STUDIES ON THE PHYTOPLANKTON OF THE FIRTH OF CLYDE

A thesis submitted to the University of Glasgow
for the degree of Doctor of Philosophy
in the Faculty of Science

by

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CHAPTER 1

CHAPTER 1

INTRODUCTION

Scientific investigations have been carried out in the Clyde Sea area since the late nineteenth century, most of it from the Marine Biological Station at Millport. Much of the early work was undertaken by H. R. Mill (1889) who carried out a comprehensive physical survey of the area. He replaced the loosely applied term "Firth and Lochs of Clyde" with the name by which this area is now better known, "the Clyde Sea area". This region lies between latitudes $55^{\circ}5'$ to $56^{\circ}17'$ North and longitudes $4^{\circ}30'$ to $5^{\circ}40'$ West and has a surface area of about 1136 sq. miles (2942.24 Km^2).

The Clyde Sea area is in communication with the Atlantic via the narrow north channel, some 10 miles wide, which runs between the Mull of Kintyre and Tor Point (Northern Ireland). The western boundary of this basin is formed by the long, narrow peninsula of Kintyre, separating it from the Atlantic. The limit of this area was stated by Mill as being the line from the Mull of Kintyre to Galloway, below which the area adjoins the Irish Sea. Topographically, the area is divided into a submarine plateau, deep channels and basins, whereas geologically the Clyde Sea area belongs to two distinct regions, being separated by the Great Fault.

Across the mouth of the area lies the Great Plateau which has an average depth of 24 fathoms (43.89 m). Northwards lies the Arran basin with the Isle of Arran to the west. This basin has an average depth of 34 fathoms (62 m) and reaches 107 fathoms (195.7 m) at its deepest point. To the northwest the deep inlet of Loch Fyne stretches into Argyll, while directly to the north of this basin lie the Islands of Bute and Cumbrae which split-up the channel into narrow sounds. These are continued northwards in a remarkable series of deep fjordic inlets

which cut deep into the Cowal Peninsula. This region of islands and sea lochs is referred to as the "Firth of Clyde" and is generally less than 20 fathoms (36.5 m) deep. The Firth is joined in the east by the shallow estuary of the Clyde, the only large river entering the area with the exception of the River Leven. The estuary, which has an average depth of 5 fathoms (9 m), extends inland from a line joining Gourock to Cloch Point.

Tidal conditions and general hydrography of the area have been discussed by Mill (1901), Barnes & Goodley (1961), Allen (1966) and Collar (1971). In comparison with other estuaries the tidal ranges are relatively small. According to Allen (1966) they are largely semi-diurnal although a diurnal influence of up to ten percent of the range may be apparent at times. At Cumbrae the mean Spring range is 9.6 feet (2.92 m) and the neap range is 5.8 feet (1.76 m). This becomes amplified as it passes up the Firth reaching a Spring range of 13.5 feet (4.11 m) in Glasgow. Mill (1889) showed that within the Clyde Sea area, excluding the plateau and estuary, the delay of high water from the outer to the inner Firth is only 17 minutes.

Mill (1901) stated that tidal currents are, as a rule, not very rapid in the wider channels, with current strength being greatest in the north channel where the water becomes thoroughly mixed with each ebb and flow. It has been suggested that the Spring maximum rate in the Arran Basin is three knots, and that generally the ebb stream is opposite the flood and of equal velocity and duration.

Barnes and Goodley (1961) gave a revised picture of tidal movements and showed that the currents in the wide outer Firth are weaker than suggested by Mill. Even in channels currents were generally weak except if increased by local topography. The Spring rate for the main tidal streams were given as 1.5 to 2.0 knots. The ingoing streams of the main Firth divide and run through the channels east and west of the

Cumbraes with respective tidal velocities of 2 and 1.5 knots.

Mill (1901) noted that currents were increased or decreased to a marked degree according to the direction and strength of the wind. This superimposition of non-tidal movement on tidal streams has received more attention recently by Dooley & Steele (1969). They found that the surface inshore wind driven currents near a coast moved at up to 1.6% of the wind speed and responded rapidly to changes in wind direction. However, offshore water movement was found to be more complex with the flow being part of the large-scale wind-induced circulation of the inner Firth. Johnston et al. (1971) found that tidal currents off the Ayrshire coast were very small and that any transport was a consequence of residual flow. This flow was in the direction of the prevailing wind.

More recent data from Steele et al. (1973) show that the estuarine circulation is barely detectable from current measurements. The estuarine inflow was detected along the eastern shores of the Firth where the water appears to originate from the Irish Sea. Except in this narrow strip the salinity of the surface water is relatively low and constant over the whole Firth to the estuary. The upper water flows southwards above the depth of the strong pycnocline at 15 m, with the amount of fresh water in this layer rarely exceeding 2%.

No published data appear to be available for the circulatory pattern in the Fairlie Channel. However, from private communications and personal observation, it seems probable that there is an anti-clockwise circulation of (surface) water within the Channel. This results in a continued southward flow of the water at Keppel Pier throughout the tidal cycle, with the exception of one hour, around low tide, when the direction changes to northward.

The climatology of the area has been reviewed by Mill (1889) and Barnes (1955). The latter author showed that the temperature trends are typical of the north temperate zone and the rainfall is typical

of a wet oceanic climate.

The air temperature measured at the Marine Station, Millport (Barnes, 1955) showed an annual maximum monthly mean of 14.1°C in July while the coldest month, 4.3°C, is February. The rainfall in the area is not excessive, being around 45 inches (1143 mm) per year, less than normal for Scotland, and only slightly more than the mean for the U.K. Generally December is the wettest month with 5.42 inches (137.6 mm) and the driest is May with only 1.82 inches (46.2 mm). The prevailing winds in this area are usually from the south-west quadrant, except for March and May when north-easterlies predominate. The difference in the mean hourly wind speeds is only 5 knots between the windiest month, October (13.22 knots), and the calmest month, June.

The entire sea area includes 1136 square miles with land drainage from 3350 square miles (Mill, 1889). The greatest single drainage area is that of the River Clyde, 1140 square miles, not including the estuary itself, while the Leven drains from the Loch Lomond catchment area of 295 square miles. The relative sizes of the two catchment areas is balanced by the much higher average rainfall in the Leven drainage area. In fact, the Leven provides the major fresh water inflow during dry weather and normal flow conditions (Collar, 1971).

Barnes & Goodley (1958) showed that the land rainfall was higher than that at sea with 55.24 inches (1403 mm) per year, supplying 1.162×10^{10} cubic metres. The islands have a rainfall of 47.87 inches (1215.8 mm) supplying 0.07×10^{10} cubic metres, whereas the sea and loch surface receive 42.74 inches (1085.6 mm) supplying 0.387×10^{10} cubic metres per annum. When the annual loss by evaporation has been taken into account (14") it is found that two cubic miles of fresh water enter the Firth of Clyde each year, or 8.4% of the total volume. A similar annual exchange of water must take place to preserve the balance.

Mill (1889) carried out a considerable amount of his work on the

salinity of the Clyde Sea area generally taking samples at the surface and bottom. The highest mean salinity was found in the north channel, 34.2‰ falling to around 33‰ at the Cumbraes. Within narrow channels the salinity of surface waters was apt to be lowered by spells of wet weather or even heavy rain, however, this 'freshening' was not found at any depth. Barnes (1955) calculated the mean (surface) salinity of the outer Firth as 32 to 33‰ falling as low as 27‰ to the east of Cumbrae and 7‰ to the west, during periods of high fresh water runoff. Depressions of up to 5‰ are usual in coastal waters.

Both Mill (1889) and Barnes (1955) showed the clear reduction in surface (and bottom) salinity in the Clyde Sea area during winter months reaching a minimum of 31.26‰ (at Millport) in January. A maximum, 32.98‰, was recorded by Barnes in June while Mill found a surface maximum between July and September. Both authors correlated this change with the pattern of seasonal rainfall changes. Mill stated that a change in rainfall takes two months to produce its full effect on salinity while Barnes showed a delay of one month.

Tidal variations in the salinity at Millport were reported by Barnes (1955) who grouped the salinity data into twelve, hourly intervals from high tide and calculated the daily anomalies. A distinct oscillation, with the maximum salinity at high tide, was found. This tidal effect is less regular than might be expected. This is related to tidal currents (at Keppel Pier) with a possible reverse eddy.

Except in the estuary, where stratified layers of fresh water on top of salt water often occur (Allen, 1966) temperature and salinity usually vary only gradually. Consequently the Firth of Clyde is not a typical estuary, but may be regarded in many respects as a shallow sea (Johnston et al., 1971). Mill (1889) attributed the small differences in vertical distribution of salinities to mixing processes. He also made the distinction that fresh water was lost by mixing in each tidal

outflow and not by the flowing out of a fresh water layer. Within the estuary Mill found an average of 50% sea water by volume whereas throughout the Clyde Sea area the percentage never fell below 90%.

The net annual income of 2 cubic miles of fresh water into the Clyde Sea area has to be balanced by a considerably greater exchange of water with the open sea (Barnes & Goodley, 1958). Steele et al., (1973) from a consideration of current strengths and temperature-salinity profiles gave the period of renewal of water in the Firth of Clyde as up to four weeks. However, the retention time of the main basin may be reduced to a number of days at periods when wind-driven currents predominate. These currents may reach 0.5 knots throughout the water column; rapid changes in salinity at such times indicate coupling with water of the north channel.

Mill (1901) demonstrated the influence of the intrusion of warm oceanic water on the annual sea temperatures in the area. Between 1886 and 1888 the mean air temperature was 8.3°C while the mean temperature of the upper 5 fathoms was 9.4°C. On a seasonal basis the sea is at its warmest in August, when the monthly mean is 13.72°C. The coldest month is February when the mean temperature is 6.96°C. In Summer a delay of a month between water and air temperature changes was apparent.

