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ZOOPLANKTON OF THE CAPE PENINSULA UPWELLING REGION

by L. HUTCHINGS

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ABSTRACT

The vertical and horizontal distribution of meso-zooplankton in the vicinity of an extremely active upwelling site in the southern Benguela Current is described. Zooplankton samples collected in oceanic, newly-upwelled and mature upwelled water showed that temperature, chlorophyll and time of day had considerable effects on the vertical distribution of different species.

Most species underwent limited daily vertical migrations within the upper mixed layer, while concentrations of animals decreased markedly below the thermocline except where sinking had occurred, when an inverted distribution, particularly of juveniles, was observed.

The Bray-Curtis dissimilarity coefficient was used to distinguish sample groups within the data. Differences in environmental parameters between groups were examined using the Mann-Whitney U-test. Species groups were separated using both the Bray-Curtis and McConnaughey coefficients and their relative merits are discussed. Samples from the upper mixed layer in upwelled water contained the greatest zooplankton standing crop in terms of dry weight, with Centropages brachiatus the most abundant organism. The frontal zone, with a strong thermal gradient, contained animals with distinct warm and cold water affinities as well as a group of species closely associated with the temperature gradient.

The near-surface distribution of the bulk of the population, combined with the lack of cool-water continuity to the south, poses especial problems for the maintenance of the upwelled-water community in the area during the upwelling season. It is suggested that sinking at the oceanic front combined with periodic shoreward flow of the upper layers when the southerly wind stress is relaxed, are sufficient to allow zooplankton to replenish rapidly from the north and offshore.

The horizontal distribution of zooplankton standing crop is described firstly on a broad time and spatial scale, based on quarterly cruises of a grid of stations up to 60 km offshore along 150 km of coastline. It is shown that the Cape Peninsula area is subject to considerably more variability than the area

further north, due both to upwelling events and to shoreward intrusions of oligotrophic oceanic water. This results in lower standing crops of zooplankton in the south.

Samples collected at monthly intervals between October 1970 and March 1973 off the Cape Peninsula showed three generalised patterns of distribution along the upwelling plume: a summer pattern, with offshore peaks of zooplankton standing crop; an autumn period, when the peak standing crop occurs closer to the coast; and a winter pattern where low concentrations occur everywhere except very close inshore. These patterns are subject to considerable variation during different wind regimes.

Short-term changes in zooplankton standing crop and species composition in a 20 km by 60 km area at the base of the upwelling plume were examined during two periods; one where gentle steady upwelling persisted during four days and a second period where a complete cycle of onshore and offshore winds occurred during six days. Changes in the distribution of sample groups identified using the Bray-Curtis coefficient are related to hydrographic changes. Three species groups, separated using the McConnaughey coefficient, reflect the occurrence of warm, cold and frontal zone areas. The information statistic is used to identify "core" species of the cool water group, which constitutes the bulk of the standing crop.

The horizontal distribution of these abundant species clearly demonstrates the isolation of the cool water group from minor upwelling sites to the east and from the waters south of the subtropical convergence. The annual cycle of zooplankton in the southwest Cape is described and the relative importance of zooplankton as grazers, nutrient regenerators, and as a source of food for the pelagic fish is discussed in relation to other areas. It is clear that physical events control the quantities of plankton present in the area, and zooplankton may be limiting as a food source for juvenile pelagic fish.

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GENERAL INTRODUCTION

During investigations into the nature and mechanisms of upwelling off the Cape Peninsula from 1968 to 1974, zooplankton samples were collected in conjunction with detailed observations of physical and chemical parameters. The general features of the upwelling system has been reported elsewhere, (Andrews, 1974, Andrews, Hutchings and Visser, in press) including the fluctuations in zooplankton biomass over sampling time intervals ranging from four hours to one month.

The report by Andrews, Hutchings and Visser "Upwelling in the southern Benguela Current" has been submitted as a supplement to this thesis as it contains essential background information on the oceanography of the study area. It has been accepted for publication by 'Progress in Oceanography' subject to updating of certain sections by W.R.H. Andrews, who left the Sea Fisheries Branch in 1974. All the sections on zooplankton were contri= buted by the author of this thesis, who also revised the chapter on wind and primary production and contributed jointly to the discussion.

The cruise strategy for the December 1969 survey was planned by W.R.H. Andrews and G.A. Visser, who both supervised the collection, processing and interpretation of physical, chemical and phytoplankton data. Zooplankton sampling and processing were done by the author of this thesis, including the species identifi= cation, standing stock measurements and the writing of a computer program to calculate percentage composition and ranking of species.

The monthly monitoring cruises were run jointly by Andrews and the author, with the same division of disciplines as for December 1969 with regard to interpretation. Technicians, after in-service training, gradualy assumed responsibility for the logistics of cruise preparation and sample processing.

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The quarterly 1974 cruises were supervised by the author with considerable technical support with regard to data collection and processing.

This thesis constitutes a more detailed examination of the zooplankton data, including the distribution of different species. Emphasis has been placed on both the numerically dominant species and on those animals which contribute a large proportion of the biomass and therefore form a major pathway of energy flow between the nutrient-rich upwelled water and the phytoplankton and the large stock of pelagic, planktivorous fish which constitute the basis of the 400 000 m ton purse-seine fishery of the south-west Cape (Centurier-Harris and Crawford 1974b). This fishery extends from Port Nolloth in the north to Cape Agulhas in the south (Centurier-Harris and Crawford, 1974a; Crawford, Shelton and Hutchings, 1978). The Cape Peninsula is in the middle of the fishing area although the highest yields are caught in St Helena Bay and in Walker Bay, 130 km on either side. Upwelling also occurs at these sites, but unpublished temperature data indicate that upwelling there is considerably less active than at the site off the Cape Peninsula. The major spawning ground for pilchards and anchovy, the two most important species in the fishery, lies immediately south of the Cape Peninsula, in the area between Cape Point and Cape Agulhas. Developing eggs and larvae drift northwards from October to January, mainly beyond the oceanic front which separates the cooler, upwelled waters from warmer waters offshore, and recruit, as juveniles, to the commercial fishery from the north (Crawford, Shelton and Hutchings, 1978). The major spawning period coincides with the increase in the frequency of strong southerly to southeasterly winds, which drive the upwelling cycle (Andrews, 1974), resulting in an increasing biomass of zooplankton in the well-developed upwelling plume off the Cape Peninsula. (Andrews *et al.*, in press). Arthur (1976) concluded that eggs and nauplii of copepoda comprised the most important components in the diets of larval pilchard (*Sardinops caerula*) and anchovy (*Engraulis mordax*) in the California current region, and preliminary feeding studies

indicate a similar situation in the Benguela Current (King and McCleod (1976); S. Davies, S.F.B., unpublished data).

Much qualitative data on zooplankton distribution off South Africa has been reported, based largely on samples collected with N70V nets and other Discovery- type equipment (Kemp, Hardy and MacKintosh 1929) as well as with continuous pumps (Nepgen (1957), Heydorn (1959), Van Zyl (1960), Kollmer (1963), Siegfried (1963), De Decker (1964), Unteruberbacher (1964), De Decker and Mombeck (1965), Lazarus (1974), Stander and De Decker (1969). De Decker (1968), De Decker (1973), Lazarus (1974), Stander and De Decker (1969). N70 nets have filtering surfaces with multiple mesh apertures, and were operated according to wire depth, without monitoring of flow or actual depth, so little quantitative information on the abundance of species can be obtained from the data. In this investigation, zooplankton was collected with WP-2 nets (Fraser, 1966; UNESCO, 1968) equipped with N10 depth-recording flowmeters (Currie and Foxton (1957)), and with a 7,6 cm centrifugal pump with water meter and 50 - 100 metres of flexible reinforced suction hose (Hutchings et al. (1970)).

Vertical hauls from close to the bottom to the surface were made in December 1969, together with pump samples to 50 metres while similar WP-2 net duplicate hauls were done in January 1971, with pump samples to 100 metres and in February 1971. From March 1971 to December 1974, WP-2 net hauls were made from close to the bottom to the base of the thermocline, and from that depth to the surface. The thermocline was not rigidly defined as a 1°C change per 10 metres (Duncan, 1964), but as the region of maximum vertical thermal gradient. Inspection of chemical data showed that small temperature gradients were usually accompanied by large changes in chlorophyll"a" and nutrient concentrations (Andrews, 1974; Andrews et al., in press) and the WP-2 net hauls generally separated the zooplankton in the phytoplankton-rich euphotic zone from zooplankton below the upper layer. Most samples were collected during daylight hours, although sampling was continuous during the December 1969 cruise (Africana stations only), the January 1971 cruise and the December 1971 anchor stations, when approximately one third of the samples were collected during darkness. Sample handling and storage generally followed the recommendations of UNESCO (1968), and has been described by

Andrews et al., (in press).

CRUISE STRATEGIES

Two basic cruise patterns were employed; the first was a rapid, repeated survey of an active upwelling centre off the west side of the Cape Peninsula using two ships, which occupied a grid of 34 stations, in fixed order for a four-day and a six-day period, in December 1969. The second was a line of stations which extended north-west and then west-northwest from the Cape Peninsula, generally following the plume of upwelled water as it moved northwards and offshore. This was sampled monthly from October 1970 to March 1973, and thereafter once per quarter until December 1974, except for December 1973. Variations on this second pattern included sampling along the monitoring line of stations three times in six days in January 1971, (the Bioupwelling cruise) and sampling at a fixed point, 15 km from the shore every four hours over a 24 hour period (Anchor stations) in December 1971. In 1974 three lines north of the Cape Peninsula, parallel to the monitoring line, were also sampled on a quarterly basis during the West Coast Monitoring Cruises. This provided a comparison between the Cape Peninsula upwelling system and the upwelling site centred off Cape Columbine.

The analysis of the zooplankton has been separated into three parts. The first part described changes in the distribution of the standing stock over different time intervals in relation to other environmental features. This has been reported in Andrews et al (in press), which is appended. The second in third parts form this thesis. The second part concerns the vertical distribution of species within the upwelling centre under different hydrological conditions. The third part consists of grouping zooplankton species observed at

the centre of upwelling using numerical classification techniques and describing the horizontal distribution of these groups over short periods of time. Notes on the distribution of zooplankton to the north of the Cape Peninsula in relation to hydrographic conditions, (based on the 1970-1973 monthly monitoring and the quarterly 1974 west coast monitoring data) are also presented in the thesis.

The crucial question of zooplankton dynamics in upwelling areas concerns the maintenance of the population within an unstable environment; this work provides information on the relative importance of different organisms, their vertical and horizontal distribution during different phases of the upwelling cycle and basic details of community structure. Much laboratory and field work will be necessary to assess the population dynamics and energy flow through the most common zooplanktonic organisms at the southern end of the Benguela Current but that is beyond the scope of this thesis.

TABLE 1: Details of "Pump" stations occupied by R.S. Africana II between 3 - 16 December 1969

Grid station	Date	Local time	Light/ dark	Wind speed ($m\ sec^{-1}$)	Wind direction (°)	Wave height (metres)	Wave period (secs)	Chlorophyll 'a' content mgm^{-2}, 0 - 50 m
146	4-12-69	0105-0212	Dark	14	170°	-	-	34
143	4-12-69	0927-1014	Light	9	180°	2,5	6-7	70
141	4-12-69	1413-1505	Light	9	190°	2,5	6-7	12
334	11-12-69	0303-0347	Dark	13	190°	-	-	214
432	12-12-69	0333-0417	Dark	3	180°	-	-	124
513	13-12-69	0145-0227	Dark	6	330°	-	-	177
612	14-12-69	0205-0346	Dark	6	200°	-	-	149
623	14-12-69	0950-1028	Light	5	220°	4,0	8-9	181
633	14-12-69	1529-1611	Light	11	180°	3,0	8-9	103
643	15-12-69	0419-0502	Dark	13	150°	-	-	220

THE VERTICAL DISTRIBUTION OF ZOOPLANKTON IN THE CAPE PENINSULA UPWELLING SYSTEM, DECEMBER 1969

1. INTRODUCTION

Several workers have used the suction hose principle for sampling zooplankton. (Gibbons and Fraser (1937), Wiborg (1948), Barnes (1949), Aron (1958), Cassie (1958), O'Connell and Leong (1963), Cassie (1964), Grindley (1964), Harver (1966), Beers, Stewart and Strickland (1967), Whaley and Taylor (1968) and Anraku (1975)) with pipes ranging from 1,3 cm to 7,6 cm in diameter and with pumping rates varying from a few litres to nearly 1 000 litres per minute. They have usually been employed in shallow, highly variable environments, where the spatial resolution of the pump and hose system is superior to conventional plankton nets, and the animals are not sufficiently concentrated or are too mobile to allow the use of large-capacity sampling bottles.

While a pump and hose system theoretically samples at a fixed point in the water column, ships drift and the action of waves move the pipe opening over a considerable area while the sample is being collected. For instance R. S. Africana II, the ship used for pumping operations, lies beam-on to the sea and wind during sampling and can drift at speeds of up to 50 cm per second, and her trawler-type hull allows for considerable rolling motion. Therefore during a single eight minute pumping operation an area of up to 3 to 4 metres high by 240 metres long could be traversed. Wind speed and direction and wave height and period have been tabulated in Table I to indicate the sampling conditions during each pump station. As wave height and period were estimated by officers on the bridge, wave data are only available during daylight hours.

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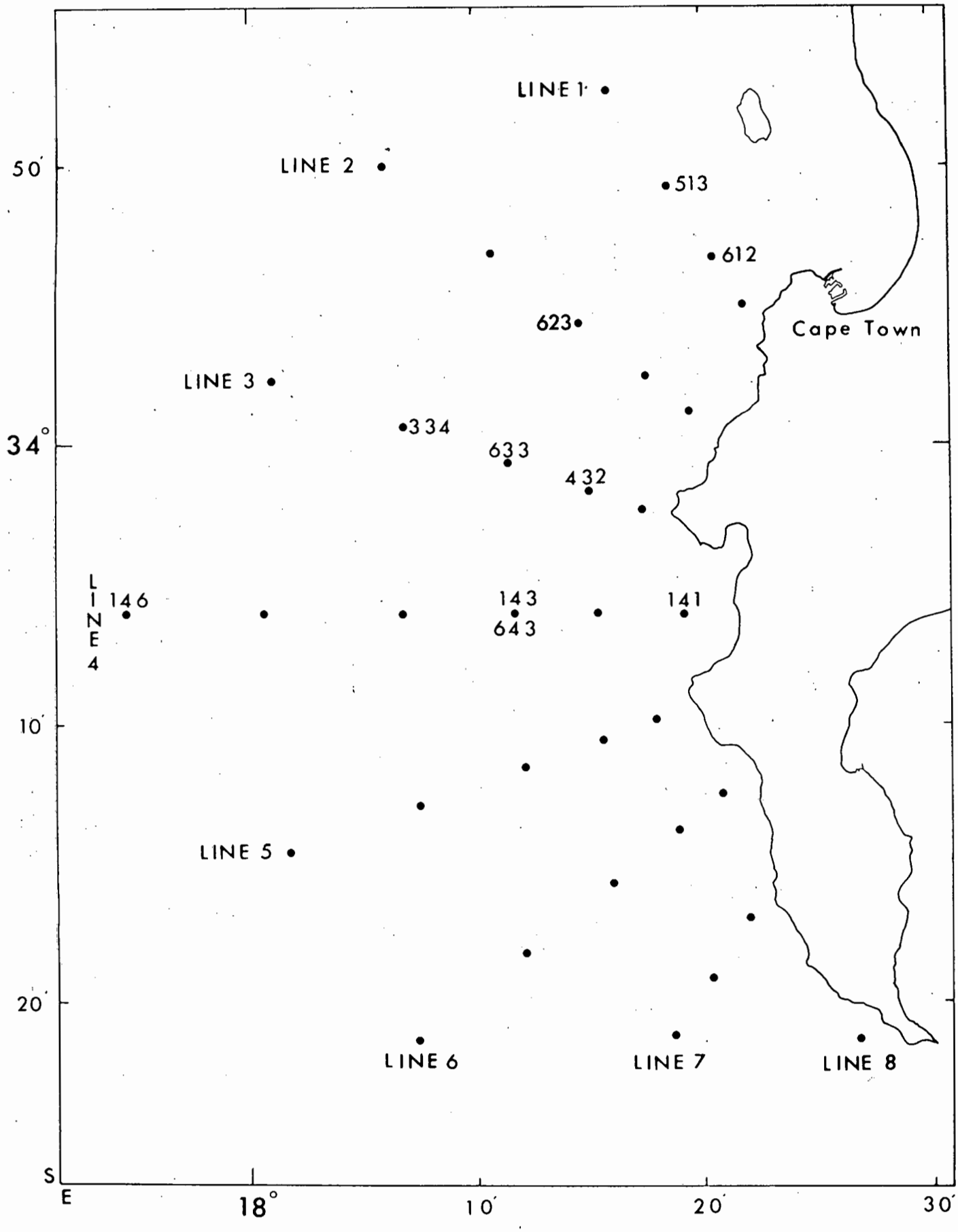

Fig. 1. Location of sampling stations where pump samples were collected in the upper 50 metres between 3rd and 16th December 1969. The first figure refers to the circuit number, the second to the line number and the third number indicates the station sequence from the coast.

During an intensive two-ship survey of an upwelling site in the southern Benguela Current between 3rd and 16th December 1969, (Andrews 1974; Andrews et al., in press), a series of 50 zooplankton samples were collected with a 7,6 cm centrifugal pump and flexible hose at 10 selected stations (Fig. 1), to supplement the samples collected routinely with a vertically hauled WP-2 net (Fraser 1966) from close to the bottom to the surface at all other stations. The pump samples provided information on the depth distribution of meso-zooplankton at this extremely active site, where rates of upwelling temporarily attain 20 - 40 metres per day (Andrews (1974), Bang (1976), Andrews et al. (in press)). Strong temperature and salinity gradients exist in both the horizontal and vertical planes and an examination of physical-chemical data allowed four water types to be distinguished (Andrews (1974), Andrews et al. in press): (a) Oceanic water, warmer than 18°C, poor in chlorophyll 'a' and nutrients; (b) Upwelling water, between 8°C and 10°C, poor in chlorophyll 'a' but rich in nutrients; (c) Shelf water, of less than 8°C, with similar characteristics to upwelling water, but always lying beneath the euphotic zone; (d) Mixed water, intermediate between oceanic water and upwelling water in characteristics, with highly variable chlorophyll and nutrient concentrations, depending on the age of the upwelled component, the degree of mixing to which it is subjected and the nature of the water with which it mixed. At the inshore edge at the southern end of the Cape Peninsula newly-upwelled water would mix directly with oceanic water, as the front approaches close to the coast. Further north newly upwelled water would mix with aged upwelled water at the inner edge of the plume while at the outer boundary a considerable proportion of the mixed water would be oceanic in origin, as pockets of oceanic water leak across the front, especially during periods of onshore winds or as the south-east wind stress relaxes (Bang and Andrews, 1974).

The relative proportions of the different water types varied widely within the survey area during different meteorological regimes, and the zooplankton biomass distribution altered considerably from day to day (Andrews et al., in press). The depth distribution of the species should provide some insight as to how the different species of zooplankton were affected by the rapidly changing environment. With this in mind, the vertical distribution has been examined in oceanic, mixed and upwelled water types, with very different temperature stratifications and chlorophyll, oxygen and nutrient concentrations.

2. METHODS

Zooplankton samples were pumped at 10 of the 124 stations occupied by the R.S. Africana II during the cruise (Fig. 1). Selection of the pump stations was, as always, a compromise between the necessity to complete each grid circuit as quickly as possible and the need to sample as many water types for zooplankton as was practical. Zooplankton displaced volumes and sample appearance from the WP-2 net hauls, chlorophyll filter colour, thermal stratification, and distance from the shore were all considered when selecting stations, but the time factor limited the number of stations chosen for pumping operations to 10. The construction and use of the pump has been described earlier (Hutchings, Robertson and Allen 1970), but the method of sampling will again be outlined here. 50 metres of 7,6 cm internal diameter flexible hosing, were lowered over the side attached to the hydrographic wire, secured approximately two metres from the pipe opening together with a 25 kg weight to maintain depth. A coarse wire grid of 2,5 cm aperture width was fitted flush over the end of the pipe to prevent the entry of large objects should the pipe accidently touch bottom. The sections of pipe, each 10 or 20 metres in length, were joined together with air-tight "Perrot" quick-release fittings. A rope secured just below the first joint and attached to the

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gunwhale relieved tension on the piping passing over the gunwhale, thus preventing kinking. Approximately 400 litres, twice the dead volume of the pumping system, were flushed through before filtration commenced at a particular depth. After passing through the pump, a Saunders valve, (to create an artificial back- pressure to prevent cavitation) and a full flow helical-vane water meter, the water speed was reduced by expanding the outlet pipe to 15 cm diameter before being filtered by a conical net with 200 um mesh aperture, similar to the WP-2 net mesh. The net was arranged so that trickle of water entered the collecting bucket (mesh aperture 180 um), removing the filtered animals from the main flow of water. The net was rubbed down immediately prior to attaching or removing the collecting bucket to avoid contamination of the succeeding sample.

Samples were collected at 50, 30, 20, 10 metres and in the 0-5 metre layer consecutively, alternating with flushing. The sampling depth was altered using the hydrographic winch to raise the pipe opening; the piping lay freely in the water, attached only at both ends. A constant length of piping is necessary to maintain a constant friction head and pumping rate.

At six of the 10 pump stations WP-2 net hauls were made from the bottom to 50 metres and from 50 metres to the surface, for comparison with the pump hauls. NIO depth-recording flowmeters (Currie and Foxton, 1957), were used to determine the depth attained and the volume of water filtered. Samples were processed in a similar manner to the pump samples.

Samples were washed into glass test tubes and preserved in 10% v/v. Formalin, neutralised with marble chips. In the laboratory, displaced volumes were determined with filtered seawater using the Yashnov method as modified by Robertson (1970). Samples were then split in two with a Folsom splitter, and one half was dried at 60°C for 24 hours after rinsing with fresh water (Lovegrove, 1966). The other half was examined under a binocular

microscope and organisms were identified to species level where possible. All specimens larger than approximately 5 mm in their largest dimension were removed and counted; smaller organisms were subsampled with a wide-mouthed pipette in variable fractions to a minimum of 1/10 of the sample, depending on the abundance of animals within the sample. A random two hundred animals were identified, and the whole subsample counted to provide an estimate of the total numbers of small animals present. Approximately 800 - 1 300 organisms were present in each subsample, except for very small samples.

Profiles of zooplankton displaced volume and dry weight, derived from pump samples, were integrated manually to provide estimates of the standing stock of zooplankton under one square metre.

Temperatures, salinities, chlorophylls, oxygens and nutrients were sampled and analysed as outlined in Andrews et al. (in press).

Numerical analysis of the samples was as follows: Zooplankton concentrations (number m^{-3}) were log-transformed (Barnes 1951; Field and Robb 1970; Field 1970, 1971) and dissimilarities between pump samples were calculated using the Bray-Curtis measure and additional runs were made including the WP-2 net samples. Group-average sorting was used to present the results in the form of a dendrogram. The presence of many zero values and some very high concentrations as well as the stress on dominance in this investigation suggested that these techniques would produce the most "useful" results (Field and Robb 1970. Field 1971, Clifford and Stephenson 1975).

The information statistic (Field 1969, 1971) was applied to the station groupings to determine which species differed significantly between the groups. while differences in temperature and chlorophyll"a" concentrations were examined using the Mann-Whitney statistic (Mann and Whitney (1947) quoted in Zar, 1974; Field 1971).

TABLE 2: Comparison of net and pump estimates of zooplankton standing stock in the 50 - 0 m layer: pump-derived profiles were drawn and integrated manually

Station	146	143	141	334	432	513	612	623	633	643
Disp. vol. mℓ m^{-2} pump	4,1	5,9	8,2	10,3	6,7	7,8	10,5	6,0	5,9	20,9
Disp. vol. mℓ m^{-2} net	18,0	5,2	3,9	8,0	13,0	12,3	14,0	1,5	8,4	7,3
Pump/net ratio	0,2	1,1	2,1	1,3	0,5	0,6	0,7	4,0	0,7	2,9
Dry weight mg m^{-2} pump	185	208	547	766	722	688	1 000	333	333	2 861
Dry weight mg m^{-2} net	1 424	446	466	1 006	1 148	1 336	744	398	701	2 808
Pump/net ratio	0,1	0,5	1,2	0,8	0,6	0,5	1,3	0,8	0,5	1,0

Species associations were examined using both Bray-Curtis and McConnaughey (1964) coefficients for comparison. The latter coefficient was modified slightly to allow similarities to be expressed as percentages and group-average sorting was applied to both sets of coefficients to display the data in dendrogram form.

3. RESULTS

3.1 Comparison of net and pump standing stock estimates

Table II shows that although pump estimates ranged from 0,3 to 0,4 times (mean = 1,4) the quantity caught by the WP-2 net on a displaced volume basis, and from 0,1 to 1,3 times (mean = 0,8) the dry weight value, the Wilcoxon paired-sample test (Zar 1974) showed no significant differences in the estimates ($p < 0,05$) Neither light regime nor wind speed showed any relation to the ratios between the samplers. (Tables 1 & 2). The very low pump/net ratio at station 146 may have been due to shattering of gelatinous organisms, common at this station, as they passed through the pump, with a subsequent loss of retention of the organisms by the filter meshes. The variation between sampler estimates may be due to inaccuracies inherent in the construction of profiles from relatively few point samples, or due to the fact that the space-time characteristics of the two samplers provide different probabilities of encountering patches of organisms. For example the pipe opening would remain at a particular depth (± 3 - 4 metres) for up to eight minutes, collecting 4,5 cubic metres of water, while the net would pass through the same four-metre depth zone in three to four seconds, filtering one cubic metre of water. If animals existed in patches strongly stratified in the vertical plane, the pump would be a less "efficient" sampler than the net; conversely, if the animals exist in a number of discrete patches in the horizontal plane, the pump should provide the better estimates.

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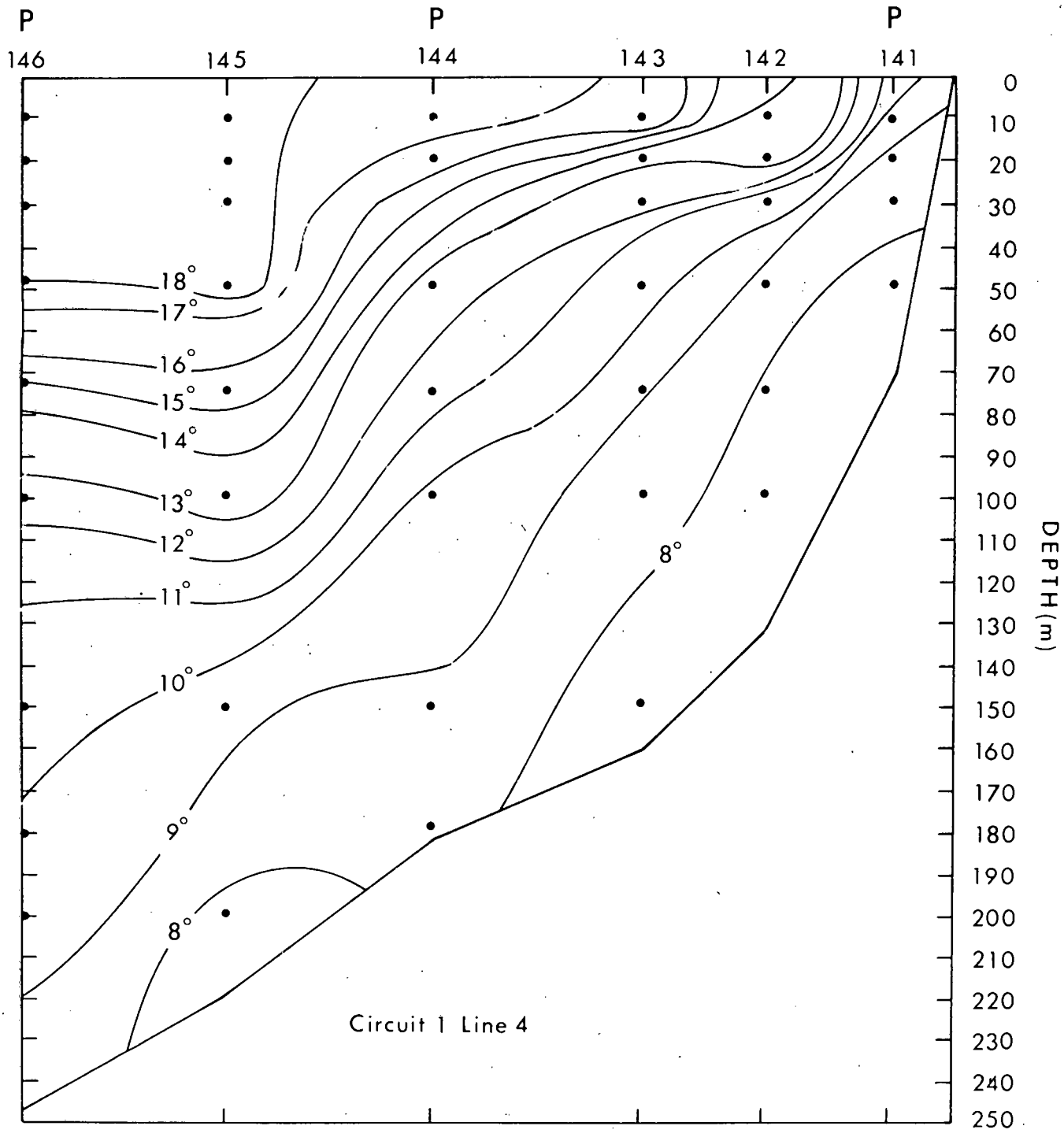


Fig. 2. Vertical section of temperature (^{o}C) along line 4 during circuit 1. Sampling duration along the line was 10,5 hours. P denotes location of pump stations.

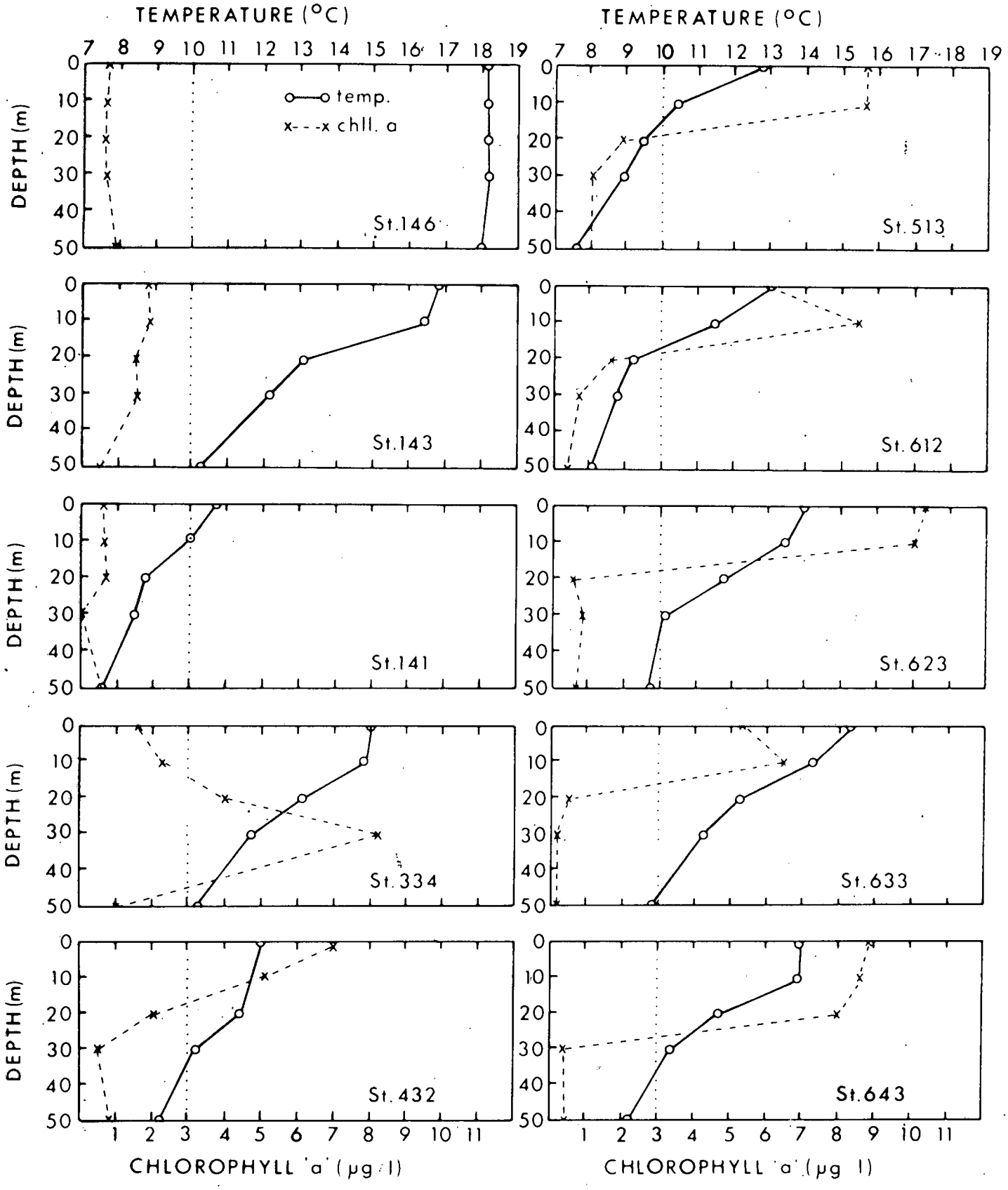


Fig. 3. Vertical profiles of temperature (°C) and chlorophyll 'a' (ug $^{-1}$) at the 10 pump stations. The dotted line through 10°C and 3 ug $^{-1}$ serves as a reference line.

3.2 Environmental features of the pump stations

Stations 146 143, and 141, sampled between 0100 hrs and 1500 hours on 4 December, represent the transition from warm oceanic water, through a frontal system, to recently upwelled water. Fig. 2 shows a vertical temperature section along line 4 on circuit 1, when the pump was used.

At station 146, (Fig. 3) sampled in the dark, 10 miles beyond the oceanic front, the water was nearly isothermal in the upper 50 metres (18,30° - 17,9°), with a strong thermocline at 75 metres, below the depth of the pump samples. Chlorophyll "a" concentrations were negligible (0,6 - 0,7 ug/l) in the upper 30 metres but increased to 1,0 ug/l at 50 and 75 metres, the maximum concentrations encountered at this station. Uniform, high salinities (35,4‰), high oxygen (5 - 5,7 ml/l) and low nutrient concentrations were present in the upper 50 metres.

Station 143, sampled at 0900 hours, was situated in the frontal zone, and a sharp thermocline was present between the 16,8°C surface water and the 13°C water at 20 metres. Salinity decreased from 35,3 in the upper 30 metres to 35,1 at 50 metres. A decrease in oxygen and chlorophyll "a" concentrations and an increase in nutrients occurred across the thermocline.

At station 141, sampled at 1430 hours, newly upwelled water was present, with the surface temperature of 10,8°C decreasing to 7,5°C at 50 metres. Chlorophyll "a" concentrations were negligible throughout the water column, varying between 0 and 0,7 ug/l, similar to concentrations in warm oceanic water. Salinity (34,57 - 34,75‰), and oxygen concentrations (4,25 - 4,94 ml/l) were low but nutrient concentrations were very high (nitrates 20,8 - 25,4 ug-at 1, silicates 16 - 22,7 ug-at 1), indicating potentially productive water. As the south-east wind had blown only briefly, the newly-upwelled water was limited to a narrow strip close to the coast and at station 142, five kilometres seaward, the surface temperature was 14,5°C (Fig. 2).

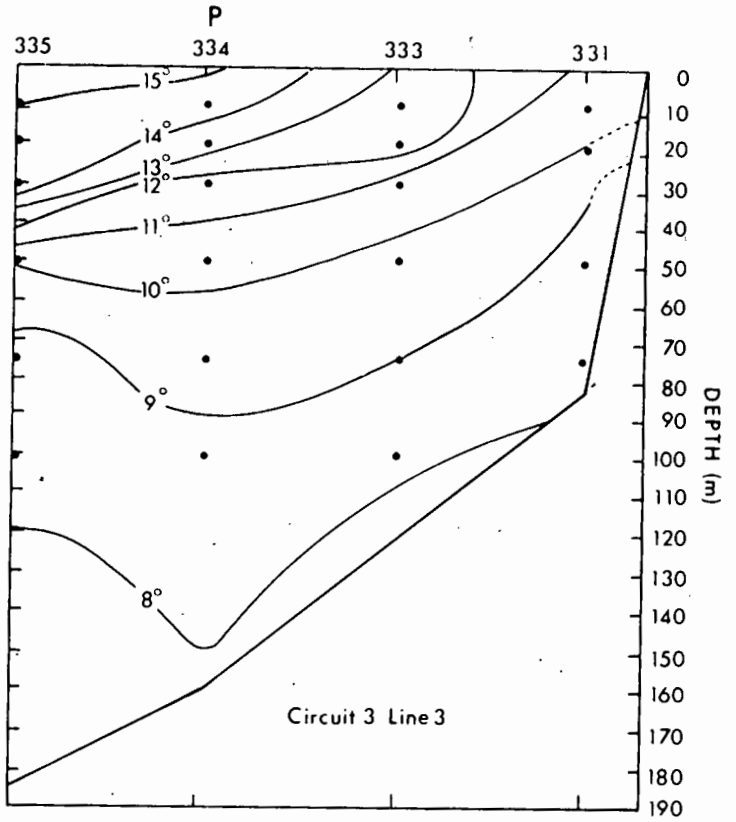


Fig. 4. Vertical section of temperature (^{o}C) along line 3, during circuit 3. Sampling duration was 5,5 hours. P denotes location of pump stations.

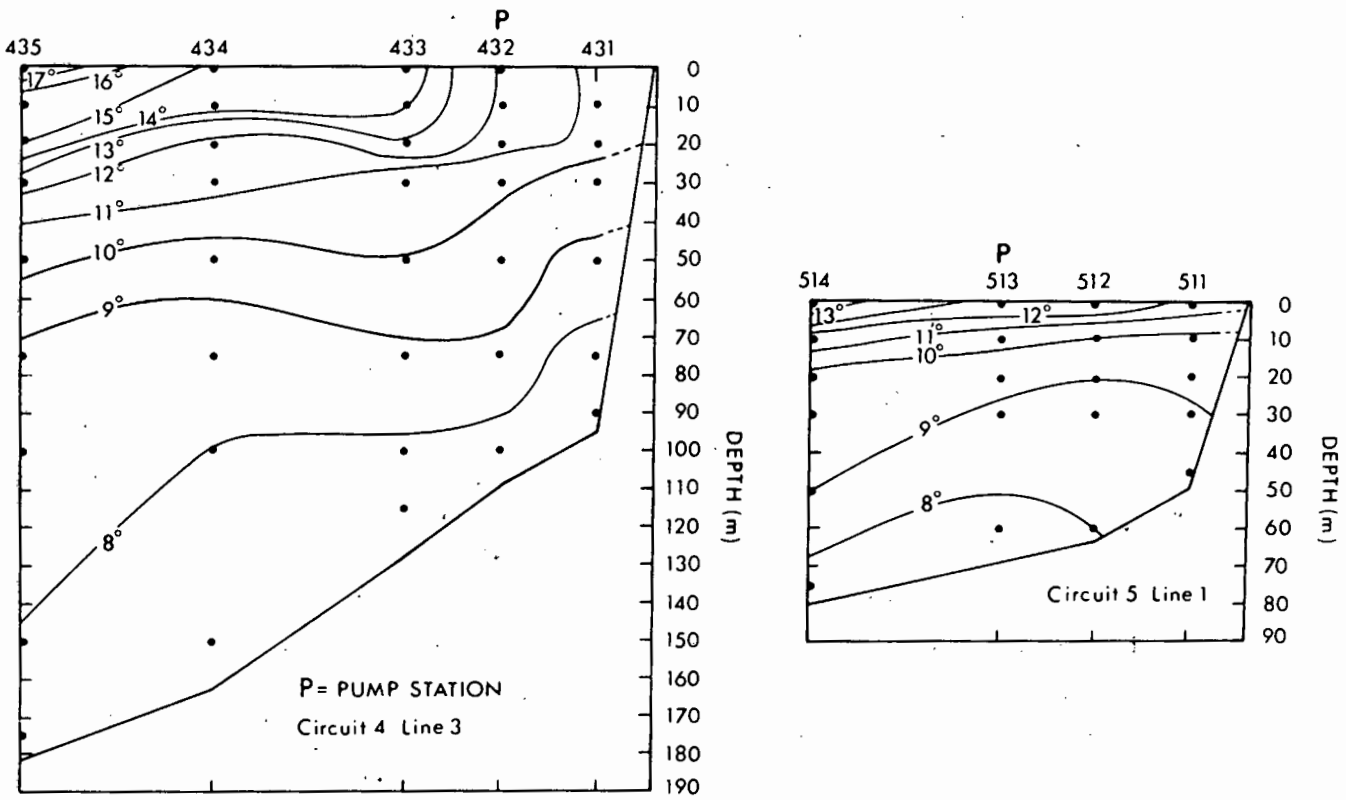


Fig. 5. Vertical temperature sections of: (a) Circuit 4, Line 3, 12/12/69 (duration 6,3 hours) (b) Circuit 5, Line 1, 13/12/69 (duration 4 hours). P denotes location of pump stations.

Station 334, situated approximately 16 kilometres from the coast, was sampled at 0300 hours on 11 December, at the end of a three-day period of strong south-easterly wind which caused upwelling inshore. The temperature and salinity in the upper 20 metres at this station suggested some sunwarming and mixing of upwelled water and oceanic water (temperature 13,1° - 15,0°C, salinity 35,0 - 35,16°/₀₀), but the chlorophyll"a" distribution was somewhat unusual in that a marked subsurface maximum was present at 30 metres, reaching 8,3 ug/l, despite the presence of seemingly adequate concentrations of nutrients in the upper 20 metres. (Nitrate 8,5 - 8,6 ug-at l, silicate 16,8 - 18,2 ug-at l, phosphate 1,05 ug-at l-). Both dissolved oxygen concentrations and zooplankton species composition were consistent with the presence of a subsurface chlorophyll maximum. Some evidence of localised sinking was apparent below 50 metres from examination of temperature data, (fig. 4) and this may be the remnant of a much greater sinking process, evidence of which has been obliterated in the upper layers. It appears unlikely that meso-zooplankton could have removed the phytoplankton crop in the upper layers because biomass estimates were not particularly high at this station. It is possible that macro= plankton in the surface layers grazed down the phytoplankton and were not sampled by the pump or the WP-2 net, but the high nutrient levels suggest that phytoplankton had never colonized the water to any extent, either due to a low optimum light level or temperature for the species encountering this particular parcel of water, or due to rapid advection to lower layers.

Station 432 was sampled 24 hours later, after the south-east wind had veered to the south west and decreased in strength, signalling the onset of downwelling conditions. However, cool (10° - 11,9°C) (Fig. 3, Fig. 5(a)) low-saline (34,9°/₀₀) water was still present in the upper 30 metres, and chlorophyll"a" concentrations decreased uniformly from 7,2 ug/1 at the surface to 0,5 ug/1 at 30 metres. High nutrient and dissolved oxygen con= centrations in the upper 10 metres indicated a vigorously growing

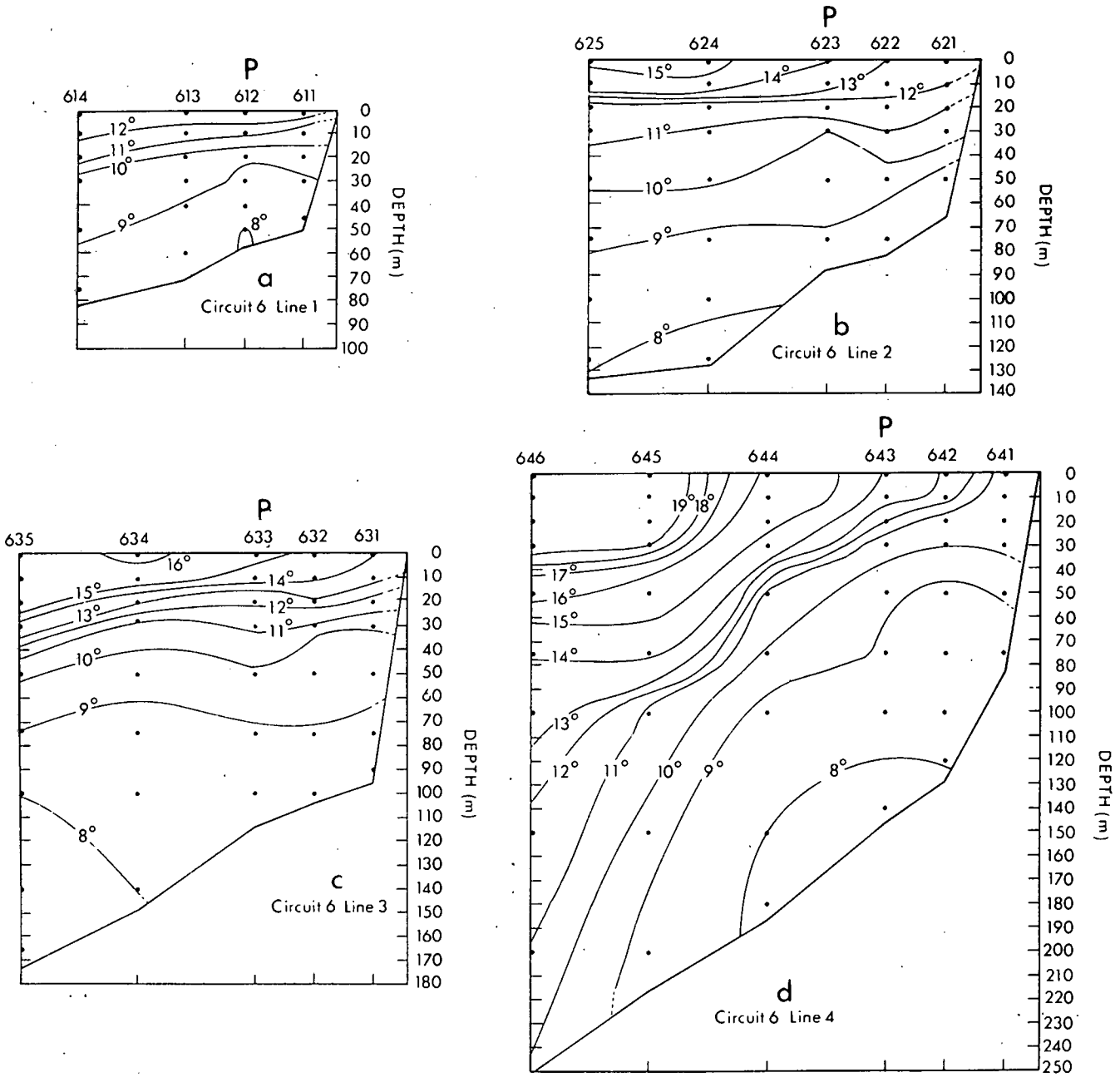


Fig. 6. Vertical temperature sections during Circuit 6 of (a) Line 1, 14/12/69 (duration 3,75 hours) (b) Line 2, 14/12/69 (duration 5,75 hours) (c) Line 3, 14/12/69 (duration 7 hours) and (d) Line 4, 14-15/12/69 (duration 10,3 hours). P denotes location of pump stations.

phytoplankton population. Dissolved oxygen values decreased and nutrients increased below 10 metres, showing that production at greater depths was probably light-limited due to self-shading.

Station 513 was sampled at 0200 hours on 13 December after approximately two days of westerly (onshore winds), which caused downwelling close to the coast (Andrews et al., in press), although the effect was diminished towards the northern end of the Peninsula during westerly winds, (Fig. 5b) because of the SW - NE orientation of the coastline. The surface temperature at 513 was 12,7°C but decreased rapidly to 10,3° at 10 metres and then more slowly to 7,5° at 50 metres. The low surface salinity (34,79°/$_{oo}$) indicated that sunwarming rather than mixing had raised surface temperatures. High chlorophyll "a" (8,6 ug/l), dissolved oxygen (6,3 - 7,3 ml/l), and nutrient concentrations in the upper 10 metres again indicated a rapidly growing phytoplankton population. Below 10 metres temperature, chlorophyll "a" and oxygen decreased and nutrients increased, in a similar manner to station 432.

Station 612, sampled 24 hours later, showed very similar features to 513; a shallow, sunwarmed layer (fig. 6(a)), containing a rapidly developing stock of phytoplankton and very high dissolved oxygen levels, although in this case the nitrate at the surface was sufficiently low (0,7 ug-at N/l) to begin to inhibit phytoplankton growth (Andrews et al. in press). Below this productive zone, growth was light limited due to shading from the surface layers.

Whereas stations 432, 513 and 612 were characteristic of newly upwelled water, where sunwarming rather than mixing with other water caused changes in the thermohaline structure, the following three stations were more mature, with the higher surface temperatures, deeper thermoclines and raised salinities, compared with the previous three. The depth of the 10°C water

was a good indicator of the relative age of the upwelled water mass; at sts. 432, 513 and 612, 10°C water was present above 30 metres, while at 623, 633 and 643 it was at or below 30 metres. Sampling at the latter three stations commenced as the onshore winds ceased and the wind backed to the south-east, rapidly increasing in speed (Table I).

Station 623 (fig. 6) had a surface temperature of 14°C, decreasing to 10°C at 30 metres. The highest chlorophyll"a" concentrations encountered at the pump stations (10 ug/l) occurred in the upper 10 metres (fig. 3), and dropped abruptly to less than 1 ug/l at 20 metres. Depleted nitrate levels (1 ug/l) occurred at the surface.

Station 633 (fig. 6) had a similar subsurface temperature structure, but the surface temperature had risen to 15,3°C and chlorophyll"a" concentrations were somewhat lower, at 5 to 6 ug/l (Fig. 3). Nitrate concentrations of 1-2 ug/l were observed in the upper 10 metres. Below 10 metres chlorophyll"a" decreased to less than 1 ug/l and nitrate increased to more than 15 ug/l.

Station 643, (fig. 6) sampled 15 hours after the southerly wind began to freshen, already displayed at 2°C drop in surface temperature compared with the temperature measured 36 hours earlier on the previous circuit. The chlorophyll"a"-rich layer with concentrations of 8,0 - 8,8 ug/l was 20 metres thick, (fig. 3) penetrating well into the thermocline region, and declined to less than 0,5 ug/l at 30 metres. Nitrate values varied between 3,9 and 5,2 ug/l in the upper 20 metres, rising to more than 12 ug-at/l at 30 metres, accompanied by a decrease in oxygen levels. As this station was sampled the hydrology of the survey area was rapidly changing, with upwelled water moving offshore from the coast and displacing warmer waters to the north west.

TABLE 3: Regressions between standing stock estimates

	n	r	P	Equation
Nos(N) vs dry wt. (mg) (DW)	49	0,57	0,01	$Log_{10}N = 7,67\ Log_{10}\ DW + 1,97$
Nos(N) vs disp. vol. (mℓ) (DV)	49	0,72	0,01	$Log_{10}N = 1,3\ Log_{10}\ DV + 1,97$
DW (mg vs DV (mℓ)	49	0,66	0,01	$DW = 90\ DV - 2,46$

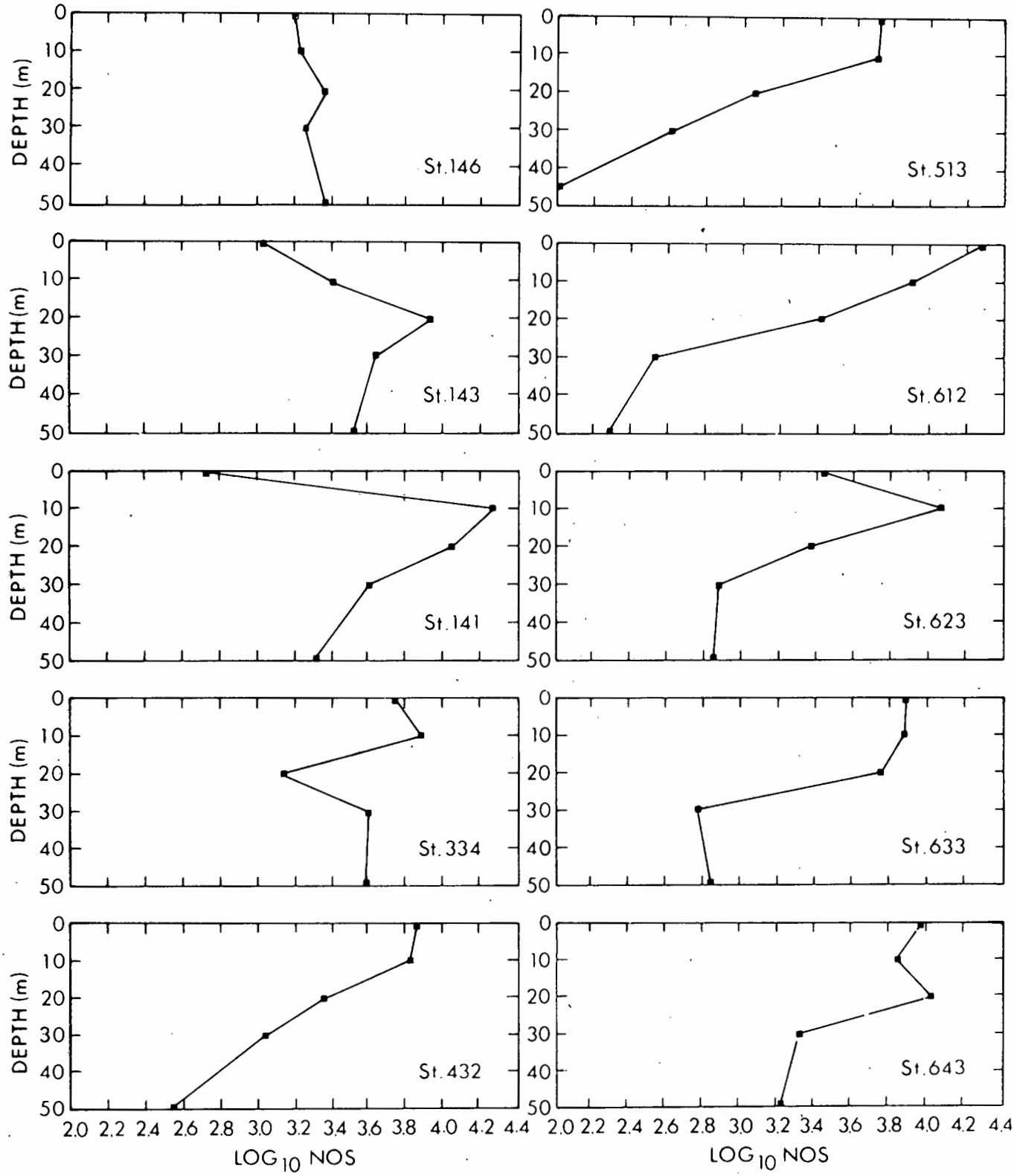


Fig. 7. Vertical profiles of zooplankton numbers (Log_{10} (no.(4,5 m^3)$^{-1}$) at the 10 pump stations.

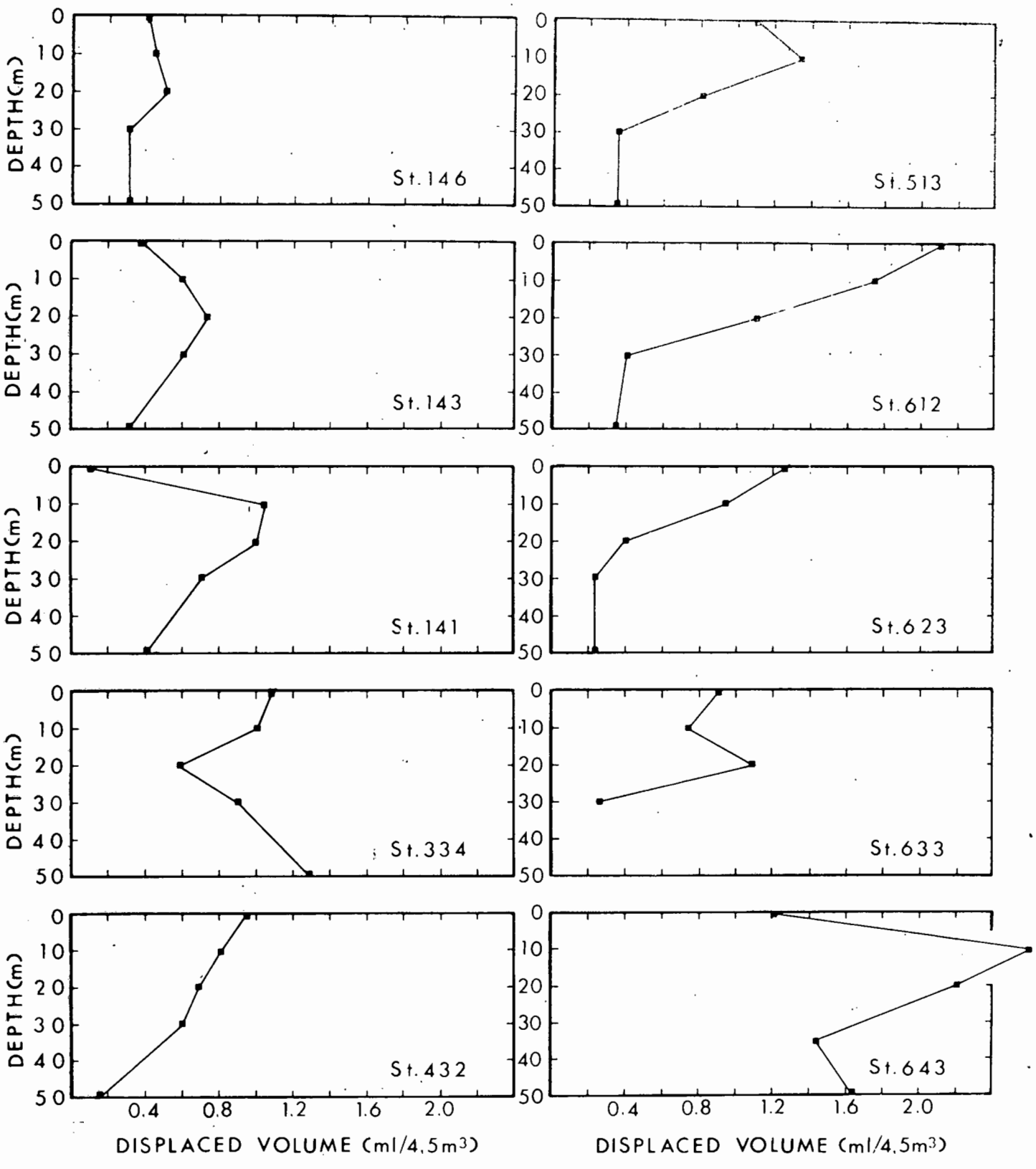


Fig. 8. Vertical profiles of zooplankton displaced volume ($ml(4,5\ m^3)^{-1}$) at the 10 pump stations.

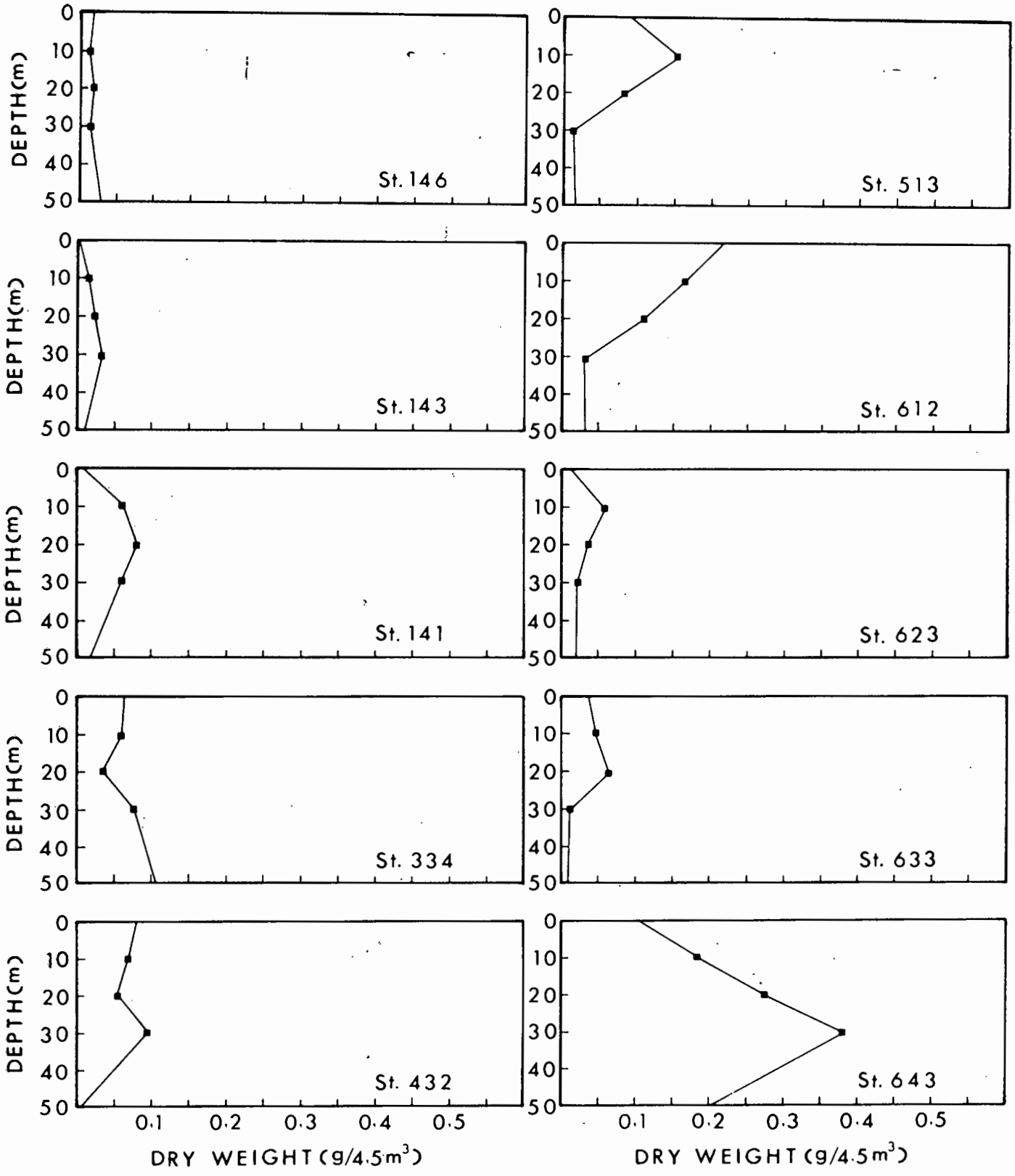


Fig. 9. Vertical profiles of zooplankton dry weight ($mg(4{,}5\ m^3)^{-1}$) at the 10 pump stations.

3.3 Relationships between standing stock estimates, taxonomic groups and environmental features (Table III and Appendix 1)

As the majority of organisms encountered during the pump series consisted of crustaceans, particularly copepoda, numbers, displaced volume and dry weight were significantly related to each other (Table III) although the relation between dry weight and numbers was less close than between the others, possibly because where large numbers of euphausids, or euphausid eggs occurred, the dry weight/displaced volume ratio was raised or lowered from the regression line respectively.

The number of species present in a pump sample (Appendix 1) was independent of the water temperature, in the range of 7,5° - 18,2°C although the percentage (by numbers) of copepods showed a significant negative correlation with temperatures ($P < 0,01$).

The concentration of organisms and the dry weight declined below 10°C and above 15°C, but considerable scatter was present in the data, especially between 10° and 14°C.

A weak correlation between zooplankton dry weight and chlorophyll "a" concentrations ($0,01 < p < 0,05$) was found but again considerable scatter decreased the usefulness of the regression.

In general, predictions about the size of the zooplankton standing stock based on absolute values of physical or chemical parameters were limited in their accuracy in this area, and are likely to depend on the biological history of an upwelled parcel of water. Any of the standing stock units may be used to describe changes in zooplankton abundance, but if a wider range of organisms are sampled this agreement is likely to deteriorate.

3.4 Changes in zooplankton standing stock and species composition with depth.

General

At six of the 10 pump stations, a subsurface maximum of zooplankton number occurred (Fig. 7), while subsurface peaks of displaced volumes occurred seven times (Fig. 8) and dry weights

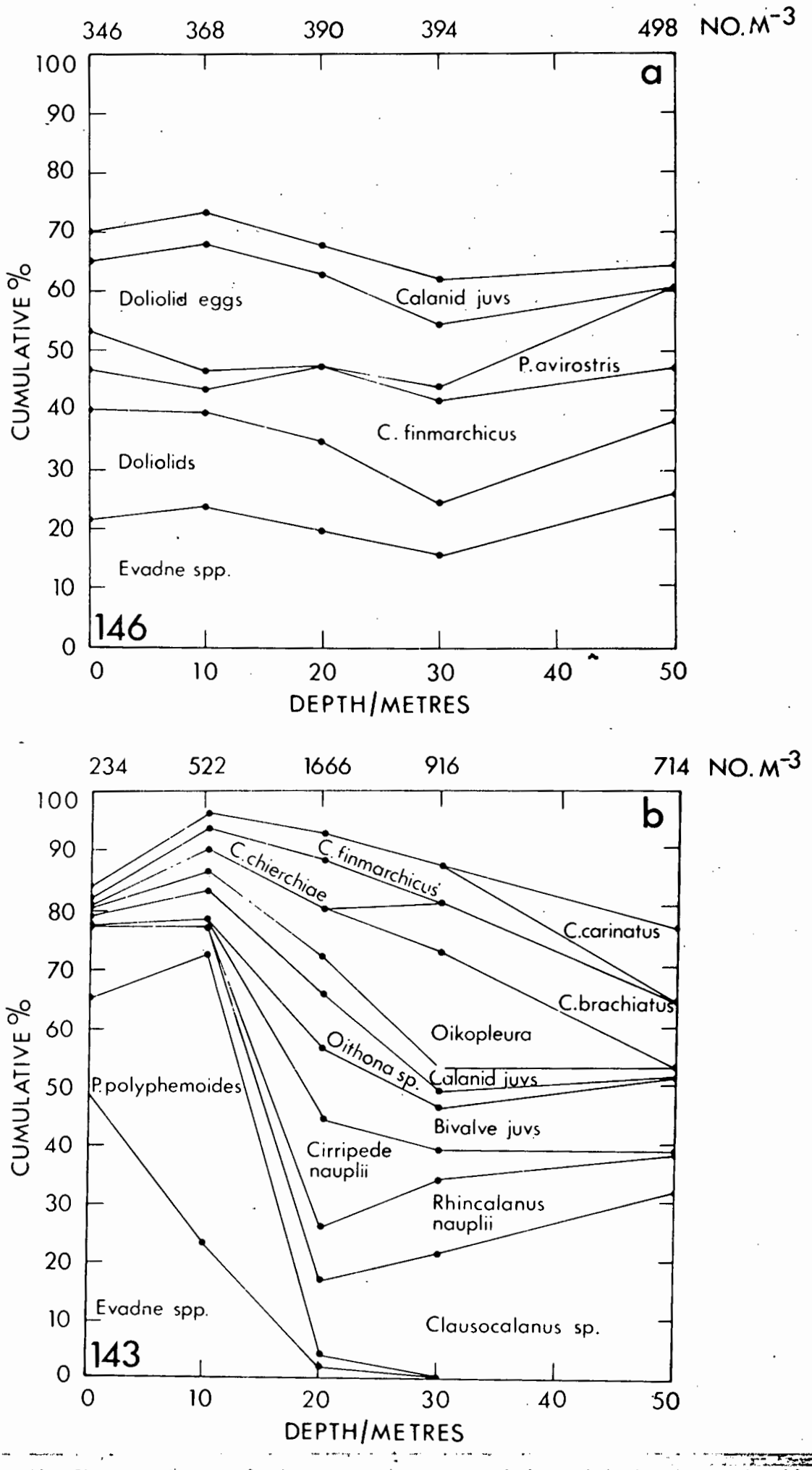
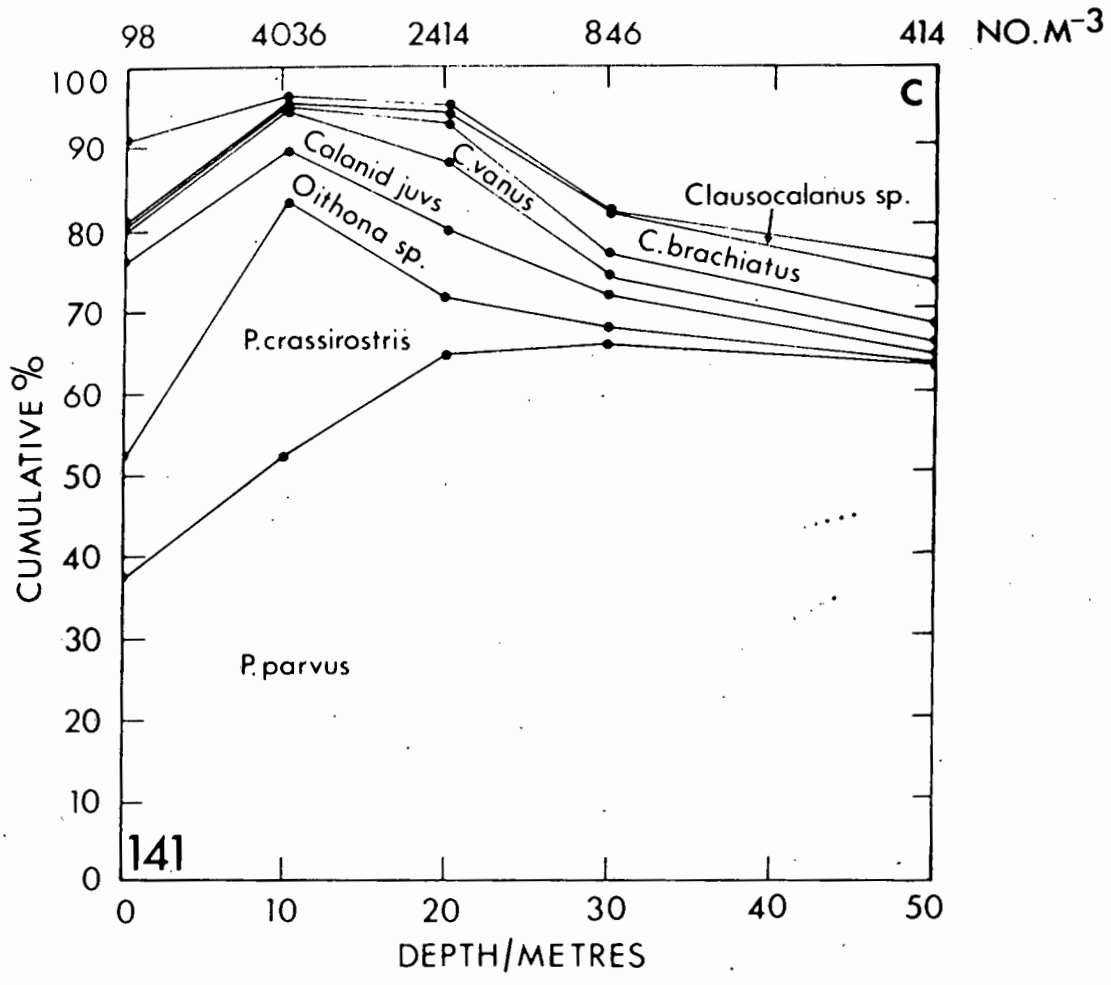


Fig. 10(a-j). Changes in zooplankton species composition with depth at the 10 pump stations. Numbers at top = number of animals per cubic metre, filtered; numbers at the side = cumulative percentage.

nine times (Fig. 9) indicating that larger organisms were present at subsurface levels. Usually these maxima were associated with thermoclines or chlorophyll"a" maxima (Figs. 3, 7, 8 and 9) and the zooplankton distribution was obviously profoundly affected by changes in temperature rather than the actual temperature. While there was a steady increase in zooplankton stocks when moving from oceanic (St. 146) to upwelled (St. 141) water, some of this may be due to proximity of the shore. The quantity of chlorophyll "a" present in the 0 - 50 m layer was relatively low when line 4 was first sampled (Appendix 1), but the other samples were collected in water with dense phytoplankton concentrations in the upper 50 metres.

Station 146 showed very uniform, low numbers and dry weight values (Figs. 7 and 9) throughout the 0 - 50 m layer, while displaced volumes (Fig. 8) also varied little but were somewhat higher, reflecting the preponderance of small, gelatinous organisms at this station. The species composition (Fig. 10(a)) remained relatively constant, with the cladoceran Evadne spinifera, doliolids and doliolid eggs dominant at all depths. Small Calanid copepodid stages I - II were of some numerical importance (7 - 12%) at 50 metres, but could not be conclusively identified as either Calanoides carinatus or Calanus finmarchicus v. australis but in view of the known preference of C. carinatus, adults for cooler waters (De Decker 1973, Herbland, Voiturez and Le Borgne 1975 , Thiriot, 1977 , and this study), they were likely to be young stages of C. fin. v. australis, considered by De Decker (1973) to be remnant population resident on the Agulhas Bank. Penilia avirostris assumed some importance (12%) at 50 metres, somewhat deeper than its normal surface-dwelling habitat (De Decker 1973). The presence of Penilia indicated that the oceanic water was largely derived from the waters on the Agulhas Bank, which is a centre of dispersion for Penilia (De Decker 1973).


98
4036
2414
846
414
NO.M-3
c
Calanid juvs
C.vanus
Clausocalanus sp.
C.brachiatus
Oithona sp.
P.crassirostris
P.parvus
141
CUMULATIVE %
DEPTH/METRES

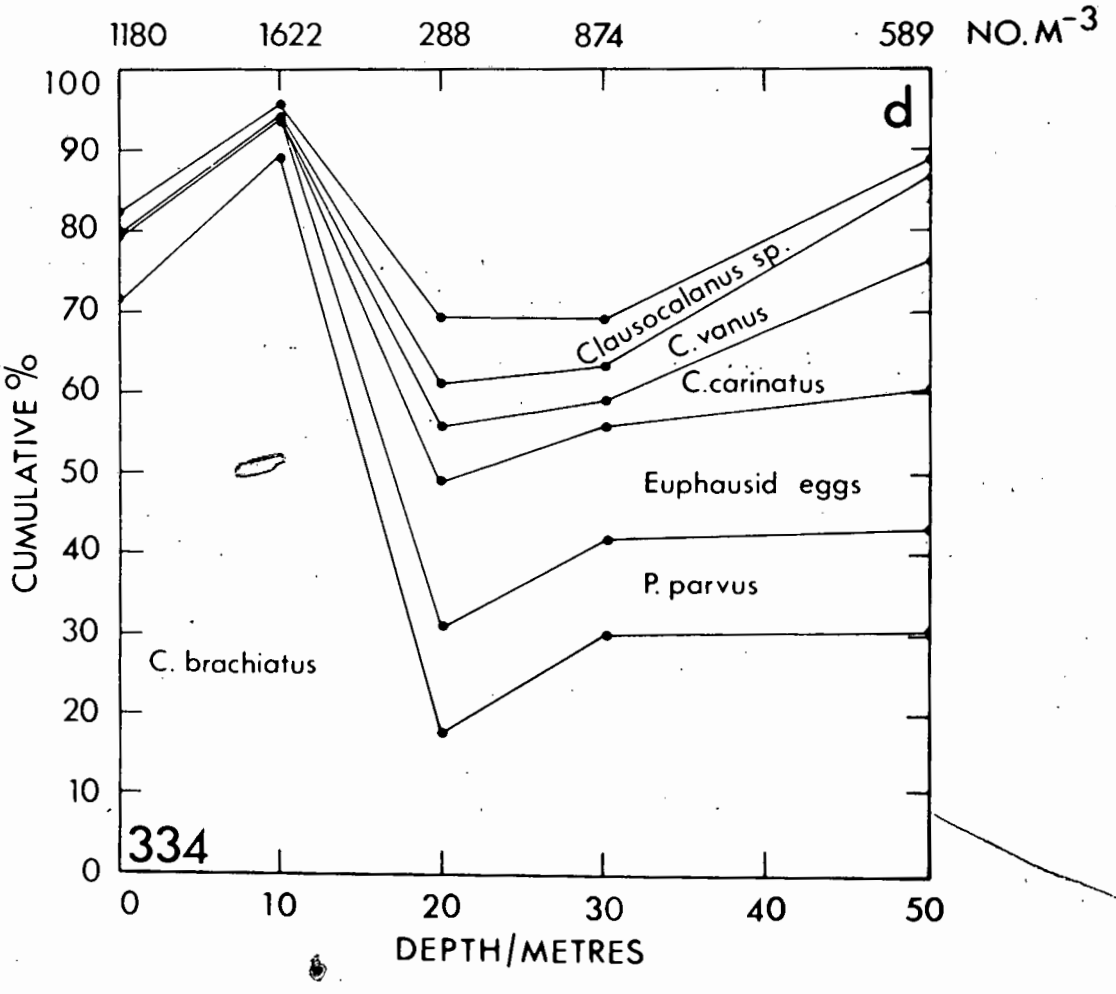

1180
1622
288
874
589
NO.M-3
d
Clausocalanus sp.
C.vanus
C.carinatus
Euphausid eggs
P. parvus
C. brachiatus
334
CUMULATIVE %
DEPTH/METRES

Fig. 10 (cont.)

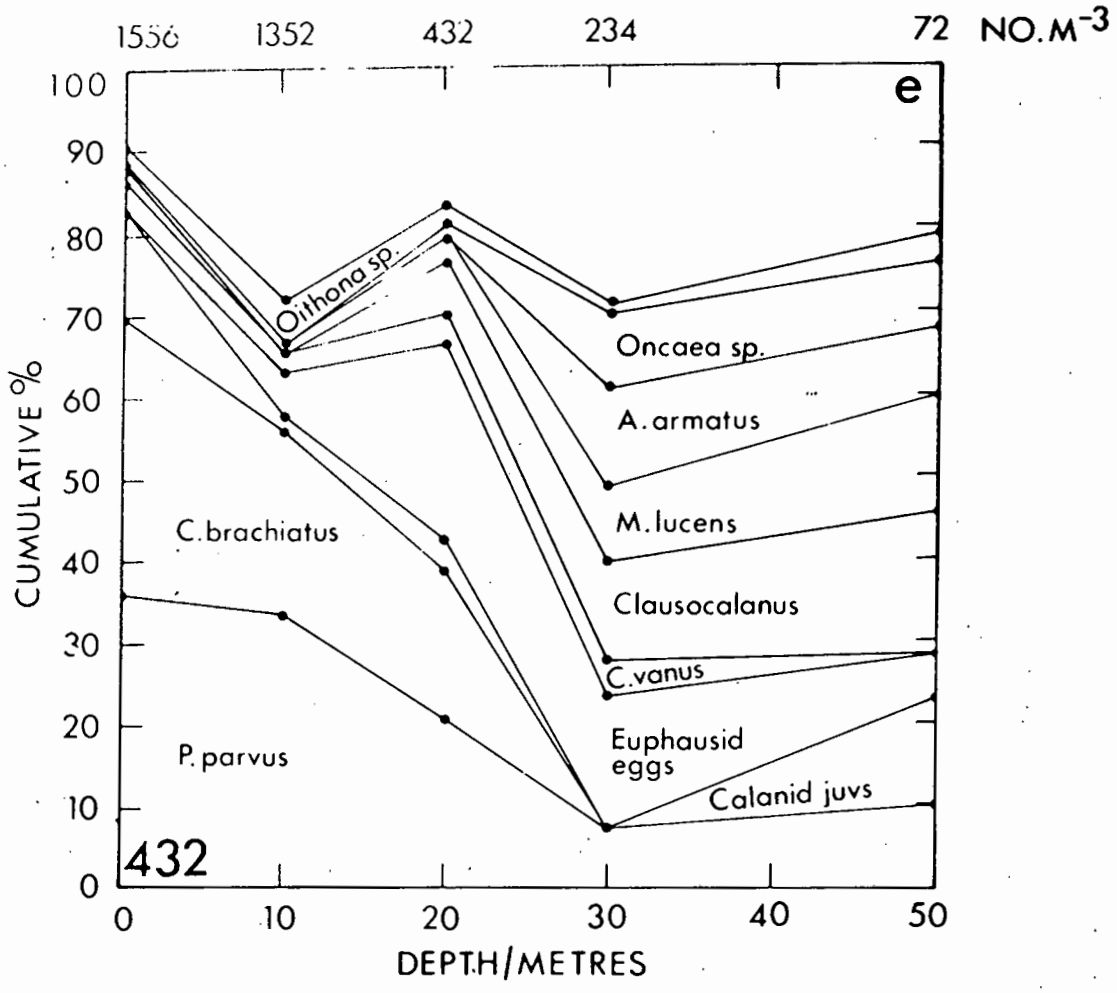
Station 143, situated within the frontal zone had a strong thermocline between 10 and 20 metres, but low chlorophyll"a" concentrations. Both numbers and displaced volumes peaked at 20 m (Figs. 7 and 8), while dry weight values showed a slight maximum at 30 metres. The warm water population above the thermocline (Fig. 10(b)) was dominated by Evadne spinifera and Podon polyphemoides which together comprised some 70% by numbers of the population, while copepods constituted 25%. These Cladocera were replaced by cirripede and Rhincalanus nauplii, Clausocalanus sp., juvenile bivalves and Oithona at 20 metres while cold-water species such as Centropages brachiatus, Calanoides carinatus and Rhincalanus nasutus became important in the 30 m to 50 metre layer, raising the percentage of copepods to 50% - 70%. Compared with net hauls, high numbers of Pseudodiaptomus nudus and Calocalanus tenuis occurred at 20 metres, confirming the preference these species have for strongly stratified water. (De Decker, S A Museum, per comm). It is highly probably that they occur in very localised patches, since high numbers are rarely collected with vertical net hauls. (Lazarus, 1974).
Podon and Evadne reflect a definite preference for warm surface waters, although Unteruberbacher (1964) considers them typical of neritic waters in South West African waters. Lazarus (1974) found them all year round at inshore stations along the west coast but numbers declined considerably during summer after a peak abundance during spring. De Decker (1973) observed that Evadne spinifera appears to be associated with centres of upwelling.

At station 141, (Fig. 10(c)) within the zone of upwelled water, copepods comprised 93% by numbers, and the small copepods Paracalanus parvus and P. crassirostris dominated, especially P. parvus, which comprised 60% by numbers below 20 metres. The second highest concentration of animals encountered during the pump series occurred at 10 metres (4036 m), but because of their

small size they did not constitute a large standing stock on a displaced volume or dry weight basis. By contrast surface concentrations of animals were very low (98 m^{-3}) probably due to avoidance of the near surface layers during daytime in the clear upwelled waters (1% light depth = 35 m). Both these species, especially P. crassirostris, reached maximum numbers close to the coast during the survey and the maintenance of the population close inshore during periods of powerful upwelling is difficult to explain.

These three stations clearly illustrate the transition from a warm water, deep thermocline situation through a stratified, shallow- thermocline region to a uniformly cold-water regime. The mixed water zone in this particular instance was quite limited (Fig. 2), as the vertical temperature distribution indicated a strong uplift of water to 20 - 30 metres between stations 144 and 145, followed by a flattening of isotherms close inshore. Wind data from Cape Point tended to confirm this deduction, and the limited water mixed water zone meant that phytoplankton stock did not reach very high concentrations on this particular occasion.

At Stations 334, (Fig. 10(d)) adult Centropages brachiatus dominated in the upper 10 metres, comprising 70% - 90% by numbers. A pronounced zooplankton minimum occurred at 20 metres (Fig. 8), the depth of the maximum thermal gradient, where displaced volumes were one half one third of the values at other depths. Numbers and dry weight (Fig.s 7 and 9) were similarly distributed. A marked change in species composition occurred at this depth, with C. brachiatus declining to less than 20% by numbers and Paracalanus parvus, Euphausid eggs, Calanoides, Ctenocalanus and Clausocalanus sp. becoming relatively more abundant. At the pronounced chlorophyll maximum at 30 metres, large numbers of juveniles of C. brachiatus, Clausocalanus sp., Calanoides and Paracalanus parvus were observed, ans these species persisted to 50 metres in similar proportions. At other stations these juveniles were closely associated with the thermocline (Fig. 11), which in turn was normally the boundary between high and low chlorophyll concentrations. The shift of the chlorophyll maximum appears to have a greater effect on the vertical distribution of juveniles than the temperature gradient. Adult C. brachiatus, on the other hand, on


1556
1352
432
234
72
NO.M-3
e
100
90
80
70
60
50
40
30
20
10
0
CUMULATIVE %
Oithona sp.
Oncaea sp.
A.armatus
M.lucens
Clausocalanus
C.vanus
Euphausid eggs
Calanid juvs
C.brachiatus
P.parvus
432
0
10
20
30
40
50
DEPTH/METRES

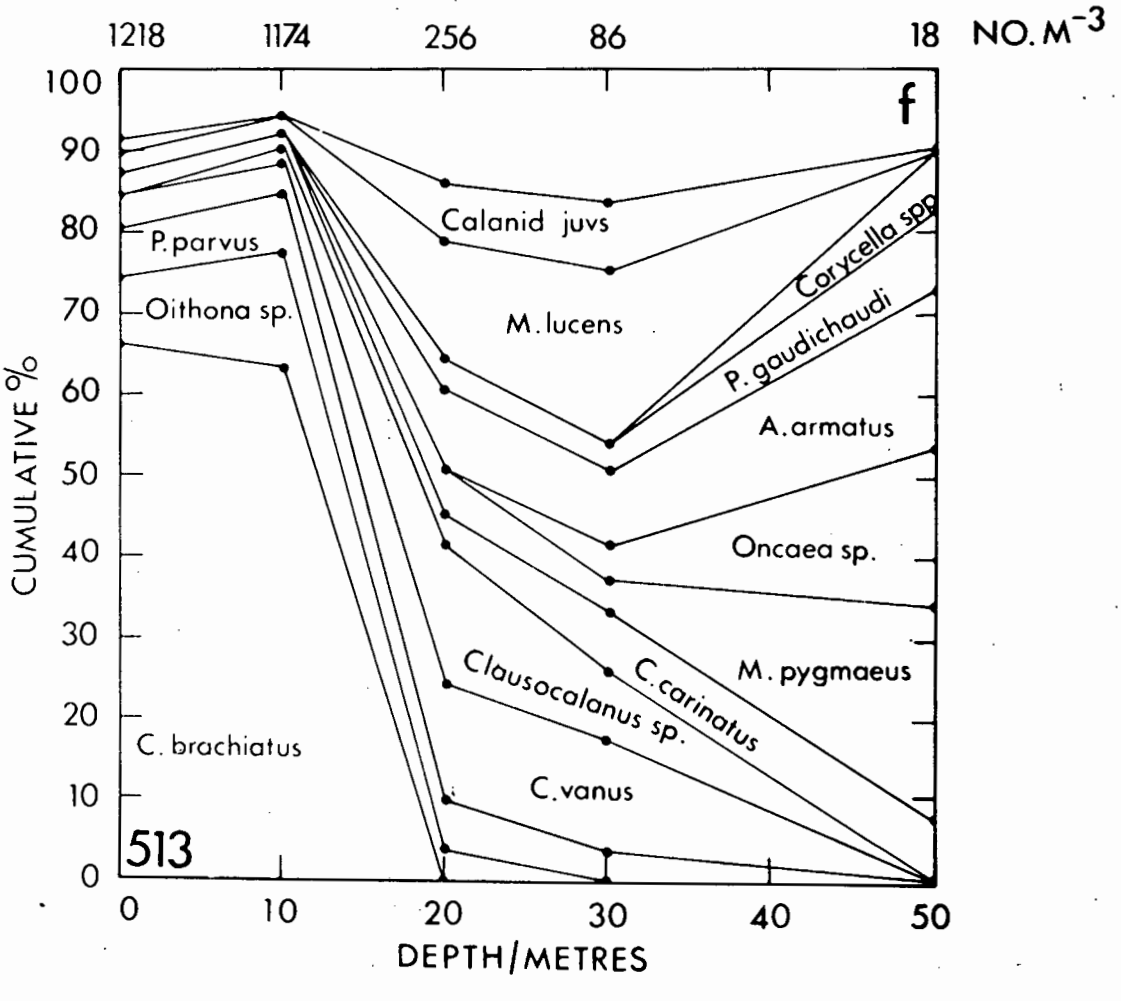
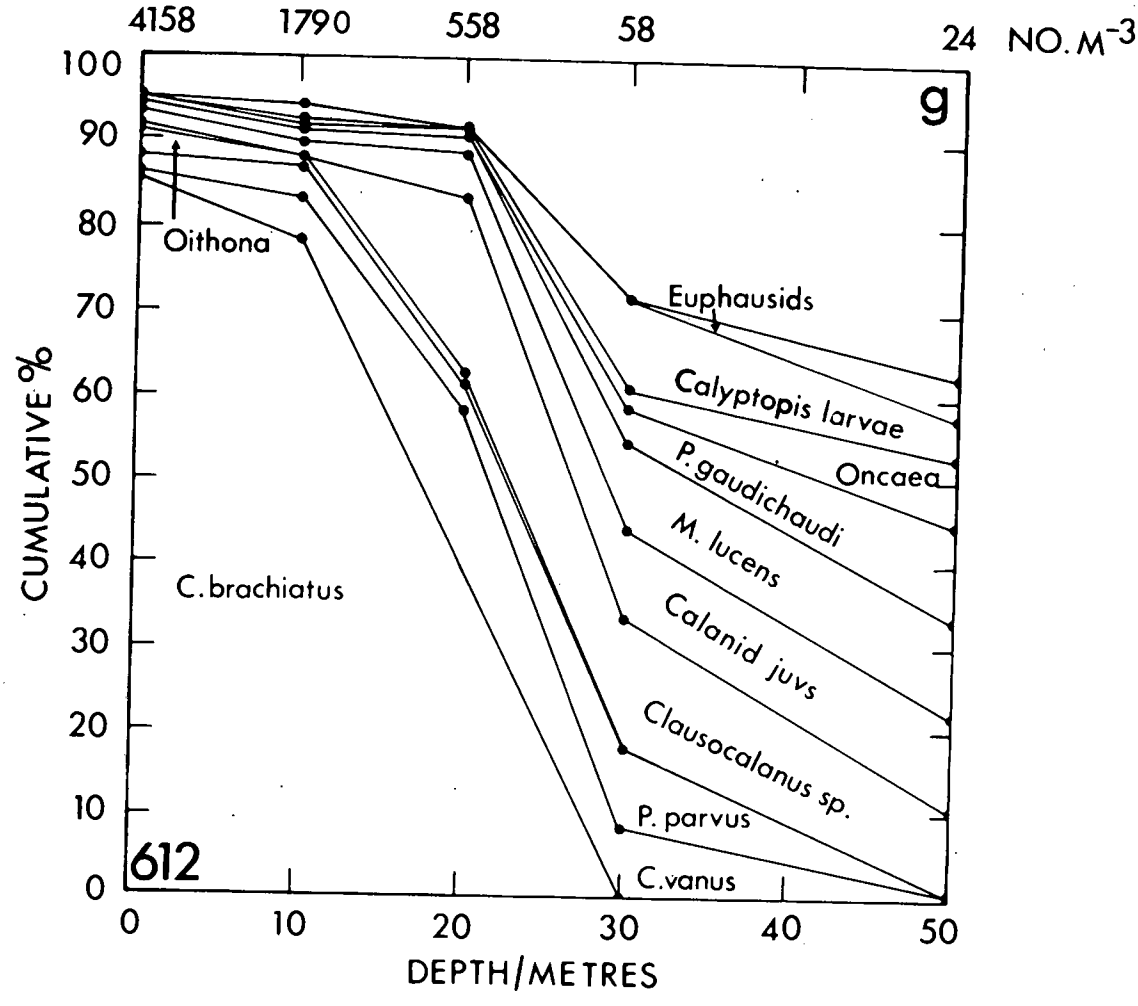

1218
1174
256
86
18
NO.M-3
f
100
90
80
70
60
50
40
30
20
10
0
CUMULATIVE %
Calanid juvs
Corycella spp.
P.gaudichaudi
M.lucens
P.parvus
Oithona sp.
A.armatus
Oncaea sp.
M.pygmaeus
C.carinatus
Clausocalanus sp.
C.vanus
C.brachiatus
513
0
10
20
30
40
50
DEPTH/METRES

Fig. 10 (cont.)


