COLONIZATION AND SUCCESSION OF PHYTOPLANKTON SPECIES IN UPWELLING PLUMES OFF THE CAPE PENINSULA

by

EMILIA TÉRÉSA OLIVIERI

A thesis submitted for the Degree of Master of Science
Department of Botany
University of Cape Town
Rondebosch, Cape Town, Republic of South Africa

1981

CONTENTS

Page

ACKNOWLEDGEMENTS

REFERENCES

PLATES

LIST OF TABLES

LIST OF FIGURES

Page

Page

ABSTRACT

Colonization and temporal changes in phytoplankton diversity and biomass in the upwelling plumes off the Cape Peninsula are described for two different communities. A drogue study showed the presence of a fast-developing mixed phytoplankton community with *Chaetoceros compressus* Laud. and *Skeletonema costatum* (Grev.) Cleve the dominant species. Monthly transect studies, however, revealed the presence of another community consistently dominated by *Nitzschia* spp. Species succession did not occur in either phytoplankton community.

Factors likely to affect the development of the phytoplankton communities and cause differences in certain community characteristics, e.g. dominance, biomass and diversity, were attributed to differences in:

(1) the origins of the source water;

(2) the wind speed and direction; and

(3) the sampling strategies employed.

The factors responsible for the successful colonization of the different species in the phytoplankton community were thought to depend on:

(1) the initial variations in species diversity and abundance of the seeded population in newly upwelled waters;

(2) the extent to which the upwelled waters mixed with neighbouring waters; and

(3) the specific selective adaptations for growth of the individual species.

Possible adaptive phytoplanktonic mechanisms in a changing environment, were discussed in terms of cell size, growth, nutrient absorption and buoyancy.

CHAPTER 1

INTRODUCTION

1.1 Succession

1.1.1 Definition

For the purpose of this thesis, phytoplankton succession may be defined as "a continuous process of self-organization, based on interactions among species and between organisms and their environment, which is manifest in many measurable changes in the ecosystem" (Margalef, 1967).

1.1.2 Different lines of investigation

The earliest studies of biological succession described the sequence of species that successively invaded a site (Cowles, 1899; Clements, 1916) with little attention being paid to environmental changes. Later a number of independent areas of investigation developed, among which two major approaches can be recognized.

The first, a deterministic approach to mathematical modelling developed by Riley (1947) and other co-workers, relates successional changes in standing stock to a number of physical, chemical and biological factors. This approach consists of a search for generalizations about the manner in which certain biological parameters (such as biomass and turnover rate) evolve during the course of succession (Margalef, 1968). However, information concerning the distribution and succession of individual species is usually lost in such studies.

The second approach involves identifying the factors causing changes in species composition from laboratory culture studies. Such studies have revealed that chemical and physical factors are primarily responsible for successional changes. Studies of how factors interact in controlling the growth of phytoplankton have progressed rapidly since Dugdale (1967) introduced the Michaelis-Menten Equation for modelling nutrient-limited growth and kinetics of nutrient uptake. Examples of this approach can be found in papers of Eppley *et al.* (1969); Paasche (1973); Parsons & Takahashi (1973); Droop (1973); Goldman & Carpenter (1974); and O'Brien (1974). To date, they have predicted successional patterns with moderate success. Although such studies have greatly increased our understanding of the physiology of species under laboratory conditions, it is often difficult to interpret results in relation to field observations.

The lack of a generally suitable model capable of describing quantitatively the process of succession has caused much uncertainty and speculation (Jassby & Goldman, 1974). Those successional trends that have been described are inconsistent and not strictly directional (Pickett, 1976). The following publications provide data useful in comparative studies of marine plankton successions; for example: Margalef (1958); Venrick (1971); Semina *et al.* (1976); Holligan & Harbour (1977); Hulburt (1977); Pingree *et al.* (1975, 1976, 1977); Reid *et al.* (1978); and Simpson *et al.* (1979).

1.1.3 Summary of successional trends

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

(1) A general increase in cell size implying a decrease in the surface area to volume ratio.

(2) A decrease in the maximum potential growth rate.

(3) An increase in the occurrence of motile forms.

The major associated environmental changes were:

(1) A decrease in turbulence.

(2) A decrease in both nutrient concentration and rate of nutrient supply.

(3) An increase in water temperature and usually salinity. Light quality and intensity may also be somewhat modified.

Margalef claimed that succession begins with some mixing process such as upwelling which results in the fertilization of the euphotic zone. The initial increase in the nutrient concentrations, turbulent mixing and stabilization of the water mass as it moves offshore, provide a sequential gradient for phytoplankton succession.

1.2 Upwelling

1.2.1 The Benguela upwelling system

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 & Currie, 1960). The Cape Peninsula upwelling system is primarily generated by the orographic force of the wind which, with a strong southeasterly component, results in offshore Ekman transport of surface water (Shannon, 1966). Upwelling rates of up to 30 m day^{-1} have been estimated in this area. Between September and May, when strong southeasterly winds predominate, a plume of cool water extends up to 100 km northwest of the Cape Peninsula. It is separated from warmer oceanic water by a distinct frontal zone. Within this plume of ageing upwelled water maximum chlorophyll concentrations have been recorded and biological activity is most intense (Andrews & Hutchings, 1980).

1.2.2 Types of mixing

Andrews & Hutchings (1980) have identified 3 water types from data collected over 5 consecutive upwelling seasons by calculating mean values of conservative (temperature, salinity) and non-conservative (oxygen, nutrients, chlorophyll 'a') parameters. The degree of mixing of different water types is variable. When calm conditions prevail simple ageing of the water occurs inshore. When southeasterly winds persist, newly upwelled water moves offshore and northwards and mixes with aged upwelled water or oceanic water. In all cases a shallow upper mixed layer develops, 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, as the nutrients and light change with time. A reversal in wind direction from southeast to northwest causes onshore transport of water resulting in active downwelling at the coast (Andrews & Hutchings, 1980).

1.3 Study Aims

The aim of this study is to describe the colonization and the temporal changes in the species diversity and biomass of phytoplankton in the upwelling plumes off the Cape Peninsula.

The first approach (mentioned earlier) will be used to search for successional trends. Certain community characteristics such as biomass, diversity, and growth rates will be investigated and successional stages in conjunction with environmental changes will be characterized.

An attempt will be made to understand the mechanisms causing the species to change, by using the published data obtained from culture studies (second approach). The possible adaptive phytoplanktonic mechanisms and implications to the upwelling system will be discussed.

This study will allow for the establishment of whether consistent patterns of phytoplankton species succession exist in the Cape Peninsula upwelling plume.

The significance of the initial species composition and abundance in newly upwelled waters on colonization and succession will be discussed in relation to the origins of the source water.

CHAPTER 2

MATERIALS AND METHODS

2.1 Introduction

Two basic methods have been employed in this investigation, due to the fact that the study of succession is inextricably linked to changes in plankton distributions (Margalef, 1967).

The first approach has been to assess the changes in phytoplankton communities after a period of upwelling, by monitoring a single parcel of water over several days. This approach has been used by Ryther *et al.* (1971); Beers *et al.* (1971); and Herbland *et al.* (1973). The build-up and decline of the phytoplankton crop could thus be documented.

The second approach has been to assess the monthly changes in phytoplankton communities from a line of stations running along the apex of the normal position of the upwelling plume. These serialized 'snapshots' have been used to provide a reconstruction of successional events over a period of six months, without an absolute time scale for each transect (i.e. distance offshore is assumed to be equated with time).

2.2 Study Methods

2.2.1 Drogue study

Cruise strategy

The drogue study (Plankton Dynamic Cruise) was undertaken between 4.12.79 and 13.12.79, 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 (Figure 2.1) which was then marked with a tetrahedral drogue set at 10 metres, 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 5.12.79. This drogue (drogue track I) showed the existence of a southward flowing current close inshore, with strong vertical mixing, which prevented significant surface sunwarming. The drogue was therefore retrieved after 46 hours and a second drogue (drogue track II) was released 10 km from the coast (33° 55,4'S, 18° 16,3'E) on 7.12.79 in water with a surface temperature of 10,4°C. The drogue (drogue track II) was followed for 5 days, sampling 3 - 4 times per day. An aerial survey showing the wind speed and direction at 500 ft and sea surface temperatures was conducted over the Cape Peninsula during the drogue study (Jury, 1980)

Sample collection

Three stations were sampled daily at 0730, 1200 and 1800 hrs. Samples were taken as close to the drogue as possible A bathythermograph cast was made, and submarine light levels were determined using a Lamhda LI-192S underwater quantum sensor. The sample depths were at the 100%, 50%, 25%, 10%, 1% light levels and then at 10 metre intervals to the bottom. Temperature was measured using a Nansen-Pettersen insulated water bottle from which salinity samples were drawn. Simultaneously, 7 or 5-litre 10S bottles were used to collect samples for measuring oxygen, nutrients, chlorophyll, particulate protein, carbohydrate, carbon and nitrogen, C^{14} uptake and for counting phytoplankton. Two sets of phytoplankton samples were collected. One set was preserved with 4% buffered formalin to be counted ashore microscopically, using the Utermöhl technique. The other set was counted electronically on board using 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

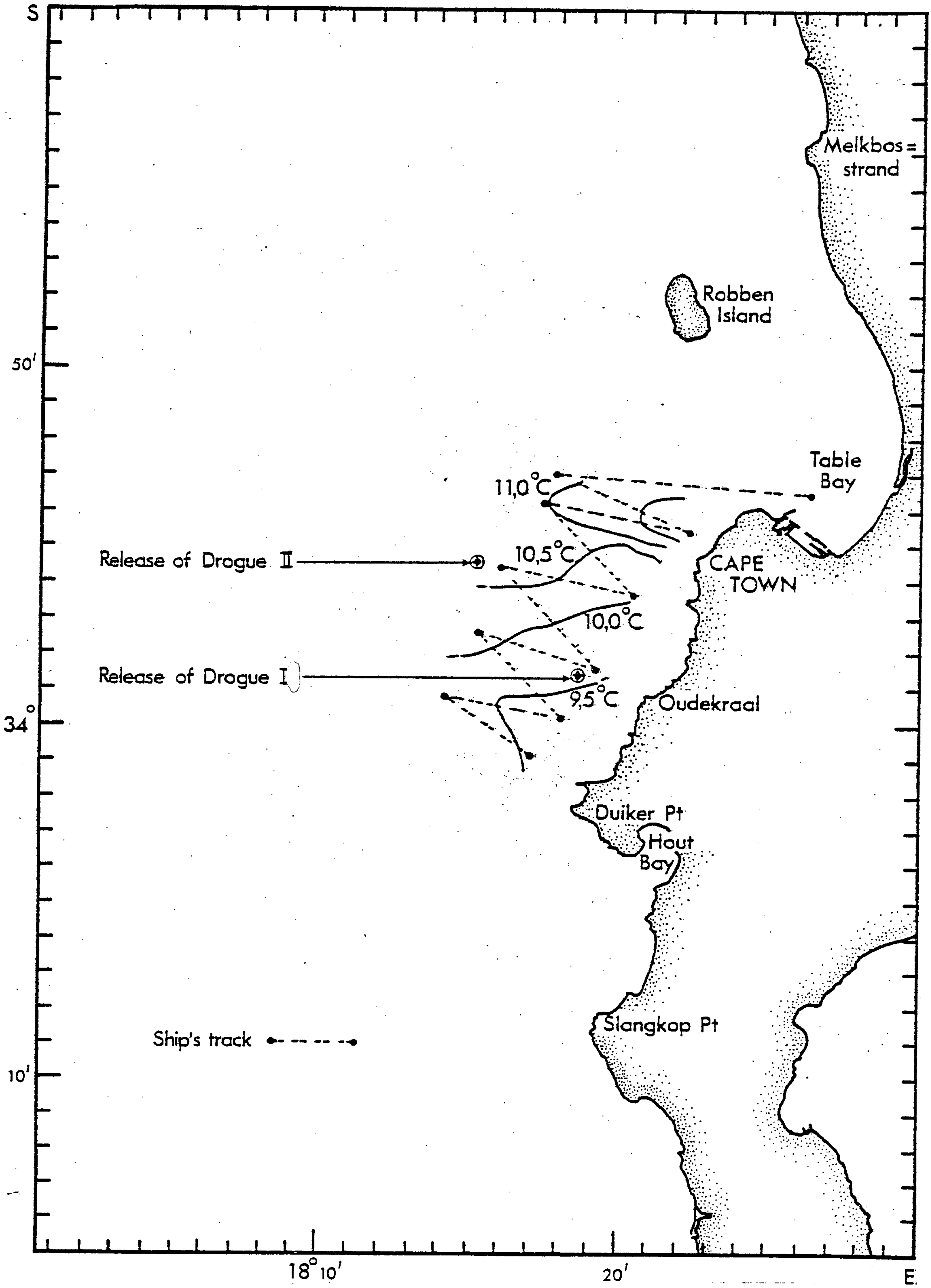


Figure 2.1 Distribution of surface temperatures °C between Cape Town and Duikerpoint off the west coast of the Cape Peninsula.

measured with a Bissett-Berman Model 6600 thermosalinograph. The drogue position, wind speed and direction were recorded every hour on the hour.

2.2.2 Transect study

Cruise strategy

The cruise consisted of sampling a line of up to 10 stations (Figure 2.2) at monthly intervals over a period of 30 months beginning in October 1970. Stations 1-7 were 8 km apart and ran due northwest of Duiker Point. Stations 8, 9 and 10 were approximately 16 km apart and ran in a west-northwesterly direction. It took two days to sample all stations with sampling proceeded from the inshore stations seawards.

Sample collection

Samples were taken at 10 metre intervals to 60 metres; at 20 metre intervals to 120 metres; at 150 metres; and at 100 metre intervals from 200 metres to the bottom. The deepest sample was usually taken within 4 metres of the bottom. Temperatures were measured with Nansen-Pettersen insulated water bottles at shallow depths and Munroe-Ekman reversing bottles at deeper levels. Samples for measuring salinity, oxygen, nutrients, chlorophyll and phytoplankton were collected in 7 or 5-litre NIO 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 the 3rd and 6th stations with a photometer (lux) and a deck reference cell.

2.3 Processing of Samples

The processing of the samples was similar for both cruises except

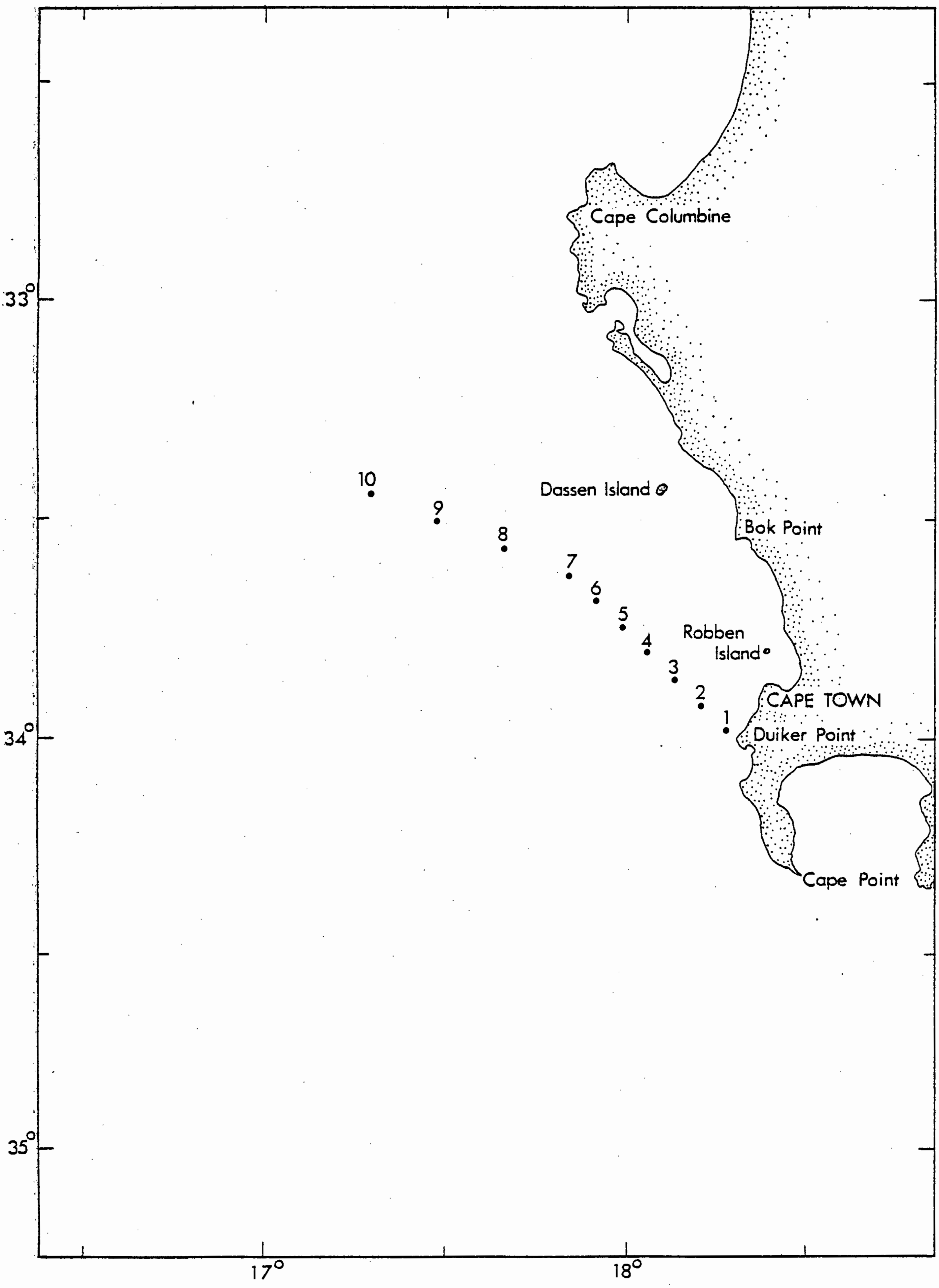


Figure 2.2 The line of ten stations sampled monthly during the transect study.

that a Coulter counter was used in the drogue study. Three analytical techniques were therefore used to measure changes in phytoplankton biomass in the drogue study.

(1) Cell size and frequency was measured microscopically.

(2) The volume and frequency of particles was measured using a Coulter counter.

(3) Chlorophyll 'a' concentrations (μg/l), were determined spectrophotometrically.

2.3.1 Salinity

Salinity samples were stored in glass bottles and analysed with an inductively-coupled autolab salinometer. Both standard Copenhagen and substandard water were used for calibrations.

2.3.2 Oxygen

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

2.3.3 Chlorophyll 'a'

One-litre water samples from the upwelling monitoring cruise were filtered on board and stored at -20°C for later spectrophotometric analysis of chlorophyll 'a'. Wavelengths and equations recommended by UNESCO (1966) were used.

2.3.4 Nutrients (phosphates, silicates, nitrates)

Samples for measuring phosphates, silicates and nitrates were deep frozen in 100 ml polythene bottles. Analyses were done ashore using a Technicon autoanalyser and following the methods of Strickland & Parsons (1968) for phosphates and nitrates, and of Grasshoff (1966) for silicates.

2.3.5 Preserved phytoplankton - Utermöhl method

Preserved phytoplankton samples were analysed by the Utermöhl (1936) method of sedimentation using an inverted microscope, but following the simplified procedure and recommendations of Willén (1976) and Hobro and Willén (1977). The sedimenting chambers used were 10 ml or 50 ml, depending on sample concentrations. Samples were well agitated and poured into settling chambers through a filling chamber. This ensured the sediment to be uniformly distributed. The recommended time of at least 3 hrs for 10 ml and 8 hrs for 50 ml was allowed for the sediment to settle (Lund *et al.*, 1958).

Most phytoplankton counts were made using a 40 x phase contrast objective. The eye-piece micrometer was calibrated for all objectives using a stage micrometer. The width of the counting strip was measured with the eye-piece micrometer and was adjusted according to the density of the sample. Strips were counted until a minimum of 2% of the total counting area was scanned. Sample counts were expressed as cells/litre. Phytoplankton were identified from the drawings and descriptions of Hustedt (1962); Hendey (1937) and Cupp (1943).

Estimates of precision were obtained by making six successive counts from one sample. The results are given in Table 2.1

Table 2.1 Replicate counts analysed at the 95% confidence level using ($\bar{x}$) arithmetic mean; (c.v.) coefficient of variation; ($\frac{s}{\sqrt{n}}$) standard error and marginal error (Hobro & Willén, 1977)

No. of Replicas	Mean (particles/ℓ) $\bar{x}$	Coefficient of Variation c.v.	Standard Error $\frac{s}{\sqrt{n}}$	Marginal Error $\frac{SE.t.\ 100}{\bar{x}}$
6	1215696	28998	11838	2.5%

The percentage marginal error obtained for all 6 counts was 2,5% at the 95% confidence level.

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

2.3.6 Unpreserved phytoplankton - Coulter counter method

Unpreserved phytoplankton samples were counted on board electonically, using a Model TA II Coulter counter following the method described by Sheldon & Parsons (1967). Briefly, this method determines the number and size of particles suspended in an electronically conductive fluid. For the purpose of this study, the 280 µm aperture tube was used, as 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 readout 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 $\mu m^3 \times 10^{-6}$/ml) was set using the procedure outlined in the Coulter counter Model TA II 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. Samples were well 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 secs) were made in the time mode, with the manometer pinched off to prevent erratic flow due to the mercury column surging at sea. Two plots per station depth were produced:

(1) Log particles/ml versus diameter intervals in micrometers.

(2) Concentration by volume (p.p.m.) versus diameter intervals in micrometers.

2.4 Numerical Analyses

2.4.1 Cluster analyses

Bray-Curtis coefficient

The Bray-Curtis (Czekanowski) per cent similarity index (PSI) (Barnes, 1951; Field & Robb, 1970; Field, 1970, 1971; and Clifford & Stephenson, 1975) was used to determine similarities between stations after cell concentrations expressed as cell counts/litre had been log transformed. Dendrograms were prepared from the Group Average Sorting Method of Clifford & Stevenson, *ibid* and Field, *ibid*.

McConnaughey (PSI)

The McConnaughey (1964) index (PSI) was similarly used to group associated species based on species absence or presence.

2.4.2 Abundance-frequency distributions

Abundance-frequency distributions were plotted for several species. The shape of the abundance-frequency distributions were examined statistically using the coefficient of variation ($cv = s/\bar{\chi}$); and a skewness statistic ($SK = [\Sigma(\chi-\chi)^3/n]/s^3$), (Glass & Stanley, 1970). These 2 indicators of curve shape were correlated with mean abundancies for several species.

CHAPTER 3

DROGUE STUDY

3.1 Results

3.1.1 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 (Figure 3.1(a)) showed the existence of a southward flowing current close inshore characterized by strong vertical mixing. The second drogue was therefore released further offshore and travelled a distance of 28,2 km in 102 hrs for a mean drift of 0,27 km/hr. 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 m/sec from the south. Evidence from wind data, recorded from the research vessel (Figure 3.1(b)) showed that an average wind speed of 7 m/sec 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, roughly parallel to the coast. The prevailing southerly winds effectively caused northward and alongshore water movements.

There were two lines of evidence to support that the drogue followed the same body of water up till 10.12.79 (day 4).

(1) The movement of the plume as observed from the aerial survey (Figure 3.2) coincided with the track of the drogue.

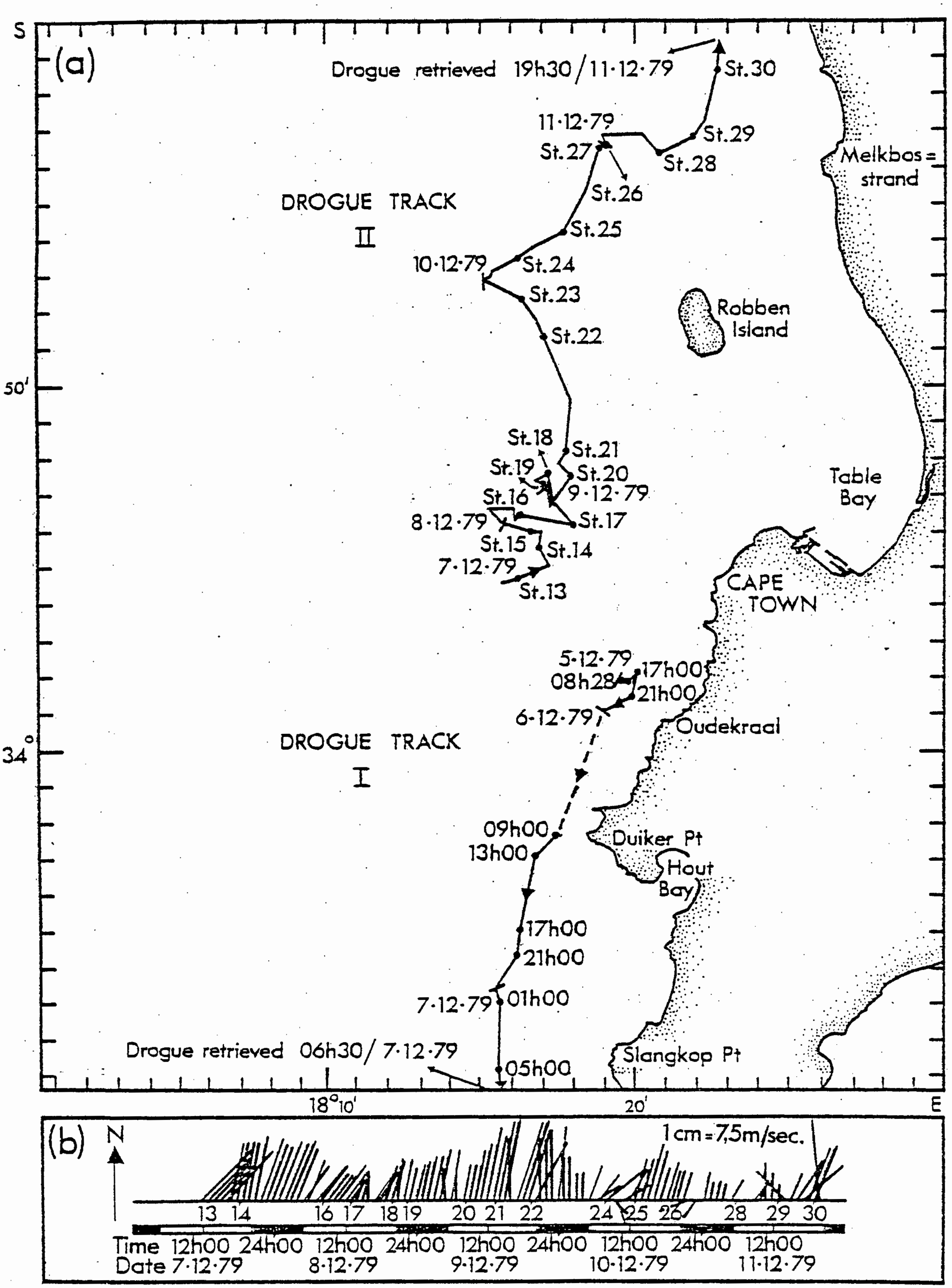
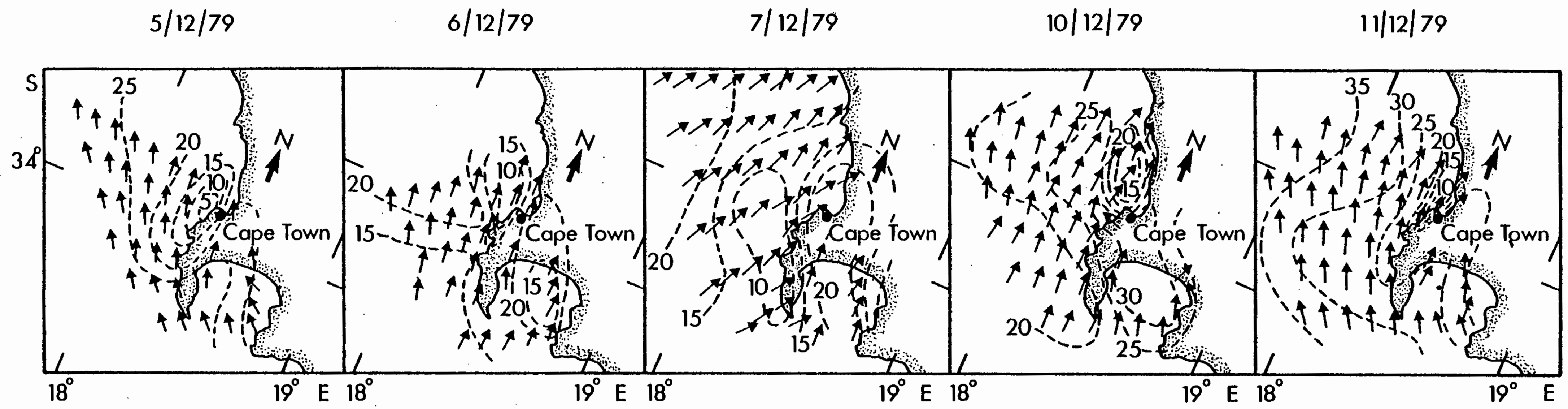
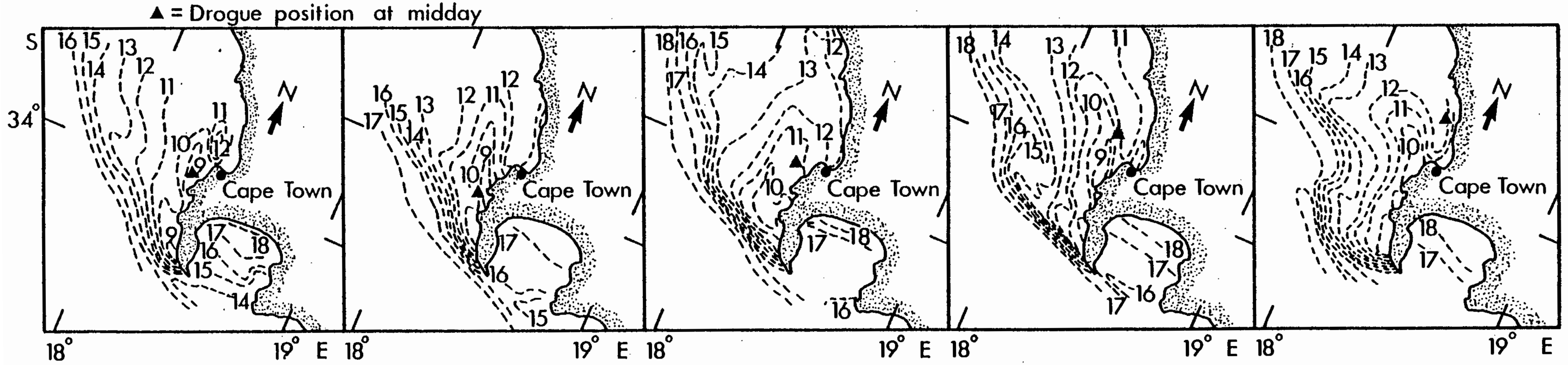


Figure 3.1(a) Drogue trajectories

(b) Wind stick diagram of drogue track II (7-11 December 1979).



WIND (knots) AT 500 FEET



SEA TEMPERATURE SURFACE (°C)

Figure 3.2 Flight maps showing wind speed and direction at 500 ft and sea surface temperatures (S.S.T). (Courtesy Jury, SFI.)

Two distinct plumes were observed on 5 and 6 December at Olifantsbos and Oudekraal during southerly and southeasterly winds. The wind then veered to the southwest on 7 December and by 10 December southerly winds had resumed, producing a single plume 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. On 11 December, however, the drogue veered shorewards whilst the plume moved off in a northwesterly direction.

(2) Several parameters measured at the 10 metre drogue depth (Figure 3.3) showed that there was a continuous increase in phytoplankton growth until Station 26 (day 4). Temperature and oxygen increased steadily by 1,9°C and 2,9 ml/l respectively. Chlorophyll 'a' concentrations increased by 21 µg/l and the cell counts increased by 1950 x 10^3 cells/l. Conversely, concentrations of nitrates, silicates and phosphates decreased by 82, 72 and 29 per cent respectively. Such increases in biomass, oxygen and temperature with the corresponding depletion of nutrients over the first four days, strongly suggested that the drogue followed a coherent body of water in which phytoplankton was actively developing. On the 5th day however, the temperature, and oxygen values declined and an apparent drop in standing stock was also evident. These features suggested that the body of water was being mixed with cooler, less mature and more recently upwelled water.

3.1.2 Measurements of Standing Stock

Comparative estimates of biomass

The chlorophyll 'a' concentrations (µg/l), inverted microscope

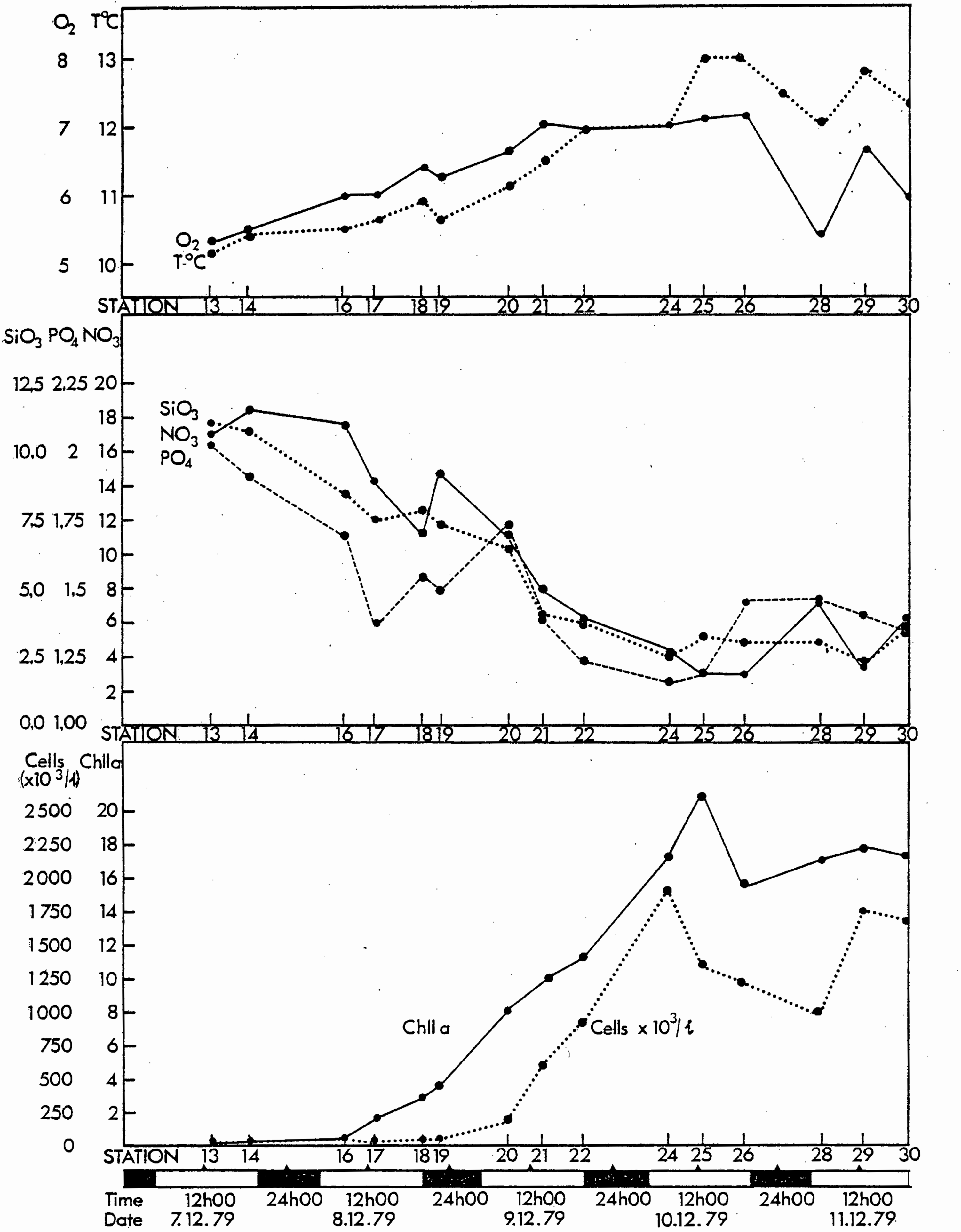


Figure 3.3 The distribution of temperature (°C), dissolved oxygen (ml/l), nitrates (µg atoms/l), silicates (µg atoms/l), phosphates (µg atoms/l), chlorophyll 'a' (µg/l), and microscopic cell counts ($\times 10^3$/l) at the 10 metre drogue depth.

counts (counts/l x 10^3), Coulter counter counts (counts/l x 10^3, and altered Coulter counter counts (i.e. minus channels 2 and 3) (counts/l x 10^3) are presented in Table 3.1 for each station at the various light levels. Values obtained for each method followed a similar trend, where an increase from station 13 - 30 was observed. The highest cell counts were concentrated between stations 24 - 26. A maximum of 2 280 cells/l x 10^3; 7 744 particle/l x 10^3; and 4 381 particles/l x 10^3 was obtained using the inverted microscope method, Coulter counter and altered Coulter counter method respectively. The Coulter counter counts showed an approximate 5 - 7 fold increase (and greater for the first few stations where high concentrations of detritus were observed) when compared directly with inverted microscope counts. However, when altered Coulter counter counts were compared with inverted microscope counts, the increase was approximately 2 - 4 fold. This suggested 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% level of significance) for correlations of chlorophyll 'a' against both electronic and microscopic counts. Similarly 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 shown to be greater than the volume representing channel 3 (134 μm^3), the Coulter counter was probably counting detritus.

