PHYTOPLANKTON GROWTH AND ZOOPLANKTON GRAZING IN THE SOUTHERN BENGUELA CURRENT

by

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To my parents,

to whom this dissertation is dedicated,

for the gratifying confidence they have in me

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ABSTRACT

The development and production of several phytoplankton communities and the consumption of these communities by herbivorous mesozooplankton were investigated in newly upwelled waters of the southern Benguela Current by means of an electronic counting and sizing technique (Coulter counter).

A feasibility study was initiated to test the accuracy of the Coulter counter (Model TAII) in estimating phytoplankton size and biomass in fresh and preserved samples from the Benguela Current. Counting phytoplankton using this method gave a higher degree of reproducibility than the inverted microscope method. Certain recommendations as to the counting procedures were made. The counting of preserved samples was shown to introduce artefacts, resulting in a 77 per cent reduction in particle volume after a year of preservation. Correlations of particle volume with chorophyll a, carbon and nitrogen were calculated, with highest correlations occurring between particle volume and chlorophyll a. Particle volume was shown to represent biomass as accurately as any of the other methods.

Three developing phytoplankton communities in newly upwelled waters (during December 1979, December 1980 and February 1981) were described in terms of their particle size frequency distributions. These communities varied in their development, diversity and species dominance. Their particle size spectra also differed

in terms of total biomass and size range of particle volume peaks. Changes in the species composition and growth were attributed to short-term wind variations by allowing upwelled developing waters to mix with different neighbouring water bodies.

Production estimates, in terms of total particulate organic matter, showed that the phytoplankton communities developed rapidly (max. doublings per day ca. 2.9 and max. carbon production ca. 21 $g.m^{-2}.d^{-1}$) with little evidence of a lag phase. The growth pattern differed for each community encountered and was shown to relate to the rate of mixing of the water column and the nutrient and light regimes. Production rates were highest in newly upwelled waters and lowest under limiting light and during periods of nitrate depletion in the upper mixed layer. Changes in the growth rates were also attributed to short-term wind variations causing different water bodies to mix, changing the nutrient regimes.

Growth was not size dependent, although on certain occasions large increases occurred between an equivalent spherical diameter (ESD) of 6 - 14 μm, suggesting growth of microflagellates. A diel variation was observed with volume increases during the day exceeding those at night. Except under extreme limiting conditions, heterotrophic growth occurred.

Comparisons of the grazing stresses, measured on these developing phytoplankton blooms, indicated that at most, only 11% of the

total daily food available was harvested, even though considerable temporal and spatial variations were observed in the food availability (2903 - 25270 $mgC.m^{-2}$), zooplankton abundance (1610 - 12253 $mg.m^{-2}$) and mesozooplankton ingestion rates (55 - 5609 $\mu gC.mg\ copepod^{-1}.hr^{-1}$). The mesozooplankton exerted little control on the developing phytoplankton blooms of newly upwelled waters.

Much of the primary production is thought to go unutilized because of the intermittent nature of the upwelling in this region. The transient nature of food availability and quality were shown to depress ingestion rates and thought to delay the reproductive responses of the mesozooplankton, limiting their biomass off the Cape Peninsula.

This study greatly enhances our understanding of the dynamic interactions between phytoplankton and herbivorous mesozooplankton in the southern Benguela System by measuring rates of processes over several short durations. Spatial and temporal variations in these processes have considerable implications on the fertility of the system and hence food resources available to the economically important fishery of the region.

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INTRODUCTION

INTRODUCTION

In a dynamic ecosystem such as the southern Benguela Upwelling System, the rapid pulsating nature of the upwelled water results in strong contrasts in sea temperatures, high surface nutrients and high biological productivity. This sporadic yet substantial productivity supports a large and commercially valuable pelagic fishery.

To understand the basic food relationships in this ecosystem, and whether pelagic fish (anchovy and pilchard amongst others) are food limited, we need to have some measure of the levels of primary productivity and an understanding of the partitioning of this production between zooplankton consumers, pelagic fish, bacteria and the sediments. The rate at which zooplankton consume and incorporate food can be one of the critical links between primary production and upper trophic levels in the southern Benguela Current.

This thesis aims to investigate the development and production of phytoplankton communities in newly upwelled waters of the southern Benguela Current and the consumption of these communities by herbivorous mesozooplankton. The ultimate intention is to determine phytoplankton turnover rates and zooplankton grazing rates, such that manageable models of productivity in this region may be constructed to predict food availability.

Over the past five years changes (growth and decay) in phytoplankton communities have been assessed, after periods of upwelling, by monitoring single parcels of water over several days with the aid of drogues. Data collected on a series of four of these drogue cruises forms the basis of this thesis. On each cruise three simultaneous experiments were conducted daily on the same water body: determining the particle size frequency distribution of the phytoplankton; measuring phytoplankton production and estimating mesozooplankton grazing rates.

The thesis consists of four complementary papers presented separately and in logical sequence. The papers deal with the following topics: -

Paper 1 deals with the methodology of automated counting and sizing of phytoplankton and other particles by means of a Coulter counter (Model TAII). It investigates the feasibility of estimating phytoplankton size and biomass in fresh and preserved samples from the Benguela Current. This technique is universally employed in the other three papers.

Paper 2 investigates the development of three phytoplankton communities in terms of their particle size frequency distributions in newly upwelled waters of the southern Benguela Current. The particle size frequency distributions and species composition of the communities are discussed in relation to their respective environments.

Paper 3 examines the diel growth patterns of four phytoplankton communities of newly upwelled waters in the southern Benguela Current. It investigates the growth rates as estimated by changes in particle volume, under varying environmental conditions, and compares these growth rates with those obtained by other methods of estimating production.

Paper 4 investigates the significance of grazing by herbivorous mesozooplankton on phytoplankton populations in waters of the southern Benguela Current. The rate of feeding is discussed in relation to food concentration, size and quality.

The data are presented in the form of separate manuscripts for the purpose of publication. Papers 1 and 2 have already been published and Papers 3 and 4 are being submitted for publication. Each paper therefore has a slight variation in format complying to the requirements of the respective journals. Presentation of the thesis in this form necessitates each section having its own reference list. The individual papers are followed by a general conclusion and by two supporting papers which were submitted for the degree of Master of Science at the University of Cape Town in 1981.

PAPER 1 - FEASIBILITY OF ESTIMATING PHYTOPLANKTON SIZE AND BIOMASS IN FRESH AND PRESERVED SAMPLES FROM THE BENGUELA CURRENT WITH A COULTER COUNTER.

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FEASIBILITY OF ESTIMATING PHYTOPLANKTON SIZE AND BIOMASS IN FRESH AND PRESERVED SAMPLES FROM THE BENGUELA CURRENT WITH A COULTER COUNTER

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Counting phytoplankton with a Coulter counter gave a higher degree of reproducibility than the inverted microscope method. Certain recommendations as to counting procedures are made. Repeating the count in the same sample resulted in underestimates of particle volume of up to 19 per cent. Replicates should be decanted into different beakers and counted separately so as to prevent any conductivity effects on the phytoplankton. In order to obtain representative particle volumes, samples should not exceed 25 mℓ at a concentration index (CI) of 5 per cent and not be less than 50 mℓ at a CI of 1 per cent. The counting of preserved samples is not recommended, because of the introduction of artefacts, resulting in a reduction of 77 per cent in particle volume after a year of preservation. Correlations of particle volume with chlorophyll *a*, carbon and nitrogen were calculated, with highest correlations occurring between particle volume and chlorophyll *a*. Total particle volume represents biomass as accurately as any other method.

Die telling van fitoplankton met 'n Coulter-teller het 'n hoër graad van reproduseerbaarheid as die omkeermikroskoop-metode gelewer. Sekere aanbevelings word gemaak wat telprosedures betref. Herhaling van die telling in dieselfde monster het tot onderskattings van partikelvolume van tot 19 persent gelei. Replikate moet in verskillende bekers oorgegiet en apart getel word om enige effekte vanwee geleivermoë op die fitoplankton te voorkom. Ten einde verteenwoordigende partikelvolumes te verkry, moet monsters nie groter as 25 mℓ teen 'n konsentrasie-indeks (KI) van 5 persent, en nie minder as 50 mℓ teen 'n KI van 1 persent wees nie. Die tel van bewaarde monsters word nie aanbeveel nie, vanweë die invoering van artefakte, wat lei tot 'n daling van 77 persent in partikelvolume na 'n jaarlange bewaring. Korrelasies van partikelvolume met chlorofil *a*, koolstof en stikstof is bereken; die hoogste korrelasies het tussen partikelvolume en chlorofil *a* voorgekom. Totale partikelvolume verteenwoordig biomassa so akkuraat soos enige ander metode.

The counting and sizing of naturally occurring particles is a fundamental requirement of many studies of the aquatic environment. Numerous methods have been employed in the past to count phytoplankton (Unesco 1978), but as yet no one method of enumerating is accepted as being superior under all circumstances and for all purposes. There are limits to the accuracy of any method and, if the limitations of any method are unknown, it is difficult to evaluate a quantitative result (Lund *et al.* 1958).

The Coulter counter was originally designed for the electronic counting of blood cells (Coulter 1953, Mattern *et al.* 1957, Grant *et al.* 1960). In the early sixties the technique was applied to counting marine unicellular organisms (Hastings *et al.* 1962, Maloney *et al.* 1962). Several workers have compared the accuracy and precision of the Coulter counter with other standard methods of plankton enumeration (El-Sayed and Lee 1963, Mulligan and Kingsbury 1968, Evans and McGill 1970, Leslie 1978). A practical manual on the uses of the Coulter counter in marine research was produced by Sheldon and Parsons (1967a), followed by a presentation of a continuous size spectrum for particulate matter in the sea (Sheldon and Parsons 1967b). In a later study Parsons (1969) demonstrated the use of the particle size spectrum in describing the structure of a plankton community. The size distribution of particles has also been presented for several water masses (Sheldon *et al.* 1967, 1972, Olivieri *et al.* 1985).

The Coulter counter technique was also developed for measuring growth of phytoplankton (Cushing and Nicholson 1966, Strickland and Parsons 1972). Primary production studies using this technique have been conducted by several workers (Parsons 1965, Cushing *et al.* 1968, Parsons, Stephens and Le Brasseur 1969, Sutcliffe *et al.* 1970, Sheldon *et al.* 1973, Sheldon 1979, Olivieri and Hutchings in preparation [a]). It has further been used in determining grazing by zooplankton on phytoplankton populations (Parsons, Le Brasseur *et al.* 1969, Hargrave and Geen 1970, Poulet 1973, Richman *et al.* 1977, Olivieri and Hutchings in preparation [b]). Coulter counter analyses in enclosure experiments have shown the structure of the phytoplankton population to be affected by predation (Gamble *et al.* 1977, Gamble 1978) and nutrient enrichment (Parsons *et al.* 1977). The limitations of the technique when applied to grazing studies are comprehensively discussed by Deason (1980), Harbison and McAlister

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(1980) and Roman and Rublee (1980).

The purpose of this study was to determine the feasibility of analysing preserved and freshly collected phytoplankton in the sea by means of a Coulter counter. The objectives of the investigation were to:

(i) test the reproducibility of the Coulter counter,
(ii) evaluate the effects of preservation on the counting and sizing of particulate matter,
(iii) assess whether the technique can give reliable estimates of phytoplankton biomass.

MATERIALS AND METHODS

Counting procedure

Phytoplankton samples were counted electronically on a Model TAII Coulter counter, following the method described by Sheldon and Parsons (1967a). Briefly, this method determines number and size of particles suspended in an electrically conductive fluid. As particles pass through the aperture the change in voltage is recorded by the positioning of an internal and an external electrode around the aperture tube. The pulses are displayed visually on an oscilloscope and are of a magnitude proportional to the size of the particles. Particle volumes are regarded as spheres and equivalent spherical diameters (ESD) are classed into diameter size intervals. The flow of the sample through the aperture is controlled by an external vacuum pump and a mercury manometer.

In all experiments a 280 μm aperture tube was used, as it counted a size range of particles appropriate for marine diatoms and minimized clogging of the aperture when counting samples from local waters. The aperture tube was initially calibrated with latex particles of known diameter and the instrument gain set for direct read-out of particle volume (ppm = $\mu m^3 \times 10^6 \cdot m\ell^{-1}$) by the procedure outlined in the Operator's Manual (Coulter Electronics 1975). Background counts were obtained from seawater filtered through 0,45 and 0,22 μm filters in series. The "noise" level was found negligible for all size intervals except the first (4 – 5,04 μm), which was therefore screened out. Before counting, samples were agitated gently with a mechanical stirrer. To minimize coincidence, samples exceeding a concentration index (CI) of 5 per cent were diluted 2-, 5- or 10-fold. In most cases either 50- or 25-mℓ aliquots were siphoned from the sample in the time mode and counted. On board ship, the manometer tube was pinched off to prevent erratic flow due to surge in the mercury column at sea.

Data are presented in the form of particle spectra, with the y axis as log particles·mℓ^{-1} or particle volume (ppm = $\mu m^3 \times 10^6 \cdot m\ell^{-1}$) and the x axis as particle diameter (μm) with diameter increments to the base of $2^{1/3}$ (Sheldon and Parsons 1967a). Values on the x axis represent the mean equivalent spherical diameters (ESD) of the diameter size intervals.

Experiment 1: Reproducibility of the Coulter counter

From various 15-ℓ sample stocks containing mixtures of live phytoplankton species:

(a) twenty separate 25-mℓ replicate subsamples were counted to test the precision of the technique in reproducing reliable repetitive counts of particle volume;
(b) five successive 25-mℓ counts were obtained from a 150-mℓ subsample to test whether the conductivity of the phytoplankton is affected by being suspended and counted in an electrically conductive fluid;
(c) ten replicate subsamples of varying quantities (12,5, 25, 50, 75 and 100 mℓ) were counted at concentration indices (CI) of 5 and 1 per cent to determine the minimum quantity required to give representative values of particle volume.

Counts were analysed at a confidence level of 95 per cent by means of the arithmetic mean, the coefficient of variation, the standard error and the marginal error of Hobro and Willén (1977). Particle spectra were compared by the paired *t*-test of Snedecor and Cochran (1967), with each size interval as a data set. The statistical variance was compared at $P = 0{,}025$ and $P = 0{,}01$.

Experiment 2: Preservation effects on particle counts

This experiment evaluated the effects of preservation of phytoplankton on particle counts and size frequency distribution. A stock sample of 1 ℓ of a mixed phytoplankton bloom was collected in December 1979 off the Cape Peninsula. A fresh subsample was counted initially, following the procedure described before. The remainder of the stock sample was preserved in 4-per-cent neutralized and buffered formalin, and subsequent subsamples were counted after 1, 3, 5, 7, and 10 days, 1 month and 1 year of preservation.

Experiment 3: Particle volume as a biomass estimate

Comparisons of the Coulter counter with other

Table I: Total particle volumes (TPV) of Experiments 1 (a, b, c) analysed at the 95-per-cent confidence level for arithmetic mean, coefficient of variation, standard error and marginal error (Hobro and Willén 1975)

Experiment number	Mean total volume (ppm = $\mu m^3 \times 10^6 \cdot m\ell^{-1}$) $\bar{X}$	Coefficient of variation C.V.	Standard error (SE) $\frac{C.V.}{\sqrt{n}}$	Marginal error (%) $\frac{SE \cdot t \cdot 100}{\bar{X}}$
1a	5.188	0.5335	0.1193	6.4
1b	2.488	0.2221	0.0993	11.1
1c (CI = 1%)	2.816	0.3953	0.1768	17.4
1c (CI = 5%)	12.998	2.0886	0.9341	20.0

methods of estimating phytoplankton biomass were obtained by linear regressions of particle volume with chlorophyll *a*, carbon and nitrogen content of particulate matter collected on five drogue cruises (Dec. 1979, Dec. 1980, Feb. 1981, Mar. 1981 and Oct. 1981). Freshly collected material was counted on the Coulter counter on board ship. One-litre water samples were filtered on board and stored at −20°C for later spectrophotometric analyses of chlorophyll *a*. Wavelengths and equations recommended by SCOR/UNESCO Working Group 17 (1966) were used. Carbon and nitrogen content were obtained by filtering water samples onto Whatman GF/C glass-fibre filters. Filters were stored frozen, then homogenized and analysed with CHN analyser.

RESULTS AND DISCUSSION

A marginal error of 6,4 per cent was obtained for the replicate counts of total particle volume of Experiment 1a (Table I). This error is well within the acceptable bounds (± 26 per cent) for routine countings as proposed by Hobro and Willén (1975). (Refer to the Appendix for raw data.) A higher degree of precision is obtained in the Coulter counter's reproducibility than in the Utermöhl microscopic method, because of unavoidable random and human errors inherent in the manual counting procedure (El-Sayed and Lee 1963).

An evaluation was made for routine countings with the Utermöhl technique by Hobro and Willén (1975). The participation of five laboratories each using their routine counting procedure showed the coefficient of variation to range between 6 and 218 per cent. The intercalibrations also revealed a difference of approximately 700 per cent between minimum and maximum total volumes computed from cell sizing, whilst errors within any one of these laboratories remained at 20–30 per cent, which was considered acceptable by the authors.

Experiment 1b was prompted by earlier observations of a noticeable reduction in counts for successive replicates from the same beaker. An acceptable marginal error of 11,1 per cent was obtained when total particle volumes were compared (Table I). Each particle spectrum was shown to be statistically similar at $P = 0.025$ (Table II and Fig. 1), even though a reduction of 19 per cent in total particle volume was evident after the first count. However, at $P = 0.1$ the first count differed significantly from the successive replicate counts. The results are therefore not conclusive. Nonetheless, it is recommended that, as a safety precaution, subsamples should be decanted into separate beakers, and then each replicate sample should be counted separately.

Recently, Flos (1984) has shown that repeating a count in the same sample introduces some change, which is dependent on the quality of particles, although as yet little is known about precisely in what sense the sample changes. Furthermore the sampling method can also change the spectrum. Less disturbed samples (less manipulated) better represent the *in situ* structure.

Table II: Experiment 1b — Particle volume spectra of five 25-mℓ subsamples, repeated successively from the same beaker, compared by the paired *t*-test of Snedecor and Cochran (1967), with each diameter size interval as a data set

Probability	$P = 0.025$					$P = 0.1$				
Count	1	2	3	4	5	1	2	3	4	5
1		—	—	—	—		+	—	—	—
2			—	—	—			—	—	—
3				—	—				—	—
4					—					—
5										

\+ Significant difference
— No significant difference

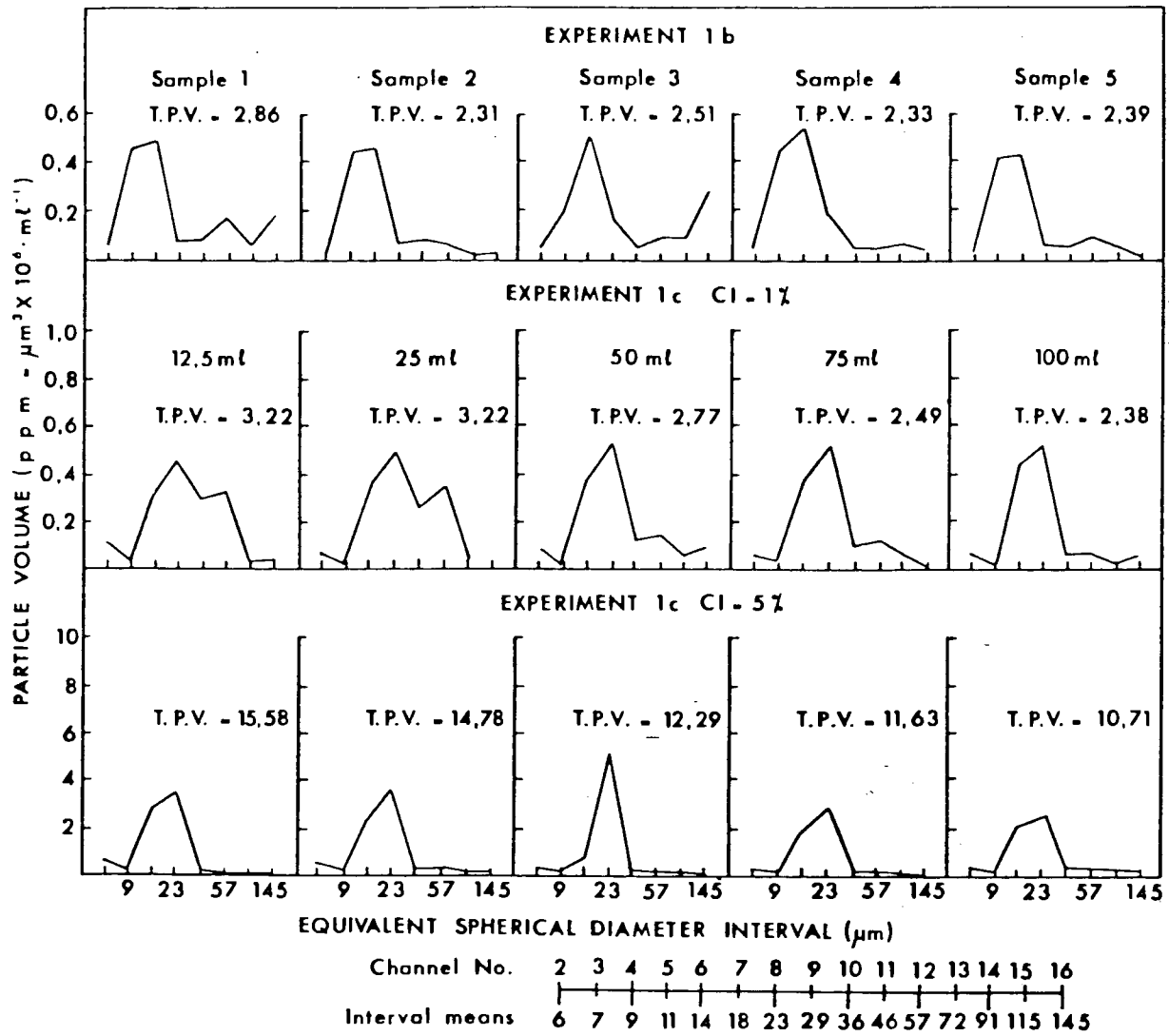

Fig. 1: Particle spectra for Experiment 1 (b and c), in which 1b tests the conductivity effects on phytoplankton and 1c the minimum sample quantity for representative counts of particle volume at CIs of 1 and 5 per cent. Alternate channel numbers are plotted with diameter increments of $2^{1/3}$ on the x axis (Sheldon and Parsons 1967a)

Experiment 1c tested the minimum sample volume at concentration indices (CI) of 5 and 1 per cent required to give representative measurements of particle volume when numerous counts have to be made in a short space of time. Acceptable marginal errors of 17,4 and 20 per cent for CIs of 1 and 5 per cent respectively were obtained when comparing total particle volumes (Table I).

Comparisons of particle spectra (Table III) showed no differences at $P = 0,05$ for both concentration indices. However, at $P = 0,1$ and CI = 1 per cent the 100- and 75-mℓ samples differed from the 12.5-, 25- and 50-mℓ samples, whilst at CI = 5 per cent the 12,5- and 25-mℓ samples differed from the 100-, 75- and 50-mℓ samples.

On this basis it is recommended that, at CI = 5 per cent, sample volume should not exceed 25 mℓ and, at CI = 1 per cent, sample volume should not be less than 50 mℓ. Inspection of the 12,5- and 25-mℓ particle spectra in Figure 1 shows particularly high

Table III: Experiment 1c — Particle volume spectra of five subsamples ranging from 12.5 to 100 mℓ compared at concentration indices (CI) of 1 and 5 per cent by the paired *t*-test of Snedecor and Cochran (1967). Each diameter size interval formed a data set

Probability	$P = 0.5$					$P = 0.1$				
Subsample (mℓ)	12.5	25	50	75	100	12.5	25	50	75	100
	CI = 1%									
12.5		—	—	—	—		—	—	—	+
25			—	—	—			—	+	+
50				—	—				+	+
75					—					—
100										
	CI = 5%									
12.5		—	—	—	—		—	+	+	+
25			—	—	—			—	+	+
50				—	—				—	—
75					—					—
100										

\+ Significant difference
— No significant difference

volume values in the 57-μm diameter size interval when compared with the 50-, 75- and 100-mℓ samples at CI = 1 per cent. However, at CI = 5 per cent, the total particle volumes decreased as the quantity measured increased, suggesting that coincidence does occur at CI = 5 per cent.

Counts are dependent on the degree of random dispersion, and it is essential when using any sensing-zone method to organize particles such that they enter the sizing zone one at a time. Coincidence is minimized when the concentration index is less than 5 per cent. In order to obtain this, dilutions of natural seawater need never exceed ten-fold and, provided the filtered seawater background count is kept to a minimum, the effect of sample dilution is negligible.

Allen (1966, cited in Leslie 1978) has found that an undercount results from distortion of pulse shape, owing to "shadowing" of pulses in close succession. To date, the exact relationship between cell size and pulse height is not clearly understood. When counting spherical, red blood cells, the pulse height is directly proportional to particle volume (Grant *et al.* 1960), although Mattern *et al.* (1957) found a better correlation between pulse height and particle diameter. Long needle-like cells have smaller pulse heights than predicted from their linear dimensions (Hastings *et al.* 1962) and, generally, phytoplankton chains tend to be underestimated because of their passing through the aperture parallel to the electric field (Leslie op. cit.). Cognizance of this fact must be taken when samples consist mostly of chain-forming diatoms or colonial forms of algae, as occurs in most samples from the Benguela upwelling region. Kachel (1976) has shown that the height and the shape of the voltage pulses cannot be directly interpreted as particle volume because they depend on (a) the constant current applied, (b) the geometrical dimensions of the orifice, (c) the electrical conductivity of the suspending medium, (d) the path of the particles through the orifice, (e) the shape of the particles and (f) the electrical conductivity of the particles.

An evaluation of the accuracy of the Coulter counter against the widely accepted Utermöhl (1936) technique for phytoplankton enumeration has been done by Olivieri (unpublished data). Although it is standard practice to count living material whenever possible, both live and preserved samples may be counted (Sheldon 1978). Hence, six preserved samples were chosen for comparison of the two counting methods. A computer program facilitated the conversion of the microscopically determined cell volumes to the diameters of equivalent spheres, providing particle spectra comparable with that of the Coulter counter. Results proved to be discouraging, with little evidence of compatability between the two different methods (Table IV). The questions then posed were two-fold: Does the spectrum of a live sample alter on preservation and, if so, does the sample material progressively deteriorate? With these questions in mind, the effects of preservation of phytoplankton on the particle size frequency distributions (particle numbers and volumes) were evaluated in Experiment 2.

Referring to Figures 2 and 3, it is clear that both the particle spectra and the total particle volumes alter on preservation. The effects of preservation on the sample counts are evident after one day of preservation, with an appreciable change occurring in the particle spectrum, although not in total particle volume. A general shift to the left is evident in the particle spectra, with increases in the numbers and volumes in the lower diameter size intervals occurring concomitant with decreases in the larger size intervals.

Microscopic examination revealed a mixed bloom of diatoms, with the chain-forming genera *Chaetoceros* and *Skeletonema* dominating. It is likely that, as the preserved sample ages, so the risk of chains breaking increases. The increase in numbers in the lower size range can also be a result of precipitates forming on preservation, which are often complicated by fluxes of non-living material (Batoosingh *et al.* 1969).

Of greater concern is the considerable loss in total

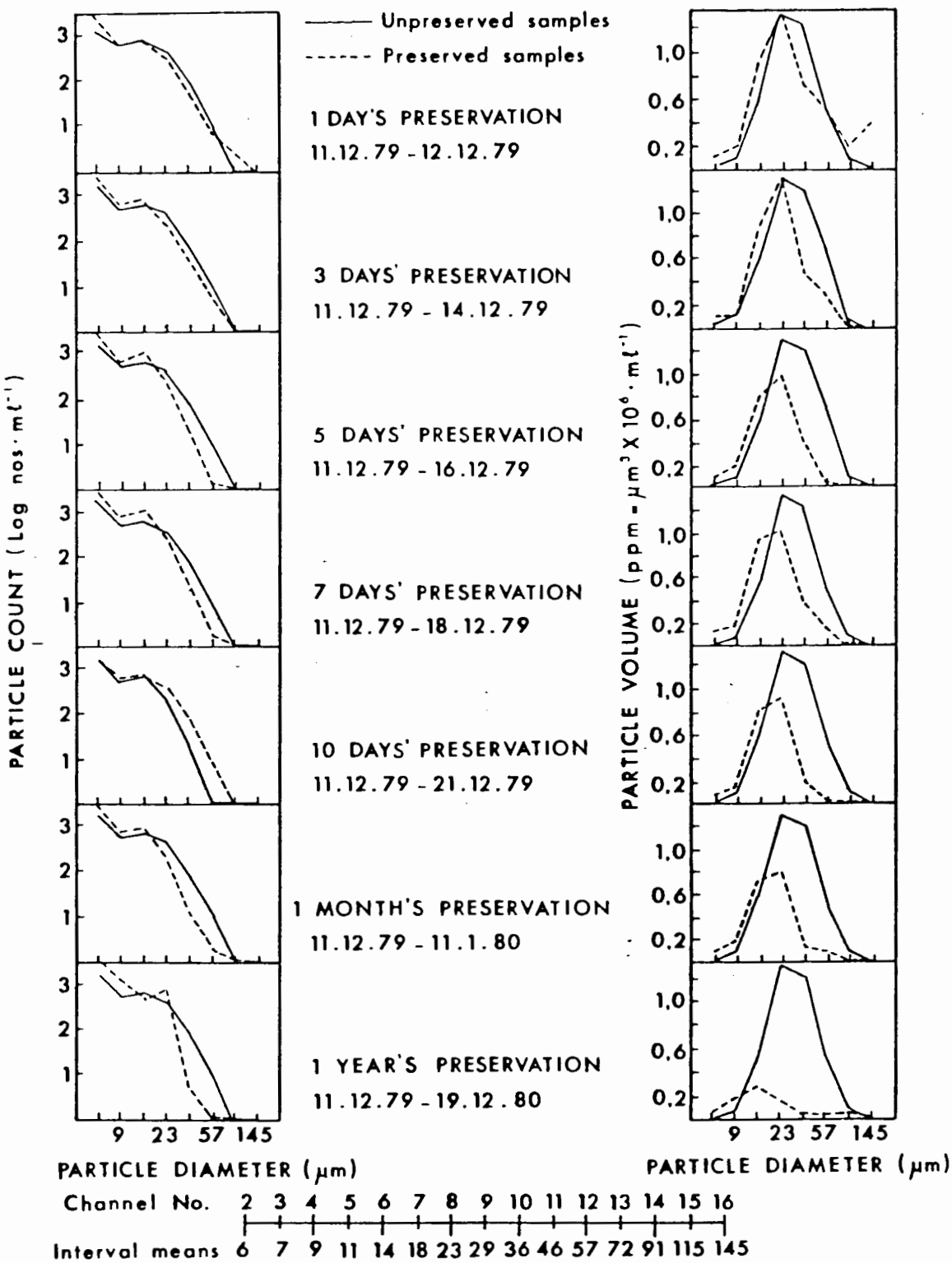

Fig. 2: Experiment 2 — Changes in particle counts after 1, 3, 5, 7, 10, 31 and 370 days of preservation for particle size frequency distributions. Alternate channel numbers are plotted with diameter increments of 2½ on the x axis (Sheldon and Parsons 1967a)

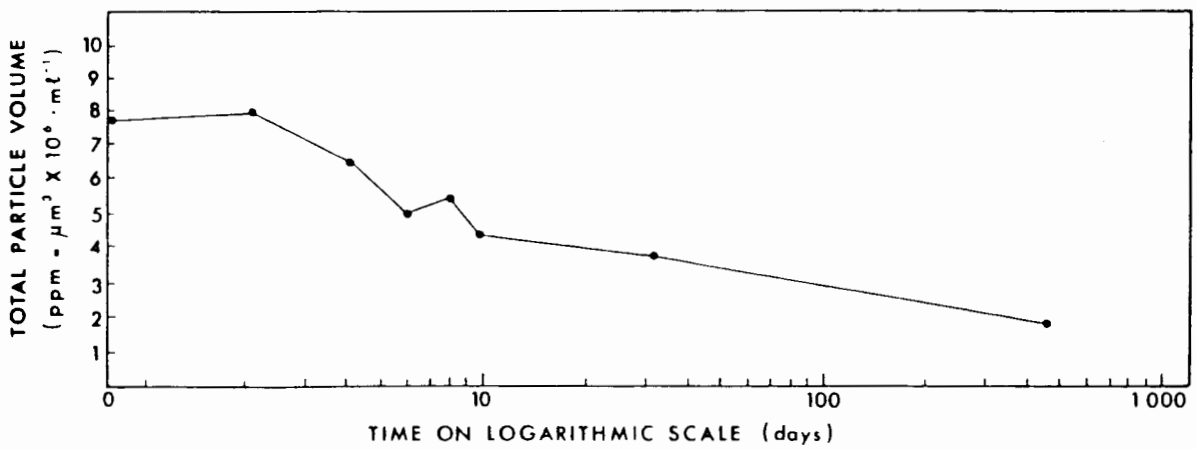

Fig. 3: Experiment 2 — Changes in total particle volume after 1, 3, 5, 7, 10, 31 and 370 days of preservation

particle volume after the first day. After five days of preservation, 35 per cent of the total particle volume is lost and, more alarmingly, after a year of preservation the total volume is reduced by 77 per cent. This general shrinkage remains unexplained. Each algal species and detrital type has a dielectric constant peculiar to itself (Leslie 1978), and it would appear that on preservation some alteration is caused in the electrical properties of both living and non-living material. Hastings *et al.* (1962) have shown that the small electrical differences between different cells of a similar size, e.g. a living dinoflagellate and a dried spore, are not sufficient to influence their sizing behaviour. In preserved samples the conductivity may be altered as the cell membrane becomes permeable, and prolonged preservation may cause cell lysis.

It has long been realized that estimates of standing stock as cell numbers alone result in inadequate measures of phytoplankton abundance (Smayda 1978). Cell volume, whether obtained directly from particle size counters or indirectly from cell volume data, has become a more acceptable measure of phytoplankton biomass.

Linear regressions and correlation coefficients of particle volume, chlorophyll *a*, carbon and nitrogen

Table IV: Comparison of the Coulter counter and inverted microscope (Utermöhl) methods of determining particle volume (ppm = $\mu m^3 \times 10^6 \cdot m\ell^{-1}$) of preserved samples

Channel number	Diameter class intervals (μm)	Sample 1		Sample 2		Sample 3		Sample 4		Sample 5		Sample 6	
		C.C.*	I.M.†	C.C.	I.M.	C.C.	I.M.	C.C.	I.M.	C.C.	I.M.	C.C.	I.M.
2	5.04 - 6.35	0.29	0.002	0.06	0.03	0.2	0.02	0.05	0	0.06	0.0004	16.1	0
3	6.35 - 8	0.39	0.02	0.03	0.04	0.2	0.02	0.05	0.005	0.09	0	6.1	0
4	8 - 10.08	0.8	0.06	0.04	0.004	0.4	0.06	0.09	0.002	0.1	0.02	14.2	1.5
5	10.08 - 12.7	1.9	0.2	0.01	0.5	0.7	0.7	0.2	1.0	0.2	0.03	58.7	0
6	12.7 - 16	3.3	0.3	0.2	0.04	0.7	1.3	0.2	2.0	0.3	0.07	146.3	0
7	16 - 20.2	3.5	2.0	0.3	0.7	0.6	3.5	0.2	2.2	0.3	0.2	166.1	7.3
8	20.2 - 25.4	2.8	3.8	0.5	0.1	0.8	2.1	0.2	1.3	0.6	0.4	92.0	19.5
9	25.4 - 32	2.0	14.2	0.8	1.1	0.7	2.8	0.3	0.8	0.7	2.9	72.1	50.5
10	32 - 40.3	1.3	30.0	0.9	4.0	0.5	9.8	0.5	4.1	0.4	1.1	179.5	90.7
11	40.3 - 50.8	1.7	15.7	1.2	1.4	0.6	3.5	0.5	0.3	0.6	2.4	404.1	23.3
12	50.8 - 64	2.0	9.2	1.1	5.9	0.5	15.9	0.5	6.6	0.7	3.2	645.1	0
13	64 - 80.6	1.5	10.0	0.8	3.9	0	9.8	0.3	4.0	0.5	1.5	660.4	0
14	80.6 - 101.6	2.3	7.1	0.2	24.3	0.4	10.9	0.6	0	0.6	4.7	423.8	0
15	101.6 - 128	0.8	102.8	0	25.9	0.8	46.7	0	7.0	0	0	96.7	0
16	128 - 162	0	149.0	0	3.0	0	10.4	0	0	0	12.4	0	0
r		0.36		-0.24		-0.26		-0.28		-0.14		0.08	

* Coulter counter
† Inverted microscope
r = Correlation coefficient

are presented in Figure 4. The data points were collected from *in situ* experiments and represent phytoplankton in different stages of growth under varying environmental conditions. The highest correlation coefficient was obtained for particle volume against chlorophyll *a*, where alterations in the environment influenced both the chlorophyll content and the particle volume linearly. Estimates of particle volume are extremely useful, particularly in studies involving phytoplankton-grazing relations and size-class contribution to primary production (Paasche 1960, Smayda 1965, 1966), from which volume in each size-class can be determined. On the other hand, chlorophyll *a* determinations, although commonly used in routine surveys, are proximate estimates of biomass and therefore inadequate, unless substantiated by other methods of determining biomass. Furthermore, high performance liquid chromatography (HPLC) techniques show that chlorophyll *a* is not always reliable as an estimate of phytoplankton biomass, particularly for nutrient-limited blooms.

Rather low correlation coefficients ($r = 0{,}52$ and 0,56) were obtained for particle volumes against carbon during the December 1980 and February 1981 drogue cruises respectively. This is not surprising, because the mixed community of phytoplankton on these cruises was composed of diatoms, having large vacuoles and therefore less carbon per organism. In the March 1981 drogue cruise a high correlation and lower intercept was obtained, as nanoplankton tended to dominate. Mullin *et al.* (1966) showed cell volume to give better estimates of cell carbon than surface area. However, plasma volume provides a more precise estimate of cell carbon in diatoms than does total volume calculated from cell dimensions (Strathmann 1967), and therefore a common regression equation for both diatoms and other phytoplankton, as given by Mullin and co-workers, may not always be appropriate.

Correlation coefficients (r) ranging from 0,33 to 0,87 were obtained for carbon against chlorophyll *a* with ratios comparable to those found in the Peru upwelling system (Strickland *et al.* 1969, Beers *et al.* 1971). The use of regression analysis for finding the ratio of algal carbon to chlorophyll *a* has been questioned (Riley 1965), especially since the chlorophyll *a* content is dependent on the environment and is influenced by temperature, light intensity and nutrient deficiency. For instance, phytoplankton grown in nutrient-limited chemostats show increasing ratios of carbon to chlorophyll *a* (Thomas and Dodson 1972), to such an extent that high ratios are found in nutrient-depleted cells. Likewise, detritus-dominated blooms will have a high carbon to chlorophyll *a* ratio, because the determined content of chlorophyll *a* is not reliable in the late bloom stages.

Low correlations were found between nitrogen and particle volume, nitrogen and chlorophyll *a*, and nitrogen and carbon. There is evidence that nutrient-limitation (Strathmann 1967) and temperature (Eppley 1972) influence the carbon and nitrogen content of cells. Taguchi (1976) reported that smaller cells are relatively nitrogen-rich, so that the ratio of nitrogen and carbon is dependent on cell size. Straight ratios from quotients of data pairs are generally biased if the intercept is large. Detrital and bacterial fractions could be present, which would not be associated with newly synthesized substances. A further interference can arise from dissolved organic matter that appears as a natural by-product of photosynthesis and grazing (Banse 1974).

Despite these shortcomings, the validity of the biomass estimates can be increased through parallel determinations of biomass by different methods. Eppley (1972) compared average specific growth rates (μ) of phytoplankton in the southern Californian coastal waters using three methods of estimation. In Method 1, μ is computed from photosynthetic rate and ATP $\times$ 250 = standing stock as carbon. (This method has been found to be inaccurate — Stuart 1982.) In Method 2, μ is calculated from photosynthetic rate and standing stock carbon computed from cell numbers and cell volumes. In Method 3, μ is computed from assimilation rate of nitrate plus ammonium plus urea per unit particulate nitrogen. Growth estimates are shown to vary by a factor of two. Even though these methods have been compared and used in conjunction with one another greater precision within each method is desirable.

SUMMARY

1. A high degree of precision is obtained in the Coulter counter's reproducibility, with a marginal error of 6,4 per cent found between replicate counts.
2. Replicates should be decanted into different beakers and counted separately, so as to prevent underestimates of particle volume.
3. The minimum sample volume required to give representative measurements of particle volume at a CI of 1 per cent is 50 mℓ and the maximum required at a CI of 5 per cent is 25 mℓ.
4. Preservation of phytoplankton affects the count-

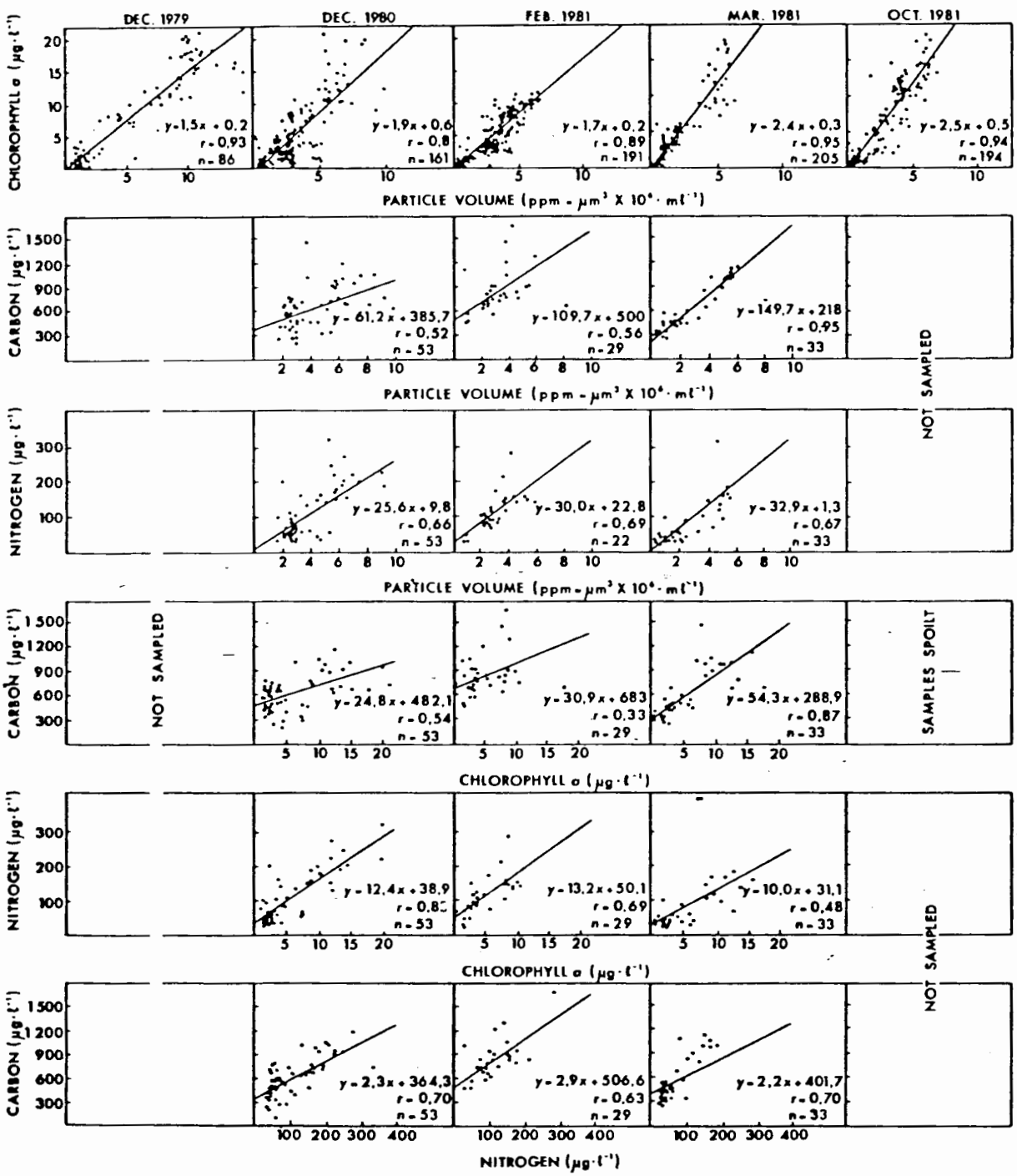

Fig. 4: Linear regressions and correlation coefficients of particle volume (ppm), chlorophyll *a* ($\mu g \cdot \ell^{-1}$), carbon ($\mu g \cdot \ell^{-1}$) and nitrogen ($\mu g \cdot \ell^{-1}$)

ing and sizing of the particles, with underestimates in particle volume of up to 77 per cent.

5. The high degree of correlation between particle volume and carbon, nitrogen and particularly chlorophyll *a* suggests that this method can be used to give reliable estimates of phytoplankton biomass, although the degree of correlation is dependent upon the quantity of detritus present.

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APPENDIX

Experiment 1a — Reproducibility of particle volume (ppm = $\mu m^3 \times 10^6 \cdot m\ell^{-1}$) within each diameter interval using the Coulter counter

Channel number	Number of replicate subsamples																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
2	0.065	0.053	0.112	0.178	0.064	0.066	0.057	0.076	0.060	0.064	0.216	0.064	0.065	0.063	0.129	0.115	0.050	0.193	0.062	0.535
3	0.038	0.029	0.050	0.039	0.053	0.044	0.043	0.038	0.030	0.030	0.111	0.043	0.037	0.036	0.043	0.035	0.027	0.092	0.035	0.051
4	0.043	0.038	0.050	0.039	0.095	0.044	0.076	0.044	0.047	0.040	0.442	0.043	0.041	0.040	0.039	0.040	0.041	0.053	0.044	0.042
5	0.087	0.077	0.078	0.072	0.074	0.082	0.737	0.076	0.077	0.080	0.077	0.077	0.074	0.080	0.078	0.075	0.073	0.092	0.084	0.079
6	0.759	0.726	0.762	0.733	0.720	0.764	1.673	0.744	0.716	0.751	0.758	0.712	0.755	0.750	0.749	0.769	0.762	0.793	0.779	0.763
7	1.734	1.668	1.725	1.648	1.640	1.730	1.149	1.752	1.641	1.784	1.747	1.647	1.690	1.715	1.743	1.677	1.692	1.817	1.690	1.704
8	1.247	1.139	1.226	1.234	1.196	1.179	0.222	1.299	1.185	1.226	1.216	1.194	1.188	1.201	1.127	1.218	1.145	1.180	1.102	1.154
9	0.249	0.245	0.258	0.231	0.259	0.317	0.161	0.277	0.208	0.227	0.310	0.205	0.230	0.197	0.189	0.235	0.210	0.184	0.230	0.163
10	0.233	0.260	0.302	0.227	0.286	0.317	0.331	0.347	0.200	0.232	0.277	0.111	0.193	0.085	0.099	0.205	0.169	0.111	0.115	0.093
11	0.390	0.250	0.521	0.366	0.392	0.475	0.184	0.656	0.119	0.282	0.398	0.201	0.235	0.201	0.133	0.250	0.246	0.164	0.150	0.102
12	0.509	0.375	0.521	0.174	0.418	0.442	0.052	0.769	0.145	0.361	0.332	0.137	0.226	0.156	0.047	0.380	0.256	0.218	0.243	0.163
13	0.222	0.163	0.179	0.077	0.312	0.055	0.085	0.378	0.060	0.074	0.260	0.060	0.088	0.067	0.099	0.195	0.055	0.087	0.115	0.014
14	0.065	0.014	0.056	0.015	0.016	0.060	0.019	0.101	0.017	0.015	0.017	0.017	0.014	0.018	0.069	0.015	0.064	0.058	0.018	0.014
15	0.016	0.019	0.017	0.019	0.016	0.126	0.024	0.019	0.021	0.015	0.017	0.017	0.018	0.121	0.022	0.015	0.018	0.019	0.018	0.019
16	0.022	0.019	0.022	0.024	0.021	0.022	—	0.025	0.026	0.020	0.022	0.026	0.023	0.027	0.026	0.020	0.023	0.019	0.027	0.019
TPV*	5.680	5.080	5.880	5.080	5.560	5.720	5.000	6.600	4.560	5.200	5.800	4.560	4.880	4.760	4.600	5.240	4.840	5.080	4.720	4.920

*TPV = Total particle volume

PAPER 2 - THE DEVELOPMENT OF PHYTOPLANKTON COMMUNITIES IN TERMS OF THEIR PARTICLE SIZE FREQUENCY DISTRIBUTION, IN NEWLY UPWELLED WATERS OF THE SOUTHERN BENGUELA CURRENT.

THE DEVELOPMENT OF PHYTOPLANKTON COMMUNITIES IN TERMS OF THEIR PARTICLE SIZE FREQUENCY DISTRIBUTION, IN NEWLY UPWELLED WATERS OF THE SOUTHERN BENGUELA CURRENT.

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Palabras clave: Fitoplancton, afloramiento, espectros de particulas, boyas, Corriente de Benguela Meridional, Sudafrica.
Key words: Phytoplankton, upwelling, particle spectra, drogues, Southern Benguela Current, South Africa.

RESUMEN: Desarrollo de comunidades fitoplanctonicas referido a la distribucion de frecuencias de tamano de sus particulas, en aguas recien afloradas de la Corriente de Benguela meridional. Se describe el crecimiento y declive de tres comunidades fitoplanctonicas en aguas recien afloradas de la Corriente de Benguela meridional. Las comunidades mostraron variaciones en su desarrollo, diversidad y dominancia especifica. Los espectros del tamano de sus particulas difirieron tambien en terminos de biomasa total y en el rango de tamanos de los maximos de concentracion de particulas. Los cambios en la composicion especifica y en el crecimiento se atribuyeron a variaciones a corto plazo del viento, que permitieron la mezcla del agua aflorada en desarrollo con diferentes masas de aguas vecinas.

SUMMARY: The growth and decay of three phytoplankton communities are described in newly upwelled waters of the southern Benguela Current. The communities varied in their development and in their diversity and species dominance. Their particle size spectra also differed in terms of total biomass and size range of the particle volume peaks. Changes in the species composition and growth were attributed to short-term wind variations by allowing upwelled developing waters to mix with different neighbouring water bodies.

INTRODUCTION

The pulsing nature of the southern Benguela upwelling system off the Cape Peninsula results in strong contrasts in sea-surface temperatures, nutrients and in high biological productivity (ANDREWS and HUTCHINGS, 1980). Investigations on the colonization, adaptations and temporal changes in the diversity and biomass of phytoplankton communities have revealed that different species can dominate or co-dominate in coastal upwelled waters (OLIVIERI, 1983 a, b; HORSTMAN, SFRI unpublished data).

The aim of this investigation is to assess the development of phytoplankton communities occurring in patches of newly upwelled waters, by following the water masses with the aid of drogues. The approach of this study is to monitor both the phytoplankton species composition and the distribution of particulate matter in the water column using electronically determined particle

size spectra. SHELDON and PARSONS (1967b) have shown that the size spectrum of particulate matter gives a realistic measure of the volume of irregularly shaped particles. In a later study, PARSONS (1969) demonstrated the use of particle size spectra in describing the structure of a plankton community. The size distribution of particles have also been presented for water masses in the Straits of Georgia, British Columbia (SHELDON et al., 1967), in the Atlantic and Pacific Oceans (SHELDON et al., 1972), and in the Sargasso Sea (SHELDON et al., 1973). More recently, Coulter counter analyses in enclosure experiments have shown the structure of the phytoplankton population to be affected by predation (GAMBLE et al., 1977; GAMBLE, 1978), and nutrient enrichment (PARSONS et al., 1977).

METHODS

Cruise Strategy

Three ship-board studies were undertaken during the upwelling season; in December 1979 (4th - 13th), December 1980 (3rd - 9th) and February 1981 (4th - 11th). In each case sea-surface temperature was mapped in the near inshore coastal region west of the Cape Peninsula, in order to locate a suitable patch of newly upwelled water which was marked with a tetrahedral drogue set at 10 meters. The development of the phytoplankton community in the patch of water was monitored over several days by following the drogue and sampling the water column alongside it three

times a day. The drogue position, wind speed and direction were recorded every hour. Drogue or patch studies have been conducted with considerable success by various workers, BEERS et al., (1971) and RYTHER et al., (1971) off Peru, HERBLAND et al., (1973) off Mauritania and NELSON and GOERING (1978) off Baja California and Spanish Saharan upwelling systems.

Sample Collection

Samples were collected daily at approximately 0830, 1300 and 1800 hours. A bathythermograph cast was made, and submarine light levels were determined using a Lambda Ll-192S underwater quantum sensor. Water samples were collected using 5 or 7-litre NIO bottles from the 100%, 50%, 25%, 10% and 1% light levels, and then at 10 meter intervals to 100 meters or 5 meters from the bottom at shallow stations. For the purpose of this study subsamples were drawn for microscopic examination, particle spectral analyses and the determination of chlorophyll a concentrations. The water column was subdivided into an upper mixed, stable and bottom layer after consideration of vertical profiles of chlorophyll a, temperature, salinity, nutrients and particle volume (ppm) (BROWN et al., in prep.).

Methods of assessing phytoplankton biomass.

Microscopic analyses

Water samples were preserved with either 4% buffered formalin (Dec. 1979) or Lugol's solution (Dec. 1980 and Feb. 1981) and were processed ashore, using the Utermöhl technique (UTERMÖHL, 1936) as modified by WILLÉN (1976) and HOBRO and WILLÉN (1977). Samples fixed in Lugol's solution were discarded because loss of molecular iodine caused degradation of the phytoplankton. Consequently microzooplankton samples (for Dec. 1980 and Feb. 1981) which had been filtered through a 37 µm mesh and preserved in 4% buffered formalin were used for microscopic examinations. Samples were selected according to the highest total particle volume occurring on each day and phytoplankton were identified from the drawings and descriptions of HUSTEDT (1962), HENDEY (1937) and CUPP (1943). Pie diagrams were compiled showing the daily species composition in terms of relative abundance and relative particle volume. Cell volumes of only the dominant species were calculated using formulae for the geometric shapes, which resembled the species in question (LARRANCE, 1964). Rare species in the "other species" category of the pie diagrams were excluded.

Particle spectral analyses

Particles in the water samples were electronically sized and counted on board using a Model TAII Coulter counter, following the method of SHELDON and PARSONS (1967a). A 280 µm aperture

tube was used, so as to include the diameter size ranges appropriate for marine diatoms in this area and to minimize clogging of the aperture. The aperture tube was calibrated with latex particles of known diameter and the instrument gain for direct readout of the part per million (ppm $= \mu m^3 \times 10^6$/ml) was set using the procedure outlined in the Coulter counter Model TAII Operator's Manual (1975). Background counts were obtained from sea water filtered through 0.45 μm, and 0.22 μm filters in series. The "noise" level was found negligible for all size intervals except the first which was therefore screened out allowing particles between equivalent spherical diameters of 5 and 145 μm to be counted and sized. Some samples were gently agitated using a mechanical stirrer, to prevent larger particles from sedimenting. To minimize coincidence, certain samples were diluted 2 or 5 fold. In most cases 50 ml counts (160 sec) were made in the time mode, with the manometer pinched off to prevent erratic flow due to the mercury column surging at sea.

The Coulter counter system was linked to a Hewlett Packard 85 calculator, which enabled the printing of particle spectra at sea. Further data manipulations were performed by transferring stores of data from HP85 magnetic tapes to an Eclipse C350 computer so that three dimensional particle spectra could be produced (where x = diameter intervals in micrometers, y = particle volume (ppm) and z = depth).

Chlorophyll 'a' determinations

One-litre samples were filtered on board onto 47 mm Nucleopore GC-50 glass fibre filters, stored deep frozen, and analysed spectrophotometrically in 90% acetone. Concentrations were determined from a standard curve (SWART and BARLOW, 1981).

RESULTS

Significant regressions between Coulter counter determined particle volume and chlorophyll a measurements were obtained from all three cruises (fig.1). Particle volume may therefore be considered a suitable index of phytoplankton biomass, as ANDREWS and HUTCHINGS (1980) demonstrated that carbon : chlorophyll a ratios were fairly constant during the upwelling season.

Each cruise is discussed separately in terms of drogue movements in relation to wind patterns, depth of the euphotic zone and upper mixed layer, and phytoplankton development in terms of particle spectra and species composition.

December 1979

The drogue was released approximately 10 km offshore in newly upwelled water of 10 - 11° C from where it travelled a total distance of 28.2 km in 102 hours for a mean drift of 0.27 km/hr (fig. 2). On the third day, however, it covered 10.6 km at a mean drift of 0.44 km/hr with an average wind speed of 10

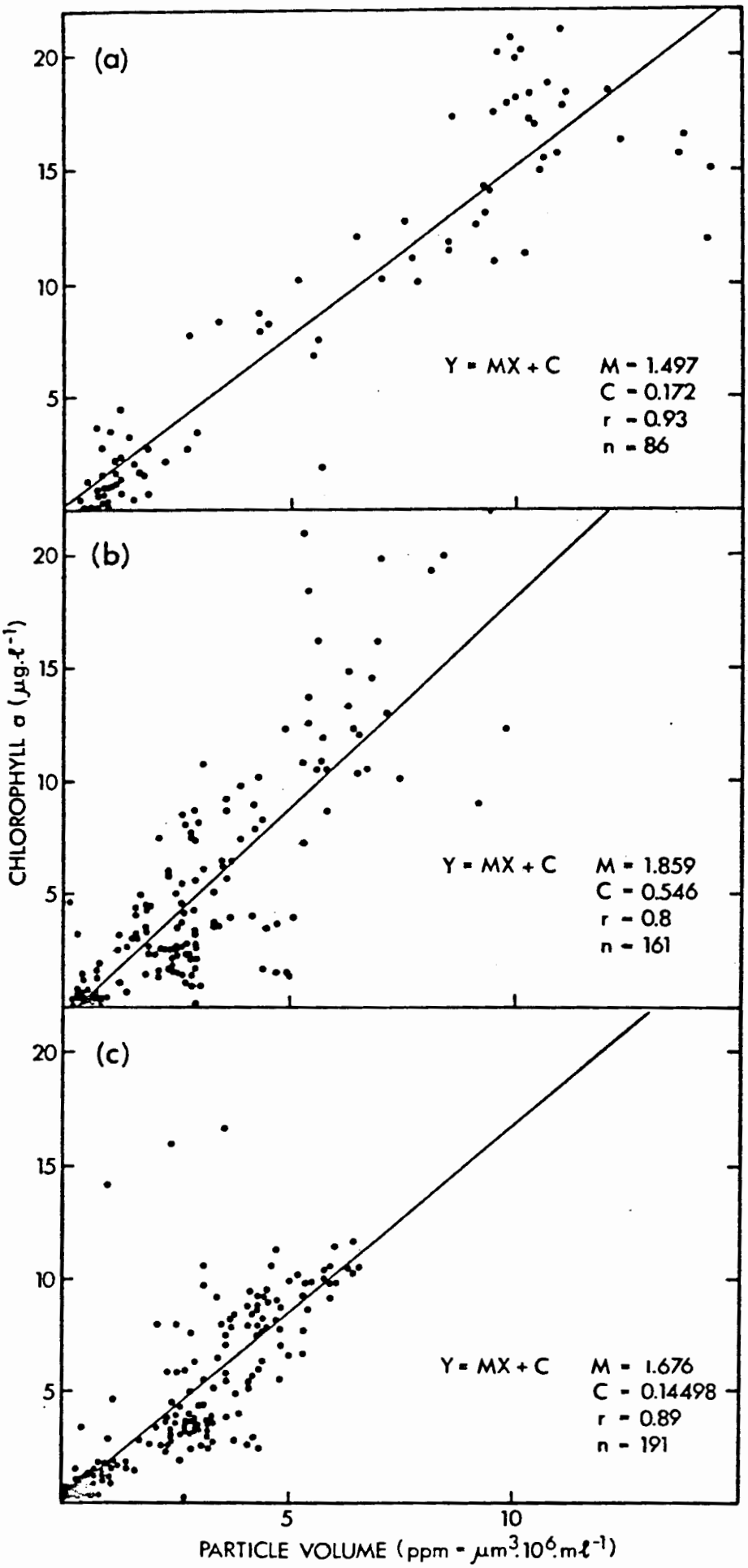

FIG. 1. - Correlation coefficients and linear regression equations for chlorophyll "a" ($\mu g.\ell^{-1}$) and particle volume (ppm) for (a) December 1979 (b) December 1980 and (c) February 1981.

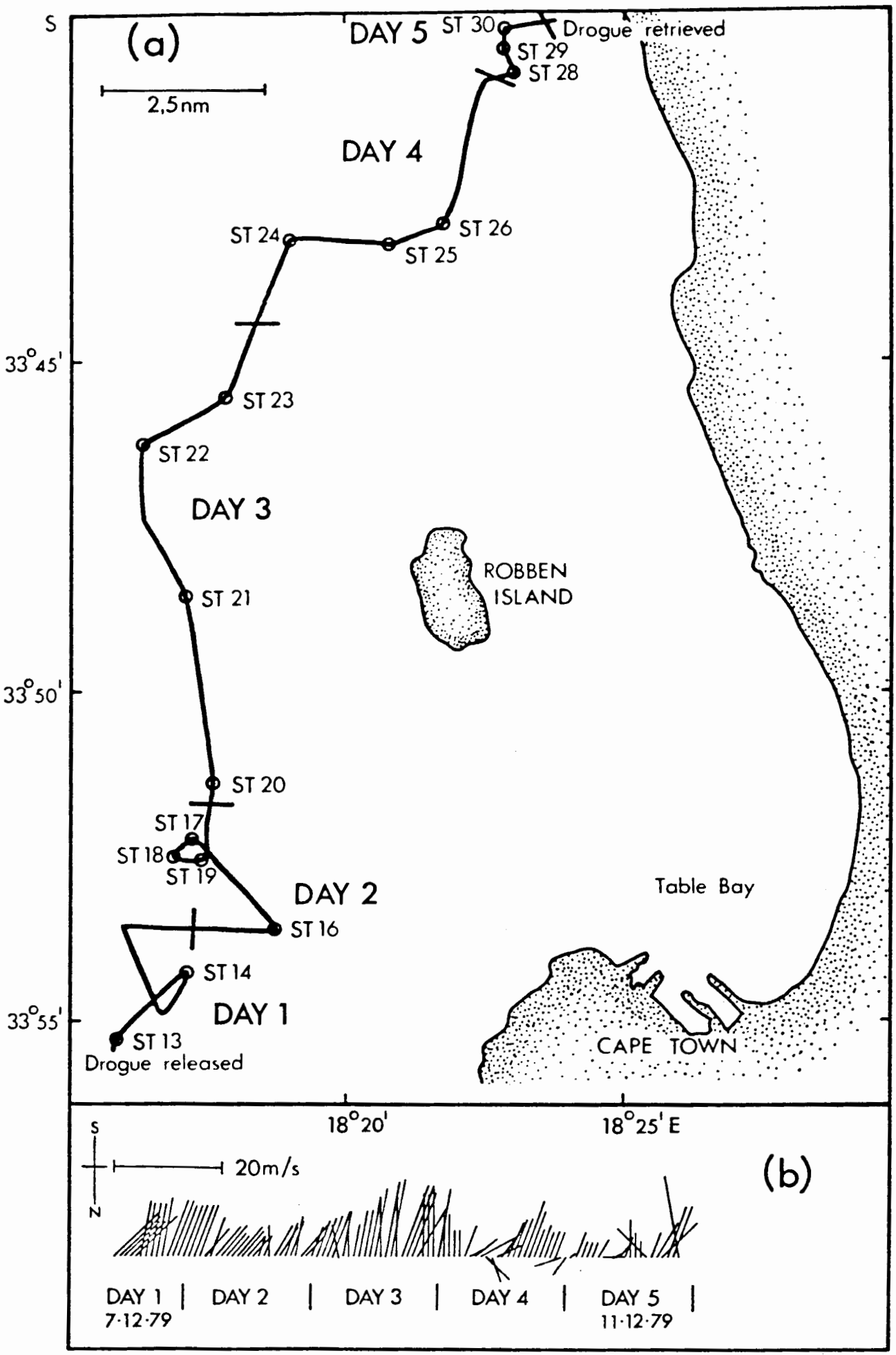

FIG. 2. - December 1979. (a) The drogue trajectory. (b) The wind stick diagram.

m/s from the south. Evidence from wind data, showed that an average wind speed of 7 m/s was experienced over the 5 day period between 7 - 11 December. For almost the entire survey period, the winds blew consistently from the south-southwest, causing northward and shoreward movement of the drogue.