The presence of a well-developed thermocline in the outer Firth during the Summer has been suggested by Barnes (1955) and in the Clyde River Purification Board annual report for 1972. The only published profiles are those of Mill (1901) who investigated the thermal conditions throughout the Clyde Sea area. The north channel remained isothermal throughout the year whereas the Arran Basin remained completely mixed till the period of maximum surface temperatures. Even at this time no distinct thermocline occurred, but a constant gradient of temperature from 12.2°C at the surface to 8.3°C at 110 metres was evident. Strong winds cause complete circulation of the water column at the Autumn equinox. The presence of a vertical temperature discontinuity was

only demonstrated in Loch Goil and Loch Fyne although Mill suggested that other deep lochs would have a similar thermal regime.

The first investigation of the chemical nature of the water mass within the Clyde Sea area was made by Mill (1889). However, this was confined to the study of sulphates and carbonates which were found to achieve a higher proportion in waters of lowered salinity. It was not until 1926 that the first annual survey of some chemical factors was carried out by Marshall & Orr (1927). They showed the seasonal changes in dissolved phosphate, pH and the percentage saturation of oxygen in Loch Striven, a deep fjordic sea loch. Phosphate reached a winter maximum of 0.75 µg at P/l at the surface in November and fell to undetectable levels in May and September. During the Spring phytoplankton increase the phosphate content of the water fell from 0.68 to 0.22 µg at P/l at the surface, while little change was evident at the bottom. The regeneration of phosphate in deep waters was shown to occur during late summer and autumn. Oxygen saturation reached its highest values of more than 135% at the surface in April and August while at the bottom a minimum of 30% was recorded during Autumn. The pH varied within fairly close limits and never exceeded 8.45 or fell below 7.75, with the lowest values in the winter.

The phosphate and nitrogen contents of the muds of the Clyde Sea area was studied by Moore (1930). The top 10 cm of the mud was generally very soft with phosphate values of up to 0.224% by weight. Deeper down, the mud became more clayey and the phosphate content fell to around 0.178%. Generally in the strongest tidal streams, the sediments possessed a lower phosphate and nitrogen content.

Following this early work on the chemistry of the Clyde little attention was given to such studies. Nevertheless within the last five years the emphasis on water pollution has given new impetus to this type of research. However, in the Clyde most of this work has been

confined to the more grossly polluted stretches of water within the estuary with little attention being given to the Clyde Sea area itself. The published data which are available generally stem from short-term studies and no seasonal surveys have been undertaken.

The Clyde estuary received the drainage from a heavily industrialized region with a population of 2.4 million people, consequently the most harmful type of pollution in this area is domestic sewage and certain industrial effluents (Clyde Estuary Study Group 1971 Report). Steele et al. (1973) showed that the daily input of soluble nitrogen compounds into the upper estuary is up to 30 tons per day. Evidently the major portion of this is ammonia which reaches up to 4 mg N/l at Glasgow Bridge (C.R.P.B. annual report 1972). In the inner Firth and around the Cumbraes little evidenceof pollution was evident. Generally in the Firth of Clyde the background winter nitrate level is 25% higher than that of the North Sea. This is due both to nutrient addition from the Clyde and the Irish Sea (Steele et al., 1973). The time taken for pollution to reach any part of the estuary will depend on the fresh water input and the tidal range. At neap tides the retention time of the estuary is less.

The nitrate enrichment of the region of the Firth in the vicinity of Irvine Bay, which may be up to 15 tons per day, was studied by Johnston et al. (1971) for a short period during April. The lowest nitrate values were found along the eastern coastline of Kintyre (5-9 µg at N/l), while in the upper Firth levels were markedly higher to the west of Cumbrae (12-14) than to the east (10.5-12 µg at N/l). Within Irvine Bay itself localized nitrate values exceeding 30 µg at N/l were found on occasions.

Considerable attention has been given recently to the problem of the distribution of toxic trace metals within the Firth of Clyde (Mackay et al., 1972; Halcrow et al., 1973; C.R.P.B. annual reports, 1970, 1972). The relatively high concentrations of Copper, Zinc, Cadmium and Mercury

found in tidal waters may reflect industrial contamination from the upper estuary, together with localized contamination due to sludge-dumping. This practice of dumping sewage sludge in the Firth in the vicinity of Garroch Head has continued for the last 70 years with a current addition of 1 million tons per year. However, the effects of this process are very localized with high concentrations of toxic metals being confined to within 2 km of the centre of the dumping area. An accumulation of organic carbon occurred here reaching 3to 8% compared with background values of 0.3 to 2.2%.

The credit for much of the work on phytoplankton in the Clyde must go to Drs. Marshall and Orr who carried out extensive quantitative surveys during the 1920's, particularly in Loch Striven. The first seasonal survey of phytoplankton was made by Marshall (1924) who studied the gut contents of Calanus over a 12 month period and related them to changes in the algal population. During the spring, Skeletonema predominated in the gut contents reflecting its predominance in the phytoplankton of the spring outburst although small quantities of Thalassiosira were also present. Skeletonema was replaced by Thalassiosira as the dominating organism in May and June with small amounts of Fragilaria and Naviculids. In July and August Chaetoceros spp. and Rhizoselenia were dominant. The large numbers of Peridinium present in the water during summer months were reflected in the gut contents whereas Ceratium which was also present was not eaten. Both Skeletonema and Thalassiosira predominated in the autumn phytoplankton while only Thalassiosira was found during the winter together with Bidulphia and Coscinodiscus. Secondary pulses of coccolithophores occurred during the summer and silicoflagellates in September.

From 1924 to 1928 Marshall & Orr (1927, 1928 & 1930) studied the phytoplankton of Loch Striven and other stations in the Clyde Sea area. In general stations were sampled weekly, although the spring diatom

outburst in Loch Striven was studied at a shorter time interval during 1927 and 1928. The pattern of seasonal succession of phytoplankton has only been published for Loch Striven on the basis of the weekly samples taken in 1926.

The earliest and largest increase of the year came in Spring when Skeletonema costatum completely dominated the population, as it did in most years in the Clyde. The greatest abundance was recorded at the beginning of April when numbers rose to 16 million cells per litre. Other diatoms were present but in very small numbers. A second small wave of Skeletonema occurred at the beginning of May followed by a larger wave of 4.5 million cells per litre. At the end of the month, the maximum of Thalassiosira (500,000) was recorded. During June Chaetoceros became dominant reaching a peak of around 1.2 million cells/l at the beginning of the month. A further wave of diatoms - Ceratulina, Skeletonema and Chaetoceros - occurred at the end of June. A pulse of Nitzschia seriata at the end of July was followed by Leptocylindricus at the beginning of August. At this time the surface sample was pure Leptocylindricus, while at 20 m only Nitzschia was observed, at 10 m a mixture was present. As these algae disappeared, Eucampia became predominant and it appears that as one plant sinks another one takes its place as the surface. A small peak of Rhizoselenia came at the start of October with a subsequent peak of Skeletonema at the beginning of November. Dinoflagellates displayed sporadic increases between April and October reaching a maximum of 40,000 cells/l at the surface.

Marshall & Orr discussed the relationship between phytoplankton and the chemical changes in the sea water. During the spring diatom increase the fall in phosphate was accompanied by a distinct lowering of silicate although no data were given. The conclusion was drawn that "it is extremely improbable that silicates are of importance as limiting factors in Loch Striven". Another nutrient which was measured but not

represented, nitrate, showed little change during the period of diatom increase. Marshall & Orr concluded that "it is obvious that there is a very close connection between the number of diatoms present and the changes in the sea water". Hunter (1970) from a reconsideration of these data suggests that the disappearance of diatoms during the Spring was due to phosphate limitation, at a concentration of around 0.12 µg at P/l, below which Skeletonema will not divide.

The timing, composition and magnitude of the Spring diatom increase in successive years were compared by Marshall & Orr (1930). They showed the general predominance of Skeletonema in the Firth of Clyde and the similarity in the time at which the increase occurs each year, generally being within a week of 20th March. Hunter (1970) considered that this was due to a threshhold being reached in the total available light energy. The original authors stated that only a comparatively constant external factor could account for the narrow time limits within which the increase took place. The actual date was dependant both on daylength, brightness and the vertical stability of the water column. Under these conditions the compensation depth increased, to around 7 m, and as soon as mixing stopped numbers increased rapidly at the surface and then spread downwards.

The spring increase in 1924 and 1925 at Keppel reached a peak of around 3.5 million cells per litre while in 1926 a total of 6 million cells/l were recorded. In 1924 and 1925 the increase was composed of Skeletonema and Thalassiosira. From 1925 to 1929 the increase began around 20th March although it was earlier in 1927. In 1924 a rise in numbers was not observed till the beginning of April. The usual delay between the first appearance of diatoms and the peak appears to be around 10 days. In Loch Striven the magnitude of the increase was always greater; in 1926 the peak was 16 million cells/l, rising to 30 million in 1927 then falling to 26 million in 1928. As at Keppel the increase was much earlier in 1927 than in the other two years. In all three years the

population was almost completely composed of Skeletonema and in 1928 the population was described as a "pure culture" of Skeletonema. Further visits to Loch Striven in 1932 and 1933 (Marshall, Nicholls & Orr, 1934) show reduced spring populations. In 1932 no spring diatom increase was observed (although it may have been missed due to irregular sampling) while in 1933 a relatively small peak of 8.5 million cells/l was found. These years were regarded as relatively poor in diatom growth although flagellates were common.