Biomass estimates determined by volume concentrations expressed as $\mu m^3 \times 10^{-9}$ (ppm) are presented in Table 3.2. An increase was evident from stations 13 - 30. High concentrations were found between stations 22 - 26, corresponding with the high cell counts. However, higher concentrations were observed at station 29 due to the general increase in cell sizes (determined from measurements of the dominant species present). A significant correlation coefficient of 0,93 (Figure 3.4) was obtained for comparisons of chlorophyll 'a' with volume concentrations (ppm).

TABLE 3.1 Chlorophyll 'a' concentrations (µg/ℓ); inverted microscope counts (counts/ℓ x 10^3); Coulter counter counts (counts/ℓ x 10^3) and altered Coulter counter counts (minus channels 2 and 3) (counts/ℓ x 10^3) are presented for each station at the various light levels.

Stations	Methods	Light levels above 1%					Depths below the 1% 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	1434	1031	1123	982	1342	-	-	-	-	-	1568	-
	Coulter Counter (-Ch. 2,3)	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	1139	1220	1292	1173	1919	-	-	-	-	2971	-	-
	Coulter Counter (-Ch. 2+3)	343	380	407	411	633	-	-	-	-	1091	-	-
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	1808	2489	1512	1073	1778	-	-	-	-	-	-	2360
	Coulter Counter (-Ch. 2+3)	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	2055	1965	1943	1675	1214	-	-	-	-	2151	-	-
	Coulter Counter (-Ch. 2+3)	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	2464	2741	2835	13410	1012	-	-	-	1032	-	-	-
	Coulter Counter (-Ch. 2+3)	1131	1277	1471	1211	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	1204	1546	431	-	-	-	-	-	-	-
	Coulter Counter (-Ch. 2+3)	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	5714	4804	3978	4175	1991	-	1304	-	-	-	-	-
	Coulter Counter (-Ch. 2+3)	3007	2836	2181	2113	761	-	369	-	-	-	-	-
21	Chlorophyll 'a'	13,288	10,215	12,769	12,642	2,284	-	1,557	0,727	1,349	1,868	-	-
	Inverted microscope	331	448	707	662	22	-	2	6	4	16	-	-
	Coulter Counter	6535	6380	6835	6510	1779	-	1193	-	-	-	-	-
	Coulter Counter (-Ch. 2+3)	3970	3880	4380	3665	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	2280	1182	875	734	1278	464	24	62	4	13	-	-
	Coulter Counter	6014	7100	6368	6552	6584	4698	-	-	-	-	-	-
	Coulter Counter (-Ch. 2+3)	3459	3886	3633	3728	3550	2605	-	-	-	-	-	-
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	1461	1388	2110	1348	24	10	6	10	12	-	-
	Coulter Counter	7073	6291	5828	6150	5810	1103	-	-	-	-	-	-
	Coulter Counter (-Ch. 2+3)	3944	3582	3379	3637	3314	311	-	-	-	-	-	-
25	Chlorophyll 'a'	15,779	17,814	17,232	21,177	20,762	8,616	2,076	0,727	2,180	-	-	-
	Inverted microscope	2118	1177	1177	1098	2095	564	17	12	59	-	-	-
	Coulter Counter	7160	7087	6454	6682	5847	3067	-	-	-	-	-	-
	Coulter Counter (-Ch. 2+3)	4113	4398	3982	4053	3570	1620	-	-	-	-	-	-
26	Chlorophyll 'a'	18,478	18,810	18,374	15,572	14,222	1,869	1,661	1,869	9,447	-	-	-
	Inverted microscope	1270	952	1001	1074	1321	265	7	10	3	-	-	-
	Coulter Counter	8277	7744	7546	7445	6104	4007	-	-	-	-	-	-
	Coulter Counter (-Ch. 2+3)	4831	4732	4472	4275	3645	2002	-	-	-	-	-	-
28	Chlorophyll 'a'	11,315	13,080	16,298	14,118	17,025	7,682	1,765	1,661	-	-	-	-
	Inverted microscope	1089	761	953	1692	1065	131	11	0,8	-	-	-	-
	Coulter Counter	6128	5067	5407	5072	5069	2224	-	-	-	-	-	-
	Coulter Counter (-Ch. 2+3)	3699	3236	3334	3223	3186	1073	-	-	-	-	-	-
29	Chlorophyll 'a'	15,052	11,959	15,675	16,506	19,309	10,173	1,557	-	-	-	-	-
	Inverted microscope	1154	1270	1461	1460	1750	549	0,2	-	-	-	-	-
	Coulter Counter	6846	7282	6975	7320	7089	4388	-	-	-	-	-	-
	Coulter Counter (-Ch. 2+3)	4335	4612	4271	4547	4144	2288	-	-	-	-	-	-
30	Chlorophyll 'a'	20,139	14,949	20,243	17,959	17,336	8,305	-	-	-	-	-	-
	Inverted microscope	1430	1538	1453	1900	1693	1694	-	-	-	-	-	-
	Coulter Counter	5587	5570	5552	5650	5639	3433	-	-	-	-	-	-
	Coulter Counter (-Ch. 2+3)	3491	3438	3453	3523	3353	1762	-	-	-	-	-	-

TABLE 3.2 Volume concentrations expressed in ppm $(\mu^3 \times 10^{-9})$ for each station at the various light levels.

Stations	Light levels above 1%					Depths below the 1% 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	34,6	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	-	-	-	-	-	-

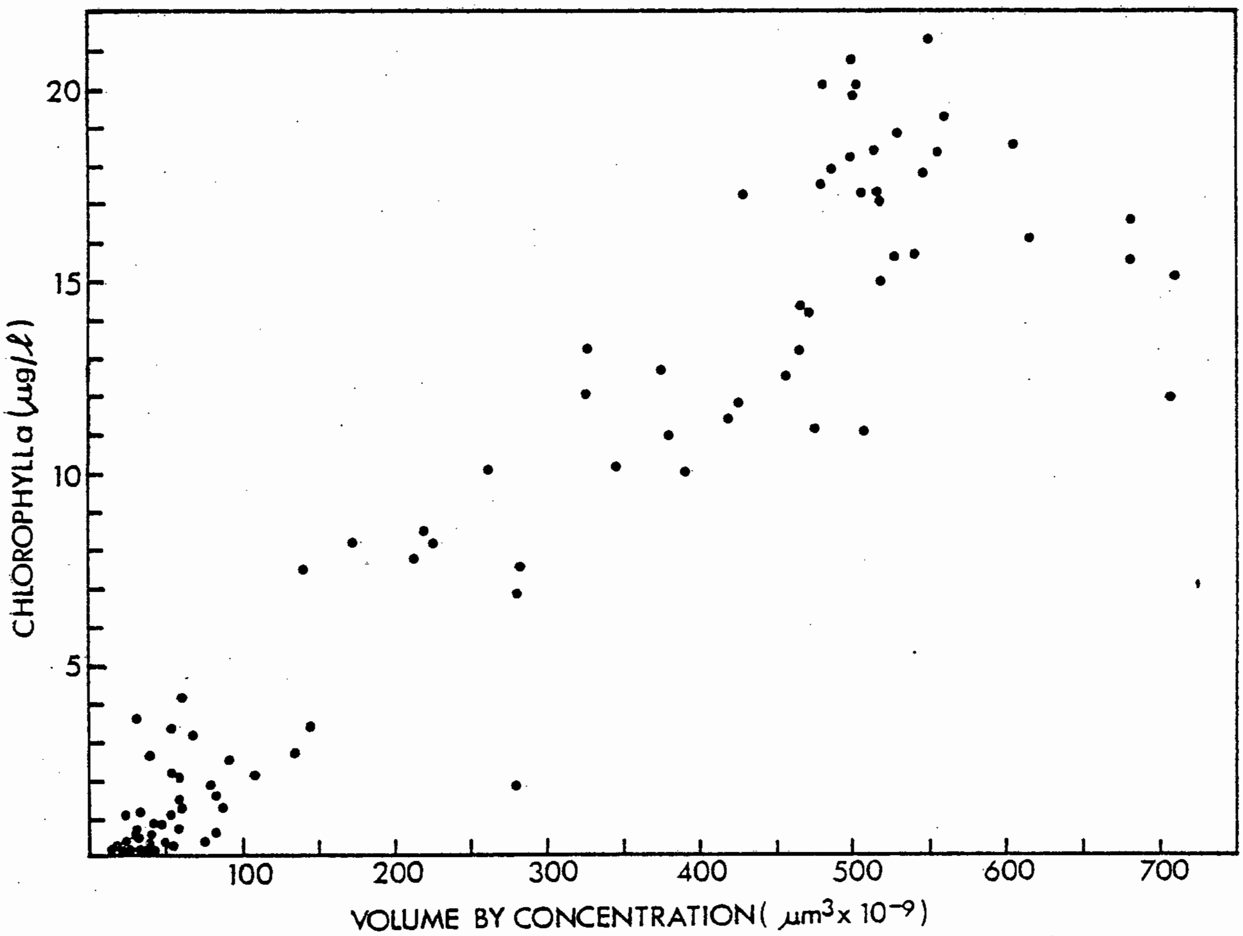


Figure 3.4 Chlorophyll 'a' versus volume by concentration (ppm) (n=88; r=0,93).

Chlorophyll 'a'

The vertical distribution of chlorophyll 'a' is illustrated in Figure 3.5(a). A rapid increase of chlorophyll 'a' occurred in the upper 10 - 20 metres, with concentrations, roughly doubling each day to reach 15 - 20 μg chlorophyll 'a'/l by station 24. This increase in biomass is clearly shown in Figure 3.5(b) where mean concentrations of chlorophyll 'a' within the euphotic zone increased from 0,2 μg/l on day 1 to 18 μg/l on day 5.

The influence that the temperature profile had on the vertical distribution of chlorophyll 'a' is shown for each station in Figure 3.6. Low levels of chlorophyll 'a' were distributed down the water column, during the first two days of the survey. On the third day the chlorophyll 'a' levels increased and the vertical distribution was shown to coincide with the depth of the mixed layer (i.e. above the 10°C isotherm).

Growth rates, expressed as cell counts x 10^3/l/day (using Cowles, 1977 growth coefficient) are illustrated in Table 3.3.

Table 3.3 Values of the daily instantaneous growth coefficient K (cells x $10^3/\ell$/day) (Cowles 1977), calculated from changes in the total number of cells present, N (cells x $10^3/\ell$) at 1230 hrs for four different depths in the upper mixed layer during the drogue study.

$$K = \frac{1}{t_2-t_1} \ln \left(\frac{N_2}{N_1}\right)$$

DAYS		1	2	3	4	5
STATIONS		13	17	21	25	29
Depth (m)	N;K					
0	N	0,5	41	331	2118	1154
	K		4,41	2,09	1,86	-0,61
5	N	-	31	707	1098	1460
	K			3,13	0,44	0,29
10	N	0,8	30	662	2095	1750
	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

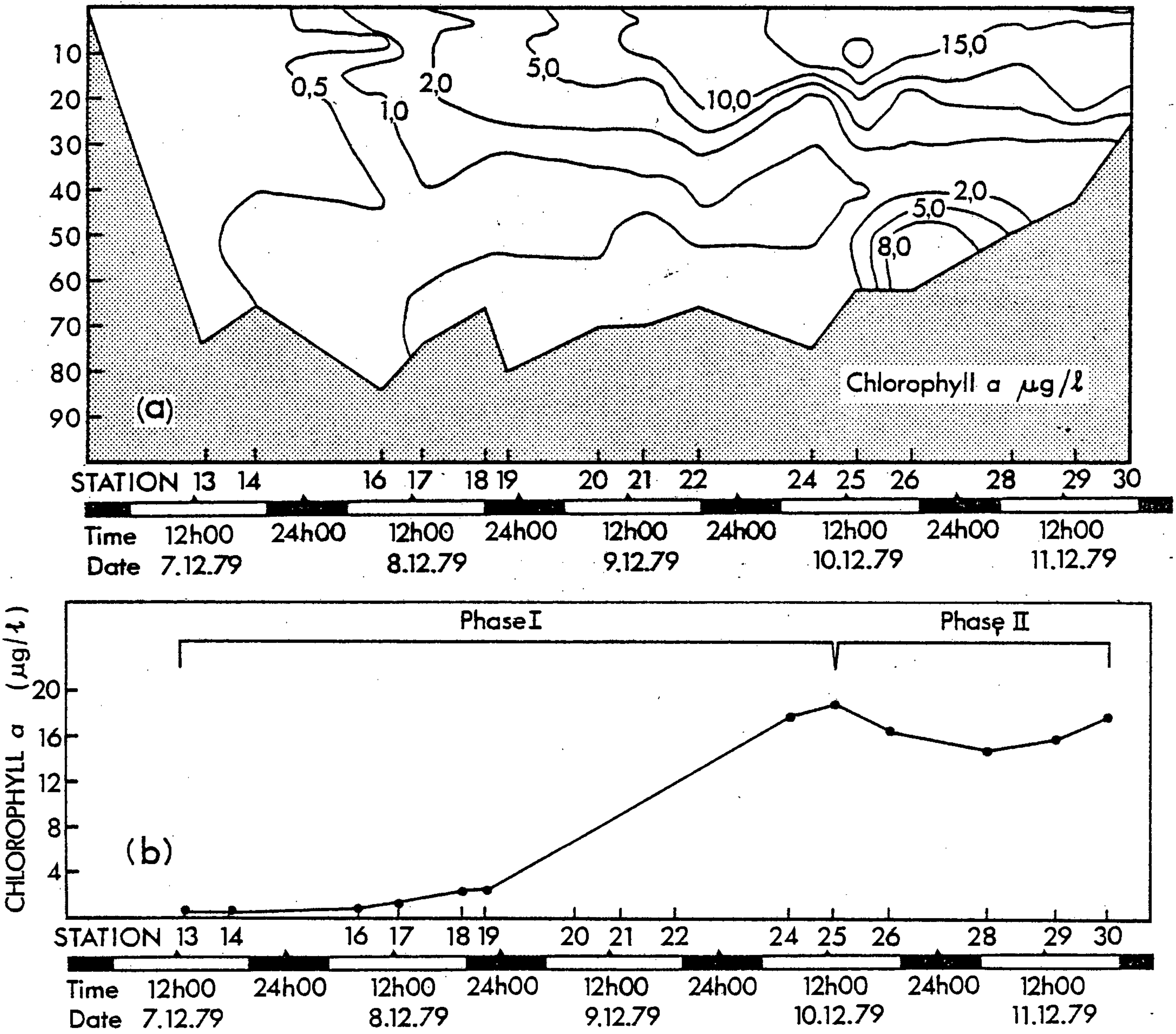


Figure 3.5(a) Vertical distribution of chlorophyll 'a' (µg/l).

(b) Changes in the mean integrated values of chlorophyll 'a' (µg/l) within the euphotic zone.

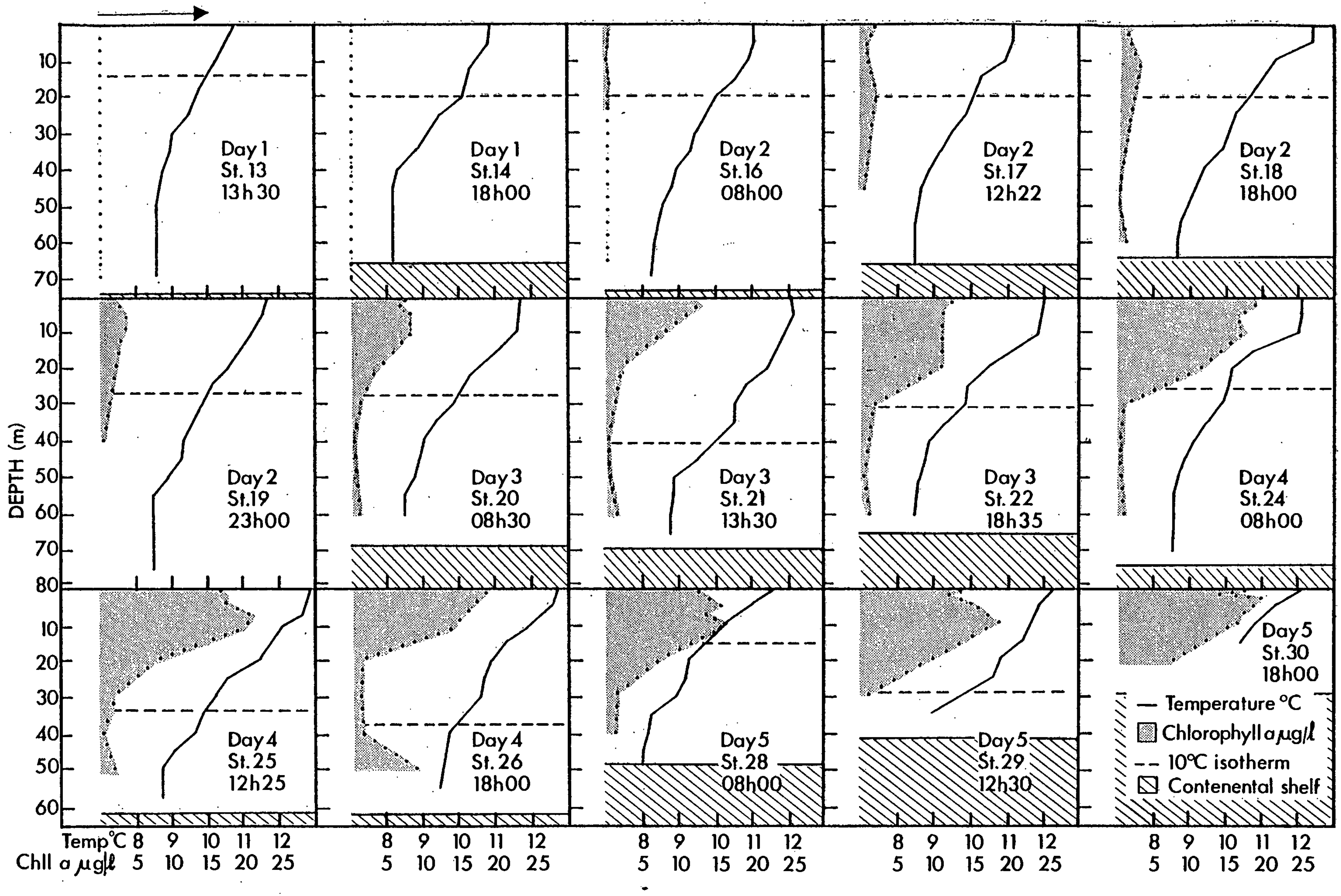


Figure 3.6 Vertical profiles of chlorophyll 'a' (μg/l) and temperature (°C) at each station along the drogue track.

The highest growth rate was observed between day 1 and day 2 at the surface and at 10 metres. The growth rates near the surface decreased towards day 4, but at 20 metres relatively high cell counts were obtained, probably as a result of phytoplankton sinking out of the euphotic zone. On day 5, the phytoplankton standing stock decreased and therefore growth rates decreased.

3.1.3 Physical and chemical changes

Temperature, salinity and density

The vertical distribution of temperature is illustrated in Figure 3.7(a). 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 depth of the 10°C isotherm increased from 14 metres at station 13 to a maximum of 40 metres at station 21 and rose again to 24 metres at station 30. The thermocline which occurred between 10 - 25 metres was most pronounced between stations 22 - 25 when temperatures increased by 2°C in one day (day 3-4). The development of the thermocline is shown in the vertical profiles of temperature and chlorophyll 'a' (refer to Figure 3.6). 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.

Salinity (Figure 3.7(b) 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 metres were less than 0,1‰, indicating that mixing processes were not significant during the study.

The surface density (Figure 3.7(c)) decreased from 26,63 (σt units) at station 13 to 26,33 (σt units) at station 26, and increased somewhat towards station 30. The isopycnals and isotherms displayed similar variations, indicating that density changes were influenced more by the

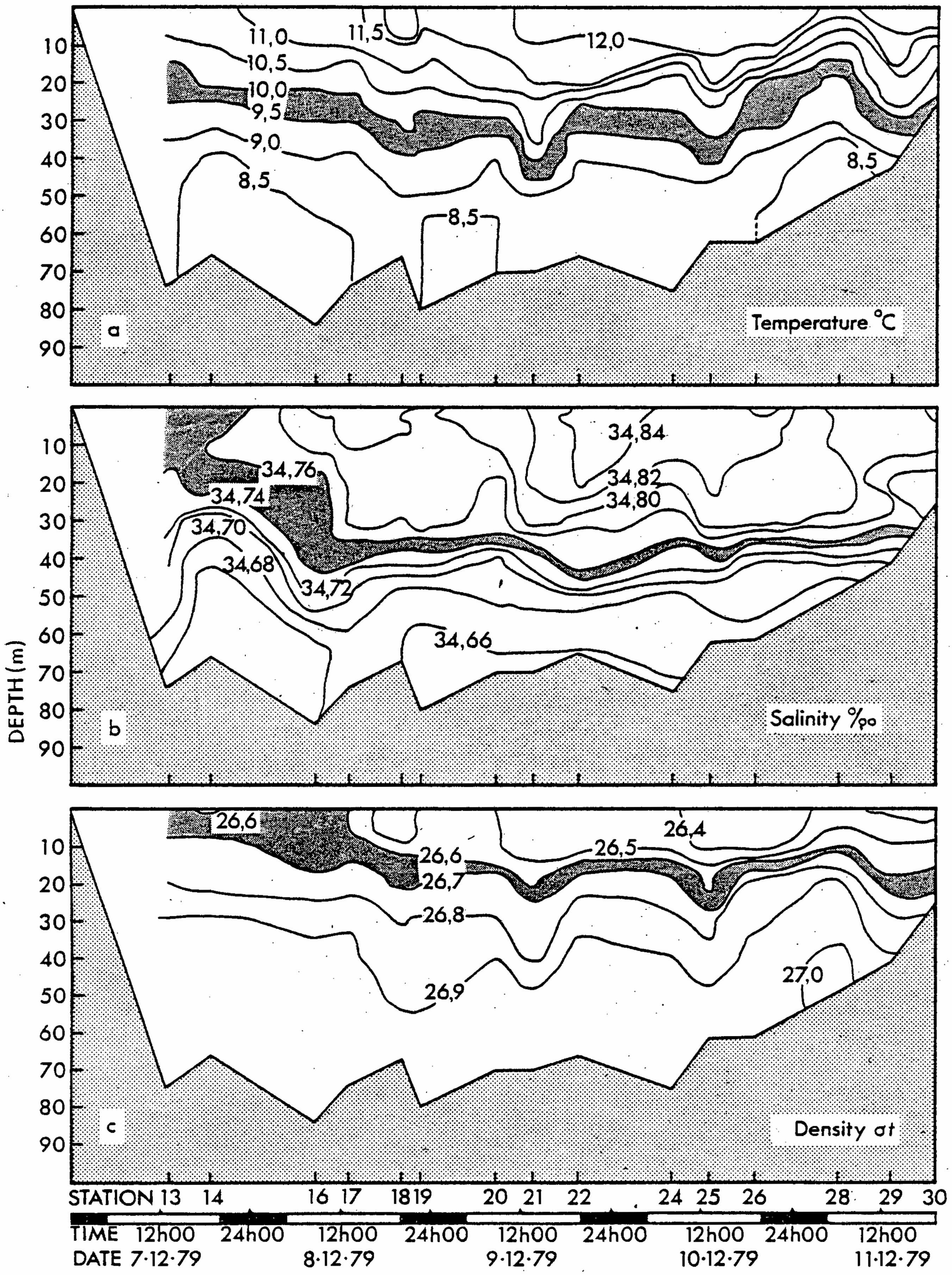


Figure 3.7(a) Vertical distribution of temperature (°C).

(b) Vertical distribution of salinity (‰).

(c) Vertical distribution of density (σt units).

temperature variations than by salinity changes. The 26,6 isopycnal appeared at the surface at station 14 and reached 20 metres by station 21. Thereafter it remained steady until station 28 when it rose to within 10 metres of the surface.

Irradiance

The midday hourly integrated light measurement ranged between 1197 and 2309 μEm²/sec. with an average measure of 1900 μEm²/sec. for the 5 day survey period (Brown, pers. comm.).

The euphotic zone defined as the depth of penetration of the 1% incident radiation ranged from 54 metres at station 13 (day 1) to 9 metres at station 30 (day 5) (Figure 3.8). 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 due to self-shading by phytoplankton. Of considerable ecological significance is the point where the 1% light level (euphotic zone) crossed the 10°C isotherm (mixed layer). The mixed layer refers to the depth to which phytoplankton surface waters are mixed by wind, waves and turbulence. If the 1% light level is below the mixed layer depth, then all the phytoplankton can grow. But if the mixed layer exceeds the 1% light level depth, then a decrease in the growth of the phytoplankton population in the water column can be expected, i.e. only if the net production above the compensation depth is less than the loss below the compensation depth. At the critical depth therefore, the losses exceed the net production and the whole phytoplankton population will decrease.

Nitrates, phosphates and silicates

The vertical distributions of the inorganic nutrients: nitrates, phosphates and silicates, are illustrated in Figure 3.9. Highest nutrient values were observed at the early stations, and in all cases the

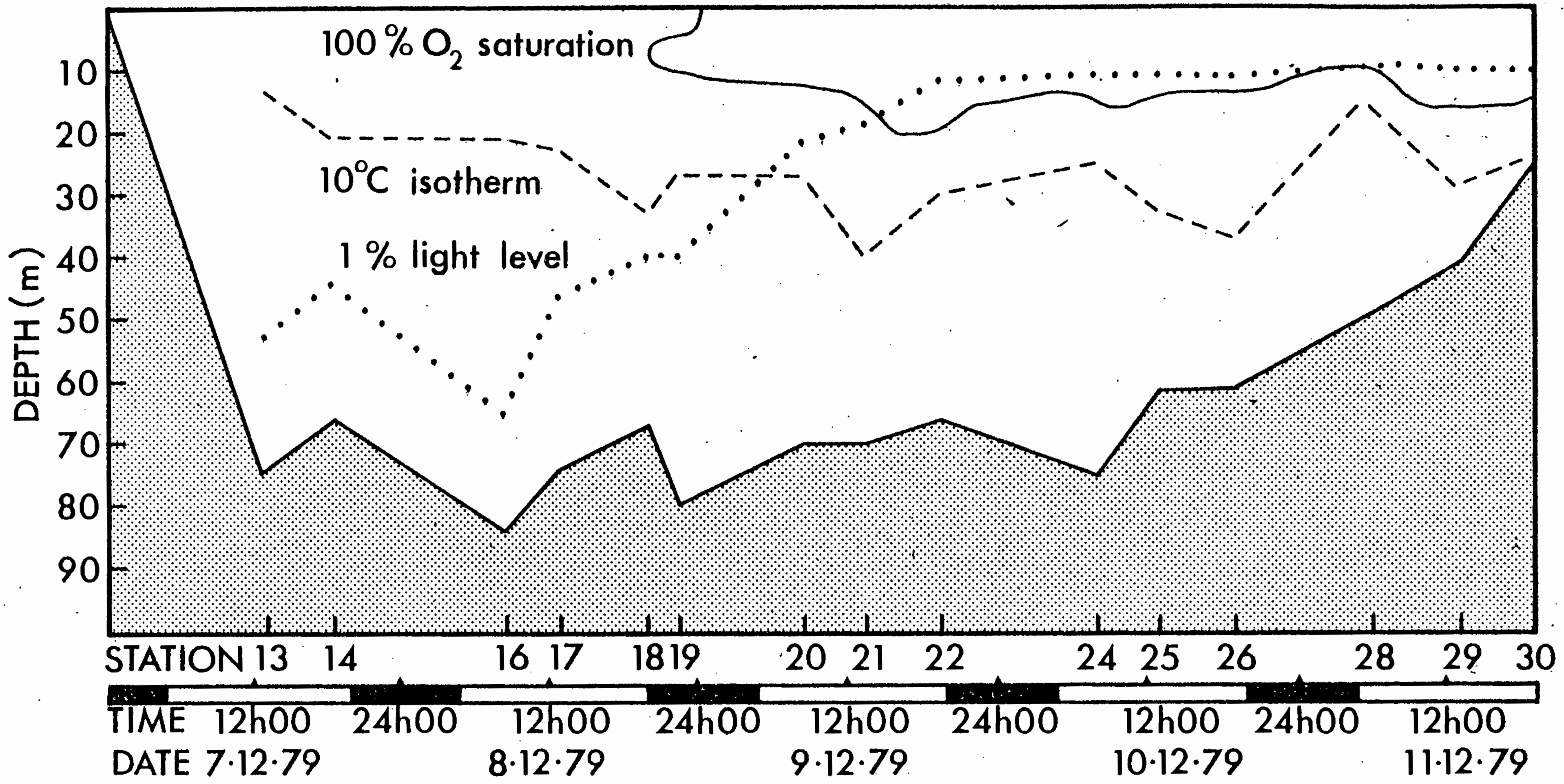


Figure 3.8 Vertical section of the 1% light level (euphotic zone), 10°C isotherm (upper mixed layer) and the 100% oxygen saturation level.

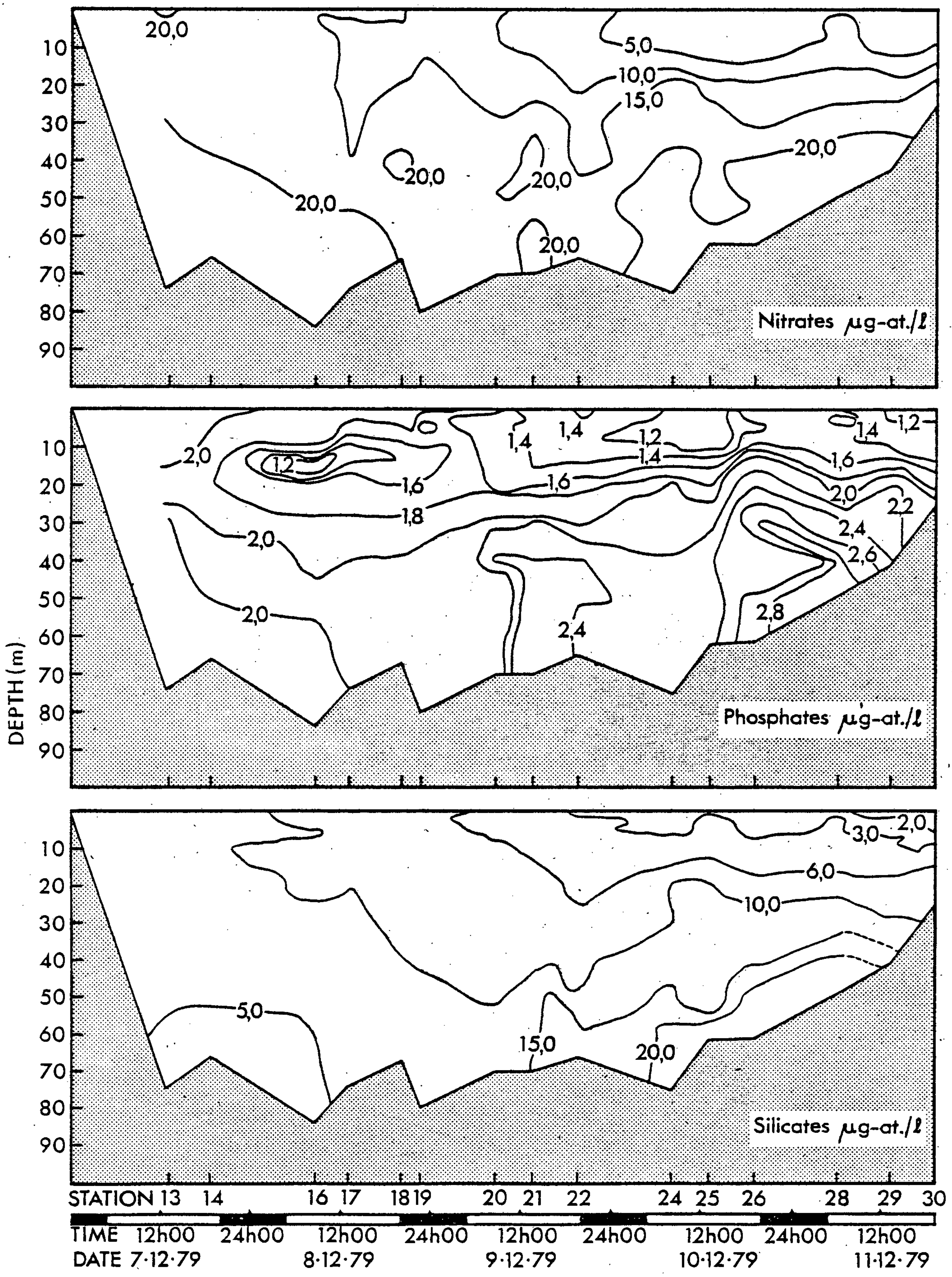


Figure 3.9 Vertical distributions of nitrates, phosphates and silicates (µg atoms/l).

nutrient concentrations were minimal where chlorophyll 'a' values were maximal. In these areas, surface nitrates fell to levels less than 0,8 µg atoms/l; phosphates to 1,00 µg atoms/l; and silicates to 1,23 µg atoms/l. At the surface, a reduction of more than 96% for nitrate, 89% for silicate and 57% for phosphate was shown. Negative correlation coefficients of -0,89; -0,85; and -0,39 were obtained for correlations of chlorophyll 'a' against nitrate, silicate and phosphate respectively.

Decreases in the mean integrated values of the nutrients (Figure 3.10) were conversely related to the increases in the mean integrated values of chlorophyll 'a'. Gradients of 20-4 µg atoms NO_3/l, 12,4-2,1 µg atoms SiO_3/l and 2,5 - 1 µg atoms PO_4/l were observed over the 5 day period for nitrates, silicates and phosphates respectively.

Dissolved oxygen and oxygen saturation

The vertical distributions of dissolved oxygen and oxygen saturation are illustrated in Figure 3.11. Initially the water was 82% saturated with oxygen, and increased up to > 140% at stations 23 - 26 before decreasing slightly. Oxygen rose from 5,12 - 8,15 ml/l in a similar fashion. The 100% saturation contour appeared initially at the surface, at station 18 (day 2) and attained a depth of 20 metres on day 3, after which it remained fairly constant. Below the thermocline the oxygen content decreased rapidly and below 50 metres the water was <60% saturated.