4158
1790
558
58
24 NO. M-3
g
100
90
80
70
60
50
40
30
20
10
0
CUMULATIVE %
Oithona
C. brachiatus
612
Euphausids
Calyptopis larvae
Oncaea
P. gaudichaudi
M. lucens
Calanid juvs
Clausocalanus sp.
P. parvus
C. vanus
0
10
20
30
40
50
DEPTH/METRES

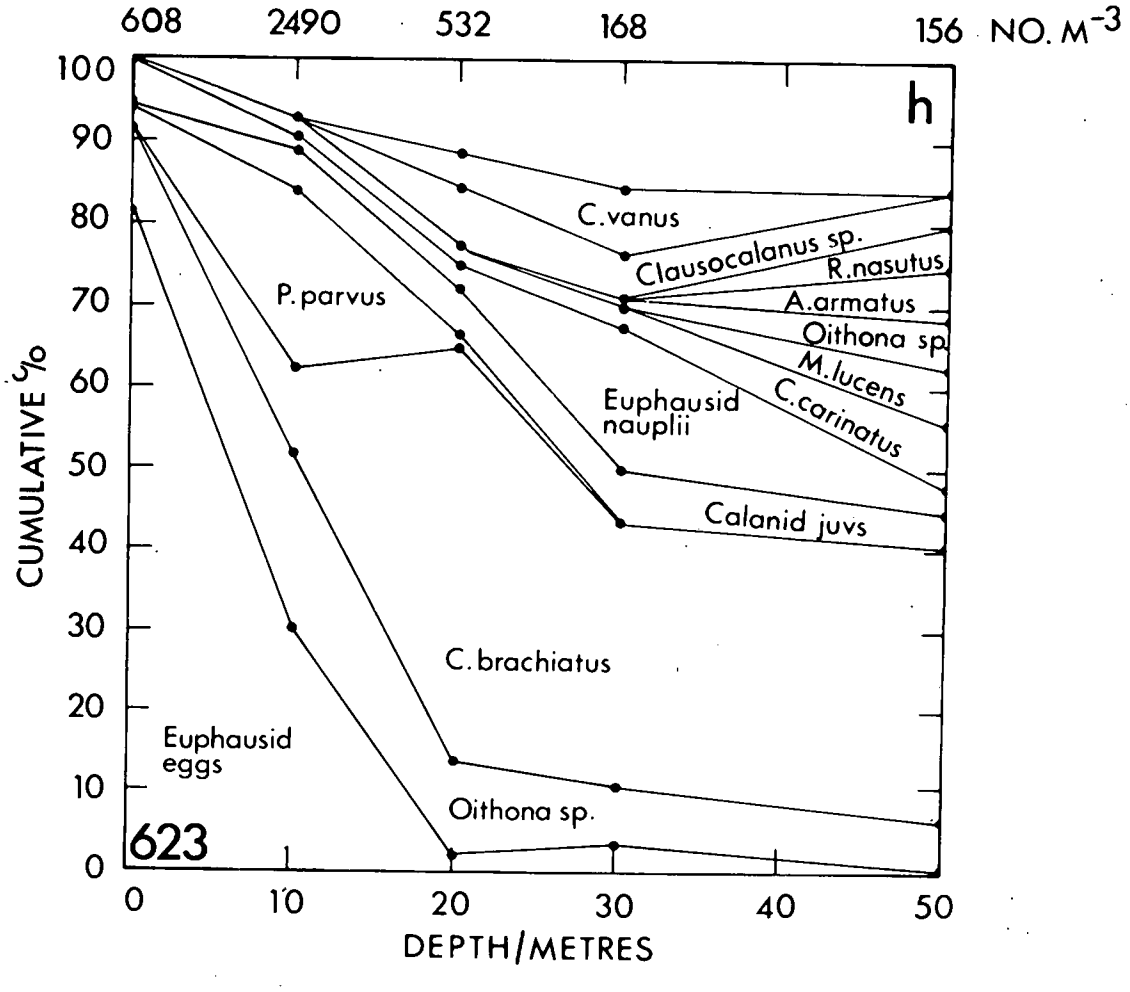

608
2490
532
168
156 NO. M-3
h
100
90
80
70
60
50
40
30
20
10
0
CUMULATIVE %
C. vanus
Clausocalanus sp.
R. nasutus
A. armatus
Oithona sp.
M. lucens
C. carinatus
Calanid juvs
P. parvus
Euphausid nauplii
C. brachiatus
Euphausid eggs
Oithona sp.
623
0
10
20
30
40
50
DEPTH/METRES

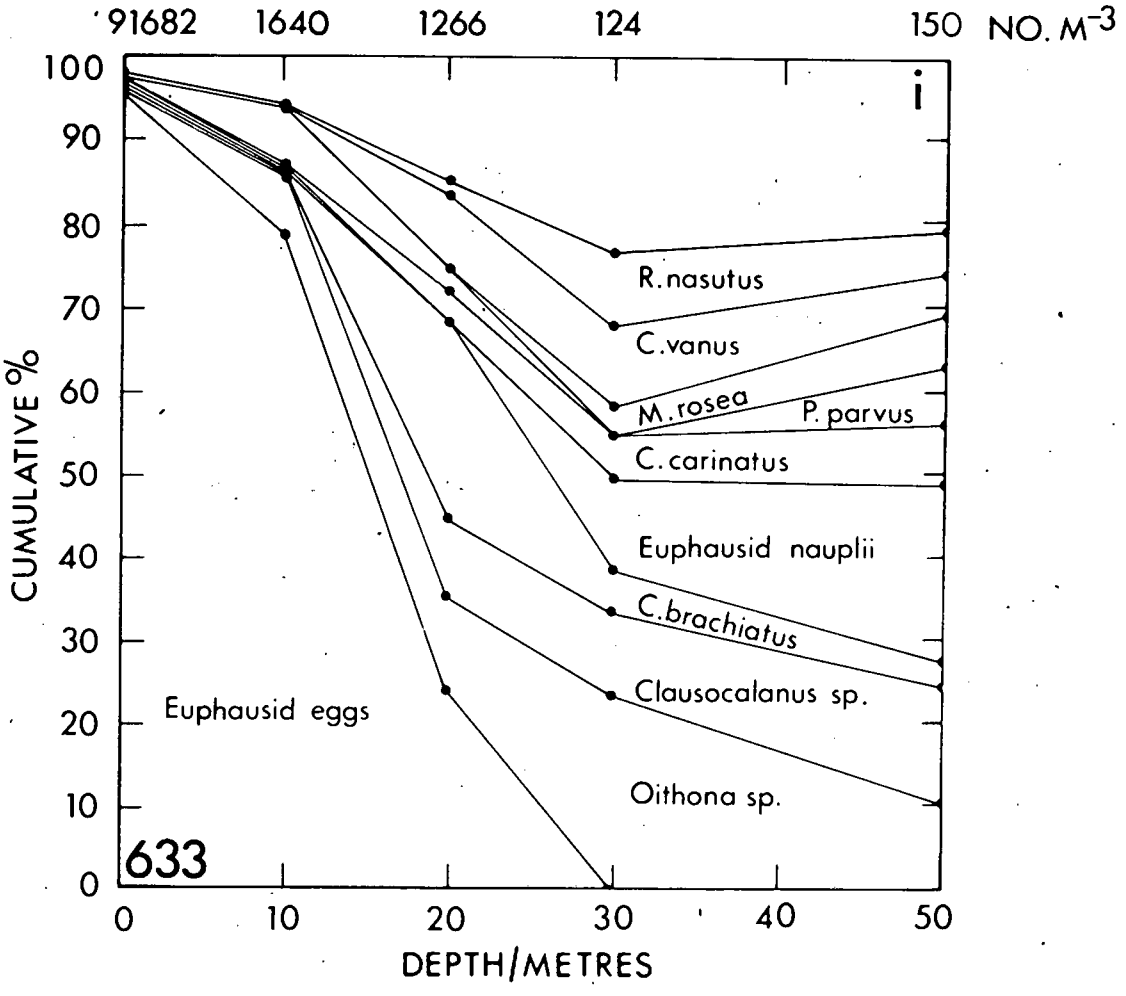
Fig. 10 (cont.)

on the other hand, are most abundant close to the surface, their normal distribution at night (see vertical distribution of species).

At station 432, C. brachiatus and P. parvus dominated in the 0 - 20 m layer and were replaced below the thermocline by lesser numbers of several species (Fig. 10(e)), including Aetideus armatus, Metridia lucens and Clausocalanus sp. P. parvus persisted to 50 metres, but C. brachiatus were limited to water warmer than 10°C, in the upper 30 metres. Displaced volumes and numbers of animals decreased markedly with depth (Figs. 7 and 8) but dry weight values (Fig. 9) increased somewhat at 30 metres before decreasing to 10 mg/4,5 m^3 at 50 metres.

Stations 513 and 612 had similar species distributions, and will be described together. C. brachiatus was clearly dominant in the upper 10 - 20 metres (Fig. 10 (f) and 10(g)), associated with high chlorophyll "a" concentrations (Fig. 3). Station 612 showed the highest concentration of organisms of all the pump samples at 10 metres (4158/m^3), of which 85% were C. brachiatus. Below the chlorophyll-rich layer numbers of animals decreased to 18-24 per cubic metre (Fig. 7) and consisted of a few specimens of Euphausia lucens, calyptopis larvae, Parathemisto, M. lucens, Clausocalanus sp., Ctenocalanus, Paracalanus parvus and juvenile Calanoides in approximately equal numbers. Displaced volumes and dry weight did not decrease as markedly because of the larger size of the specimens from the deeper layers.

At station 623 and 633, sampled in the light, euphausid eggs dominated in the upper 10 metres comprising 80- 95% by numbers, with few other organisms present (Figs. 10(h and i), although this may have been typical of the daytime distribution of the majority of the organisms. As the number of eggs declined with depth C. brachiatus, Oithona sp. And P. parvus became more important, but the concentration of organisms declined (Fig. 7). At station 633 numbers declined from 1226/m at 20 metres to 124 - 150/m in the 30 - 50 metre layer. At 623 peak concentrations of 2490/m^3


91682
1640
1266
124
150 NO. M-3
i
CUMULATIVE %
R.nasutus
C.vanus
M.rosea
P.parvus
C.carinatus
Euphausid nauplii
C.brachiatus
Clausocalanus sp.
Euphausid eggs
Oithona sp.
633
DEPTH/METRES

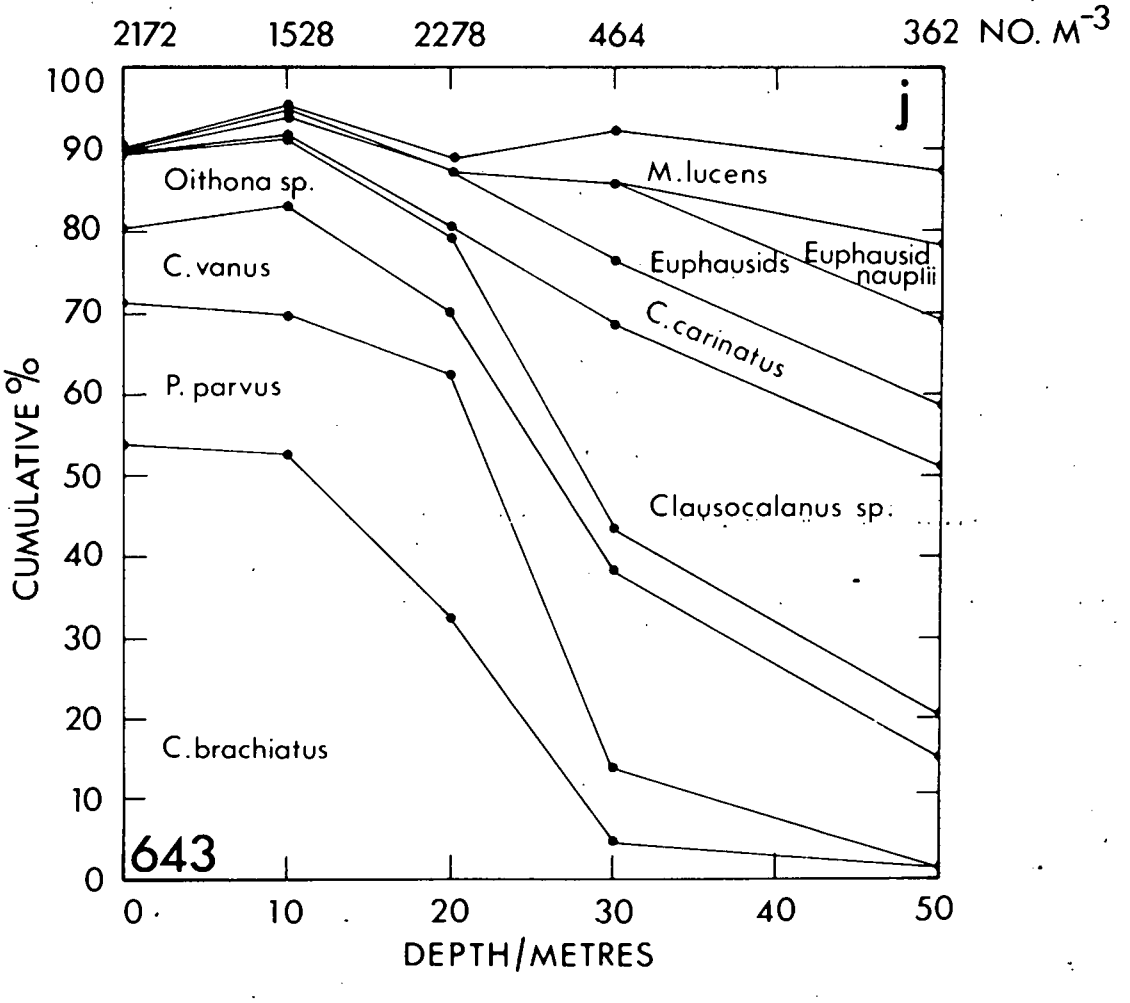

2172
1528
2278
464
362 NO. M-3
j
CUMULATIVE %
Oithona sp.
M.lucens
C.vanus
Euphausids
Euphausid nauplii
C.carinatus
P. parvus
Clausocalanus sp.
C.brachiatus
643
DEPTH/METRES

Fig. 10 (cont.)

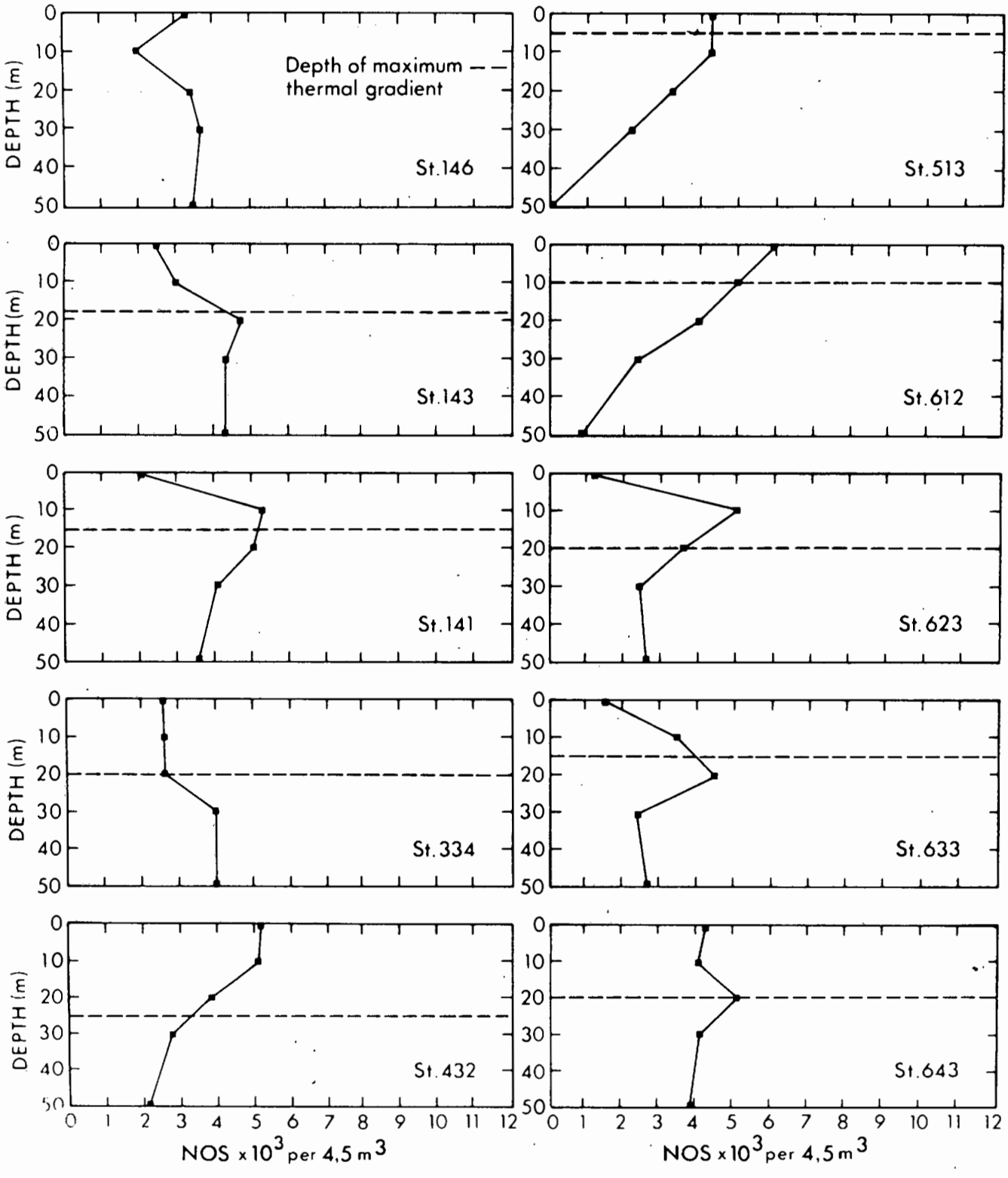


Fig. 11. Vertical profiles of number of copepod juveniles (no.$(4{,}5\ m^3)^{-1}$) at the 10 pump stations.

occurred at 10 metres, declining to 150 - 500/m^3 at deeper levels. Displaced volume profiles showed similar trends to the numbers, but dry weights showed only slight increases near the surface, reflecting the high displaced volume/dry weight ratio of the euphausid eggs. The only zooplankton species which maintained its numbers in the egg- rich layer was Oithona sp, and it is clear that grazing stress on the phytoplankton at these stations was reduced, despite the fact that the water was fairly mature upwelled water, with nutrients beginning to reach limiting levels. The zooplankton crop at these stations was relatively low (dry weight = 333 mg/m^3), and suggest that either zooplankton simply had not colonized this particular patch of phytoplankton or the euphausids, which had spawned in this water, removed the smaller copepoda, and had themselves avoided both the pump and the net during daylight hours. The high chlorophyll"a" concentrations, however, suggest that little grazing pressure had ever been applied to this particular patch of phytoplankton.

Station 643 (Fig. 10(j)) was situated in the centre of a patch of zooplankton that had begun to form 36 hours previously as the wind backed to the west on the 12/13th, and when station 643 was sampled it had reached its maximum state of consolidation before being dispersed as the wind returned to the south east (Andrews et al. in press). Centropages brachiatus and Paracalanus parvus were numerically dominant, forming 65% - 70% by numbers in the upper 20 metres, but declined in importance below 30 metres as the temperature dropped to 10°C. This distribution of P. parvus is contrasted with its distribution at station 141, where it was present at considerably higher concentrations at temperatures as low as 7,5°C. Below 20 metres Ctenocalanus, Clausocalanus sp. Calanoides, Euphausia lucens, euphausid nauplii, Parathemisto and M. lucens become more important, and because of the large size of the euphausids and hyperiids dry weight values peaked at 30 metres. Although this patch shifted some 16 kilometres to the north west subsequent to being sampled at 643, the species

22/...

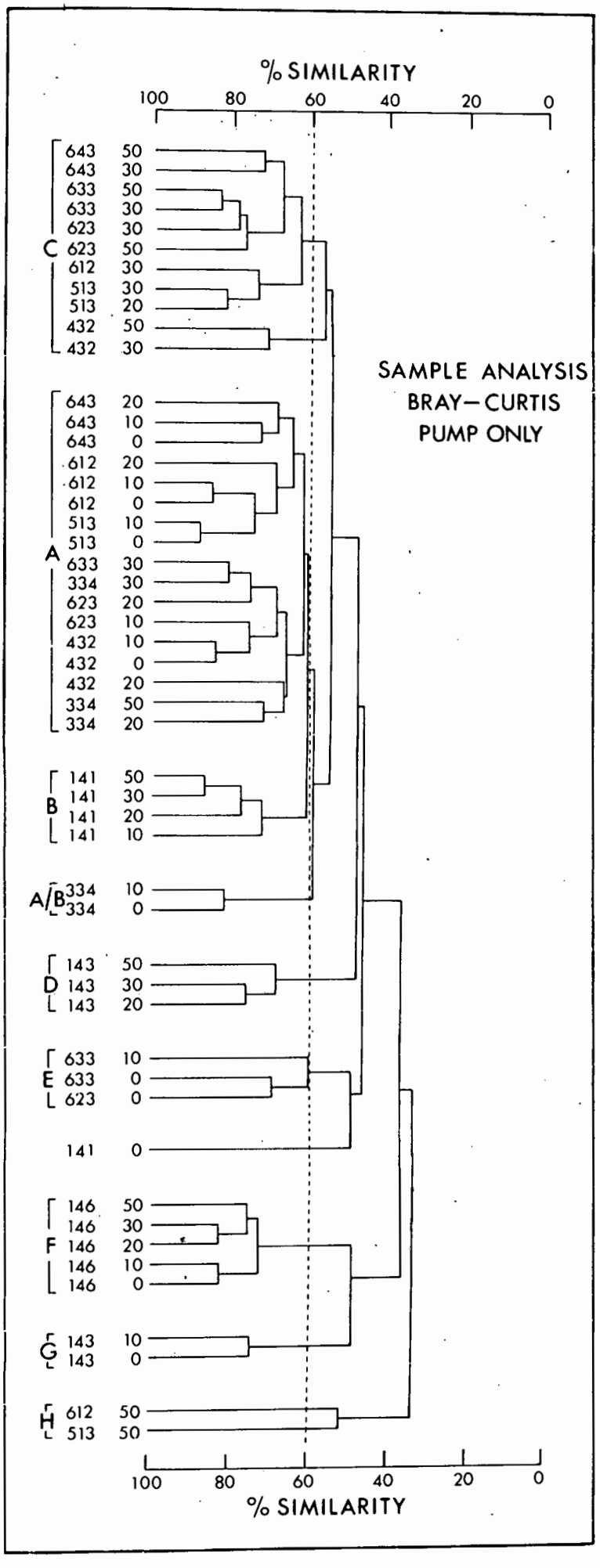


Fig. 12. Dendrogram of Bray-Curtis similarity after group-average sorting between pump samples only, showing groups A - H. Similarity coefficients calculated from species abundance expressed as number per cubic metre.

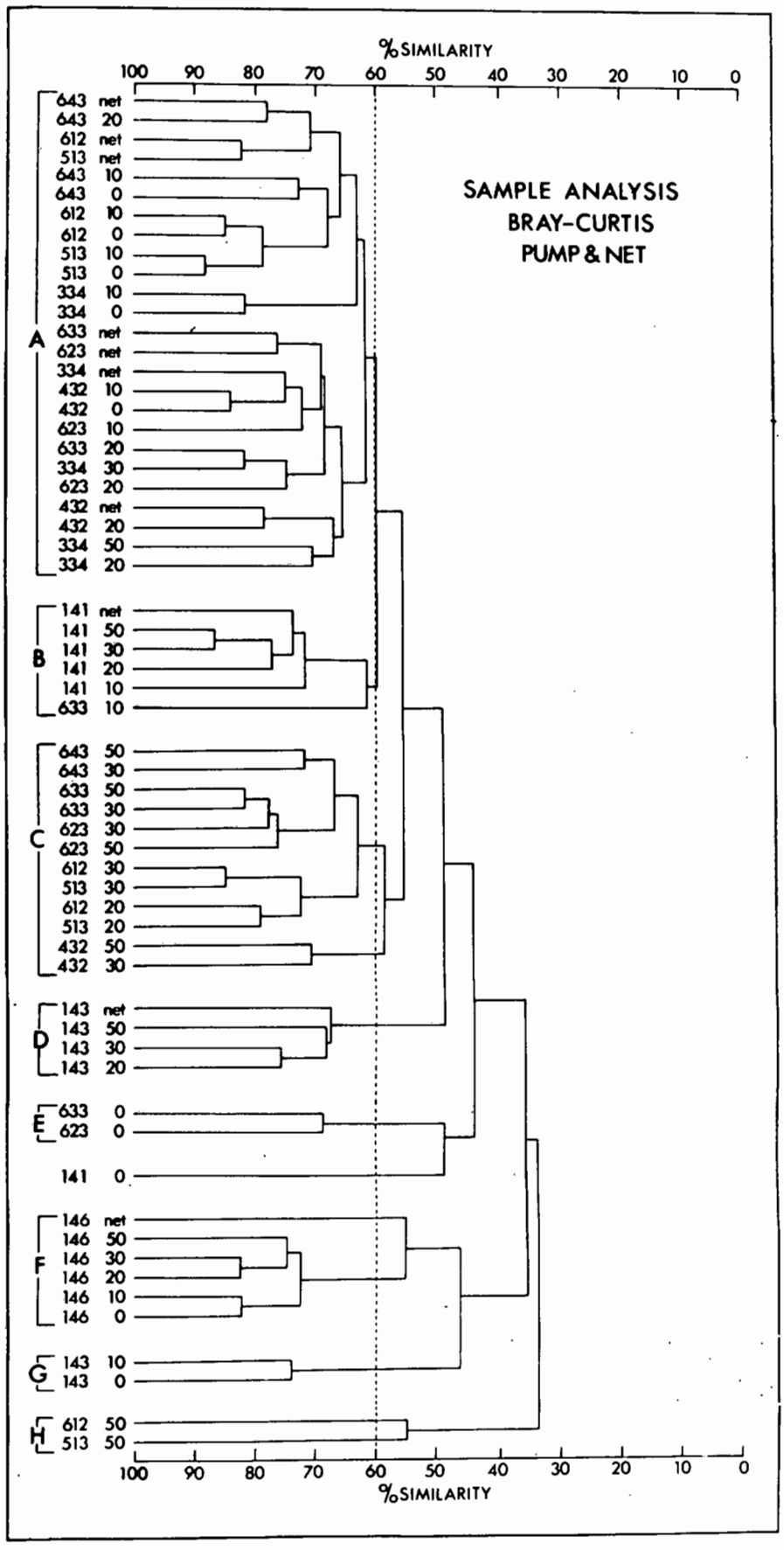


Fig. 13. As in Fig. 12, but including 50 - 0 WP-2 net samples at each pump station.

composition, as estimated by WP-2 net hauls, had remained relatively constant, (Andrews et al. in press), which, considering the strong shearing effect the wind stress is likely to exert on a stratified water colum, demonstrated the importance of the zooplankton in the upper layers compared to the whole water column.

3.5 Numerical classification of zooplankton

3.5.1 Sample groupings

Eight groups of samples were delineated by the Bray-Crutis coefficient at the 50% similarly level (Fig. 12) and addition of the net samples, which provided depth-integrated samples, did not alter the grouping to any great extent (Fig. 13).

Inspection of Figs. 12 and 13 shows that group A, the largest group, consisted of samples from the upper 20 metres at stations 432, 513, 612 and 643 as well as 30 m and 50 m samples from station 334, and were associated with high chlorophyll concentrations and cool water of 11° - 15°C. C. brachiatus, P. parvus, Ctenocalanus, Calanoides, Oithona and Clausocalanus were common in these samples and are all typical members of the southern Benguela upwelling community (Thiriot 1977). Of interest is the inclusion of deep samples from station 334 in this group, suggesting that a sinking process had occurred at this station. The surface and 10 metre samples from st. 334 form an intermediate group when only pump stations are matched but when net samples are included they form part of the A-group. Because group A pump samples generally contained the highest concentrations of animals present in the water column, net hauls at these stations were linked to them. Group B was closely linked to group A, and consisted of the 10-, 20-, 30- and 50 metre samples from station 141, the "upwelling water" station. Temperature and chlorophyll"a" concentrations are significantly lower than in Group A (Mann-Whitney U-test, $p < 0{,}05$). P parvus 40% - 60%) and P. crassirostris (15% - 30%) dominated in these samples. The near-surface sample was somewhat different, due to the marked decrease in numbers of animals and the greatly increased proportion of Oithona, which caused it to show closer similarity to the surface samples from station 623 and station 633 than to subsurface samples.

Group C. The third group consists of those samples from below the chlorophyll"a" rich layer, in cold water. Samples collected both in the light and the dark are included, as light levels below the dense chlorophyll"a" layer are likely to remain low. Characteristic species are the larger west coast species, including Metridia lucens and Aetideus armatus in relatively low numbers compared with the dominant species in groups A and B. Chlorophyll"a" concentrations and temperatures are significantly lower than in Groups A and B.

Group D. The fourth group consists of the net haul and pump samples below the thermocline at the station in the frontal zone, station 143, showing that the integrated net haul reflects the abundance of animals in the cooler waters at this station, rather than the slightly lesser numbers above the thermocline. Dominant animals were Clausocalanus, Rhincalanus nauplii, cirripede nauplii and Oikopleura. Neither temperature nor chlorophyll"a" concentrations differ significantly from those in groups A, B and C.

Group E. The fifth group consists of only three samples, station 623 0 m and station 633 0 m and 10 m, where euphausid eggs comprise 80 - 95% of the plankton, with small numbers of Oithona. Station 141 0 m is the closest to this group due possibly to the presence of Oithona and P. parvus. No difference in chlorophyll or temperature exists between group E and groups A - D.

Group F. The sixth group consists of all the samples from the warm water station, St. 146, where uniform conditions with respect to chlorophyll"a" and temperature were present in the upper 50 metres, and the diverse species composition altered little with depth (Fig. 10(a)), with Evadne, doliolids, doliolid eggs and Calanus finmarchicus dominant. Temperature is significantly higher than in group G or groups A - E, while chlorophyll"a"

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TABLE 4: Information statistic showing frequency of occurrence of species differing significantly between adjacent groups

* Significant at 5% level
** Significant at 1% level

	Σ = 17	Σ = 4
A vs B	A	B
Calyptopis	10 *	0
Euphausids	14 **	0
Euphausid eggs	9 *	0
Metridia lucens	13 *	0
Pseudodiaptomus nudus	1	4 **

	Σ = 21	Σ = 12
A B vs C	A B	C
Actideus armatus	9	10 *
Calanus finmarchicus	4 *	0
Calyptopis	10 **	0
Ctenocalanus vanus	21	10 *
Euchaeta hebes	0	2 *
Lucicutia flavicornis	0	4 **
Metridia lucens	13	11 **
Nannocalanus minor	19 **	4
Paracalanus crassirostris	21 *	10
Pseudodiaptomus nudus	5 *	0
Rhincalanus nauplii	6 *	0
Sagitta sp	21 **	8
Euphausid nauplii	7	10 **

	Σ = 32	Σ = 3
A B C vs D	A B C	D
Anchovy eggs	0	1 *
Bivalves	14	3 *
Calanoides carinatus	30 *	1
Calanus finmarchicus	4	2 *
Calocalanus tenuis	13	3 *

TABLE 4 (cont.)

	Σ = 38 ABCDE	Σ = 5 F
Calyptopis	14 *	0
Centropages brachiatus	35 **	1
Centropages chierchiae	6	3 *
Coryceaus	1	5 **
Corycella	14	5 **
Ctenocalanus	32 *	2
Doliolids	0	5 **
Euterpina acutifrons	13	5 **
Evadne spinifera	12	5 **
Gastropoda	8	5 **
Macrosetella gracilis	0	2 **
Meycenocera clausi	1	2 *
Microsetella rosea	20	5 *
Penilia	0	5 **
Pleuromamma abdominalis	9	4 *
Rhincalanus nasutus	33 **	1
Doliolid eggs	3	4 **
Tomopteriis	1	2 *

A B C D E F vs G	Σ = 42 ABCDEF	Σ = 2 G
C Calanoides	34 *	0
Calanus finmarchicus	11	2 *
Centropages brachiatus	36 **	0
Centropages chierchiae	9	2 *
Cirripede nauplii	10	2 *
Ctenocalanus	34 *	0
Nannocalanus minor	30 *	0
Penilia	5	2 **
Podon	5	2 **
Rhincalanus nasutus	34 *	0
Rhincalanus nauplii	11	2 *

TABLE 4 (cont.)

	Σ = 32 A B C	Σ = 3 D
Centropages chierchiae	2	2 *
Cirripede nauplii	5	3 **
Coryceaus	0	1 *
Corycella	11	3 *
Ctenocalanus vanus	30 *	1
Metridia lucens	23 **	0
Oikopleura	0	1 *
Parathemisto	18 *	0
Podon	1	2 **
Pseudodiaptomus	5	3 **
Rhincalanus nauplii	0	3 **
Euphausid nauplii	16 *	0

A B C D vs E	Σ = 35 A B C D	Σ = 3 E
Aetideus armatus	22 *	0
Centropages chierchiae	4	2 *
Ctenocalanus vanus	31 *	1
Euphausid eggs	13	3 *
Metridia lucens	23 *	0
Microsetella rosea	20 *	0
Euphausid nauplii	16	3 *

A B C D E vs F	Σ = 38 ABCDE	Σ = 5 F
Acartia danae	2	5 **
Acartia negligens	0	2 **
Bivalves	19 *	0
Calanoides carinatus	33 **	1
Calanus finmarchicus	6	5 **
Calocalanus pavo	0	4 **
Calocalanus tenuis	16 *	0

TABLE 4 (cont.)

A B C D E F G vs H	Σ = 45 ABCDEFG	Σ = 2 H
Clausocalanus sp	44 ⁎	1
Ctenocalanus sp	34 ⁎	0
Euchaeta hebes	2	2 ⁎⁎
Isopoda	6	2 ⁎⁎
Nannocalanus minor	30 ⁎	0

although very low, shows no significant differences from the combined groups, although it is significantly lower than groups A and E.

Group G. The warm waters above the thermocline at station 143 form the seventh group, and are the closest link to station 146 (group F) Podon and Evadne are the commonest species present. Chlorophyll "a" concentrations are similar to groups A - F, while temperatures are intermediate between groups A - E and F.

Group H. The last group consists again of only two samples, station 513 50 m and station 612 50 m. These samples were collected at night close to the bottom and contain several species more closely associated with a benthic environment than with a pelagic one. Temperature and chlorophyll "a" concentrations are obviously lower than that in the surface waters at these stations.

Species showing significantly different frequencies of occurrence between groups, based on the information statistic, are shown in Table (4). As "adjacent" groups were not displayed by the dendrograms, each group was compared with the sum of groups to which it was linked.

Differences between the species in newly upwelled water (Group B) and the more mature water (Group A) were minor, and were due mainly to a day-night difference in sampling, when Metridia lucens, and Euphausia lucens eggs, calyptopis and furcilia were collected in group A samples. Only Pseudodiaptomus nudus was characteristic of newly upwelled water and even so it was not abundant in this water compared with its abundance in group D samples in the frontal zone.

The "shallow" samples (Group A and B) were characterised by Ctenocalanus, Nannocalanus, Paracalanus crassirostris and Sagitta sp when contrasted with the "deep" samples at the same

locations, where Aetideus armatus and Metridia lucens were significantly more common.

Characteristic cool-water frontal-zone species (Group D) were Calocalanus tenuis, bivalves, cirripede nauplii, Podon, Rhincalanus nauplii, and Pseudodiaptomus.

Group E samples were distinguished only at the 5% level by the presence of euphausid eggs and nauplii with very few other significant differences in species. Group F, (station 146 samples) constituted a major change in fauna with 25 of the total of 57 species showing significant differences, of which 18 belonged to the warm water group.

The warm water frontal zone samples (Group G) showed that at the 1% level Penilia and Podon were characteristic of the frontal zone while C. brachiatus was absent from the warmer water, although present below the thermocline. The epibenthic samples (Group H) were only distinguished by Euchaeta hebes and an unidentified isopod.

These results must be treated cautiously as most groups contained very few samples and were widely spread in time. For these reasons multidimensional scaling (Kruskal 1977) of the pump samples was not attempted, although with a greater number of samples from discrete depths over a short time interval this technique should prove useful. All the samples in the cooler waters (Stations 141, 334, 432, 513, 612, 633 and 643 appear more similar to each other than frontal zone (Station 143) or oceanic water (Station 146) samples, judging from the number of significant differences in species occurrences between the groups of samples.

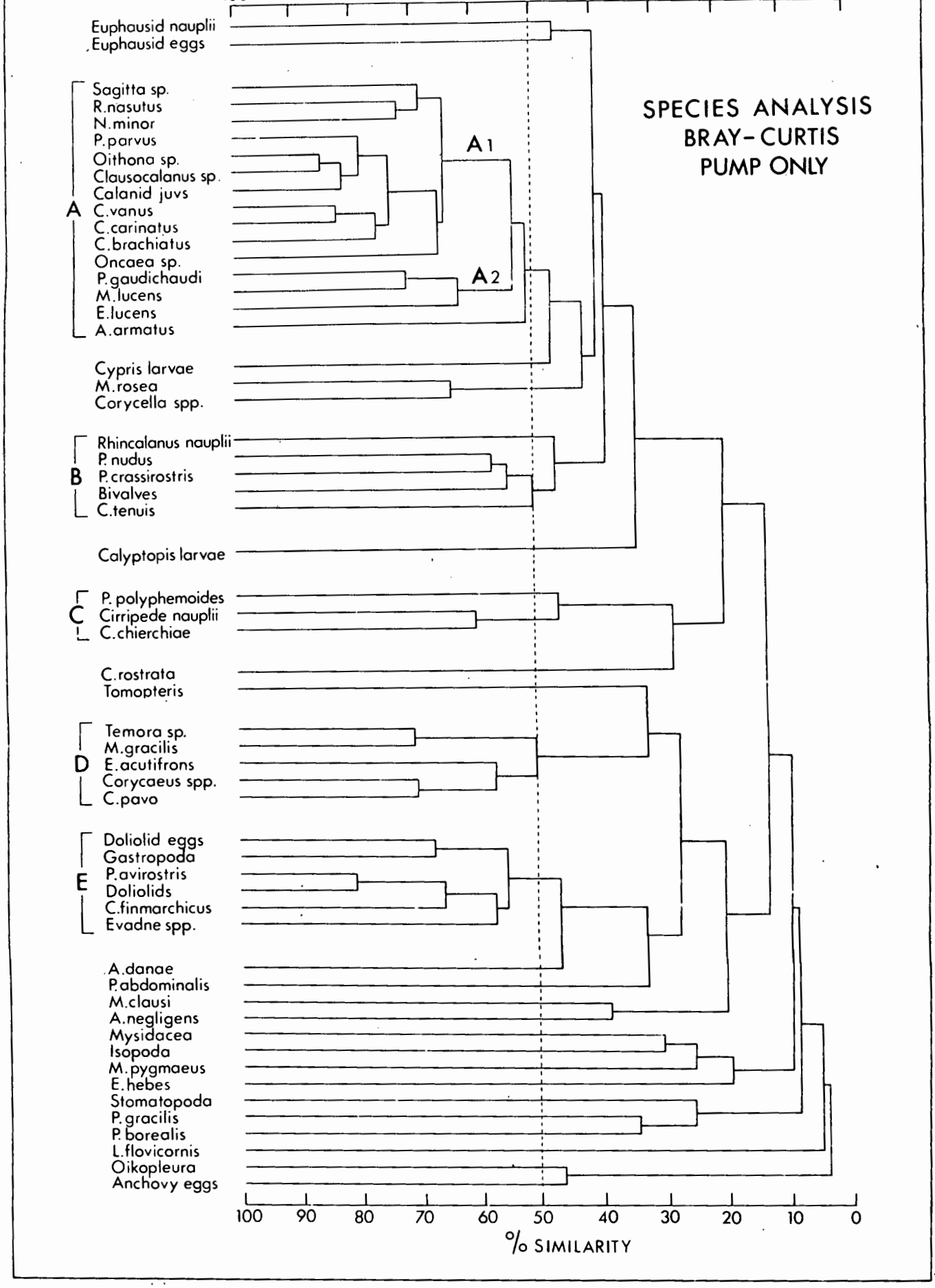

Fig. 14. Dendrogram of Bray-Curtis similarity between species based on pump samples only.

3.5.2 Species groupings - Bray-Curtis

A Bray-Curtis species analysis on the data (Fig. 14) revealed the presence of four major groups of organisms, of which the largest group could be subdivided into two further groups.

A(1) the first major group consisted of 14 members of the typical west coast community (De Decker 1973, Thiriot 1977) including as its most abundant members Centropages brachiatus, Paracalanus parvus, Ctenocalanus vanus, Oithona, Calanoides carinatus, Rhincalanus nasutus, Sagitta sp, and Nannocalanus minor, in one sub-group. These species were commonest in the upper chlorophyll-rich layers in cool (11° - 15°C) or in cold (7,5° - 11°C) water. The second sub-group (A2) consists of three larger forms, Euphausia lucens, Parathemisto gaudichaudi and Metridia lucens, which generally occurred deeper in the water column and were more abundant at night. The second group, group B, have been termed thermocline-lovers as they were most abundant at or near the thermocline, especially when a well-developed temperature gradient was present as at station 143. Typical species were Rhincalnaus nauplii, Pseudotiaptomus nudus, P. crassirostris, juvenile bivalves and Calocalanus tenuis. The third group, C, consisted of Podon, cirripede nauplii and Centropages chierchiae, which were commonest in the warmer waters at Station 143.

Group D consisted of four species which were only found in low numbers at Station 146, and were of limited significance. The fourth group, E, were all more abundant in warm water and dominated the plankton at Station 146 and in warm water at Station 143, while isolated specimens were present at stations where some mixing had occurred, such as Station 334 and Station 643. They are all species characteristic or common on the Agulhas Bank (De Decker 1973) indicating that the warm water beyond the frontal zone comprised largely Agulhas Bank water. The other species were in general only present as isolated specimens which did not closely relate to any particular water type.

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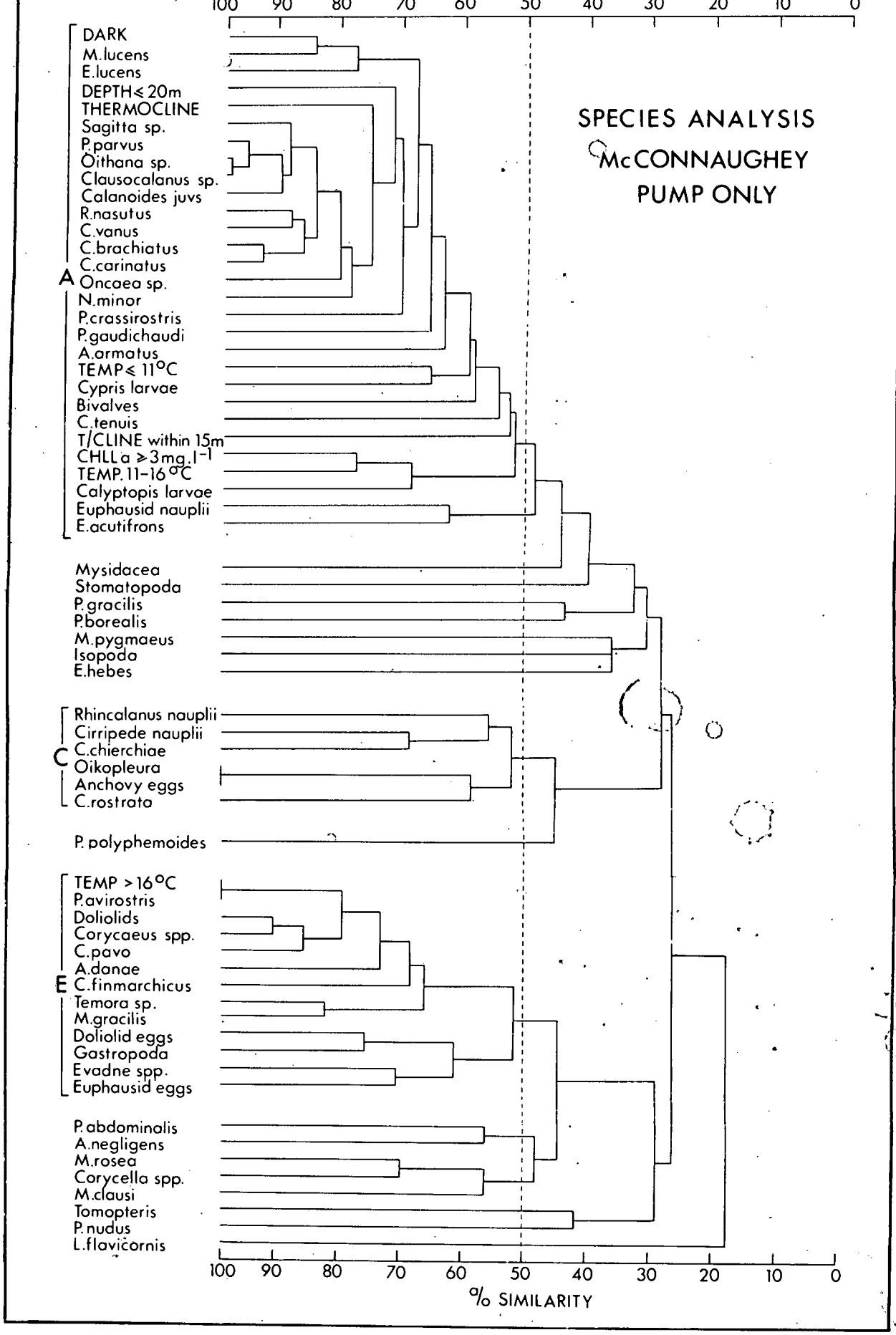

Fig. 15. Dendrogram of species similarities calculated with the McConnaughey Index, based on pump samples only. The index is calculated using the presence or absence of species.

The McConnaughey coefficient, slightly modified to provide similarity levels between species as a percentage, was less satisfactory at differentiating the groups (Fig. 15), The very tight grouping of cool-water forms (*P. parvus*, *Oithona*, *Clausocalanus*, *Calanoides*, *Centropages brachiatus* and *Ctenocalanus*) was retained, as was the warm water group (>16°C) of *Penilia*, Doliodids, *Calanus finmarchicus*, *Acartia danae* and *Calocalanus pavo*. An intermediate group between the two represented animals present in the frontal zone at Station 143. Several species appeared incorrectly linked as they were present in low numbers in many samples but were abundant at very different locations. The linking of *Evadne* (dominant at Station 143 0 and 10 m) and euphausid eggs (dominant of 623 0 m) and 633 0 m) is one example, as is *Pseudodiaptomus nudus*, which was present everywhere but reached highest numbers close to strong thermoclines, and is linked with *Calocalanus tenuis*, Cirripede nauplii and bivalves by the Bray-Curtis coefficient, but isolated using the McConnaughey index.

The use of a coefficient based on presence/absence data is useful in that environmental factors may be added, yet for use with plankton data it must be treated with caution.

3.6 The vertical distribution of species

At each pump station, except perhaps at Station 146 and Station 141, a wide variety of habitats were accessible to any organism capable of migration vertically through 50 metres. The factors most likely to effect the vertical distribution of zooplankton are time of day and predator-prey interactions (Longhurst 1976), thermal stratification (Angel 1968, 1969) and phytoplankton abundance (Anderson, Frost and Petersen 1972).

In this section, species interactions have been ignored and species distribution are related only to environmental features such as chlorophyll maxima, thermoclines, and time of sampling.

The vertical distribution of representative species of each group are described in the text and the less important species are listed in the appendix for future reference, with a short description for each species or stage.

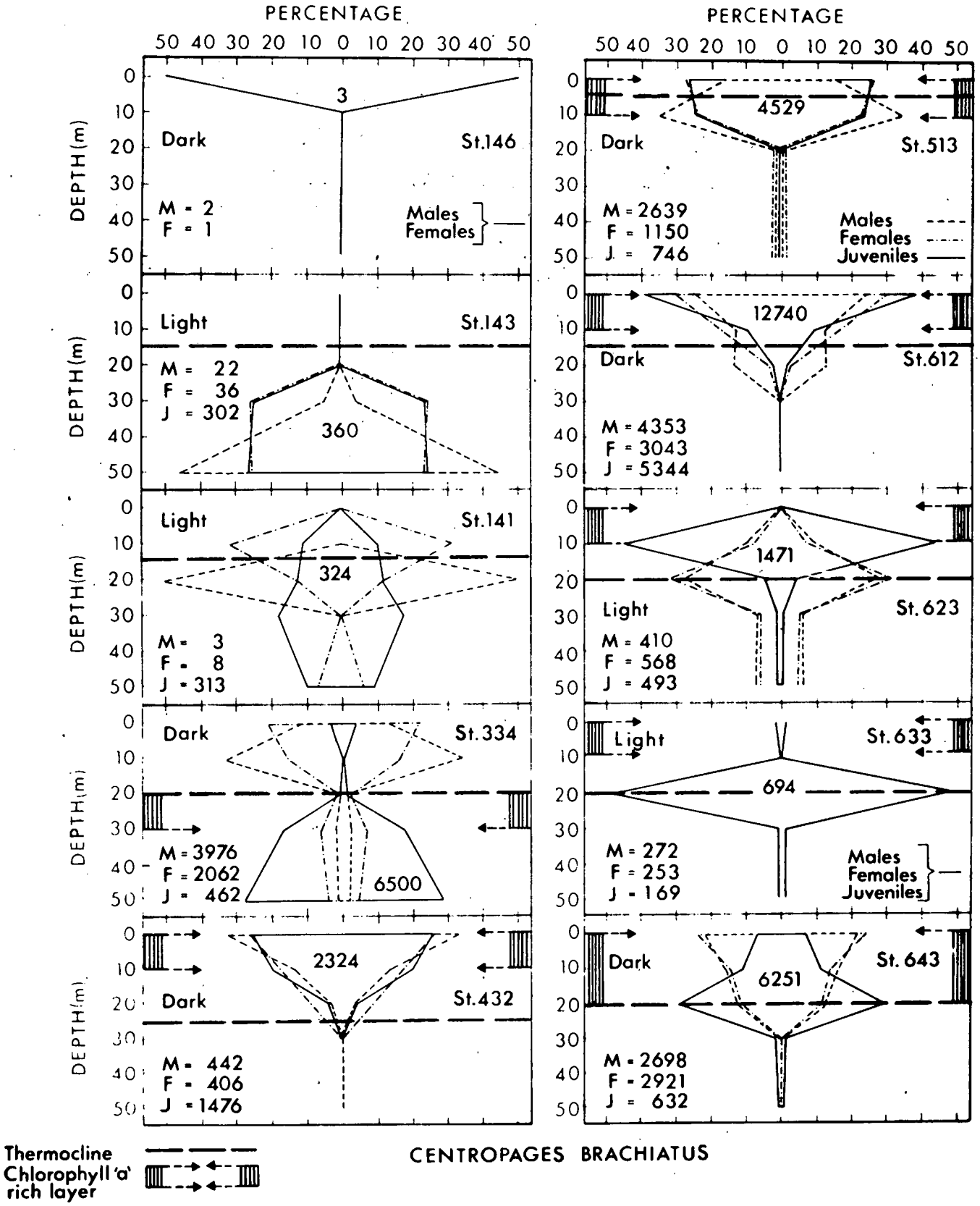

Fig. 16. Vertical distribution of *Centropages brachiatus*, showing the depth of the thermocline (– –), the chlorophyll 'a'-rich layer (◀▮▶) and light or dark. Numbers within the outline refer to the total number of animals observed in the five half-samples at a station. The percentage spread indicates the proportion of the station total observed at a particular depth. Males, females and juveniles are shown separately.

TABLE 5: Station, depth, sounding, displaced volume and dry weight of WP-2 net samples collected at pump stations

Station	Depth (m)	Sounding (m)	Disp. volume $m\ell\ m^{-2}$	Dry Wt ($mg\ m^{-2}$)
146	220 - 50	248	13,6	1,4
146	52 - 0	248	18,0	1,4
143	123 - 0	161	18,8	1,7
143	50 - 0	161	5,2	0,4
141	48 - 0	73	3,9	0,5
334	137 - 33	160	15,6	2,2
334	44 - 0	160	8,0	1,0
432	105 - 50	109	4,4	0,2
432	47 - 0	109	13,0	1,1
513	50 - 0	69	12,3	1,3
612	50 - 0	58	13,0	0,7
623	80 - 50	88	1,5	0,1
623	50 - 0	88	5,2	0,4
633	120 - 50	124	3,6	0,3
633	50 - 0	124	8,4	0,7
643	140 - 50	146	7,3	0,7
643	50 - 0	146	18,4	2,8

TABLE 6: Proportion of common species below the upper limit of the closing haul, from WP-2 net hauls at the pump stations. Total = One half no. of animals in whole water column

Species	Station	Total	% below	Species	Station	Total	% below
C. brachiatus	143	312	0	P. parvus	143	854	5,0
	146	0	-		146	738	
	334	5 786	53,5		334	1 926	63,7
	432	1 698	8,5		432	1 980	10,9
	623	5 040	12,1		623	1 138	1,2
	633	2 174	0,8		633	936	0,0
	643	5 708	0,4		643	3 954	0,9
C. vanus	143	292	100,0	Cal. carinatus	143	22	16,7
	146	248	0,8		146	4	0,0
	334	2 004	61,2		334	3 298	67,3
	432	520	11,2		432	910	13,8
	623	182	50,5		623	272	27,2
	633	694	2,0		633	1 264	11,1
	643	1 846	16,9		643	414	16,4
Oithona sp	143	3 358	23,5	M. lucens	143	1 080	76,4
	146	1 670	85,3		146	204	100,0
	334	2 132	72,6		334	330	73,3
	432	1 308	10,1		432	112	58,9
	623	852	4,9		623	20	100,0
	633	1 894	4,1		633	98	91,8
	643	1 946	9,2		643	378	35,5
R. nasutus	143	584	92,5	A. armatus	143	1 832	74,9
	146	264	100,0		146	2	100,0
	334	482	86,7		334	52	69,2
	432	64	12,5		432	194	48,5
	623	120	28,3		623	50	72,0
	633	182	19,8		633	76	100,0
	643	376	14,9		643	64	65,6

TABLE 6 (cont.)

Species	Station	Total	% below	Species	Station	Total	% below
Nannocalanus minor	143	1 136	89,1	Parathemisto gaudichaudi	143	2	100
	146	2	0,0		146	0	-
	334	52	34,6		334	358	44,8
	432	30	6,7		432	34	11,8
	623	86	4,7		623	4	0,0
	633	62	0,0		633	22	54,5
	643	116	0,0		643	112	39,3
Bivalves	143	1 872	48,9	Calocalanus tenuis	143	312	0,0
	146	0			146	248	0,8
	334	252	84,1		334	134	40,3
	432	84	0,0		432	2	0,0
	623	2	0,0		623	44	0,0
	633	126	11,1		633	112	0,0
	632	176	13,6		643	12	100,0
Euphausia lucens eggs	143	0	-	E. lucens nauplii	143	0	-
	146	0	-		146	205	100
	334	1 214	61,4		334	316	50,6
	432	1 136	3,9		432	666	48,9
	623	2 856	0,8		623	1 042	9,4
	633		0,3		633	596	43,0
	643	132	100,0		643	623	26,8
E. lucens furcilia	143	2	100	Clausocalanus sp	143	5 198	68,4
	146	80	100		146	3 360	48,6
	334	34	35,3		334	1 308	40,7
	432	28	0		432	300	44,0
	623	0	0		623	1 072	7,8
	633	2	0		633	1 044	13,2
	643	154	32,5		643	1 436	62,7

The proportion of a species at a particular depth is expressed as a percentage of the total number of that species in the upper 50 metres and is drawn as a percentage spread, i.e. (30% ..... 0 ..... 30%) = 60%. As microscopic counts were made on half samples, numbers of organisms at each depth were standardised to number per 2,25 m (i.e. Approximately the number actually observed) while the number shown on each illustration represents the sum over five depths (= number per station), where sufficient numbers of organisms were present, species are divided into males, females and juveniles and are shown independently (e.g. Total number of males at a station = 100%).

As an indication of the proportion (%) of a species below the depth range (0 - 50) sampled by the pump, use was made of WP-2 net hauls taken at the pump stations in two separate layers, 50 - 0 m and bottom - 50 m (Table 5). Table 6 shows the proportion below for selected species, giving the total number of animals present in the water column and the percentage in the lower haul.

It will be noted that on occasions some overlap in the hauls occurred, due to greater wire stray during the deeper haul (e.g. St 334, 137 - 33m and 44 - 0 m), which would tend to decrease the proportion living below the upper limit of the closing haul. At Station 143, where the "lower" haul net ascended to the surface without closing, the numbers in the 50 - 0 haul were subtracted from the number in the 123 - 0 metre haul in order to estimate the proportion living below 50 metres.

Group A species

Centropages brachiatus, (Fig. 16) numerically the dominant species in the mixed water, adults displayed a distinct downward shift during daylight (Stations 143, 623 and 633) compared with the night-time distribution (Stations 334, 432, 513, 612, 643). Adults, with roughly equal numbers of males and females, showed similar distributions except of Station 334 and Station 523, where males peaked 10 metres below the female peak. Juveniles

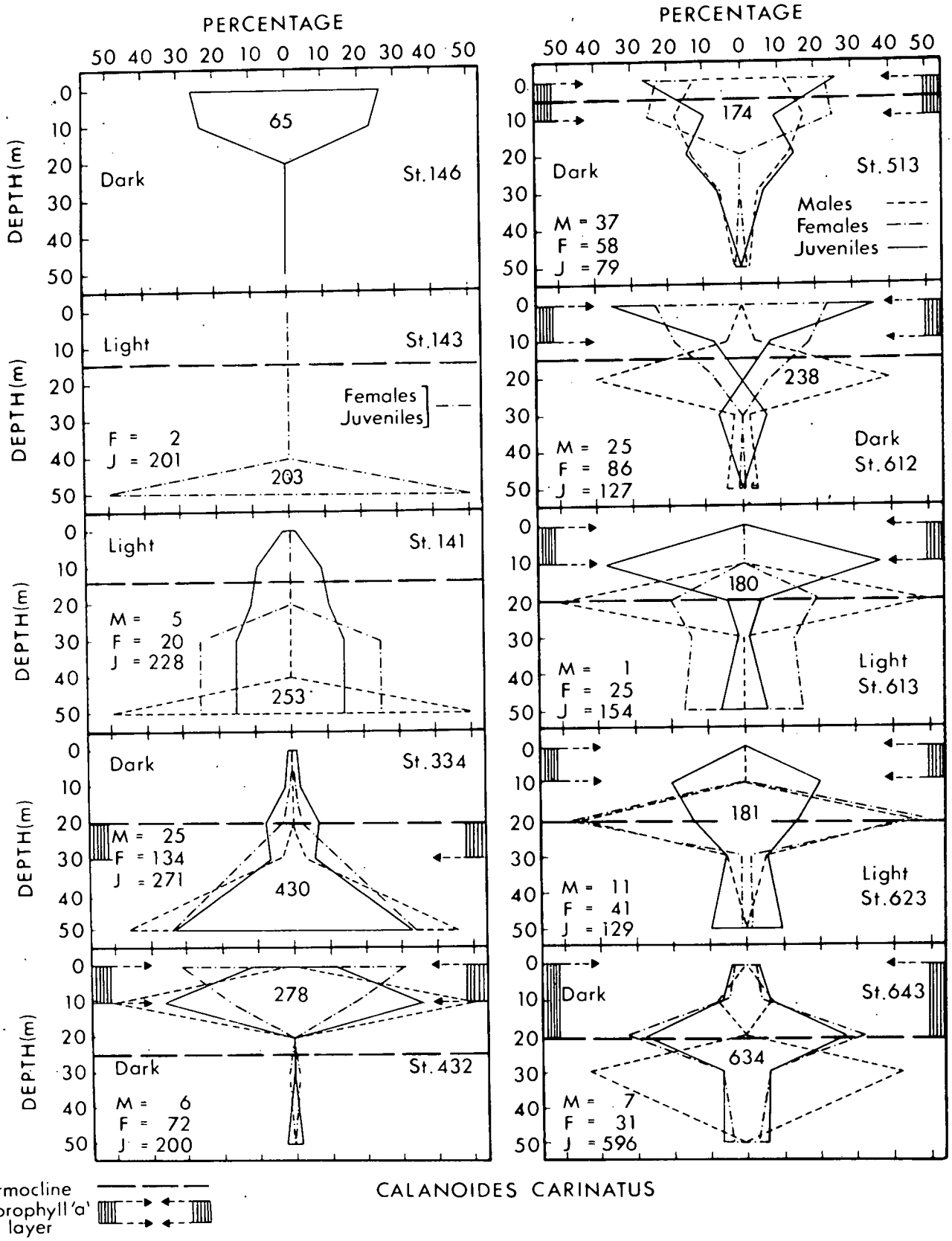

Fig. 17. Vertical distribution of *Calanoides carinatus*. Symbols as for Fig. 16.

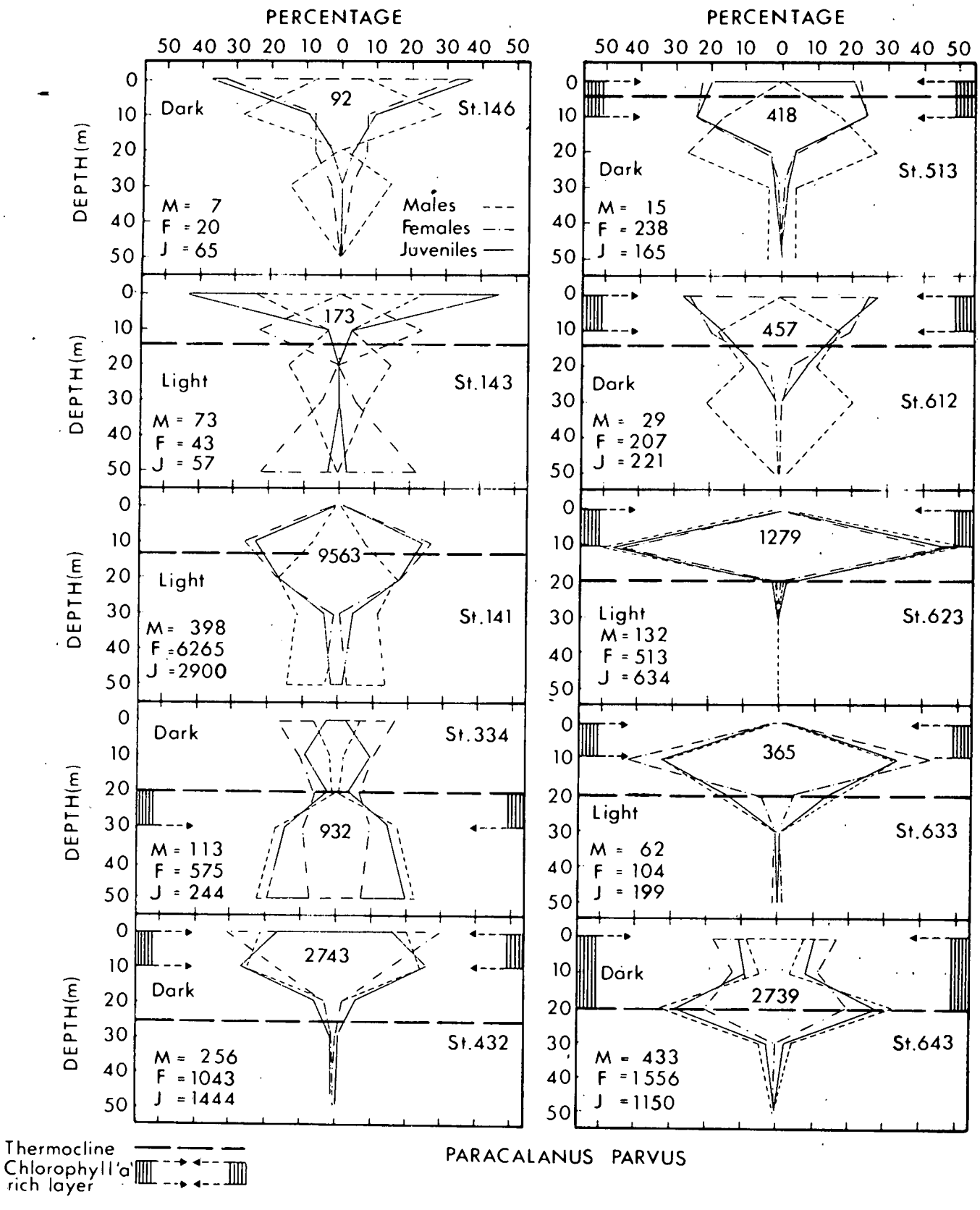

Fig. 18. Vertical distribution of *Paracalanus parvus*. Symbols as for Fig. 16.

showed a somewhat different distribution, which appeared to be related to temperature changes and they were found most commonly in the region of the thermocline, except at Station 334 where peak juveniles occurred at 50 metres, suggesting that surface water was sinking at this station. No juveniles occurred in warm water at Station 146 or Station 143.

Calanoides carinatus (Fig. 17) displayed a similar pattern to C. brachiatus, reaching maximum concentrations in mixed water near the surface at night but 10 - 20 metres deeper during daylight. At Station 334, maximum numbers occurred at 50 metres and WP-2 net hauls showed that 67% of the population occurred below 33 metres (Table 6). Adults were absent from warm waters at Station 146 and Station 143. Juveniles tended to occur closer to the surface than adults during daylight.

Paracalanus parvus (Fig. 18) was the second commonest copepod encountered in the pump samples and it showed little evidence of changes in vertical distribution with time of day. Both temperature and chlorophyll"a" appear important in determining its position in the water column, being generally at or above the thermocline in chlorophyll-rich water (Stations 432, 513, 612, 623, 633 and 643), although it is tolerant of a wide range of temperature, being present in water of 18°C at Station 146, in water of 7,5°C at station 141 and in both warm and cold water at Station 143. It reached maximum numbers at Station 141 in newly upwelled water, peaking at 10 metres, while at Station 334 maximum numbers occurred below both the chlorophyll"a" peak and the thermocline. The presence of high chlorophyll"a" seems of prime importance in determining its vertical distribution.

Ctenocalanus vanus (Fig. 19) occurred at all ten stations, were more common in cool water (Stations 141, 334, 432, 513, 612, 623, 633, 643) than in warm water (Stations 146, 143) and showed evidence of an upward shift at night (Stations 146, 432,

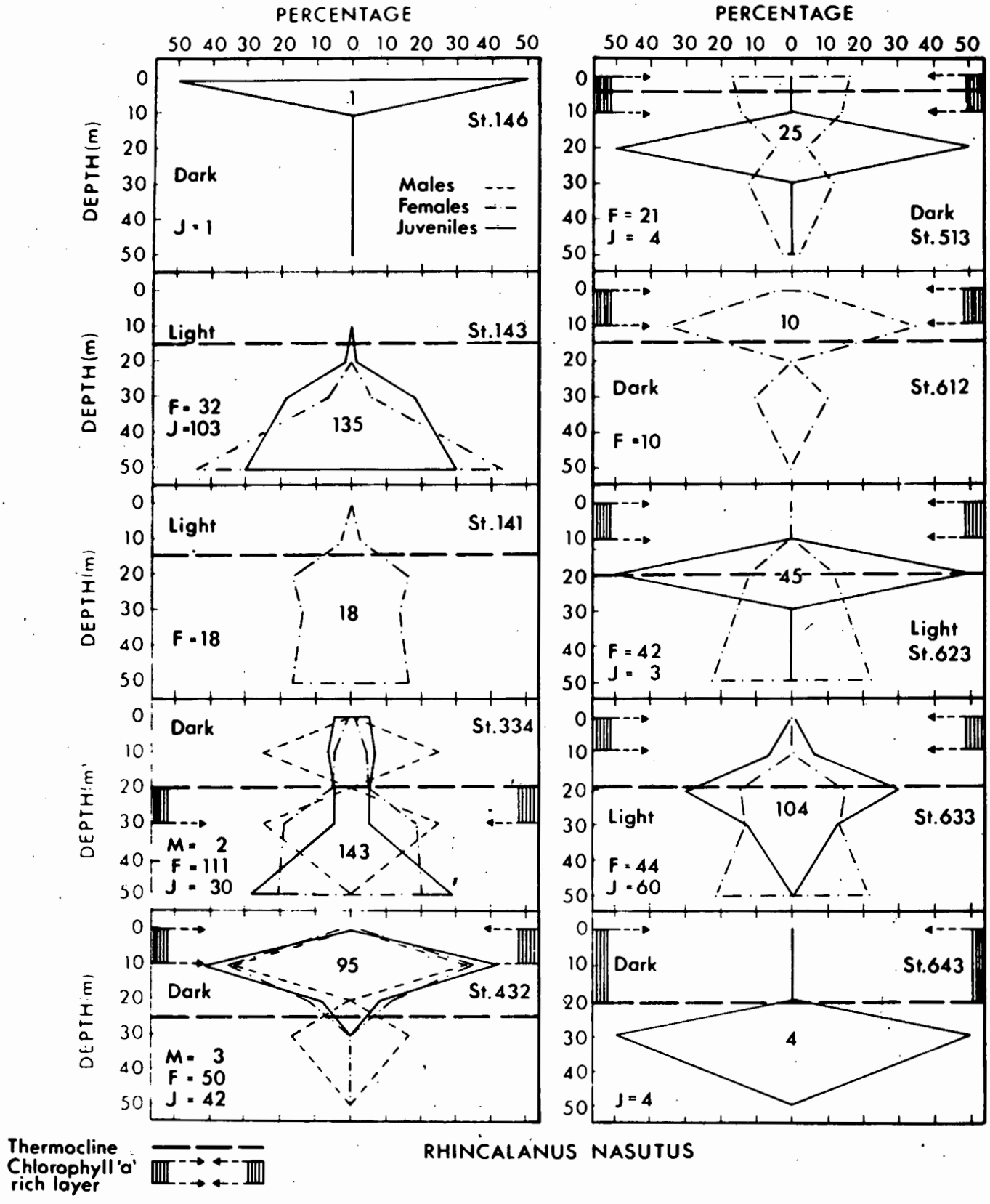

Fig. 20. Vertical distribution of *Rhincalanus nasutus*. Symbols as for Fig. 16.

513, 612, 643) compared with the daytime distribution, when they descended to the thermocline region (Stations 143, 623, 633). At station 334 Ctenocalanus abundance increased from the surface to 50 metres, although sampled in the dark, indicating that the sinking processes affected their distribution more than the temperature or chlorophyll"a" concentrations. De Decker (1964) described them as initial colonisers of upwelled waters, able to tolerate very cold water, but they were also abundant in more mature upwelled water (e.g. Station 643).

Rhincalanus nasutus (Fig. 20), although never attaining high concentrations, is nevertheless an important component of the zooplankton biomass by virtue of its large size. It showed a marked preference for cooler water, being virtually absent at Station 146 and in the warm 0 - 20 metre layer at Station 143. In water cooler than 16°C females shifted upwards during the night (Stations 432, 513, 612) compared to the daytime distribution (Stations 623, 633) when peak female abundance occurred at 50 metres. Station 334 was again an exception where females peaked at 50 metres. Juveniles, on the other hand, were associated with the thermocline or the chlorophyll"a" maximum irrespective of the time of sampling (Stations 432, 513, 623, 633), except at Station 143 when warm water maximum concentrations occurred at 50 metres. Male R. nasutus were only observed at Station 334 and Station 432, in low numbers.

Oithona sp. (Fig. 21) was common at all stations but reached maximum numbers in cooler waters, generally above the thermocline in the chlorophyll"a"-rich layer (Stations 432, 513, 612, 623, 633, 643). Where there was no temperature or chlorophyll gradient (e.g. at Station 146), it was evenly distributed through the water column while in cold water at Station 141 maximum numbers occurred at 10 and 20 metres. At Station 334 maximum concentrations were associated with the chlorophyll maximum at 30 metres, 10 metres below the thermocline.

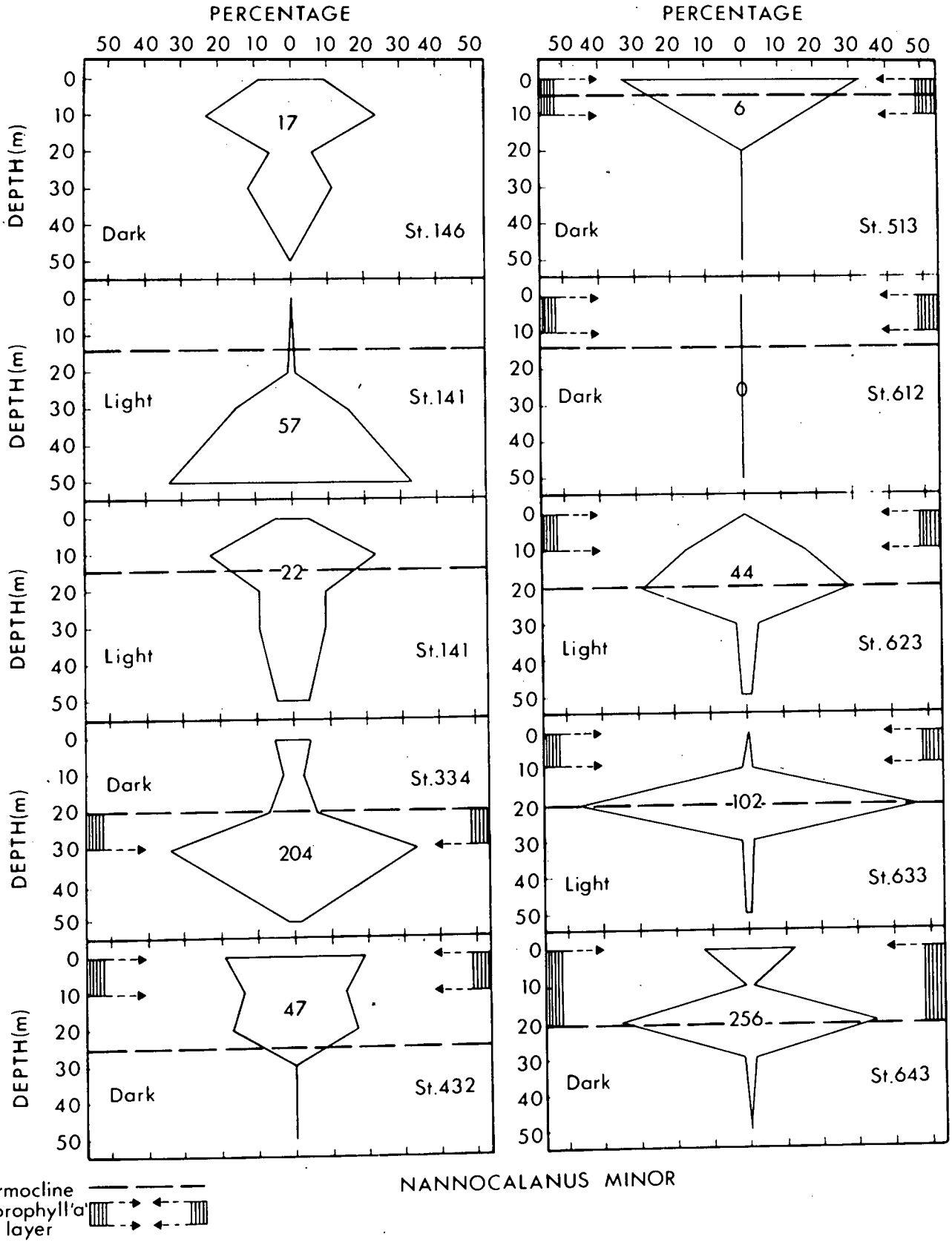

Fig. 22. Vertical distribution of *Nannoclanus minor*. Symbols as for Fig. 19

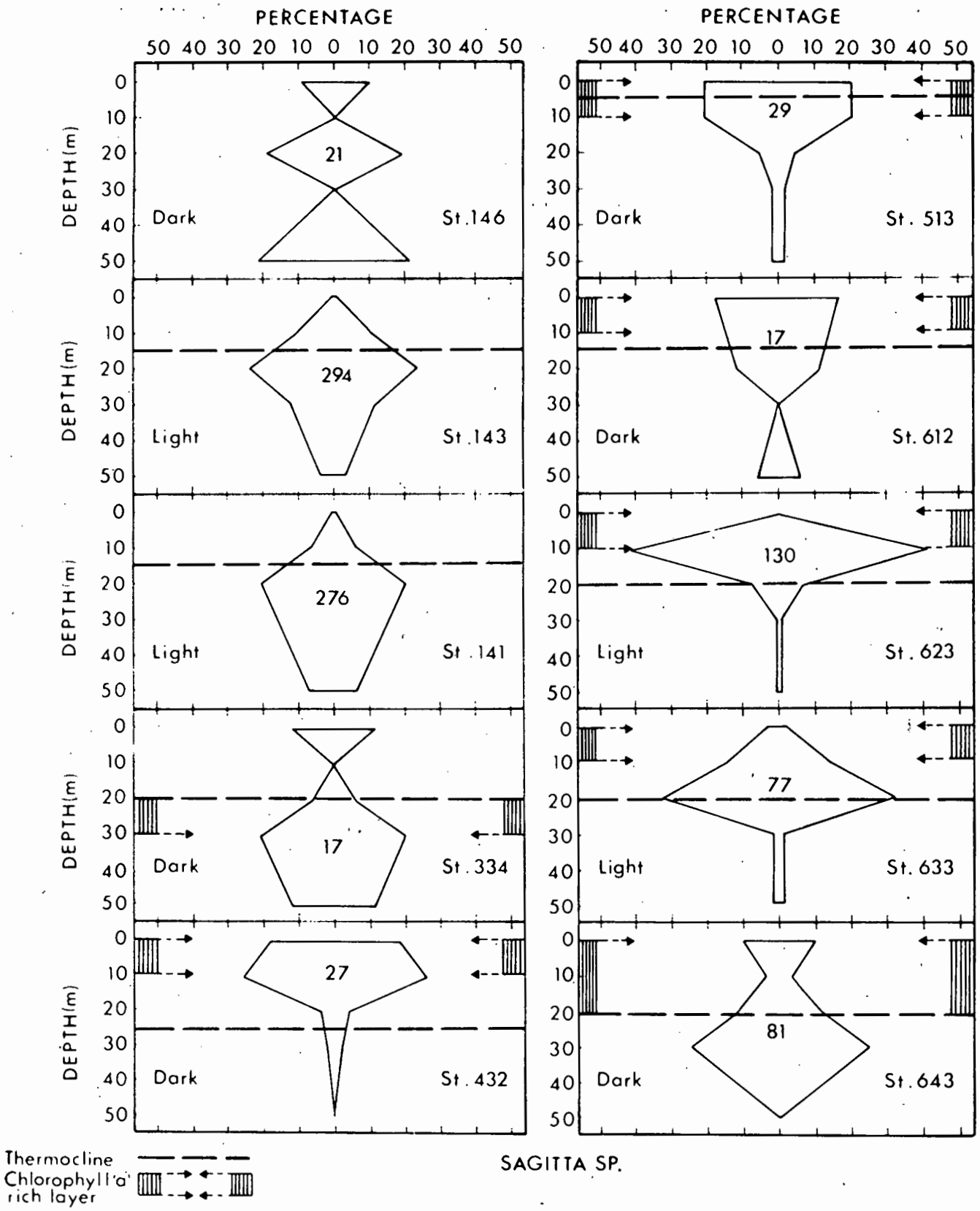

Fig. 23. Vertical distribution of *Sagitta* sp. Symbols as for Fig. 19.

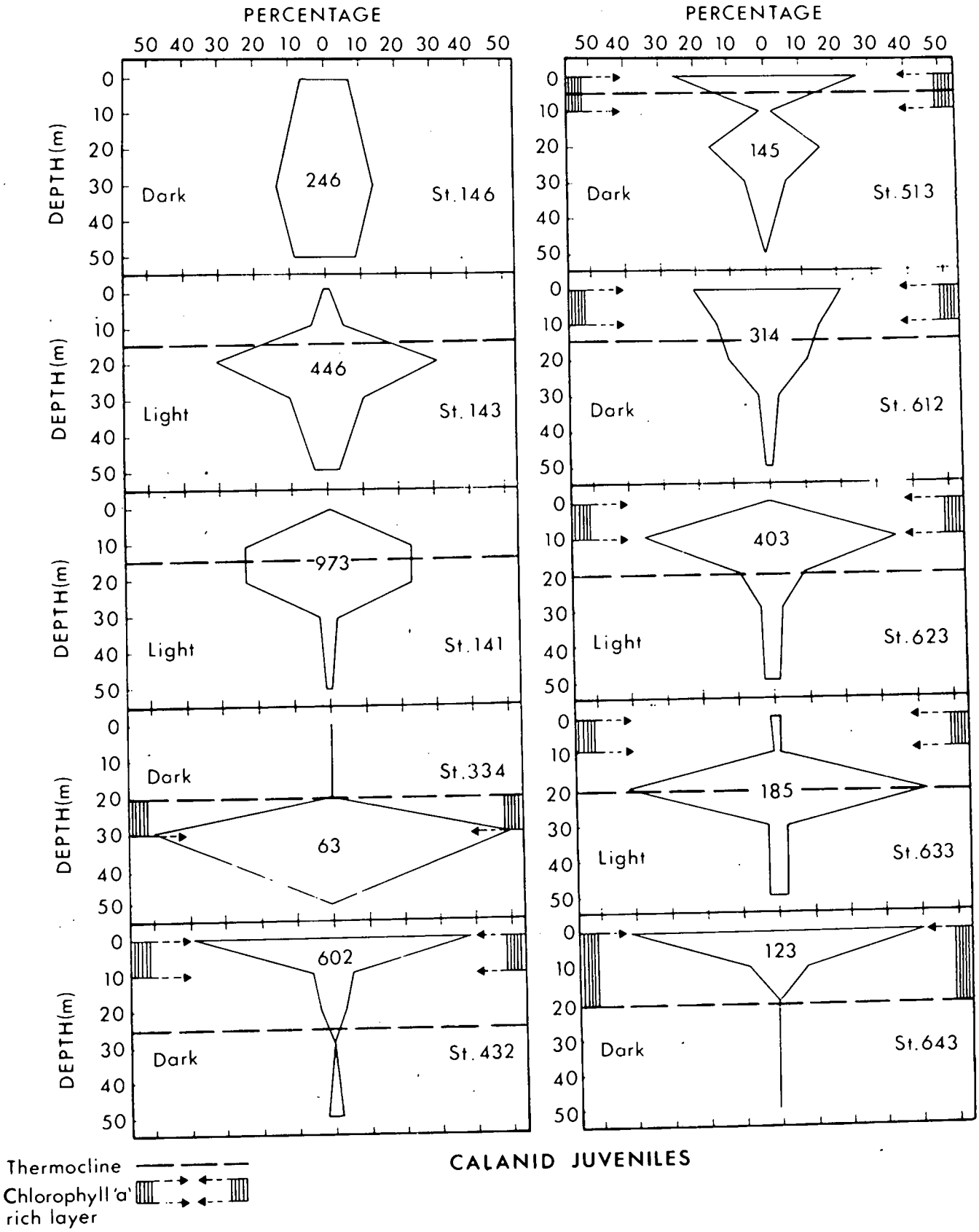

Fig. 24. Vertical distribution of *Calanid* juveniles. Symbols as for Fig. 19.

Nannocalanus minor (Fig. 22) occurred at nine of the ten pump stations, and it was most abundant at Stations 334, 633 and 643, representing more mature upwelled water. It appears to be quite temperature-tolerant, being present through the whole 0 - 50 metre layer at Station 146 as well as at Station 141. De Decker (1973) reports this species is very abundant on the Agulhas Bank and it is also present in offshore waters in South West Africa (Unteruberbacher 1964). It probably represents a species of the mixed zone, where upwelled and offshore water intermingle.

Sagitta spp. (Fig. 23). Analysis of WP-2 samples revealed that chaetognatha were dominated by S. frederici, a neritic cold-water species, and S. minima, characteristic of offshore waters (Heydorn 1959). Specimens collected with the pump, however, could not be conclusively identified due to damage to the fins so the species were counted together. However the bulk of the speciemens at all stations except Station 146 and 143 are likely to be S. frederici. There was a suggestion of an upward movement at night (Stations 432, 513, 612) compared to daytime distribution (Stations 623, 633) although at Station 334 and Station 643, also sampled in the dark, maximum numbers occurred at 30 metres, below the thermocline.. Maximum concentrations occurred at Station 141 in very cold water.

Calanid juveniles (Fig. 24) showed maximum concentrations in the chlorophyll-rich layer except at Station 633, where they peaked on the thermocline. At night maximum concentrations were at the surface (Stations 432, 513, 612, 643) while during daytime subsurface peaks occurred (Stations 141, 623, 633). In warm water, they were uniformly distributed through the upper 50 metres.

Oncaea sp occurred at all stations but were never abundant, and showed little change in concentration with depth, although they were seldom abundant at the surface.

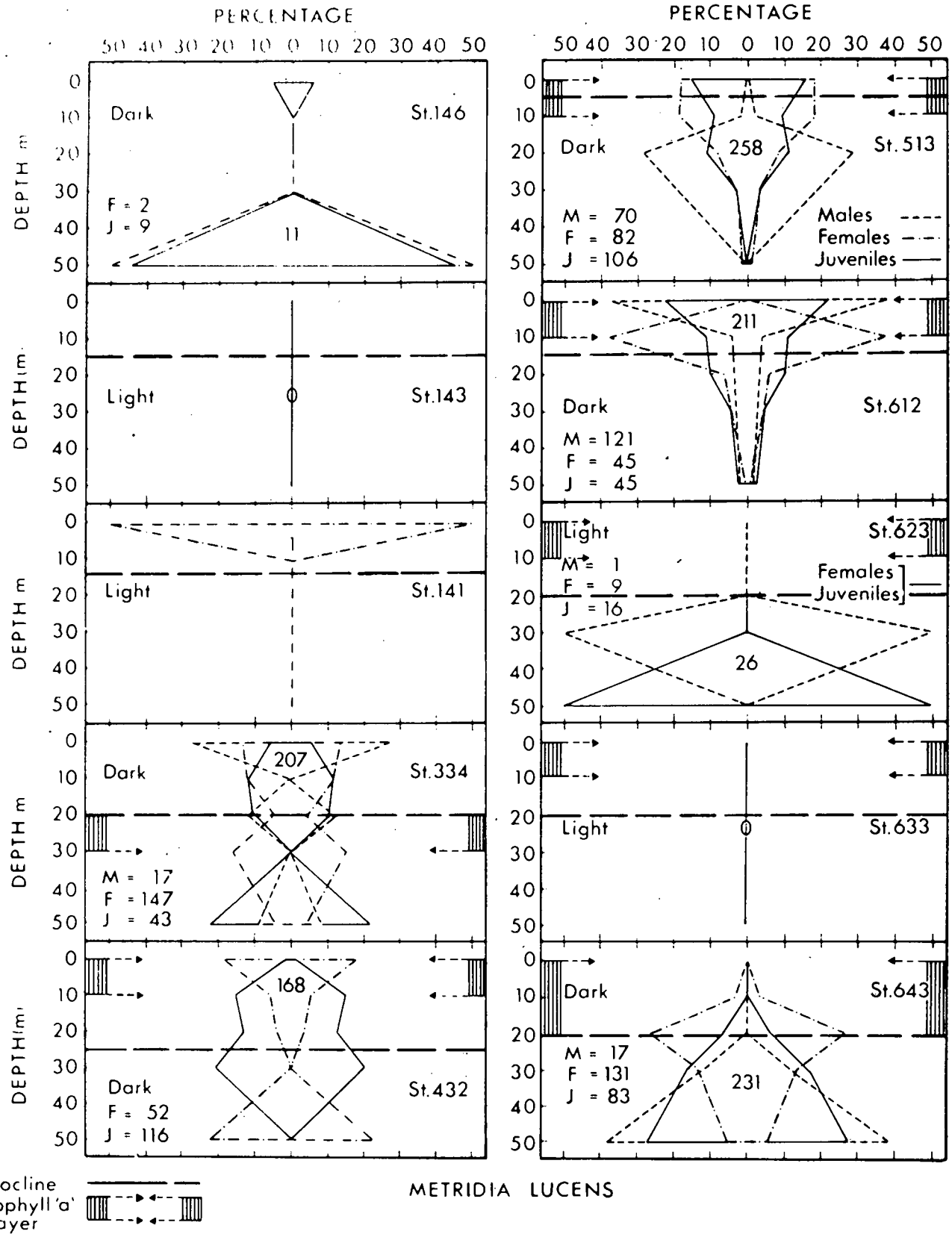

Fig. 25. Vertical distribution of *Metridia lucens*. Symbols as for Fig. 16.

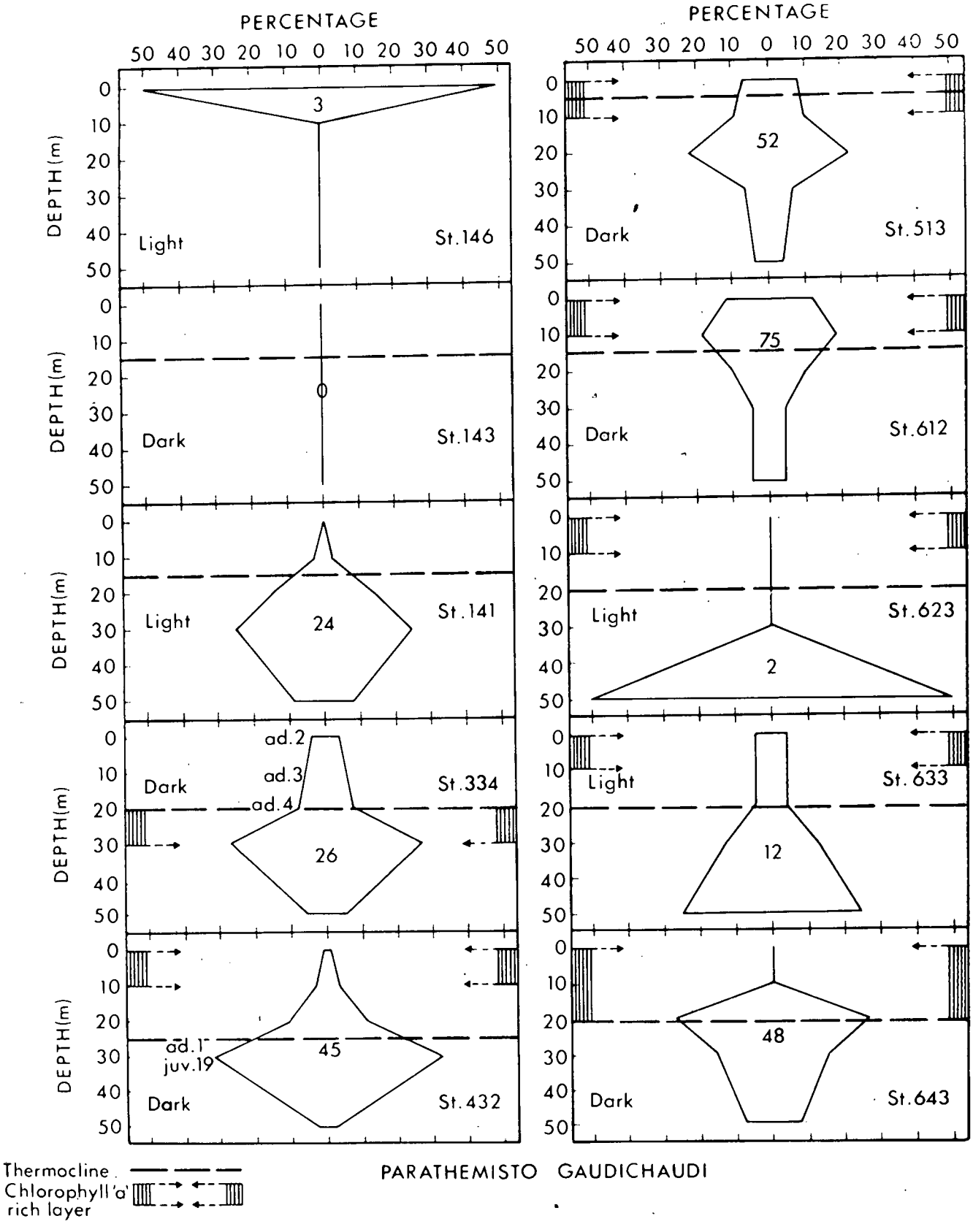

Fig. 26. Vertical distribution of *Parathemisto gaudichaudi*. Symbols as for Fig. 19.

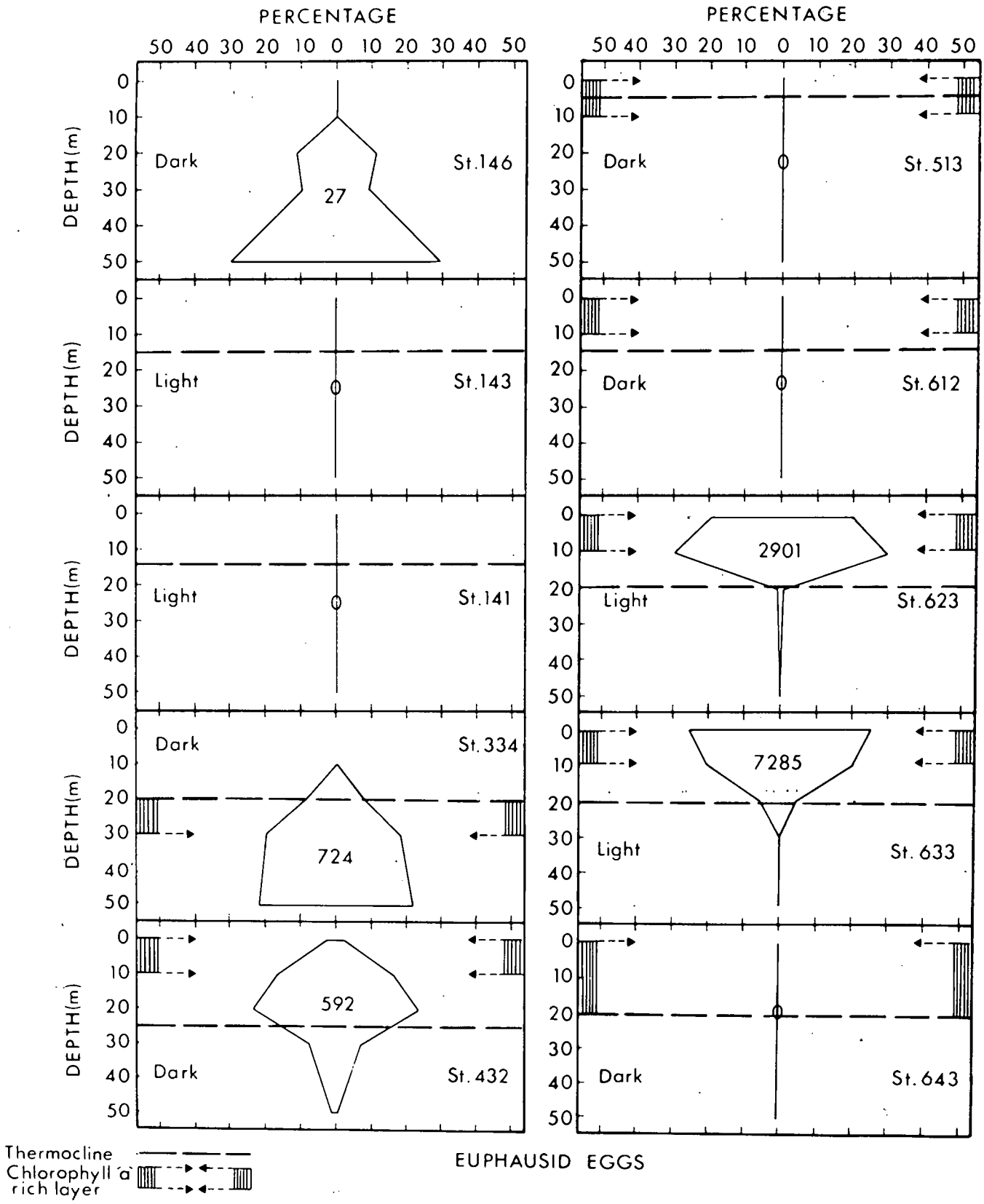

Fig. 27. Vertical distribution of Euphausid eggs. Symbols as for Fig. 19.