It is clear from this period of intensive study in the Clyde that there is a considerable difference in phytoplankton production at the same location in successive years and between stations in the same year. Unfortunately no clarification of this phenomena was made. Following this period no data are available till 1944, thereafter only qualitative observations on the contents of two-nettings have been recorded. Skeletonema featured prominently throughout.

Pyefinch (1948) noted 'heavy hauls' of Skeletonema during the middle of March in 1944 and 1945 whereas in 1946 and 1947 hauls persisted well into April with a peak at the end of March (Barnes, 1956). In Loch Striven in 1947 (S.M.B.A. annual report, 1948) the diatom increase began in early March but was interrupted by vertical mixing, which delayed the peak till the beginning of April. The recorded reduction in phosphate and nitrate was apparently insufficient to account for the cessation of diatom growth in the middle of April although no data were given. In 1948 the greatest abundance of Skeletonema was found on 11th March (Pyefinch, 1949) while in 1949 the increase lasted from 20th to 31st March with a peak around the 25th (Barnes, 1956). The population was entirely Skeletonema.

The peculiarity of the pattern in 1951 was noted by Marshall & Orr (1952) and Barnes (1956). The expected spring diatom increase did not take place, instead during March there was a much smaller increase

in the numbers of Chaetoceros and Coscinodiscus. A second pulse of Chaetoceros occurred in mid-April while the increase in Skeletonema was delayed till mid-May. In 1952 the increase came in two waves, a small increase of Skeletonema in mid-March and a larger increase in mid-April (Barnes, 1956). In 1954 and 1956 the increase was towards the end of March while in 1957 it came at the beginning of March (Edwards, 1958). 1958 was quite different with the early predominance of a Coscinodiscus species, Skeletonema not being common till mid-April. Thalassiosira and Chaetoceros persisted in large numbers till May.

Marshall & Orr (1962) again recorded the spring plankton increase in Loch Striven in 1960 and 1961. In the former year the increase came in two waves in mid-March and mid-April and consisted mainly of Skeletonema. The maximum abundance in the following year was higher (14.6 million) and occurred earlier but was of similar composition. The first measurements of chlorophyll a in the Clyde were made by Butler et al. (1970) who showed that chlorophyll a reached peaks in early April, in mid-May and in early September (1968) with a maximum abundance of 1.2 µg/l in May. In 1969 Butler recorded the spring outburst of phytoplankton which reached 12.5 million cells/litre, with a corresponding peak of 0.6 µg/l on 5th April. The spring population in this year had the unique feature of being dominated by Thalassiosira with Skeletonema much less numerous. He attributed this phenomenon to the low water temperature (5.5°C on March 18th) which favoured Thalassiosira.

To summarize these data it is clear that in almost all years a spring diatom increase takes place in the Clyde. There is a general predominance of Skeletonema with varying amounts of Thalassiosira. Only in a single year was Thalassiosira recorded as being dominant whereas in the years in which the increase failed other species, notably Coscinadiscus and Chaetoceros, have appeared. The increase often appeared very suddenly and declined again just as rapidly, with a total span of

around two weeks. In some instances the increase commences but is then reduced by adverse conditions, followed by the main pulse. The magnitude of the pulse in Loch Striven varies from less than 8 million to 30 million cells/l, whereas at Keppel numbers range from 3.5 to 12 million cells/l. The spring pulse is generally apparent during the second half of March or early April.

Apart from the vernal rise in diatom numbers the summer and autumn phytoplankton have received little attention. However, it is known that dinoflagellates, particularly Peridinium and Ceratium are common during the summer, although they seldom achieve dominance in temperate waters (Tett, 1971). According to Hunter (1970) an autumn increase often occurs with Skeletonema being the principal component. This follows the complete circulation of the water mass and nutrient replenishment from deep waters by vertical mixing.

Recent work by Johnston et al. (1971) from a single three day survey of the Firth of Clyde carried out in April, 1970 established chlorophyll a levels of 0.6 to 1.11 µg/l at the beginning of the month. The carbon^{14} productivity was around 1 mg C^{14} per cubic metre per hour at 6.0°C. This gives a chlorophyll to carbon ratio of 2.08 to 2.14.

The seasonal variation of phytoplankton and the annual cycle of nutrients in the Clyde Sea area have been given little attention in comparison with studies on animals or macrophytic plants. The only detailed work on this aspect of the biology of the Clyde has been confined to a partially enclosed sea loch, Loch Striven, in the upper Firth. Here, the seasonal succession of phytoplankton was studied on a weekly basis for a single year (1926) and the Spring increase in diatoms was studied in relation to changes in phosphate levels. Most other surveys which have been carried out have been fairly brief (less than three months) and have been restricted to the Spring period. In general, there appears to be a fairly poor documentation of the quantitative

seasonal succession of phytoplankton in British coastal waters.

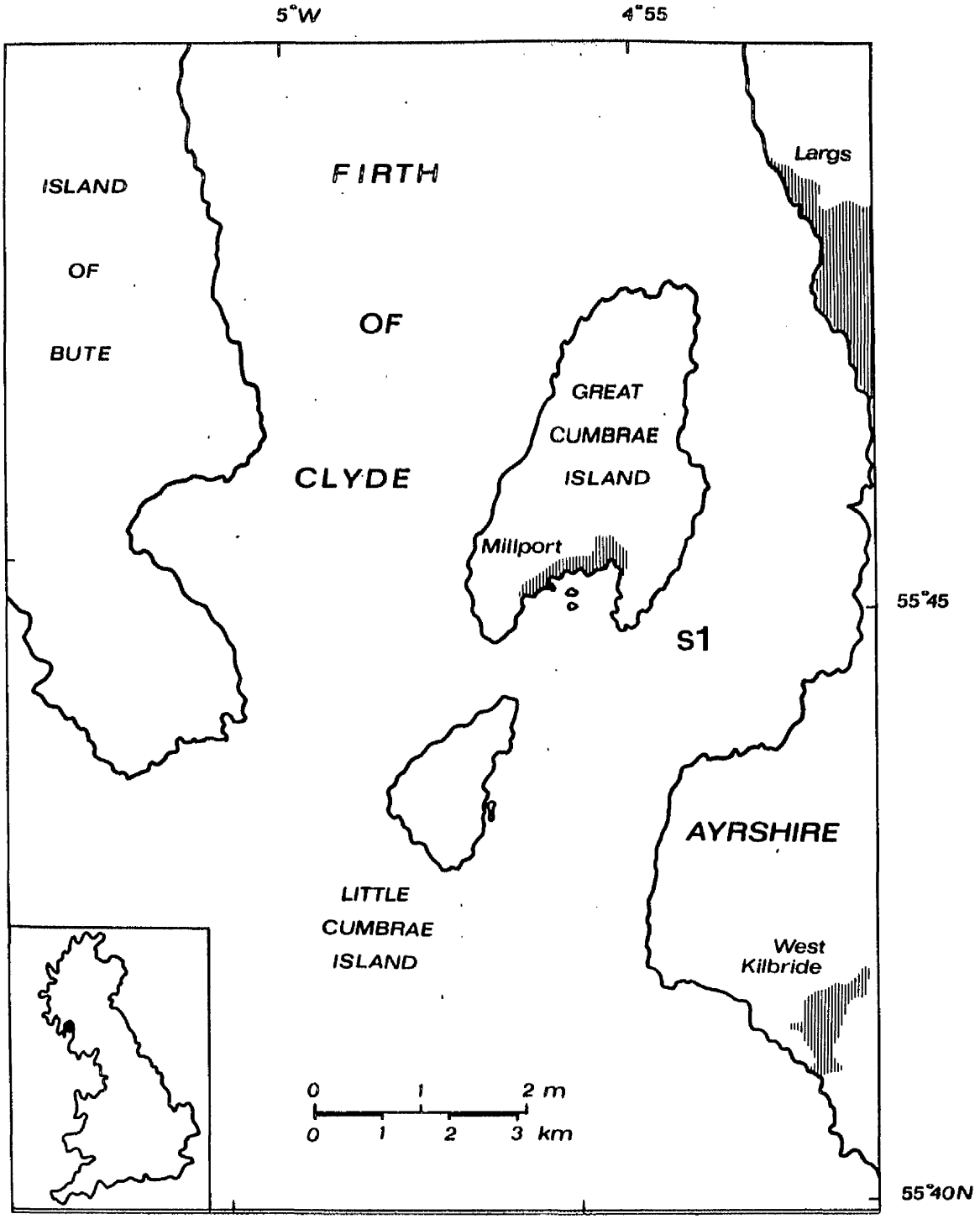
The present investigation is the first, in this area, to combine three different methods of assessing the phytoplankton standing crop; from direct enumeration, chlorophyll estimations and total particle volume, and the first report of the annual cycles of silicate, nitrate and nitrite.

This survey will fill a gap in the background information on the seasonal chemical, physical and biological changes in this area and will provide a baseline for future studies. At present there is no evidence of eutrophication in the outer Firth or the sea lochs (Clyde Estuary Study Group, 1971) although future industrial development will put the region under considerable pressure in years to come. A particular case in point is the proposed future developments on the Hunterston peninsula (opposite the Isle of Cumbrae). This will not only alter the coastline but will also bring the possibility of environmental pollution from the proposed iron-ore, steel and oil developments.

The rapidly changing nature of tidal, coastal waters necessitates a sampling programme with the shortest possible time interval. For this survey samples were generally taken twice daily, providing more detailed information about the variation taking place than for any other coastal waters. The diurnal variation of chemical and environmental factors have been studied for two 24 hour periods (during July and August) with samples being taken at two hourly intervals.

The usual method of sampling surface waters (by bucket) has been replaced by a completely new method. This makes it possible to take integrated samples from the upper 5 cms of the water column from a moving boat. This fills a gap in the methods of sampling surface waters for ecological purposes.