3.1.4 Phases of development

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

(1) *Phase I (Stations 13 - 25) Day 1 - Day 3^1/2*

Certain trends of both the physical and chemical parameters associated

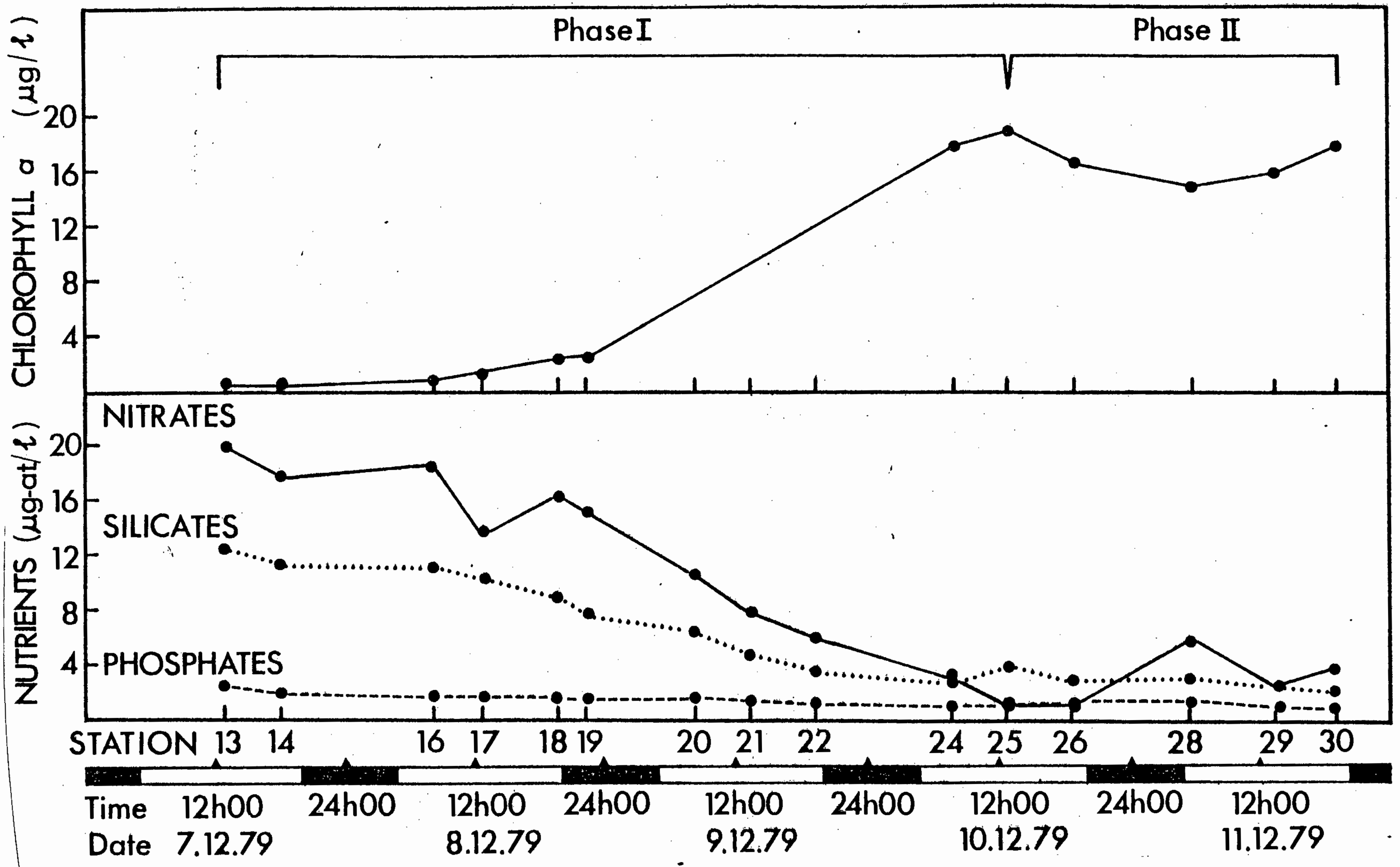


Figure 3.10 Changes in the mean integrated values of nutrients (NO_3; SiO_3; PO_4) µg atoms/ℓ and chlorophyll 'a' µg/ℓ within the euphotic zone.

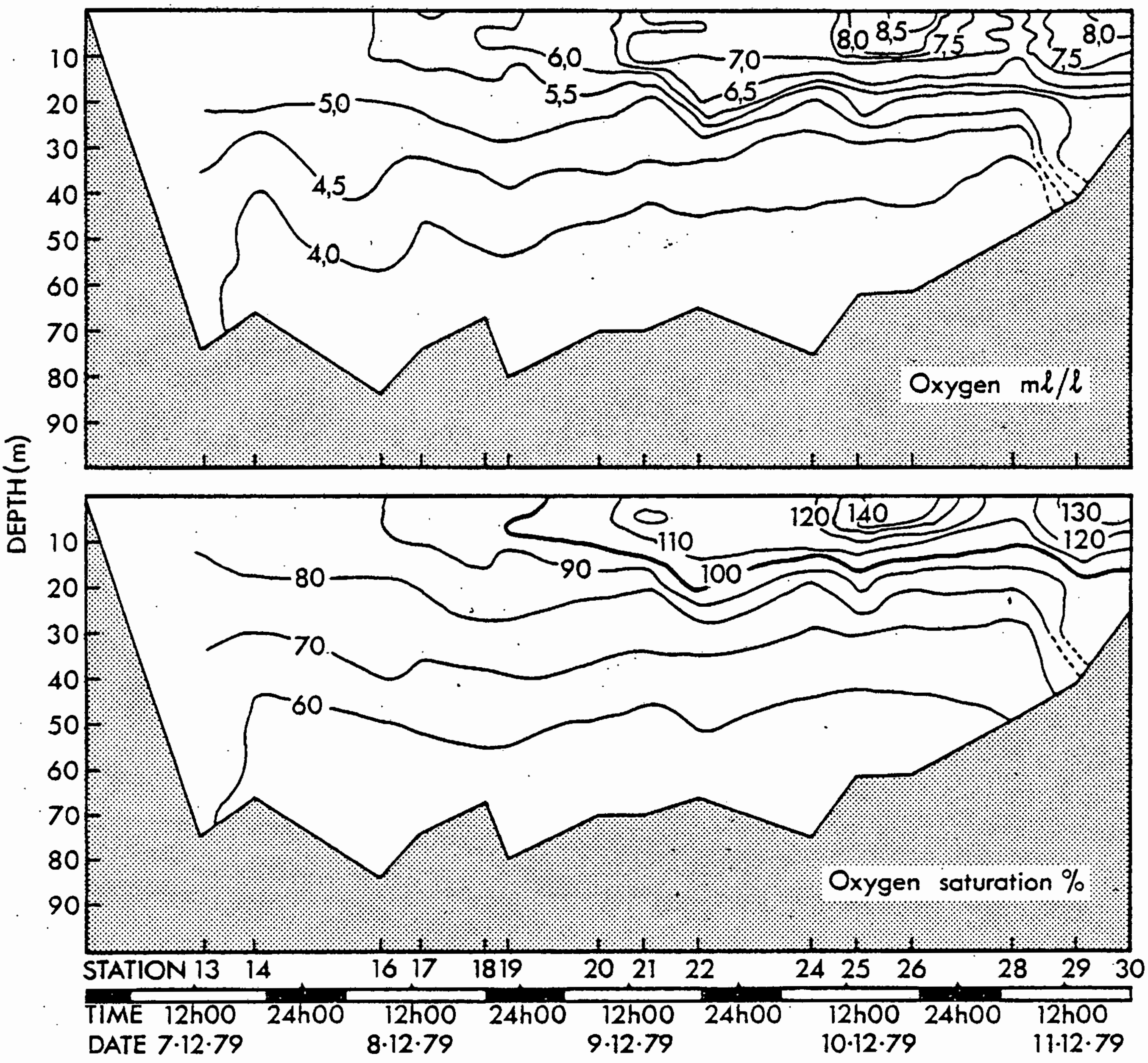


Figure 3.11 Vertical distributions of dissolved oxygen (ml/l) and oxygen saturation (%).

with the growth of the phytoplankton, were observed in this phase. At the start of Phase I cool, nutrient-rich water rose to 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 (26,63 σt units). The instability of the water column was linked to strong turbulent mixing which resulted in the upward movement of nutrients. High nutrient concentrations were observed initially at the surface (20,68 µg atoms NO_3/l; 2,29 µg atoms PO_4/l; 11,61 µg atoms SiO_3/l). 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. Yet the phytoplankton standing stock (using chlorophyll 'a' as a measure of biomass) was low, 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 x 10^3 cells/l/day was detected at the surface between day 1 and 2 which was not evident from changes in the chlorophyll 'a' levels (due to 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 into the upwelled waters. A lag period in growth was not detected in this survey, but may well have taken place prior to sampling. (Upwelling occurred off Oudekraal on the 5.12.79 (drogue track I) and sampling commenced two days later on the 7.12.79 (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 of 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 metres at station 20. Light became limiting as the euphotic zone became shallower and the phytoplankton was mixed below the 1% light level. The phytoplankton stock showed an increase of 18,8 µg/l of chlorophyll 'a' until day 4. This rapid increase compares favourably with an increase of 11,9 µg/l in 2,5 days as found by Ryther *et al.* (1971) in coastal waters off Peru, where a similar drogue study was performed. A concomitant decrease in nutrient concentration and increase in oxygen concentration was equally observed over this period. Nitrates and silicates were taken up at a faster rate than phosphates. This agrees with the results of Andrews & Hutchings (1980) who studied the rate of uptake of these nutrients by phytoplankton in local waters.

(2) *Phase II (Stations 25 - 30) Day 3^1/2 - Day 5*

A change in the physical and chemical parameters was observed in this phase. Decreases in surface temperatures 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 due to 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 until the end of day 4. A senescent phase had not been reached during this survey.

3.1.5 Vertical distribution of species

The grouping of species according to similar vertical distributions of abundance together with specific cell characters appears in Table 3.4. The vertical distributions of species were grouped with respect to varying light levels. Seventy per cent of the species showed a tendency to be distributed within the euphotic zone and were characterized by Group 1. Fourteen per cent of the species were characterized by Group 2, i.e. occurring below the euphotic zone, and 16% by Group 3, i.e. occurring throughout the water column.

A general trend in cell shape was displayed. Species occurring within the euphotic zone showed a higher proportion of cylindrical-shaped cells relative to thread-like shaped cells. Conversely, the

Table 3.4 The grouping of species according to similar vertical distributions with respect to light, together with cell characters.

Species Group Type	Species	SPECIES CELL CHARACTERISTICS								
		Cell Size				Cell Shape				
		S	I	L	Trend	T	D	C	S	Trend
Group 1 (within euphotic zone)	C. brevis		I		I = L			C		C > T
	C. teres		I					C		
	C. affinis		I					C		
	C. subsecundus		I					C		
	C. glandazii		I					C		
	H. haukii		I					C		
	C. gracilis		I					C		
	C. constrictus		I					C		
	C. laciniousus		I					C		
	A. japonica		I					C		
	H. sinensis		I					C		
	C. didymus		I					C		
	L. punctata	S						C		
	C. decipiens			L				C		
	C. lorenzianus			L				C		
	C. bergonii			L				C		
	E. zoodiacus			L				C		
	S. costatum	S	→	L				C		
	C. compressus	S	→	L				C		
	C. debilis	S						C		
	Navicula sp	S				T				
	N. longissima	S				T				
	N. pacifica	S				T				
	R. delicatula	S				T				
	Thalassiothrix sp		I			T				
	N. pungens		I			T				
	R. fragilissima			L		T				
	N. seriata			L		T				
	R. stolterfothii			L		T				
	T. rotula			L			D			
	T. aestivalis			L			D			
	T. decipiens			L			D			
✱	Ciliate sp			L					S	
✱	Dinoflagellate sp 1			L					S	
✱	Dinoflagellate sp 2			L					S	
Group 2 (below euphotic zone)	T. frauenfeldii		I		I > L	T				T > C
	T. nitzschioides		I			T				
	P. directum		I			T				
	R. setigera		I			T				
	R. imbricata			L		T				
	B. delicatulum		I					C		
	L. borealis		I					C		
	D. brightwellii			L				C		
Group 3 (above and below euphotic zone)	N. delicatissima	S			L	T				
	R. alata			L		T				
	Coscinodiscus sp.			L			D			
	C. criophilum			L				C		
✱	Tintinnid sp			L		-	-	-	-	
✱	Peridinium			L					S	

KEY

S = Small
I = Intermediate
L = Large
T = Thread-like

D = Disc
C = Cylindrical
S = Spherical
✱ = Non diatom

proportion of thread-like shaped to cylindrical-shaped species increased below the euphotic zone. Most of the different shapes were found in Group 3. No trend in cell size was displayed. *S. costatum* and *C. compressus* occurred within the euphotic zone and varied from small-intermediate-large throughout the survey. Referring to Figure 3.12, a general increase in cell size for both these species was apparent from station 13 - 30. A 2,6 fold increase in volume for *S. costatum* was observed with the volume ranging between 328 μm³ and 857 μm³, and likewise a 2,5 fold increase in volume was observed for *C. compressus*, with the volume ranging between 157 μm³ and 391 μm³. The means of the mean length ranges and mean width ranges in *S. costatum* and *C. compressus* increased from stations 13 to 30 by 4 and 2,4 μm; and 0,1 and 1 μm respectively.

3.1.6 Species diversity, abundance and occurrence

Relative abundance of species

In the 113 samples analysed, 49 species were identified. They are listed in rank order in Table 3.5. The grouping of species according to total abundance (expressed as total counts/l x 10³ of all 113 samples) is illustrated in Figure 3.13(a). Six per cent of the species were represented by Group 1 (dominant); 39% by Group 2 (most common); 20% by Group 3 (common) and 34% by Group 4 (rare). The distribution of 94% of species below 12 000 cells/l x 10³, and only 6% above 55 946 cells/l x 10³, clearly indicated that *C. compressus*, *S. costatum* and *Chaetoceros debilis* Cleve (present in Group 1) were dominant with respect to total abundance.

The total abundance of species (absolute concentration) and relative changes in species composition (as cumulative per cent) along the drogue track at approximately 10 metres are illustrated in Figure 3.13(b). Samples at this depth were shown to be dominated by the three species mentioned above. The total cumulative per cent for these species ranged between 55 - 94%. *C. compressus* was shown on average, to represent half of the total abundance at all stations,

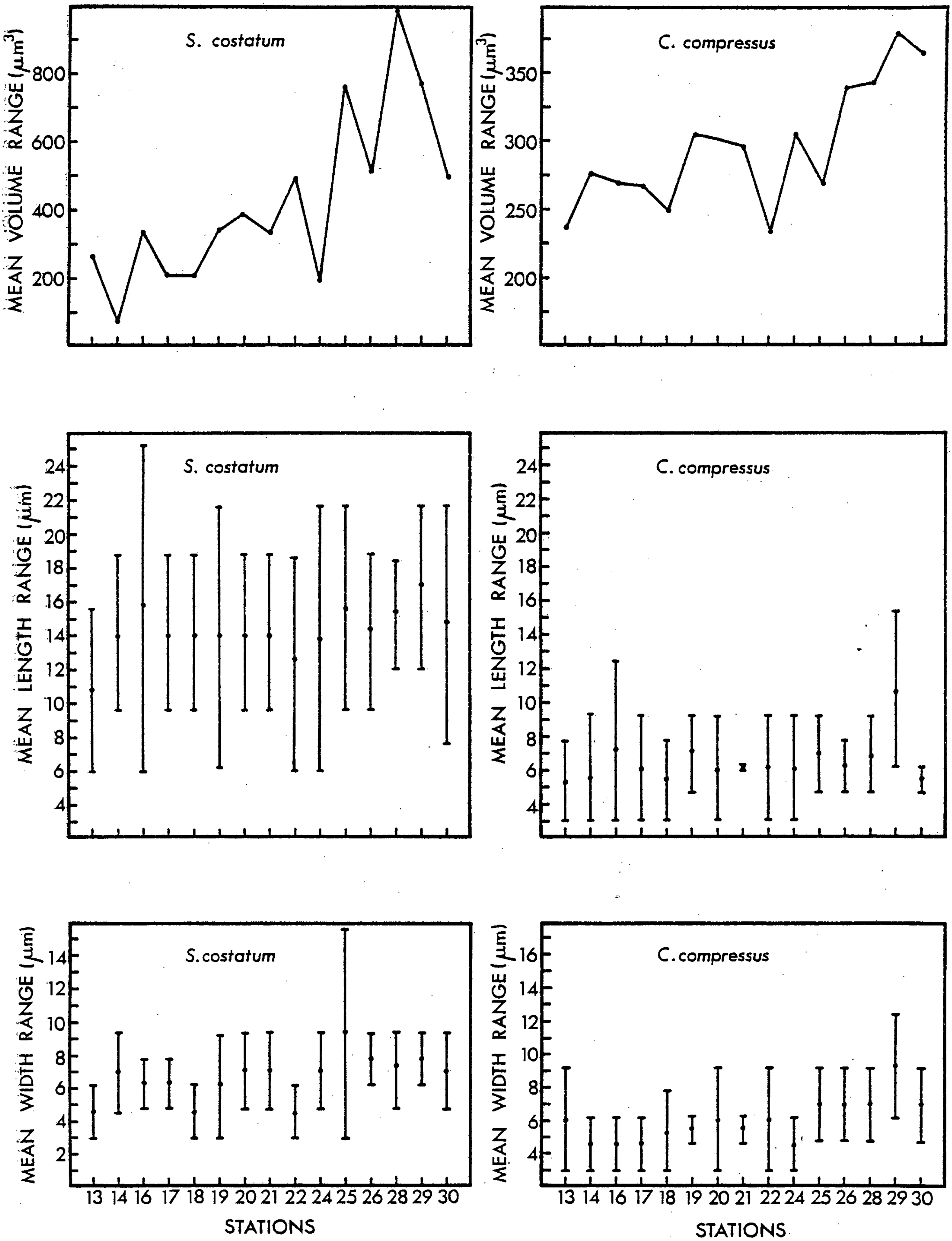


Figure 3.12 Changes in the mean volume (µm³); mean length (µm) and mean width (µm) of *S. costatum* and *C. compressus* at each station over the 5 day survey period.

Table 3.5 Rank ordering of species with respect to total abundance (total counts/ℓ x 10^3 of all samples).

See Figure 3.13(a)

Group	Rank	Species
Group 1	1.	C. compressus
	2.	S. costatum
	3.	C. debilis
Group 2	4.	N. pungens
	5.	A. japonica
	6.	T. aestivalis
	7.	Navicula species
	8.	C. laciniousus
	9.	N. seriata
	10.	C. constrictus
	11.	H. haukii
	12.	R. fragilissima
	13.	T. decipiens
	14.	N. longissima
	15.	C. bergonii
	16.	C. lorenzianus
	17.	C. didymus
	18.	L. punctata
	19.	C. affinis
	20.	C. decipiens
	21.	R. stolterfothii
	22.	H. sinensis
Group 3	23.	E. zoodiacus
	24.	N. delicatissima
	25.	N. pacifica
	26.	Tintinnid species
	27.	C. teres
	28.	Coscinodiscus species
	29.	C. subsecundus
	30.	R. delicatula
	31.	C. gracilis
	32.	C. criophilum
Group 4	33.	C. glandazi
	34.	Peridinium species
	35.	R. alata
	36.	L. borealis
	37.	Ciliate species
	38.	Dinoflagellate species 1
	39.	Thalassiothrix species
	40.	C. brevis
	41.	B. delicatulum
	42.	T. rotula
	43.	T. frauenfeldii
	44.	R. imbricata
	45.	Dinoflagellate species 2
	46.	R. setigera
	47.	P. directum
	48.	T. nitzschioides
	49.	D. brightwelli

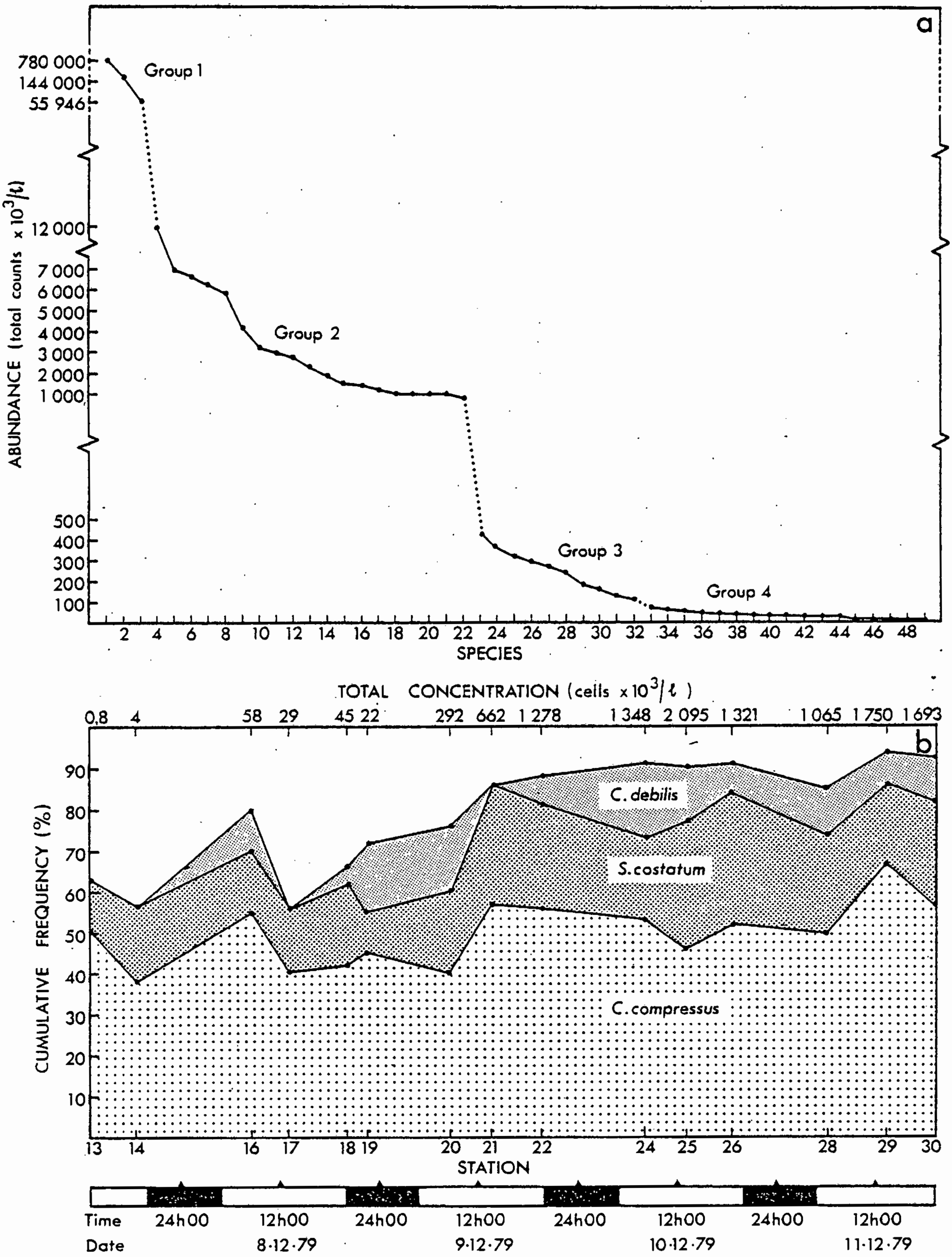


Figure 3.13(a) Species total abundance expressed as total cells/l x 10^3.

3.13(b) Changes in species composition (cumulative percent) and total cell concentrations (cells x 10^3/l) at approximately 10 metres using the inverted microscope cell counts.

(cumulative per cent ranged between 38 - 67%). The total number of cells at 10 metres increased rapidly along the drogue track from station 13 - 30, with a peak in cell concentrations at station 25. Inspection of Table 3.6 shows the relative growth rates (K) at 10 metres (cell counts x 10^3/l/day) measured daily at 12.30 hrs of *C. compressus*, *S. costatum* and *C. debilis* using Cowles (1977) growth coefficient. The growth rates of both *C. compressus* and *S. costatum* were particularly high between day 1 and 3 and then decreased towards day 5. *C. debilis* made its first appearance at 10 metres on day 2 where comparatively lower growth rates were observed.

Table 3.6 Values of the daily instantaneous growth coefficient K (cells x 10 ^{3}/ℓ/day) (Cowles 1977), calculated for C. compressus, S. costatum and C. debilis from changes in the number of cells present, N (cells x 10 ^{3}/ℓ) at 1230 hrs at 10 meters

DAYS		1	2	3	4	5
STATIONS		13	17	21	25	29
Species	N;K					
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

■ occurring at station 16
□ " " " 20

Species groups based on frequency of occurrence

The species occurring at the different stations along the drogue track are listed in Table 3.7(a). The seeding population at station 13 comprised 21 species, which was 43% of the total number of species recorded in the study. Of these, 9 species (38%) persisted abundantly

Table 3.7(a) The occurrence of species at different stations.

Species	STATIONS														
	13	14	16	17	18	19	20	21	22	24	25	26	28	29	30
S. costatum	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
N. seriata	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
N. pungens	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
N. longissima	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Navicula species	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
H. haukii	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
C. compressus	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
C. didymus	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
C. debilis	X		X	X	X	X	X	X	X	X	X	X	X	X	X
Coscinodiscus sp	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
R. fragilissima	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
E. zoodiacus	X	X	X		X		X	X	X	X	X	X	X	X	X
T. decipiens	X	X	X	X	X	X	X	X			X	X	X	X	X
Tintinnid species	X	X	X	X	X	X	X	X	X	X	X	X	X		
Peridinium species	X	X		X	X			X		X	X	X		X	
N. pacifica	X	X	X	X	X	X	X	X	X	X					
N. delicatissima	X	X	X	X	X	X	X				X		X		X
R. delicatula	X	X	X	X	X	X	X	X	X						
C. criophilum	X						X			X	X		X	X	X
Dinoflagellate sp 1	X			X	X				X					X	
Dinoflagellate sp 2	X	X	X			X									
Ch. gracilis		X	X	X	X	X	X	X	X	X	X	X	X		
Ch. lorenzianus		X		X	X		X	X	X	X	X	X	X	X	X
Rh. imbricata		X						X	X	X	X				
Rh. setigera		X				X		X	X						
T. rotula		X	X		X										
C. laciniousus			X	X	X	X	X	X	X	X	X	X	X	X	X
C. constrictus			X			X	X	X	X	X	X	X	X	X	X
C. brevis			X	X	X	X									
A. japonica				X	X	X	X	X	X	X	X	X	X	X	X
C. decipiens				X	X	X	X	X	X	X	X	X	X	X	X
R. stolterfothii				X	X	X	X	X	X	X	X	X	X		
C. bergonii				X	X	X	X			X	X	X	X	X	X
C. teres				X	X	X	X		X	X	X	X		X	
L. punctata					X	X	X	X	X	X	X			X	X
Ciliate sp					X				X		X	X			
C. affinis						X	X	X	X		X	X	X		X
R. alata						X	X			X	X			X	
T. frauenfeldii						X				X		X	X		
C. subsecundus							X		X					X	
D. brightwellii							X								
T. aestivalis								X	X	X	X	X	X	X	X
H. sinensis									X		X	X	X	X	X
Thalassiothrix sp									X			X		X	
C. glandazii									X						
T. nitzschioides										X					
B. delicatulum											X			X	
L. borealis												X			
P. directum														X	

38%

43%

Table 3.7(b) Change of species with respect to station 13

Total no. of species	21	23	23	27	31	31	32	29	34	31	34	31	28	31	23
No. of "new" species added	21	5	5	9	12	14	14	12	18	15	17	16	12	15	10
No. of species "lost"	-	3	3	3	2	4	3	4	5	5	4	6	5	5	8
Total change	-	8	8	12	14	18	17	16	23	20	21	22	17	20	18
% change in species	-	35	35	44	45	58	53	55	68	64	62	71	61	65	78

Table 3.7(c) Change of species from station to station

Total no. of species	21	23	23	27	31	31	32	29	34	31	34	31	28	31	23
No. of "new" species added	21	5	4	8	4	6	5	3	6	6	6	3	2	9	2
No. of species "lost"	-	3	4	4	0	0	4	7	1	9	3	6	4	6	10
Total change	-	8	8	12	4	12	9	10	7	15	9	9	6	15	12
% change in species	-	35	35	44	13	38	28	35	21	48	27	29	21	48	52

throughout the course of the study. Thus changes in the species composition relative to station 13 (Table 3,7(b)) were by the addition of new species. It is important to note that the addition of new rare species, could be underestimated at certain stations where smaller aliquots of concentrated samples were sedimented. On average there was a 34% change in species diversity between adjacent stations (Table 3.7(c)). The greatest change in diversity was found between stations 29 and 30, and the least change between stations 17 and 18.

A dendrogram grouping of species according to the McConnaughey index (based on species presence or absence), is illustrated in Figure 3.14. Inspection of the dendrogram showed a tight grouping of ten species (Group 1) at the 75% similarity level. Nine species (Group 2(1)) were shown to be associated with Group 1 at the 50% similarity level. Five further small groups were also delineated at the 50% level, one of 4 species (Group 2(2)), another of 3 species, and three groups of 2 species each (Group 2(3)) linked individually to these groups as chains. Group 3 comprised 35% of the total species, which were linked below the 50% similarity level.

Table 3.8 shows the grouping of species according to the McConnaughey index together with each species total abundance grouping, vertical abundance grouping, cell characteristics and mean relative growth rates, based on cell counts at 10 metres over the 5 day period.

Group 1 represented 20% of the total species. The most common species (from abundance groupings) were present in this group with *C. compressus*, *S. costatum* and *C. debilis* representing 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 growth rates were observed for species of this group, particularly for the dominant species *C. compressus* and *S. costatum*.

Group 2 represented 44% of the total species present, of which 18% was represented by Group 2(1), 8% by Group 2(2) and 18% by Group 2(3). Species in Group 2(1) were shown to belong to Group 2 (most common) with respect to the total abundance grouping, occurring within the euphotic

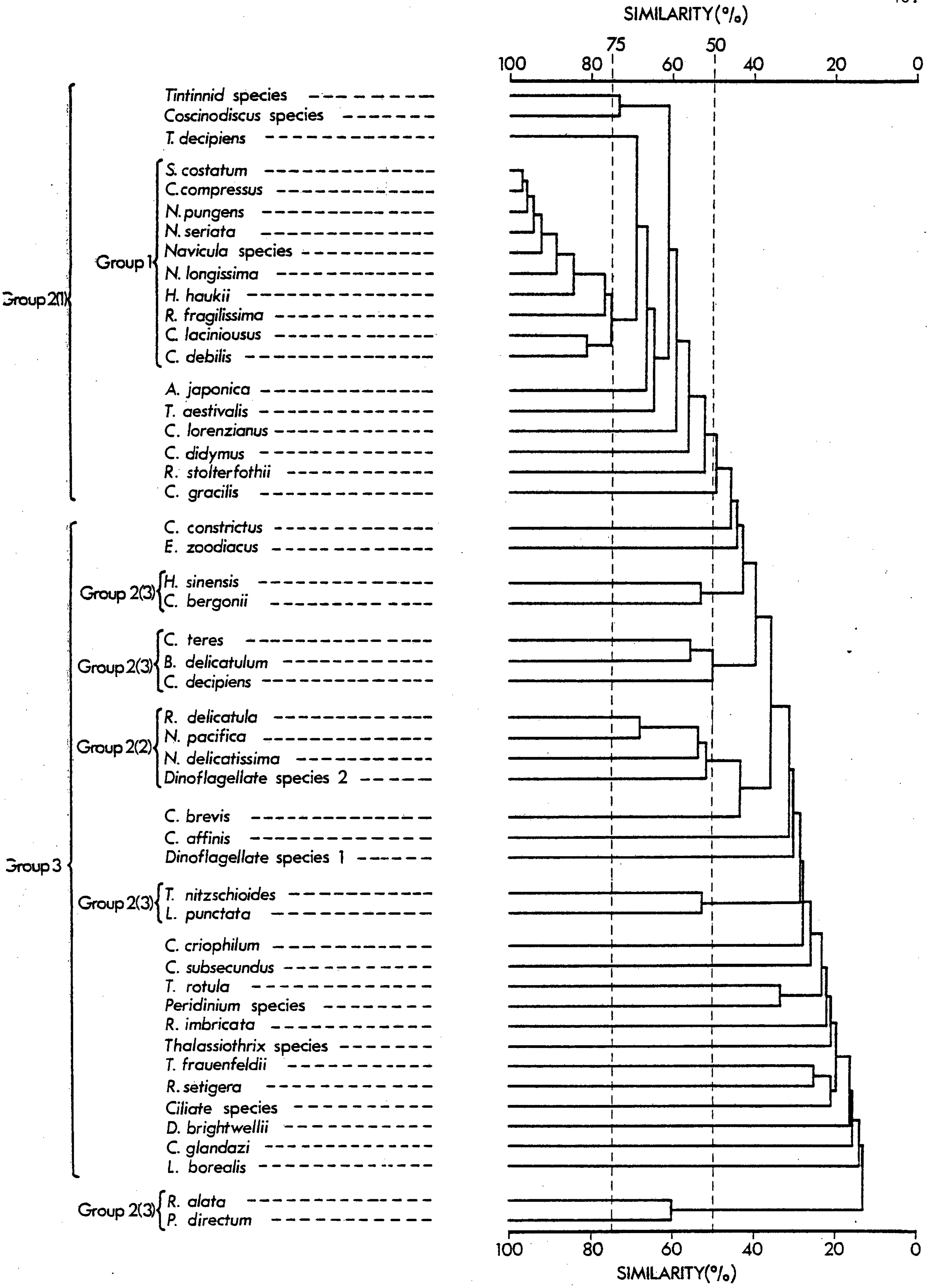


Figure 3.14 A dendrogram showing species grouping according to the McConnaughey index.

Table 3.8 Grouping of species according to the McConnaughey index together with each species total abundance grouping, vertical distribution grouping, cell characteristics and relative growth rates over the 5 day survey period.