During the initial stages of the study, the 1% light level (commonly regarded as the bottom of the euphotic zone) extended to approximately 50 meters, which, combined with the uniformly mixed water column provided ideal conditions for phytoplankton growth (fig. 3(a)). As mixing and sunwarming proceeded, an upper mixed layer developed increasing to approximately 20 meters while the euphotic zone became much shallower, averaging 10 - 12 meters.

The vertical profiles of particle volume (fig. 4) and the particle spectra (fig. 5) showed that a phytoplankton bloom developed rapidly over the 5 day period with particle volume increasing from < 1.0 ppm on Day 1 to > 10 ppm on Day 4 and 5. This 10 fold increase in biomass occurred within the upper 10 - 20 meters with particle volume roughly doubling daily. Low particle volumes were evident on Day 1 (fig. 5). Particle volume increased somewhat on Day 2 between ESD (equivalent spherical diameter) of 9 - 57 μm and then peaked on Day 3, 4 and 5 at roughly 18 μm with the bulk of the volume spread over an ESD range of 14 - 57 μm.

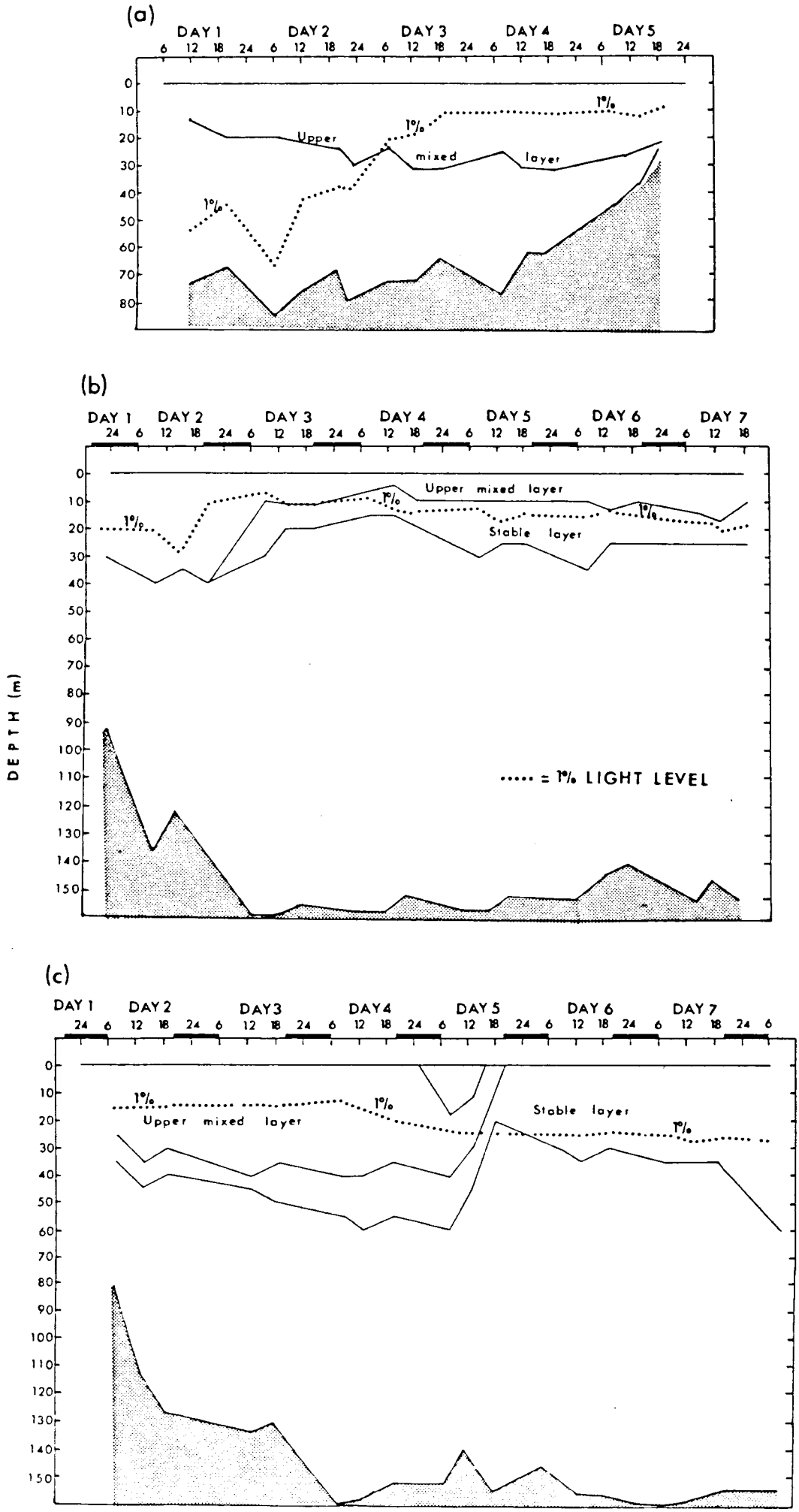

FIG. 3. - The vertical sections of the 1% light level (euphotic zone) the upper mixed layer, and stable layer for (a) December 1979 (b) December 1980 and (c) February 1981. (Upper mixed and stable layers were determined using temperature, chlorophyll "a" and nutrient profiles)

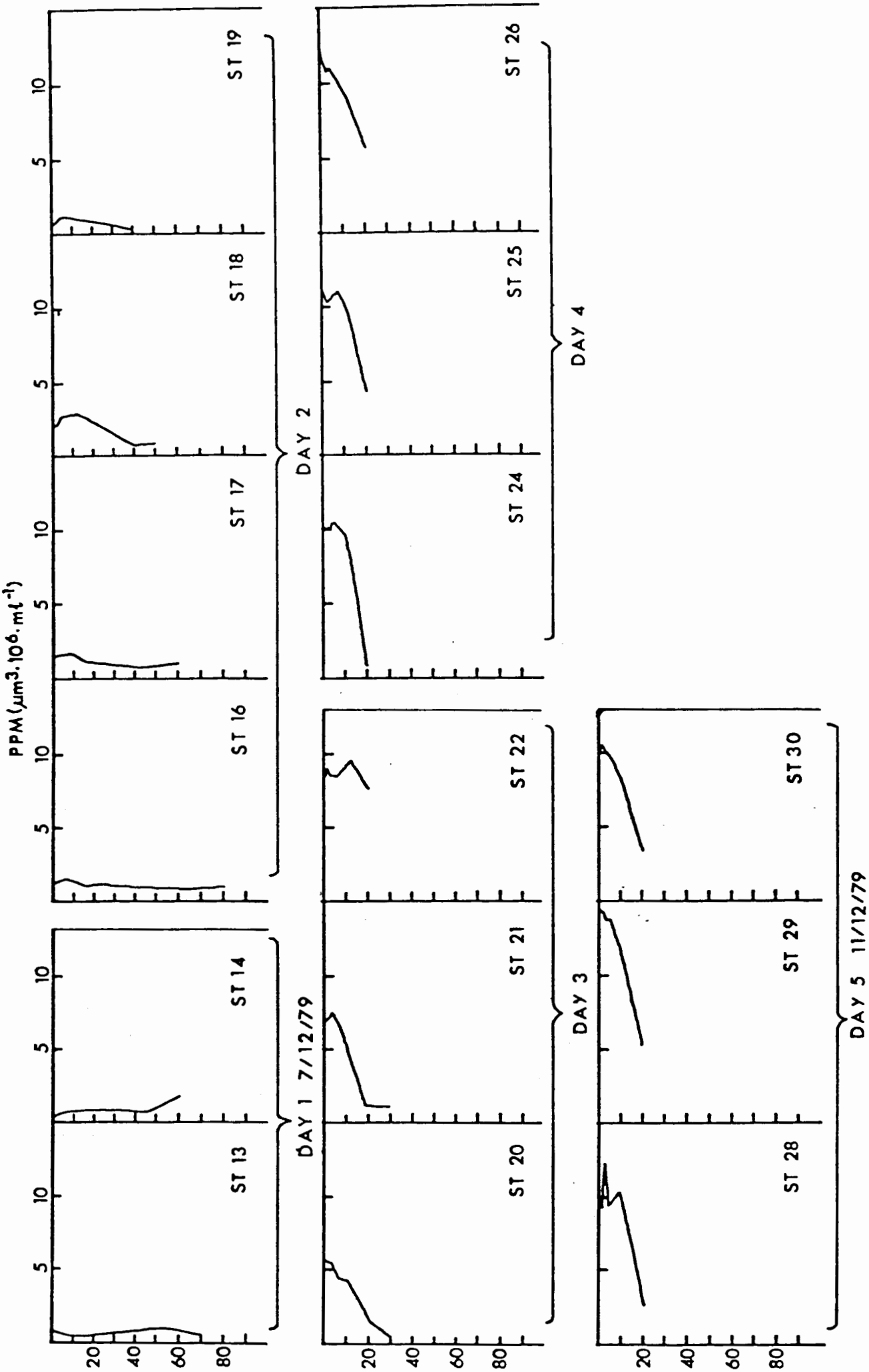

FIG. 4. - Vertical profiles of total particle volume (ppm) at each station along the drogue track for December 1979.

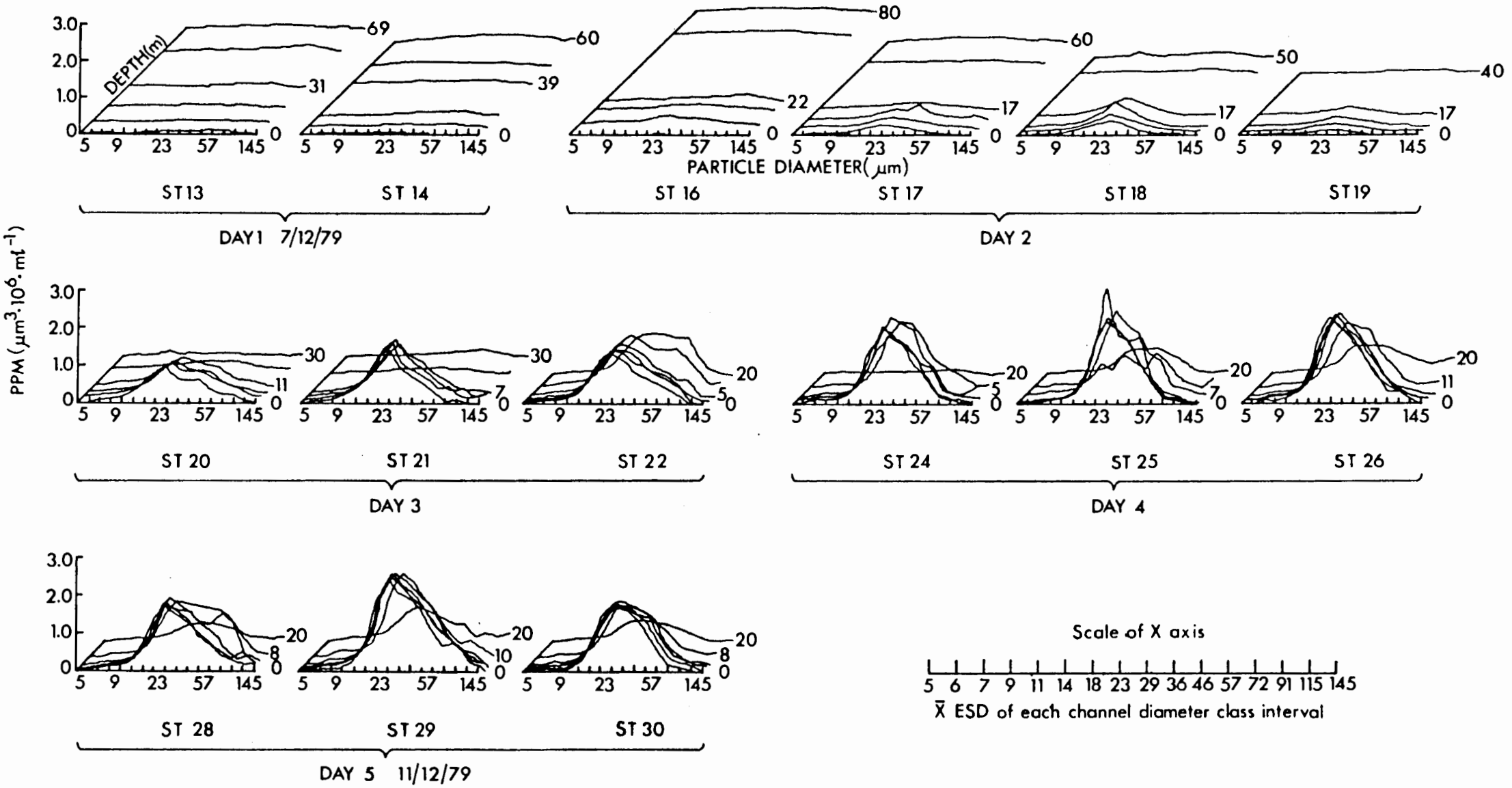

FIG. 5. - Three dimensional particle spectra plotted for each station between 7 - 11 December 1979 where x = particle diameter (μm) with diameter increments of $2^{1}/_{3}$ (Sheldon and Parsons, 1967a), y = particle volume (ppm) and z = depth (m).

A mixed phytoplankton community developed with three species dominating (fig. 6). Chaetoceros compressus Laud. was by far the largest contributor in terms of numbers, representing on average half of the cells, whilst Skeletonema costatum (Grev.) comprised the bulk of the total particle volume. The microscopic measurements in Table I show that on average the ESD of chains of preserved Chaetoceros compressus and Skeletonema costatum are 14 µm (range 9 - 23 µm) and 28 µm (range 15 - 36 µm) respectively. These diameters fall well within the bounds of the particle volume peaks (fig. 5). It would not seem unreasonable therefore, to assume that realistic biomass estimates can be obtained from the particle spectra based on these approximations of chain and cell sizes.

December 1980

The drogue covered a total distance of 170 km in 140 hours at an average mean drift of 1.21 km/hr (fig. 7). The winds were consistent and strong from the south during the first three days of the cruise averaging 8.7 m/s. On Day 4, the winds dropped and veered from gentle southwesterlies to northwesterlies to northerly and backed to southwesterlies on Day 5. Strong southerly winds recommenced on Days 6 and 7. The drogue moved in a northerly direction between the 100 and 200 meter isobaths. A relatively short distance was covered on Day 4 and 5 due to the lull and change in wind direction. The longest distance was covered on Day 7 at a mean drift of 1.96 km/hr with winds averaging

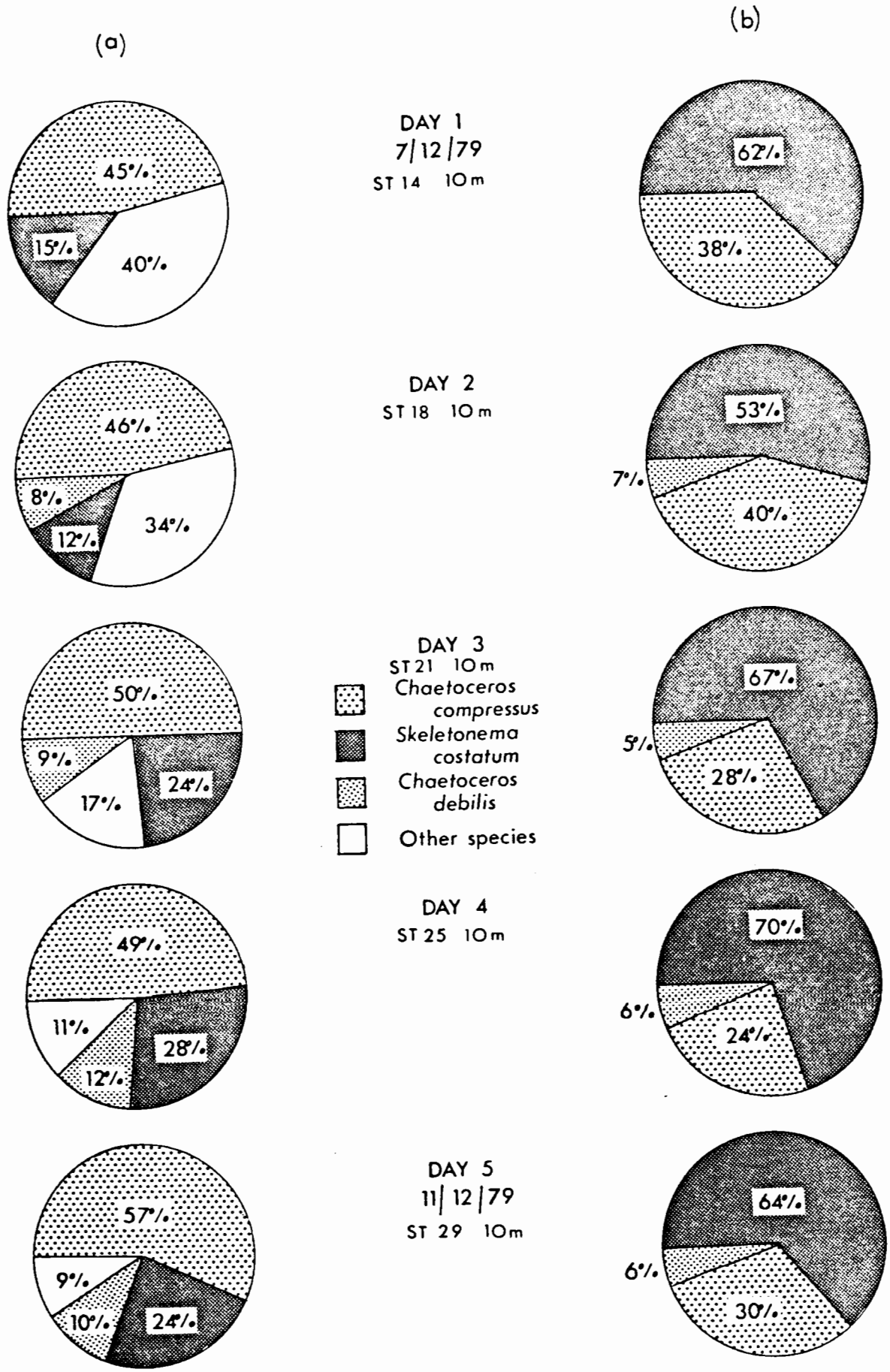

FIG. 6. - Pie diagrams showing the daily species composition for December 1979 in terms of (a) relative abundance by numbers (b) relative particle volume (excluding all species in the "other species" category).

Table I - Equivalent spherical diameters (ESD) of the dominant phytoplankton species obtained from average cell and chain volumes.

Phytoplankton Species	$\overline{X}$ Cell Dimensions (μm)			$\overline{X}$ Cell Volume (μm³)	$\overline{X}$ ESD of a Cell (μm)	Average Cell No. per chain (Range)	Range in ESD of Chains (μm)	$\overline{X}$ Chain Volume (μm³)	$\overline{X}$ ESD of a Chain (μm)
	Length	Width	Height						
Chaetoceros compressus	9.2	6.1	6.1	342.3	9	1 - 15	9 - 23	1711.5	14
Chaetoceros spp.	9.2	6.1	6.1	342.3	9	1 - 15	9 - 23	1711.5	14
Lauderia spp.	36.7	27.5	25.5	27754.4	38	1 - 6	38 - 72	111017.6	62
Nitzschia spp.	76.5	4.6	-	1237.3	13	1 - 17	13 - 30	6186.5	22
Skeletonema costatum	15.3	9.2	-	1690.6	15	1 - 20	15 - 36	10143.5	28
Thalassiosira spp.	36.7	18.4	-	19454.5	33	1 - 9	33 - 72	97272.5	54.2

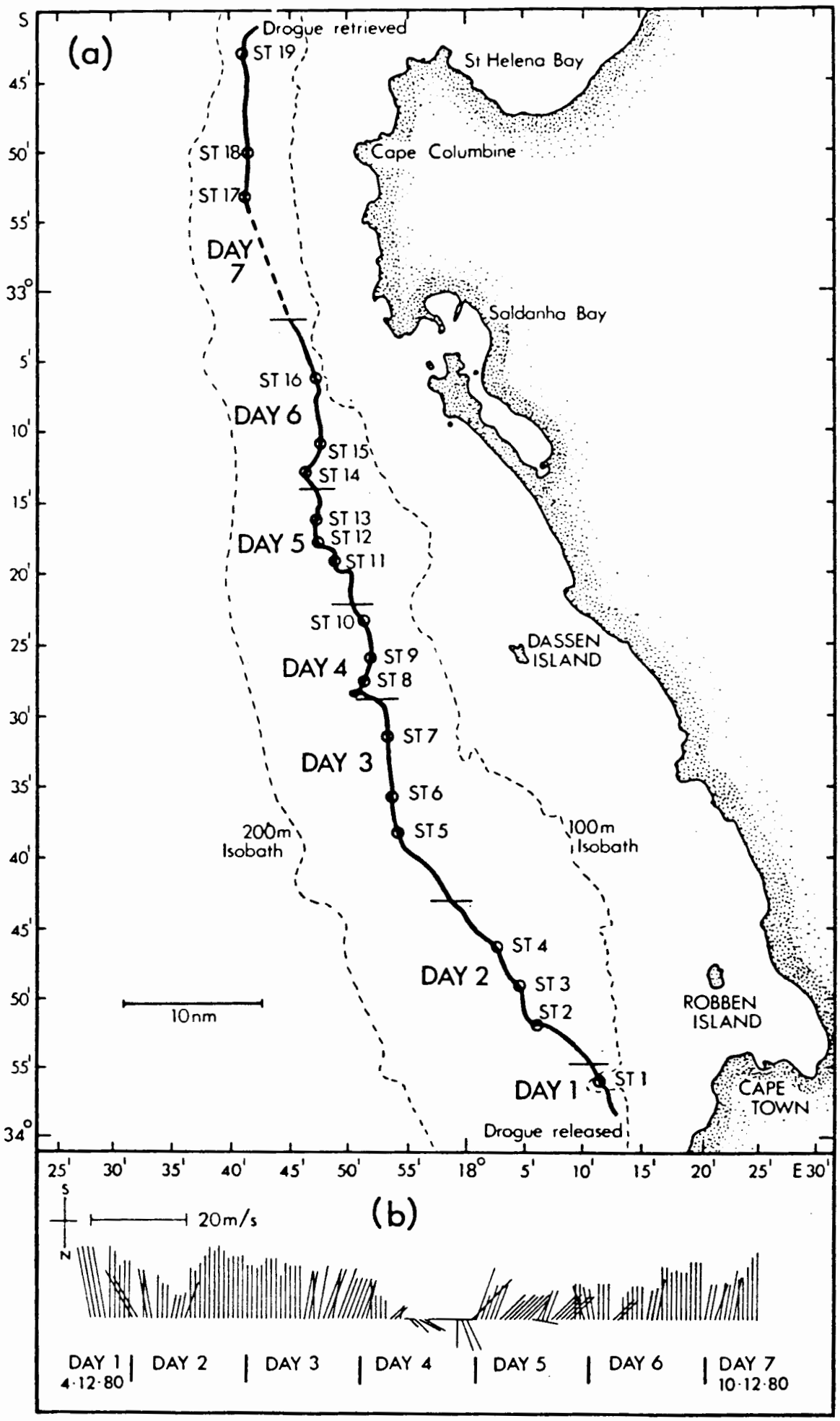

FIG. 7. - December 1980. (a) The drogue trajectory. (b) The wind stick diagram.

a speed of 9.8 m/s as the drogue was apparently entrained in the Cape Columbine Jet (NELSON and HUTCHINGS, 1983).

A relatively uniform euphotic zone of roughly 20 meters was evident throughout the seven day period (fig. 3 (b)) as in the absence of strong upwelling prior to the cruise, a patch of slightly aged upwelled water of 11 - 12° C, with moderate chlorophyll a concentrations was selected for launching the drogue. The strong prevailing winds resulted initially in a deep upper mixed layer, down to 40 meters, but it subsequently rose to approximately 10 meters with a subsurface stable layer forming between 10 and 40 meters as the wind speed decreased.

Particle volume (figs. 8 and 9) showed an initial moderate crop of phytoplankton occurring within the upper 40 meters during the early part of the cruise, followed by an increase from < 2 ppm (Day 1) to > 8 ppm (Day 3) in the upper 20 meters as the water column stabilized. In the following days the phytoplankton bloom peak sank down to roughly 30 meters as observed by a subsurface maximum in particle volume occurring on Days 6 and 7. During the initial phase, peaks were apparent at ESD's of 23 µm and very slightly around 91 µm. In the following days, when the maximum concentrations shifted to subsurface levels, a more bimodal distribution was observed, with peaks at 23 µm and 91 µm ESD.

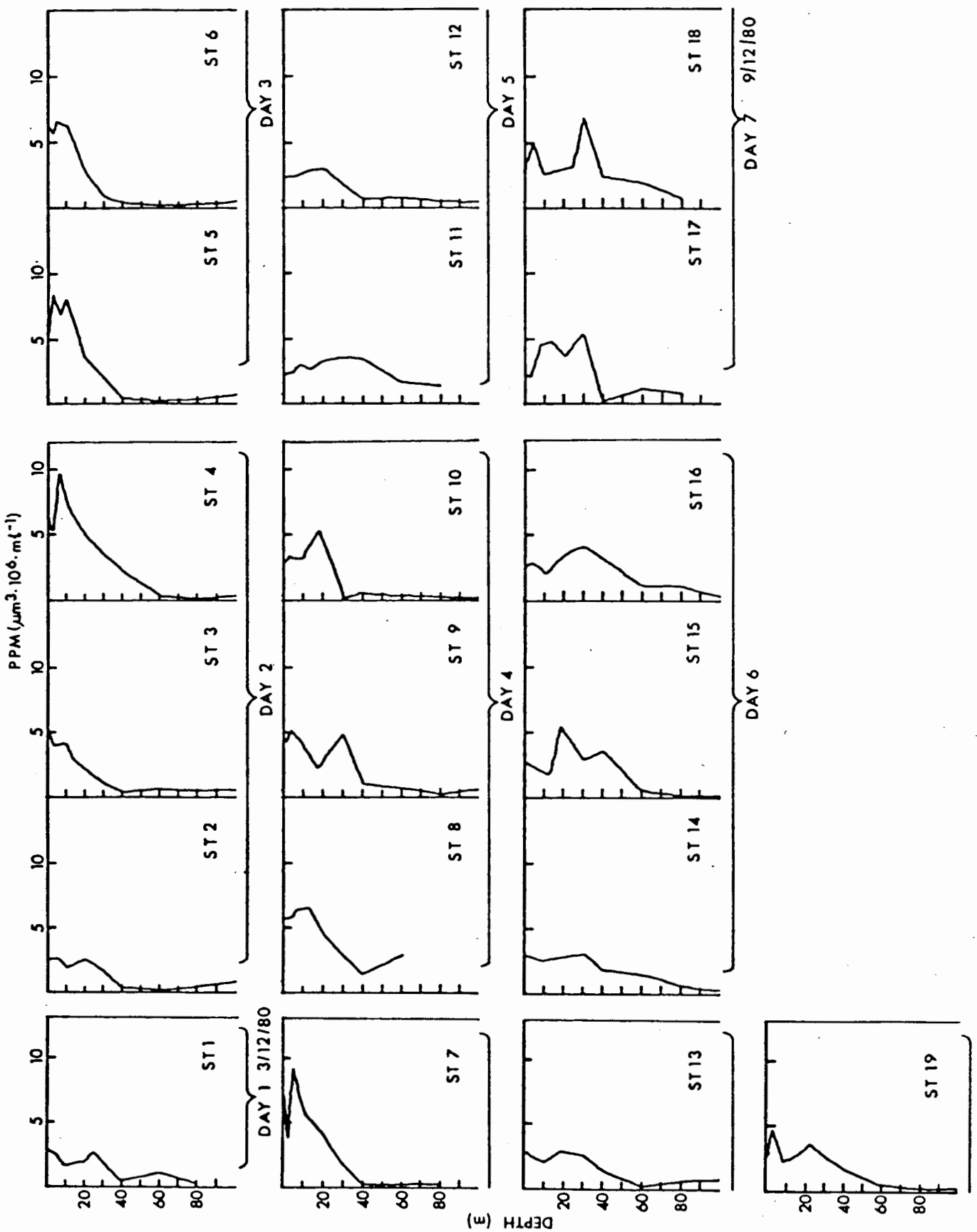

Fig. 8 Vertical profiles of total particle volume (ppm) at each station along the drogue track for December 1980.

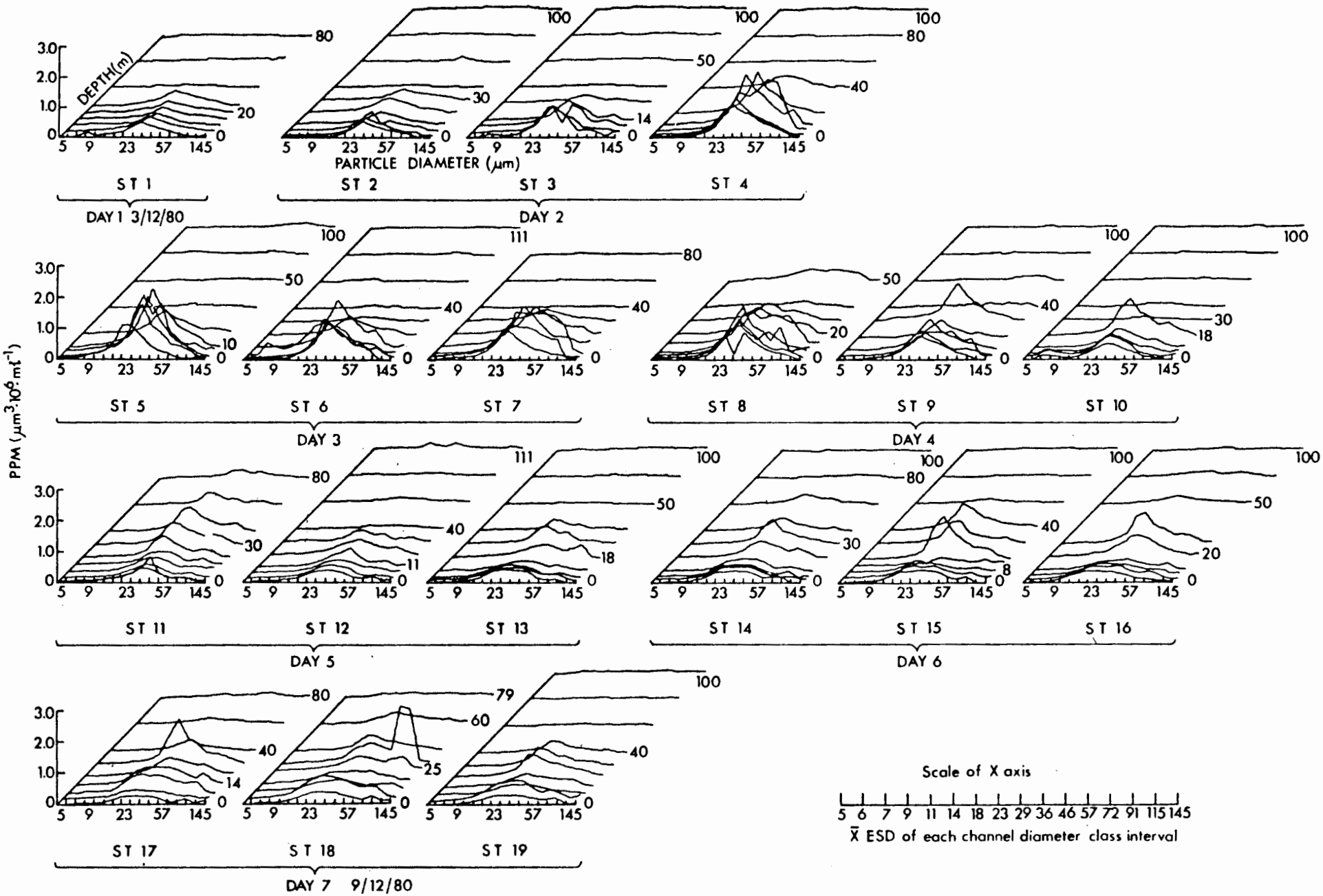

FIG. 9. - Three dimensional particle spectra plotted for each station between 3 - 9 December 1980 where x = particle diameter (μm) with diameter increments of $2^{1/3}$ (Sheldon and Parsons, 1967a), y = particle volume (ppm) and z = depth (m).

The species composition varied in terms of diversity, relative abundance and relative particle volume (fig. 10). Both Nitzschia and Chaetoceros spp. represented on average more than 80% of the total numbers with Skeletonema costatum, Lauderia spp., and a mixture of other species contributing the remaining 20%. Nitzschia spp. dominated initially until Day 3 and Chaetoceros spp. until Day 7. The particle volume was represented by mainly Nitzschia, Lauderia and Thalassiosira spp. The latter two species, although not abundant, were important in terms of volume (Table I). Their contribution is evident in many of the spectra as a secondary peak between 46 - 91 μm ESD (fig. 9). In addition to this the $\bar{X}$ ESD of a Nitzschia spp. chain (22 μm) coincided initially with the particle volume peak, during the first three days.

February 1981

Figure 11 shows the drogue trajectory in relation to the wind. The drogue moved in a northwesterly direction initially during the first three days of the cruise when very strong southerlies blew of approximately 20 m/s . On Day 4 the winds dropped, then swung to gentle north-northwesterlies and back again to moderate 10 - 15 m/s southwesterlies on Days 5 and 6. During this short lull, the drogue meandered extensively before moving south to a position some 16 km offshore from the site of its initial release. The drogue covered a total distance of 144 km in 162 hours averaging a drift of 0.89 km/hr. The largest

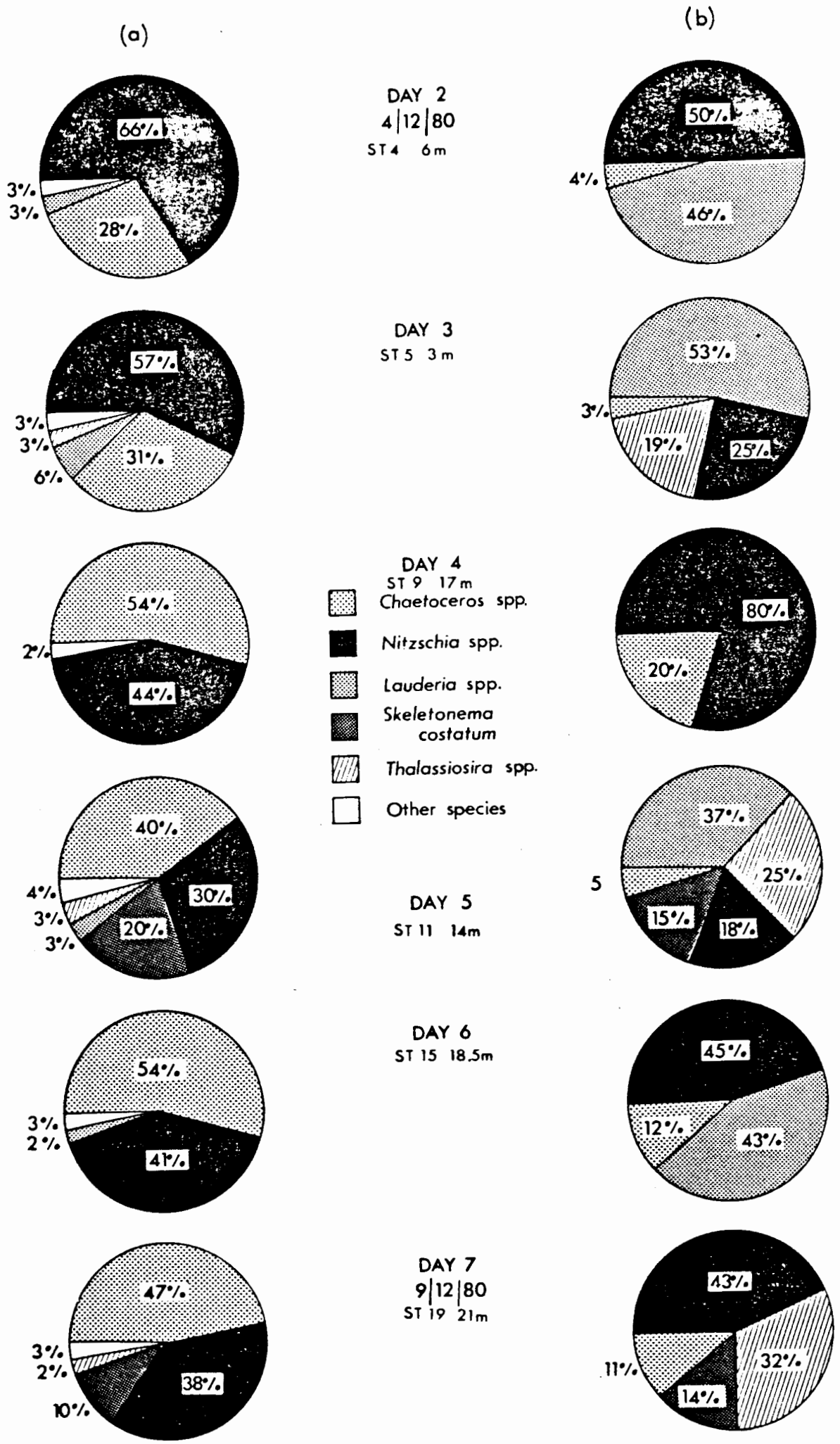

FIG. 10. - Pie diagrams showing the daily species composition for December 1980 in terms of (a) relative abundance by numbers (b) relative particle volume (excluding all species in the "other species" category).

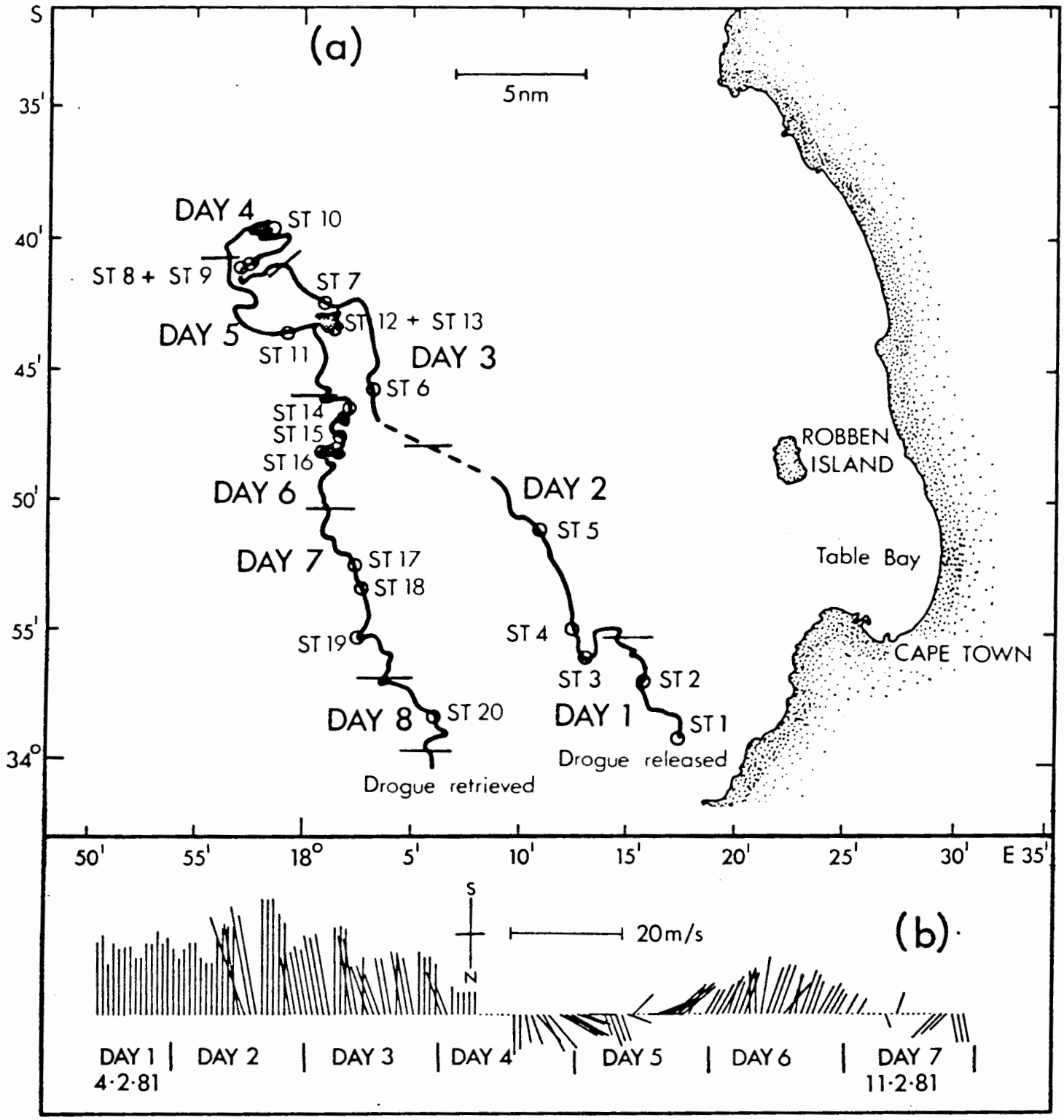

FIG. 11. - February 1981. (a) The drogue trajectory. (b) The wind stick diagram.

distance covered was on Day 2 when strong south-southeasterly winds blew at an average speed of 15 m/s.

The strong prevailing southerly winds initially caused deep mixing of the water column down to 60 meters (fig. 3(c)). But as the winds dropped, the effect of sunwarming gradually stabilized the surface waters. The 1% light level averaged 15 meters for the first three days then deepened to 20 meters for the remaining four days, just above the thermocline.

Low particle volumes were evident on Day 1 at the surface (< 1 ppm) with a subsurface maximum (> 3 ppm) occurring at roughly 25 meters at Station 1(fig. 12). Although vigorous upwelling had preceded the drogue launching, a moderately well-developed bloom was already apparent, indicating very early and successful seeding into newly upwelled water (9.5 - 10.1 °C). Particle volume was distributed uniformly down the water column to approximately 60 meters and increased slowly to > 4 ppm up till Day 3. A gradual decrease in particle volume was evident in the following days with relatively shallower biomass maxima occurring within the upper 20 - 50 meters as the upper layers stabilized when the wind abated. Particle peaks were evident up till Day 4 peaking between 18 - 57 μm ESD (fig. 13). On the following Days (5, 6 and 7) the size and shape of the particle spectra changed. A broader and flatter spectrum was evident in the upper layers and a different spectrum with a peak developing at roughly 72 μm occurred in the lower layers of the water column.

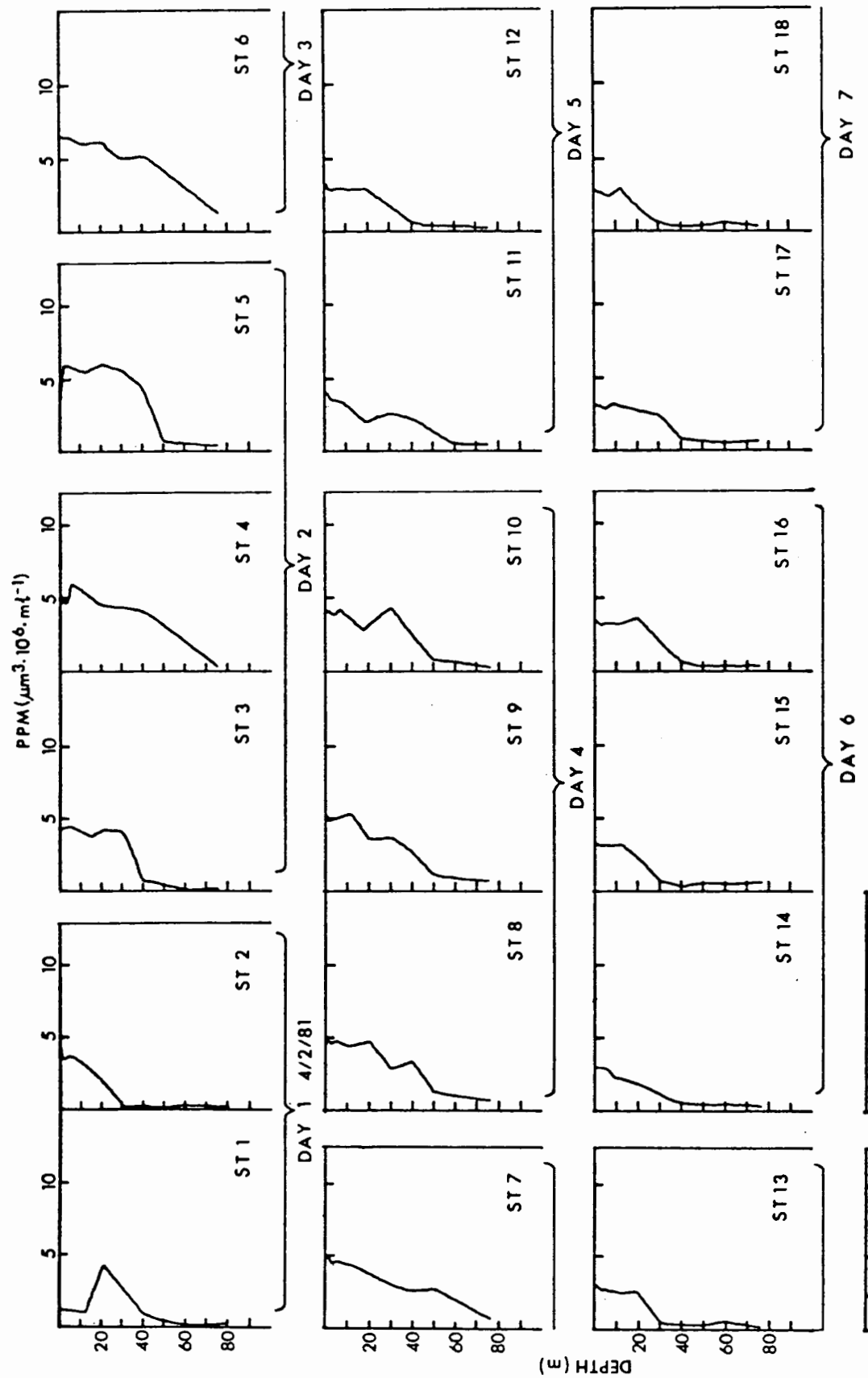

FIG. 12. - Vertical profiles of total particle volume (ppm) at each station along the drogue track for February 1981.

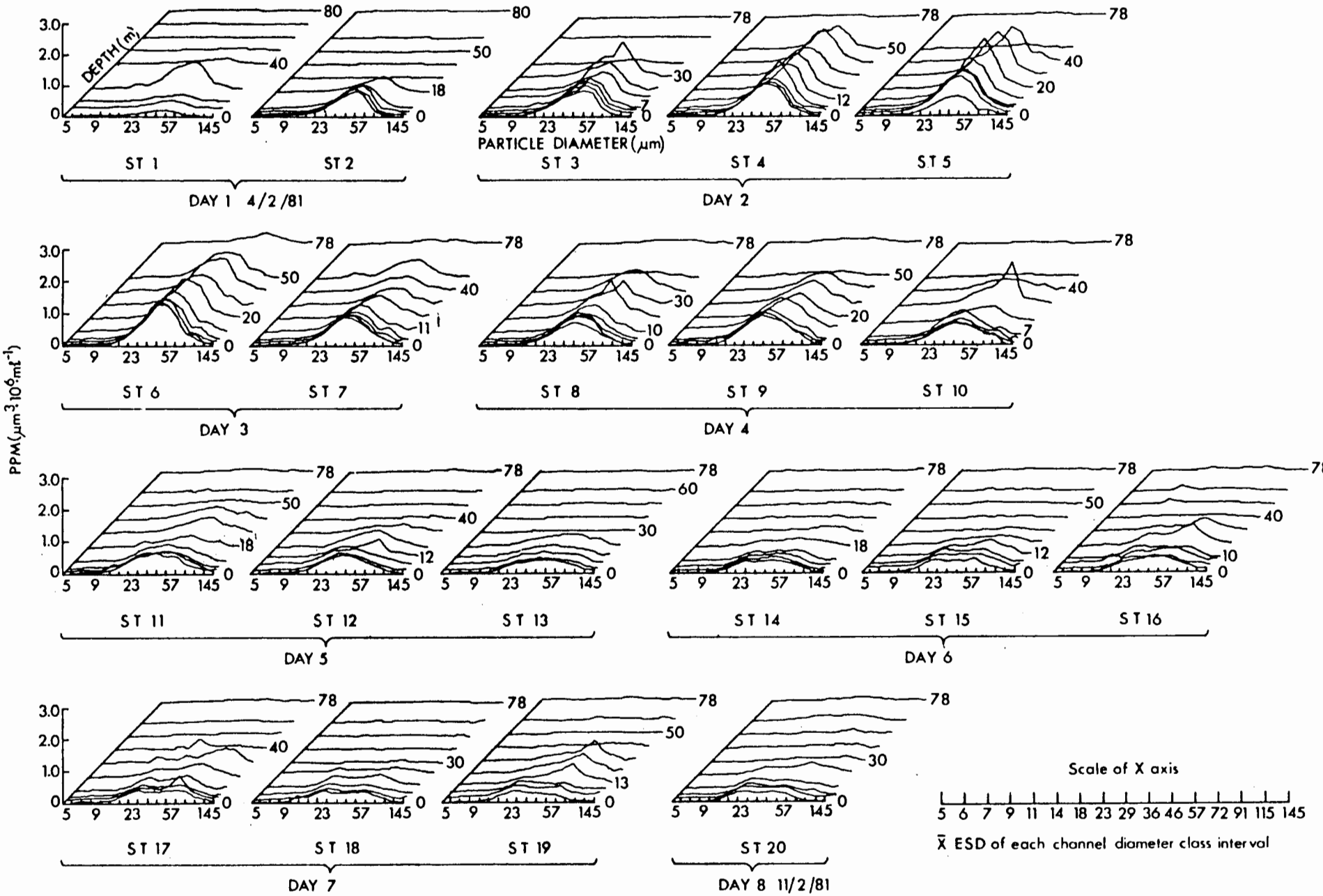

FIG. 13. - Three dimensional particle spectra plotted for each station between 4 - 11 February 1981 where x = particle diameter (μm) with diameter increments of $2^{1/3}$ (Sheldon and Parsons, 1967a), y = particle volume (ppm) and z = depth (m).

A mixed phytoplankton community developed with Chaetoceros spp. dominating with respect to total abundance up till Day 6 and Nitzschia spp. dominating on Day 7 (fig. 14). Roughly 50% of the particle volume was represented by Thalassiosira spp. up till Day 4 and again on Day 7. Lauderia spp. appeared for the first time on Day 5 and dominated to Day 6. Referring to Table I the $\bar{X}$ ESD of a Thalassiosira spp. chain is 54.2 µm, falling within the biomass peak observed up till Day 4 in Figure 14. On Day 5 when the particle spectra showed distinct changes, the peak developing at roughly 72 µm could be attributed to the dominance of Lauderia spp. (range in ESD = 38 - 72 µm).

DISCUSSION

There are some biases in preserving phytoplankton in formalin as many naked flagellates smaller than 10 µm may not be recognizable. This biases species composition towards the more robust forms, although numerous microscopic examinations of fresh samples in coastal waters off the Cape Peninsula have consistently shown the predominance of diatoms during bloom conditions. Likewise BLASCO et al., (1980, 1981), and SCHNACK and ELBRÄCHTER (1981) showed that inshore waters of the northwest African upwelling region are dominated by large proportions of small centric diatoms, whereas in the offshore waters microflagellates tend to predominate. Additional underestimates of the smaller cells may have been caused through the collection of particles on a 37 µm mesh. This however does not present a major bias as the chain forming

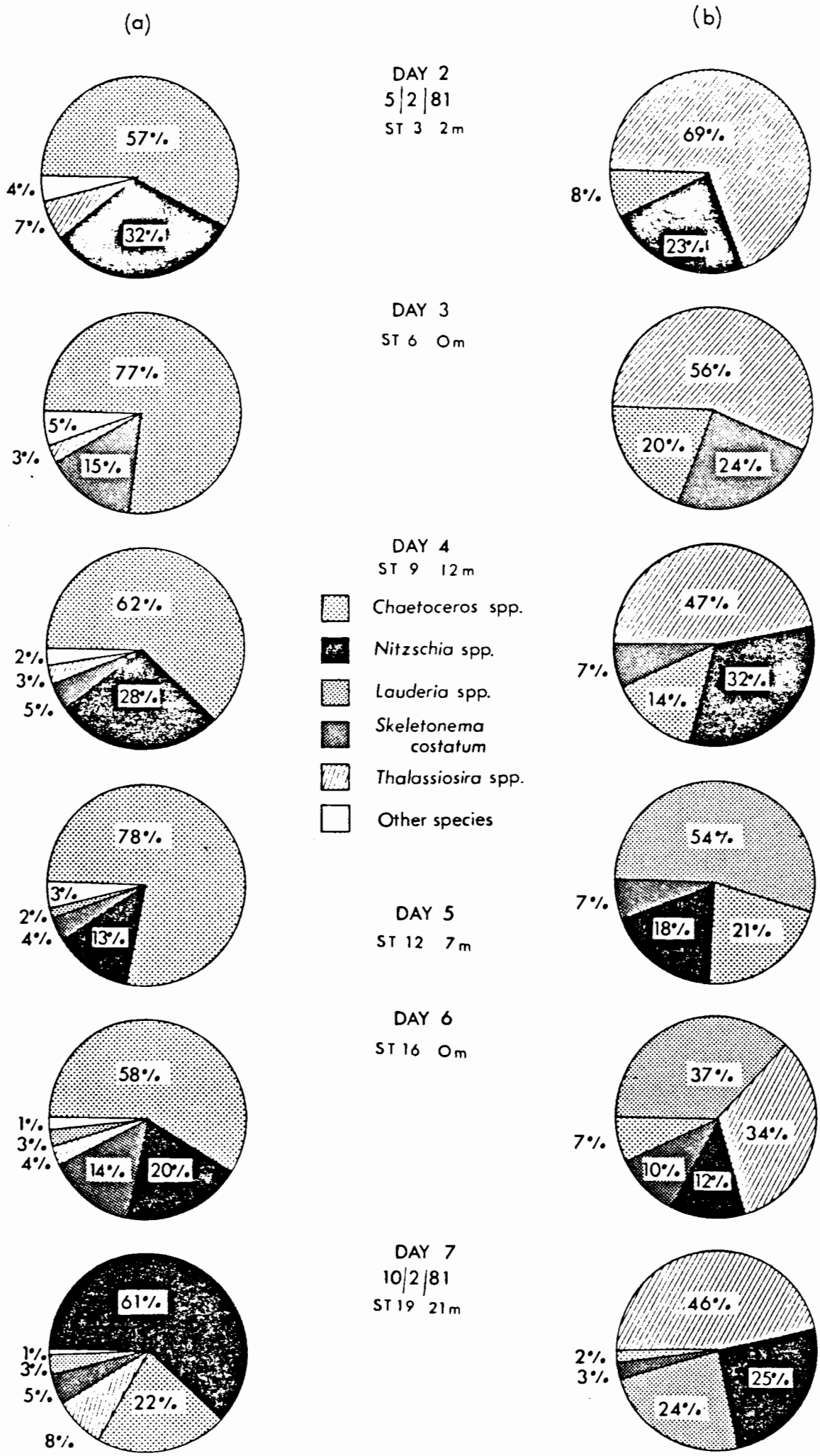

FIG. 14. - Pie diagrams showing the daily species composition for February 1981 in terms of (a) relative abundance by numbers (b) relative particle volume (excluding all species in the "other species" category).

diatoms dominated the biomass of the particle spectra derived from unfiltered water samples (figs. 9 and 13). These chains had average lengths > 37 μm (Table I) and so were adequately retained on the mesh.

It becomes evident from the above results, that rapid changes in the structure of phytoplankton communities can occur during the upwelling season, and can only be adequately monitored by following single parcels of water over a period of days with rapid repetitive sampling. In general the drogue movement at 10 meters, was shown to be largely influenced by the speed and direction of the wind. Discontinuities in the sequence of phytoplankton development can occur as an artefact of attempting to follow phytoplankton patches with drogues. These may occur by either winds causing horizontal shear of the water masses due to the flow being faster at the surface than at greater depths, or by vertical mixing due to strong winds. In addition the scales of motion affecting small particles are clearly different from those affecting the drogue itself.

In December 1979, the strong and uninterrupted southerly winds prior to the cruise produced clear, newly upwelled water close inshore with a very low initial seed population. The euphotic zone extended well below the surface initially, but as sunwarming proceeded so the water column stabilized, in the absence of strong winds, allowing a vigorous Chaetoceros/Skeletonema bloom to develop within three days. The particle volumes increased 3

fold until Day 3, reaching total volumes of 14 ppm by Day 5 when the patch began moving northwards. These results show that the growth of phytoplankton in local upwelling regions can be very rapid and the standing crop is 10 fold higher than that found off the Chilian upwelling region (SHELDON et al., 1972). However, the distribution of particle size and volume does vary geographically. Low particle volumes are found in the South Atlantic, North and South Pacific and the Sargasso Sea, with roughly equal concentrations of material occurring in all size grades. Whereas seasonal variations in the particle spectra occur in temperate waters where phytoplankton bloom in spring and autumn (MORRIS and SKEA, 1978; HITCHCOCK, 1978) and take weeks rather than days to develop.

Strong southerly winds during the initial phases of December 1980 and February 1981 caused vigorous mixing of the water column. In December 1980 the drogue was released in slightly aged water (11.8° C). A bloom co-dominated by Nitzschia and Chaetoceros spp. developed within the upper 20 meters. Thereafter, the brief wind reversal on Day 4 caused a discontinuity in the sequence of events, as was evident from the increase in the species diversity and the change in the particle spectra by Day 5. Although Nitzschia spp. and Chaetoceros spp. still co-dominated in terms of numbers, Skeletonema and Thalassiosira spp. increased in importance by volume. During the latter part of the study, the phytoplankton bloom sank down to 30 meters, below the euphotic zone, but remained within the subsurface stable layer.

During the February 1981 cruise, newly upwelled water was selected on the basis of surface temperature (10.2 °C) but seeding had already taken place, as was evident by the presence of moderately high particle volumes. As the drogue moved to the northwest a Chaetoceros dominated community was well mixed throughout the upper 50 - 60 meters. This community grew relatively slowly as the depth of the upper mixed layer exceeded the 1% light level, subjecting the population to low average light levels. The cessation of wind on Day 4, resulted in considerable eddying and there were changes in the species composition in the upper layers. The sudden appearance and dominance of Lauderia spp. (in terms of biomass) suggests that water in the vicinity of the drogue may have mixed with a neighbouring parcel of water. Alternatively, differential growth because of altered light and nutrient concentration may have caused the sudden change in species dominance. As there was no distinct alteration in the nutrient regime in the vicinity of the drogue, the change in vertical mixing may have altered the light regime to favour Lauderia spp.

From such brief sampling it is still unclear, whether hydro-dynamic forces (SEMINA, 1972), or the competitive nutrient kinetics (PARSONS and TAKAHASHI, 1973), or effects by grazing (STEELE and FROST, 1977; STEELE and HENDERSON, 1981) are responsible for determining species composition and cell size. HARRISON and TURPIN (1982) suggest that temperature, light intensity, specific nutrient flux, and nutrient supply are "coarse tuning" factors in

controlling the selection of major phytoplankton groups. Whereas "fine tuning" factors such as frequency of limiting nutrient addition, form of the limiting nutrient, allelopathy and parasitism, control selection within groups. Cell size selection is controlled by buoyancy, temperature, frequency of control addition, and size selective grazing. The importance of water stability, through its action on sinking and nutrient supply, does vary with fluctuations in wind velocity, which in turn determines the sequence of the species succession and the diversity of the phytoplankton community. Blooms of large-celled and chain-forming diatoms in coastal upwelling areas (TONT, 1976) are promoted by their upward vertical transport as well as by the higher nutrient concentrations associated with upwelling (MARGALEF, 1974). EPPLEY et al., (1978) showed that daily stirring of enclosed water columns, led to the maintenance of large phytoplankton cells. HARRISON and DAVIS (1979) using outdoor continuous cultures showed that at high specific nutrient flux, small, fast growing centric diatoms e.g. Skeletonema costatum (Grev.) Cleve and Chaectoceros spp. tend to dominate with low percentage of flagellates. Whereas at low specific nutrient flux a mixture of larger, slower growing centric diatoms, small flagellates and pennate diatoms are obtained. Studies on natural assemblages of phytoplankton grown in chemostats by THOMAS et al., (1980) show that pumping in high-nutrient water results in a decrease of crop diversity, whereas pumping of low-nutrient water results in a mixture of species. According to DAVIS (1982) who summarized MARGALEF's (1962) successional stages, bloom diatoms appear

initially reaching peak abundance within 4 - 8 days and then sink from the euphotic zone. These blooms are then followed by larger/slow growing diatoms, microflagellates, and large dino-flagellates. Our study clearly encompasses only the bloom diatom stage, as such seeding into newly upwelled water played the dominant role, with too short a survey period to allow a true succession of species to be observed. In view of the strong lateral and vertical mixing, it is unlikely that succession would ever take place without mixing masking the process. A sudden loss of particles from the deeper levels of the water column was evident as the turbulence decreased and the upper layers stabilized. This material could have sedimented to the bottom, or could have been re-entrained into upwelled source water as "preconditioned" seed cells capable of immediate rapid growth. In this case a very short lag phase would be observed, as in our Feb. 1981 study. Research in other upwelling regions (Peru and North-West Africa) show the existence of sub-surface on-shore counter-currents, which play an important role in the recycling of the upwelling water (BARBER and SMITH, 1981; HERBLAND et al., 1973).