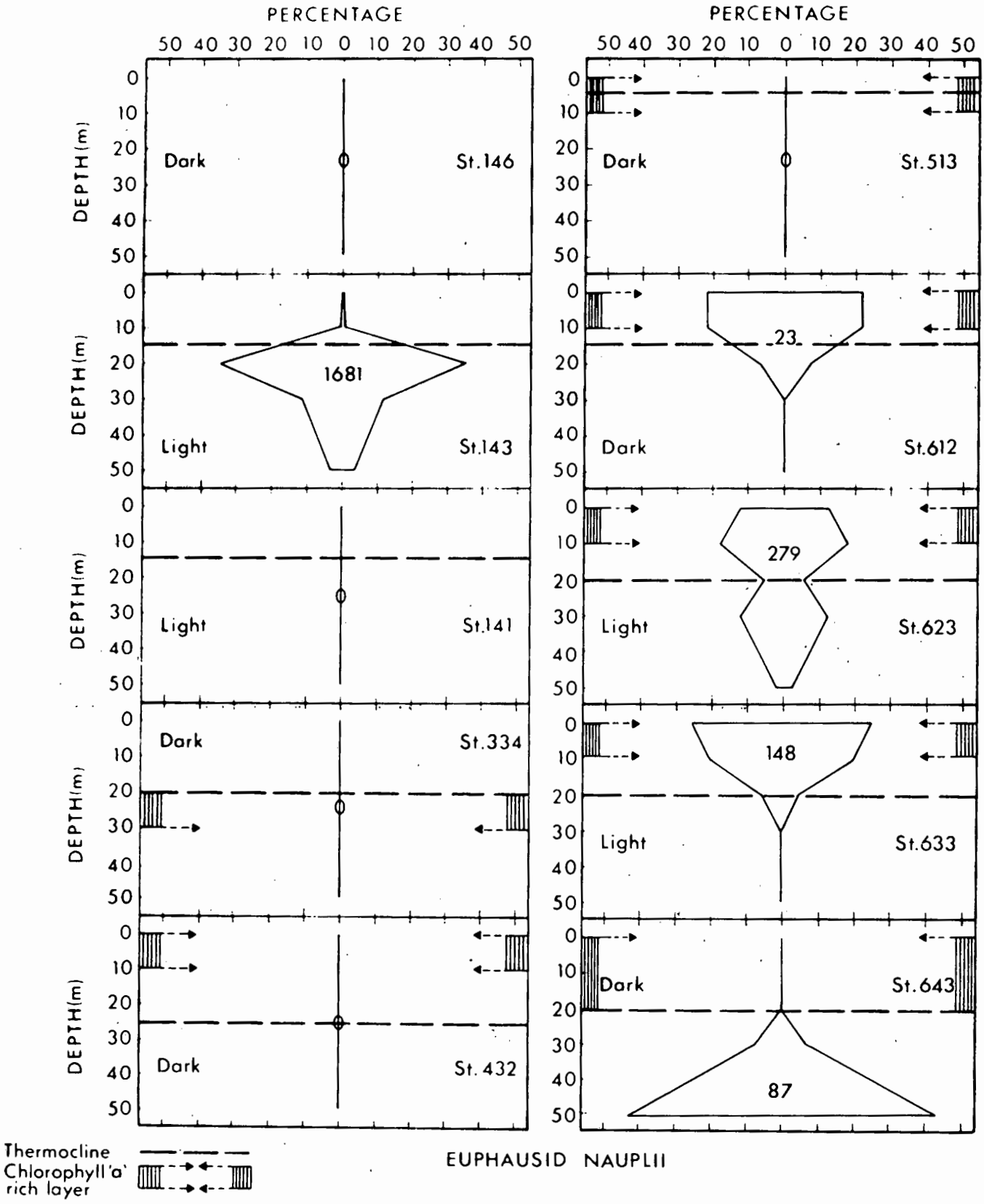

Fig. 28. Vertical distribution of Euphausid nauplii. Symbols as for Fig. 19.

Metridia lucens (Fig. 25) was very scarce during daylight in the upper 50 metres (Stations 146, 143, 623, 633), although WP-2 net hauls from close to the bottom to 50 metres revealed its presence in the water column at these stations, confirming its strong tendency to migrate vertically (Enright 1977). Certain night-time distributions (Stations 334, 432) indicate that only part of the population migrates right to the surface or into the chlorophyll-maximum layer, which may be related to sex or stage of development. At stations 513 and 612 a much higher proportion of males relative to females were present compared with other stations.

Parathemisto gaudichaudi (Fig. 26) was more abundant by night than by day and maximum numbers always occurred at subsurface depths, sometimes immediately below the chlorophyll-rich layer or the thermocline (Stations 334, 432, 513) or penetrating into these regions (Stations 334, 612, 643). The lack of animals during daylight may be due to avoidance of the sampler in the upper layers.

Euphausid eggs (Fig. 27) were very abundant at Stations 623 and 633 in the upper 20 metres above the thermocline, with fewer numbers at Station 432 above the thermocline and at Station 334 below the thermocline, with a small number at Station 146 peaking at 50 metres.

Nauplii (Fig. 28) were very abundant at the thermocline at Station 143 with lesser numbers at Stations 612, 623 and 633 in the chlorophyll-rich layer, and below the thermocline and chlorophyll-rich layer at Station 643. Calyptopis larvae (Fig. 29) were present at all stations except Station 141 and Station 513, and were closely associated with the chlorophyll-rich layer. A few specimens were present at Station 146 and Station 143.

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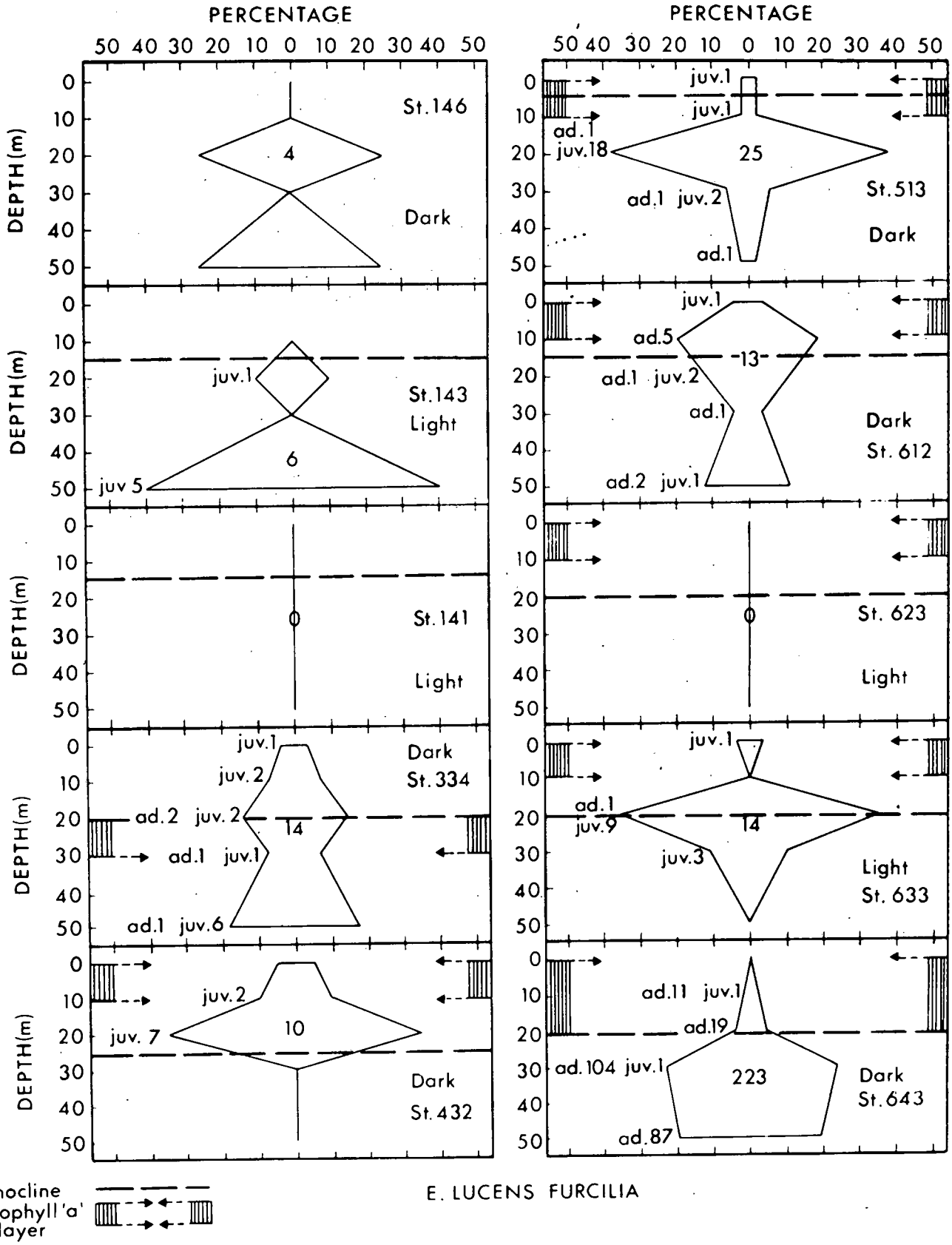

Fig. 30. Vertical distribution of *Euphausia lucens* furcilia. Symbols as for Fig. 19.

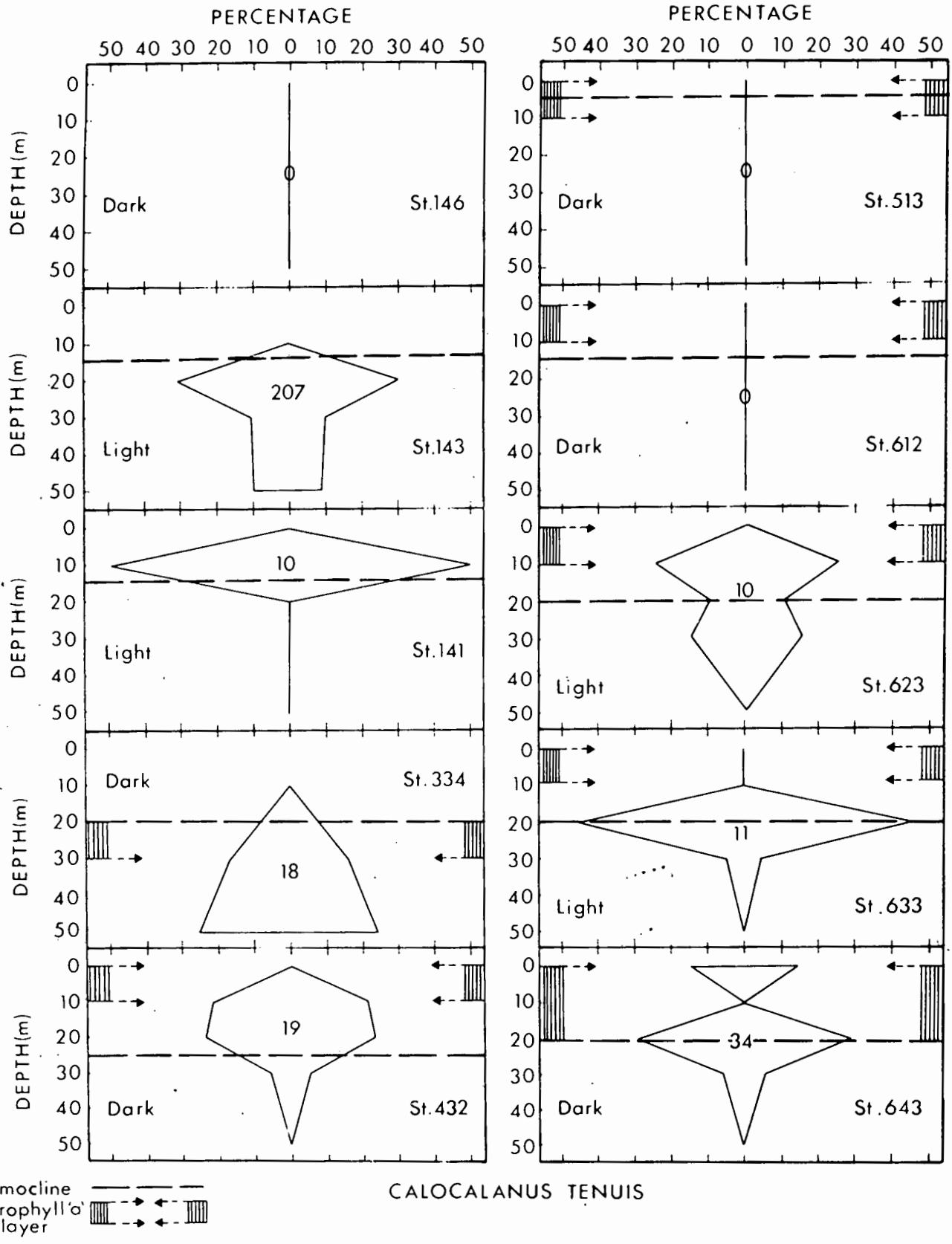

Fig. 32. Vertical distribution of *Calocalanus tenuis*. Symbols as for Fig. 19

upwelling. These organisms appears to prefer the frontal region between cool and warm water.

Bivalve juveniles were present at all stations except at Station 146, while maximum concentrations (216/m^3) occurred at Station 143, at the thermocline. They showed an identical distribution to Calocalanus tenuis at other stations, being strongly associated with the thermocline except at Station 334 where only a few specimens were present at 50 m.

Pseudodiaptomus nudus was most abundant at the thermocline at Station 143 and elsewhere was always within 15 metres of the thermocline, except at 334 where 80% occurred at 50 metres, all below the thermocline.

Zooplankton in the warm water group (D) were common only at Station 146, where they were usually evenly distributed in the upper 50 metres, and at Station 143 in the upper 10 metres. Isolated specimens, always in low numbers, appeared in cooler waters and can be considered as stray migrants, although their presence indicates some degree of mixing with oceanic water. The species are listed with their occurrences below:

Doliolids: Station 146, 0 - 50 m, 870
Doliolid eggs: Station 146, 0 - 30 m, 535.
Calanus finmarchicus (stages IV - VI): St. 146, 0 - 50 m, 103; St. 143, 20 - 30 m, 165; St. 141 20 - 30 m 8; St. 334, 30 m, 2; St. 513, 10 m 1.
Penilia: Station 146, 0 - 50 m, 300; Station 143, 0 - 10 m, 18.
Evadne spinifera: St. 146, 0 - 50 m, 1012; St. 143, 0 - 20 m, 590; St. 432, 0 - 50 m, 38; St. 623, 00 m, 1; St. 643, 0 m,1.
Gastropoda: St. 146, 0 - 50 m, 134; St. 432, 0 - 30 m, ; St. 623, 10 m, 30 - 50 m., 19; St. 633, 10 m, 2.

Both Calanus finmarchicus and Penilia avirostris are typical members of the Agulhas Bank community (De Decker 1973) and indicate that much of the oceanic water bordering the upwelling centre during this time was derived from the mixed waters of the Agulhas Bank rather than the Agulhas Current itself. Carter (1977) lists characteristic species of the core of the Agulhas Current off Natal as Meycenocera clausi, Clausocalanus paululus and Acartia danae, and the fact that at least two of these three species were present in the area indicates a possible influence of the Agulhas Current, although their numbers were very much fewer than the numbers of Agulhas Bank species.

4. DISCUSSION

The numerical analysis of the data distinguishes the important groups of zooplankton in this area. The first and largest group comprise some 14 species typical of the cool upwelled waters of the Benguela Current. According to Lazarus (1974) the majority of these species are herbivorous in this area. Apart from Metridia lucens, there is little extensive vertical migration and the majority of the animals remain in the upper layers where chlorophyll "a" concentrations are highest. The second group consists of "frontal zone" species which border on the cool upwelled water. Strong vertical temperature gradients exert a considerable influence on the distribution of the animals in this zone, clearly separating them into warm and cold components with a few species, such as Calocalanus tenuis associating closely with the thermocline. The third group are of less importance in terms of biomass, and inhabit the nutrient-poor warm waters beyond the frontal zone. During this survey these comprised several species characteristic of the Agulhas Bank region and these animals are transported northwards (Bang 1976, Bang and Andrews 1974), steadily diminishing in numbers but nevertheless still indicating that some elements of the Agulhas Current persist in the Benguela Current even up to latitudes of 27° - 30°S (De Decker, pers comm), long after physical-chemical characteristics of Agulhas water have been blurred into insignificance through mixing.

Care mist be exercised in any extrapolation of the groups delineated here to other area around the South African coastline, or to different times of the year. The groupings are based on relatively few locations, spread out in time in an area of great vertical instability and which has a unique location with regard to wind regime, bottom topography and influences from different water masses. Of importance is the lack of continuity of cool surface water southwards, especially during summer months when upwelling intensity is greatest. This precludes a passive drift of organisms at the surface from temperate latitudes to replenish those species which are driven offshore and equatorwards during upwelling events. This is in direct contrast to the other major upwelling areas off North-West Africa, Peru/Chile and Oregon/California where surface water continuity to higher latitudes exists.

Upwelling does occur in False Bay and in the Walker Bay - Cape Agulhas region, but the movement of cool upwelled water westwards around Cape Point is a rare occurrence (Sea Fisheries Branch, unpublished data). Warm water of 15° - 22°C is transported westwards, (Duncan and Nell, 1964; Bang and Andrews, 1974; Bang 1976), but this water is generally unsuitable for the zooplankton of the upwelled water community, whose normal habitat is either neritic or subsurface cool water (De Decker 1964; De Decker & Mombeck 1965; De Decker 1973; Thiriot 1977). Recruitment of zooplankton to the surface waters of the Cape Peninsula area is therefore most likely to occur from the north or from below.

Upwelling water in this area is of South Atlantic Central water origin (Shannon 1966), itself made up of a mixture of South Atlantic surface water and Antarctic Intermediate water (Clowes 1950). Its constant physical-chemical characteristics (Andrews et al. in press) suggest that little biological activity has occurred in it for a considerable period of time;

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therefore it cannot support sufficient zooplankton to explain the rapid increase in plankton abundance following its uplift into the euphotic zone close to the coast. Consequently most of the colonisation of recently-upwelled water is likely to occur from short term current reversals and eddies in the vicinity of the Cape Peninsula.

The colonisation of freshly upwelled water by zooplankton has not been studied in detail despite the large effort directed towards the study of biological events after upwelling (Walsh et al. 1970; Dugdale 1972; Walsh, 1977). Therefore the mechanisms whereby zooplankton species maintain themselves in upwelling areas is relatively unknown, although research is progressing off Oregon (Peterson and Miller, 1975, 1977, Peterson 1976), off North West Africa (Angel 1969; Angel and Fasham 1973; Hargreaves 1975; Baker 1975; Thiriot 1977).

The stimulus for copepoda to initiate egg production is generally abundant food (Marshall and Orr, 1955), and implies that in order for herbivorous zooplankton to increase their population numbers they must consistently encounter high phytoplankton concentrations. Yet except on rare occasions, such as sustained strong upwelling, the zooplankton standing stock was consistently high close to the coast (Andrews et al, in press). They also showed that strong south easterly winds rapidly displaced the phytoplankton offshore and maximum phytoplankton concentrations occurred just inshore of the oceanic front while zooplankton maxima offshore showed an erratic distribution which was not closely linked to the distribution of phytoplankton, although the offshore maxima were more common during the summer months.

The presence of the majority of organisms in the mixed layer even during daylight enables them to move rapidly offshore with the newly upwelled water as it ages and allows them to feed extensively on the developing phytoplankton

population. These include the species Centropages brachiatus, Paracalanus parvus, Ctenocalanus vanus, Calanoides, Rhincalanus nasutus, Oithona and others.

Very little quantitative data on the lateral and cross circulation patterns are available for our area (Duncan and Nell 1964; Shannon 1966; Bang and Andrews 1974; Bang 1976), although field experiments using radar and radiotracked drogues are underway at present (Boyd, Nelson, Sea Fisheries Branch, pers. comm), and preliminary results indicate that there is considerable variability in the currents inshore of the oceanic front with strong evidence of counter currents heading shorewards and southwards, even during active upwelling conditions, but particularly when the wind stress decreases. Duncan and Nell (1964), using surface drift indicators, describe a counter current inshore between Table Bay and Saldanha Bay and De Decker (S A Museum, pers. comm) has noted dense zooplankton concentrations in the Table Bay area during summer months. It is thus likely that a considerable proportion of animals are returned to the Cape Peninsula via this counter current. More definite evidence of its existence and of its variability with time are needed. The nature of the December 1969 cruise did not lend itself to a study of recruitment of zooplankton back to the Peninsula, but rather to the movement of animals away from the near-coastal zone, as the sampling grid extended only 35 kilometres offshore, and the onshore winds encountered during the cruise were of short duration, Nevertheless, the vertical distribution of zooplankton at station 334 is instructive, as it suggests that any sinking motion, proposed by Andrews et al. (in press) to be common at the frontal zone where mixed water meets lighter oceanic water, transports considerable numbers of near- surface dwelling zooplankters downwards and these may move shorewards in the upwelling water. The species which increased in abundance with depth included C. brachiatus, P. parvus, C. vanus and C. carinatus, all typical members of the upwelling community.

Assuming these animals have generation times of a similar period to laboratory reared animals of a similar size at similar temperatures i.e. 20 - 90 days at 12° - 15°C (Mullin and Brooks 1967, 1970; Corkett 1970; Paffenhoffer & Harris 1976; McLaren 1978), recycling time of about 50 days is indicated. Lazarus (1967) notes that Jasus lalandii phyllosoma larvae spend 11 months at sea, spreading out northwards, westwards and southwards from the centre of dispersion at the commercial fishing grounds between Cape Point and Cape Columbine as the larvae age, yet as they reach the end of their planktonic existence they are distributed more or less westward of the commercial grounds, indicating little active transport elsewhere.

Considerable eddy formation occurs in the fast flowing Agulhas Current with recycling times varying from several weeks to two - three years (Bang and Pearce in Heydorn et al. 1978) allowing animals of varying longevity to use very different mechanisms of recruitment. The Benguela is considerably more sluggish (Shannon 1966; Bang 1976) and increased cross circulation can be expected, facilitating recycling of planktonic animals.

The low-oxygen counter current (Hart and Currie 1960; De Decker 1970; Andrews et al. in press) is another possible mechanism for returning animals to the Cape Peninsula area during the summer months, as closing net hauls (WP-2), taken in March and June 1974, show and average of 40% (range 15% - 91%) of the zooplankton stock at any one station exists in water with with dissolved oxygen content of less than 3 ml/l. A preliminary inspection of these samples shows the presence of typical members of the upwelling community (Centropages brachiatus, Calanoides carinatus, Oithona sp., Ctenocalanus vanus, Paracalanus parvus, Rhinalanus nasutus and others), so they are presumably able to tolerate low oxygen concentration to some extent. However the replenishment of zooplankton to the near-coastal zone occurs too rapidly to be due entirely to this current, and replenishment

also occurs in October to December; before the counter current reaches the west coast of the Peninsula (Andrews *et al.* in press). It is likely that alternative means of returning to the south east are employed. As more information on the current regimes off the Cape Peninsula and to the north is forthcoming, greater insight into the movement of zooplankton will be possible.

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30m	4,546	916	15,20	7,90	29	96
50m	"	714	11,00	5,85	26	76
141,0 m	"	98	2,20	1,67	15	98
10m	"	4 036	23,10	14,34	19	99
20m	"	2 414	22,00	17,69	16	98
30m	"	846	15,40	13,07	25	93
50m	"	414	8,58	4,49	27	94
334,0 m	"	1 180	23,76	13,99	20	99
10m	"	1 622	22,00	13,37	19	100
20m	"	288	12,76	7,79	28	78
30m	"	874	19,80	17,55	30	83
50m	6,365	589	28,28	23,11	26	81
432,0 m	4 546	1 556	20,90	18,57	23	96
10m	"	1 352	17,60	16,15	25	89
20m	"	492	14,96	12,41	32	65
30m	"	72	3,30	2,02	17	85
513,0 m	"	1 218	24,20	20,37	18	97
10m	"	1 174	29,70	34,10	21	95
20m	"	256	17,60	21,56	21	85
30m	"	86	7,70	3,08	20	88
50m	"	18	7,70	3,87	16	80
612,0 m	"	4 158	46,19	46,94	16	98
10m	"	1 790	38,28	35,42	18	96
20m	"	558	24,20	23,84	19	95
30m	5 455	58	9,17	7,30	20	96
50m	5 001	24	8,00	7,52	23	77
623,0 m	4 546	608	27,50	3,17	10	12
10m	"	2 490	20,90	12,63	21	63
20m	"	532	8,80	7,70	19	90
30m	"	168	5,50	4,62	23	78
50m	"	156	5,50	4,62	24	93
633,0 m	"	1 682	19,80	8,05	21	3
10m	"	1 640	16,50	10,47	21	18
20m	"	1 226	24,20	14,12	26	73
30m	"	124	5,50	2,20	24	85
50m	"	150	-	2,51	24	74
643,0 m	"	2 172	26,18	23,89	17	97
10m	"	1 528	57,19	41,53	16	98
20m	"	2 278	48,61	60,80	21	98
30m	"	464	9,90	84,51	23	86
50m	"	362	36,08	45,09	24	80

Volume filtered (m^3), concentration of organisms number (m^{-3}) dis
weights (mg m^{-3}), number of species per sample (n), % copepod by
copepod juveniles (number m^{-3}) temperature (°C) and chlorophyll'a
each pump sample.

APPENDIX 2

The vertical distribution of rarer species at the pump stations

The following species are of less numerical importance and the absence of sufficient numbers reduces the significance of their distributions. As more data on vertical distributions become available, records for comparison purposes will be useful. Two alphabetical lists follow, one for less common species where a tentative conclusion or comparison is possible and a second list for reference purposes only.

Acartia danae. This species occurred at four stations (146, 143, 334 and 643) and was not found deeper than 20 metres, both by day and by night. Its preference appears to be warm water but because of its near surface distribution it can be swept into cool water during downwelling conditions. Carter (1977) considers it characteristic of the "core region" of the Agulhas Current off Natal.

Centropages chierchiae is a common warm water inhabitat from Natal to South West African waters (Unteruberbacher 1964, De Decker 1964, Carter 1977) and it was most abundant at Station 146 and Station 143, with occasional specimens at Station 334, Station 432 and Station 633. As such it closely resembles Agulhas Bank species, but its maximum at the thermocline at Station 143 suggests that it is more a "frontal zone" species similar to cirripede nauplii.

Cirripede nauplii were most abundant at Stations 143 (914), where most were found at 20 - 30 metres just below the thermocline. Lesser numbers occurred at 30 - 50 metres at Station 334 (15), at 20 - 50 metres at Station 432 (63) and at 0 - 10 metres at 633 (5). There was no consistent day-night difference inddistribution.

Corycella sp. Occurred at six of the pump stations, but never in high numbers (3 - 19 per station). No consistent depth distribu= tion was observed, with peaks in numbers at 50 metres at stations 143, 334, 513 633 and 643, at 0 m at Station 643 and at 10 m at

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Station 141. Cypris larvae occurred at all 10 stations, in numbers ranging from two (Station 146) to 34 (Station 141). No clear pattern of distribution could be discerned, except that they wer slightly more abundant in cooler waters.

Microsetella rosea was also present at all 10 stations, in numbers ranging from one to 184 per station. Although most abundant at Station 146, where it was evenly distributed in the upper 50 metres, the number of animals peaked at 20 metres at Station 143, at 10 metres at Station 141 both at the thermocline, below the thermocline at Station 334, 513, 612, 623, 633 and 643 and only at Station 432 did maximum occur above the thermocline. It is clearly tolerant of a wide range of conditions.

Microcalanus pygmeaus occurred in small numbers at five of the 10 stations and only at Station 141 and Station 513 did numbers rise above 20 per station. It remained persistently in very cold waters of 10,75° or less, except for a single occurrence in 18°C water at Station 146.

Podon polyphemoides was found at five stations, all on lines three and four. It was common only at Station 143 (699) where it was limited to the warm water above the thermocline. It was also present at Station 334 and Station 643 in far lesser numbers (6 - 20 per station).

Its preferenceappears to be warm water in the vicinity of the frontal zone.

The following list of species are provided for reference purposes only. The station, depth range and number of specimens observed are recorded.

Acartia negligens: St. 146, 0 m, 50 m, 4.
Anchovy eggs: St. 143 0 m, 30 m, 6.
Calanus tenuicornis: St. 643, 50 m, 1.

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Calocalanus pavo: St. 146, 20 m, 11.
Calocalanus plumulosus: St. 146, 20 - 30 m, 2.
Candacia sp. (juveniles): St. 146, 20 - 30 m, 2; St. 143, 30 - 50 m, 8; St. 141, 50 m, 2; St. 334, 10 - 30 m, 3; St. 432, 10 m 1; St. 633, 20 m 1.
Decapod larvae: (two types) St. 141, 30 - 50 m, 13; St. 143, 50 m, 14; St. 146, 20 - 30 m, 4; St. 432, 20 - 30 m, 3; St. 633, 10 m, 2.
Eucalanus sp (juveniles): St. 146, 20 m, 1; St. 143, 10 m, 50 m, 15; St. 141, 30 m 1; St. 334, 10 - 20 m, 2; St. 432, 20 m, 3; St. 623, 20 - 30 m, 2; St. 643, 10 m, 1.
Eucalanus acus: St. 513, 50 m, 1; St. 612, 30 m, 1.
Eucalanus attentuatus: St. 432, 30 m, 2.
Eucalanus crassus: St. 633, 20,m, 50 m, 3.
Euchaeta sp (juveniles): St. 141, 50 m, 1; St. 334, 50 m, 1; St. 432, 20 m, 3.
Euchaeta hebes: St. 513, 20 m, 50 m, 2; St. 612, 50 m, 1; St. 623 50 m, 1., appears to be epibenthic.
Euterpina acutifrons: St. 146. 0 - 50 m, 24; St. 432, 20 m, 3; St. 513, 50 m, 1; St. 633, 50 m, 1.
Heterorhabdus sp (juveniles): St 612, 50 m, 2; St. 623, 50m, 1.
isopoda: St. 141, 30 - 50 m 16; St. 334, 20 m, 1; St. 513, 30 - 50 m, 2; St. 612, 20 - 50 m, 6.
Lucicutia flavicornis: St. 432, 30 - 50 m, 9; St. 633, 30 - 50 m, 2.
Macrosetella gracilis: St. 146, 30 m, 3.
Meycenocera clausi: St. 146, 10 m, 50 m, 3; St. 141, 0 m 1; St. 334, 20 m, 1.
Mysidacea: St. 432, 20 m, 3; St. 513, 0 - 30 m, 18; St. 612, 0 - 30 m, 81; St. 543, 50 m, 1.
Oikopleura: St. 143, 30 m, 408.
Ostracoda: St. 612, 50 m, 2; St. 623, 50 m, 1.
Paracartia africana: St. 633, 0 m, 2.

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Phyllosoma: St. 141, 20 - 30 m, 2; St. 612, 0 m 3.
Pleuromamma abdominalis: St. 146, 0 - 50 m, 18; St. 334, 20 - 30 , 21; St. 432, 20 - 50 m, 8; St. 612, 20 m, 1; St. 623, 50 m, 2; St. 543, 20 m, 50 m 4.
Pleuromamma borealis: St. 334, 20 m, 1; St. 643, 30 - 50 m, 5.
Pleuromamma gracilis: St. 146, 30 m, 3; St. 334, 0 - 10 m, 50 m, 22; St. 643, 30 - 50 m, 3.
Pleuromamma sp (juveniles): St. 141, 10 m, 1; St. 513, 20 m, 2; St. 633, 50 m, 1; St. 643, 20 - 30 m, 25.
Sappharina sp: St. 143, 30 m, 2.
Scolecethricella sp (juveniles): St. 146, 0 m, 10 m, 30 m, 3; St. 143, 50 m, 6; St. 432, 20 m, 3; St. 612, 50 m, 1; St. 623, 50 m, 4.
Scolecethrix sp: St. 623, 50 m, 1; St. 633, 30 m, 50 m, 2.
Sergestid larvae: St. 633, 0 m, 1.
Stomatopoda (alima larvae): St. 143, 50 m, 1; St. 334, 20 - 50 m, 2; St. 612, 10 m, 30 m, 2; St. 633, 20 m, 1; St. 643, 50 m, 2.
Temora stylifera: St. 146, 0 m, 30 m, 50 m, 5; St. 643. 0 m, 10.
Temora turbinata: St. 334, 0 m 1.
Tomopteris: St. 146 10 - 20 m, 2; St. 141, 50 m, 1.
Zoea larvae: St. 146, 10 - 20 m, 2; St. 143, 30 - 50 m, 18; St. 141, 50 m, 2; St. 334, 20 - 30 m, 4; St. 432, 0 - 10 m, 12; St. 141, 50 m, 2; St. 334, 20 - 30 m, 4; St. 432, 0 - 10 m, 12; St. 633, 20 m, 1.

THE HORIZONTAL DISTRIBUTION OF ZOOPLANKTON

1. INTRODUCTION

Little information on the horizontal variation of zooplankton biomass and species composition in the Benguela Current has been published, although there are many accounts of the distribution of individual taxonomic groups in relation to hydrological features. (Nepgen 1957, Heydorn 1959, Van Zyl 1960, Kollmer 1963, Siegfried 1963, De Decker 1964, Stander and De Decker 1964, Unterüberbacher 1964, Lazarus 1967, De Decker 1968, Masson 1971, De Decker 1973, and Lazarus 1975).

Unpublished settled volume data from N 70 V hauls (Sea Fisheries Branch) show little change in volume of plankton inshore and offshore around the southwestern Cape coast, but considerable change in species composition occurs with crustaceans and occasionally Ctenophores or medusae dominant in the cool water inshore and tunicates offshore. Kollmer (1963) and Unterüberbacher (1964) noted that zooplankton and phytoplankton settled volumes peaked some distance offshore in the Walvis Bay region, at the head of the upwelling plume that develops immediately south of Walvis Bay, while Visser et al (1974) and Wessels et al (1975) showed that zooplankton and phytoplankton maxima occurred in belts parallel with the coastline. The phytoplankton maxima occurred inshore in cool upwelled water with zooplankton further offshore, although little information on seasonal changes is available. Settled volume data based on N70 net hauls without monitoring flow rates indicate little more than trends, as the species composition of the plankton can considerably alter both the numbers of organisms caught by the net and the settled volume, rendering interpretation difficult.

Andrews et al. (in press) made use of flowmeters, WP-2 nets and dry weight values to assess changes in zooplankton abundance on a seasonal basis in a restricted area off the Cape Peninsula. They showed that high zooplankton concentrations were consistently present close to the coast and high values extended offshore during

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summer. During periods of particularly strong upwelling the near-coastal zone was temporarily depleted of zooplankton. They concluded that advection was the most important factor affecting both the quantity and distribution of zooplankton in the area.

While Andrews et al (in press) emphasised the fluctuations in zooplankton biomass with time, this report describes in more detail changes in both biomass and species composition at the southern boundary of the Benguela Current. In contrast to other major upwelling regions, there is a lack of surface continuity between the upwelled component of the Benguela Current and the more temperate waters to the south, due to the intrusion of warm Agulhas Current and Agulhas Bank water west of Cape Agulhas. (Clowes 1954, Shannon 1966, Bang 1971, 1973, De Decker 1973). This warm water approaches close to the coast in the vicinity of the Cape of Good Hope for much of the year, restricting the movement of cool water forms to the east or west around Cape Point. Thus upwelling sites to the east of Cape Point (Cram 1969; Tromp et al in prep), are effectively isolated from the upwelling on the west side of the Cape Peninsula, except during exceptionally prolonged periods (Longer than 8 - 10 days) of strong south-easterly winds, when cool water extends right around the coast from Cape Agulhas to north of Cape Columbine. These occasions however, rarely occur more than once or twice per year (Andrews et al, in press) and may be considered insignificant in terms of plankton transport. Although many cool water species do extend east of the Cape of Good Hope, they seldom occur in great numbers. (De Decker, 1973).

The first part of this report describes the distribution of zooplankton between Cape Columbine and the Cape Peninsula in 1974, when four lines of 8 - 10 stations were sampled once per quarter (Fig. (1)) from north to south (West Coast monitoring cruises). Zooplankton standing crop is related to hydrological features, phytoplankton distribution and season to provide a broad view of the southern Benguela Current region.

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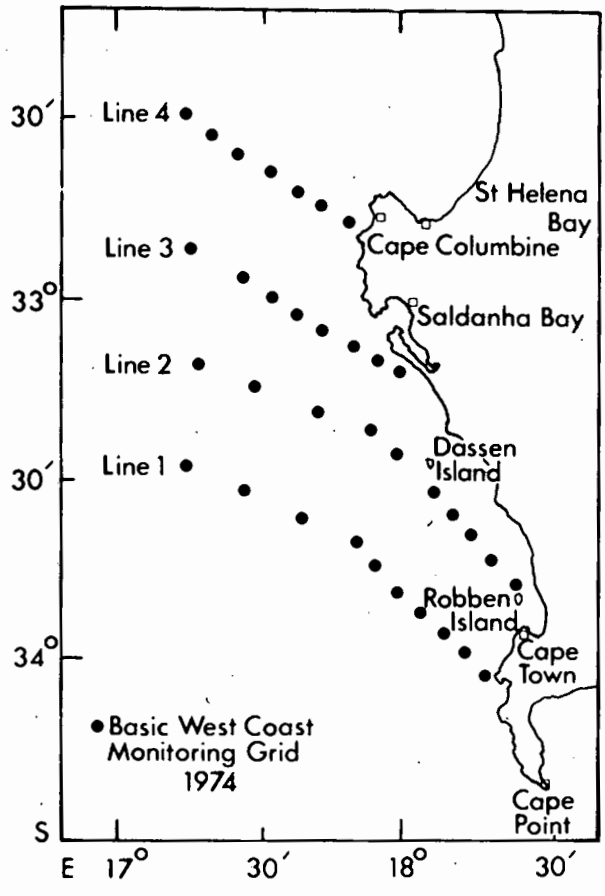

Fig. 1 Basic station grid, 1974. West Coast Monitoring Cruises, sampled March, June, October and December.

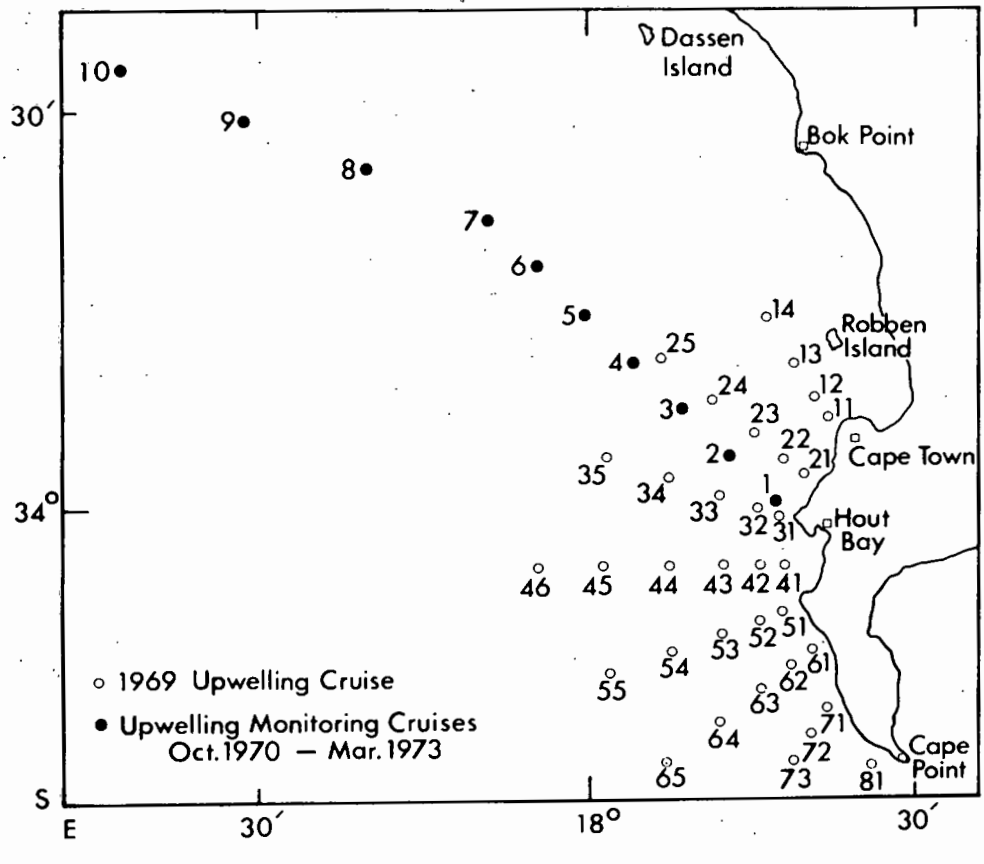

Fig. 2 Station grids of December 1969 upwelling cruise and 1970-73 monthly upwelling monitoring cruises.

The second part reports on data obtained during monthly surveys over two days along the axis of the upwelling plume which developes from the Cape Peninsula, where distance along the plume may be equated with time and seasonal changes could be discerned. (Upwelling Monitoring Cruises) (Fig. 2). While the main features of the changes in zooplankton biomass were reported by Andrews et al (1979), more detail is provided here.

Wind plays an important role in determining the near surface distribution of hydrological and biological parameters and the recent wind history prior to each monthly or quarterly cruise is discussed where relevant.

The third part of this report deals with short term variation in zooplankton standing crop and species composition in a 60 x 40 kilometre area at the base of the plume off the Cape Peninsula western coast. (Fig. 2). Warm surface water of Agulhas Bank and South Atlantic origin abuts sharply against cool upwelled water of South Atlantic central water origin (Shannon 1966) in a complex and very dynamic manner (Bang and Andrews 1974; Bang 1976), with significant changes occurring within twelve hours of a change in wind speed or direction. The sampling period between repeated circuits of the grid of 34 stations (Fig. (2)) varied from 32 to 48 hours, which although not optimal, still provided great insight into factors affecting the distribution of zooplankton in the area on a short time scale and provides explanations for the zooplankton distribution observed during the more extensive surveys conducted at longer time intervals.

From these three very different types of cruises a picture of the annual cycle of zooplankton in this unstable area can be described.

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1. QUARTERLY SURVEY OF WESTERN CAPE COAST

1.1 METHODS

1.1.1 Sampling

During the West Coast Monitoring cruises zooplankton was collected with WP-2 nets (UNESCO 1968) in divided hauls, one through the upper mixed layer, where a large proportion of the phytoplankton was observed, and a second haul from the bottom to the pycnocline. Corrections were made for wire stray, while depth and flow were monitored using calibrated N.I.O. flowmeters (Currie and Foxton 1957).

Samples for salinity, oxygen nutrient chlorophyll'a' and particulate carbon analyses were collected at discrete depths using 5-litre all plastic N.I.O. bottles. Surface temperature and salinity were measured continuously using a Bissett-Berman model 9060 thermo-salinograph while a mechanical bathythermograph and a bucket thermometer was used on station. Analysis of the samples was as described in Andrews *et al* (in press).

1.1.2 Processing

Procedures for zooplankton and phytoplankton standing crop determinations were as follows. The depth of the suspected chlorophyll'a' maximum, was selected for particulate organic carbon analysis, and two replicate one-litre samples were analysed by wet oxidation with dichromate (Strickland and Parsons 1968). In 77% of the cases the depth selected as the chlorophyll'a' maximum was either correct or the chlorophyll'a' concentration at that depth differed by less than 20% from the maximum chlorophyll'a' concentration. The chlorophyll'a' depth profile was integrated by computer using the mean of a cubic polynomial and a straight line fit and the chlorophyll'a' in the upper 50 metres, (where 80-85% of the chlorophyll'a' in the water column was found) was converted into units of carbon using the carbon/chlorophyll'a' ratio obtained at that station. When chlorophyll'a' concentrations were less than 1,0 $\mu g \ell^{-1}$ carbon/chlorophyll'a' ratios were discarded, because of

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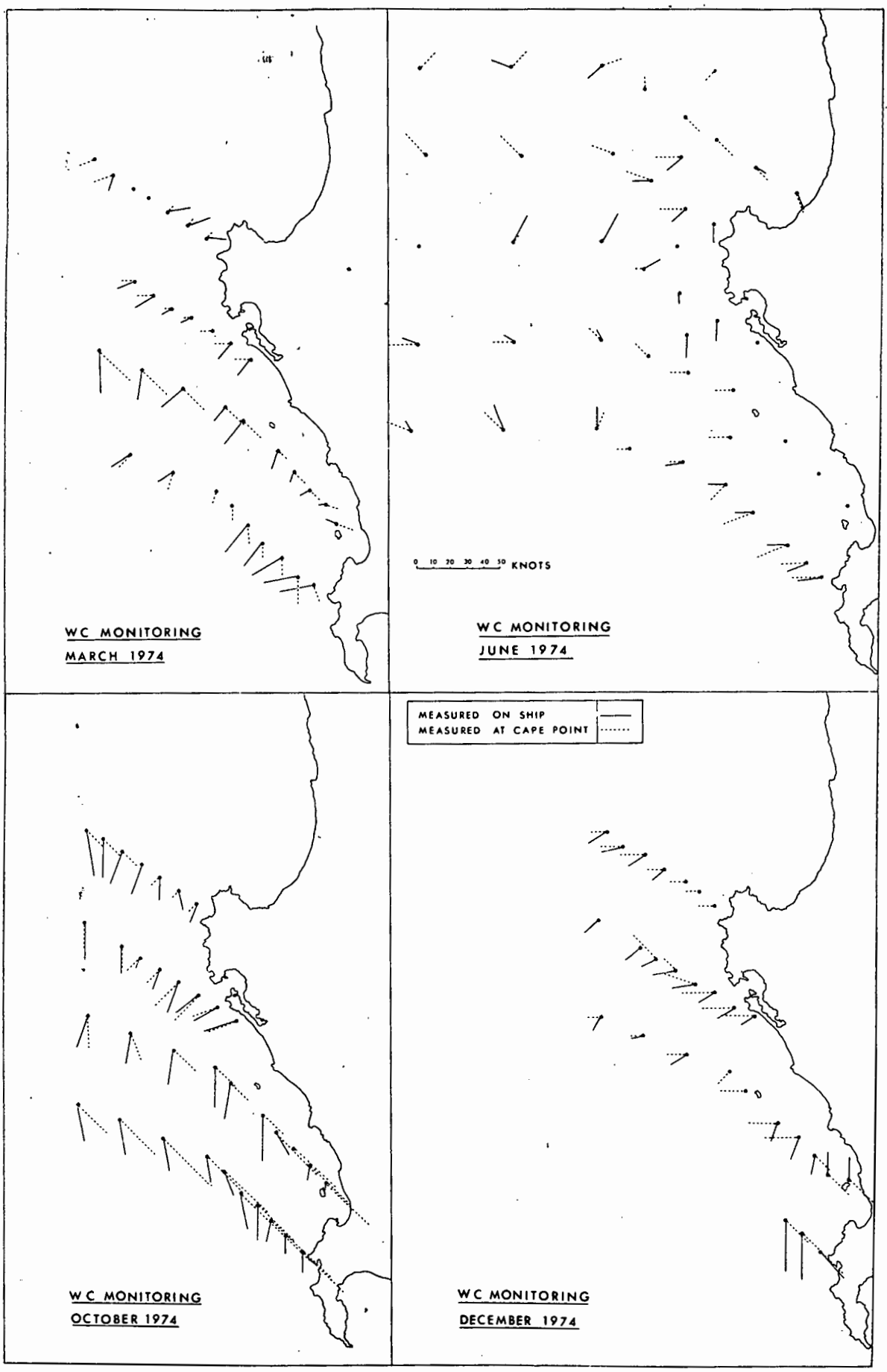

Fig. 3 Wind, measured at sea and at Cape Point during West Coast Monitoring Cruises, 1974.

uncertain accuracy of the chlorophyll'a' determination, as only one litre of water was filtered.

Displaced volumes were measured on board in filtered seawater using a modified Yashnov meter (Robertson 1970), before being deep-frozen at -20°C. Ashore, samples were split in two using a Folsom splitter and one half was dried at 60°C for 24 hours for the measurement of dry weight. Replicate subsamples of dried, homogenized zooplankton were analysed for organic carbon by wet oxidation with dichromate, and the dry weight of zooplankton converted to carbon per square metre.

Nutrients, chlorophyll, dissolved oxygen, temperature and salinity were determined as described by Andrews et al (in press).

The distribution of surface temperature, chlorophyll'a' carbon/ chlorophyll'a' ratio, particulate carbon, zooplankton carbon and the zooplankton carbon as a percentage of particulate carbon are shown in figs (4) to (7).

Wind data, measured at Cape Point lighthouse using a deflection-plate anemometer, were used to describe wind events prior to a cruise. These reading show good agreement with ships anemometer measurements speeds measured at 10-15 metres with regard to direction although southeast winds at sea level are lower because of the location of the lighthouse at about 300 metres, in the centre of the a coastal jet (= wind maximum) which develops during southeasterly winds (M. Jury, S.F.B., pers commn). North of the Cape Peninsula the wind tends to recurve, and to flow from a more southerly to southwesterly direction (Hutchings 1977). It become more diurnal in nature as low pressure areas develop over the land-mass in midafternoon during the summer months. Wind measured at Cape Point and at sea during the cruise are shown in fig. (3) and it shows that wind records at Cape Point provide a satisfactory picture for present purposes of the wind in the whole area, apart from the area immediately north of the Cape Peninsula where a wind-shadow effect develops in the lee of the mountains during periods of strong

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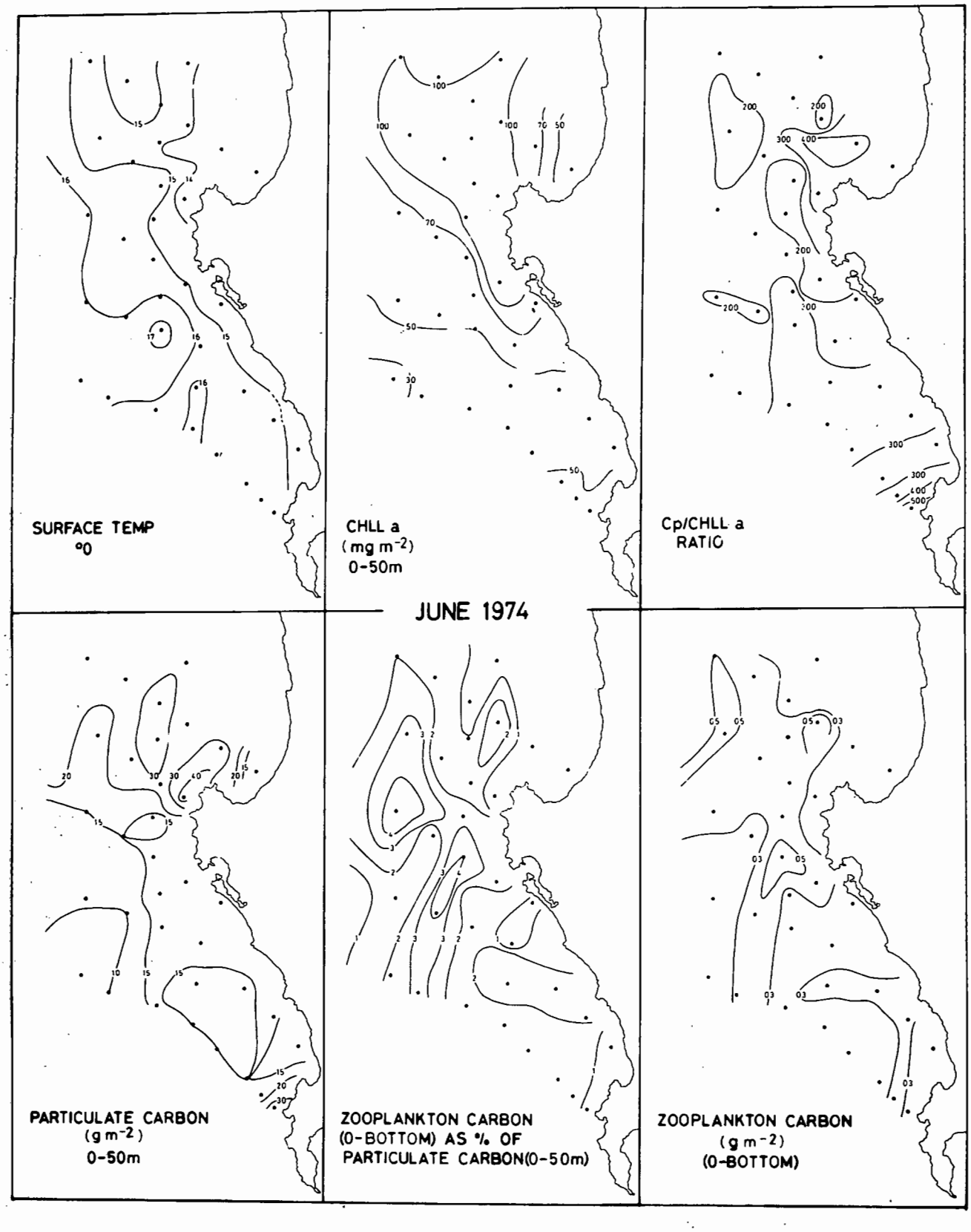

Fig. 4 Distribution of chlorophyll "a" (mg m^{-2}), carbon/chll "a" ratio, particulate carbon (gC m^{-2}), zooplankton carbon (g m^{-2}) and zooplankton as a percentage of particulate carbon during the June 1974 West Coast Monitoring Cruise.

southeasterly winds.

1.2 RESULTS AND DISCUSSION

In view of the known rapid changes in the zooplankton distribution during changing hydrographic events it is perhaps optimistic to look for meaningful distributions during cruises of four to five days duration, undertaken once per quarter, yet quiescent conditions prevailed in the week before and in the early stages of each cruise (Fig. (3)) so seasonal features were not obscured by superficial short term events.

The data will be treated as a sequence from mid-winter, when upwelling was minimal, through spring and summer the peak upwelling period, to autumn, when upwelling activity is still vigorous but light levels are declining.

1.2.1 Winter (Fig. (4))

The June cruise was preceeded by six days of strong westerly (onshore) winds blowing between seven and fifteen metres per second, followed by calm conditions during the cruise (Fig. (3)) and very typical winter conditions were observed. Small inshore/ offshore surface temperature gradients were present, with a slight drop in temperature to less than 14°C inshore north of Cape Columbine, while chlorophyll'a' was highest to the north west of Cape Columbine (more than 100 mg Chlorophyll'a' m^{-2}). Carbon: chlorophyll'a' ratios were very high, ranging between 119 and 1060 (mean = 308). The distribution of particulate carbon resembles the chlorophyll'a' distribution, with highest values to the north west of Cape Columbine and low values offshore in water warmer than 15°C. The very high carbon values inshore off the Cape Peninsula probably reflect detritus with a very high carbon: chlorophyll'a' ratio.

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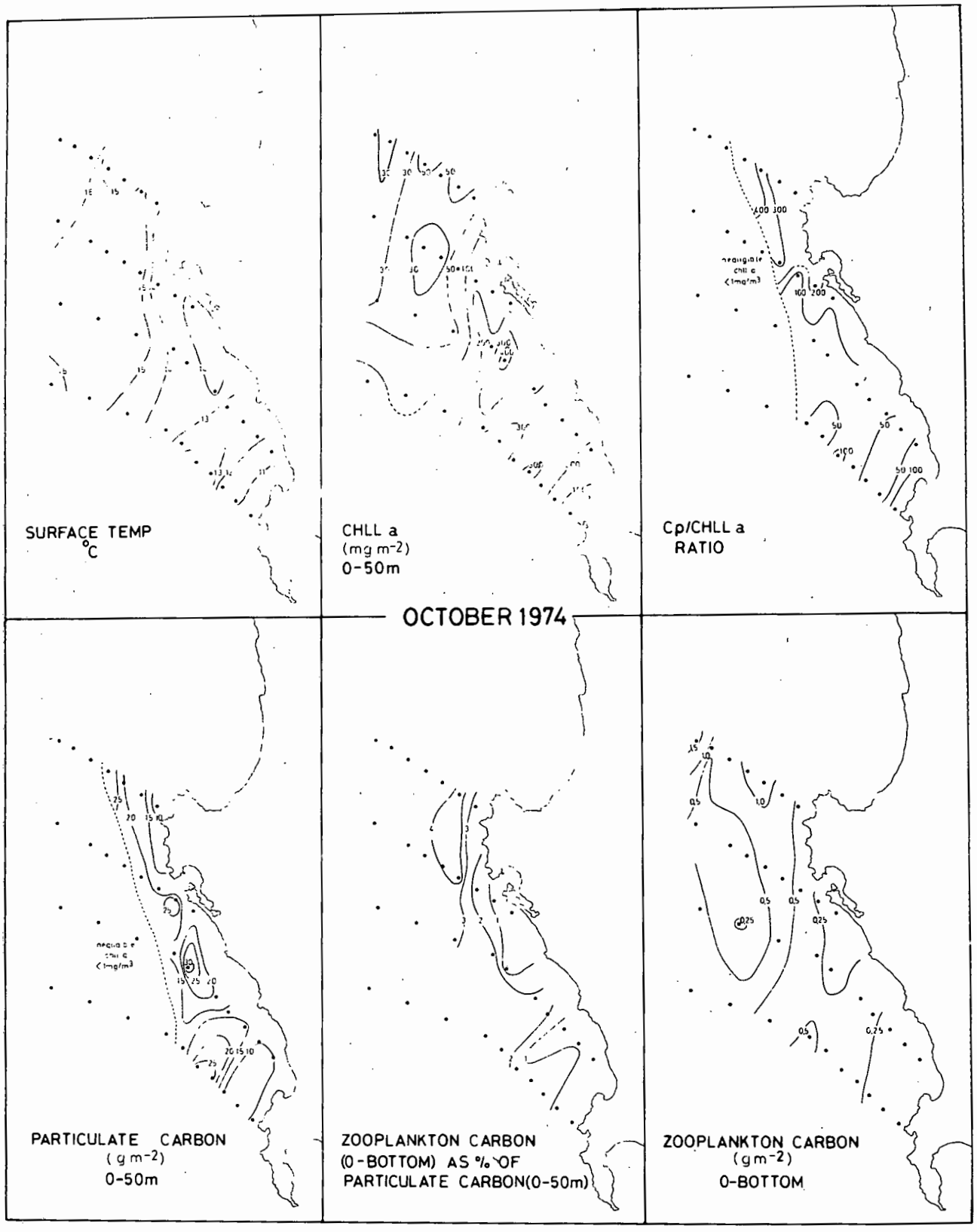

Fig. 5 As for Fig. 4, in October 1974.

Zooplankton quantities were low, and rose above 0,5 g carbon per square metre at only two stations north of Cape Columbine and at one station west of Saldanha Bay. Zooplankton carbon content varied from 24% to 53,4% of the dry weight (mean = 40.4%) with lower percentages offshore. Zooplankton formed from one to four percent of the particulate carbon with a mean of 2,03%.

1.2.2 Spring (Fig. (5))

In October, at the beginning of the peak upwelling period, the cruise was preceded by northwest or westerly winds apart from a brief three-day south easterly wind, four days before the cruise began. The wind backed from southwest to southeast and freshened after the northern two lines were sampled,(Fig. (3)) and represented the second major southeast wind event after winter. Oceanic water, represented by temperatures of greater than 15°C, approached close to the coast in the Saldanha Bay - Cape Columbine region, while upwelling activity was indicated in the south,with temperatures increasing from less than 10,5°C close to the coast to 14°C - 15°C some 60 km to the north west. Chlorophyll'a' concentrations increased steadily to a peak of more than 400 mg chlrophyll'a' m^{-2} along the temperature gradient, and fell sharply to less than 100 mg chlorophyll'a' m^{-2} further north. Carbon-chlorophyll'a' ratios initially decreased from 100 close inshore to 30-50, then rose to 70-80 at the centre of the chlorophyll'a' patch before increasing to more than 400 further north. Consequently particulate carbon values were evenly distributed over the whole region, with concentrations of 20 gC m^{-2} on each line. Zooplankton quantities were very low in the south (0,25 gC m^{-2}), reached maximum values on the Cape Columbine line (1,5 gC m^{-2}), and contributed a similar proportion of the particulate carbon as in winter (0,4% - 4%, mean = 1,8%). It is clear that early in the upwelling "season" zooplankton off the Cape Peninsula has not had sufficient time to develop, for although average standing stocks had risen approximately 50%, (Table 1), compared with the June cruise, this increase was entirely on the northern two lines, off Saldanha Bay and Cape Columbine, exactly opposite to the development of

TABLE 1: Means and Standard Deviations of chlorophyll'a', particulate carbon and zooplankton at West Coast Monitoring Stations 1974.

	Means and Standard Deviations for all stations			
	March	June	Oct.	Dec. 1974
Chll 'a'(0-50 m) mg m^2	181±107	65±35	140±114	226±196
Cp/Chll 'a' ratio	92±69	278±100	126±113	120±90
Cp (0-50 m) g m^2	16,3±10,3	19,2±9,2	15,4±8,6	25,3±16
Zooplankton dry weight O_m-bottom g m^2	1,96±0,91	0,71±0,41	1,08±0,83	1,09±0,79
Zooplankton % carbon	48,4±6,5	40,2±7,1	43,0±7,8	49,9±5,5
Zooplankton carbon O_m-bottom g m^2	0,96±0,46	0,30±0,15	0,47±0,35	0,54±0,4
Zooplankton (O_m-bottom)as percentage of particulate carbon (0-50 m)	7,5%±5,8	1,9%±1,3	1,8%±1,3	1,3%±1,6

TABLE 2: Mean zooplankton standing stock (dry wt. g m^{-2}) along lines 1-4, West Coast Monitoring Cruises 1974. Lines numbered from south to north.

	March		June		Oct.		Dec.	
Line	Dry wt ($g\ m^{-2}$)	Rank	Dry wt ($g\ m^{-2}$)	Rank	Dry wt ($g\ m^{-2}$)	Rank	Dry wt ($g\ m^{-2}$)	Rank
1	2,03	3	0,89	2	0,75	3	-	-
2	1,41	4	0,52	4	0,58	4	0,73	3
3	2,18	2	0,78	3	1,02	2	1,24	2
4	2,35	1	1,05	1	2,01	1	1,87	1

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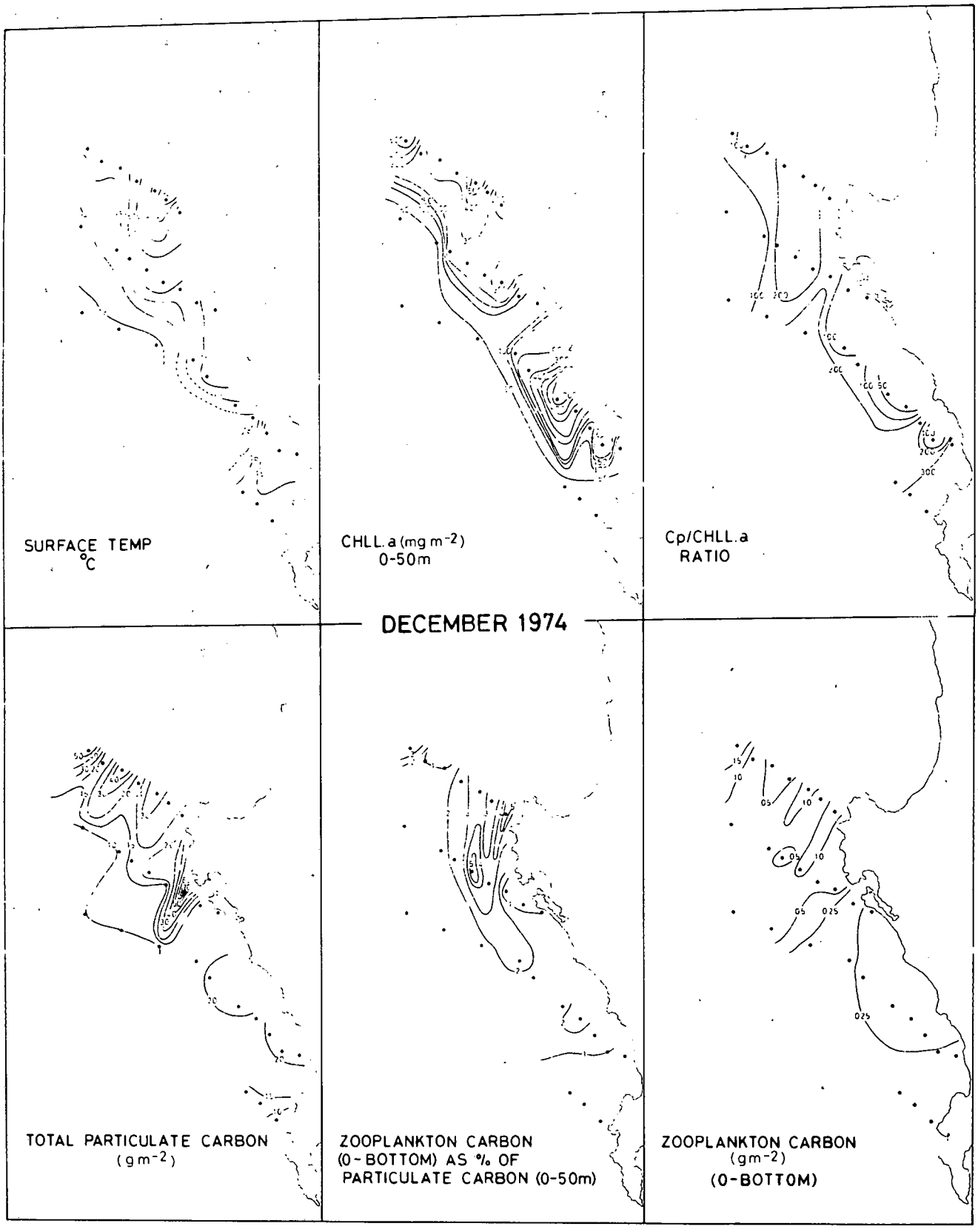

Fig. 6 As for Fig. 4, in December 1974.

chlorophyll'a' concentrations in the south.

1.2.3 Summer (Fig.(6))

The frequency of southeast winds increased during November, alternating with wind reversals to the west and north west over periods of three to seven days. In the week preceding the December cruise, the southeast wind blew at speeds between 2,5 m sec^{-1} and 15 m sec^{-1}, for six days before veering to the west and blowing at speeds between 7,5 - 10 m sec^{-1} on the 3rd December. Calm conditions were present as the cruise commenced on the 4th (Fig. (3). The west wind freshened again and persisted until the 6th, when it backed to the southwest and then to the south on the 7th, when it increased in speed. The onshore winds had caused a strong coastward movement of warm surface water in the south, (Bang and Andrews 1974; Bang 1976), with water of 15° - 18°C close inshore from Saldanha Bay to Table Bay, while remnants of upwelling off Cape Columbine were shown by surface water of less than 12°C, with a strong frontal zone immediately to the west. Chlorophyll'a' peaked at subsurface depths, immediately below the warm water and concentrations of 20-59 $\mu g\ \ell^{-1}$ were observed on the three northern lines, particularly in the vicinity of Dassen Island. High chlorophyll'a' values (greater than 400 mg m^{-2}) were observed in three large patches: inshore and offshore on the Cape Columbine line and at Dassen Island. Low carbon/chlorophyll'a' ratios (<50) in the Dassen Island patch reduced its "significance" when converted into units of carbon, although considerable production by phytoplankton was observed when water samples from the subsurface chlorophyll maximum layer were incubated at light-saturating levels, indicating that much of the phytoplankton at those depths was viable (Sea Fisheries Branch, unpublished data).

Zooplankton standing crop was low in the whole area affected by the intrusion, with low dry weight values of less than 1,0 gm^{-2} (0,5 $gC\ m^{-2}$), especially on the three stations on the Cape Peninsula line. North of Saldanha Bay zooplankton increased to

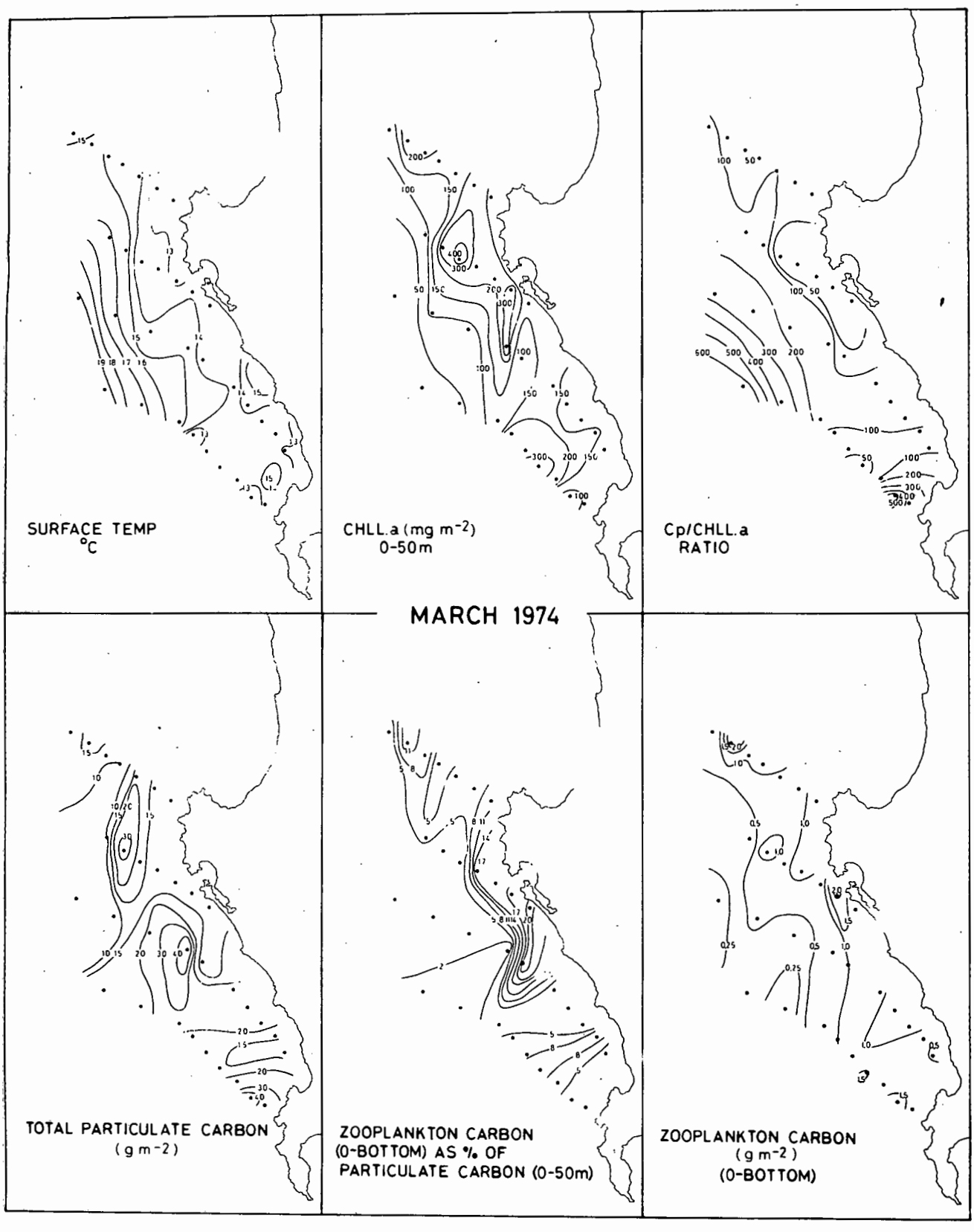

Fig. 7 As for Fig. 4, in March 1974.

1 - 3 g dry wt. m^{-2} (0,5 - 1,5 gC m^{-2}), especially on the Cape Columbine line, in the area unaffected by the warm water intrusion. As a consequence zooplankton concentrations and distribution closely resemble those observed two months earlier, despite the very different hydrological conditions, and the zooplankton again constituted a very small fraction of the particulate carbon (0,3%-5,9%, mean = 2,1%).

The lack of zooplankton in the south is at present inexplicable, as it was previously suggested (Andrews et al (in press)) that zooplankton was displaced shorewards of the Cape Peninsula line of stations during warm water intrusions. While the zooplankton standing crop at the first three stations on the Peninsula line was less than one third that at the inshore three stations on the next line, the average zooplankton standing crop is very low compared to what is generally observed in midsummer (Andrews et al), and it is clear that no large-scale shoreward displacement of zooplankton had occurred. There are two possible explanations for this. Firstly the WP-2 nets may have clogged in the dense patches of phytoplankton at subsurface depths, and so have underestimated zooplankton abundance, although flowmeter records did not indicate clogging problems. Secondly the spacing between lines was considerable, and dense concentrations of zooplankton may have existed between them. More closely spaced stations under similar circumstances are required to resolve the fate of zooplankton during warm water intrusions.

1.2.4 Autumn (Fig. (7))

Typical summer wind conditions were observed prior to the March cruise, with strong southeasterly winds persisting for three to seven days followed by calms or wind reversals of one or two days duration. The cruise itself took place in a relatively calm period immediately after a short southeast blow of 3 1/2 days, and mild southwesterly winds or calms prevailed during the entire cruise,

while gentle southerly winds were recorded at Cape Point (Fig. (3)).

A broad belt of cool water (13-15°C) was present inshore along the whole coast between the Peninsula and Cape Columbine with a sharp frontal zone separating it from oceanic water offshore, represented by water of 16-19°C. Of some importance were the isolated patches of water warmer than 15°C inshore of the sampling lines, detected with the ship's continuous thermosalinograph. In particular the warm patch between the Peninsula and Dassen Island lines may indicate a counter current (Duncan and Nell 1969) returning to the Peninsula, between the two plumes of cold water which represent recent upwelling both off the Peninsula and close inshore north of Table Bay where wind funnelling occurs. (Andrews and Cram 1969). Chlorophyll'a' concentrations were high, although slightly less than December values, probably due to falling light levels. Patches of high chlorophyll occurred off the Cape Peninsula, and in the Dassen Island - Saldanha Bay region some 20 - 40 kilometres offshore, with very low concentrations in the oceanic water. Carbon - chlorophyll'a' ratios again showed a strong inverse relationship to chlorophyll'a' concentrations, so the distribution of particulate carbon was displaced slightly offshore from the chlorophyll'a' patch in the north and shorewards on the Cape Peninsula line, due largely to a very high carbon/chlorophyll'a' ratio at station 2. Zooplankton was abundant (1 gC m^{-2}) in much of the cool inshore region in the south, but was only abundant close inshore off Saldanha Bay before broadening out on the Cape Columbine line. Relative to December zooplankton formed a considerably greater proportion of particulate carbon (2% - 20%, $\bar{x}$ = 7,5%), especially near Saldanha Bay, when zooplankton constituted more than 20% of the particulate carbon present in the upper layers.

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1.2.5 General

The variability of the Cape Peninsula area is contrasted with the Cape Columbine/Saldanha Bay area, where although similar topographic features such as canyons (Simpson and Forder 1968) and capes exist, the strong southeast winds experienced at the Cape Peninsula do not occur and are replaced with milder yet more frequent southerly winds. This, together with the close proximity of the shallow St Helena Bay area, with its permanent eutrophic nature due to persistent upwelling (Sea Fisheries Branch, unpublished data) ensures consistently higher plankton stocks in the north throughout the year than further south.

The unstable hydrological regime at the southern end of the grid is clearly demonstrated by the October and December cruises, where both upwelling and downwelling profoundly affected the quantity of zooplankton present. In the next section, it will be shown that the normal midsummer distribution of zooplankton off the Cape Peninsula in the absence of warm water intrusions consists of one or more peaks of zooplankton exceeding 2 - 3 g dry weight m^{-2} extending up to 60 - 70 kilometres offshore along the monitoring line, but this is unlikely to have been the case under circumstances experienced during December 1974.

2. MONTHLY MONITORING OF THE UPWELLING PLUME

It is clear from the description of short-term events by Andrews et al (in press) that considerable short term variability in zooplankton occurs at any fixed point in the Cape Peninsula upwelling system, and samples collected at time intervals of larger than 36 - 48 hours are subject to serious aliasing. Sampling in a northwesterly direction, as done during the upwelling monitoring cruises, does integrate time to some extent, especially during the summer months when the main movement of water is in that direction, although changes are likely to be considerable over a period of more than one week. With the realisation that aliasing could be problematical, the distribution of zooplankton is described below

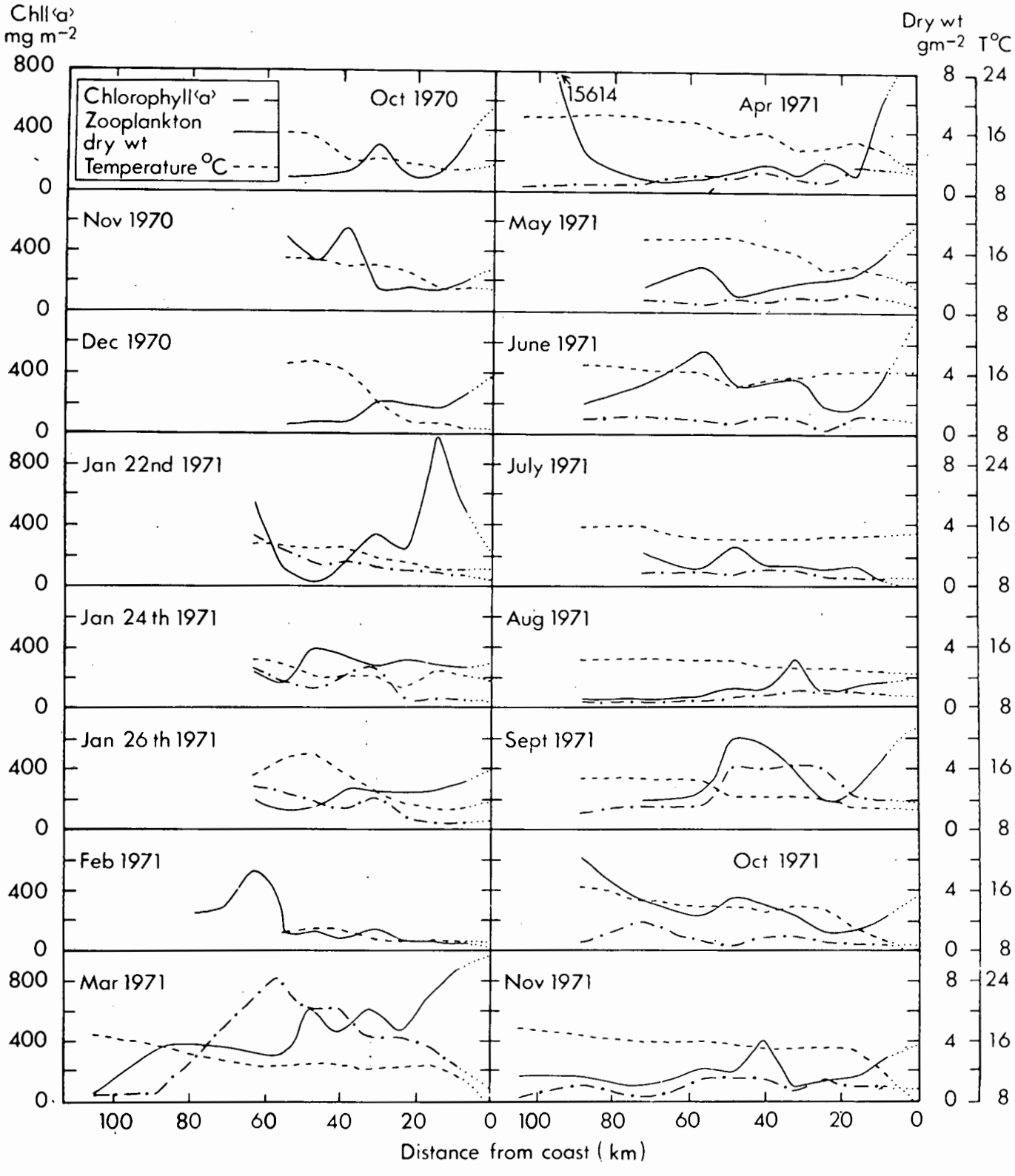

Fig. 8(a) Zooplankton (g m^{-2}, surface to bottom), chlorophyll "a" (mg m^{-2}, 0-50 m) and surface temperature (^{o}C) along upwelling monitoring line October 1970 - March 1973.

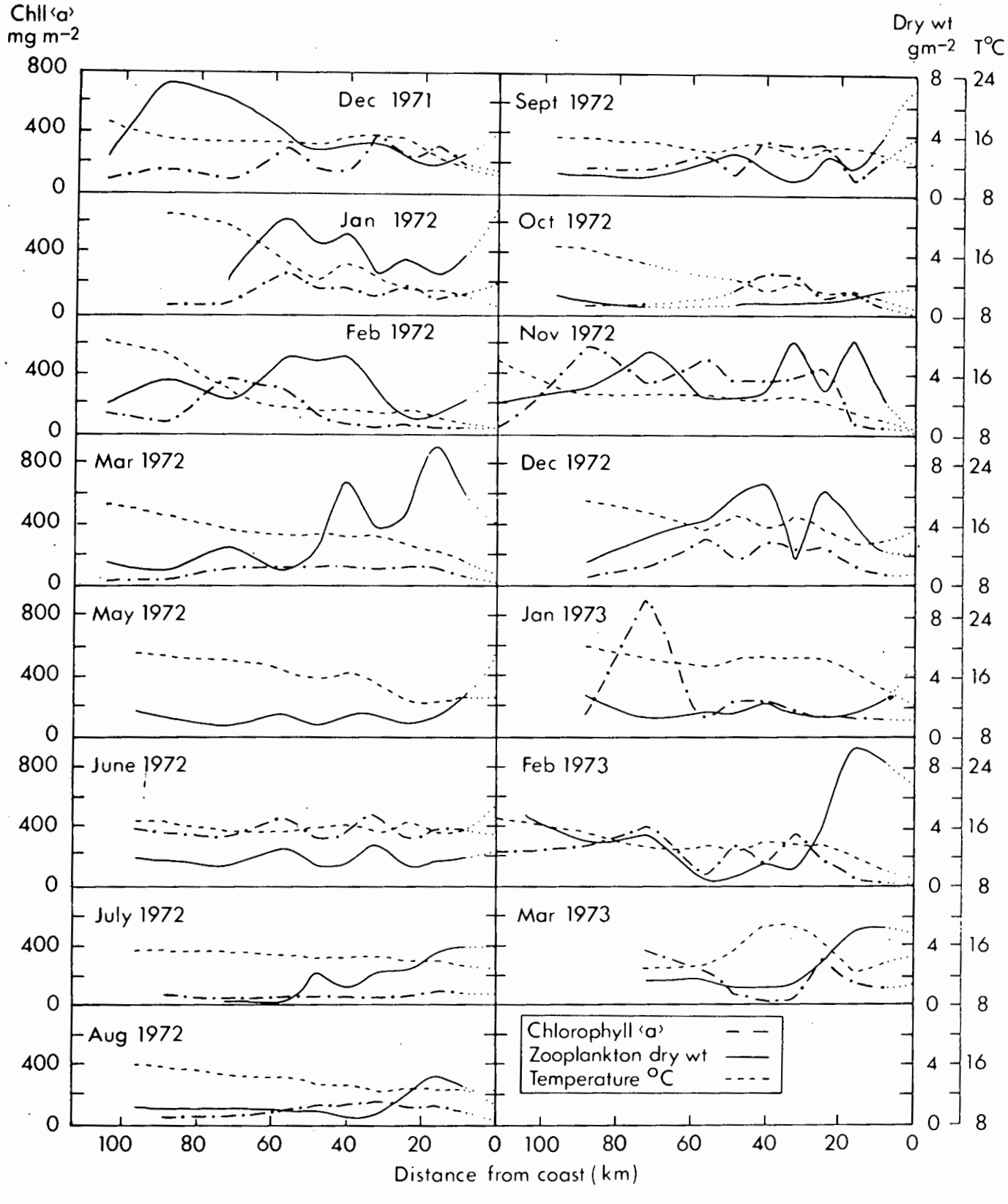

Fig. 8(b) Zooplankton (g m^{-2}, surface to bottom), chlorophyll "a" (mg m^{-2}, 0-50 m) and surface temperature (^{o}C) along upwelling monitoring line October 970 - March 1973

in relation to temperature, chlorophyll and the wind regime.

2.1 METHODS

Sampling and processing methods were similar to those employed during the quarterly surveys, except:

(i) only a surface sample was collected for particulate carbon analysis;

(ii) zooplankton samples were preserved in 5% v/v buffered formalin after measurement of the displaced volume and

(iii) zooplankton standing stock was assessed as dry weights rather than carbon

(iv) Temperature was measured at discrete depths using a Nansen Pettersen insulated bottle.

2.2 RESULTS AND DISCUSSION

Fig. (8) shows the distribution of zooplankton standing crop in the water column, surface temperature and chlorophyll'a' in the 0-50 m layer in the 33 transects made between October 1970 and March 1973. While the zooplankton profiles show considerable variation, two general patterns of distribution are observed:
(i) a summer pattern, showing multiple offshore peaks of high zooplankton dry weight as well as a smaller peak close inshore;
(ii) a winter pattern of lower concentration, more evenly spread along the monitoring line, with only minor peaks, usually inshore.
The profiles from March to May show intermediate stages, still with high standing crop values but always peaking close to the coast.

The summer profiles were highly variable over short time periods, for example in January 1971, when the shortened line was repeated three times in six days, although in this instance the quantity of zooplankton along the line of stations altered by less than one

third during the three replicates. The displacement of zooplankton offshore is clearly shown by the February 1971 cruise, sampled immediately after a sustained southeast wind. The surface temperature 58 km from the coast was only 10,6°C and the entire inshore zone was depleted of zooplankton, with a rapid increase in abundance beyond 60 km. By contrast in March 1971 when sampling commenced after a week of westerly to northwesterly winds, high zooplankton concentrations occurred along the whole line to 90 km from the coast, with highest concentrations inshore. As the frequency of strong southeasterly winds declined zooplankton concentrations decreased through April and May 1971, apart from an incidental night-time catch of euphausids at the outermost station in April. The June profile was obviously anomalous and shows features more typical of summer, i.e. high values and offshore peaks of abundance. An unseasonally strong southeaster blew for five days immediately prior to the cruise and obviously displaced zooplankton offshore although neither phytoplankton nor surface temperature patterns suggested any enrichment of the water by upwelling. Temperature effects could have been masked by oceanic water moving rapidly shoreward on cessation of the wind stress (Bang and Andrews, 1974) while the phytoplankton crop was either rapidly grazed down or did not grow rapidly due to low light levels. It appears that the zooplankton crop was physically accumulated along the line of stations by advection from the coastal region.

The period from July 1971 to June 1972 illustrated a coherent seasonal cycle of zooplankton. Low concentrations were uniformly spread over the whole transect in July and early September with small inshore/offshore temperature gradients indicating minimal upwelling activity. With the increasing frequency of southeast winds and increased light levels in spring both zooplankton and chlorophyll 'a' concentrations increased markedly by late September, while upwelling in October dispersed the phytoplankton and displaced the zooplankton offshore. November was subject to onshore winds and a warm water intrusion, with surface temperatures of greater than 15,0°C close inshore and anomalously low zooplankton concentrations. By December a typical summer pattern has developed, with high phytoplankton concentrations forming multiple peaks and a well developed zooplankton crop which reached maximum concentrations about 90 km from the coast,

decreasing rapidly as surface temperatures rose above 16°C. From December 1971 until March 1972 the peak in zooplankton shifted shoreward, with warm water moving gradually inshore. Concentrations declined rapidly to low levels in May, when typical winter conditions were again established and persisted through until September 1972.

Changes through the next summer were less clear, due to considerable "noise" from short term events. Salps offshore and upwelling inshore in October 1972 limited the zooplankton standing crop to the lowest observed during the entire sampling period, while November showed a four-fold increase in standing crop along the line, with three peaks of abundance extending to 80 km and considerable quantities of phytoplankton between the third and ninth stations. High concentrations of zooplankton and phytoplankton continued in December, although warm water limited the offshore extent of high values. In January warm water intruded close to the coast and zooplankton levels were considerably diminished although the phytoplankton crop, by virtue of large subsurface concentrations (20-50 μg chll'a' ℓ^{-1}) remained high. By February 1973, the water was some 4°C cooler due to renewed upwelling and zooplankton show two peaks of abundance with a distinct minimum between stations 4 and 7. Chlorophyll'a' concentrations showed a similar trend, although there was no marked changes in hydrological conditions in the area to explain these minima. In March 1973 a patch of warm water raised temperatures and depressed zooplankton and phytoplankton levels between 15 and 50 kilometres from the coast. Cool water of 13,6°C was present at st. 8, with rising plankton concentrations, and the transect did not extend sufficiently far offshore to reach oceanic water.

It is of obvious that both warm water intrusions and powerful upwelling during summer restrict the development of high zooplankton standing stocks, so it is of interest to examine meteorological and hydrological conditions leading up to the peak zooplankton concentrations which were observed, as these may be regarded as

optimal for zooplankton in the area. Highest average standing stocks to 100 km offshore along the transect occurred in March 1971; June 1971; December 1971 and November - December 1972.

In all cases the zooplankton was fairly uniformly distributed over a wide area, rather than a combination of low and very high concentrations. Secondly, apart from the anomalous June 1971 transect which has already been discussed, the other peaks occurred during the summer-autumn period. Thirdly the wind regime prior to each cruise was characterised by a lack of sustained strong winds from any one direction in the week prior to the cruise, with frequent wind reversals, although attempts to quantify wind data into various speed and direction categories and relate it to zooplankton abundance in the plume throughout the year were not successful. This may be due to minor reorientations of the upwelling plume (M. Jury S.F.B. pers. comm) which were not detected because only a single line of stations was sampled.

The distribution of high zooplankton standing stock up to 60-90 kilometres offshore is in contrast to the situation in Oregon where very high standing crops only occur within 25 kilometres of the coast, in the zone of most frequent upwelling (Peterson 1976).

3. SHORT-TERM REPETITIVE GRID SURVEY AT THE BASE OF THE PLUME

3.1 METHODS

3.1.1 Sampling

Temperature was measured using a bathythermograph and a Nansen Pettersen sampling bottle, while water samples for salinity, oxygen, nutrients and chlorophyll'a' were collected with 7-litre N.I.O. bottles at discrete depths. Zooplankton was collected with vertically-hauled WP-2 nets hauled from close to the bottom to the surface, after allowance for wire stray. At 10 stations where the pump was used, divided hauls were made from close to the bottom to

50 metres and from 50 metres to the surface. Depth and flow were monitored using N.I.O. flowmeters (Currie and Foxton 1957). Where no flowmeter records were available, readings extracted from the regression between wire length and volume filtered for the whole cruise were used to estimate the volume of water filtered.

3.1.2 Processing

Analysis of salinity, oxygen, nutrients and chlorophyll'a' was done according to the methods described in Andrews et al (in press). Depth profiles of chlorophyll'a' were integrated manually to provide estimates of the phytoplankton standing stock in the upper 75 metres.

Zooplankton samples were processed in a similar manner to those collected during the monthly surveys, with one-half used for dry weight determinations and the other half used for species analysis, which was done in the following way: All organisms longer than one centimetre (principally euphausids and hyperiids) were removed, identified and counted. If numerous, their proportion in terms of displaced volume was measured. It was assumed that they were not quantitatively sampled, and dry weight values for the whole sample were adjusted in proportion to the volume measurement of these larger organisms. Medium-sized organisms 5-10 mm in length, were counted in the whole half-sample while smaller organisms were subsampled using a wide-mouthed pipette as described in the report on the vertical distribution of zooplankton. All counts were adjusted to the number per cubic metre of water filtered.

Dry weight values, based on WP-2 net hauls made from bottom to surface, after standardisation to the quantity beneath one square metre, have been used to describe changes in zooplankton abundance, as displaced volume measurements are often unduly weighted by the presence of gelatinous organisms which are usually more abundant in upwelling water and in warm water. In this study, large medusae and ctenophores were removed before measuring displaced volumes, and there is reasonable agreement between dry weights and displaced volumes (See appendix 2) except for occasional samples where large numbers of small gelatinous organisms were present. Standing stock measures, depth of haul, volume filtered and sounding are shown in Appendix 2.

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Distribution maps of zooplankton dry weight were constructed from complete circuits of the grid of stations, using the northern (R.S. Africana II) and southern (R.S. Sardinops) circuits which overlapped best in time (Appendix 1). The period between consecutive circuits varied from 32 to 48 hours, while sampling was temporarily stopped between 6th and 10th December 1969 when the vessels returned to port.