Species Group Type			Species	Total Abundance Grouping	Vertical Distribu= tion Grouping	SPECIES CELL CHARACTERISTICS									Mean Relative Growth Rate(K) Cells x 10^{3}/l/ day at 10 m
						S	I	L	Trend	T	D	C	S	Trend	
Group 1 >75% (P.S.I.)			S. costatum	1	1	S	⟶	L	-			C		-	2,03
			C. compressus	1	1	S	⟶	L				C			2,00
			N. pungens	2	1		I			T					1,00
			N. seriata	2	1			L		T					1,27
			Navicula species	2	1	S				T					1,46
			N. longissima	2	1	S				T					1,03
			H. haukii	2	1		I					C			0,29
			R. fragilissima	2	1			L		T					1,09
			C. laciniousus	2	1		I					C			1,06
			C. debilis	1	1	S						C			1,11
GROUP 2 >50% P.S.I.	(1)	⌶	Tintinnid sp	3	3			L	I = L	-	-	-	-	-	0,79
			Coscinodiscus sp	3	3			L			D				1,30
			T. decipiens	2	1			L			D				0,72
			A. japonica	2	1		I					C			1,04
			T. aestivalis	2	1			L			D				0,23
			C. lorenzianus	2	1			L				C			0,39
			C. didymus	2	1		I					C			1,10
			R. stolterfothii	2	1			L		T					3,69
			C. gracilis	3	1		I					C			1,61
	(2)		R. delicatula	3	1	S			S	T				T	-
			N. pacifica	3	1	S				T					-
			N. delicatissima	3	3	S				T					1,87
		⌶	Dinoflagellate sp 2	4	1			L					S		-
	(3)		C. teres	3	1		I		I > L			C		C > T	3,19
			R. delicatulum	4	2		I					C			-
			C. decipiens	2	1			L				C			-
			H. sinensis	2	1		I					C			1,53
			C. bergonii	2	1			L				C			0,74
			T. nitzschioides	4	2		I			T					-
			L. punctata	2	1	S						C			-
			R. alata	4	3			L		T					-
			P. directum	4	2		I			T					-
Group 3 >50% (P.S.I.)			C. constrictus	2	1		I		I = L			C			0,58
			E. zoodiacus	3	1			L				C			-
			C. brevis	4	1		I					C			-
			C. affinis	2	1		I					C			0,43
		⌶	Dinoflagellate sp 1	4	1			L					S		-
			C. criophilum	3	3			L				C			-
			C. subsecundus	3	1		I					C			-
			T. rotula	4	1			L			D				-
		⌶	Peridinium sp	4	3			L					S		0,75
			R. imbricata	4	2			L		T					-
			Thalassiothrix sp	4	1		I			T					-
			T. frauenfeldii	4	2		I			T					-
			R. setigera	4	2		I			T					-
		⌶	Ciliate sp	4	1			L					S		-
			D. brightwellii	4	2			L				C			-
			C. glandazii	4	1		I					C			-
			L. borealis	4	2		I					C			-

KEY

= Small
= Intermediate
= Large
= Thread-like

D = Disc
C = Cylindrical
S = Spherical
⌶ = Non diatom

zone. Cell size was either intermediate or large, and shape was variable. *Cosinodiscus* spp. and *Tintinnid* spp. were fairly uncommon though found throughout the water column. The relative growth rates of these species were lower than those found for species in Group 1 except for *Rhizosolenia stolterfothii* H. Péra where a growth rate of 3,69 was measured, being higher than the growth rates of the dominant species. Species in Group 2(2) were fairly uncommon, small thread-like and found within the euphotic zone. A large spherical dinoflagellate (species 2) was shown to be rare. Species in Group 2(3) were either most common and occurring within the euphotic zone, or rare and occurring below the euphotic zone or throughout the water column. Cells were intermediate, large and cylindrical rather than thread-like. *Chaetoceros teres* Cleve was shown to possess a very high growth rate.

Group 3 represented 35% of the total species present. Species belonging to this group were mostly rare and occurred either above 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 intermediate sized species, with a cylindrical shape, were confined to the euphotic zone. Relative growth rates of these species were low. In summary no clear trends in cell characteristics could be linked to any group.

Sample groups based on species abundance

Inspection of the dendrogram according to the Bray-Curtis coefficient (Clifford & Stephenson, 1975) (Figure 3.15) showed the delineation of three distinctive groups at the 50% similarity level. The grouping of samples using this abundance-weighted technique was strongly biased towards grouping samples with similar cell concentrations rather than similar species, despite log-transformation of the cell concentrations (Barnes, 1951; Field & Robb, 1970; and Field, 1970, 1971). The reason being, that a weak species grouping was obtained with the McConnaughey index, i.e. essentially only one group was isolated at the 75% similarity level. An information statistic was therefore not applied. By contrast Hutchings (1979) found very distinct groupings of

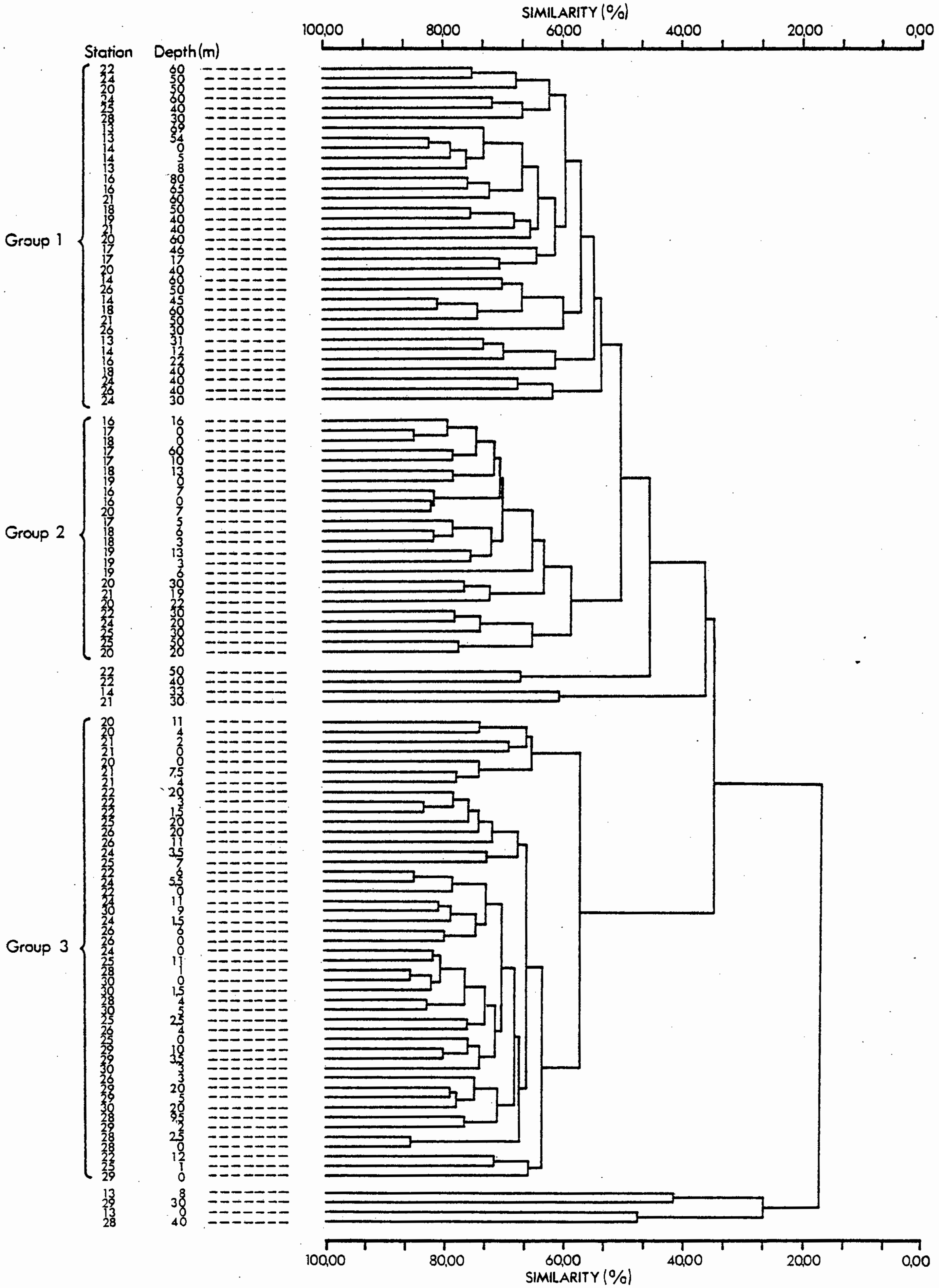


Figure 3.15 A dendrogram showing the grouping of samples according to the Bray-Curtis coefficient.

samples and zooplankton species when a wide variety of watermasses were sampled. Hopson (SFI pers. comm.) found a very homogenous sample grouping in the uniform conditions prevalent in the St Helena Bay area, based on an analysis of zooplankton species.

The grouping of sample abundance relative to stations is summarized in Figure 3.16.

Group 1

This group was characterized by samples occurring throughout the water column in the initial stages of Phase I, i.e. station 13 and 14, and well below the euphotic and mixed layer zone between stations 16 - 30. Abundance expressed as concentration (cells/l) was shown to be low for this group. Samples occurring at the early stations had low cell concentrations as seeding was taking place, whereas species occurring in samples below the euphotic zone were inhibited by low light levels.

Group 2

This group represented the transition from low cell concentrations as was found in the initial stages of Phase I, to high cell concentrations as was found in the latter stages of Phase I. Samples were all found above the upper mixed layer. In the initial stages, the samples were found above the euphotic zone whereas in the latter stages they were found below, often near the bottom of the upper mixed layer.

Group 3

Most of the samples of this group, were found above the euphotic zone in the latter stages of Phase I and in Phase II. These samples had similar high cell concentrations.

Species abundance-frequency distributions

Lewis (1977) has shown that certain ecological interpretations can be made using species abundance-frequency distributions. Shapes of abundance-frequency distributions of several species have been quantified statistically, using

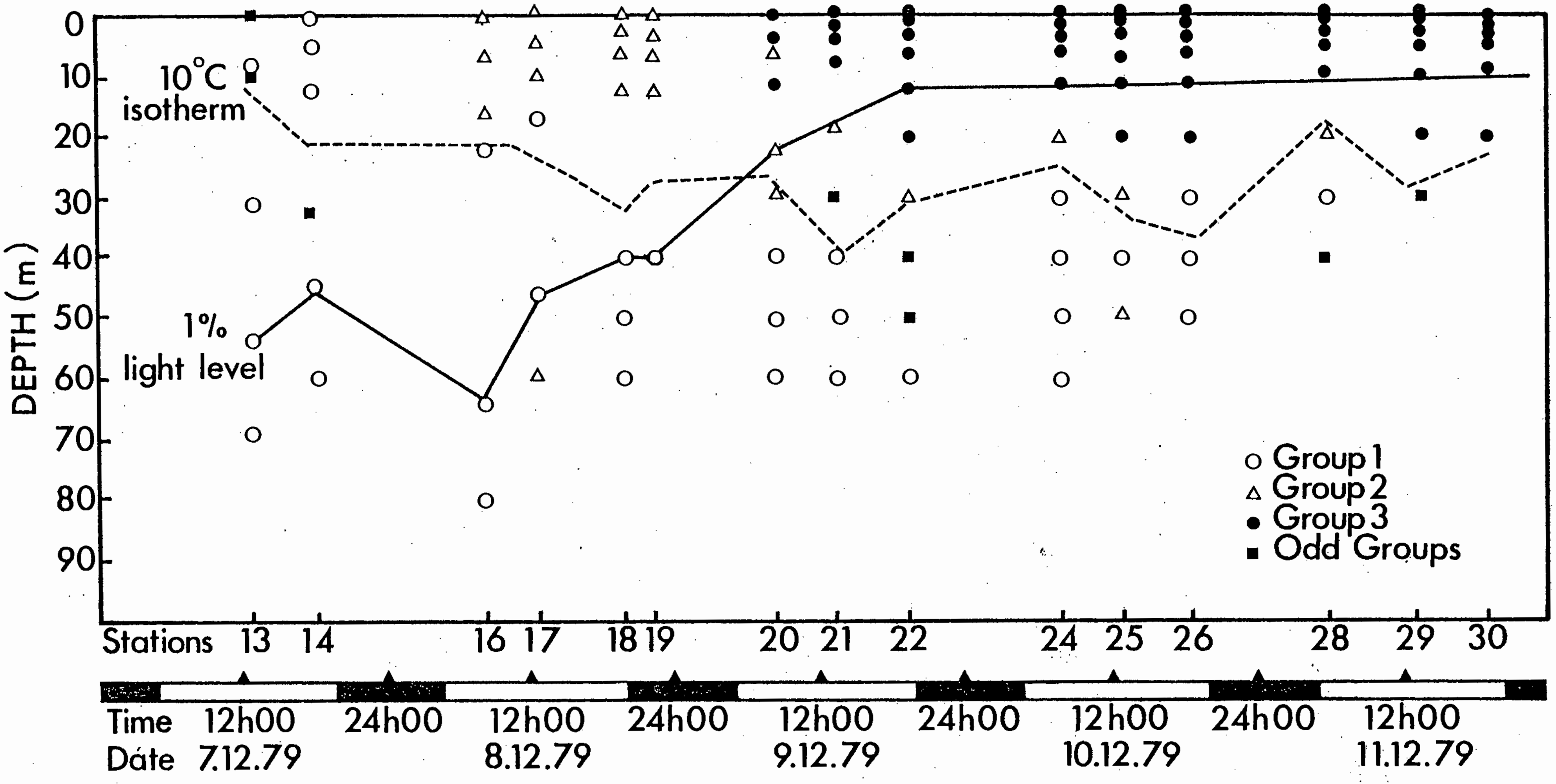


Figure 3.16 Distribution of sample groups derived from the Bray-Curtis coefficient.

(1) coefficient of variation (C.V.)

(2) a skewness statistic (S.K.) (Glass & Stanley, 1970).

Abundance-frequency distributions for selected species appear in Figure 3.17. All frequency distributions are asymetrical and skewed to the left, but the degree of skew varies greatly between species. Values of C.V. and S.K. for these species appear in Table 3.9.

Table 3.9 The distribution of cell concentrations (x $10^3/\ell$) expressed as mean ($\bar{x}$), standard deviation(s), coefficient of variation (C.V.), and skewness statistic (S.K.) for various species (Glass & Stanley, 1970).

No.	Species	$\bar{x}$	s	C.V.	S.K.
1	C. compressus	9,0	17,1	1,9	2,95
2	S. costatum	14	24,2	1,7	2,16
3	N. pungens	13,3	22,5	1,7	2,11
4	N. longissima	22	35	1,6	1,08
5	T. decipiens	7,1	12,1	1,7	2,27
6	T. aestivalis	5,8	5,5	0,9	0,82
7	A. japonica	6,4	9,5	1,5	1,98
8	C. teres	2,7	2,5	0,9	1,53
9	C. decipiens	6,5	7,2	1,1	0,98

Nos. 1 - 4 = Group 1) Grouping of species based
5 - 7 = Group 2(1)) on the McConnaughey index
8 + 9 = Group 2(3))

Species with a high C.V. also had a high variation about the mean. Group 1 (from species grouping McConnaughey index) showed the highest values of C.V. and S.K., which in ecological terms would suggest that these species have marked powers of increase under a relatively narrow range of favourable conditions, but drop radically in abundance at other times. Species with low C.V. and skew (Group 2(1) + (3)) would mean that they lack the ability to produce impressive growth surges but persist more effectively under less favourable conditions. Group 1 species could therefore be described as r-selected species or opportunistic weedy species (Hutchinson 1961).

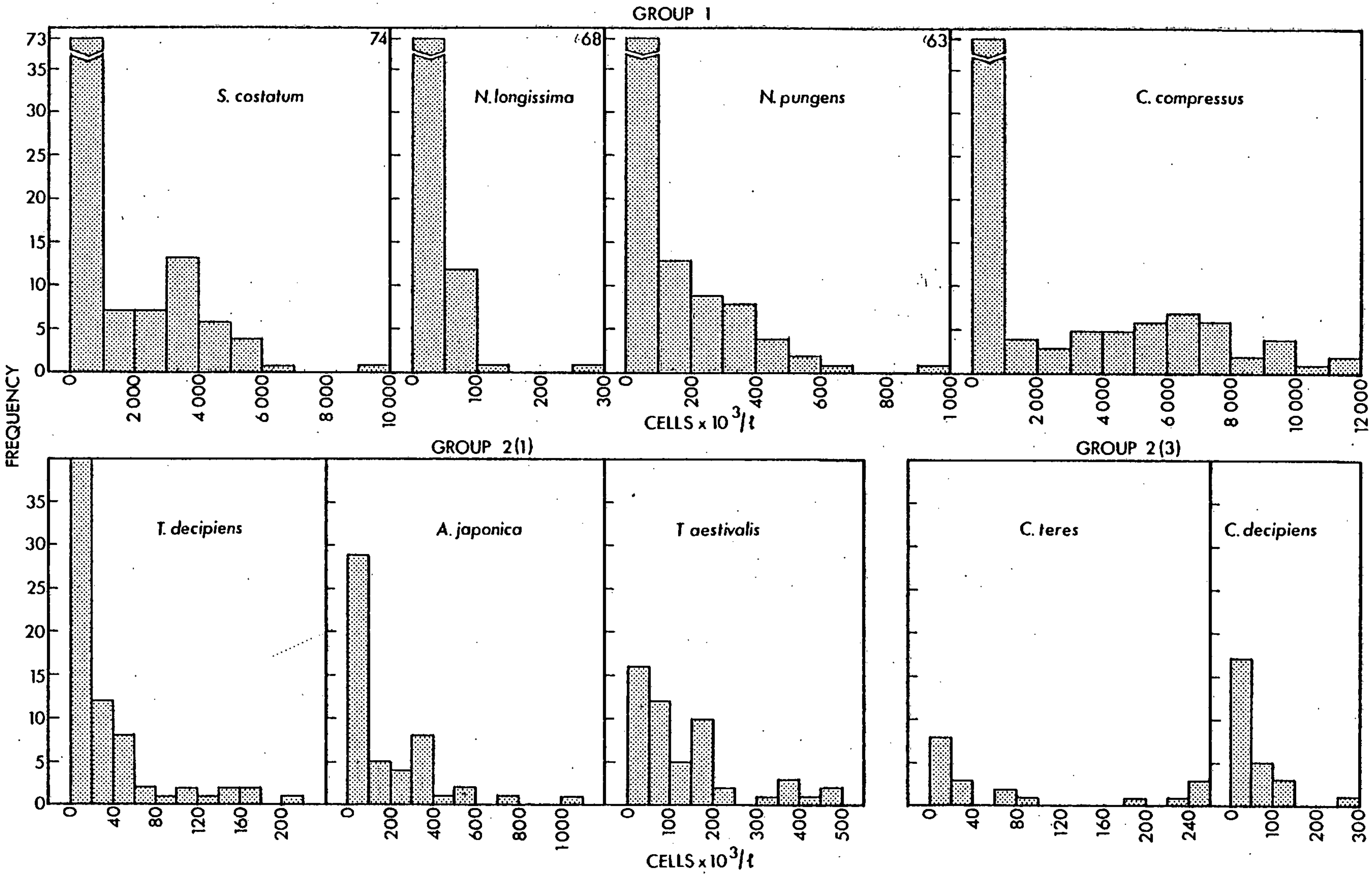


Figure 3.17 Abundance-frequency distributions of various species.

3.2 Discussion

3.2.1 Trends discernible from the analyses of species diversity, abundance and occurrence

A mixed phytoplankton bloom comprising 49 species developed with *C. compressus*, *S. costatum* and *C. debilis* always being dominant. These 3 species dominated with respect to abundance and frequency of occurrence. Seven other species were shown to have a high frequency of occurrence and were grouped together with the dominants at the 75 per cent similarity index, in accordance with the McConnaughey index. The remaining 39 species occurred infrequently and in total with the above-mentioned 7 species, contributed on average 19% of the cumulative abundance in samples measured at the drogue depth.

3.2.2 Survival strategies of the three dominants in relation to changes in the environment

The prime question arising at this point is: Why should these three species successfully colonize and out-compete the remaining species of the seeded population in a changing environment? The possible survival strategies of these species in adapting to environmental changes in terms of light, nutrients and stability of the water column, will be discussed.

Morphological changes in relation to growth, nutrient absorption and buoyancy

An increase in cell size of *C. compressus* and *S. 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. It is worth mentioning however, that there are two apparently divergent views on the question of the environmental control on cell size

(Hecky & Kilham, 1974).

(1) The "nutrient" view (Parsons & Takahashi, 1973) simply suggests that the ambient nutrient concentrations determine cell surface to volume ratios. Thus large cells are succeeded by small cells as nutrients diminish. This view is based entirely on 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 (1973) have used these relationships to explain the seasonal succession in the cell size of coastal phytoplankton.

(2) The "physical" view (Semina, 1972; and Semina *et al.* 1976) suggests that the mean cell size of a phytoplankton population depends on the velocity of vertical water movements and on the density gradient of the pycnocline (i.e. the role of the hydrodynamic forces is emphasized). Later, Hecky and Kilham (1974) expressed the opinion that inherent kinetics of nutrient absorption and the sinking rates of different kinds of cells are important.

Growth and nutrient uptake

The small size of cells in the newly upwelled waters was assumed to enhance their growth and nutrient absorption rates profoundly (based on experimental evidence of several authors: Findlay (1972); Fogg (1965); and Friebele *et al.* (1978)). Generally the species that grow most rapidly and utilize high concentrations of nutrients are small, with a high surface to volume ratio. Maintenance of these species in this initially turbulent environment depends on their intrinsic multiplication rates. As was mentioned earlier, these dominants grew faster in the upwelled waters between days 1 and 2, than between days 3 and 5 when average cell size had increased and the water column had begun to stabilize. The dominants were also shown to possess high mean growth rates when compared with mean growth rates of other species at 10 metres (Table 3.8). These high growth rates allowed the dominants to selectively out-compete the 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 division rate gives a good indication of the rates of nutrient absorption as determined by surface/volume ratios. This finding confirmed Fogg's view (1965) that size is generally most important since it determines the surface/volume ratio and thus the relative rate of nutrient intake for growth. The initially high surface/volume ratios found in the dominants therefore resulted in faster division rates which in turn accounted for their selection and dominance over the other species.

Friebele *et al.* (1978) have succeeded in demonstrating that phosphate uptake rate is a power function of the surface to volume ratio of a cell. Although the uptake rate per cell is largest for large cells, the uptake rate per μm^3 cell volume is highest for small cells. Based on this evidence the small cells of the dominants would consequently possess a competitive advantage, since their uptake rate per cell mass would be faster than those of larger-celled species. The nutrient-rich upwelled waters, would therefore select species with small cell sizes and high intrinsic uptake and growth rates. It is worth mentioning that although the dominants possessed high division rates, they may catabolize a larger fraction of their biomass than larger celled species. Law (1975) has shown that large unicellular diatoms have a lower respiratory catabolism than smaller-celled species.

As the upwelled waters aged, cell sizes increased and surface/volume ratios decreased. The implications are that these cells will have relatively lower nutrient absorption rates 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 & Thomas (1969) compared half saturation constants (K_s) for a coastal diatom *Asterionella japonica* and *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 & Guillard (1971) have shown that physiological races of marine phytoplankton are adapted to high or low nutrient levels. Species succession may very well be controlled by these specific differences and by the temporal changes in the nutrient concentrations. Although the nutrient concentrations were rapidly depleted in 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 would possibly occur at a later stage when nutrient conditions would be limiting for the dominants.

An important aspect to consider, however, is the fact that species also have different abilities to store non-limiting nutrients. Different concentrations of internal nutrient pools can determine the outcome of competition for nutrients (Davis *et al.*, 1978). Perhaps *C. compressus*, *S. costatum* and *C. debilis* stored sufficient concentrations of nutrients during the initial stages of the drogue study when nutrients were abundant, to support a considerable portion of their growth in the latter stages where nutrient concentration had decreased considerably. Perhaps the actual competition took place during the early stages of the study, prior to the appearance of reduced nutrient concentrations. Harrison *et al.* (1977) have demonstrated a significant increase in the surface to volume ratio of *S. costatum* and *C. debilis* in response to nutrient limitation. This finding is in contrast to the observations of the large cells found in the latter stages of the study, although here again the nutrient conditions were not defined as being limiting. Based on the evidence of Harrison *et al.* (1977) it would seem very likely however, that an association between cell size and certain physiological properties does exist.

Buoyancy

The large cells of the dominants occurring during the latter stages of the drogue study will have problems in remaining afloat. Morphological features such as cell size, shape, colony formation and cell protuberances have all been considered to affect form resistance and influence buoyancy. According to Munk & Riley (1952) the rate of sinking increases with increasing cell size, but is not uniform in cells of different shapes. The following shapes are shown in the order of decreasing sinking rate, for particles of different sizes:-

$$\begin{array}{rl|l} & \xrightarrow{\text{decreasing}} & \\ 5\mu m \text{ in } Ø : & \text{plate} > \text{cylinder} > \text{sphere} & \\ 50\mu m \text{ in } Ø : & \text{cylinder} > \text{plate} > \text{sphere} & \downarrow \text{ decreasing} \\ 500\mu m \text{ in } Ø : & \text{cylinder} > \text{sphere} > \text{plate} & \end{array}$$

Applying these criteria to species of this drogue study, shows that the medium-large cylindrical cells of the dominants will sink less rapidly than the plate or even thread-like cells, e.g. *Nitzschia* species. The dominants are all chain forming diatoms, and the ecological implications thereof are yet 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 & Boleyn (1965) have shown that chain formation in *S. costatum* does not increase its rate of sinking. The numerous silicon rods interconnecting the cells, are thought to be responsible for increases in micro-turbulent conditions between and near the rods causing an increase in frictional drag and thus decreasing the sinking rate. Cell protuberances are traditionally viewed as positive traits for suspension, but silica-bearing setae as found in the case of *Chaetoceros* species however, increase the density of the cell and so increase the sinking rate. On the other hand, the setae of *Chaetoceros* and horns of *Ceratium* are assumed to increase the surface of absorption of the cell (Margalef, 1978a). The increase of cell size without any special modification has been considered by Smayda (1970) to somehow represent a positive adaptation to floatation.

The physiological regulation of cell density is also an effective means of modifying the suspension of phytoplankton (Beklemischev, *et al.*, 1961). He suggests 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 to total cell size) has also been considered as a means of floatation (Gross & Zeuthen, 1948).

Other physiological mechanisms such as light and photoperiod have been shown to influence buoyancy. For example, Steele & Yentsch (1960) showed that *S. costatum* reduces its sinking rate when placed in the dark.

The age and physiological state of cells in phytoplankton populations may also influence the sinking rate of cells. Titman & Kilham (1976) have shown that in lakes *Asterionella* cells sink 4 times more rapidly during their stationary phase of growth than during their exponential phase. Eppley *et al.* (1967) similarly showed that cells with lower photosynthetic rates sank at a more rapid rate than faster-growing phytoplankters.

There is also evidence that the depletion of nutrients increases the sinking rates of *S. costatum* (Steele & Yentsch, 1960). The practical advantage of increasing cell size and sinking rates of phytoplankton in this study, would be evident in an environment where surface nutrients were becoming depleted. In fact, the phytoplankton losses from the euphotic zone were high during the latter stages of this drogue study when more than two-thirds of the mixed layer occurred below the 1% light level. It is difficult however, to say whether the loss of phytoplankton was due solely to mixing (wind velocities increased slightly towards the latter stages of the study) or due to sinking by cells adapting morphologically or physiologically to the environment. If the loss of phytoplankton was caused by a decrease of cell buoyancy then this may have been caused by the increase in cell size. There is evidence at present, to support that phytoplankton can grow and adapt to lower light levels in areas of high nutrient concentrations (Knoechal & Kalff, 1978; Estrada, 1974; and Blasco & Packard, 1974).

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-oxidation at high light levels. Certainly Jørgensen (1964) has shown 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 adaptions from one light intensity to another may be caused by cells changing their content of photosynthetically active pigments or by changing the enzymes involved in photosynthesis. Yentsch & Ryther (1959) showed that chlorophyll 'a' content was highest in the early stages of succession and Eppley (1980) found that the cellular pigment content adjusted rapidly with changes in the quantity and quality of light. The ratio of carotenoids to chlorophyll 'a' (D_{430} : D_{665}) has also been shown to increase with succession (Margalef, 1967) with lowest values being measured in the initially turbulent conditions. When progressing from the initial to the latter stages of the drogue study a decrease in the ratio of chlorophyll 'a'/cell numbers was observed at the surface and at the lower limit of the mixed layer depth.

In addition to changes in pigment content and ratio, 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 & 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% 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 be advantageous for the phytoplankters to adapt to low levels of irradiance. Since 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 dominants were adapting to the reduced light levels. Light adaptation by the dominants could only have been confirmed if the survey had continued for a few more days and a large subsurface population comprising the same dominants developed.

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

Certain studies on the physiological properties of the dominant species need to be investigated in order to unravel the relationships existing between nutrient uptake light and water stability. An estimate of their physiological state has however, been determined. Decreases in their growth rates and increases in their cell size as the waters aged, implied that initially the dominants possessed high absorption rates and could therefore grow actively. But as their specific growth rates decreased towards the latter stages of the study a stationery or slow-growing phase became evident. Barlow (1981) showed that during this phase (i.e. under low nutrient and low light levels) the rate of protein production for the whole phytoplankton population decreased considerably 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 nutrient utilization and slower respiratory catabolism.

3.2.3 Other possible factors influencing species dominance

Diatom populations can modify their environment by reducing nutrient levels, or altering light intensity via shading and selective absorption and reflection, and also they can alter the chemistry of the water by way of exudates. Specific studies undertaken by Menzel & 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 & Ryther (1969) performing enrichment experiments showed that only the 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 increases in growth of the dominants at the start of the study. Provasoli & Pinther (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 this to trigger the succession of species in temperate waters.

Temperature has been shown by Goldman & 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 as was observed during this 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 the effect of nutrients was irrelevant. Munk and Riley (1952) have suggested that predation has allegedly triggered the development of dwarfism, gigantism, chain forming, and diverse protuberances in the phytoplankton as anti-predation devices. Preliminary studies on the losses of phytoplankton populations by zooplankton grazing in local waters is presently being investigated by Hutchings & Olivieri (in prep.). Strickland *et al.* (1969) have attributed low phytoplankton standing stocks in Peruvian waters to result from grazing by anchoveta.

3.2.4 Summary

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

Small cells were shown to possess high growth rates. The dominants were assumed to possess high absorption rates 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 dominants increased and therefore nutrient absorption rates decreased. The ability of the dominants to store non-limiting nutrients during the initial stages of the study was considered a possible adaptation to the diminishing nutrient concentrations. The dominants were not thought to adapt to these conditions by physiologically altering their nutrient uptake abilities.

Morphological features such as cell size, shape, colony formation and cell protuberances of the dominants were considered to affect form resistance and influence their suspension. The medium-large cylindrical cells of the dominants were postulated to sink less rapidly than plate or thread-like cells. Phytoplankton losses from the euphotic zone were high and the increase in cell size was considered a mechanism in adapting to low surface nutrients by increasing the rate of sinking. The possession of large cells during the slow-growing phase was considered advantageous for the storage of intracellular nitrogen and the accumulation of polysaccharides.

The dominants were assumed to possess a special mechanism protecting them against photo-oxidation during the initial stages of the study when the water column was unstable. The cells were thought to adapt physiologically to the changes in the light intensity by (a) adjusting their pigment content and/or their enzymes involved in photosynthesis, (2) changing their morphology and/or arrangement of their chloroplasts.

It was postulated that the dominants possessed some ability to adjust their physiology, in the second half of the study, to the decreasing light levels, as they maintained their dominance over the remaining species without showing a decline in cell concentrations. Evidence to support that the dominants may have adapted to the low light levels, had the survey continued a few more days, was shown by several authors.

Other factors influencing species dominance were considered. The modification of the environment by the way of exudates was considered a possible strategy. The small temperature gradient was thought to have no effect on the dominance of the three species. Grazing was considered important in determining the course of succession.

The three dominant species were postulated to be r-selected species or opportunistic weedy species.

CHAPTER 4

TRANSECT STUDY

4.1 Results

4.1.2 Monthly transects

September 1972

Wind data were not recorded during this month. The vertical distributions of certain parameters, are illustrated in Figure 4.1. The temperature, salinity and density isolines, showed no indications of inshore upwelling. The 10°C isotherm rose rapidly 56 km offshore (station 7), from below 100 metres to about 50 metres, 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 metre depth. A weak gradient of surface salinity and temperature was also apparent. Upwelling had obviously ceased some time before the transect was sampled.

A well-developed subsurface (10 - 50 metres) chlorophyll 'a' maximum was evident inshore between station 3 - 5, where values of up to 14,4 µg/l were measured. A separate patch of chlorophyll 'a' reaching values of 7,6 µg/l was observed in the frontal zone, further offshore (station 7) at a depth of 30 metres. An isolated patch of chlorophyll 'a' of 8,6 µg/l, suspected to consist of decomposed material with a high phaeophytin content, was found close to the bottom at 80 metres at station

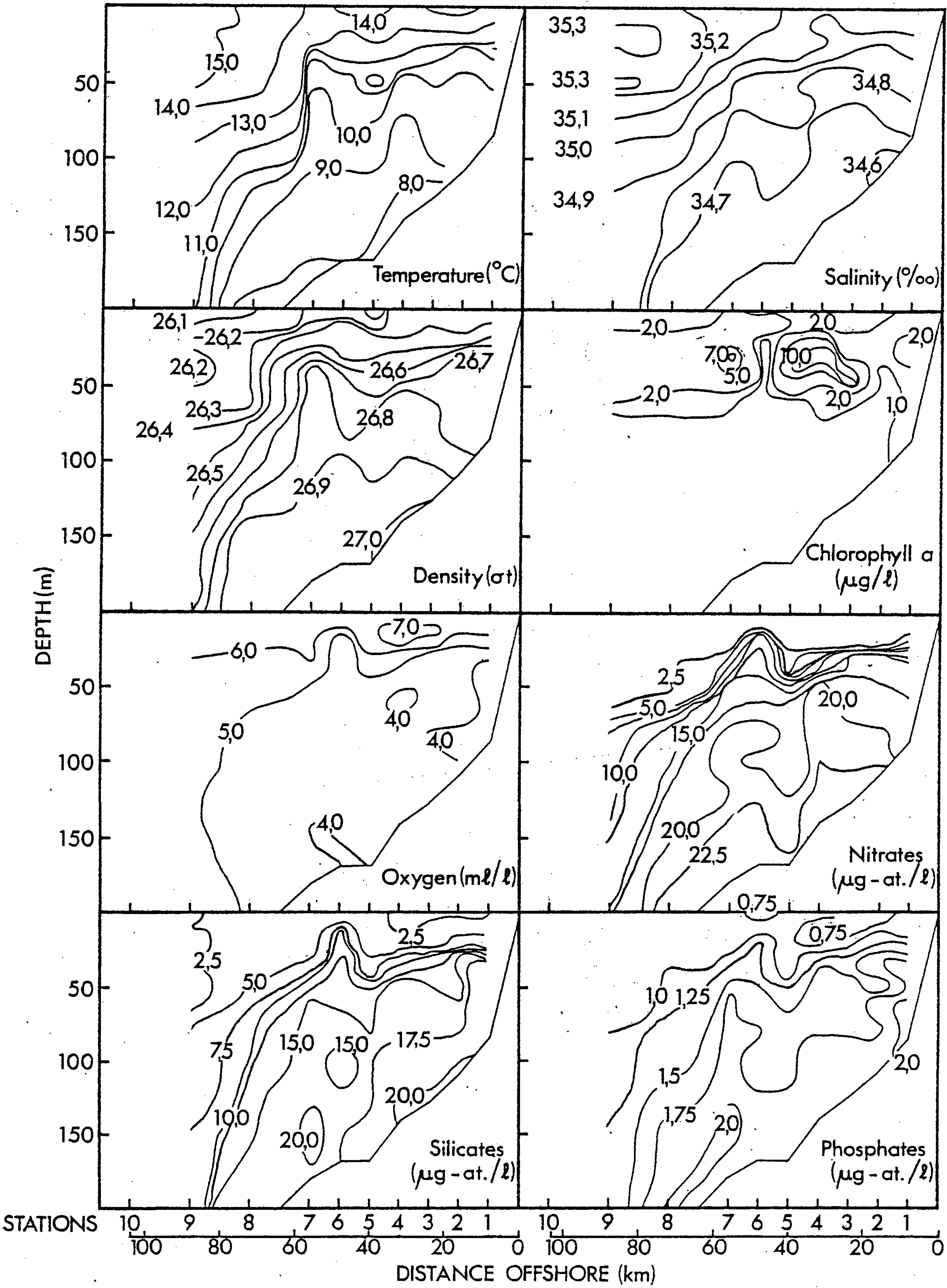


Figure 4.1 Vertical distributions of temperature °C; salinity ‰; density σt; chlorophyll 'a' μg/l; dissolved oxygen ml/l; nitrates μg atoms/l; silicates μg atoms/l; and phosphates μg atoms/l for September 1972.

1. High dissolved oxygen values coincided with chlorophyll 'a' maxima where levels of up to 7,74 ml/l were measured at station 3. These high oxygen levels at the surface indicated that phytoplankton production had taken place prior to sampling.