The development of electronic methods has greatly simplified the process of counting and sizing marine particles and of evaluating the role of various-sized organisms in a plankton community. However, this method provides no taxonomic detail on the species present in a phytoplankton community. A major drawback is that the nature of the suspended particulate matter

is not known unless substantiated with qualitative microscopic observations. PARSONS (1963) and ZEITSCHEL (1970) believed that much of the particulate material is detritus and according to SUTCLIFFE et al., (1970) the concentration in the phytoplankton size ranges should be reduced by a factor of at least two. However, HOBBIE et al., (1972) have shown that the suspended matter in the western North Atlantic is mostly organic, even though less than half of the particulate organic carbon is associated with living material (SUTCLIFFE et al., 1970). Also, SHELDON et al., (1973) found more than half of their samples to be live material when estimating production of particles in the surface waters of the Sargasso Sea. Variable quantities of detrital material could be present in newly upwelled source waters. FIELD et al., (1981) show that during active upwelling off the Cape Peninsula, flushing of detrital material from inshore kelp beds occurs, and some of this may persist offshore, although rapid sinking of large detrital fragments probably reduces this effect. The extreme clarity of newly upwelled water on many occasions off the Cape Peninsula (e.g. fig. 3(a)), suggests that the detrital load is very small, and given the near-optimal light and nutrient conditions, a large proportion of the particulate matter during the first 3 - 5 days may be living material. The contribution of faecal material is uncertain and would vary with grazing activity, although OLIVIERI and HUTCHINGS (in prep.) suggest this would be a minor consideration. Therefore in this region of the southern Benguela Current, the electronic counting and sizing technique is particularly valuable for monitoring the

rapid changes which occur after newly upwelled water is brought to the surface. The unique location of this active upwelling centre at the southern extremity of the Benguela Current, and the very clear upwelled water which regularly appears, makes it a rewarding site for detailed studies of subsequent changes in the marine food chain, unfettered by enclosures.

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PAPER 3 - VOLUMETRIC ESTIMATES OF PHYTOPLANKTON PRODUCTION IN NEWLY UPWELLED WATERS OF THE SOUTHERN BENGUELA CURRENT.

VOLUMETRIC ESTIMATES OF PHYTOPLANKTON PRODUCTION IN NEWLY UPWELLED WATERS OF THE SOUTHERN BENGUELA CURRENT.

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Abstract

Production estimates, in terms of total particulate organic matter, was studied in four developing phytoplankton communities in newly upwelled waters, in the southern Benguela Current. Rapid growth (max. doublings per day ca. 2.9 and max. carbon production ca. 21g.m^{-2}.d^{-1}) of phytoplankton upwelled from source water occurred with little evidence of a lag phase. The growth pattern differed for each community encountered and was shown to relate to the rate of mixing of the water column and the nutrient and light regimes. Production rates were highest in newly upwelled waters and lowest under limiting light and during periods of nitrate depletion in the upper mixed layer. Changes in the growth rates were also attributed to short-term wind variations causing different water bodies to mix, changing the nutrient regimes.

Growth was not size dependent, although on certain occasions large increases occurred between an equivalent spherical diameter

(ESD) of 6-14 µm, suggesting growth of microflagellates. A diel variation was observed, with volume increases during the day exceeding those at night. Except under extreme limiting conditions, heterotrophic growth occurred.

Introduction

Primary production off the west coast of southern Africa varies significantly both spatially and over seasonal and shorter time scales (Henry et al. 1977; Andrews and Hutchings 1980; Brown 1980; Borchers and Field 1981; Carter 1982; Field et al. 1980a). Investigations by Brown (1984) have led to a better understanding of the factors regulating primary production in the Cape Peninsula upwelling system, variations of nutrients and light in the upper mixed layer being considered the major environmental regulators of primary production.

The aim of this study was to investigate the growth pattern of four developing phytoplankton communities off the Cape Peninsula, placing emphasis on the influence of environmental factors, and diel variation in the growth rates.

The first approach was to monitor changes in the biomass of various phytoplankton communities over a time span of several days, by tagging parcels of newly upwelled water with the aid of drogues (Olivieri et al. 1985). The second approach was based on assessing phytoplankton growth rates from serial measurements

of particle volume (ppm) over a 24 h experimental period, using an electronic particle counter. In this study, the major emphasis was placed primarily on the quantitative increases in particle volume rather than on the qualitative nature of the particles. Some of the first workers to develop this method for production studies were Cushing and Nicholson (1966) who used a mathematical growth relationship to estimate detrital concentrations. Their method can produce anomalies if small errors are made in the experimental procedure. A variation of this method is described by Strickland and Parsons (1968). According to Sheldon (1979) accurate measurements of phytoplankton growth by particle counting can only be obtained if the detrital material is estimated directly from microscopic measurements. Production studies using this technique have been conducted by several workers (Parsons 1965; Cushing et al. 1968; Parsons et al. 1969; Sutcliffe et al. 1970; Sheldon et al. 1973; Sheldon and Dunbrack 1981).

Methods

Preliminary growth experiments performed on three successive days on the December 1979 drogue cruise (Olivieri unpublished data), showed measurable volume increases. These findings prompted further detailed investigations, of daily growth experiments on four drogue cruises, by following parcels of upwelled water off the west coast of the Cape Peninsula in December 1980, and February, March and October 1981.

For descriptions of the cruises and sample collection techniques refer to Olivieri et al. (1985).

Experimental procedure

One-ℓ duplicate experimental bottles and a 250 ml initial bottle were drawn at the midday station, at the 100 and 50 % light levels for December 1980, February 1981, March 1981, and at the 100, 50 and 1 % light levels for the October 1981 drogue cruises. The reliability of replicate incubation was tested using the Paired t-test of Snedecor and Cochran (1967). The statistical variance was compared at $P = 0.05$.

Experimental bottles were placed in clear perspex deck incubators filled with running seawater and allowed to roll around by the movement of the ship, causing sufficient agitation. The seawater passing through the incubators never rose more than $1^{\circ}C$ above sea temperatures. Simulated light intensities were obtained by covering the experimental bottles with varying layers of stainless steel gauze, tested using a Licor quantum light meter for % P.A.R. transmission.

Particle growth was established by measuring the particle volume ($ppm = \mu m^3 . 10^6 . ml^{-1}$) of the initial bottle at the start of the experiment and subsequently counting subsamples of the experimental bottles at 2 - 3 hourly intervals over a 24 h incubation

period.

The particle size and volume were measured with a Model TA II Coulter counter using a 280 µm aperture tube, following the method of Sheldon and Parsons (1967a). Modifications to this basic technique have already been described by Olivieri et al. (1985). It should be noted, however, that growth was measured between equivalent spherical diameters (ESD) of 5.04 - 145 µm, so that most of the nanoplankton growth is excluded. Growth measurements reported here therefore represent minimal production estimates.

The Coulter counter system was linked to a Hewlett Packard 85 calculator, which corrected for background counts and enabled the printing of particle spectra at sea. Further data manipulations were performed by transferring data from HP85 magnetic tapes to a mainframe Eclipse C350 computer ashore. Computer programs facilitated the computation of the mean values of duplicate counts for each experimental and initial bottle, integration of the production values within the euphotic zone (zero growth was assumed at the 1 % light level, when production studies were not carried out at this light level), and plotting of growth curves (incubation time against production).

Specific growth rates were calculated within the euphotic zone using both day and night growth rates (autotrophic and heterotrophic) and just day growth rates (autotrophic), where

specific growth rate ($\mu.d^{-1}$) = ℓn (particle volume)$_{t_1}$ - ℓn (particle volume)$_{t_0}$,

division rate (div.d^{-1}) = $\frac{\mu.d^{-1}}{\ell n\, 2}$ (equivalent to Eppley's (1972) doublings per day) and

generation time (d) = $\frac{\ell n\, 2}{\mu.d^{-1}}$, for each experiment.

Cushing and Nicholson's method (1966) for determining the detrital content was not used, as the number of data points were too few to give a statistically significant variance on the calculated detrital content. Likewise, accurate detrital estimates could not be obtained from regressions of chlorophyll a : carbon because of poor correlations, although these ratios compared favourably with Boyd et al. (in press) and Cowles (1977). No detrital background was therefore assumed, so that the specific growth rates discussed in this paper refer to minimum doublings per day, and maximum generation times. The detrital content of upwelled water in the Cape Peninsula seems to be low, similar to the findings of Sheldon and Dunbrack (1981) off Peru.

For comparative purposes estimates of the carbon content of the total particulate volume were obtained using Cowles (1977) linear regression equation for the Peruvian upwelling area.

carbon ($\mu g.l^{-1}$) = 41.76 volume ($\mu m^3 . 10^6 . ml^{-1}$) + 13.38

Correlations between particle volume : carbon were low although

ratios were found to fall within the range of the generally accepted values found by Mullin et al. (1966) and Eppley et al. (1970).

Results

Daily production (Fig. 1(a) and Table 1) was highest at the start of the December 1980 drogue cruise, doublings per day decreasing from 2.96 on Day 1 to 0.61 by Day 5. Negligible growth occurred on Days 6 and 7, with generation times (d) increasing to 1.4. Autotrophs accounted for most of the daily growth, except on Day 4, when night production exceeded day production, and generation times (d) increased from 0.41 - 2.31 by Day 7. Similar growth curves were observed at the 100 and 50% light levels (Olivieri unpublished data) following the same trends as the integrated growth curves for each drogue cruise.

No definite trends in the growth of the varying size intervals could be distinguished from the particle spectra (Fig. 1(b)). During the first three days (2, 3, 4) the initial spectrum at the 100 and 50% light levels differed. At the 100% light level volume increased over most size intervals, whilst at the 50% light level a reduction in volume was observed in the large size intervals. A small peak (ESD 57 - 91 μm) was evident on the initial spectrum of Day 5, unaccountable by the volume increases of Day 4. Over the remaining days (5, 6, 7) volume increases were reduced overall, except in the smaller diameter size intervals,

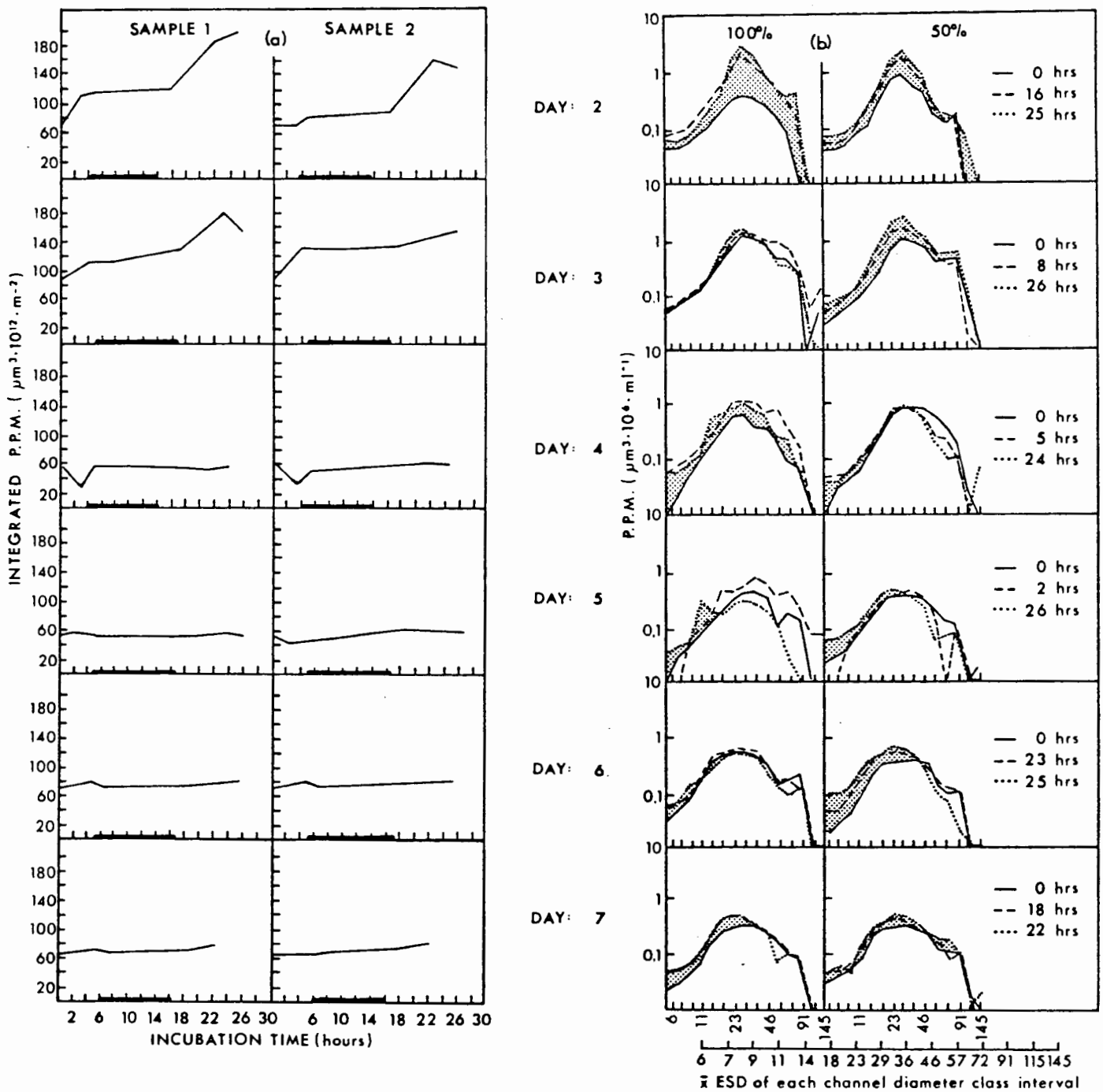

Fig. 1. December 1980. (a) Daily integrated growth curves showing production within the euphotic zone. (b) Particle spectra selected from specific counts at the 100 and 50% light levels for each production experiment. Shading represents growth.

Table 1. December 1980 - Specific growth rates calculated within the euphotic zone using both day and night growth rates (autotrophic and heterotrophic) and just day growth rates (autotrophic), where I = initial biomass; Ph(d) = hourly daylight production; Ph(n) = hourly night production; Pd = daily production; specific growth rate ($\mu.d^{-1}$) = ℓn (particle volume)$_{t_1}$ - ℓn (particle volume)$_{t_0}$; division rate (div.d^{-1}) = $\frac{\mu.d^{-1}}{\ell n 2}$; and generation time (d) = $\frac{\ell n 2}{\mu.d^{-1}}$.

Day	Sample	I ($\mu m^3 . 10^{12} . m^{-2}$)	Ph(d) ($\mu m^3 . 10^{12} . m^{-2} . hr^{-1}$)	Ph(n) ($\mu m^3 . 10^{12} . m^{-2} . hr^{-1}$)	Pd ($\mu m^3 . 10^{12} . m^{-2} . d^{-1}$)	$\bar{x}$ Pd ppm ($\mu m^3 . 10^{12} . m^{-2} . d^{-1}$)	$\bar{x}$ Pd carbon ($mgC . m^{-2} . d^{-1}$)	Specific Growth Rate ($\mu.d^{-1}$)	Division Rate D.R. (div.d^{-1}) or (doublings.d^{-1})	Generation Time (G.T.) (d)	† $\bar{x}$ Pd ($\mu m^3 . 10^{12} . m^{-2} . d^{-1}$)	† ($\mu.d^{-1}$)	† (Div.d^{-1}) or doubling.d^{-1})	† G.T.(d)
*														
2	S1	75.14	33.60	4.63	535.15	535.15	22361	2.09	3.02	0.33	327.60	1.68	2.42	0.41
	S2		27.98	8.32	487.54	487.54	20373	2.01	2.90	0.34	272.81	1.53	2.21	0.45
3	S1	90.01	23.40	5.66	365.46	274.16	11462	1.37	1.97	0.53	227.13	1.26	1.82	0.55
	S2		15.26	-1.33	182.85									
4	S1	62.74	-6.20	17.47	81.99	91.37	3839	0.90	1.30	0.77	-	-	-	-
	S2		-2.14	13.47	100.75									
5	S1	54.65	3.26	-1.78	23.55	28.90	1220	0.43	0.61	1.65	38.31	0.53	0.77	1.31
	S2		-2.36	6.02	34.25									
6	S1	71.77	4.10	-5.84	-13.73	-	-	-	-	-	41.25	0.45	0.65	1.54
	S2		2.92	-3.56	- 2.93									
7	S1	66.66	3.11	-0.80	33.07	46.94	1973	0.53	0.76	1.40	23.06	0.30	0.43	2.31
	S2		1.62	3.69	60.80									

* S1 and S2 are significantly different at P = 0.05
† only autotrophic growth is considered.

where a slight shift in the spectrum was observed, possibly indicating the breakage of larger chain-forming diatoms.

Consistent, strong southerly winds caused the drogue to move in a northerly direction during the December 1980 cruise. A moderate crop of phytoplankton occurred within the upper 20 m initially, and then sank to roughly 40 m (Olivieri et al. 1985). The strong winds resulted initially in the upper layer being mixed down to 40 m with nitrate concentrations of up to 10 $\mu M.m^{-3}$ (Fig. 2). As wind speed declined, the upper mixed layer shallowed to 10 m with low nitrate concentrations ($< 1\ \mu M.m^{-3}$), whilst a subsurface stable layer formed between 10 - 40 m, containing moderately higher levels of nitrates. The euphotic zone remained at roughly 20 m throughout the seven day period.

It becomes evident from (Fig. 3(a) and Table 2) that daily production was generally high throughout the February 1981 drogue cruise with doublings per day highest on Day 1, and decreasing to almost half on Day 3 and 6 with generation times (d) ranging between 0.41 and 0.61. Daytime production rates greatly exceeded night production over the first four days, but later (Days 5, 6, 7) heterotrophic activity increased. Autotrophic growth decreased during this period, with doublings per day decreasing to 1.13 and generation times (d) increasing to 0.89. It is important to note that the relationship between generation time and doublings per day for an autotroph is different to that for a heterotroph, as autotrophic growth can only occur during daylight hours.

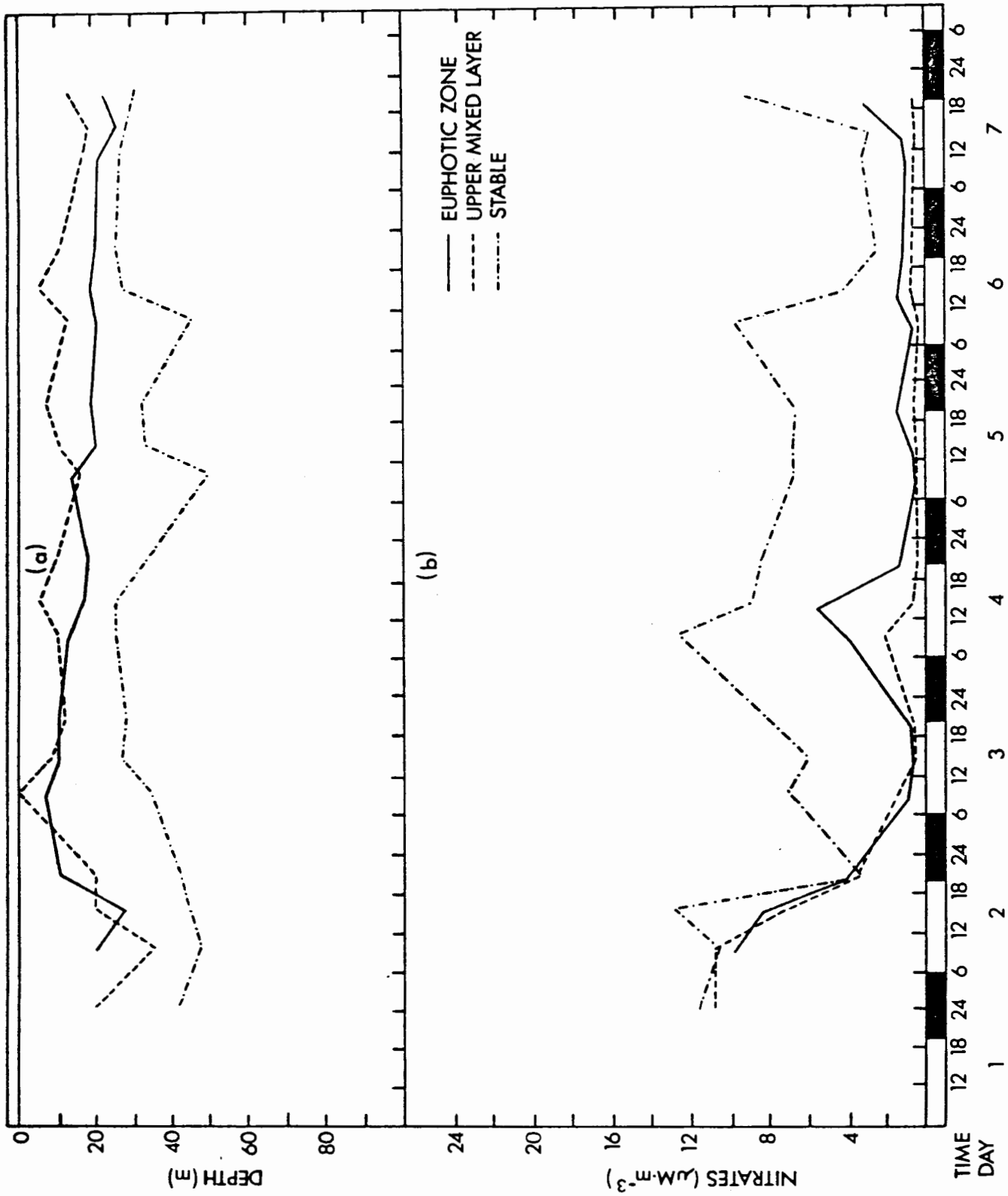

Fig. 2. December 1980. Vertical sections of (a) the 1% light level (euphotic zone), the upper mixed layer, and stable layer, (b) nitrates $\mu M.m^{-3}$ within each layer.

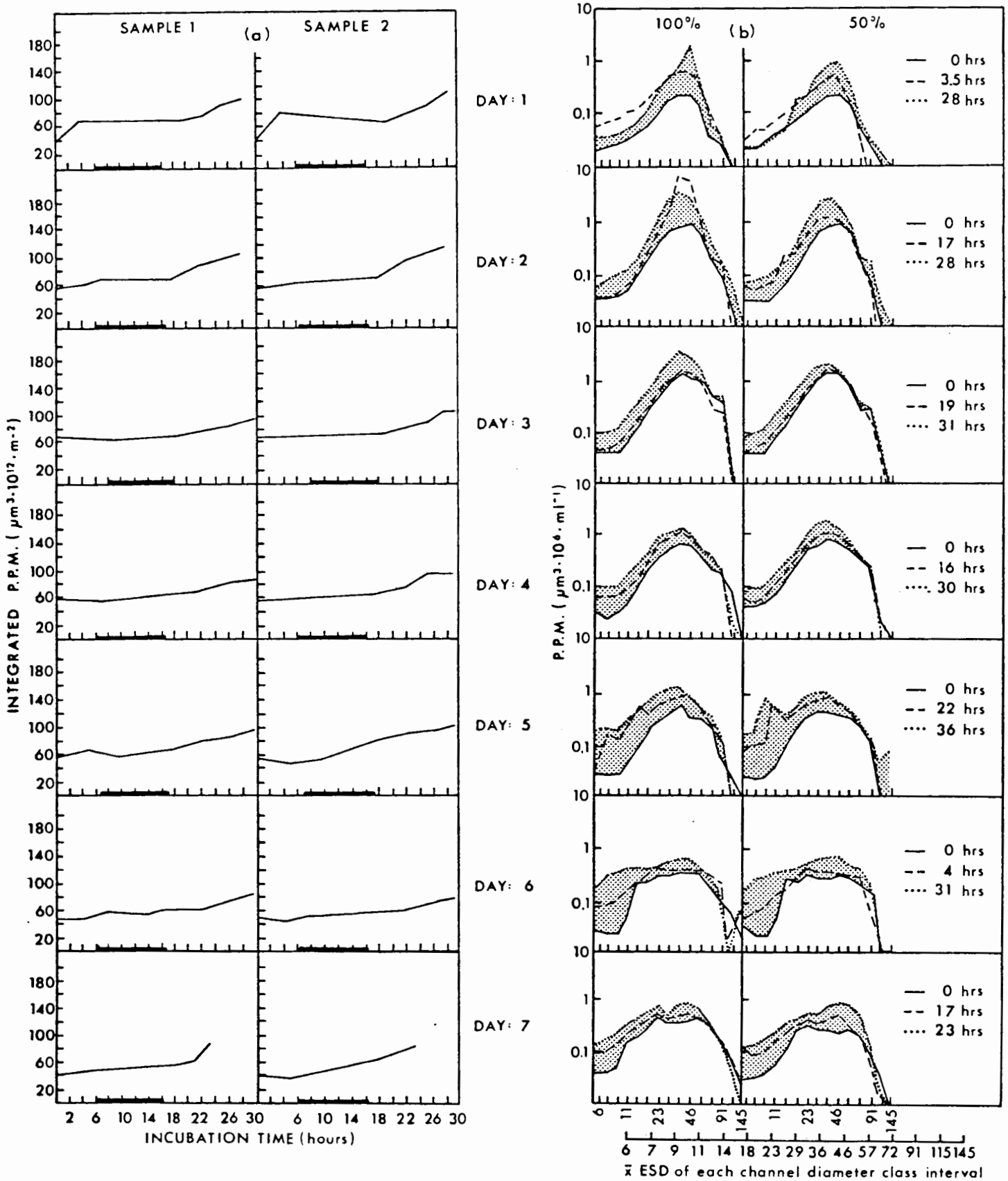

Fig. 3. February 1981. (a) Daily integrated growth curves showing production within the euphotic zone. (b) Particle spectra selected from specific counts at the 100 and 50% light levels for each production experiment. Shading represents growth.

Table 2. February 1981 - Specific growth rates calculated within the euphotic zone using both day and night growth rates (autotrophic and heterotrophic) and just day growth rates (autotrophic), where I = initial biomass; Ph(d) = hourly daylight production; Ph(n) = hourly night production; Pd = daily production; specific growth rate ($\mu.d^{-1}$) = ℓn (particle volume)$_{t_1}$ - ℓn (particle volume)$_{t_0}$; division rate ($div.d^{-1}$) = $\frac{\mu.d^{-1}}{\ell n 2}$; and generation time (d) = $\frac{\ell n 2}{\mu.d^{-1}}$.

Day	Sample	I ($\mu m^3 . 10^{12} . m^{-2}$)	Ph(d) ($\mu m^3 . 10^{12} . m^{-2} . hr^{-1}$)	Ph(n) ($\mu m^3 . 10^{12} . m^{-2} . hr^{-1}$)	Pd ($\mu m^3 . 10^{12} . m^{-2} . d^{-1}$)	$\bar{X}$ Pd ppm ($\mu m^3 . 10^{12} . m^{-2} . d^{-1}$)	$\bar{X}$ Pd carbon ($mgC . m^{-2} . d^{-1}$)	Specific Growth Rate ($\mu.d^{-1}$)	Division Rate D.R. ($div.d^{-1}$) or (doublings.d^{-1})	Generation Time (G.T.) (d)	† $\bar{X}$ Pd ($\mu m^3 . 10^{12} . m^{-2} . d^{-1}$)	† ($\mu.d^{-1}$)	† ($Div.d^{-1}$) or doubling.d^{-1})	† G.T. (d)
1	S1	43.72	13.27	-0.31	201.90	198.96	8322	1.72	2.48	0.41	144.65	1.46	2.11	0.47
	S2		15.60	-5.09	196.92									
2	S1	58.94	13.49	2.55	228.29	259.55	10852	1.68	2.43	0.41	152.10	1.28	1.85	0.54
	S2		16.93	3.70	290.80									
* 3	S1	69.62	6.36	1.93	117.95	117.95	4939	0.99	1.43	0.70	63.60	0.65	0.94	1.07
	S2		11.44	1.92	199.99	199.99	8365	1.35	1.95	0.51	114.40	0.97	1.40	0.72
* 4	S1	56.32	7.30	4.11	149.58	149.58	6260	1.30	1.87	0.53	73.00	0.83	1.20	0.84
	S2		12.58	2.91	224.32	224.32	9381	1.61	2.32	0.43	125.80	1.17	1.69	0.59
5	S1	55.46	13.16	-0.62	207.36	224.25	9378	1.62	2.33	0.43	112.05	1.11	1.6	0.63
	S2		9.25	11.68	241.14									
* 6	S1	48.58	6.35	3.84	132.62	132.62	5552	1.32	1.90	0.53	63.50	0.84	1.21	0.83
	S2		5.70	5.44	134.79	134.79	5642	1.33	1.92	0.52	57.00	0.78	1.13	0.89
7	S1	43.30	6.02	3.94	122.68	147.38	6168	1.47	2.14	0.47	54.00	0.81	1.17	0.86
	S2		4.78	10.26	172.08									

* S1 and S2 are significantly different at P = 0.05
† only autotrophic growth is considered.

A distinct change in the initial spectrum (Fig. 3(b)) was evident between Days 1 - 4 and Days 5 - 7, where the spectrum peak broadened from approximately (29 - 57 μm ESD) to (14 - 72 μm ESD). Growth during the first four days occurred mainly between 6 - 57 μm ESD and peaking between 29 - 57 μm ESD, whilst in the latter days (5, 6, 7) maximum growth tended towards the smaller diameter size intervals, peaking on Day 7 at 29 - 72 μm ESD.

The strong southerly winds initially caused the drogue to move in a northwesterly direction (Olivieri et al. 1985). During this period deep mixing of the water column occurred down to 40 m with nutrient concentrations reaching up to 18 $\mu M.m^{-3}$ (Fig. 4). As the winds dropped, the drogue meandered extensively and then moved southwards whilst sunwarming gradually stabilized the surface waters. The 1% light level depth averaged 15 m for the first three days, then deepened to 20 m for the remaining four days, just above the thermocline.

Daily production during the March 1981 drogue cruise, (Fig. 5(a) and Table 3) increased steadily till Day 6 reaching doublings per day of 2.81 and a generation time (d) of 0.36 but decreasing on Days 4 and 7. Daily production rates exceeded night production except on Day 3, where a counting error seems likely to have occurred with the 50% S1 sample. During this cruise the heterotrophs accounted for very little of daily production.

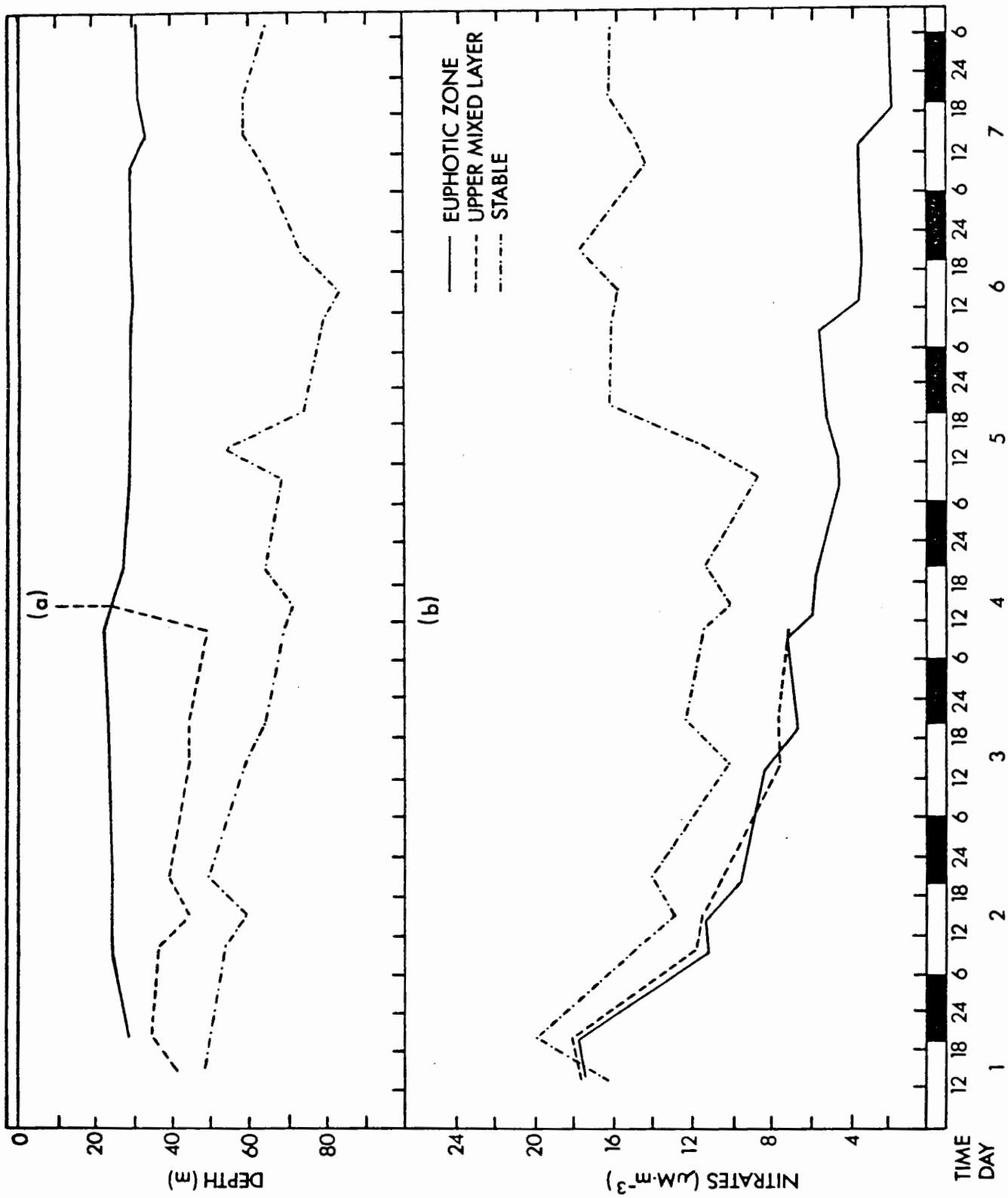

Fig. 4. February 1981. Vertical sections of (a) the 1% light level (euphotic zone), the upper mixed layer, and stable layer, (b) nitrates $\mu M.m^{-3}$ within each layer.

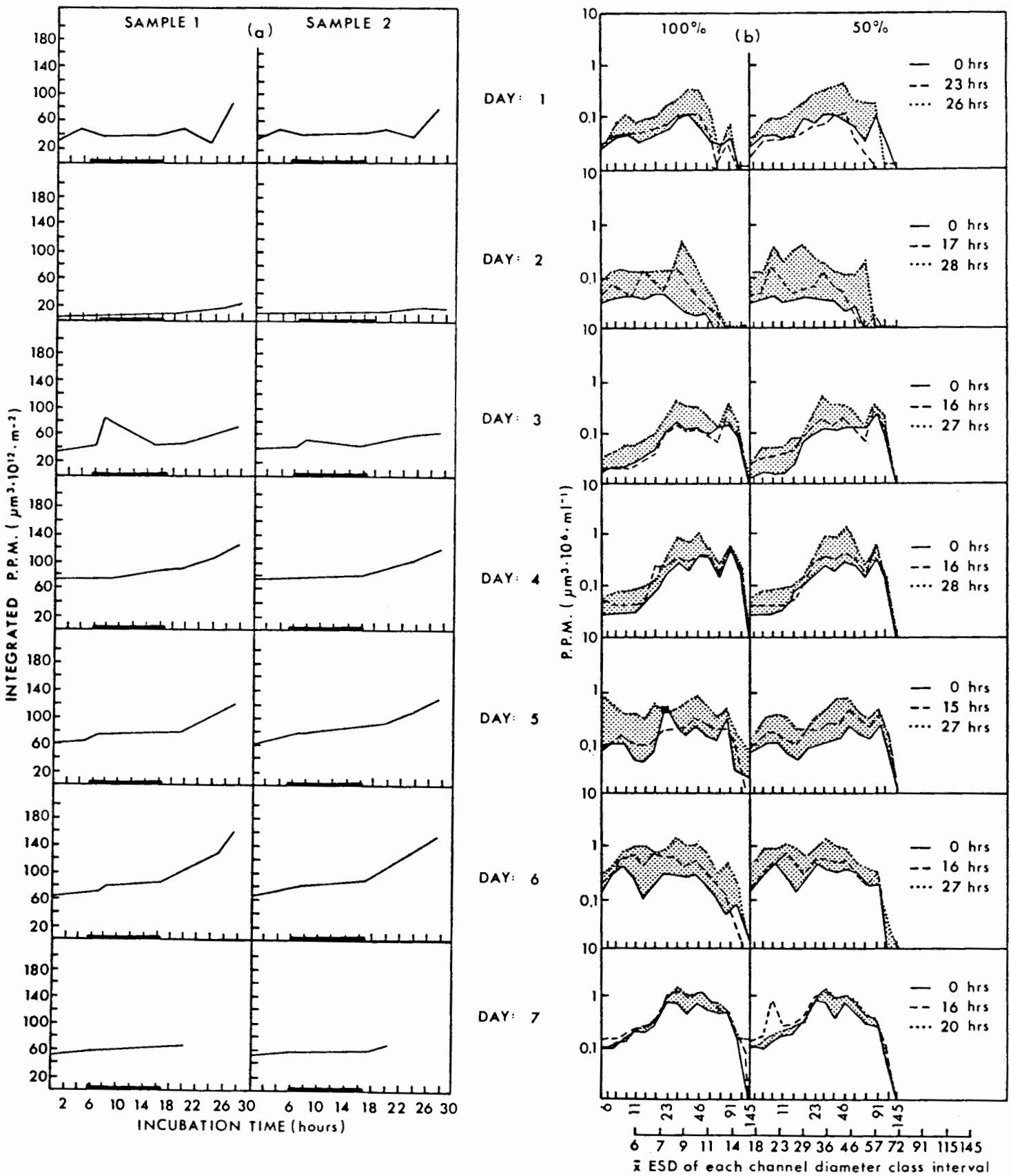

Fig. 5. March 1981. (a) Daily integrated growth curves showing production within the euphotic zone. (b) Particle spectra selected from specific counts at the 100 and 50% light levels for each production experiment. Shading represents growth.

Table 3. March 1981 - Specific growth rates calculated within the euphotic zone using both day and night growth rates (autotrophic and heterotrophic) and just day growth rates (autotrophic), where I = initial biomass; Ph(d) = hourly daylight production; Ph(n) = hourly night production; Pd = daily production; specific growth rate ($\mu.d^{-1}$) = ℓn (particle volume)$_{t_1}$ - ℓn (particle volume)$_{t_0}$; division rate ($div.d^{-1}$) = $\frac{\mu.d^{-1}}{\ell n 2}$; and generation time (d) = $\frac{\ell n 2}{\mu.d^{-1}}$.

Day	Sample	I ($\mu m^3 . 10^{12} . m^{-3}$)	Ph(d) ($\mu m^3 . 10^{12} . m^{-3} . hr^{-1}$)	Ph(n) ($\mu m^3 . 10^{12} . m^{-3} . hr^{-1}$)	Pd ($\mu m^3 . 10^{12} . m^{-3} . d^{-1}$)	$\bar{X}$ Pd ppm ($\mu m^3 . 10^{12} . m^{-3} . d^{-1}$)	$\bar{X}$ Pd carbon ($mgC.m^{-3} . d^{-1}$)	Specific Growth Rate ($\mu.d^{-1}$)	Division Rate D.R. ($div.d^{-1}$) or (doublings.d^{-1})	Generation Time (G.T.) (d)	† X Pd ($\mu m^3 . 10^{12} . m^{-3} . d^{-1}$)	† ($\mu.d^{-1}$)	† ($Div.d^{-1}$) or doubling.d^{-1})	† G.T. (d)
1	S1	35.43	6.04	-4.64	38.55	43.45	1828	0.80	1.15	0.87	65.78	1.05	1.52	0.66
	S2		5.92	-3.49	48.34									
2	S1	10.13	3.42	1.45	63.36	60.22	2528	1.94	2.80	0.36	35.86	1.51	2.18	0.46
	S2		3.10	1.31	57.43									
3	S1	40.51	8.33	17.90	292.25	225.45	9429	1.76	2.67	0.39	84.49	1.13	1.63	0.61
	S2		7.05	5.96	158.65									
4	S1	74.54	9.32	6.97	201.23	194.00	8115	1.29	1.85	0.54	111.98	0.92	1.33	0.75
	S2		11.04	2.89	187.03									
* 5	S1	62.42	12.32	6.90	243.36	243.36	10176	1.59	2.29	0.44	135.52	1.15	1.66	0.6
	S2		14.26	7.15	273.53	273.53	11436	1.68	2.43	0.41	156.86	1.26	1.82	0.55
6	S1	65.65	20.83	10.58	400.42	393.43	16443	1.95	2.81	0.36	241.51	1.54	2.22	0.45
	S2		23.08	5.83	386.44									
7	S1	52.37	2.69	2.97	68.30	61.67	2589	0.78	1.12	0.89	31.08	0.47	0.68	1.48
	S2		2.96	1.76	55.03									

* S1 and S2 are significantly different at P = 0.05
† only autotrophic growth is considered.

Large increases in volume, probably masked by detritus at these low concentrations, occurred over most diameter size intervals during Days 1 and 2 (Fig. 5(b)). Growth on Days 3 and 4 occurred in all sizes, with the bulk spread over 6 - 57 μm ESD. A distinct peak (6 - 14 μm ESD) in the initial spectra of Days 5 and 6 was evident, though preferential growth in this range was not evident. Negligible volume increases occurred on Day 7 where a change in the spectrum became evident.

Winds were strong and consistent from the south throughout the cruise, changing from an easterly to a westerly direction later, and causing a north and westward flow of surface water (Fig. 6). Low particle volumes were evident from the particle spectra up till Day 4 with a peak developing in the larger diameter size intervals down to 60 m. Thereafter, the bloom began to develop with volumes beginning to increase in the smaller size fraction.

A very deep upper mixed layer with extremely high nutrient concentrations reaching 23 $\mu M.m^{-3}$ occurred throughout most of the cruise (Fig. 7). High nutrient concentrations (14 $\mu M.m^{-3}$) occurred within the euphotic zone down to 60 m, and then decreased gradually to (2 $\mu M.m^{-3}$) on Day 7 as the euphotic zone shallowed to 10 m.

Daily production estimates (Fig. 8(a) and Table 4) were high during the first two days of the October 1981 drogue cruise with

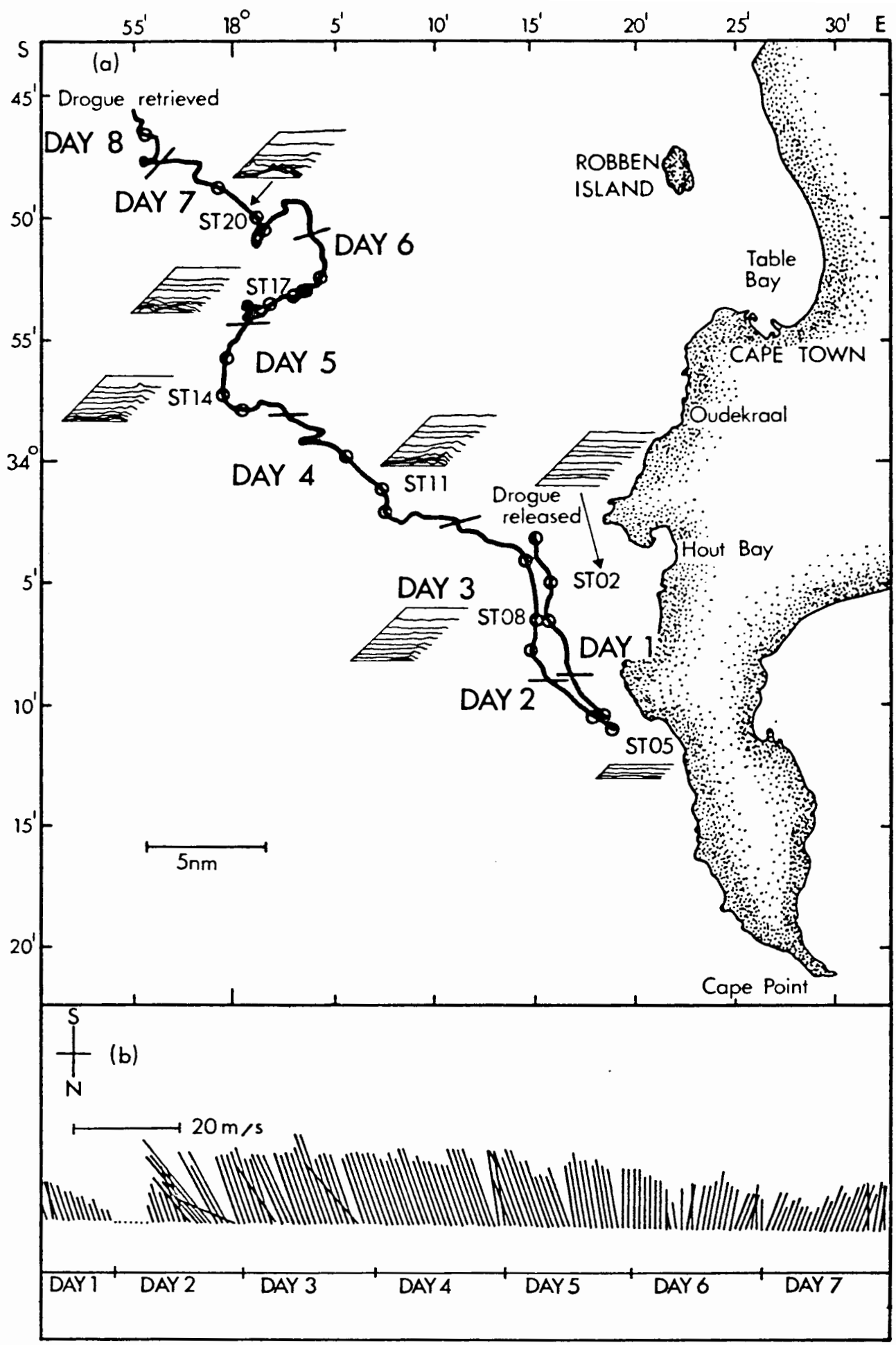

Fig. 6. March 1981. (a) The drogue trajectory together with three dimensional particle spectra where x = particle diameter (5 - 145 μm) with diameter increments of $2^{1/3}$ (Sheldon and Parsons 1967a) y = particle volume (ppm = $\mu m^3 .10^6 .ml^{-1}$) and z = depth (m). (b) Wind stick diagram.

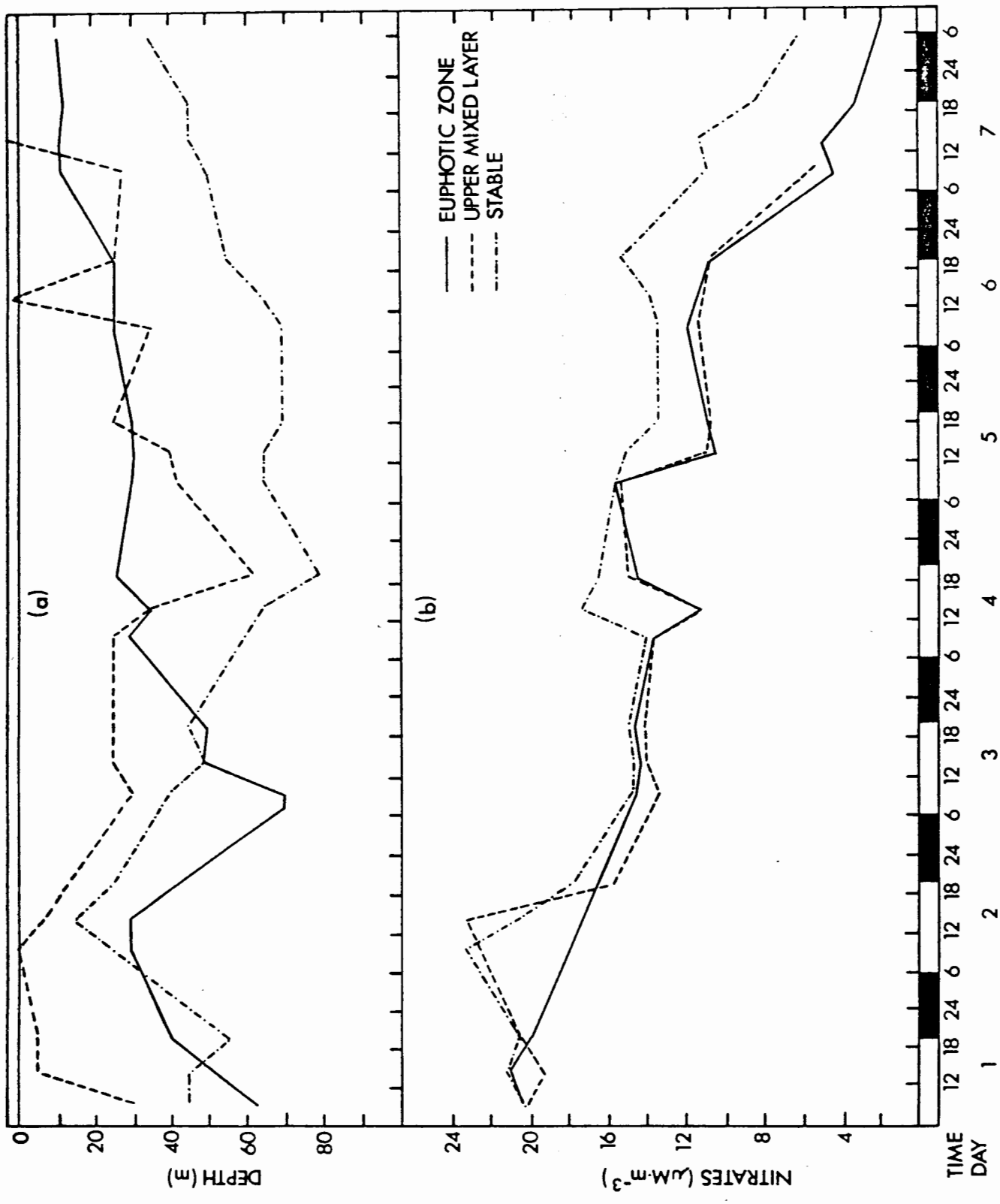

Fig. 7. March 1981. Vertical sections of (a) the 1% light level (euphotic zone), the upper mixed layer, and stable layer, (b) nitrates $\mu M.m^{-3}$ within each layer.

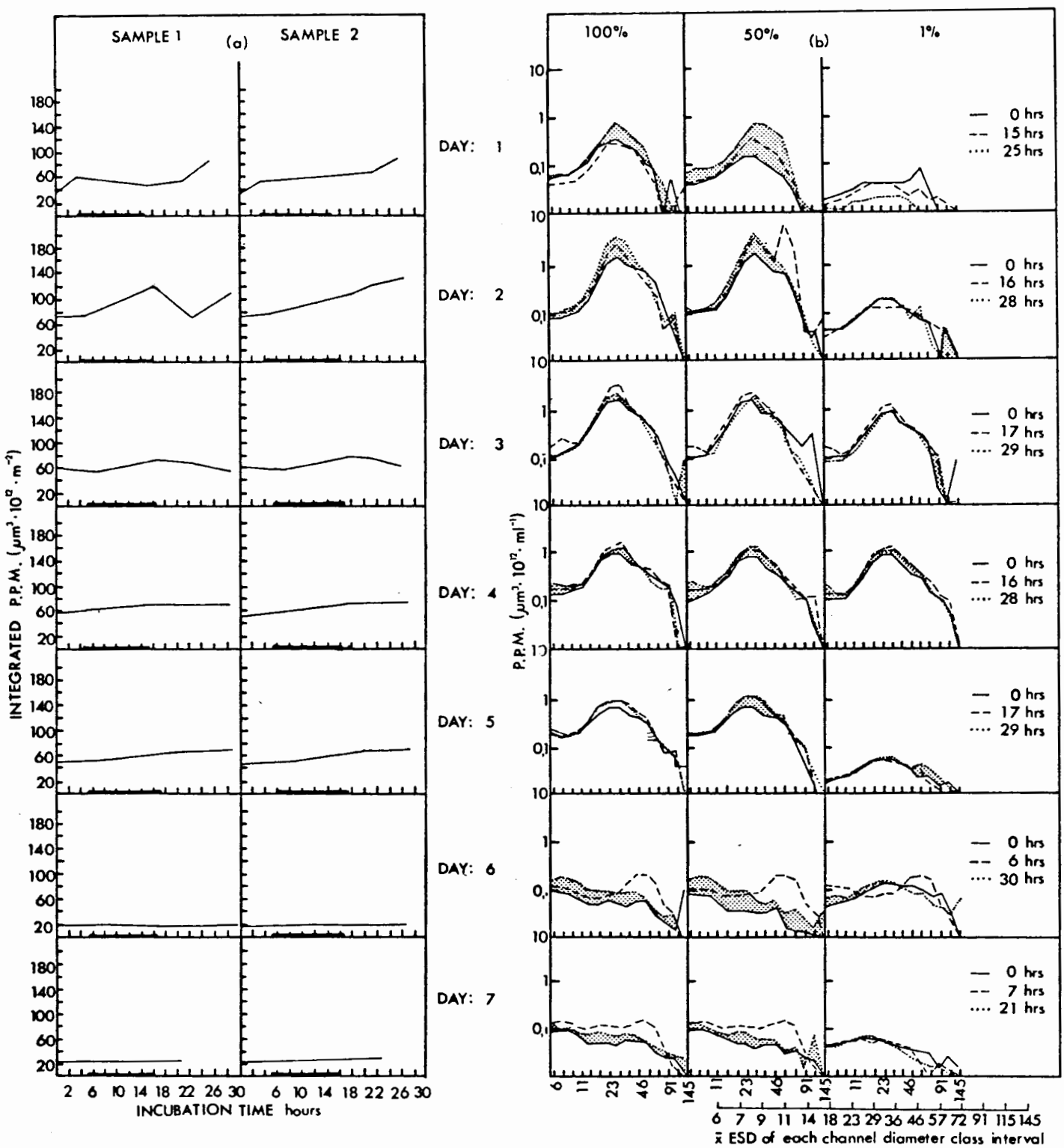

Fig. 8. October 1981. (a) Daily integrated growth curves showing production within the euphotic zone. (b) Particle spectra selected from specific counts at the 100, 50 and 1% light levels for each production experiment. Shading represents growth.

Table 4. October 1981 - Specific growth rates calculated within the euphotic zone using both day and night growth rates (autotrophic and heterotrophic) and just day growth rates (autotrophic), where I = initial biomass; Ph(d) = hourly daylight production; Ph(n) = hourly night production; Pd = daily production; specific growth rate ($\mu.d^{-1}$) = ℓn (particle volume) $_{t_1}$ - ℓn (particle volume) $_{t_0}$; division rate (div.d^{-1}) = $\frac{\mu.d^{-1}}{\ell n 2}$; and generation time (d) = $\frac{\ell n 2}{\mu.d^{-1}}$.

Day	Sample	I ($\mu m^3 . 10^{12} . m^{-3}$)	Ph(d) ($\mu m^3 . 10^{12} . m^{-3} . hr^{-1}$)	Ph(n) ($\mu m^3 . 10^{12} . m^{-3} . hr^{-1}$)	Pd ($\mu m^3 . 10^{12} . m^{-3} . d^{-1}$)	$\bar{X}$ Pd ($\mu m^3 . 10^{12} . m^{-3} . d^{-1}$)	$\bar{X}$ Pd carbon ($mgC . m^{-3} . d^{-1}$)	Specific Growth Rate ($\mu.d^{-1}$)	Division Rate D.R. (div.d^{-1}) or (doublings.d^{-1})	Generation Time (G.T.) (d)	† $\bar{X}$ Pd ($\mu m^3 . 10^{12} . m^{-3} . d^{-1}$)	† ($\mu.d^{-1}$)	† (Div.d^{-1}) or doubling.d^{-1})	† G.T.(d)
1	S1	36.67	11.19	-5.41	86.86	129.11	5405	1.48	2.13	0.49	121.68	1.46	2.11	0.47
	S2		9.97	3.76	171.35									
2	S1	71.68	-17.91	22.00	-40.96	-	-	-	-	-	-	-	-	-
	S2		15.67	12.80	348.15	348.15	14552	1.77	2.55	0.39	180.21	1.26	1.82	0.55
3	S1	60.59	-5.21	6.68	-10.89	-	-	-	-	-	-	-	-	-
	S2		-4.18	7.37	10.52	10.52	453	0.16	0.23	4.33				
4	S1	52.96	2.08	4.87	76.01	84.61	3547	0.96	1.38	0.73	19.03	0.31	0.45	2.23
	S2		1.58	7.50	93.20									
5	S1	49.60	2.93	6.47	105.64	105.71	4428	1.14	1.65	0.61	33.36	0.51	0.74	1.36
	S2		2.63	6.92	105.78									
6	S1	17.80	2.25	-0.82	25.84	22.47	951	0.82	1.18	0.85	21.45	0.79	1.14	0.88
	S2		1.48	-0.30	19.10									
7	S1	23.91	0.36	0.84	14.75	16.32	695	0.52	0.75	1.34	4.18	0.16	0.23	4.3
	S2		0.40	1.04	17.89									

† only autotrophic growth is considered.

doublings per day of 2.55 and generation times (d) 0.39. A sudden sharp drop in production was evident on Day 3, ($div.d^{-1}$ = 0.23 and generation time (d) = 4.33) but increased again towards Day 6, and then dropped slightly again on Day 7. However, increases during this period can be accounted by the increase in heterotrophic activity. Daily production rates generally exceeded night production, except during this period (Days 3 - 5).

The initial spectra at the three light levels were similar, though volume increases were greatest at the 100 and 50% light level and negligible at the 1% light level (Fig. 8(b)). Volume increases on Day 1 were greatest at the 50% light level especially between 18 - 47 μm ESD. Similar spectra were observed on Days 2 - 5 with most growth occurring between 18 - 46 μm ESD on Day 2. This peak was not evident on Days 6 and 7, instead high volume increases occurred between 29 - 91 μm ESD after only 7 h of incubation, whereas a general volume decrease resulted after 20 h of incubation.

During this month the drogue moved in many directions due to the frequent wind reversals (Fig. 9). Calm conditions, followed by gentle southwesterlies caused the drogue to move in a northeasterly direction on Day 1 in waters with low particle volumes. A reversal in the wind direction to northwesterly, caused the drogue to loop twice and then move southwards as the winds persisted till Day 3. A well-developed bloom within the upper 5 m was evident, which could possibly have been advected from

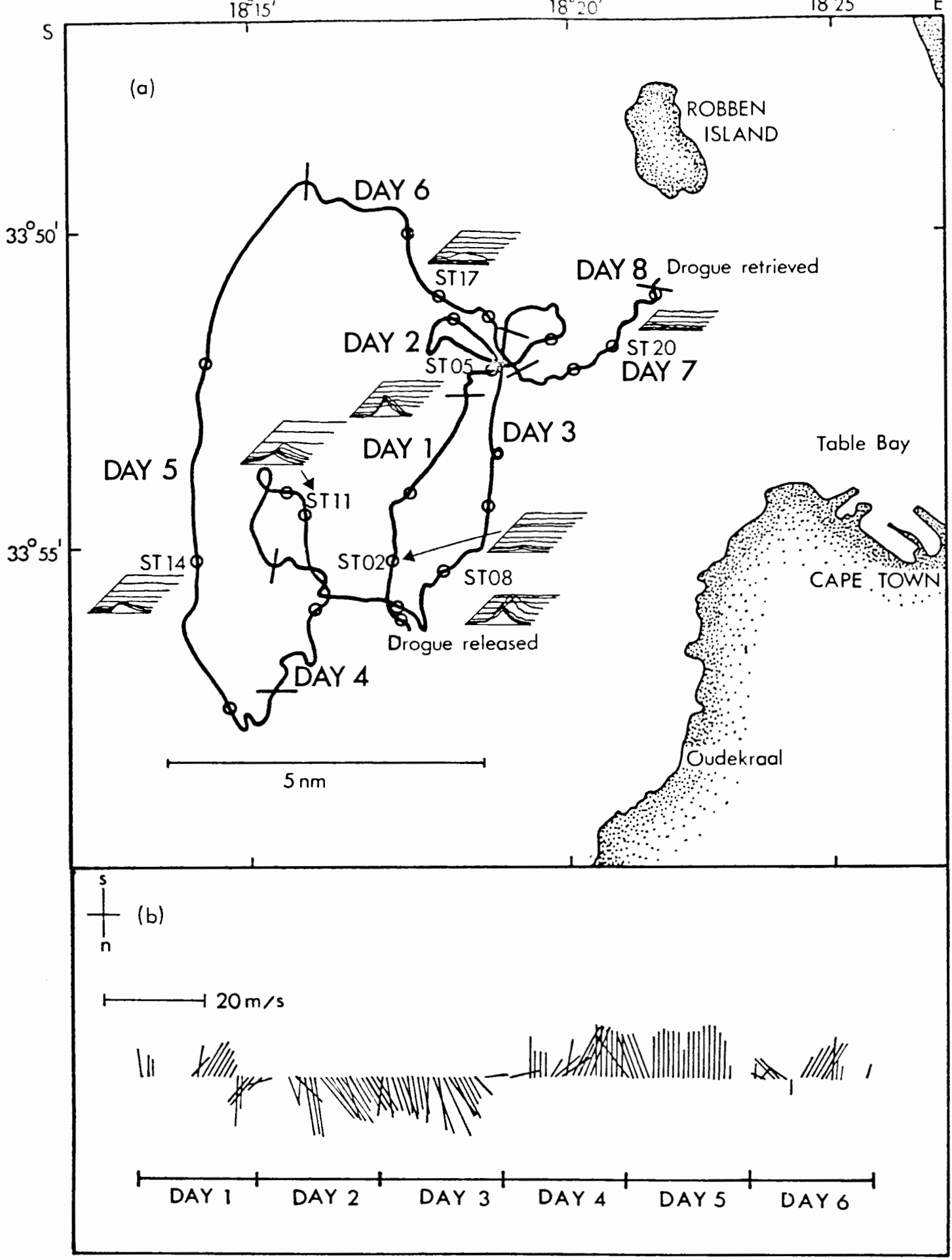

Fig. 9. October 1981. (a) The drogue trajectory together with three dimensional particle spectra where x = particle diameter (5 - 145 μm) with diameter increments of $2^{1/3}$(Sheldon and Parsons 1967a) y = particle volume (ppm = $\mu m^3 .10^6 . ml^{-1}$) and z = depth (m). (b) Wind stick diagram.

further north. At the end of Day 3, the winds turned to westerlies, and the drogue looped again before moving in a northward direction by Days 4 and 5. Low particle volumes were evident as mixing occurred down to approximately 25 m on these two days. Particle volume dropped even further on Days 6 and 7 as the winds changed to southwesterlies, causing shoreward movement of the drogue.