Fig 1

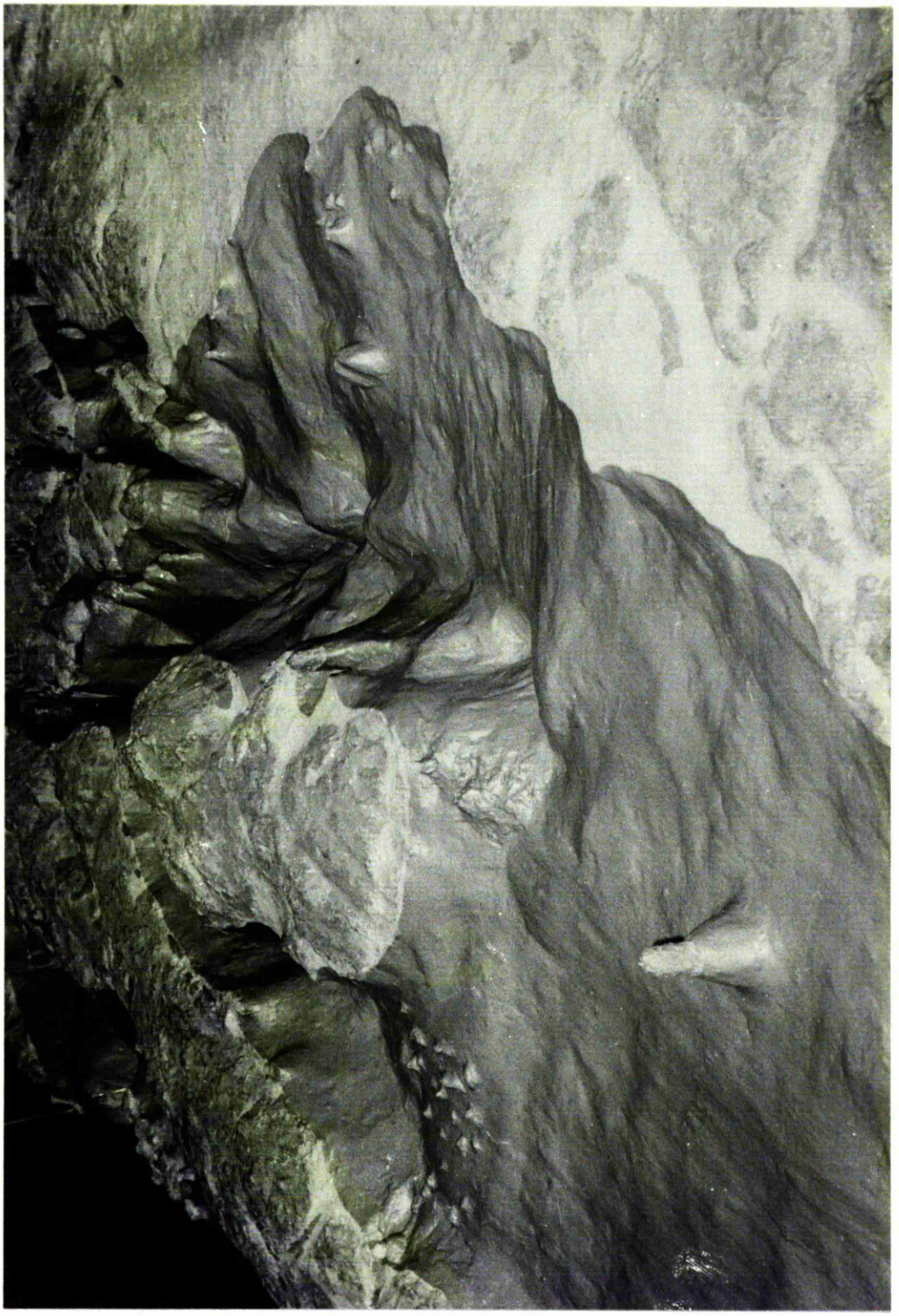

5°W
4°55
ISLAND
OF
BUTE
FIRTH
OF
CLYDE
Largs
GREAT
CUMBRAE
ISLAND
Millport
S1
55°45
AYRSHIRE
LITTLE
CUMBRAE
ISLAND
West
Kilbride
0 1 2 m
0 1 2 3 km
55°40N

Description of the area studied:

Figure 1 shows the geological location of the Isle of Great Cumbrae Latitude 55°57 N, Longitude 4°46 W (West Coast of Scotland). At the south-east corner of this island is situated the Marine Biological Station (at Keppel) at which this study was based. The mainland coast to the east is that of Ayrshire while, to the west the island is bordered by the southern part of the Island of Bute. Southwards from Cumbrae toward more open sea lies the smaller island of Wee Cumbrae. Deep channels run down both sides of the island of Great Cumbrae, the Fairlie Channel to the east being the location from which most samples for this study were taken. This channel has a maximum depth of 19 fathoms (35 m) between Keppel pier and the limit of Hunterston sands (the perch). The width of the deep channel is about 1.4 Km. Depth profiles of salinity, temperature, etc. were taken at the deepest point (S1 on Figure 3). To the south of Cumbrae is the Arran basin: the deepest region (in excess of 80 fathoms) lies south of the most southerly point of Bute (Garroch Head). Samples were taken on occasions throughout the area covered by Figure 1, although the majority of sampling was confined to a detailed study of the Fairlie Channel.

Samples were regularly taken from Loch Long and Gareloch. Loch Long is a long narrow loch with a maximum depth of 35 fathoms opening into the mouth of the Estuary, while Gareloch, which extends from estuary, has shallower sides and a maximum depth of 22 fathoms.

Fig 2



CHAPTER 2

CHAPTER 2

METHODS

1. The determination of orthophosphate phosphorus

Nearly all methods for the determination of phosphate in natural waters are photometric and most are based on the development of the heteropoly blue formed after reduction of 12 molybdophosphoric acid which forms under well-defined acid conditions. Combined forms of phosphate do not react with the molybdenum (Olsen, 1966), these include both dissolved and particulate, organically combined phosphorus and condensed phosphates (such as detergent polyphosphates). Thus the normal analysis measures only inorganic orthophosphate phosphorus.

In waters containing very high levels of phosphate, the yellow colour of the molybdophosphoric acid may be read directly although it is normally reduced to the intensely coloured heteropoly blue compound. Reduction is carried out in the aqueous phase with either stannous chloride or ascorbic acid as the usual reductants (Burton, 1973). Stannous chloride has the disadvantage of being rapidly oxidised in air and the final colour development is very temperature and salinity dependant (Martin, 1972). Ascorbic acid as a reducing agent suffers from none of these drawbacks and is now used in 90% of marine analyses (Burton, 1973). The procedure of Murphy & Riley (1962) has now become the standard method for sea water analysis (Olsen, 1966) and involves treating the sample with a single reagent consisting of: acidified molybdate, ascorbic acid and antimony. The acidity is chosen to allow the conversion of phosphate in the presence of a large excess of silicate (Murphy & Riley, 1958), while the antimony is added to reduce the time of colour formation (Murphy & Riley, 1962). The method used in the present study is that described by Strickland & Parsons (1968) which is based on the method of Murphy & Riley with the acid and molybdate concentrations recommended

by Stephens (1963).

This procedure has no interference with silicate up to 10 p.p.m. and has a salt error of less than 1%. The final colour is stable for 24 hours and its development is temperature independent between 15 and 30°C; the use of a single reagent solution also recommends it. The accuracy is 1% at a concentration of 20 µg P/l (0.64 µg at /l) and the minimum limit of detection is 1 µg P/l (0.03 µg at /l) (Olsen, 1966).

Immediately after collection, samples were filtered through a 25µ nylon mesh to remove zooplankton and particulate matter and then frozen (to -20°C) within an hour. Freezing is a commonly used method for preserving samples and seems satisfactory under most circumstances provided that it is done rapidly after collection (Strickland & Parsons, 1968). Chloroform preservative was not included since it may cause the release of up to 25% of phosphate from zooplankton (Burton, 1973).

Analyses were made immediately after thawing and warming samples to room remperature, with duplicate 100 ml aliquots of each sample being analysed. The widely used phosphate standard, Potassium dihydrogen phosphate was used during this study at a concentration of 3 µg at P/l. The final colour development was measured for samples (in duplicate), standards (in triplicate), and blanks of distilled water (in duplicate) on an SP600 spectrophotometer at 885 mµ. A new calibration factor was determined for each set of analyses, generally around 13 for a 4 cm glass cell.

2. The determination of orthosilicate silicon

Silicon appears to be present in natural waters in three main forms; orthosilicate in true solution, colloidal silicate and seston ic material such as clay particles and organisms (Hutchinson, 1957). Martin (1972a) considers that at the normal pH of sea water the dissolved form is largely undissociated orthosilicic acid (H_4SiO_4) and only 5% exists as ions.

The method for the determination of silicate depends on the reaction of orthosilicic acid with molybdate, producing a silico-molybdate complex which is yellow in colour (Martin, 1972a). Lund (1965) considers that the orthosilicate which is estimated by the standard molybdate method is available to diatoms while the more highly polymerized forms (colloidal silica) are not. This view is supported by Strickland & Parsons (1968) who state that the "reactive silicate" measured by this method probably gives a meaningful measure of the amount of silicon available to plant cells.

The commonly used colorimetric methods for silicate determination are based on that of Dienert & Wandenbulcke (1923); this involves the reaction of molybdate at pH 1.2 with silicate (and any phosphate present) to give heteropoly acids. The addition of oxalic acid is necessary to destroy any molybdophosphoric acid formed. The intensity of the yellow colour produced is proportional to the concentration of silicate, and although A.P.H.A. (1965) suggests that a part may be unreactive, Burton & Leatherland (1970) found no unreactive silicate, even in samples with a high concentration of this nutrient. The yellow colour may be read directly if the silicate content of the water is high (more than 50 µg at Si/l) but is usually reduced in a second step to the intensely coloured heteropoly blue compound (Martin, 1972a).