The nutrient concentrations observed within 10 metres of the surface, were very low and decreased somewhat irregularly along the line of stations. Higher nutrient levels 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 sub-surface chlorophyll 'a' maximum was generally associated with the thermocline at 30 - 40 metres, between stations 3 and 7 except at station 6, where a maximum occurred at 10 metres, well above the thermocline (Figure 4.2).

Integrated values of chlorophyll 'a', oxygen and nutrients within the euphotic zone (0 - 50 metres) are illustrated in Figure 4.3. (The 1% light level depth was shown by Andrews & Hutchings (1980) to vary from station to station, and in fact was often shallower than 50 metres. Nonetheless non-conservative parameters were integrated to this depth in order to compensate for mixing processes.) A simultaneous increase offshore in chlorophyll 'a' and oxygen was observed at stations 5 and 7 together with a decrease in nutrients. Station 6 appears anomalous, with a marked increase in nutrients and rapid decrease in chlorophyll 'a' and oxygen, just inshore from the frontal zone.

Samples preserved in 4% formalin, were counted after a period of 7 years. The effects of long-term preservation on the cells was, 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 chlorophyll 'a' measurements.

Selected cell counts and species identifications were performed on samples exceeding 1 µg/l of chlorophyll 'a'. The highest phytoplankton cell counts (381 x 10^3 cells/l at station 3) occurred where sub-surface chlorophyll 'a' concentration was maximal (Table 4.1). Samples analysed at the surface consisted of detritus. Twenty one

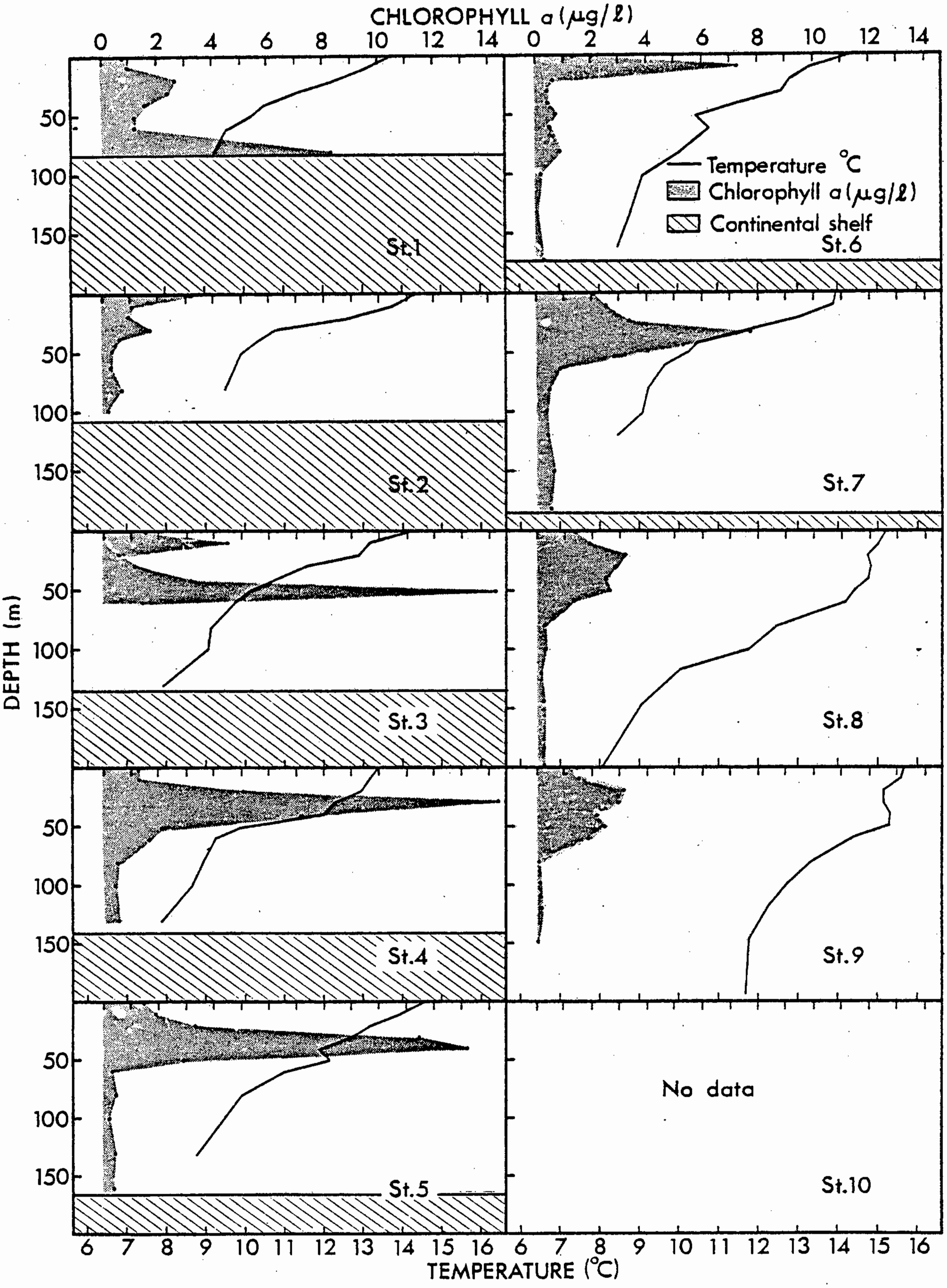


Figure 4.2 Vertical profiles of temperature °C and chlorophyll 'a' µg/l for September 1972.

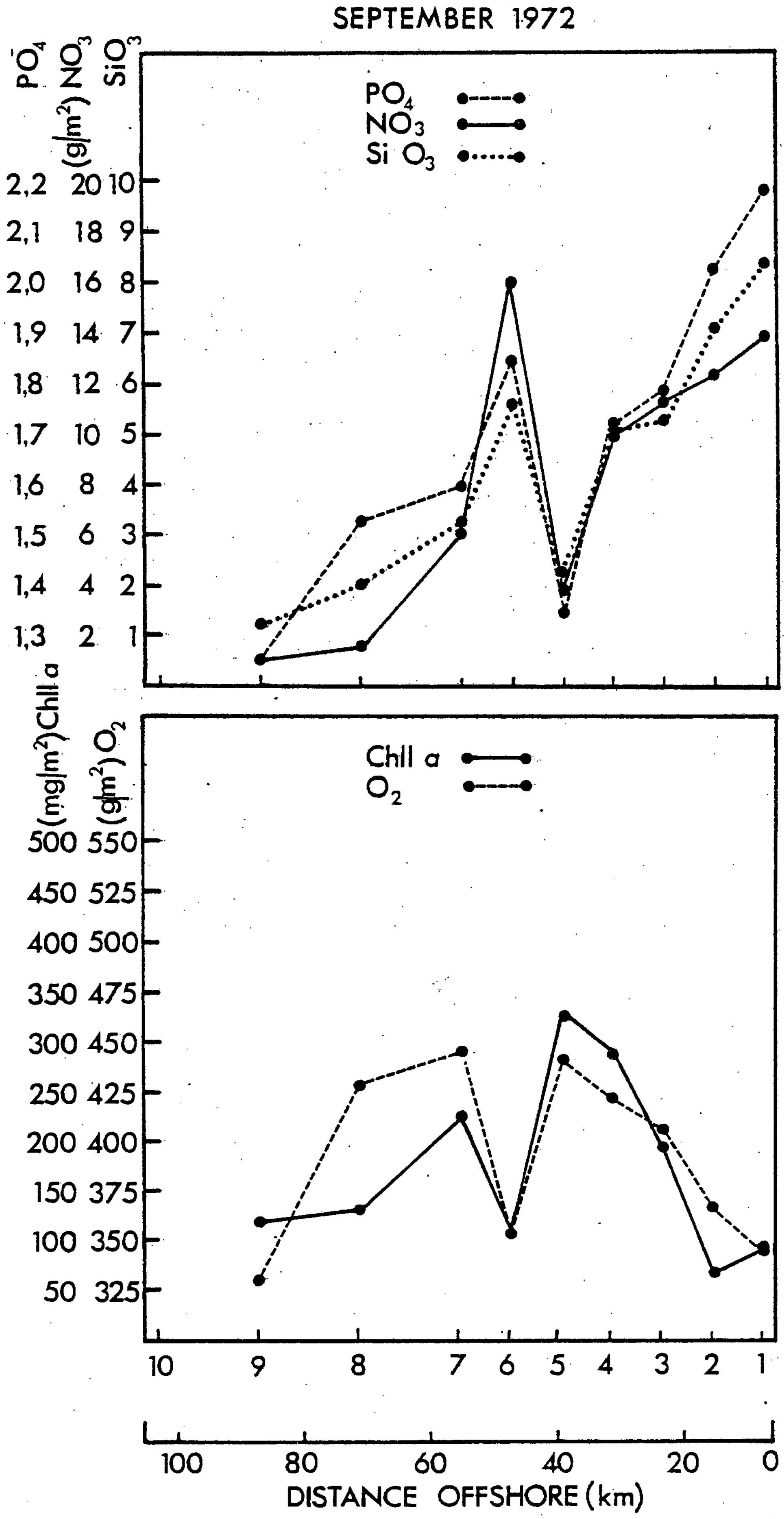


Figure 4.3 Changes within the euphotic zone (0-50 metres) of chlorophyll 'a' mg/m²; dissolved oxygen g/m²; nitrates g/m²; silicates g/m²; and phosphates g/m² for September 1972.

Table 4.1 Species identifications and microscopic cell counts of samples exceeding 1 µg/ℓ of chlorophyll 'a' during September 1972.

Depth	Station 1			Station 2			Station 3			Station 4			Station 5			Station 6			Station 7			Station 8			Station 9			Station 10		
	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	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=23940	7	7,4	Δ=98% T=182860	3	2,7	Detritus	-	1,9	▒	▒	1,7	Detritus	-			
20	3,0	Detritus	-	1,1	Δ=69% ▲=28% T=332140	6	0,7			5,1	Detritus	-	3,4	Detritus	-	0,7			3,7	Detritus	-	3,3	▒	▒	3,2	▒	▒			
30	2,5	▲=67% ✱=16% T=71620	5	1,8	Δ=70% ▲=25% T=17434	4	1,3			14,4	Δ=87% ▲=10% T=179600	5	11,6	Δ=77% ▲=21% T=350320	4	0,5			7,6	Detritus	1	3,0	▒	▒	3,0	▒	▒			
40	1,7	▲=41% Δ=32% T=27580	6	0,8			3,2	Δ=72% ▲=26% T=381200	3	7,0	Δ=85% ▲=10% T=115860	4	13,3	Δ=90% ▲= 8% T=362069	5	0,5			5,4	Δ=85% ▲= 9% T=79798	5	2,6	▒	▒	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	Δ=72% ▲=25% T=54983	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
Δ = Nitzschia seriata
✱ = Nitzschia delicatissima
✿ = Ciliate sp.

KEY

Chl = Chlorophyll 'a' µg/ℓ
D = Diversity (species)
T = Total
☐ = Chl 'a' < 1 (counts not done)
▒ = Samples missing

species were identified along the transect with two species *Nitzschia pungens* var. *atlantica* Cleve and *Nitzschia seriata* Cleve together comprising approximately 90% of the cells in most samples. *N. pungens*, a small, thread-like cell dominated at station 1, whereas the larger *N. seriata* was the dominant species in the remaining samples.

A dendrogram grouping of samples using the Bray-Curtis coefficient showed two broad groupings (Figure 4.4). In the absnece of marked changes in the species composition the grouping reflected the relative abundance of species. Group 1 samples were associated with low levels of chlorophyll 'a' and low phytoplankton cell counts. Group 2 consisted of samples within and bordering the chlorophyll 'a' maxima. The tight grouping of 5 samples at the 76% similarity level within this group, corresponded with the high phytoplankton cell counts found above the thermocline within the chlorophyll 'a' maxima.

October 1972

This transect was sampled on the 5 and 6 October during a period of moderate southwesterly winds of 10 - 20 knots. Prior to this, gentle southeasterly winds of 5 - 15 knots prevailed between 1 and 3 October. These strengthened to 35 knots by 4 October. A short lull then followed before the wind changed to southwesterly.

Active upwelling occurred during the sampling period, indicated by the temperature, salinity and density distributions (Figure 4.5). 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 offshore between stations 1 and 2. Offshore, sunwarming together with vertical and horizontal mixing processes caused the surface water temperatures and salinities to rise by 6,75°C and 0,63‰ respectively, with the front situated between stations 6 and 8, 40 - 60 km offshore.

A relatively small near-surface patch of chlorophyll 'a' <2 µg/l was distributed between the front and the newly upwelled water (stations 3 - 6). Highest values for chlorophyll 'a' (10,2 µg/l) and dissolved oxygen concentrations (6,1 ml/l) occurred at station 4. The dissolved oxygen values did not alter much in the euphotic zone except for a

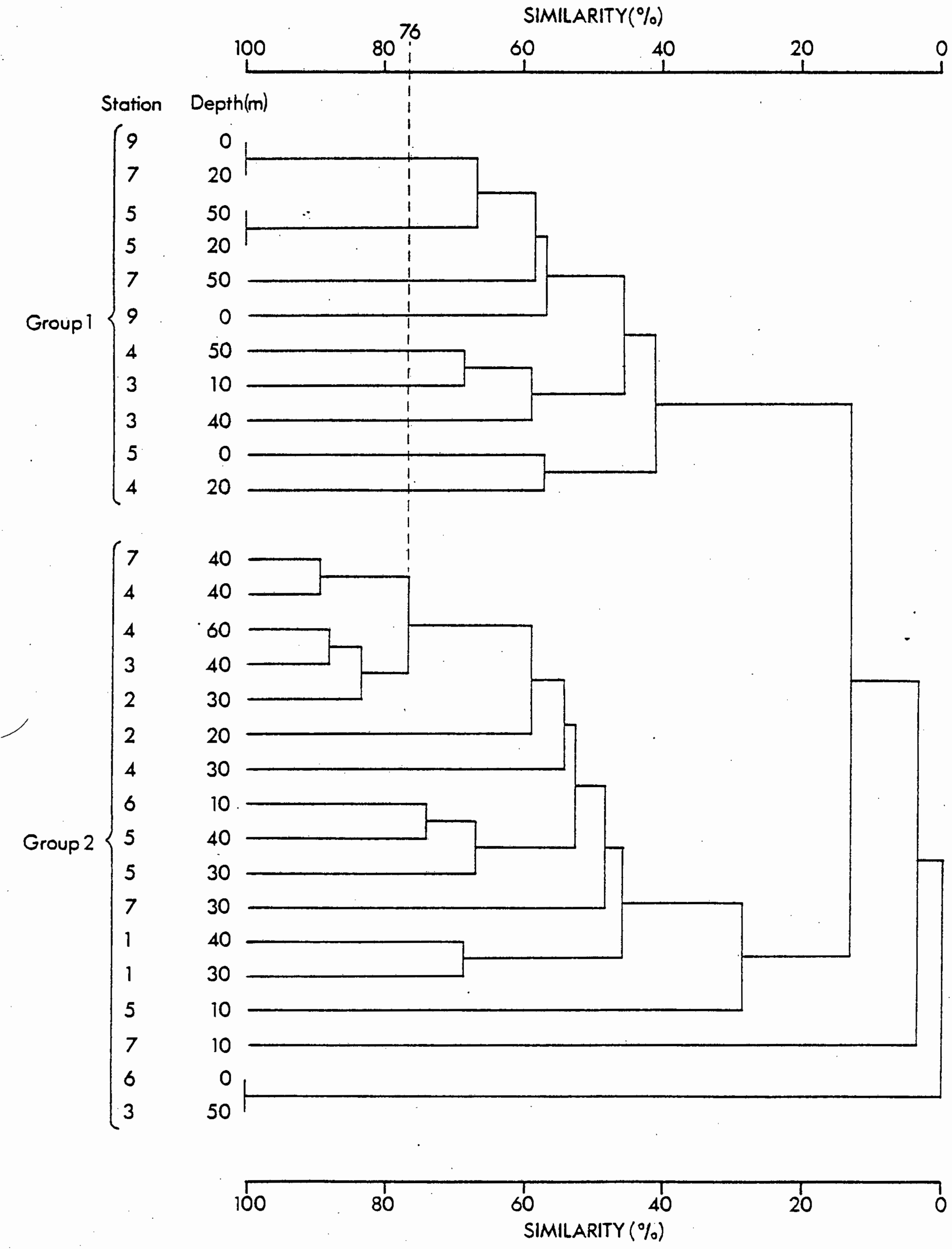


Figure 4.4 A dendrogram showing the grouping of samples according to the Bray-Curtis coefficient for September 1972.

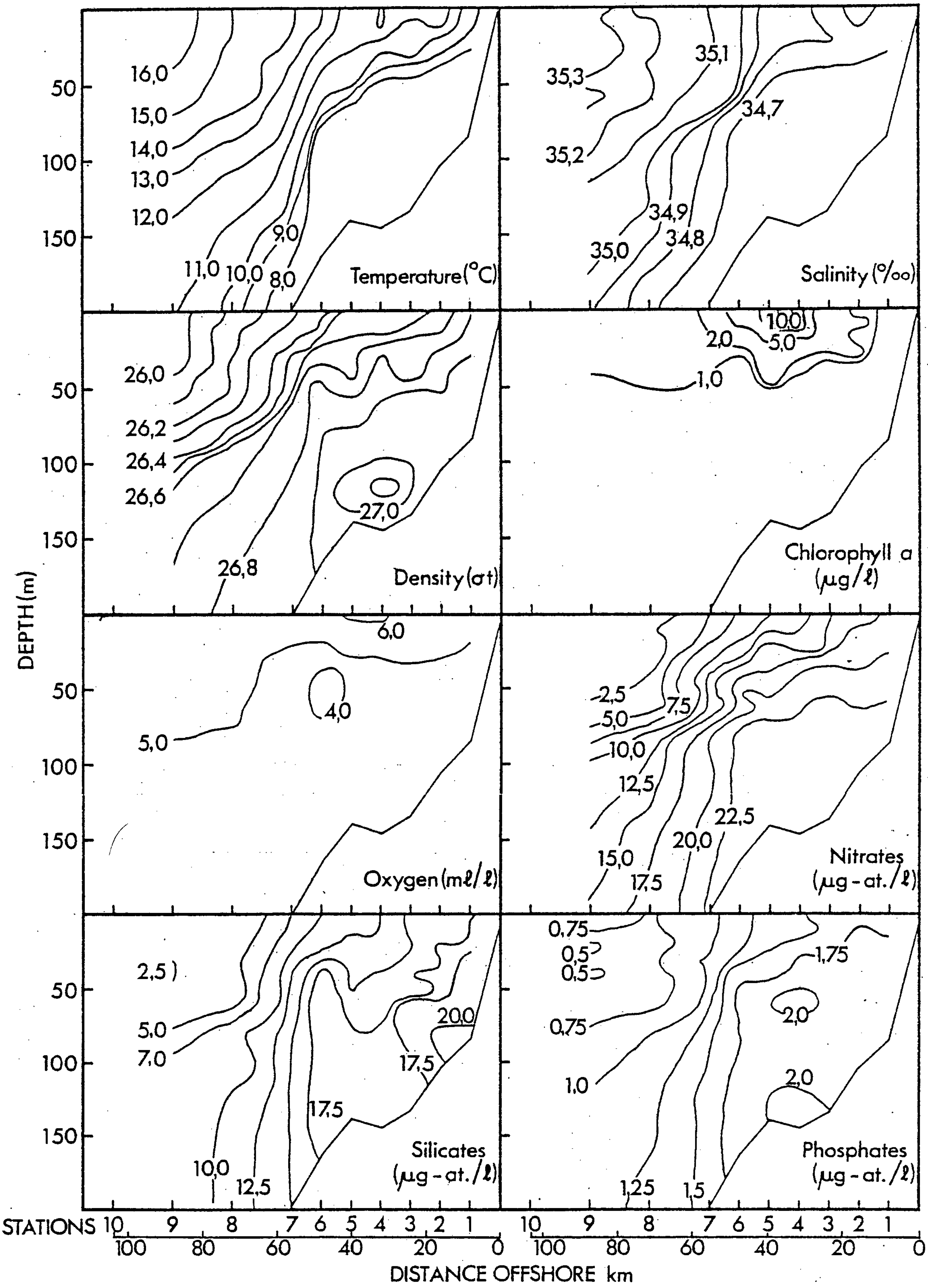


Figure 4.5 Vertical distributions of temperature °C; salinity ‰; density σt; chlorophyll 'a' μg/ℓ; dissolved oxygen mℓ/ℓ; nitrates μg atoms/ℓ; silicates μg atoms/ℓ; and phosphates μg atoms/ℓ for October 1972.

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 metres.

The surface nutrients displayed similar trends. Initially high nutrient concentrations were observed close inshore, where active upwelling was occurring, decreasing somewhat in the high chlorophyll 'a' patch and reaching minimum values beyond the front. High nutrient concentrations were found to coincide with the patch of low oxygen water observed at station 6 between 40 - 70 metres, within the frontal zone, suggesting that regeneratory processes were occurring.

Vertical profiles of temperature and chlorophyll 'a' (Figure 4.6) clearly indicated that the surface chlorophyll 'a' maxima 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 4.7. A concomitant decrease in nutrients and increase in oxygen and chlorophyll 'a' was shown until station 3. Between stations 3 and 5, the sudden increase in chlorophyll 'a' without a corresponding increase in dissolved oxygen content, suggested that the phytoplankton was in the early stages of a bloom.

Evidence from microscopic cell counts and identifications (Table 4.2) revealed that the surface chlorophyll 'a' maximum represented detrital material. In fact, the phytoplankton standing stock was very low, and confined to station 6 where a maximum of 380 x 10^3 cells/l were found at 30 metres. In this instance, it would seem probable that the low standing stocks could have resulted from cellular degradation due to poor preservation. Andrews & Hutchings (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 nitzioides* Hust. were strongly dominant constituting 90% of the cells in most samples. *Chaetoceros* species alone contributed about 80% of the total abundance in most samples.

November 1972

This transect was sampled on 8 and 9 November during a period of

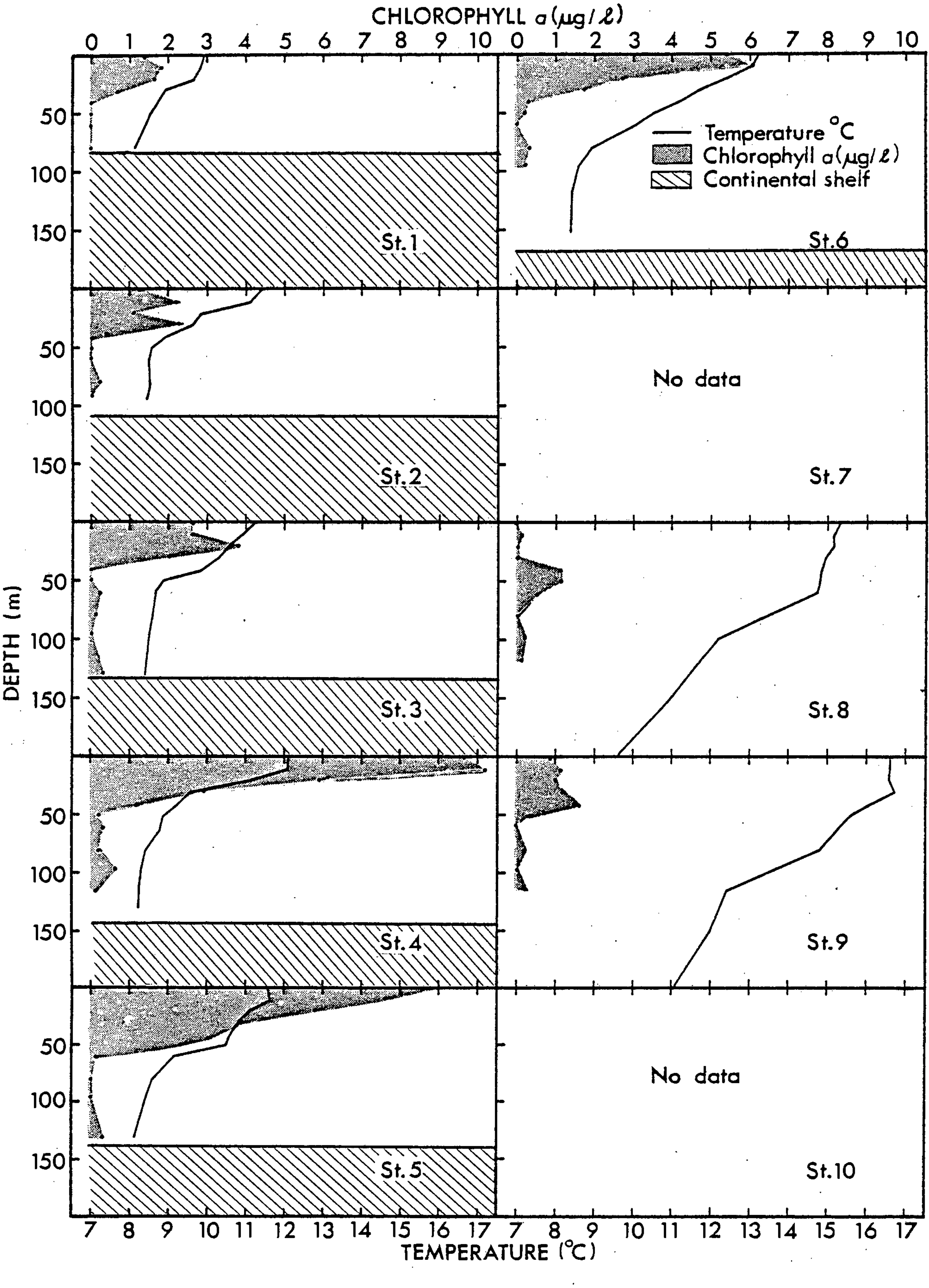


Figure 4.6 Vertical profiles of temperature °C and chlorophyll 'a' µg/l for October 1972.

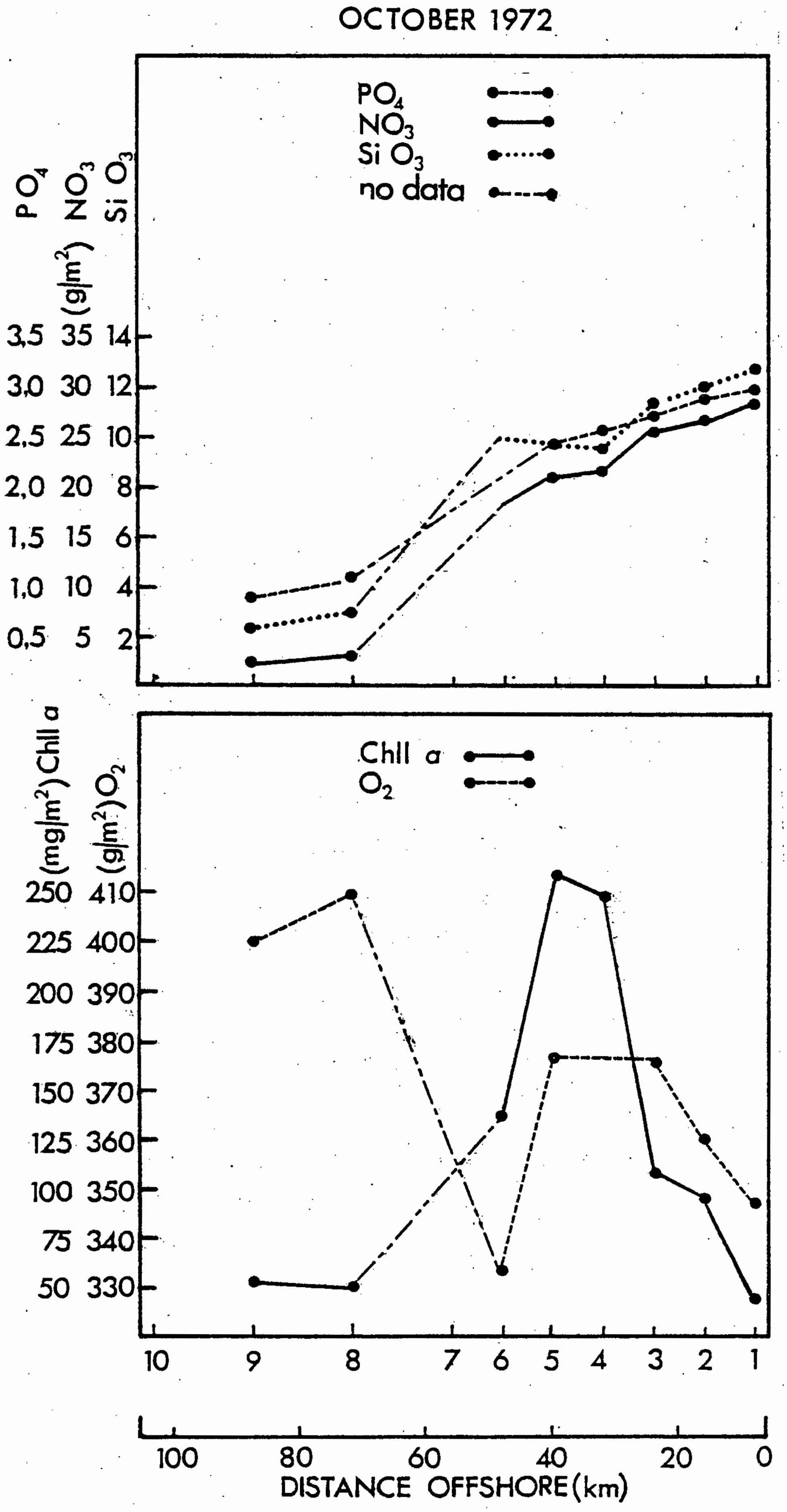


Figure 4.7 Changes within the euphotic zone (0-50 metres) of chlorophyll 'a' mg/m²; dissolved oxygen g/m²; nitrates g/m²; silicates g/m²; and phosphates g/m² for October 1972.

Table 4.2 Species identifications and microscopic cell counts of samples exceeding 1 µg/ℓ of chlorophyll 'a' during October 1972.

Depth	Station 1			Station 2			Station 3			Station 4			Station 5			Station 6			Station 7			Station 8			Station 9			Station 10		
	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D
0	0,7			1,3	Detritus	-	2,6	Detritus	-	9,6	Detritus	-	8,8	Detritus	-	5,4	□= 56% O= 29% T=81909	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=77987	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=328865	3				-			1,0					
30	0,4			2,2	Detritus	-	2,0	Detritus	-	2,6	Detritus	-	3,9	Detritus	-	1,7	O=70% □=20% T=37987	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 species

KEY

Chl = Chlorophyll 'a' µg/ℓ
D = Diversity (species)
T = Total
□ = Chl 'a' < 1 µg/ℓ

35 knot strong southeasterly winds. Previously, between the 1st and 4th, 30 - 40 knot southeasterlies prevailed. On the 5th the wind veered to northwesterlies (5 - 10 knots) and reversed again on the 6th to strong southeasterlies (20 - 30 knots). There was a lull on the 7th before strong southeasterlies commenced again on the 8th and 9th.

Sustained upwelling prior to the transect, resulted in a broad belt of mixed water, with the front some 20 km further offshore than in October. Active upwelling was evident within 10 km of the shore, where temperature, salinity, and density isolines, vertically intersected the sea surface (Figure 4.8). The mixed water zone was nearly isohaline between 10 and 100 km offshore, to a depth of 40 - 50 metres, but changed dramatically across the front, rising by 0,5‰ within 18 km. The pycnocline gradually deepened up till 60 km offshore and then deepened very rapidly across the front. A strongly defined front was evident offshore, where marked temperature and salinity gradients separated warm saline oceanic waters from cooler and less saline aged upwelled waters.

Chlorophyll 'a' concentrations were highest in the upper 10 - 20 metres between stations 2 and 7, reaching a maximum of 22,7 µg/l at 10 metres at station 4, and dropping rapidly below the pycnocline. At station 9, 100 km offshore, chlorophyll 'a' concentrations of >2,7 µg/l extended to 120 metres, the maximum depth sampled for chlorophyll 'a', clearly demonstrating sinking of dense, productive, upwelled water at the frontal zone. Dissolved oxygen levels increased simultaneously with increases in chlorophyll 'a'.

Inshore surface waters possessed high nutrient concentrations while offshore the concentrations diminished simultaneously with the increases in chlorophyll 'a'. A reduction of 96% for nitrate, 86% for phosphate and 68% for silicate occurred at the surface from the inshore stations to the offshore stations.

Vertical profiles of chlorophyll 'a' and temperature (Figure 4.9) showed the existence of a shallow thermocline between stations 2 and 7, coinciding with the distribution of maximum chlorophyll 'a' concentrations.

Integrated values (Figure 4.10) of chlorophyll 'a' and oxygen, within the euphotic zone, increased, with a concomitant decrease in

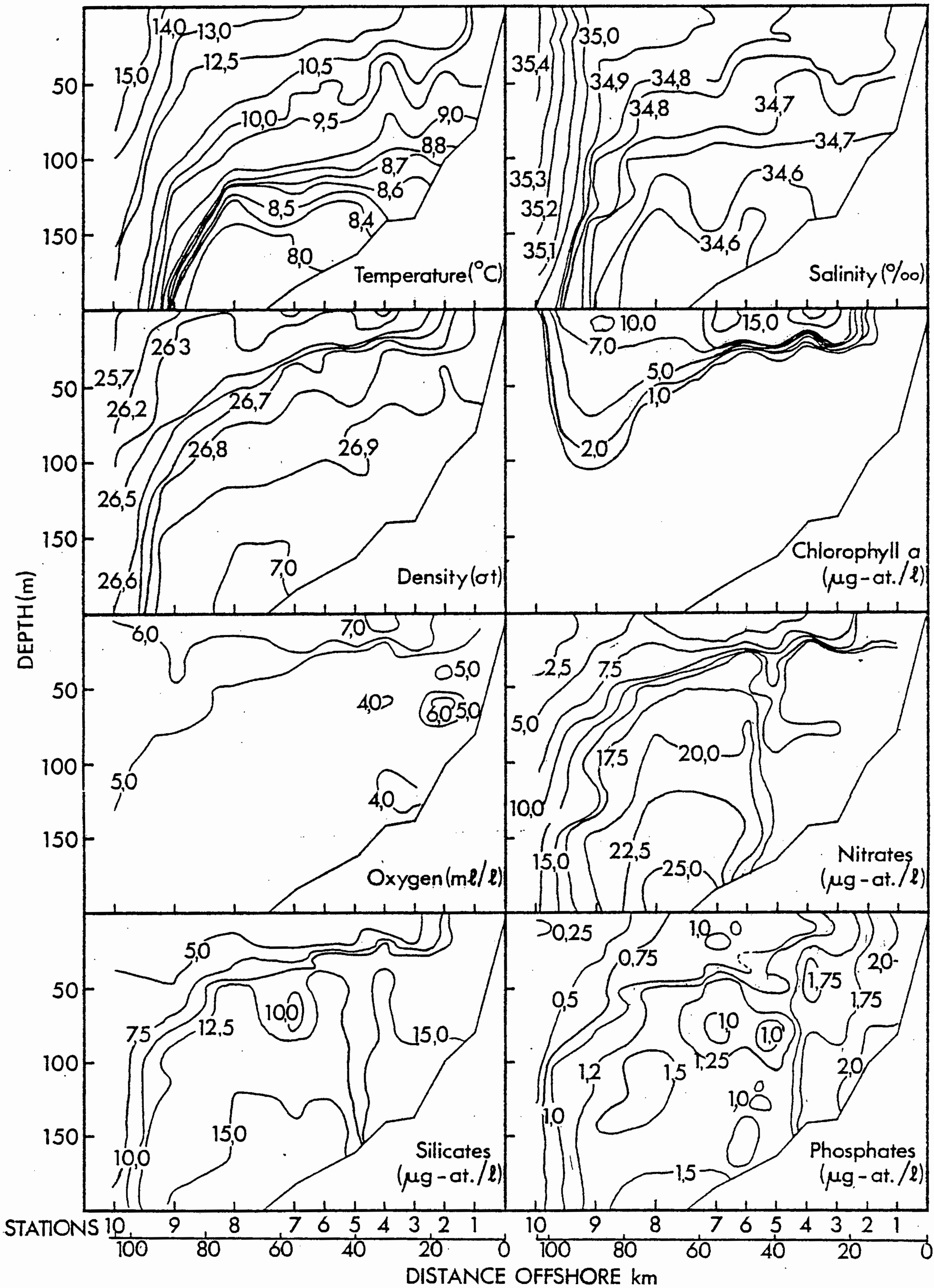


Figure 4.8 Vertical distributions of temperature °C; salinity ‰; density σt; chlorophyll 'a' µg/l; dissolved oxygen ml/l; nitrates µg atoms/l; silicates µg atoms/l; and phosphates µg atoms/l for November 1972.