The euphotic zone extended roughly down to 45 m on Day 1 and contained high nutrient concentrations initially (Fig. 10). As the euphotic zone shallowed to approximately 10 m on Day 3 the nutrient levels dropped rapidly. Nutrient levels were very low within the relatively shallow upper mixed layer.

Discussion

Each drogue cruise presented an opportunity of studying the growth of phytoplankton under varying sets of environmental conditions. Although the production rates for the cruises fell within the same range, each set followed a different sequence peculiar to the specific environmental conditions encountered. Growth rates during the December 1980 drogue cruise declined due to nutrient and then light limitation. This was evidenced by a well developed bloom sinking from a nutrient depleted upper layer into a deeper light limited, nutrient-rich stable layer. Doublings per day declined from 2.96 - 0.76. Likewise, during the October 1981 drogue cruise after the first two days, both light and

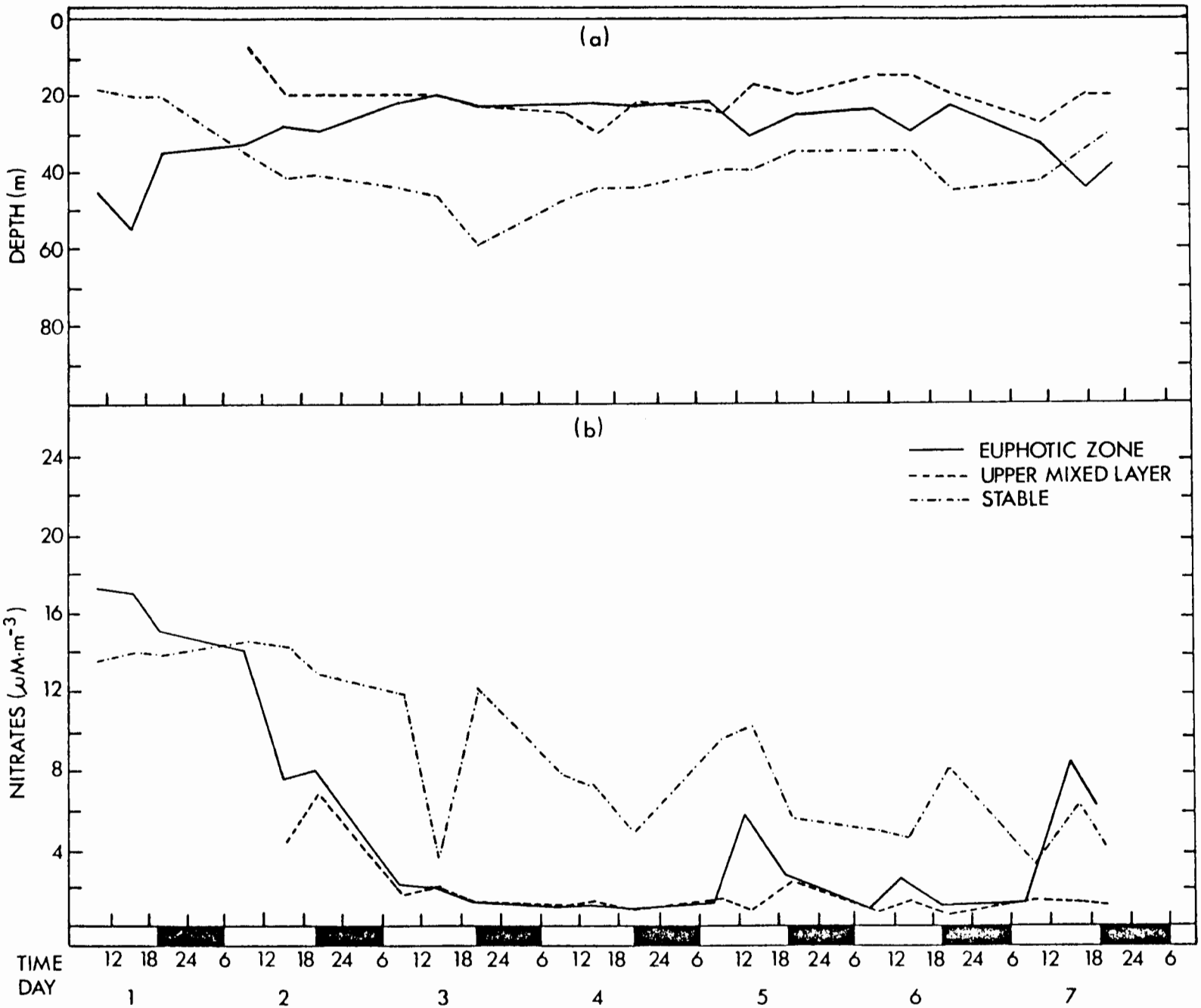

Fig. 10. October 1981. Vertical sections of (a) the 1% light level (euphotic zone), the upper mixed layer, and stable layer, (b) nitrates $\mu M.m^{-3}$ within each layer.

nutrients became limiting, reducing doublings per day to 0.75 by Day 7. During the February and March 1981 drogue cruises, nutrients were in abundance and growth rates were influenced by the intense vertical mixing which in turn altered the mean light levels in the upper mixed layer. Growth was not light limited as minimal doublings per day of 1.12 were observed.

The strong southerly winds during the December 1980 drogue cruise caused a deep upper mixed layer to form, with nitrate concentrations reaching up to 10 $\mu M.m^{-3}$ and high production rates ($\mu.d^{-1}$ = 2.05). When nitrate concentrations declined to levels < 1 $\mu M.m^{-3}$) on Days 3 and 4 doublings per day decreased by over half, indicating that the bloom was entering a declining phase of growth. Diatoms have the ability to store non-limiting nutrients (Davis et al. 1978; Dortch 1982) such that internal nitrogen reserves may have been utilized to sustain average doublings per day of 1.5. Production rates decreased further by Days 5 and 6 as the bloom sank from the nutrient depleted upper mixed layer into the stable layer. Steele and Yentsch (1960) have shown Skeletonema costatum to increase its sinking rates in nutrient depleted waters. In such an environment where surface nutrients are rapidly depleted, it would be advantageous for phytoplankton to increase their cell size so as to accelerate their sinking rates. In a previous drogue study (Olivieri 1983a) the increase in cell size of the two dominating species was considered as a strategy in adapting to a changing environment towards limiting conditions. A notable shift in the particle size frequency distribution was

not detected, suggesting that age and physiological state of the bloom could have influenced their sinking rates. Asterionella cells sink four times more rapidly during their stationary phase of growth than during their exponential phase (Tilman and Kilham, 1976). Also cells with lower photosynthetic rates sink more rapidly than faster-growing cells (Eppley et al. 1967). Examination of the changes in the biochemical composition of this community during Days 5 - 7 (Barlow 1984a) reveal that the phytoplankton conserve the synthesis of protein at the expense of carbohydrates, indicating that cells in the stable layer were still viable with adequate supplies of nutrients. He suggests that this may be a physiological mechanism whereby a community maintains itself until mixing processes ameliorate the light conditions.

The February 1981 drogue cruise presented an opportunity of studying the growth responses of the phytoplankton communities encountered during strong turbulent mixing, followed by stabilization. Strong, uninterrupted, southerly winds up till Day 3, induced deep mixing of the surface layer, with nutrients in the upper mixed layer in excess of 18 $\mu M.m^{-3}$. Production rates up till Day 2 were extremely high. Of considerable ecological significance is the critical light depth which represents the theoretical light level under which phytoplankton growth is light limited in the upper mixed layer. During the first five days the upper mixed layer greatly exceeded the 1% light level depth, though production rates did not substantially decrease. Levasseur et al. (1984)

have shown that in the St. Lawrence estuary the mean light intensity in the upper mixed layer determines the occurrence of diatoms, whilst strong density stratification selects for flagellates.

Production rates increased towards Day 5 as the winds on Day 4 abated, allowing an upper stable layer to form. Olivieri et al. (1985) suggest that mixing of surface waters with neighbouring parcels of water may have occurred in the vicinity of the drogue, as considerable eddying caused by the wind reversal and changes in the species composition were found in the upper surface layers. The dominance of Lauderia species (Olivieri et al. 1985) was evidenced by a noticeable broadening of the particle spectra by Day 6, although appreciable growth occurred mainly in the smaller diameter size range (6-14 μm) and only towards Day 7 in the larger diameter size intervals (29-72 μm). Studies using controlled experimental enclosures (Davis 1982) reveal that microflagellates (10 μm) preceed the succession of dinoflagellates and form an additional, functional group to the three successional stages described by Margalef (1962). These organisms would not be identified in previous analyses of species composition because of poor preservation techniques. It could be possible that the rapid growth (6 - 14 μm) occurring between Days 5 - 7 was grazed upon, as increases in this size fraction were undetectable from the initial spectra of Days 6 and 7. Microflagellates in enclosures have been shown to grow in rough equilibrium with microzooplankton that feed on them (Davis 1982).

From the data, it would appear that initially in the turbulent environment, a fast growing diatom-dominated bloom developed and continued to coexist with an actively growing microflagellate bloom as the water column stabilized. Advection, caused by a reversal in the wind direction accounted for the change in the species composition.

The March 1981 drogue cruise presented an ideal opportunity of studying the early stages of bloom development in a continually turbulent environment. Our 'on deck' experiments give a measure of the daily potential production but failed to simulate the in situ turbulent conditions. In such a vertically mixed column, assumptions cannot be made concerning the integrated light histories of the plankton samples from the various light level depths, as their residence time at various light intensities will vary with the rate of mixing. Nonetheless, the transient response to fluctuating irradiances does not necessarily cause photoinhibition (Marra 1978b). Diatoms have been shown to tolerate high and low irradiances without a decrease in photosynthetic rate (Platt et al. 1980). Harrison et al. (1981) showed that phytoplankton populations off the northern coast of Peru adapt particularly to light inhibition, by endogenous adjustments, regulated over diurnal time scales.

The high production estimates indicate that the detectable lag in the standing crop (from particle spectra) is not associated

with conditioning of the water, as occurs off Peru (Barber et al. 1971) by the synthesis of growth enhancing compounds. Instead, this apparent lag is probably attributed to low phytoplankton concentrations present in the source water and the inability to quantify these low concentrations accurately, particularly when mixed and diluted down the water column. Barlow (1984b) showed that in the mixed layer this population adjusted physiologically, by incorporating carbon into sugar synthesis. As light conditions changed, later in the cruise, a shift in the carbon metabolism towards synthesizing protein, was favoured.

The presentation of data in the form of particle spectra are difficult to follow in detail, but are intended to show primarily how smaller or larger particles may be favoured to grow. Growth was not size dependent, although an appreciable increase in the smaller size fraction (6 - 14 µm ESD) was apparent in the standing crop on Days 5 and 6. While turbulence and advection may have contributed to certain losses of phytoplankton, zooplankton grazing (McAllister et al. 1960; Malone 1971; Steele and Frost 1977) may exert a major influence on the cell size of natural phytoplankton communities. For example Davis (1982) has postulated that herbivores could eliminate or greatly reduce diatom populations, favouring the growth of microflagellates. Although this hypothesis has not yet been tested, the particle spectra on Days 4 to 5 suggest that this may have occurred.

Difficulties in the interpretation of the events arising from the continual variation in the wind speed and direction occurred during the October 1981 drogue cruise. The short-term wind variation experienced on Day 1 caused a definite quantitative change in the standing crop, unattributable to the growth rates of Day 1. Surface mixing of these newly upwelled waters occurred with neighbouring, mature water bodies, advected from further north due to the northwesterly winds predominating. This variation had a diluting effect on the nutrient concentrations, where by the end of Day 2 a 72% reduction in nitrates occurred in both the euphotic and upper mixed layer. Over longer time scales the dilution of nutrients has been shown to result in the selective advantage for growth of certain species from natural phytoplankton assemblages (Turpin and Harrison 1979; 1980; Thomas et al. 1980).

A distinct decline in production occurred on Day 3 as both nutrients and light conditions became limiting. In addition a change in the diel growth rates was observed between Days 3 - 5, where night production rates significantly exceeded the daylight rates. In waters off the Cape Peninsula, Brown (1980) suggests that limiting nutrients influence both periodicity of the photosynthetic activity and the time of peak production. The high night production rates may have resulted from different periodicities in cell division in the species present, so that the nutrient demands could be separated temporarily. Under limiting light conditions, photoperiod appears to govern growth rate (Hobson

1974), and the timing of cell division (Humphrey 1979; Nelson and Brand 1979) is influenced by periodic nutrient supplies.

On Days 6 and 7 the production rates decreased even further as the duration of the non-limiting conditions increased. Under these conditions, production estimates are subject to error, as it is likely that bacterial and heterotrophic activity predominated. Production experiments off Peru similarly indicate that night growth is due to protozoans or accumulations of non-living material (Sheldon and Dunbrack 1981). Flagellates have been observed to grow rapidly in the dark (Sheldon et al. 1973) and inspection of the particle spectra on Days 6 and 7 would suggest that this was happening. Cognizance should be taken of the fact that secondary production will introduce errors in the interpretation of data.

Important to note is that phytoplankton production estimates discussed in this paper are based on the assumptions that no detritus is present in the samples, and if present, no accountable growth of this non-living fraction occurs. Variable quantities of detrital material could be expected in Type 2 - 3 waters (Barlow 1982) so that specific growth rates representative of communities in the slow-growing phase (December 1980) or senescent phase (October 1981) would be underestimated. However, the extreme clarity of newly upwelled water on most occasions, suggests that the detrital load is very small initially, and given the near-optimal light and nutrient conditions, a large proportion of the

particulate matter during the first 3 - 5 days of active growth is probably living material.

Production rates calculated during this study show that the growth of phytoplankton is extremely rapid, with doublings per day and particulate carbon ranging between (0.23 - 2.96) and (453 - 21367) $mgC.m^{-2}.d^{-1}$ respectively. These doublings fit within the limits of the maximum expected values predicted from Eppley's (1972) exponential equation given a range of temperatures. Similar doublings per day (2.23 for Nitzschia closterium, using cell numbers) are quoted in the Peruvian upwelling system- (Hendrikson et al. 1982). The carbon estimates are higher than those obtained by the C^{14} method (Brown unpublished data) due to the possible inclusion of non photosynthetic growth and non-living material in the Coulter counter method. Likewise, Sutcliffe et al. (1970) in a comparative study obtained higher values using the Coulter counter method, in one instance a seven fold difference being observed. Differences are also attributed to errors occurring when one conversion factor is used to estimate carbon from cell volume. Carbon is shown to vary with cell size and species, viz, plasma volume is more precise of cell carbon in diatoms than is cell volume. However, this method is certainly more versatile than the C^{14} method and cell volume adequately represents biomass.

Acknowledgements

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PAPER 4 - THE RÔLE OF HERBIVOROUS MESOZOOPLANKTON ON NEWLY DEVELOPED PHYTOPLANKTON BLOOMS IN THE SOUTHERN BENGUELA CURRENT.

THE RÔLE OF HERBIVOROUS MESOZOOPLANKTON ON NEWLY DEVELOPED PHYTOPLANKTON BLOOMS IN THE SOUTHERN BENGUELA CURRENT.

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Abstract

The impact of mesozooplankton grazing was measured for the first time on four developing phytoplankton populations in newly upwelled water off the Cape Peninsula. Comparisons of the grazing stresses indicated that at most, only 11% of the total daily food available was consumed, averaging 2%. Considerable temporal and spatial variations were observed in the food availability (2903 - 25270 $mgC.m^{-2}$), zooplankton abundance (1610 - 12253 $mg.m^{-2}$) and average ingestion rates (55 - 5609 $\mu gC.mg\ copepod^{-1}.hr^{-1}$). The mesozooplankton exerted little control on the developing phytoplankton blooms of newly upwelled waters.

Much of the primary production is thought to go unutilized because of the intermittent nature of the upwelling in this region. The transient nature of food availability and food quality were shown to depress ingestion rates and thought to delay the reproductive responses of the mesozooplankton, limiting their biomass off the Cape Peninsula.

Introduction

The frequent occurrence of coastal wind-driven upwelling, along the Cape Peninsula and south west coast of Africa, is coupled with a pulsed enrichment of nutrients, allowing rapid development of phytoplankton blooms, consisting principally of diatoms (Olivieri 1981a; 1981b; Olivieri et al. 1985). Phytoplankton form the base of relatively short food chains leading to harvestable fish (Ryther 1969). In coastal waters an understanding of both qualitative and quantitative trophic interactions between phytoplankton and zooplankton are important links in these food chains (Parsons and Le Brasseur 1970).

Olivieri et al. (1985) have reported the changes in the biomass of various phytoplankton communities over a time span of several days, by tagging parcels of newly upwelled water with the aid of drogues. Rates of production and growth patterns are described for these communities which are shown to develop within 5 - 10 days (Olivieri and Hutchings in press.).

The primary objective of this study was to examine the impact of community grazing on these naturally developing phytoplankton blooms. The question posed was: To what extent do herbivorous zooplankton graze developing phytoplankton blooms in the Cape Peninsula Upwelling System? In order to answer this, both growth and grazing experiments were conducted simultaneously on deck using water collected alongside the drogue, in each case

changes in total particle volume were measured with a Coulter counter. Feeding rates were related to zooplankton abundance and phytoplankton production to assess the effect of zooplankton grazing on the developing phytoplankton community.

Methods

Daily feeding experiments were performed during a series of four drogue surveys which was conducted off the west coast of the Cape Peninsula over the period December 1980 - October 1981. Details of the cruise strategies and Coulter counter methods are given in Olivieri et al. (1985). A Coulter counter Model TAII fitted with a 280 µm aperture tube yielded information on the size frequency distribution of particulate matter between 5.04 - 145 µm equivalent spherical diameters (ESD).

Phytoplankton samples were obtained at each station by collecting water with 18-ℓ IOS plastic bottles (poured through a 200 µm mesh to remove mesozooplankton) from four depths within the euphotic zone (50, 25, 10 and 1% light levels), determined using a Lambda L1-192S underwater quantum sensor. To establish initial food concentrations, an initial bottle at each depth was analysed at the beginning of each grazing experiment. One-ℓ control and duplicate experimental bottles were used to contain the feeding media. The reliability of replicate incubations was tested using the Paired t-test of Snedecor and Cochran (1967). The statistical variance was compared at $P = 0.05$.

At each sampling station zooplankton were collected using a WP-2 or Bongo net (200 μm mesh) hauled vertically from the bottom to the thermocline depth, and from that depth to the surface. The dusk samples were usually collected well after dark to obtain night-time zooplankton distribution. For grazing experiments, organisms were retrieved at < 0.5 $m.s^{-1}$ from above the thermocline in the upper mixed layer. The contents of the nets were gently emptied into a 4.5ℓ bucket containing filtered surface sea water.

After making the field collections, the zooplankton were selected by eye using a wide-mouthed Pasteur pipette. To set up each feeding experiment, individuals (ranging between 3 and 86) were placed in separate plastic dishes containing 20 - 25 mls filtered sea water, and then added to each experimental bottle. Duplicate experimental bottles did not always have the same number and species of zooplankton. Zooplankton species and stages used in the grazing experiments are listed in Table 1. Centropages brachiatus and Calanoides carinatus were the most commonly used organisms.

Bottles were then placed on a plankton wheel and rotated at three rpm to prevent settling. Grazing experiments were all conducted in the dark to minimize algal growth and were kept at temperatures similar to the water mass from which the samples were collected. After a period of 24 h the experimental bottles and their corresponding controls were removed from the wheel. The zooplankton were removed from the experimental bottles with a 200 μm mesh as

TABLE 1. Zooplankton species and stages used in the grazing experiments.

Species	Small	Medium	Large
Centropages brachiatus	II - III	IV - V	
Calanoides carinatus		II - III	IV - VI
Ctenocalanus vanus	II - V		
Clausocalanus spp.	III - V		
Oithona sp.	IV - VI		
Paracalanus parvus	III - V		
" crassirostris	IV - VI		
Metridia lucens		II - IV	V - VI
Actideus armatus		II - IV	V - VI
Rhinocalanus nasutus		I - II	III - VI
Cirripede nauplius	*		
Euphausid nauplius		*	
" furcilia			*
Calyptopis larvae		*	

subsamples of the contents of the bottles were poured into 175 ml beakers for Coulter counter analyses. The control samples were also filtered through the mesh, to ensure equal treatment. Zooplankton were preserved in 4% formalin and stored in separate plastic test tube containers for final counting, sizing and identification. Total dry weights were obtained by drying the experimental animals for 30 min at room temperature in a desiccator and weighing on a Cahn electrobalance (Berg 1979).

The Coulter counter system was linked to a microcomputer, which allowed for rapid automation of data. Data analyses were performed by transferring stores of data on magnetic tapes to a mainframe Eclipse C350 computer. Since initial, experimental and control counts were determined, it was possible to estimate phytoplankton growth and take this into account in calculating the grazing rates. Calculations using the equations of Frost (1972) were applied to each size category of the particle spectrum in order to obtain a growth constant, grazing coefficient, food availability, filtration rate and ingestion rate (IR) ($\mu m^3 .10^6 .mg\ copepod^{-1} .hr^{-1}$). Total volume ingestion rates were converted to carbon ingestion rates by using Cowles (1977) linear regression equation for the Peruvian upwelling area.

$$Carbon\ (\mu g.l^{-1}) = 41.76\ volume\ (\mu m^3 .10^6 .ml^{-1}) + 13.38.$$

Grazing by the copepod community was calculated by averaging the ingestion rates within the euphotic zone and multiplying these rates by the proportion of zooplankton dry weight biomass within the upper mixed layer (assuming a 24 h feeding period) and by the balance below this layer (assuming a 12 h feeding period). Daily zooplankton consumption was then calculated using both phytoplankton net production and biomass estimates from the same water bodies reported in Olivieri and Hutchings (in press).

Results

The daily particle size distributions of the initial, control and experimental bottles for the December 1980 drogue cruise are illustrated in Figure 1. Maximum ingestion rates ($314\ \mu m^3 .10^6 .mg\ cop^{-1}.hr^{-1}$) occurred in the larger size range on Day 2 at the 50% light level (2 m) where a vigorous bloom, dominated by Nitzshia and Chaetoceros spp., developed within the upper 20 m (Olivieri et al. 1985). Much of the material grazed was accounted by growth occurring in the control bottles. Growth could have been triggered by slight exposures to light on deck prior to incubating the bottles. An increase in the feeding activity was further evidenced at the 10 and 1% light level (9 - 14 m) after Day 4 when limiting nutrients in the surface layers caused the bloom to sink to subsurface nutrient-rich layers. High ingestion rates occurred concomitantly with high bloom concentrations.

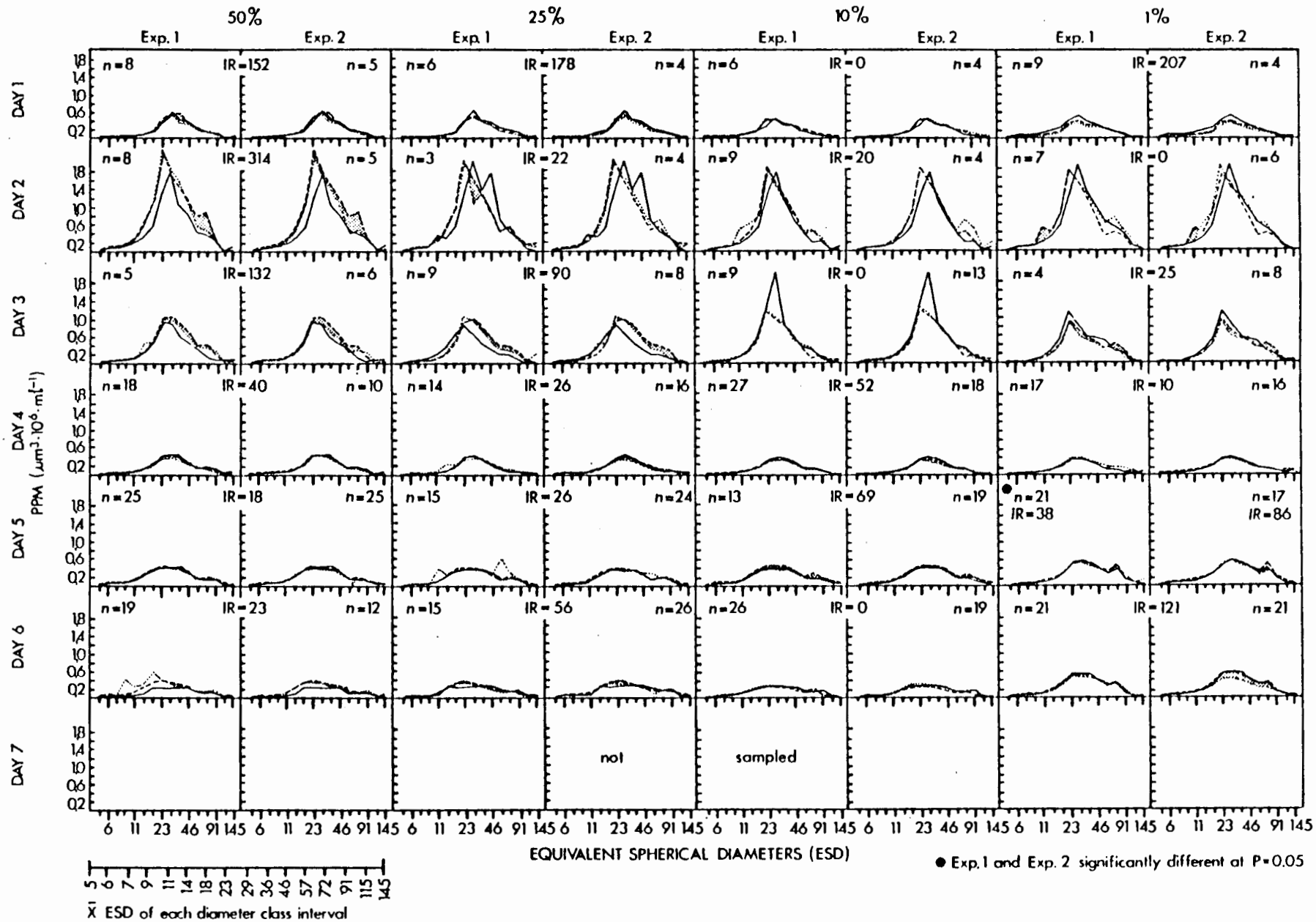

Fig. 1. December 1980 Daily particle size distributions of initial bottles (solid line), control bottles (dotted line) and experimental bottles (dashed line) at the 50, 25, 10 and 1% light levels. Shaded areas represent ingestion.

During the February 1981 drogue cruise (Fig. 2), relatively high ingestion rates occurred on Day 1 within the euphotic zone even though cell volumes in the control bottles decreased remarkably. This loss was not likely to be due to senescence, as the bloom was actively growing during this period (Olivieri and Hutchings, in press). Instead, the possible inclusion of nauplii (< 200 μm fraction) could have caused this slight underestimation. During Days 2 and 3 the total ingestion rates dropped, even though apparent grazing from the 1% depth was evident. The feeding activity increased by Day 4 till Day 6, coinciding with the change in the particle spectra and species composition that accompanied the change in the drogue's direction (Olivieri et al. 1985). In addition to this a greater proportion of smaller animals were used in the grazing experiments during this period.

During the March 1981 drogue cruise (Fig. 3) little feeding activity was apparent until Days 6 and 7 when ingestion rates reached 132 $\mu m^3 .10^6 .mg\ cop^{-1}.hr^{-1}$ at the 1% light level (11 - 25 m). The low ingestion rates can be attributed to strong winds creating turbulent mixing in the upper mixed layer and diluting the already low phytoplankton concentrations through the upper 40 - 60 m (Olivieri and Hutchings, in press). Only towards Days 6 and 7, when the winds declined, did phytoplankton levels rise sufficiently for grazing.

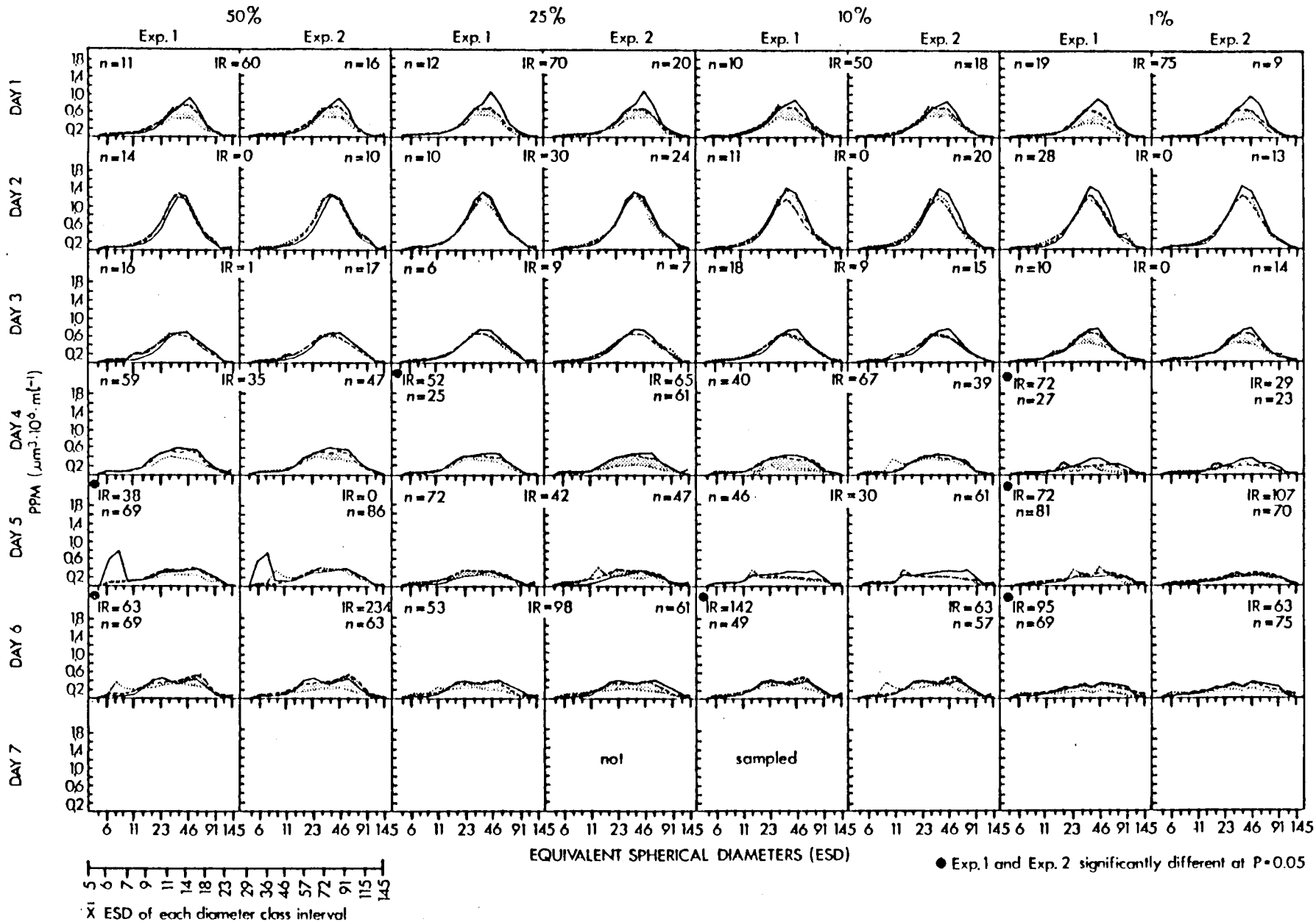

Fig. 2. February 1981 Daily particle size distributions of initial bottles (solid line), control bottles (dotted line) and experimental bottles (dashed line) at the 50, 25, 10 and 1% light levels. Shaded areas represent ingestion

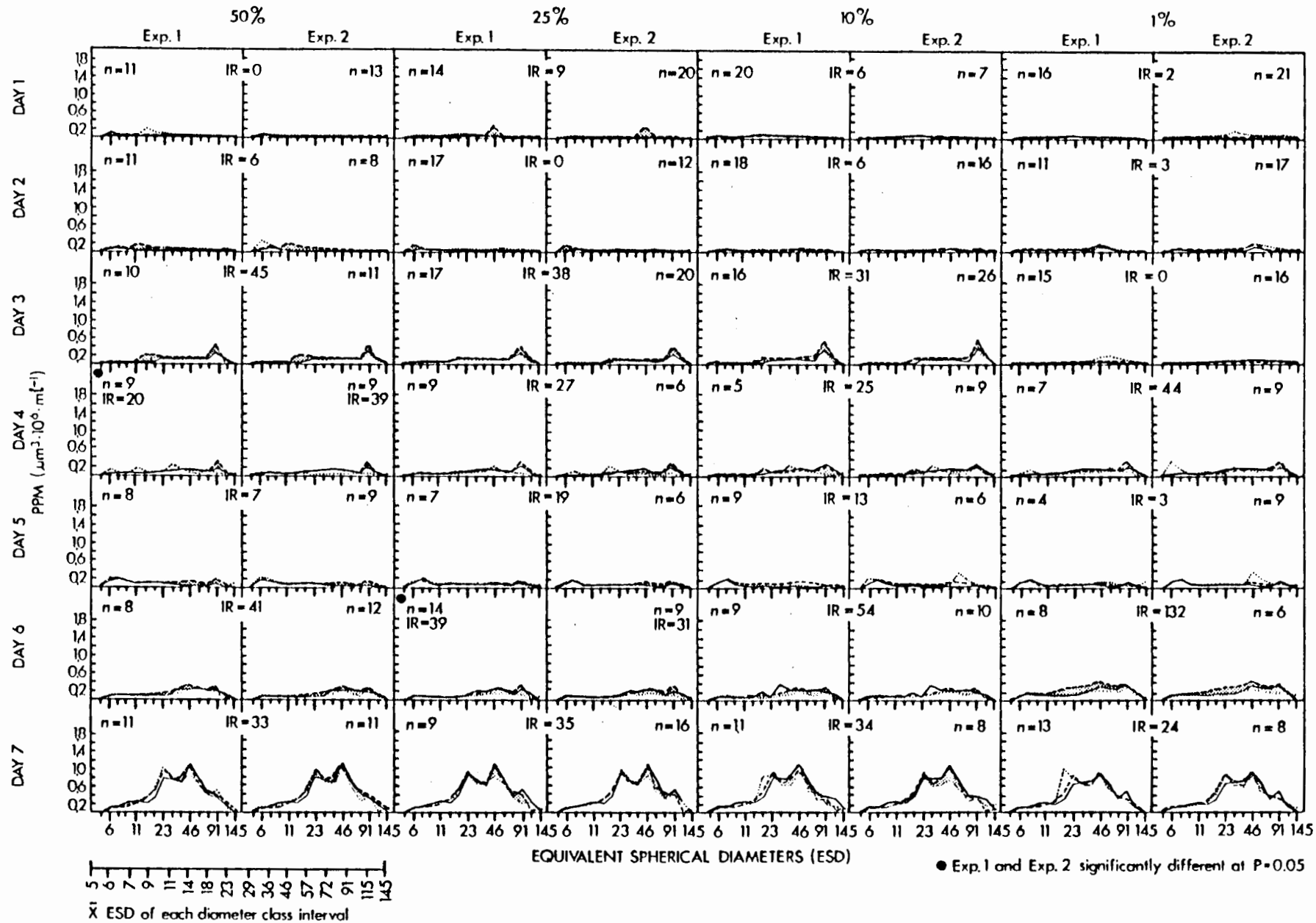

Fig. 3. March 1981 Daily particle size distributions of initial bottles (solid line), control bottles (dotted line) and experimental bottles (dashed line) at the 50, 25, 10 and 1% light levels. Shaded areas represent ingestion.

The grazing curves during the October 1981 drogue cruise (Fig. 4) show little grazing activity on Days 1 and 7 but increasing ingestion rates throughout the euphotic zone between Days 2 - 6. During this month, the drogue moved in a convoluted manner due to the frequent wind reversals (Olivieri and Hutchings, in press) and from Day 3 a radical decline in the daily production occurred as both nutrients and light conditions became limiting. However, the daily particle size distributions of the control bottles during Days 3 and 4 show substantial growth (ESD 23 - 46 µm) due to heterotrophic activity (Olivieri and Hutchings, in press).

Discussion

Artefacts in grazing experiments.

Although mostly chain-forming diatoms dominated in our experiments, particle production, due to chain breakages and cell fragmentation, could not be discerned from the lower size ranges. Particle size modifications have been shown to occur in many grazing studies (Conover 1966; Martin 1970; Paffenhöfer 1971; Poulet 1974; O'Connors et al. 1976; Allan et al. 1977; Gamble 1978; Poulet and Marsot 1978; Richman et al. 1977; 1980). Recently Alcaraz et al. (1980) using specialized filming techniques have shown that from an average chain of twelve Rhizosolenia cells, four cells will be successfully ingested whilst the remaining eight escape with the filtering current. These modifications of the particles through the grazing mechanism complicate any interpretations of size selectivity studies. Particularly since Deason

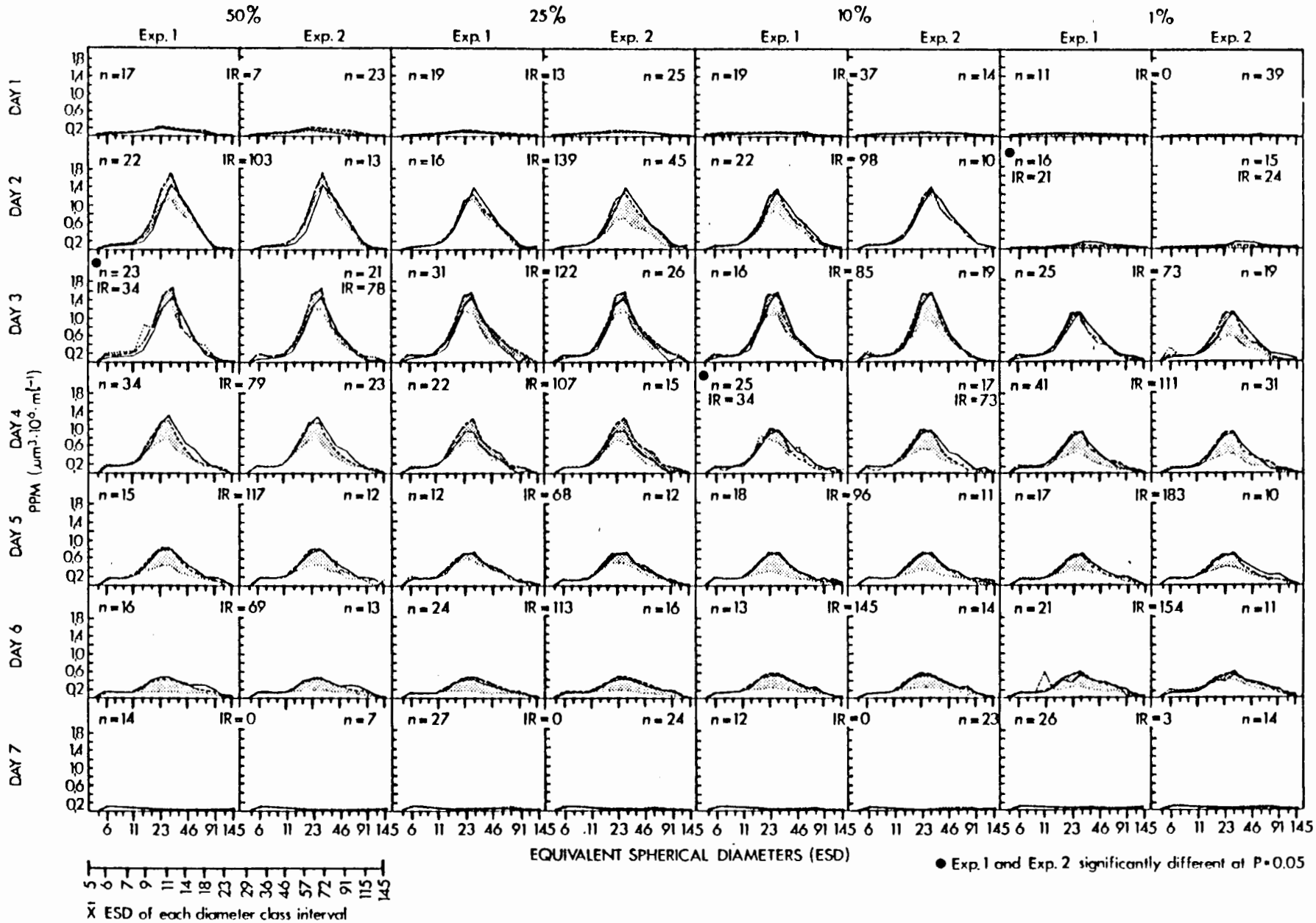

Fig. 4. October 1981 Daily particle size distributions of initial bottles (solid line), control bottles (dotted line) and experimental bottles (dashed line) at the 50, 25, 10 and 1% light levels. Shaded areas represent ingestion.

(1980) has shown that breakage of chain-forming diatoms can create artifacts resembling feeding behaviour even when filtration rate is constant. Unfortunately cell breakage can only be detected experimentally if it greatly exceeds the feeding rate.

Conditions in the control and experimental bottles differ as copepods excrete ammonia and increase the concentration of dissolved organic carbon by breaking cells during feeding (Lampert 1978). Ingestion rates may be underestimated if remineralization occurred, increasing the growth rate of the phytoplankton in the experimental bottles. Roman and Rublee (1980) show that adding NH_3 to control bottles to simulate grazing excretion resulted in an 18% increase in cell concentration. This could also cause differential growth of various sized particles, obscuring any effects of size selective feeding. Although it is not the intention of this study to look at size selective feeding, growth in the experimental bottles seldom exceeded that found in the control bottles. However, the exact amount underestimated still remains unknown particularly when nutrients became limiting for phytoplankton growth.

Faecal pellets.

A further underestimation of ingestion rates can occur by the ingestion of faecal material over the duration of the experiments. Paffenhöfer and Knowles (1979) have shown that late copepodids of Calanus spp. remove all faecal pellets in experimental bottles once phytoplankton are depleted. They also show that pellets

produced by nauplii of Eucalanus spp. are eaten by adult females of the same species at similar rates to phytoplankton of the same size. However, in most of our grazing experiments, adult stages were used, so that ingestion rates would not be affected unless nauplii were present at the onset of the experiments in the experimental bottles.

Faecal pellets can be produced at rates as high as 200 pellets. $cop^{-1}.d^{-1}$ (Gaudy 1974). Faecal pellet dimensions produced in laboratory cultures of Acartia spp. and Calanus spp. range between 200 $\pm$ 55 μm in length, by 40 $\pm$ 10 μm in width and 600 $\pm$ 100 μm in length, by 70 $\pm$ 15 μm in width respectively, and show little bacterial degradation of the pellet membrane during the first 24 h at low temperatures of 10 - 15 ^{o}C (Honjo and Roman 1978). If each copepod produced 200 pellets per day (pellet volume = 210000 μm^3 given pellet L = 600 μm, W = 70 μm, H = 5 μm) then 20 copepods will produce 0.84 $\mu m^3 .10^6 .ml^{-1} .d^{-1}$. Although faecal pellets were not microscopically sized or counted during our grazing experiments, it seems likely that little degradation occurred and in most experiments faecal pellet production was a low proportion of the total food available (1 - 10 $\mu m^3 .10^6 .ml^{-1}$)

The above mentioned containment effects underestimate the present grazing rates. However comparisons of estimates using this method with estimates obtained by three other methods show that measurements are in fair agreement (Kiørboe et al. 1985).

Ingestion rates and food concentrations.

Ingestion by copepods as a function of concentration has been expressed by numerous mathematical models [viz. rectilinear model (Frost 1972), Ivlev curve (Parsons et al. 1967) and Michaelis-Menten model (Mullin et al. 1975)] each involving a saturation-type relationship. However, the existence of saturated feeding in the natural environment has seldom been shown (Reeve and Walter 1977; Mayzaud and Poulet 1978; Koeller et al. 1979; Huntley 1981). A linear relationship poorly described the feeding behaviour of the various copepod species to the ambient food concentrations in our experiments (Fig. 5). This can however be explained by species-specific differences in ingestion rates (Arnold 1971). Saturated feeding rates have been shown to occur somewhere beyond 40 $\mu m^3 .10^6 .ml^{-1}$ when concentrating naturally occurring particles from the Bedford Basin (Mayzaud and Poulet 1978). Yet O'Connors et al. (1980) have shown saturated feeding to occur beyond 5 $\mu m^3 .10^6 .ml^{-1}$ at Long Island Sound. It is difficult to interpret from our data whether saturation did occur, as this depends on both the food type and feeding organisms. Nevertheless it would seem unlikely that saturated feeding rates were attained during our study, particularly since ambient food concentrations ranged between >1 and 7 $\mu m^3 .10^6 .ml^{-1}$. Extrapolation of equations for calculating ingestion rate as a function of food concentration and copepod weight, seldom give realistic results (Dagg and Grice 1980)as they are generally derived from laboratory feeding experiments.

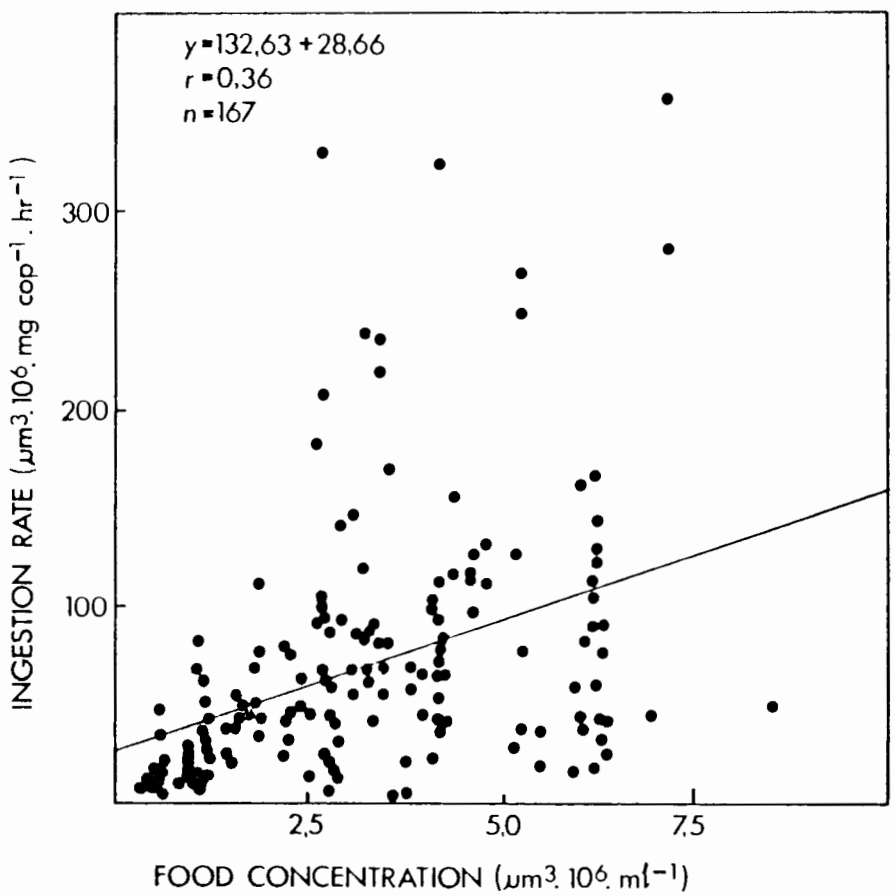

Fig. 5. The relationship between ingestion rate and food concentration.

Food quality.

Although a poor relationship exists between ingestion rate and ambient food concentration a relationship may exit between ingestion rate and food quality. Average daily ingestion rate followed similar trends as the daily production:biomass within the euphotic zone (Fig. 6) suggesting that feeding of the living component of the particulate material was being favoured as opposed to the non-living component. Detritus has been considered a possible food source for zooplankton, particularly in near-shore areas (Poulet 1976) where the main nutritional value of macrophytic detritus lies in the ciliates and bacteria associated with it (Heinle et al. 1977; Roman 1977). However, in our coastal waters, the regular appearance of clear upwelled water suggests that the detrital content plays a minor nutritive role. During the March 1981 drogue cruise, the presence of detritus through turbulent mixing may have subdued the ingestion rates, when the drogue was close inshore. Paffenhöfer and Strickland (1970) have shown that deep-water detritus is not eaten. Senescent algal cultures have also been shown to reduce feeding rates (Conover 1956; Paffenhöfer and Strickland 1970), suggesting that the age of the phytoplankton bloom affects the grazing rate. During the October 1981 drogue cruise, when the bloom became senescent, the increased ingestion rates were as a result of the increase in heterotrophic activity.

Zooplankton distribution and abundance.

No definite periodicity in the movement, during either early

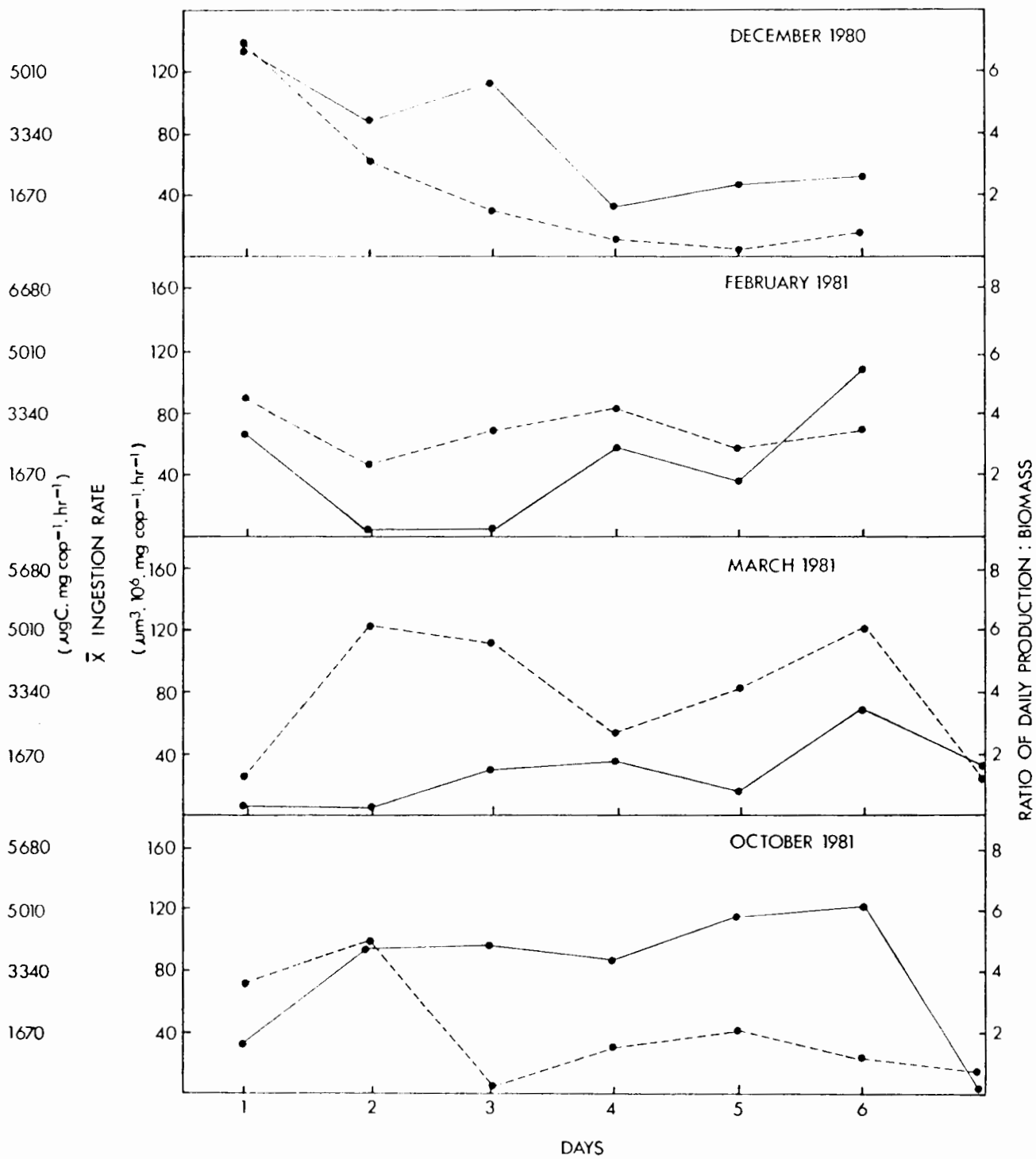

Fig. 6. Average ingestion rates (solid line) and the ratio of daily production: biomass (dashed line) within the euphotic zone for the various drogue cruises.

morning, midday or evening, could be discerned from the vertical distributions of the zooplankton (Fig. 7). This confirms previous studies by Hutchings (1979) and Pillar (1984) where little vertical migration of the mesozooplankton was shown to occur. Zooplankton abundance was highest during the latter period of the February 1981 drogue cruise when levels increased from 2683 - 12253 $mg.m^{-2}$ (dry weight) by Day 5. Zooplankton abundance remained fairly steady and low throughout the December 1980 drogue cruise as opposed to the March 1981 drogue cruise when high abundance was experienced throughout. Low abundance was observed during the October 1981 drogue cruise.

Zooplankton consumption estimates.

It becomes evident from the daily biomass, production and consumption estimates presented in Table 2 and Figure 8 that on average only 1% of the production and biomass was consumed during the December 1981 drogue cruise even though ingestion rates were very high during this cruise. Only 4% of the daily production was grazed as the phytoplankton community became nutrient limited and production decreased in the upper layer. During the February 1981 drogue cruise a strong turbulent environment was succeeded by stabilization (Olivieri and Hutchings, in press) with production remaining fairly high and constant throughout. Consumption was very low in the turbulent environment but increased in the stable environment such that by Day 6, approximately 11% of the daily production was consumed. The increased grazing stress during this period coincided with increases in the average ingestion

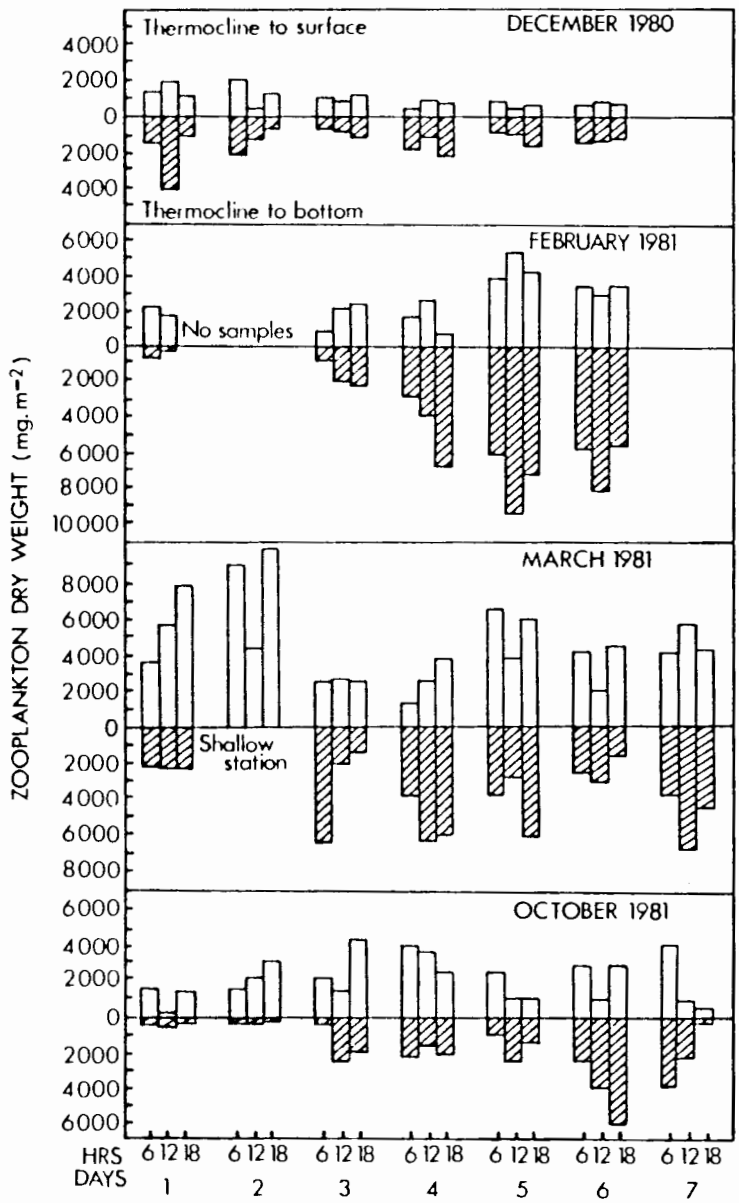

Fig. 7. Zooplankton abundance (dry weights) above and below the thermocline hauled vertically using a WP-2 net (57 cm and 200 μm mesh) for the various drogue cruises.

Table 2. Daily zooplankton consumption (%) for the various drogue cruises, calculated using average ingestion rates within the euphotic zone, total zooplankton biomass and phytoplankton production and biomass.

Month	Daily exp.	$\bar{X}$ IR within euphotic zone ($\mu m^3 .10^4 .mgcop^{-1}.hr^{-1}$) OR ($\mu gC.mgcop^{-1}.hr^{-1}$)		Zooplankton biomass dry weight ($mg.m^{-2}$)		Total daily volume consumed ($\mu m^3 .10^{12}.m^{-2}$) OR ($mgC.m^{-2}$)		Daily production and biomass ($\mu m^3 .10^{12}.m^{-2}$) OR ($mgC.m^{-2}$)		Daily consumption %
		Volume	Carbon	Above Thermocline	Below Thermocline	Volume	Carbon	Volume	Carbon	
D										
E	1	134	5609	1477	2267	8.5	368	604.8	25270	1.4
C	2	89	3730	1263	1397	4.2	189	472.1	19728	0.9
E	3	119	4983	1140	933	4.6	206	304.8	12742	1.5
M	4	33	1392	703	1780	1.3	68	232.9	9739	0.6
B	5	44	1851	640	1200	1.3	68	170.3	7125	0.8
E	6	50	2101	700	1770	1.9	93	224.0	9368	0.9
R										
1980										
F										
E	1	64	2686	1833	850	3.5	160	415.1	17348	0.8
B	2	8	348	1195	1610	0.4	30	505.6	21127	0.08
R	3	5	222	1893	1460	0.3	26	392.8	16417	0.08
U	4	53	2227	2093	4547	5.6	247	368.0	15381	1.5
A	5	34	1433	4600	7653	6.9	302	218.2	9125	3.2
R	6	107	4482	3370	6550	17.1	728	266.8	11155	6.4
Y										
1981										
	1	5	222	5927	2243	0.8	47	101.3	4244	0.8
M	2	4	180	8147	-	0.8	47	69.2	2903	1.2
A	3	29	1224	2647	3303	2.9	135	294.8	12324	1.0
R	4	32	1378	2717	5440	4.2	189	276.2	11548	1.5
C	5	11	473	5573	4297	2.1	101	310.8	12992	0.7
H	6	66	2770	3640	2483	7.8	339	491.9	20555	1.6
1981	7	32	1350	4850	5067	5.7	251	266.0	11122	2.1
O	1	31	1308	1173	457	1.0	55	156.6	6553	0.6
C	2	91	3814	2400	433	5.7	251	420.1	17557	1.4
T	3	94	3939	2727	1670	8.1	352	133.5	5588	6.1
O	4	88	3688	3453	2053	9.5	410	210.8	8816	4.5
B	5	116	4858	1553	937	5.6	247	200.0	8365	2.8
E	6	121	5066	2323	3120	11.3	485	99.6	4173	11.4
R	7	1	55	1860	2327	0.1	18	345.3	14433	0.03
1981										

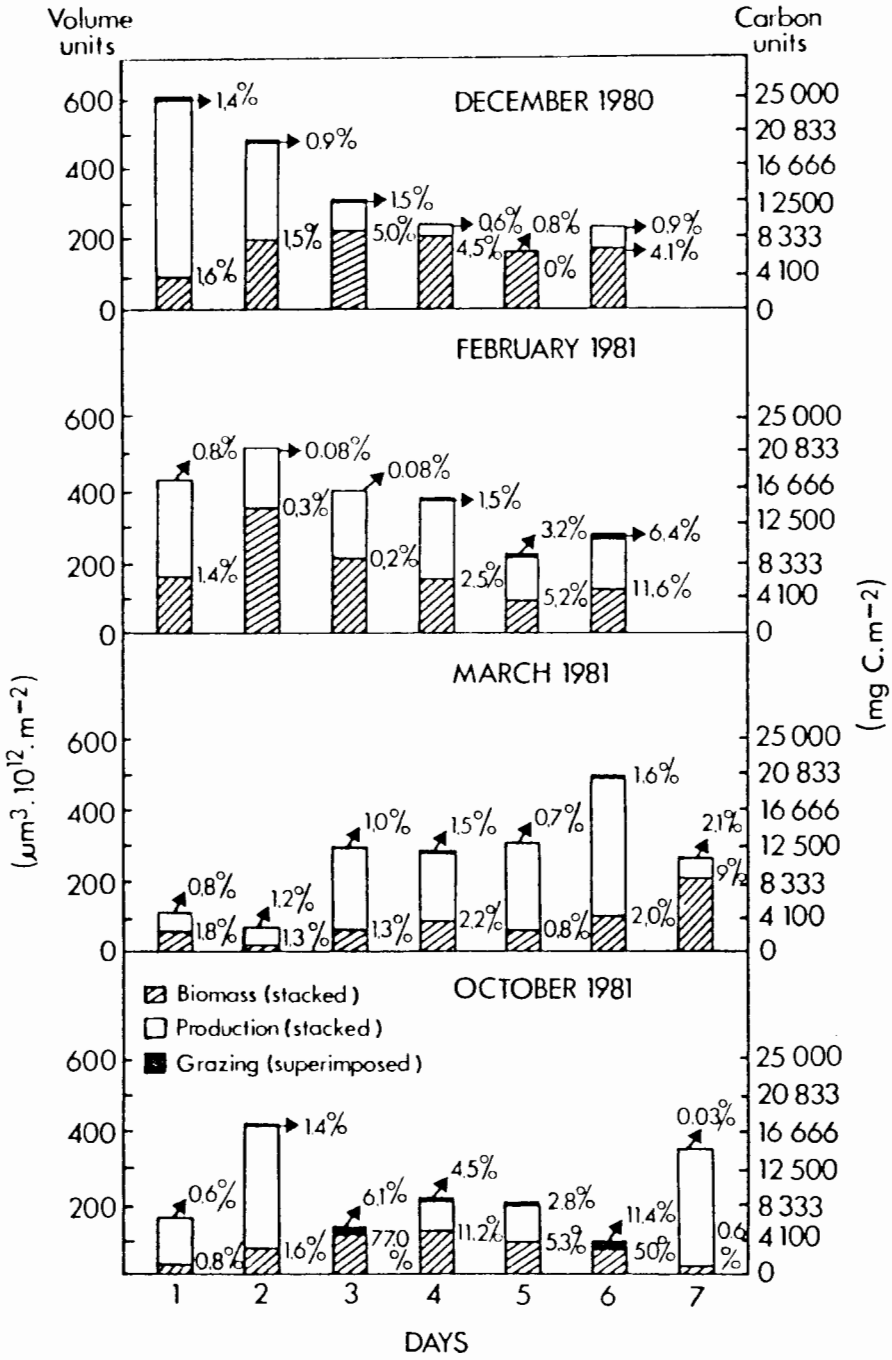

Fig. 8. Histograms showing daily biomass, production and consumption estimates for the various drogue cruises. The top value represents percent daily production plus biomass consumed, whilst the bottom value represents percent daily production consumed.

rates and zooplankton abundance. A continually turbulent environment was experienced during the March 1981 drogue cruise with production escalating till Day 6. The grazing stress fluctuated but remained very low till Day 7, when 9% of the daily production was consumed. Grazing may have been limited by the turbulent mixing of the water column and the quality of the food present, as average ingestion rates were low, although zooplankton abundance was high throughout this cruise. The grazing stress was highest during the October 1981 drogue cruise as by Day 3 both nutrients and light limited further bloom development. As much as 77% of the daily production was harvested on Day 3, although consumption never exceeded more than 11% of the total food available. The possibility of omnivorous feeding cannot be excluded, as growth could only be accounted by heterotrophic activity. Eucalanus and Paracalanus spp. have been shown to be omnivores but primarily opportunistic herbivores (Turner 1984).