3.1.3 Numerical analysis

The similarity between stations on each complete circuit was calculated using the Bray-Curtis similarity measure after log-transformation of zooplankton species numbers per cubic metre of water filtered. Species associations were similarly determined and were also grouped on a presence/absence basis using the association index of McConnaughey (1964) together with eight environmental factors: warm, ($>$ 16°C), cool (11°-16°C) and cold ($<$11°C) water, presence of thermocline, distance from shore, day or night, high (>3 $\mu g \ell^{-1}$) chlorophyll 'a' concentrations and deep ($>$ 200 metres) water.

The information statistic (Field 1969; 1971) was used to distinguish species differing significantly between the station groups identified in the dendrograms. The Mann-Whitney U-test was used to assess environmental differences between station groups. (Appendix 3)

The horizontal distribution of zooplankton dry weight and station groupings are compared with changes in the hydrology and phytoplankton of the area. Surface temperature has been used to indicate hydrological changes as it shows a close similarity to changes in salinity and is a sensitive indicator of active upwelling.

For convenience, the survey has been broken into two periods; the first part between the 3rd and the 6th of December was conducted during gentle southwesterly winds inshore which maintained approximately "steady-state" conditions with regard to the hydrology. The second part of the survey, conducted between the 10th and 16th of

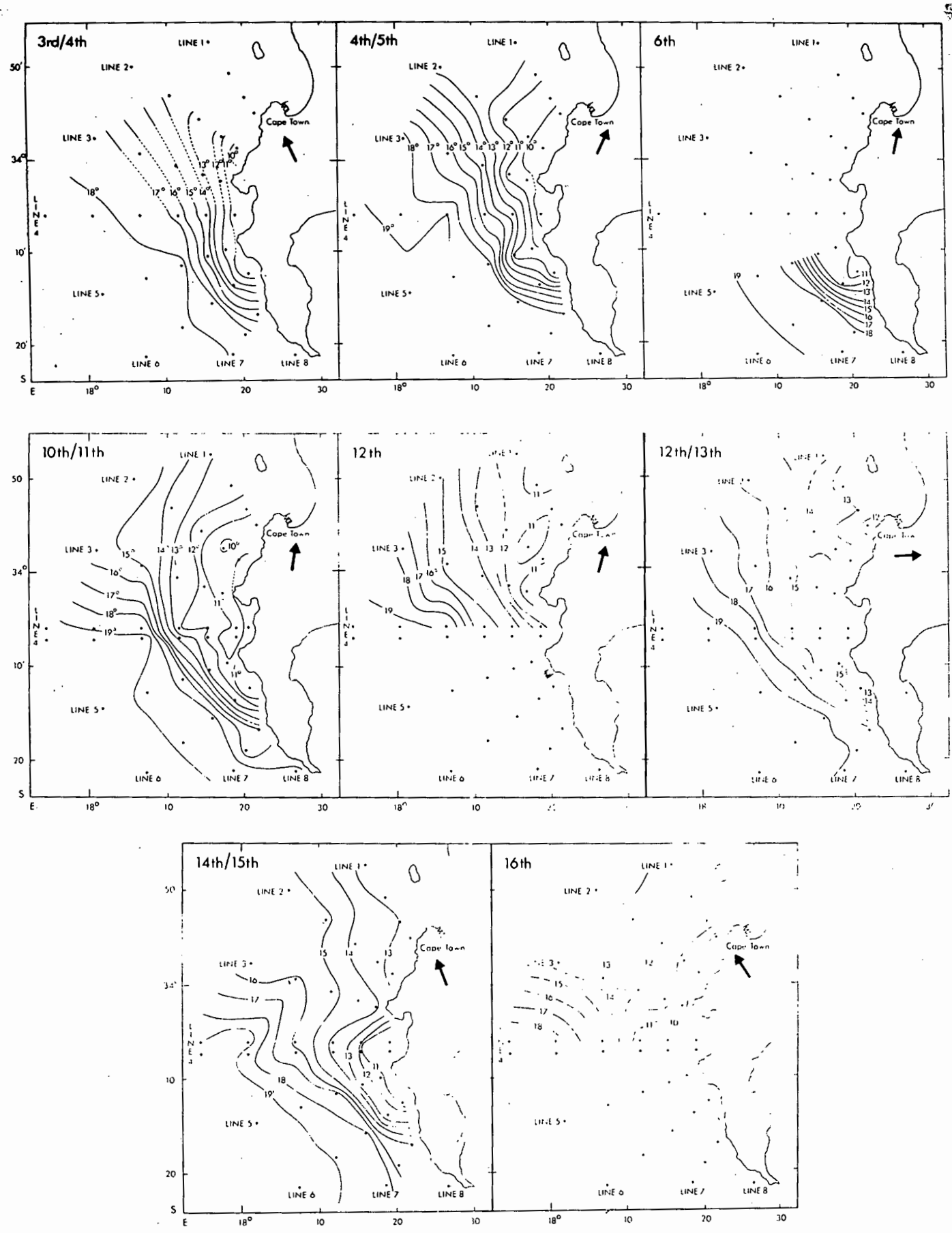

Fig. 9 Horizontal distribution of surface temperature (^{o}C) 3rd-16th December 1969. Arrow indicates predominant wind direction.

December, demonstrated a complete although brief wind cycle, as a weak depression passed the Cape Peninsula. Hydrological conditions changed from gentle upwelling to downwelling and back to vigorous upwelling within this period, and the movement of patches of zooplankton and phytoplankton provide great insight into the short-term processes affecting plankton populations located at an active upwelling site.

3.2 RESULTS AND DISCUSSION

3.2.1 At steady state

During the first part of the cruise (3rd-6th December) the wind blew steadily from 160° to 240°, at 5-10,5 m sec^{-1} and caused moderate upwelling close inshore (Fig. 9), with surface temperatures below 10°C at st. 121, and between 10° and 11°C along the whole inshore strip to st. 361 on 3/4 December. The water cooled on 4th/5th December north of Duiker Point (Hout Bay) where the tangential wind stress was greatest, (M. Jury, S.F.B. pers comm.) and warmed up slightly further south, where the wind was slightly onshore. This situation persisted on 6th December, when only the southern half was sampled. A strong surface thermal front was apparent close inshore in the south, running between stations 61 and 63, 51 and 53, and 41 and 43, but weakening and moving offshore between lines three and four. Line six showed a temperature gradient of 7°-8°C, while the gradient was 2,7°C along line 2.

The chlorophyll'a' distribution (Fig. 10), showed enhanced values just seaward of the front in the south, decreasing inshore in newly upwelled water and offshore in oceanic water. Quantities of chlorophyll'a' were two to three times higher in the northern half of the grid, reaching 250 mg m^{-2} on lines one and two. The centre of this patch shifted northwards on the 4th/5th in response to increased upwelling inshore. On the 6th December, considerably higher concentrations of chlorophyll'a' were present in the south,

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reaching 209 mg m^{-2} at station 552, suggesting on onshore accumulation due to the wind. Zooplankton dry weight distribution (Fig. 11) on 3/4 showed a zooplankton maximum lying immediately west of the chlorophyll'a' maximum in the south, with higher values widespread in the north. On the 4th/5th zooplankton was concentrated close to the coast, centred off Hout Bay and inshore of the phyto= plankton maximum, suggesting that zooplankton was drawn towards the centre of upwelling. On the 6th December a similar zooplankton pattern to that observed on the 3rd/th was apparent, with enhanced zooplankton on the outer edge of the front.

The conditions experienced in the period between 3rd and 6th December were approximately in a steady state with regard to upwelling and Figs. (10) and (11) show that considerable changes in zooplankton and phytoplankton standing crop occurred during these conditions.

3.2.2 Changes during a wind reversal

On the resumption of the cruise on the 10th December, moderate southerly to southwesterly winds were blowing after a 24 hour period of strong southeast wind on the 8th December, and a similar temperature distribution (Fig. 9) to that observed during the period from 3-6 was observed, with cool water of 10°-11° inshore in the northern part and a well defined frontal zone reaching the coast between lines 6 and 7. These conditions persisted until the 12th when the wind veered to the west and pushed warm water shore= wards especially in the north, so the 15°C isotherm moved some eight kilometres along line three and increased surface temperatures 2°C on lines 1 and 2. This onshore wind had a marked effect on the chlorophyll'a' distribution, (Fig. 10) which formed a dense patch inshore on lines 2 to 4, tripling in quantity from 100-200 mg m^{-2} to 400-450 mg m^{-2} over a period of 36 hours in the vicinity of stations 32 and 42. As the wind backed again to the south and then the east and rapidly increased in speed on the 14th and 15th, upwelling was initiated in the south and cool water began to push westwards

on lines 4-6, with warm water still intruding in the north (Fig. 9). The shearing motion separated the dense chlorophyll'a' into two patches, the one moving northwards to centre around st. 22, the other westward to st. 44, without concentrations in either diminishing (Fig. 10). On the 16th, with a wind of 25-30 m sec^{-1} from 160°-180°, cold water of less than 10°C covered the whole inshore area in the northern part (Fig. 9), causing the northern patch of phytoplankton previously centred around st. 22 to disperse completely, while the patch at st. 44 had moved northwards to st. 35 and the maximum chlorophyll'a' had decreased from 450 to 350 mg m^{-2} (Fig. 10).

Zooplankton distribution during the period from the 10th to the 16th showed different changes to the phytoplankton. On the 10th/11th (Fig. 11) maximum zooplankton levels were centred about st. 34 and st. 35, immediately beyond the phytoplankton maximum which extended to line 1. A belt of raised zooplankton levels extended southwards, parallel to and just seaward of the oceanic front, to line 7. Low concentrations were present in the cold inshore strip. On the 12th, both zooplankton and phytoplankton peaks had shifted to the north east as the water warmed and maximum zooplankton values were centred at stations 14 and 25. A second patch became apparent on the 12th/13th at the height of the downwelling period just seaward of the dense phytoplankton patch inshore on lines 3 and 4 (Fig. 11), while a remnant of the northern patch was present at station 14, west of Robben Island. As the wind backed to the east and part of the phytoplankton moved westward, the zooplankton crop increased in concentration from 1,5 g dry wt. m^{-2} to more than 2,6 g m^{-2} and was centred around stations 43 and 44, coincident with the phyto= plankton patch (Fig. 11). The northern patch of phytoplankton was associated with zooplankton levels about one-fifth that of the southern patch. High zooplankton concentrations appeared on line 1 and seemed to be derived either from the Robben Island/Table Bay area or they had moved southward from north of the sampling

area. Slightly raised zooplankton levels running parallel with the frontal zone persisted in the south during this period (Fig. 11) despite the marked changes occurring elsewhere. On the 16th cold water had completely displaced the high zooplankton concentrations along line 1 and the southern patch had shifted some 15-18 kilometres northward to centre around at 34, inshore of the remnant of the phytoplankton, indicating a faster dispersal of phytoplankton.

3.2.3 General

These events show that water movements may be responsible for the initiation and development of discrete patches of zooplankton and phytoplankton, and it is clear that very different grazing pressures were exerted on the two phytoplankton patches displayed in figs. 10 and 11. Elementary calculations based on the area and average standing stocks of zooplankton and phytoplankton within the patches show that in order for zooplankton grazing to account for the changes in phytoplankton abundance between the 14th/15th and 36 hours later, a ration of approximately 100 x to 200 x the body-weight of the zooplankton must have been consumed. It is clear that physical turbulence played the dominant role in the phytoplankton dynamics of the two patches (See Beers et al 1971).

The northern phytoplankton patch, despite the lack of grazing pressure on it, dispersed more rapidly than the southern are because it was closer to the centre of the upwelling plume. It is clear that much of the dissimilarity between zooplankton and phytoplankton along the axis of the upwelling plume (Andrews et al (in press) is due to differences in the response of plankton populations at the base of the plume to water movements. The southeasterly wind which began on the 14th/15th persisted until the 19th and assuming that the zooplankton patch maintained its speed and integrity it would be displaced some 60-70 km to the northwest, and phytoplankton still further. However mixing and dispersion must decrease the rate of drift considerably.

3.2.4 Quantitative changes in zooplankton standing crop.

Quantitative changes in chlorophyll'a', oxygen and nutrients in the photic (0-50 m) and subphotic (50-100 m) layers were made by Andrews et al (in press), who divided the area into two zones separated along line 4. It was shown that during active upwelling nutrients increased and chlorophyll'a' and oxygen in the photic layer decreased, while the reverse was true during downwelling conditions. A cruder approach has been adopted for assessing changes in zooplankton, more in keeping with the known large variability to which zooplankton net hauls are subject (Cassie, 1968). Polygons were drawn through the midpoints between stations and the zooplankton collected at the station was considered representative of the area within the polygon. The survey area was divided into north (lines 1-4), south (lines 5-8), inshore (stations 1-3) and offshore (stations 4-6) regions, and the quantities in each zone are listed in Table (3). Therefore the figures are not directly comparable with those for phytoplankton and nutrients in Andrews et al (in press). The area was divided up in the above manner because the most marked changes occurred in the northern inshore area, while in the southern zone the frontal zone showed little change despite the widely varying winds, and if the area had been divided into northern and southern zones along line 4 little change in zoo= plankton would have been observed.

Table (3) demonstrates the importance of the northern part, particularly the "offshore" zone which contained 33%-50% of the total zooplankton, while the southern inshore area contained the least. During the period from the 3rd to the 6th changes were not clear due to incomplete circuits. For instance on the 3rd/4th one-half of the northern part was omitted and little can be inferred about the quantity of zooplankton present. In the south, while the total zooplankton remained constant between circuits on the 3rd/ 4th and the 4th/5th, there was a shift shorewards under the influence

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TABLE 3: Changes in the quantity of zooplankton present in the survey area from bottom to surface during the December 1969 cruise, divided into northern (Lines 1-4) and southern (Lines 5-8) sectors as well as inshore (stations 1-3) and offshore (stations 4-6) zones. Values are in metric tons dry weight.

	3rd/4th	4th/5th	6th	10th/11th	12th	12th/13th	14th/15th	16th
North Inshore	Incom= plete	1016,801	-	435,278	396,217	647,577	579,328	450,345
North Offshore	Incom= plete	816,406	-	1071,931	1228,439	1136,820	1734,476	1357,673
North (total)	1520,437	1833,207	-	1507,209	1624,656	1784,397	2313,804	1808,018
South Inshore	278,937	336,400	403,807	252,343	-	164,229	281,568	-
South Offshore	353,269	257,300	414,147	440,123	-	239,042	427,247	-
South (total)	632,226	593,700	817,954	692,466	-	403,271	708,815	-
Total (North and South	2152,643	2426,907	-	2199,675	-	2187,668	3022,619	-

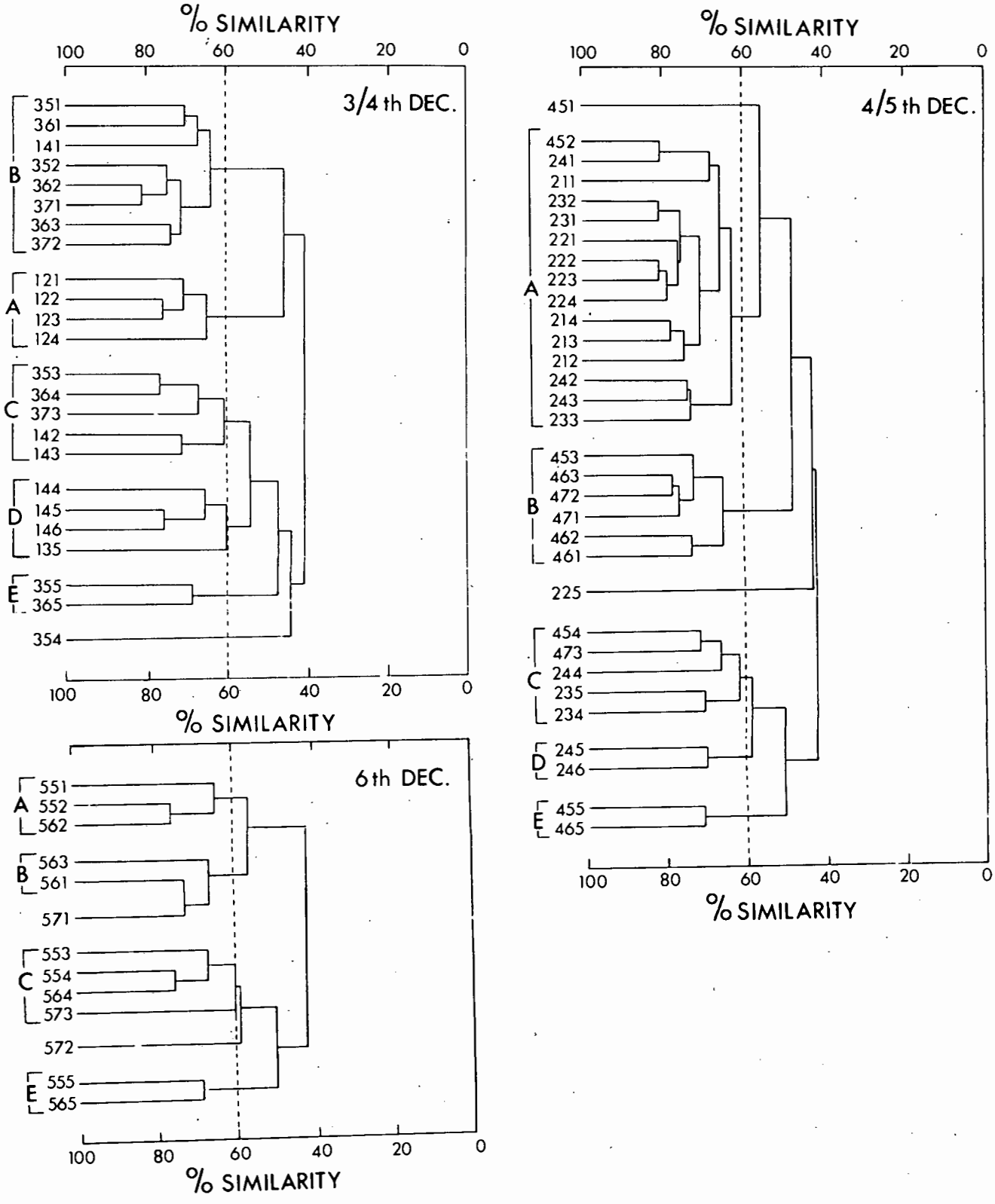
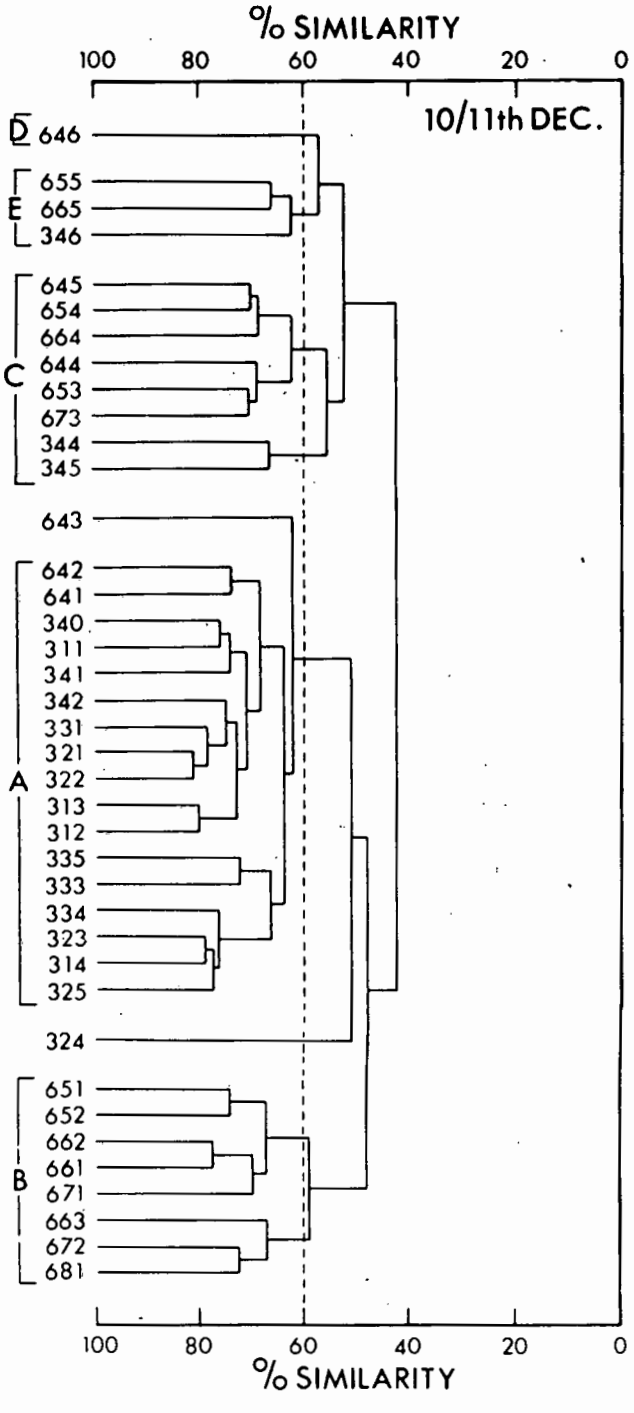


Fig. 12 Dendrograms of Bray-Curtis similarity between stations, 3rd- 6th December 1969.



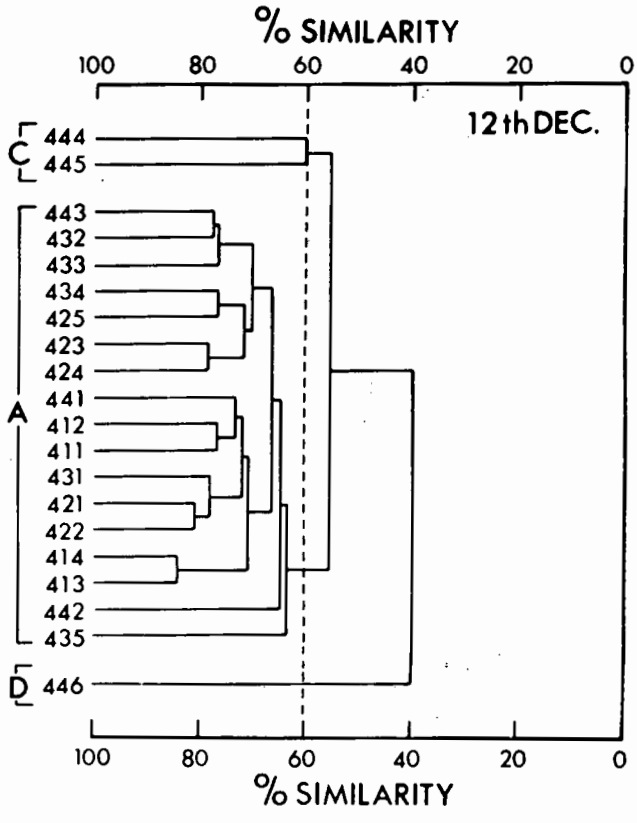


Fig. 13 Dendrograms of Bray-Curtis similarity between stations
(a) 10th-12th

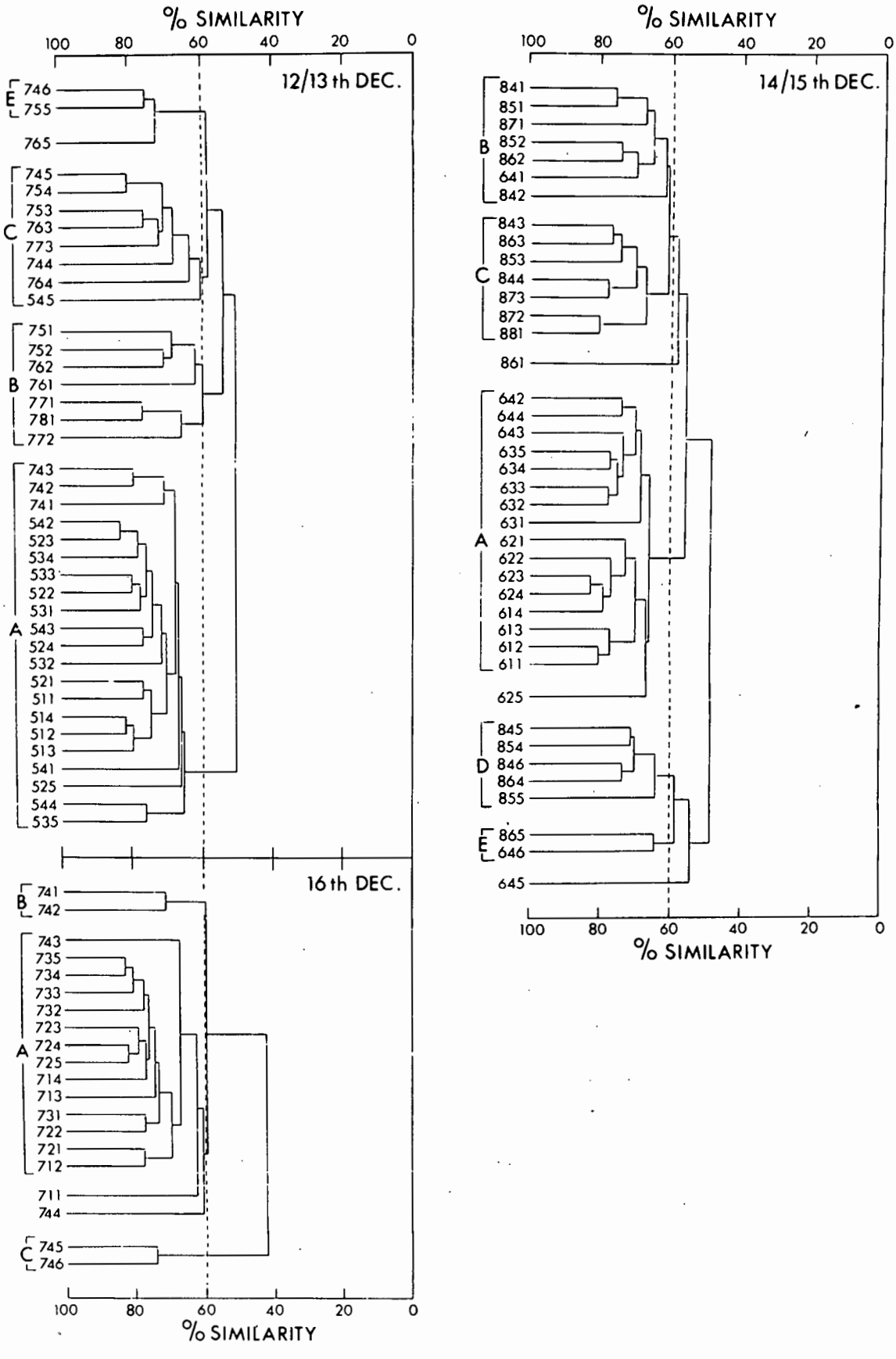


Fig. 13 Dendrograms of Bray-Curtis similarity between stations

(b) 12th-16th December 1969.

of southwesterly winds and the total quantity in the south rose by one third on the 6th as these winds continued.

During the period from the 10th-16th, zooplankton in the northern zone rose from 1507 m tons (dry weight) to 2300 m tons during the period of onshore winds, followed by a rapid decrease within 36 hours to 1808 m tons as upwelling recommenced. The southern zone decreased from 692 m tons to 403 m tons at the start of the downwelling period on the 12th, but recovered to 708 m tons by the 14th/15th.

Considering the whole 2 500 km^2 survey area, repeated circuits showed variations of 10-15%, about a mean of 2 400 m tons between repeated circuits, apart from a 40% increase on the 14th/15th at the end of the downwelling period. The 18% decrease in the northern zone as upwelling developed on the 16th suggests that much lower quantities of zooplankton would have been found in the area had sampling continued for a further three days. Thus changes in zooplankton abundance follow the trends in phytoplankton in the upper 50 meters noted by Andrews et al (in press), namely an increase in standing stock during downwelling conditions and a decrease during upwelling.

3.2.5 Numerical analysis of species changes

Dendrograms showing the station groupings based on Bray-Curtis coefficients are shown in Figs 12 and 13. At the 60% level five major groups were distinguished in complete circuits and three or four groups for the half-circuits on the 6th, 12th and 16th December. The relative geographical locations of these groups remained constant over the whole period and groups were labelled in the same sequence (Fig. 14). Group A samples always occurred in the northern part of the grid and were typical of the phyto=plankton-rich upwelled west coast waters, lying inshore of the frontal zone. Group B samples occupied the southern inshore region where the front approached the coast and cool upwelled

water was close to or at the surface, although phytoplankton concentrations were low due to the water moving offshore and northwards before dense concentrations could develope. This group showed contained many species also common in group A samples and could be termed the "pioneering" species of the Benguela upwelled component. It is of interest that it is "open-ended" to the south on occasions and could extend into False Bay. Bordering the A and B groups and running parallel with the oceanic front (Fig. 9) was group C, termed the frontal zone group, which generally contained a mixture of cool and warm water forms as well as species which showed a distinct preference for the frontal zone. Offshore from group C were two warm water groups D and E, characterised by a high diversity of zooplankton, deep thermoclines and deep soundings.

Despite great changes in the distribution of temperature (Fig. 9) chlorophyll'a' (Fig. 10) and zooplankton biomass (Fig. 11) the distribution of the groups varied little during the survey. Group A extended southwards inshore on the 4th/5th and the 6th December but thereafter remained north of line 5. Group B only extended northwards to line 4 on the 14th/15th and 16th December, when strong upwelling was occurring. Group C maintained an intermediate position in the south, where little change in the physical structure of the water occurred, but its location on line 4 altered considerably. On the 3rd/4th it was at stations 42 and 43, on the 4th/5th at 44, on the 10th-13th at 44 and 45, on the 14th/15th at 43 and 44 and on the 16th and 45 and 46. These changes are in sympathy with movements of the frontal zone along line 4. The general warming processes (Fig. 9) observed during downwelling conditions on the 12th/13th - 14th/15th, which caused such marked changes in the vertical distribution of chlorophyll'a', nutrients, temperature salinity and oxygen (Andrews et al in press) did not alter the zooplankton species distribution to any great extent, apart from the intrusion of an insignificant number of warm

water species into the cool water zone.

Group D remained centred around the outer stations on line 4, occasionally encompassing station 35 or 55, while group E stations were centred around stations 55 and 65 during the whole survey period, and were always closely similar to group D. The Mann-Whitney U-test was applied to temperature, depth of thermocline and chlorophyll'a' data (Appendix 3) to detect significant differences in environmental parameters between the groups. The results can be summarised as follows:-

Surface temperature: $A < B < C = D = E$ ($P < 0,05$)

Depth of thermocline: $A = B < C < D = E$ ($P < 0,05$)

Chlorophyll'a' in water column: $A > B = C = D = E$ ($P < 0,05$)

The information statistic tests showed that when concentrations of animals were compared between the station groups nearly half the species showed significant differences, and little could be inferred about characteristic species. On the basis of frequency of occurrence the test showed greater powers of discrimination with 12-54 species showing significant differences between groups. Numbers were further limited by considering only those species which showed a frequency of occurrence of 80% or more within one group. These species are listed in Table (4), together with the total number of species which differed significantly between the groups. Positive and negative signs indicate the affinity of the species for a particular group. Large differences existed between groups A and B (46 species) and A and C (54 species) while fewer differences were apparent between A and D (31 species) and B and C (40 species). Fewest differences were observed between the warm water groups C, D and E, with only 12-17 species differing significantly, despite the high diversity of species at these stations.

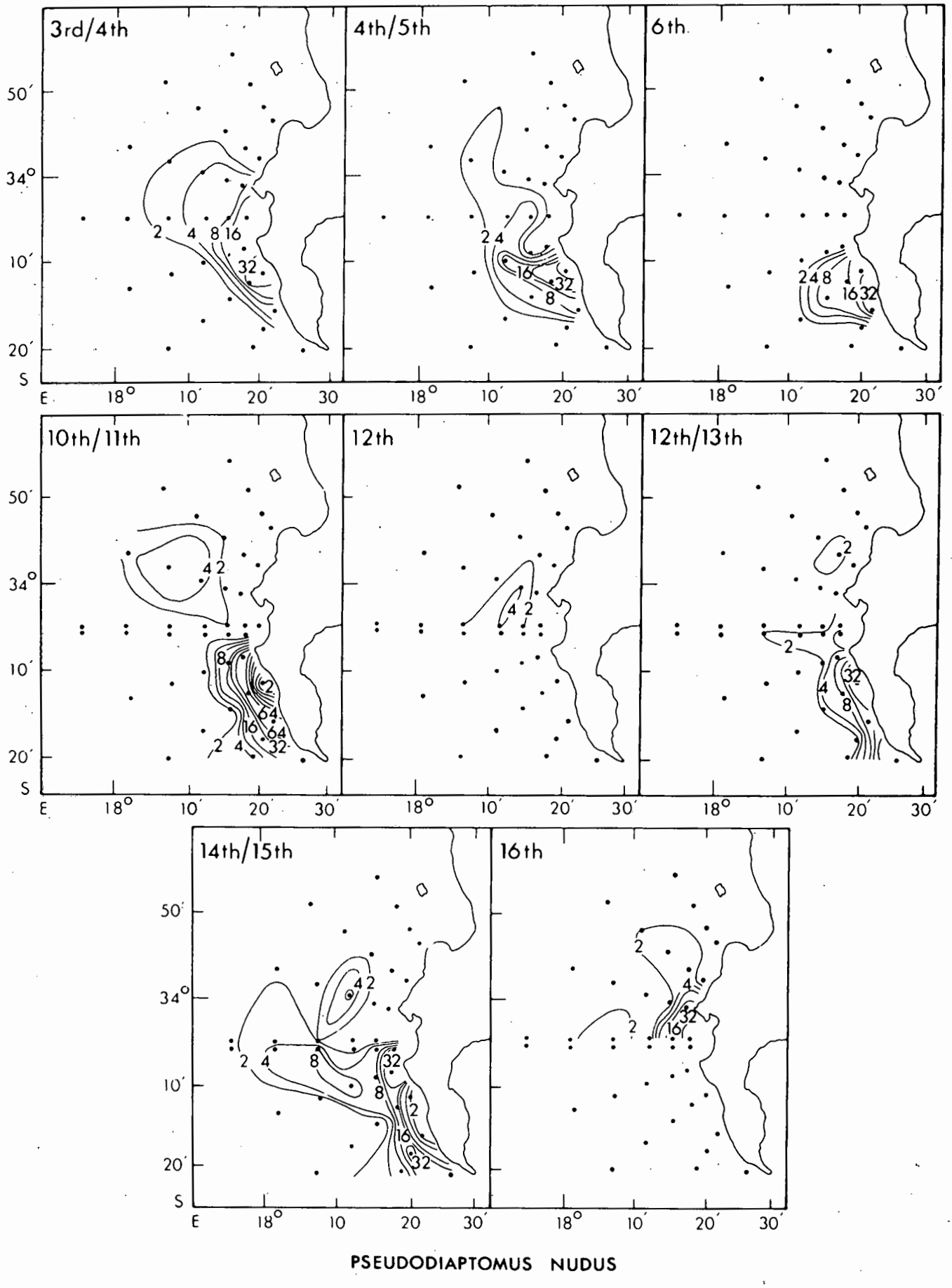
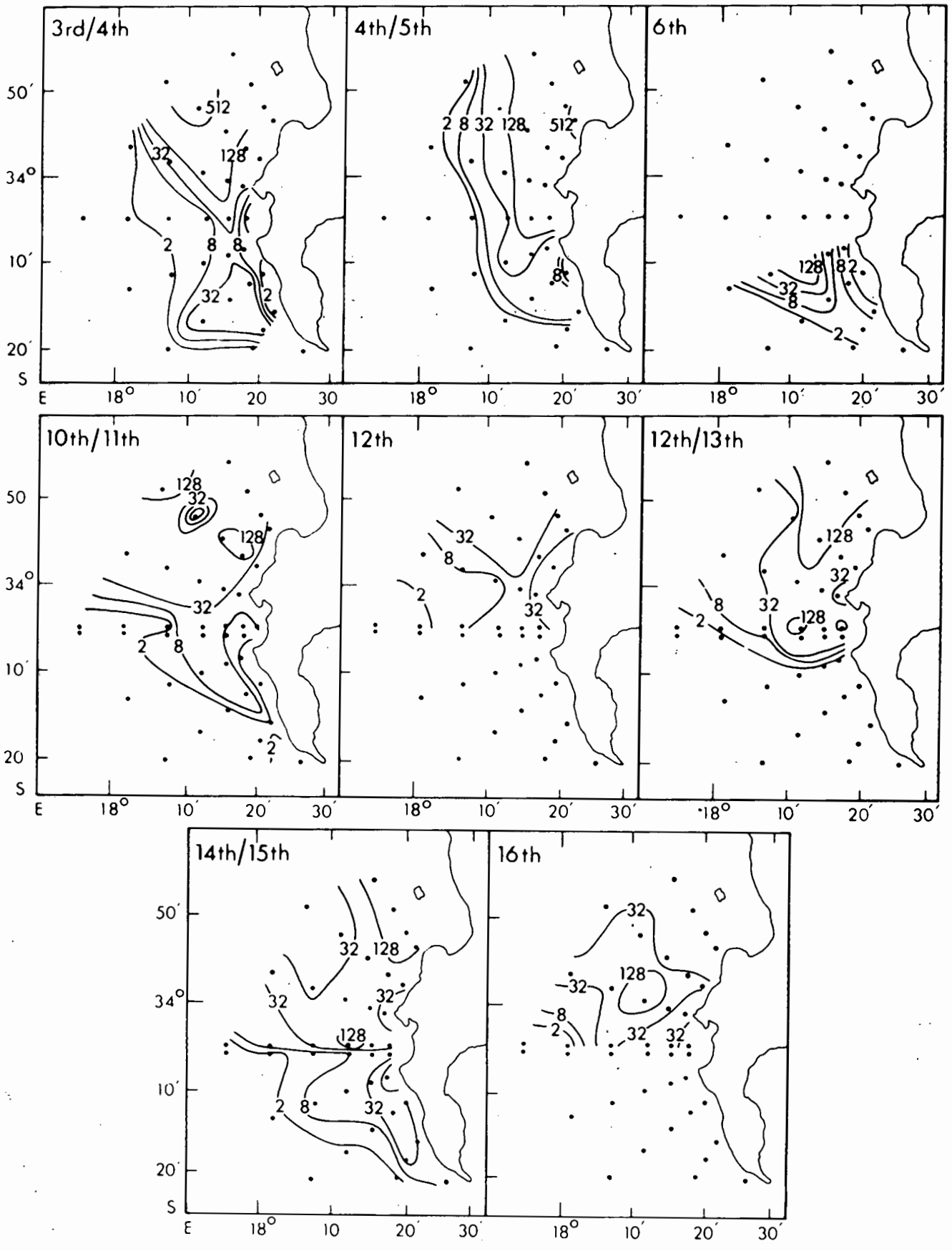


Fig. 15 Horizontal distribution of Pseudodiaptomus nudus, characteristic of Group B stations, 3rd-16th December 1969 (No. m^{-3}).



CENTROPAGES BRACHIATUS

Centropa

Fig. 16 Horizontal distribution of Centropages brachiatus, characteristic of Group A and B stations, and the most abundant cool water zooplankton (No. m^{-3}).

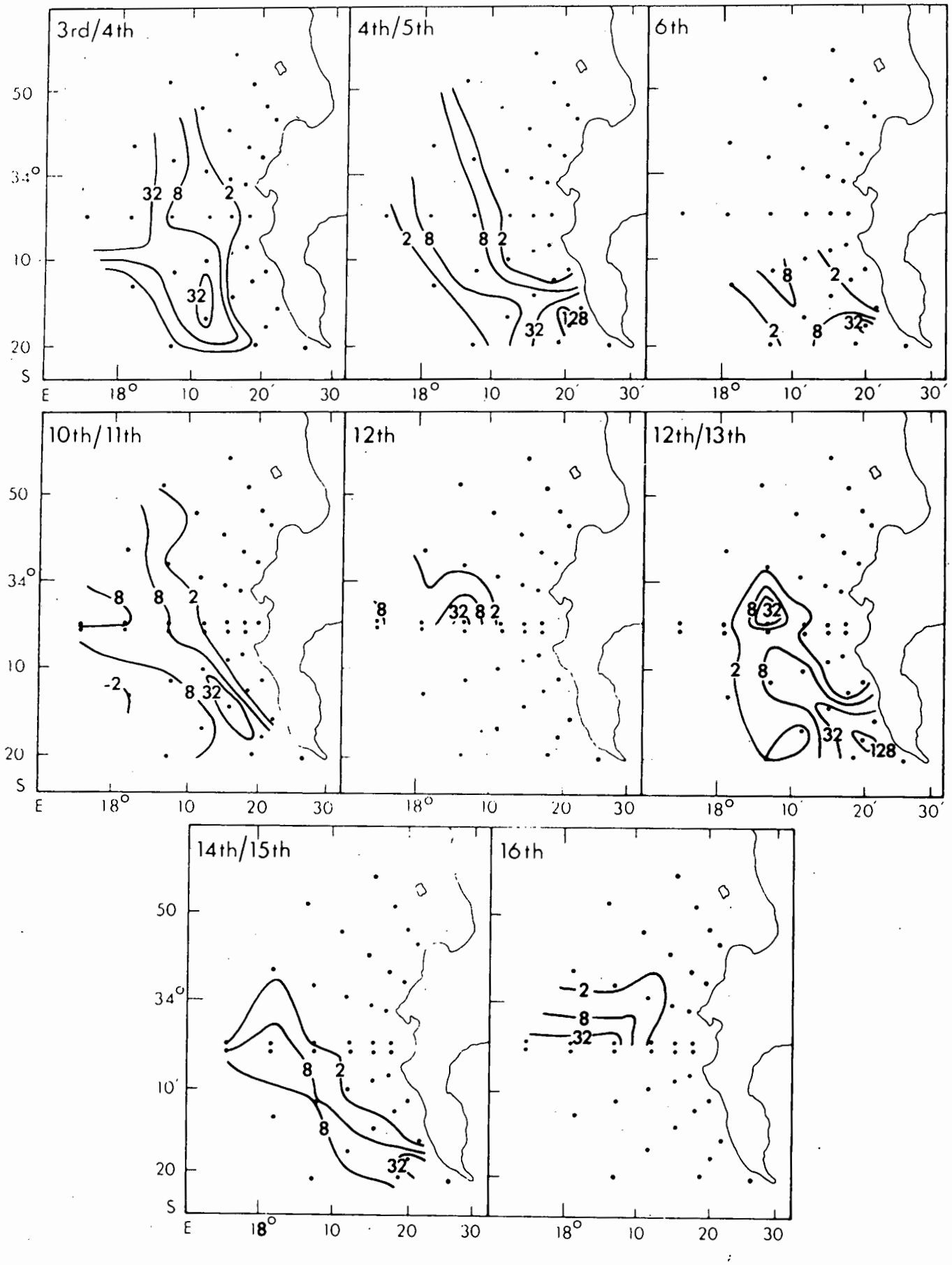


Fig. 17 Horizontal distribution of Penilia avirostris, characteristic of Group C stations and an indicator of Agulhas Bank water, 3rd-16th December 1969 (No. m^{-3}).

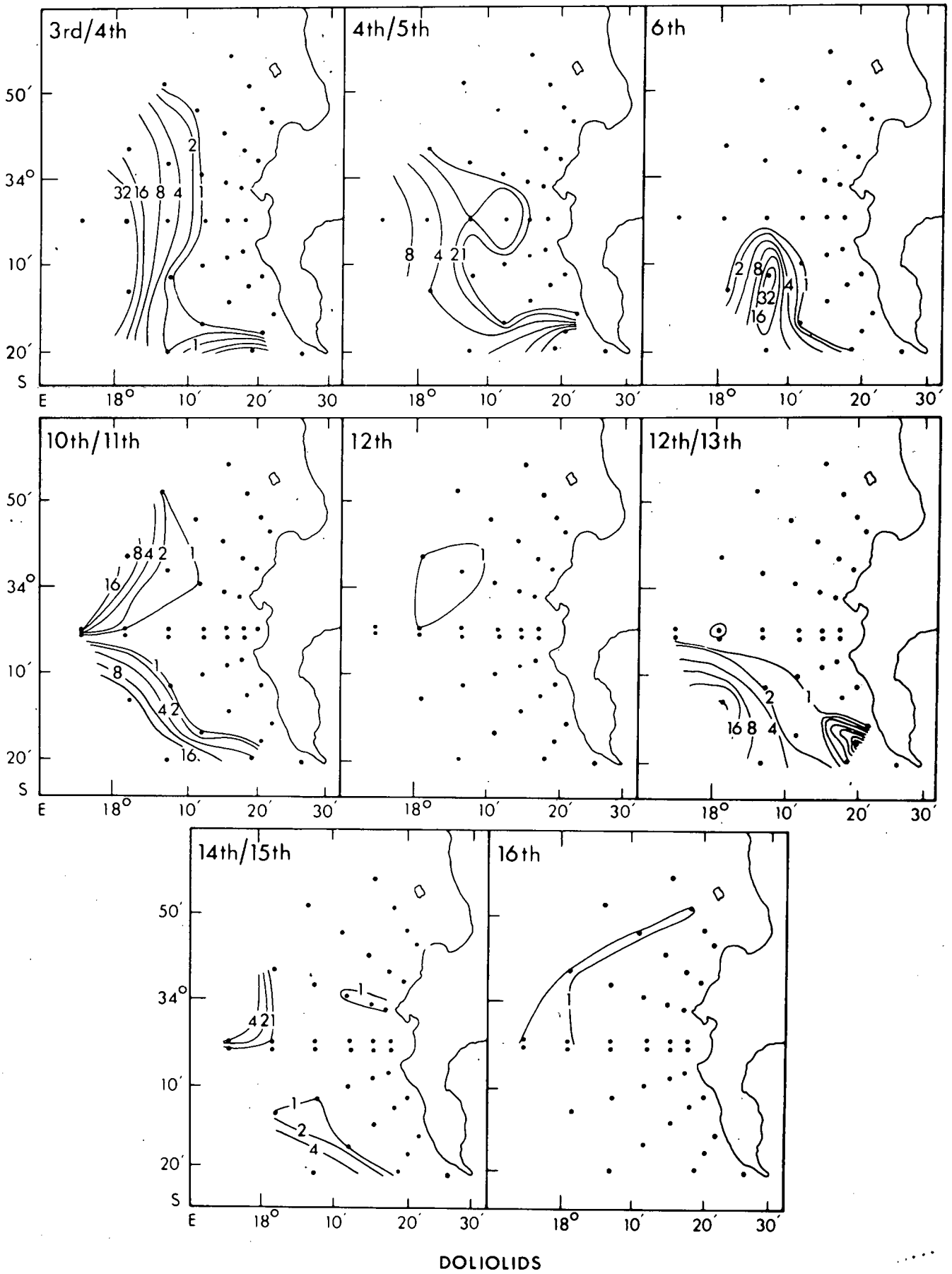


Fig. 18 Horizontal distribution of doliolids, characteristic of Groups C, D and E, 3rd-16th December 1969 (No. m^{-3}).

Few of the very abundant species showed significant differences in occurrence between the station groups Table (4). Group A stations were characterised by four species from the cool-water group, when compared with group B, while two cool water species (Bivalve juveniles and Nannocalanus) three warm water species (Centropages chierchiae, Evadne and decapod larvae (type 3)) and one frontal zone species (Pseudopiaptomus) (Fig. 15) distinguished group B. Centropages brachiatus (Fig. 16) was significantly more common in group A than in group C or D and similarly more common in group B than group C. Groups C and D are distinguished from groups A and B by Penilia (Fig. 17), Doliolids (Fig. 18), Doliolid eggs and Eucalanus attennuatus, all warm water species, yet cool water species Aetideus armatus and Microcalanus distinguished group C from D and E offshore. Gastropoda juveniles and euphausids distinguished D from C, while calyptopis larvae and Sappharina sp separated group E from C. Only Eucalanus attennuatus and Sagitta minima separated group D from E, and these two groups could be combined.

The major distinction between the groups of stations occurs between A and B, the cool water groups. and C, D, and E, representing warmer water. Some of the group B stations had a thin film of warm water in the upper layers and strong thermoclines and most of the differences between A and B are due to this and to the fact that group B stations were always sampled in daylight while group A samples were collected by day and by night. In addition, the higher chlorophyll'a' concentrations at group A stations possibly decreased the net detection range of the larger species such as Euphausia and Parathemisto and in concert with night hauls probably contributed to the greater frequency of occurrence of these animals at group A stations than group B stations. S. frederici was significantly more abundant in group B than in group A, but this was due to the chaetognaths not being identified to species until the sixth circuit (14th/15th) of the R.S. Africana II stations. All the R.S. Sardinops stations in the south were analysed fully for

TABLE 4: Characteristic Species in Groups A - E, based on $p \leq .01$ and presence in at least 80% of the samples within a group.

Species	A	B	Species	A	C
Bivalves	-	+	Centrop. brachiatus	+	-
Centrop. chierchiae	-	+	Doliolids	+	+
Decapod larvae type 3	-	+	Doliolid eggs	-	+
Euphausia lucens	+	-	Eucal. attennuatus	-	+
Euphausid nauplii	+	-	Euphausia lucens	+	-
Evadne sp.	-	+	Euphausid nauplii	+	-
Metridia lucens	+	-	Nannocalanus minor	-	+
Nannocalanus minor	-	+	Paracal. crassirostris	+	-
Parathemisto	+	-	Parathemisto	+	-
Pseudodiaptomus	-	+	Penilia	-	+
Sagitta frederici	-	+	Sagitta sp.	+	-
Total species signifi= cant at 1% level	18	32	Total species signifi= cant at 1% level	9	46
	50			55	

Species	A	D	Species	B	C
Acartia danae	-	+	Bivalves	+	-
Calanoides	+	-	Centrop. brachiatus	+	-
Centrop. brachiatus	+	-	Cypris	+	-
Doliolids	-	+	Doliolids	-	+
Doliolid eggs	-	+	Eucal. attennuatus	-	+
Evadne	-	+	Metridia lucens	-	+
Gastropoda	-	+	Paracal. crassirostris	+	-
Larval fish	-	+	Penilia	-	+
Oikopleura	-	+	Pseudopiaptomus nudus	+	-
Paracal. crassirostris	+	-	Sagitta frederici	+	-
Parathemisto	+	-	Total species signifi= cant at 1% level	9	31
Penilia	-	+			
Total species signifi= cant at 1% level	11	20		40	
	31				

TABLE 4: (cont.)

Species	C	D
Aetideus armatus	+	-
Euphausia lucens	-	+
Gastropoda	-	+
Microcalanus	+	-
Total species signifi= cant at 1% level	8	4
	12	

Species	C	E
Aetideus armatus	+	-
Calyptopis	-	+
Microcalanus	+	-
Sappharina	-	+
Total species signifi= cant at 1% level	13	4
	17	

Species	D	E
Eucal. attenuatus	-	+
Sagitta minima	-	+
Total species signifi= cant at 1% level	6	6
	12	

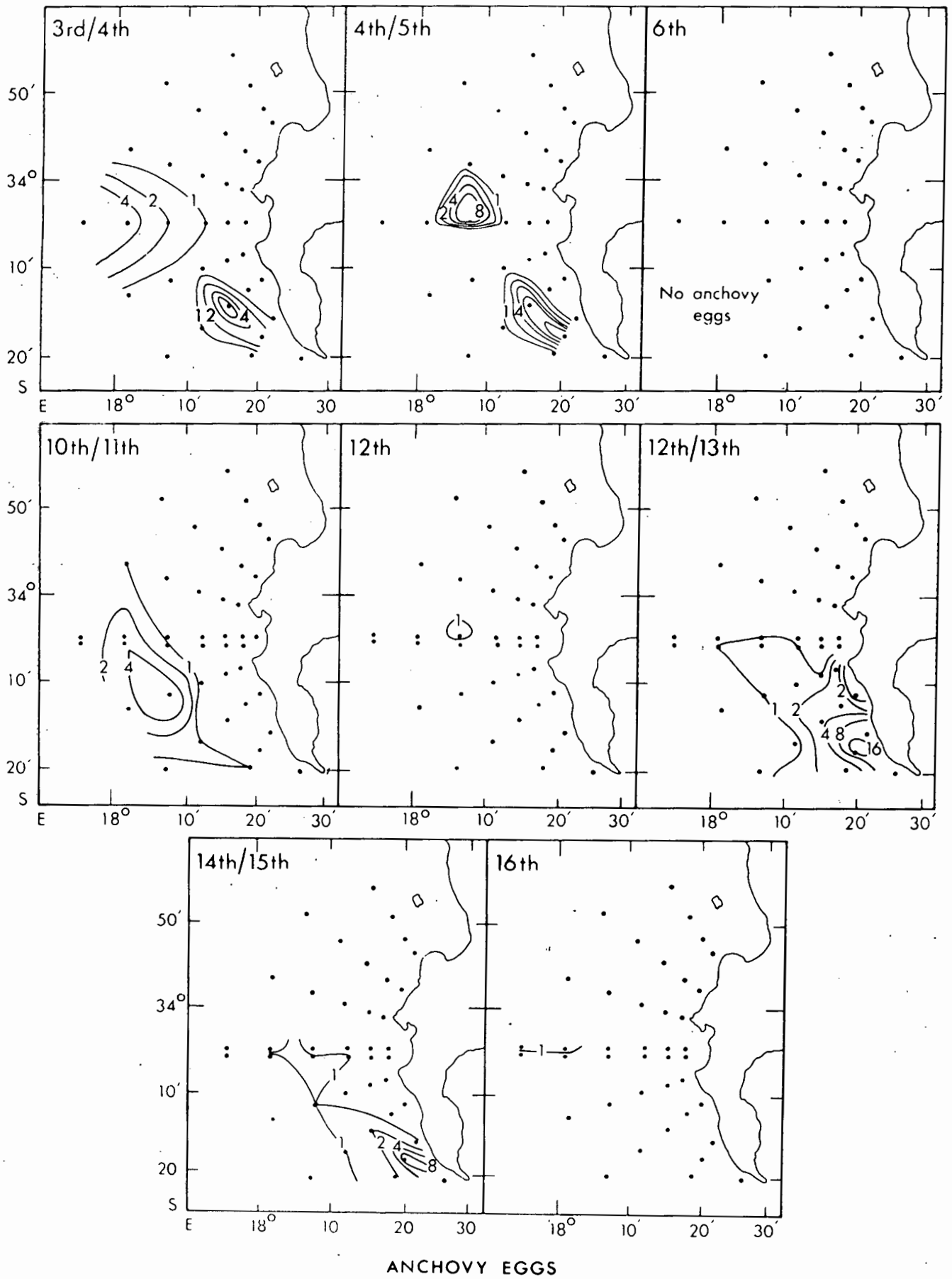


Fig. 19 Horizontal distribution of Anchovy (Engraulis capensis) eggs, 3rd-16th December 1969 (No. m^{-3}).

chaetognaths and a very clear distinction between the distributions of S. minima and S. frederici was apparent, confirming the findings of Heydorn (1959) and Masson (1974). Comparison of the distribution of S. minima, S. frederici and Sagitta spp in the northern zone shows that chaetognath concentrations were higher in the south than in the north, and the same relative distribution of species occurred, with S. frederici more common inshore and S. minima offshore. Because of incomplete analyses, the distribution of chaetognaths has not been illustrated. Although the inclusion of Sagitta spp in the numerical analysis is not strictly correct they constituted a very small proportion of the population in any one sample, and are unlikely to significantly distort the similarity coefficients.

Anchovy eggs (Fig. 19) were patchy, although restricted to group C or D samples close to the frontal zone, and showed a distribution similar to bivalves, cirripede nauplii, Calocalanus tenuis, Podon, Evadne, Penilia, Rhincalanus nauplii and Nannocalanus minor. Their concentration is undoubtedly underestimated as eggs are generally restricted to the upper layers above the thermocline (Shelton and Hutchings, 1979). Numbers per square metre ranged between 2 and 672 per sample.

These species are all common on the Agulhas Bank (De Decker, 1973) and represent a community which appears to be transported north-westwards in a narrow conduit (Bang 1976). Of this group only anchovy, as juveniles and adults, penetrate successfully into the coldest waters of the Benguela Current, while the other species either decrease in importance or remain on the outskirts of the coldest parches of upwelled water. (De Decker 1973; Unterüberbacher 1964). Nannocalanus minor, although present in the core of the cool water species group, reached maximum concentrations at group C stations. It was present at many group A stations in low numbers and in the study on the vertical distribution it was considered to be present only in mature upwelled water.

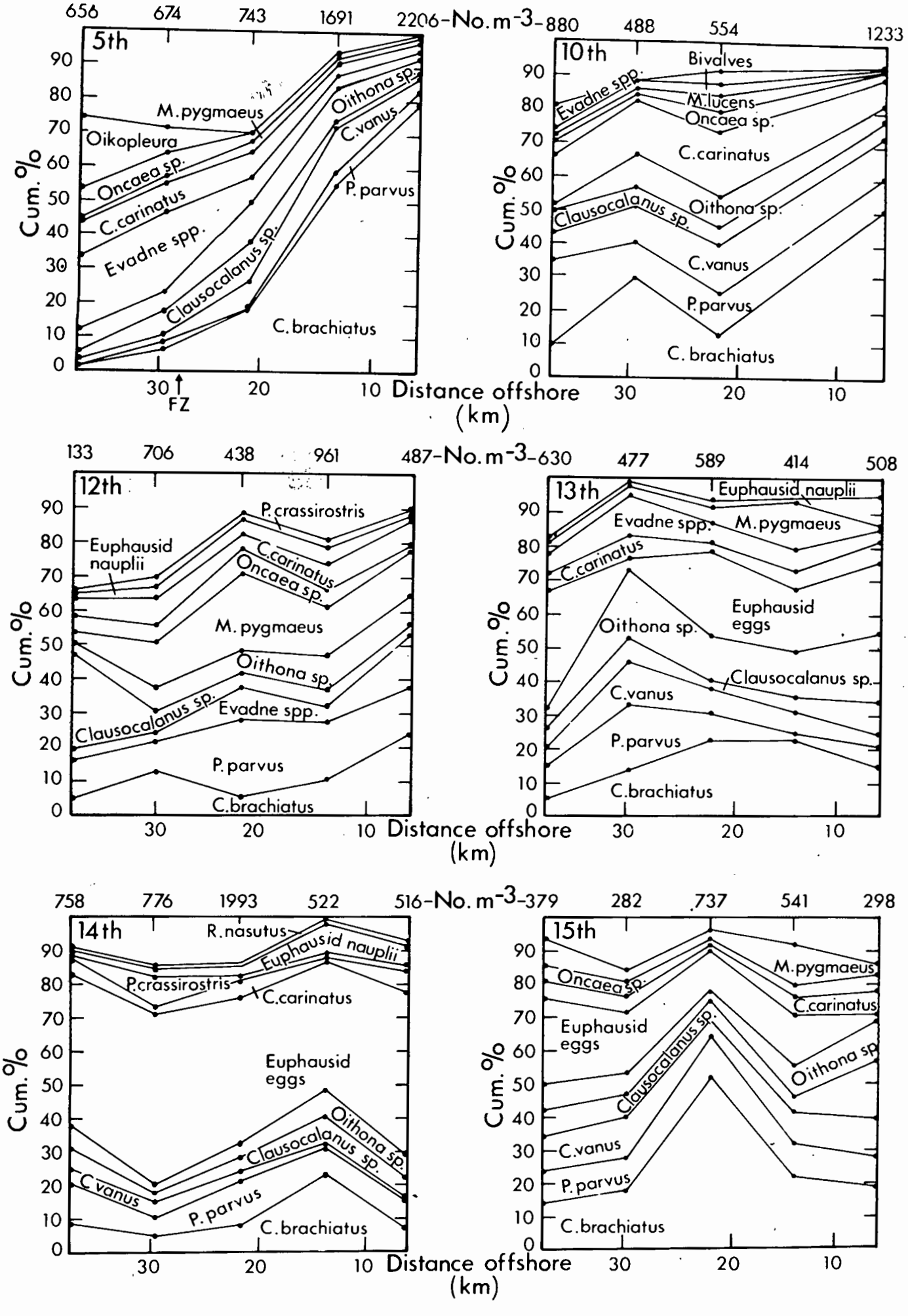


Fig. 20 Changes in relative abundance of zooplankton along line 3, 5th-15th December 1969. Numbers at top are no. m^{-3}.

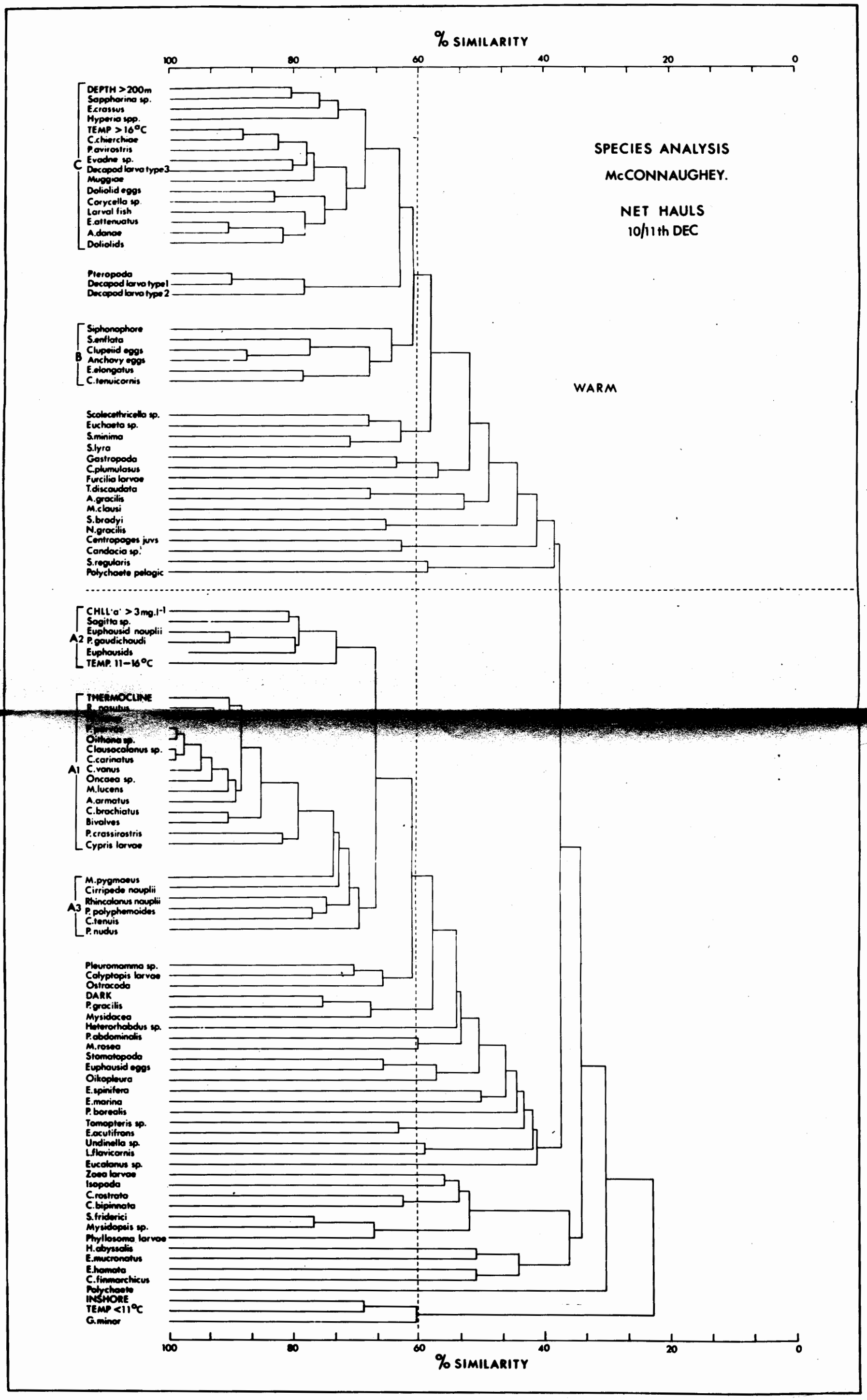


Fig. 22 Dendrogram showing species grouping based on the McConnaughey coefficient, 10th/11th December 1969.

frontal zone group was ill-defined in these analyses; certain species such as Calocalanus tenuis, Podon, cirripede nauplii and Evadne (group A3) were grouped differently with different circuits.

Further examination of the "cold water" group during separate circuits (Table 5) showed that seven species occurred within the group on every occasion. These were Rhincalanus, Oithona, Clausocalanus, Calanoides, Ctenocalanus, Paracalanus parvus and Centropages brachiatus, while a further three species, Nannocalanus, juvenile bivalves and Oncaea were absent only once. Metridia lucens and Aetideus armatus were excluded from the group when the northern half was incompletely sampled, on the 3rd/4th and the 6th December. Microcalanus was always closely linked with the group but on only four occasions was it within the 80% similarly level. Sagitta frederici and Paracalanus crassirostris always co-occurred within the group and did so on four of the eight circuits. Their centres of abundance were within the B-group of stations so whenever the southern zone alone was sampled (6th) or when strong upwelling occurred (16th) they were included in the group.

The remaining eight species only occasionally occurred within the grouping, principally when only the northern zone was sampled on the 12th and on the 16th December, when the greatest number of species were linked above the 80% similarity level.

The first 12 species in Table (5) accounted for some 70-90% of the numbers of zooplankton present at group A stations, except when large numbers of euphausid eggs were present (Fig. 20). Most of these animals persist throughout the inshore region of the Benguela Current (De Decker 1964; Kollmer 1963; Unterüberbacher 1964 and Thiriot 1977), and together with the larger euphausids, which may have been undersampled in daylight during this investigation, they constitute the main invertebrate grazers along the west coast.

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TABLE 5: "Core" Species of the Cool-Water Group, selected at 80% similarity during the 8 circuits, based on the McConnaughey Coefficient.

	Species	3rd/4th	5th	6th	10th/11th	12th	12th/13th	14th/15th	16th	Score
1.	Rhincalanus nasutus	+	+	+	+	+	+	+	+	8
2.	Oithona	+	+	+	+	+	+	+	+	8
3.	Clausocalanus sp	+	+	+	+	+	+	+	+	8
4.	Calanoides carinatus	+	+	+	+	+	+	+	+	8
5.	Ctenocalanus vanus	+	+	+	+	+	+	+	+	8
6.	Paracalanus parvus	+	+	+	+	+	+	+	+	8
7.	Centropages brachiatus	+	+	+	+	+	+	+	+	8
8.	Nannocalanus minor	-	+	+	+	+	+	+	+	7
9.	Bivalves	+	+	+	+	-	+	+	+	7
10.	Oncaea	+	+	-	+	+	+	+	+	7
11.	Metidia lucens	-	+	-	+	+	+	+	+	6
12.	Aetideus armatus	-	+	-	+	+	+	+	+	6
13.	Microcalanus pygmeaus	-	+	-	-	+	+	-	+	4
14.	Sagitta frederici	-	-	+	-	+	-	+	+	4
15.	Paracanus crassirostris	-	-	+	-	+	-	+	+	4
16.	Cypris	-	-	+	-	-	-	+	-	2
17.	Parathemisto gaudichaudi	-	-	-	-	+	-	-	+	2
18.	Sagitta m nima	-	-	-	-	-	-	+	+	2
19.	Euphausid nauplii	-	-	-	-	+	-	-	+	2
20.	Heterorhabdus sp.	-	-	-	-	-	-	-	+	1
21.	Calyptopis larvae	-	-	-	-	-	-	-	+	1
22.	Euphausids	-	-	-	-	+	-	-	-	1
23.	Euphausid eggs	-	-	-	-	+	-	-	-	1
	Number of species:	9	13	12	12	18	13	16	20	

In summary changes in the distribution of species groups were maximal along line 4 and declined progressively to the north and south. To the north, where wind stress is lessened in the lee of Table Mountain, the area is relatively unaffected by upwelling or warm water intrusions. South of line four the position of the frontal zone remained fairly constant and smaller changes in species distributions occurred. The strong upwelling experienced on the 15th/16th of December displaced some 40% of the zooplankton in the northern zone offshore without materially altering the species composition, apart from a shift of Group C stations westward and group B stations northward. It is unfortunate that it was not possible to follow the flushing of plankton from the coastal zone for a longer period.

Highest zooplankton standing stock levels were associated with group A stations (Figs. 11 and 14) while the enhanced levels parallel with the front in the southern zone comprised group B or C stations.

From the point of view of monitoring biological events after upwelling, it was obviously preferable to sample in a north westerly direction, in order to smooth out short term irregularities as much as possible, and to monitor the most abundant group of organisms which colonise the newly upwelled water.

4. CONCLUSION

4.1 THE ANNUAL CYCLE OF ZOOPLANKTON

The description of events during the December 1969 cruise explains why stationssampled one per month both by UCT (unpublished) and the Sea Fisheries Branch (1959-1969 unpublished) off the Cape Peninsula show a confused picture, with warm water species alternating with cool water species in different months. The species composition obviously depended to a large extent on the wind regime preceeding the time of sampling by a matter of perhaps 24-36 hours. There is

some shoreward movement of zooplankton during wind reversals, although the wind reversal observed in December 1969 was of short duration and the wind blew only briefly from the northwest. If sustained northwesterly or westerly winds persisted it is likely that the shoreward and southward movement of zooplankton would bring zooplankton back to the coastal area from the north and northwest and could extend southwards past the Cape of Good Hope. Tuna sportfishermen have reported the sudden appearance of "cool discoloured water" over a broad front in the area southwest of Cape Point following northwesterly winds after a spell of south-easterly winds and this water is likely to come from the north considering the limited movement of cool water westward around Cape Point.

The data also suggest that the correlation between zooplankton and phytoplankton standing crops along the length of the upwelling monitoring transect observed by Andrews et al (in press) is due to passive accumulation of organisms in the same area during upwelling rather than an active migration by mesozooplankton into patches of phytoplankton, as postulated by Cushing (1953) for the North Sea. The abundance of small animals in the upper mixed layer facilitates rapid offshore transport, ensuring at least partial co-occurrence of herbivores and phytoplankton, although their relative speeds as they drift northward appear different (Andrews et al, (in press)). The deeper distribution of larger organisms, (Euphausia lucens furcilia, Parathemisto, Metridia lucens and Aetideus armatus) is difficult to reconcile with their similar rate of movement compared to the smaller zooplankters. Their close similarity to high chlorophyll'a' concentrations suggests that they have superior swimming powers and may congregate in certain area of high phytoplankton abundance, although this co-occurrence could be on artifact due to a decrease in avoidance response of these more motile forms in turbid water.

Stahishia

Rock 'my soul

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The transport of water northwards and offshore is obviously extremely complex as plumes of cool water emanate from numerous small centres of upwelling and coalesce (Andrews and Cram, 1969; Andrews et al in press) and changes in wind regime alter the intensity and orientation of the plume. At the beginning of the upwelling period only a small proportion of the zooplankton swept offshore will encounter suitable concentrations of phytoplankton, and an even smaller proportion of the developing young stages will be successful at locating food. As light levels and the frequency of upwelling events increase, the probability of zooplankton/phytoplankton encounters also rises, ensuring a gradual increase in the zooplankton population to peak values in summer and autumn (December to March). The zooplankton observed at any time does not on its own indicate the potential growth of which it is capable, but taking phytoplankton concentrations, light and nutrient levels into account some idea of the potential can be gained. The anomalous June 1971 cruise gives further insight into the dynamics of zooplankton in this area. The standing stock observed in June was roughly double that of the previous month, yet both phytoplankton crop and potential production remained low, due possibly to low light levels (Andrews et al in press). It is unlikely that the zooplankton could have converged on the patch and grazed it down, as sampling commenced soon after the wind ceased, before phyto= plankton had time to develop high concentrations. The relative paucity of zooplankton offshore during winter as well as their lack of mobility also mitigate against active migration. It is more likely that zooplankton was physically accumulated in the area and therefore showed a limited potential for further growth due to low food concentrations, both for the adults and young.

Similar events probably occur during summer, but the phytoplankton is then able to grow vigorously and sustain the zooplankton, and is also sufficiently wide-spread to greatly increase the probability of further cohorts having enhanced survival rates,

following the reasoning of Mullin (1976). In autumn, the reverse process occurs with diminishing light levels, frequency of upwelling and phytoplankton vigour. This basic pattern of the upwelling community is altered by short term events and is dependent on the immediate history of the waters along the monitoring line, thus exposing the limitations of sampling along a single line of stations in such a complex area.

The frontal zone community off the Cape Peninsula and presumably along the frontal zone northwestwards is only likely to exist during summer months when prevailing currents move from east to west about Cape Point (Duncan and Nell 1966, Bang 1976). During winter months when onshore (westerly) winds predominate, surface currents indicate a west to -east movement, the frontal structure breaks down and upwelling activity is minimal. Oceanic water invades close to the coast and zooplankton standing stock levels decline in the vicinity of the Cape Peninsula while the Agulhas Bank species (De Decker 1973) are likely to be restricted to the east of Cape Point over the Bank itself.

The more stable conditions to the north in the northern vicinity of Cape Columbine, allow for the maintenance of higher stocks of zooplankton there compared to the area south of Dassen Island. The large shallow area of St Helena Bay, the more consistent if less dramatic upwelling, and the lack of warm water intrusions all contribute to this phenomenon, and it is not surprising that the yield of pelagic fish from the Cape Columbine area is considerably higher then from the upwelling plume off the Cape Peninsula (Centurier-Harris and Crawford 1974).

The Cape Peninsula upwelling system must contribute significantly to the enrichment of the Southern Benguela Current but the fraction of the potential productivity (calculated by Andrews et al 1970) which is lost to the euphotic zone by sinking and by non-cooccurrence of phytoplankton and grazers is extremely difficult to quantify. Walsh (1977) reports that in a steady-state upwelling situation zooplank-

ton would be transported some 190 km downstream over a period of 15 days. However without adequate means of replenishment, as shown to be the case in this study, the Cape Peninsula would be depleted of zooplankton for long periods of time subsequent to a powerful upwelling event, especially considering that the longshore flow in the coastal jet can attain 120 cm sec^{-1} (Bang and Andrews 1974). The Cape Peninsula upwelling system is clearly anomalous compared with Peru, Baja California and North West Africa, due to a combination of bottom topography, wind regime and water masses and extrapolation of models developed under steady state conditions cannot be applied successfully to our area. Changes in wind stress occur over intervals of 3-6 days and the presence of the Cape Canyon (Simpson and Forder 1968) may allow the frontal zone to move close inshore near Saldanha Bay as energy inherent in the coastal jet current is expended downwards instead of moving horizontally (Bang and Andrews 1974). This would tend to "shut off" the Cape Peninsula cell to some extent and limit the movement of zooplankton northward.

4.2 THE IMPORTANCE OF ZOOPLANKTON IN THE SOUTHERN BENGUELA CURRENT COMPARED TO OTHER AREAS

4.2.1 Standing crop

Cushing (1971) has compared the cycle of production in upwelling areas with the classic cycles in temperate zones. The spring bloom is represented by a slow upward movement of water through the euphotic zone, allowing "seeded" phytoplankton to develop rapidly as light increases, resulting in a dense bloom of algae at the centre of upwelling. Decay follows as the water is moved more rapidly offshore. Grazing is initiated some 20-30 days after the beginning of the cycle when zooplankton from temperate waters on the poleward side (downstream), as well as zooplankton brought up from depths, begin to accumulate and feed on patches of phyto= plankton, thus stimulating secondary production which results in a

rapid rise of zooplankton standing crop to levels far above those of surrounding waters. The sustained nature of the upwelling allows the zooplankton to maintain high levels throughout the upwelling season and persist in the whole zone of upwelling before being dispersed at the "other end" of the upwelling system. There is, therefore, a gradual dispersal of phytoplankton away from the regions of most intense upwelling with additional inputs at the inshore edge along the whole upwelling zone. These conditions may apply to most upwelling zones, but the southern Benguela region is clearly anomalous in several respects, the most important being the separation of cool Benguela water from cool temperate waters to the south by the intrusion of warm oligotrophic Agulhas water, which forces the Sub-tropical convergence southwards. This can be seen clearly in the illustration of Wooster and Reid (1963) (Fig. 1) which shows that even in July when the west wind drift reaches its northernmost limit, water between 10°C and 15°C is deflected southwards, separated from the South African coast by warm water, while off the west coasts of South America, North America and Europe/N.W. Afriva cool waters deflect equatorward close to the coast. This warm water, which usually persists to depths well below the euphotic zone, prevents large quantities of phytoplankton or herbivorous zooplankton from entering the Benguela Current from the south. This effect is even more marked in summer. (De Decker, 1973; Visser, 1969; Shannon, 1966).

Secondly, the presence of a tongue of warm water close to the coast as well as critically-orientated canyons pointed directly towards pronounced capes contribute to the establishment of a very high-energy situation off the Cape Peninsula (Bang, 1976) where water of less than 10°C is already uplifted some 150-200 metres to lie within 50 metres of the surface before any wind stress is applied. Couple to this tall ($>$ 1000 m) mountans close ot the coast which funnel and accelerate the wind to create stronger-than-average southeasterly winds, and it is not surprising that rates of upwelling approach

30-40 metres per day (Andrews et al 1970; Andrews, 1974). The source water of upwelling is South Atlantic Central Water (Hart and Currie, 1960; Shannon, 1966) and this displays very constant physical and chemical characteristics over different upwelling seasons (Andrews, 1974; Andrews et al in press). It is noticeably poor in phytoplankton and powerful upwelling is characterised by the appearance of clear cold blue water, with secchi disc visibility of up to 25 metres. Colonisation of this water is relatively rapid and the zone of clear water seldom extends more than six to ten kilometres from the coast. This combination of cape, canyon and rate of upwelling produces a plume of upwelled water (Walsh, 1977) rather than a longshore belt or block structure, and provides the Benguela Current with a southern boundary far mor distinct than any other major upwelling region. (Wooster and Reid, 1963; Cushing, 1971; Walsh, 1977).

Walsh (1977), reporting on results produced by SCOR W.G.36, estimates a longshore movement of up to 190 kilometres during a 15-day period of constant winds. This ought to lead to an increased adult population some 200 km downstream, assuming a generation time of 18-20 days at 15°C (Paffenhofer, 1970) as is observed off Cape Timiris. (Herbland et al 1973). Such a situation could hardly apply to the southern Benguela Current as this would lead to a marked depletion in zooplankton at the base of the plume early in the upwelling season (October to December) when in fact this does not occur. It thus implies that rates of removal from the Peninsula area are not as high or replenishment to the area from the north is more rapid than in the generalised case assumed by Walsh (1977). Replenishment from further south can be discounted. Removal rates are likely to be even higher than the rates assumed by Walsh, due to the presence of the Good Hope Jet (Bang and Andrews 1974) where equatorward speeds reach 120 cm sec^{-1}, and upwelling rates temporarily attain 4 x 10^{-2} cm per sec, double Walsh's assumed figure, although Bang (1976) cautions

against the use of such a high rate of upwelling except in limited areas, and suggests that a figure of $1,4 \times 10^{-2}$ cm/sec may be more applicable over an extended area. The rate of northward drift may decrease considerably to the north of the Cape Peninsula, where the Cape Canyon limits the offshore extent of the jet, which is itself a shelf-edge feature (Bang and Andrews (1974)). This would redirect biological material coastwards where it could be entrained in a southward flowing surface compensation current (Duncan and Neill 1966) or in the oligoxic De Decker Undercurrent (De Decker, 1970; Bang, 1976). Probably of greater importance is the change in the currents and eddies during intermittent upwelling. Bang and Andrews (1974) mention the leaking of oceanic water shorewards on relaxation of the upwelling wind stress and Andrews (1974) and Andrews et al (in press) suggest that downwelling occurs whenever onshore winds blow. Shelton and Hutchings (1979) show temperature sections during anomalous north-westerly winds in summer which strongly suggest a southerly flow inshore. Upwelling winds (southerly to easterly) seldom persist for more than five to seven days before relaxation or reversal of winds and this would facilitate the movement of zooplankton southward and shoreward.

Peterson (1976) describes the possible mechanisms for the maintenance of the five commonest copepod species the upwelling zone off Oregon, where a two-cell circulation system as well as continuity north and south exists. He demonstrates the importance of the relaxation phase in enabling the coastal zooplankton to maintain themselves.

The intermittency of the upwelling from a point source would generate a poor control of phytoplankton by zooplankton grazing (Walsh, 1977). The distribution of phytoplankton and zooplankton between the 10th and 16th December substantiate and document this clearly. The instability of the region should limit the zooplankton in the Cape Peninsula area compared with other areas, due to there being a lesser probability of zooplankton encountering

suitable food concentrations - the "ins" and "outs" of Mullin (1976). It is therefore of interest to compare the biomass of zooplankton in the southern Benguela current with other areas of upwelling, bearing in mind the problems of seeding, colonisation and replenishment which are in many ways unique to this area. Comparisons are as always confounded by the wide variety of standing stock units and sampling gear used in the different areas. Volumetric measures per unit of water filtered are generally employed, although dry weights and carbon values were also employed, so standing stock figures can be converted, with dry wet approximately 10% of displaced volume and carbon content roughly 40%-50% of the dry weight, for samples dominated by crustaceans, which often form the greatest standing stock in upwelling areas. Thus direct comparisons are only possible with the results of Herbland et al (1973) off N.W. Africa. Mesh size, however, is possibly the most important parameter in zooplankton gear to consider and most workers have used a mesh of between 100 /um (Beers et al, 1971; Smith and Whitledge, 1977) and 555 /um (Longhurst 1967; Kramer and Smith 1972). Net mesh is of critical importance because nets with mesh width above 300 /um may lose up to two-thirds of the mesozooplankton (Lasker 1970). while smaller nets with bridles can underestimate euphausid abundance, Several workers have used numerical abundance (numbers per cubic metre) as a measure of standing crop, and comparable figures for the southern Benguela Current are only available during the peak of the upwelling period, in December 1969.

Table (6) indicates that summer zooplankton levels off the Cape Peninsula are not noticeably lower than stocks in other upwelling areas, with the exception of N.W. Africa and Oregon. This differs somewhat with Cushing's (1971) estimates of zooplankton standing crop for upwelling areas. His estimate of zooplankton standing crop off N.W. Africa appear too low compared with the estimates of Smith and Whitledge (1977), Walsh (1977) and Blackburn and

TABLE 6: Comparison of zooplankton stocks in different upwelling areas and in temperate seas. Values in brackets are approximate conversions from other units of standing stock.

Area		Volume ml/1000m³	Volume ml/m²	Dry wt. mg/m³	Dry wt. mg/m²	Numbers No/m³	Numbers No./m² x10³	Gear	Mesh Width Um	Depth metres	Reference	Comments
Southern Benguela	1.	83	10	83	(1000)	300-700		WP-2	200	30-240	This report	December 1969. Mean of 227 stations.
	2.	571	24	-	2570	3525	148	"	"	42	" "	December 1969. Highest concentration of organisms.
	3.	(127)	(23)	12,7	2300			"	"	180 (mean)	Andrews et al (in press)	1970-1973 Mean dry weight along plume.
	4.	792	79	100	9962			"	"	100	Andrews et al (in press)	1971. Highest dry weight per square metre.
	5.				1090-1960			"	"	200 (mean)	Hutchings (1975)	1975. Mean of 30-34 stations, west coast monitoring repeated in October, December and March.
	6.	245						N70V	200-460	100	De Jager (1954)	Converted from settled volume by reducing to ⅓. Summer samples only. Mean values approximately ½ summer values.
	7.	157						"	"	"	De Decker (1973)	Converted from settled volume by deducing to ⅓.
	8.	320	64	104				?	?	200	Cushing (1971)	
Northern Benguela	1.	315	32					N70V	200-460	100	Kollmer (1963)	Converted from settled volume as above. Mean of 38 coastal and routine stations repeated monthly for 1958-1959.
	2.	207	20					"	"	"	Unterüberbacker (1964)	Converted from settled volumes as above 1959-1962.
	3.	(100)		10				WP-2	200	100	Wessels et al (1974)	Estimated mean depth of li hi fishing.
	4.	750	150	98				?	?	200	Cushing (1971)	
	5.			12-145				Bottle 10 ℓ			Hobson (1971)	100 ml subsample examined
Guinea	1.	770-1280						ICITA	280		Mensah (1975)	Peak values during upwelling period. Mainly Calanoides.
	2.	315	63							200	Cushing (1971)	
N.W. Africa	1.			14-130	500-8000			WP-2	200	20-50	Herbland et al (1973) Binet(1973)	Followed a drogue over nine days during peak upwelling period.
	2.		20-200					Bongo	100	100	Blackburn and Nellen (1975)	Along line of stations on 21°40'N sampled repeatedly
	3.				1600-13190			"	"	"	Smith and Whitledge (1977)	Along line of stations on 21°40'N sampled repeatedly.
	4.		25-150					"	"	"	Walsh (1977)	Pers. comm from Clutter and Blackburn. As above.
	5.		20-38					IOS/RMT	333	1000	Hargreaves(1975)	Canary Islands to Cape Blane Jan.-Feb. 1968, July 1972.
	6.	533	106					?	?	200	Cushing (1971)	

TABLE 6: (cont.)

Area		ml/1000m³	ml/m²	mg/m³	mg/m²	No/m³	No/m² x10³	Gear	Mesh Width Um	Depth metres	Reference	Comments
Oregon	1.					1000-16000		Bongo	240	80	Peterson and Miller (1975)	Median density at four stations in upwelling period.
	2.			50-200							Peterson (1976)	
	3.					365-4350		"	"	"	Peterson and Miller (1977)	Median density at four stations year round 1969-172.
	4.	500	70					?	?	140	Cushing (1971)	
California	1.	300						CALCOFI	555	140	Kramer and Smith (1972)	Zooplankton 5 ml at upwelling centres during peak upwelling. Volumes should be increased 3-fold to include mesozoo= plankton (Lasker 1970)
	2.	300	42					"	"	"	Cushing 1971	
Baja California	1.	11,5-20,8				238-280		"	"	"	Longhurst 1967	June and August 1964. In upwelled waters.
	2.	200	28					"	"	"	Cushing 1971	
Peru	1.		30-60					?	?	?	Reid 1962	
	2.		16					Ring net	240	100	Walsh et al (1971)	In upwelling plume. Mean of 58 stations.
	3.			12	1200	1000-4000		Bongo	103	100	Beers et al (1971)	In phytoplankton patch, June 1969
	4.	200	60					?	?	300	Cushing (1971)	
Fraser River Plume		50-1300						-25m²	330	100	Parsons et al (1969)	Spring - summer
North Sea					3000-10000			?	?	?	Steele (1974)	In spring - summer.

and Nellen (1975) although Hargreaves (1975) shows results which are somewhat lower than Cushing's estimates. Similarly he expresses a two-fold difference in zooplankton standing crop between S.W. Africa and the zone south of the Orange River, but this does not appear to be the case.

His estimate of generation time of about two months can be viewed against more recent work on generation lengths of temperate marine copepods (Paffenhöfer, 1970; Mensah 1975; Evans, 1977; McClaren, 1978) which show somewhat shorter generation times for Calanus species at 8-15°C, while for other genera also common in southern Benguela waters, such as Centropages, generation times of 20-25 days are estimated (McClaren 1978).

Short generation times and resistance to prolonged periods of starvation (Dagg, 1977) are probably characteristics well suited to zooplankton of unstable areas, where food is of a highly transient nature, although reaching very high concentrations. Assuming a mean generation time of 30 days for the mesozooplankton at an average standing crop of 2,3 g dry wt m^{-2} (0,92 g C m^{-2}) we can estimate a secondary production figure of some 8-11 g C m^{-2} $year^{-1}$, compared to a potential primary production of some 3,7 kg C m^{-2} (estimated actual production about one-third of this level). Even if considerable loss through sinking occurred, food is unlikely to be limiting for zooplankton in this area. The unstable environment would allow the coexistence of numerous species all with similar feeding habits (Poulet, 1978) as observed in most upwelling and inshore areas, and the limiting factor governing population size would appear to be the probability of the weakly motile organisms encountering suitable food from one generation to the next. This imposes a temperate zone type of fluctuation on the zooplankton in the southern extremity of the Benguela Current, very different from the short-term phytoplankton production cycles. North of Cape Columbine upwelling is more consistent and zooplankton levels are greater than in the Cape Peninsula to Cape Columbine area, with smaller changes in seasonal

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abundance (Sea Fisheries, unpublished data).

The values quoted in Table (6) are in some cases based on single cruises and seasonal abundance may vary 2-4 fold (Kramer and Smith 1972; Peterson and Miller, 1977; Lasker, 1970; Andrews et al in press). Estimates made with the WP-2 net are likely to undersample the larger, more mobile forms and the values may be raised by about one-third to one-half. These results emphasise the problems of replenishment of zooplankton in the Cape Peninsula are and also raise questions as to how the zooplankton population maintains reasonably high levels in this unstable environment.

4.2.2 Grazing

Beers et al (1971) estimate that in Peruvian waters in winter (June) ciliates, consuming three times their own body weight per day could account for about 15% of the daily phytoplankton production and grazing by Calanus at rates estimated using the data of Mullin and Brooks (1970), could consume only 2% of the primary production, while itself consituting 27% of the "net" zooplankton present. The total net-zooplankton grazing would be about 10% of the daily primary production. The other 75% loss was considered to be due to diffusive mixing with surrounding waters, with rates of upwelling between 17 and 35 m/day. Walsh (1975) calculated that in autumn anchoveta and zooplankton could account for 80% of the production of phytoplankton. Herbland et al (1973) consider that off Cape Timiris grazing by mesozooplankton accounted for nearly all the decline in phytoplankton standing crop, when a patch of upwelled water drifted into high concentrations of zooplankton which rapidly removed all the production as well as the accummulated biomass within a short while before the zooplankton was in turn consumed by pelagic fish. The daily ration of zooplankton was estimated to be 17-28% of its body weight per day.

Parsons et al (1969) working in the Fraser River plume, estimate the ration of Calanus christatus at 10%-60% of body carbon per day while Cal. pacificus has a ration of 15-20% and the smaller Pseudocalanus a ration of 45%.

Andrews et al (1970) estimated daily production in a 20x40 km area off the Cape Peninsula as 3166-7500 m tons C per year. If this area has a mean zooplankton stock of some 2 400 m. tons dry weight (this study), at a daily ration of 40% they could acount for 12,8%-30% of the daily production. Andrews et al (in press) estimated that zooplankton formed from 4% to 25% of the phytoplankton crop and averaged 18% of the daily potential production (approximately three-fold higher than actual production) in their seasonal study along a plume of upwelling of the Cape Peninsula. This report (West Coast monitoring cruises 1974) shows that a similar situation persists up to Cape Columbine, 100 kilometres to the north of the Cape Peninsula. Andrews (1974) and Andrews et al (in press) suggest that strong sinking motions can carry surface waters below the euphotic zone at the frontal zone, where cool waters about against warmer oceanic water. As the frontal zone has been found to recurve towards the coast in the region of the Cape Canyon, a considerable proportion of the phytoplankton production in the Cape Peninsula plume may be lost to the upper layers within a short time as it moves northwards and sinks beneath the lighter oceanic water.

4.2.3 Nutrient regeneration

As no direct measurements of nutrient regeneration have been made in this study, the importance of zooplankton as regenerators in relation to standing crop and productivity measurements in other areas will be described and the importance with regard to the local situation will be inferred from these results.

Whitledge and Packard (1971) report that zooplankton nutrient excretion is insignificant compared with uptake rates by phyto= plankton while anchovy excretion is some 10-fold higher, Herbland et al (1973) estimate that zooplankton regenerate some 28% of the phytoplankton nutrient requirements off N.W. Africa, with levels of zooplankton and phytoplankton slighter higher than levels in the southern Benguela Current (chlorophyll'a' 200-400 g m^{-2}, production 5-10 g C m^{-2} day^{-1}, mesozooplankton 30-130 mg dry wt m^{-3}). Smith and Whitledge (1977) estimate that regeneration from a large zooplankton crop (1,6 - 13,1 g dry wt m^{-2}) with a moderate level of primary production (1-3 g C m^{-2}/day, Huntsman and Barber (1977)), could supply some 25% of the total nitrogen compared with 35% from the benthos and 13% from nekton. In all, some 75% of the nitrogen could be regenerated, thus prolonging the residence time of nutrients in the euphotic zone considerably.

Without accurate data on primary production rates it is extremely difficult to anticipate the relative importance of regeneration in the southern Benguela Current although two factors merit consideration. The first is that nitrate appears to be the limiting nutrient which would imply a lack of regenerated nitrogen in the form of ammonia or urea, in the Cape Peninsula area (Andrews et al (in press)). The second is the presence of oligoxic water (De Decker 1970) which extends southwards from S.W. Africa as a narrow band on the shelf and is occasionally entrained into the euphotic zone (Sea Fisheries Branch, unpublished data). Considering the high rates of upwelling, the close proximity of the oligoxic water to the surface and the small zooplankton crop relative to the phytoplankton, zooplankton regeneration is likely to be of limited importance in the southern Benguela upwelling system.

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4.2.4 Food potential for pelagic fish

There is no doubt that the pelagic fish in upwelling areas are important consumers of both zooplankton and phytoplankton (Davies, 1957; Cushing, 1971; Walsh, 1977) changing their mode of feeding to whatever is most abundant at the time. Both off Peru and in the Benguela the commonest species of zooplankton occur most frequently in the stomach contents of adult anchovy or pilchards. (Rojas de Mendiola 1975; Lazarus 1975; King and McCleod 1976). Arthur (1976) shows that the diet of developing larvae of Sardinops, Engraulis and Trachurus off California consists largely of young stages of copepods. As concentrations of these young stages are critical for successful feeding (O'Connell and Raymond. 1970) it is reasonable to assume that the commonest organisms produce the large numbers of eggs and nauplii necessary to maintain the developing young fish. Interactions across the frontal zone between larval fish on the warm water side and the young stages of zooplankton on the cool water side should prove of interest in our area. As juveniles, pilchards and anchovy penetrate close to the coast into the coolest waters (Stander and Le Roux, 1968) and the proportion of phytoplankton in their diet increases as the gill-rakers develop. During this phase of rapid growth, when numbers are declining, the maximum biomass of the cohort can be expected (P.E. Smith pers. comm) and it is likely that fluctuations in fish recruitment can be expected to have strong links to the availability of the zooplankton resource in these nursery areas.