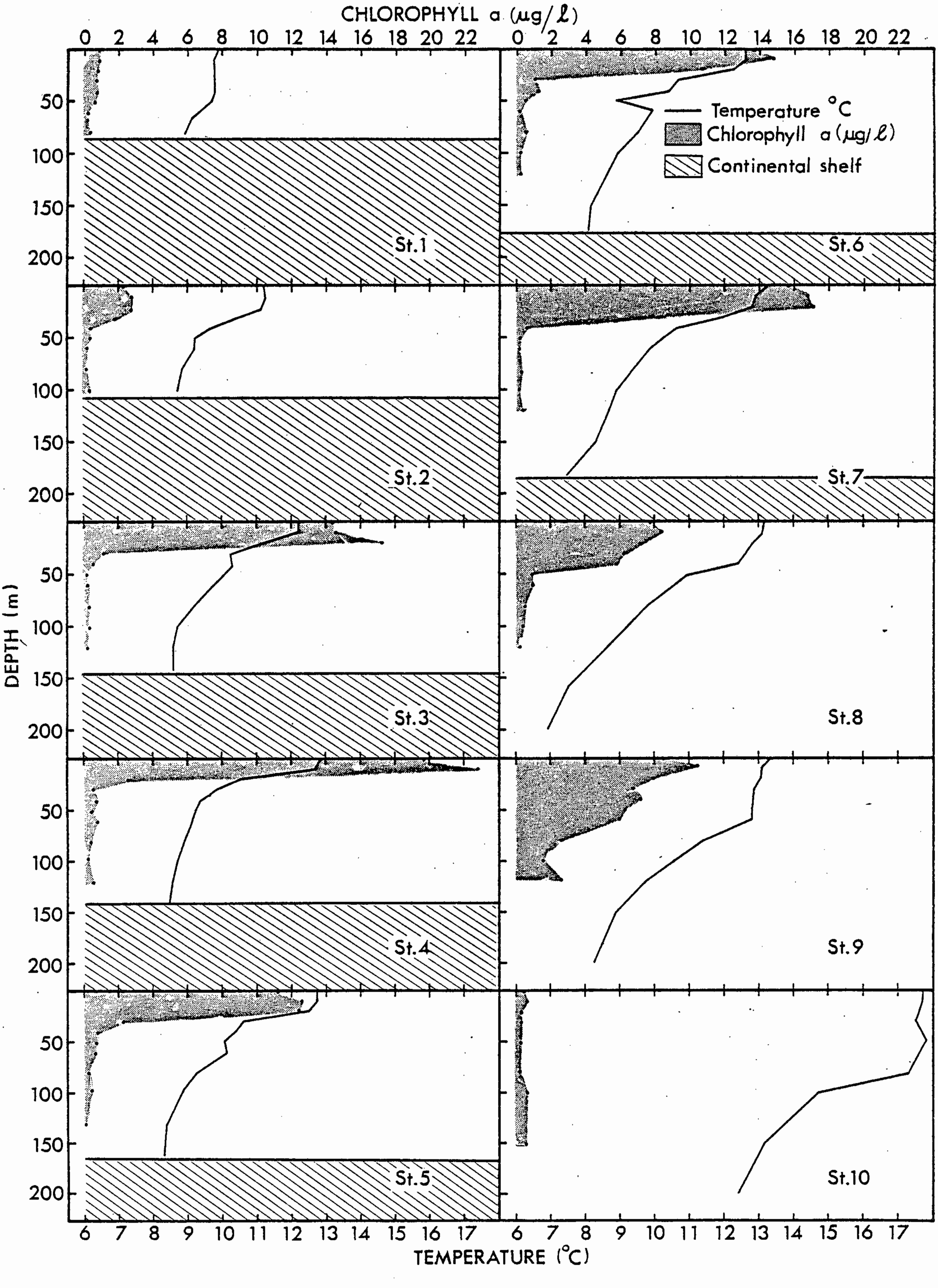


Figure 4.9 Vertical profiles of temperature °C and chlorophyll 'a' μg/l for November 1972.

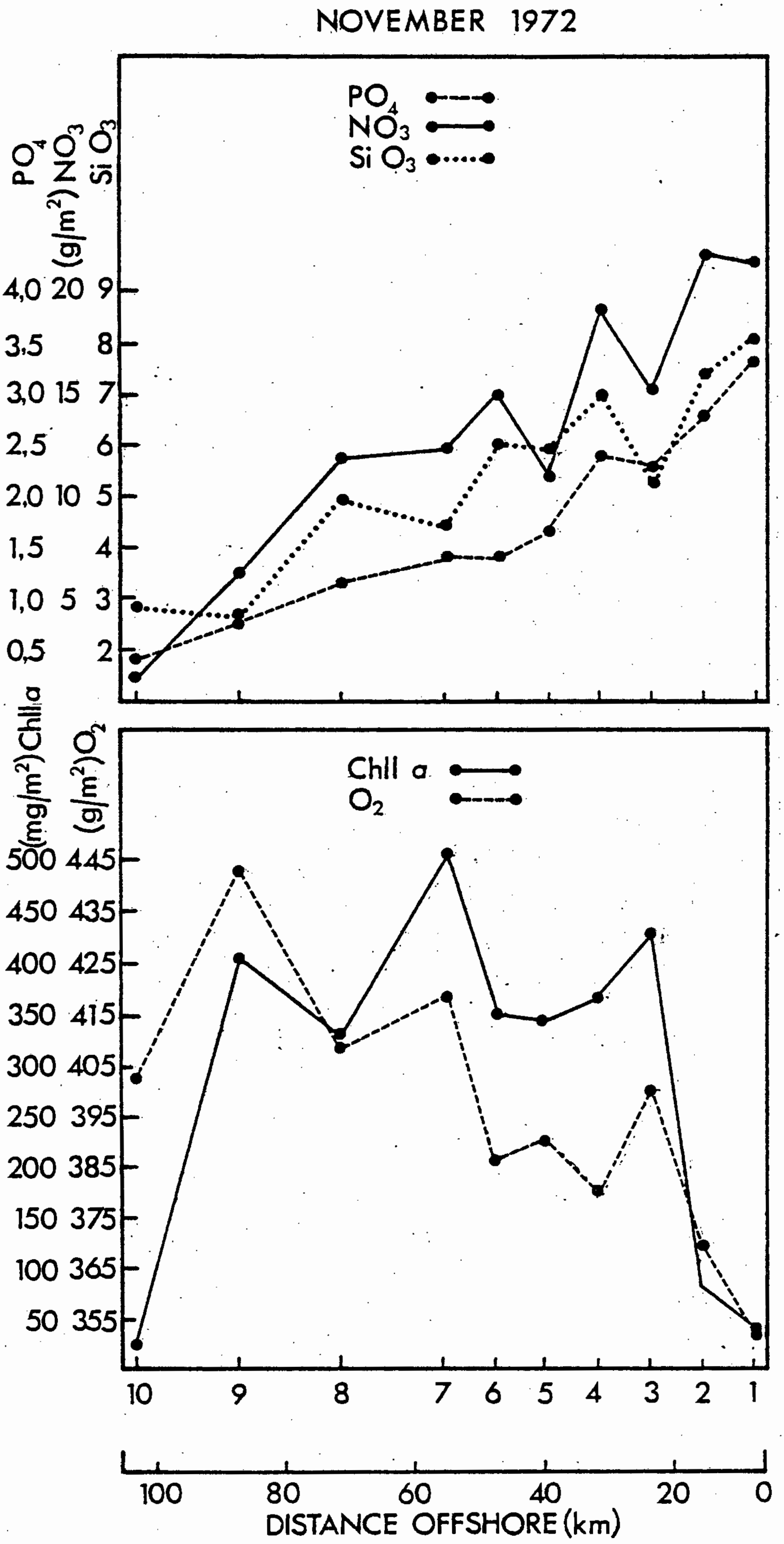


Figure 4.10 Changes within the euphotic zone (0-50 metres) of chlorophyll 'a' mg/m²; dissolved oxygen g/m²; nitrates g/m²; silicates g/m²; and phosphates g/m² for November 1972.

nutrient concentrations. Within the euphotic zone nitrates were utilized at a faster rate than either phosphates or silicates.

The phytoplankton standing stock, as determined from cell counts (Table 4.3) was considerably higher than in October. Cell counts of 1100 x 10^3 cells/l were measured at station 5 at 10 metres. The highest concentration of cells was distributed between stations 3 and 7 within the upper 20 metres. Nine species in total were identified with a *Nitzschia* species dominant at most stations on the transect. *Thalasiothrix frauenfeldii* Grun. and *Skeletonema costatum* represented a minor proportion of the samples until station 4. *Chaetoceros* spp. appeared at station 5 and increased in abundance, constituting 50 - 82% of the sample.

December 1972

Sampling commenced on the 12th during moderate (20 knots) southeasterlies and then changed on the 13th to southerly winds. Previously, between the 1st and 11th, west and northwesterly winds of up to 15 knots prevailed with intermittent calms.

Conditions were similar to those in November, with a broad belt of mixed, aged upwelled water, but with no upwelling inshore (Figure 4.11). Inshore at the front, the waters were relatively stable with a marked pycnocline between the coast and 60 km (station 7) offshore, beyond which the isopycnals deepened rapidly. A warm water eddy was centred at station 6. The front, less well defined than in November, occurred between stations 7 and 8.

A shallow chlorophyll 'a' maximum in the upper 20 metres occurred between stations 2 and 5. High dissolved oxygen levels were found at the surface and within the chlorophyll 'a' maximum. Oxygen-depleted water of <3ml/l appeared along the shelf between stations 4 - 7.

Nutrient concentrations were lowest in the areas rich in chlorophyll 'a' and in offshore oceanic water. Rapid decreases were observed below the pycnocline.

Vertical profiles of temperature and chlorophyll 'a' showed that the chlorophyll 'a' maximum followed the thermocline as it deepened offshore (Figure 4.12).

Table 4.3 Species identifications and microscopic cell counts of samples exceeding 1 µg/ℓ of chlorophyll 'a' during November 1972.

Depth	Station 1			Station 2			Station 3			Station 4			Station 5			Station 6			Station 7			Station 8			Station 9			Station 10		
	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D
0	0,9	●=100%		2,2	●=98% ▽= 5% T=53294	2	15,4	●=95% ■= 5% T=165760	2	19,7 ⬚	⬚	⬚	11,0	●=94% O= 5% T=309523	4	13,6	●=75% O=22% T=337634	4	15,6	●=90% O= 9% T=249495	3	7,8	●=100% T=144118	2	7,7	Detritus	-	0,4		
10	0,9	●=50% O=50%		2,8	●=91% ■= 9% T=94792	2	15,5	●=100% T=372960	1	22,7	●=89% ■=10% T=442424	5	12,6	●=80% ■=17% T=1100000	3	14,8	●=98% T=280640	2	16,8	●=64% O=34% T=193269	3	8,4	●=91% □= 7% T=71845	5	10,5	●=65% □=32% T=129897	4	0,5		
20	0,8			2,8	Detritus	-	17,3	●=100% T=336160	1	2,6	Detritus	-	12,5	●=84% O= 5% T=282243	5	10,6	●=85% O=15% T=151852	3	17,1	●=83% O=17% T=488764	3	7,2	●=94% O= 4% T=114407	5	7,9	O=51% ●=45% T=180952	4	0,4		
30	0,6			0,9			1,2			0,4			2,3	●=96% ▽= 3% T=79167	3	1,0	Detritus	-	8,1	●=76% O=22% T=94180	3	6,2	Detritus	-	6,8	O=50% ●=33% □=10% T=41178	5	0,3		
40	0,8			0,2			0,7			0,5			0,8			1,2	Detritus	-	0,6			5,8	Detritus	-	7,2	O=82% ●=10% T=68932	4	0,3		
50	0,5			0,2			0,3			0,3			0,7			0,5			0,2			0,9			6,3	●=91% O= 8% T=126316	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			1,5	Detritus	-			

KEY OF SPECIES

●= Nitzschia species
O= Chaetoceros species
▽= Thalassiothrix frauenfeldii
■= Skeletonema costatum
□= Thalassiosira nitzschioides

KEY

Chl = Chlorophyll 'a' µg/ℓ
D = Diversity (species)
☐ = Chl 'a' < 1 µg/ℓ
⬚ = Missing sample
T = Total

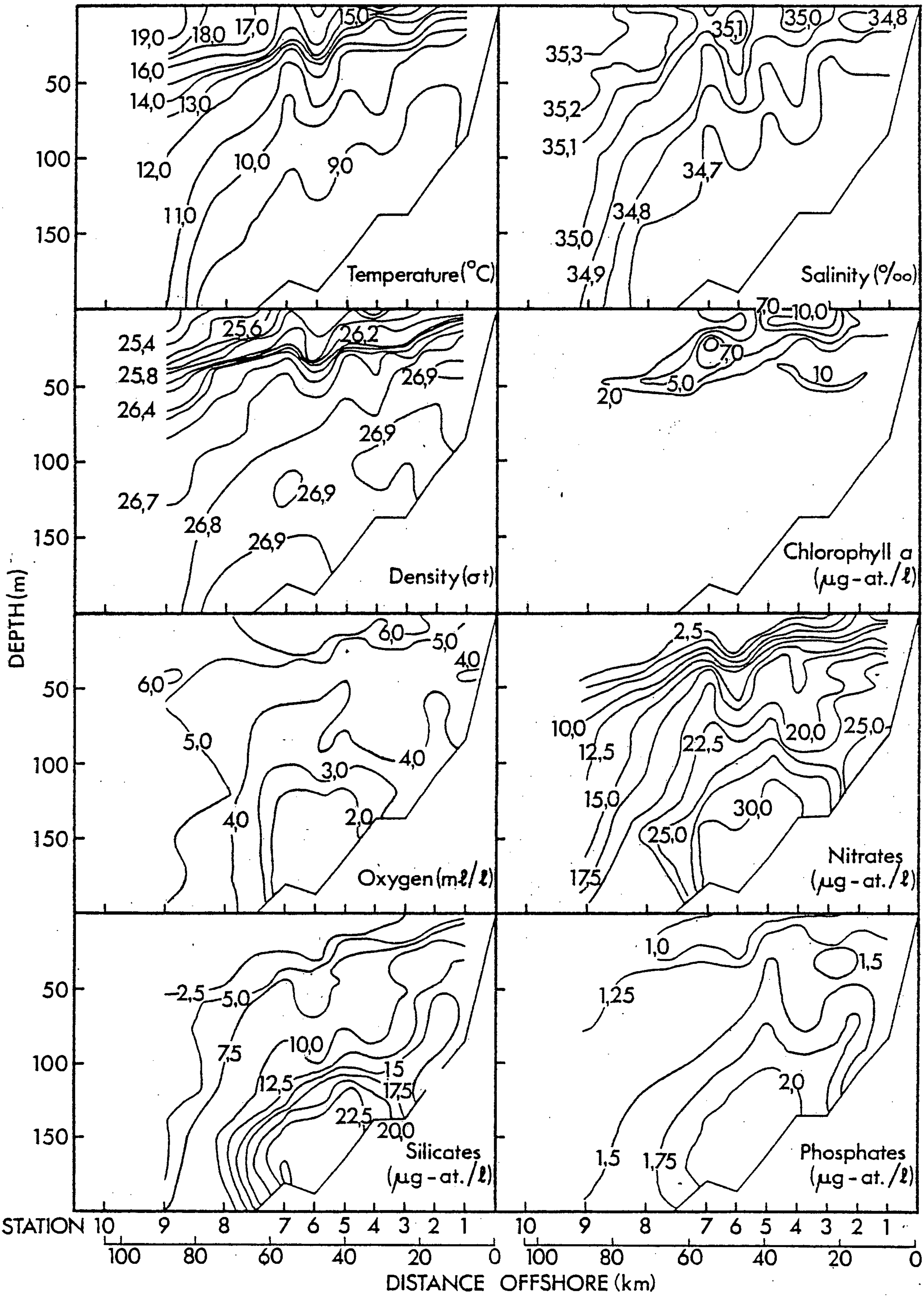


Figure 4.11 Vertical distributions of temperature °C; salinity‰; density σt; chlorophyll 'a' μg/l; dissolved oxygen ml/l; nitrates μg atoms/l; silicates μg atoms/l; and phosphates μg atoms/l for December 1972.

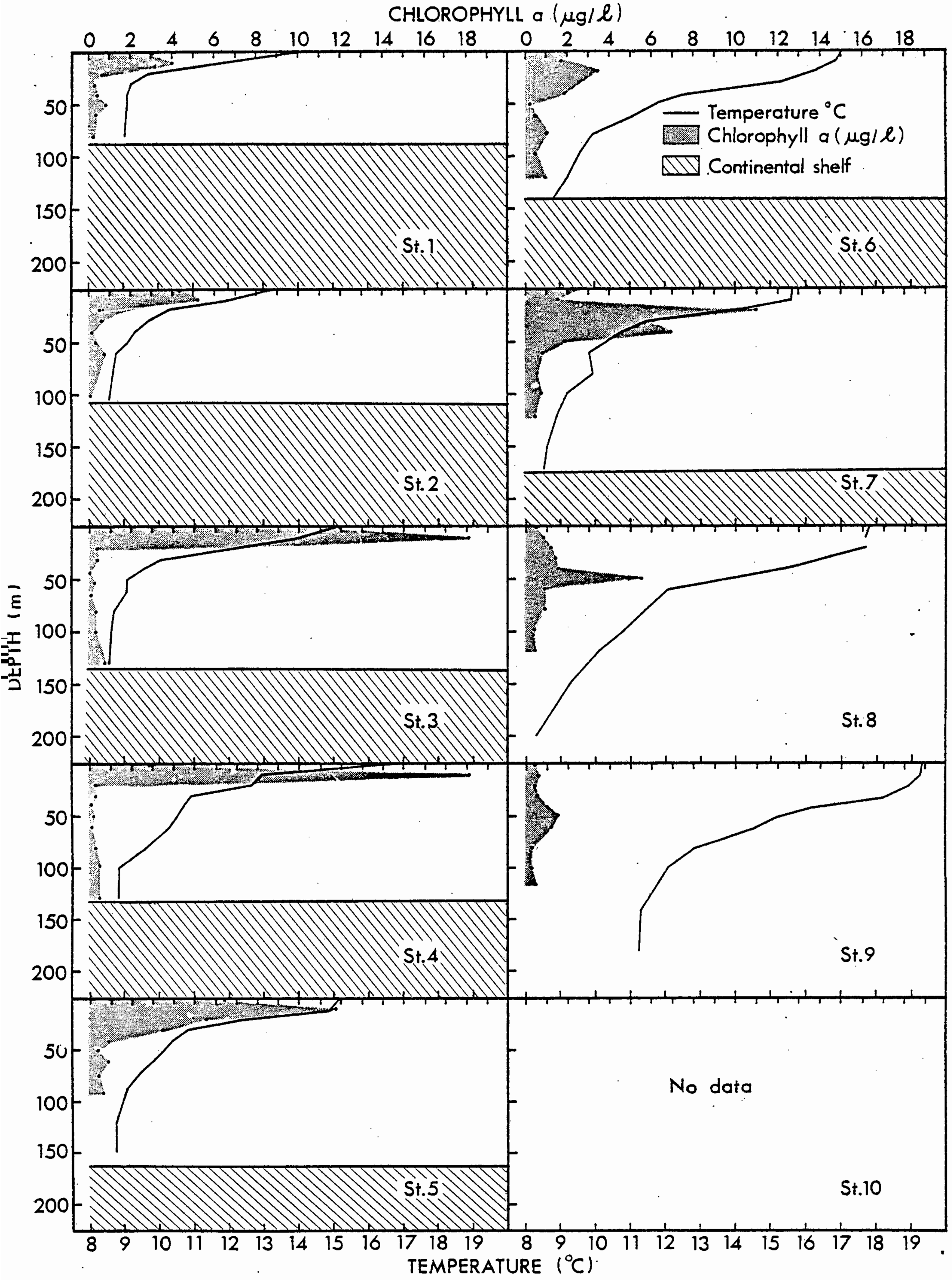


Figure 4.12 Vertical profiles of temperature and chlorophyll 'a' for December 1972.

Integrated values of non-conservative parameters within the euphotic zone are illustrated in Figure 4.13. The nutrients dropped somewhat irregularly down the plume. The sharpest drop occurred between stations 5 and 6 as the patch of oceanic water was sampled. This drop in nutrients was not accompanied by an increase in chlorophyll 'a'. Chlorophyll 'a' was highest 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 the oxygen content differed little on crossing the front.

Peak cell concentrations at 10 metres at station 4 (434 x 10^3 cells/l) coincided with the shallow chlorophyll 'a' maximum and shallow thermocline (Table 4.4). Similarly at station 7 (40 metres) a high value of 422 x 10^3 cells/l coincided with the offshore sub-surface chlorophyll 'a' maximum and the thermocline depth. Fifteen species were identified in total but again *Nitzschia* spp. dominated all samples, even in the deep chlorophyll 'a' maximum at station 8. *S. costatum* occurred only at the surface at station 3 and represented 6% of the total abundance in that sample. All other species were rare.

January 1973

Strong southeasterly winds which blew for 3 days between the 12th and 15th, were followed by a calm and then by a southwesterly wind of 5 - 10 knots on the 16th when sampling commenced. A gentle southerly wind (10 knots) blew on the second day of sampling (7th).

Observations made from the vertical distributions of various parameters (Figure 4.14) revealed no upwelling, with strong stratification of the water column. A 20 - 30 metre deep layer of oceanic water, separated from cooler waters by a very strong pycnocline, came close to the coast.

A sub-surface chlorophyll 'a' maximum developed in the vicinity of the thermocline (Figure 4.15). Levels of 51,8 µg/l chlorophyll 'a' were recorded at 30 metres at station 8. Nutrients were depleted within the upper layers where dissolved oxygen levels were uniformly high.

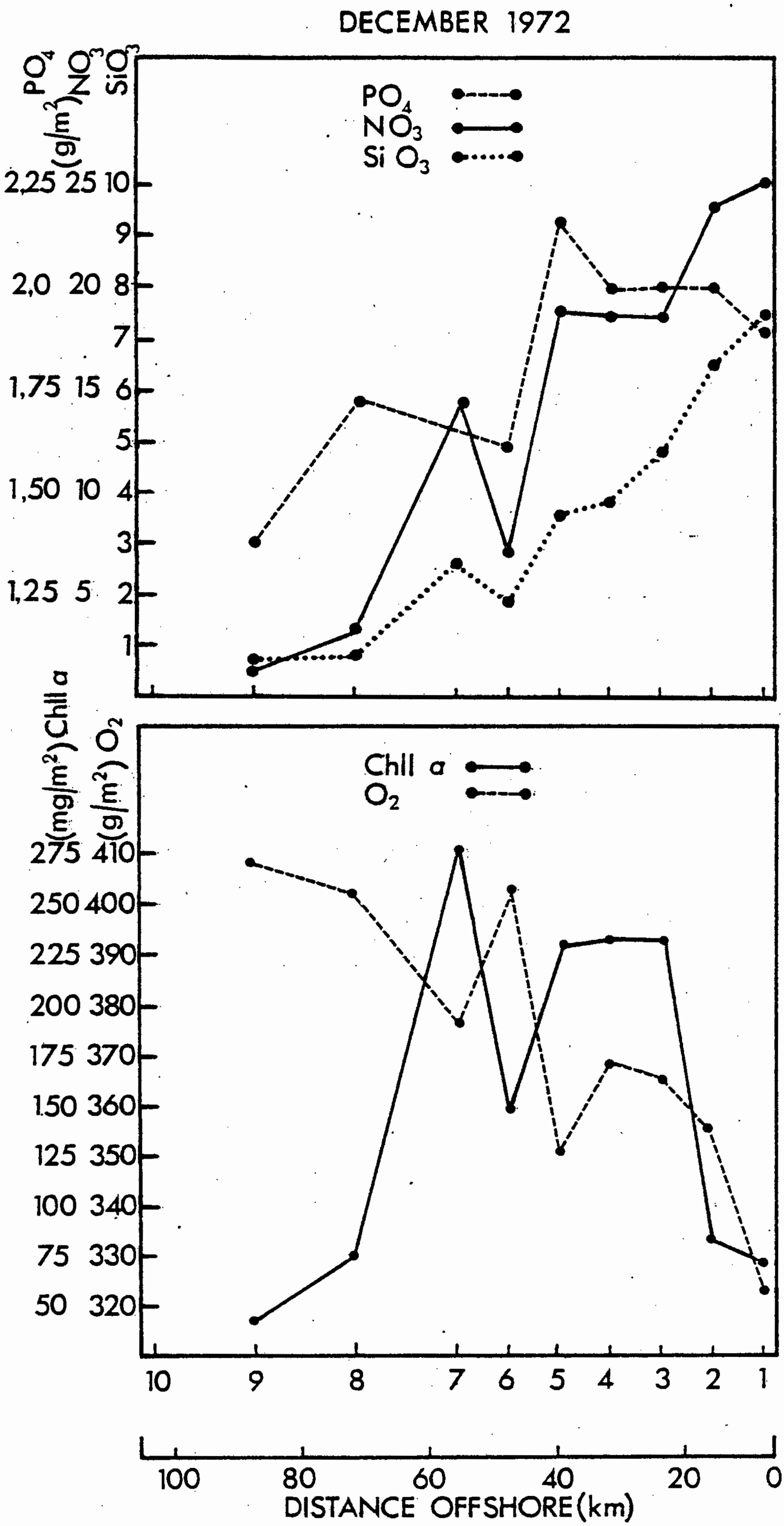


Figure 4.13 Changes within the euphotic zone (0-50 metres) of chlorophyll 'a' mg/m²; dissolved oxygen g/m²; nitrates g/m²; silicates g/m²; and phosphates g/m² for December 1972.

Table 4.4 Species identifications and microscopic cell counts of samples exceeding 1 µg/ℓ of chlorophyll 'a' during December 1972.

Depth	Station 1			Station 2			Station 3			Station 4			Station 5			Station 6			Station 7			Station 8			Station 9			Station 10		
	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D
0	3.0	Detritus	-	4.1	Detritus	-	11.7	●=93% ■= 6% T=121569	3	2.8	●=97% T=96899	4	6.5	●=100% T=316527	2	2.0	Detritus	-	2.2	Detritus	-	0.5			0.4					
10	4.0	●=100% T=213757	1	5.1	●=100% T=48511	1	9.3	●=100% T=140845	1	18.5	●=100% T=433816	2	11.7	●=99% T=390935	2	1.8	Detritus	-	1.5	Detritus	-	0.8			0.5					
20	0.5			0.3			6.1	●=99% T=206025	3	0.3			5.5	●=100% T=142424	1	3.3	Detritus	-	1.0	●=98% T=195145	3	1.1	Detritus	-	0.3					
30	0.3			0.6			1.2	Detritus	-	0.3			3.2	●=100% T=112037	1	5.9	●=91% T=101156	5	6.2	●=95% T=79314	2	1.2	Detritus	-	0.4					
40	0.4			0.1			0.8			0			1.0	Detritus	-	2.7	Detritus	-	6.9	●=98% T=422343	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=217554	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 species
■ = Skeletonema costatum

KEY

Chl = Chlorophyll 'a' µg/ℓ
D = Diversity (species)
☐ = Chl 'a' < 1 µg/ℓ
T = Total

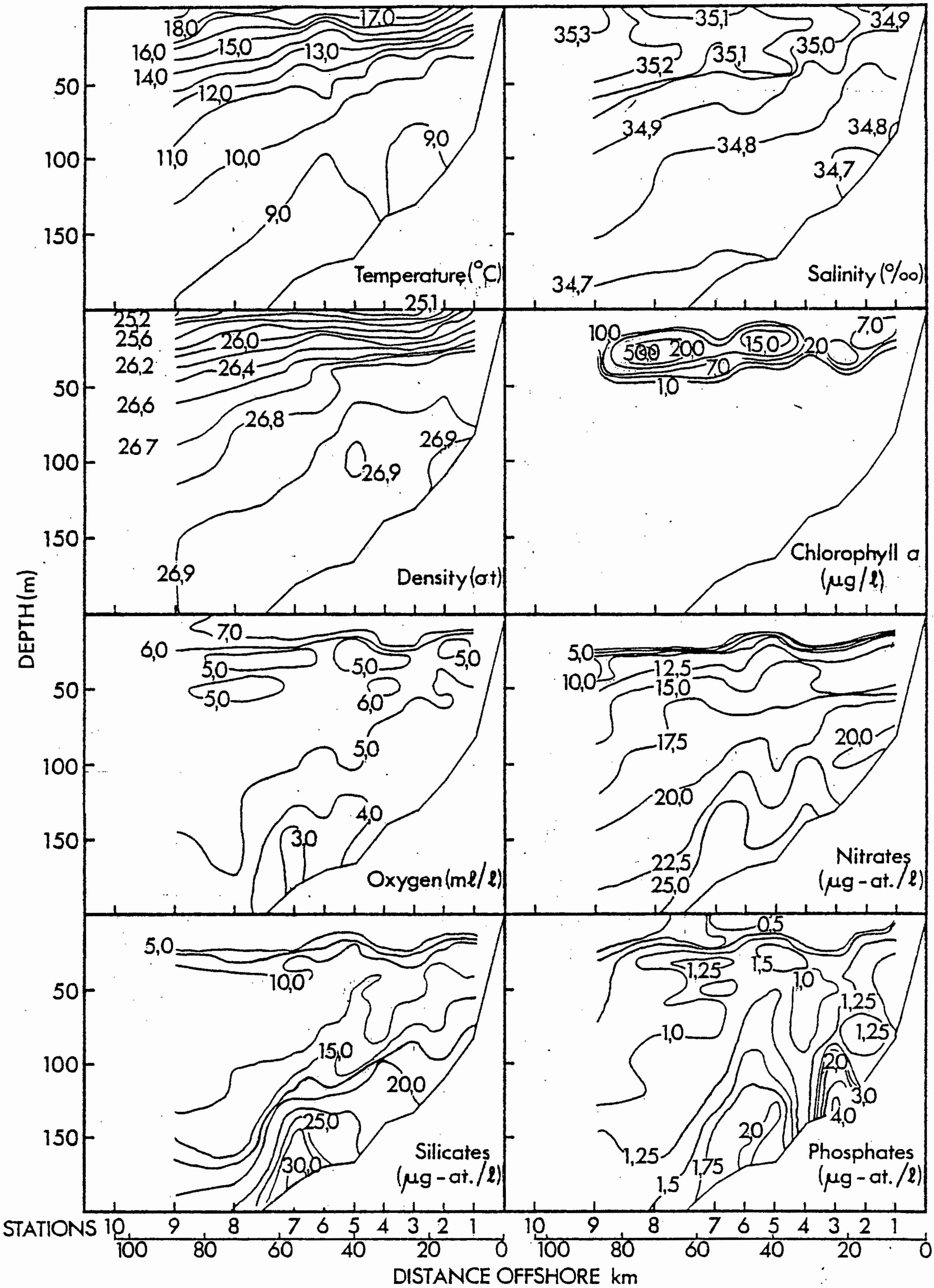


Figure 4.14 Vertical distributions of temperature °C; salinity ‰; density σt; chlorophyll 'a' μg/l; dissolved oxygen ml/l; nitrates μg atoms/l; silicates μg atoms/l; and phosphates μg atoms/l for January 1973.

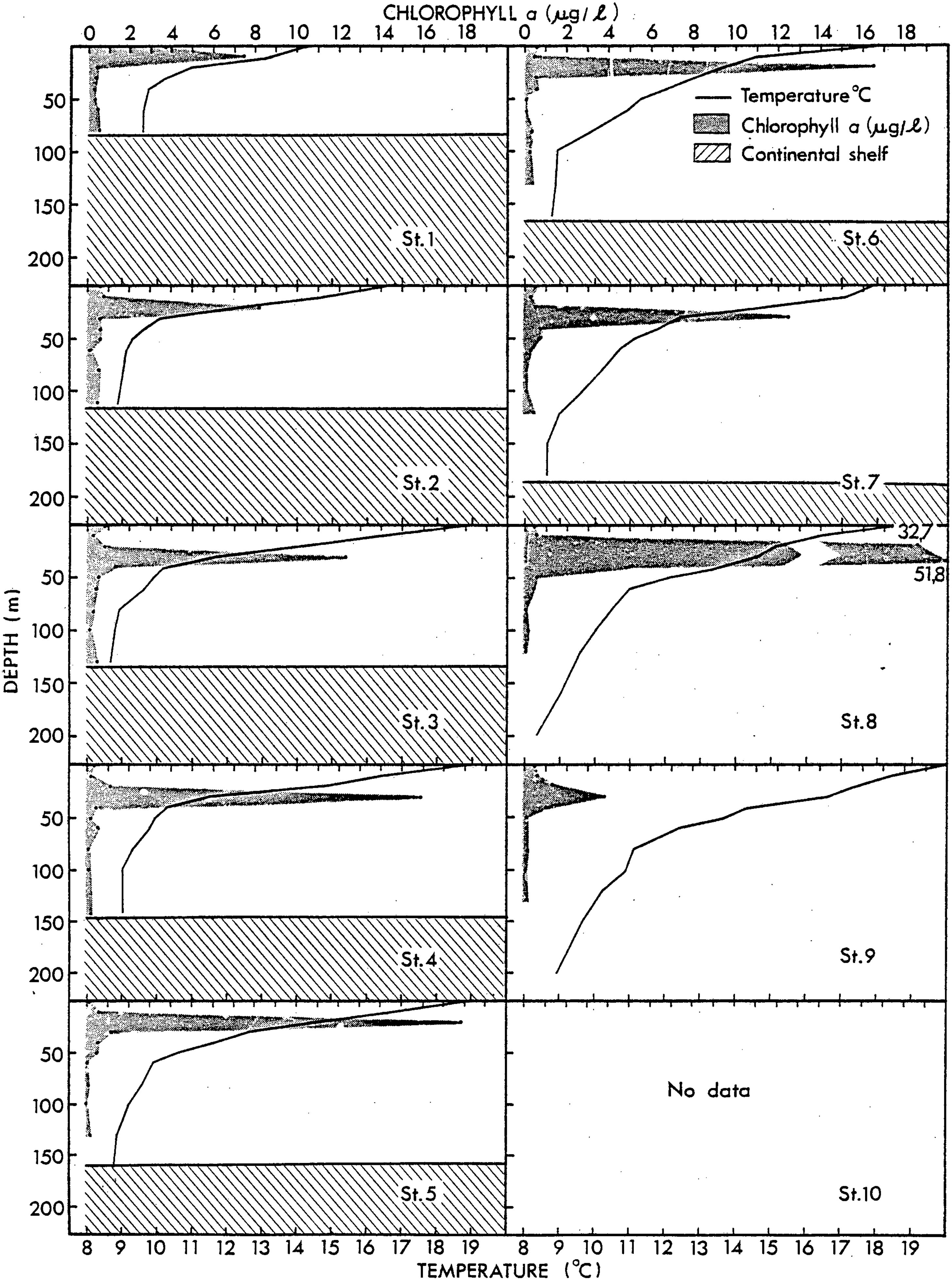


Figure 4.15 Vertical profiles of temperature °C and chlorophyll 'a' µg/l for January 1973.