In order to obtain estimates of community grazing, a better understanding of the actual feeding behaviour of copepod species is necessary. The assumption was made that the zooplankton represented a homogenous entity such that average ingestion rates adequately represented the grazing rates for the whole zooplankton community. This assumption, however, is not strictly true as copepod species have different ingestion rates with different threshold feeding behaviours (Cowles 1977). The mesozooplankton is only a fraction of the total zooplankton present (approximately 40 - 50%) (Verheye and Hutchings in prep.). The rest comprises

mostly euphausids which are undersampled by the vertically-hauled net. Recently it has been shown that copepod feeding behaviour is dependent on a sensory mode allowing active handling and capture of selected food particles (Alcaraz et al. 1980; Koehl and Strickler 1981; Paffenhöfer et al. 1982; Strickler 1982) such that phytoplankton is not equally available or nutritious for all zooplankton.

Grazing behaviour has also been shown to change with copepod development (Allan et al. 1977; Poulet 1977; Fernández 1979). Paffenhöfer (1971) has shown that young stages of herbivorous copepods have higher grazing rates than their adult counterparts and are responsible for the major part of consumption of phytoplankton. Grazers < 200 µm may have been present in the incubation bottles with their grazing contribution possibly matching that of the larger organisms. Presently too little is known about the distribution of nauplii to evaluate their role in grazing. Grazing rates are also substantially higher in adult females than in males (Raymont and Gross 1941; Mullin 1963). The actual grazing impact is therefore dependent on species and age composition and also the diel movements of the copepod species present. A definite feeding rhythm is found in most copepods, in addition to their vertical movements (Petipa 1958; Mackas and Bohrer 1976, Boyd and Smith 1980; Runge 1980) although no definite periodicity in the feeding activities could be discerned from the vertical distributions of the zooplankton.

Conclusion

The rate of transfer of organic material from phytoplankton to zooplankton is important in understanding pelagic fish yield, as grazers have been shown to play important roles in controlling and modifying phytoplankton populations (Menzel and Ryther 1961; Cushing 1968; Hargrave and Geen 1970; Steele and Frost 1977; Sonntag and Parsons 1979; Dagg and Turner 1982; Dagg et al. 1982). It is evident that the grazing impact of mesozooplankton on developing phytoplankton communities is very low in the Cape Peninsula Upwelling System. Only 11% of the total daily food available was harvested, even though considerable temporal and spatial variations were observed in the food availability (2903 - 25270 $mgC.m^{-2}$), zooplankton abundance (1610 - 12253 $mg.m^{-2}$) and average ingestion rates (55 - 5609 $\mu gC.mg\ cop^{-1}.hr^{-1}$).

In other upwelling areas Dagg et al. (1980) showed that less than 5% of the daily phytoplankton production was consumed by large copepods off Peru. By contrast Herbland et al. (1973), off North Africa, and Longhurst (1967), off Baja California, showed rapid exploitation of phytoplankton when encountered by high zooplankton abundance. The grazing stress in coastal regions of the Bering Sea is equivalent to 6%, as opposed to 25% in the mid-shelf region and 18% in the oceanic and outer-shelf regions. (Dagg et al. 1982). In the open subarctic Pacific Ocean, Mc Allister (1972) estimates that an average of 40% of the annual

primary production is ingested and Kremer and Nixon (1978) estimate between 31% and 82% of the annual primary production is consumed in the Narragansett Bay.

Phytoplankton production in the Cape Peninsula is both seasonal and extremely rapid, although large variations in productivity result from the intermittent nature of upwelling in this region (Hutchings 1981; Nelson and Hutchings 1983; Olivieri and Hutchings in press). Wind reversals often cause high accumulations of phytoplankton to occur close inshore, and storms readily disperse and disrupt phytoplankton within the water column. These periodic instabilities, of the order of days to weeks, cause much of the primary production to go unutilized. Therefore an efficient phytoplankton-zooplankton interface is not likely to exist in this upwelling region, unless prolonged stability of the horizontal and vertical structures of the phytoplankton occurs.

Upwelling areas are characterized by zooplankton populations of low diversity and high standing stocks (Walsh 1976). Hutchings (1979) has shown that in the Cape Peninsula estimates of zooplankton standing stocks compare favourably with estimates in other upwelling areas although higher and more consistent biomasses are recorded just north of the Cape Peninsula in the St. Helena Bay area. Little is known about the dynamics of the zooplankton populations and whether they encounter enough food to meet their nutritional requirements. Parsons and Le Brasseur (1970) have shown that even in neritic areas where food is abundant ingestion

rates do not always meet the requirements for growth and reproduction. Borchers and Hutchings (in press) have shown, off the Cape Peninsula, that adult Calanoides carinatus are resistant to prolonged periods of starvation and the populations may be controlled to some degree by poor adaptation of the juvenile stages to intermittent food supplies. At the extreme south of the Benguela Current there are constraints on re-seeding of zooplankton into upwelling plumes (Hutchings 1979). Our study shows that the few zooplankton species which seed the newly upwelled patches exert little control on the phytoplankton communities. Moreover, their delayed reproductive response means that young and naupliar stages appear when food concentrations diminish through sinking, turbulence or advection. The important factor limiting zooplankton populations in the Cape Peninsula Upwelling System is probably the transient nature of food availability and the inability of the species to consistently return to the site of high primary production.

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CONCLUSION

CONCLUSION

This thesis constitutes a first attempt at understanding the development and production of phytoplankton communities in newly upwelled waters of the southern Benguela Current and the utilization of this production by mesozooplankton. Several general conclusions can be drawn from this study in addition to those detailed in the preceeding papers.

The electronic counting and sizing technique, has proved to be extremely valuable in monitoring the rapid changes that occur in the marine food chain off the Cape Peninsula. Although this method showed that preserved phytoplankton samples introduce artifacts, it provided a quick and accurate method for measuring freshly collected material. Particle volume was shown to accurately represent phytoplankton biomass. This added a useful dimension to the interpretation of trophic interactions, where consideration of the changes in particle concentration relative to size could be emphasized. The versatility of this method in (a) assessing the development of phytoplankton communities (b) determining phytoplankton production rates and (c) mesozooplankton grazing rates, simultaneously from the same water body, has resulted in all data being expressed in the same units. This has obviated the introduction of errors when conversions of data obtained from different methods have to be made.

The combined use of the Coulter counter and inverted microscope techniques, proved to be very effective in assessing the development of the phytoplankton communities in newly upwelled waters. These communities were adequately monitored by following single parcels of water over a period of days with rapid repetitive sampling. Rapid changes in the structure of the communities were shown to occur during the December 1979 and the December 1980 - February 1981 upwelling seasons. Differences in the community characteristics (eg. species dominance, diversity and biomass) were inextricably linked to fluctuations in wind speed and direction. Short-term variations in wind caused surface mixing of the newly upwelled waters with neighbouring water bodies, resulting in changes in nutrient concentrations and species composition. True succession of the species was not observed during these cruises due to the strong lateral and vertical mixing which may have masked the process. Longer survey periods would be required to observe species succession off the Cape Peninsula.

The upwelled waters, during each cruise, were primed with the same chain-forming diatoms, supporting the view that the upwelled water originates from a constant source. The colonization and succession of species depends ultimately on the initial numbers (cell concentrations) and on the specific selective adaptations for growth of the individual species.

The phytoplankton communities of the newly upwelled waters were shown to develop within 3 - 5 days with extremely rapid growth

rates (max. doublings per day ca. 2.9 and max. carbon production ca. 21g.m^{-2}.d^{-1}) and little evidence of a lag phase. Variations of nutrients and light in the upper mixed layer were considered the major environmental regulators of the primary production. Differences in the growth rates were attributed to the rate of mixing of the water column, which in turn altered the light regime and short-term wind variations causing different water bodies to mix and change the nutrient regime.

These production measurements, expressed in terms of rates, have provided basic information on the fertility of the southern Benguela in terms of distribution in space and time of rich food resources for zooplankton, pelagic and mesopelagic fish. High enough food concentrations were attained, during certain periods, for saturated feeding of mesozooplankton, however, their impact on the system was shown to be small relative to the food available. Only 11% of the total daily food available was harvested even though considerable temporal and spatial variations were observed in the food availability (2903 - 25270 mgC.m^{-2}), zooplankton abundance (1610 - 12253 mg.m^{-2}) and average ingestion rates (55 - 5609 µgC.mg copepod^{-1}.hr^{-1}).

Periodic instabilities of the horizontal and vertical structures of the phytoplankton caused much of the primary production to go unutilized. An inefficient phytoplankton-zooplankton interface exists, resulting from intermittent halts in the upwelling process. Although little is known about the dynamics of the

mesozooplankton in the Cape Peninsula region, their biomass is thought to be limited by periods of reduced food abundance. The transient nature of food availability and food quality were shown to depress ingestion rates and could delay their reproductive responses.

Insight into understanding the quantitative trophic interactions between phytoplankton and herbivorous mesozooplankton, off the Cape Peninsula, has been gained in terms of measuring rates of processes. However, to assess the food potential of this region accurately and to construct manageable models of oceanic productivity, qualitative studies are necessary. Areas which require further investigation in order to achieve this goal include measuring: (a) contribution of nanoplankton production to the system (b) importance of nauplii grazing (c) species specific ingestion rates of the important mesozooplankton species in order to obtain estimates of their specific nutritional requirements.

PAPER 5 - COLONIZATION, ADAPTATIONS AND TEMPORAL CHANGES IN DIVERSITY AND BIOMASS OF A PHYTOPLANKTON COMMUNITY IN UPWELLED WATER OFF THE CAPE PENINSULA, SOUTH AFRICA, IN DECEMBER 1979.

S. Afr. J. mar. Sci. 1: 97–109
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COLONIZATION, ADAPTATIONS AND TEMPORAL CHANGES IN DIVERSITY AND BIOMASS OF A PHYTOPLANKTON COMMUNITY IN UPWELLED WATER OFF THE CAPE PENINSULA, SOUTH AFRICA, IN DECEMBER 1979

E.T. OLIVIERI

The colonization, adaptations and temporal changes in the species diversity and biomass of phytoplankton in an upwelling plume off the Cape Peninsula are described. Certain community characteristics such as biomass, diversity and growth rates were investigated so that successional stages as a result of environmental changes could be characterized. A mixed phytoplankton bloom comprising 49 species developed with *Chaetoceros compressus* Laud. and *Skeletonema costatum* (Grev.) Cleve the dominant species. The factors responsible for these species successfully colonizing and dominating are examined with respect to their specific selective adaptations for growth. An attempt is made to determine the mechanism whereby these species dominated, by proposing several possible adaptations in terms of cell size, growth, nutrient absorption and buoyancy. Increase in cell size along the drogue trajectory is considered as a strategy in adapting to the changing environmental conditions.

Die kolonisasie, aanpassings en veranderinge met verloop van tyd in die spesieverskeidenheid en biomassa van fitoplankton in 'n opwellingspluim teenoor die Kaapse Skiereiland word beskryf. Bepaalde gemeenskapskenmerke soos biomassa, verskeidenheid en groeikoerse is ondersoek sodat die stadiums van opeenvolging as gevolg van omgewingsveranderinge gekarakteriseer kon word. 'n Gemengde fitoplankton-opbloeiing wat 49 spesies behels, het ontwikkel, met *Chaetoceros compressus* Laud. en *Skeletonema costatum* (Grev.) Cleve as oorheersende spesies. Die faktore wat daarvoor verantwoordelik was dat hierdie spesies met welslae gekoloniseer en oorheers het, word ondersoek wat hul spesifieke selektiewe aanpassings vir groei betref. Daar word 'n poging aangewend om die meganisme te bepaal deur middel waarvan hierdie spesies oorheers het, deur verskillende moontlike aanpassings aan die hand te doen ten opsigte van selgrootte, groei, die absorpsie van voedingsoute en dryfvermoë. Toename in selgrootte met die dryfankertrajek langs word oorweeg as 'n strategie in die aanpassing by die veranderende omgewingstoestande.

The Benguela upwelling system off the west coast of southern Africa is regarded as one of the major upwelling systems of the world's oceans (Hart and Currie 1960). The Cape Peninsula upwelling system is primarily generated by the orographic force of the wind which, with a strong southerly component, results in off-shore Ekman transport of surface water (Shannon 1966). Between September and May, when strong south-easterly winds predominate, a tongue of cool water extends up to 100 km north-west of the Cape Peninsula. Within this plume of ageing upwelled water, maximum chlorophyll concentrations have been recorded and biological activity is most intense (Andrews and Hutchings 1980).

Margalef (1978) has claimed that colonization and succession of phytoplankton begin with a mixing process such as upwelling, which causes fertilization of the euphotic zone. The initial increase in the nutrient concentrations, followed by turbulent mixing and stabilization of the water mass as it moves off shore, provide a gradient of phytoplankton succession.

The approach of this investigation has been to assess the changes in a phytoplankton community by monitoring a single parcel of newly upwelled water over several days. This approach has been used by Beers *et al.* (1971), Ryther *et al.* (1971) and Herbland *et al.* (1973).

MATERIALS AND METHODS

Cruise strategy

The drogue study was undertaken between 4 December and 13 December 1979, midway through the upwelling season. The surface temperature distribution was mapped in the area between Oudekraal and Duiker Point in order to locate a suitable patch of newly upwelled water (Fig. 1). This water was then marked with a tetrahedral drogue set 10 m deep and attached to a surface float equipped with a flag and a flashing light. The drogue was lowered into the water at a position approximately 5 km off Oudekraal (33°58,1'S, 18°19,5'E) on 5 December. This drogue (Drogue Track I) showed the existence of a southward-flowing current close inshore, with strong vertical mixing which prevented significant surface sun-warming. The drogue was therefore retrieved after 46 hours and a second drogue was released 10 km from the coast (33°55,4'S, 18°16,3'E) on 7 December in water with a surface temperature of 10,4°C. The drogue (Drogue Track II) was followed for five days, sampling 3—4 times per day. An aerial survey, showing the wind speed and direction at 500 feet (c. 150 m) and sea surface temperatures, was con-

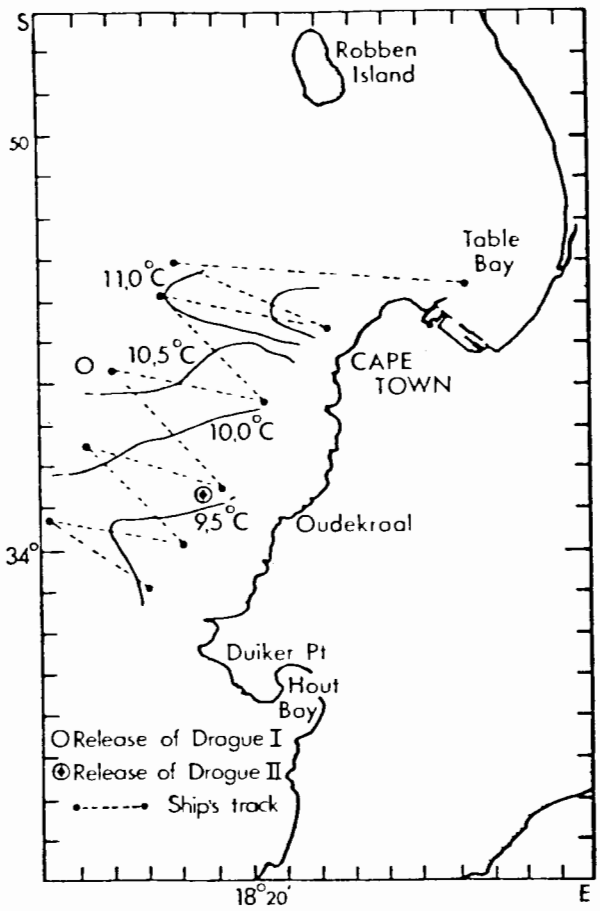

Fig 1: Distribution of surface temperature between Cape Town and Duiker Point off the west coast of the Cape Peninsula

ducted over the Cape Peninsula during the drogue study (Jury 1980).

Sample collection

Samples were taken daily at 07h30, 12h00 and 18h00 as close as possible to the drogue. Concurrently, a bathythermograph cast was made, and submarine light levels were determined with a Lambda LI-1925 underwater quantum sensor. The sample depths were at the 100-, 50-, 25-, 10- and 1-per-cent light levels, and then at 10-m intervals to the bottom. Temperature was measured by means of a Nansen-Pettersson insulated water bottle, from which salinity samples were also drawn. Simultaneously, 7- or 5-ℓ I.O.S. bottles were used to collect samples for determination of concentrations of oxygen, nutrients, chlorophyll, particulate protein, carbohydrate, carbon and nitrogen, for measuring ^{14}C uptake and for counting phytoplankton. Two sets of phytoplankton samples were collected. One set was preserved with 4-per-cent buffered formalin to be counted ashore microscopically by the Utermöhl technique (Utermöhl 1936). The other set was counted electronically on board with a Model TA II Coulter counter, fitted with a 280 μm aperture tube.

Irradiance was monitored continuously with a surface quantum sensor and integrator. Continuous surface temperatures and salinities were measured with a Bissett-Berman Model 6600 thermosalinograph. The drogue position and wind speed and direction were recorded every hour on the hour.

Processing of samples

Salinity samples were stored in glass bottles and analysed with an inductively coupled Autolab salinometer. Both standard Copenhagen and substandards were used for calibrations. Oxygen samples were analysed on board by means of the classical Winkler technique. Mostert (1966) has described the basic reagents used for this analysis. Samples for measuring phosphates, silicates and nitrates were deep-frozen in 100-mℓ polythene bottles. Analyses were carried out ashore on a Technicon Autoanalyser, following the methods of Strickland and Parsons (1972) for phosphates and nitrates, and of Grasshoff (1966) for silicates.

Three analytical techniques were employed to measure changes in phytoplankton biomass.

Technique 1 — One-litre water samples for chlorophyll *a* were filtered on board and stored at −20°C for later spectrophotometric analysis. Wavelengths and equations recommended by the SCOR/UNESCO Working Group 17 (1966) were used.

Technique 2 — Preserved phytoplankton samples were analysed by the Utermöhl (1936) method of sedimentation with an inverted microscope, but following the simplified procedure and recommendations of Willén (1976) and Hobro and Willén (1977). The sedimenting chambers were 10 mℓ or 50 mℓ, depending on sample concentration. Samples were well agitated and poured into settling chambers through a filling chamber, thus ensuring uniform distribution of the sediment. The recommended time of at least 3 hours for the 10-mℓ and 8 hours for the 50-mℓ chambers was allowed for the sediment to

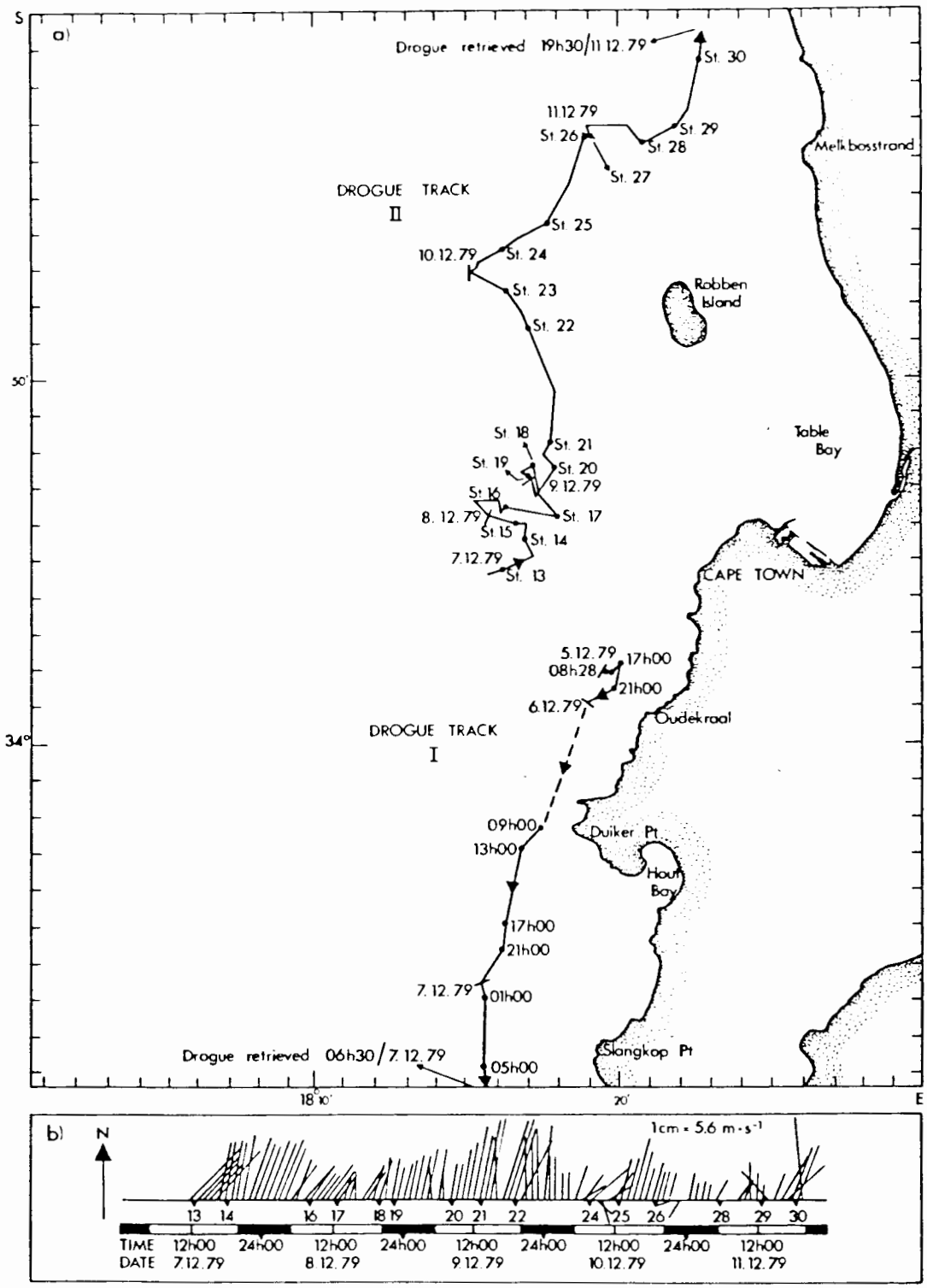

Fig 2. Drogue Track II (7—11 December 1979) — a) drogue trajectories, b) wind stick diagram

Table I Replicate counts analysed at the 95-per-cent confidence level for arithmetic mean, coefficient of variation, standard error and marginal error (Hobro and Willén 1977)

Number of replicates n	Mean (particles $\cdot\ell^{-1}$) $\bar{x}$	Coefficient of variation c.v.	Standard error $\frac{c.v.}{\sqrt{n}}$	Marginal error $\frac{SE \cdot t \cdot 100}{\bar{x}}$ (%)
6	1 215 696	28 998	11 838	2.5

$t_{(95\%)5} = 2.571$

settle (Lund *et al.* 1958).

Most phytoplankton counts were made through a 40× phase-contrast objective. The micrometer eyepiece was calibrated for all objectives with a stage micrometer. The width of the counting strip was measured with the micrometer eyepiece and adjusted according to the density of the sample. Strips were counted until a minimum of 2 per cent of the total counting area was scanned. Sample counts were expressed as cells $\cdot\ell^{-1}$. Phytoplankton species were identified from the drawings and descriptions of Hendey (1937), Cupp (1943) and Hustedt (1962).

Estimates of precision were obtained by making six successive counts from one sample. The results are given in Table I. The percentage marginal error obtained for all six counts was 2,5 per cent at the 95-per-cent confidence level.

At each station, 50 measurements of cell length and width were made of the dominant species (*Chaetoceros compressus* Laud. and *Skeletonema costatum* (Grev.) Cleve) per sample, and the cell volume was determined by approximating the cell shape to that of a cylinder (Larrance 1964).

Technique 3 — Unpreserved phytoplankton samples were counted on board electronically, with a Model TA II Coulter counter, following the method described by Sheldon and Parsons (1967). For the purpose of this study the 280 μm aperture tube was used, because it included a diameter size range appropriate for marine diatoms and minimized clogging of the aperture. The aperture tube was calibrated with latex particles of known diameter and the instrument gain for direct read-out of the part per million (p.p.m. = the proportion of the volumes of all the suspended material measured relative to the total volume of the fluid in the sample, expressed as $\mu m^3 \times 10^6 \cdot m\ell^{-1}$) was set according to the procedure outlined in the Coulter counter Model TA II Operator's Manual (Coulter Electronics 1975). Background counts were obtained from seawater filtered through 0,45 μm and 0.22 μm filters in series. The "noise" level was found to be negligible for all size intervals except the first, which was therefore screened out. Samples were well agitated by a mechanical stirrer to prevent larger particles from sedimenting. In order to minimize coincidence, certain samples were diluted two-or five-fold. In most cases 50-mℓ counts (160 seconds) were made in the time mode, with the manometer isolated to prevent erratic flow caused by the mercury column surging at sea. Two plots per station depth were produced:

(i) logarithm of particles $m\ell^{-1}$ versus diameter intervals in micrometers;
(ii) concentration by volume (p.p.m.) versus diameter intervals in micrometers.

Numerical analyses

The Bray-Curtis (Czekanowski) per-cent similarity index (PSI) (Barnes 1952, Field 1970, Field and Robb 1970, Clifford and Stephenson 1975) was used to group samples with similar concentrations, after cell concentrations expressed as cell counts$\cdot\ell^{-1}$ had been log-transformed. Dendrograms were prepared from the Group Average Sorting Method of Field (*op. cit.*) and Clifford and Stephenson (*op. cit.*). The McConnaughey (1964) index (PSI) was similarly used to group associated species based on species absence or presence.

RESULTS

Drogue movements in relation to wind patterns

At the onset of the cruise (4 December), three days of steady southerly winds had caused moderate upwelling close inshore with surface temperatures of 9—10°C. The first drogue released 5 km off the coast (Fig. 2a) showed the existence of a southward-flowing current close inshore characterized by strong vertical mixing. The second drogue was therefore released further off shore, and this one travelled a distance of 28,2 km in 102 h, with a mean rate of drift of 0,27 km$\cdot$h^{-1}. On the third day, however, it covered 10,6 km at a mean drift of 0,44 km$\cdot$h^{-1} while the average wind speed was 10 m$\cdot$s^{-1} from the south. Evidence from wind data (Fig. 2) recorded on the research vessel showed that an average wind speed of 7 m$\cdot$s^{-1} was experienced over the five-day period 7—11 December. For almost the entire survey period, the winds blew consistently from the south-south-west, roughly parallel to the coast, causing

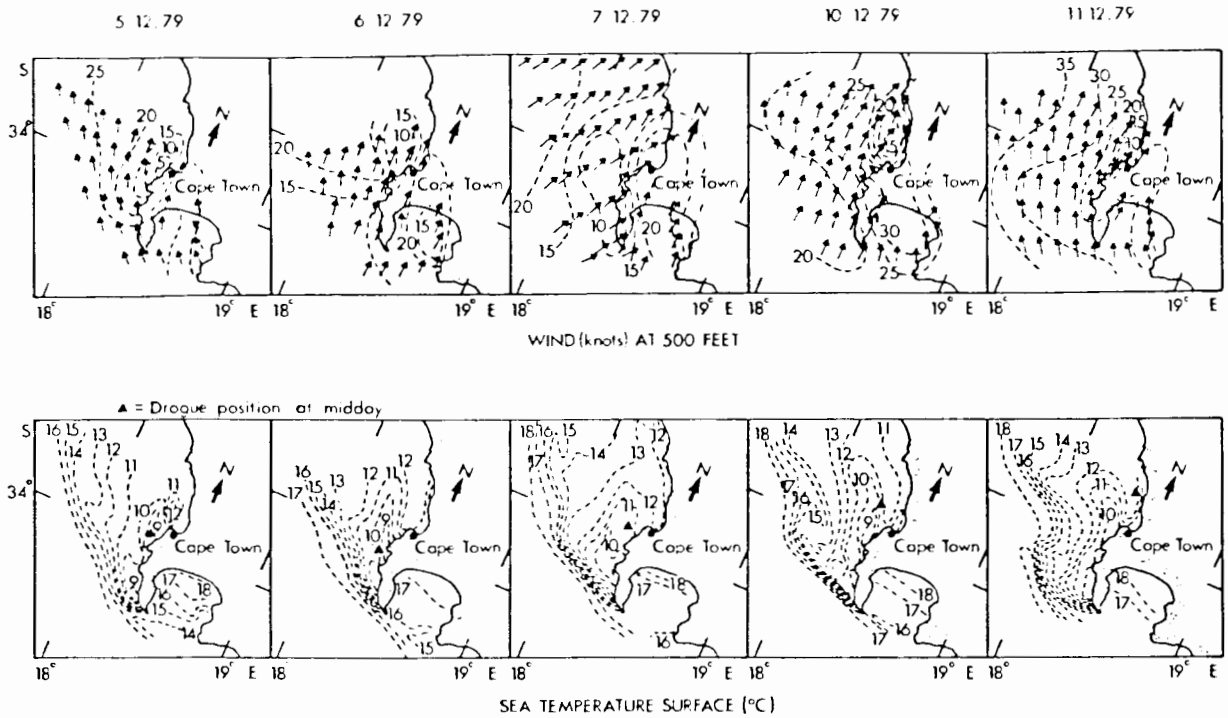

Fig 3: Flight maps showing wind speed and direction at 500 feet (150 m) and sea surface temperatures (reproduced by courtesy of M. R. Jury, formerly Sea Fisheries Research Institute)

northward (longshore) water movement.

There were two lines of evidence to support the theory that the drogue followed the same body of water until 10 December (Day 4).

(i) The movement of the plume as observed from the aerial survey (Fig. 3) coincided with the track of the drogue during the first four days. Two distinct plumes were observed on 5 and 6 December at Olifantsbos and Oudekraal during southerly and south-easterly winds. The wind then veered to the south-west on 7 December and, by 10 December, southerly winds had resumed, resulting in a single plume being produced off Oudekraal. The positioning of this plume was in accordance with the drogue track, which was shown to be orientated along the axis of the plume. However, on 11 December the drogue veered shorewards while the plume moved off in a north-westerly direction.

(ii) Several parameters measured at the 10-m depth of the drogue (Fig. 4) showed that there was a continuous increase in phytoplankton growth until Station 26 (Day 4). Temperature and oxygen increased at the same time by 1,9°C and 2,9 $m\ell \cdot \ell^{-1}$ respectively. Chlorophyll *a* concentrations increased by 21 $\mu g \cdot \ell^{-1}$ and the cell counts increased by $1\,950 \times 10^3$ cells$\cdot \ell^{-1}$. In contrast, concentrations of nitrates, silicates and phosphates decreased by 82, 72 and 29 per cent respectively. Such increases in biomass, oxygen and temperature with a corresponding depletion of nutrients over the first four days strongly suggest that the drogue followed a coherent body of water in which phytoplankton was actively developing. However, on the fifth day the temperature and oxygen values declined and an apparent drop in standing stock was also evident. Such features suggest that the water body was mixing with cooler, less mature, more recently upwelled water.

Comparative estimates of biomass

The concentration of chlorophyll *a*, inverted micro-

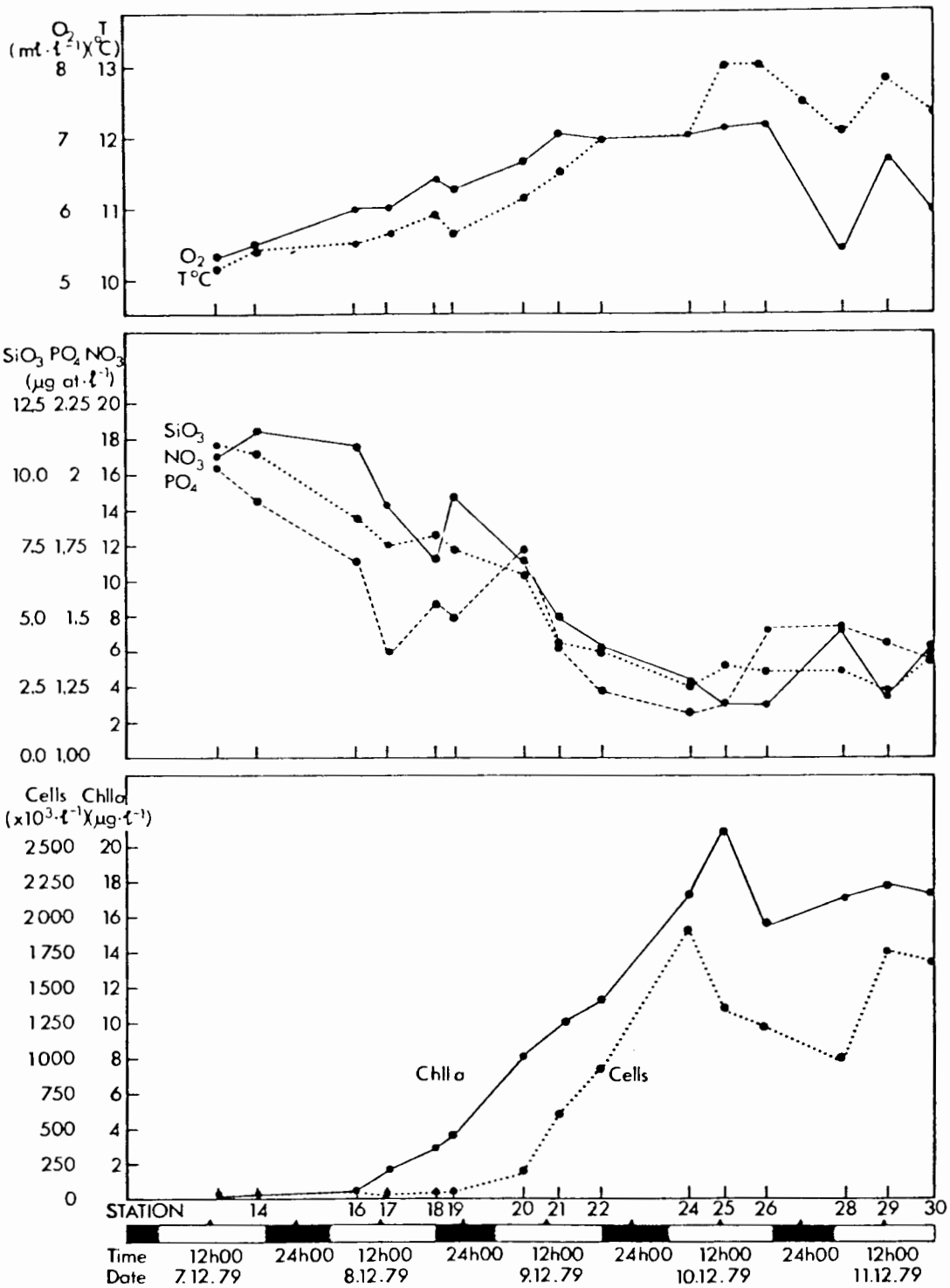

Fig 4: Distribution of temperature, dissolved oxygen, nitrate, silicate, phosphate, chlorophyll *a* and microscopic cell counts at the 10-m drogue depth

Table II: Chlorophyll *a* concentrations (μg ℓ^{-1}), inverted microscope counts (cells × 10^3 ℓ^{-1}), Coulter counter results (cells × 10^3 ℓ^{-1}) and edited Coulter counter results, without Channels 2 and 3 (Cells × 10^3 ℓ^{-1}) for each station at the various light levels

Station	Method	Light levels above 1 per cent					Depth (m) below the 1-per-cent light level						
		100	50	25	10	1	20	30	40	50	60	69	80
13	Chlorophyll *a*	0,104	0	0,104	0,208	0,415	—	—	—	—	—	0,104	—
	Inverted microscope	0,5	0,8	11	4	10	—	—	—	—	—	9	—
	Coulter counter	1 434	1 031	1 123	982	1 342	—	—	—	—	—	1 568	—
	Edited Coulter counter	459	344	362	241	475	—	—	—	—	—	564	—
14	Chlorophyll *a*	0,104	0,104	0,208	0,208	0,727	—	—	—	—	0,623	—	—
	Inverted microscope	8	9	4	2	11	—	—	—	—	5	—	—
	Coulter counter	1 139	1 220	1 292	1 173	1 919	—	—	—	—	2 971	—	—
	Edited Coulter counter	343	380	407	411	633	—	—	—	—	1 091	—	—
16	Chlorophyll *a*	1,349	0,415	1,142	0,727	0,934	—	—	—	—	—	—	0,934
	Inverted microscope	47	58	25	4	13	—	—	—	—	—	—	37
	Coulter counter	1 808	2 489	1 512	1 073	1 778	—	—	—	—	—	—	2 360
	Edited Coulter counter	705	913	571	394	661	—	—	—	—	—	—	777
17	Chlorophyll *a*	1,972	1,619	1,557	2,181	0,623	—	—	—	—	1,038	—	—
	Inverted microscope	41	31	30	9	7	—	—	—	—	35	—	—
	Coulter counter	2 055	1 965	1 943	1 675	1 214	—	—	—	—	2 151	—	—
	Edited Coulter counter	902	868	837	467	399	—	—	—	—	853	—	—
18	Chlorophyll *a*	2,699	2,118	2,633	3,426	0,830	—	—	—	0,623	1,453	—	—
	Inverted microscope	35	23	49	46	5	—	—	—	4	9	—	—
	Coulter counter	2 464	2 741	2 835	13 410	1 012	—	—	—	1 032	—	—	—
	Edited Coulter counter	1 131	1 277	1 471	1 211	329	—	—	—	366	—	—	—
19	Chlorophyll *a*	3,633	2,741	4,371	3,426	0,415	—	—	—	—	—	—	—
	Inverted microscope	37	30	118	22	5	—	—	—	—	—	—	—
	Coulter counter	909	944	1 204	1 546	431	—	—	—	—	—	—	—
	Edited Coulter counter	373	424	570	614	209	—	—	—	—	—	—	—
20	Chlorophyll *a*	7,563	6,851	8,201	7,890	3,218	—	1,246	0,727	0,934	1,142	—	—
	Inverted microscope	150	305	71	292	48	—	12	6	7	4	—	—
	Coulter counter	5 714	4 804	3 978	4 175	1 991	—	1 304	—	—	—	—	—
	Edited Coulter counter	3 007	2 836	2 181	2 113	761	—	369	—	—	—	—	—

Continued overleaf

Table II: *(Continued)*

Station	Method	Light levels above 1 per cent					Depth (m) below the 1-per-cent light level						
		100	50	25	10	1	20	30	40	50	60	69	80
21	Chlorophyll *a*	13,288	10,215	12,769	12,642	2,284	—	1,557	0,127	1,349	1,868	—	—
	Inverted microscope	331	448	707	662	22	—	2	6	4	16	—	—
	Coulter counter	6 535	6 380	6 835	6 510	1 779	—	1 193	—	—	—	—	—
	Edited Coulter counter	3 970	3 880	4 380	3 665	605	—	437	—	—	—	—	—
22	Chlorophyll *a*	10,07	12,582	11,834	11,419	11,004	11,108	2,284	1,142	0,830	1,453	—	—
	Inverted microscope	2 280	1 182	875	734	1 278	464	24	62	4	13	—	—
	Coulter counter	6 014	7 100	6 368	6 552	6 584	4 698	—	—	—	—	—	—
	Edited Coulter counter	3 459	3 886	3 633	3 728	3 550	2 605	—	—	—	—	—	—
24	Chlorophyll *a*	18,374	19,932	18,167	17,025	17,544	1,453	1,038	0,727	0,830	1,453	—	—
	Inverted microscope	923	1 461	1 388	2 110	1 348	24	10	6	10	12	—	—
	Coulter counter	7 073	6 291	5 828	6 150	5 810	1 103	—	—	—	—	—	—
	Edited Coulter counter	3 944	3 582	3 379	3 637	3 314	311	—	—	—	—	—	—
25	Chlorophyll *a*	15,779	17,814	17,232	21,177	20,762	8,616	2,076	0,727	2,180	—	—	—
	Inverted microscope	2 118	1 177	1 177	1 098	2 095	564	17	12	59	—	—	—
	Coulter counter	7 160	7 087	6 454	6 682	5 847	3 067	—	—	—	—	—	—
	Edited Coulter counter	4 113	4 398	3 982	4 053	3 570	1 620	—	—	—	—	—	—
26	Chlorophyll *a*	18,478	18,810	18,374	15,572	14,222	1,869	1,661	1,869	9,447	—	—	—
	Inverted microscope	1 270	952	1 001	1 074	1 321	265	7	10	3	—	—	—
	Coulter counter	8 277	7 744	7 546	7 445	6 104	4 007	—	—	—	—	—	—
	Edited Coulter counter	4 831	4 732	4 472	4 275	3 645	2 002	—	—	—	—	—	—
28	Chlorophyll *a*	11,315	13,080	16,298	14,118	17,025	7,682	1,765	1,661	—	—	—	—
	Inverted microscope	1 089	761	953	1 692	1 065	131	11	0,8	—	—	—	—
	Coulter counter	6 128	5 067	5 407	5 072	5 069	2 224	—	—	—	—	—	—
	Edited Coulter counter	3 699	3 236	3 334	3 223	3 186	1 073	—	—	—	—	—	—
29	Chlorophyll *a*	15,052	11,959	15,675	16,506	19,309	10,173	1,557	—	—	—	—	—
	Inverted microscope	1 154	1 270	1 461	1 460	1 750	549	0,2	—	—	—	—	—
	Coulter counter	6 846	7 282	6 975	7 320	7 089	4 388	—	—	—	—	—	—
	Edited Coulter counter	4 335	4 612	4 271	4 547	4 144	2 288	—	—	—	—	—	—
30	Chlorophyll *a*	20,139	14,949	20,243	17,959	17,336	8,305	—	—	—	—	—	—
	Inverted microscope	1 430	1 538	1 453	1 900	1 693	1 694	—	—	—	—	—	—
	Coulter counter	5 587	5 570	5 552	5 650	5 639	3 433	—	—	—	—	—	—
	Edited Coulter counter	3 491	3 438	3 453	3 523	3 353	1 762	—	—	—	—	—	—

Table III: Volume concentrations for each station at the various light levels

Station	Volume concentrations in p.p.m. ($\mu m^3 \times 10^4$) at light levels											
	Light levels above 1 per cent					Depth (m) below the 1-per-cent light level						
	100	50	25	10	1	20	30	40	50	60	69	80
13	44,3	27,2	26,6	39	54,4	—	—	—	—	—	33,9	—
14	19,5	43,1	43,1	40,5	33,0	—	—	—	—	88,1	—	—
16	60,4	76,1	53,8	58,4	41,9	—	—	—	—	—	—	47,4
17	77,2	79,4	84,6	55,2	36,0	—	—	—	—	51,5	—	—
18	92,4	109	135	144,5	32,7	—	—	—	40,7	—	—	—
19	34,8	41,8	60,4	52	34,2	—	—	—	—	—	—	—
20	279,5	276,5	223,5	216	71,4	—	25,5	—	—	—	—	—
21	328	348,5	375,5	324,5	58,3	—	56	—	—	—	—	—
22	389,5	454	426,5	424,5	476,5	382,5	—	—	—	—	—	—
24	516	501	501	521,5	477	39,7	—	—	—	—	—	—
25	544,5	547,5	513,5	550	497	212,5	—	—	—	—	—	—
26	604,5	536	557	528	464	286,5	—	—	—	—	—	—
28	510	463,5	614,5	470	519,5	135,6	—	—	—	—	—	—
29	714	709	681	684	567,5	262	—	—	—	—	—	—
30	482	523	504	488	427,5	171,5	—	—	—	—	—	—

scope counts, Coulter counter results and edited Coulter counter results (i.e. minus Channels 2 and 3) are presented in Table II for each station at the various light levels. The results from the Coulter counter showed an increase of approximately 5—7 times when compared directly with counts made with the inverted microscope. However, when the edited Coulter counter results were compared with counts made with the inverted microscope, the increase was approximately two- to four-fold. This suggests that the high counts obtained in the lower channels of the Coulter counter particle-size spectra consisted almost entirely of detritus.

A high correlation coefficient of 0,91 was obtained (at the 95-per-cent level of significance) for correlations of chlorophyll *a* against both electronic and microscopic counts. Also, a significant correlation coefficient of 0,7 was obtained for comparisons of electronic counts with microscopic counts. Omitting Channels 2 and 3 (of particle-size spectra) for the electronic counts increased *r* to 0,82. As the smallest mean volume (157 μm^3) of the dominant species was greater than the volume representing Channel 3 (134 μm^3), the Coulter counter was probably counting detritus.

Biomass estimates determined by volume concentrations (p.p.m.) are presented in Table III. An increase was evident between Stations 13 and 30. A

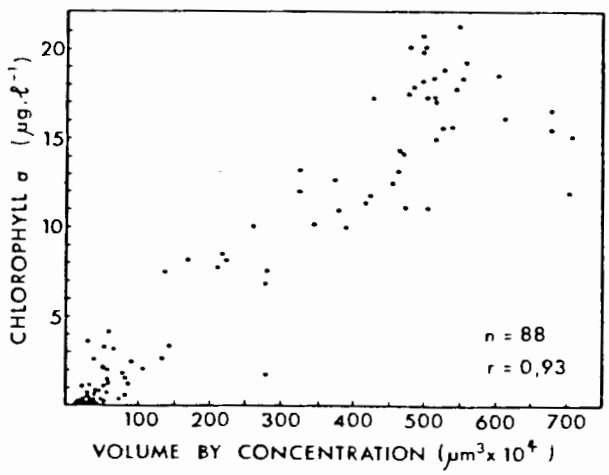

Fig. 5: The relationship between chlorophyll *a* and volume by concentration (p.p.m.)

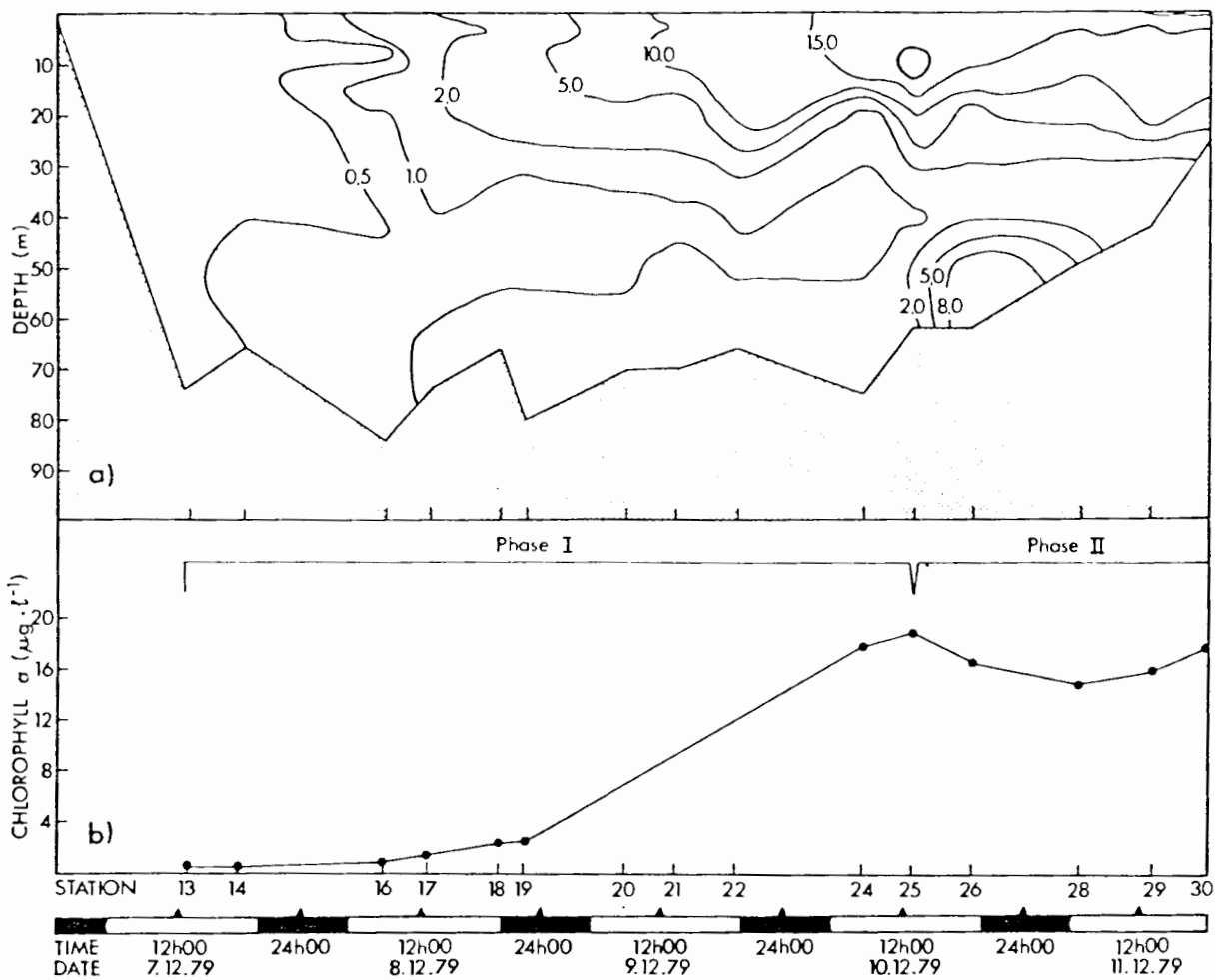

Fig. 6: a) Vertical distribution of chlorophyll *a*; b) changes in the mean integrated values of chlorophyll *a* within the euphotic zone

significant correlation coefficient of 0,93 (Fig. 5) was obtained for comparisons of chlorophyll *a* with volume concentrations (p.p.m.).

Chlorophyll *a*

The vertical distribution of chlorophyll *a* is illustrated in Figure 6a. A rapid increase occurred in the upper 10—20 m, with concentrations roughly doubling each day to reach 15—20 μg chlorophyll $a \cdot \ell^{-1}$ by Station 24. This increase in biomass is clearly shown in Figure 6b, where the mean concentration of chlorophyll *a* within the euphotic zone increased from 0,2 $\mu g \cdot \ell^{-1}$ on Day 1 to 18 $\mu g \cdot \ell^{-1}$ on Day 5.

The vertical profiles of chlorophyll *a* and temperature (closely related to density and indicative of the degree of vertical mixing) are shown in Figure 7. Low levels of chlorophyll *a* were encountered down the water column during the first two days of the survey, but on the third day the chlorophyll *a* levels increased within the upper mixed layer (i.e. above the 10°C isotherm).

Growth rates, determined using the growth coefficient of Cowles (1977), are illustrated in Table IV.

The highest growth rate was observed between Days 1 and 2 at both the surface and 10 m. The

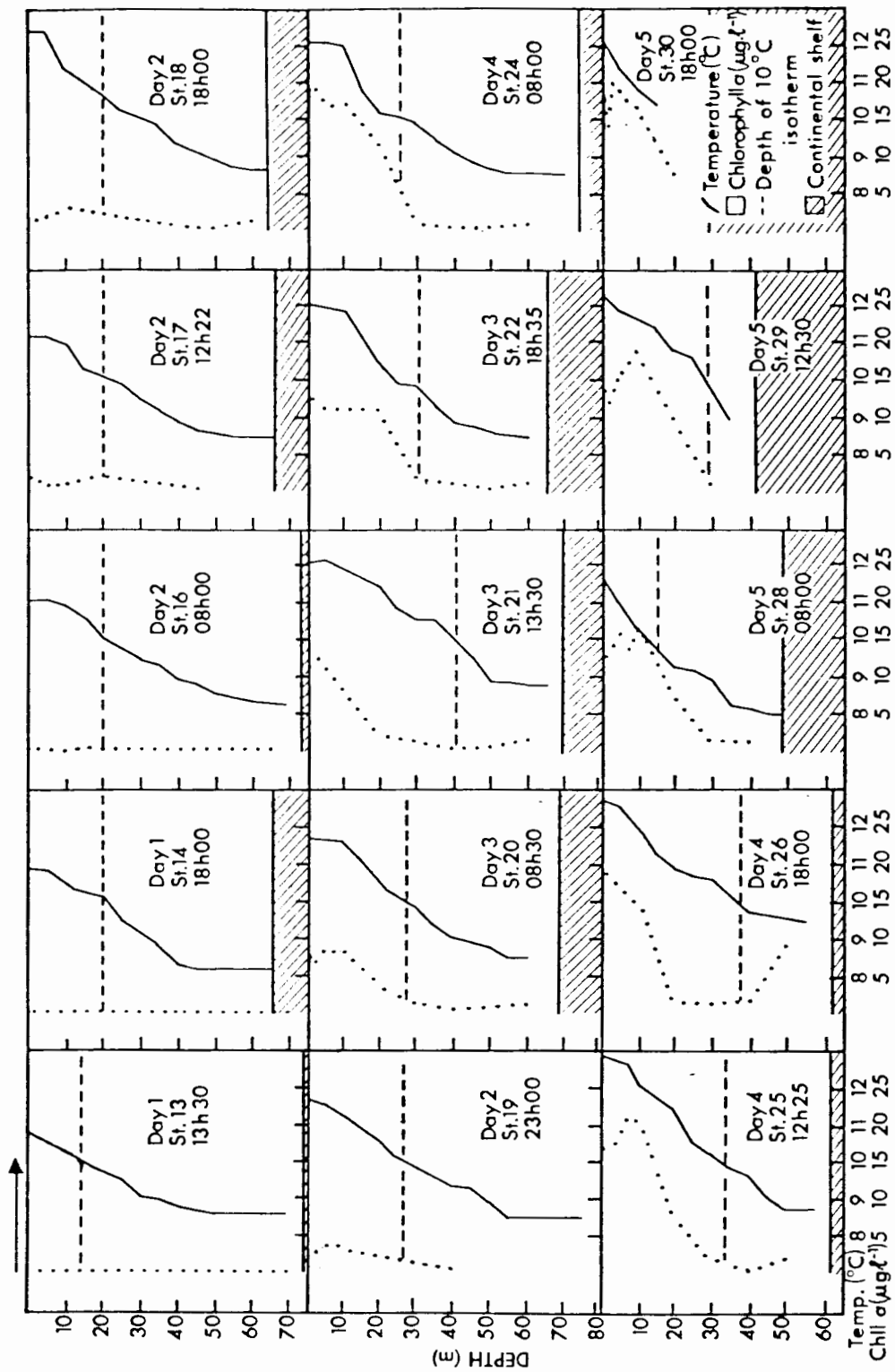

Fig. 7: Vertical profiles of chlorophyll *a* and temperature at each station along the drogue track

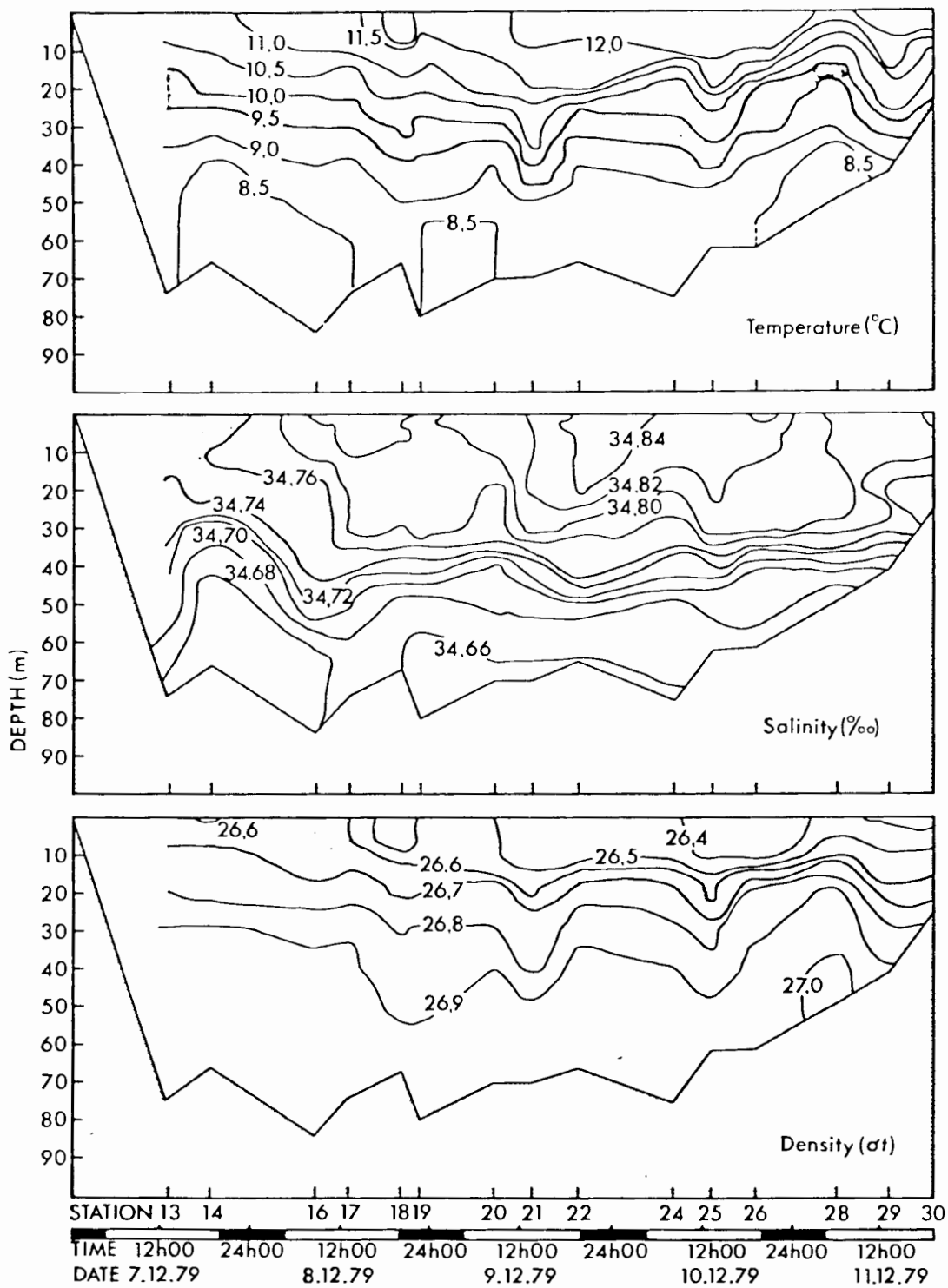

Fig. 8: Vertical distribution of temperature, salinity and density

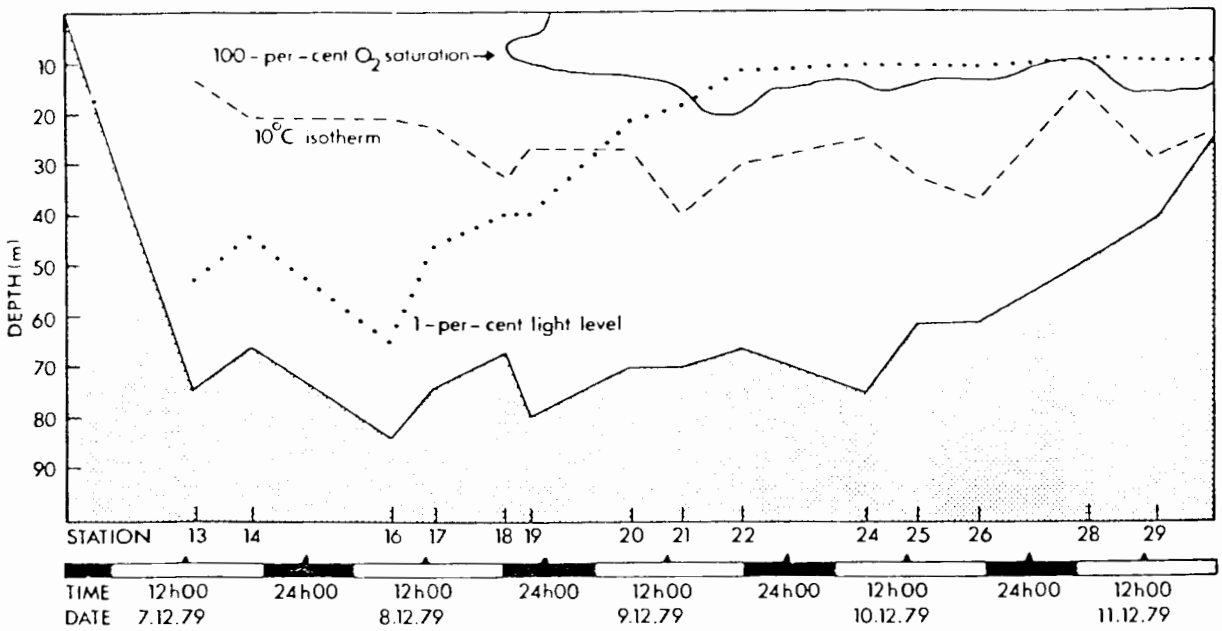

Fig. 9. Vertical section of the 1-per-cent light level (euphotic zone), 10°C isotherm (upper mixed layer) and the 100-per-cent oxygen saturation level

growth rates near the surface decreased towards Day 4, but relatively high cell counts were obtained at 20 m, probably because phytoplankton cells were sinking out of the euphotic zone.