The adaptation of the different organisms to life in turbulent, unstable waters is a subject gradually becoming more important, as the initial dramatic results of upwelling research are viewed with proper perspective. Despite the enormous funds and effort devoted to the study of the mechanisms of upwelling there has been little direct application of the results of mainly shortterm experiments to the management of fisheries within upwelling zones, and management advice has not benefitted as much as could be expected

from the research effort. The key to these unstable areas is in a study of the life cycles of individuals at all levels in the food chain, ranging from colonisation and succession of phytoplankton species in upwelled waters to the detailed life history of the pelagic and mesopelagic fishes which live in the upwelling zones. This presupposes a detailed knowledge of the prevailing currents in the area during different meteorological events and during different seasons, which at present is unavailable for the southern Benguela Current region.

This report represents the first quantitative study of mesozooplankton in the Benguela Current and objective methods of classification were used to separate communities of organisms and relate these to a comprehensive set of hydrological and biological parameters. It has been shown that the location of the study area at the southern extremity of the Benguela Current imposes severe restrictions on the movements of animals and possible mechanisms for the maintenance of the cool-water population have been outlined. These will be useful in the planning of further research on zooplankton in the area.

Because of the rapid, erratic changes in the hydrology, the tracing of cohorts in natural population is likely to be difficult and much work on captive laboratory populations will be necessary to evaluate the role of zooplankton grazers and nutrient regenerators in the southern Benguela.

Zooplankton occupies a central position in the pelagic food web of the southern Benguela Current and fluctuations in the zooplankton population would have effects both on phytoplankton and on pelagic fish stocks.

Monitoring of the important species identified in this report and more detailed information on their life cycles are necessary for a better understanding of the upwelling ecosystem of the southern Benguela Current.

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APPENDIX I

A list, in sequence, of all stations begun each day of the 1969 Upwelling Cruise by R.S. Sardinops (s---) and R.S. Africana II (a---). The first figure refers to circuit number, the second to line number and the third to station.

)ec.	2nd	3rd	4th	5th	6th	10th	11th	12th	13th	14th	15th	16th
	s155	s281	s373	s473	s573	s681	s655	s781	s755	s881	s855	a746
	s154	s273	s372	s472	s572	s673	s654	s773	s754	s873	s854	a745
	s153	s272	s371	s471	s571	s672	s653	s772	s753	s872	s853	a744
	s152	s271	s361	s461	s561	s671	s652	s771	s752	s871	s852	a743
		s261	s362	s462	s562	s661	s651	s761	s751	s861	s851	a742
		s262	s363	s463	s563	s662	s641	s762	s741	s862	s864	a741
		s263	s364	s464	s564	s663	s642	s763	s742	s863	s845	
		s264	s365	s465	s565	s664	s643	s764	s743	s864	s844	
		s265	s355	s455	s555	s665	s644	s765	s744	s865	s843	
		s251	s354	s454	s554	a311	s645	a422	s745	a611	s842	
		s252	s353	s453	s553	a312	s646	a421	s746	a612	s841	
		s253	s352	s452	s552	a313	a333	a431	a512	a613	a644	
		s254	s351	s451	s551	a314	a334	a432	a513	a614	a643	
		s255	a146	a223		a325	a335	a433	a514	a625	a642	
		a124	a145	a222		a324	a346	a434	a525	a624	a641	
		a123	a144	a221		a323	a345	a435	a524	a623	a711	
		a122	a143	a231		a322	a344	a446	a523	a622	a712	
		a121	a142	a232		a321	a342	a445	a522	a621	a713	
		a135	a141	a233		a331	a341	a441	a521	a631	a714	
			a211	a234			a340	a442	a531	a632	a725	
			a212	a235			a411	a443	a532	a633	a724	
			a213	a246			a412	a444	a533	a634	a723	
			a214	a245			a413	a511	a534	a635	a722	
			a225	a244			a414		a535	a646	a721	
			a224	a243			a425		a545	a645	a731	
				a242			a424		a544		a732	
				a241			a423		a543		a733	
									a542		a734	
									a541		a735	

APPENDIX 2

Zooplankton samples collected during December 1969
Africana II Stations

Station	Sounding (m)	Depth fished (m)	Vol. filtered m^3	Disp vol. $m\ell\ m^{-2}$	Vol. ratio small/total	Wet wt. gm^{-2}	Dry wt. gm^{-2}
Circuit 1							
124	126	103-0	25,83	25,68		31,84	2,92
123	96	98-0	23,70	20,72		27,12	2,40
122	82	80-0	19,40	14,52		16,80	2,12
121	67	65-0	16,00	20,80		23,28	2,76
135	181	94-0	23,43	15,24		11,92	0,82
146	248	300-60	55,50	13,60		9,52	1,38
146	248	52-0	13,02	18,00		21,92	1,42
145	220	167-0	59,29	19,36		15,92	1,91
144	196	220-0	52,27	13,68		12,16	1,02
143	161	123-0	30,83	18,80		9,20	1,72
143	161	50-0	12,50	5,20		4,16	0,45
142	132	125-0	31,25	7,64		9,76	0,65
141	73	67-46	5,25	2,80		3,92	0,25
141	73	48-0	12,08	3,92		7,04	0,47

Zooplankton samples collected during December 1969
Africana II Stations

Station	Sounding (m)	Depth fished (m)	Vol. filtered m^3	Disp vol. $m\ell\ m^{-2}$	Vol. ratio small/total	Wet wt. gm^{-2}	Dry wt. gm^{-2}
Circuit 2							
211	44	42-0	10,41	23,60		29,78	2,57
212	58	60-0	14,80	13,24		14,24	1,55
213	73	77-0	19,17	1 ,40		13,68	1,33
214	82	82-0	20,38	12,00		12,24	1,65
225	137	140-0	34,97	6,96		8,72	0,70
224	124	127-0	31,67	13,80	0,5	15,76	2,04
223	89	100-0	25,00	33,20	0,5	37,44	4,39
222	87	88-0	21,87	31,56	0,3	36,00	3,95
221	67	68-0	17,08	26,40	0,5	28,40	3,48
231	96	92-0	22,91	64,40	0,2	72,00	7,93
232	108	114-0	28,54	28,40		31,92	3,31
233	122	121-0	30,19	12,60		13,20	1,25
234	163	160-0	38,22	9,80		13,20	0,67
235	187	180-0	42,91	8,92		9,44	0,79
246	247	240-0	56,96	9,20		15,20	0,56
245	217	210-0	49,93	11,20		8,96	0,62
244	185	180-0	43,75	9,88		6,26	0,78
243	152	150-0	35,88	12,40		12,24	1,18
243	152	50-0	12,00	7,20		8,40	0,71
243	152	82,50	7,00	3,64		3,52	0,34
242	113	110-0	26,51	26,32	0,7	28,16	3,16
241	78	78-0	19,45	68,00	0,2	67,36	10,98

Zooplankton samples collected during December 1969
Africana II Stations

Station	Sounding (m)	Depth fished (m)	Vol. filtered m^3	Disp Vol. $m\ell\ m^{-2}$	Vol. ratio small/total	Wet wt. gm^{-2}	Dry wt. gm^{-2}
Circuit 3							
311	45	40-0	10,00	1,80		2,40	0,20
312	56	58-0	14,58	4,40		4,80	0,38
313	69	75-0	18,75	6,76		0,72	0,07
314	84	75-0	18,75	3,76		5,52	0,63
325	137	117-0	29,17	11,52		14,24	1,13
324	128	128-0	31,96	5,28		13,68	0,41
323	91	75-0	18,75	11,20		11,20	1,60
322	80	87-0	21,85	5,00		6,32	0,48
321	68	65-0	15,97	5,64		6,40	0,49
331	84	80-0	19,49	6,56		7,92	0,70
333	120	115-0	27,68	14,60		13,60	1,29
334	160	137-33	26,02	15,60		14,24	2,20
334	160	44-0	11,05	8,00		9,76	1,01
335	184	143-0	35,83	24,96	0,6	25,52	4,07
346	247	220-0	54,87	10,80		8,32	0,71
345	216	220-0	52,27	9,20		10,56	0,64
344	192	200-0	47,59	14,00		12,24	1,14
342	126	130-0	32,42	6,96		9,60	0,80
341	84	83-0	20,83	3,52		3,28	0,29
340	53	50-0	12,46	2,00		2,32	0,21

Zooplankton samples collected during December 1969
Africana II Stations

Station	Sounding (m)	Depth fished (m)	Vol. filtered m^3	Disp vol. $m\ell\ m^{-2}$	Vol. ratio small/total	Wet wt. gm^{-2}	Dry wt. gm^{-2}
Circuit 4							
411	51	45-0	11,29	4,20		4,80	0,38
412	57	54-0	13,54	2,40		2,72	0,39
413	60	54-0	13,54	3,60		3,36	0,37
414	79	77-0	19,17	5,80		7,04	0,53
425	135	130-0	31,20	14,80		15,84	1,98
424	124	122-0	30,41	16,80		20,16	2,89
423	95	102-0	25,42	9,92		12,24	1,09
422	80	77-0	19,17	5,80		9,52	0,93
421	69	60-0	15,08	6,00		7,04	0,69
431	95	90-0	22,54	6,88		12,72	0,78
432	109	108-50	14,37	4,40		3,92	0,21
432	109	47-0	11,84	12,96		8,60	1,15
432	109	92-0	22,91	9,20		10,72	0,82
433	128	125-0	30-02	8,80		8,24	0,98
434	163	150-0	35,88	8,16		8,64	0,73
435	182	174-0	43,46	4,80		4,80	0,31
446	234	230-0	54,61	10,36		9,76	0,67
445	204	200-0	47,59	8,52		12,16	0,72
444	179	175-0	41,73	24,12		30,00	3,44
443	146	140-0	34,96	10,08		11,04	1,23
442	104	100-0	24,17	4,20		4,88	0,77
441	80	63-0	15,75	5,68		12,72	0,46

Zooplankton samples collected during December 1969
Africana II Stations

Station	Sounding (m)	Depth fished (m)	Vol. filtered m^3	Disp vol. $m\ell\ m^{-2}$	Vol. ratio small/total	Wet wt. gm^{-2}	Dry wt. gm^{-2}
Circuit 5							
511	49	45-0	11,29	1,20		3,92	0,41
512	53	50-0	12,50	1,04		3,84	0,41
513	69	39-0	9,79	12,32		14,16	1,34
514	80	75-0	18,75	15,52		16,08	2,27
525	128	125-0	37,05	6,64		6,16	0,64
524	126	130-0	31,20	12,40		12,08	1,03
523	95	95-0	23,00	10,44		12,64	1,20
522	80	75-0	18,32	6,36		8,96	0,95
521	66	60-0	14,80	4,40		5,68	0,48
531	90	75-0	18,32	5,20		8,80	0,59
532	90	75-0	18,32	8,20		8,00	0,72
533	117	112-0	26,98	10,00		12,00	1,51
534	153	150-0	35,88	15,16		15,84	1,60
535	181	175-0	41,73	2,08		8,96	1,68
545	212	205-0	48,76	8,72		10,56	0,83
544	192	185-0	44,08	40,96	0,2	42,24	4,49
543	159	150-0	35,88	27,28	0,5	27,04	3,01
542	130	125-0	30,02	19,28	0,5	18,32	3,00
541	79	70-0	17,14	16,40	0,5	18,40	2,45

Zooplankton samples collected during December 1969
Africana II Stations

Station	Sounding (m)	Depth fished (m)	Vol. filtered m^3	Disp vol. $m\ell\ m^{-2}$	Vol. ratio small/total	Wet wt. gm^{-2}	Dry wt. gm^{-2}
Circuit 6							
611	51	45-0	11,29	6,40		7,36	0,89
612	58	53-0	13,16	14,40		16,08	2,00
613	71	65-0	15,97	13,88		13,36	2,14
614	82	75-0	18,32	16,60		16,40	2,50
625	133	130-0	31,20	25,92		24,64	0,38
624	128	125-0	30,02	11,68		6,56	0,71
623	88	80-50	7,78	1,48		1,44	0,14
623	88	50-0	12,46	5,16		6,00	0,40
622	82	75-0	18,31	12,80		8,64	0,46
621	66	60-0	14,80	4,20		4,64	1,58
631	96	90-0	21,83	10,00		8,96	0,85
632	104	100-0	24,17	7,60		8,08	0,67
633	124	120-50	17,14	3,56		2,96	0,30
633	124	50-0	12,46	8,40		8,88	0,70
634	159	129-0	32,27	13,00		11,36	1,28
635	184	180-0	42,91	10,60		14,32	1,03
646	250	250-0	59,30	11,28		11,36	0,71
645	217	220-0	52,27	20,72		55,36	2,23
644	187	180-0	42,91	54,16		58,72	8,76
643	146	140-50	21,83	7,28	0,5	8,40	0,74
643	146	50-0	12,46	18,40	0,5	19,92	2,81
642	129	125-0	30,26	10,20		12,72	0,94
641	82	75-0	18,32	7,20		7,84	0,43

Zooplankton samples collected during December 1969
Africana II Stations

Station	Sounding (m)	Depth fished (m)	Vol filtered m^3	Disp vol. $m\ell\ m^{-2}$	Vol. ratio small/total	Wet wt. gm^{-2}	Dry wt. gm^{-2}
Circuit 7							
711	42	35-0	89,48	1,80		1,28	0,07
712	51	45-0	11,29	2,40		2,72	0,18
713	71	68-0	16,68	5,20		6,56	0,27
714	82	75-0	18,32	2,80		2,56	0,25
725	128	120-0	28,85	10,00		10,64	1,00
724	122	120-0	28,85	10,40		12,72	0,69
723	93	90-0	21,83	5,60		4,80	0,52
722	86	80-0	19,49	7,80		8,32	1,08
721	68	65-0	15,97	3,20		3,84	0,22
731	95	100-0	24,17	6,40		5,76	0,45
732	104	105-0	25,34	11,00		10,64	1,11
733	122	120-0	28,85	17,60		20,32	2,01
734	164	160-0	38,22	21,60		25,44	2,78
735	183	180-0	42,91	16,40		18,32	1,79
746	247	240-0	56,95	17,00		13,68	1,62
745	214	200-0	47,59	13,08		14,88	1,33
744	186	180-0	42,91	17,00		17,76	1,45
743	148	150-0	35,88	11,20		12,56	0,88
742	108	110-0	26,51	12,00		14,24	1,73
741	69	70-0	17,14	11,40		12,24	1,25

Zooplankton samples collected during December 1969
R.S. Sardinops Stations

Station	Sounding (m)	Depth fished (m)	Vol. filtered m^3	Disp vol. $m\ell\ m^{-2}$	Vol. ratio small/total	Wet wt. gm^{-2}	Dry wt. gm^{-2}
Circuit 1							
155	240	235-0	62,47	5,12		4,60	0,38
154	226	220-0	58,00	6,80		7,76	0,63
153	162	155-0	40,00	15,20		15,00	1,71
152	91	85-0	20,00	10,80		10,80	1,07

Zooplankton samples collected during December 1969

R.S. Sardinops Stations

Station	Sounding (m)	Depth fished (m)	Vol. filtered m^3	Disp vol. $m\ell\ m^{-2}$	Vol. ratio small/total	Wet wt. gm^{-2}	Dry wt. gm^{-2}
Circuit 2							
281	56	50-0	10,21	6,40		7,24	0,73
273	146	140-0	33,09	12,08		13,32	1,09
272	55	50-0	10,21	9,60		9,40	0,83
271	36	30-0	4,56	4,20		3,20	0,27
261	27	22-0	2,30	7,24		6,40	0,35
262	48	45-0	8,79	7,20		5,36	0,42
263	109	104-0	25,46	13,20		12,48	1,07
264	240	235-0	62,47	6,40		5,60	0,44
265	263	250-0	66,70	7,08		7,60	0,59
251	36	30-0	4,56	8,72		9,60	0,41
252	91	85-0	20,09	8,60		9,64	0,94
253	164	160-0	41,28	10,40		12,36	0,99
254	226	220-0	58,23	13,60		15,52	1,32
255	240	235-0	62,47	7,20		7,60	0,83

Zooplankton samples collected during December 1969
R.S. Sardinops Stations

Station	Soun= ding (m)	Depth fished (m)	Vol. filtered m^3	Disp vol. $m\ell\ m^{-2}$	Vol. ratio small/total	Wet wt. gm^{-2}	Dry wt. gm^{-2}
Circuit 3							
373	157	140-0	30,09	8,40		9,60	0,93
372	58	55-0	11,62	12,00		11,96	0,94
371	36	32-0	5,12	2,84		2,40	0,21
361	27	22-0	2,30	5,60		4,60	0,29
362	54	50-0	10,21	8,08		7,20	0,76
363	109	105-0	25,73	11,12		10,00	1,04
364	240	235-0	62,47	12,00		13,12	0,89
365	265	260-0	69,53	9,20		9,68	0,60
355	245	245-0	65,30	8,20		8,24	0,38
354	226	220-0	58,23	10,20		11,24	0,78
353	164	160-0	41,28	18,20		20,80	1,58
352	91	85-0	20,09	6,60		6,84	0,72
351	36	33-0	5,40	2,72		2,32	0,15

Zooplankton samples collected during December 1969

R.S. Sardinops Stations

Station	Sounding (m)	Depth fished (m)	Vol. filtered m^3	Disp vol. $m\ell\ m^{-2}$	Vol. ratio small/total	Wet wt. gm^{-2}	Dry wt. gm^{-2}
Circuit 4							
473	146	125-0	31,39	7,20		6,76	0,60
472	50	45-0	8,79	8,00		8,80	0,49
471	36	30-0	4,56	2,40		2,96	0,24
461	23	20-0	1,73	3,00		3,12	0,25
462	50	45-0	8,79	8,40		8,32	0,59
463	109	105-0	25,74	9,60		10,60	0,95
464		235-0	62,47	SAMPLE DISCARDED			
465	263	258-0	68,96	9,00		8,00	0,74
455	240	235-0	62,47	5,60		6,40	0,37
454	226	220-0	58,23	10,08		11,60	0,73
453	164	160-0	41,28	16,80		18,76	1,98
452	91	85-0	20,09	32,08	0,3	32,08	5,26
451	36	33-0	5,40	2,84		2,80	1,31

Zooplankton samples collected during December 1969
R.S. Sardinops Stations

Station	Sounding (m)	Depth fished (m)	Vol. filtered m^3	Disp vol. $m\ell\ m^{-2}$	Vol. ratio small/total	Wet wt. gm^{-2}	Dry wt. gm^{-2}
Circuit 5							
573	146	140-0	35,63	7,28		8,80	0,69
572	50	45-0	8,79	4,40		4,40	0,33
571	36	33-0	5,40	4,40		4,80	0,24
561	27	24-0	2,86	4,96		5,00	0,33
562	48	45-0	8,79	5,88		6,40	0,56
563	109	104-0	25,46	22,28	0,37	23,56	2,54
564	240	235-0	62,47	10,92		10,48	0,89
565	263	260-0	69,53	8,32		7,60	0,45
555	240	235-0	62,47	8,88		8,84	0,68
554	226	223-0	59,08	14,80		14,04	1,29
553	158	123-0	30,83	20,84	0,58	20,84	2,46
552	82	78-0	18,12	5,60		6,08	1,04
551	34	30-0	4,56	2,00		1,40	0,09

Zooplankton samples collected during December 1969
R.S. Sardinops Stations

Station	Sounding (m)	Depth fished (m)	Vol. filtered m^3	Disp Vol. $m\ell\ m^{-2}$	Vol. ratio small/total	Wet wt. gm^{-2}	Dry wt. gm^{-2}
Circuit 6							
681	46	42-0	7,95	6,00		4,08	0,29
673	146	140-0	35,63	8,40		10,40	1,18
672	50	45-0	8,79	5,96		6,00	0,50
671	36	30-0	4,56	4,00		2,92	0,17
661	27	24-0	2,86	3,60		2,08	0,19
662	50	47-0	9,36	5,60		4,84	0,53
663	109	105-0	25,74	11,20		11,24	1,03
664	240	235-0	62,47	10,32		9,60	0,54
665	263	260-0	69,53	6,76		5,60	0,78
655	240	240-0	63,88	12,80		10,68	0,98
654	226	220-0	58,23	10,00		8,76	0,78
653	159	155-0	39,87	11,60		13,28	1,43
652	90	85-0	20,09	6,00		8,40	0,81
651	36	33-0	5,40	5,20		7,92	0,74
641	77	75-0	17,27	5,28		6,36	0,46
642	130	125-0	31,39	6,08		7,64	0,77
643	160	155-0	39,87	8,80		11,52	1,27
644	197	194-0	50,88	10,00		11,92	0,90
645	224	220-0	58,23	7,20		7,88	0,45
646	250	245-0	65,29	6,88		7,68	0,44

Zooplankton samples collected during December 1969
R.S. Sardinops Stations

Station	Sounding (m)	Depth fished (m)	Vol. filtered m^3	Disp vol. $m\ell\ m^{-2}$	Vol. ratio small/total	Wet wt. gm^{-2}	Dry wt. gm^{-2}
Circuit 7							
781	45	42-0	7,93	3,60		4,88	0,44
773	146	130-0	32,81	4,81		6,20	0,51
772	34	30-0	4,56	2,80		4,44	0,25
771	27	25-0	3,14	1,20		3,16	0,12
761	27	25-0	3,14	5,28		7,56	0,78
762	50	45-0	8,79	2,80		4,80	0,28
763	109	105-0	25,74	6,32		8,20	0,79
764	240	230-0	61,05	5,28		7,60	0,44
765	263	258-0	68,96	3,64		6,28	0,36
755	240	235-0	62,47	4,40		5,12	0,44
754	226	220-0	58,23	5,60		8,28	0,56
753	159	155-0	39,87	7,00		9,16	0,70
752	90	85-0	20,09	5,92		8,40	0,59
751	36	33-0	5,40	2,04		2,84	0,20
741	77	74-0	16,99	6,80		8,00	0,68
742	130	125-0	31,39	6,60		9,96	0,66
743	160	155-0	39,87	10,00		15,64	1,00
744	197	194-0	50,88	8,00		10,88	0,80
745	224	220-0	58,23	6,60		10,00	0,66
746	250	245-0	65,29	6,40		7,56	0,64

Zooplankton samples collected during December 1969
R.S. Sardinops Stations

Station	Sounding (m)	Depth fished (m)	Vol. filtered m^3	Disp vol. $m\ell\ m^{-2}$	Vol. ratio small/total	Wet wt. gm^{-2}	Dry wt. gm^{-2}
Circuit 8							
881	45	40-0	7,38	5,20		6,08	0,47
873	142	135-0	34,22	8,20		11,40	1,24
872	37	34-0	5,69	4,40		6,40	1,24
871	36	33-0	5,40	5,60		6,76	0,62
861	27	24-0	2,86	2,76		4,84	0,42
862	50	45-0	8,79	5,60		5,92	0,41
863	109	105-0	25,74	5,12		6,84	0,63
864	224	220-0	58,23	6,40		8,76	0,41
865	263	259-0	69,25	4,00		6,04	1,21
855	240	235-0	62,47	1,60		7,60	0,67
854	226	225-0	59,64	7,00		8,36	0,61
853	159	155-0	39,87	10,40		13,00	1,58
852	90	85-0	20,09	5,96		6,88	0,47
851	36	33-0	5,40	5,20		6,72	0,65
846	250	245-0	65,29	6,40		7,00	0,48
845	224	220-0	58,23	11,60		9,60	0,88
844	195	190-0	49,81	13,12		16,96	1,67
843	159	155-0	39,87	11,20		11,52	1,18
842	130	125-0	31,39	5,20		5,60	0,58
841	72	68-0	15,29	6,36		7,56	0,88

APPENDIX 3

Surface temperature (°C,) Depth of maximum temperature gradient (metres), and chlorophyll'a' (mg m^{-2}) in the 0-75 m layer at the station groups.

GROUP A- stations

Station	Surf. temp. °C	DΔt max. m	chlla mg m^{-2}	Station	Surf. temp. °C	DΔt max. m	chlla mg m^{-2}
124	13,46	151	222	325	15,78	15	159
123	12,84	15	255	323	11,53	15	173
122	11,27	25	109	322	9,91	0	119
121	9,88	0	34	321	11,02	5	30
211	9,78	0	50	331	10,70	15	111
212	10,16	15	55	333	12,73	25	173
213	11,68	15	811	334	15,03	15	234
214	12,52	15	252	335	15,46	40	390
224	12,57	25	231	342	12,02	15	197
223	10,74	15	59	341	10,96	5	64
222	10,07	0	30	340	11,36	5	60
221	9,65	0	9	641	10,47	0	19
231	10,10	0	24	642	11,29	25	53
232	10,20	0	35	411	11,65	5	189
233	14,33	5	103	412	11,25	15	207
243	15,28	25	80	413	10,81	20	110
242	13,52	5	84	414	11,17	15	211
241	9,88	0	30	425	15,28	15	265
562	14,58	15	18	424	12,96	25	206
552	11,37	5	33	423	11,87	15	198
551	11,06	5	19	422	10,25	0	89
311	10,40	0	680	421	11,17	5	73
312	11,40	5	143	431	10,41	0	98
313	12,47	25	294	432	11,92	25	144
314	13,13	5	344	433	14,11	25	173

Station	Surf. temp. °C	DΔt max. m	chlla mg m^{-2}	Station	Surf. temp. °C	DΔt max. m	chlla mg m^{-2}
434	14,47	15	142	632	14,71	25	273
433	17,76	25	78	633	15,30	15	102
443	15,25	15	181	634	16,09	25	111
442	14,63	5	196	635	15,79	25	293
441	12,17	5	229	644	15,91	40	471
511	11,58	5	166	643	13,87	35	236
512	13,00	5	160	642	12,69	15	93
513	12,69	5	185	712	11,38	5	112
514	14,50	5	168	713	12,73	5	273
524	15,65	25	198	714	12,73	5	336
523	13,72	5	352	725	13,64	25	202
522	13,96	5	266	724	12,84	40	201
521	13,57	5	219	723	11,53	40	189
531	14,70	15	211	722	10,61	0	90
532	14,31	5	469	721	9,38	0	32
533	15,72	15	242	731	10,49	25	79
534	16,71	15	259	732	12,17	40	239
535	17,95	15	193	733	12,85	25	266
544	18,38	25	317	734	13,10	40	262
543	15,80	15	311	735	13,01	40	356
542	14,27	15	310				
541	14,24	25	195				
741	15,07	25	214				
742	15,96	25	429				
743	16,88	25	47				
611	12,62	5	200				
612	13,00	5	144				
613	12,47	15	266				
614	12,67	25	270				
624	15,17	15	85				
623	13,97	15	186				
622	13,07	15	453				
621	12,21	15	76				
631	14,00	15	225				

$\bar{x}$=1470

n=103

$\bar{\bar{x}}$=14 m

GROUP B - stations

Station	Surf. temp. °C	D▲t max. m	chlla mg m^{-2}	Station	Surf. temp. °C	D▲t max. m	chlla mg m^{-2}
141	10,75	10	18	881	18,60	15	32
372	17,38	25	53	873	19,17	25	82
371	15,25	15	30	872	18,54	15	35
361	10,28	15	8	871	16,50	5	108
362	12,99	25	24	862	15,45	5	120
363	17,42	35	80	863	17,58	15	62
352	14,53	5	38	853	14,25	15	59
351	11,40	5	11	852	10,81	15	85
472	18,44	20	50	851	10,17	10	28
471	18,03	5	20	841	10,26	5	41
462	14,58	5	18	842	10,60	25	105
463	18,18	20	40	843	13,54	35	79
453	18,49	20	57	844	16,95	25	55
571	15,91	5	23	742	9,59	0	35
561	10,76	5	20	741	9,53	0	26
563	18,19	20	56			x=625	
681	18,08	20	29			n= 47	
672	16,88	20	26			$\bar{x}$= 13	
671	16,61	10	15				
661	10,37	10	24				
662	12,71	5	29				
663	18,48	25	38				
652	12,94	15	47				
651	11,14	5	19				
781	18,78	15	27				
772	18,99	15	26				
771	18,51	5	20				
761	12,19	5	25				
762	17,71	5	24				
752	15,85	5	186				
751	15,40	5	143				
641	10,38	10	70				

GROUP C - stations

Station	Surf. temp. °C	DΔt max. m	chlla mg m^{-2}	Station	Surf. temp. °C	DΔt max. m	chlla mg m^{-2}
143	16,84	15	100	854	17,84	15	48,5
142	14,33	25	79,5	845	18,18	25	53,5
373	17,97	25	22	846	18,57	40	34
364	18,22	40	17,5	746	19,38	40	23,5
353	18,16	40	77,5	745	19,56	40	27
234	16,54	15	57				
235	18,38	40	26			x=1095	
244	19,00	25	52			n=36	
473	18,47	40	24			$\bar{x}$=30,4 m	
454	18,99	40	49				
573	18,46	30	34				
572	18,26	25	21				
564	18,79	25	21,5				
345	18,91	30	65				
344	18,98	25	66,5				
673	18,68	40	40				
664	18,95	30	39				
654	18,93	40	21				
653	17,46	30	37				
644	19,16	15	41				
645	19,48	40	29,5				
545	19,45	40	63				
773	18,99	40	41				
763	19,02	15	87				
764	19,41	40	77				
754	19,34	40	59				
753	18,68	15	161.5				
744	18,70	15	41				
745	19,56	30	27				
864	19,38	25	18,5				
855	18,98	40	17,5				

GROUP D - stations

Station	Surf. temp. °C	D4t max. m	chlla mg m^{-2}
135	17,81	25	97
146	18,15	75	81
145	18,13	75	74,5
144	17,68	30	70,5
246	19,19	50	32
245	18,80	50	40
646	19,45	50	36
646	19,39	50	22
865	19,61	50	19
		x=455	
		n= 9	
		$\bar{x}$= 51 m	

GROUP E - stations

Station	Surf. temp. °C	D4t max. m	chlla mg m^{-2}
365	18,86	40	55
355	18,85	40	23
465	19,22	40	12
455	19,26	40	19
565	19,66	40	16
555	19,19	40	17
665	19,50	40	25
655	19,21	40	47
346	19,30	40	70
765	19,54	50	61
755	19,19	40	40
		x=450	
		n= 11	
		$\bar{x}$= 41 m	

UPWELLING IN THE SOUTHERN BENGUELA CURRENT

by

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Abstract

The seasonal and short-term variability of a semi-permanent upwelling site in the Southern Benguela Current is described. Wind is the major factor controlling the rate of upwelling or downwelling at this centre and during vigorous upwelling a plumelike structure extending up to 100 kilometres northwest of the Cape Peninsula developes, separated from warmer oceanic water by a distinct frontal zone. Intense biological activity occurs within the zone between the newly-upwelled water and the frontal zone.

Rates of upwelling were measured indirectly using temperature, nutrient and isanostere data and averaged 20 meters per day, with a maximum rate of 30 m uplift per day. Nitrate was found to be the primary limiting nutrient in the area and production conforms to Michaelis - Menten kinetics with a $Ks_{(NO_3^-)}$ between 0.38 and 1.12 ug-atom N/litre and a PI (max) of 17.4 - 19.0 mg C/mg chlorophyll a/hour. The mean standing stock of phytoplankton was 11.2 g C/m^2 which doubled on average about once per day. The zooplankton standing crop averaged 0.8 gC/m^2 with maximum values in summer about two - to three-fold higher than winter levels. Zooplankton appeared unable to effectively graze down the phytoplankton crop and both zooplankton and phytoplankton were limited by physical processes in the area.

A periodic intrusion of oligoxic water was observed between December and July, transporting regenerated nutrients southwards. This water mass could be distinguished from local regeneration processes by the ratios of nitrate to silicate.

1. Introduction

The oceanography of the inshore waters off the west coast of southern Africa is dominated by an upwelling system which can be regarded, as with those found off Peru, California and North-West Africa, as one of the major upwelling systems of the world's oceans. The extent and importance of this upwelling system has been recognised for several decades and received particular attention after Hart and Currie's (1960) work. More recent work in upwelling areas has not been so concerned with outlining the extent over which upwelling occurs but rather with the nature of the process itself. Changes occur very rapidly in upwelling areas and many recent surveys have included repeated visits to a small part of the system. In this paper we shall outline the results of research in a very small area (approximately 65 km X 45 km) of the South Atlantic immediately adjacent to the Cape Peninsula. In a preliminary survey (Andrews and Cram, 1969) it was found that this area contained a very active and quite discrete upwelling site. This upwelling site is situated in the centre of a mixed species pelagic fishery (Centurier-Harris and Crawford 1974 a) with an annual catch of some 400 000 metric tons (Centurier-Harris and Crawford 1974 b). Changes in the intensity and duration of the upwelling in this area can be expected to exert a considerable influence on the fishery. Our subsequent investigations were designed to further elucidate the nature of the processes occurring in this site.

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Two basic approaches of data collection were tried - rapid repeated surveys of the area during the peak of the upwelling season; and monthly visits over a period of 30 months to a line of stations running along the apex of the normal position of the upwelling plume. Together, both approaches gave us data which had depth in both the short-term and in the seasonal directions. The [illegible] the Cape Peninsula is particularly intense and probably not typical of the Benguela Current, although there is considerable evidence that there are other sites along the west coast of southern Africa where upwelling is particularly active (Copenhagen, 1953; Cram, unpublished ART data). Its geographical location at the extreme south of the western seaboard places the sea off the Peninsula in a unique position both oceanographically and meteorologically. It seems likely that this upwelling site is the most southerly one contributing significantly to the Benguela Current (see Chapter 4); and the wind regimes over the Peninsula are considerably more variable than those found further north (Weather Bureau, Republic of South Africa - Daily Weather Bulletin). Winds tend to be of greater velocity and are subject to very rapid directional changes (Chapter 3). However the results show that in spite of its relative geographical isolation from the bulk of the Benguela Current this upwelling site is indeed an important integral part of the same oceanographic system.

3/...

In this study temperature data are more numerous than other conservative data and a heavy reliance has been placed on them. Although in the open ocean temperature is not normally as reliable a conservative property as salinity, in this area, where temperature gradients are large, heat exchange through processes other than mixing is likely to be insignificant. Bang (1973) found a good relationship between sigma-t and temperature in the area.

4/...

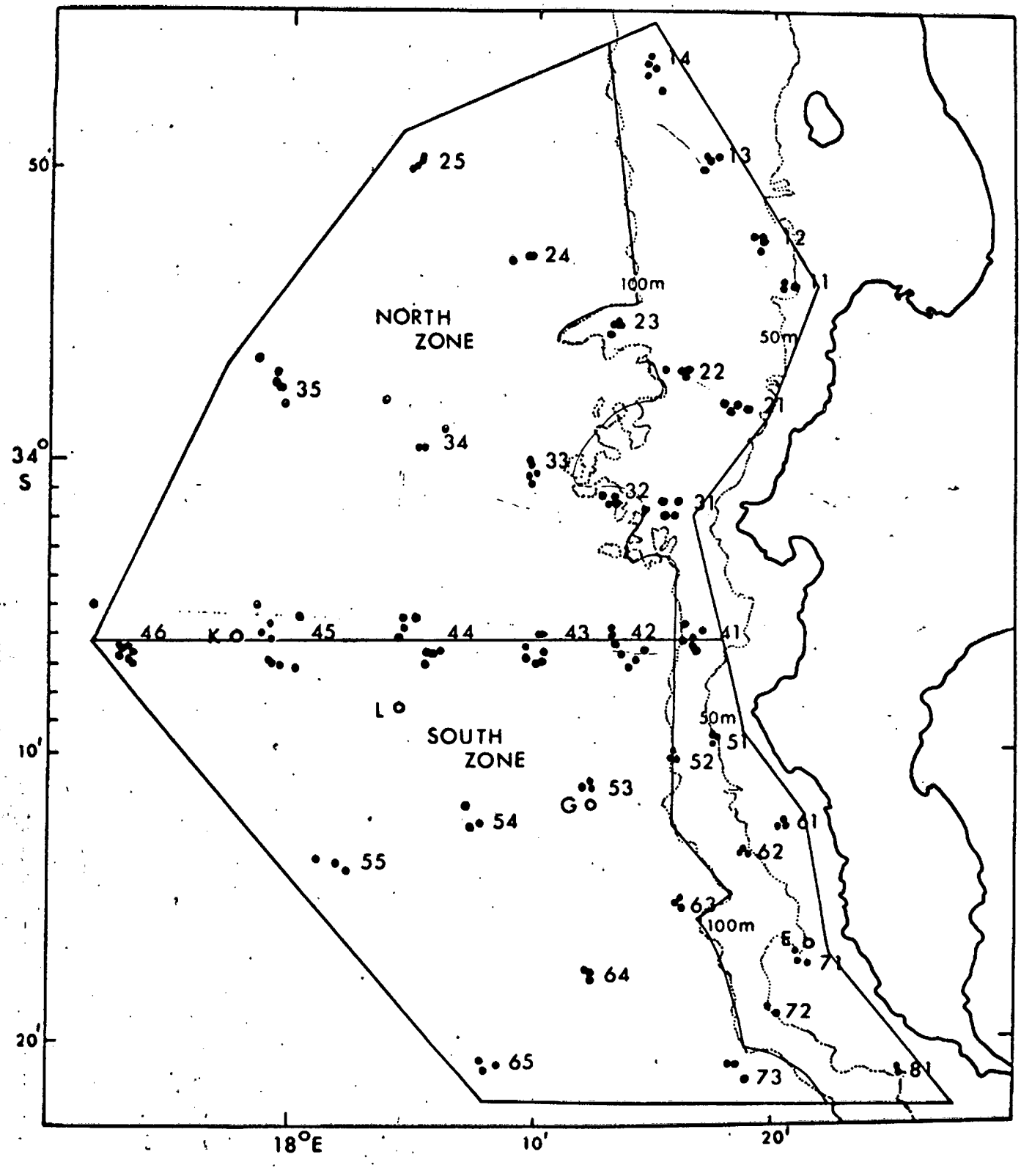
50'
34° S
10'
20'
18°E
10'
20'
NORTH ZONE
SOUTH ZONE
100m
50m
100m
50m
14
13
12
1
25
24
23
22
21
35
34
33
32
31
46
45
44
43
42
41
K
L
G
E
51
52
53
54
55
61
62
63
64
65
71
72
73
81

Fig. 2.1.

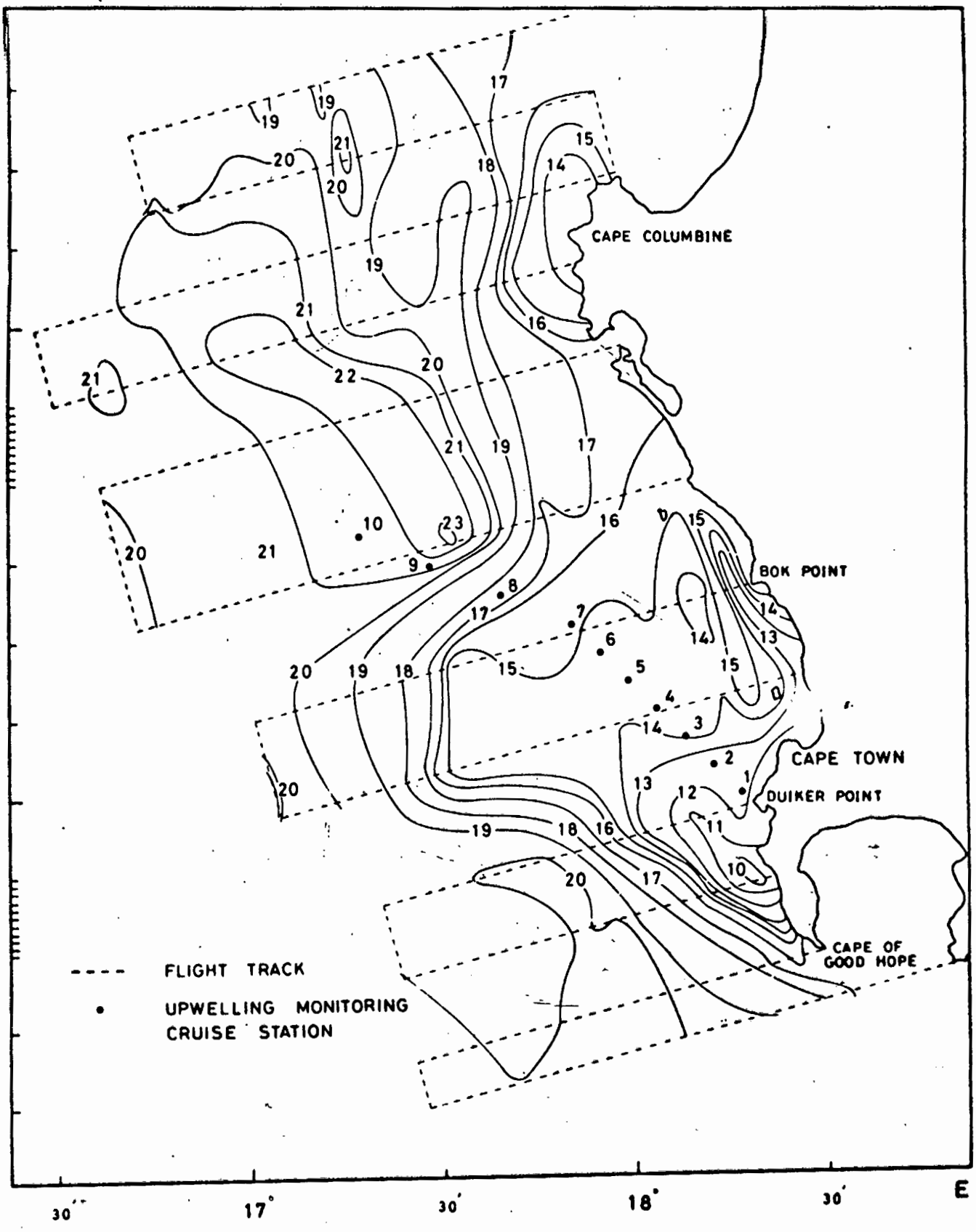
CAPE COLUMBINE
BOK POINT
CAPE TOWN
DUIKER POINT
CAPE OF GOOD HOPE
FLIGHT TRACK
UPWELLING MONITORING CRUISE STATION
30°
33°
30°
34°
30°
S
30'
17°
30'
18°
30'
E

Fig 2.2

2. The Cruises

The 1969 Upwelling Cruise was undertaken in December. It consisted of a grid of 35 stations on 8 lines radiating from the Peninsula (Fig. 2.1). The northern stations (Lines 1-4) were occupied by R.S. Africana II while the ones in the south (Lines 4-8) were done by R.S. Sardinops. On completing its section of the grid each ship returned to its first station (11 and 81 respectively) and started again. There were some interruptions in the early portion of the cruise and data were obtained only erratically from 2 to 6 December. However from 10 to 16 December samples were collected on schedule. At 250 stations temperature, salinity, phosphate, silicate, nitrate, chlorophyll a and oxygen were sampled at standard depths to the bottom. Zooplankton samples, a bathythermograph cast and, during daylight, Secchi disc readings were also taken. (Chlorophyll a was only sampled to 75 m or 100 m and nutrient samples were not obtained at 150 m or 250 m unless these were the deepest sampling depths). Some results from the 1968 Upwelling Cruise have been used. This was similar to the 1969 Cruise although the stations were more widely spaced (see Andrews and Cram, 1969).

The Upwelling-Monitoring cruises ran each month for a 30-month period from October 1970. To start with, a line of 7 stations 9 km apart, running due north-west of Duiker Point, was sampled. From March 1971 the line was extended into oceanic water by adding up to three stations (according to the season)

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approximately 20 km apart on a line running west-noth-west (Fig. 2.2). The line was worked from the inshore station oceanwards with the exception of cruises done in the initial five months. The first five stations were done in one day and the remainder the next day. Samples were taken at 10 m intervals to 60 m; at 20 m intervals to 120 m; at 150 m; and at 100 m intervals from 200 m to the bottom. The deepest sample was usually taken within four meters of the bottom.

3. Sampling and processing

Samples were obtained from 5- or 7- litre N.I.O. water bottles. Temperatures were measured simultaneously with Nansen-Pettersen insulated water bottles at shallow depths and Munroe-Ekman reversing bottles at deeper levels. Reversing bottles were not used on the 1969 Upwelling Cruise and the depth quoted is uncorrected wire length. Depths used in the rate of upwelling calculations were corrected with the aid of bathythermograph data.

Salinity samples were stored in glass bottles and analysed with an inductively-coupled Autolab salinometer. Oxygen samples were analysed on board using standard Winkler techniques. One-litre samples were filtered on board for subsequent spectrophotometric analysis for chlorophyll a, b and c. The wavelengths and equations recommended by UNESCO (1966) were used. After sampling for chlorophyll to the bottom for a 12-month period on Upwelling-Monitoring Cruises sampling was restricted to the upper 120 m. Samples for reactive phosphate, silicate and nitrate analyses were stored deep frozen in 100ml polythene bottles after the addition of three drops of a saturated mercuric chloride solution. Analyses of these nutrients were done ashore on a Technicon autoanalyser using the methods of Strickland and Parsons (1968), Grasshoff (1966) and Strickland and Parsons (1968) respectively. Nitrite was not specifically analysed and all nitrate results given in this paper include nitrite.

Two-litre samples from the surface at each station sampled from March 1972 to March 1973 were filtered through Whatman GF/C

7/...

papers for total carbon analysis. The method of wet oxidation with potassium dichromate described by Strickland and Parsons (1968) was used.

During the Upwelling-Monitoring Cruises, at Stations 3 and 6, 22 km and 50 km north west of Duiker Point respectively, water samples were taken from four depths in the upper 30 to 40 m and placed in 300 ml BOD bottles. Two light bottles and one dark bottle from each depth were incubated for a six-hour period at light intensities equal to 100%, 59%, 55% and 44% of the intensity of bright sunlight at 0700 hours in mid-summer, about 1,5 hours after sunrise. This light level is approximately 17% of the maximum radiation level measured at midday in mid-summer. The rather irregular Light Levels used were due to recalibration of the incubator in 1977 using a quantum meter (LI-185, Lamda Instruments). Two Atlas Kolorlux 400 watt lamps were used as light sources and wire-mesh screens were used as neutral filters. During incubation samples were kept cool with surface water and were rotated at about 1 rpm to minimise settling and possible irregularities in the lighting. Gross production, in units of mg C m-3 hr-1 was obtained from the difference between the oxygen concentrations of the dark and light bottles after multiplication by 89.3. Initial oxygen concentrations at each depth were also measured and the net production calculated from the differences between these and the concentrations in the light bottles. Photometer measurements were also made at these stations to below the level of 1% of surface light by comparing outputs of surface and

submerged photoelectric cells. At other stations occupied during daylight Secchi disc readings were taken.

During the December 1969 Upwelling cruise zooplankton was collected at each station by vertically towing a WP-2 net, (Unesco 1968) fitted with a N.I.O. depth recording flowmeter (Currie and Foxton (1957)), between the bottom and the surface. At 10 stations in the northern part of the grid additional samples were taken by filtering 4,5 m^3 of water pumped from 5 discrete depths (1 m, 10 m, 20 m, 30 m and 50 m) through a 200 /u mesh filter. Water was delivered to the filter at approximately 550 litres per minute, as measured by a full-flow helical vane water meter. At these 10 stations separate WP-2 net hauls were made from the bottom to 50 meters (closing) and from 50-0 meters. The displaced volumes of samples were determined in filtered sea water using a modified Yashnov meter (Robertson 1970), before preservation in 10% V/V buffered ($CaCO_3$ chips) formalin. (100% formalin = 40% formaldehyde solution). Excess water was removed by filtering, at 5 cm Hg vacuum for one minute after the meniscus had disappeared, through the 200 /u mesh gauze. Samples were later split into two parts using a Folsom splitter and one half was rinsed with one litre of fresh water, dried at 60°C for 24 hours (Lovegrove 1966) and ashed at 800°C for two hours for the determination of dry weight and ash free dry weight. The other half was preserved for taxonomic analysis. Large organisms (greater than about 0,75 cm in their largest dimension) were removed manually and counted before the smaller organisms were subsampled using a wide-mouthed pipette after agitation. Between 10% and 50% of the sample was examined depending on the density

of organisms, to ensure that 800 to 1 200 small organisms were counted. A random 200 organisms were identified (for species composition). Species percentage composition by numbers was calculated for each station.

In January 1971 a line of seven stations 9 km apart, running north-west from the Peninsula, was sampled three times in six days. 2.25 m^3 pump samples were collected at 8 depths to 100 metres at each station. Duplicate WP-2 net hauls from bottom to surface were also taken. Displaced volumes, dry and ash weights were assessed as before except that samples were preserved in 4% V/V buffered formalin solution, and no species composition data are available at present.

From March 1971 to March 1973 monthly samples were collected along the upwelling monitoring line. Two WP-2 net hauls were collected at each station, one from as close to the bottom as possible up to the maximum temperature gradient and the second haul from that depth to the surface. If no marked gradient was apparent, hauls were made from the bottom to 50 metres and from 50 metres to the surface. Most samples were collected during daylight hours. In December 1971 station 03, approximately 24 km from the coast, was occupied for 24 hours; 2,25 m^3 pump samples were collected at 8 different depths to 100 metres every 4 hours (Depth of station = 140 m). The displaced volume profiles were integrated manually to provide estimates of zooplankton abundance in the 0-100 metre layer.

10/...

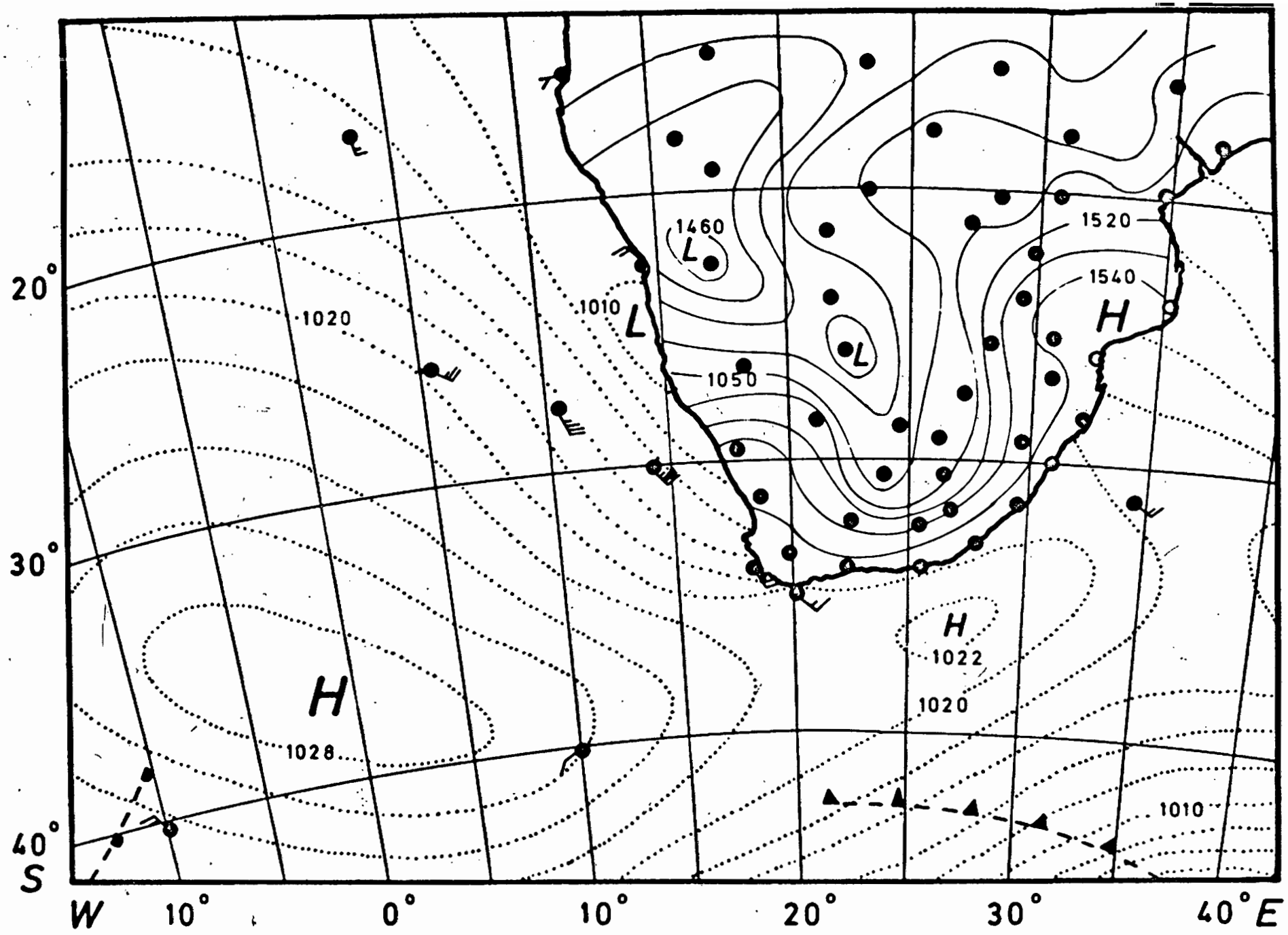

Fig. 4.\ Synoptic weather map of Southern Africa showing typical summer atmospheric pressure system. (From Weather Bureau, 197 .)

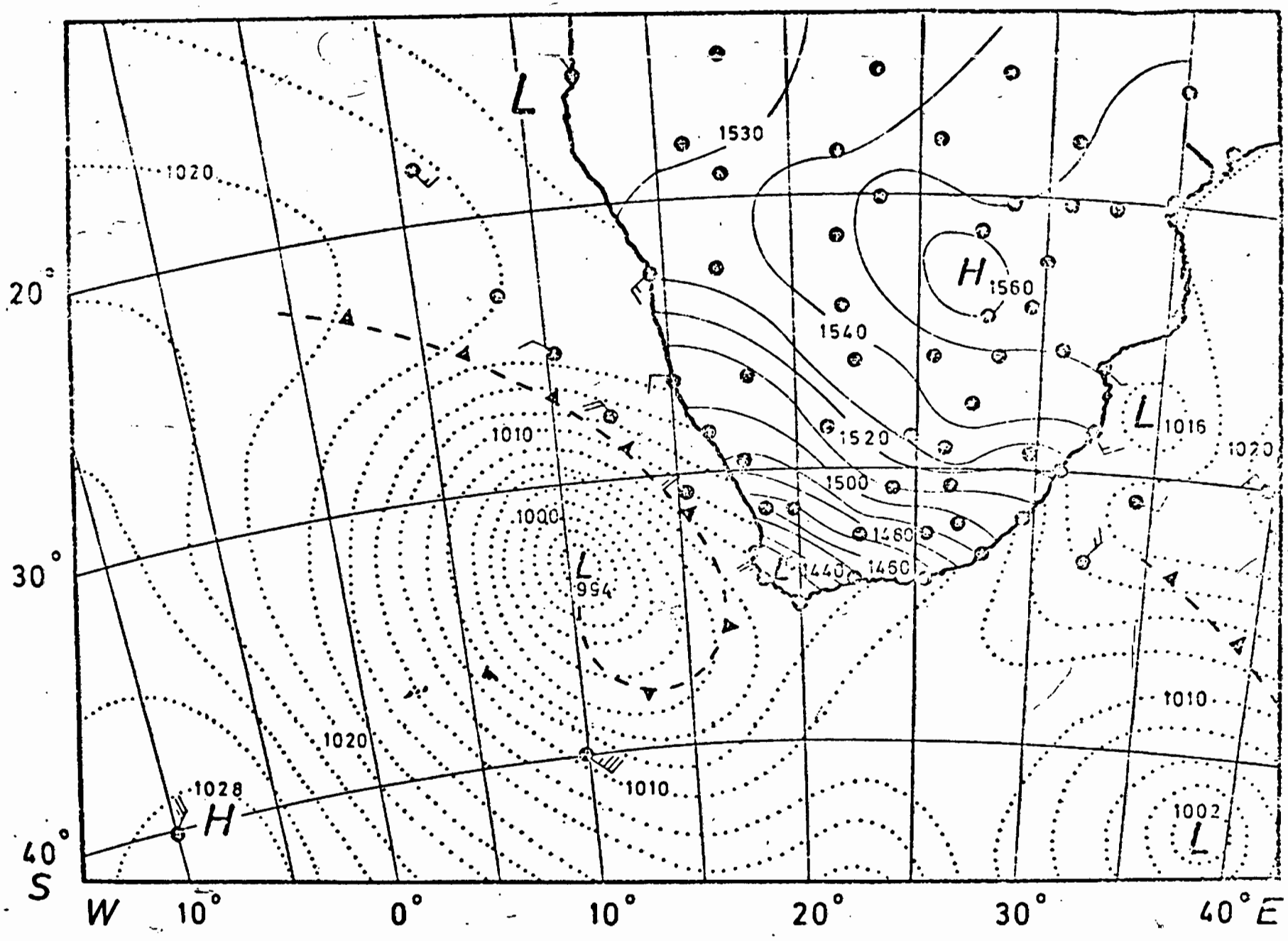

Fig 4.2 Synoptic weather map of Southern Africa showing typical winter atmospheric pressure system (from Weather Bureau, 1971).

4. Wind

Lying at 34°S, the Cape Peninsula is subject to the influence of the south east trade winds during the summer (Fig. 4.1) and the westerly variables during winter (Fig. 4.2), and a pronounced seasonal cycle is evident in the wind data from Cape Point lighthouse (Fig. 4.3).

During spring, summer, and autumn the anticyclonic subtropical high pressure cell, which is a permanent feature of the South Atlantic, periodically ridges eastwards south of the continent (Fig. 4.1) and south-easterly winds predominate during this period, making up more than 50% and up to 70% of the total winds for several months. (Fig. 4.3) Peak frequencies occur in spring and late summer with a noticeable hull in strong (8 m/sec) winds during midsummer. These is little evidence of any diurnal periodicity during this period; south-easterly "blows", with wind velocities of 18-25 m/sec, typically last for four to five days before the passage of a depression weakens the high pressure ridge and the wind abates or reverses (Fig. 4.4). Occasional gales continue for up to eight to twelve days, but these are exceptional and rarely occur more than once or twice per year.

During winter low pressure cells are driven from west to east, under the action of an atmospheric circumpolar wave, across the southern Cape Province, and northwesterly winds dominate during this period, although to a lesser extent than the south-easterly winds dominate during summer. South-easterly winds still occur, but they are of short duration and constitute less than 10% of the total winds.

11/...

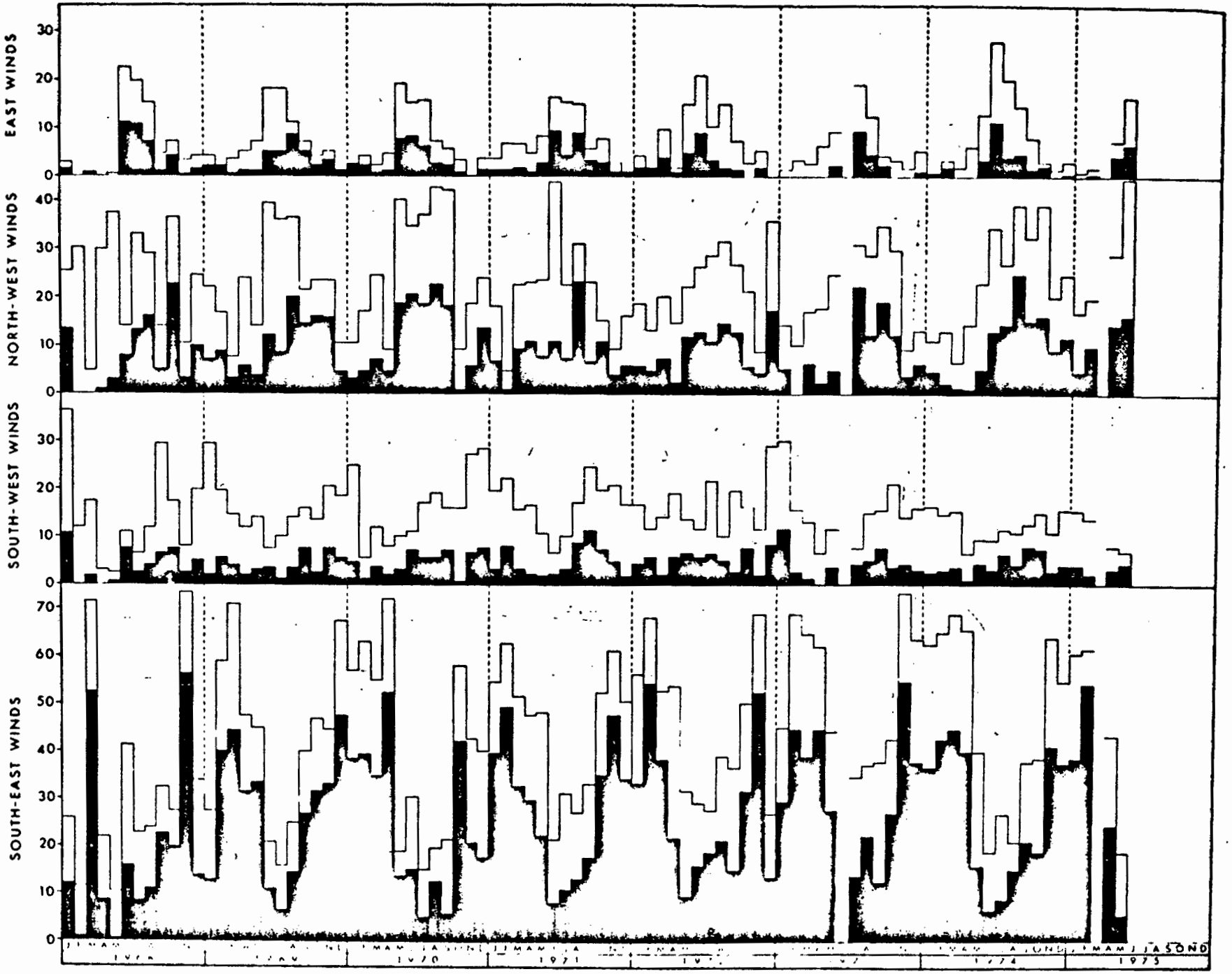

Fig 4.3

CAPE POINT LIGHTHOUSE WIND ANALYSIS

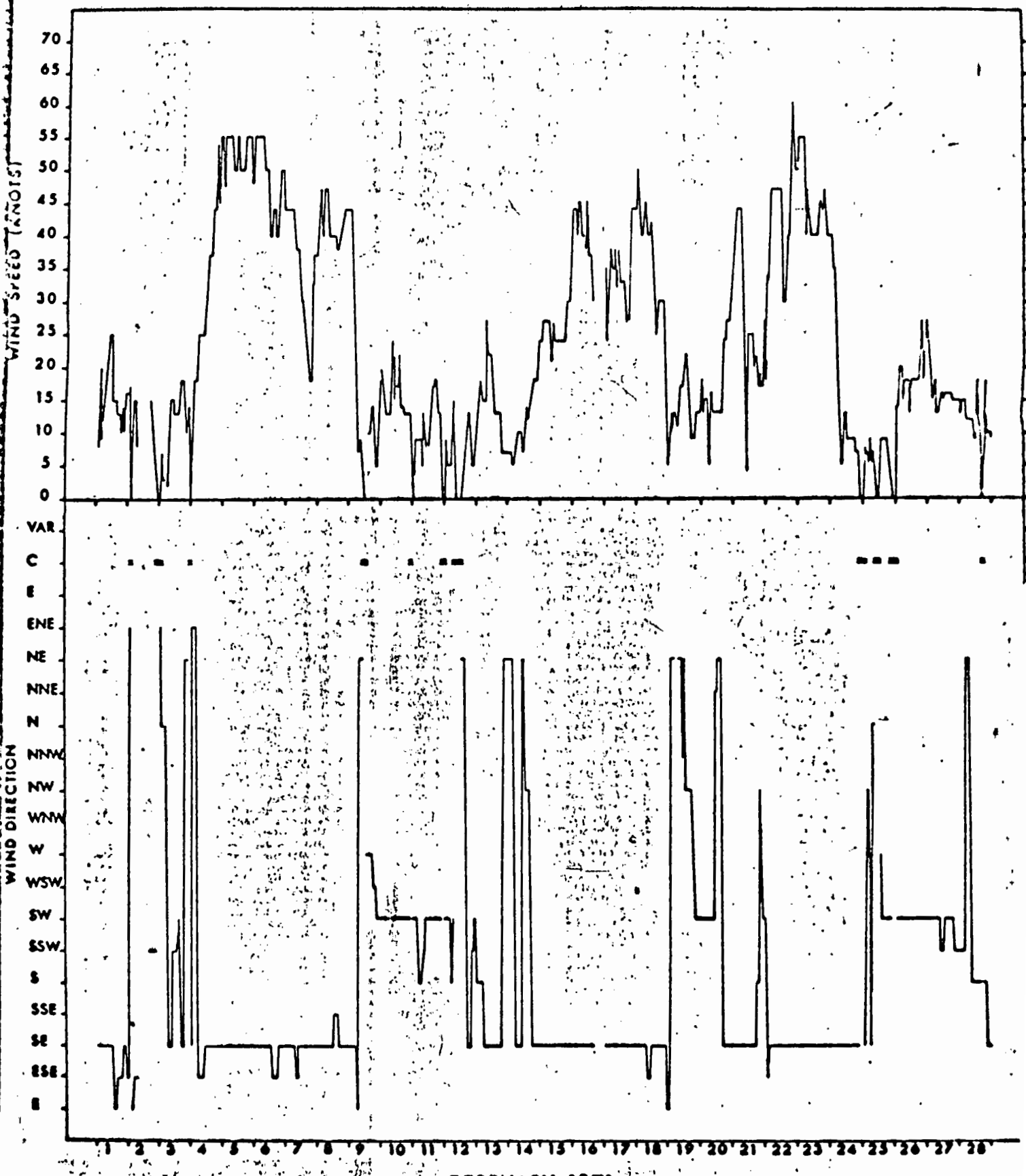
WIND SPEED (KNOTS)
70
65
60
55
50
45
40
35
30
25
20
15
10
5
0
WIND DIRECTION
VAR
C
E
ENE
NE
NNE
N
NNW
NW
WNW
W
WSW
SW
SSW
S
SSE
SE
ESE
E
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28
FEBRUARY-1971

Fig 4

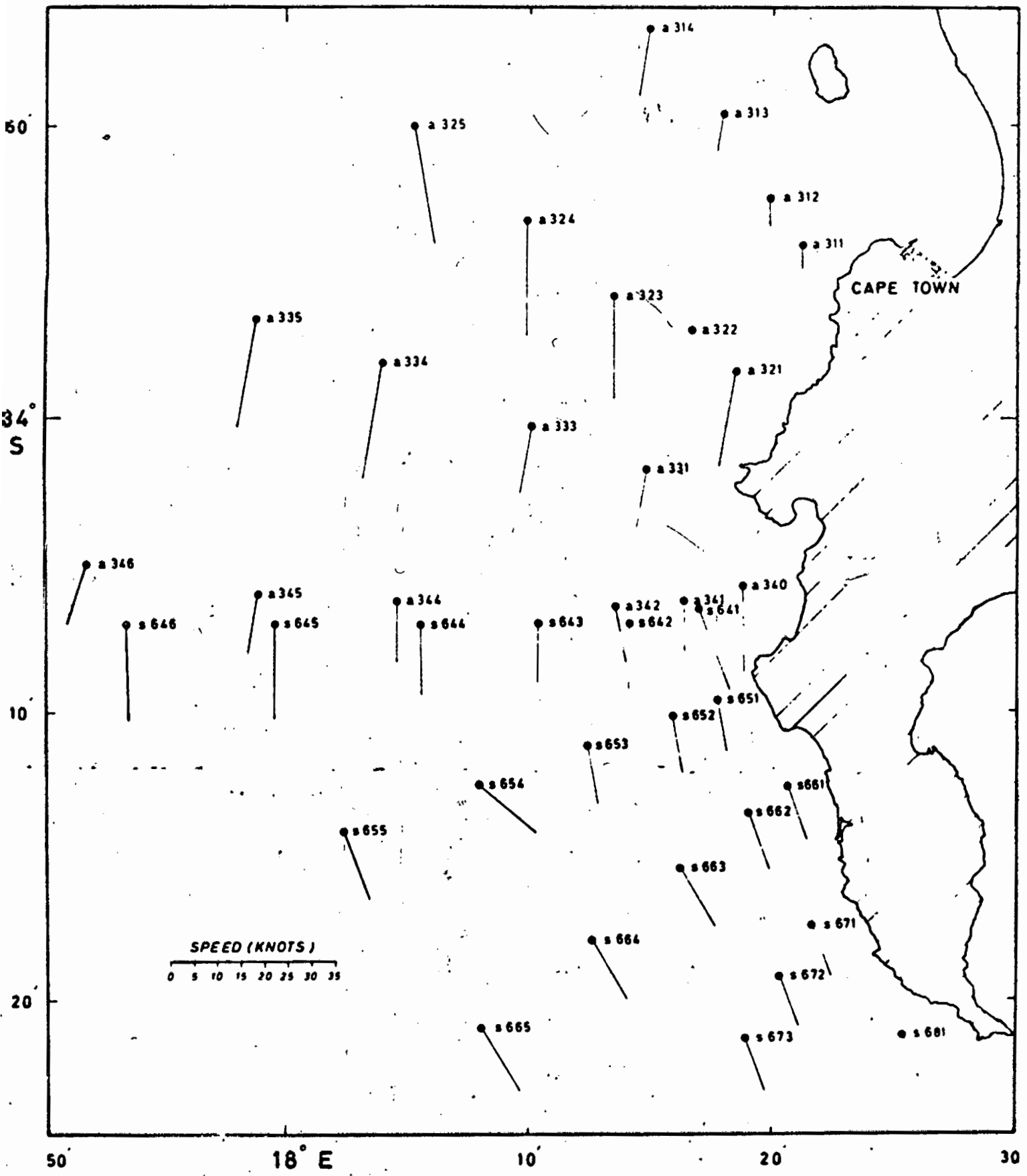
a 314
a 313
a 325
a 312
a 324
a 311
CAPE TOWN
a 323
a 335
a 322
a 334
a 321
a 333
a 331
a 346
a 340
a 345
a 344
a 342
a 341
s 641
s 646
s 645
s 644
s 643
s 642
s 651
s 652
s 653
s 654
s661
s 662
s 655
s 663
s 671
s 664
s 672
s 665
s 673
s 681
SPEED (KNOTS)
0 5 10 15 20 25 30 35
60
34° S
10
20
50
18° E
10
20
30

Fig 4.5

There are few data to throw light on the distribution of wind stress in the area although Bang and Andrews (1974) suggest that there is a rapid decrease in meridional wind stress west of a near-shore maximum during south-easterly winds. Within the first few kilometers off the shore local wind conditions vary along the length of the Peninsula due to the shielding and funneling effects of the mountains that form its backbone. The region north-west of Cape Town docks is shielded by the high mountains of the Table mountain complex at the northern end of the Peninsula.

When data from Cape Point lighthouse were compared with those obtained simultaneously from research ships in the study area it was found that there was very close directional agreement between the two sets (Fig. 4.5) but that the velocities recorded on the ships were only 0.6 of those recorded at the lighthouse. The lighthouse is situated 100 m above sea level in a very exposed position.

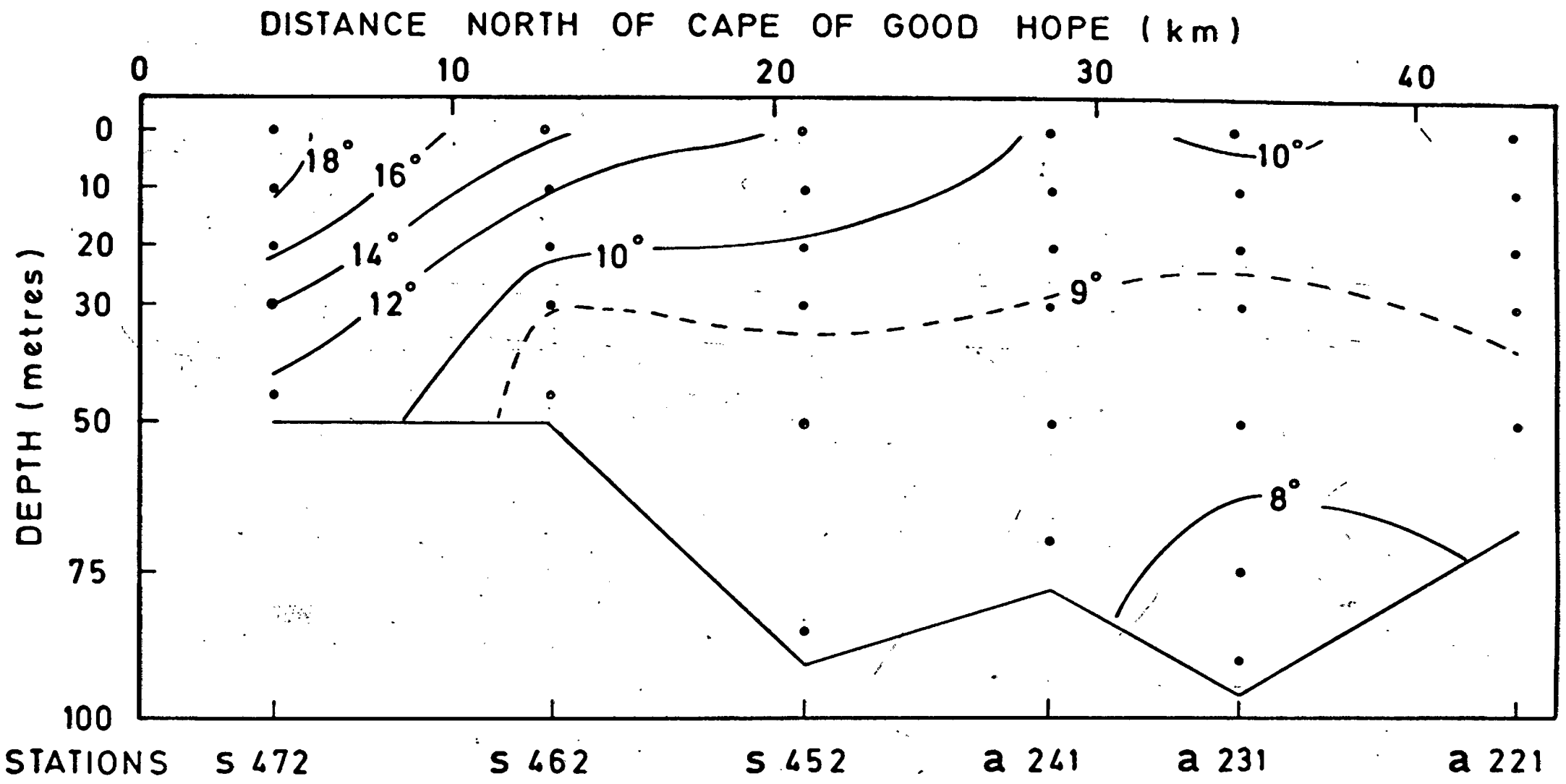

Fig. 5.1 Vertical temperature distribution 7 km from coast along the Cape Peninsula on 5 December 1969.

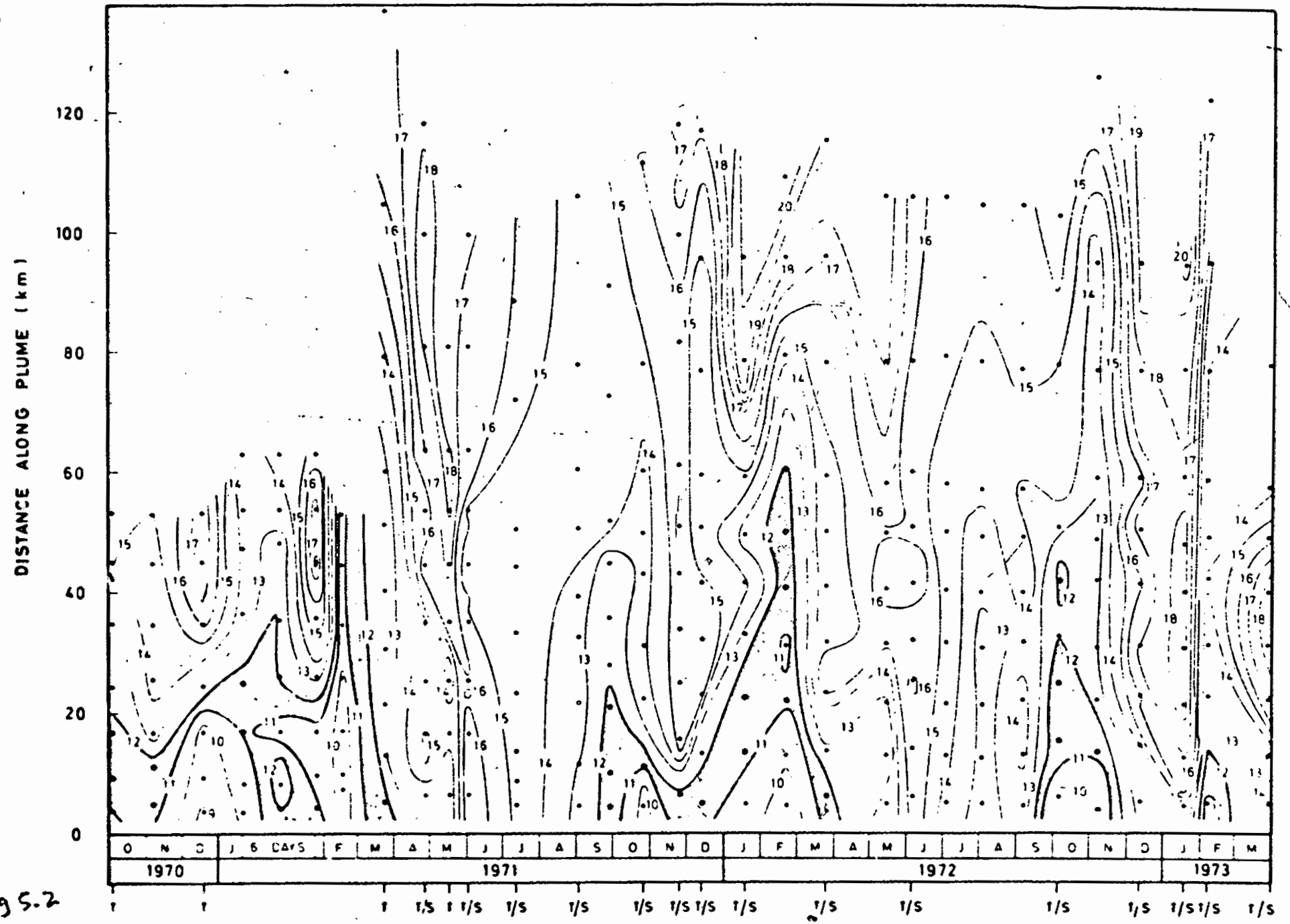
DISTANCE ALONG PLUME (km)
120
100
80
60
40
20
0
O N D J 6 DAYS F M A M J J A S O N D J F M A M J J A S O N D J F M
1970
1971
1972
1973
f
f
f
f/s
f
f/s
f/s
f/s
f/s
f/s
f/s
f/s
f/s
f/s
f/s
f/s
f/s
f/s
f/s

Fig 5.2

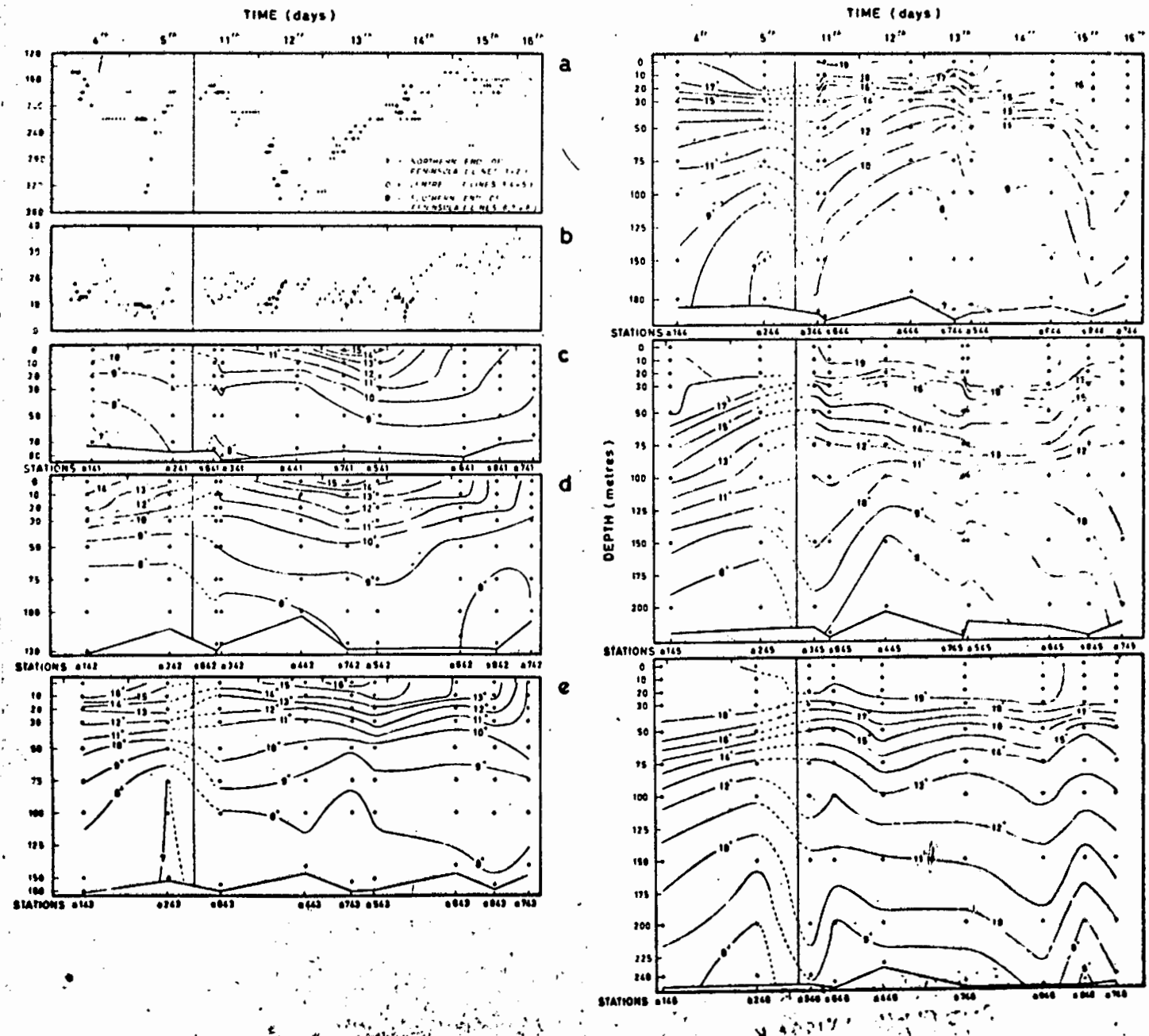
TIME (days)
WIND
DIRECTION
SPEED (knots)
a
b
c
d
e
DEPTH (metres)
STATIONS
TIME (days)
f
g
h
DEPTH (metres)
STATIONS

Fig 5.3

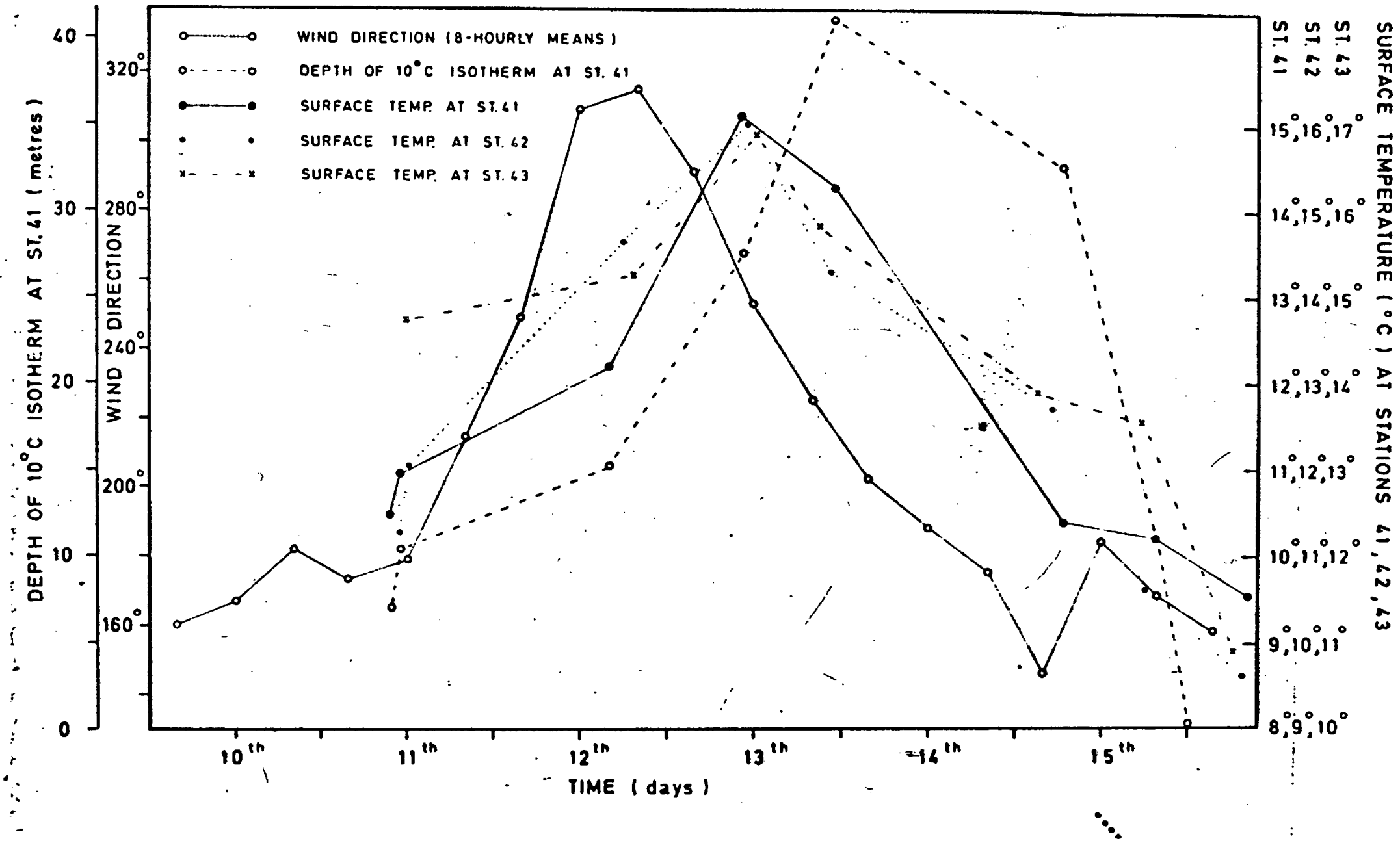
WIND DIRECTION (8-HOURLY MEANS)
DEPTH OF 10°C ISOTHERM AT ST. 41
SURFACE TEMP. AT ST. 41
SURFACE TEMP. AT ST. 42
SURFACE TEMP. AT ST. 43
DEPTH OF 10°C ISOTHERM AT ST. 41 (metres)
WIND DIRECTION
SURFACE TEMPERATURE (°C) AT STATIONS 41, 42, 43
ST. 41
ST. 42
ST. 43
40
30
20
10
0
320°
280°
240°
200°
160°
15°,16°,17°
14°,15°,16°
13°,14°,15°
12°,13°,14°
11°,12°,13°
10°,11°,12°
9°,10°,11°
8°,9°,10°
10th
11th
12th
13th
14th
15th
TIME (days)

Fig 5.4

5. The upwelling plume

After surveys made in 1968 Andrews and Cram (1969) reported the existence during upwelling of one or more plumes of cold water, isolated from South Atlantic Surface Water by a well-defined front, running in a north-westerly direction from the Cape Peninsula. Subsequent surveys have confirmed these findings and shown that the upwelling system off the Cape Peninsula is a fairly distinct oceanographic feature with a second distinct upwelling system off Cape Columbine, 150 km to the north (Fig. 2.2). Hart and Currie (1960) and Shannon (1966) showed that water upwelling off the west coast of South Africa was of South Atlantic Central Water origin and that this flowed eastward, under the South Atlantic Surface Water, before upwelling near the coast. Our data support these findings and indicate the isolation of the Cape Peninsula upwelling site from those reported on the south coast (Cram 1970), as during upwelling conditions isotherms deepen at the extreme southern tip of the Peninsula (Fig.5.1).

The plume of cold surface water is a common feature throughout the summer months, but disappears almost entirely for several winter months and generally follows the pattern expected of a wind-generated upwelling system with a cycle of wind as outlined in the previous chapter, even to the extent of showing a noticeable reduction in size during the mid-summer lull in south east winds (Fig. 5.2). Yet imposed on this seasonal cycle is a pronounced short-term variability which is also evidently wind-generated. This was particularly well documented on the second half of the

1969 Upwelling Cruise when a fairly typical cycle of wind conditions and the concomitant changes in oceanographic conditions in the area were observed.

On 10 and 11 December the wind blew from the south at between 7.5 and 10 m/sec until midday on 11 December when it slowly veered westwards (Fig. 5.3). Twenty four hours later it was blowing from between 320° and 340° at 9 m/sec. Early on 13 December it started backing eastwards and by late on 14 December until the end of the cruise on 16 December it was blowing from between 150° and 170° at speeds greater than 14 m/sec. This cycle of wind conditions was accompanied by spectacular changes in the oceanography of the area, with the partial disappearance of the plume during north-westerly winds and its almost immediate reappearance on the return of brisk south-easterly winds. Similar changes were recorded by Andrews and Cram (1969) (see their Fig. 1) but on this occasion more detailed observations were made. Of particular interest are the data from Line 4 of the grid (Fig. 2.1) which was sampled 7 times during this cycle. Time-depths sections of temperature have been drawn for all six stations along this line and are shown in Fig. 5.3. The relationship between wind direction and temperature was most direct inshore.

Some of these data have been compared graphically with eight-hourly means of the wind-direction during this cycle in an attempt to determine the response time of the ocean to changes in wind direction (Fig. 5.4). From this figure it is evident

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the response of the surface layers is more rapid than that of deeper layers and, assuming that all winds north of west cause net transport of (warm) water shorewards, is almost immediate. The slower response time of deeper waters could be entirely the result of the greater inertial forces that have to be overcome in these layers.

Similar trends were found with other parameters. The salinity of the surface layer increased during north-westerly winds as did the chlorophyll and oxygen contents whilst nitrate and phosphate levels were higher during south-easterly winds.

The plume then is a semi-permanent feature off the Peninsula in the upwelling season. Its surface features are masked during north-westerly winds but it only completely disappears during the winter. In the summer it can change its dimensions dramatically. The most intense upwelling tends to occur off the central part of the Peninsula with the result that surface water tends to flow back towards the coast in the more wind-protected areas to the north.

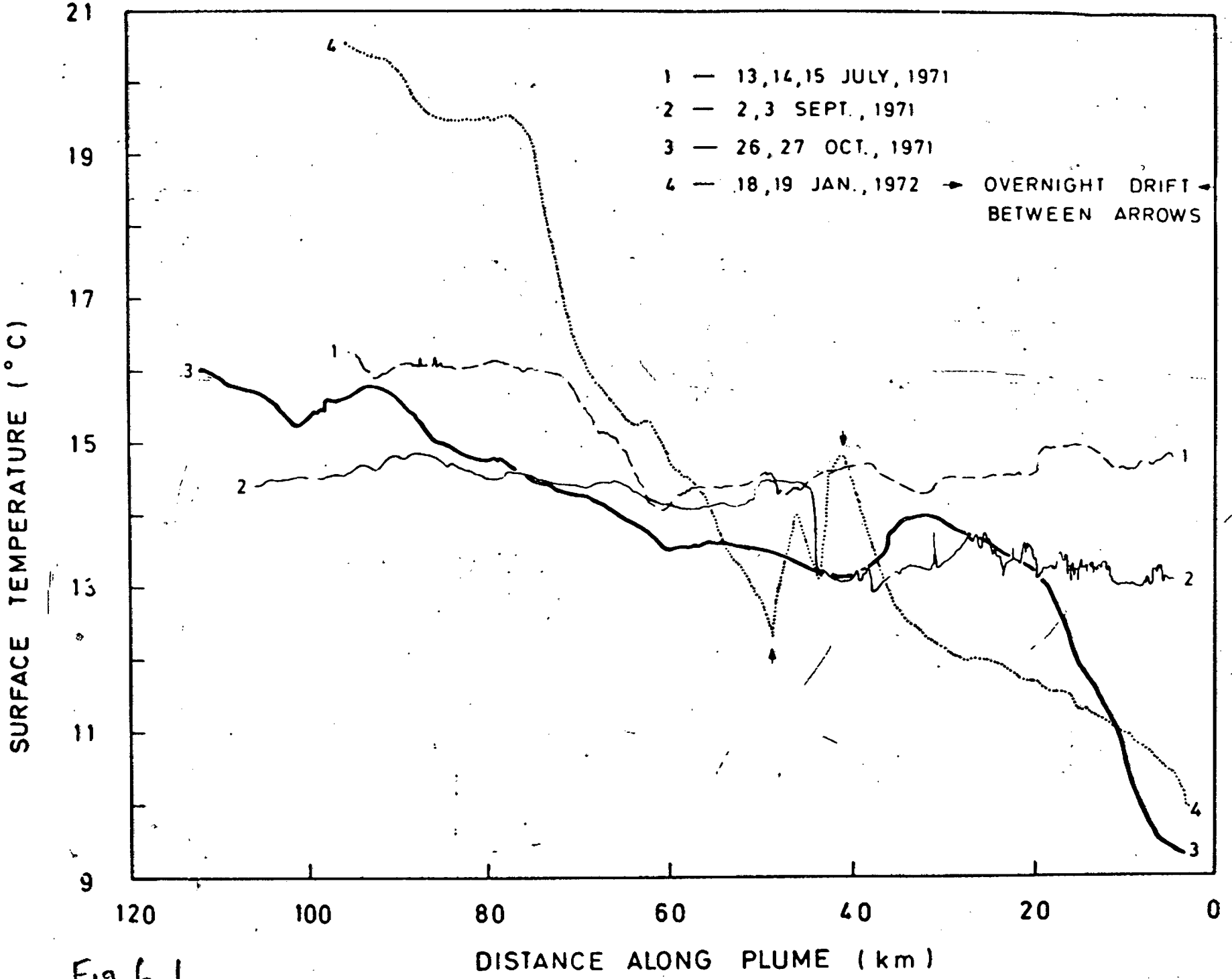

1 — 13,14,15 JULY, 1971
2 — 2,3 SEPT., 1971
3 — 26,27 OCT., 1971
4 — 18,19 JAN., 1972 → OVERNIGHT DRIFT ←
BETWEEN ARROWS
SURFACE TEMPERATURE (°C)
21
19
17
15
13
11
9
120
100
80
60
40
20
0
DISTANCE ALONG PLUME (km)

Fig 6.1

6. The Front

Strong temperature and salinity gradients are evident between the warm oceanic waters offshore and the cold upwelling waters inshore. (Fig. 2.2) The intensity and position of these gradients relative to the shore is dependent on the strength and direction of the wind and varies both seasonally and in the short term. At its most intense a temperature differential of over 10°C can develop as was observed in January 1972 (Fig. 5.2 and 6.1) and January 1973 (Fig. 2.2). At its weakest the front is hardly evident as was found in the winter months of 1971 (Figs. 5.2 and 6.1). The front is most intense at the southern end of the Peninsula.