No trends were discernible from integrations of the non-conservative parameters within the euphotic zone (Figure 4.16). Chlorophyll 'a' was low, except for a sharp increase at station 8. Nutrient enrichment occurred at stations 2 and 5, and dissolved oxygen was highest at station 3 when chlorophyll 'a' was lowest.

Low cell counts were associated with the chlorophyll 'a' maximum except at station 8 where high chlorophyll 'a' levels occurred and 788 x 10^3 cells/l were recorded at 30 metres (Table 4.5). (This count is likely to be an underestimate of the actual numbers due to the fact that the phytoplankton cells, especially *Nitzschia* spp., were poorly preserved.) Five species were identified. Again, *Nitzschia* spp. dominated all samples and *S. costatum* formed a small proportion to the total abundance at stations 6 and 8. Detritus occurred in all samples.

February 1973

Strong 35 knot, southeasterly winds prevailed between the 3rd and 6th. 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 (Figure 4.17). Surface temperatures increased and density decreased until station 5. This suggested that the stabilizing effect of sunwarming on the water column allowed a chlorophyll 'a' maximum to develop between stations 3 and 5. Mixing processes due to 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 metres offshore. The oceanic front was only apparent 100 km offshore between stations 9 and 10.

Chlorophyll 'a' was broadly distributed in two patches, inshore and offshore, both in the upper 20 metres (Figure 4,18). High levels of dissolved oxygen were measured within the chlorophyll 'a' maximum.

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

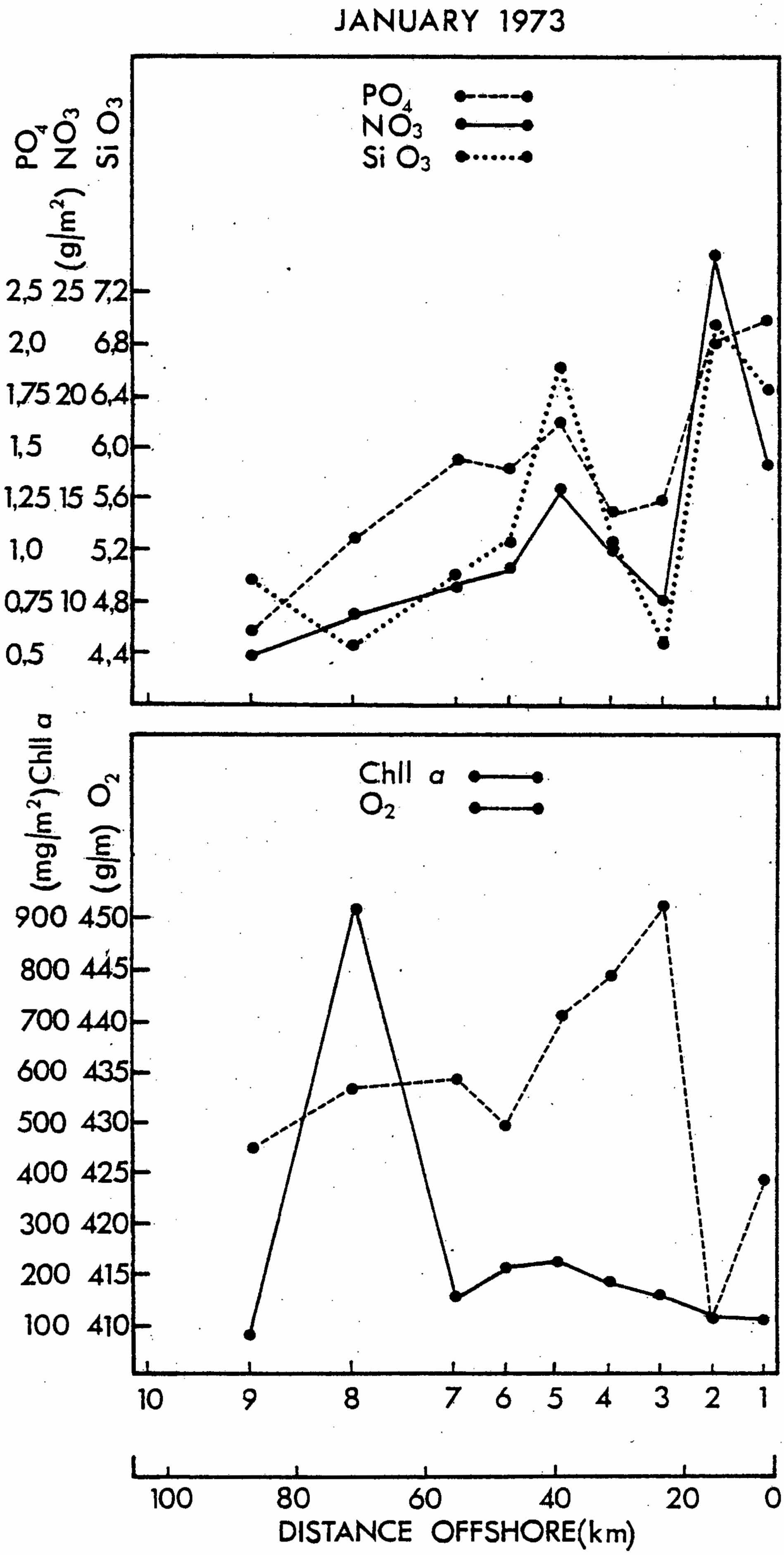


Figure 4.16 Changes within the euphotic zone (0-50 metres) of chlorophyll 'a' mg/m²; dissolved oxygen g/m²; nitrates g/m²; silicates g/m²; and phosphates g/m² for January 1973.

Table 4.5 Species identifications and microscopic cell counts of samples exceeding 1 μg/ℓ of chlorophyll 'a' during January 1973.

Depth	Station 1			Station 2			Station 3			Station 4			Station 5			Station 6			Station 7			Station 8			Station 9			Station 10		
	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	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=71795	1	16,4	●=91% ■= 9% T=77295	2	0,4			32,7	◤●=97% ■= 3% T=480300	2	1,6	Detritus	-			
30	0,3			0,6			12,1	●=100% T=135200	1	16,0	●=81% T=192308	1	1,1	Detritus	-	0,6			12,4	Detritus	-	51,8	◤●=100% T=788618	1	3,8	Detritus	-			
40	0,2			0,6			1,4	●=100% T=26570	1	0,3			0,6			0,6			0,8			4,9	●=100% T=78269	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 species
■ = Skeletonema costatum

KEY

Chl	= Chlorophyll 'a' μg/ℓ
D	= Diversity (species)
T	= Total
☐	= Chl 'a' < 1 μg/ℓ
◤	= Inaccurate counts

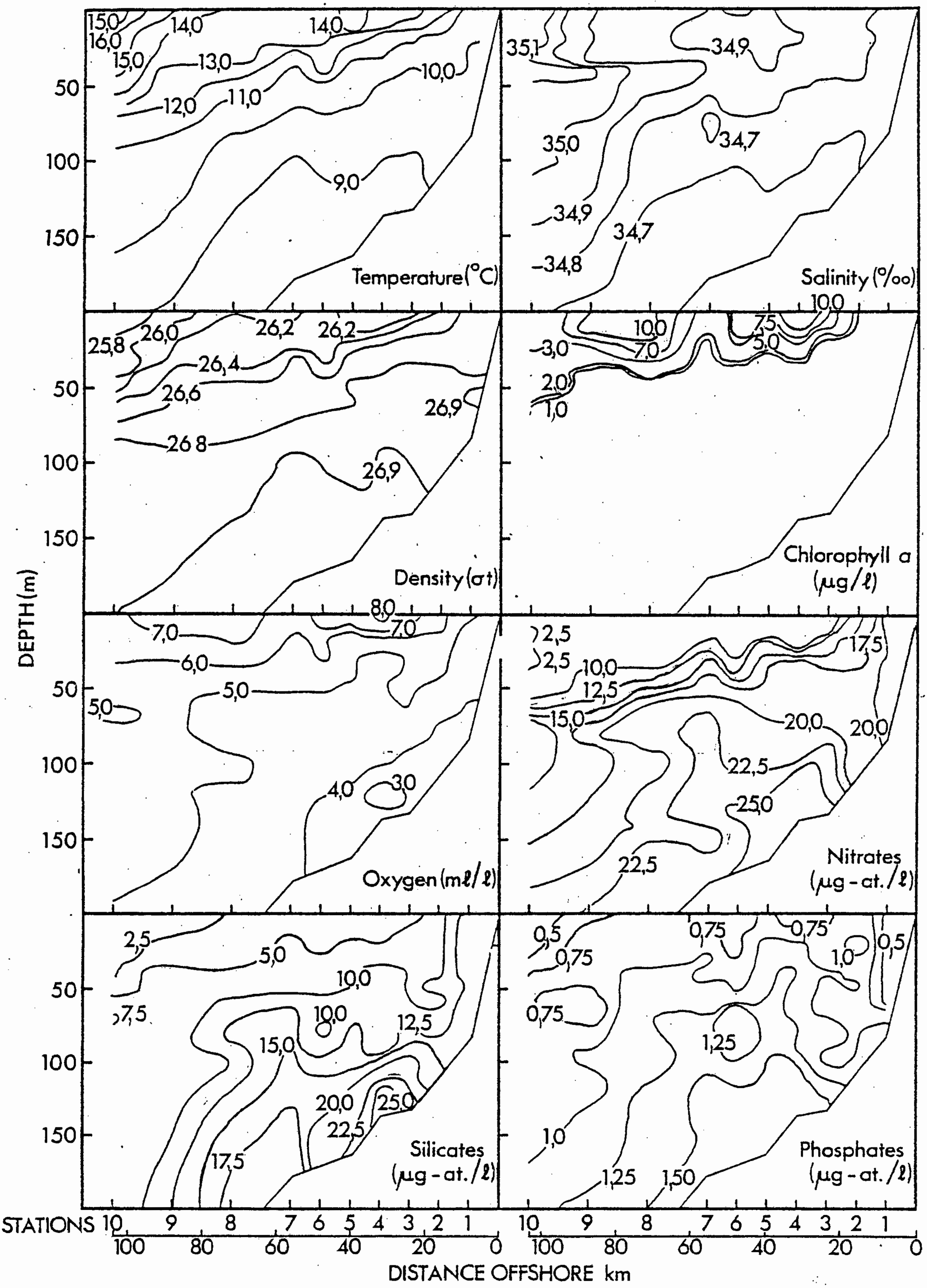


Figure 4.17 Vertical distributions of temperature °C; salinity ‰; density σt; chlorophyll 'a' μg/l; dissolved oxygen ml/l; nitrates μg atoms/l; silicates μg atoms/l; and phosphates μg atoms/l for February 1973.

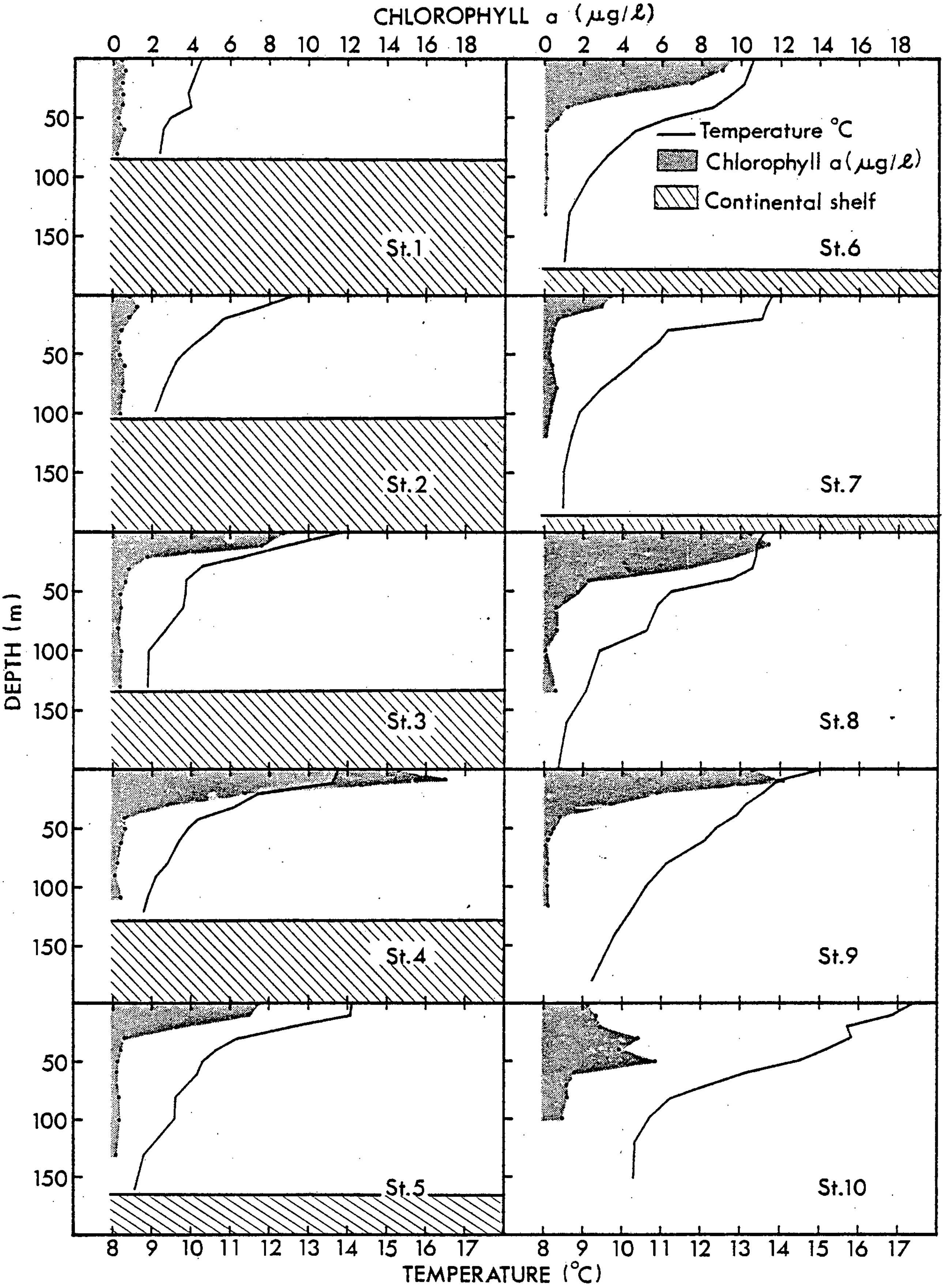


Figure 4.18 Vertical profiles of temperature °C and chlorophyll 'a' μg/l for February 1973.

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 (Figure 4.19).

High cell concentrations corresponded with high levels of chlorophyll 'a', inshore at stations 4 and 5 and offshore at station 8(Table 4.6). Inshore samples and those in which chlorophyll 'a' exceeded 1 µg/l (stations 6 and 7) contained detritus. Eight species in total were identified. *Nitzschia* spp. dominated throughout the transect. *Chaetoceros* spp. occurred together with *Nitzschia* spp. in the inshore chlorophyll 'a' maximum and *S. costatum* and a dinoflagellate species occurred together with *Nitzschia* in the offshore patch.

4.2 Discussion

4.2.1 Changes through the upwelling season

Physical changes

A rapid response in the distribution of the hydrographic parameters was caused by short-term wind events throughout the upwelling season. Andrews & 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 orientation of the plume by the inshore and offshore movement of the frontal zone and by the extent and depth to which the mixed water belt had been formed.

By analysing the changes in the distribution of the hydrographic parameters the monthly transects were categorized into 3 different bloom stages.

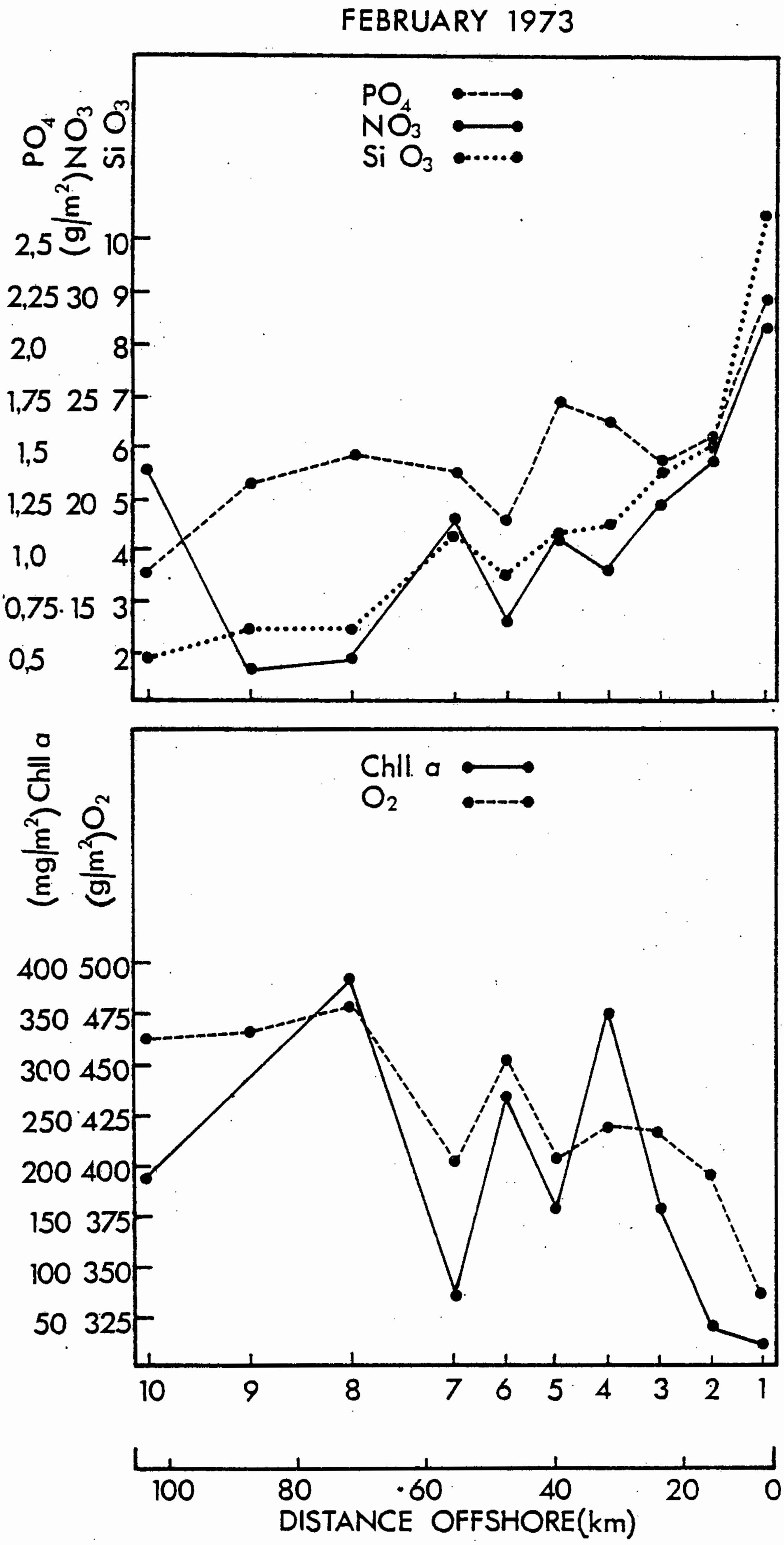


Figure 4.19 Changes within the euphotic zone (0-50 metres) of chlorophyll 'a' mg/m²; dissolved oxygen g/m²; nitrates g/m²; silicates g/m²; and phosphates g/m² for February 1973.

Table 4.6 Species identifications and microscopic cell counts of samples exceeding 1 µg/ℓ of chlorophyll 'a' during February 1973.

Depth	Station 1			Station 2			Station 3			Station 4			Station 5			Station 6			Station 7			Station 8			Station 9			Station 10		
	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D	Chl	Count/ℓ	D
0	0,4	Detritus	-	0,9			8,6	Detritus	-	14,4	●=95% O= 5% T=430416	2	7,4	●=99% T=354160	3	9,5	Detritus	-	3,4	Detritus	-	10,5	●=91% ■= 9% T=460366	2	10	●=87% Δ=10% T=242254	4	2,1	Detritus	-
10	0,5	Detritus	-	1,1			7,6	Detritus	-	16,9	●=89% O=11% T=578671	2	6,9	●=96% T=237681	4	9,0	Detritus	-	2,9	Detritus	-	11,5	●=99% T=429524	2	12,1	Detritus	-	2,6	Detritus	-
20	0,3			0,8	Detritus	-	1,8	Detritus	-	6,7	●=96% O= 4% T=547312	2	3,3	●=100% T=171717	1	7,4	Detritus	-	0,7			9,8	●=100% T=367708	2	5,8	Detritus	-	2,8	Detritus	-
30	0,3			0,4			0,8			2,7	●=100% T=200000	1	0,6			3,7	Detritus	-	0,5			7,4	●=99% T=118095	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=123288	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=315686	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 species
O = Chaëtoceros species
■ = Skeletonema costatum
Δ = Dinoflagellate species

KEY

Chl = Chlorophyll 'a' µg/ℓ
D = Diversity (species)
T = Total
☐ = Chl 'a' < 1 µg/ℓ

(1) Early developing blooms

This included the October transect when 4 days of gentle southeasterly 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.

(2) Maturing blooms

The development of mature blooms occurred during November and February when strong and favourable winds for upwelling caused the upward displacement of isolines close inshore. Figure 4.20 shows the southeast wind component to be dominant over the six month period, particularly during November and February where a broad belt of mixed water extended far offshore, and a distinct frontal zone was evident between stations 9 and 10, approximately 100 km offshore.

(3) Interrupted mature blooms

Short-term reversals, prior to sampling in September were thought to be responsible for the onshore flow of oceanic water, detected by high salinity levels inshore. The front was situated approximately 50 km offshore where a well defined upper mixed layer was apparent.

Similarly in January, a lull in the southeast 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 late in November between the 10th and 30th when strong southeasterlies prevailed. The front was more well defined than in January and occurred offshore between stations 7 and 8 approximately 30 km further inshore than during November and February. A broad belt of mixed aged upwelled water with no upwelling inshore was also evident.

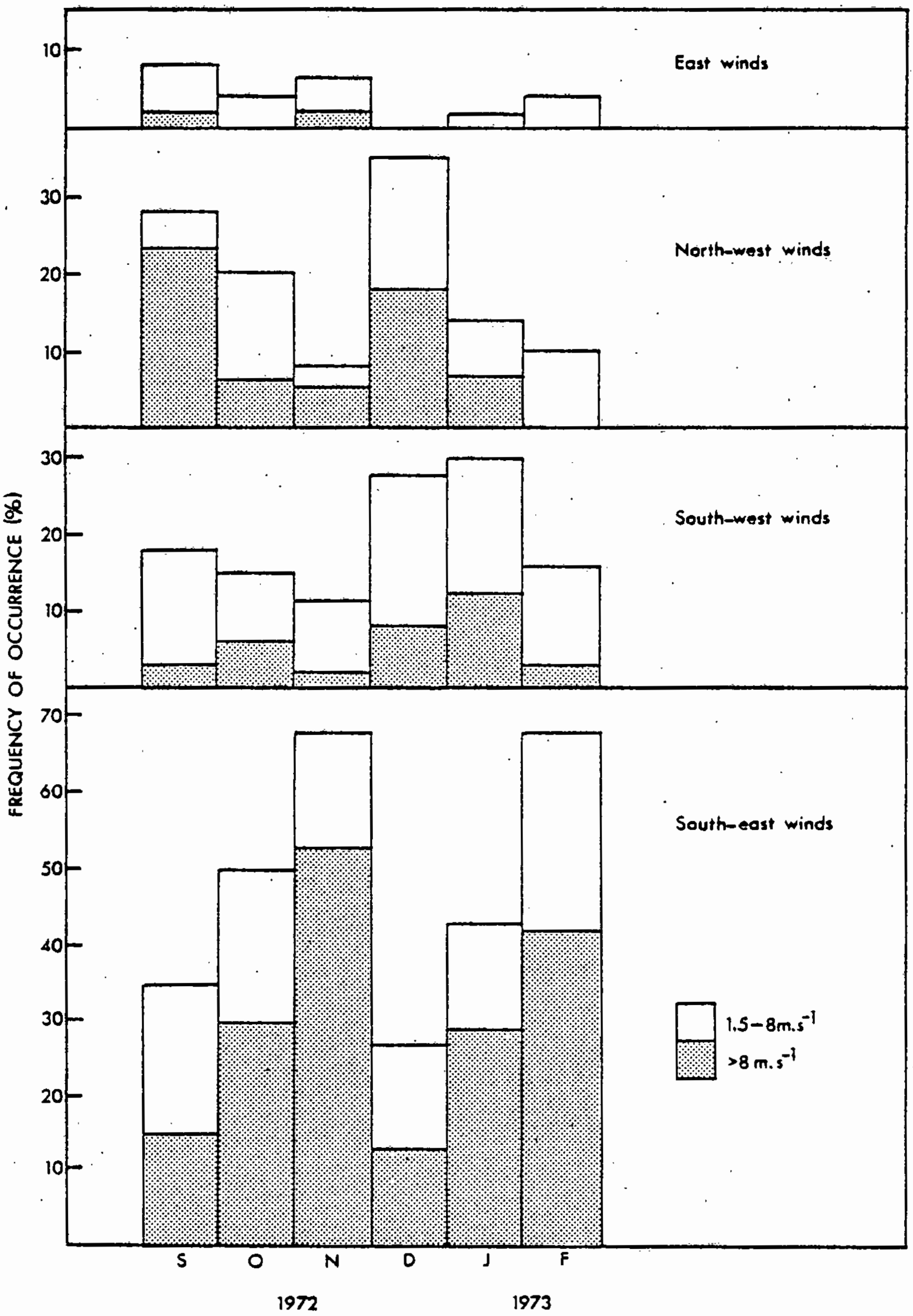


Figure 4.20 Percentage occurrence of four wind categories at Cape Point lighthouse over the 6 month period (Andrews & Hutchings, 1980).

Inspection of the monthly surface temperatures and salinities (Figure 4.21) showed the appearance of cool, less saline water inshore and warmer, more saline water offshore. The highest temperature and salinity gradients occurred during November where a difference of 7,81°C and 0,66‰ was evident. An overall increase in temperature and salinity occurred in the offshore surface waters towards January and 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 good relationship between temperature and density in the study area was shown to exist. 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, inorganic nutrients at the surface declined seawards from high levels close inshore, where active upwelling had occurred, to lower and sometimes limiting levels offshore. Nitrates were shown to decrease faster than either phosphates or silicates. Andrews & Hutchings (1980) showed nitrate to be the major limiting nutrient in this region by looking at the overall atomic ratios of nutrient utilization. They also showed that the phytoplankton populations were physiologically adapted to high nutrient concentrations typical of fast-growing coastal populations when compared with McIsaacs & Dugdale's (1969) results.

Integrated values of each nutrient within the euphotic zone are compared on a monthly basis and illustrated in Figure 4.22(a). The steepest nutrient gradient occurred during October when phytoplankton standing stocks were lowest. It would seem likely that gradients due to nutrient depletion by phytoplankton were accentuated by the close proximity of oceanic and newly upwelled waters, with only a narrow belt of mixed water occurring between these waters.

Changes in biomass

Integrated values of chlorophyll 'a' within the euphotic zone are

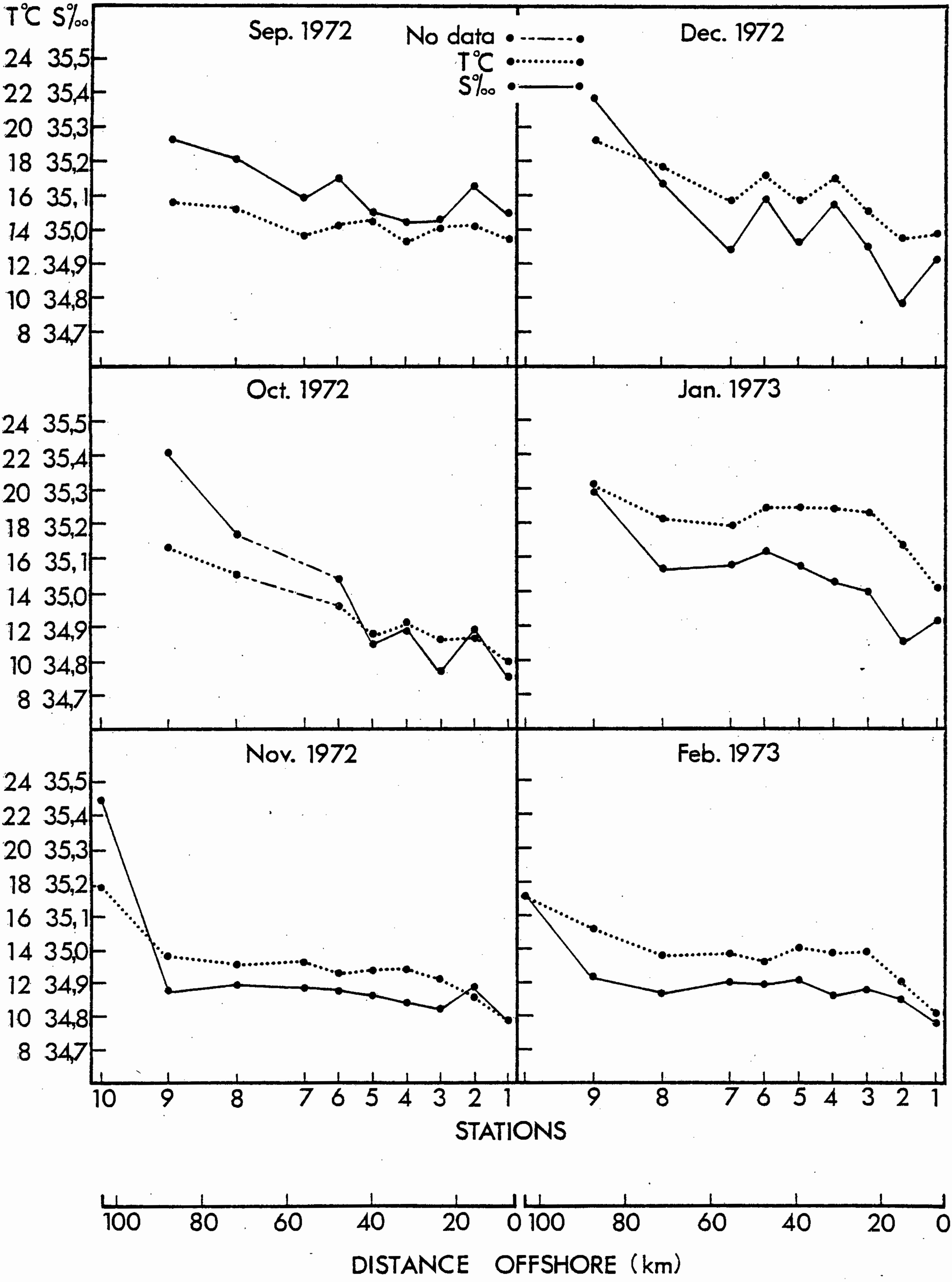


Figure 4.21 Changes in the monthly surface temperatures °C and salinities ‰.

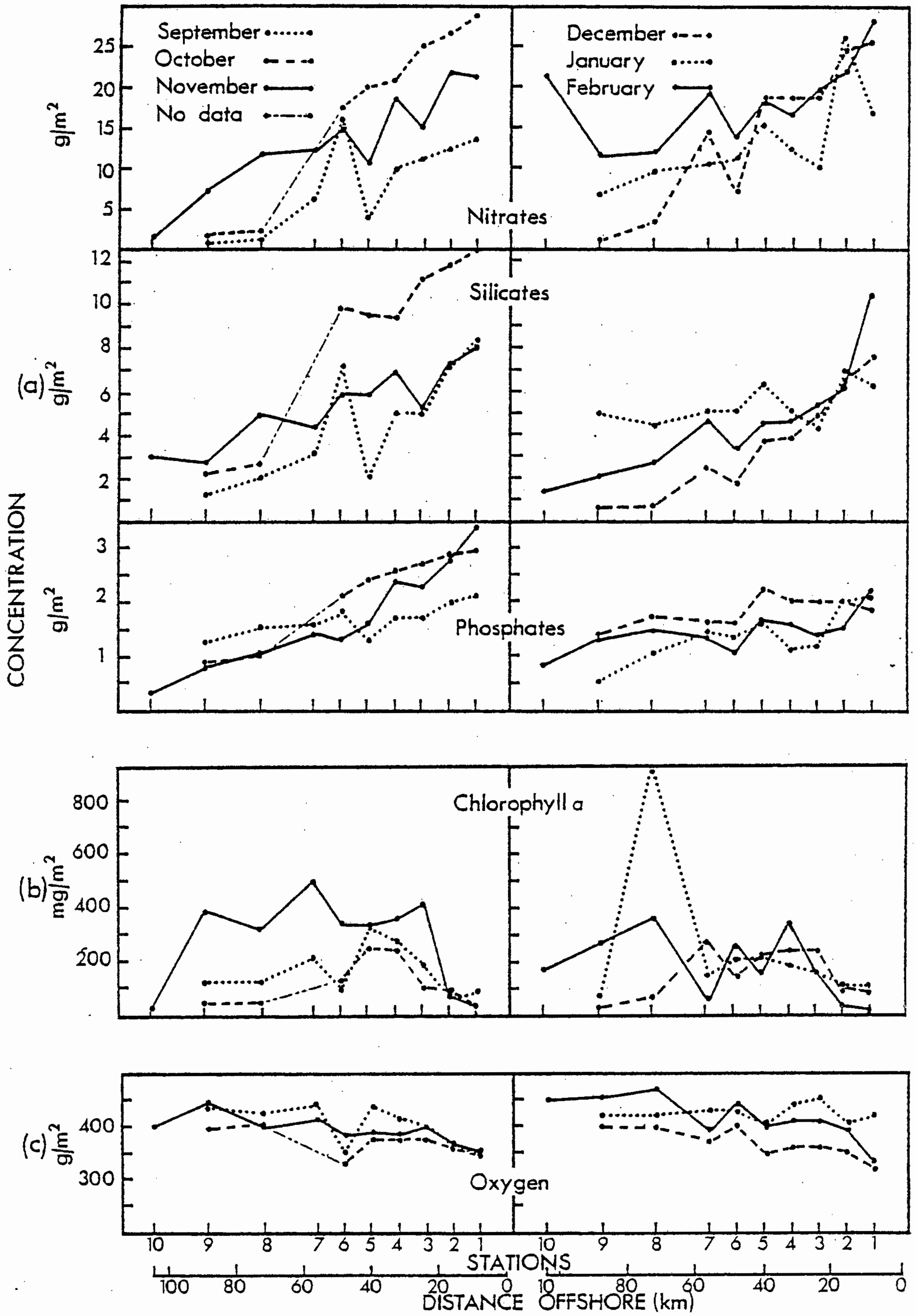


Figure 4.22 Monthly changes within the euphotic zone (0-50 metres) of (a) nitrates, silicates and phosphates g/m²; (b) chlorophyll 'a' mg/m² and (c) dissolved oxygen g/m²

compared on a monthly basis and illustrated in Figure 4.22(b). The highest standing stocks were shown to occur during November when the mixed water belt was best developed. The highest concentration in the phytoplankton population occurred in January when the invasion of oceanic water shorewards appeared to cause phytoplankton to passively accumulate on the strong pycnocline. Chlorophyll 'a' levels reached 51,8 μg/l but with surprisingly low cell counts of 788 x 10^3 cells/l. 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). Generally, higher cell counts were associated with high chlorophyll 'a' concentrations, although all counts were much lower than found during the drogue study.