Table IV: Values of the daily instantaneous growth coefficient K, calculated from changes in the total number of cells present N at 12h30 for four different depths in the upper mixed layer during the drogue study

Depth (m)	N or K	Day (Station)				
		1(13)	2(17)	3(21)	4(25)	5(29)
0	N	0.5	41	331	2 118	1 154
	K	4.41	2.09	1.86	-0.61	
5	N	—	31	707	1 098	1 460
	K	3.13		0.44	0.29	
10	N	0.8	30	662	2 095	1 750
	K	3.62	3.09	1.15	-0.18	
20	N	10	0.9	22	564	549
	K	-2.41	3.20	3.24	-0.03	

N measured in cells $\times 10^3 \cdot \ell^{-1}$

K units as defined by Cowles (1977):

$$K = \frac{1}{t_2 - t_1} \log_n \frac{N_2}{N_1} \text{ cells} \times 10^3 \cdot \ell^{-1} \cdot \text{day}^{-1}$$

Temperature, salinity and density

The vertical distribution of temperature is illustrated in Figure 8. Gradual warming was evident, with surface temperature rising 2°C along the drogue transect to Day 4 and then declining slightly. As the surface waters warmed, the 12°C isotherm appeared at the surface at Station 18.

The 10°C isotherm was used, somewhat arbitrarily, to define the lower limit of the upper mixed layer, being the lower limit of the steepest temperature gradient and also coinciding with the bottom of the chlorophyll-rich layer. The depth of the 10°C isotherm increased from 14 m at Station 13 to a maximum of 40 m at Station 21, but it rose again to 24 m at Station 30. The thermocline, which occurred at 10—25 m, was most pronounced between Stations 22 and 25, where temperatures increased by 2°C in one day (Day 3—4).

Salinity (Fig. 8) varied little with depth or time, with a range of less than 0,2‰. Isohalines deepened slightly between Days 1 and 2 and rose again on Day 5, but changes in the upper 10 m were less than 0,1 ‰ indicating that lateral mixing processes were not significant during the study.

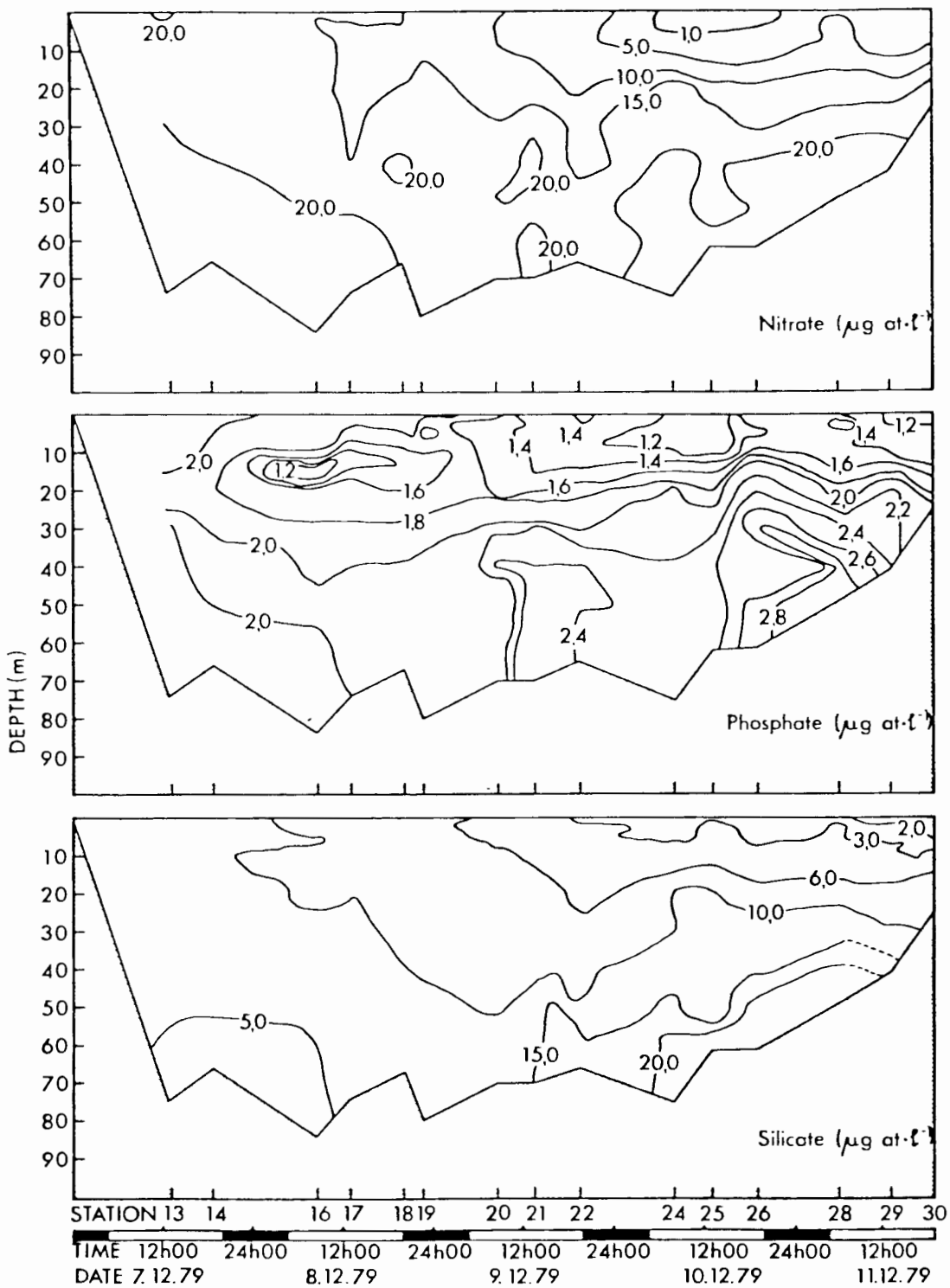

Fig. 10. Vertical distribution of nitrate, phosphate and silicate

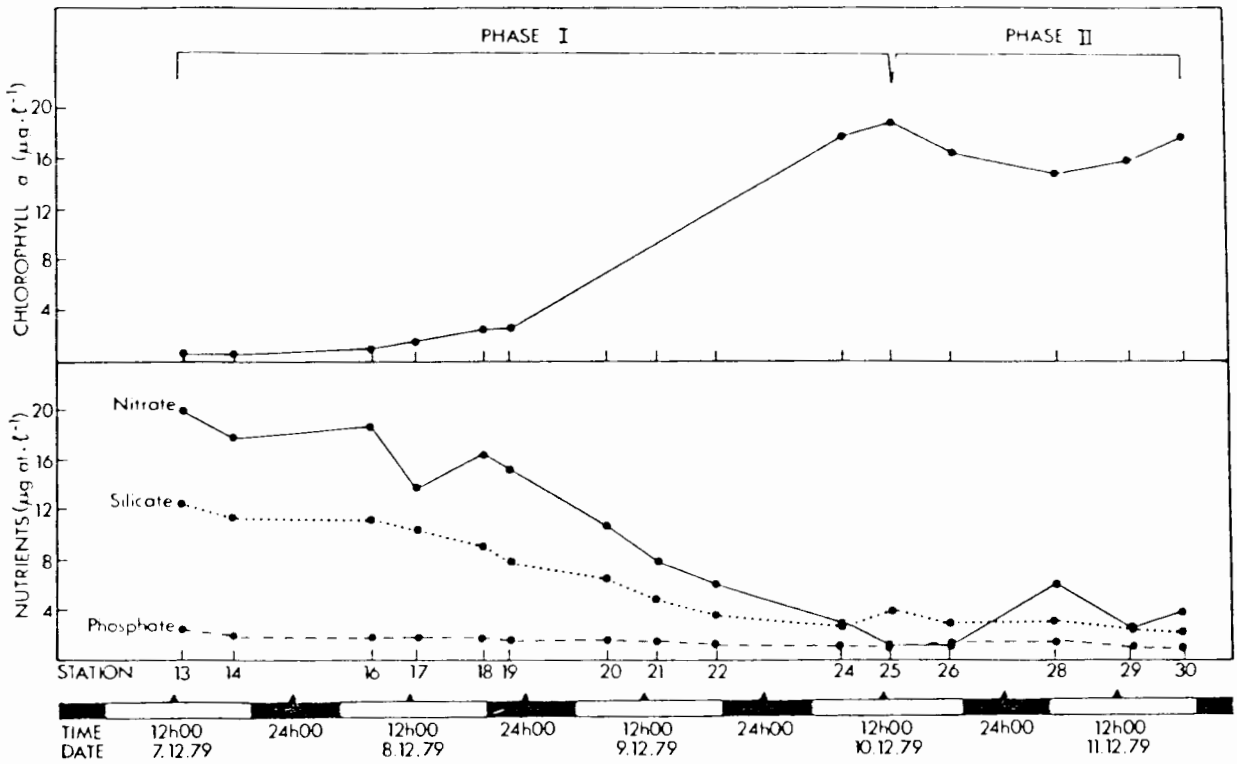

Fig. 11: Changes in the mean integrated values of chlorophyll *a* and nutrients within the euphotic zone

Isopycnals displayed variations similar to those of isotherms (Fig. 8), indicating that density changes were influenced more by variations in temperature than by changes in salinity.

Irradiance

The midday hourly integrated light measurement ranged between 1 197 and 2 309 $\mu E \cdot m^{-2} \cdot s^{-1}$, with an average measure of 1 900 $\mu E \cdot m^{-2} \cdot s^{-1}$ for the five-day survey period (P.C. Brown, Sea Fisheries Research Institute, personal communication).

The euphotic zone ranged from 54 m at Station 13 (Day 1) to 9 m at Station 30 (Day 5) — see Fig. 9. During the initial stages of the study the euphotic zone extended well below the 10°C isotherm into upwelled water, such that the compensation depth (where the photosynthetic rate equals the respiratory rate) lay below the mixed layer. As mixing and sun-warming proceeded, the depth of the mixed layer increased slightly while the euphotic zone became much shallower owing to self-shading by phytoplankton. Of considerable ecological significance is the point where the 1-per-cent light level (euphotic zone) rose into the upper mixed layer.

Nitrates, phosphates and silicates

The vertical distributions of inorganic nutrients (nitrates, phosphates and silicates) are illustrated in Figure 10. Highest nutrient values were observed at the early stations, and in all cases minimal nutrient concentrations corresponded with maximal chlorophyll *a* values. At the surface, reductions of more than 96 per cent for nitrate, 89 per cent for silicate and 57 per cent for phosphate were shown. Decreases in the mean integrated values of the nutrients (Fig. 11) were inversely related to the increases in the mean integrated values of chlorophyll *a*.

Dissolved oxygen and oxygen saturation

The vertical distributions of dissolved oxygen and oxygen saturation are illustrated in Figure 12. Initially the water was 82 per cent saturated with oxygen,

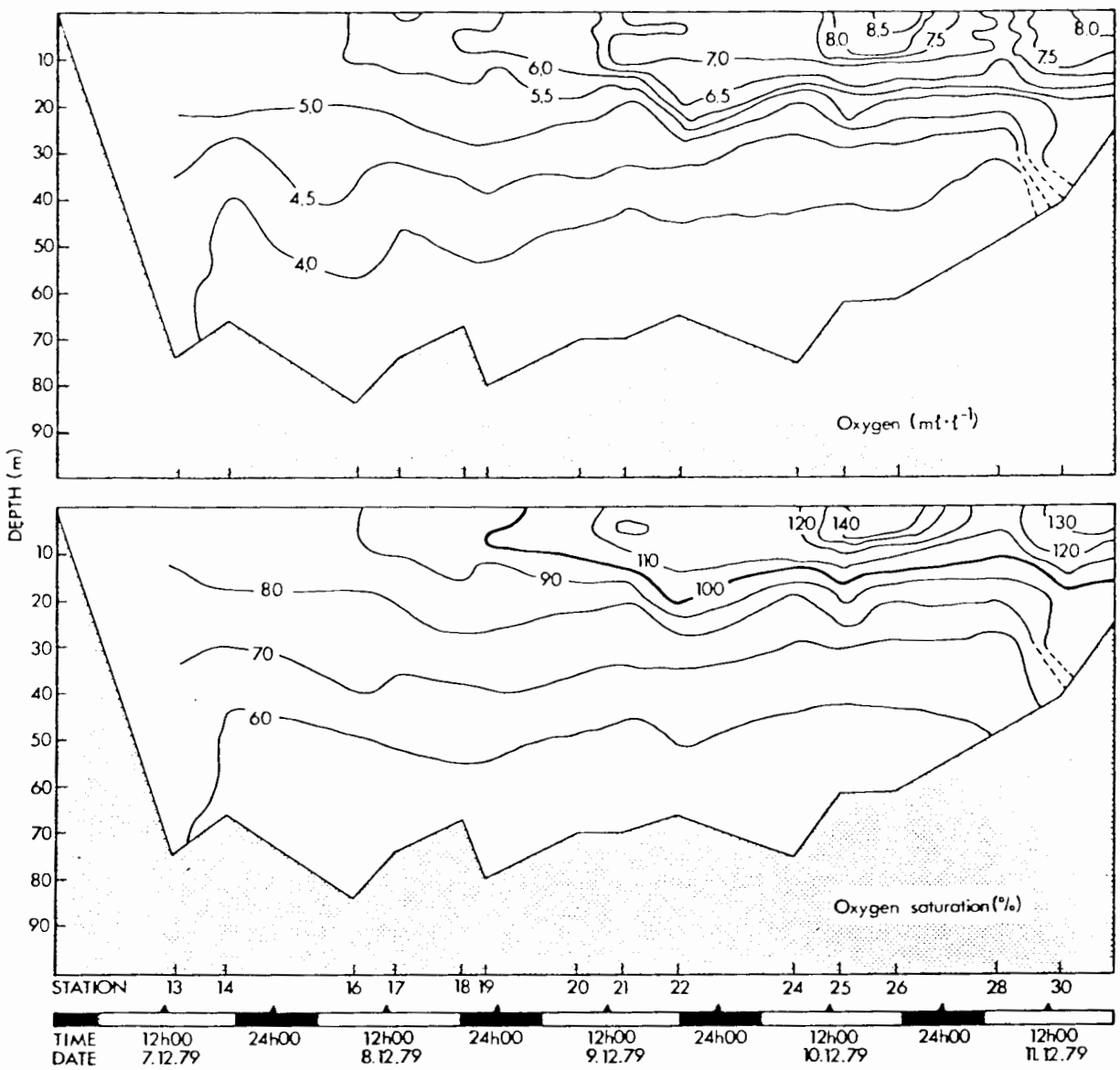

Fig. 12: Vertical distribution of dissolved oxygen and oxygen saturation

increasing to >140 per cent at Stations 23—26 before decreasing slightly. The 100-per-cent saturation contour appeared initially at the surface at Station 18 (Day 2) and attained a depth of 20 m on Day 3, after which it remained fairly constant. Below the thermocline the oxygen content decreased rapidly, and below 50 m the water was <60-per-cent saturated.

Phases of development

The water masses along the drogue transect have been conveniently characterized into two developmental phases.

Phase I (Stations 13–25, Days 1–3) — At the start of

Phase I cool, nutrient-rich water was at the surface. This upwelled water was characterized by a low surface temperature (10,84°C), a low salinity (34,75‰) and a relatively high density (σt = 26,63). The water column was uniformly mixed and rich in nutrients. High concentrations were observed initially at the surface (20,68 μg at. $NO_3 \cdot \ell^{-1}$, 2,29 μg at. $PO_4 \cdot \ell^{-1}$, 11,61 μg at. $SiO_3 \cdot \ell^{-1}$). Light was non-limiting during the initial stage, as was shown by the existence of a deep euphotic zone.

In terms of the survival requirements of the phytoplankton, the growth conditions were optimal. However, the phytoplankton standing stock (taking chlorophyll *a* as a measure of biomass) was low for the first 12 hours, suggesting an apparent growth lag. Inspection of the daily growth rates denied the existence of a growth lag period. A growth rate of $4{,}41 \times 10^3$ cells $\cdot \ell^{-1} \cdot day^{-1}$ was detected at the surface between Days 1 and 2, which was not evident from changes in the level of chlorophyll *a* (because of the very low numbers of cells present in the water column). Barber *et al.* (1971) have shown planktonic diatoms to undergo a lag period of 2—4 days in freshly upwelled waters off Peru. This lag period was associated with a lack of prior conditioning of the water, based on their hypothesis that growth-enhancing compounds are synthesized by the phytoplankton and released in the upwelled waters. A lag period in growth was not detected in this survey, but it may well have taken place prior to sampling. (Upwelling occurred off Oudekraal on 5 December — Drogue Track I — and sampling commenced two days later on 7 December — Drogue Track II.)

As the waters progressed northwards, the effect of surface heating increased surface temperatures, stabilizing the water column by increasing the surface buoyancy in the upper mixed layer. Evidence of this could be seen from a deepening of the 26,6 isopycnal from the surface at Station 14, to 15 m at Station 20. Light became limiting as the euphotic zone became shallower and the phytoplankton was mixed below the 1-per-cent light level. The phytoplankton stock showed an increase of 18,8 $\mu g \cdot \ell^{-1}$ of chlorophyll *a* up to Day 4. This rapid increase compares favourably with the increase of 11,9 $\mu g \cdot \ell^{-1}$ in 2,5 days found by Ryther *et al.* (1971) in coastal waters off Peru, where a similar drogue study was performed. A decrease in nutrient concentration concomitant with an increase in oxygen concentration was also observed over this period. Nitrates and silicates were taken up at a faster rate than phosphates. This agrees with the results obtained by Andrews and Hutchings (1980), who studied the rate of uptake of these nutrients by phytoplankton in local waters.

Table V. Grouping of species according to similar vertical distributions in respect of light, and the cell characteristics

Species group type	Species	Cell characteristic			
		Size	Trend	Shape	Trend
Group 1 (within euphotic zone)	*Chaetoceros brevis*	I	I=L	C	C>T
	Chaetoceros teres	I		C	
	Chaetoceros affinis	I		C	
	Chaetoceros subsecundus	I		C	
	Chaetoceros glandazi	I		C	
	Hemiaulus hauckii	I		C	
	Chaetoceros gracilis	I		C	
	Chaetoceros constrictus	I		C	
	Chaetoceros laciniosus	I		C	
	Asterionella japonica	I		C	
	Hemiaulus sinensis	I		C	
	Chaetoceros didymus	I		C	
	Lauderia punctata	S		C	
	Chaetoceros decipiens	L		C	
	Chaetoceros lorenzianus	L		C	
	Cerataulina bergonii	L		C	
	Eucampia zoodiacus	L		C	
	Skeletonema costatum	S-L		C	
	Chaetoceros compressus	S-L		C	
	Chaetoceros debilis	S		C	
	Navicula sp.	S		T	
	Nitzschia longissima	S		T	
	Nitzschia pacifica	S		T	
	Rhizosolenia delicatula	S		T	
	Thalassiothrix spp.	I		T	
	Nitzschia pungens	I		T	
	Rhizosolenia fragilissima	L		T	
	Nitzschia seriata	L		T	
	Rhizosolenia stolterfothii	L		T	
	Thalassiosira rotula	L		D	
	Thalassiosira aestivalis	L		D	
	Thalassiosira decipiens	L		D	
	Ciliate spp. •	L		S	
	Dinoflagellate sp. 1 •	L		S	
	Dinoflagellate sp. 2 •	L		S	
Group 2 (below euphotic zone)	*Thalassiothrix frauenfeldii*	I	D>L	T	T>C
	Thalassionema nitzschioides	I		T	
	Pleurosigma directum	I		T	
	Rhizosolenia setigera	I		T	
	Rhizosolenia imbricata	L		T	
	Bacteriastrum delicatulum	I		C	
	Lauderia borealis	I		C	
	Ditylum brightwellii	L		C	
Group 3 (above & below euphotic zone)	*Nitzschia delicatissima*	S	L	T	—
	Rhizosolenia alata	L		T	
	Coscinodiscus spp.	L		D	
	Corethron criophilum	L		C	
	Tintinnid spp.•	L			
	Peridinium sp.•	L		S	

Key: S = small
I = intermediate
L = large
• = non-diatom species
T = threadlike
D = discoid
C = cylindrical
S = spherical

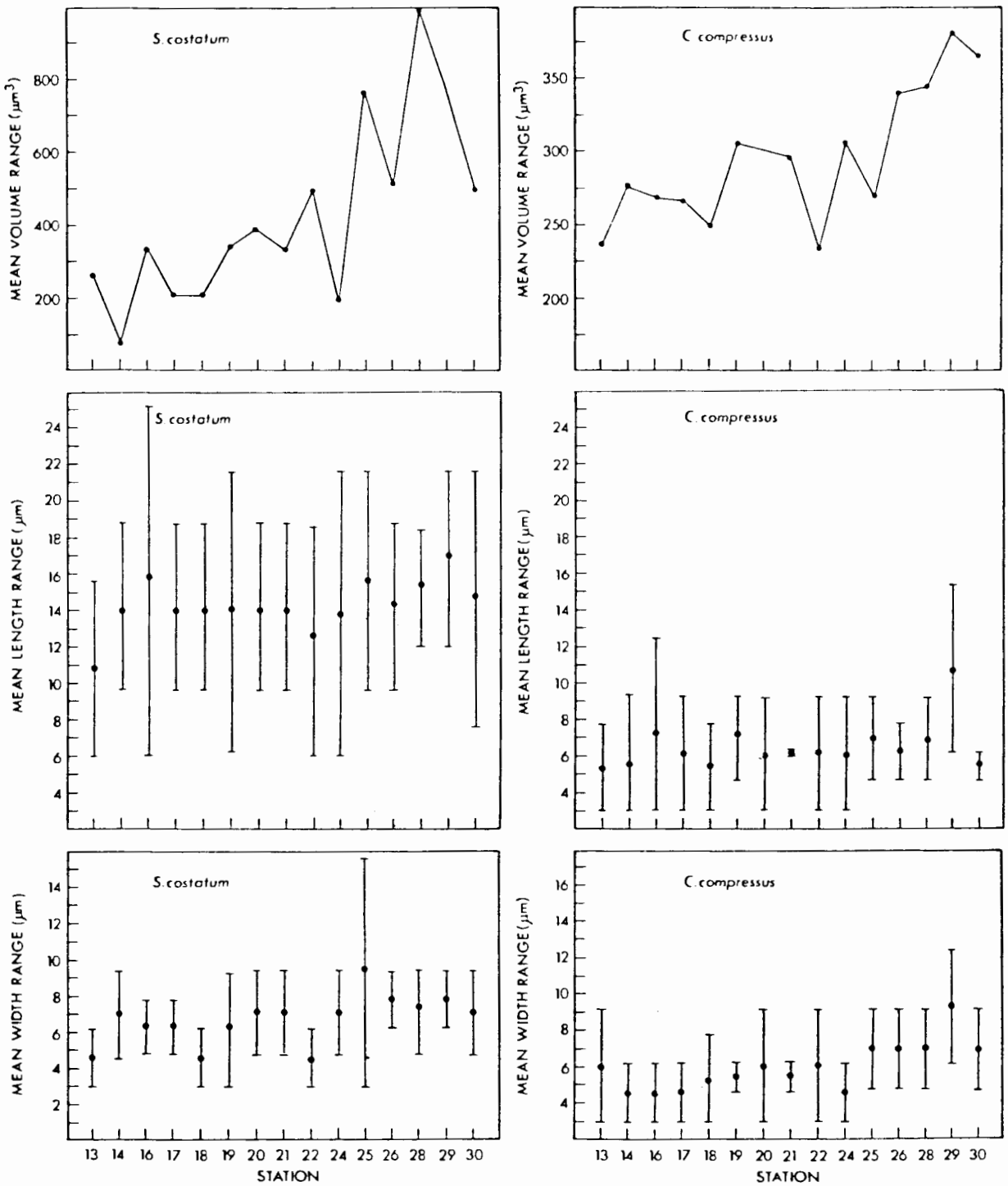

Fig. 13: Changes in mean volume, mean length and mean width of *Skeletonema costatum* and *Chaetoceros compressus* at each station over the five-day survey period

Table VI. Rank order of species in respect of total abundance (total cell count $\times 10^3 \cdot \ell^{-1}$ of all samples)

Group	Order	Species
1	1	*Chaetoceros compressus*
	2	*Skeletonema costatum*
	3	*Chaetoceros debilis*
2	4	*Nitzschia pungens*
	5	*Asterionella japonica*
	6	*Thalassiosira aestivalis*
	7	*Navicula* sp.
	8	*Chaetoceros laciniosus*
	9	*Nitzschia seriata*
	10	*Chaetoceros constrictus*
	11	*Hemiaulus hauckii*
	12	*Rhizosolenia fragilissima*
	13	*Thalassiosira decipiens*
	14	*Nitzschia longissima*
	15	*Cerataulina bergonii*
	16	*Chaetoceros lorenzianus*
	17	*Chaetoceros didymus*
	18	*Lauderia punctata*
	19	*Chaetoceros affinis*
	20	*Chaetoceros decipiens*
	21	*Rhizosolenia stolterfothii*
	22	*Hemiaulus sinensis*
3	23	*Eucampia zoodiacus*
	24	*Nitzschia delicatissima*
	25	*Nitzschia pacifica*
	26	Tintinnid spp.
	27	*Chaetoceros teres*
	28	*Coscinodiscus* spp.
	29	*Chaetoceros subsecundus*
	30	*Rhizosolenia delicatula*
	31	*Chaetoceros gracilis*
	32	*Corethron criophilum*
4	33	*Chaetoceros glandazi*
	34	*Peridinium* sp.
	35	*Rhizosolenia alata*
	36	*Lauderia borealis*
	37	Ciliate spp.
	38	Dinoflagellate sp. 1
	39	*Thalassiothrix* spp.
	40	*Chaetoceros brevis*
	41	*Bacteriastrum delicatulum*
	42	*Thalassiosira rotula*
	43	*Thalassiothrix frauenfeldii*
	44	*Rhizosolenia imbricata*
	45	Dinoflagellate sp. 2
	46	*Rhizosolenia setigera*
	47	*Pleurosigma directum*
	48	*Thalassionema nitzschioides*
	49	*Ditylum brightwellii*

Phase II (Stations 25–30, Days 3–5) – Decreases in surface temperature and in the phytoplankton standing stock, and increases in the concentration of inorganic nitrate, suggested that the body of water was being mixed with inshore, less mature water. Losses in the phytoplankton population were therefore the result of mixing of different water bodies. Evidence that the phytoplankton population was entering a stationary phase at the end of Day 4 was shown by the depletion of nutrients at the surface and within the shallow euphotic zone. Growth had slowed down, as was evident from the reduced growth rates just before the end of Day 4. A senescent phase was not reached during this survey.

Vertical distribution of species

The grouping of species according to similar vertical distributions of abundance, together with specific cell characteristics, appears in Table V. The vertical distributions of species were grouped for varying light levels. Seventy per cent of the species occurred within the euphotic zone, these species showing a higher proportion of cylindrical-shaped cells than threadlike cells. Conversely, the ratio of threadlike to cylindrical-shaped species increased below the euphotic zone. Group 3 contained species of most of the different shapes. No trend in cell size was displayed. *Skeletonema costatum* and *Chaetoceros compressus* occurred within the euphotic zone as small, intermediate and large cells throughout the survey. A 2,6-fold increase (328 — 857 μm^3) in cell volume of *S. costatum* took place between Stations 13 and 30, and a 2,5-fold increase (157—391 μm^3) in cell volume of *C. compressus* was observed at the same time (Fig. 13). These volumes refer to individual cells rather than to a mean, as given in the Figure.

Total abundance of species

In the 113 samples analysed, 49 species were identified. They are listed in rank order in Table VI. The grouping of species according to total abundance is illustrated in Figure 14a. Only 6 per cent of the species were Group 1 (dominant species), 39 per cent were Group 2 (most common), 20 per cent were Group 3 (common) and 34 per cent were Group 4 (rare). The discovery that 94 per cent of the species were less abundant than 12 000 cells $\times 10^3 \cdot \ell^{-1}$, but that only 6 per cent were more abundant than 55 946 cells $\times 10^3 \cdot \ell^{-1}$ clearly indicates that *Skeletonema costatum*, *Chaetoceros compressus* and *C. debilis* (the Group 1 species) were dominant in respect of total abundance.

The total abundance of species at each station and relative changes in species composition along the drogue track at approximately 10 m (drogue depth) are illustrated in Figure 14b. Samples at this depth

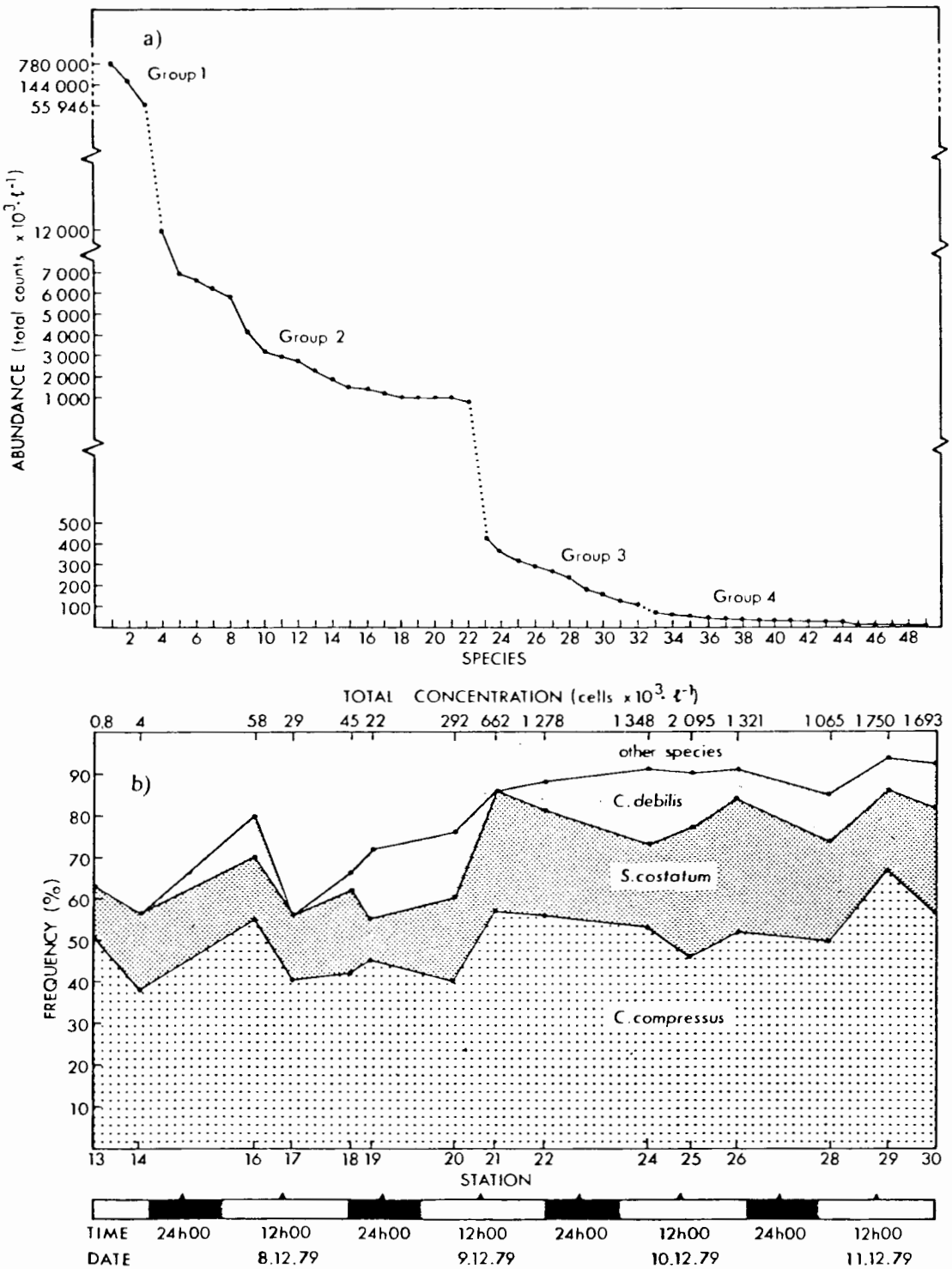

Fig. 14: a) Species total abundance; b) changes in species composition and total cell concentration at approximately 10 m determined from counts made by inverted microscope

Table VII. Values of the daily instantaneous growth coefficient K (units as defined by Cowles 1977) calculated for *Chaetoceros compressus*, *C. debilis* and *Skeletonema costatum* from changes in the number of cells present N at 12h30 at a depth of 10 m

Species	N or K	Day (Station)				
		1(13)	2(17)	3(21)	4(25)	5(29)
C. compressus	N	0.4	12	381	972	1169
	K	3.4	3.5	0.94	0.19	
S. costatum	N	0.1	5	194	646	338
	K	3.9	3.7	1.2	-0.7	
C. debilis	N	—	6*	48#	270	145
	K	2.0	1.5	-0.6		

Values for Stations 16 (*) and 20 (#)
N measured in cells $\times 10^3 \cdot \ell^{-1}$
K measured in cells $\times 10^3 \cdot \ell^{-1} \cdot \text{day}^{-1}$

were shown to be dominated by the three species classified as Group 1 (dominant).

The growth rates of both *C. compressus* and *S. costatum* (Table VII) were particularly high between Days 1 and 3 but then decreased towards Day 5. *C. debilis* made its first appearance at 10 m on Day 2, when comparatively low growth rates were observed.

Species groups based on frequency of occurrence

The species occurring at the different stations along the drogue track are listed in Table VIII. The seeding population at Station 13 was made up of 21 species, 43 per cent of the total number of species recorded during the study. Of these, nine species (18 per cent of the total recorded) persisted abundantly throughout the course of the study. Therefore, change in the species composition relative to Station 13 (Table VIII) was mainly by addition of new species. It must be noted that the addition of new, though apparently scarce, species during the course of the study could have been underestimated at certain stations where smaller aliquots of concentrated samples were sedimented. On average, there was a 34-per-cent change in species diversity between adjacent stations (Table VIII). The greatest change in diversity was found between Stations 29 and 30 (52 per cent), and the least change between Stations 17 and 18 (13 per cent).

A dendrogram grouping of species according to the McConnaughey index (based on species presence or absence), is given in Figure 15. The dendrogram shows a tight grouping of 10 species (Group 1) at the 75-per-cent level of similarity. Nine species forming Group 2 (1) are associated with Group 1 at the 50-per-cent level of similarity. Five further small groups are also delineated at the 50-per-cent level, and 35 per cent of the species (Group 3) are linked below the 50-per-cent level of similarity.

Table IX shows the grouping of species according to the McConnaughey index, together with the total-abundance and vertical-abundance grouping of each species, the cell characteristics and the mean relative growth rates based on cell counts at 10 m over the five-day period.

Group 1 consisted of 20 per cent of the total number of species recorded. The most common species (from abundance groupings) were present in this group, with *Chaetoceros compressus*, *C. debilis* and *Skeletonema costatum* being the dominant species. In this group, the species that occurred most frequently throughout the study were also the most abundant. Species cell size and shape varied and all species were distributed within the euphotic zone. High relative rates of growth were observed for species of this group, particularly for the dominant species *C. compressus* and *S. costatum*.

Group 2 contained 44 per cent of the total species present, 18 per cent of which were in Group 2(1), 8 per cent were in Group 2(2) and 18 per cent were in Group 2(3). Species in Group 2 (1) were classified in Group 2 (most common) on the basis of total abundance and the fact that they occurred within the euphotic zone. Cell size was either intermediate or large, and their shape was variable. *Coscinodiscus* spp. and certain species of Tintinnidae were fairly uncommon though they were found throughout the water column. The relative growth rates of all Group 2 species except *Rhizosolenia stolterfothii* H. Péra were lower than those of species in Group 1. The growth rate of *R. stolterfothii* (3,69 cells $\times 10^3 \cdot \ell^{-1} \cdot \text{day}^{-1}$) was higher than the growth rates of even the dominant species of Group 1. Species in Group 2(2) were fairly uncommon, small and threadlike, and were found within the euphotic zone. A large, spherical dinoflagellate (species 2) was present, but rare. Species in Groups 2(3) were classified as such either because they were most common and within the euphotic zone, or because they were rare and below the euphotic zone or throughout the water column. Cells were mostly intermediate and large, and cylindrical more often than threadlike. *Chaetoceros teres* Cleve had a very high rate of growth.

Group 3 had 35 per cent of the total species recorded. Most species belonging to this group were

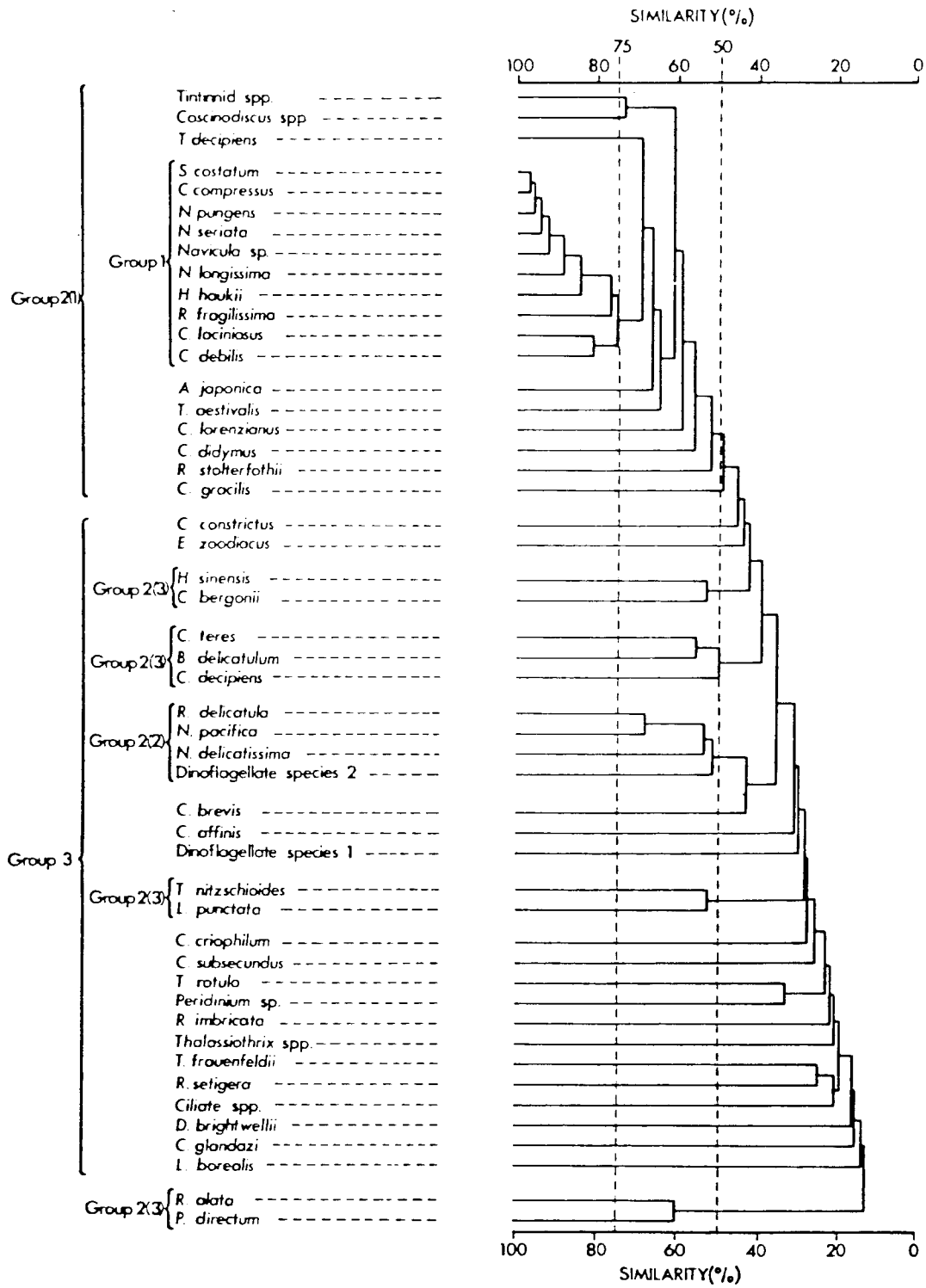

Fig. 15: Dendrogram showing species grouping according to the McConnaughey index

Table VIII. Occurrence of species at different stations

Species		Station														
		13	14	16	17	18	19	20	21	22	24	25	26	28	29	30
Skeletonema costatum		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Nitzschia seriata		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Nitzschia pungens		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Nitzschia longissima		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Navicula sp.	38%	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Hemiaulus haukii	38%	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Chaetoceros compressus	43%	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Chaetoceros didymus	43%	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Chaetoceros debilis	43%	X		X	X	X	X	X	X	X	X	X	X	X	X	X
Coscinodiscus spp.		X	X	X	X	X	X	X	X	X	X	X	X	X	X	
Rhizosolenia fragilissima		X	X	X	X	X	X	X	X	X	X	X	X	X	X	
Eucampia zoodiacus		X	X	X		X		X	X	X	X	X	X	X	X	X
Thalassiosira decipiens		X	X	X	X	X	X	X	X			X	X	X	X	X
Tintinnid spp.		X	X	X	X	X	X	X	X	X	X	X	X	X		
Peridinium sp.		X	X		X	X			X		X	X	X		X	
Nitzschia pacifica		X	X	X	X	X	X	X	X	X	X					
Nitzschia delicatissima		X	X	X	X	X	X	X				X		X		X
Rhizosolenia delicatula		X	X	X	X	X	X	X	X	X						
Corethron criophilum		X						X			X	X		X	X	X
Dinoflagellate sp. 1		X			X	X				X					X	
Dinoflagellate sp. 2		X	X	X			X									
Chaetoceros gracilis			X	X	X	X	X	X	X	X	X	X	X	X		
Chaetoceros lorenzianus			X		X	X		X	X	X	X	X	X	X	X	X
Rhizosolenia imbricata			X						X	X	X	X				
Rhizosolenia setigera			X				X		X	X						
Thalassiosira rotula			X	X		X										
Chaetoceros laciniosus				X	X	X	X	X	X	X	X	X	X	X	X	X
Chaetoceros constrictus				X			X	X	X	X	X	X	X	X	X	X
Chaetoceros brevis				X	X	X	X									
Asterionella japonica					X	X	X	X	X	X	X	X	X	X	X	X

(Continued overleaf)

Table VIII (*Continued*)

Species	Station														
	13	14	16	17	18	19	20	21	22	24	25	26	28	29	39
Chaetoceros decipiens				X	X	X	X	X	X	X	X	X	X	X	X
Rhizosolenia stolterfothii				X	X	X	X	X	X	X	X	X	X	X	X
Cerataulina bergonii				X	X	X	X			X	X	X	X		
Chaetoceros teres				X	X	X	X		X	X	X	X		X	
Lauderia punctata					X	X	X	X	X	X	X			X	X
Ciliate spp.					X				X		X	X			
Chaetoceros affinis						X	X	X	X		X	X	X		X
Rhizosolenia alata						X	X			X	X			X	
Thalassiothrix frauenfeldii						X				X			X	X	
Chaetoceros subsecundus							X		X					X	
Ditylum brightwellii							X								
Thalassiosira aestivalis								X	X	X	X	X	X	X	X
Hemiaulus sinensis									X		X	X	X	X	X
Thalassiothrix spp.									X			X		X	
Chaetoceros glandazi									X						
Thalassionema nitzschioides										X					
Bacteriastrum delicatulum											X			X	
Lauderia borealis												X			
Pleurosigma directum														X	
Change of species with respect to station 13															
Total species	21	23	23	27	31	31	32	29	34	31	34	31	28	31	23
"New" species added	21	5	5	9	12	14	14	12	18	15	17	16	12	15	10
Species "lost"	—	3	3	3	2	4	3	4	5	5	4	6	5	5	8
Change by number	—	8	8	12	14	18	17	16	23	20	21	22	17	20	18
Change (%)	—	35	35	44	45	58	53	55	68	64	62	71	61	65	78
Change of species from station to station															
Total species	21	23	23	27	31	31	32	29	34	31	34	31	28	31	23
"New" species added	21	5	4	8	4	6	5	3	6	6	6	3	2	9	2
Species "lost"	—	3	4	4	0	0	4	7	1	9	3	6	4	6	10
Change by number	—	8	8	12	4	12	9	10	7	15	9	9	6	15	12
Change (%)	—	35	35	44	13	38	28	35	21	48	27	29	21	48	52

Table IX: Grouping of species according to the McConnaughey index, total abundance and vertical distribution the cell characteristics and relative growth rates over the five-day survey period

Species group type		Species	Total abundance grouping	Vertical distribution grouping	Cell characteristic				Mean relative growth rate at 10 m (cells $> 10^3$ l^{-1} day^{-1})
					Size	Trend	Shape	Trend	
Group 1 >75% (PSI)		*Skeletonema costatum*	1	1	S-L		C		2,03
		Chaetoceros compressus	1	1	S-L		C		2,00
		Nitzschia pungens	2	1	I		T		1,00
		Nitzschia seriata	2	1	L		T		1,27
		Navicula sp.	2	1	S		T		1,46
		Nitzschia longissima	2	1	S	—	T	—	1,03
		Hemiaulus hauckii	2	1	I		C		0,29
		Rhizosolenia fragillissima	2	1	L		T		1,09
		Chaetoceros laciniosus	2	1	I		C		1,06
		Chaetoceros debilis	1	1	S		C		1,11
Group 2 50—75% (PSI)	(1)	• Tintinnid spp.	3	3	L		—		0,79
		Coscinodiscus spp.	3	3	L		D		1,30
		Thalassiosira decipiens	2	1	L		D		0,72
		Asterionella japonica	2	1	I		C		1,04
		Thalassiosira aestivalis	2	1	L	I=L	D	—	0,23
		Chaetoceros lorenzianus	2	1	L		C		0,39
		Chaetoceros didymus	2	1	I		C		1,10
		Rhizosolenia stolterfothii	2	1	L		T		3,69
		Chaetoceros gracilis	3	1	I		C		1,61
	(2)	*Rhizosolenia delicatula*	3	1	S		T		—
		Nitzschia pacifica	3	1	S	S	T	T	—
		Nitzschia delicatissima	3	3	S		T		1,87
		• Dinoflagellate sp.2	4	1	L		S		—
	(3)	*Chaetoceros teres*	3	1	I		C		3,19
		Bacteriastrum delicatulum	4	2	I		C		—
		Chaetoceros decipiens	2	1	L		C		—
		Hemialus sinensis	2	1	I		C		1,53
		Cerataulina bergonii	2	1	L	I>L	C	C>T	0,74
		Thalassionema nitzschioides	4	2	I		T		—
		Lauderia punctata	2	1	S		C		—
		Rhizosolenia alata	4	3	L		T		—
		Pleurosigma directum	4	2	I		T		—
Group 3 <50% (PSI)		*Chaetoceros constrictus*	2	1	I		C		0,58
		Eucampia zoodiacus	3	1	L		C		—
		Chaetoceros brevis	4	1	I		C		—
		Chaetoceros affinis	2	1	I		C		0,43
		• Dinoflagellate sp.1	4	1	L		S		—
		Corethron criophilum	3	3	L		C		—
		Chaetoceros subsecundus	3	1	I		C		—
		Thalassiosira rotula	4	1	L	I=L	D	—	—
		• Peridinium sp.	4	3	L		S		0,75
		Rhizosolenia imbricata	4	2	L		T		—
		Thalassiothrix spp.	4	1	I		T		—
		Thalassiothrix frauenfeldii	4	2	I		T		—
		Rhizosolenia setigera	4	2	I		T		—
		• Ciliate sp.	4	1	L		S		—
		Ditylum brightwellii	4	2	L		C		—
		Chaetoceros glandazi	4	1	I		C		—
		Lauderia borealis	4	2	I		C		—

Key: S = small; I = intermediate; L = large; • = non-diatom species; T = threadlike; D = discoid; C = cylindrical; S = spherical

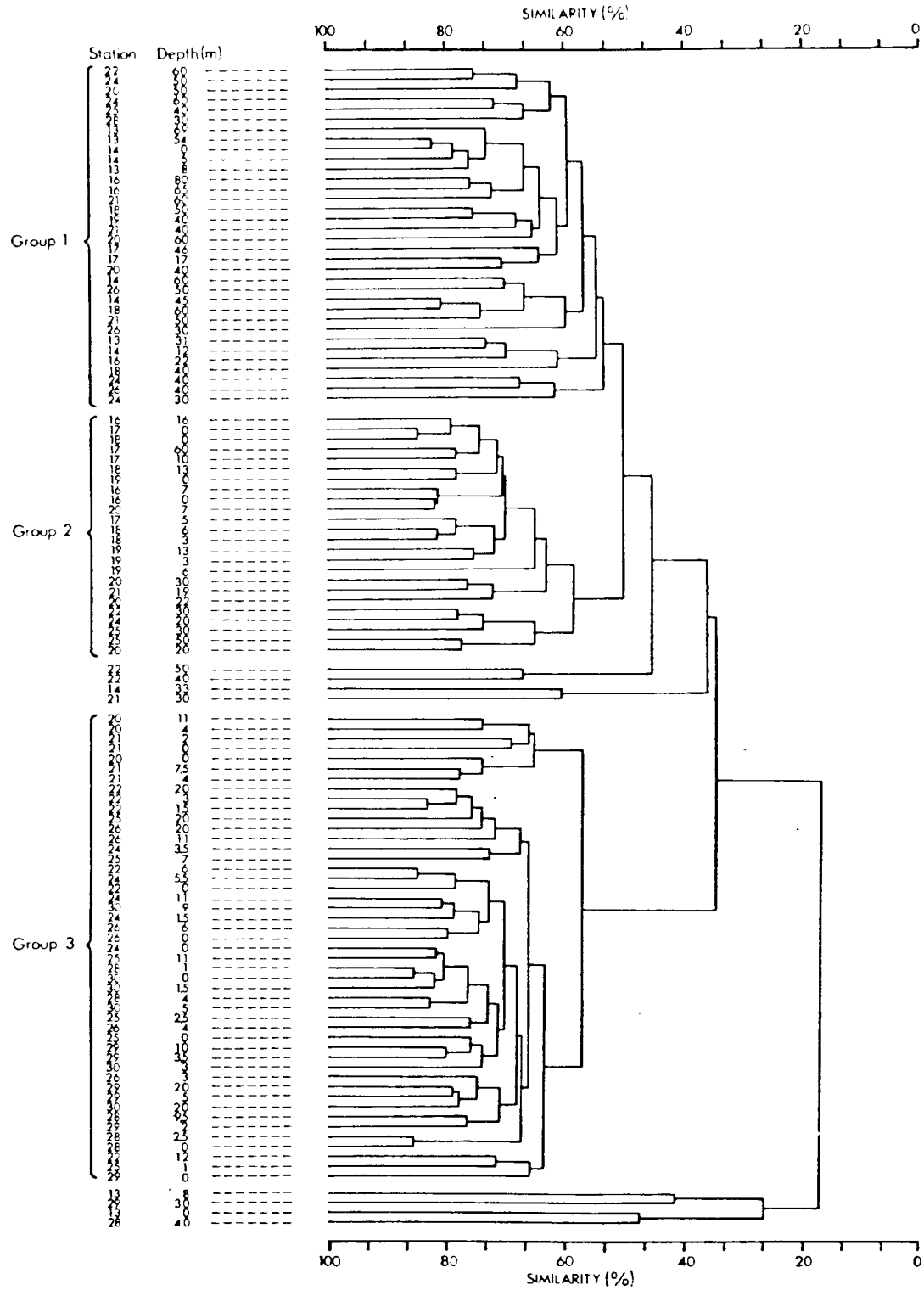

Fig. 16: Dendrogram showing the grouping of samples according to the Bray-Curtis coefficient

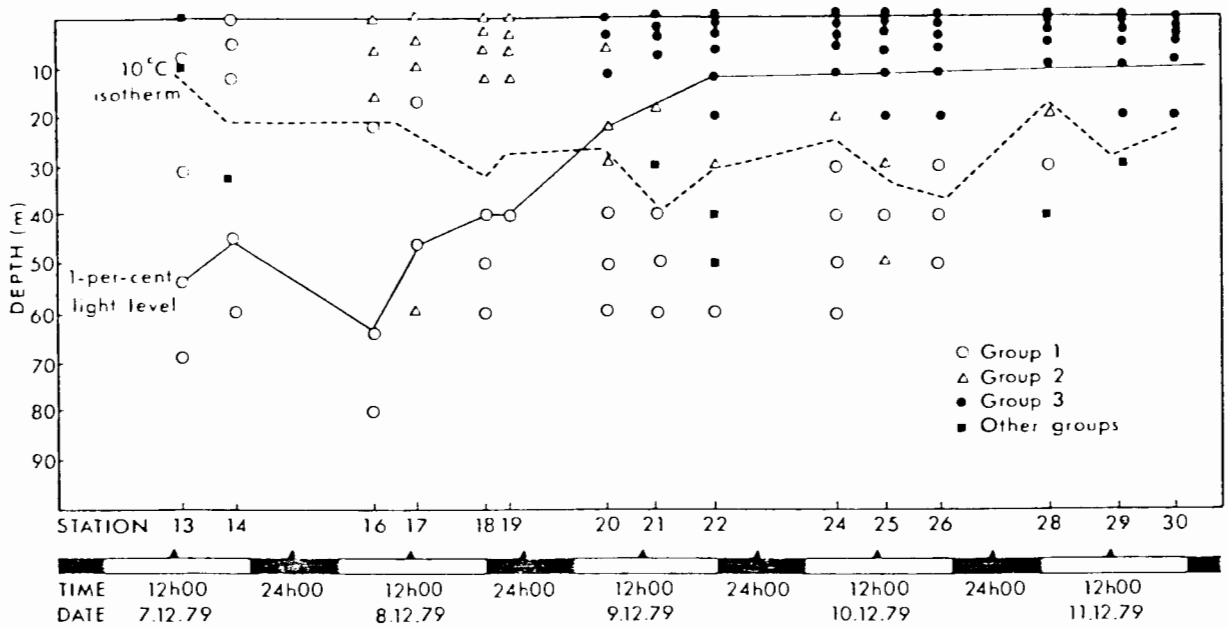

Fig 17: Distribution of sample groups derived from the Bray-Curtis coefficient

rare, and they occurred either within or below the euphotic zone. Cell size was either intermediate or large and shapes were highly variable. *Chaetoceros constrictus* Gran and *Chaetoceros affinis* Laud., two fairly common cylindrical species of intermediate size, were confined to the euphotic zone. Their relative rates of growth were low.

In summary, no clear trend of cell characteristics could be linked to any of the three groups.

Sample groups based on species and cell concentrations

Inspection of the dendrogram according to the Bray-Curtis coefficient (Clifford and Stephenson 1975) showed the delineation of three distinctive groups at the 50-per-cent similarity level (Fig. 16). The grouping of samples by this abundance-weighted technique was strongly biased towards the grouping of samples with similar cell concentrations rather than towards similar species, despite the fact that the cell concentrations were log-transformed (Barnes 1952; Field 1970, 1971; Field and Robb 1970). The reason for this finding was that the species grouping obtained with the McConnaughey index was rather weak, i.e. it was only possible to isolate a single group at the 75-per-cent level of similarity. An information statistic could not, therefore, be applied. By contrast, Hutchings (1979) found very distinct groupings when he sampled zooplankton species from a wide variety of water masses. A homogenous sample grouping in the uniform conditions prevalent in the St Helena Bay area was found by S. Hopson (formerly Sea Fisheries Research Institute, personal communication) on the basis of analysis of zooplankton species.

The grouping of sample abundance relative to stations is summarized on Figure 17.

Group 1 — This group was characterized by samples throughout the water column in the initial stages of Phase I, i.e. at Stations 13 and 14, then well below the euphotic and mixed-layer zone between Stations 16 and 30. Abundance expressed as concentration (cells $\cdot \ell^{-1}$) was low for this group. Samples taken at the early stations, as seeding was taking place, had low cell concentrations, and species occurring in samples below the euphotic zone (at the later stations) were inhibited by low light levels. It would appear that the seeding population was composed of similar species to those occurring in the dysphotic depths north of the upwelling site.

Group 2 — This group represented a transition from low cell concentrations, as found in the initial stages of Phase I, to high cell concentrations, as found in the later stages of Phase I. Samples were all derived from waters above the upper mixed layer. In the initial stages, the samples came from within the euphotic zone, whereas in the later stages they were derived from below that zone, often near the bottom of the

upper mixed layer.

Group 3 — Most of the samples of this group were found within the euphotic zone in the later stages of Phase I and in Phase II. The samples were characterized by high cell concentrations.

DISCUSSION

An increase in cell size of both *Chaetoceros compressus* and *Skeletonema costatum* was observed when progressing from Phase I to Phase II of the drogue study. This progressive change was interpreted as an adaptive mechanism for the survival and maintenance of these species in the changing environment. There are two apparently divergent views on the question of environmental control over cell size (Hecky and Kilham 1974). Data from the present survey cannot be said to support either viewpoint.

(i) The "nutrient" view (Parsons and Takahashi 1973) simply suggests that the ambient nutrient concentrations determine ratios of cell surface : volume. Thus large cells are succeeded by small cells as nutrients diminish. This view is based entirely on the relationships between cell size and uptake and growth rates observed in laboratory cultures, mainly from the work of Eppley *et al.* (1969) and Eppley and Thomas (1969). Parsons and Takahashi *(op. cit.)* have used these relationships to explain the seasonal succession in the cell size of coastal phytoplankton.

(ii) The "physical" view (Semina 1972, Semina *et al.* 1976) suggests that the mean cell size of a phytoplankton population depends on the velocity of vertical water movement and on the density gradient of the pycnocline (i.e. the role of the hydrodynamic forces is emphasized, with large cells occurring under turbulent conditions and small cells under stable conditions). Hecky and Kilham (1974) expressed the opinion that the inherent kinetics of nutrient absorption and the sinking rates of different types of cells are important.

Growth and nutrient uptake

The small size of cells in the newly upwelled waters was assumed (based on the experimental evidence of Findlay 1972, Fogg 1965 and Friebele *et al.* 1978) to profoundly enhance their rates of growth and nutrient absorption. In general, the species that grow most rapidly and that utilize high concentrations of nutrients are small, with a high ratio of surface : volume. Maintenance of these species in this initially turbulent environment depends on their intrinsic multiplication rates. As mentioned earlier, these dominant species grew faster in the newly upwelled waters of Days 1 and 2 than when average cell size had increased and the water column had begun to stabilize (Days 3—5). These dominants have already been shown to have high mean rates of growth when compared with the mean rates of growth of other species at 10 m (see Table IX). Their high growth rates resulted in the dominants selectively out-competing other species.

Findlay (1972) has shown that the relative growth rate of *Coscinodiscus* increases with increasing surface : volume ratio. He has shown, in effect, that the rate of division is a good indication of the rate of nutrient absorption as determined by surface : volume ratio. This finding confirmed Fogg's (1965) view that size is generally most important, because it determines the ratio of surface : volume and therefore the relative rate of nutrient intake for growth. The initially high ratio between surface and volume in the dominant species resulted in faster division rates, which in turn accounted for their selection and dominance over the other species.

The nutrient-rich upwelled waters would therefore favour species with small cell size and high intrinsic uptake and growth rate. Although the dominants possess high rates of division, they may catabolize a larger fraction of their biomass than larger-celled species. Laws (1975) has shown that large unicellular diatoms have a lower respiratory catabolism than smaller-celled species.

As the upwelled waters aged, cell size increased and surface : volume ratio decreased. The implications are that these cells have relatively lower rates of nutrient absorption in an environment where nutrients are being depleted. Dugdale (1967) and others have shown that phytoplankton species differ in their ability to absorb nutrients. Eppley and Thomas (1969) compared the half-saturation constant (K_s) of the coastal diatom *Asterionella japonica* with that of *Chaetoceros gracilis* from the open sea. They showed the coastal species to possess a higher K_s value for nitrate uptake than the open-sea species.

Carpenter and Guillard (1971) have shown that physiological races of marine phytoplankton are adapted to either high or low levels of nutrients. Species succession may well be controlled by these specific differences and by the temporal changes in nutrient concentrations. Although the nutrient concentrations were rapidly depleted during this study, it is unlikely that nutrients ever became limiting for a sufficiently long period of time to affect any selection.

The succession of species with lower K_s values could possibly occur at a later stage when nutrient conditions would be limiting for the dominant species.

The fact that species also have different abilities to store non-limiting nutrients must also be considered. Different concentrations of internal pools of nutrients can determine the outcome of competition for nutrients (Davis *et al.* 1978). It is quite possible that *Chaetoceros compressus*, *C. debilis* and *Skeletonema costatum* were able to store sufficient nutrients during the initial stages of the drogue study, when nutrients were abundant, to support much of their growth in the later stages when nutrient concentration had decreased considerably. The actual competition could, therefore, have taken place during the early stages of the study, prior to the reduction in concentration of nutrients. Harrison *et al.* (1977) demonstrated a significant increase in the ratio of surface : volume for *S. costatum* and *C. debilis* in response to nutrient limitation. Their finding is not supported by that for the large cells taken in the later stages of the present study, although the nutrient conditions could not actually be defined as limiting.

Buoyancy

The large cells of the dominant species during the later stages of the study would have had problems in remaining at a stable position in the water column. An increase in cell size without any special modification has been considered by Smayda (1970) to somehow represent a positive adaptation to flotation. Morphological features of the cells, such as size, shape, colony-forming ability and protuberances are all thought to affect form resistance and to influence buoyancy.

According to Munk and Riley (1952), the rate of sinking accelerates with increasing cell size but is not uniform for cells of different shapes. The following shapes are given in order of decreasing sinking rate for particles of different sizes:

decreasing →

5 μm in diameter: plate > cylinder > sphere
50 μm in diameter: cylinder > plate > sphere
500 μm in diameter: cylinder > sphere > plate.

↑ decreasing

Application of these criteria to the species found during this drogue study would suggest that the medium-large cylindrical cells of the dominant species would sink less rapidly than the plate-shaped or even threadlike cells, e.g. *Nitzschia* spp.

The dominant species are all chain-forming diatoms, and the ecological implications thereof are still poorly understood (Smayda 1970). The formation of chains generally increases the rate of sinking because of the accompanying reduction in relative surface area. However, Smayda and Boleyn (1965) showed that chain formation in *Skeletonema costatum* did not increase its rate of sinking. They considered the numerous silicon rods interconnecting the cells to be responsible for increases in micro-turbulent conditions between and near the rods, resulting in an increase in frictional drag and a decrease in sinking rate.

Cell protuberances are traditionally viewed as positive traits for suspension, but silica-bearing setae, such as found in *Chaetoceros* spp., increase the density of the cell and hence the sinking rate. On the other hand, the setae of *Chaetoceros* and horns of *Ceratium* spp. are assumed to increase the absorptive surface of the cell (Margalef 1978).