The usual reductants are stannous chloride or metol-sulphite, of which the former gives slightly higher sensitivity but suffers from temperature and salinity dependence and lack of stability (Strickland

& Parsons, 1968). Consequently metol-sulphite is now commonly used giving full colour development in one hour when silicate is less than 50 µg at Si/l and in three hours for higher concentrations. The salinity error is small (less than 3% between 25‰ to 35‰) and the colour is stable for at least three hours. The method used in the present study is based on the procedure of Mullin & Riley (1955) as described by Strickland & Parsons (1968).

This involves the reaction of duplicate 25 ml aliquots of sample with acidified ammonium molybdate solution followed (after 10 minutes) by the addition of a second solution containing oxalic acid, sulphuric acid and metol-sulphite reductant. The extinction was measured after three hours at 812 mµ in a 4 cm cuvette. As suggested by Strickland & Parsons (1968) Na_2SiF_6 was used as a convenient silicate standard. A concentrated aqueous solution is stable indefinitely and was freshly diluted to 4 µg at Si/l for calibration purposes. For each set of analyses samples and blanks (silicate-free distilled water) were carried through the procedure in duplicate and standards in triplicate (generally the calibration factor was around 23).

Samples for analysis were filtered through a 25µ nylon mesh immediately after collection and then stored in a polythene bottle. Freezing (to -20°C) was carried out within the hour, a procedure which ensures satisfactory preservation for many months (Strickland & Parsons, 1968). For concentrations up to 30 µg at Si/l Burton and Leatherland (1970) found there was no change in the "reactive silicate" content after freezing for two days. The precision of the method at the 10 µg at Si/l level is better than ±2%.

3. The determination of nitrate nitrogen

Early procedures for the determination of nitrate generally relied on the formation of coloured compounds with various reagents, such as Brucine, Stychnidine and Phenoldisulphonic acid (Martin, 1972a). However, the method now recommended by Strickland & Parsons (1968), and used in the present investigation, depends on the reduction of nitrate to nitrite and the subsequent colorimetric determination of nitrite by a diazotization method. This procedure, developed by Wood et al. (1967) involves passing a sample treated with tetrasodium E.D.T.A. through a column of copperized cadmium in which nitrate is quantitatively reduced with an efficiency of 99 ±1%. The possible reaction given by the authors is:-

$$NO_3^- + Cd + EDTA^{4-} + H_2O \longrightarrow NO_2^- + Cd\,EDTA^{2-} + 2OH^-$$

This reaction proceeds under neutral or alkaline conditions. Copper serves as a cathode in the redox couple and the complexing agent tetrasodium EDTA sequesters cadmium to prevent the precipitation of $Cd(OH)_2$ and subsequent loss of efficiency (Martin, 1972a). The method is rapid, accurate and dependable, in the range 0-60 µg at N/l in sea or fresh waters. The salt error and interference from ions is negligible.

A special column is required for this determination, with a 25 cm length of copperized cadmium filings, which have been previously pitted with nitric acid to increase their surface area. The flow rate for the optimum reduction to take place is 6 ml per minute which is controlled by a metering tap. New reducing columns were prepared every three months.

Samples for analysis were treated with EDTA and two 50 ml aliquots passed through the reducing column. The first 20 ml of column effluent was discarded, following which 15 ml of effluent was collected and diluted to 30 ml with distilled water. Blanks consisted of 0.0015 N HCl to which 1 ml EDTA solution had been added, thus bringing the pH to that of sea water. Standard nitrate solutions were made up from a concentrated

standard of potassium nitrate diluted with sea water of low nitrate content. Duplicate blanks and triplicate standards were carried through each set of analyses. The samples were then treated as nitrite samples by the method of Bendschneider & Robinson (1952) and measured in a 1 cm cell at 543 mμ. The calibration factor was generally around 48.

4. The determination of nitrite-nitrogen

Under acid conditions, nitrite ion reacts with an aromatic amine to form a diazo compound which is then coupled with a second aromatic amine to form an azo dye. The intensity of the final red colour is proportional to the amount of nitrite present. A rapid colour development and good sensitivity result from the use of sulphanilamide as the diazotizing agent and N-(1-naphthyl) ethylenedi-amine dihidrochloride as the coupling agent as recommended by Bendschneider & Robinson (1952), described in Strickland & Parsons (1968).

This procedure, used throughout the present investigation, involves the addition of 1 ml sulphanilamide solution to a 50 ml sample aliquot (in duplicate) followed after two to six minutes by 1 ml of naphthylene hydrochloride. The maximum colour is developed after 10 minutes and is stable for two hours, during which time the extinction is measured at 543 mμ in a 4 cm cell. Samples for analysis were frozen immediately after collection which, according to Mackereth (1963) provides adequate preservation. However, Strickland & Parsons (1968) advise against too prolonged storage of frozen samples for this determination. Re-calibration of the method was found to be only necessary when stock solutions were changed.

5. Determination of pH

The pH is the logarithm of the hydrogen ion concentration and can be measured colorimetrically or electrometrically. The colorimetric method suffers from interference from turbidity, salinity and colloidal matter, and is only suitable for rough estimation (APHA, 1965). The electrometric method is considered standard and has a higher precision (Welch, 1952). In the present study a Pye Model 292 pH meter was used, with a glass electrode in combination with the saturated calomel reference electrode.

The pH was determined on unfiltered samples immediately on return to the laboratory. Since the current from the glass electrode is temperature dependent, the temperature of the sample was measured to 1°C and the instrument set accordingly. The electrode was standardized on each occasion using a buffer solution near to the expected pH of the sample, in this case pH 8. The standardization was made within 3°C of the temperature of the sample.

6. Salinity determination

Determinations of salinity may either be made directly from the conductivity of the sea water or by estimating the chlorosity using the Mohr-Knudson titration method. The choice of method is mainly determined by the level of accuracy required. Within an estuary an accuracy between ±0.1‰ to ±0.01‰ is sufficient, both as an ecological parameter and as a quantitative tool for tracing water masses (Martin, 1972a). For this degree of precision conductivity is the best choice, and was used in the present investigations.

The salinity and temperature bridge used in the present investigation was the MC5 Mk II supplied by Electronic Switchgear and recommended by the National Institute of Oceanography. It is designed for rapid *in situ* measurements. The electrolytic conductivity is measured by a cell moulded from mica loaded epoxy resin fitted with carbon composition electrodes. This electrode fulfils the same function as the normal platinised-platinum electrode in minimizing polarization errors. The measuring head is connected to 100 metres of cable, and contains a thermistor, as a compensator for temperature errors and as a sensing element for temperature readings. The accuracy of this instrument over the most favourable range is ±0.05‰.

The salinity bridge was calibrated against standard sea water of known chlorosity. When taking temperature and salinity measurements *in situ* a small amount of agitation is necessary to keep the tube flushed, however, when working from ship-board there is usually sufficient motion. In fast currents a heavy sinker was lowered first on a wire and the probe was loosely attached and slid down. The bridge was recalibrated from time to time using a secondary standard (a large volume of sea water of known salinity in a polythene container).

7. Estimation of standing crop - Total Particle Volume

The electronic dimensional particle counter (Coulter counter Model B) which was originally used for counting blood cells and different organisms in pure culture has recently been applied to the study of mixed populations of plankton (Mulligan & Kingsbury, 1968; Evans & McGill, 1973).

In principle the Coulter counter depends on the changes produced in the current passing through an electrolyte (sea-water) as particles of differing resistivity pass through the electric field. Practically, the sea water (and suspended particles) is sucked through a minute aperture across which an electric field is maintained. The change in resistance as a particle passes through the pore is proportional to the volume of the particle. The pulse is amplified and counted, giving an estimate of the number of particles in suspension. In the present study a 280 μ pore size was used since smaller apertures (100 μ or less) became easily blocked.

The range of size over which counts are made can be limited by the threshold settings. The upper threshold only allows particles less than some predetermined value to be counted while the lower threshold setting only allows larger particles to register. Counts can be made in a particular size interval or over a complete spectrum of sizes. Each aperture size has a different relationship between particle volume and electrical pulse strength, this must be found by a calibration process. Standard size particles are used in calibration with a diameter within the range 20 to 40% of the aperture size. In this case ragweed pollen grains with a mean volume of 3900 μ^3 were used, suspended in particle-free sea water. A cumulative frequency distribution is made at suitable machine settings. From these data the threshold setting corresponding to the mean particle volume is found. In this case the setting was 39 at a sensitivity of one-eighth, giving the relationship:

1 threshold unit = $100\mu^3$ at this sensitivity. The reproducibility depends only on the actual count; for a count of 2000 the accuracy is $\pm 3.3\%$ while a count of 200 may vary by up to $\pm 6\%$. Recalibration of the machine was carried out at three monthly intervals or when its location was changed.

Samples were counted immediately on return from the field with 2 ml duplicate volumes being counted for each set of threshold intervals. Knowing the volume range of the interval, the volume is found by multiplying the actual count by the lower volume for the interval. The cumulative addition of the volume for each interval gives the total particle volume (T.P.V.) (Sheldon & Parsons, 1966). From this entity information about the seston and its size distribution may be obtained. This method is also particularly useful in detecting gradients of suspended matter (living and dead) (Vollenweider, 1969). This author also considers that in most instances the number of detritus particles is higher than that of living cells.