Increases in dissolved oxygen occurred within the chlorophyll 'a' maximum layer although integrated values within the euphotic zone, compared on a monthly basis (Figure 4.22(c)) do not reveal this. The reason is that although the upwelled waters possess constant concentrations of dissolved oxygen (Andrews & Hutchings, 1980) their concentrations of dissolved oxygen varied initially, suggesting a mixing of the upwelled waters with possibly surrounding more mature waters. 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 & Hutchings (1980) to differ from "distant" oxygen-depleted water in their nitrate to silicate ratios. The significance 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 consisted, by in large, of detrital material, although *T. nitzschioides* and *Chaetoceros* spp. were abundant. In the remaining months *Nitzschia* spp. constituted approximately 90% of the total abundance in all samples. *Chaetoceros* spp. and *S. costatum* constituted a small percentage of the total abundance during November and January.

Thus *Nitzschia*, a genus of pennate diatoms, was the main contributor to the high chlorophyll 'a' concentrations measured throughout the coastal waters, over the six month period, when a wide variety of upwelling conditions were experienced. This dominance by *Nitzschia* occurred despite the continued presence (in low numbers) of *C. compressus* and *S. costatum* which were the dominant species in the drogue study.

CHAPTER 5

CONCLUSION

5.1 Patterns of Succession

One of the main aims of this thesis was to establish whether consistent patterns of phytoplankton distributions exist in the Cape Peninsula upwelling plumes. The different investigational strategies employed during this study (drogue and transect study) showed unequivocally that two different phytoplankton communities were encountered. The drogue study was associated with a fast developing mixed phytoplankton bloom with *Chaetoceros compressus* and *Skeletonema costatum* the dominant species, whereas *Nitzschia* was shown to persist throughout the upwelling season of September 1972 - February 1973. Species succession did not occur in either phytoplankton community.

5.2 Factors affecting the Development of Phytoplankton Communities in the Cape Peninsula Upwelling Plumes

Differences in certain community characteristics, e.g. species dominance, diversity and biomass may be inextricably linked to:

(1) The origins of the source water.

(2) Wind speed and direction.

(3) The sampling strategies employed.

5.2.1 The origins of the source water

The colonization of phytoplankton species depends on the phytoplankton species present in the upwelled source water, which in turn is determined by processes that regulate where the upwelled water will be drawn from, and what kind of water will be present at that time and depth. That is to say that the quantitative and qualitative content of the biological material in the upwelled waters, depends on the origin of the source water and the types of sediments encountered. The upwelled waters in both studies were shown to be primed with similar species, supporting the view 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.

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 & Hutchings (1980) showed this water to possess constant chemical and physical properties. Recent results from CUEX data, suggest that the Cape Point Canyon might play an important role in funneling this water onto the shelf, establishing a perennial subsurface cold water plume (Shannon *et al.* 1980).

The isolation of the Cape Peninsula upwelling system from other upwelling regions further north led Andrews (1974) to suggest that "The upwelling water contains little or no contamination from recycling and no biologically productive water enters the region from other upwelling areas". Shannon (1970) has shown the existence of an inshore southward moving surface counter-current between 34°S and 30°S and the drogue track I from the Plankton Dynamics Cruise 1979 confirms this as far south as Slangkop (Figure 2.1). It would seem likely that as the upwelled water approaches the surface close inshore, appreciable mixing of this water with the southward moving counter-current could occur. Also the appearance of oxygen-depleted water along the shelf (shown by De Decker (1970) to originate in the northern waters) could cause considerable seeding of the source water by contributing phytoplankton material (auxospores, resting spores) to the Cape Peninsula upwelling system.

It would seem necessary that greater emphasis be placed in the near future on investigating the advective variations in the subsurface and alongshore 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 onshore counter-current. For instance Smith & Barber (1980) showed that the cross-shelf circulatory pattern off Peru, physically sorted the phytoplankton according to their specific sinking rates or vertical migration speeds. Phytoplankton were shown to recirculate in the upwelling system by sinking out of the offshore flowing surface layer into the subsurface onshore flowing layer. Herbland *et al.* (1973) suggested that a similar mechanism existed in the upwelling system off NW Africa. The undercurrent was suggested to play an important role in the re-cycling of the upwelling water.

5.2.2 Wind speed and direction

The northward and alongshore drogue trajectory in December 1979 was effectively determined by the predominance of the southerly winds, whereas in the transect study, a northwesterly flow of surface waters along the transect line, only occurred during southeasterly winds. Variations in the wind strength and direction can change the location of the upwelling plume resulting in either a translation or dilation of the upwelling system. In other words short-term variations in wind speed and direction could have caused quantitative and qualitative changes in the transect study where a fixed line of stations was sampled, and distance offshore not approximated with time. Fluctuations in the intensity of the upwelling events may also cause surface mixing of the newly upwelled waters with neighbouring aged water bodies, causing variations in the nutrient concentrations close inshore. This dilution of nutrients may result in the selective advantage for growth of certain species. The importance of water stability, through its action on sinking and nutrient supply to the euphotic zone will vary with fluctuations in wind velocity and in turn will determine the sequence of species succession and diversity of the plankton community. For example, studies on natural assemblages of phytoplankton grown in chemostats by Thomas *et al.* (1980) showed that pumping in high-nutrient water (simulating a high rate of upwelling), resulted in a decrease of crop diversity whereas pumping of low-nutrient water resulted in a mixture of species. Turpin & Harrison (1979) likewise showed that low frequency pulsing of nutrients selected for large, long-chained, centric diatoms.

5.2.3 The sampling strategies employed

Drogue studies have been conducted elsewhere with considerable success. Although the same body of water was being followed (shown earlier by the coherent changes in the parameters at 10 metres), it is nonetheless pertinent to mention some limitations of the use of drogues. The horizontal shear of the water flow, the slippage of water past the drogue, diffusion and vertical mixing processes are important factors likely to cause differences between the flow velocities of the 4 m² drogue and the much smaller phytoplankters. Such differences could cause quantitative changes in the assessment of certain community characteristics. The transect studies on the other hand, indicated in a general way, the relationships of the biological properties to changes in the environmental factors of the upwelled waters off the Cape Peninsula. However, because of time lags in sampling relative to the development of the phytoplankton community, fine scale relationships can be masked. An important limitation is that one cannot analyse accurately the rates of change of quantities from the transect data.

This study is the first of its kind to describe the species composition of the phytoplankton community in our local waters. Analyses of 3 drogue studies, completed subsequently, will proceed in a similar manner, but will include the decline of the phytoplankton blooms. So far, results showed that *Chaetoceros, Skeletonema, Nitzschia* and *Thalassiosira* spp. were the dominant species in the mixed phytoplankton blooms. Similarly Horstman (pers. comm.) showed that *Chaetoceros, Skeletonema* and *Thalassiosira* spp. were the dominants off the west coast (Cape Peninsula) during the summers of 1964, 1966 and 1967. *Nitzschia* spp. was not shown to dominate, which casts some doubt on the dominance of this genus throughout the upwelling season described in this study. It is important to consider, that the dominance of *Nitzschia*, could in fact be an artifact of preservation.

However from this study it would seem justifiable to state that:

(1) The phytoplankton communities which develop in the Cape Peninsula upwelling plumes differ in their community characteristics.

(2) Consistent patterns of species succession do not exist.

(3) The factors responsible for the successful colonization of the different species in the phytoplankton communities are likely to be:

  a) the initial variations in species diversity and abundance of the seeded population in newly upwelled waters;

  b) the extent to which the upwelled waters mix with neighbouring waters; and

  c) the specific selective adaptations for growth of the Individual species (i.e. their intrinsic growth and absorption rate as determined by cell size)

The progressive change in cell size in the mixed bloom of the drogue study was interpreted as an adaptive strategy for the successful colonization of *C. compressus* and *S. costatum*. The environmental trends accompanying these changes complied, in a broad sense, with Margalef's (1968) hypothesis, in that a decrease in turbulence and nutrient concentrations was accompanied by increases in water temperature and modification of light quality and intensity. It would seem probable that a second phase of succession could have developed if the sampling had been extended several days.

Similarly, the monthly transect studies represented an adequate temporal gradient in the environmental factors, i.e. from turbulent, high nutrient conditions to sometimes stable and low nutrient conditions. The integrated values of the non-conservative parameters within the euphotic zone, in the transect study, were similar to those of the drogue study. The small scale discrepancies were attributed to time lags in sampling and therefore possibly sampling on the confines of the initial phytoplankton patch or missing the patch altogether.

More emphasis and attention should be directed, in future studies towards laboratory investigations of certain phytoplankton attributes such as nutrient requirements, growth rates, adaptation to light, and palatability to zooplankton. The ecological implications of these attributes have been discussed and shown to be relevant to the succession of species.

ACKNOWLEDGEMENTS

I wish to express my sincere thanks and appreciation to:

Dr C. Hay (Botany Department) for his invaluable suggestions, reassuring support and sense of humour.

Dr L. Hutchings (S.F.I.) for his able guidance, enthusiasm and brisque criticisms.

Mr D. Horstman and Mr D. Alexander (S.F.I.) for their assistance in photographing and identifying the phytoplankton.

Mr R. Koegenberg (S.F.I.) for his aid in running the computor programs.

Mr T. van Dalsen, Miss M. Herbert and Miss A. Mehl (S.F.I.) for their efficiency in the drawing of the figures.

Mr B. Wessels, Mrs D. Lichtman and Mr A. Payne (S.F.I.) for their help in the search for references.

Miss M. van Niekerk for her unfailing willingness to help with the draft copies, and Mrs L. Freeland for her prompt, accurate and speedy typing.

The Director of Sea Fisheries Institute, for his permission to use the results of this project for an M.Sc. degree.

The Plankton Dynamics Scientific staff, especially Miss P. Brown, Mr R. Barlow and Dr L. Hutchings for their steadfast support and co-operation.

The technical staff of the phytoplankton section, for their cordial assistance.

The officers and crew of the *R.S. Africana II* for helping to make the field work of this project as pleasant as possible (in stifling the calls for huey!).

The Fisheries Development Corporation for financial assistance.

All the friends - too numerous to name - who have provided assistance and encouragement.

Miss P. Helme *especially*, for her constant side-line support in times of stress.

My parents, for the gratifying confidence they have in me.

REFERENCES

ANDREWS, W.R.H. 1974 - Selected aspects of upwelling research in the southern Benguela Current. *Tethys* 6(1-2): 327-340.

ANDREWS, W.R.H. and L. HUTCHINGS 1980 - Upwelling in the southern Benguela Current. *Prog. Oceanogr.* 9(1): 81 pp.

BARBER, R.T., DUGDALE, R.C., MacISAAC, J.J. and R.L. SMITH 1971 - Variations in phytoplankton growth associated with the source and conditioning of upwelled waters. *Investigación pesq.* 35: 121-193.

BARBER, R.T. and J.H. RYTHER 1969 - Organic chelators: factors affecting primary production in the Cromwell Current upwelling. *J. exp. mar. Biol. Ecol.* 3: 191-199.

BARLOW, R.G. 1981 - Phytoplankton physiology in a near-shore region of the southern Benguela current. Ph.D. thesis, University of Cape Town: 129 pp.

BARNES, H. 1951 - The use of transformations in marine biological statistics. *J. Cons. perm. int. Explor. Mer* 18: 61-71.

BEERS, J.R., STEVENSON, M.R., EPPLEY, R.W. and E.R. BROOKS 1971 - Plankton populations and upwelling off the coast of Peru, June 1969. *Fishery Bull., U.S.* 69(4): 859-876.

BEKLEMISHEV, C.W., PETRIKOVA, M.N. and H.J. SEMINA 1961 - On the cause of the buoyancy of plankton diatoms. *Tr. Inst. Oceanol.* 51: 33-36.

BLASCO, D. and T.T. PACKARD 1974 - Nitrate reductase measurements in upwelling regions. 1. Significance of the distribution off Baja California and Northwest Africa. *Tethys* 6(1-2): 239-246.

BROWN, T.E. and F.L. RICHARDSON 1968 - The effect of growth environment on the physiology of algae: light intensity. *J. Phycol.* 4: 38-54.

CARPENTER, E.J. and R.R.L. GUILLARD 1971 - Intra specific differences in nitrate half-saturation constants for three species of marine phytoplankton. *Ecology* 52: 183-185.

CLEMENTS, F.E. 1916 - *Plant Succession. An Analysis of the Development of Vegetation.* Washington; Carnegie Institute: 512 pp.

CLIFFORD, H.T. and W. STEVENSON 1975 - *An Introduction to Numerical Classification.* New York; Academic Press: 229 pp.

COULTER ELECTRONICS 1975 - *Coulter Counter Model TA II Operator's Manual.* Hialeah, Florida; Coulter Electronics Inc.

COWLES, H.C. 1899 - The ecological relations of the vegetation on the sand dunes of Lake Michigan. *Bot. Gaz.* 27: 95-117.

COWLES, T.J. 1977 - Copepod feeding in the Peru upwelling system. Ph.D. thesis, Duke University: 165 pp.

CUPP, E.E. 1943 - Marine plankton diatoms of the west coast of North America. *Bull. Scripps Instn Oceanogr.* 5(1): 238 pp.

CUSHING, D.H. 1964 - The work of grazing in the sea. In *Grazing in Terrestrial and Marine Environments.* Crisp, D.J. (Ed.). Oxford; Blackwell: 207-225.

DAVIS, C.O., BREITNER, N.F. and P.J. HARRISON 1978 - Continuous culture of marine diatoms under silicon limitation. 3. A model of Si-limited diatom growth. *Limnol. Oceanogr.* 23(1): 41-52.

DE DECKER, A.H.B. 1970 - Notes on an oxygen-depleted subsurface current off the west coast of South Africa. *Investl Rep. Div. Sea Fish. S. Afr.* 84: 24 pp.

DROOP, M.R. 1973 - Some thoughts on nutrient limitation in algae. *J. Phycol.* 9: 264-272.

DUGDALE, R.C. 1967 - Nutrient limitation in the sea: dynamics, identification and significance. *Limnol. Oceanogr.* 12: 685-695.

EPPLEY, R.W. 1972 - Temperature and phytoplankton growth in the sea. *Fishery Bull., U.S.* 70(4): 1063-1085.

EPPLEY, R.W. 1980 - Primary productivity in the sea. *Nature, Lond.* 286(5769): 109-110.

EPPLEY, R.W., HOLMES, R.W. and J.D.H. STRICKLAND 1967 - Sinking rates of marine phytoplankton measured with a fluorometer. *J. exp. mar. Biol. Ecol.* 1: 191-208.

EPPLEY, R.W., ROGERS, J.N. and J.J. McCARTHY 1969 - Half-saturation "constants" for uptake of nitrate and ammonium by marine phytoplankton. *Limnol. Oceanogr.* 14: 912-920.

EPPLEY, R.W. and W.H. THOMAS 1969 - Comparison of half-saturation constants for growth and nitrate uptake of marine phytoplankton. *J. Phycol.* 5: 375-379.

ESTRADA, M. 1974 - Photosynthetic pigments and productivity in the upwelling region of N.W. Africa. *Tethys* 6(1-2): 247-260.

FIELD, J.G. 1970 - The use of numerical methods to determine benthic distribution patterns from dredgings in False Bay, South Africa. *Trans. Roy. Soc. S. Afr.* 39: 183-200.

FIELD, J.G. 1971 - A numerical analysis of changes in the soft-bottom fauna along a transect across False Bay, South Africa. *J. exp. mar. Biol. Ecol.* 7: 215-253.

FIELD, J.G. and F.T. ROBB 1970 - Numerical methods in marine ecology. 2. Gradient analysis of rocky shore samples from False Bay. *Zool. Afr.* 5(2): 191-210.

FINDLAY, I.W.O. 1972 - Effects of external factors and cell size on the cell division rate of a marine diatom *Coscinodiscus pavillardii* Forti. *Int. Revue ges. Hydrobiol.* 57(4): 523-533.

FOGG, G.E. 1965 - *Algal Cultures and Phytoplankton Ecology.* London; Athlone Press: 126 pp.

FRIEBELE, E.S., CORRELL, D.L. and M.A. FAUST 1978 - Relationship between phytoplankton cell size and the rate of orthophosphate uptake: *in situ* observations of an estuarine population. *Mar. Biol.* 45: 40-52.

GLASS, G.V. and J.C. STANLEY 1970 - *Statistical Methods in Education and Psychology.* Englewood Cliffs; Prentice-Hall: 595 pp.

GOLDMAN, J.C. and E.J. CARPENTER 1974 - A kinetic approach to the effect of temperature on algal growth. *Limnol. Oceanogr.* 19(5): 756-766.

GOLDMAN, J.C. and J.H. RYTHER 1976 - Temperature-influenced species competition in mass cultures of marine phytoplankton. *Biotechnol. Bioeng.* 18: 1125-1144.

GRASSHOFF, K. 1966 - Automatic determination of fluoride, phosphate and silicate in sea water. In *Automation in Analytical Chemistry*. New York Mediad Incorporated: 304-307.

GROSS, F. and E. ZEUTHEN 1948 - The buoyancy of plankton diatoms: a problem of cell physiology. *Proc. R. Soc. (B)* 135(880): 382-389.

GUILLARD, R.R.L. and P. KILHAM 1977 - The ecology of marine diatoms. In *The Biology of Diatoms*. *Botanical Monographs* 13. Werner, D. (Ed.). Oxford; Blackwell: 372-469.

HARRISON, P.J., CONWAY, H.L., HOLMES, R.W. and C.O. DAVIS 1977 - Marine diatoms grown in chemostats under silicate or ammonium limitation. 2. Cellulas chemical composition and morphology of *Chaetoceros debilis*, *Skeletonema costatum*, and *Thalassiosira gravida*. *Mar. Biol.* 43: 19-31.

HART, T.J. and R.I. CURRIE 1960 - The Benguela Current. *"Discovery" Rep.* 31: 123-298.

HECKY, R.E. and P. KILHAM 1974 - Environmental control of phytoplankton cell size. *Limnol. Oceanogr.* 19(2): 361-366.

HENDEY, N.I. 1937 - The plankton diatoms of the southern seas. *"Discovery" Rep.* 16: 151-364.

HERBLAND, A., LE BORGNE, R. and B. VOITURIEZ 1973 - Production primaire, secondaire et regeneration des sels nutritifs dans l'upwelling de Mauritanie. *Doc. Scient. Centre Rech. Océanogr. Abidjan. Orstom* 4(1): 1-75.

HOBRO, R. and E. WILLéN 1977 - Phytoplankton countings. Intercalibration results and recommendations for routine work. *Int. Revue ges. Hydrobiol.* 62(6): 805-811.

HOLLIGAN, P.M. and D.S. HARBOUR 1977 - The vertical distribution and succession of phytoplankton in the western English Channel in 1975 and 1976. *J. mar. biol. Ass. U.K.* 57(4): 1075-1093.

HULBURT, E.M. 1977 - Coexistence, equilibrium, and nutrient sharing among phytoplankton species of the Gulf of Maine. *Am. Nat.* 111(981): 967-980.

HUSTEDT, F. 1962 - Die Kieselalgen Deutschlands, Österreichs und der Schweiz mit Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete. *Rabenhorsts' Kryptogamen-Flora* 7(1): 920 pp. (Facsimile reprint in 1962 by Johnson Reprint Corp., New York.).

HUTCHINGS, L. 1979 - Zooplankton of the Cape Peninsula upwelling region. Ph.D. thesis, University of Cape Town: 225 pp.

HUTCHINSON, G.E. 1961 - The paradox of the plankton. *Am. Nat.* 95: 137-145.

JASSBY, A.D. and C.R. GOLDMAN 1974 - A quantitative measure of succession rate and its application to the phytoplankton of lakes. *Am. Nat.* 108(963): 668-693.

JØRGENSON, E.G. 1964 - Chlorophyll content and rate of photosynthesis in relation to cell size of the diatom *Cyclotella meneghiniana*. *Physiologia Pl.* 17: 407-413.

JURY, M.R. 1980 - Characteristics of summer wind field and air-sea interactions over the Cape Peninsula upwelling region. M.Sc. thesis, University of Cape Town: 131 pp.

KNOECHEL, R. and J. KALFF 1978 - An *in situ* study of the productivity and population dynamics of five fresh-water planktonic diatom species. *Limnol. Oceanogr.* 23(2): 195-218.

LARRANCE, J.D. 1964 - A method for determining volume of phytoplankton in a study of detrital chlorophyll 'a'. A thesis submitted in partial fulfillment of the requirements for the degree of master of science, University of Washington: 107 pp.

LAWS, E.A. 1975 - The importance of respiration loss in controlling the size distribution of marine phytoplankton. *Ecology* 56: 419-426.

LEWIS, W.M. 1977 - Ecological significance of the shapes of abundance-frequency distributions for coexisting phytoplankton species. *Ecology* 58(4): 850-859.

LUND, J.W.G., KIPLING, C. and E.D. LE GREN 1958 - The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. *Hydrobiologia* 11: 143-170.

MacISAAC, J.J. and R.C. DUGDALE 1969 - The kinetics of nitrate and ammonium uptake by natural population of marine phytoplankton. *Deep Sea Res.* 16: 45-57.

McCONNAUGHEY, B.H. 1964 - The determination and analysis of plankton communities. *Mar. Res. Indonesia* spec. no.: 1-40.

MARGALEF, R. 1958 - Temporal succession and spatial heterogeneity in phytoplankton. In *Perspectives in Marine Biology*. Buzzati-Traverso, A. (Ed.). Berkeley; University of California Press: 323-349.

MARGALEF, R. 1967 - Some concepts relative to the organization of phytoplankton. *Oceanogr. mar. Biol.* 5: 257-289.

MARGALEF, R. 1968 - *Perspectives in Ecological Theory*. Chicago; University of Chicago Press: 111 pp.

MARGALEF, R. 1978a - Life forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol. Acta* 1(4): 493-509.

MENZEL, D.W. and J.H. RYTHER 1961 - Nutrients limiting the production of phytoplankton in the Sargasso sea, with special reference to iron. *Deep Sea Res.* 7: 276-281.

MOSTERT, S.A. 1966 - Distribution of inorganic phosphates and dissolved oxygen in the S.W. Indian Ocean. *Investl Rep. Div. Sea Fish. S. Afr.* 54: 24 pp.

MUNK, W.H. and G. RILEY 1952 - Absorption of nutrients by aquatic plants. *J. mar. Res.* 11: 215-240.

O'BRIEN, W.J. 1974 - The dynamics of nutrient limitation of phytoplankton algae: A model reconsidered. *Ecology* 55: 135-141.

PAASCHE, E. 1973 - The influence of cell size on growth rate, silica content and some other properties of four marine diatom species. *Norw. J. Bot.* 20: 197-204.

PARSONS, T.R. and M. TAKAHASHI 1973 - Environmental control of phytoplankton cell size. *Limnol. Oceanogr.* 18(4): 511-515.

PARSONS, T.R., TAKAHASHI, M. and B. HARGRAVE 1977 - *Biological Oceanographic Processes.* *2nd Ed.* Oxford; Pergamon: 84-85.

PICKETT, S.T.A. 1976 - Succession: An evolutionary interpretation. *Am. Nat.* 110: 107-119.

PINGREE, R.D., HOLLIGAN, P.M., MARDELL, G.T. and R.N. HEAD 1976 - The influence of physical stability on spring, summer and autumn phytoplankton blooms in the Celtic Sea. *J. mar. biol. Ass. U.K.* 56(4): 845-873.

PINGREE, R.D., MADDOCK, L. and E.I. BUTLER 1977 - The influence of biological activity and physical stability in determining the chemical distributions of inorganic phosphate, silicate and nitrate. *J. mar. biol. Ass. U.K.* 57(4): 1065-1073.

PINGREE, R.D., PUGH, P.R., HOLLIGAN, P.M. and G.R. FORSTER 1975 - Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English Channel. *Nature, Lond.* 258: 672-677.

PROVASOLI, L. 1963 - Organic regulators in phytoplankton fertility. In *The Sea.* Hill, M.N. (Ed.). New York; Wiley - Interscience: 165-219.

PROVASOLI, L. and I.J. PINTNER 1953 - Ecological implications of *in vitro* nutritional requirements of algal flagellates. *Ann. N.Y. Acad. Sci.* 56: 839-851.

REID, F.M.H., STEWART, E., EPPLEY, R.W. and D. GOODMAN 1978 - Spatial distribution of phytoplankton species in chlorophyll maximum layers off southern California. *Limnol. Oceanogr.* 23(2): 219-226.

RILEY, G.A. 1947 - Factors controlling phytoplankton populations on Georges Bank. *J. mar. Res.* 6: 54-73.

RILEY, G.A. 1963 - Theory of food chain relations in the ocean. In *The Sea* 2. Hill, M.N. (Ed.). New York; Wiley - Interscience: 438-463.

ROBBINS, W.J. 1951 - Euglena and vitamine B_{12}. *Gdn. J. N.Y. bot. Gdn.* 1(6): 171-173.

RYTHER, J.H., MENZEL, D.W., HULBURT, E.M., LORENZEN, C.J. and N. CORWIN 1971 - The production and utilization of organic matter in the Peru coastal current. *Investigación pesq.* 35(1): 43-59.

SCOR/UNESCO WORKING GROUP 17 1966 - Determination of photosynthetic pigments. In *Determination of Photosynthetic Pigments in Sea-water.* Unesco Monographs on oceanographic Methodology 1: 9-18.

SEMINA, H.J. 1972 - The size of phytoplankton cells in the Pacific Ocean. *Int. Revue ges. Hydrobiol.* 57: 117-205.

SEMINA, H.J., TARKHOVA, I.A. and A.N. TRUONG NGOC 1976 - Different patterns of phytoplankton distribution, cell size, species composition and abundance. *Mar. Biol.* 37: 389-395.

SHELDON, R.W. and T.R. PARSONS 1967 - A continuous size spectrum for particulate matter in the sea. *J. Fish. Res. Bd Can.* 24(5): 909-915.

SHANNON, L.V. 1966 - Hydrology of the south and west coasts of South Africa. *Investl Rep. Div. Sea Fish. S. Afr.* 58: 52 pp.

SHANNON, L.V. 1970 - Oceanic circulation off South Africa. *Fish. Bull. S. Afr.* 6: 27-33.

SHANNON, L.V., NELSON, G. and M.R. JURY 1980 - Hydrological and meteorological aspects of upwelling in the southern Benguela Current. *IDOE International Symposium on Coastal Upwelling, Los Angeles, 4 February 1980.* (in press).

SIMPSON, J.H., EDELSTEN, D.J., EDWARDS, A., MORRIS, N.C. and B.P. TETT 1979 - The Islay Front: Physical Structure and Phytoplankton Distribution. *Estuarine Coastal mar. Sci.* 9: 713-726.

SMAYDA, T.J. 1970 - The suspension and sinking of phytoplankton in the sea. *Oceanogr. mar. Biol.* 8: 353-414.

SMAYDA, T.J. and B.J. BOLEYN 1965 - Experimental observations on the flotation of marine diatoms. 1. *Thalassiosira* cf. *nona, Thalassiosira rotula* and *Nitzschia seriata. Limnol. Oceanogr.* 10: 499-509.

SMITH, W.O. and R.T. BARBER 1980 - Circulation, sinking and vertical migration as determinants of phytoplankton success in the upwelling center at 15°S. *IDOE International Symposium on Coastal Upwelling, Los Angeles, 4 February 1980.* (in press).

STEELE, J.H. and C.S. YENTSCH 1960 - The vertical distribution of chlorophyll. *J. mar. biol. Ass. U.K.* 39(2): 217-226.

STRICKLAND, J.D.H., EPPLEY, R.W. and B. ROJAS DE MENDIOLA 1969 - Phytoplankton populations, nutrients and photosynthesis in Peruvian coastal waters. *Bol. Inst. Mar Peru* 2: 37-45.

STRICKLAND, J.D.H. and T.R. PARSONS 1968 - A practical handbook of seawater analysis, 2nd Ed. *Bull. Fish. Res. Bd Can.* 167: 310 pp.

THOMAS, W.H., POLLOCK, M. and D.L.R. SEIBERT 1980 - Effects of simulated upwelling and oligotrophy on chemostat-grown natural marine phytoplankton assemblages. *J. exp. mar. Biol. Ecol.* 45(1): 25-36.

TILMAN, D. and S.S. KILHAM 1976 - Phosphate and silicate growth and uptake kinetics of the diatoms *Asterionella formosa* and *Cyclotella meneghiniana* in batch and semi-continuous culture. *J. Phycol.* 12: 375-383.

TURPIN, D.H. and P.J. HARRISON 1979 - Limiting nutrient patchiness and its rôle in phytoplankton ecology. *J. exp. mar. Biol. Ecol.* 39(2): 151-166.

UTERMöHL, H. 1936 - Quantitative Methoden zur Untersuchung des Nannoplanktons. *Abderhalden Handb. biol. Arb. Meth.* 9(2): 1879-1937.

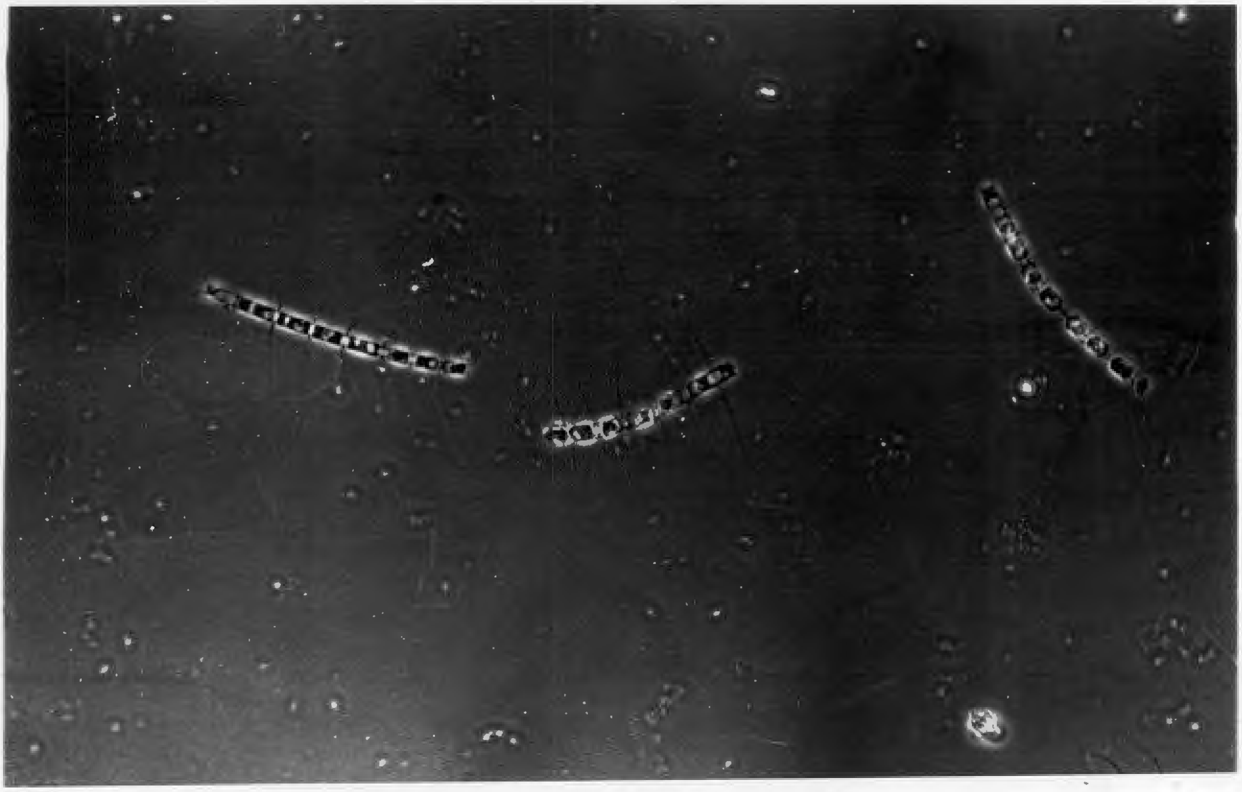
VENRICK, E.L. 1971 - Recurrent groups of diatom species in the North Pacific. *Ecology* 52: 614-625.

WILLéN, E. 1976 - A simplified method of phytoplankton counting. *Br. phycol. J.* 11: 265-278.

YENTSCH, C.S. and RYTHER, J.H. 1959 - Absorption curves of acetone extracts of deep water particulate matter. *Deep Sea Res.* 6: 72-74.

Nitzschia seriata Cleve (400 x magnification)

PLATE II *Nitzschia pungens* var *atlantica* Cleve (400 x magnification)



Chaetoceros compressus Laud. (400 x magnification)

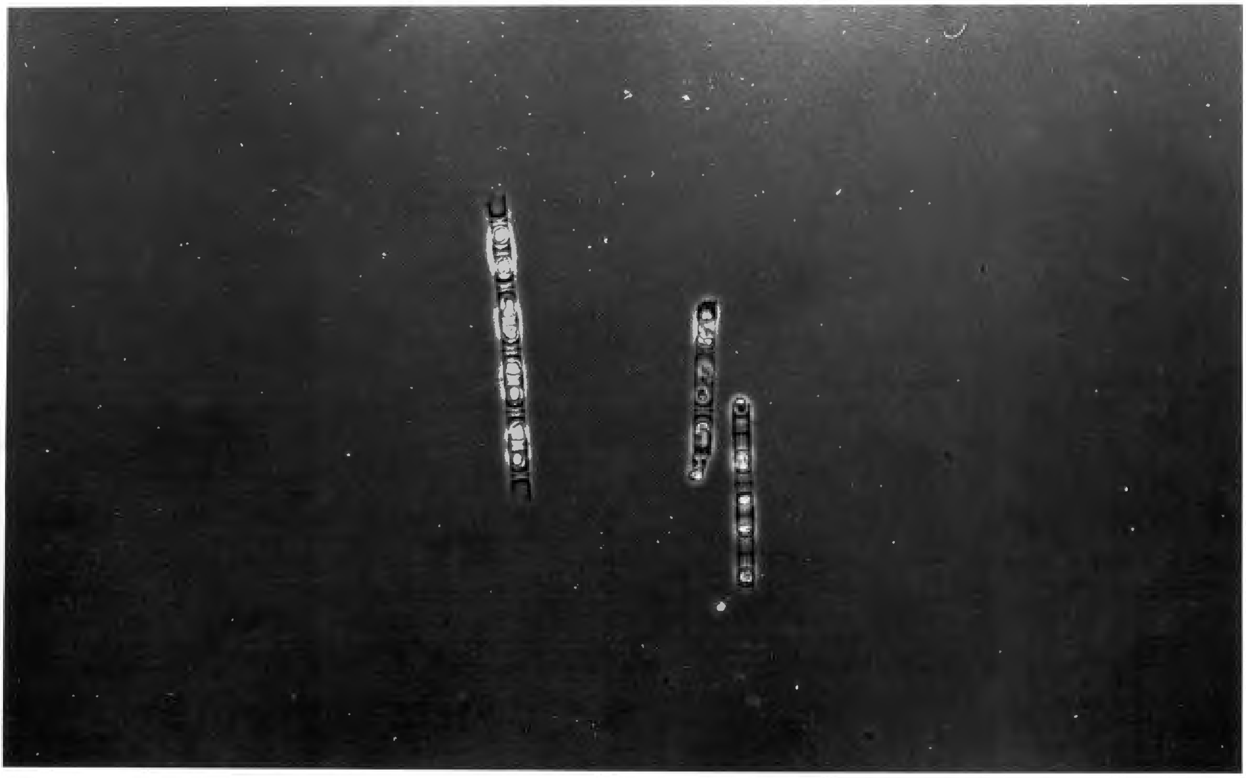


PLATE I *Skeletonema costatum* (Grev.) Cleve (400 x magnification)