The physiological regulation of cell density is also an effective means of modifying the suspension of phytoplankton (Beklemishev *et al.* 1961). They suggest that buoyancy could be controlled by the regulation of the ionic composition of the cell sap by the exclusion of heavier divalent ions. The importance of vacuole size (ratio of vacuole : total cell size) has also been considered to be a means of flotation (Gross and Zeuthen 1948).

Other physiological mechanisms, such as light and photoperiod, have been shown to influence buoyancy. For example, Steele and Yentsch (1960) demonstrated that the sinking rate of *S. costatum* is lower in the dark.

The age and physiological state of cells in phytoplankton populations may also influence the sinking rate of cells. Tilman and Kilham (1976) have shown that, in lakes, *Asterionella* cells sink four times more rapidly during their stationary phase of growth than during their exponential phase. Eppley *et al.* (1967) also showed that cells with lower photosynthetic rates sink more rapidly than faster-growing phytoplankters.

There is also evidence that depletion of nutrients increases the sinking rate of *S. costatum* (Steele and Yentsch 1960). The practical advantage of increasing cell size and accelerating sinking rates of phytoplankton would be evident in an environment where surface nutrients were becoming depleted. In fact, phytoplankton losses from the euphotic zone were high during the later stages of this drogue study when more than two-thirds of the mixed layer was below the 1-per-cent light level. However, it is difficult to determine whether the loss of phytoplankton was the result solely of mixing (wind velocities increased slightly towards the later stages of the study) or also

of sinking by cells adapting morphologically or physiologically to the environment. If the loss of phytoplankton was caused by a lowered cell buoyancy, then this may have been due to increased cell size.

There is evidence at present to support the hypothesis that phytoplankton can grow and adapt to lower light levels in areas of high nutrient concentrations (Blasco and Packard 1974, Estrada 1974, Knoechal and Kalff 1978).

Adaptation to varying light levels

During the course of this study, the three dominant species were distributed within the euphotic zone. Initially the euphotic zone was deep, and turbulence (caused by upwelling) mixed the phytoplankton throughout the unstable water column. Under these conditions, the circulating phytoplankters were exposed to constantly changing light conditions. Presumably they had a special mechanism protecting them from photo-inhibition at high light levels. Certainly, Jørgensen (1964) showed that diatoms can tolerate being transferred from low to extremely high irradiances without showing signs of chlorophyll inactivation or a decrease in their photosynthetic rate.

Physiological adaptations to movement from one light intensity to another may be caused by cells changing either their content of photosynthetically active pigments or the enzymes involved in photosynthesis. Yentsch and Ryther (1959) showed that chlorophyll *a* content was highest in the early stages of succession, and Eppley (1980) found that the quantity of cellular pigment adjusted rapidly to changes in the quantity and quality of light. The ratio of carotenoids to chlorophyll *a* ($D_{430} : D_{665}$) has also been shown by Margalef (1967) to increase with succession, with lowest values being measured in the initially turbulent conditions. When progressing from the initial to the later stages of this drogue study, a decrease in the ratio of chlorophyll *a* : cell numbers was observed at the surface and at the lower depth limit of the mixed layer.

In addition to changes in pigment ratio and content, a change in the arrangement of the chloroplasts has been found in cells adapted to low light (Parsons *et al.* 1977). Adaptations by altering the morphology of the chloroplasts have been reported by Brown and Richardson (1968), who showed that the size of the chloroplasts in *Nitzschia* increased with increasing irradiance.

In the second half of the study the 1-per-cent light level was relatively close to the surface, and approximately two-thirds of the phytoplankton population was found below the euphotic zone where nutrients were more concentrated than in the surface waters. Under these conditions it would seem advantageous for the phytoplankters to adapt to low levels of irradiance. Because the cell concentrations remained constant (until the population was diluted by mixing with newly upwelled water on Day 5), it may be assumed that the dominant species were adapting to the reduced light levels. However, such light adaptation by the dominant species could only have been confirmed if the survey had continued for a few more days and a large sub-surface population of the same species developed.

There is considerable evidence to show that cells below the euphotic zone can adapt to lower light levels. For example, for the upwelling areas off Baja California and North-West Africa, Blasco and Packard (1974) showed (by measuring the distribution of nitrate reductase) that phytoplankters were able to assimilate nitrates in low light conditions when nitrates were unavailable in the euphotic zone. Estrada (1974) also showed that phytoplankton cells at deep levels were more efficient at utilizing dim light than those at the surface. Knoechel and Kalff (1978) showed that certain diatoms grew quite actively at deeper levels, where nutrient concentrations were high, by altering their P_{max} (maximum photosynthetic rate).

Studies on the physiological properties of dominant species need to be carried out in order to determine the relationships existing between nutrient uptake, light and water stability. An estimate of the physiological state of the dominants has been made by Barlow (1981). Decreases in their growth rates combined with increases in their cell sizes as the waters aged implied that, initially, the dominants possessed high absorption rates and could therefore grow actively. Nevertheless, because their specific growth rates decreased towards the later stages of the study, a stationary or slow-growing phase was evident. Barlow *(op. cit.)* showed that, during this phase (i.e. under low nutrient concentrations but relatively high light levels), the rate of protein production for the whole phytoplankton population decreased considerably concomitant with an increase in cellular reserves of polysaccharides. The advantage of large cells in a slow-growing phytoplankton population is therefore evident, particularly when the accumulation of polysaccharides and the conservation of intracellular nitrogen reserves takes place as a result of slower utilization of nutrients and slower respiratory catabolism.

Other factors possibly influencing species dominance

Diatom populations can modify their environment

by reducing the nutrient levels, or by altering light intensity by shading, selective absorption and reflection. They can also alter the chemistry of the water by way of exudates. Specific studies undertaken by Menzel and Ryther (1961) showed that iron was the effective compound of a trace-metal mixture responsible for increased phytoplankton production in the Sargasso Sea. Likewise Barber and Ryther (1969), performing enrichment experiments, showed that addition of a strong chelator or an undefined zooplankton extract could improve phytoplankton growth in nutrient-rich, newly upwelled water. The release of natural organic chelators by some organisms in the newly upwelled waters could well have been responsible for increased growth of the dominants at the start of the present study. Provasoli and Pintner (1953) showed that marine algae require vitamins, and that these vitamins are produced by microbes and some phytoplankton (Robbins 1951). The species-specific requirements for vitamins have not been determined for diatoms in local waters, but Provasoli (1963) has shown that specific vitamins can trigger the succession of species in temperate waters.

Temperature was shown by Goldman and Ryther (1976) to strongly influence the outcome of phytoplankton competition in mass cultures maintained on wastewater-seawater mixtures. Temperature races within marine species have been defined, i.e. clones of species isolated from different areas display different temperature optima (Eppley 1972). It would seem unlikely that the dominance of the three species could have been influenced by the small temperature differences that were observed during the survey.

Grazing, particularly size-selective feeding, is of particular importance in determining the fate of phytoplankton blooms and the course of successions (Riley 1963). Cushing (1964) pointed out that the control of diatom blooms in the North Sea could be attributed solely to grazing, and that the effect of nutrients was irrelevant. Munk and Riley (1952) have suggested that predation has triggered the development of dwarfism, gigantism, chain-forming, and diverse protuberance in phytoplankton as anti-predation devices. Strickland *et al.* (1969) have attributed low phytoplankton standing stocks in Peruvian waters to grazing by anchoveta. Preliminary studies on the losses from phytoplankton populations by zooplankton and pelagic fish grazing in local waters are at present being made at the Sea Fisheries Research Institute.

SUMMARY

A mixed bloom of phytoplankton containing 49 species developed with *Chaetoceros compressus*, *C. debilis* and *Skeletonema costatum* dominating in respect of abundance and occurrence. Certain survival strategies were employed by the dominants in order to successfully maintain their numbers in a changing environment. Their progressive increase in cell size as the waters aged is interpreted as an adaptive mechanism for their successful colonization and maintenance.

Small cells were shown to possess fast rates of growth. The dominants are assumed to have possessed high rates of absorption and a high respiratory catabolism in the initial stages of the survey, when light and nutrients were optimal for growth. As the waters aged the cell size of the dominant species increased, and therefore the rates of nutrient absorption decreased. The ability of the dominants to store non-limiting nutrients during the initial stages of the study is considered to be a possible adaptation to the diminishing concentrations of nutrients. The dominants are not thought to have adapted to these conditions by physiologically altering their capability of nutrient uptake.

Morphological features of the cells of the dominants, such as size, shape, colony-forming ability and protuberances are considered to affect form resistance and thus to influence their suspension in the water column. The medium-large cylindrical cells of the dominants are postulated to sink less rapidly than plate-shaped or threadlike cells. Phytoplankton losses from the euphotic zone were great, and the increase in cell size is considered to be a mechanism of adapting to low concentrations of surface nutrients by increasing the rate of sinking. Large size of cell during the slow-growing phase is regarded to be advantageous for the storage of intracellular nitrogen and the accumulation of polysaccharides.

The dominant species are assumed to have possessed a special mechanism of protection against photo-inhibition during the initial stages of the study, when the water column was unstable. The cells are thought to have adapted physiologically to changes in light intensity by, firstly, adjusting their pigment content and/or their enzymes involved in photosynthesis and, secondly, changing their morphology and/or arrangement of their chloroplasts. It is postulated that the dominant species possessed some ability to adjust their physiology to the decreasing light levels, in the second half of the study, because they maintained their dominance over the remaining species without evidence of a decline in cell concentration.

Other factors influencing species dominance were considered. The modification of the environment by way of exudates is seen as a possible strategy. The small temperature gradient is thought to have had no

effect on the dominance of the three species, but grazing is important in determining the course of succession.

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PAPER 6 - A DESCRIPTION OF THE HYDROGRAPHY AND PHYTO-PLANKTON COMMUNITIES IN THE UPWELLED WATERS OF THE CAPE PENINSULA, SOUTH AFRICA, SEPTEMBER 1972 - FEBRUARY 1973.

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A DESCRIPTION OF THE HYDROGRAPHY AND PHYTOPLANKTON COMMUNITIES IN THE UPWELLED WATERS OF THE CAPE PENINSULA, SOUTH AFRICA, SEPTEMBER 1972 — FEBRUARY 1973

E. T. OLIVIERI

Monthly changes in phytoplankton communities were assessed from a line of stations running along the apex of the normal position of the upwelling plume. Changes in the environment and certain community characteristics permitted a reconstruction of a series of successional events over a six-month period to be made. The width of the phytoplankton-rich zone was shown to vary according to changes in hydrography. The genus *Nitzschia* was shown to dominate over this period, although other investigators have shown different genera to have dominated at other times. Consistent phytoplankton distributions and succession of species were not apparent in this study. The factors responsible for successful colonization of the different species in the phytoplankton communities are likely to be the initial variations in species diversity and abundance of the seeded population in newly upwelled waters, the extent to which upwelled waters mix with neighbouring waters and the specific selective adaptations for growth of individual species.

Maandelikse veranderinge in fitoplanktongemeenskappe is beoordeel volgens 'n lyn stasies wat strek al langs die spits van die normale posisie van die opwellingspluim. Veranderinge in die omgewing en bepaalde gemeenskapskenmerke het 'n rekonstruksie van 'n reeks opeenvolgingsgebeurtenisse binne 'n tydperk van ses maande moontlik gemaak. Daar is bevind dat die wydte van die planktonryke sone wissel na gelang van veranderinge in hidrografie. Dit het geblyk dat die genus *Nitzschia* gedurende die tydperk van ses maande oorheers het, hoewel vorige navorsers aangetoon het dat ander genera op ander tye oorheers het. In hierdie studie was daar nie blyke van konsekwente verspreidings van fitoplankton en opeenvolging van fitoplanktonspesies nie. Die faktore wat verantwoordelik is vir suksesvolle kolonisasie van die verskillende spesies in die fitoplanktongemeenskappe is waarskynlik aanvanklike variasies in spesieverskeidenheid, die mate waarin opgewelde waters met naburige waters meng, en die spesifieke selektiewe aanpassings vir groei van afsonderlike spesies.

The Cape Peninsula upwelling system is primarily generated by the prevailing south-easterly winds, which cause newly upwelled water to move off shore and northwards to mix with aged upwelled water or oceanic water (Andrews and Hutchings 1980). A shallow, upper mixed layer is formed, ideal for phytoplankton development. The vertical stability of the water column and the nature of the source water are likely to be the critical factors responsible for the selective development of phytoplankton species, because the nutrients and light intensity change with time.

Margalef (1958, 1968) has summarized the literature dealing with plankton successions in different marine areas. More recently, Guillard and Kilham (1977) have slightly modified his successional stages and the following ecological trends are discernible:

(i) a general increase in cell size that implies a decrease in the ratio of surface area to volume;
(ii) a decrease in the maximum potential growth rate;
(iii) an increase in the occurrence of motile forms.

The major associated environmental changes are a decrease in turbulence, nutrient concentration and rate of nutrient supply and an increase in water temperature and usually salinity. Light quality and intensity may also be somewhat modified.

The aim of this study is to assess the monthly changes in phytoplankton communities from sampling a line of stations running along the successive apices of the normal position of the upwelling tongue. These serialized "snap-shots" have been used to provide a reconstruction of a series of successional events over a period of six months, without an absolute time scale for each transect (i.e. distance off shore is assumed to be equated with time).

Certain community characteristics, such as biomass and diversity, are investigated in conjunction with environmental changes. The main aim of the study was to determine whether consistent patterns of phytoplankton species succession exist in the southern Benguela Current. The significance of the initial species composition and abundance in newly upwelled waters as regards colonization and succession are discussed in relation to the origins of the source water.

MATERIALS AND METHODS

Cruise strategy

The cruises consisted of a line of up to 10 stations (Fig. 1) sampled at monthly intervals over a period of 30 months starting in October 1970. Stations 1 — 7 were 8 km apart and ran due north-west of Duiker Point. Stations 8, 9 and 10 were approximately 16 km apart and ran in a west-north-westerly direction. It

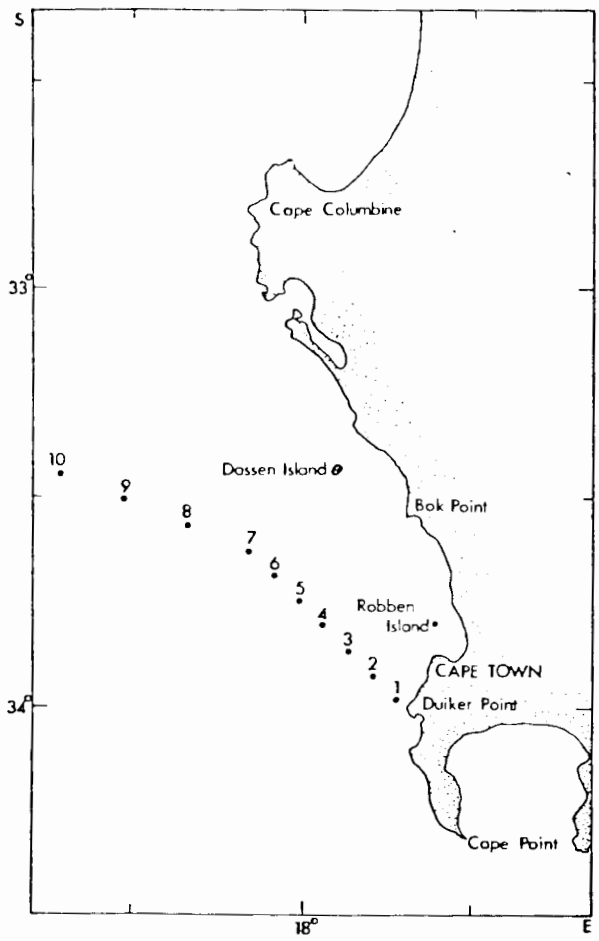

Fig. 1: The line of ten stations sampled monthly during the transect study

took two days to sample all stations, sampling proceeding from the inshore stations seawards. Six cruises, in future referred to as transects, one each month from September 1972 to February 1973 and covering one upwelling season, were selected for detailed analysis of phytoplankton species. Seasonal changes in the hydrography, chlorophyll *a*, nutrients and zooplankton are described by Andrews and Hutchings (1980).

Sample collection

Samples were taken at 10-m depth intervals to 60 m, then at 20-m intervals to 120 m, at 150 m and at 100-m intervals from 200 m to the bottom. The deepest sample was usually taken within 4 m of the bottom. Temperatures were measured by means of Nansen-Pettersson insulated water bottles at shallow depths and with Munro-Ekman reversing bottles at deeper levels. Samples for measuring salinity, oxygen, nutrients, chlorophyll and phytoplankton were collected in 7- or 5-ℓ I.O.S. bottles. Wind data were obtained from the Cape Point lighthouse, and wind speed and direction were also recorded from the research vessel. Submarine light levels were measured at Stations 3 and 6 with a photometer and a deck reference cell.

Processing of samples

Salinity samples were stored in glass bottles and analysed on an inductively coupled Autolab salinometer. Both standard Copenhagen and substandards were used for calibrations.

Oxygen samples were analysed on board by the classical Winkler technique. Mostert (1966) has described the basic reagents used in this analysis.

Water samples were filtered on board and stored at −20°C for later spectrophotometric analysis of chlorophyll *a*. Wavelengths and equations recommended by the SCOR/UNESCO Working Group 17 (1966) were used.

Samples for the determination of phosphate, silicate and nitrate were deep-frozen in 10-mℓ polythene bottles. Analyses were carried out ashore with a Technicon Autoanalyser, following the methods of Strickland and Parsons (1972) for phosphate and nitrate and of Grasshoff (1966) for silicate.

Preserved phytoplankton

Preserved phytoplankton samples were analysed by the Utermöhl (1936) method of sedimentation with an inverted microscope, but following the simplified procedure and recommendations of Willén (1976) and Hobro and Willén (1977). Estimates of precision were obtained by making six successive counts from one sample. The marginal error obtained for all six counts was 2,5 per cent at the 95-per-cent confidence level.

Samples were preserved in 4-per-cent formalin, and were counted after a period of seven years. The effects of long-term preservation on the cells were in some cases shown by losses of the intra-cellular content and by the formation of excessive detritus. Cellular degradation was assumed to have occurred when microscopic counts disagreed considerably with the measurements of chlorophyll *a*. Phytoplank-

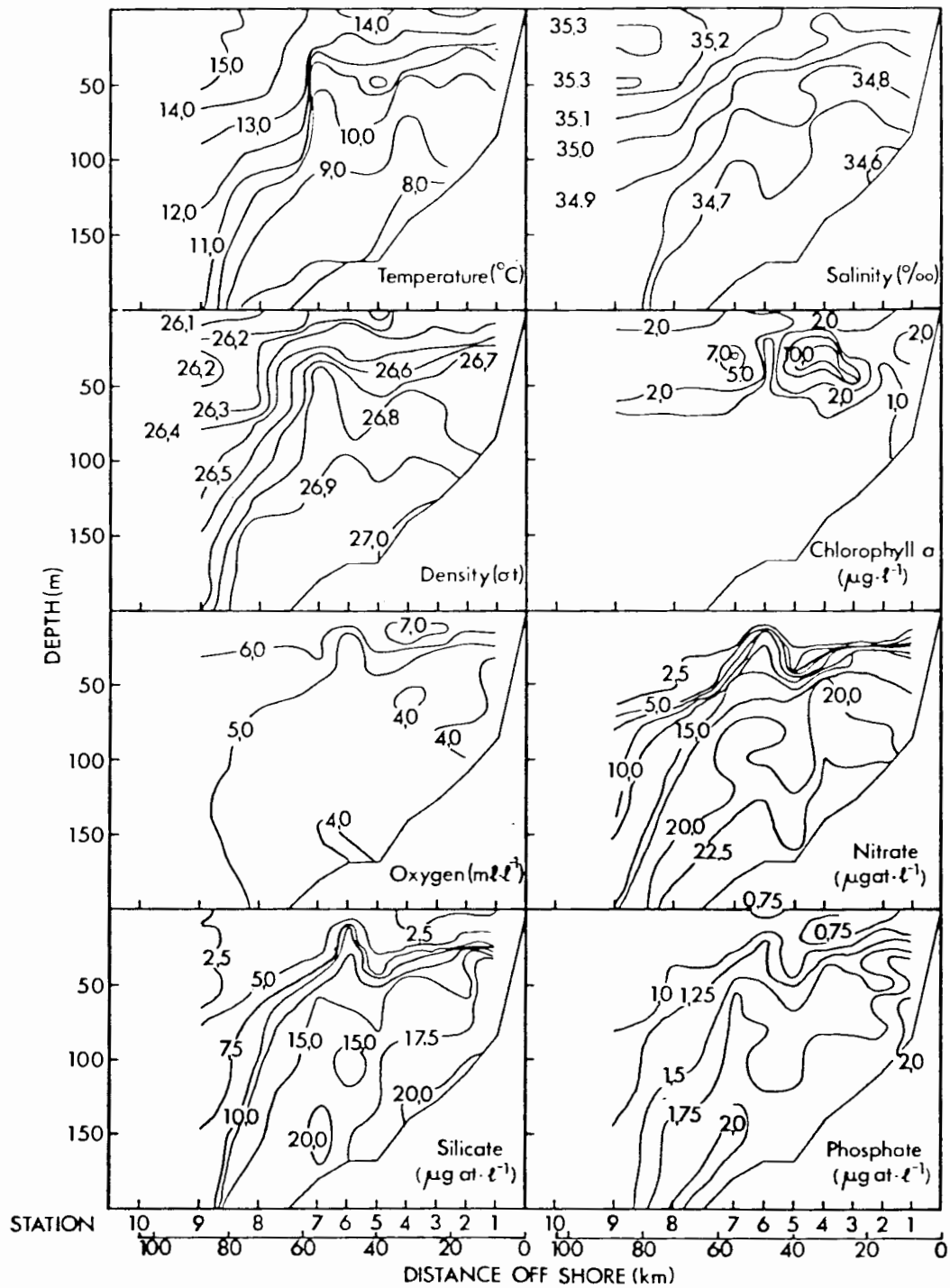

Fig 2: Vertical distributions of temperature, salinity, density, chlorophyll a, dissolved oxygen, nitrate, silicate and phosphate, September 1972

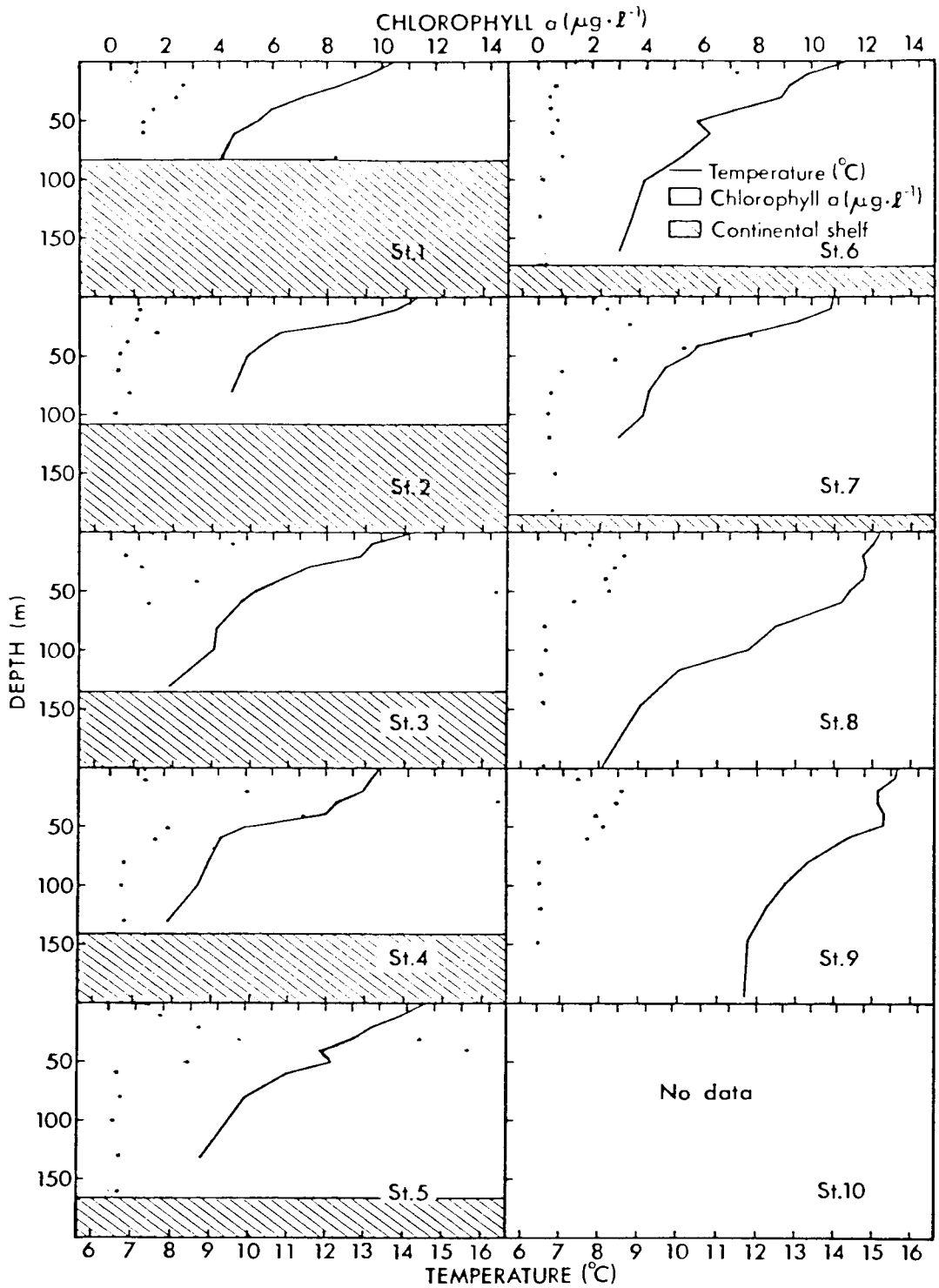

Fig. 3. Vertical profiles of temperature and chlorophyll *a*. September 1972

ton species were identified from the drawings and descriptions of Hendey (1937), Cupp (1943) and Hustedt (1962).

Data presentation

Hydrographic data were displayed in three ways to show changes along the transect:

(i) vertical sections of temperature, salinity, density, chlorophyll *a*, oxygen and nutrients were drawn to indicate the state of upwelling;
(ii) vertical profiles of chlorophyll *a* and temperature indicated the stability of the water column in relation to distribution of plant pigment;
(iii) integrated values of chlorophyll *a* and nutrients to a depth of 50 m were plotted against distance off shore to indicate the sequence of events.

RESULTS

Monthly transects

September 1972 — Wind data were not recorded during this month. The temperature, salinity and density isolines showed no indications of inshore upwelling (Fig. 2). The 10°C isotherm rose rapidly 56 km off shore (Station 7), from below 100 m to about 50 m, and then maintained this depth to the coast. The isohalines and the isopycnals showed similar patterns, indicating a well-defined upper mixed layer of some 30—40 m depth. A weak gradient of surface salinity and temperature was also apparent. Upwelling had obviously ceased some time before the transect was sampled, because active upwelling in this region is characterized by water cooler than 10°C breaking the surface (Andrews and Hutchings 1980).

A well-developed subsurface (10—50 m) chlorophyll *a* maximum was evident inshore between Stations 3 and 5, where values of up to 14,4 $\mu g \cdot \ell^{-1}$ were measured. A separate patch of chlorophyll *a* that reached 7,6 $\mu g \cdot \ell^{-1}$ was observed in the frontal zone, farther off shore (Station 7) at a depth of 30 m. An isolated patch of chlorophyll *a* of 8,6 $\mu g \cdot \ell^{-1}$, suspected to consist of decomposed material with a high phaeophytin content, was found close to the bottom at 80 m at Station 1. High values of dissolved oxygen coincided with chlorophyll *a* maxima, and levels of up to 7,74 $m\ell \cdot \ell^{-1}$ were measured at Station 3. These high levels of dissolved oxygen at the surface indicated that phytoplankton production had taken place prior to sampling.

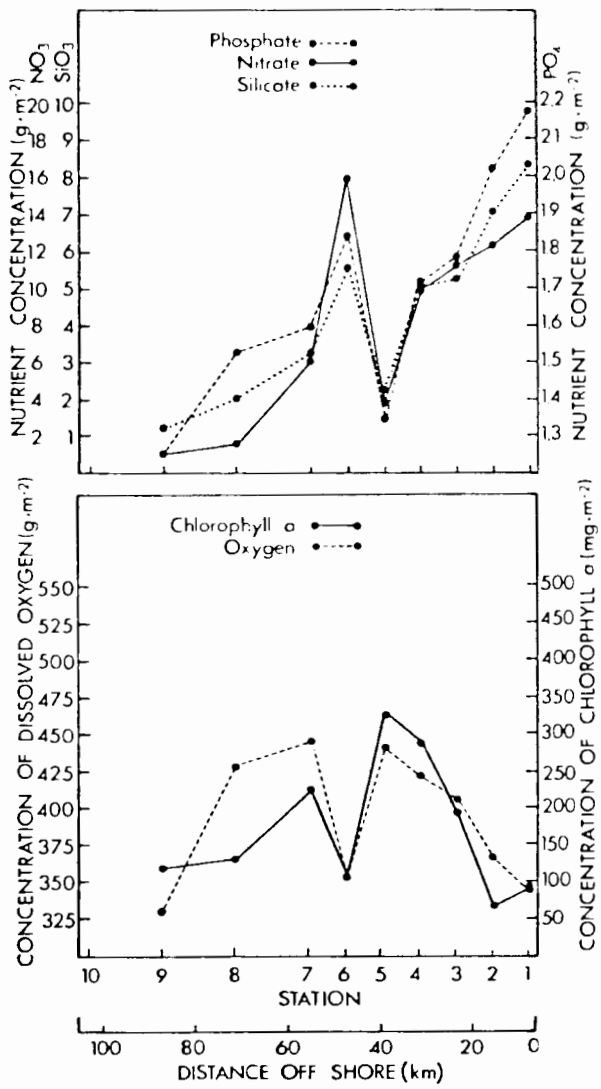

Fig 4: Changes within the euphotic zone (0—50 m) of chlorophyll *a*, dissolved oxygen, nitrate, silicate and phosphate, September 1972

The nutrient concentrations observed within 10 m of the surface were very low and decreased somewhat irregularly along the line of stations. Higher concentrations of nutrients were found within and below the chlorophyll *a* maxima. High negative correlation coefficients were obtained for correlations between chlorophyll *a* and concentrations of nitrate, silicate and phosphate.

Vertical profiles of chlorophyll *a* and temperature showed that the subsurface chlorophyll *a* maxi-

Table I: Species identifications and microscopic cell counts of samples exceeding 1 $\mu g \cdot \ell^{-1}$ of chlorophyll *a* during September 1972

Depth (m)	Station 1			Station 2				Station 3			Station 4			Station 5			Station 6			Station 7			Station 8			Station 9			Station 10		
	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D
0	0,9			3,3	Detritus	—	1,4	Detritus	—	1,4			1,6	Detritus	—	1,5	Detritus	—	2,2	Detritus	—	1,5			1,6	Detritus	—			
10	1,1			1,2	Detritus	—	4,7	Detritus	—	1,4			1,9	▲=61% ★=10% T=23 940	7	7,4	△=98% T=182 860	3	2,7	Detritus	—	1,9			1,7	Detritus	—			
20	3,0	Detritus	—	1,1	△=69% ▲=28% T=332 140	6	0,7			5,1	Detritus	—	3,4	Detritus	—	0,7			3,7	Detritus	—	3,3			3,2					
30	2,5	▲=67% ★=16% T=71 620	5	1,8	△=70% ▲=25% T=17 434	4	1,3			14,4	△=87% ▲=10% T=179 600	5	11,6	△=77% ▲=21% T=350 320	4	0,5			7,6	Detritus	1	3,0			3,0					
40	1,7	▲=41% △=32% T=27 580	6	0,8			3,2	△=72% ▲=26% T=381 200	3	7,0	△=85% ▲=10% T=115 860	4	13,3	△=90% ▲= 8% T=362 069	5	0,5			5,4	△=85% ▲= 9% T=79 798	5	2,8			2,3					
50	1,4			0,4			14,2	Detritus	—	2,0	Detritus	—	3,1	Detritus	—	0,6			2,9	Detritus	—	2,8			2,4					
60	1,4			0,3			1,5			1,7	△=72% ▲=25% T=54 983	3	0,4			0,5			1,1			1,5			2,1					
80	8,6			0,8			—			0,7			0,5			0,7			0,7			0,4			0,2					
100				0,3			—			0,6			0,3			0,3			0,5			0,4			0,2					

KEY OF SPECIES
▲=*Nitzschia pungens*
△=*Nitzschia seriata*
★=*Nitzschia delicatissima*
★=*Ciliate spp.*

KEY
Chl= Chlorophyll *a* ($\mu g \cdot \ell^{-1}$)
D = Diversity (species)
T = Total (cells ℓ^{-1})
□ = No count made
■ = Samples missing

mum was generally associated with the thermocline at 30—40 m between Stations 3 and 7 except at Station 6, where a maximum occurred at 10 m, well above the thermocline (Fig. 3).

Integrated values of chlorophyll *a*, oxygen and nutrients within the euphotic zone (0—50 m) are illustrated in Figure 4. A simultaneous peak off shore in chlorophyll *a* and oxygen was observed at Stations 5 and 7, concomitant with lower nutrients. Station 6, just inshore of the frontal zone, appeared somewhat anomalous, with higher concentrations of nutrients, but lower chlorophyll *a* and oxygen.

Selected cell counts and species identifications were performed on most of the samples in which the concentration of chlorophyll *a* exceeded 1 $\mu g \cdot \ell^{-1}$. The highest phytoplankton cell counts (381×10^3 cells $\cdot \ell^{-1}$ at Station 3) occurred where subsurface chlorophyll *a* concentration was maximal (Table I). Samples analysed at the surface consisted of detritus. A total of 21 species was identified along the transect, with two species, *Nitzschia pungens* var. *atlantica* Cleve and *N. seriata* Cleve together representing approximately 90 per cent of the cells in most samples. The small, threadlike *N. pungens* dominated at Station 1, whereas the larger *N. seriata* was the dominant species in the remaining samples.

October 1972— This transect was sampled on 5 and 6 October, during a period of moderate south-westerly winds of 10—20 knots. Prior to the survey period, gentle south-easterly winds of 5—15 knots prevailed between 1 and 3 October. These had strengthened to 35 knots by 4 October. A short lull then followed before the wind veered to south-westerly.

Active upwelling occurred during the sampling period, indicated by the temperature, salinity and density distributions (Fig. 5). The vertical displacement of the isohalines towards the coast was indicative of strong upwelling. The 10°C isotherm and the 26,6 isopycnal inclined upwards over the shelf and broke the surface 8 km off shore between Stations 1 and 2. Off shore, sun-warming and vertical and horizontal mixing processes caused the surface water temperatures and salinities to rise by 6,75°C and 0,63‰ respectively. The oceanic front was situated between Stations 6 and 8, 40—60 km off shore.

A relatively small near-surface patch of chlorophyll *a* ($<2 \mu g \cdot \ell^{-1}$) was distributed between the front and the newly upwelled water (Stations 3—6). Highest values for chlorophyll *a* (10,2 $\mu g \cdot \ell^{-1}$) and dissolved oxygen (6,1 $m\ell \cdot \ell^{-1}$) were found at Station 4. The concentrations of dissolved oxygen did not alter much in the euphotic zone, except for a small increase at the surface between Stations 4 and 5. A small patch of low-oxygen water was found at Station 6, between 40 and 70 m deep.

The surface nutrients displayed similar trends. Initially, high nutrient concentrations were observed close inshore, where active upwelling was occurring. The concentrations then decreased somewhat in the patch of high chlorophyll *a* concentration and reached minimum values beyond the front. High concentrations of nutrients coincided with the patch of low-oxygen water observed at Station 6 between 40 and 70 m deep, i.e. within the frontal zone, suggesting that regeneratory processes were taking place.

Vertical profiles of temperature and chlorophyll *a* (Fig. 6) clearly showed that the surface chlorophyll *a* maximum was confined between Stations 4 and 6, where a shallow thermocline was evident.

Integrated values of chlorophyll *a*, oxygen and nutrients within the euphotic zone are illustrated in Figure 7. A decrease in nutrients and a concomitant increase in oxygen and chlorophyll *a* was evident out to Station 3. Between Stations 3 and 5, the sudden increase in chlorophyll *a*, without a corresponding increase in dissolved oxygen, suggests that the phytoplankton was in the early stages of a bloom.

Evidence from microscopic cell counts and identifications (Table II) revealed that the surface chlorophyll *a* maximum represented detrital material. The phytoplankton standing stock was very low, and it was in fact confined to Station 6, where a maximum of 380×10^3 cells $\cdot \ell^{-1}$ was found at 30 m. In this instance, it would seem probable that the low standing stocks determined could have resulted from cellular degradation because of poor preservation. Andrews and Hutchings[4] (1980) measured high gross production values during this month, which suggested that the phytoplankton population was growing vigorously. Six species in total were identified, but *Chaetoceros* spp. and *Thalassionema nitzschioides* Hust. were strongly dominant, contributing 90 per cent of the cells in most samples. *Chaetoceros* spp. alone contributed about 80 per cent of the total abundance in most samples.

November 1972 — This transect was sampled on 8 and 9 November during a period of strong south-easterly winds (3,5 knots). Between 1 and 4 November south-easterlies of 30—40 knots had prevailed. On the 5th, the wind had veered to the north-west (5—10 knots) but had reversed again on the 6th to the south-east (20—30 knots). There was a lull on the 7th before a strong south-easterly wind commenced again on the 8th and lasted through the 9th.

Sustained upwelling prior to the transect resulted in a broad belt of mixed water with the front some 20 km further off shore than in October. Active up-

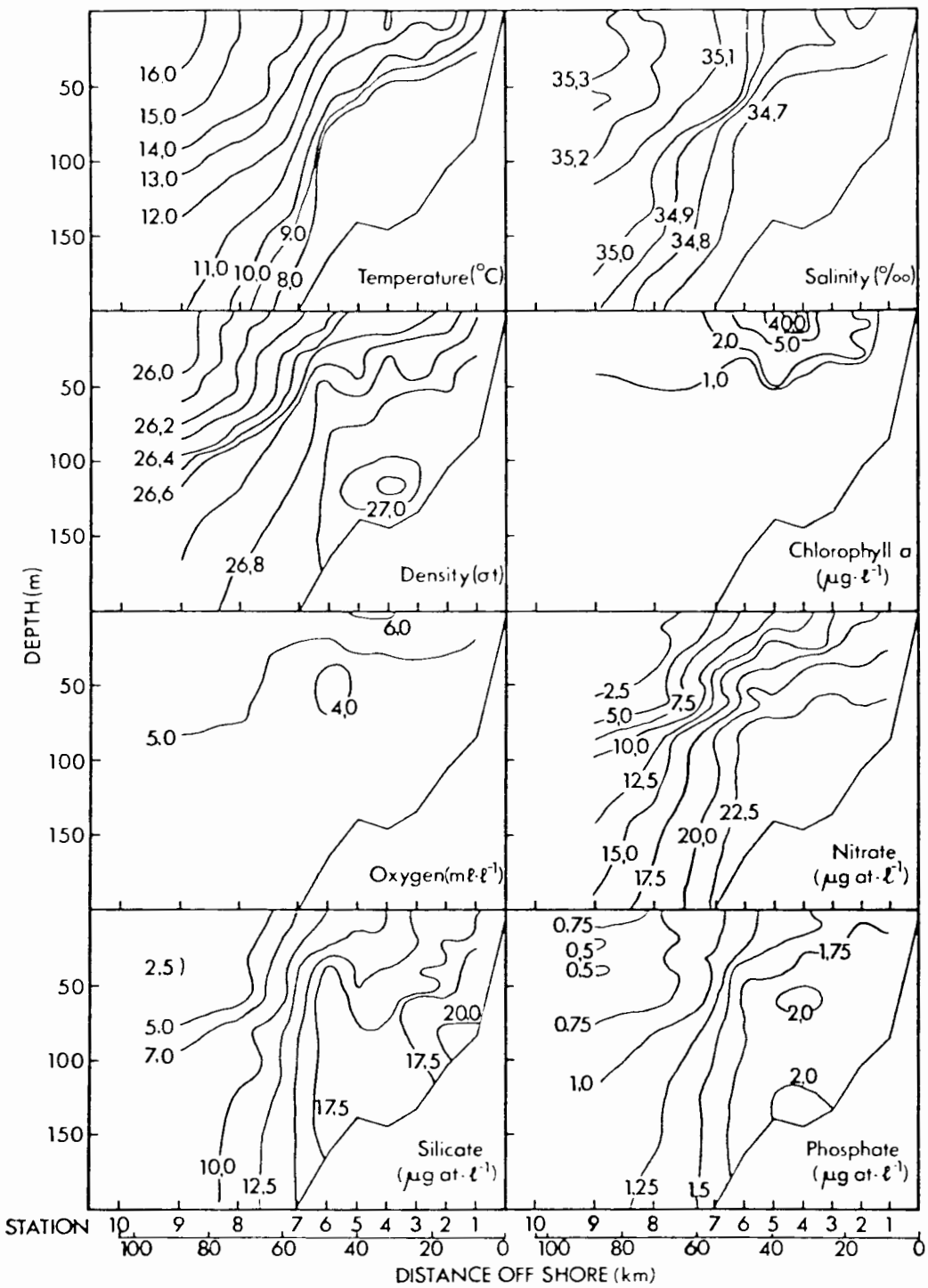

Fig. 5 Vertical distributions of temperature, salinity, density, chlorophyll *a*, dissolved oxygen, nitrate, silicate and phosphate, October 1972

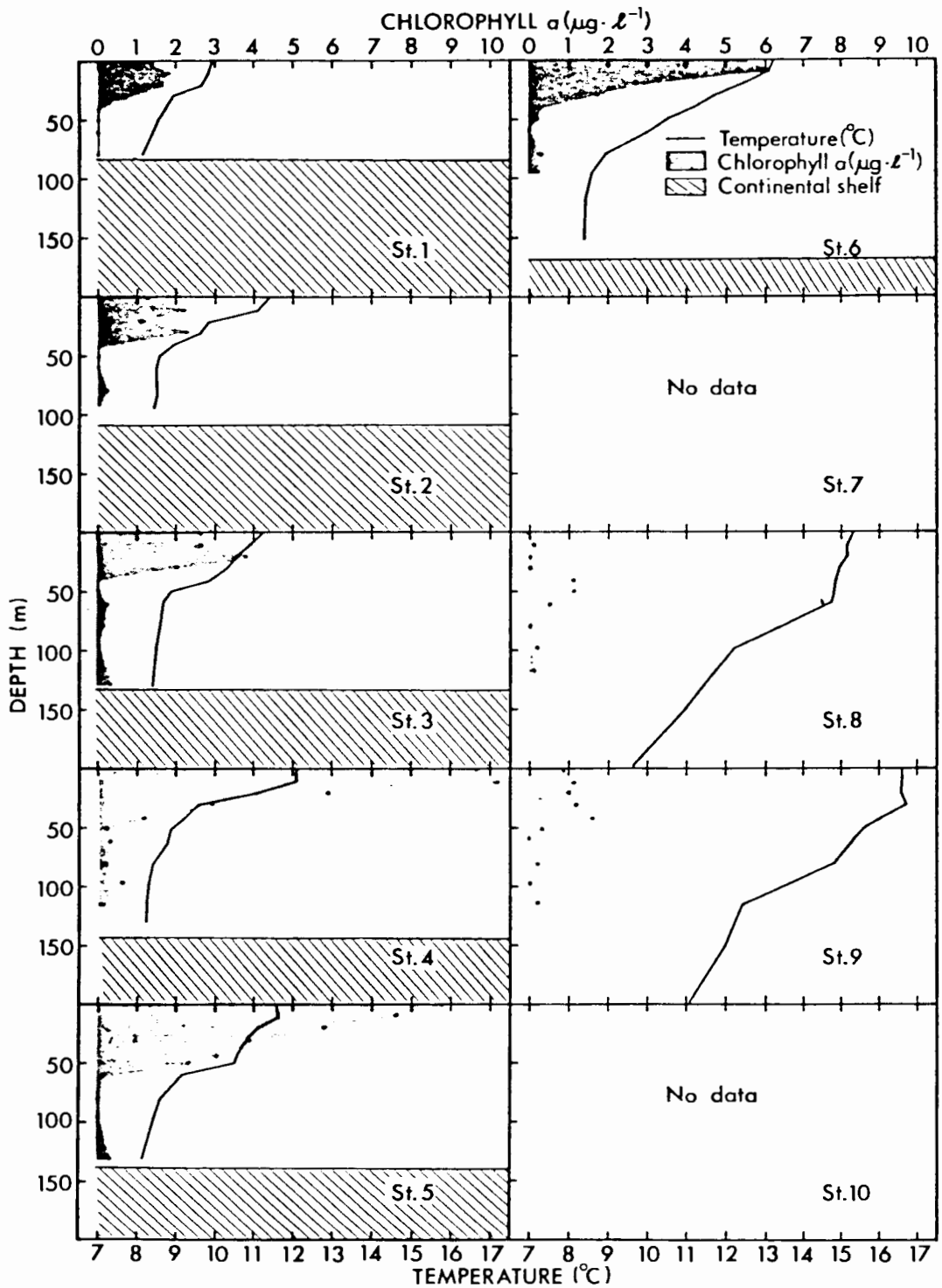

Fig. 6: Vertical profiles of temperature and chlorophyll *a*, October 1972

Table II: Species identifications and microscopic cell counts of samples exceeding 1 $\mu g \cdot \ell^{-1}$ of chlorophyll *a* during October 1972

Depth (m)	Station 1			Station 2			Station 3			Station 4			Station 5			Station 6			Station 7			Station 8			Station 9			Station 10		
	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D
0	0,7			1,3	Detritus	—	2,6	Detritus	—	9,6	Detritus	—	8,8	Detritus	—	5,4	□=56% O=29% T=81 909	5				0			0,9					
10	0,9	Detritus	—	2,2	Detritus	—	2,6	Detritus	—	10,2	Detritus	—	7,6	Detritus	—	6,1	O=88% □= 6% T=77 987	4				0,9			1,1					
20	0,8	Detritus	—	1,1	Detritus	—	3,8	Detritus	—	5,9	Detritus	—	5,8	Detritus	—	2,7	O=95% □= 4% T=37 987	3				—			1,0					
30	0,4			2,2	Detritus	—	2,0	Detritus	—	2,6	Detritus	—	3,9	Detritus	—	1,7	O=70% □=20% T= 37 987	3				—			1,1					
40	0			0			0			1,2			3,0	Detritus	—	0,3						1,1	Detritus	—	1,6	Detritus	—			
50	0			0			0			0,2			2,3			0,2						1,1	Detritus	—	0,3					
60	0			0			0,2			0,3			0,1			0						0,5			0					
80	0			0,2			0,1			0,2			0			0,3						0			0,2					
100	0			0			0			0,6			0			0,2						0,2			0					

KEY OF SPECIES
□=*Thalassionema nitzschioides*
O=*Chaetoceros* spp.

KEY
Chl= Chlorophyll *a* ($\mu g \cdot \ell^{-1}$)
D = Diversity (species)
T = Total (cells ℓ^{-1})
□ = No count made

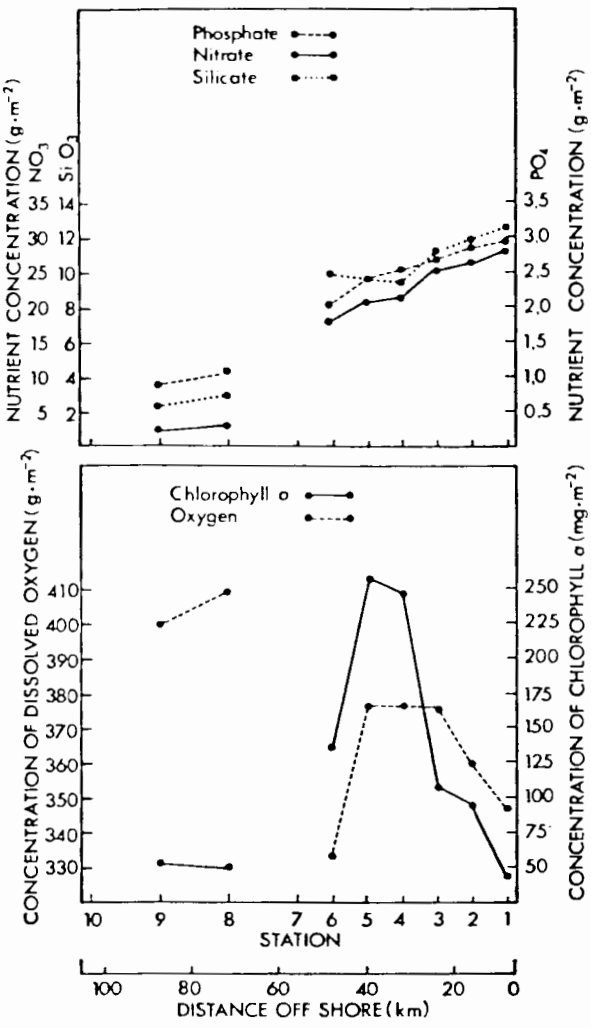

Fig 7: Changes within the euphotic zone (0—50 m) of chlorophyll a, dissolved oxygen, nitrate, silicate and phosphate, October 1972

welling was evident within 10 km of the shore, where temperature, salinity and density isolines intersected the sea surface (Fig. 8). The zone of mixed water was nearly isohaline between 10 and 100 km off shore, to a depth of 40—50 m, but it changed dramatically across the front, salinity rising by 0,5‰ within 18 km. The pycnocline gradually deepened off shore to 60 km, and then it deepened very rapidly across the front. The front was strongly defined off shore, marked temperature and salinity gradients separating warm saline oceanic waters from cooler, less-saline older upwelled waters.

Concentrations of chlorophyll *a* were highest in the upper 10—20 m between Stations 2 and 7, reaching a maximum of 22,7 $\mu g \cdot \ell^{-1}$ at 10 m at Station 4, but dropping rapidly below the pycnocline. At Station 8, 100 km off shore, concentrations of chlorophyll *a* greater than 2,7 $\mu g \cdot \ell^{-1}$ extended to 120 m, the maximum depth sampled for chlorophyll *a*, clearly demonstrating sinking of dense, productive, upwelled water at the frontal zone. Levels of dissolved oxygen increased simultaneously with increases in chlorophyll *a*.

Inshore surface waters possessed high concentrations of nutrients, whereas off shore the concentrations diminished simultaneously with increases in chlorophyll *a*. Reductions of 96 per cent for nitrate, 86 per cent for phosphate and 68 per cent for silicate were evident at the surface between the inshore and off-shore stations.

Vertical profiles of temperature and chlorophyll *a* (Fig. 9) showed the existence of a shallow thermocline between Stations 2 and 7, coinciding with the distribution of maximum concentrations of chlorophyll *a*.

Integrated values of chlorophyll *a* and oxygen within the euphotic zone increased (Fig. 10), with a concomitant decrease in nutrient concentration. Within the euphotic zone, nitrates were utilized at a faster rate than phosphates or silicates.

The phytoplankton standing stock, as determined from cell counts (Table III), was considerably higher than in October. Cell counts of $1\,100 \times 10^3$ cells $\cdot \ell^{-1}$ were measured at Station 5 at 10 m. The highest concentration of cells was distributed between Stations 3 and 7 within the upper 20 m. Nine species in total were identified, with *Nitzschia* spp. dominant at most stations on the transect. *Thalassiothrix frauenfeldii* and *Skeletonema costatum* represented a minor proportion of the samples only up to Station 4. *Chaetoceros* spp. appeared at Station 5 and increased in abundance further off shore, constituting 50—82 per cent of the cell count 20—40 m deep at Station 9.

December 1972 — Sampling commenced on 12 December during moderate (20 knots) south-easterly winds. On the 13th, the wind veered to the south. Previously, between 1 and 11 December, west and north-west winds of up to 15 knots with intermittent calms prevailed.

Conditions were similar to those in November, there being a broad belt of mixed, aged upwelled water, but no upwelling inshore (Fig. 11). Inshore of the front the waters were relatively stable, with a marked pycnocline between the coast and 60 km (Station 7) off shore. Beyond this, the isopycnals deepened rapidly. A warm-water eddy was centred at

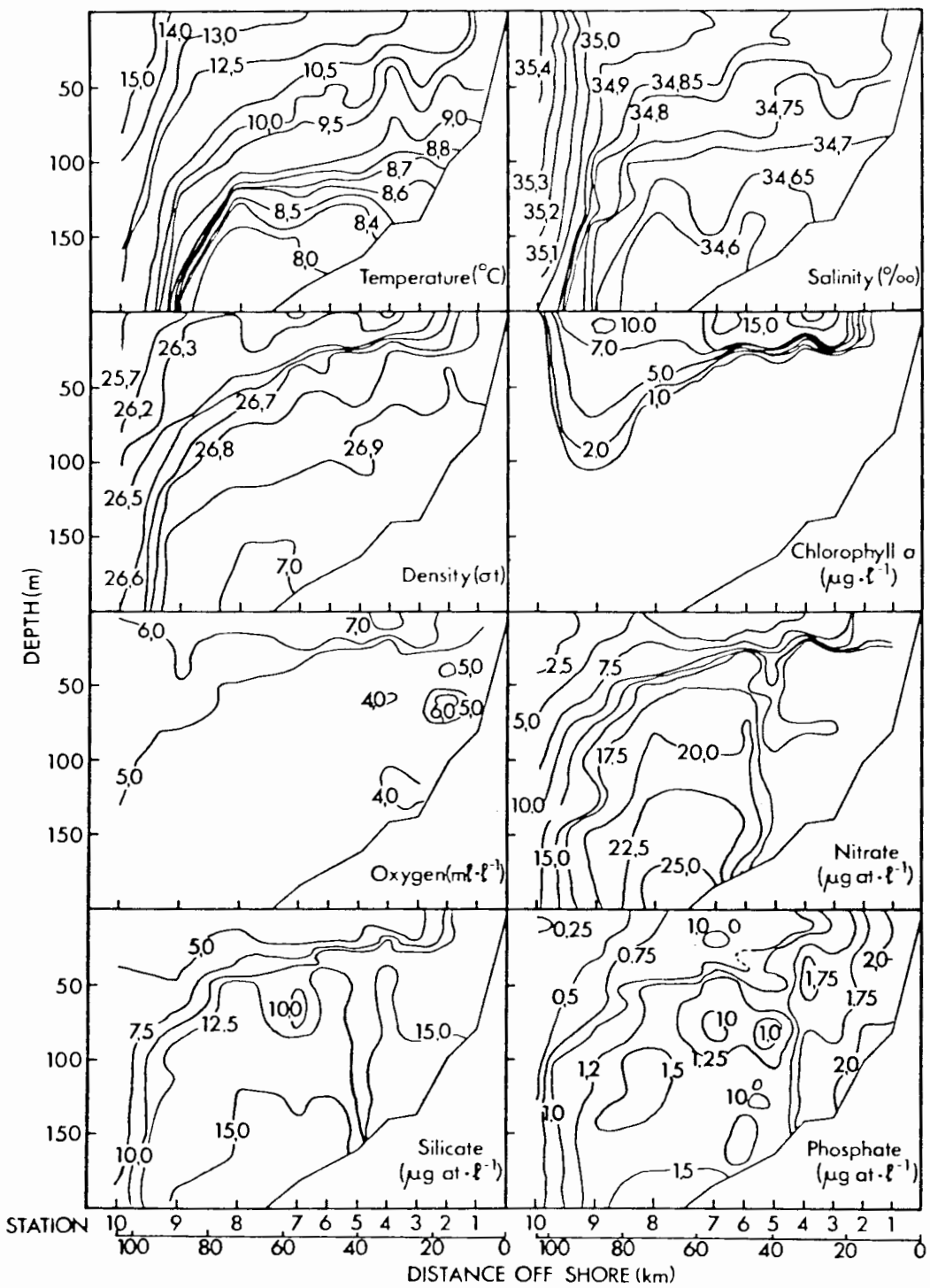

Fig. 8: Vertical distributions of temperature, salinity, density, chlorophyll *a*, dissolved oxygen, nitrate, silicate and phosphate, November 1972

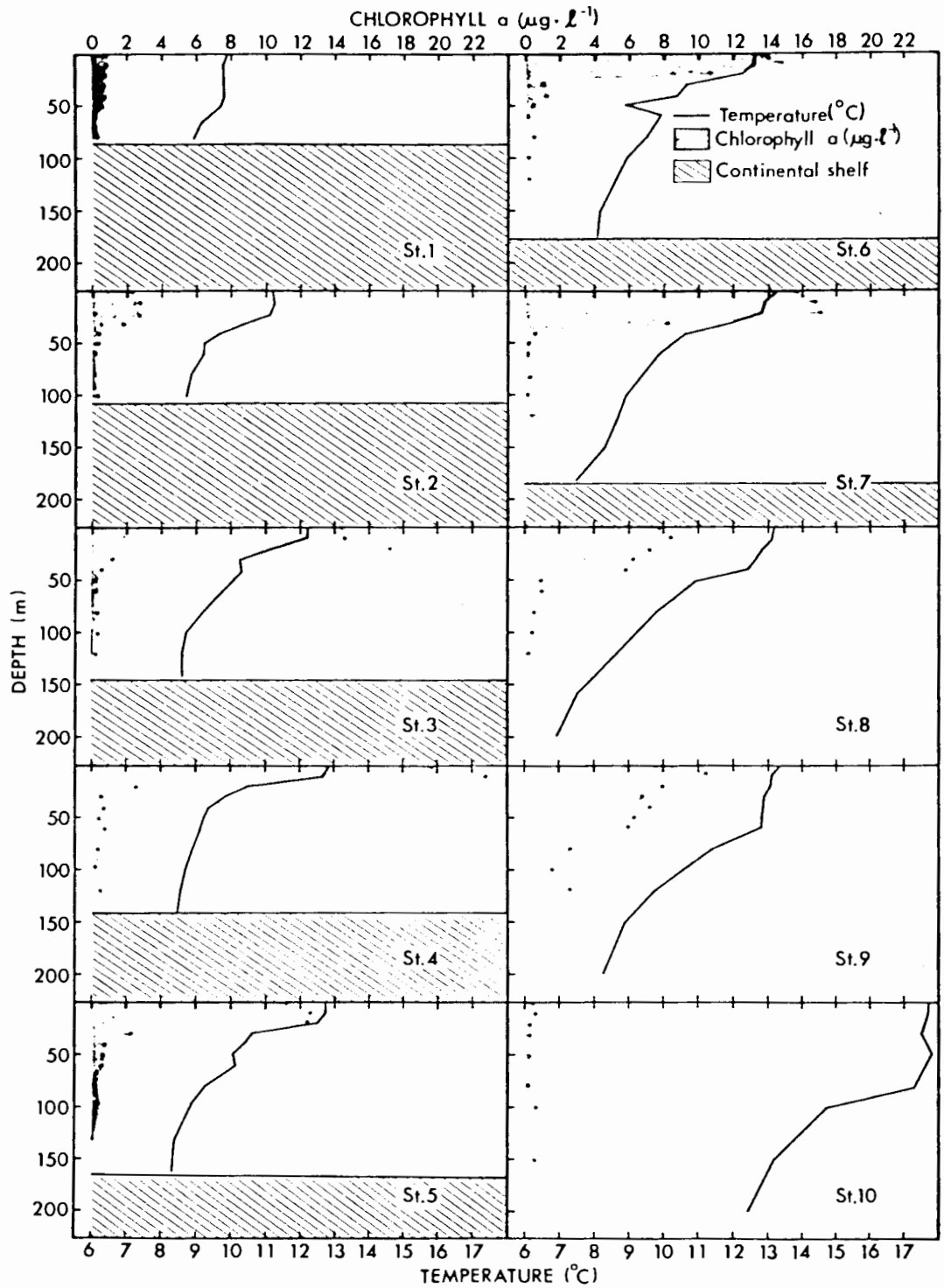

Fig. 9: Vertical profiles of temperature and chlorophyll a, November 1972

Table III: Species identifications and microscopic cell counts of samples exceeding 1 $\mu g \cdot \ell^{-1}$ of chlorophyll *a* during November 1972

Depth (m)	Station 1			Station 2			Station 3			Station 4			Station 5			Station 6			Station 7			Station 8			Station 9			Station 10		
	Chl	Count ℓ^{-1}	D	Chl	Count ℓ^{-1}	D	Chl	Count ℓ^{-1}	D	Chl	Count ℓ^{-1}	D	Chl	Count ℓ^{-1}	D	Chl	Count ℓ^{-1}	D	Chl	Count ℓ^{-1}	D	Chl	Count ℓ^{-1}	D	Chl	Count ℓ^{-1}	D	Chl	Count ℓ^{-1}	D
0	0,9	●=100%		2,2	●=98% ▽= 5% T=53 294	2	15,4	●=95% ■= 5% T=165 760	2	19,7			11,0	●=94% ○= 5% T=309 523	4	13,6	●=75% ○=22% T=337 634	4	15,6	●=90% ○= 9% T=249 495	3	7,8	●=100% T=144 118	2	7,7	Detritus	—	0,4		
10	0,9	●=50% ○=50%		2,8	●=91% ■= 9% T=94 792	2	15,5	●=100% T=372 960	1	22,7	●=89% ■=10% T=442 424	5	12,6	●=80% ■=17% T=1 100 000	3	14,8	●=98% T=280 640	2	16,8	●=64% ○=34% T=193 269	3	8,4	●=91% □= 7% T=71 845	5	10,5	●=65% □=32% T=129 897	4	0,5		
20	0,8			2,8	Detritus	—	17,3	●=100% T=336 160	1	2,6	Detritus	—	12,5	●=84% ○= 5% T=282 243	5	10,6	●=85% ○=15% T=151 852	3	17,1	●=83% ○=17% T=488 764	1	7,2	●=94% ○= 4% T=114 407	5	7,9	○=51% ●=45% T=180 952	4	0,4		
30	0,6			0,9			1,2			0,4			2,3	●=96% ▽= 3% T=79 167	3	1,0	Detritus	—	8,1	●=76% ○=22% T=94 180	3	6,2	Detritus	—	6,8	○=50% ●=33% □=10% T=41 178	5	0,3		
40	0,8			0,2			0,7			0,5			0,8			1,2	Detritus	—	0,6			5,8	Detritus	—	7,2	○=82% ●=10% T=68 932	4	0,3		
50	0,5			0,2			0,3			0,3			0,7			0,5			0,2			0,9			6,3	●=91% ○= 8% T=126 316	3	0		
60	0,2			0,1			0,3			0,5			0,7			0,2			0,2			1,0			6,0	Detritus	2	0,6		
80	0,3			0,1			0,4			0,4			0,2			0,6			0,3			0,6			2,7	Detritus	2	0,5		
100				0,2			0,4			0,2			0,4			0,3			0,2			0,4			1,6	Detritus	—			

KEY OF SPECIES
● = *Nitzschia* spp
○ = *Chaetoceros* spp
▽ = *Thalassiothrix frauenfeldii*
■ = *Skeletonema costatum*
□ = *Thalassionema nitzschioides*

KEY
Chl = Chlorophyll *a* ($\mu g \cdot \ell^{-1}$)
D = Diversity (species)
□ = No count done
□ = Missing sample
T = Total cells ℓ^{-1}

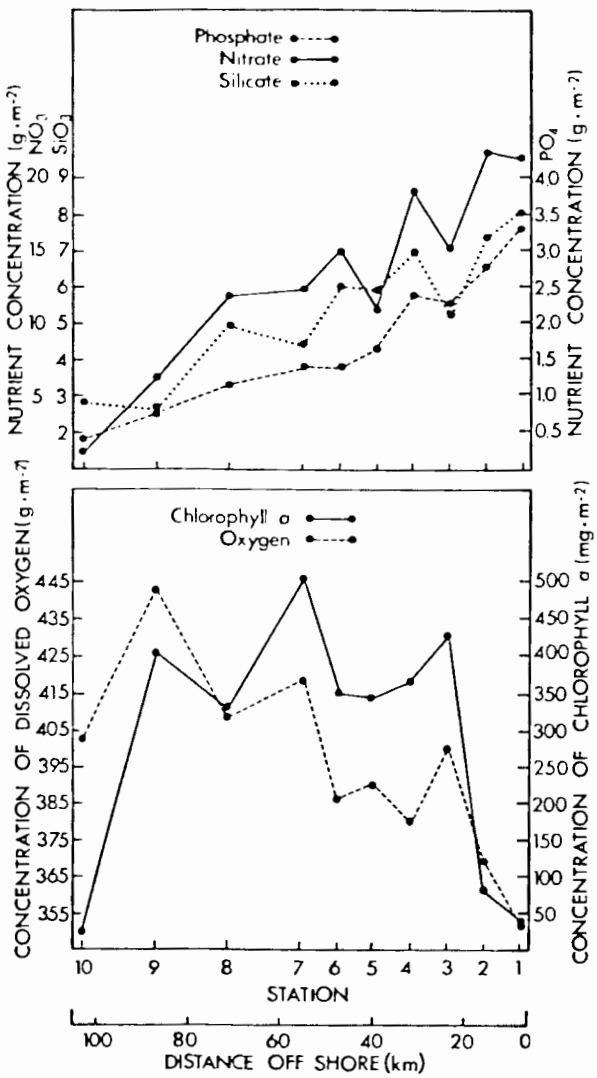

Fig. 10 Changes within the euphotic zone (0—50 m) of chlorophyll *a*, dissolved oxygen, nitrate, silicate and phosphate, November 1972

Station 6. The front, less well defined than in November, lay between Stations 7 and 8.