The waters either side of the front show distinct seasonal variations. Inshore temperatures tend to be lower during the summer months due to upwelling whilst offshore there is an increase in temperature of oceanic waters in late summer due to an overall warming of South-East Atlantic Surface Water and to an increase in the flow of Agulhas Bank Water around the Cape of Good Hope (Shannon, 1966).

Bang and Andrews (1974) have found that the front is associated with a powerful north-flowing jet current extending to 200 metres. Some authors (e.g. Shannon, 1966) regard the front as the site of uplift of water during upwelling, but the continuity between the front and the jet and the association of the steep temperature gradients with maximum chlorophyll concentrations (Fig. 6.2) suggest a sinking of water down the front under the oceanic water.

Such a movement, rather than the reverse, as postulated by Shannon (1966), would be expected from the dynamics of the system. Coriolis force would cause a westward movement on the coastal surface waters and this westward-flowing component would tend to flow along the isopycnals and thus down the thermocline to be entrained in part into the jet current.

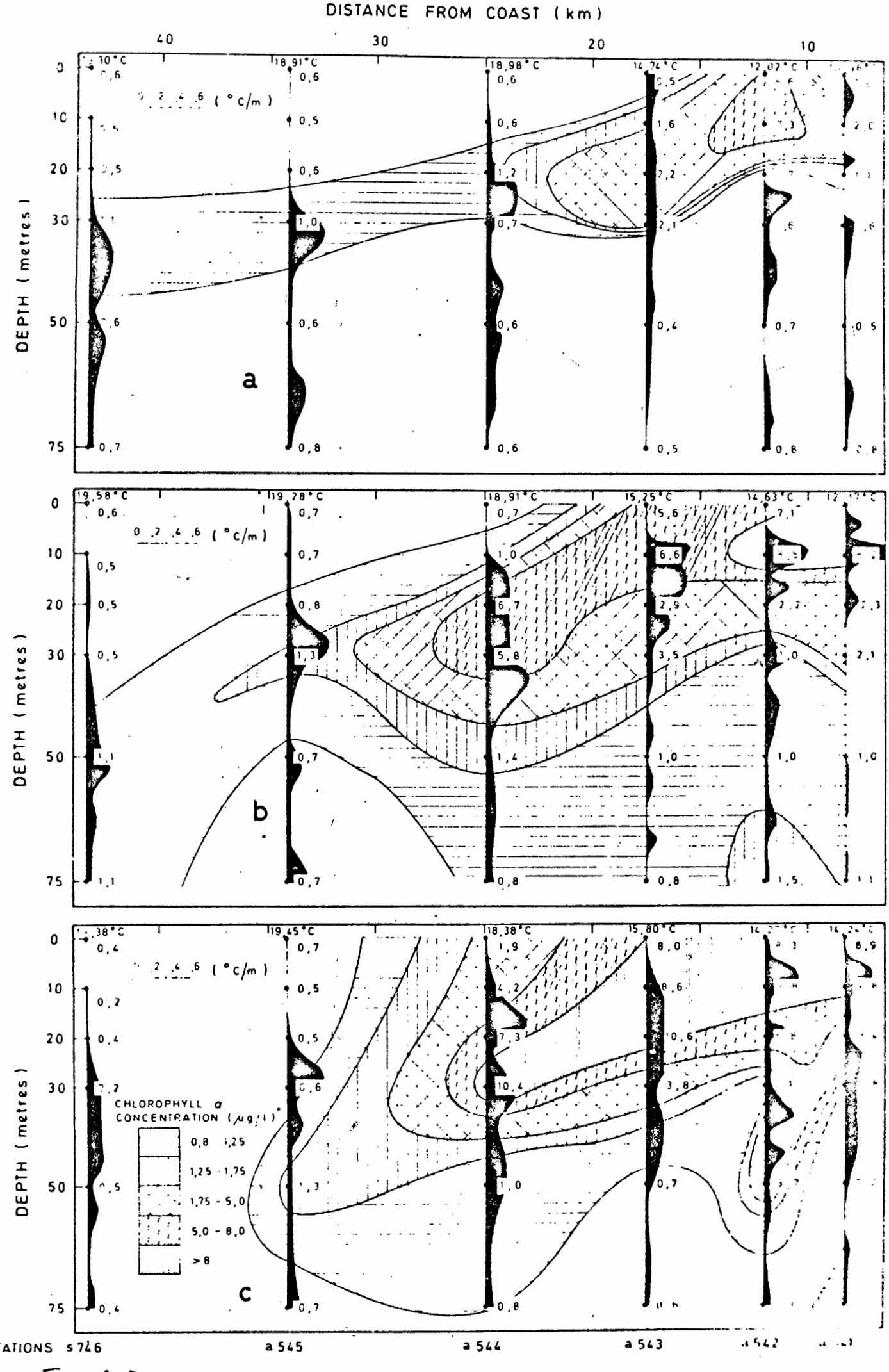

DISTANCE FROM COAST (km)
40
30
20
10
DEPTH (metres)
0
10
20
30
50
75
0 .2 .4 .6 (°C/m)
a
b
c
CHLOROPHYLL a
CONCENTRATION (µg/l)
0,8 - 1,25
1,25 - 1,75
1,75 - 5,0
5,0 - 8,0
>8
STATIONS s 746
a 545
a 544
a 543
a 542

Fig 6.2

7. Downwelling

Although the upwelling plume is a semi-permanent feature of the area during the summer months, northerly-winds do cause onshore transport of water which can result in active downwelling as indicated by a downturning of isolines of conservative properties close to the coast (c.f. Fig. 7.1 and 7.2). Downwelling would seem a relatively minor feature, having only a superficial and temporary effect on the upwelling plume. However it is noticable that the chlorophyll a and oxygen distributions change quite dramatically, showing a marked increase inshore during downwelling (c.f. Figs. 7.1 and 7.2). This would seem to result from an increased vertical stability coupled with a reduction of the northward flow of surface waters.

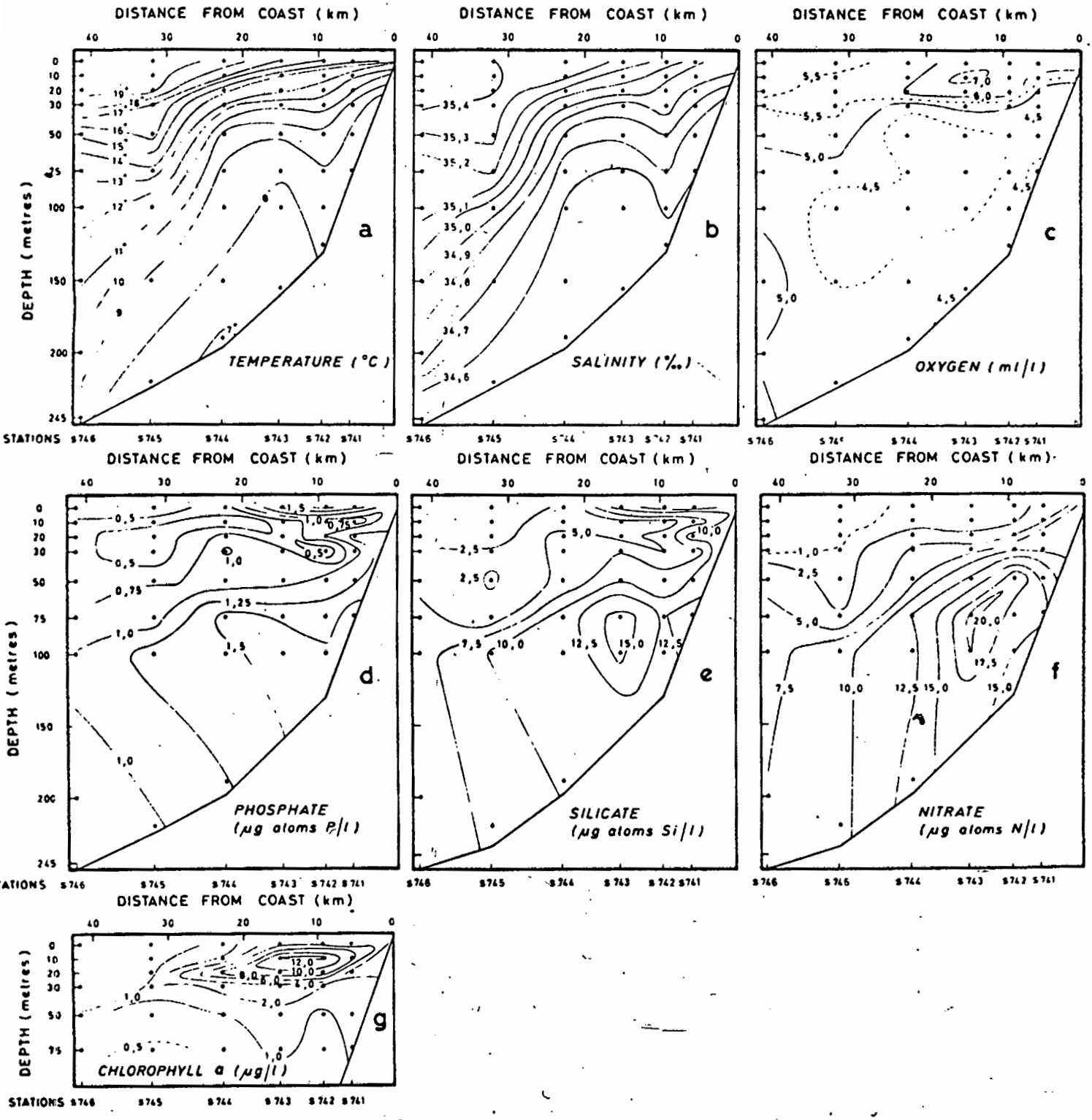

DISTANCE FROM COAST (km)
DEPTH (metres)
STATIONS
TEMPERATURE (°C)
SALINITY (‰)
OXYGEN (ml/l)
PHOSPHATE (µg atoms P/l)
SILICATE (µg atoms Si/l)
NITRATE (µg atoms N/l)
CHLOROPHYLL a (µg/l)
a
b
c
d
e
f
g

Fig 7.1

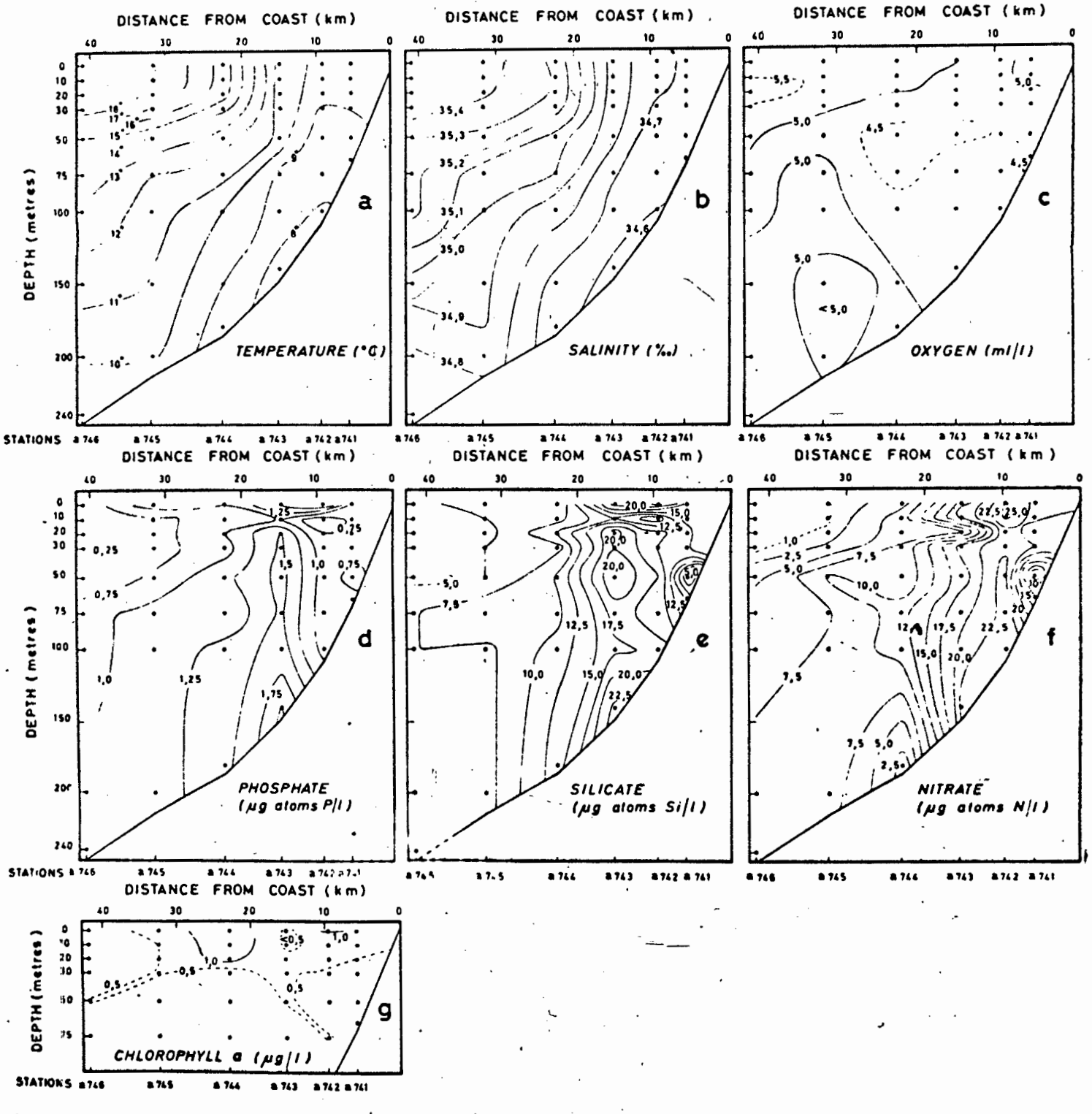

DISTANCE FROM COAST (km)
DEPTH (metres)
STATIONS
a
TEMPERATURE (°C)
b
SALINITY (‰)
c
OXYGEN (ml/l)
d
PHOSPHATE (µg atoms P/l)
e
SILICATE (µg atoms Si/l)
f
NITRATE (µg atoms N/l)
g
CHLOROPHYLL a (µg/l)

Fig 7.2.

8. Characteristics of the Water Types

As might be expected, the nutrient and oxygen concentrations in the area vary both in the short term, with the state of upwelling, and in the long term, with the season. Data from the December 1969 Upwelling Cruise are used to establish a preliminary categorisation of the water masses in the survey area.

Definite trends exist in the relation between temperature and the nutrient, chlorophyll and oxygen concentrations (Fig. 8.1). All data, irrespective of depth, were classified according to temperature and the mean and standard deviation of values within each 0.5°C fraction were determined. There are two plateaus, corresponding to temperatures of colder than 10°C and warmer than 18°C with a slope between them (except in the case of chlorophyll where a peak occurs at intermediate temperatures). Using these graphs as a basis and applying an intuitive interpretation of water movements in the study area it seemed appropriate to separate the water of the region into four water types:-

(i) Oceanic Water - lying outside the oceanic front and above the thermocline;

(ii) Upwelling Water - water upwelling into the photic zone;

(iii) Mixed Water - formed when Oceanic and Upwelling Waters come into contact;

(iv) Shelf Water - lying under the Upwelling Water.

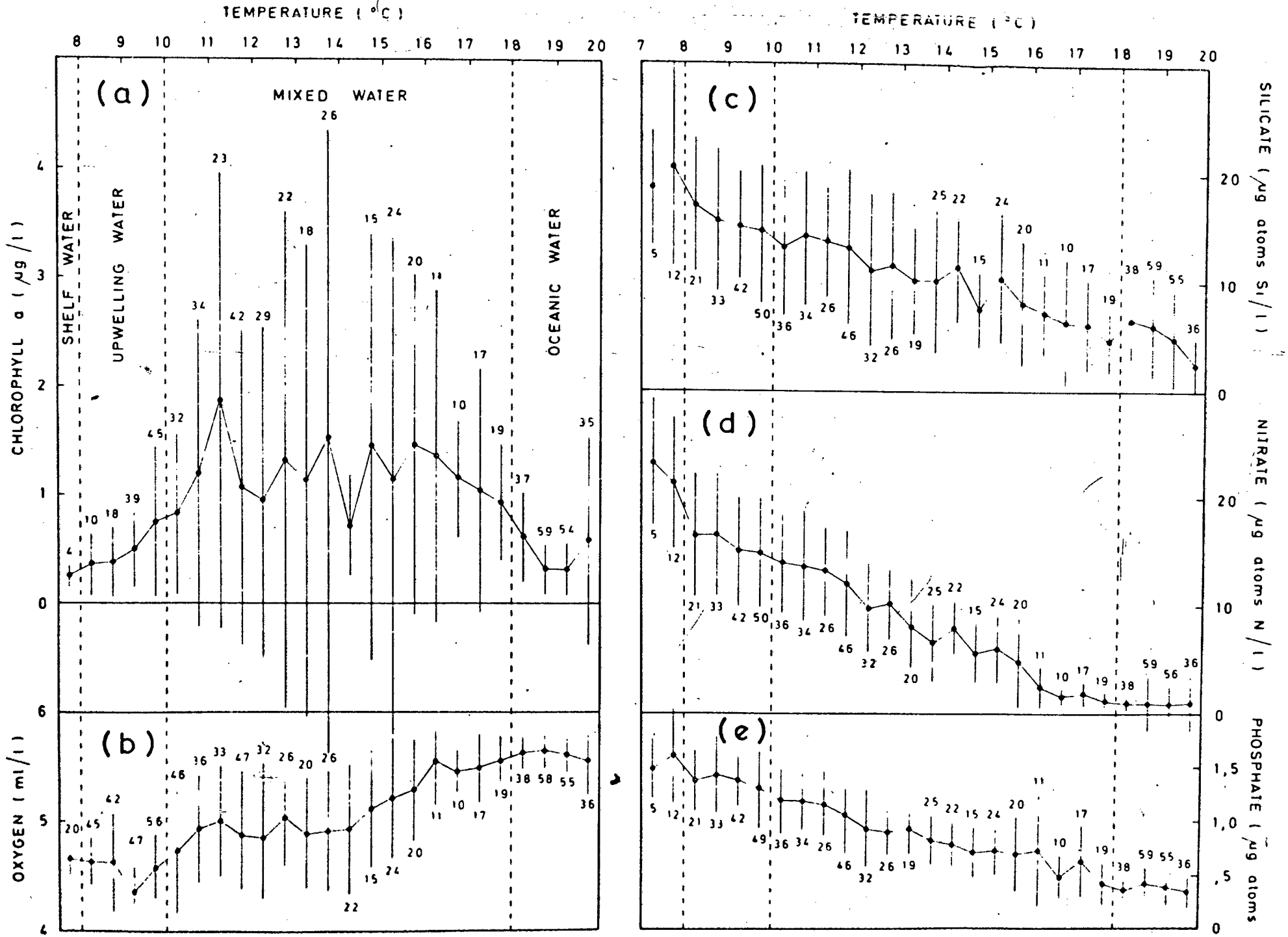

TEMPERATURE (°C)
(a)
MIXED WATER
SHELF WATER
UPWELLING WATER
OCEANIC WATER
CHLOROPHYLL a (µg / l)
(b)
OXYGEN (ml / l)
(c)
SILICATE (µg atoms Si / l)
(d)
NITRATE (µg atoms N / l)
(e)
PHOSPHATE (µg atoms P / l)

Fig 9.1

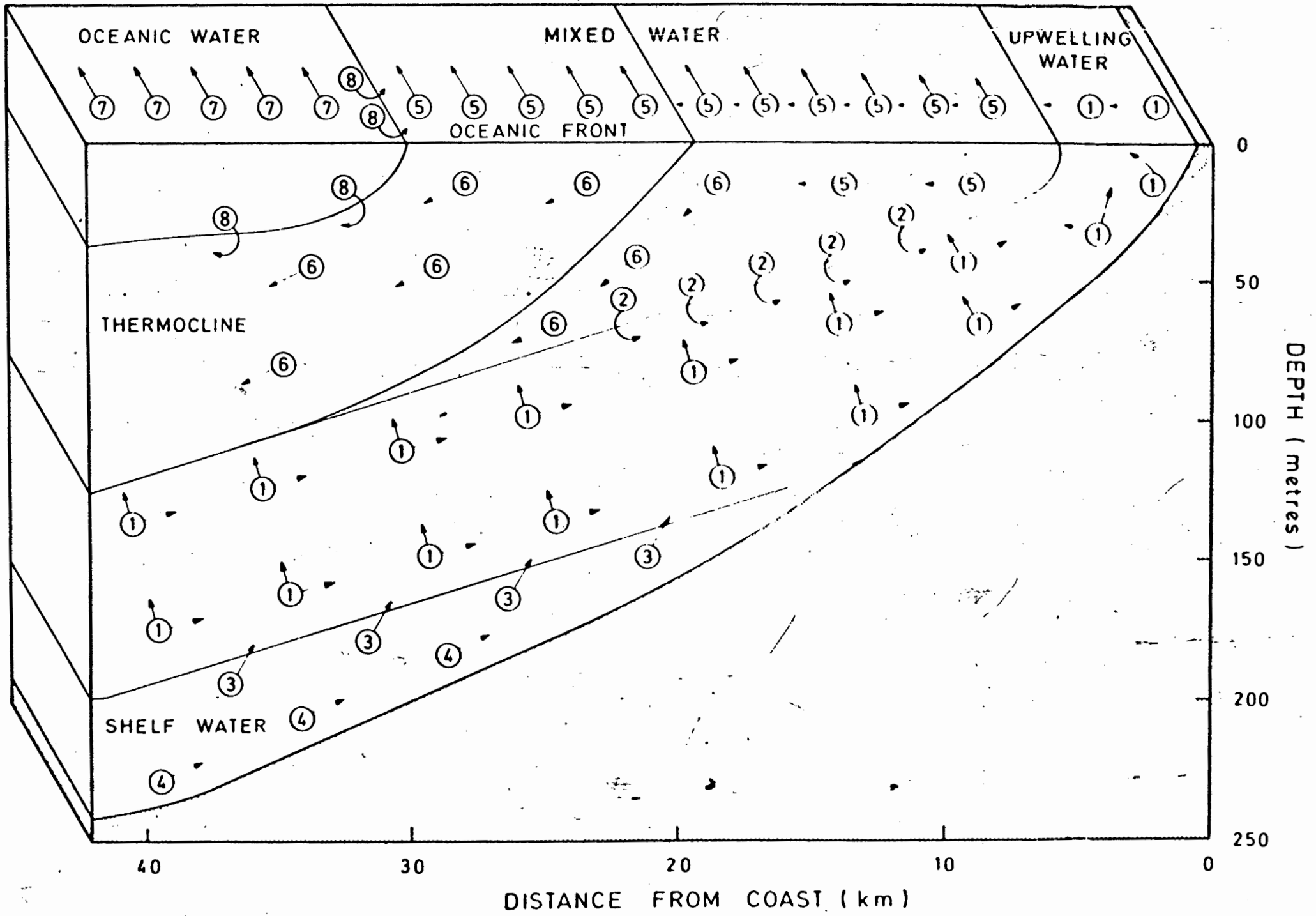

OCEANIC WATER
MIXED WATER
UPWELLING WATER
OCEANIC FRONT
THERMOCLINE
SHELF WATER
0
50
100
150
200
250
DEPTH (metres)
40
30
20
10
0
DISTANCE FROM COAST (km)

Fig 8.2

These water types were seen to appear each upwelling season and to have relatively constant conservative and non-conservative characteristics over five such seasons (Table 1). Oceanic Water is defined in the present context as water of temperature greater than 18°C. This water type is probably a mixture of South Atlantic Surface Water and Agulhas Surface Water, is more saline than other water in the area, contains little phytoplankton and very low amounts of nitrate. Upwelling Water is defined as water of temperature between 8°C and 10°C. Water colder than this was not encountered within the photic zone on any of the cruises and, although there have been reports of water colder than this at the surface, these occurrences are rare and can be regarded as abnormal. Although the upper limit of 10°C to this water type is rather arbitrarily set, no water colder than this is found at the surface unless winds favourable for upwelling are blowing. Upwelling Water is of South Atlantic Central Water origin (Hart and Currie 1960, Shannon 1966), is less saline than Oceanic Water, contains little phytoplankton and is rich in nutrients. Shelf Water is defined as water of temperature less than 8°C. This water type is similar to Upwelling Water in origin but since it remains below the photic zone, and it varies seasonally (see Chapter 10) it plays little part in the upwelling system, and it has been treated separately.

The greatest proportion of all water encountered on the cruise falls into the Mixed Water type. Mixed Water has variable conservative and very variable non-conservative characteristics due, in part, to its origin and, in part, to the intense biological

activity that occurs within it. Off the Cape Peninsula it generally forms a wedge shape, between the coast and the frontal zone, narrowing in the south. The relationships between these water types is shown in diagrammatic form in Figure 8.2.

PARAMETER	SEASON	OCEANIC WATER			UPWELLING WATER			SHELF WATER		
		Mean	S.D.	N.	Mean	S.D.	N.	Mean	S.D.	N.
TEMPERATURE	1968-69	-	-	-	9,20	±0,52	257	7,59	±0,34	13
	1969-70	18,73	±0,45	214	8,97	±0,56	526	7,57	±0,37	182
°C	1970-71	-	-	-	9,03	±0,53	115	7,86	±0,11	5
	1971-72	20,05	±1,17	21	9,05	±0,55	164	7,25	±0,83	21
	1972-73	18,80	±0,59	11	9,17	±0,48	167	7,20	±0,61	11
SALINITY	1968-69	-	-	-	34,69	±0,06	257	34,57	±0,07	13
	1969-70	35,42	±0,07	214	34,69	±0,09	503	34,56	±0,07	170
°/oo	1970-71	-	-	-	34,68	±0,07	110	34,58	±0,10	5
	1971-72	35,37	±0,11	21	34,69	±0,08	162	34,51	±0,11	17
	1972-73	35,22	±0,16	11	34,72	±0,07	166	34,50	±0,07	10
OXYGEN	1968-69	-	-	-	4,65	±0,39	146	4,57	±0,30	10
	1969-70	5,54	±0,34	211	4,53	±0,37	522	4,56	±0,22	177
ml/l	1970-71	-	-	-	4,19	±0,50	111	3,89	±0,14	4
	1971-72	5,36	±0,18	21	4,19	±0,57	160	4,36	±0,48	19
	1972-73	6,51	±0,75	11	4,35	±0,76	166	4,73	±0,20	8
PHOSPHATE	1968-69	-	-	-	1,65	±0,82	59	-	-	-
	1969-70	0,39	±0,17	213	1,36	±0,31	487	1,55	±0,32	134
/ug atoms P/1	1970-71	-	-	-	-	-	-	-	-	-
	1971-72	0,47	±0,17	21	1,42	±0,42	162	1,46	+0,24	19
	1972-73	0,55	±0,32	11	1,55	±0,44	167	1,61	±0,33	9
SILICATE	1968-69	-	-	-	-	-	-	-	-	-
	1969-70	5,1	±4,6	213	16,3	±5,8	487	19,6	±5,9	133
/ug atoms Si/1	1970-71	-	-	-	15,1	±5,7	114	18,7	±4,0	5
	1971-72	1,3	±1,5	21	16,6	±6,6	162	21,4	±5,2	18
	1972-73	2,8	±1,3	11	15,0	±4,7	167	17,8	±2,7	9

TABLE 1 The characteristics of three water types off the Cape Peninsula over five consecutive upwelling seasons. Data for 1968-69 season from November 1968 Upwelling Cruise; for 1969-70 from December 1969 Upwelling Cruise; for 1970-71 from January 1971 Upwelling Cruise; for 1971-72 from Upwelling-Monitoring Cruises in November and December 1971 and January and February 1972; and for 1972-73 from Upwelling-Monitoring Cruises in November and December 1972 and January and February 1973.

Cont.

PARAMETER	SEASON	OCEANIC WATER			UPWELLING WATER			SHELF WATER		
		Mean	S.D.	N.	Mean	S.D.	N.	Mean	S.D.	N.
NITRATE	1968-69	-	-	-	19,0	±4,0	59	-	-	-
	1969-70	0,8	±2,0	214	17,8	±5,3	488	20,9	±6,2	134
/ug atoms N/1	1970-71	-	-	-	19,9	±4,4	115	21,3	±2,5	5
	1971-72	0,8	±0,1	21	24,3	±3,8	162	26,0	±3,8	19
	1972-73	0,6	±0,2	11	21,3	±4,3	166	24,7	±3,0	10
CHLOROPHYLL A	1968-69	-	-	-	-	-	-	-	-	-
	1969-70	0,4	±0,5	210	0,9	±0,9	405	0,6	±0,4	53
/ug/1	1970-71	-	-	-	0,5	±0,6	105	0,3	±0,2	5
	1971-72	0,6	±0,6	21	0,6	±0,6	147	0,7	±0,6	13
	1972-73	0,5	±0,2	11	0,4	±0,3	126	-	-	-

TABLE 1 (cont.) The characteristics of three water types off the Cape Peninsula over five consecutive upwelling seasons. Data for 1968-69 season from November 1968 Upwelling Cruise; for 1969-70 from December 1969 Upwelling Cruise; for 1970-71 from January 1971 Upwelling Cruise; for 1971-72 from Upwelling-Monitoring Cruises in November and December 1971 and January and February 1972; and for 1972-73 from Upwelling-Monitoring Cruises in November and December 1972 and January and February 1973.

9. Non-conservative Variables in the Upwelling Season

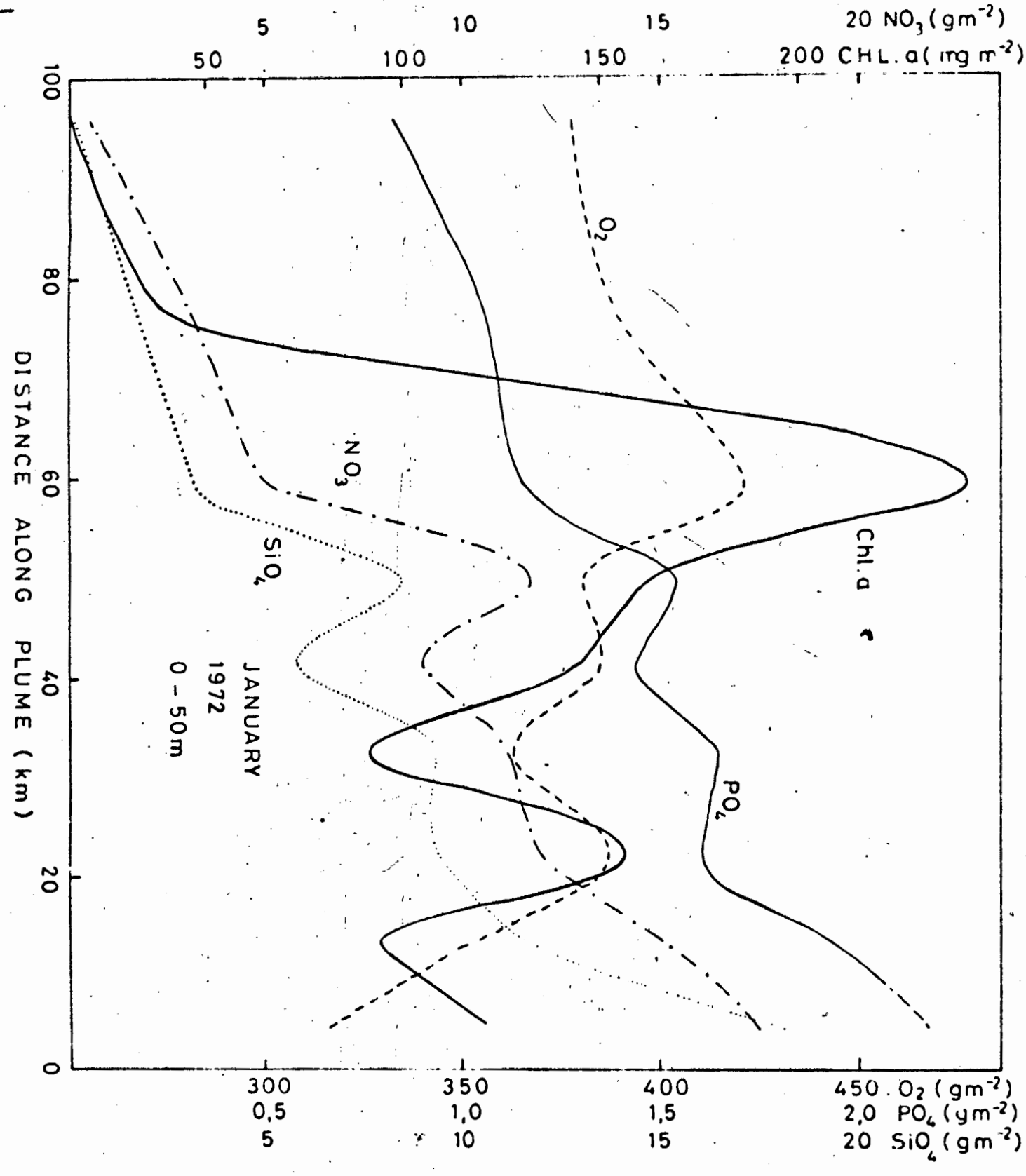
The distributions of the conservative properties in the study area are determined largely by upwelling and mixing processes. The non-conservative parameters are controlled in addition by biological activity. Further since the chlorophyll *a* concentrations in Upwelling Water and Oceanic Water are similar and those of oxygen differ by only 1 ml/l (Table 2) mixing becomes relatively unimportant in determining their distributions so that these variables can be regarded as good indicators of local biological activity. High chlorophyll *a* and oxygen concentrations were found in the wedge-shaped volume of Mixed Water, with exceptionally high values at the northern tip of the plume.

In contrast high nutrient concentrations were found in deeper waters offshore extending to the surface inshore and were generally associated with Upwelling and Shelf Waters.

It was found convenient in the interpretation of non-conservative data to assume a 50 m photic zone. Photometer measurements indicate that in fact the level of 1% of surface light is often shallower but this is compensated by considerable vertical instability. Total amounts of each measured non-conservative parameter in this photic layer (0 - 50 m) were obtained by interpolation (see Chapter 11). Similar treatment of data in the next 50 m depth category, termed the 'sub-photic layer (50 - 100 m), was also carried out.

22/...

Fig 9.1


5
10
15
20 NO_3 (gm^{-2})
50
100
150
200 CHL. a ($mg\ m^{-2}$)
100
80
60
40
20
0
DISTANCE ALONG PLUME (km)
O_2
NO_3
SiO_4
Chl.a
PO_4
JANUARY
1972
0 - 50m
300
350
400
450 O_2 (gm^{-2})
0,5
1,0
1,5
2,0 PO_4 (gm^{-2})
5
10
15
20 SiO_4 (gm^{-2})

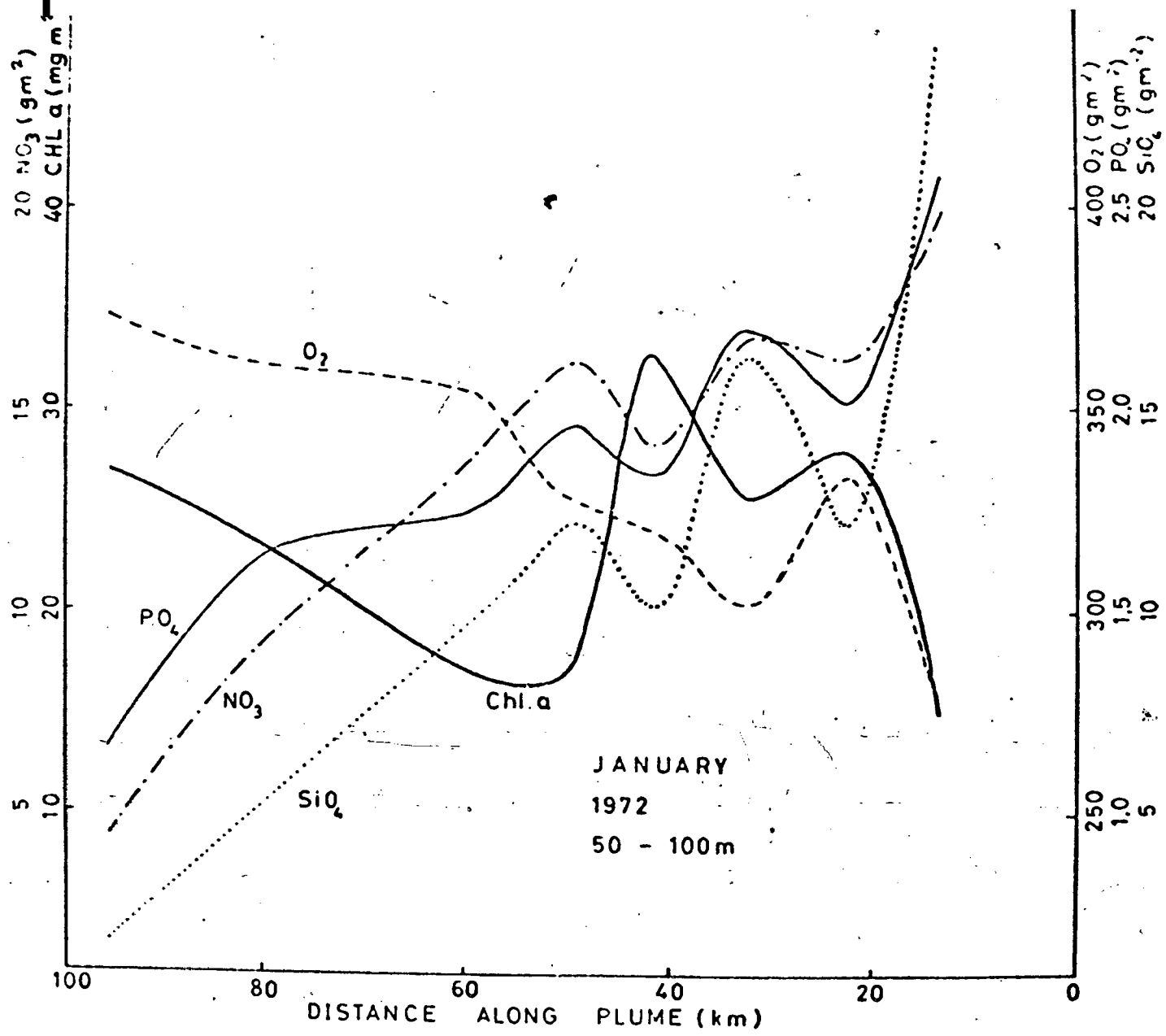
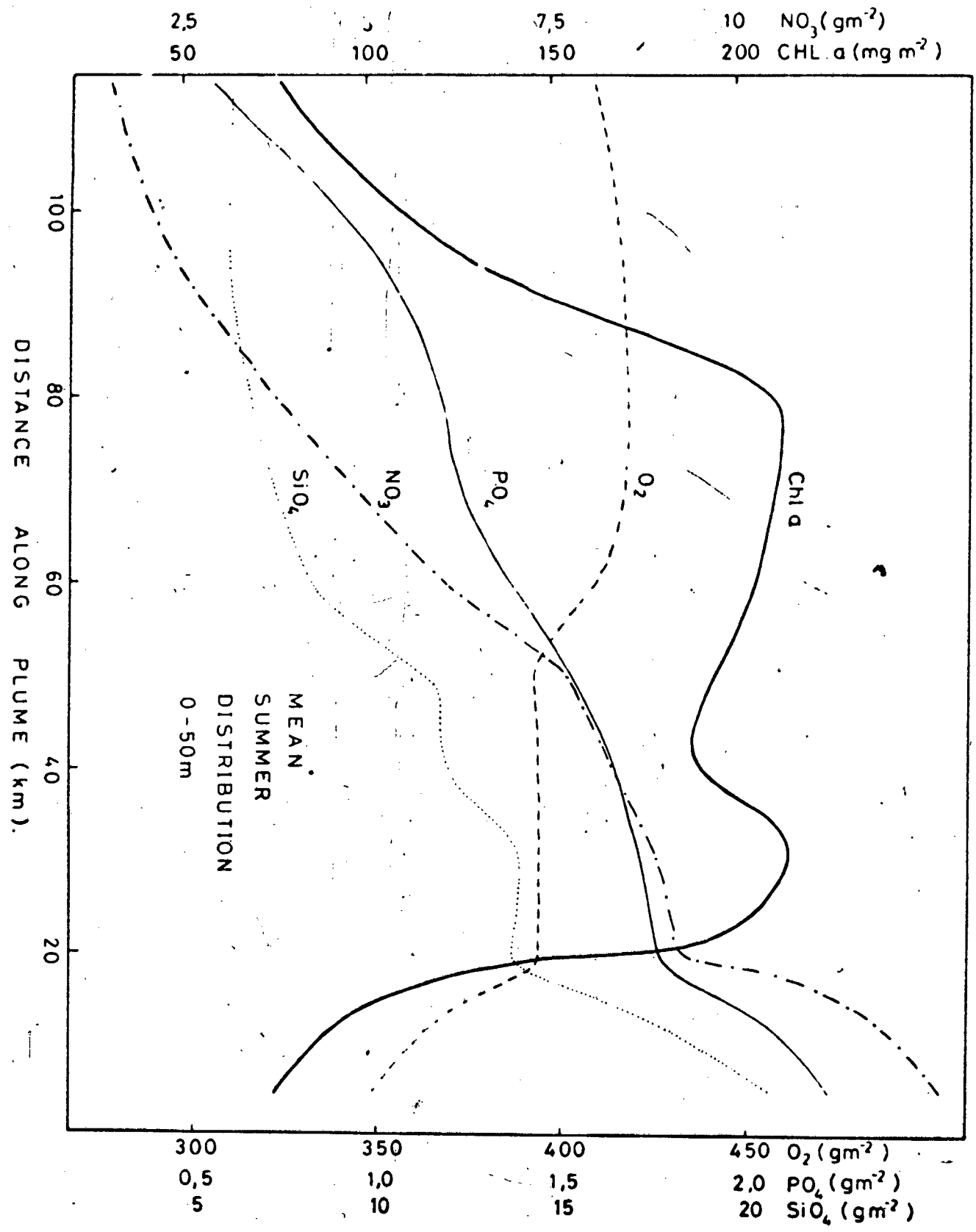


Fig 9.2 Distribution of nitrate, silicate, phosphate, oxygen and chlorophyll a in the sub-photic layer in a section along the upwelling plume in January 1972.


2,5
50
7,5
150
10 NO3 (gm-2)
200 CHL a (mg m-2)
100
80
60
40
20
DISTANCE ALONG PLUME (km).
SiO4
NO3
PO4
O2
Chl a
MEAN SUMMER DISTRIBUTION 0-50m
300
0,5
5
350
1,0
10
400
1,5
15
450 O2 (gm-2)
2,0 PO4 (gm-2)
20 SiO4 (gm-2)

If it is assumed that there is a north-westerly flow of surface waters down the centre of the plume measurements made along the axis of the plume partially reflect the temporal changes. Monthly integrated profiles of non-conservative properties along the plume of both the photic and sub-photic layers were rather variable although the main features were similar through much of the upwelling season. As examples Figs. 9.1 and 9.2 show profiles of nitrate, silicate, phosphate, oxygen and chlorophyll a in the photic and sub-photic layers in January 1972 and in Fig. 9.3 mean summer distributions, obtained by averaging data from the twelve Upwelling-Monitoring cruises between September and February of 1971-2 and 1972-3, are shown.

The nutrients drop somewhat irregularly down the plume from the coast with related irregularities in both layers. Oxygen distribution tends to mirror those of the nutrients, peaking in the photic layer inshore of the oceanic front, which normally lies between 60 and 80 km from Duiker Point, during summer months and falling on the oceanward side of it. Chlorophyll a follows a similar pattern. In the sub-photic layer chlorophyll a is maximal about 20 to 40 km from Duiker Point, falls in the region of the photic layer peak, rising again offshore of the front to a level higher than that of the layer above. This offshore rise in the sub-photic layer is probably caused by a westward flow of phytoplankton-rich water down the thermocline (Fig. 6.2). Irregularities found in individual profiles do not appear in average profiles and the offshore peak of chlorophyll a in the photic layer also largely disappears due to positional fluctuations of

23/...

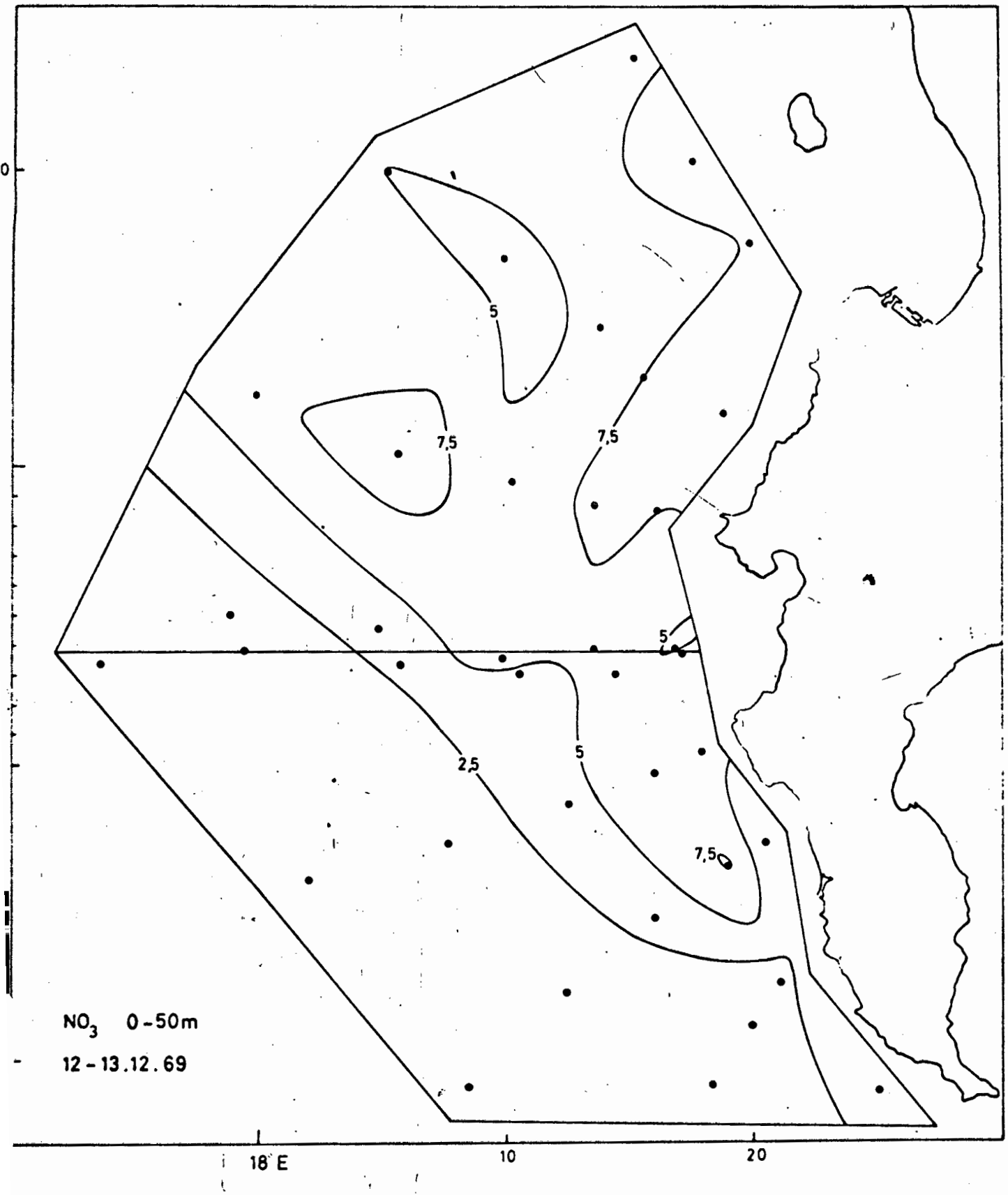


Fig 9.4

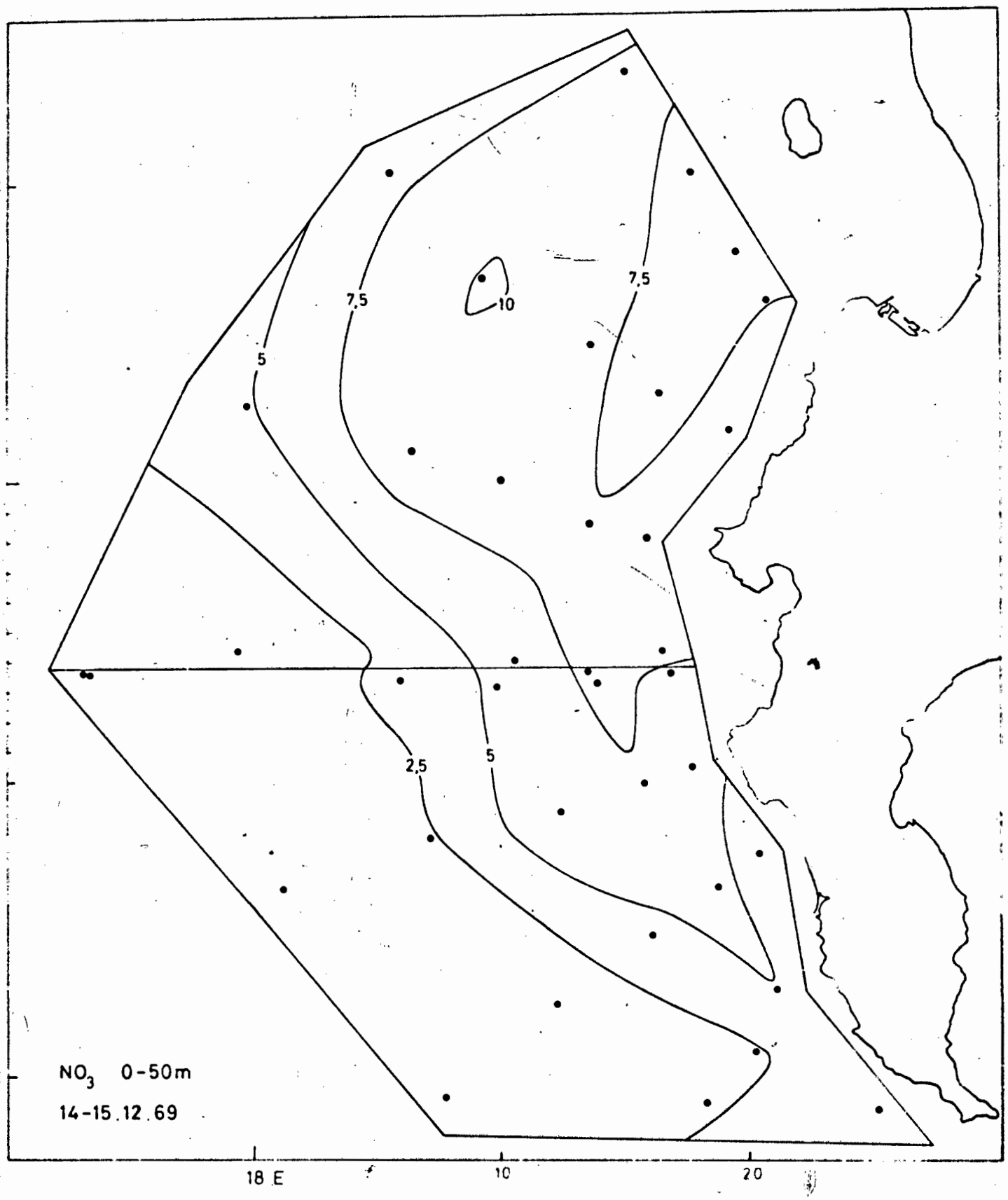


Fig 9.5

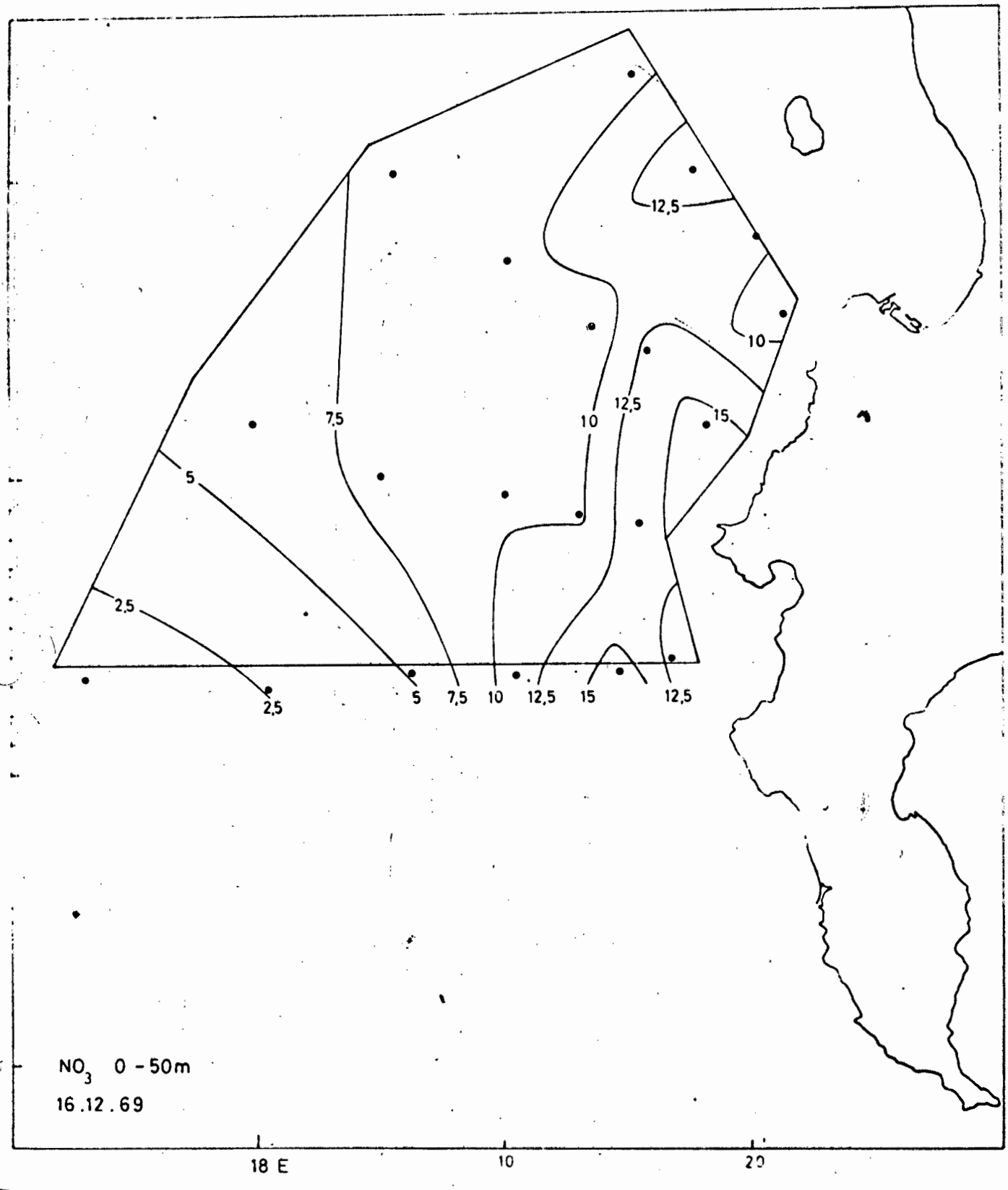

12,5
10
7,5
10
12,5
15
5
2,5
2,5
5
7,5
10
12,5
15
12,5
34
S
NO3 0 - 50m
16.12.69
18 E
10
20

Fig 9,6

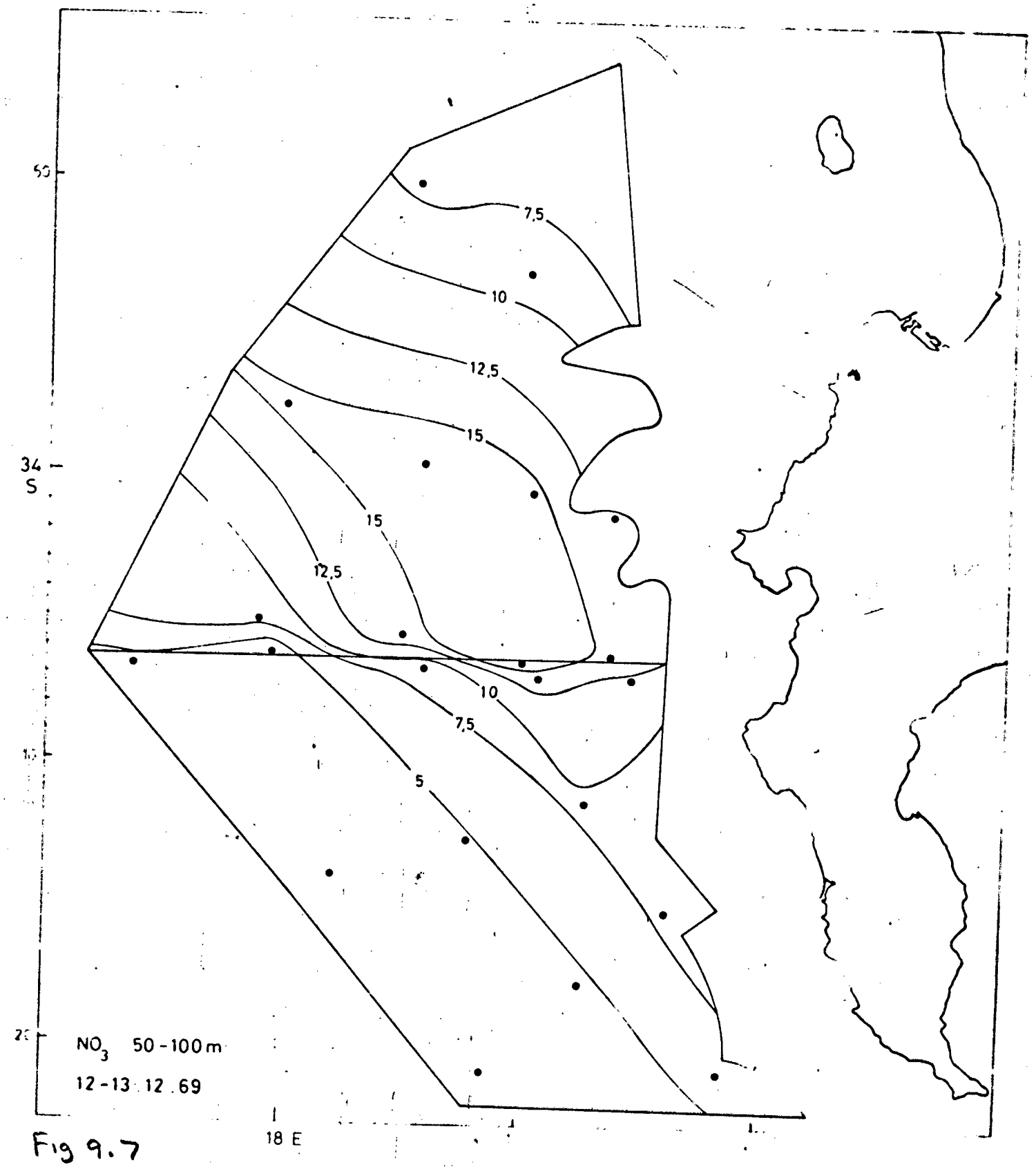


Fig 9.7

the oceanic front. Positional fluctuations were not so large inshore and a clearer position than that offshore emerges. An exponential increase of the chlorophyll a content within the inshore 20 km is accompanied by a decrease in nutrient content and an increase in oxygen levels.

The horizontal distribution of nutrients, chlorophyll a and oxygen showed considerable day to day variation, due largely to changes in upwelling conditions. For example when conditions swung from downwelling to intense upwelling between 12 and 16 December integrated nitrate values of the photic layer off the Cape Peninsula showed a substantial increase (Fig. 9.4, 9.5 and 9.6). The highest levels were found close to the coast during upwelling. The distribution of nitrate in the sub-photic layer was more uniform, although reflecting many of the features seen in the layer above (e.g. c.f. Fig. 9.4 and 9.7). Distributions of phosphate, silicate, chlorophyll a and oxygen (not illustrated) showed similar trends although chlorophyll a distribution was considerably more patchy.

10. Seasonal Changes

The seasonal wind cycle described in Chapter 4 has a profound influence on the oceanography of the region and there is a well-defined upwelling season which extends approximately from late September to March. Each measured parameter is influenced by the local wind cycle. In addition larger scale seasonal occurences have their influences and an investigation of individual parameters allows considerable insight into the interrelationships of the local and larger scale scycles.

(a) Temperature

In winter months surface water is of rather uniform temperature whilst in summer the inshore waters decrease in temperature and those offshore increase so that a 10 or 11°C difference is sometimes found between inshore and offshore surface waters (Fig. 5.2). In the deeper layers (Fig. 10.1) the isotherms sink from March to July and rise rapidly again in September and October, in the early part of the upwelling season, due apparently to an intrusion of cold water.

(b) Salinity

Isohalines show very similar trends to isotherms (Fig. 10.2). Of particular interest is the regular appearance at the bottom of low salinity water in September and October, associated with the cool water.

25/...

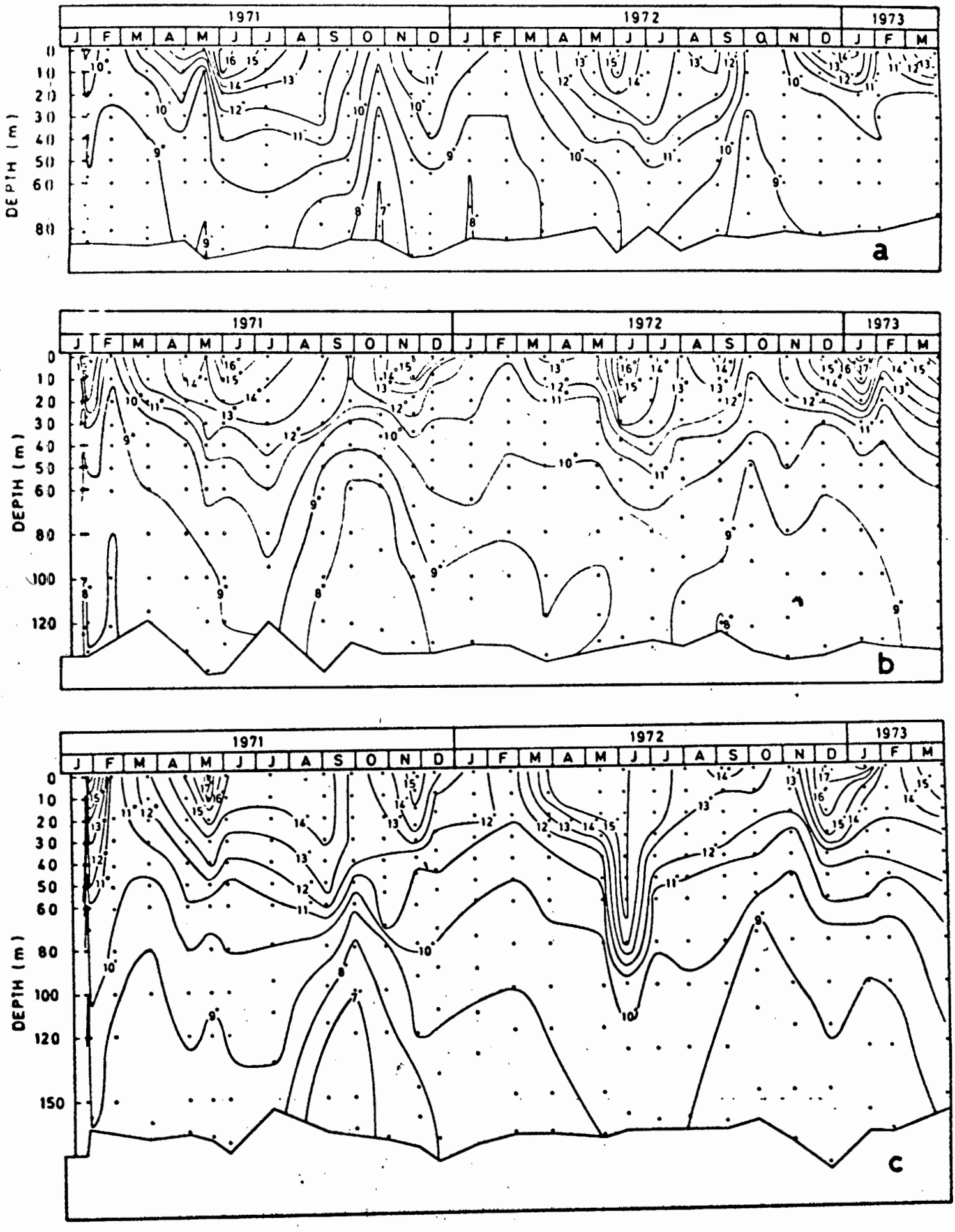

1971
1972
1973
J F M A M J J A S O N D J F M A M J J A S O N D J F M
DEPTH (m)
0 10 20 30 40 50 60 80
a
1971
1972
1973
J F M A M J J A S O N D J F M A M J J A S O N D J F M
DEPTH (m)
0 10 20 30 40 50 60 80 100 120
b
1971
1972
1973
J F M A M J J A S O N D J F M A M J J A S O N D J F M
DEPTH (m)
0 10 20 30 40 50 60 80 100 120 150
c

Fig 10.1

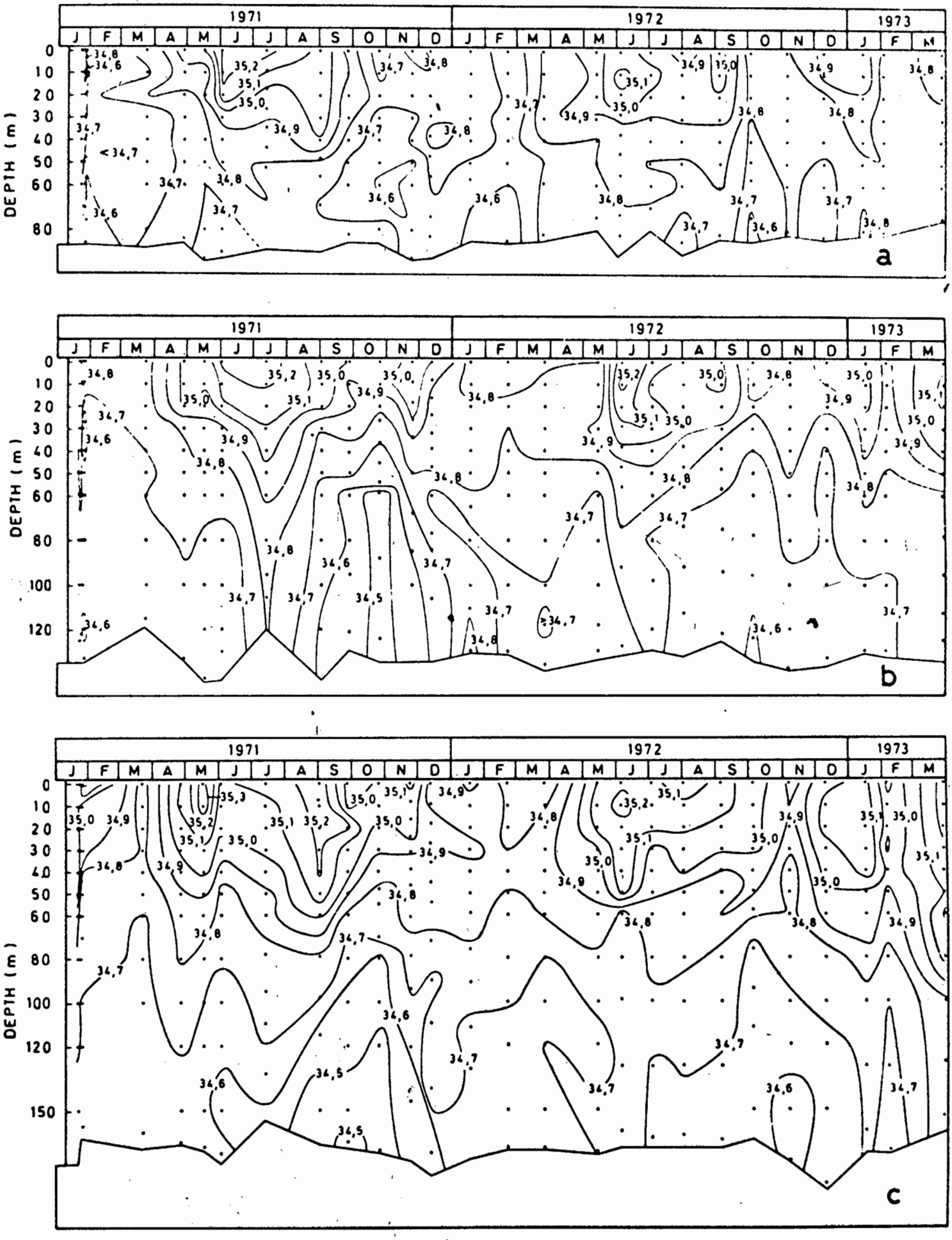

1971
1972
1973
J F M A M J J A S O N D J F M A M J J A S O N D J F M
DEPTH (m)
0 10 20 30 40 50 60 80
a
1971
1972
1973
J F M A M J J A S O N D J F M A M J J A S O N D J F M
DEPTH (m)
0 10 20 30 40 50 60 80 100 120
b
1971
1972
1973
J F M A M J J A S O N D J F M A M J J A S O N D J F M
DEPTH (m)
0 10 20 30 40 50 60 80 100 120 150
c

Fig 10.2

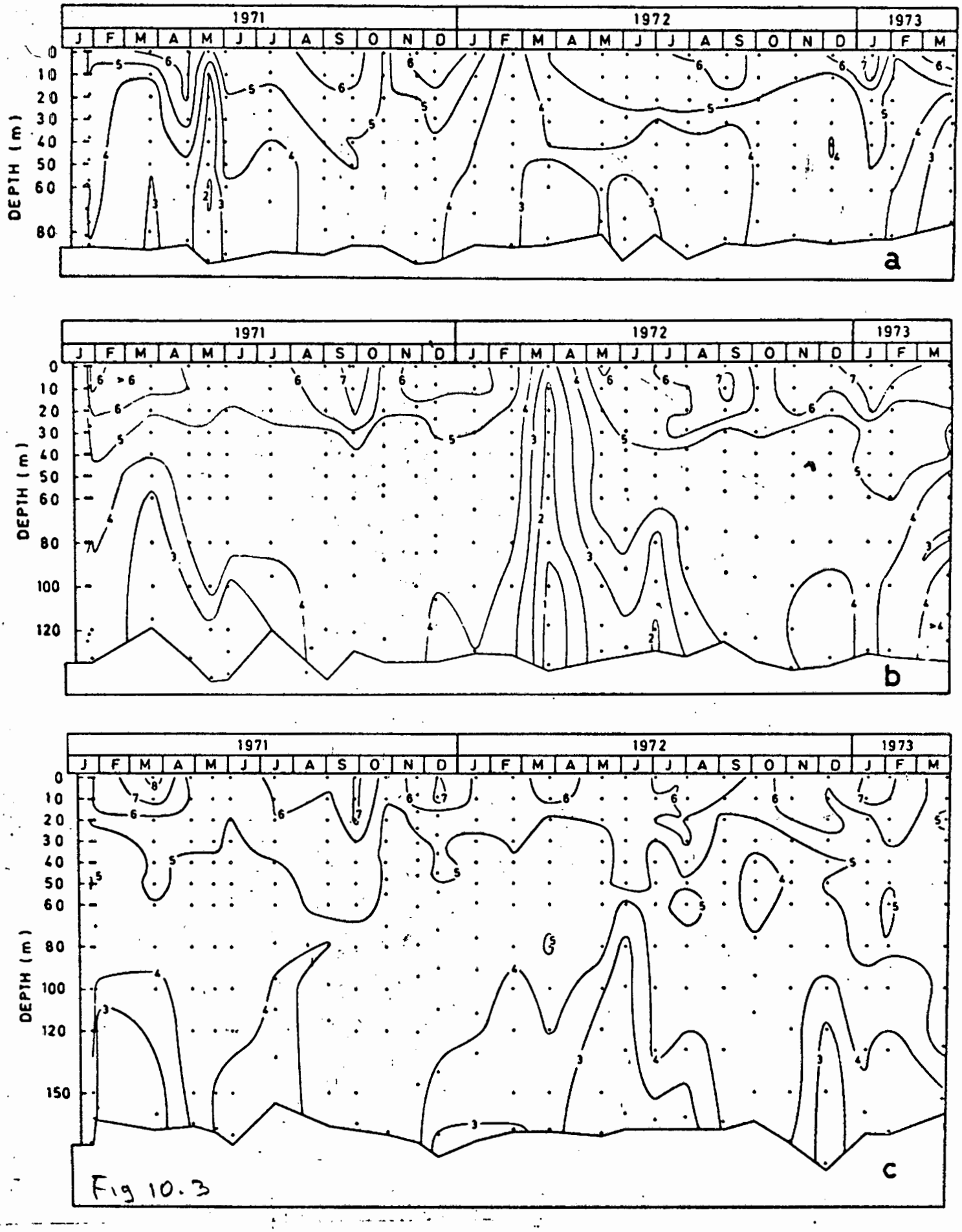

1971
1972
1973
J F M A M J J A S O N D J F M A M J J A S O N D J F M
DEPTH (m)
0 10 20 30 40 50 60 80
a
1971
1972
1973
J F M A M J J A S O N D J F M A M J J A S O N D J F M
DEPTH (m)
0 10 20 30 40 50 60 80 100 120
b
1971
1972
1973
J F M A M J J A S O N D J F M A M J J A S O N D J F M
DEPTH (m)
0 10 20 30 40 50 60 80 100 120 150
c

Fig 10.3

Fig 10.4

Fig 10.4

(c) Oxygen

The oxygen content of surface waters showed marked variation but any seasonal pattern was largely masked by less regular fluctuations. High surface oxygen concentrations were generally associated with periods of less intense upwelling when temperatures and salinities were also high (Fig. 10.3). This is particularly noticeable in summer when the oxygen content of surface waters rose above 7 ml/l on occasions, due to phytoplankton production.

The regular appearance of oxygen-depleted water near the bottom in late summer is the most noticeable feature. It coincided with the appearance of warm, saline water at the bottom. This oxygen-depleted water is only found until late winter and its disappearance is associated with the appearance of cold, low-salinity water at the bottom. A southward-flowing current, described by De Decker (1970), would seem to be responsible for much of this oxygen-depleted water. This current has very constant temperature and salinity characteristics (viz 9°C and 34.7‰ and carries oxygen-depleted water from the "azoic area" in the Walvis Bay region along the shelf of the west coast of southern Africa (De Decker 1970). In Fig. 10.4 a plot of the oxygen concentration of oxygen-depleted water sampled on the Upwelling-Monitoring cruises against temperature is shown. This figure can be compared directly with De Decker's (1970) Fig. 5 which shows a similar plot for data taken along the west coast from 32°S southwards. Oxygen-depleted water was confined to a narrow temperature range, particularly at oxygen concentrations of < 2 ml/l.

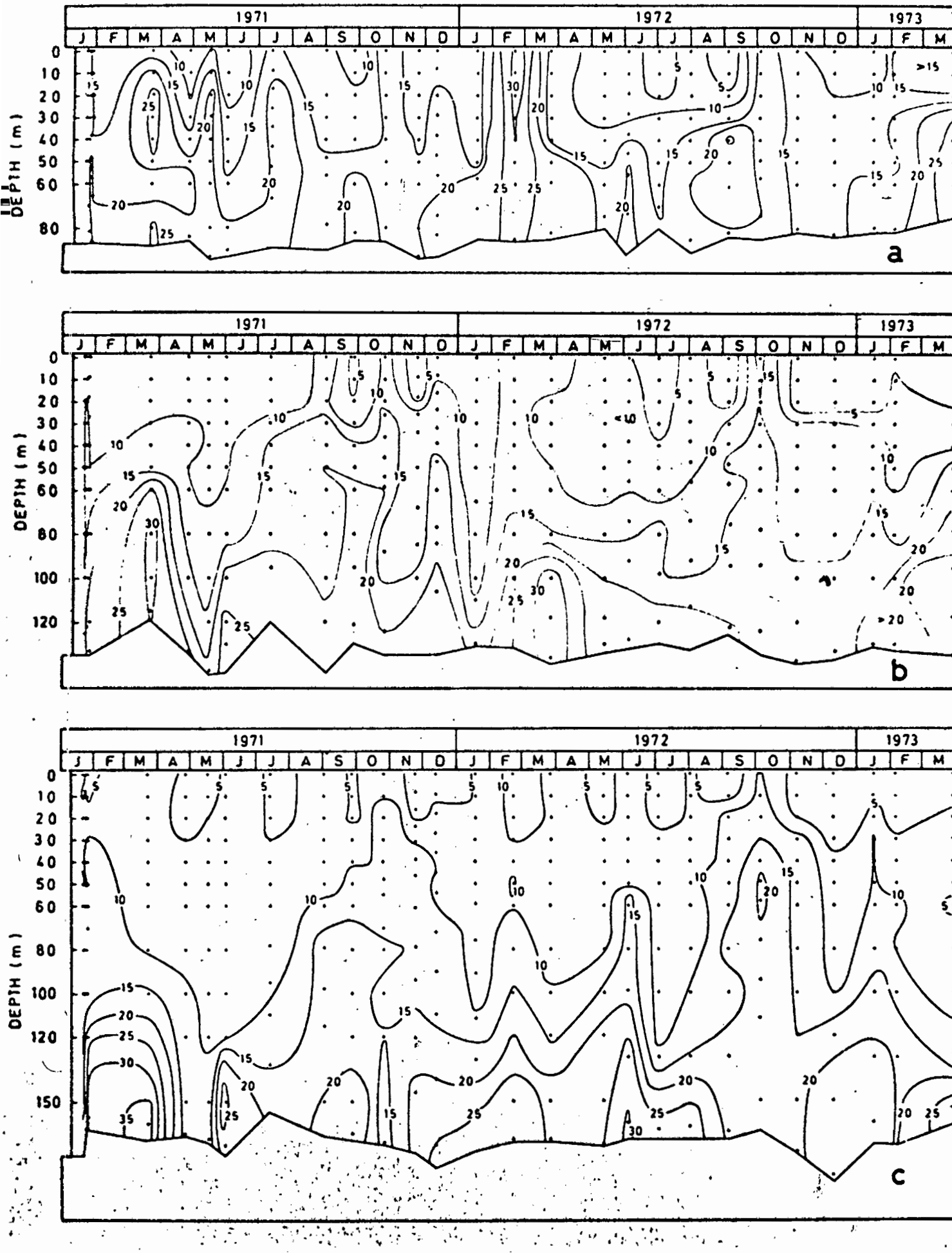

1971
1972
1973
J F M A M J J A S O N D J F M A M J J A S O N D J F M
DEPTH (m)
0 10 20 30 40 50 60 80
a
1971
1972
1973
J F M A M J J A S O N D J F M A M J J A S O N D J F M
DEPTH (m)
0 10 20 30 40 50 60 80 100 120
b
1971
1972
1973
J F M A M J J A S O N D J F M A M J J A S O N D J F M
DEPTH (m)
0 10 20 30 40 50 60 80 100 120 150
c

Fig 10.5

Several data (circles- Fig. 10.4) did not fall in this range and instead appeared to conform to a linear relationship (between oxygen and temperature) approximately originating at 9.25°C and 1.25 ml/l. These data were obtained in March 1972 at Stations 3 and 4 with the exception of the two readings arrowed, which were obtained five weeks later at Station 6 (at 60 m and 80 m). An interpretation of this linear relationship is that on this one occasion low oxygen-content water was mixed with surface waters of normal (4.4 ml/l) oxygen content and higher temperature. The arrowed readings are considered to be remnants of the same water. It might be expected that each time upwelling occurs, oxygen-depleted water would be brought to the surface, since oxygen-depleted water and Upwelling Water have similar temperature characteristics. Yet, assuming this interpretation is correct, this process was only detected once on this study and remained undetected by De Decker (1970). The infrequency of occasions on which oxygen-depleted water was detected entrained in the upwelling system indicates that it probably normally lies beneath the Upwelling Water. That a certain amount of mixing of oxygen-depleted water normally occurs is indicated by the increase of the temperature range with increasing oxygen concentration (Fig. 10.4), indicating that the core of low-oxygen water was mixing with both warmer and cooler waters with higher oxygen concentrations.

(d) Silicate

Reactive silicate concentration is closely and inversely related to dissolved oxygen concentration with the result that the seasonal distribution of silicate illustrated in Fig. 10.5

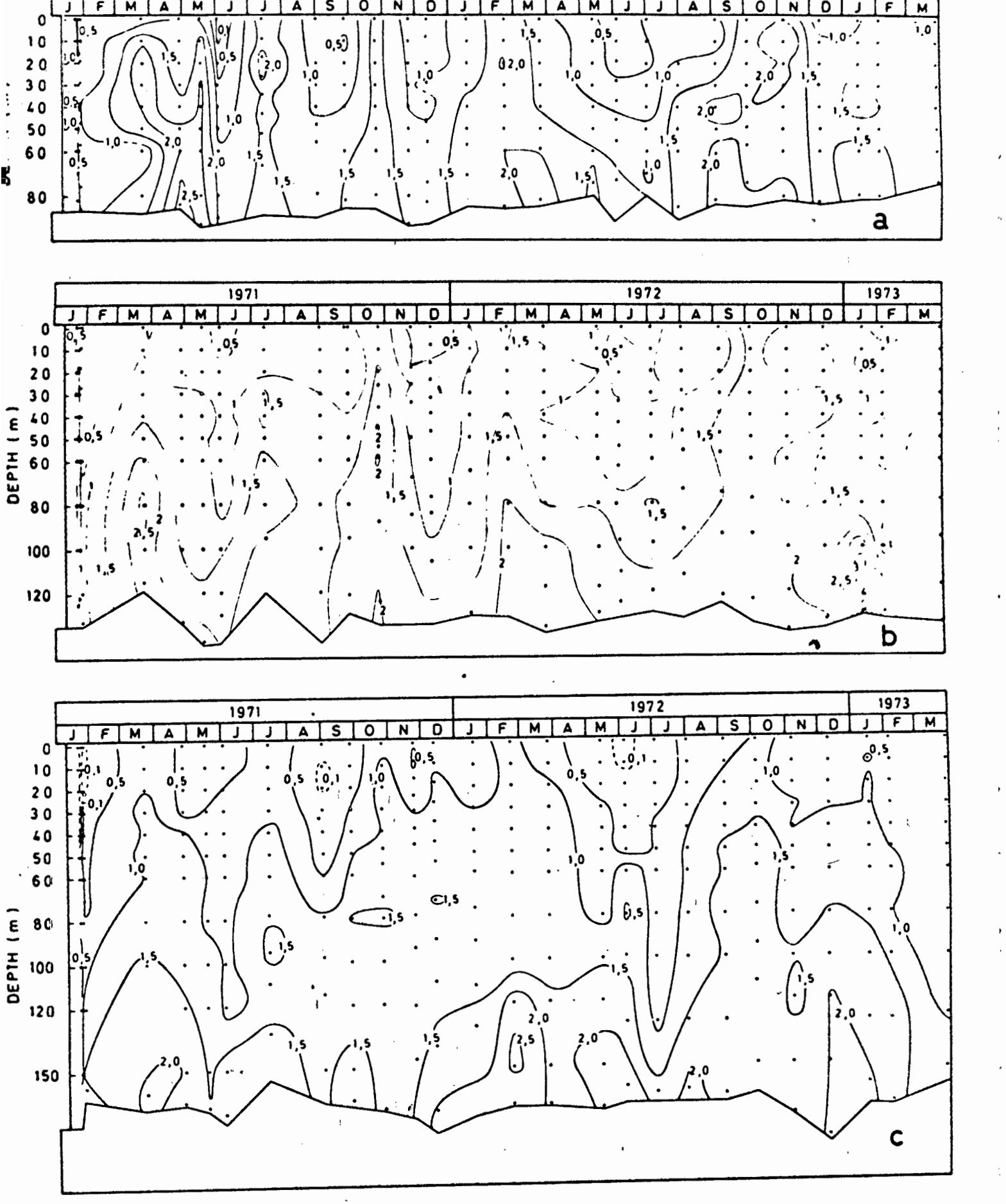

1971
1972
1973
J F M A M J J A S O N D J F M A M J J A S O N D J F M
DEPTH (m)
0 10 20 30 40 50 60 80 100 120 150
a
b
c

Fig 10.6

mirrors that of oxygen (Fig. 10.3). The cold bottom water that appears around October each year is relatively poor in silicate, containing about 20 /ug atoms Si/l or less. Low oxygen bottom water is relatively rich in silicate containing 25 to 40 /ug atoms Si/l.

Surface waters generally contained lower concentrations than bottom waters and values rarely reached more than 10 /ug atoms Si/l. Upwelling therefore causes silicate enrichment of surface waters as is particularly evident at Station 6 (Fig. 10.5(c)) where the 10 /ug atom Si/l isoline rose and peaked in October and January or February each year and sank in the winter months. The uplift in June 1972 was caused by an intrusion of oxygen-depleted water to unusually shallow depths (Fig. 10.3).

(e) Phosphate

Inorganic phosphate concentration is closely correlated with reactive silicate concentration (Fig. 10.6). Phosphate concentrations of > 2 /ug atoms P/l were found in oxygen-depleted water near the bottom. Somewhat lower concentrations were associated with cold bottom water. At surface and intermediate depths the highest phosphate concentrations were found during periods of upwelling. Low concentrations at these levels were found in winter and in mid-summer when upwelling was relatively inactive.