Parsons (1965) demonstrated the use of the Coulter counter in following the growth of Skeletonema costatum. He selected instrument settings in which the volume of an individual cell is placed in the second or third threshold category (i.e. 4 to 8 or 8 to 12). Chain lengths of up to 25 cells may be plotted on one scale and the changing distribution of chain lengths with time may be studied.

Mulligan & Kingsbury (1968) investigated plankton dynamics in artificial ponds and showed that the biomass was more precisely determined by the Coulter counter than by chlorophyll a estimations or dry weight. These authors indicated that the amount of chlorophyll a per cell is dependent on the physiological state of the cell and the class of the algae, and is not linearly related to cell volume. However, within a pond of high productivity there was a fairly good correlation between the three factors. In comparison with direct microscopic

enumeration of phytoplankton a much larger amount of data could be collected in a given time by the Coulter counter, although numbers were found to be consistently smaller. In one of the few studies on natural populations using this technique Evans & McGill (1973) showed that the total particle volume broadly reflected the summer growth and autumn decline in the numbers of phytoplankton. They also showed a linear relationship between chlorophyll a and total particle volume in excess of 0.8 mm^3.

8. Estimation of standing crop - Chlorophyll a determination

The spectrophotometric determination of chlorophyll a as an estimate of standing crop is extensively used both in limnology and oceanography. Most estimations are based on the method of Richards & Thompson (1952) although considerable modifications and improvements have been made. The basis of the method is the extraction of the photosynthetic pigments by 90% acetone after concentration of the cells and the subsequent measurement of the extinction values at the absorbancy peaks of chlorophylls a, b and c. With the knowledge of the specific absorption coefficients for each pigment the actual concentration in mg/l can be calculated.

A re-evaluation of these coefficients by Parsons & Strickland (1963) indicated that the values used by Richards & Thompson (1952) were too low by up to 25% and consequently the pigments had been overestimated. These authors also suggested a blank correction, measured at 750 mμ which should be subtracted from the extinctions measured at all other wavelengths. On the basis of this work they produced the revised equations which are now in standard use, and require readings at the following wavelengths 665, 645, 630 and 750 mμ. To estimate the concentration of chlorophyll a corrected extinctions are substituted in the following equation: $C = 11.6\ E_{665} - 1.31\ E_{645} - 0.14\ E_{630}$.

Although the original method used continuous centrifugation to concentrate the phytoplankton, filtration with millipore or glass fibre filters is now more commonly used. Before filtration the sample is treated with a suspension of Magnesium carbonate which prevents acidity and the consequent formation of phaeophytins (chlorophyll degradation pigments). According to Strickland & Parsons (1968) corrections for the presence of these products can generally be ignored unless bottom deposits are disturbed.

The advantages of using 90% acetone in preference to methanol (which

may have a higher extraction efficiency) has been considered in Recommended Procedures for Measuring Productivity (1969). It appears that chlorophyll a is more stable in acetone, the absorption band in the red is sharper and the extinction coefficient is higher. Other solvents may be used and although there is considerable information on the extraction and absorption of chlorophyll in ether this solvent cannot be used directly (but a quantitative transfer can be made) (Talling & Driver, 1961). The greater efficiency of 90% methanol in extraction has been questioned by these authors who have shown that it is no more efficient in extracting pigments from diatoms and blue-green algae than 90% acetone. Relying on the fact that most of the absorbance at 665 mm is due to chlorophyll a Talling & Driver gave a simplified equation for the measurement of this pigment involving only a single reading at 665 mm. For 90% acetone, $C_a = 11.9\ E_{665}$ while for 90% methanol, $C_a = 13.9\ E_{665}$.

The procedure used in this investigation follows Strickland & Parsons (1968) with the modified trichromatic equation of Parsons & Strickland (1963) and based on Richards & Thompson (1952). Immediately on collection, samples for chlorophyll estimation were filtered through a 300μ mesh to remove zooplankton followed by storage in subdued light till they were returned to the laboratory (usually less than one hour). Samples were treated with a few drops $MgCO_3$ suspension, and a suitable volume was measured for filtration, usually between 1 to 4 litres. The measured volume was then passed through a Whatman GF/C glass fibre filter in the dark at 1°C without the application of suction. The prepared filter was then either stored in a darkened desiccator at -20°C where the chlorophyll remains stable for several months, or extracted immediately with 90% acetone.

The extraction involves macerating the filter in ice-cold 90% acetone using a tissue grinder, this process being carried out in subdued light

since the pigment is extremely sensitive at this stage. The glass fibre-acetone pulp is then quantitatively transferred to a stoppered centrifuge tube and made up to 12 ml. After allowing 20 hours for extraction in a dark refrigerator the tubes are allowed to warm to room temperature and then centrifuged at 5000 r.p.m. for five minutes to bring down the glass fibres and debris. The clear supernatant is decanted into a 1 cm spectrophotometer cell and extinctions are read at 750, 665, 645, 630 and 480. All readings are corrected for cell to cell blanks and the concentration of chlorophyll is estimated according to the standard equation or nomogram (Battin, 1967).

9. Estimation of standing crop - Enumeration of phytoplankton

Although it is possible to obtain a quantitative assessment of the phytoplankton standing crop from the methods previously described, direct microscopic examination, identification and enumeration of individual species in terms of cell numbers is of extreme importance in any ecological study. For this purpose concentration of the algae is necessary, either by filtration, sedimentation or centrifugation. The choice of a suitable method for the present study was based on the practical limitations which the sampling programme imposed and on an examination of the relative merits of each method.

If a continuous centrifuge is available large volumes of sea water (1 litre or more) may be concentrated. This procedure permits the observation of living flagellates, but its applicability may be limited by the bouyancy of some components of the phytoplankton (Margalef, 1971). A quantitative method, involving the filtration of up to 5 litres of water through a continuous centrifuge was described by Wood (1962). The concentrated material is stained with acridine orange and examined under ultra-violet light in a haemocytometer. The quantitative transfer can be achieved providing that certain precautions are taken (Lund & Talling, 1957).

The errors inherent in the use of haemocytometers and other counting chambers have been considered in detail by Lund & Talling (1957). Replicate series of counts were found to show significantly different deviations probably owing to the large size of some organisms, haemocytometers being devised for very small cells (Lund, Kipling & le Cren, 1958). MacNabb (1960) found that the use of such chambers yields inconsistent results due to the non-random distribution of organisms. The errors involved in sub-sampling are considerable and Edmondson (1971) recommended replicate series of counts. A further disadvantage of this method lies in the

combined working depth of liquid and thick, optically-flat coverslip, which prevents the use of an oil immersion lens for critical examination. In general, this method is more useful for cultures of algae than for natural populations (Lund & Talling, 1957).

The inverted microscope method (Lund, Kipling & le Cren, 1958) has been widely used for the enumeration of samples sedimented with Lugol's solution. To allow for the slow sinking rate of some organisms, the sedimentation time in hours must be at least three times the height of the cylinder in centimetres (Margalef, 1971). The practical disadvantages of this well-proven method lie in the space required for the storage of sedimenting samples, the length of sedimentation time and the large number of cylinders which would have been required for the present programme of continuous sampling (described later).

The first description of a technique involving filtration of samples through a membrane filter was given by Cole & Jones (1949). This involves partial filtration and resuspension of the retained material in a small volume of liquid. However, separation of the organisms from the filter may be difficult in some cases (Margalef, 1971). The retained material was counted in a haemocytometer after resuspension in 1 ml of filtered sea water.

A technique for the direct enumeration of freshwater phytoplankton concentrated on a molecular filter was given by McNabb (1960). Samples preserved with formalin were filtered through a Millipore HA filter. Clearing was carried out in immersion oil which replaced the water in the filter in 24 hours at room temperature. Algae were found to be well-preserved and distributed at random on the filter. Estimation of the numbers of each species was made by scoring 30 random fields for presence or absence of individuals of that species rather than by the more laborious process of counting. The scoring of 30 random fields was stated to be sufficient for this procedure. The percentage frequency

can be converted to the theoretical density according to a table given by the author. Both MacNabb (1960) and Legendre & Watt (1972) showed that the theoretical density closely approximates the actual density calculated from the more time-consuming process of counting individuals.

Holmes (1962) proposed a modification of the method, suitable for use with marine samples. This involved washing the upper surface of the filter with successively diluted volumes of sea water followed (after a rinse in fresh water), with increasing concentrations of ethanol and staining with alcoholic fast green. Clearing was carried out in beechwood-creosote or xylene and preservation was generally good for diatoms, dinoflagellates and chrysophyceae, while naked flagellates and thin-walled diatoms were poorly preserved. In contrast with MacNabb (1960), Holmes found the organisms to be non-randomly distributed on the filter surface.

DeNoyelles (1968) devised a modified procedure based on MacNabb's method using a microfiltration unit. Phytoplankton on the filter surface were stained with aniline blue and eosine Y in aqueous solution. This treatment selectively stains the cytoplasm leaving the debris unstained. The filter was enumerated with or without clearing, although in the latter case a very high light intensity was needed. The phytoplankton showed a random distribution on the filter and were enumerated either by scoring presence and absence or by counting individuals.

In the present investigation the method of MacNabb (1960) was used with a few modifications. Fresh samples rather than preserved ones were used, filtration being completed within a short time of the completion of sampling. The estimation of actual density from the theoretical density was not used, instead algae were counted as numbers of individuals per field, a more time-consuming but more accurate process.

The direct application of this method to sea water samples has been

achieved for the first time without the necessity of passing the filter through successively dilute volumes of sea water. The wet filter is merely covered with a few drops of 'Uvinert' immersion oil, which has been found to replace the salt water within 24 hours at room temperature without the formation of salt crystals. This property was not found in other clearing agents tested.