A shallow chlorophyll *a* maximum was found in the upper 20 m between Stations 2 and 5. Levels of dissolved oxygen were high at the surface and within the chlorophyll *a* maximum. Oxygen-depleted water (<3 m$\ell \cdot \ell^{-1}$) appeared along the shelf between Stations 4 and 7.

Nutrient concentrations were lowest in the areas rich in chlorophyll *a* and in off-shore oceanic water. Below the pycnocline, the nutrient concentrations decreased rapidly.

Vertical profiles of temperature and chlorophyll *a* showed that the chlorophyll *a* maximum followed the thermocline as it deepened off shore (Fig. 12).

Integrated values of non-conservative parameters within the euphotic zone are illustrated in Figure 13. The nutrients dropped somewhat irregularly down the plume. The sharpest drop occurred between Stations 5 and 6, as the patch of oceanic water was progressively sampled. This drop in nutrients was not accompanied by an increase in chlorophyll *a*, highest concentrations of which were found at Station 7, just inshore of the front. The oxygen distribution differed from the chlorophyll *a* distribution in that an erratic increase persisted down the plume. As the oceanic water had a near-surface distribution, the dissolved-oxygen content was always high and, on crossing the front, there was little change in this parameter.

Peak cell concentrations at 10 m at Station 4 (434 $\times 10^3$ cells $\cdot \ell^{-1}$) coincided with the shallow chlorophyll *a* maximum and shallow thermocline (Table IV). Similarly at Station 7 (40 m), a high value of 422 $\times 10^3$ cells $\cdot \ell^{-1}$ coincided with the off-shore subsurface chlorophyll *a* maximum at the thermocline. A total of 15 species was identified, but again *Nitzschia* spp. dominated all samples, even in the deep chlorophyll *a* maximum at Station 8. *Skeletonema costatum* occurred only at the surface at Station 3 and represented 6 per cent of the total number of cells in that sample. All other species were scarce.

January 1973 — Strong south-easterly winds, which blew for 3 days between 12 and 15 January, were followed by a calm and then by a south-west wind of 5—10 knots on the 16th when sampling commenced. A gentle southerly wind (10 knots) blew on the second day of sampling (17th).

The vertical distributions of various parameters (Fig. 14) revealed no upwelling, but there was strong stratification of the water column. A layer of oceanic water 20—30 m deep was separated from cooler waters by a very strong pycnocline close inshore.

A subsurface chlorophyll *a* maximum developed in the vicinity of the thermocline (Fig. 15). A value of 51.8 $\mu g \cdot \ell^{-1}$ chlorophyll *a* was recorded at 30 m at Station 8. Nutrients were depleted within the upper layers where levels of dissolved oxygen were uniformly high.

No trends were discernible from integrations of the non-conservative parameters within the euphotic zone (Fig. 16). Chlorophyll *a* was low, except for a peak at Station 8. Nutrient enrichment occurred at Stations 2 and 5, and dissolved oxygen was highest at

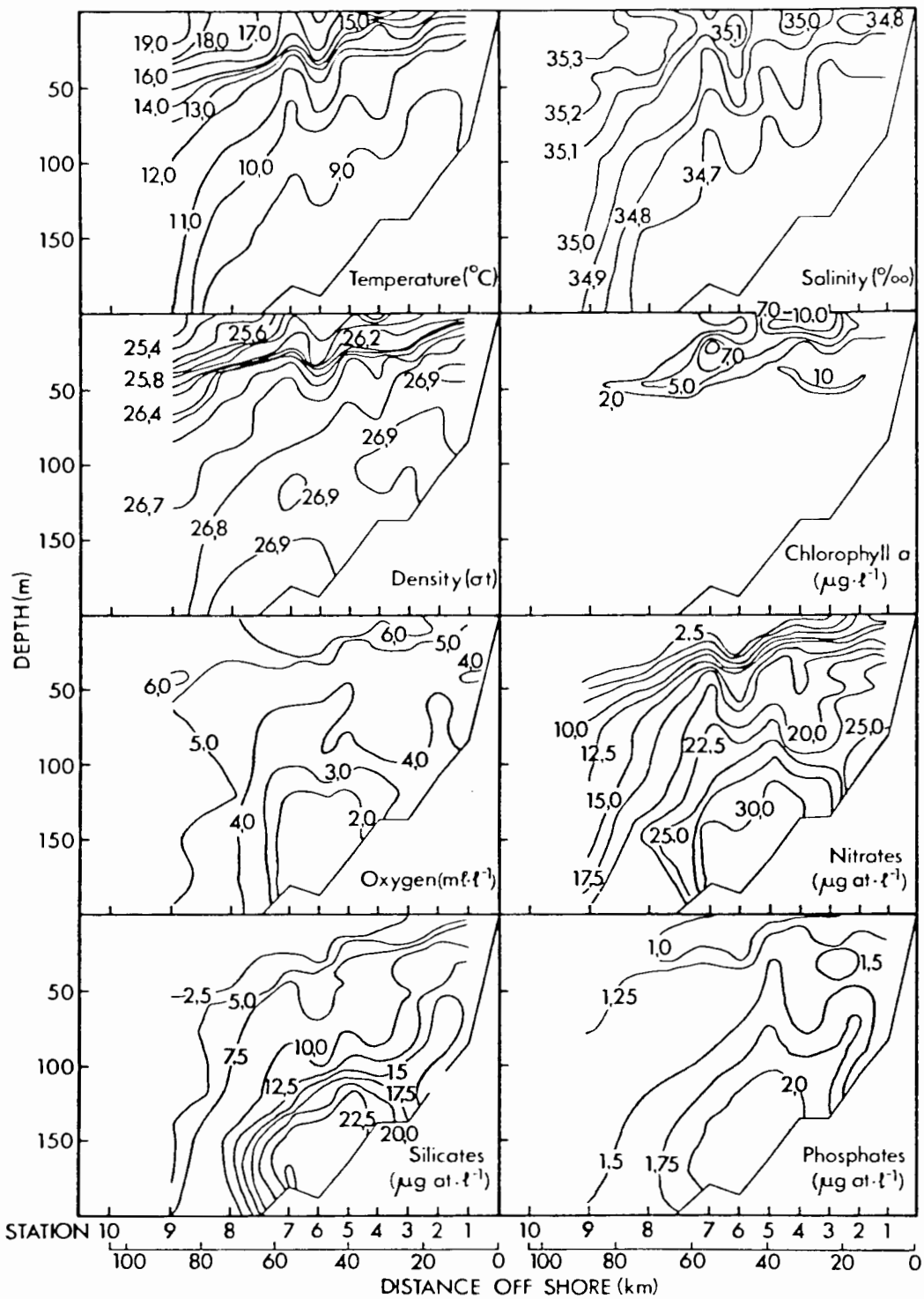

Fig. 11: Vertical distributions of temperature, salinity, density, chlorophyll *a*, dissolved oxygen, nitrate, silicate and phosphate, December 1972

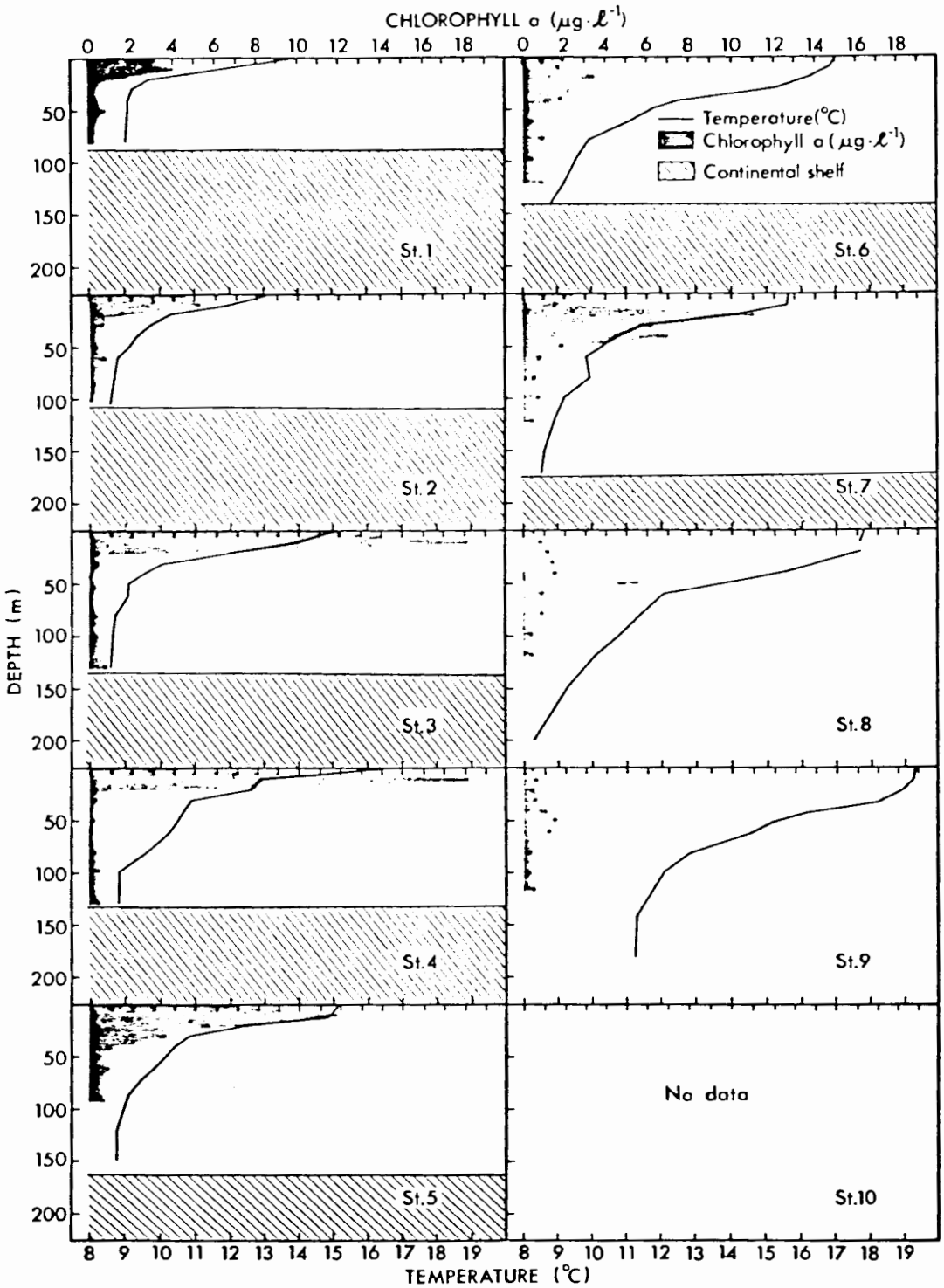

Fig. 12: Vertical profiles of temperature and chlorophyll *a*, December 1972

Table IV: Species identifications and microscopic cell counts of samples exceeding 1 $\mu g.\ell^{-1}$ of chlorophyll *a* during December 1972

Depth (m)	Station 1			Station 2			Station 3			Station 4			Station 5			Station 6			Station 7			Station 8			Station 9			Station 10		
	Chl	Count $.\ell^{-1}$	D	Chl	Count $.\ell^{-1}$	D	Chl	Count $.\ell^{-1}$	D	Chl	Count $.\ell^{-1}$	D	Chl	Count $.\ell^{-1}$	D	Chl	Count $.\ell^{-1}$	D	Chl	Count $.\ell^{-1}$	D	Chl	Count $.\ell^{-1}$	D	Chl	Count $.\ell^{-1}$	D	Chl	Count $.\ell^{-1}$	D
0	3,0	Detritus	—	4,1	Detritus	—	11,7	●=93% ■= 6% T=121 569	3	2,8	●=97% T=96 899	4	6,5	●=100% T=316 527	2	2,0	Detritus	—	2,2	Detritus	—	0,5			0,4					
10	4,0	●=100% T=213 757	1	5,1	●=100% T=48 511	1	9,3	●=100% T=140 845	1	18,5	●=100% T=433 816	2	11,7	●=99% T=390 935	2	1,8	Detritus	—	1,5	Detritus	—	0,8			0,5					
20	0,5			0,3			6,1	●=99% T=206 025	3	0,3			5,5	●=100% T=142 424	1	3,3	Detritus	—	1,0	●=98% T=195 145	3	1,1	Detritus	—	0,3					
30	0,3			0,6			1,2	Detritus	—	0,3			3,2	●=100% T=112 037	1	5,9	●=91% T=101 156	5	6,2	●=95% T=79 314	2	1,2	Detritus	—	0,4					
40	0,4			0,1			0,8			0			1,0	Detritus	—	2,7	Detritus	—	6,9	●=98% T=422 343	4	1,3	Detritus	—	1,0	Detritus	—			
50	0,8			0,2			0,3			0,1			0,4			0,3			1,8	Detritus	—	5,5	●=97% T=217 554	3	1,4	Detritus	—			
60	0,5			0,7			0,5			0			0,9			0,5			0,9			0,7			1,2	Detritus	—			
80	0,3			0,3			0,3			0,2			0,4			1,0			0,6			0,7			0,2					
100							0,3			0,4			0,6			0,6			0,8			0,3			0,2					

KEY OF SPECIES
● = *Nitzschia* spp.
■ = *Skeletonema costatum*

KEY
Chl = Chlorophyll *a* ($\mu g.\ell^{-1}$)
D = Diversity (species)
□ = No count made
T = Total (cells ℓ^{-1})

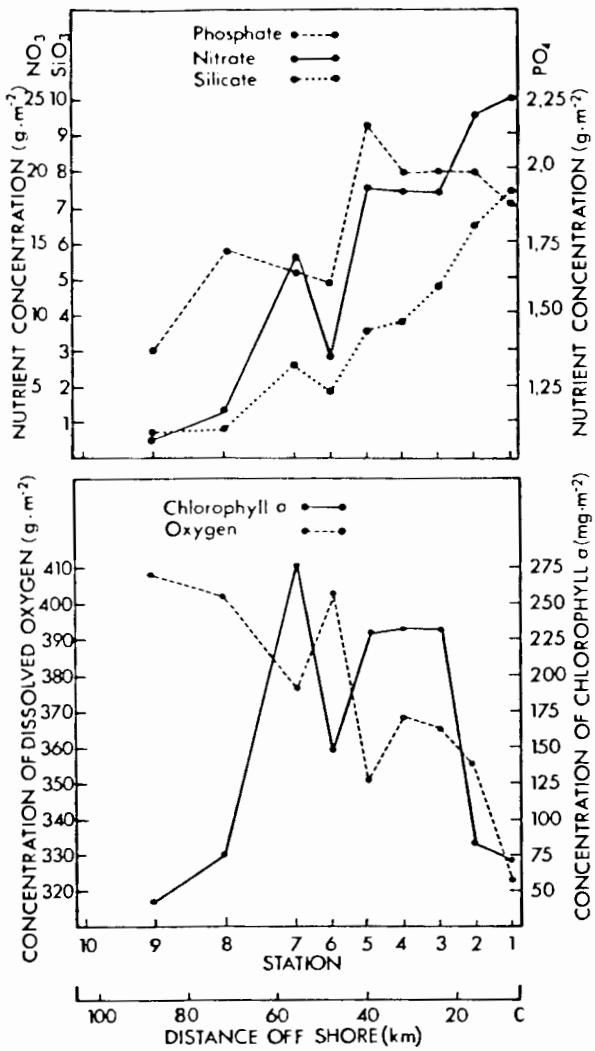

Fig. 13: Changes within the euphotic zone (0—50 m) of chlorophyll a, dissolved oxygen, nitrate, silicate and phosphate, December 1972

Station 3 when chlorophyll *a* was lowest.

Low cell counts were associated with the chlorophyll *a* maximum, except at Station 8 where high concentrations of chlorophyll *a* were found with high cell counts, e.g. 788×10^3 cells $\cdot \ell^{-1}$ at 30 m (Table V). (This count is likely to be an underestimate of the actual numbers because the phytoplankton cells, especially *Nitzschia* spp., were poorly preserved.) Five species were identified. Again *Nitzschia* spp. dominated all samples and *Skeletonema costatum* represented a small portion of the total only at Stations 6 and 8. Detritus occurred in all samples.

February 1973 — Strong south-easterly winds (35 knots) blew between 3 and 6 February. On the 6th and 7th, during the sampling period, the velocity increased to 45 knots.

Conditions approximated those of November and December, in that there was a broad belt of mixed water with evidence of moderate upwelling close inshore (Fig. 17). Surface temperatures increased and density decreased out to Station 5. As a result, the stabilizing effect of sun-warming on the water column allowed a chlorophyll *a* maximum to develop between Stations 3 and 5. Mixing processes caused by strong winds overnight were thought to be responsible for a cooling in the upper layers between Stations 6 and 8. The pycnocline was not well defined, but isopycnals gradually deepened from the surface at Station 2 to 60 m further off shore. The oceanic front was only apparent 100 km off shore between Stations 9 and 10.

Chlorophyll *a* was broadly distributed in two patches, one inshore and one off shore, both in the upper 20 m (Fig. 18). High levels of dissolved oxygen were measured within the chlorophyll *a* maximum.

High concentrations of nutrients were found close inshore, and low levels of nutrients were measured within the chlorophyll *a* maximum. The sudden influx of nutrients at Station 7 was evidently caused by mixing processes.

A trend for nutrients to decrease sporadically down the plume as chlorophyll *a* increased was evident, particularly at Stations 4, 6 and 8, where the chlorophyll *a* maximum was found. The increase in nutrients at Station 7 was associated with a decrease in chlorophyll *a* and oxygen (Fig. 19).

High cell concentrations corresponded with high levels of chlorophyll *a* inshore at Stations 4 and 5 and off shore at Station 8 (Table VI). Inshore samples and those in which chlorophyll *a* exceeded 1 $\mu g \cdot \ell^{-1}$ (Stations 6 and 7) contained detritus. A total of eight species was identified. *Nitzschia* spp. dominated throughout the transect. *Chaetoceros* spp. occurred together with *Nitzschia* spp. in the inshore chlorophyll *a* maximum, and *Skeletonema costatum* and a dinoflagellate species occurred together with *Nitzschia* in the off-shore patch.

DISCUSSION

Changes through the upwelling season

Physical changes — A rapid response manifest in the distribution of the hydrographic parameters was

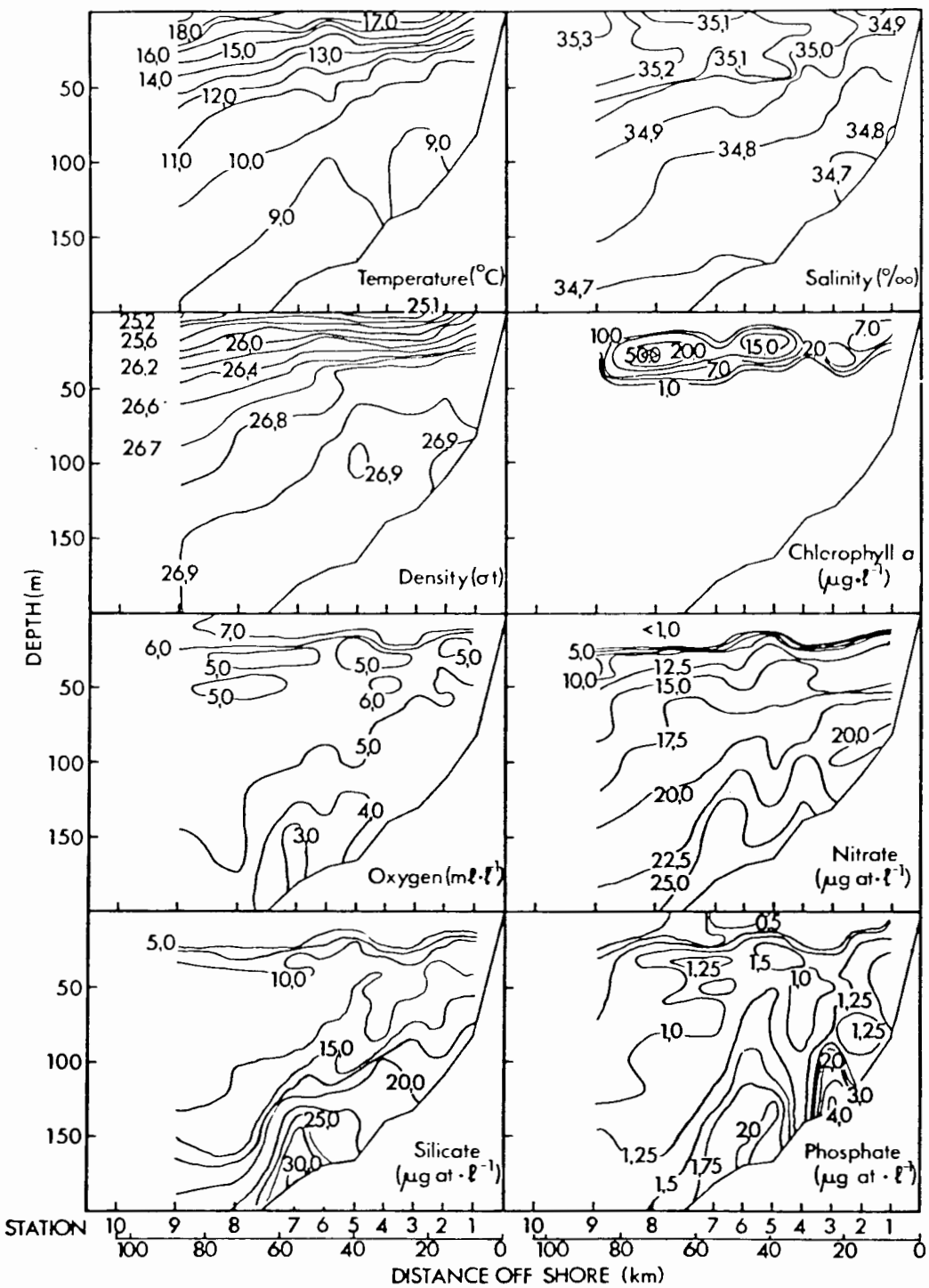

Fig 14: Vertical distributions of temperature, salinity, density, chlorophyll *a*, dissolved oxygen, nitrate, silicate and phosphate, January 1973

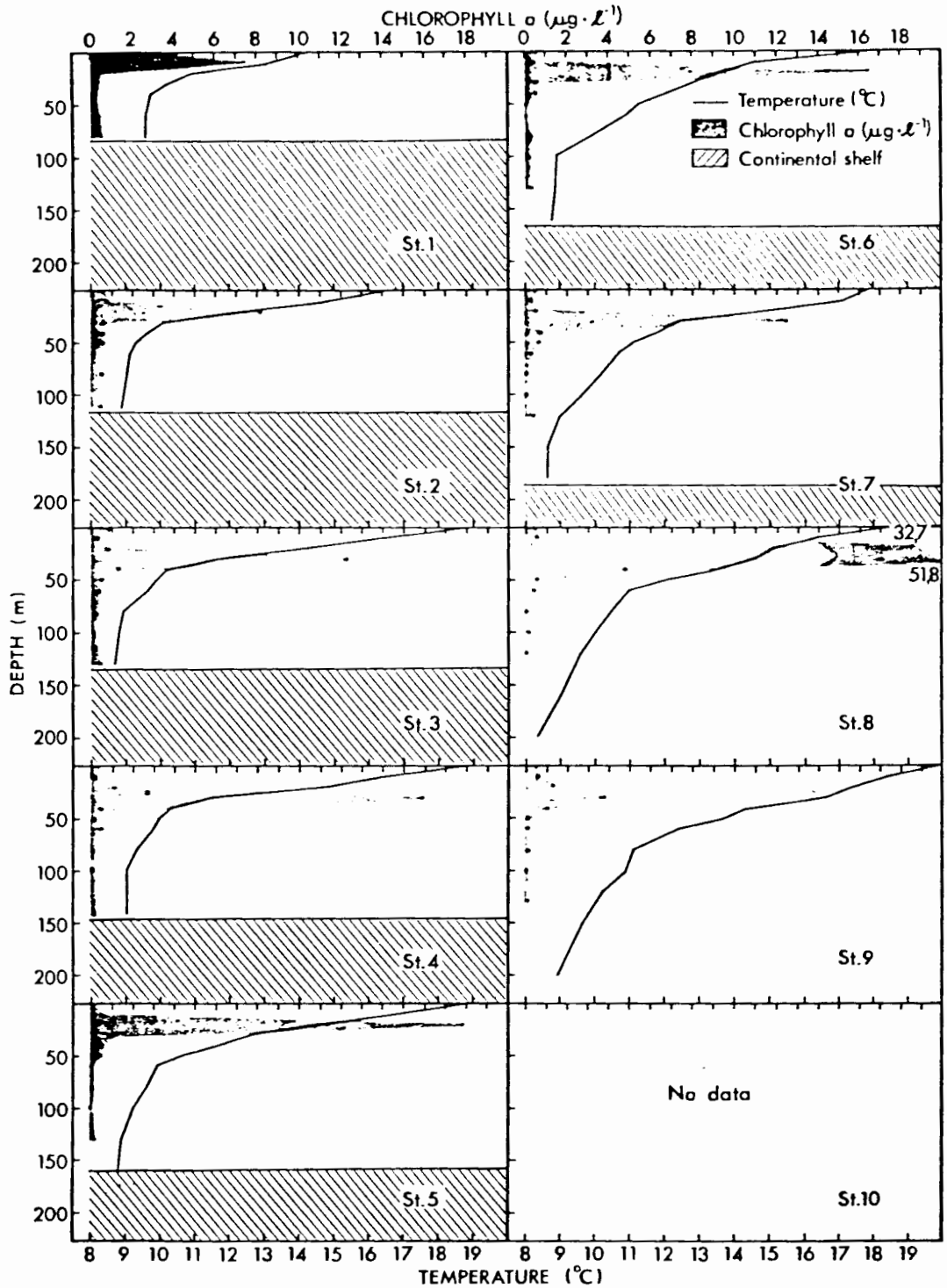

Fig. 15: Vertical profiles of temperature and chlorophyll a, January 1973

Table V: Species identifications and microscopic cell counts of samples exceeding 1 $\mu g \cdot \ell^{-1}$ of chlorophyll *a* during January 1973

Depth (m)	Station 1			Station 2			Station 3			Station 4			Station 5			Station 6			Station 7			Station 8			Station 9			Station 10		
	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D
0	3,0	Detritus	—	0,8			0,8			0,2			0,1			0,6			0,4			0,5			0,5					
10	7,4	Detritus	—	0,9			0,2			0,1			0,5			0,5			0,2			0,6			0,7					
20	0,5			8,2	Detritus	—	0,8			1,1			17,8	●=100% T=71 795	1	16,4	●=91% ■= 9% T=77 295	2	0,4			32,7	●=97% ■= 3% T=480 300	2	1,6	Detritus	—			
30	0,3			0,6			12,1	●=100% T=135 200	1	16,0	●=81% T=192 308	1	1,1	Detritus	—	0,6			12,4	Detritus	—	51,8	●=100% T=788 618	1	3,8	Detritus	—			
40	0,2			0,6			1,4	●=100% T=26 570	1	0,3			0,6			0,6			0,8			4,9	●=100% T=78 269	1	1,1	Detritus	—			
50	0,2			0,6			0,6			0,1			0,5			0			0,7			0,6			0,2					
60	0,4			0,1			0,4			0,3			0			0			0,3			0,4			0,1					
80	0,6			0,5			0,3			0			1			0,4			0,1			0			0,2					
100				0,4			0,1			0			0			0,2			0,2			0,2			0					

KEY OF SPECIES
●= *Nitzschia* spp.
■= *Skeletonema costatum*

KEY
Chl= Chlorophyll *a* ($\mu g \cdot \ell^{-1}$)
D = Diversity (species)
T = Total (cells ℓ^{-1})
□ = No count made
• = Inaccurate counts

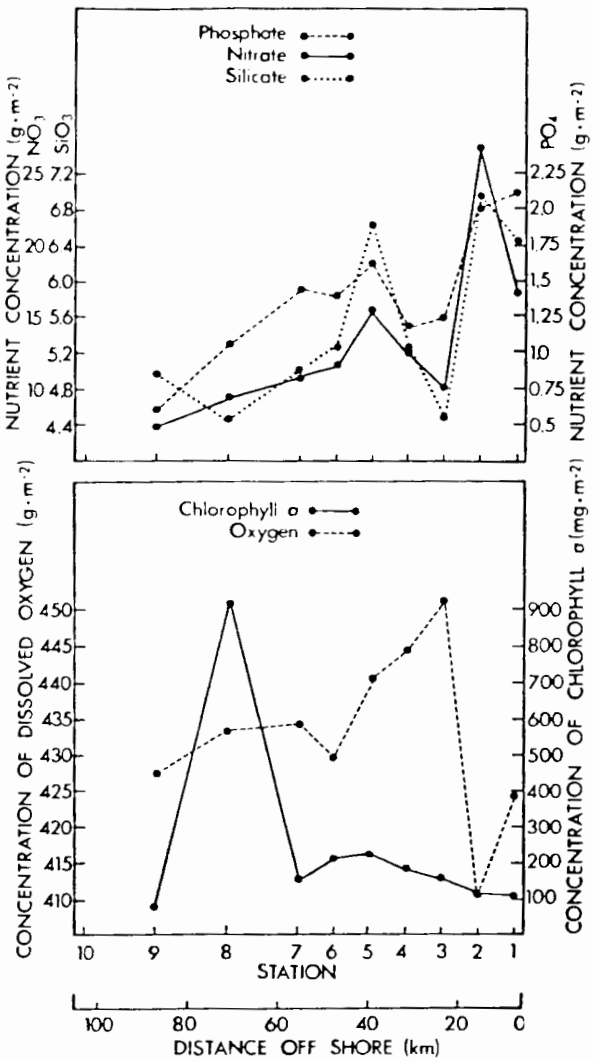

Fig 16: Changes within the euphotic zone (0—50 m) of chlorophyll *a*, dissolved oxygen, nitrate, silicate and phosphate, January 1973

caused by short-term wind events throughout the upwelling season. Andrews and Hutchings (1980) showed that upwelling was principally driven by the local surface winds, which determined the behaviour of the hydrographic parameters on a time scale of 12—18 hours. Short-term variability in the wind regime was shown to alter the intensity and the orientation of the plume by inshore and off-shore movement of the frontal zone and by the extent and the depth to which the belt of mixed water had been formed.

By analysing the changes in the distribution of the hydrographic parameters, the monthly transects were shown to display a varying width of phytoplankton-rich zone.

(i) "Limited" zones, which included the October transect, when 4 days of gentle south-easterly winds prior to sampling caused active upwelling inshore. The zone of mixed water was limited and the front occurred close inshore between Stations 6 and 7.

(ii) "Extensive" zones, which were identified when the development of mature blooms during November and February after strong and favourable winds for upwelling caused the upward displacement of isolines close inshore. Also, nutrient-rich water (i.e. NO_3>2,5 $\mu g \cdot \ell^{-1}$) was found up to 100 km off shore. Figure 20 shows the south-east wind component to be dominant over the six-month period, particularly during November and February. In these months a broad belt of mixed water extended far off shore, and a distinct frontal zone was evident between Stations 9 and 10, approximately 100 km off shore.

(iii) "Suppressed" zones, which were found when short-term reversals prior to sampling in *September* were thought to have been responsible for the onshore flow of oceanic water, as detected by high levels of salinity inshore. The front was situated approximately 50 km off shore where a well-defined upper mixed layer was apparent. Similarly in *January*, a lull in the south-east winds prior to sampling caused an intrusion of warm, saline oceanic water and the disappearance of surface upwelling inshore. A well-defined front was not evident. Unfavourable winds for upwelling occurred in *December* but sustained, powerful upwelling prior to sampling was thought to have occurred between 10 and 30 November, when strong south-easterlies prevailed. The front was better defined than in January and occurred off shore between Stations 7 and 8, approximately 30 km closer to land than during November and February. A broad belt of mixed, aged upwelled water with no upwelling inshore was also evident.

Inspection of the monthly surface temperatures and salinities (Fig. 21) showed the appearance of cool, less saline water inshore and warmer, more saline water off shore. The steepest temperature and salinity gradients were found during November, differences of 7,81°C and 0,66‰ being recorded. An overall increase in temperature and salinity occurred in the off-shore surface waters towards January and

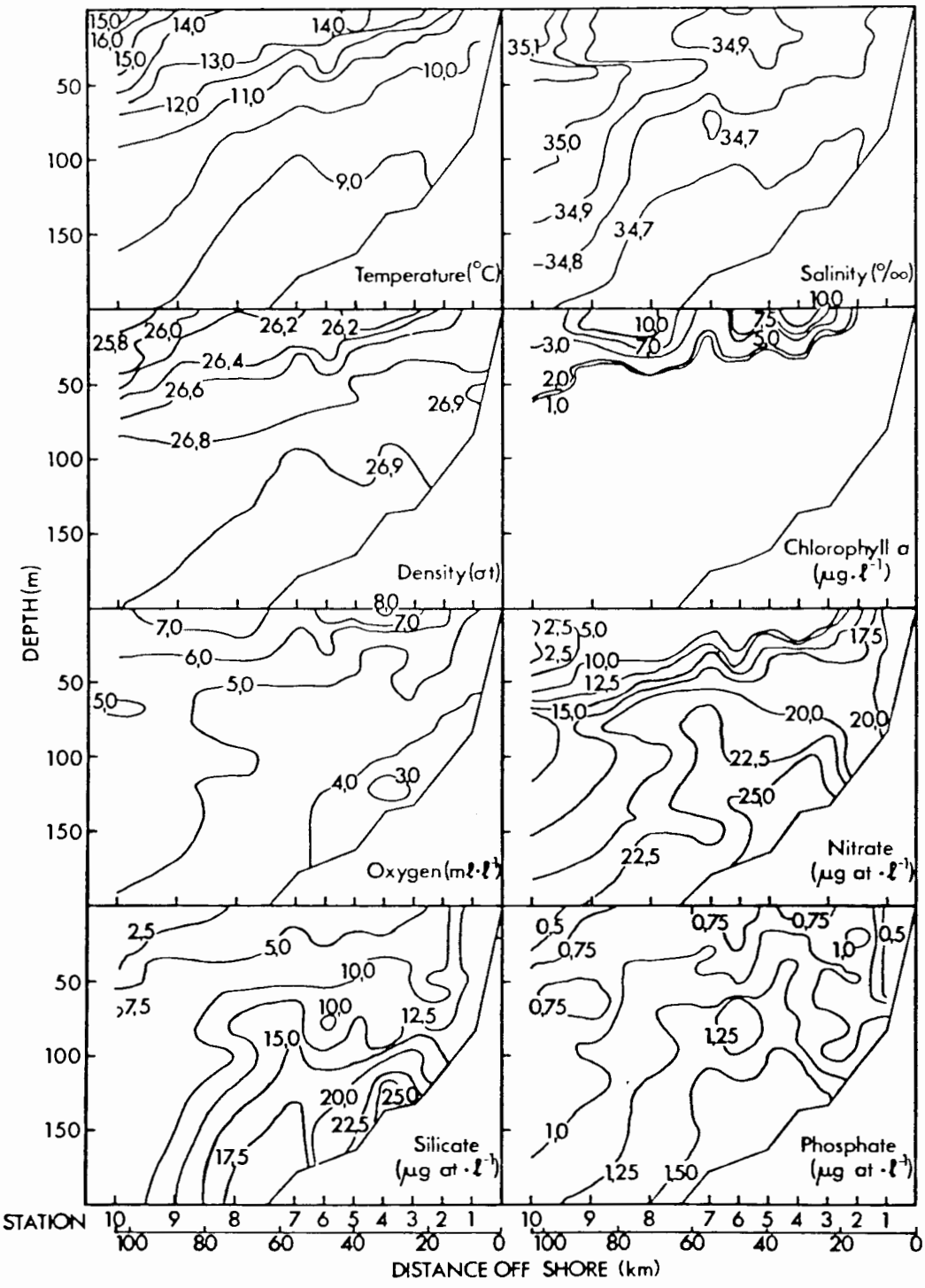

Fig. 17: Vertical distributions of temperature, salinity, density, chlorophyll *a*, dissolved oxygen, nitrate, silicate and phosphate, February 1973

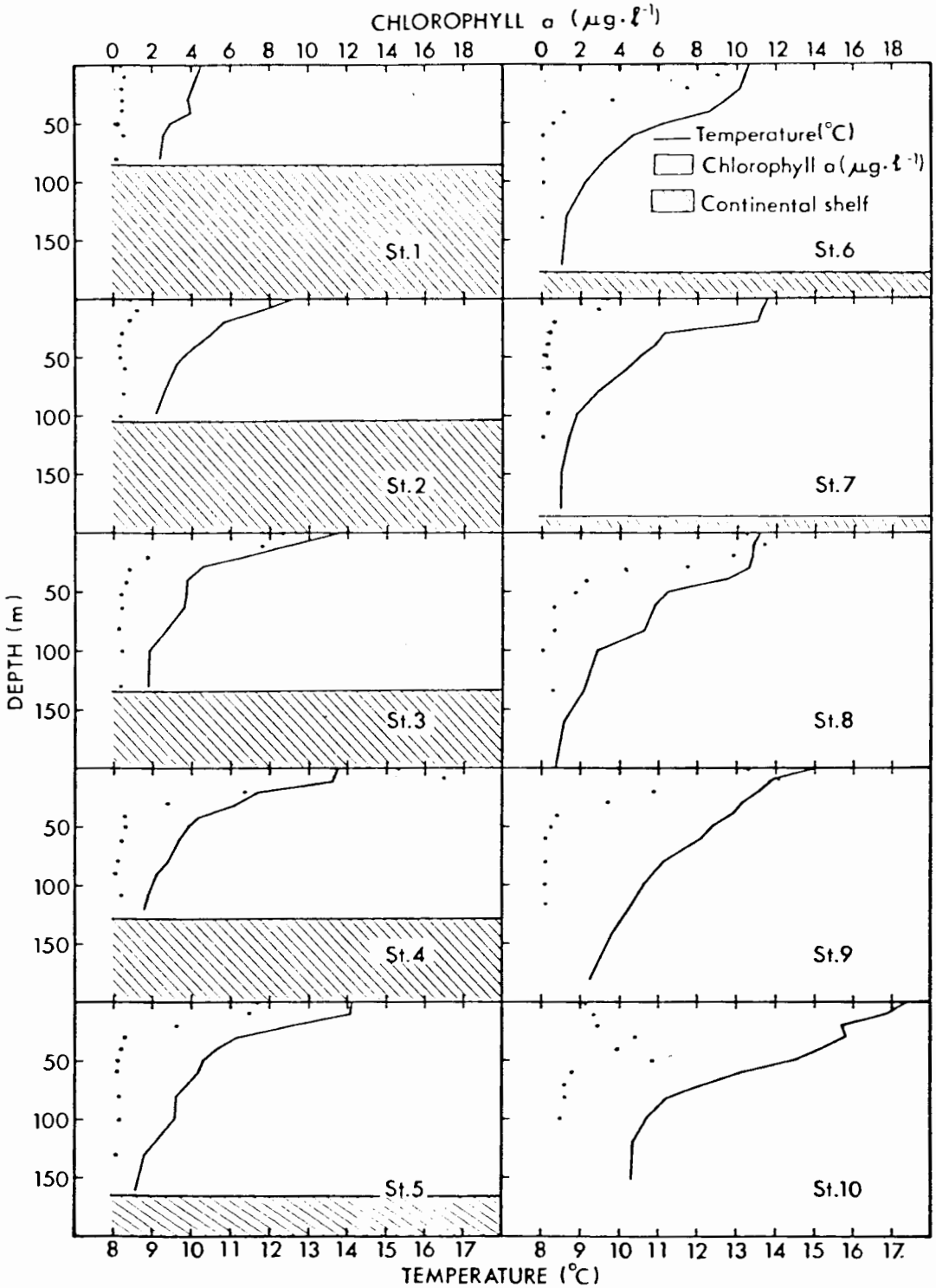

Fig. 18: Vertical profiles of temperature and chlorophyll *a*. February 1973

Table VI: Species identifications and microscopic cell counts of samples exceeding 1 $\mu g \cdot \ell^{-1}$ of chlorophyll *a* during February 1973

Depth (m)	Station 1			Station 2			Station 3			Station 4			Station 5			Station 6			Station 7			Station 8			Station 9			Station 10		
	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D	Chl	Count $\cdot \ell^{-1}$	D
0	0,4	Detritus	—	0,9			8,6	Detritus	—	14,4	●=95% O= 5% T=430 416	2	7,4	●=99% T=354 160	3	9,5	Detritus	—	3,4	Detritus	—	10,5	●=91% ■= 9% T=460 366	2	10,0	●=87% +=10% T=242 254	4	2,1	Detritus	—
10	0,5	Detritus	—	1,1			7,6	Detritus	—	16,9	●=89% O=11% T=578 671	2	6,9	●=96% T=237 681	4	9,0	Detritus	—	2,9	Detritus	—	11,5	●=99% T=429 524	2	12,1	Detritus	—	2,6	Detritus	—
20	0,3			0,8	Detritus	—	1,8	Detritus	—	6,7	●=96% O= 4% T=547 312	2	3,3	●=100% T=171 717	1	7,4	Detritus	—	0,7			9,8	●=100% T=367 708	2	5,8	Detritus	—	2,8	Detritus	—
30	0,3			0,4			0,8			2,7	●=100% T=200 000	1	0,6			3,7	Detritus	—	0,5			7,4	●=99% T=118 099	2	3,2	Detritus	—	4,4	Detritus	—
40	0,3			0,3			0,7			0,6			0,4			1,2	Detritus	—	0,3			2,2	●=99% T=123 288	2	0,9			3,9	Detritus	—
50	0,2			0,3			0,4			0,6			0,2			0,6			0,2			1,7	Detritus	—	0,5			5,7	●=99% T=315 686	3
60	0,3			0,4			0,4			0,4			0,2			0,3			0,4			0,6			0,2			1,5	Detritus	—
80	0,2			0,5			0,3			0,2			0,3			0,2			0,6			0,6			0,2			1,1	Detritus	—
100							0,4			0,1			0,3			0,3			0,3			0,1			0,2			1,1	Detritus	—

KEY OF SPECIES
● = *Nitzschia* spp.
O = *Chaetoceros* spp.
■ = *Skeletonema costatum*
+ = Dinoflagellate sp.

KEY
Chl = Chlorophyll *a* ($\mu g \cdot \ell^{-1}$)
D = Diversity (species)
T = Total cells $\cdot \ell^{-1}$
□ No count made

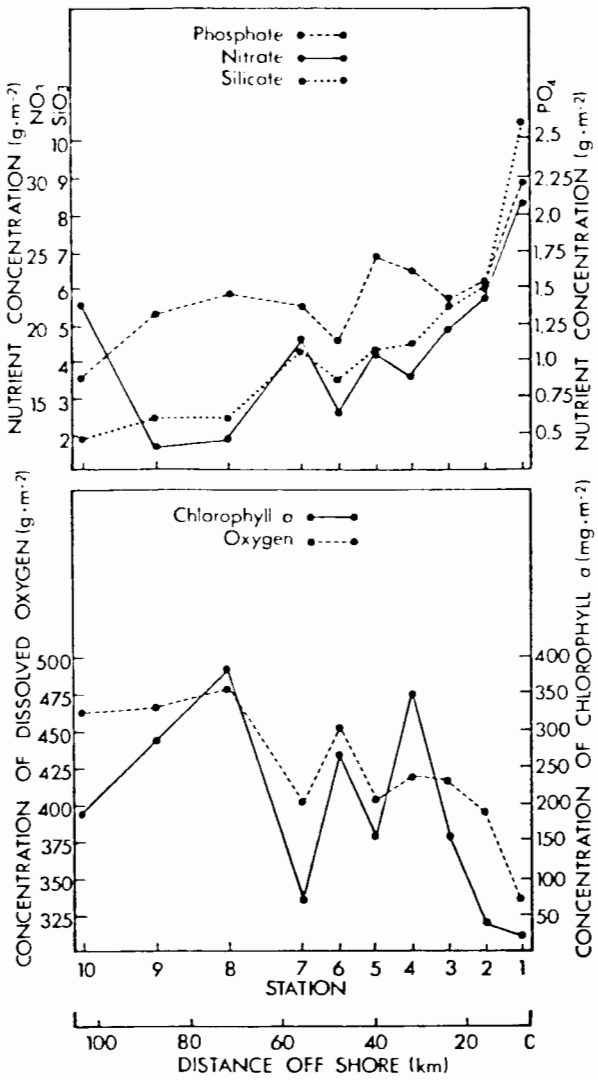

Fig. 19 Changes within the euphotic zone (0—50 m) of chlorophyll *a*, dissolved oxygen, nitrate, silicate and phosphate, February 1973

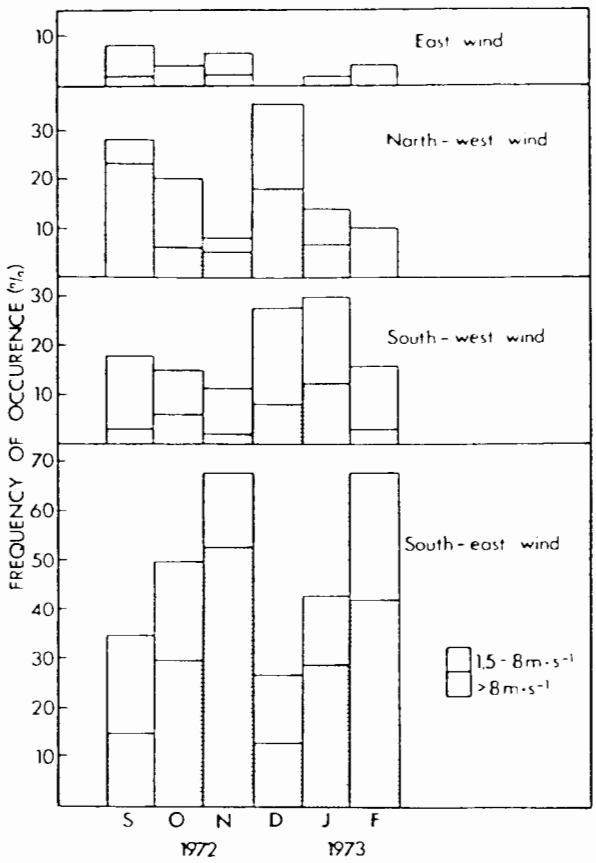

Fig. 20 Frequency of occurrence of four wind categories at Cape Point lighthouse over the six-month period (after Andrews and Hutchings 1980)

February. This has been shown by Shannon (1966) to result from a flow of Agulhas Bank water around the Cape of Good Hope in late summer. A sharp thermocline often developed from surface heating, and an associated pycnocline resulted in the stabilization of the water column.

Chemical changes — Throughout the period of sampling, the concentrations of inorganic nutrients at the surface declined in a seaward direction from high levels close inshore, where active upwelling had occurred, to lower and sometimes limiting levels off shore. Nitrates declined faster than either phosphates or silicates. Andrews and Hutchings (1980) showed nitrate to be the major limiting nutrient in this region by investigating the overall atomic ratios of nutrient utilization. They also showed, by using the criteria proposed by MacIsaac and Dugdale (1969), that the phytoplankton populations were physiologically adapted to high nutrient concentrations typical of fast-growing coastal populations.

Values of each nutrient integrated down to 50 m are compared on a monthly basis and illustrated in Figure 22. The steepest nutrient gradient occurred during October, when phytoplankton standing stocks were lowest. It would seem likely that gradients caused by nutrient depletion from phytoplankton uptake were accentuated by the close proximity of

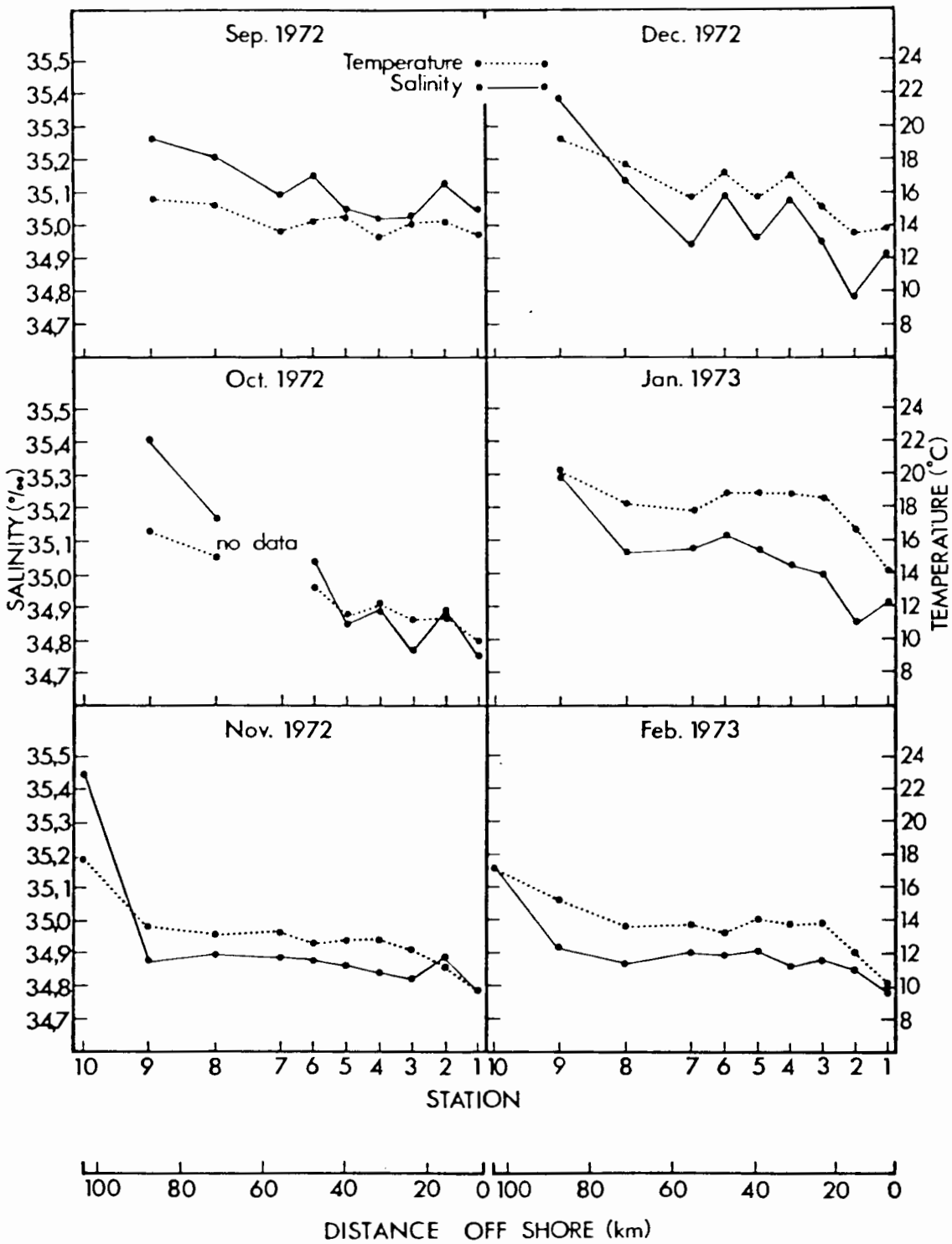

Fig 21: Changes in monthly surface temperature and salinity

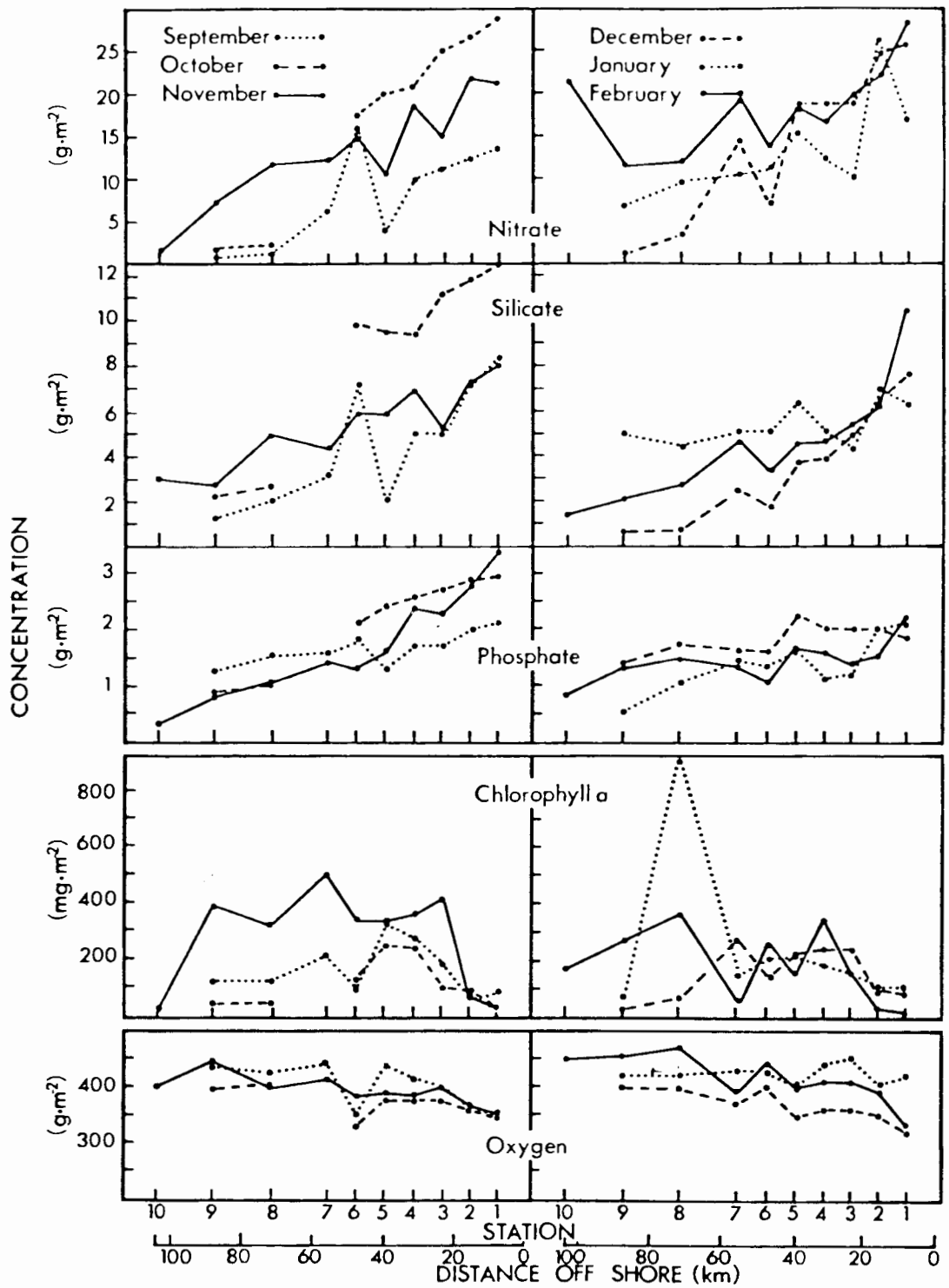

Fig. 22: Monthly changes within the euphotic zone (upper 50 m) of nitrate, silicate, phosphate, chlorophyll *a* and dissolved oxygen

oceanic and newly upwelled waters, with only a narrow belt of mixed water between these waters.

Changes in biomass — Values of chlorophyll *a* integrated down to 50 m are compared on a monthly basis and illustrated in Figure 22. The highest standing stocks were found during November, when the mixed-water belt was best developed. The highest concentration in the phytoplankton population was in January, when the invasion of oceanic water shorewards appeared to cause phytoplankton to passively accumulate on the strong pycnocline. Levels of chlorophyll *a* reached 51,8 $\mu g \cdot \ell^{-1}$, but with surprisingly low cell counts of 788×10^3 cells $\cdot \ell^{-1}$. The chlorophyll *a* maximum on the other transects was generally found above or within the thermocline. A surface chlorophyll *a* maximum was observed during upwelling months (October, November, February), when the thermocline was relatively shallow. A subsurface chlorophyll *a* maximum was associated with the development of a deep thermocline and sinking at the front (November, December) or an invasion of oceanic water (September, January). In general, higher cell counts were associated with high concentrations of chlorophyll *a*.

Increases in dissolved oxygen occurred within the chlorophyll *a* maximum layer, although integrated values within the euphotic zone, compared on a monthly basis (Fig. 22) do not reveal this. A possible reason could be the mixing of the upwelled waters with surrounding more mature waters, resulting in variations in the initial concentrations of dissolved oxygen. Low-oxygen water appeared close to the shelf between Stations 4 and 7 during December, January and February. The appearance of oxygen-depleted water in late summer originates from an "azoic area" in the Walvis Bay region along the shelf off South West Africa (De Decker 1970). "Local" oxygen-depleted water off the Cape Peninsula was shown by Andrews and Hutchings (1980) to differ from "distant" oxygen-depleted water in the ratio of nitrate : silicate. The effect of this low-oxygen water on the species diversity and abundance in the upwelled water should be considered in future seeding and colonization studies.

Phytoplankton species

The waters were primed with 21 species during the early spring bloom (September) although only two *Nitzschia* spp. dominated. *N. pungens* was found close inshore and was succeeded by *N. seriata*, a larger-celled species. During October, the phytoplankton standing stock seemed to have consisted, by and large, of detrital material, but it is possible that cellular degradation because of poor preservation was responsible. However, *Thallassionema nitzschioides* and *Chaetoceros* spp. were abundant. In the remaining months, *Nitzschia* spp. constituted approximately 90 per cent of the total cell count in all samples. *Chaetoceros* spp. and *Skeletonema costatum* made up a small percentage of the total during November and January.

Nitzschia, a genus of pennate diatoms, was the main contributor to the high concentrations of chlorophyll *a* measured throughout the coastal waters over the six-month period, when a wide variety of upwelling conditions were experienced.

Patterns of succession

Consistent patterns of phytoplankton distribution do not seem to exist in the Cape Peninsula upwelling plumes. Analysis after a drogue study in 1979 off the Cape Peninsula showed that a mixed phytoplankton bloom was dominated by *Chaetoceros compressus* and *Skeletonema costatum* (Olivieri 1981). In contrast, this study showed *Nitzschia* spp. to persist throughout the upwelling season from September 1972 to February 1973. This dominance by *Nitzschia* occurred despite the continued presence (in low numbers) of *C. compressus* and *S. costatum*.

According to D.A. Horstman (Sea Fisheries Research Institute, personal communication), species of the genera *Chaetoceros, Skeletonema* and *Thalassiosira* were the dominants off the west coast of the Cape Peninsula during the summers of 1964, 1966 and 1967. It is evident, therefore, that a wide diversity of species can dominate coastal waters at various stages of maturity and mixing after upwelling.

Variations in source water

Unfortunately, there is very little information on the cross-shelf circulatory patterns and on the actual origins and surface mixing of the upwelled waters with neighbouring waters. Shannon (1966) showed the upwelled water to be of Central South Atlantic origin and Andrews and Hutchings (1980) showed it to possess constant chemical and physical properties. Recent results suggest that the Cape Point Valley may play an important role in funneling this water onto the shelf, hence establishing a perennial subsurface cold-water plume (Shannon *et al.* 1981).

The quantitative and qualitative content of the biological material in the upwelled waters depends on the origin of the source water and the type of

sediments encountered. The upwelled waters in the above-mentioned studies were shown to be primed with similar species, supporting the views that a constant source of water upwells, and that the colonization of species depends ultimately on their initial numbers (cell concentrations) and on the specific selective adaptations for growth of individual species.

Greater emphasis should be placed in future on investigating the advective variations in the subsurface and longshore flow systems, if the successional sequence of the phytoplankton is to be predicted. This, of course, does not exclude the aspect of successful maintenance of the phytoplankton community once it has been initiated. Research in other upwelling regions has shown the existence of subsurface on-shore counter-currents. For instance, Barber and Smith (1981) showed that the cross-shelf circulatory pattern off Peru physically sorted the phytoplankton according to their specific sinking rates or speeds of vertical migration. Phytoplankton cells were shown to recirculate in the upwelling system by sinking out of the surface layer flowing off shore into the subsurface layer flowing on-shore. Herbland *et al.* (1973) suggested that a similar mechanism exists in the upwelling system off North-West Africa. The undercurrent was suggested to play an important role in the re-cycling of the upwelling water.

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