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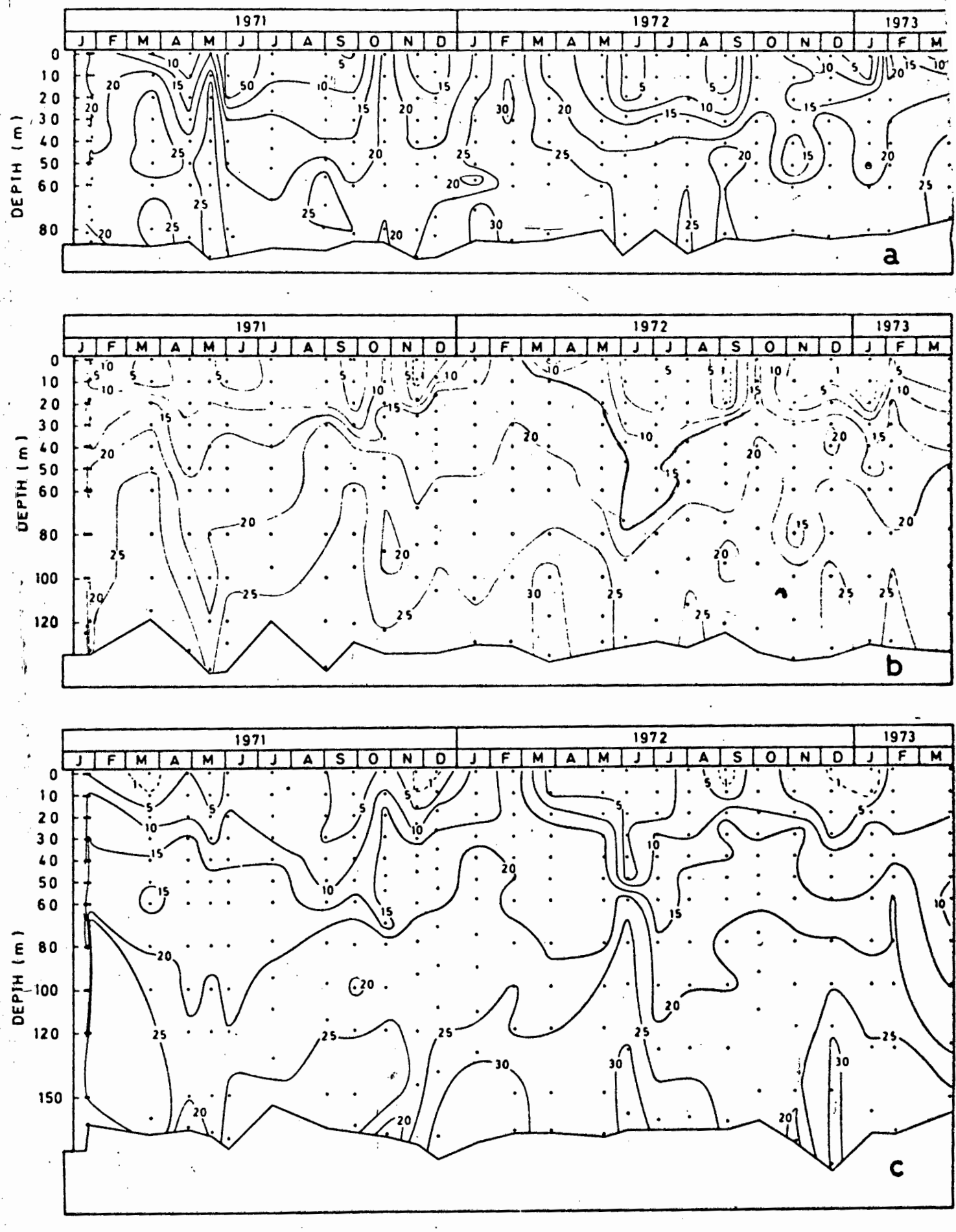
1971
1972
1973
J F M A M J J A S O N D J F M A M J J A S O N D J F M
DEPTH (m)
0 10 20 30 40 50 60 80
a
1971
1972
1973
J F M A M J J A S O N D J F M A M J J A S O N D J F M
DEPTH (m)
0 10 20 30 40 50 60 80 100 120
b
1971
1972
1973
J F M A M J J A S O N D J F M A M J J A S O N D J F M
DEPTH (m)
0 10 20 30 40 50 60 80 100 120 150
c

Fig 10.7

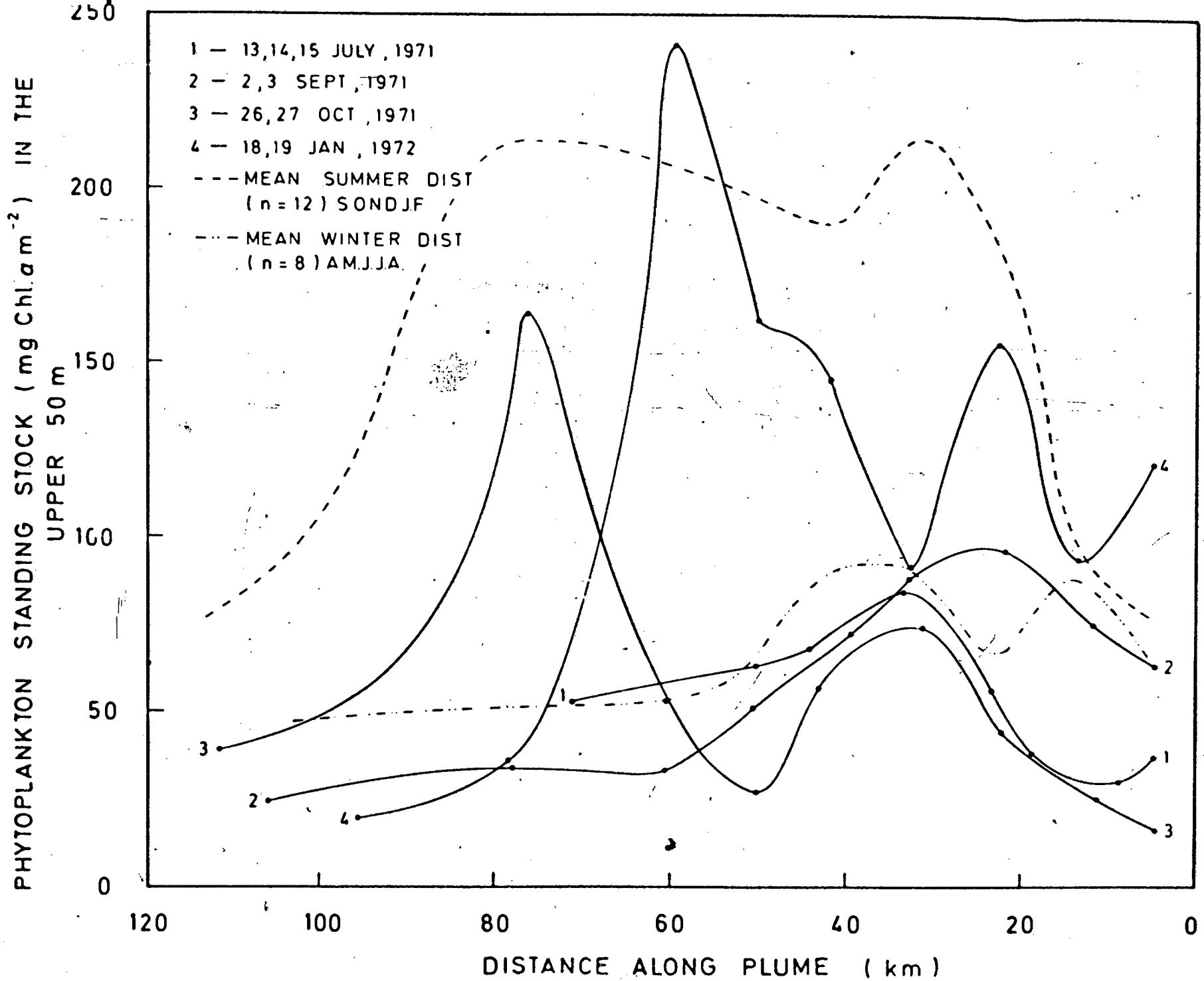
1 — 13,14,15 JULY, 1971
2 — 2,3 SEPT, 1971
3 — 26,27 OCT, 1971
4 — 18,19 JAN, 1972
---MEAN SUMMER DIST (n = 12) SONDJF
-·-·-MEAN WINTER DIST (n = 8) AMJJA
PHYTOPLANKTON STANDING STOCK (mg Chl.a m^{-2}) IN THE UPPER 50 m
250
200
150
100
50
0
120
100
80
60
40
20
0
DISTANCE ALONG PLUME (km)

Fig 10.8

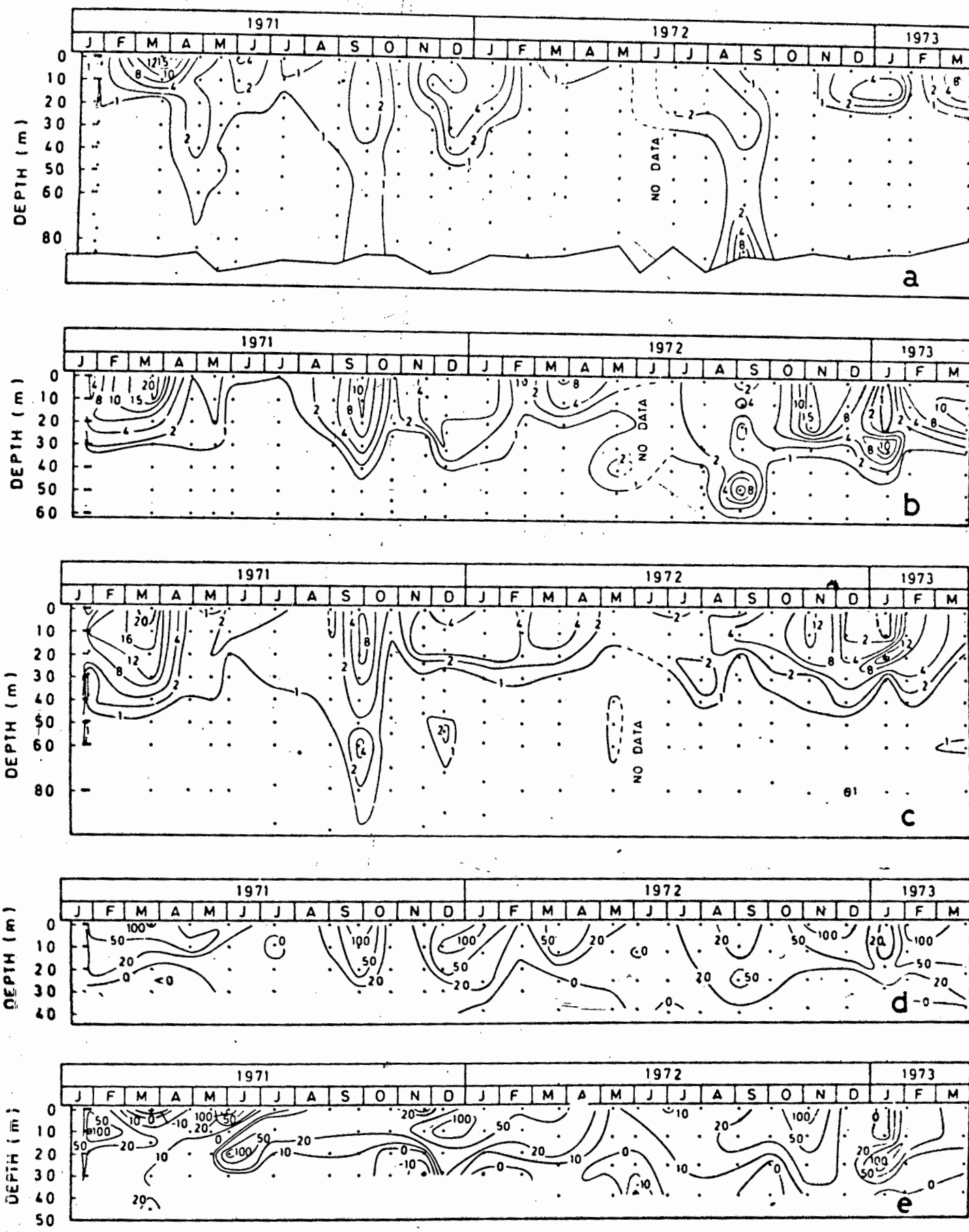

Fig 10.9

(f) Nitrate

Nitrate is closely correlated with reactive phosphate and the seasonal distribution of both (Fig. 10.7) is similar (Fig. 10.6). The relationship between high nitrate concentration and oxygen-depleted water is not as close as the one between silicate and oxygen-depleted water, yet nitrate concentrations of >30 µg atoms N/l were always found in water with a dissolved oxygen content of <4 ml/l. Surface nitrate becomes depleted, falling below 1 µg atom N/l, during calm periods in summer. In winter, when upwelling is minimal, the nitrate content of surface waters is diminished but not to the same extent as in summer.

(g) Phytoplankton

The standing stock of phytoplankton is considerably higher during the upwelling season than between the months of April and August (Figs. 10.8 and 10.9). Although the variation in the summer months in considerable, the levels bear a close relation to measured oxygen levels (Fig. 10.3) and primary production rates (Fig. 10.9). Strong upwelling displaces the phytoplankton out of the area and it is during quiescent periods that high concentrations, high production and high <u>in situ</u> oxygen levels are found. Nutrient depletion also restricts summer phytoplankton growth. This will be discussed in more detail later (Section 12).

DATE	CHLOROPHYLL a (Tons)			OXYGEN (x 10^3 tons)			NITRATE (x 10^3 tons)			SILICATE (x 10^3 tons)			PHOSPHATE (x 10^3 tons)		
December 1969	North Zone	South Zone	Total	North Zone	South Zone	Total	North Zone	South Zone	Total	North Zone	South Zone	Total	North Zone	South Zone	Total
10-11	192	22.7	214	391	337	729	8.64	3.12	11.76	20.92	8.02	28.94	1.75	0,95	2.70
12	149	-	-	392	-	-	8.94	-	-	22.56	-	-	1.81	-	-
12-13	216	72,0	288	419	347	767	6.40	2.33	8.73	15.93	6.17	22.10	1.47	0.89	2.36
14-15	204	43.0	247	437	332	769	7.07	2.87	9.93	17.05	7.02	24.07	1.51	0.91	2.42
16	198	-	-	415	-	-	9.46	-	-	22.17	-	-	1.90	-	-
Mean	192	45.9	238	411	339	750	8.10	2.77	10.87	19.73	7.07	26.80	1.68	0.92	2.60
Maximum	216	72.0	288	437	347	784	9.46	3.12	12.58	22.56	8.02	30.58	1.90	0.95	2.85
Minimum	149	22.7	172	391	332	723	6.40	2.33	8.73	15.93	6.17	22.10	1.47	0.89	2.36
Difference			116			60.9			3.85			8.49			0.49
Atomic Ratio of		C	-43.2*	:	O	-243	:	N	17.5	:	Si	19.1	:	P	1
$\frac{\text{Min}}{\text{Max}}$ x 100%			59.7%			92.2%			69.4%			72.3%			82.8%

TABLE 2 Total amounts of chlorophyll a, oxygen, nitrate, silicate and phosphate contained in the photic layer of the areas shown in Fig. 2.1 on five successive surveys in December 1969. Also shown are the mean, maximum and minimum amounts of each parameter (Northern and Southern zones were treated separately and summed), the differences between maxima and minima, the atomic ratios of the differences and the minima expressed as percentages of the maxima; chlorophyll a data converted to carbon using ratio of chlorophyll a: carbon = 1 : 70. (TABLE 5)

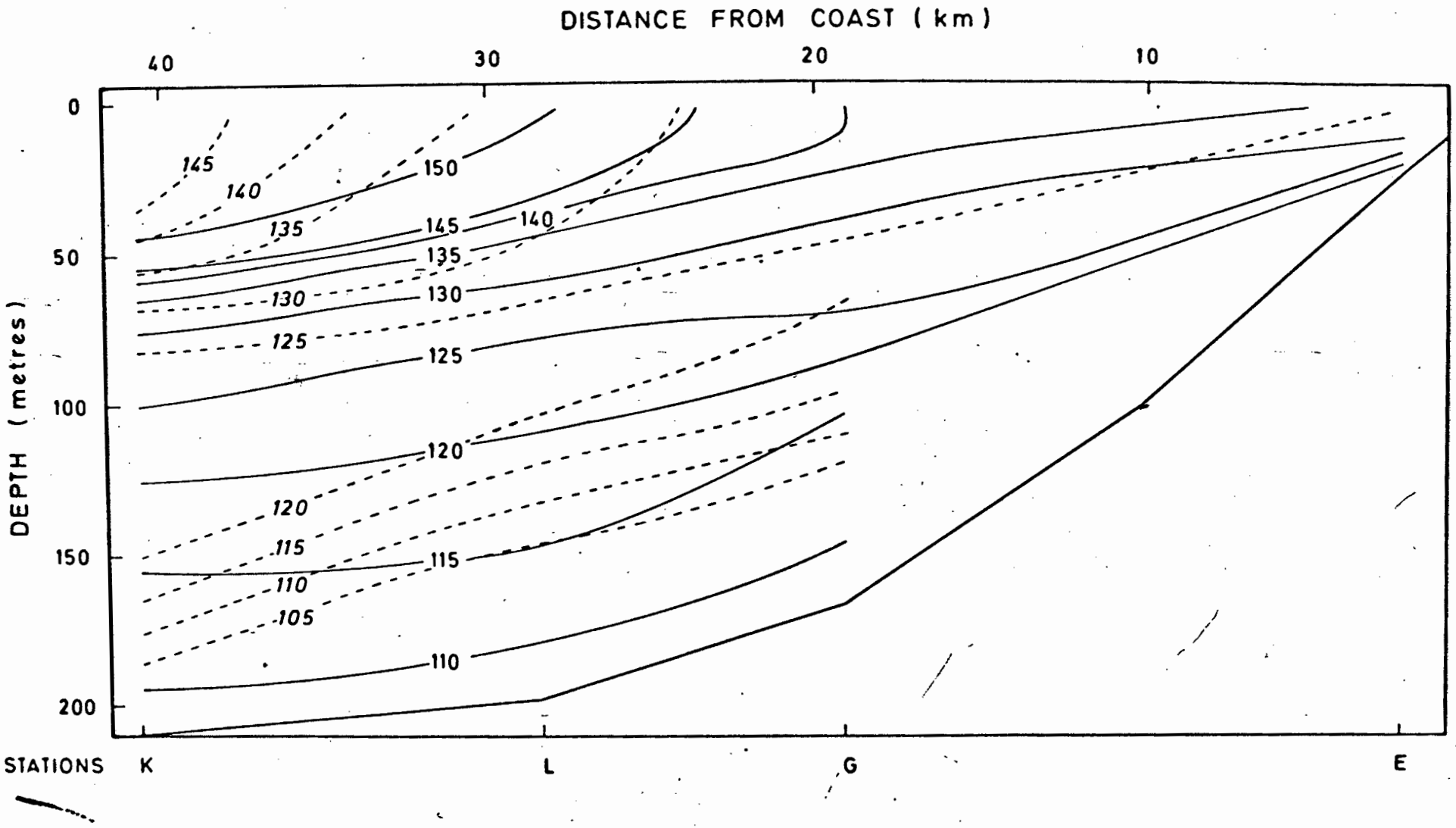
DISTANCE FROM COAST (km)
40
30
20
10
0
50
100
150
200
DEPTH (metres)
145
140
135
130
125
120
115
110
105
STATIONS
K
L
G
E

Fig 11.1

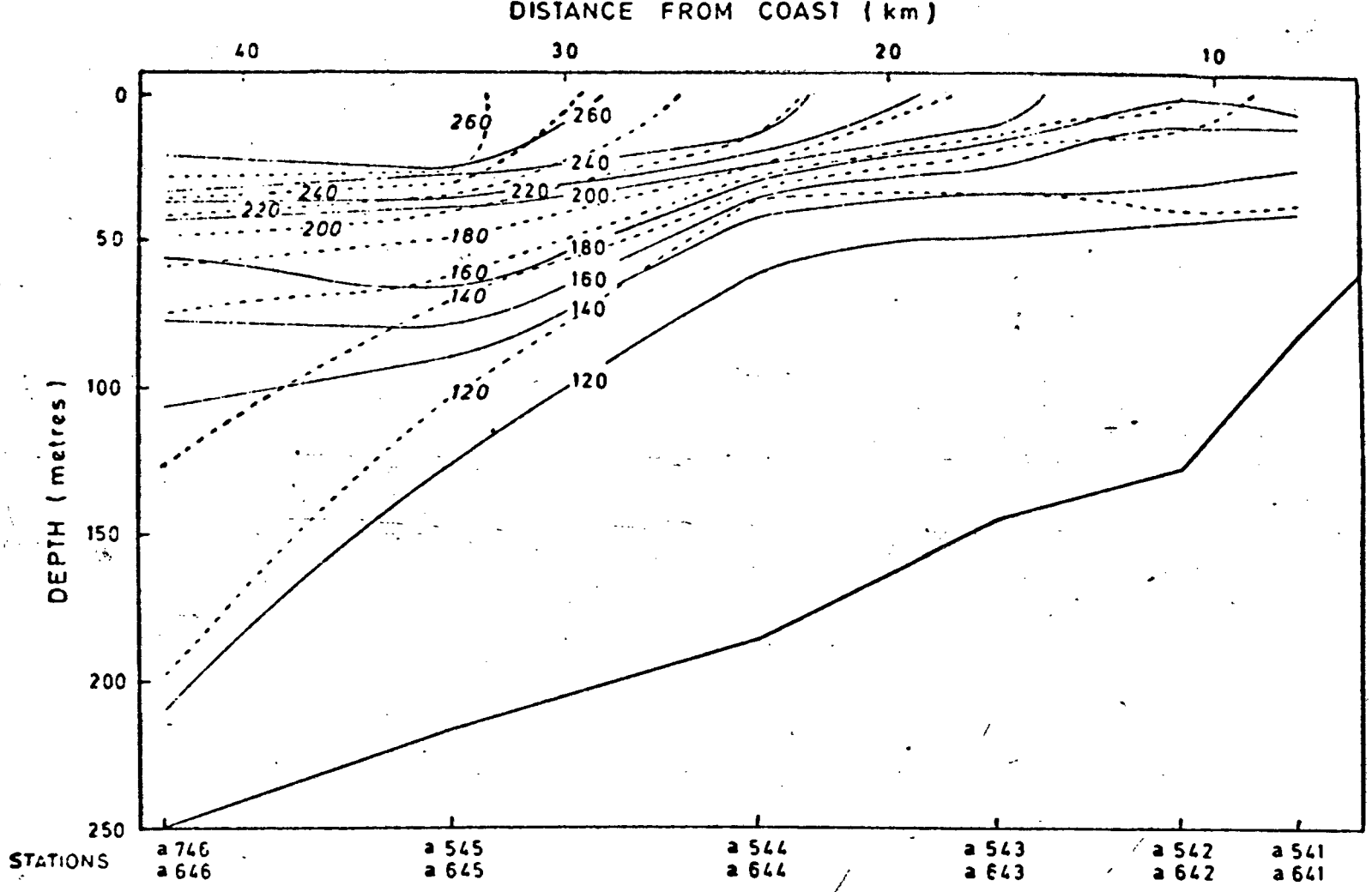

Fig 11.2 Vertical distribution of thermosteric anomaly (cl/ton) along Line 4 of 1969 Upwelling Cruise during the development of upwelling. Solid lines represent distribution on 13/12/69 and dotted lines distribution about 30 hours later

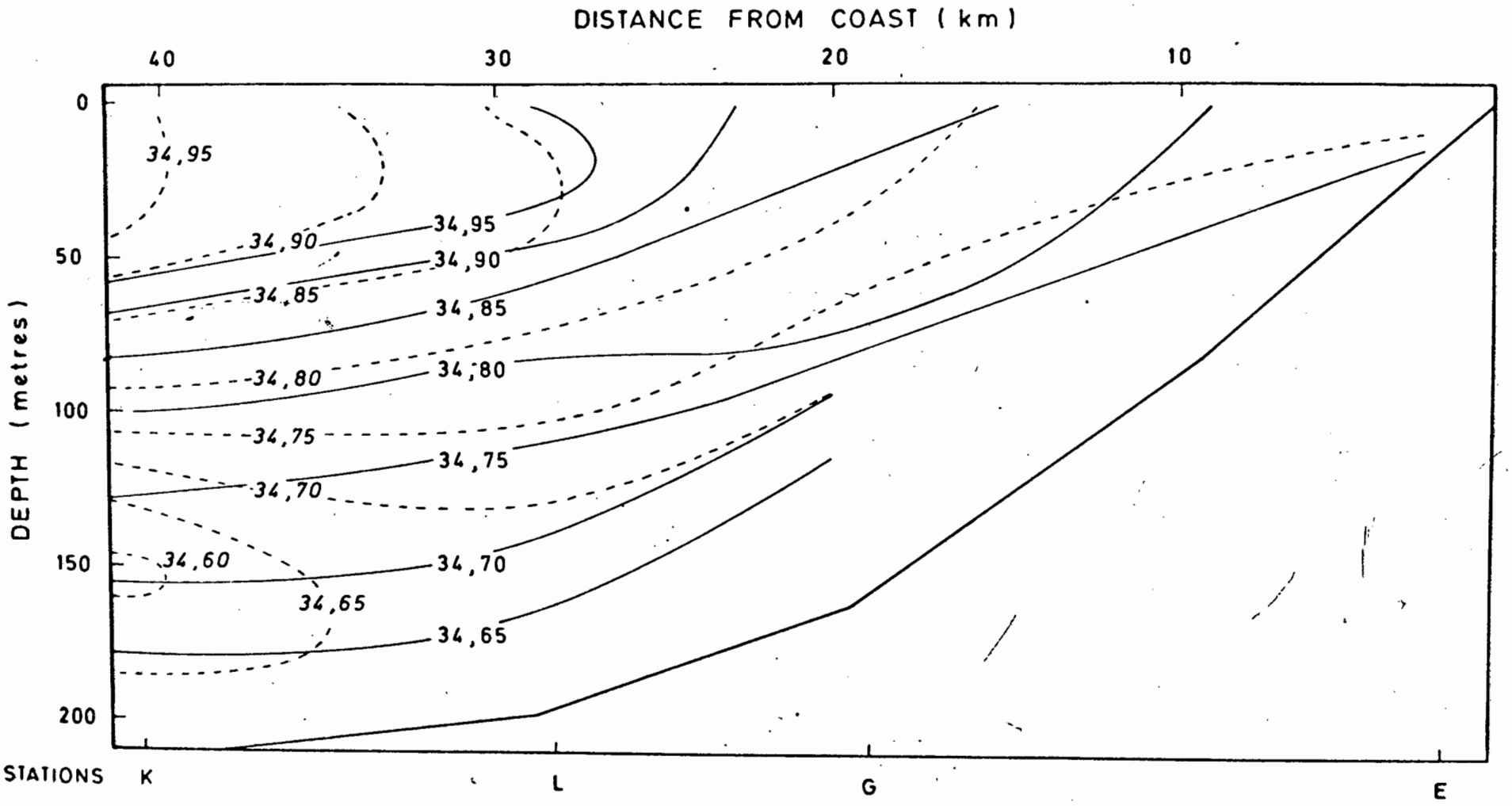
DISTANCE FROM COAST (km)
40
30
20
10
0
50
100
150
200
DEPTH (metres)
34,95
34,90
34,85
34,80
34,75
34,70
34,60
34,65
34,95
34,90
34,85
34,80
34,75
34,70
34,65
STATIONS
K
L
G
E

Fig 11.3

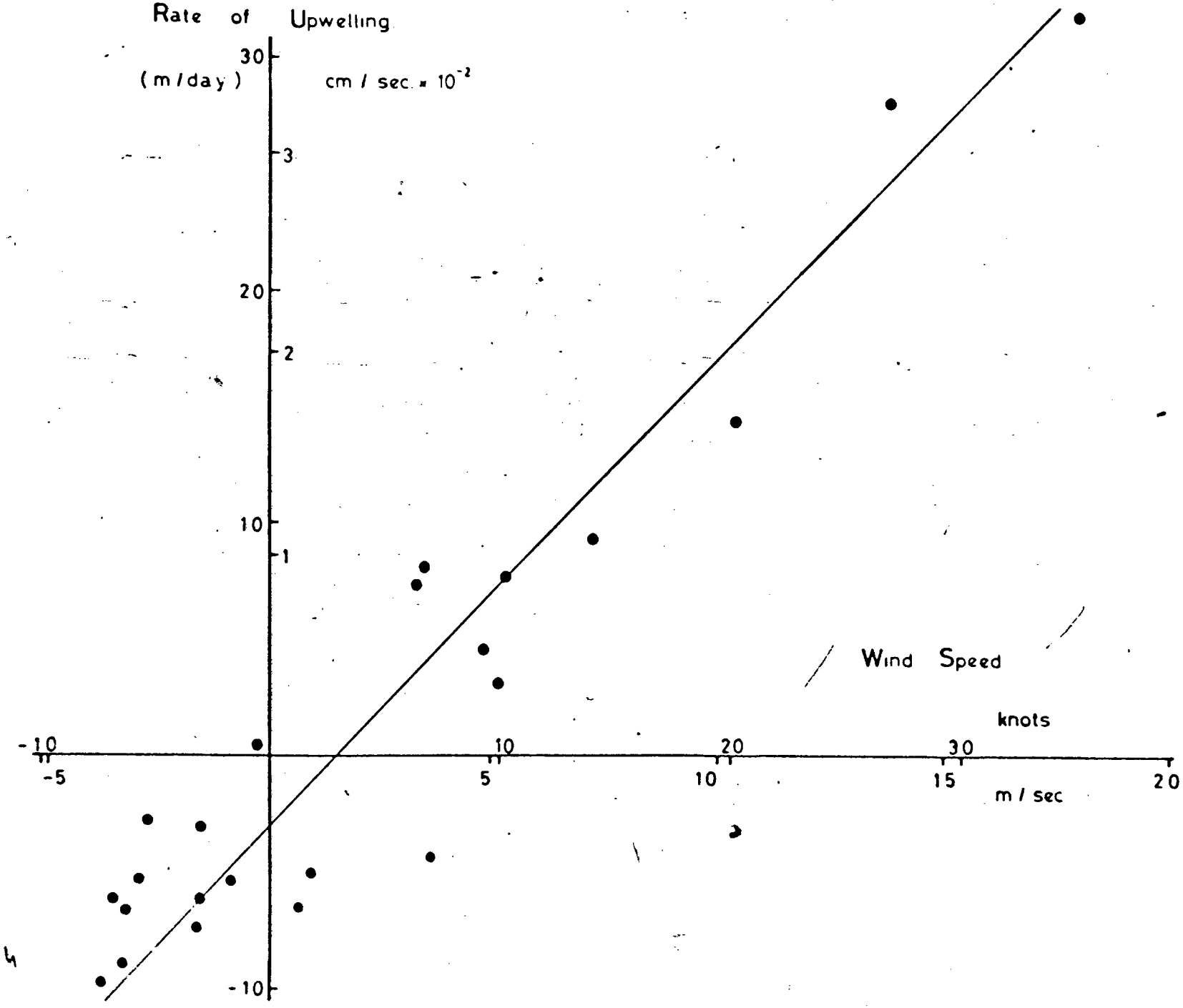
Rate of Upwelling
(m/day)
cm / sec. × 10^{-2}
30
20
10
-10
3
2
1
-10
-5
10
5
20
10
30
15
20
knots
m / sec
Wind Speed

Fig 11.4

11. The Rate of Upwelling

Determination of the rate of upwelling is of interest for it provides a numerical comparison with other areas. Of even more interest is the relation of the rate of upwelling to wind conditions. We have tried several methods in the hope of providing extra perspective on the subject.

Conventionally the rate of upwelling has been calculated from the apparent rate of uplift of isanosteres (lines of constant thermosteric anomaly, δt). Data from selected lines of stations from the 1968 and 1969 Upwelling cruises showing maximum displacement between repeat visits were used. These were Line EGLK on 19 and 20 November 1968 and Line 4 on 13 to 16 December 1969 (Figs. 11.1 and 11.2). All cases where vertical displacement took place were used and averaged. Various other lines of stations or time series of individual stations and separate parameters (temperature and salinity) were used to verify the results.

During the initial stages of upwelling vertical sections show the isanosteres within 10 miles of the coastline are distributed more or less parallel to each other. As upwelling progresses this configuration is disturbed, with some of the isanosteres in the shallower layers being tilted sharply upwards and away from the coast (e.g. Station L: Fig. 11.1; and Stations 42 and 43; Fig. 11.2). This phenomenon is even more clearly demonstrated by the vertical distribution of salinity (Fig. 11.3).

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There is an inherent inaccuracy in the method due to the fact that some of the apparent uplift must be due to mixing processes. The magnitude of this effect cannot be calculated at present but some of the mixing effects must be masked by mixing over the whole water column. The apparent discrepancy in the vertical distribution of isanosteres at Station K (Fig. 11.1) is due to an intrusion of low salinity water that occurred below 100 metres (Fig. 11.3).

The average apparent rate of uplift during periods of active upwelling varied between 20 m/day and 21.5 m/day with an overall average of 21 m/day for both cruises.

Shannon (1966) calculated that a rate of upwelling of 11 m/day off the west coast of South Africa would be produced from a wind velocity of 5 m/sec. Wind velocities encountered prior to obtaining the data for our rate of upwelling calculations was greater than 10 m/sec. Using the same assumptions as Shannon (1966) this would give a rate of upwelling of over 22 m/day (Shannon - personal communication). Walsh and Dugdale (1971) calculated the rate of upwelling for a specific area off the Peruvian coast where wind velocities were only one third to one half of those encountered during this study and found it to vary between 51.8 and 2.6 m/day.

The rate of uplift below 50 metres is much less than in surface layers, because greater lateral replacement of water is possible. The rate of upwelling at nearshore stations is also relatively low and can be explained by the shielding effects of

the mountainous Cape Peninsula and increasing bottom friction. No such shielding effect is mentioned by Walsh and Dugdale (1971) who find maximum upwelling rates close to the coast.

In order to estimate the relation between wind and the prevailing rate of upwelling it has been necessary to utilize bathythermograph data. Since there is a good relationship between temperature and density in the study area (Bang, 1973) the rate of upwelling can readily be calculated from the upward displacement of isotherms. Vertical temperature sections were drawn from bathythermograph data obtained on the 1969 Upwelling cruise and all available pairs of sections were compared. The time period between each pair of sections varied between 12 and 48 hours with 36 hours the most common time interval. Data from other cruises proved unsuitable for this type of analysis.

From each pair of sections an isotherm showing the maximum normal displacement (i.e. excluding displacement due to intrusions or obvious mixing) was selected and the mean vertical displacement per unit of time measured. On some sections displacement was all upwards, on others it was all downward whilst on yet others both motions were observed.

Wind-stress factors were calculated on the assumption that winds blowing between south and east are favourable for upwelling, those blowing between north and west cause downwelling and those blowing between south-south-west and west-south-west and between north-north-east and east-north-east have negligible effect. On

several occasions geographically intensive airborne radiation thermometer flights over the area have been made on consecutive periods of about two weeks and the results obtained tend to support this assumption (D.L. Cram - personal communication). Each hourly wind-speed reading from Cape Point lighthouse between pairs of vertical temperature sections and for a period of 12 hours prior to the first section was multiplied by +1 if favourable for upwelling, by -1 if favourable for downwelling or made equal to zero if falling into neither category. The resulting wind factors were then averaged to give a mean wind speed for comparison with each rate of upwelling calculation.

A regression curve drawn through the 22 data points obtained in this way has a correlation coefficient of r = 0.95 (Fig. 11.4). The regression does not pass through zero which could indicate a hysteresis effect due to the inertia and basic instability of the upwelling system when there is no wind stress to support it. The highest rate of upwelling measured was 32 m/day, rather higher than that independently estimated from isanostere data from the same cruise. The rate of upwelling per unit of wind speed is rather lower than that assumed by Shannon (1966). The isanostere method used averaged all vertical displacement of isolines whereas the bathythermograph data used the average displacement of the isoline showing the maximum vertical displacement on the assumption that this would partially eliminate the inherent underestimation due to mixing.

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The third method of estimating the rate of upwelling that we have used measures the volume of water uplifted into a certain known area and utilises nutrient and oxygen data. Total amounts of these parameters in a layer of water of known dimensions were determined by interpolation. Quantitative changes of parameters were assessed by comparing the total amounts found on successive surveys.

(a) Vertical Interpolation

At each station interpolations between measurements made at discrete depths were calculated using the mean of a straight-line fit and a cubic polynomial fit; interpolated values were integrated over two depth ranges, 0-50 m and 50-100 m. The 0-50 m depth range corresponds approximately to the photic zone and, for convenience, has been termed the photic layer; the 50-100 m depth range has been termed the sub-photic layer. The photic layer can be regarded as a distinct layer, separated from the sub-photic layer by a thermocline and from the open ocean by an oceanic front. The sub-photic layer cannot be regarded as being as distinct a layer as the photic layer.

(b) Horizontal Interpolation

Horizontal sections of both layers were drawn from station integrals by linear interpolation between stations. Each horizontal section was then integrated, after determining the area and mean content between pairs of isolines, by simple multiplication and addition.

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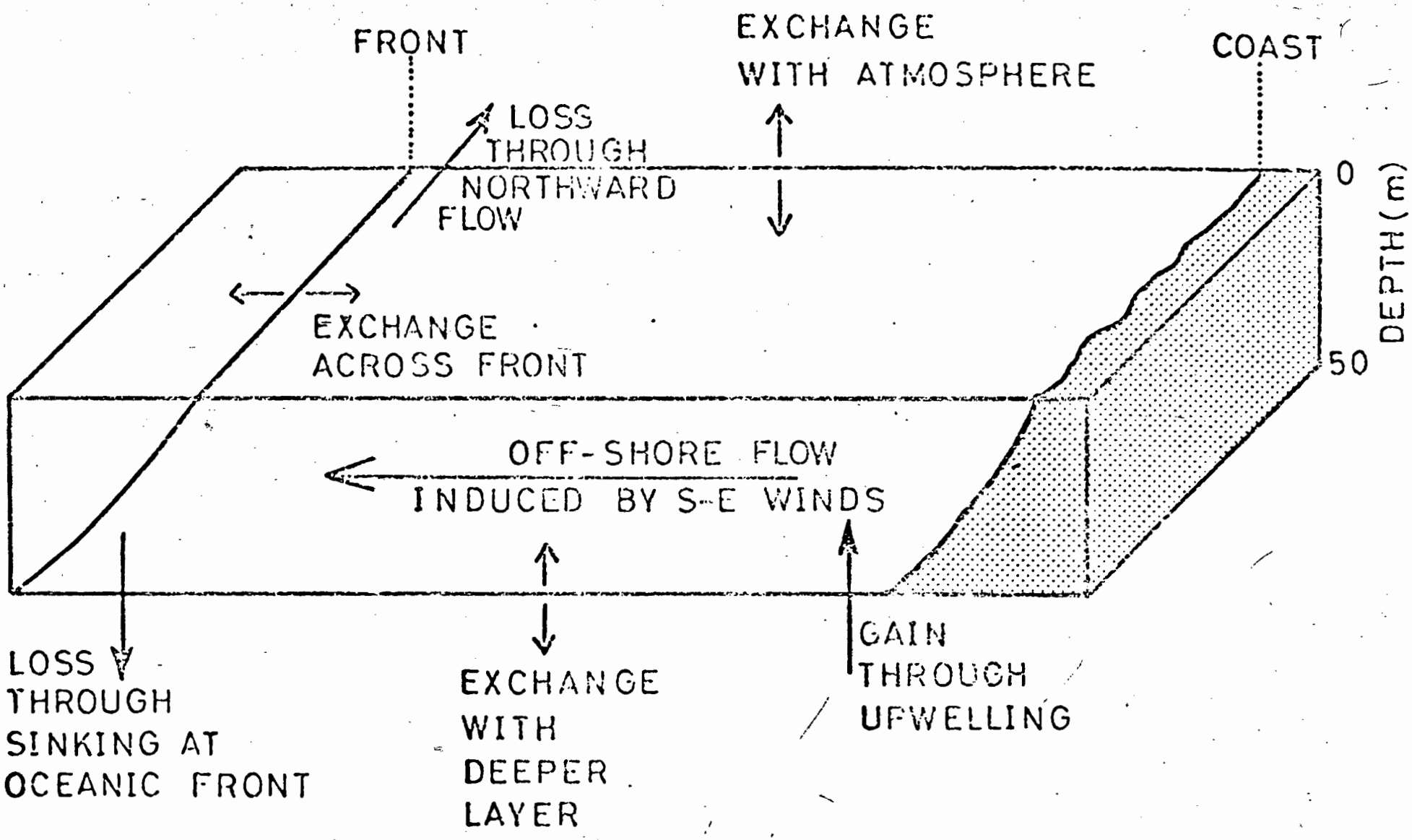

Fig 11.5 Diagram of the photic layer off the Cape Peninsula during upwelling.

The method was applied to data collected on five successive surveys of an area off the Cape Peninsula between 10 and 16 December 1969 (Fig. 2.1). Data were collected by R.S. Africana II in the northern part of the study area on five surveys and on R.S. Sardinops in the south on three surveys. Conditions in the period swung from the upwelling conditions of 10 and 11 December to the downwelling conditions of 12 and 13 December and back to the intense upwelling found on 16 December. The areas of the photic and sub-photic layers over which integration was calculated are shown in Fig. 2.1. Isolines were drawn to the boundaries seen in this figure before integration. For convenience the southern and northern zones were integrated separately. Results are shown in Tables 3 and 4.

In the interpretation of the results it has been necessary to make certain assumptions. A schematic drawing of the photic layer is shown in Fig. 11.5. During quiescent or downwelling conditions it is assumed that there are no exchanges across either the oceanic front or the thermocline. The layer is then regarded as a closed system and the decrease in nutrients that is found when upwelling is inactive is ascribed to biological utilization. Similarly during upwelling conditions the photic layer can be regarded as a steady-state flow system, similar to the closed system of quiescent conditions, but with an inshore flow of nutrient-rich water into the layer due to upwelling and a flow of nutrient-poor water out of the layer due to an offshore sinking down the thermocline and to a northward drift out of the area. Arrows have been drawn in Fig. 11.5 to represent the flow through

the layer during upwelling. Thus the increase in nutrients that occurs when upwelling conditions return after a spell of quiescent or downwelling conditions can be ascribed to the difference between the gross gain in nutrients due to an uplift into the layer and the losses that occur through water flowing out of the layer and through biological utilization.

The sub-photic layer is less distinct than the photic layer and changes that occur in it cannot be readily interpreted.

The rate of upwelling was calculated by ascribing the increase of nutrients in the photic layer between the surveys of 14 and 15, and 16 December totally to upwelling and dividing it by the concentration of each nutrient in Upwelling Water (Table 1). No account has been taken of the loss of water containing nutrients beneath the thermocline and to the north of the area (Fig. 11.5) and the method will therefore tend to underestimate the rate of upwelling. Data for the southern zone from the survey of 10 and 11 December were submitted for the missing part of the survey of 16 December on the assumption that amounts of nutrients in the zone are roughly equal on all occasions when upwelling is active. In fact there were rather larger amounts of nutrients in the northern zone on 16 December than on 10 and 11 December (Table 2) so that this substitution probably results in an underestimation of the uplift.

Three separate estimates of the volume of water uplifted in this period were obtained using nitrate, phosphate and silicate data (Table 4). These have been averaged to give a mean rate of

DATE	OXYGEN ($\times 10^3$ tons)			NITRATE ($\times 10^3$ tons)			SILICATE ($\times 10^3$ tons)			PHOSPHATE ($\times 10^3$ tons)		
December 1969	North Zone	South Zone	Total	North Zone	South Zone	Total	North Zone	South Zone	Total	North Zone	South Zone	Total
10-11	264	248	512	9.52	4.44	13.96	18.65	9.00	27.65	1.72	1.01	2.73
12	259	-	-	9.72	-	-	19.03	-	-	1.60	-	-
12-13	262	244	505	9.35	4.25	13.60	15.55	8.42	23.97	1.42	1.09	2.51
14-15	263	247	510	9.72	4.19	13.92	16.75	7.98	24.72	1.55	1.04	2.51
16	266	-	-	10.82	-	-	19.20	-	-	1.79	-	-
Mean	263	246	509	9.83	4.29	14.12	17.94	8.47	26.41	1.62	1.05	2.67
Maximum	266	248	514	10,82	4.44	15.26	19.70	9.00	28.70	1.79	1.09	2.88
Minimum	259	244	503	9.35	4.19	13.54	15.55	7.98	23.53	1.42	1.01	2.43
Difference			11.35			1.72			6.17			0.45
Atomic Ratio of Differences		O	-48.0	:	N	8.5	:	Si	12.6	:	P	1
$\frac{\text{Min}}{\text{Max}} \times 100\%$			97.9%			88.7%			82.0%			84.4%
$\frac{\text{Diff. 50-100m}}{\text{Diff. 0-50m}} \times 100\%$			17.0%			47.0%			62.8%			91.8%

TABLE 3 Total amounts of oxygen, nitrate, silicate and phosphate contained in the sub-photic layer of the areas shown in Fig. 2.1 on five successive surveys in December 1969. Also shown are the mean, maximum and minimum amounts of each parameter (Northern and Southern zones were treated separately and summed), the difference between maxima and minima, the atomic ratios of the differences, the minima expressed as percentages of the maxima and the differences of the sub-photic layer expressed as percentages of the photic layer.

Nutrient	Amount Uplifted[1] (tons/day)	Concentration in Upwelling Water (mg/m^3)	Volume of Water Uplifted (m^3/day)
Nitrate	2.12×10^3	249.2	8.5×10^9
Silicate	4.90×10^3	461.3	10.6×10^9
Phosphate	0.34×10^3	42.2	8.2×10^9
		Mean =	9.1×10^9

TABLE 4 Estimation of the volume of upwelling off the Cape Peninsula from nutrient data: [1]data obtained from Table 1 by subtracting the results of the survey of 14 and 15 December from those of 16 December and substituting the southern zone results of 10 and 11 December in place of the missing part of the survey on 16 December.

upwelling. Comparison between the estimate of the mean rate of upwelling in m^3/day given in Table 5 and those given earlier in this chapter in m/day can only be made indirectly since there is no quantitative information on the area over which the estimates of the rate of upwelling in m/day apply. A mean rate of upwelling of 9.1×10^9 cubic metres of water per day was found. An uplift of this volume is equivalent to a mean rate of upwelling over the 2,033 km^2 area of the whole study area of about 4.5 m/day. Or, if all upwelling took place at the maximum rate of 30 m/day in a narrow strip, 9.1×10^9 m^3/day would be uplifted in a strip 5 km wide along the 60 km length of the coastline of the Cape Peninsula.

Observational data on upwelling show that the process does not conform to either of these extremes but rather is intermediate between them. This last estimate of the rate of upwelling readily fits into such an intermediate picture. Each method of quantifying upwelling thus is seen to confirm and complement each other method.

12. Quantitative Changes in Nutrients and Phytoplankton

The amounts of nutrients and phytoplankton in both the photic and sub-photic layers were determined on five separate occasions between 10 and 16 December 1969. The total quantity of each parameter in each layer has been determined by interpolation for these five surveys and results are shown in Tables 2 and 3. Changes can be assessed by comparing the total quantities of each parameter. Provided that the area is surveyed at frequent intervals, fluctuations can be detected simply by comparing the quantities of each parameter found on successive surveys and then equating these with processes such as nutrient utilization or, as in the previous chapter, nutrient enrichment due to upwelling.

Integrated nitrate values of the photic layer during the swing from the downwelling conditions of 12 and 13 December to the upwelling conditions of 16 December are shown in Figs 9.4 to 9.6. Fig. 9.7 shows integrated nitrate values of the sub-photic layer on the survey of 12 and 13 December. During upwelling nitrate levels in the photic layer were high, particularly inshore (Fig. 9.6). Nitrate levels were somewhat lower overall during downwelling (Fig. 9.4) and intermediate conditions (Fig. 9.5). During the latter conditions maximum nitrate levels were found offshore in a cyclonic eddy. The distribution of nitrate in the sub-photic layer was considerably more uniform reflecting many of the features seen in the layer above.

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Distributions of phosphate, silicate, chlorophyll and oxygen (not shown) showed similar trends although chlorophyll was more patchy. Oxygen and chlorophyll were indirectly related and silicate and phosphate directly related to nitrate.

The trends observed in the horizontal sections are confirmed quantitatively by the results shown in Tables 2 and 3. During upwelling nutrient levels are generally higher and chlorophyll a and oxygen levels generally lower than during downwelling or quiescent conditions. For example a comparison of results obtained from the survey of 10 and 11 December with those obtained on 12 and 13 December shows that in this period of minimal upwelling, 25.7% of the nitrates, 23.6% of the silicates and 12.6% of the phosphates disappeared from the photic layer. This decrease was accompanied by a corresponding increase in chlorophyll a of 25.8% (Table 2). If these changes are the result of biological utilization the total nitrate content of the layer would be exhausted after 7.8 days, that of silicate after 8.5 days and that of phosphate after 15.9 days.

In contrast, between the downwelling conditions encountered on the survey of 12 and 13 December and the upwelling conditions encountered on the survey of 16 December, amounts of nitrate, silicate and phosphate in the photic layer on the northern zone increased respectively by 37.8%, 31.6% and 25.6% and the amount of chlorophyll a declined by 9.4%. The increase in nutrients during this period may be ascribed to a net gain through upwelling.

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Oxygen responded more slowly to fluctuations in upwelling and oxygen maxima did not always correspond with nutrient minima. Yet the oxygen content increased by 11.2% between the surveys of 10 and 11, and 14 and 15 December and decreased by 5.4% between 14 and 15, and 16 December.

The sub-photic layer also showed a definite response, although of smaller magnitude, to fluctuations in general oceanographic conditions, with larger amounts of nutrients being found during upwelling conditions. Variations of the oxygen content of this layer were insignificant.

13. Phytoplankton

(i) General observations

Chlorophyll measurements were made to at least below the photic zone at all stations. In addition total carbon determinations and production measurements were made at selected stations. Species analysis of the phytoplankton was carried out at a large number of stations but the results have not been fully analysed.

The seasonal changes of the phytoplankton have been briefly outlined in Chapter 10. Generally phytoplankton is more abundant during the summer but variation in standing stocks between cruises was very large. It was found that production levels generally reflected standing stocks and also that there was good agreement between measured production and in situ oxygen levels (c.f. Figs 10.3 and 10.9), levels above 4 ml/l being generally accompanied by high production. It is noticeable that poor standing stock levels were accompanied by low nutrient levels. If Fig. 10.9 is compared with Fig. 10.5, 10.6 and 10.7 it becomes immediately evident that low levels of nitrate are associated with low production and standing stock. During our 3-year monthly sampling program nitrate levels fell below 1 /ug atom N/1 on four occasions.

In November 1971 surface nitrate levels of < 1 /ug atom N/1 were found oceanwards of Station 2. Nitrate depletion was not as widespread in December and was only found oceanwards of Station 5 in the upper 10 m. There were definite signs of a restriction of production and standing stock levels of surface waters in both

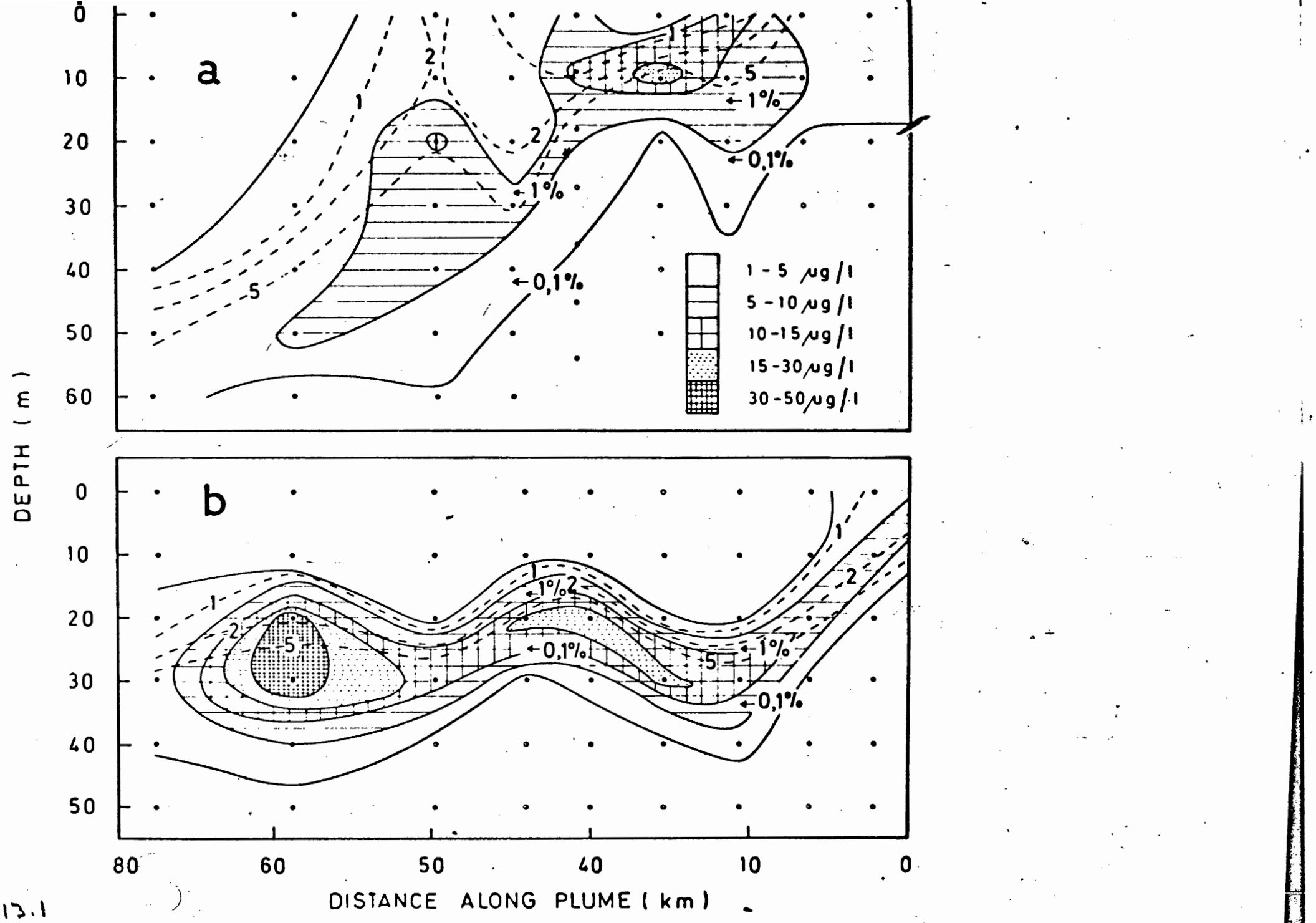
a
b
DEPTH (m)
0
10
20
30
40
50
60
80
60
50
40
10
0
1
2
5
1%
0,1%
1 - 5 µg / l
5 - 10 µg / l
10 - 15 µg / l
15 - 30 µg / l
30 - 50 µg / l
DISTANCE ALONG PLUME (km)

Fig 12.1

months at Station 6. At Station 3 the sign were less apparent but on the December cruise production was considerably higher at 10 m than at the surface.

Nitrate depletion was evident at the surface in September 1972 along the whole transect and to a depth of 20 m except at Stations 1 and 6. Both standing stock and production levels were apparently profoundly affected by these low nitrate levels. This was particularly evident at Station 3 where large standing stock and production levels were only found in the nitrate-rich waters below.

Nitrate depletion was widespread in December 1972 and persisted until after the cruise in January 1973. Standing stock levels in the upper 20 m at Station 3 dropped from 15 /ug chlorophyll a/l in November to 1 /ug/l in January 1973.* A similar drop occurred at Station 6. In Fig. 13.1 vertical sections of chlorophyll a for the December 1972 and January 1973 cruises with the 1, 2 and 5 /ug atom N/l nitrate isolines superimposed on them are shown. In December a fairly typical chlorophyll distribution, with signs of offshore sinking beneath the thermocline (Chapter 7) was apparent. There was some indication of a reduced standing stock in nitrate-depleted waters. By the January cruise the standing stock was completely restricted to water of >1 /ug atom N/l and reached its highest measured level, 51.8 /ug chlorophyll a/l, at 30 m at Station 8. Surface production levels dropped in a corresponding manner to those of chlorophyll a and

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were negative* at 0 and 13 m at Station 6 in January 1973.

The highest standing stocks encountered on this 27-month survey were found in March 1971 and were associated with limited nitrate depletion of surface waters. Nitrate levels >1 µg atom N/l were only found at the surface at Stations 2 and 6. Production measurements made on this cruise provided some rather unexpected results. Considerable oxygen consumption was measured at both stations in both light and dark bottles. For example at Station 3 the oxygen concentrations of the light bottles at 0, 10, 20 and 30 m dropped by 1.69, 3.07, 2.55 and 1.35 ml/l in the 6-hour incubation period from initial concentrations of 5.42, 6.19, 4.16 and 2.93 ml/l respectively. Depletion of dark bottles was not so great except at the surface where the oxygen content fell by 2.81 ml/l. At Station 6 similar, although less dramatic, changes were measured.

A picture of the effects of low nitrate concentrations on phytoplankton, with increasing degrees of nitrate depletion causing increasing restriction of phytoplankton growth, can be constructed from these observations. In the first stage, for example as at Station 3 in November 1971 and at Stations 3 and 6 in December 1972, production was not obviously curtailed although nitrogen-limiting levels had been reached. Perhaps

* Negative gross production figures were obtained when there was a higher oxygen consumption in the light bottles than in the dark bottle and probably result from light-accelerated bacteriological decomposition of phytoplankton.

other forms of nitrogen were available. In the intermediate stage, as in September 1972, production in Surface waters was suppressed and the standing stock curtailed. The final stage was reached when production was reduced to near zero levels and the standing stock became drastically reduced as found in the surface waters on the January 1973 cruise. The March 1971 results did not fit neatly into the picture. Clearly they were obtained during the death and decomposition of a large phytoplankton bloom. Possibly rapidly falling nitrate concentrations triggered the decomposition before widespread limiting conditions made their appearance. Other factors may also have played a part in restricting growth of the bloom.

Decompositon of phytoplankton would appear to be an active process in the area and is detectable when oxygen consumption is apparent. Since oxygen depleted water has been shown to flow into the area from the north (Capter 10) in situ oxygen values cannot be taken as evidence of local decomposition. However there is evidence that the bacterial decomposition of phytoplankton is accelerated by or activated in the presence of light so that negative gross production, evident as a higher oxygen consumption in light bottles than in dark ones, can be taken to result from light-accelerated decomposition of phytoplankton. Moscovits (1958) showed that the growth rate of a marine Pseudomonas is increased in the presence of an illuminated Nitzschia culture and it would appear that a similar effect occurs in this area in natural phytoplankton.

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Negative gross production seems to occur after two distinct types of environmental conditions. The first one is the end result of nitrate depletion and is shown by negative production in surface waters; for example, at Station 6 in March 1971, November 1971 and January 1973. When nitrate concentrations fall to levels where the phytoplankton population cannot maintain itself decomposition would seem to result. In the second case negative production observed each autumn below about 20 m (Fig. 10.9) appears to result from different environmental conditions. The high summer standing stocks of phytoplankton in deeper waters cannot maintain themselves in the autumn as light levels fall and so decomposition occurs.

(ii) Daily and annual production rates

Incubator estimates of gross daily production have been obtained from hourly production rates by integrating against depth to 30 m with a hand drawn curve and multiplying by the number of hours between sunrise and sunset less two. These figures are likely to be an overestimate of the actual in situ production rates for several reasons. Firstly, the rotating disc to which the bottles were clamped was constructed of white translucent plastic and the light levels were adjusted with the photometer facing the light source. Subsequent measurements with a more compact quantum sensor (LICOR 185, Lambda Instruments Co.) allowed measurements of the reflected light and the light transmitted through the disc from the opposite light source. These were sufficient to raise the supposed 25% and 12.5% light

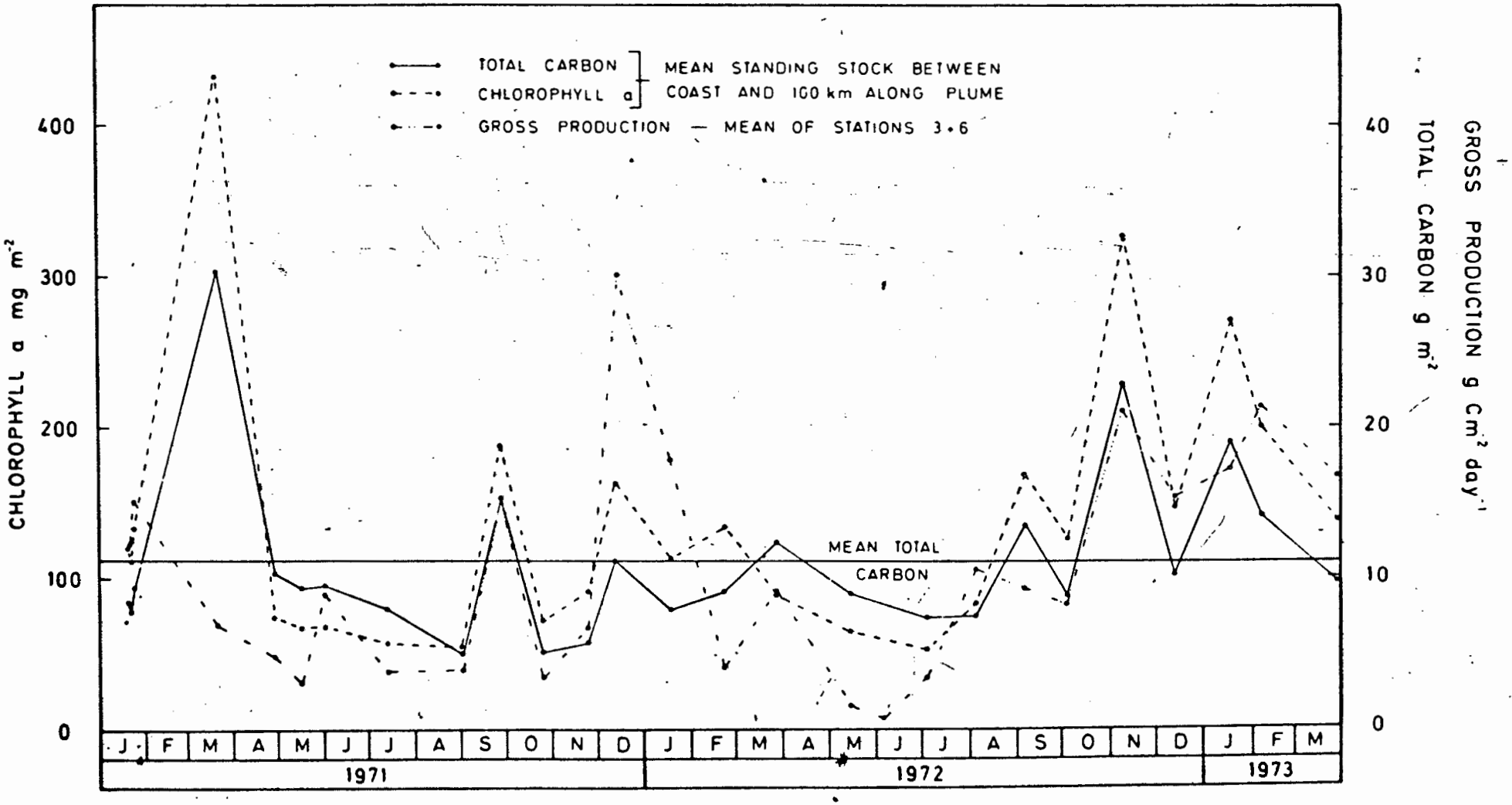
TOTAL CARBON
CHLOROPHYLL a
MEAN STANDING STOCK BETWEEN COAST AND 100 km ALONG PLUME
GROSS PRODUCTION — MEAN OF STATIONS 3-6
CHLOROPHYLL a mg m⁻²
TOTAL CARBON g m⁻²
GROSS PRODUCTION g Cm⁻² day⁻¹
MEAN TOTAL CARBON
0
100
200
300
400
10
20
30
40
J F M A M J J A S O N D J F M A M J J A S O N D J F M
1971
1972
1973

Fig 13.2.

levels to approximately 55% and 44% of the surface sample intensity respectively.

Secondly samples were collected at equal intervals in the upper 30 - 40 metres in order to measure production rates throughout the phytoplankton-rich layer. Since the 50% light level averaged only 2,4 metres and the 1% light level 24 metres during the 30 month period, it is obvious that subsurface samples were incubated at light levels far above ambient light levels. Their response to this sudden increase in light would depend on the previous light history of the cells (Ryther (1956) Yentsch and Lee (1966), Steeman Nielsen and Jorgensen (1968) Beardall and Morris (1976)).

Samples were incubated in running water pumped from 3-4 metres depth, and at temperatures which were up to 6° - 8°C warmer than <u>in situ</u> temperatures on occasions. This could considerably alter the growth rates of the algae.

Therefore our estimates are at best measurements of the potential production in light-saturating conditions, rather than actual <u>in situ</u> rates of growth. Daily potential production rates at Stations 3 and 6 were averaged for the presentation of seasonal results shown in Fig 13.2. The overall production level was very high with a discernible seasonal pattern, maximum values being found in summer and minimum values in winter. Production was also low in October and February when upwelling activity was at its highest. A maximum value of 37 g C m^{-2} day^{-1} in the upper 30 metres was measured at Station 3 in

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December 1971 while the potential production to the 1% light level (13 m) was about half this figure.

An estimate of the annual potential production of the area has been obtained by integrating mean daily rates obtained at Station 3 and 6 over the 24-month period of measurements using a straight-line fit. The annual potential production was found to be 3.7 kg C m^{-2} yr^{-1}, more than ten times as high as Ryther's (1969) estimate for upwelling areas.

(iii) Standing stock

The standing stock of phytoplankton was determined from chlorophyll a data after these had been converted into units of carbon. The conversion factors used to transform chlorophyll data from all depths were obtained from surface comparisons of chlorophyll a and total carbon (Table 5). There is a relationship between chlorophyll a and total carbon in most areas of the ocean (e.g. Lorenzen, 1968) and although the variation in Table 5 is considerable the relationship between these two measurements is good enough to be utilized to determine the standing stock of phytoplankton in units of carbon. A conversion factor of 140 for chlorophyll a to carbon has been used for calculating winter standing stocks (March to July, except March 1973), one of 70 for summer (October to February and March 1973), one of 90 for August and one of 80 for September.

Station	March 1972	June 1972*	July 1972	August 1972	October 1972	November 1972	December 1972	February 1973	March 1973
1	186	24"	95	71	245'	362'	85	1460'	105
2	114	113	301	137	187"	115	62	294'	87
3	122	207	179	97	373"	36	38	54	64
4	135	85	134	53	92	36	92	42	237'
5	100	192	202	57	80	39	54	62	492'
6	101	150	92	47	30	36	77	68	69
7	127	100	69	185	-	33	90	132	42
8	174	116	70	81	159"	39	97	49	66
9	211	48"	44"	117"	-	44	292'	07	-
10	179'	-	-	-	-	529	-	159"	-
Mean	141	138	143	91	67	48	75	68	72

TABLE 5 Total carbon: chlorophyll a ratios (8) results excluded from calculations of mean because chlorophyll a 1 ug/l; (") results excluded for other reasons - data from inshore and offshore stations did not always conform to remaining data. The mean winter ratio, calculated from March, June and July 1972 results (n=24) is 141 ± 56. The mean summer ratio, calculated from October, November and December 1972 and February and March 1973 results (n=32) is 65 ± 26. November 1972 ratios were lower than other summer values and 70 is assumed to be the normal summer ratio. (*) June 1972 chlorophyll results were unreliable and were discarded. For the purpose of calculating these ratios the means of each station of May and June 1972 were used, as there was little change in the oceanography during this period.

At each station the standing stock under a square meter of sea surface was estimated by integrating discrete chlorophyll $\underline{a}^{a}$ measurements by computer using a curve obtained from the mean of straight line and cubic polynomial fits. The mean monthly standing stock was found by integrating station values using a simple straight line fit to 100 km and dividing by the distance. These data, before and after transformation into units of carbon, are shown, contrasted with production data, in Fig. 13.2.

The standing stock of phytoplankton does show some seasonal variation but the seasonal variation of the carbon to chlorophyll ratio, with larger values being found in winter, reduces the range of variation considerably. Thus during the two year period values rarely fell below half or rose above twice the mean phytoplankton standing stock which had a value of 11.2 g.C m^{-2}.

14. Nutrient and Phytoplankton Relationships

(i) Nutrient utilization

Nutrients are necessary for phytoplankton growth and are normally taken up in constant proportions which can be expressed in terms of atomic ratios of change. These ratios also apply to the regeneration of nutrients, which occurs in similar proportions. In the open ocean P: N: Si: O, where O is the change in oxygen resulting from consumption or primary production, is normally 1 : 16 : 16: -272 (Richards, 1958: Redfield et al., 1963). Yet the proportions in which nutrients are utilized can vary and are related to factors such as the physiology of the phytoplankton and the concentrations of the nutrients.

The overall local atomic ratios of utilization have been determined on three sets of data using two separate methods. The first set of data, from the 1969 Upwelling Cruise, were subjected to an analysis outlined in Chapters 11 and 12 which involved a proportional comparison of net changes of nutrients in the area. The second and third sets of data, from Upwelling Monitoring cruises extending respectively from November 1971 to February 1972 and from November 1972 to February 1973, were each subjected to the following analysis: nitrate, silicate and oxygen concentrations were each treated as functions of phosphate concentration (Table 6). The amount of organic matter produced per atom of nutrient has been estimated by converting chlorophyll a concentrations to carbon, using the relevant conversion ratio (chlorophyll a : carbon = 1 : 70 – Chapter 13) and subjecting the converted data to

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the analyses described above.

The overall proportions in which nutrients were utilized and oxygen and carbon produced during summer conditions are shown in Table 7. Carbon: phosphate ratios of the analyses of Upwelling Monitoring cruise data have been excluded from the table because of the low correlation coefficients obtained (Table 6). The atomic ratios of the mean nutrient contents of the area, determined from the mean contents of the photic and sub-photic layers (Tables 2 and 3), are shown in Table 8 for comparison with the ratios of utilization.

The atomic ratios of the mean nutrient contents of the area, N:P and Si:P, do not differ significantly between the photic and sub-photic layers but are considerably lower than the ratios of utilization, N: P and Si: P. The ratio, N:P, is also lower than the "normal" ratio of occurrence. The ratios of utilization, N: P and Si: P, are somewhat higher than normal. Normal ratios of occurrence are N:P = 15:1, Si:P = variable; normal ratios of utilization are N: P = 16:1, Si: P = 16:1 (Redfield et al., 1963).

Nitrate and silicate are utilized relative to phosphate in greater proportions than those in which they occur and it may be surmised that these nutrients, and particularly nitrate with the most unfavourable ratios, are more likely to limit phytoplankton growth than phosphate.

Further insight into nutrient utilization can be gleaned from variations in proportions between nutrients after increasing

Relationship	Date	n	Correlation Coefficient (r)	Regression Equation
PO_4 vs NO_3	11/71-2/72*	387	0.85	y = 0.051x + 0.187
	11/72-2/73*	252	0.68	y = 0.043x + 0.586
PO_4 vs SiO_4	11/71-2/72	423	0.70	y = 0.049x + 0.483
	11/72-2/73	412	0.71	y = 0.056x + 0.633
PO_4 vs O_2	11/71-2/72	418	-0.75	y = 2.96 - 0.39x
	11/71-2/73	407	-0.72	y = 2.77 - 0.31x
PO_4 vs	11/71-2/72*'	205	-0.41	y = 1.10 - 0.072x
Chlorophyll a	11/72-2/73*'	191	-0.28	y = 1.20 - 0.017x

TABLE 6 Correlation coefficients and regression equations of phosphate on nitrate, silicate, oxygen and chlorophyll a respectively for two consecutive summers. Data from Upwelling-Monitoring cruises; * excluding nitrate values <1 ug atom N/l; ' excluding data from depths>50 m. All units in ug atoms/l except oxygen, ml/l, and chlorophyll a ug/l.

		Phosphate	Nitrate	Silicate	Oxygen	Carbon
Nutrient content	(a)	1	9.3	11.3	-	-
	(b)	1	11.7	10.8	-	-
Nutrient utilization and phytoplankton production	(a)	1	19.1	17.5	-243	-43.2
	(b)	1	19.7	20.0	-227	-
	(c)	1	23.3	17.7	-293	-

TABLE 7 Atomic ratios of the mean nutrient contents and rates of utilization of nutrients and production of oxygen and phytoplankton carbon. The ratios of the nutrient contents were obtained (a) from Table 1 and (b) from Table 2 and apply to the 0-50 m layer and the 50-100 m layer respectively. The ratios of utilization and production were obtained (a) from Table 1 (1969 data), (b) from the slopes of the regression equations given in Table 4 (1971-9172 data) and (c) as (b) but using data from the 1972-1973 upwelling season.

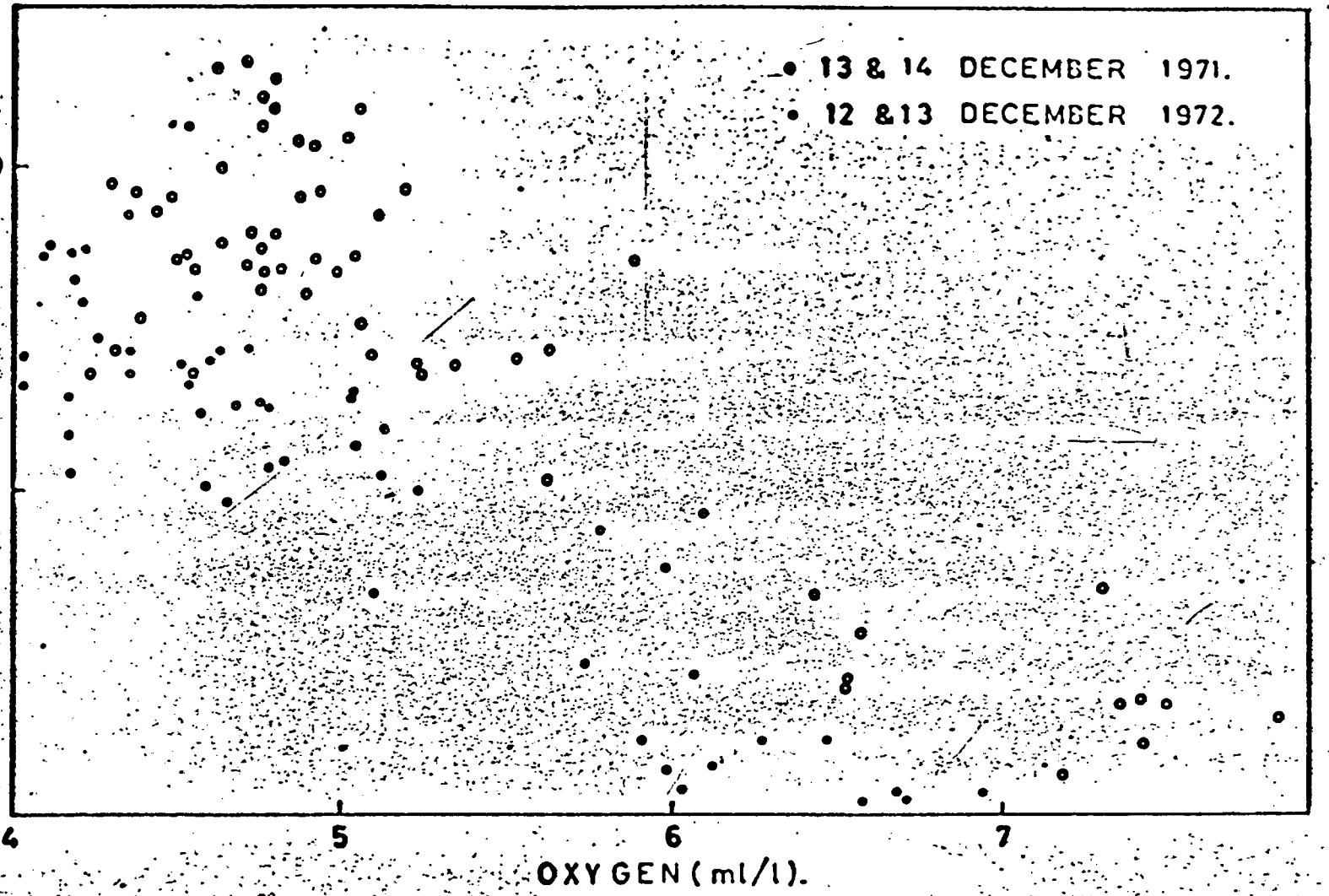

Fig 14.1 Relationship between oxygen and N:P ratios for oxygen concentrations of >4 ml/l. Data from Upwelling-Monitoring Cruises of December 1971 and December 1972.

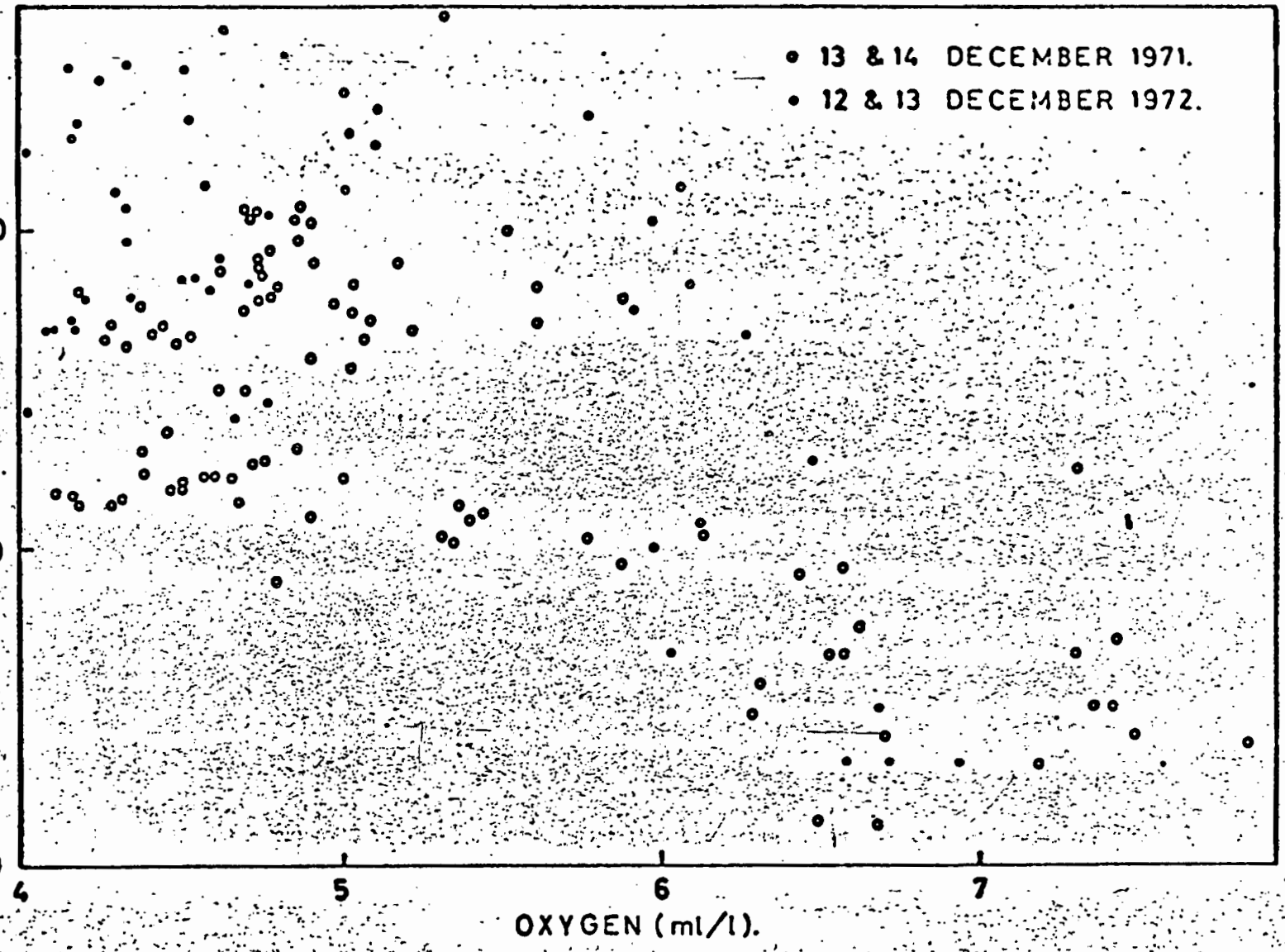

Fig 14.2 Relationship between oxygen and N:Si ratios for oxygen concentrations of 4 ml/l. Data from Upwelling-Monitoring Cruises of December 1971 and December 1972.

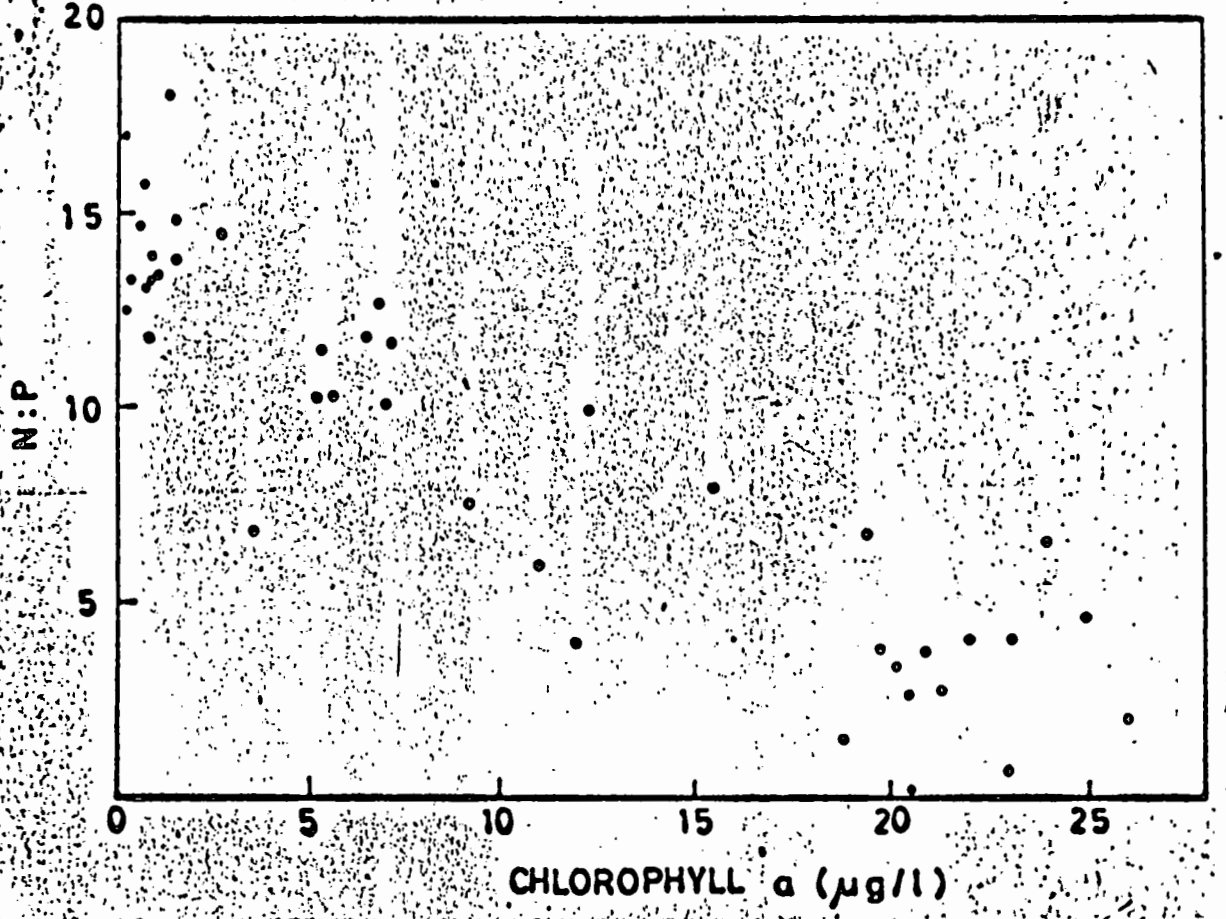

Fig 14.3 Relationship between chlorophyll a and N:P ratios. Data from the photic zone of the March 1971 Upwelling-Monitoring Cruise excluding the inshore and two offshore stations.

amounts of phytoplankton growth. Dissolved oxygen levels above 4 ml/l are closely related to primary production in the region (Chapter 13) and in this context oxygen data have been plotted against N:P and N:Si ratios (Figs 14.1 and 14.2). Data from the December 1971 and the December 1972 Upwelling Monitoring cruises were used as representative of normal growth conditions. The graphs show that nitrate was used faster than either phosphate or silicate. The N:P ratio declined from approximately 16:1 at oxygen concentrations of between 4 and 5 ml/l to between 10:1 and 0.1:1 at oxygen concentrations above 6 ml/l (Fig 14.1). Similarly the N:Si ratio decreased with increasing oxygen content, indicating that as oxygen was produced, nitrate declined relative to silicate (Fig 14.2).

Similar relationships were found between chlorophyll a content and N:P and N:Si ratios. An example is given in Fig 14.3 in which chlorophyll a concentrations of the upper 50 m on the March 1971 Upwelling Monitoring cruise have been plotted against the N:P ratios. Data from the inshore station and the two offshore stations were excluded since the former was in cold Upwelling Water and the latter were outside the oceanic front. Nitrate decreased relative to phosphate as the standing stock increased.

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These examples serve to show that, as oxygen or chlorophyll levels, both of which are related to phytoplankton growth, increase, nitrate decreases relatively faster than either phosphate or silicate. This indicates that nitrate is the primary limiting nutrient in the region.

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Strickland (1960) defines the Productivity Index (PI) as a measure of the specific rate of phytoplankton growth. This index is obtained from the productivity in mg C m^{-3} hr^{-1} per mg chlorophyll *a* m^{-3} per unit of light intensity but the light intensity term can be ignored if PI data, which have been obtained in light-saturated conditions, are used. This assumption was made by Krasnick and Caperon (1973) who obtained a hyperbolic relationship between such PI data and limiting nutrient data.

Rates of growth and nutrient uptake are described by Michaelis-Menten kinetics and conform to hyperbolic relationships (MacIsaac and Dugdale, 1969). The relationship between growth rate and nutrient concentration can be described by $PI = PI_{max} S/(K_s + S)$, where PI is the growth rate, S is the nutruent concentration, PI_{max} is the maximum growth rate and K_s is the half-saturation constant, during steady-state growth.

Productivity Indices were calculated from selected gross production and chlorophyll *a* data obtained on Upwelling-Monitoring cruises. Data were selected on the basis that they were obtained (a) in the spring and summer (October to February) when growth can

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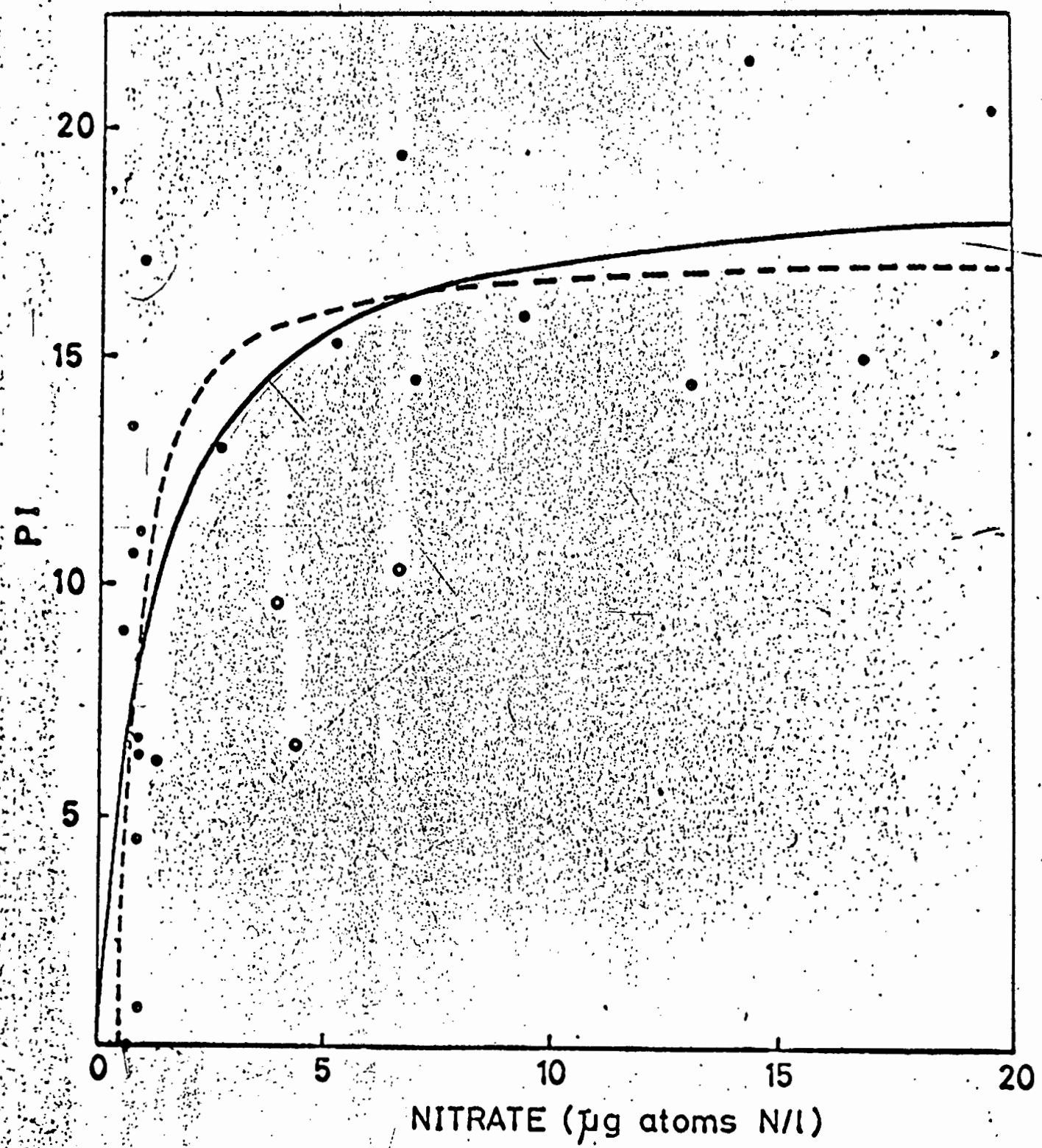

Fig 14.4 Relationship between Productivity Index (mg C/mg chl a/hr) and nitrate concentration. Solid curve : least-squares hyperbola, $PI = PI_{max}S/(K_s+S)$, assuming a zero intercept where PI_{max} = 1.11 µg atoms N/l and K_s = 18.97 mg C/mg chl a/hr. Dashed curve : as solid curve but assuming intercept at 0.5 µg atoms N/l where PI_{max} = 0.88 µg atoms N/l and K_s = 17.41.

be expected to occur; (b) at the surface or 10 m, where it was assumed that phytoplankton was adapted to light-saturated conditions. (c) during steady state growth (In practice it was not possible to determine whether conditions of steady state growth were ever reached - the absence of steady state growth might be expected during active upwelling and three data points with relatively low PI's, which were obtained in October 1971 and October 1972 in recently upwelled water, were excluded).

The selected PI data were plotted against environmental nitrate concentrations. A hyperbolic curve was fitted to them using a program written by G. Caperon* which calculates the best fit by a least squares analysis. Three data points obtained early in 1973, a period of anomalous conditions, did not conform to the hyperbolic relationship and were excluded from these calculations (hollow dots-Fig 14.4)

Krasnick and Caperon (1973) found hyperbolic relationships between PI and total fixed nitrogen and between PI and ammonia concentration in a tropical estuary. Because of the scatter of their data they made the assumption that growth only reaches zero at a nutrient concentration of zero although Caperon and Meyer (1972) have shown that this is not normally the case for nitrate-limited situations. Two alternative hyperbolas were fitted to

* Hawii Institute of Marine Biology

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the present data. The first one (continuous curve-Fig 14.4) was based on the assumption that growth ceases at zero nitrate concentration whilst the second (dashed curve-Fig 14.4) was based on the assumption that growth ceases as an arbitary concentration of 0.5 /ug atoms N/l. Values of PI_{max} of 18,97 and 17.41 mg C/mg chlorophyll a/hr and of K_s of 1.12 and ~~0.38~~ 1,05 ug atoms N/l respectively were obtained from the two alternative calculations. The resulting curves are not very different from each other although the non-zero intercept curve appears to fit the data marginally better and would conform closer to the findings of Caperon and Meyer (1972).

The values of PI_{max} and K_s reported by Macisaac and Dugdale (1969) and Krasnick and Caperon (1973) are not directly comparable with those reported above. Macisaac and Dugdale (1960) determined the uptake rate of nitrate at different concentrations of substrate under laboratory conditions and report a provisional value of 1 /ug atom N/l for the K_s of fast-growing species of phytoplankton. Krasnick and Caperon (1973) report values of K_s for an oligotrophic environment, which are respectively 0.13 /ug atoms N/l for total fixed nitrogen and 0.0049 /ug atoms N/l for ammonia, and which are considerably lower than either of the alternative values reported here for nitrate in a eutrophic environment. A high half-saturation constant is a definite indication of the adaptation of the phytoplankton population to high nitrate levels (Krasnick - personal communication).

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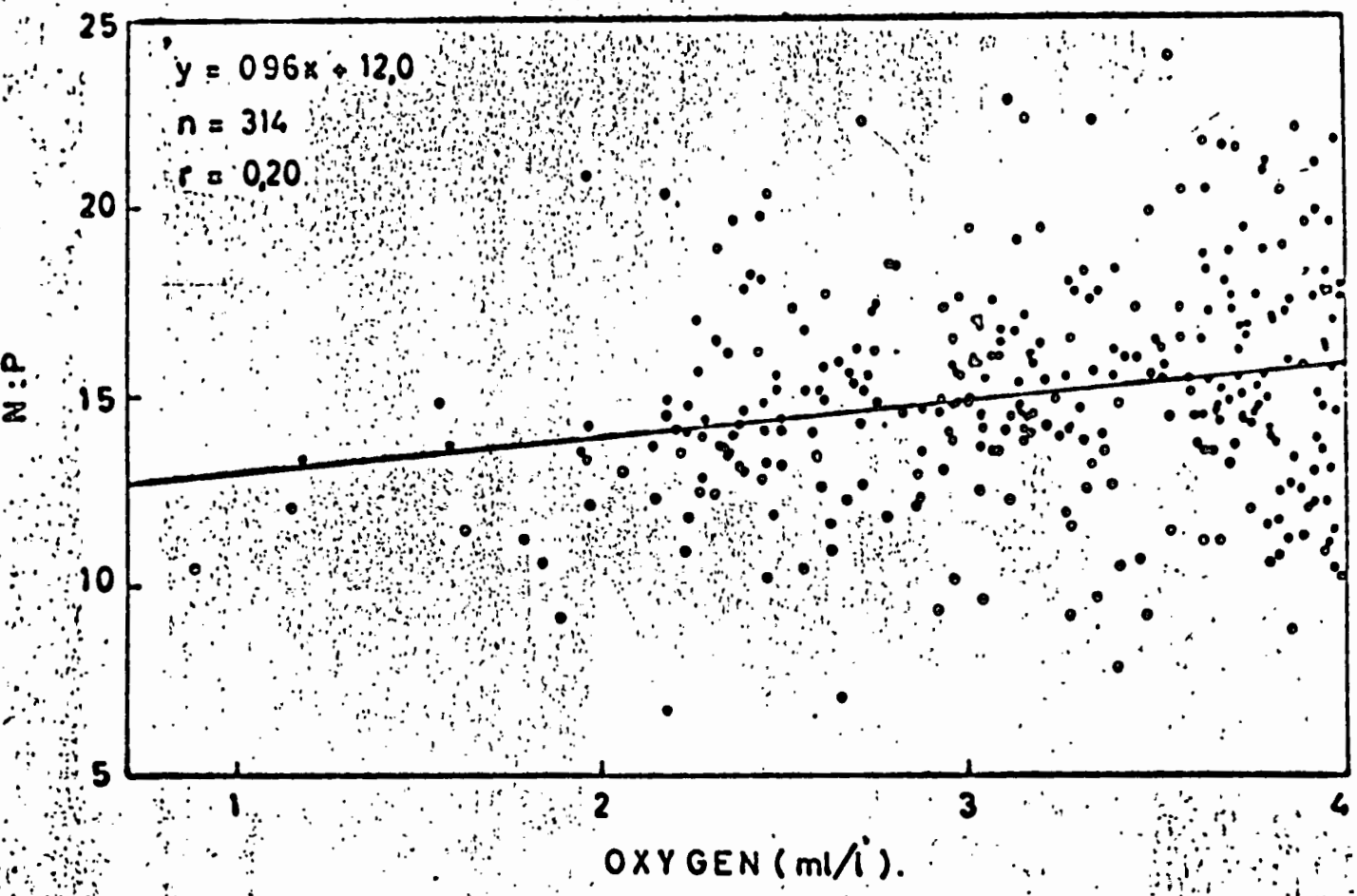

Fig 14.5 Relationship between oxygen and N:P ratios for oxygen concentrations of <4ml/l. Data from all Upwelling-Monitoring Cruises.

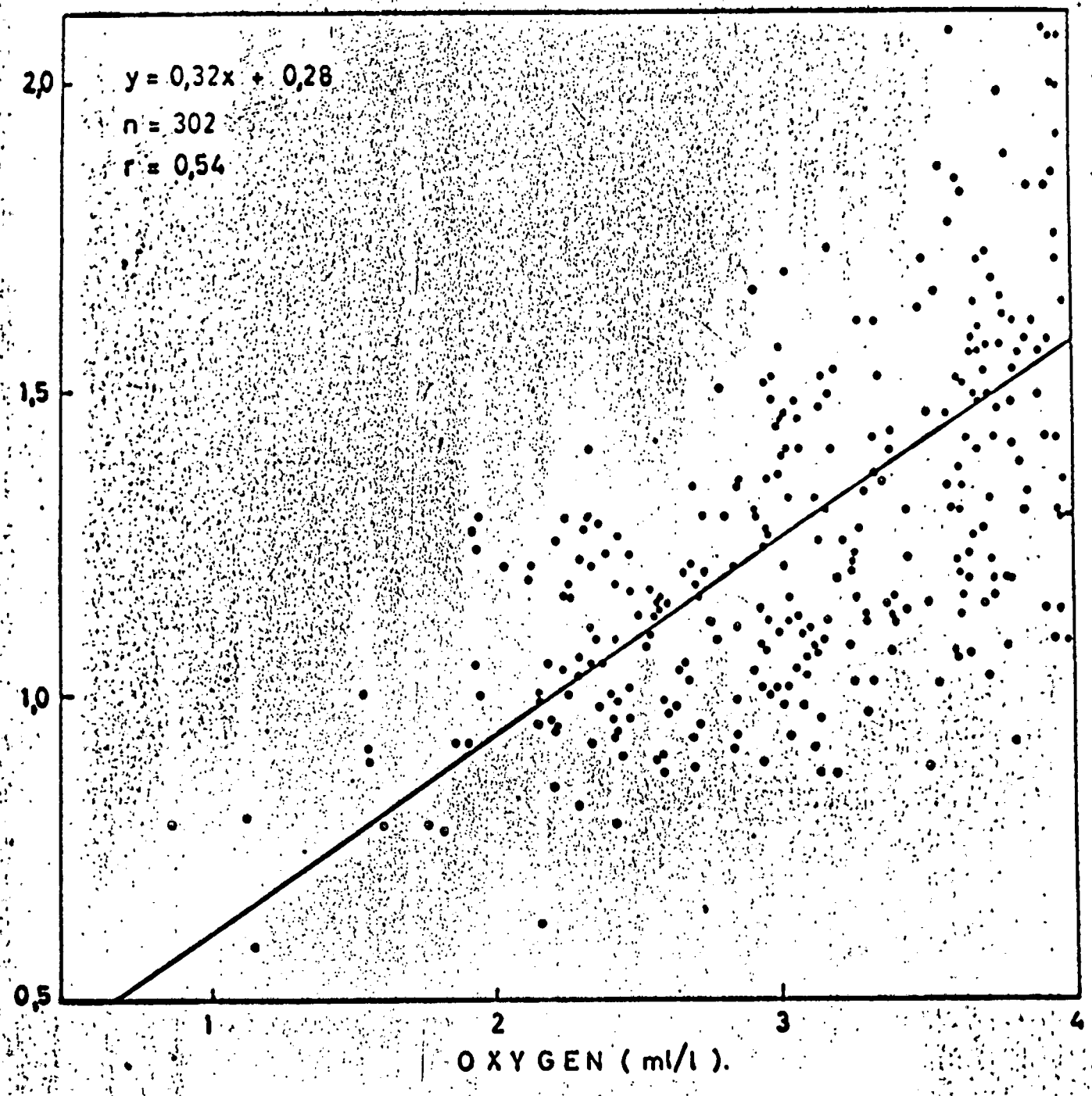

Fig 14.6 Relationship between oxygen and N:Si ratios for oxygen concentrations of <4 ml/l. Data from all Upwelling-Monitoring Cruises.