The sample volume filtered was 250 ml or 100 ml depending on the density of the phytoplankton population. 25 mm millipore HA filters with a 0.45μ pore size were used, giving a final filtered area of 15 mm. Clearing in 'Uvinert' immersion oil was complete in 24 hours at 25°C in the dark, although more rapid clearing may be effected by raising the temperature. Organisms were enumerated using a high power (x40) objective, generally under phase contrast but occasionally on bright field. An oil immersion objective was used on occasions for identification purposes.

The contention by MacNabb (1960) and de Noyelles (1968) that the phytoplankton were randomly distributed on the filter was confirmed in the present investigation. The Chi-squared values calculated from five sets of 30 counts fell between 14.2 and 18.1. This gives a probability of better than 0.02 that the distribution is random. The non-random distribution of organisms on the filter described by Holmes (1962) may have resulted from the redistribution of organisms during the numerous desalting, dehydrating and staining steps involved in his method.

The enumeration of organisms on the filter is subject to the same statistical requirement as the scanning of sedimented organisms with the inverted microscope (Holmes, 1962). The statistical basis of the counting procedure was considered in detail by Lund, Kipling & le Cren (1958) who gave 95% confidence limits for various counts. These are applied to the results of the present investigation in the following Table.

TABLE 1. Size of Count and Accuracy for Present Investigation using x40 Objective with 250 ml of Samples Filtered

No. of organism	Cells per litre	Approximate 0.95 confidence limits: Accuracy expressed as percentage of the count	Range
4	640	100%	0 - 1280
16	2560	50%	1280 - 3840
100	16000	20%	12800 - 19200
400	64000	10%	57600 - 70400
1600	256000	5%	243200 - 268800

According to Lund et al. (1958) the accuracy required in estimating phytoplankton populations is not normally very large. Most ecological experiments are concerned with generations and in such studies an accuracy of 50% is quite adequate. For a random distribution it is possible to determine the 90% confidence limits for any count made, this is indispensable for the purposes of comparing with other counts. In general, if one count lies within the confidence limits of another there is no significant difference between them.

MacNabb (1960) investigated the errors of the technique and stated that the sub-sampling error and the difference between separate sets of enumerations from the same filter were not significant. The counting procedure applies to complete organisms which may be cells, filaments or colonies. Chain-forming diatoms were recorded as chains, the total being multiplied by the mean number of cells per chain. The 95% confidence limits are applicable to these cases (Lund et al., 1958).

The membrane filtration technique thus possesses numerous advantages over methods of counting. A semi-permanent, easily stored filter, returning even the smallest organisms in such a manner that they are

randomly distributed can be prepared for enumeration in 24 hours or less. Living and dead phytoplankton are easily distinguishable by their natural pigmentation even after periods in excess of 30 months. Bacillariophyceae, Dinophyceae, Chrysophyceae and Chlorophyceae are generally well preserved although various organisms may respond differently to treatment.

CHAPTER 3

CHAPTER 3

SAMPLING METHODS AND SAMPLING PROGRAMME

a) Introduction

Estuaries and neritic areas may be considered heterogeneous in comparison with the open sea. The main factors influencing this situation are tidal currents, topographical configuration of the sea-bed, fresh-water runoff and sources of pollution. Such areas may be characterized by uneven vertical and horizontal distribution of nutrients and patchy distribution of phytoplankton. The quantitative aspects of phytoplankton patchiness have been reviewed by Bainbridge (1957) who showed that in open seas and oceans the plankton patches were between 10 and 60 miles in diameter. In partially enclosed areas phytoplankton patches were found to be about 2 km in diameter. Platt (1970) showed that in coastal waters patches of phytoplankton may be between 0.5 and 1.5 miles across. This spatial heterogeneity is poorly understood and poses formidable sampling problems, if we are to observe the changes which really characterize the area under consideration.

The scale of heterogeneity in near-shore environments was discussed by Platt (1970). He subjected the phytoplankton distribution (in terms of chlorophyll a measurements) to analysis of variance and partitioned the total variance into effects due to sample replication and effects due to true differences between stations. The important conclusion was drawn that the variance between sample replicates at the same station was of the same order as the analytical variance. Platt revealed significant differences between stations at densities as high as 10 per 0.0625 sq. miles. The maximum between station variance was found at a density of 10 stations per square mile where the maximum value of the between-station component was tenfold higher than the between-replicate component. The maximum coefficient of variation for a single observation

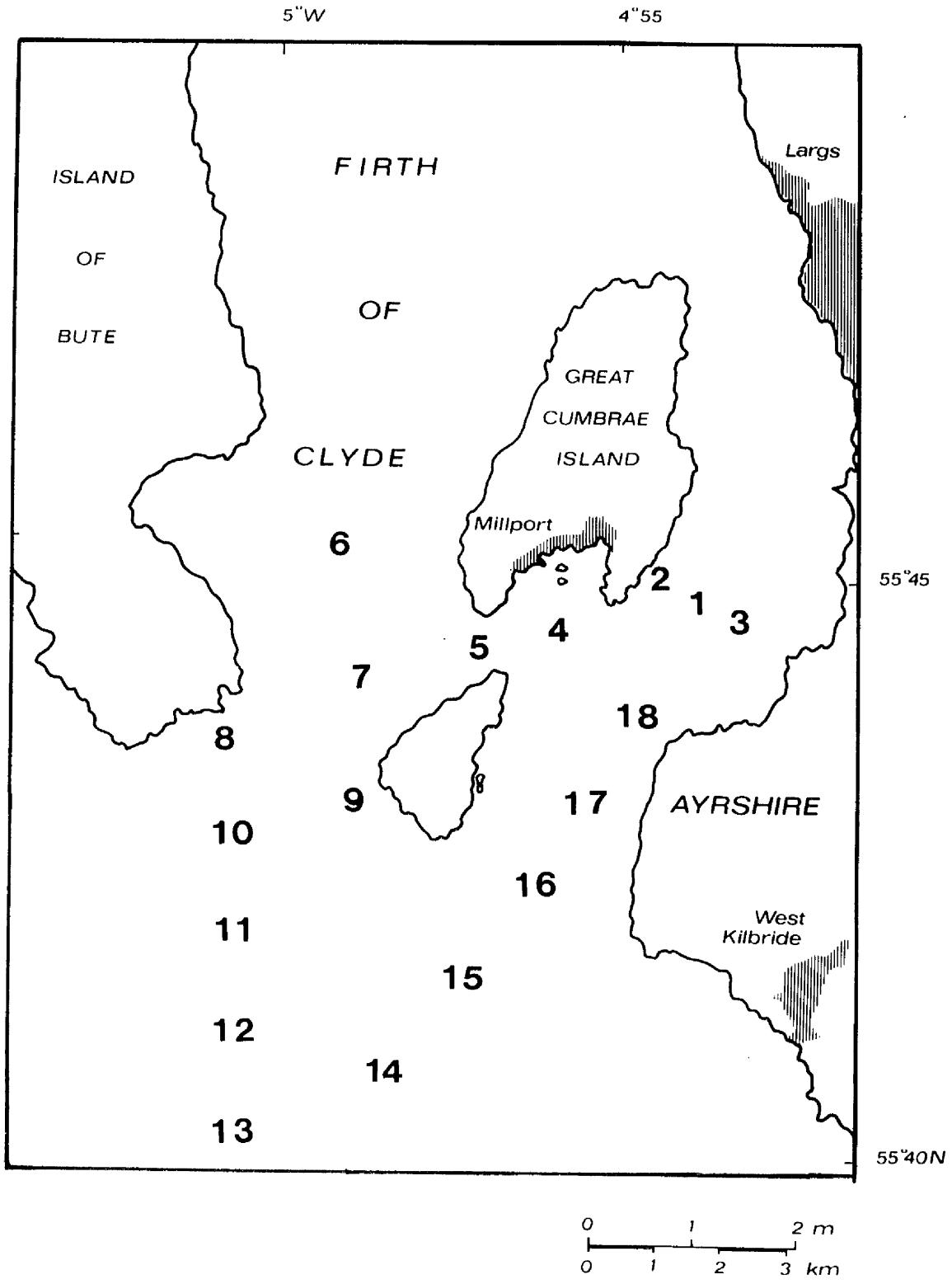
is up to 70% whereas the analytical technique has a precision of better than 10%.

The suggestion that the sample replicates taken at the same time from a single station show a similar variance to the experimental error, involved in estimating the standing crop, was also confirmed by Lund et al. (1958). They analysed the errors involved in lake sampling by applying the Chi-squared test for randomness to various series of samples, as estimated by direct enumeration of cells. Out of 36 replicate series of samples, 35 were found to be randomly distributed. It is possible to apply confidence limits to the actual counts and to make comparisons from individual samples taken from different locations or different depths.

The adequacy of sampling from a single station was questioned by Lund & Talling (1957). They considered that the erratic fluctuations seen in graphs depicting the rise and fall of planktonic populations may be a consequence of over dispersion. In areas where non-random distributions are found 'multiple mobile sampling' was suggested as a solution. This involves integration by numerous replication of samples or by towing an integrating device behind a moving boat. The use of a pumping system as an integrating device was described by Beers et al. (1967) who collected samples at depths of up to 100 metres at a speed of 3 knots. (A sampling method based on this technique has been used in the present study and is described in sub-section (e)).