(ii) Nutrient regeneration

Regeneration occurs when organic compounds are broken down releasing inorganic nutrients, and is invariably accompanied by the consumption of oxygen (Redfield et al., 1963). A major consumption of oxygen will lead to the formation of oxygen-depleted water which can be regarded as an indicator of a type of biological activity normally accompanied by nutrient regeneration. Oxygen depletion off the Cape Peninsula is frequently encountered, particularly in the autumn, and is indicated by dissolved oxygen concentrations of less than 4 ml/l.

Calvert and Price (1971) have investigated aspects of nutrient regeneration in the Benguela system with data obtained off South West Africa. They found large concentrations of nutrients associated with low oxygen concentrations and which resulted from regeneratory processes. They also studied the proportions in which nutrients are regenerated and found low Si: P ratios offshore and high Si: P ratios inshore. Since silicate is regenerated more slowly than phosphate, low ratios can be regarded as indicators of recent regeneration.

The relative proportions of nutrients in oxygen-depleted water off the Cape Peninsula have been investigated. N:P and N:Si ratios obtained in oxygen-depleted water on Upwelling Monitoring cruises are shown plotted against oxygen concentration in Figs 14.5 and 14.6. A slight relative decrease in the

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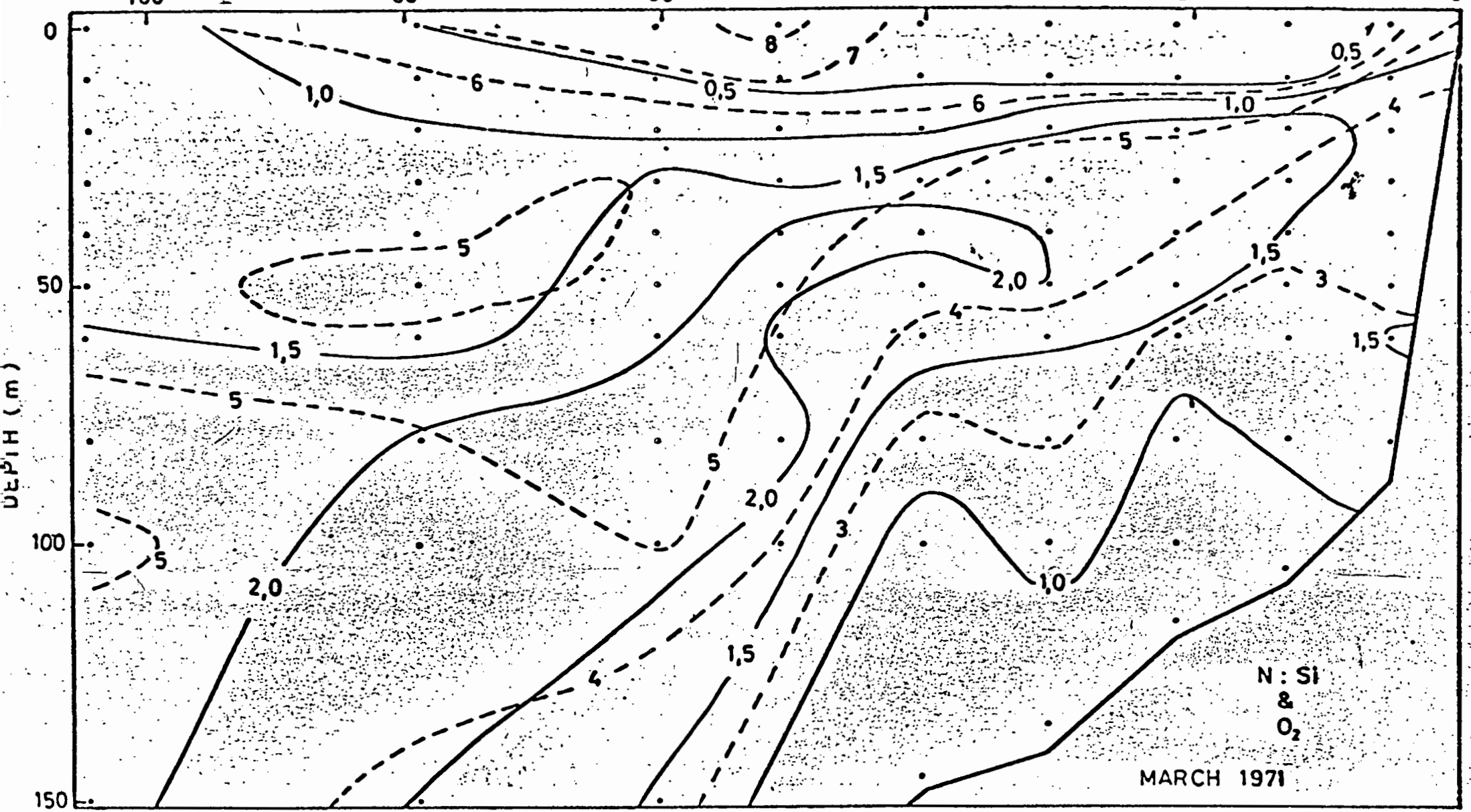

Fig 14.7 Vertical section of N:Si ratios (solid lines) of the March 1971 Upwelling-Monitoring Cruise superimposed on a vertical section of dissolved oxygen concentration in ml/l.(dashed lines).

N:P ratio with decreasing oxygen can be seen (Fig 14.5) whilst in contrast the N:Si ratio decrease rapidly with decreasing oxygen concentration, from 1.5 at 4 ml/l to 0.6 at 1 ml/l (Fig 14.6).

An investigation of the spatial distributions of N:Si ratios with relation to distributions of oxygen concentration throws more light on the latter relationship. In Fig 14.7 a vertical section of the N:Si ratios of the March 1971 Upwelling Monitoring cruise with a vertical section of the dissolved oxygen concentration superimposed on it is shown. Low N:Si ratios were associated with high oxygen values at the surface and low oxygen values near the bottom. The low ratios at the surface can be explained by high phytoplankton production causing nitrate depletion (Figs 14.1 to 14.3), whilst those near the bottom conform to the relationship shown in Fig 14.6. High ratios, > 2.0, were found in an intermediate zone where oxygen levels were relatively uniform at about 5 ml/l.

Ratios as high as these were found only on a few occasions, and then, almost invariably at similar stations and depths as in Fig 14.7. The highest ratios were recorded in December 1971 and their development from more usual ratios was observed over a 3-month period. In October 1971 N:Si ratios lay between 1.0 and 1.7, except in surface waters, particularly offshore, where nitrate utilization caused ratios to drop below 1.0. Ratios only rose above 1.5 at a few depths offshore of Station 6. By November ratios of 1.5 were widespread in intermediate depths but no ratios

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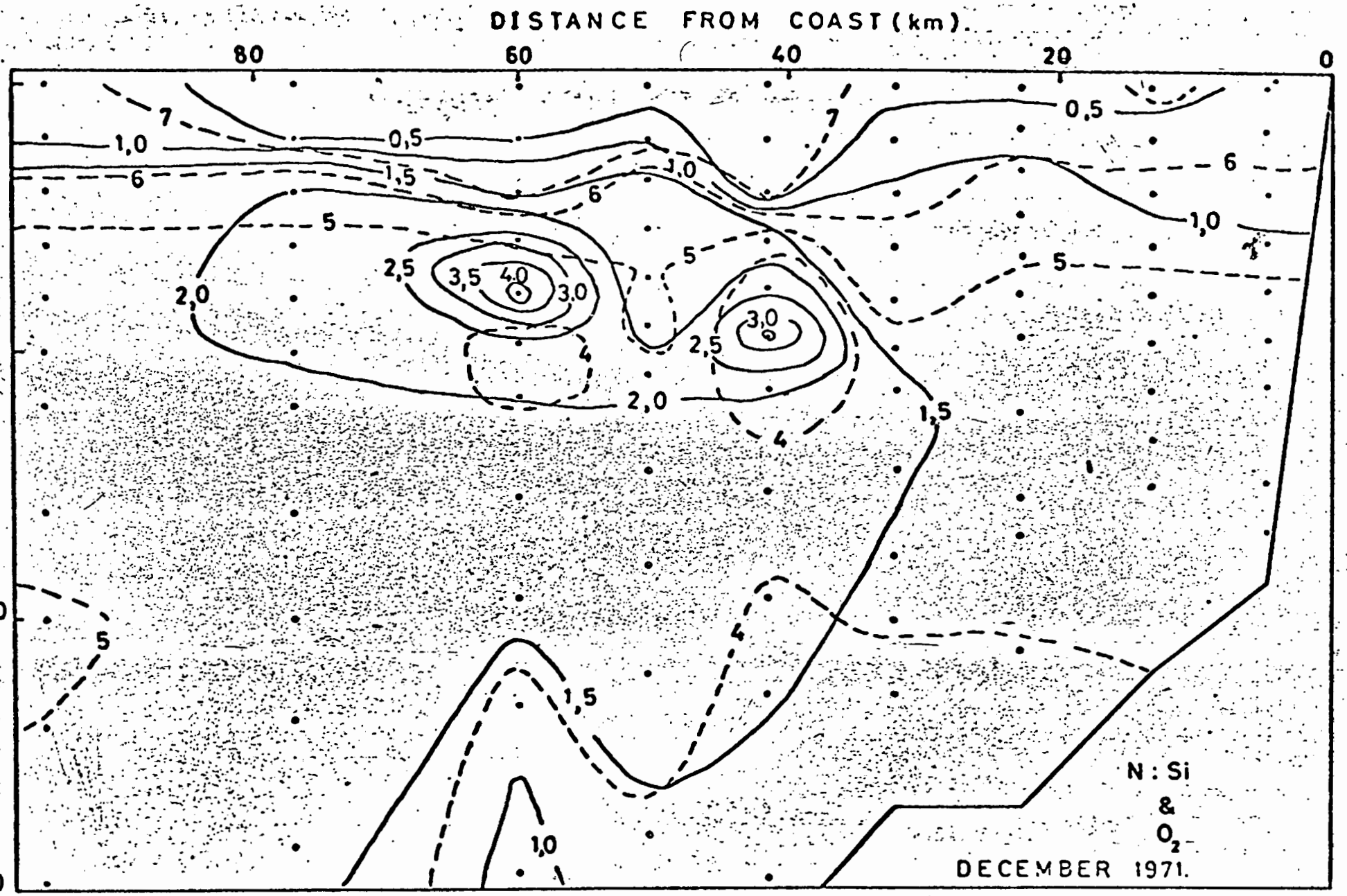

Fig 14.8 Vertical section of N:Si ratios(solid lines) of the December 1971 Upwelling-Monitoring Cruise superimposed on a vertical section of dissolved oxygen concentration in ml/l (dashed lines).

as high as 2 were recorded. Nitrate utilization caused surface ratios to drop as low as 0.22. The December results are presented in Fig 14.8 in a similar manner to those of March 1971 in Fig 14.7. Surface ratios as low as 0.13 were recorded and, in intermediate depths between Stations 4 and 8, widespread ratios of 2, with a maximum of 4,28, were found. High ratios were associated with oxygen minimum in which levels fell below 4 ml/l. Near the bottom, where more oxygen-depleted water was present, low N:Si ratios were found.

It is evident that there are two bodies of oxygen-depleted water present and that these can readily be distinguished by the N:Si ratio characteristics. High ratios are associated with an oxygen minimum of intermediate depth that does not necessarily reach the defined oxygen-depletion levels. Low ratios are associated with oxygen-depleted water lying near the bottom. Local oxygen depletion would seem to cause the oxygen minimum associated with high N:Si ratios whilst low ratios characterise oxygen-depleted waters brought into the area by a current flowing south over the shelf. Oxygen-depleted water off the Cape Peninsula may then be classified according to its origin as either "local" or "distant".

The high N:Si ratios that characterise local oxygen-depleted waters probably result from a faster regeneration of nitrate than of silicate. Calvert and Price (1971) present evidence to show that silicate regenerates relatively slowly off South West Africa and Dugdale (1972) concludes that regeneration of silicate off

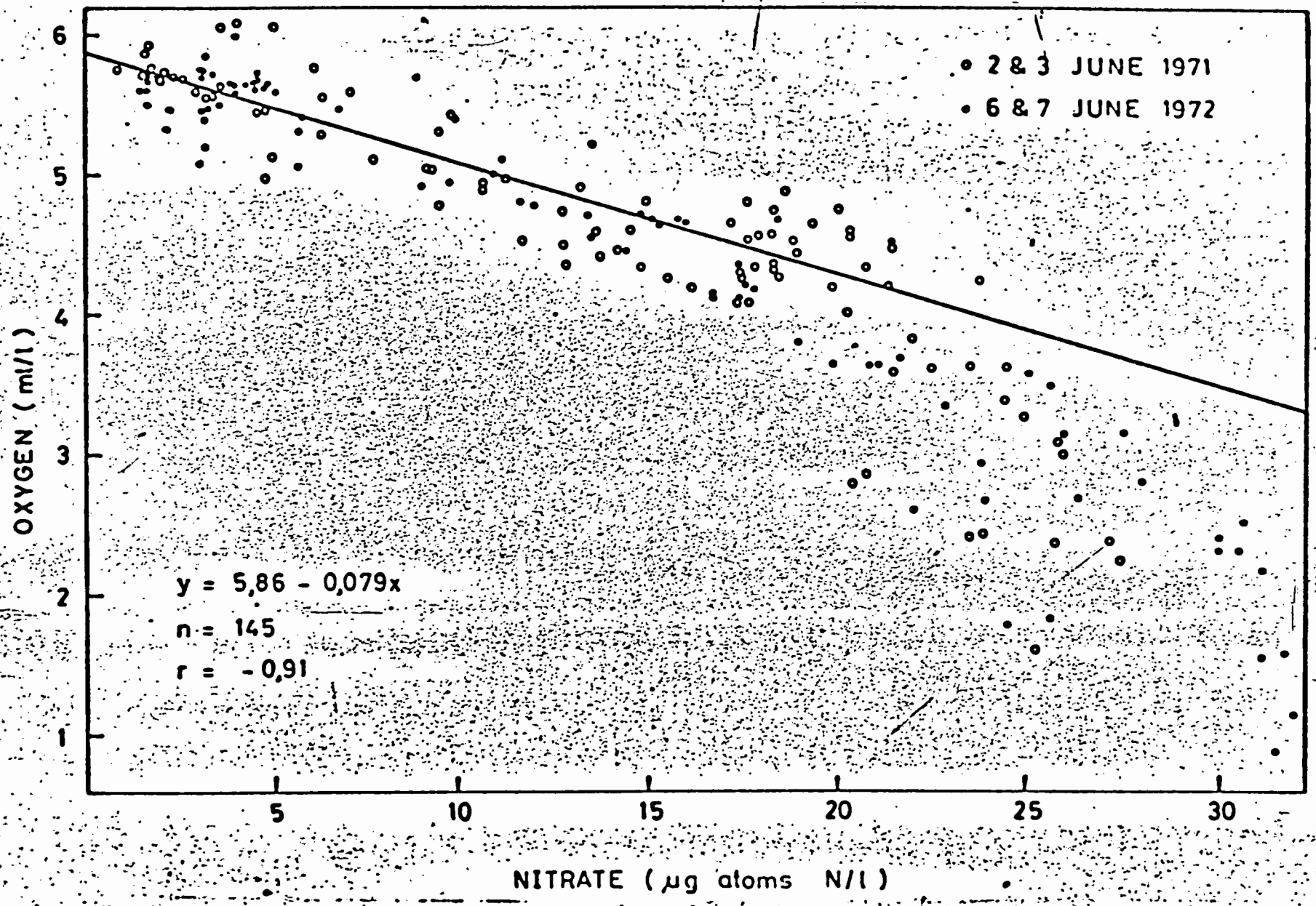

Fig 14.9 Relationship between oxygen and nitrate concentration. Regression and correlation coefficient calculated from data of oxygen concentrations of >4 ml/l only. Data from Upwelling-Monitoring Cruises of June 1971 and June 1972.

Peru occurs "at such a relatively slow rate that all silicate taken up in the euphotic zone may be considered as new". An explanation of the low N:Si ratios that characterise distant oxygen-depleted waters can be found in the nature of the area in which these waters are formed. In the azoic areas in the region of Walvis Bay very low oxygen values are found and on occasions completely anoxic conditions occur close to the bottom (Hart and Currie, 1960). In such conditions nitrate reduction is likely to take place. Calvert and Price (1971) show that there is an increase in the nitrite concentration close to the bottom over the shelf of South West Africa that results from nitrate reduction. Quantitatively the increase in nitrite was less than the decrease in nitrate for nitrite reduction results in the production of molecular nitrogen.

All nitrate results presented in this paper include nitrite since separate analyses of nitrite were not carried out. Yet plots of nitrate (+ nitrite) against oxygen (e.g. Fig 14.9) show a marked reduction of nitrate levels at low oxygen concentrations, providing additional evidence of the process of nitrate reduction to molecular nitrogen in the Benguela system. The low N:Si ratios that are found near the bottom are thus, at least partially, a result of nitrate reduction. The nature of the process of silicate regeneration will also have a profound influence on these ratios.

Silicate regeneration is rather a slow process, Since animals have little use for silicates (in contrast to nitrates

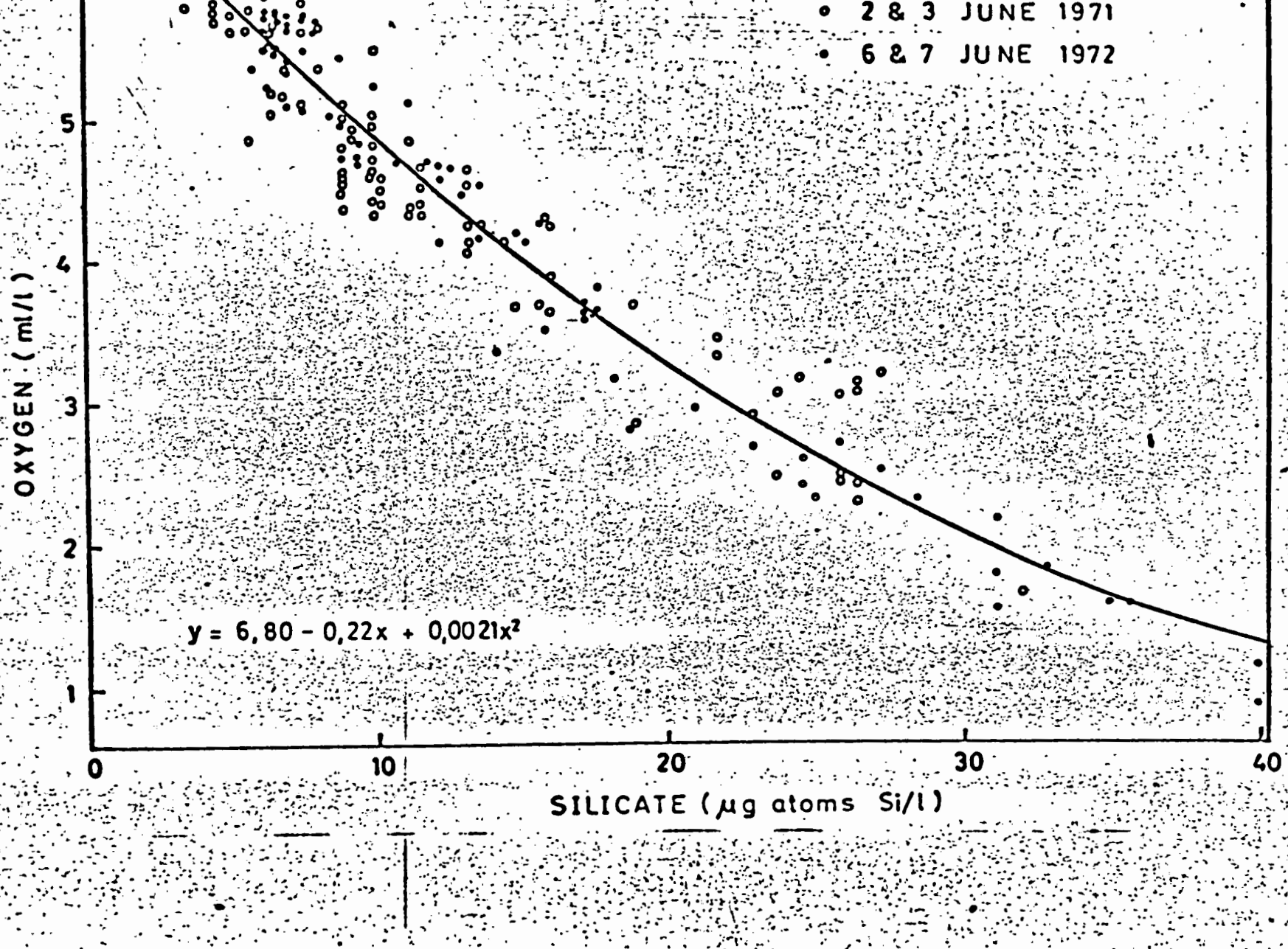

Fig 14.1f Relationship between oxygen and silicate concentration. Data from Upwelling-Monitoring Cruises of June 1971 and June 1972.

and phosphates which are metabolised by them) regeneration was considered to be purely physical process involving mainly the solubility of diatom tests. Richards (1958), however, put forward the idea that silicate was related to biological processes and was regenerated in a constant proportion to other nutrients. In a laboratory experiment with decomposing phytoplankton Grill and Richards (1964) were unable to find support for this hypothesis and found instead that silicate was regenerated in a changing proportion relative to phosphate.

A plot of oxygen and silicate data obtained off the Cape Peninsula in any season reveals a parabolic relationship, with silicate increasing relative to oxygen more rapidly at lower oxygen levels. A parabolic relationship is particularly clear in winter when data points are less scattered. The regression calculated by a least-squares analysis from data obtained in June 1971 and June 1972 (Fig 14.10) shows that at a dissolved oxygen content of 2 ml/l O: Si = -272:33.4; at one of 3 ml/l O: Si = 272:23.8; at one of 4 ml/l O: Si = -272:19.3; at one of 5 ml/l O: Si = -272:16.8; and at one of 6 ml/l O: Si = -272:15.3. In the summer a parabolic regression fits the data only marginally better than a linear regression.

Richards (1958) found the silicate concentration of the oxygen-depleted waters of the Cariaco Trench was greater than would be expected from the phosphate concentration. She suggested that this could be due to re-solution of bottom deposits accompanied by upward diffusion or to resolution of the skeletal

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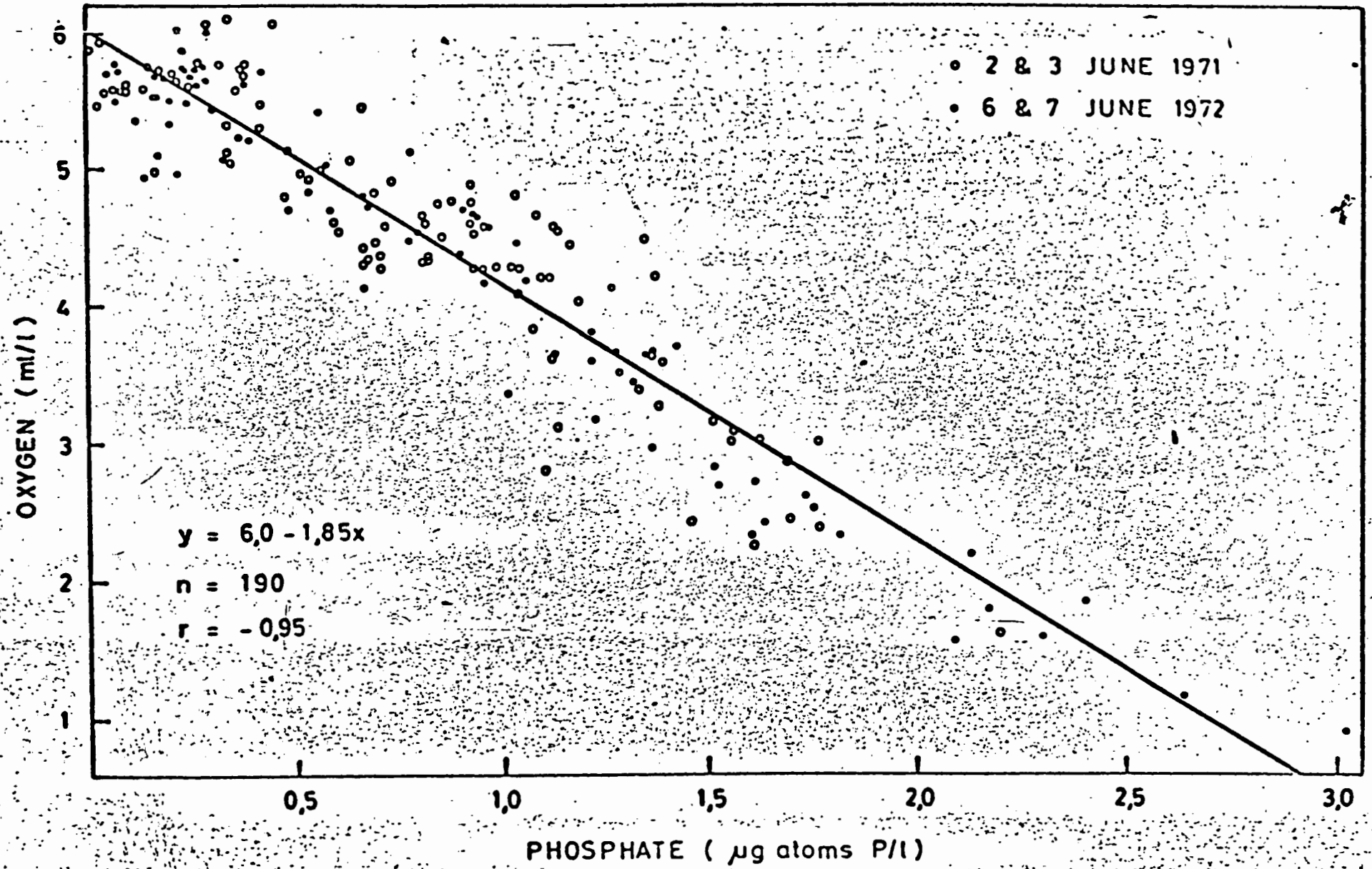

Fig 14.1) Relationship between oxygen and phosphate concentration. Data from Upwelling-Monitoring Cruises of June 1971 and June 1972.

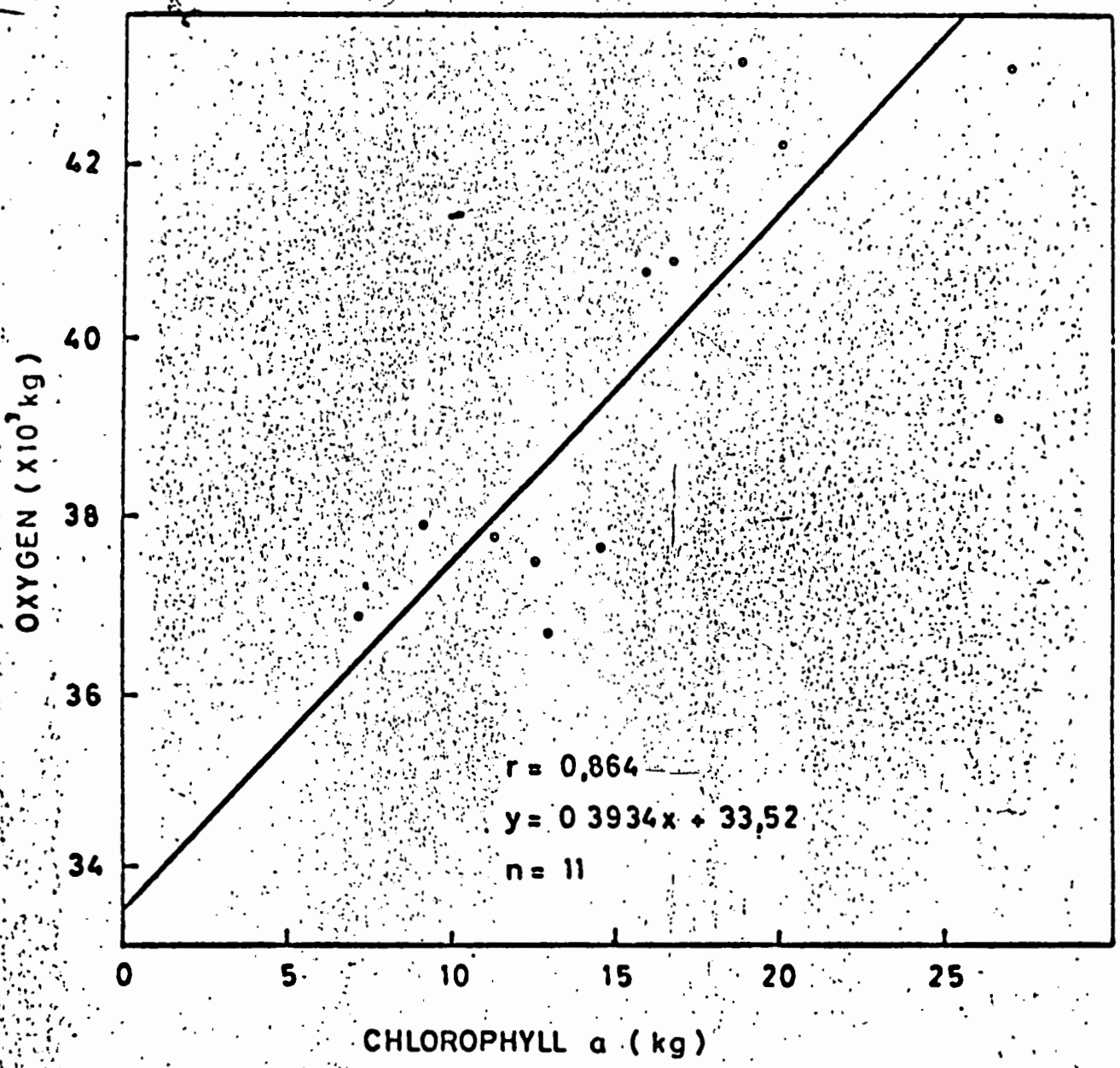

Fig 14.12 Relationship between integrated values of oxygen and chlorophyll a in a strip 1 m wide and 100 km long of the photic layer in a section along the upwelling plume.

remains of sinking diatoms. Mortimer (1971) found that silicate was liberated from bottom sediments in the Great Lakes at oxygen levels of below 1.4 ml/l, thus increasing the relative proportion of silicate. Oxygen concentrations in the azoic area off Walvis Bay fall below this level (Hart and Currie, 1960) and it may be assumed that resolution of silica from the sediments occurs in this region. Such a process would cause an increased proportion of silicate relative to oxygen with a similar relationship to the parabola shown in Fig 14.10.

Regeneration of phosphate is known to occur relatively rapidly (Redfield et al., 1963). A close linear relationship between oxygen and phosphate holds throughout the range of both variables throughout the year (e.g. Fig 14.11), indicating that regeneration of this nutrient in the Benguela system in unaffected by the oxygen concentration.

(iii) Seasonal changes in total nitrogen

Nitrate has been shown to be the primary limiting nutrient in the Cape upwelling area but is only one of a number of forms, both organic and inorganic, in which nitrogen occurs. The total amount of nitrogen in the area will include ammonia and that bound in the detritus and in the phytoplankton. There is no information on amounts of nitrogen occurring as ammonia or bound in the detritus and, for the present, these portions will have to be ignored. Estimates of the portion bound in the phytoplankton have been made and, as a preliminary step towards estimating the

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total nitrogen, have been added to the amount occurring as nitrate (+ nitrate).

Integrals of oxygen, nutrients and chlorophyll a in the photic layer were obtained from profiles, such as those shown in Fig 9.1, by linear interpolation between stations lying between the shore and 100 km down the plume. Each integral is an estimate of the total amount of oxygen, nutrients or chlorophyll a in a strip along the upwelling plume, 100 km in length, 1 m in width and 50 m in depth.

A plot of integrated amounts of chlorophyll and oxygen within the 100 km strip for the months September to February 1971-2 and 1972-3 (Fig 14.12) confirms the observation (Chapter 9) that they are closely and directly related and enables the regression, $y = 0.3934\ z + 33.52$, to be obtained. An estimate of the resident dissolved oxygen content can be made by extending the regression line until the chlorophyll a content is equal to zero. Estimates of the biologically produced oxygen content were obtained by subtracting the resident dissolved oxygen content, which has a value of 33.5×10^3 kg, from each monthly integrated oxygen value. There is a conceptual similarity between the biologically produced oxygen and the apparent oxygen utilization (Redfield et al., 1963) but in this specific instance the former concept is considered to be more meaningful.

The data for biologically produced oxygen content were used to provide estimates of amounts of nitrogen bound in phytoplankton. It was assumed that for each 272 atoms of oxygen produced 22.2

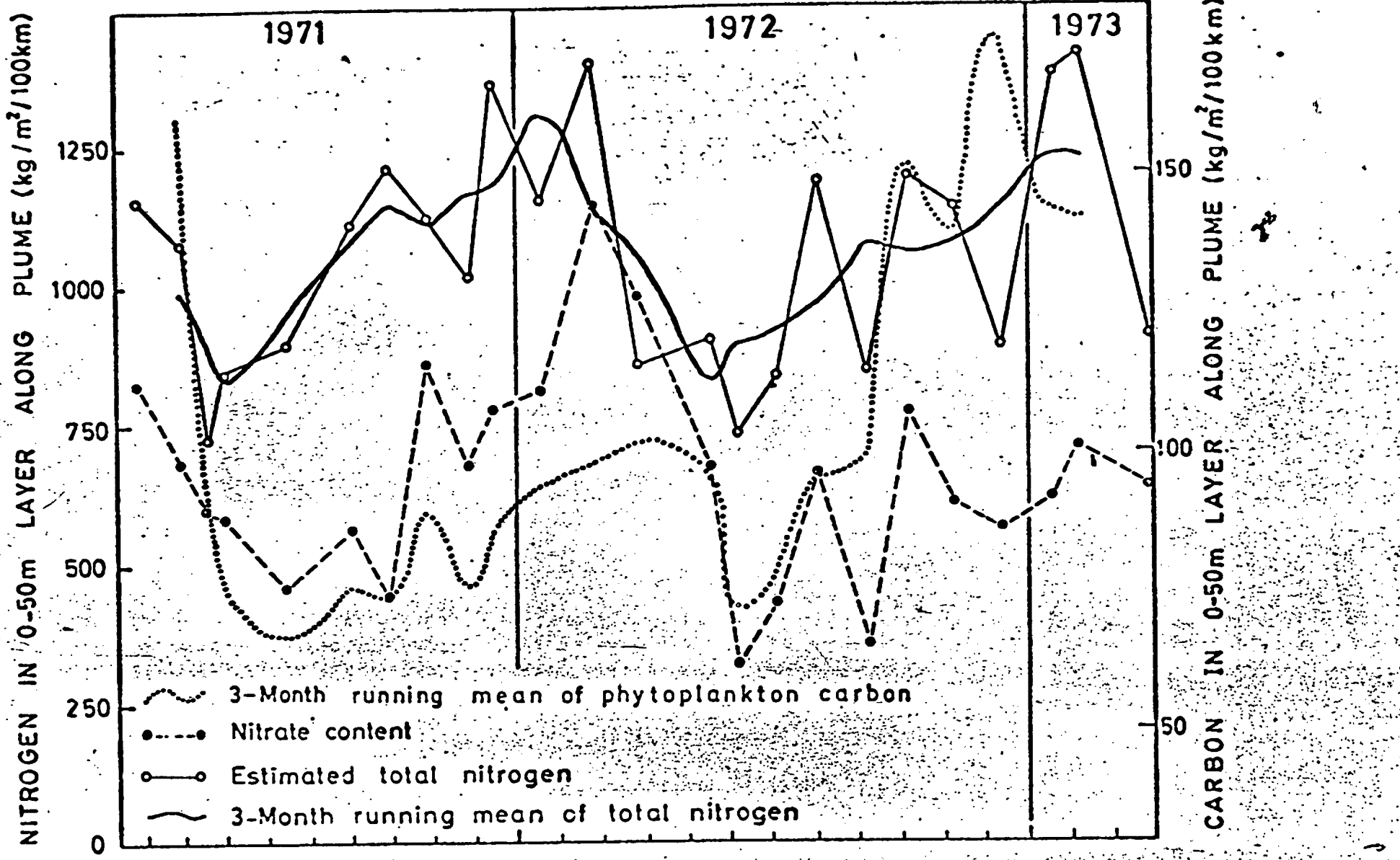

Fig 14.13 Seasonal cycles of nitrate, total nitrogen and total carbon.

atoms of nitrogen had been taken up by phytoplankton (mean of results given in Table 7). Each monthly value of biologically produced oxygen content was thus converted into estimates of bound nitrogen which were then added to the corresponding monthly integrated nitrate values. Monthly estimates of integrated nitrate, bound nitrogen and their sums are shown in Fig 14.13; as a preliminary measure sums of integrated nitrate and bound nitrogen have been equated with total nitrogen. Three-month running means of the preliminary estimates of total nitrogen were calculated and are also shown in Fig 14.13.

The three-month running means of these preliminary estimates of total nitrogen show a well-defined seasonal cycle that was remarkably similar in both years studied. This contrasts with the differences seen in the nitrate contents and in the three-month r running means of phytoplankton standing stocks (Fig 14.13) of the same period. Nitrate levels were considerably higher and phytoplankton standing stocks considerably lower in the summer of 1971-2 than in the succeeding summer.

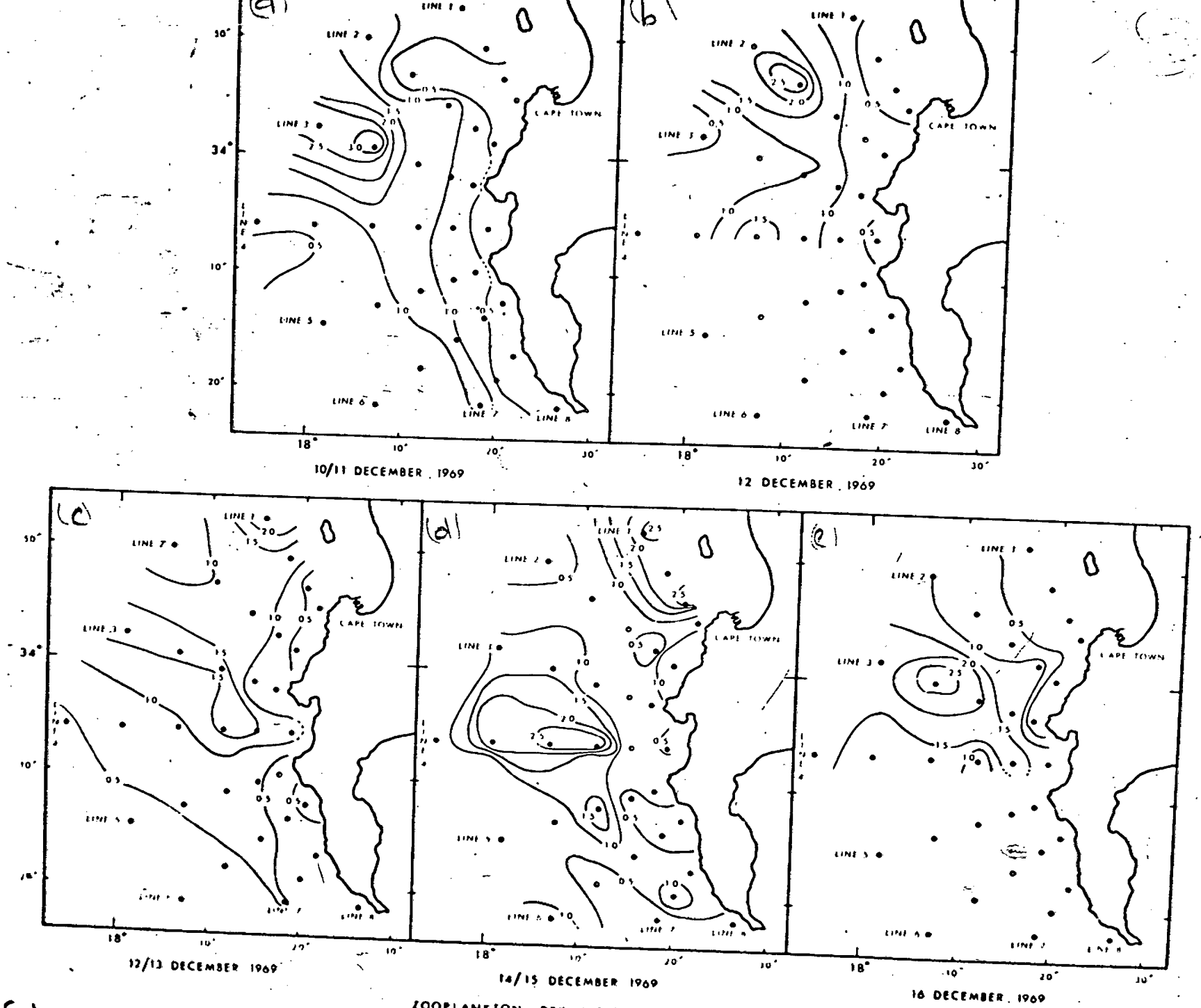

Fig 15.1

ZOOPLANKTON DRY WEIGHTS (g/m³)

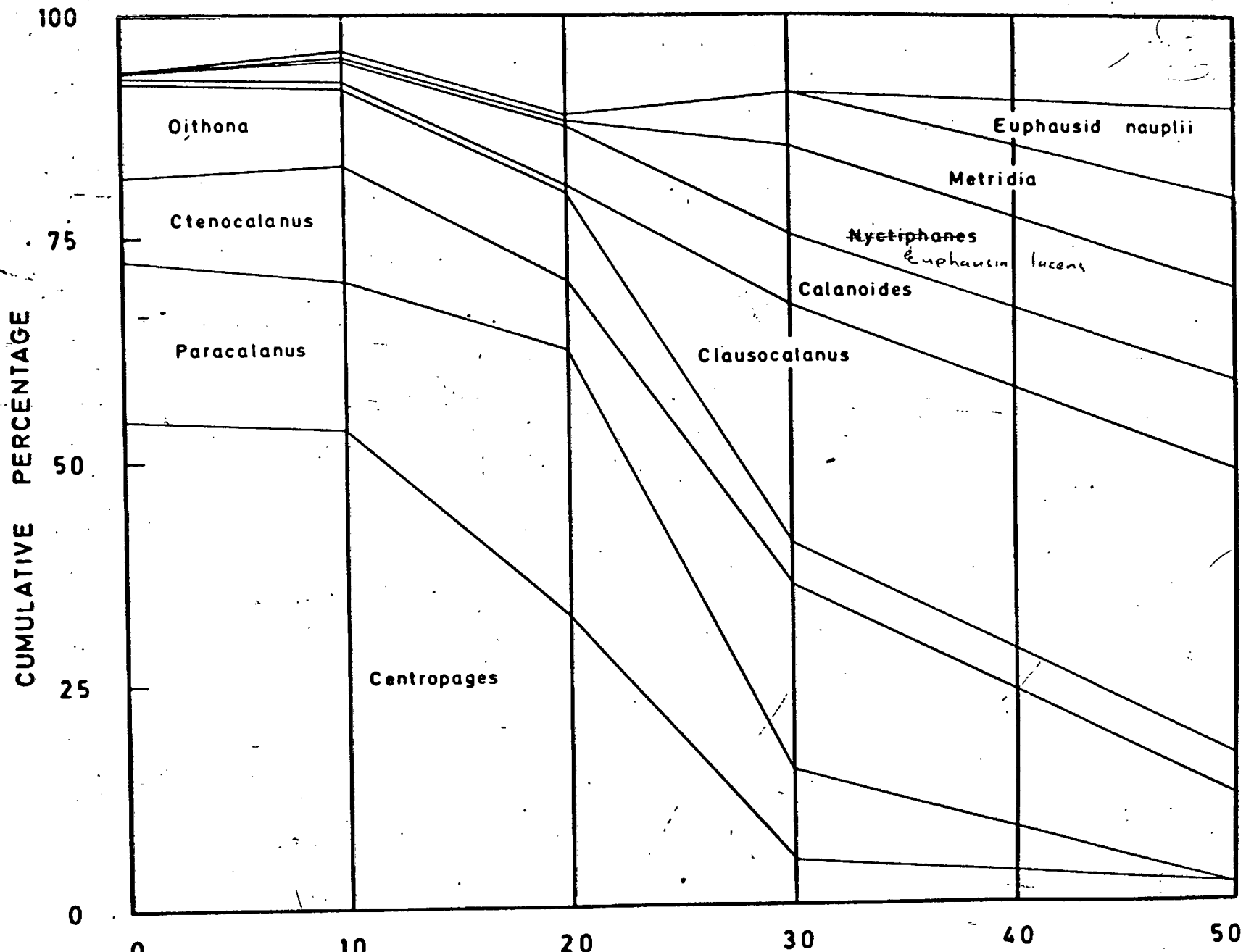

Fig 15.3

SPECIES COMPOSITION AT St. 643 PUMP SAMPLES 14 DECEMBER

15. The Zooplankton

In an area of such instability, the zooplankton exhibits a marked variability, both in space and time. Zooplankton has been sampled over various time scales ranging from 4 minute intervals through 4 hours, 34-36 hours, and 48 hours to 30 day intervals. Most stations were 9 or 18 kilometers apart. Except for the monthly monitoring trips all other samples were collected during December or January, in the middle of the peak upwelling period. It is felt that a description of the zooplankton variability over various time scales is the most appropriate way of presenting the data.

(i) Replicate Hauls

Table (8) shows the correlation coefficient between duplicate WP-2 net hauls (from bottom to surface, with approximately four minutes between hauls) taken in January and February 1971 along the upwelling monitoring line of stations.

Approximately 14% (5 in 34) of the pairs of hauls showed evidence of patchiness, with large differences between the displaced volumes and dry weights of replicate hauls. Subsequent to these hauls single hauls above and below the maximum temperature gradient were made.

(ii) Diurnal variation at a fixed point

In December 1971 the integrated displaced volumes of samples collected every four hours at 8 different depths with the pump to 100 meters at a moored buoy (Table 9) were found to vary three -

fold over a twenty-four hour period. Integrated chlorophyll a values also varied three fold during the same period in an inverse manner to the zooplankton, as water masses varying in the relative quantities of phytoplankton and zooplankton moved past the fixed point.

(iii) Daily variation at the centre of upwelling

In December 1969 the variability of zooplankton over the whole centre of upwelling was observed at 24-36 hours intervals for a continuous six day period.

Dry weight was used as an estimate of zooplankton abundance, as displaced volumes were unduly biased by jelly-like organisms, which were common in newly upwelled water and in warm oceanic water. Zooplankton was generally more abundant in the mixed water zone than in other water types. Increased zooplankton concentrations were also observed in the southern part in a narrow belt running parallel with the coastline, associated with the strong temperature and salinity gradients of the frontal zone.

Several patches of high zooplankton concentration could be seen in the northern part of the grid (Fig 15.1, (a-e)). The patch on line 4 (Fig 15.1(c)) appeared to develop as warm water began to intrude coastwards along line 3 during a brief period of onshore (westerly) winds (Fig 5-3) and was associated with high chlorophyll a concentrations. A low zooplankton crop was associated with a second patch of high chlorophyll a values centred on line 2.

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	n	r	p
Volume filtered by net	31	0,92	0,01
Displaced Volume	35	0,87	0,01
Dry weight	34	0,68	0,01

TABLE 8 Comparison of replicate hauls collected with a WP-2 net towed from bottom to surface on the Bio-upwelling cruise in January 1971 and the upwelling-monitoring cruise in February 1971.

Local time	0500 hrs	0930	1235	1630	2130	0030	0430
Zooplankton (ml/m^2) (0-100 m)	40	27	19	13	27	27	22
Chlorophyll a (g/m^2) (0-100 m)	141	238	207	419	293	203	207

TABLE 9 Variation in integrated zooplankton displaced volume and Chlorophyll a at a moored buoy in December 1971, Station 3

As the wind backed to the east the patch consolidated, increased in size, and moved slightly westwards. As the wind stress increased, this patch moved steadily northwards, but did not appear to be dispersed as rapidly as the phytoplankton, although the number of organisms in the patch decreased from approximately 90, 000/m^2 to 36, 000/m^2 over the three-day period. Because of suspected avoidance of the relatively slow-moving net by large organisms, hyperiid amphipods and euphausids were excluded from the dry weight values. In some instances these larger organisms were responsible for 40 to 70% by volume of the sample, although in terms of numbers small copepods constituted 80 to 90% of the total. Species changes in the plankton patch in terms of percentage frequency by numbers are shown in figure (15.2) and appear to be relatively small, indicating that the patch retained its integrity to some extent over the three day period. However, pump samples taken in the dark (0145-0500 hours) on December 15th in the centre of the patch showed marked changes in the species composition with depth (Fig 15.3); Centropages brachiatus and Paracalanus parvus, which dominated in the upper 20 meters, were replaced by Clausocalanus spp., Calanoides carinatus, Nyctiphanes capensis, Metridia lucens and euphausid nauplii in the 30 m and 50 m samples. Numbers of organisms dropped rapidly below 20 meters, from about 1100/m^3 at 20 metres to 220/m^3 at 30 and 50 metres. In terms of numbers, the organisms in the upper 20 metres completely dominated the 50-0 metre layer and this suggests that a layer about 20 m thick was being moved

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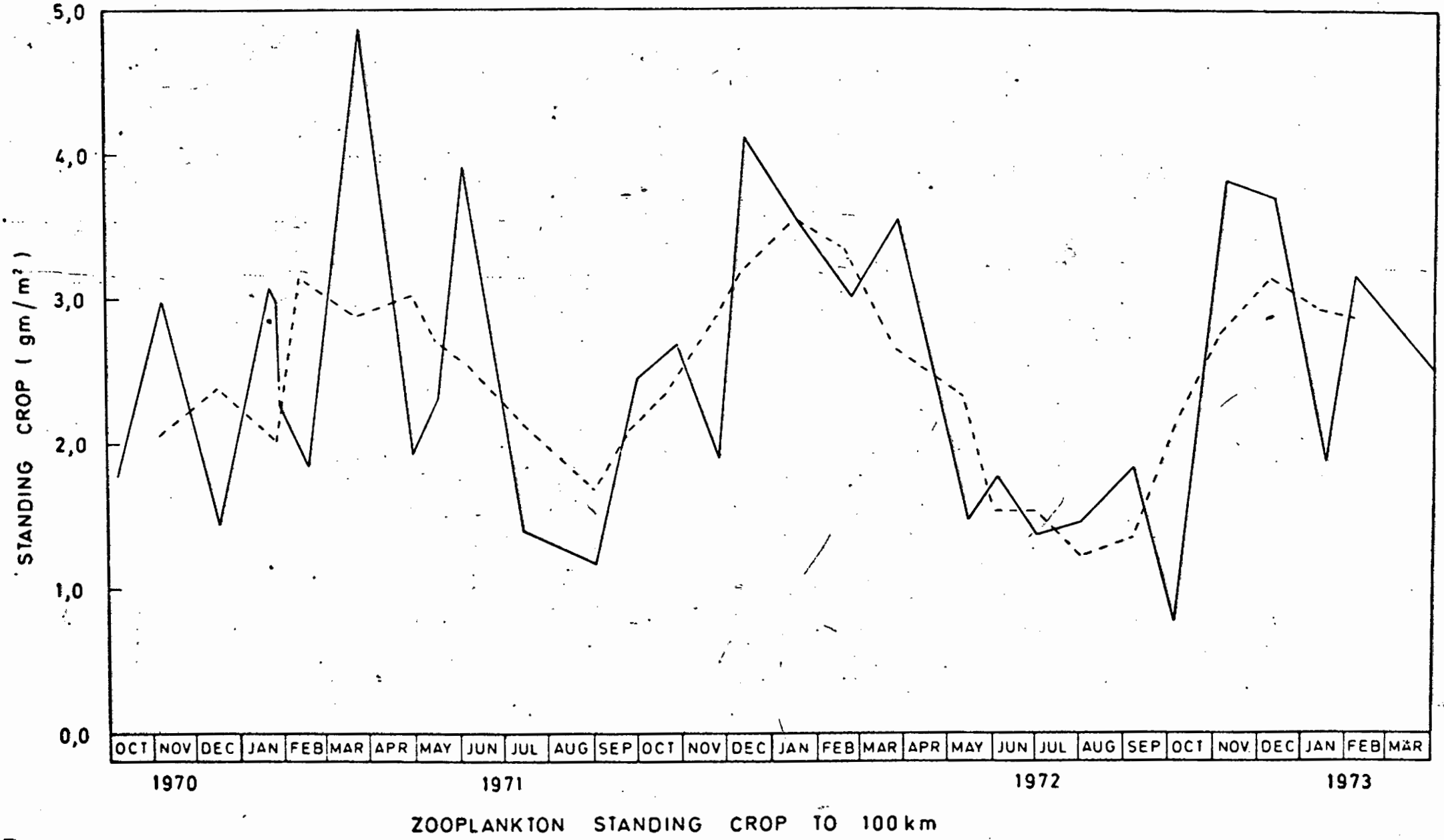
5,0
4,0
3,0
2,0
1,0
0,0
STANDING CROP (gm/m²)
OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MÄR
1970
1971
1972
1973
ZOOPLANKTON STANDING CROP TO 100 km

Fig 15.4

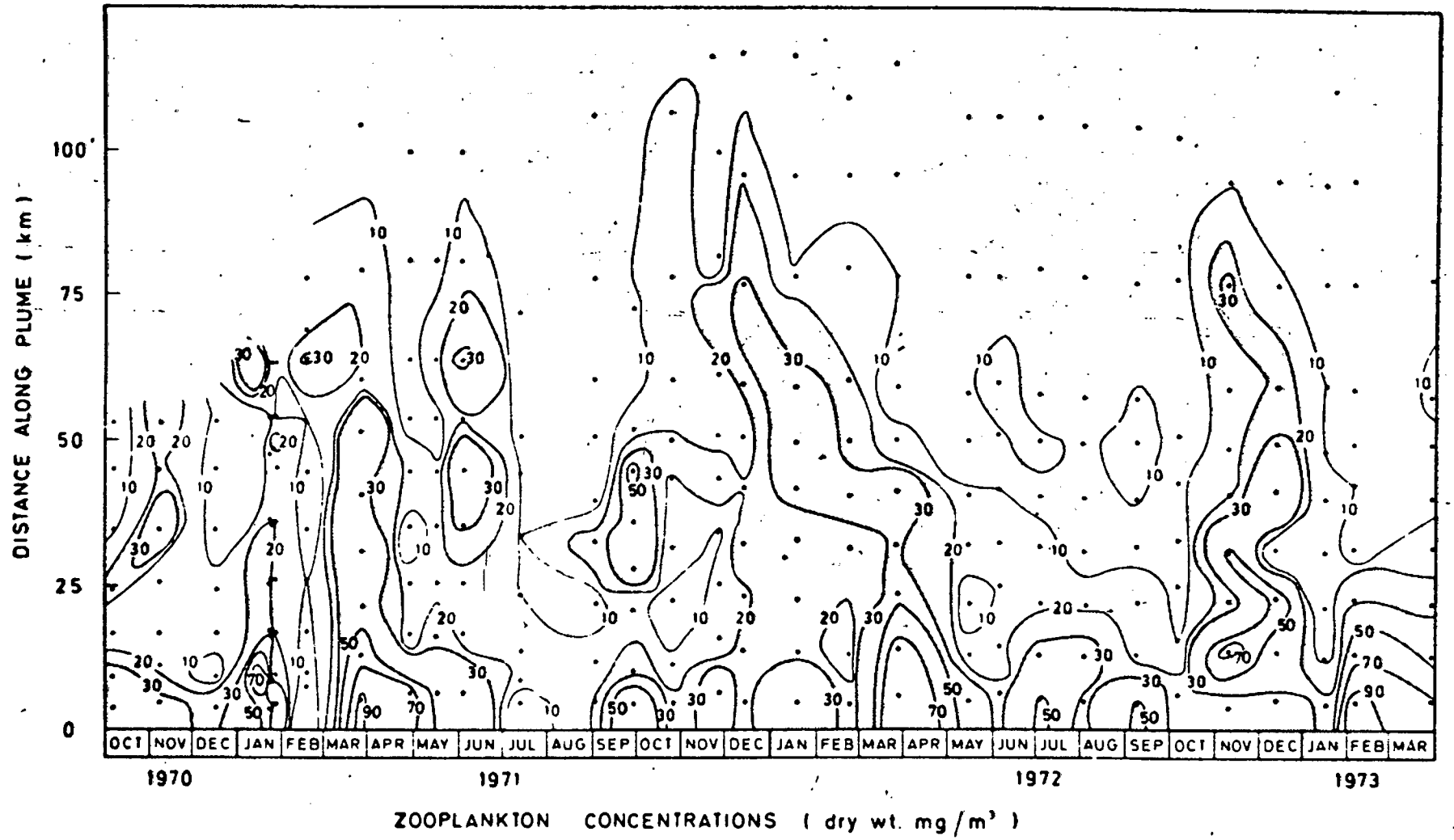
DISTANCE ALONG PLUME (km)
100
75
50
25
0
OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR
1970
1971
1972
1973
ZOOPLANKTON CONCENTRATIONS (dry wt. mg / m³)

Fig 15.5

bodily offshore. With wind as the dominant moving force one would expect very marked horizontal shearing of the water column, with more rapid dispersal of organisms living near the sea surface.

Despite the fact that euphausids and hyperiids were more abundant in the deeper layers and were probably not quantitatively sampled the area of peak abundance of these organisms coincided with the location of the patch on all three occasions, indicating they were moving at about the same rate.

(iv) Variation along the monitoring line

In January 1971 the zooplankton dry weight beneath a strip one metre wide and 65 kilometres long was estimated by linear interpolation between 8 stations along the monitoring line. The dry weight was found to vary by 3% and 30% in successive 48-hour periods respectively with a mean value of 175 kilograms dry weight for the three estimates.

(v) The Annual Cycle of Zooplankton

The standing stock of zooplankton along the monitoring line showed considerable variability between successive monthly cruises (Fig 15.4). A comparison of surface temperature (Fig 5.2) and zooplankton standing stocks (Fig 15.5) shows that high zooplankton concentrations were sandwiched between cold ($< 10°C$) water inshore and warm ($> 16°C$) water offshore. Intrusions of warm water limited zooplankton to the inshore region in May, July, 2/3rd September and November in 1971; in May to September 1972 and January 1973.

Sustained upwelling displaced zooplankton offshore in February and October in 1971 and in February 1972. Very low standing stocks were observed when warmer water intrusions abutted sharply against cold upwelled water close inshore (December 1970, October 1972). A regression of the width of the mixed water zone (estimated from consideration of the rate of change of surface temperature and the chlorophyll a content of the upper layers) against the zooplankton standing stock showed a significant positive correlation ($n=30$, $r=0,6$, $p = < 0.01$), but when the zooplankton was lagged one month the correlation dropped to 0.03 indicating that much of the fluctuations of the zooplankton population (e.g. 400% change from October to November 1972) were due to changes in the physical environment. A smoothed curve (fig. 15.4) based on three-month running means, showed a regular seasonal fluctuation in the zooplankton standing crop with a summer maximum of two to three times the winter minimum, with a mean standing stock of 2.3 g dry weight per square metre. The maximum zooplankton standing stock observed was 100g dry weight/m^2 at the 1st station in January 1971. Differences between mean summer (October to March) stocks of the three years investigated were not considered significant, with less than 20 % variation between years.

(vi) Horizontal Distribution of Zooplankton

Zooplankton standing stocks were irregularly distributed along the monitoring line during the summer months, but generally maximum values were observed 40 to 110 km from the coast and minimum values at 20 - 50 km offshore. In winter highest standing stocks were observed close to the coast with very low values offshore.

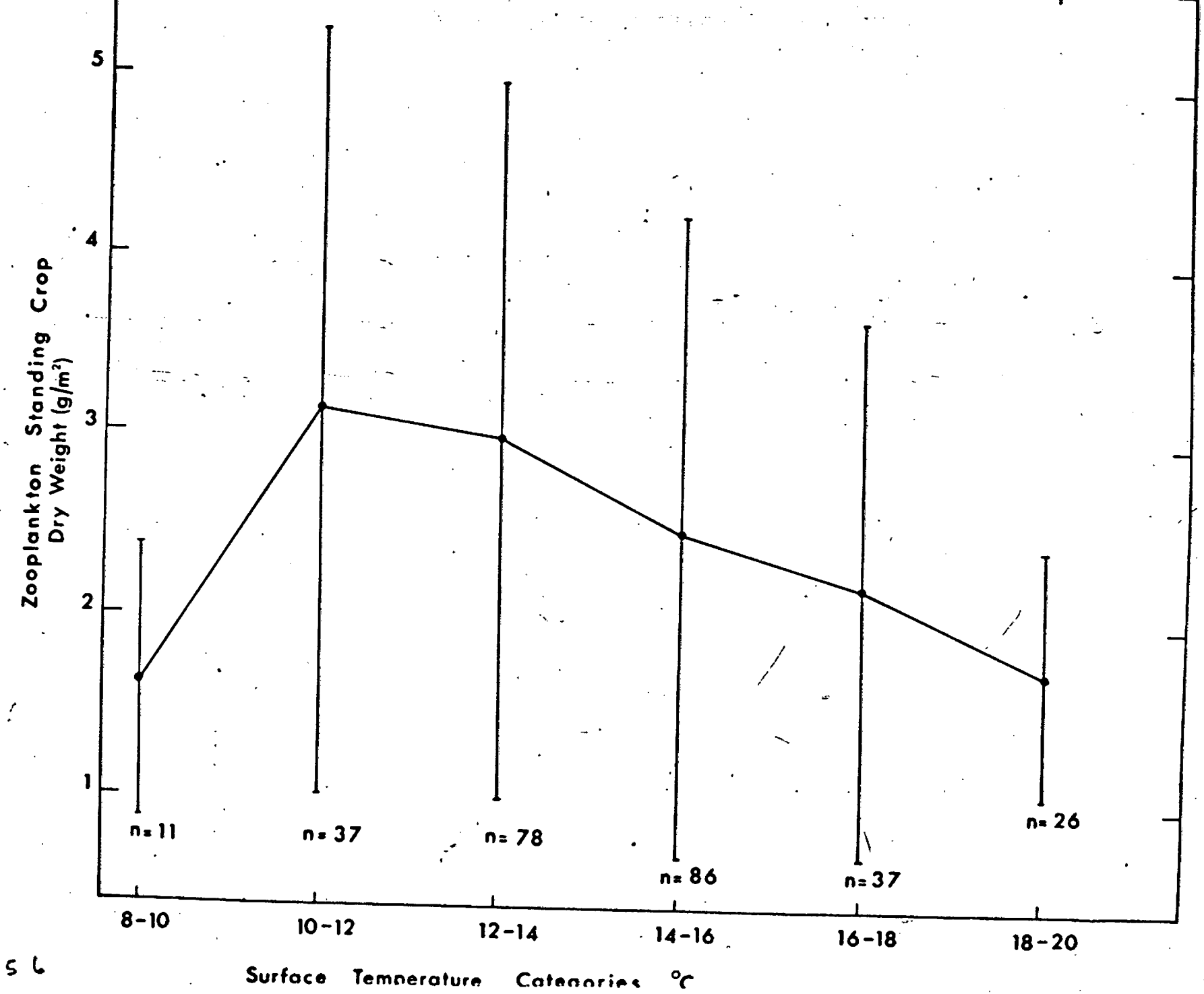
Zooplankton Standing Crop
Dry Weight (g/m²)
5
4
3
2
1
n= 11
n= 37
n= 78
n= 86
n= 37
n= 26
8-10
10-12
12-14
14-16
16-18
18-20
Surface Temperature Categories °C

Fig 15 b

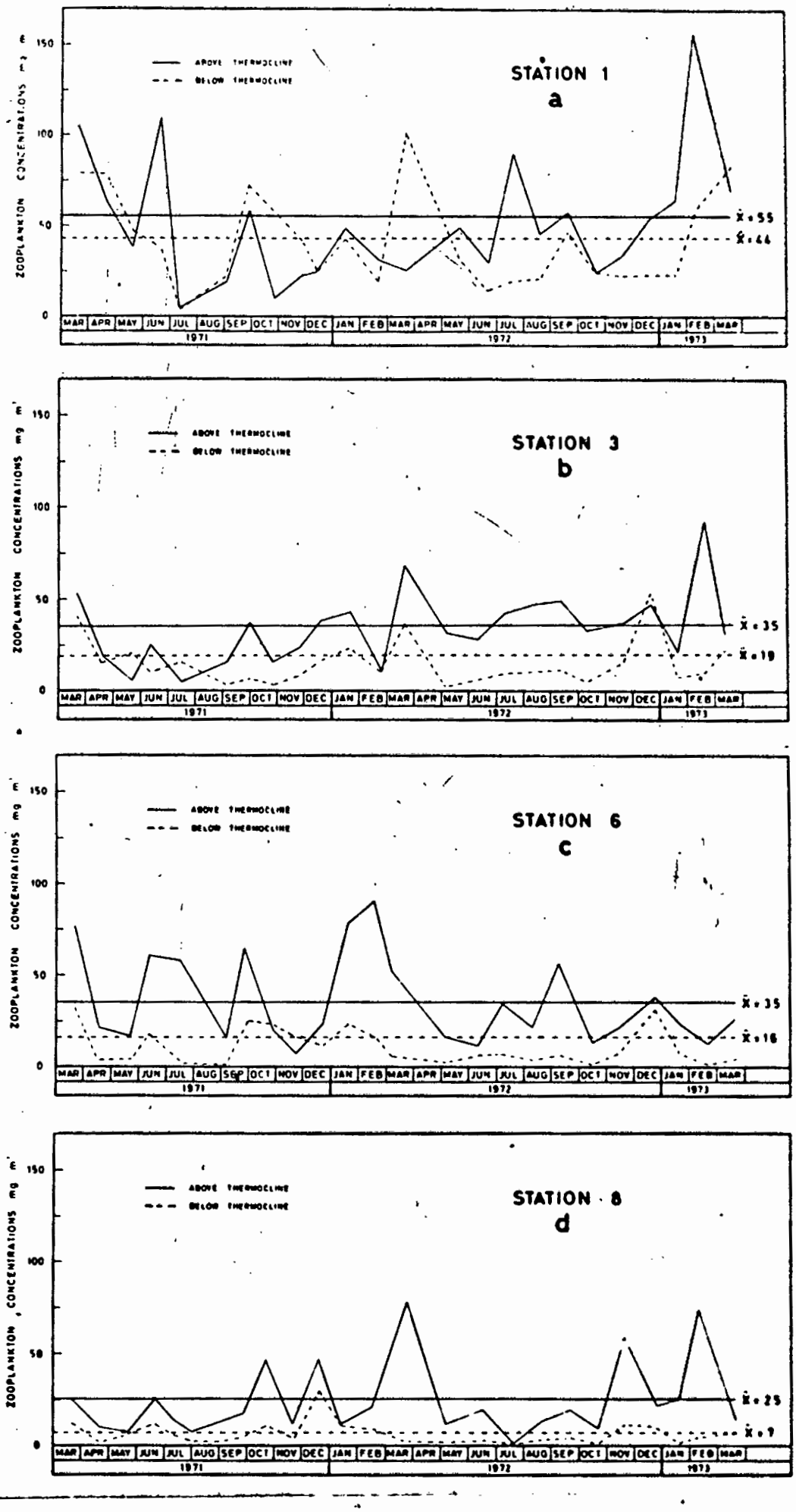
ZOOPLANKTON CONCENTRATIONS mg m³
ABOVE THERMOCLINE
BELOW THERMOCLINE
STATION 1
a
X̄ = 55
X̄ = 44
STATION 3
b
X̄ = 35
X̄ = 19
STATION 6
c
X̄ = 35
X̄ = 16
STATION 8
d
X̄ = 25
X̄ = 9
0
50
100
150
MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR
1971
1972
1973

Fig 15.7

A plot of zooplankton standing crop in various surface temperature categories (Fig 15.6) shows that in winter (April - September) maximum standing crops were found between 10°C and 14°C surface temperature, while in summer maximum stocks were observed at temperatures between 12°C and 14°C, although much scatter was evident in the data.

(vii) Vertical distribution of Zooplankton

Separate net hauls above and below the thermocline generally divided the zooplankton into that associated with high phytoplankton concentrations and that living below the phytoplankton-rich layer. Most samples were collected during daylight hours. At 90% of the stations zooplankton was more abundant in the upper layers indicating that the bulk of the population did not exhibit any vertical migrations into the upper layers during the night. Only close inshore was zooplankton more homogeneously distributed through the water column (Fig 15.7 a-d)).

Dry weight concentrations in near-surface water varied widely, but fluctuations appeared to be more seasonally linked offshore. Relative to the upper layers concentrations below the thermocline dropped off rapidly down the plume and in winter reached very low levels offshore with few exceptions. High concentrations were found very close to the coast during the whole sampling period.

(viii) Zooplankton- Phytoplankton Relationships

Eddy formation caused by changes in wind direction as well as different response times to upwelling events appear to be responsible for the lack of coherence between the distribution of zooplankton and phytoplankton down the monitoring line. Zoo-

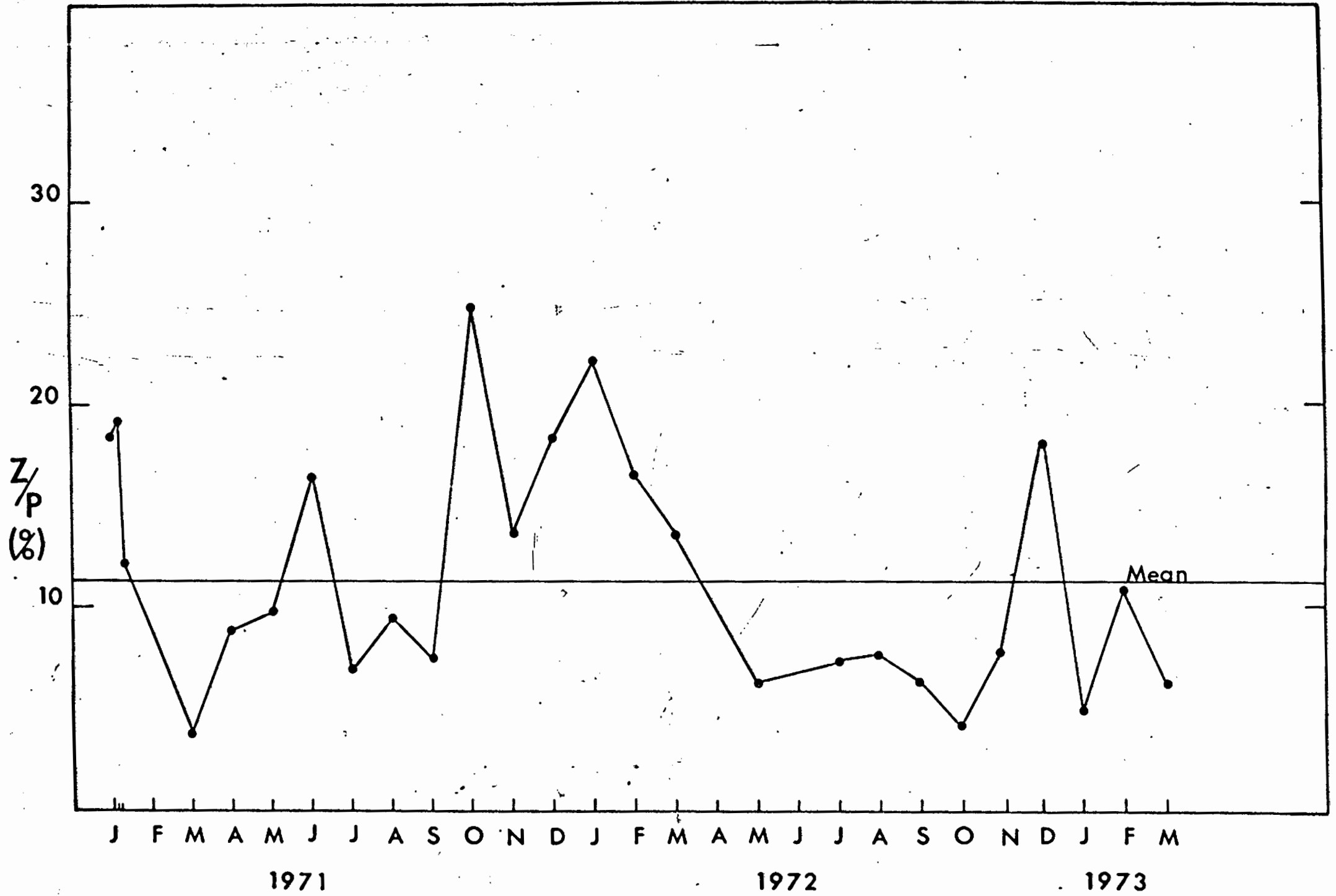
30
20
10
Z/P
(%)
Mean
J F M A M J J A S O N D J F M A M J J A S O N D J F M
1971
1972
1973

Fig 15 8

TIME

plankton maxima occurred inshore, coincident with and offshore of the phytoplankton maxima during different monitoring line cruises. Yet the quantity of zooplankton (dry weight) along the monitoring line was significantly related to the abundance of phytoplankton measured in terms of chlorophyll a (n=27 r=0.57, p =< 0.01). The quantity of chlorophyll a present in turn was less well related to the width of the belt of mixed water (r=0.35, n=25, p= < 0.05) as much subsurface chlorophyll a occurred during warm water intrusions.

The zooplankton crop formed from 4% to 25% of the phyto= plankton crop with a mean value of 12% (n=26) when both are expressed in units of carbon (Zooplankton carbon content = 40 - 50% of dry weight, Hutchings unpublished data), and the ratio followed a fairly distinctive seasonal cycle (Fig 15.8) with maximum values in summer, although large variations do occur in all seasons.

The June 1971 cruise was anomalous in several respects; a strong SE wind (30-45 knots) persisted for five days immediately prior to the cruise followed by calm conditions. High zooplank= ton concentrations were observed, but relatively low phytoplankton stocks, (due possibly to limiting light conditions) resulting in an unseasonally high zooplankton/phytoplankton ratio.

During intrusions of warm water, the zooplankton and phytoplankton populations appear to react in different ways. Very dense concentrations of phytoplankton were observed in the

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region of the thermocline immediately below the warm water, e.g. January 1973, (Fig 13.1) while the zooplankton disappeared and was presumably displaced towards the coast, east of the monitoring line, resulting in a marked reduction in the ratio of zooplankton to phytoplankton (November 1971, January 1973).

A correlation significant between the 5% and 1% levels was observed between average zooplankton standing stock along the monitoring line and the gross production (mean of 03+06); ($r=0.46$, $n=24$, $0.01 > p > 0.05$). The zooplankton standing crop averaged 18% of the daily phytoplankton gross production per day, with a minimum in October 1972 (4%) and a maximum (124%) in June 1972. No seasonal pattern was evident. As the gross production figures are probably maximum estimates, little ecological significance can be attached to this relationship.

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16. Discussion

It is evident that the strong seasonal pattern in local winds accounts for much of the seasonal variation in the oceanography of the area, with the upwelling season coinciding with the period of high percentage south-easterly winds. There is a semi-permanent nature to the upwelling plume in the upwelling season. This would seem to be related to the existence of the jet current described by Bang and Andrews (1974) which is thought to persist at the edge of the continental shelf throughout the upwelling season. The general oceanic circulation of the South Atlantic Ocean also makes an impact on the local seasonal cycle. The appearance of large volumes of cold, dense water on the shelf in the late winter (Chapter 10) is probably due to the increased intensity of the South Atlantic gyre at this time (Bang - personal communication). The shelf waters would then have a northward flow. The local south-easterly winds that follow this appearance would tend to keep the dense water on the shelf and result in the formation of a jet current. The existence of the jet current seems to cause a reversal of flow of the waters on the shelf, a reversal which results in the appearance of oxygen-depleted water flowing from the north.

The transport of oxygen-depleted waters from azoic areas off South West Africa in a southward-flowing current may correspond with the Benguela Counter Current (Hart and Currie, 1960, De Decker, 1970). Some idea of the dimensions of the current can possibly be obtained from the local distribution of oxygen-

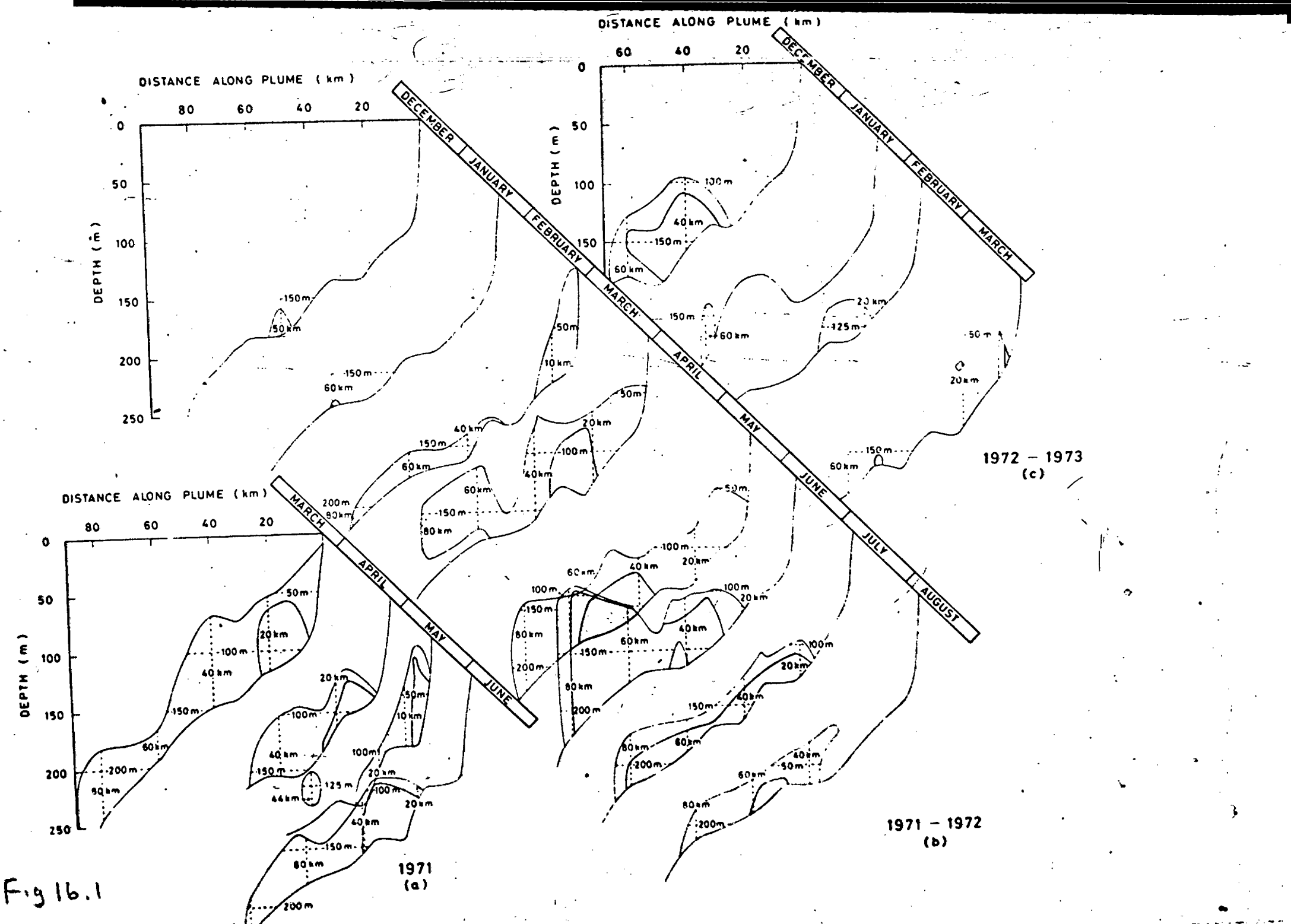
DISTANCE ALONG PLUME (km)
80 60 40 20 0
DEPTH (m)
0 50 100 150 200 250
DECEMBER JANUARY FEBRUARY MARCH APRIL MAY JUNE JULY AUGUST
150m
50 km
60 km
50m
10 km
20 km
40 km
100 m
200m
80 km
125 m
44 km
1971
(a)
1971 – 1972
(b)
1972 – 1973
(c)

Fig 16.1

depleted water. Oxygen-depleted water persists off the coast of South West Africa through the year (Stander, 1964). It would take some time, perhaps one or two months, for oxygen-depleted water to reach the Cape from South West Africa in the Benguela Counter Current so the presence of such water locally indicates a southward flow of about that duration.

The "normal" oxygen concentration of water on the shelf lies above 4 ml/l and, strictly speaking, any value below it is depleted. However, oxygen levels depleted due to local decomposition of phytoplankton must be excluded from the picture. Oxygen-depleted water of the counter current falls in a very narrow temperature range viz 8.5 - 9.5°C (De Decker, 1970). For the purposes of this investigation oxygen levels lower than 3.2 ml/l and a temperature range of 8.5 - 9.5°C were used to delineate the counter current. And, since it was noticed that there was a particularly well-mixed layer of water within these delineations which usually had an oxygen content of 2.5 ml/l, waters below this level have been assumed to form the core of the current.

A series of vertical sections of the "current" (O_2 = 3.2 - 2.5 ml/l) and the "core" (O_2 < 2.5 ml/l) were assembled in a three-dimensional diagram showing variations with depth, distance and time (Fig 16.1). Vertical interpolations between oxygen values were done by computor using means of cubic polynominal and straight-line fits; horizontal interpolations were done manually. A complete sequence of sections was only obtained in 1971-2 but data from the end of the preceeding and the beginning of the

succeeding season were also obtained. There was considerable variation of the penetration of the counter current from month to month and annually. De Decker (1970) observed a similar variability. In 1971-2 oxygen-depleted water made its first appearance, albeit to a very limited extent, in December 1971. The core first appeared in March 1972, persisted until August 1972, two months longer than in the previous year, thus remaining in the area for a period of about 20 weeks. A calculation of the cross-sectional area of the core, based on the assumption that it runs north-south and was thus not sectioned normally by the transect, reveals a dimension of approximately 7×10^5 m^2. At a velocity of 0.1 - 0.3 m/sec an southward-flowing transport of $7 - 21 \times 10^4$ m^3/sec would result. This compares with Bang and Andrews (1974) estimate of the transport in the Good Hope Jet of 7×10^6 m^3/sec.

Superimposed on the seasonal picture are quite dramatic short-term variations, mainly caused by fluctuations in wind conditions. Thus although the upwelling plume is prevalent during the upwelling season which extends from October to February of March strong north westerly winds can cause the conditions to change so much as to result in downwelling (Chapter 7).

Although the dramatic nature of the oceanographic variability tends to complicate matters we have tried to extract from our observations a general picture of the area during upwelling. Water types remain constant during the season (Chapter 8) a fact

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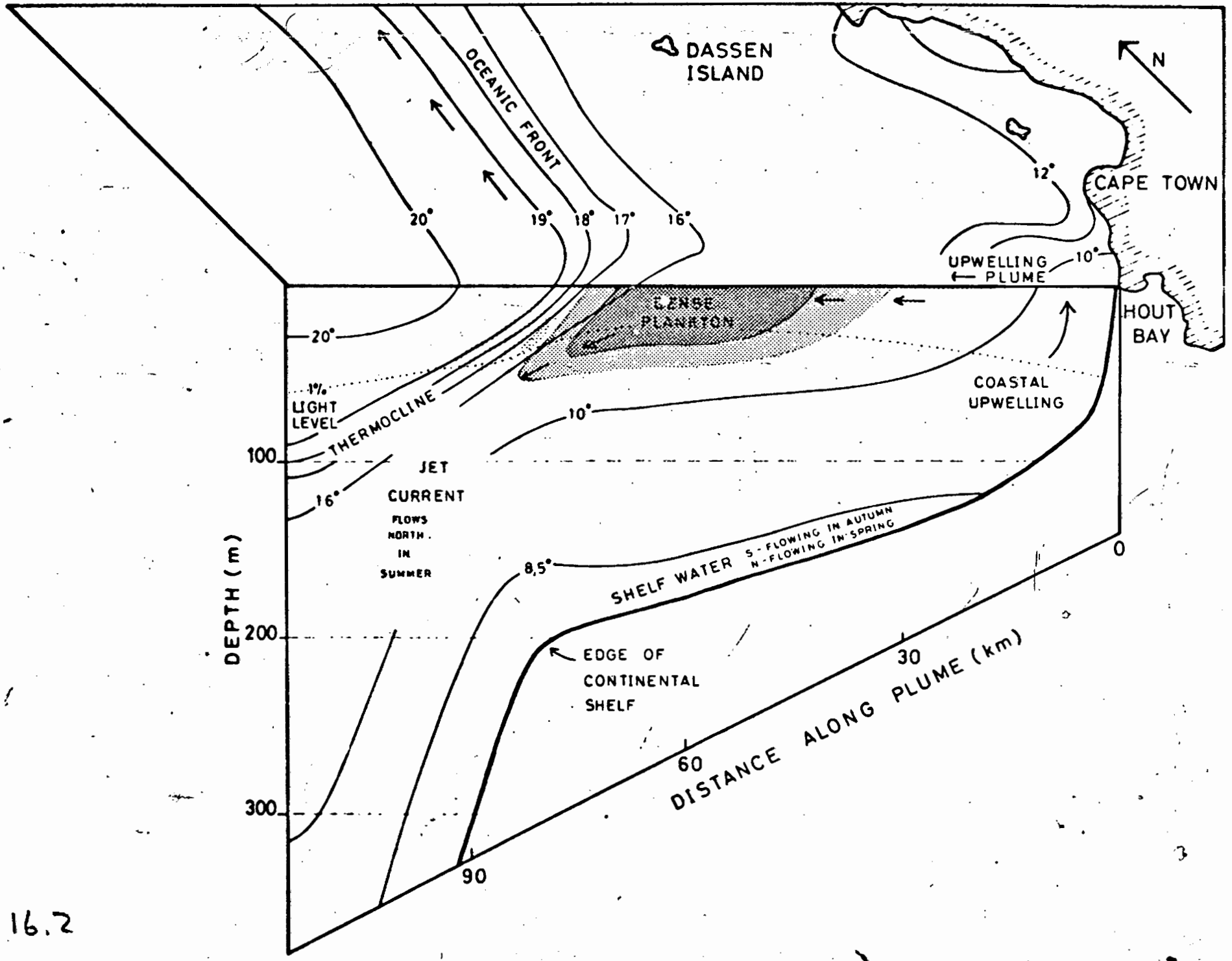
DASSEN ISLAND
N
OCEANIC FRONT
20°
19°
18°
17°
16°
12°
CAPE TOWN
UPWELLING PLUME
10°
HOUT BAY
DENSE PLANKTON
20°
1% LIGHT LEVEL
THERMOCLINE
10°
COASTAL UPWELLING
100
16°
JET CURRENT FLOWS NORTH IN SUMMER
8,5°
SHELF WATER S-FLOWING IN AUTUMN N-FLOWING IN SPRING
0
DEPTH (m)
200
EDGE OF CONTINENTAL SHELF
30
60
DISTANCE ALONG PLUME (km)
300
90

Fig 16.2

which encouraged us in our attempt. A diagram showing a section along the plume incorporating our ideas is given in Fig 16.2. Upwelling occurs maximally a few kilometers from the coast bringing large volumes of nutrient-rich Central Water into the photic zone. Surface waters are transported offshore in a semi-permanent (in the summer) upwelling plume. Some of these waters sink below the thermocline (Chaper 6) whilst others join the body of the sluggish Benguela Current. On the shelf lies a separate water type whose origin varies seasonally. The numbers that we have triend to attach to this picture we feel have credibility. Upwelling rates of 30 m/day are as high as any reported but this upwelling site would seem to be particularly active. The graph of wind vs upwelling (Fig 11.4) should be useful in future research.

Maximum upwelling coincides with the maximum amount of light and it might be expected that this would contribute to the already good conditions for biological growth provided by the upwelling of nutrient-rich water and result in very high levels of productivity. Our method of estimating primary production did not allow for accurate extrapolation to <u>in situ</u> rates of production, yet we were able to demonstrate that very high growth rates are possible in this area, and the incubator-derived results showed a close relation with the <u>in situ</u> oxygen and chlorophyll <u>a</u> levels (Fig 10.9). The large quantities of chlorophyll <u>a</u> between the 1% light level and the bottom of the surface mixed layer indicates wither that the phytoplankton are adapted to low light

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levels or there is continual rapid mixing of the upper layers during periods of strong winds with the phytoplankton alternating between low and high light intensities.

Maximum levels of primary production found off the Cape Peninsula are considerably higher than those reported for other upwelling areas. However, this paper is the first reported seasonal study of production in such an area and Hobson's (1971) reported range (n = 8) of 0.61 - 3.3 g C m^{-2} day^{-1} for May 1968 off South West Africa and the University of Washington's reported range (n = 10) of 1.1 - 9.2 g C m^{-2} day^{-1} for April 1969 off Peru (taken from Hobson, Menzel and Barber, 1973) are not significantly lower than our range (n = 6) for April and May of 1971 and 1972 of 1.4 - 6.6 g C m^{-2} day^{-1}. The figures are not directly comparable for several reasons: the South West African and Peruvian results are based on C_{14} measurements, equivalent to net production, whilst our results are based on measurements of oxygen evolution, equivalent to gross production; the South West African and Peruvian results were obtained closer to the peak of the upwelling season and at lower latitudes than were our results.

Our estimate of the annual production of 3.7 kg C m^{-2} is perhaps more realistic for upwelling areas than previous lower estimates which have not been based on seasonal data. Production at 3.7 kg C m^{-2} per annum is equivalent to a mean turnover rate of the estimated mean phytoplankton standing stock of 11.2 g C m^{-2} of about once per day (11.2 x 365 x 1 = 4.1 kg C m^{-2} p.a.)

It would appear that considerable quantities of zooplankton are lost to the near coastal zone off the Cape Peninsula during

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active upwelling conditions as they are entrained into the body of cool, low salinity water which moves northward and offshore. As little biological material appears to be brought into the area from the south or west replenishment of the zooplankton must also come from the north. Duncan and Nell (1969), from surface drift card recoveries, report on the existence of a counter current close inshore on the west coast between Cape Town and Saldanha Bay. Lessened wind stress in the lee of the mountain massif of the Cape Peninsula and the fluid flow past the peninsula could encourage the formation of such a counter current inshore of the main plume. When upwelling ceases, surface waters return rapidly towards the coast and may transport zooplankton back into the area.

The extreme variability of the physical environment may play an important role in limiting the development of large zooplankton stocks in the area, although maximum standing stock values reported here are as high as those observed in other upwelling regions (Beers et al (1971), Herbland et al (1975) Mensah (1975)). Few studies on a seasonal basis have been attempted in other upwelling areas with the notable exception of the California Current region, (Isaacs, Fleminger and Miller (1969), Smith 1971), Isaacs, Fleminger and Miller (1971), Fleminger, Isaacs and Wyllie 1974)) so the consistency of high zooplankton standing stocks cannot be compared with results elsewhere.

The transport of zooplankton offshore and northwards does mean that zooplankton enters the zone of high phytoplankton

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abundance within a few days, while if the population had to migrate into the area and gradually build up by growth and reproduction it would probably take a matter of 20 or 30 days, by which time the phytoplankton bloom after upwelling could well have been dispersed. Thus the concentration of zooplankton in the upper layers is likely to be an adaptation to the rapid, erratic movements of water in the area.

The gradual increase in zooplankton during the spring and early summer shown in the smoothed curve fig 15.4 appears to be the response of the zooplankton to the increasing quantity of mixed, productive water in the area.

There are several indications that the zooplankton population does not materially influence the phytoplankton stocks in the vicinity of the Cape Peninsula. Not only is the zooplankton standing stock a relatively minor fraction of the phytoplankton crop and the daily production, but nitrate appears to be limiting the phytoplankton production, indicating that excreted forms of nitrogen, such as ammonia, are insufficient to meet the demand. Sinking beneath the euphotic zone and transport out of the area probably account for most of the phytoplankton mortality during the peak upwelling period.

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