The frequency of sampling is also another important feature as fallacious beliefs can easily be caused by collecting samples at widely separated time-intervals. It is a well-established fact that phytoplankton outbursts are of short duration and can easily be missed (Lund & Talling, 1957). Platt (1970) demonstrated how quickly the distribution of observations in the sea may change, with a time-period which is short in comparison with the typical intervals used in ecological sampling

Fig 3


5°W
4°55
55°45
55°40N
ISLAND
OF
BUTE
FIRTH
OF
CLYDE
GREAT
CUMBRAE
ISLAND
Largs
Millport
AYRSHIRE
West
Kilbride
1
2
3
4
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6
7
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9
10
11
12
13
14
15
16
17
18
0 1 2 m
0 1 2 3 km

programmes. Lund & Talling (1958) regarded fortnightly sampling as a minimum and to obtain a full picture, an interval of three to four days is necessary. Even this frequency may be too short and may obscure important diurnal changes.

The sampling programme should be based on a preliminary study of the area followed by careful location of the sampling station or stations, determination of the optimum sampling frequency and the number of depths to be sampled.

b) Preliminary Survey

From February till the end of June, 1972 a preliminary survey was carried out within an area of about 100 Km^2, mainly to the south of the Cumbraes. The 18 sampling stations chosen, shown in Figure 3, were sampled at the surface at fortnightly intervals, providing the maximum practicable areal coverage. The fact soon emerged that the rise and fall of the nutrient content of the water was not clearly related with the estimates of standing-crop obtained from direct enumeration or from total particle volume determinations. This phenomenon was not restricted to a particular station but was general throughout the area.

For example, following the spring diatom outburst at the beginning of April in which Skeletonema predominated, an uneven reduction in silicate was evident on 10th April. Contrary to expectation the regions of lowest diatom numbers showed the greatest reduction in this nutrient. A further diatom increase, throughout the sampling region, recorded on 25th April, caused further reductions in all nutrients. A peculiar feature on this occasion was the equal nutrient status of stations 7 and 11 but their totally different population composition. Station 7 was dominated by a large population of Skeletonema (3.8 million cells per litre) while station 11 showed a large abundance of Chaetoceros sp. (1.6 million cells/l) with a smaller number of very short-chain Skeletonema. By

17th May the population was totally dominated by Chaetoceros which showed a patchy distribution but no obvious relationship with the nutrient levels. All measured nutrients showed a distinctive pattern of variation on this date with highest levels in the Fairlie Channel (stations 1 - 3) falling to very low concentrations at the most southerly stations (12 - 14). This tendency for nutrient concentrations to be highest along the Ayrshire coast and in the Fairlie Channel was reversed during the Winter and Spring when the maximum abundance of nutrients was generally located around Garroch Head (8).

This preliminary survey made it abundantly clear that this area exhibited extreme horizontal heterogeneity both in the distribution of suspended matter (living and dead) and in the variation of chemical parameters. Since the aim of this study is to assess the relationship between physical, chemical and environmental factors and the seasonal changes in the standing crop, the irregularity of the initial results made a reconsideration of the programme essential. Clearly, in the 6 to 13 day interval between sampling trips, major changes were taking place in the size and composition of the phytoplankton populations and in the utilization and recycling of nutrients.

In the light of these considerations two major changes were made in the programme of sampling. Firstly, it was decided to reduce the interval between sampling trips to the shortest practicable time - twice a day - and to concentrate on a single area, stations S1 - 3 with samples at several depths. Secondly, an integrated sampling method was introduced after an investigation of the errors inherent in the sampling methods in general use.

c) Investigation of Sampling Methods

The spatial distribution of the organisms under study is, perhaps, the major factor to be taken into consideration when designing an ecological sampling programme. The results of such a study will clearly be affected by the sampling methods used and the effect will be most obvious when organisms are over-dispersed. If organisms are randomly distributed (horizontally and vertically) throughout an area, a single small-volume sample will suffice to represent the area. However, if the non-random distribution of organisms is demonstrated, another sampling method must be employed.

Apart from the analytical or counting error involved in processing any sample, which is known, there are two further sources of error which cannot be estimated except by a further investigation:

1) Variance between replicate samples at the same station,
2) Variance between samples at closely spaced stations.

With the knowledge of these components of the total variance, confidence limits can be applied to the individual results. The only assumption which must be made is the time taken to complete the sampling is small compared with the time needed for significant changes to take place. Platt (1970) suggested a maximum time limit of 2 - 4 hours.

The indications from the preliminary survey that this area showed extreme heterogeneity was statistically investigated during a period of phytoplankton abundance (in July, 1972). Ten replicate samples were taken from station 3, to estimate the replication variance and seven samples were taken between stations 2 and 3 across the Fairlie Channel. The total distance between these stations is 1.4 Km, and the sampling interval was about 200 metres. The middle sample coincides with station S1.

1) Variance of replicate samples: 10 replicate 5 litre surface samples were taken in a short period at station 3 and the standing crop was estimated from chlorophyll a estimations. The following readings were obtained (all µg chlorophyll a/l):

0.262, 0.345, 0.262, 0.208, 0.238, 0.309, 0.226, 0.250, 0.262, 0.279.

The measures of chlorophyll a concentration were transformed by taking natural logarithms (Platt, 1970) before the Chi-squared value was calculated:

Chi-squared = 0.0185. For nine degrees of freedom this gives a better than 95% possibility of the samples being randomly extracted from the same population.

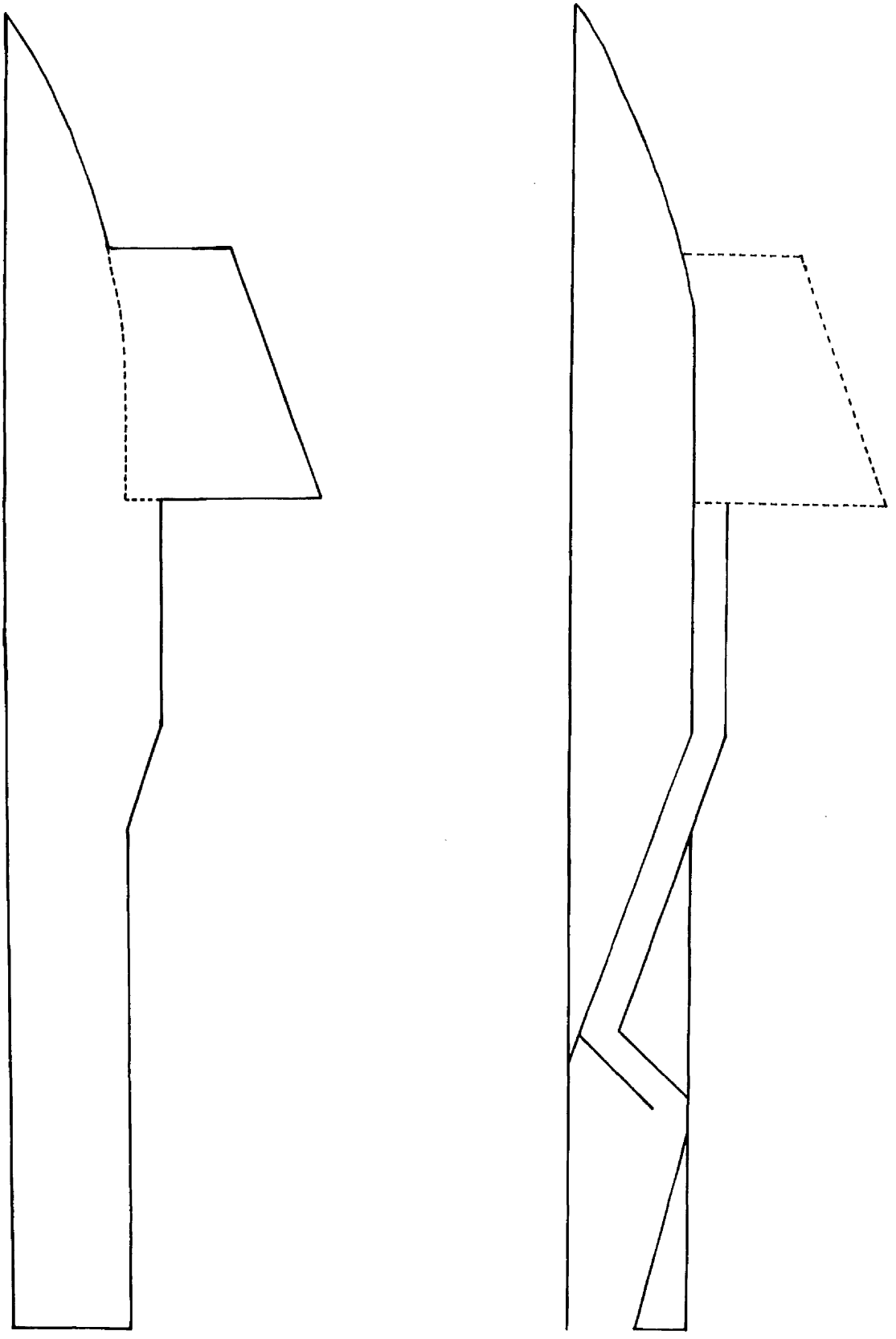
Variance = 0.00242 giving a standard deviation of 0.049. For nine degrees of freedom the 95% confidence limits are $\pm 2.26 \times 0.049$, i.e. 1.31 ±8%. The analytical technique has a precision of better than ±10% therefore the replicate variances is within this and consequently not detectable.

2) Between station variance: The standing crops at the seven locations between stations 2 and 3 (at 200 metre intervals) were estimated from the actual microscopic counts of phytoplankton. The total counts (for Chaetoceros chains) from the seven samples are as follows:-

759, 1113, 720, 689, 445, 784, 665 chains. Mean = 739.

Chi-squared value calculated for this series of counts = 219, for six degrees of freedom the possibility of the samples being randomly distributed is less than 1%. This indicates the presence of phytoplankton patches which cannot be adequately sampled from a single station. In order to achieve a meaningful result for this area it is necessary either to take numerous stations or to use a method which integrates the water from all these locations. The latter method resolves to a great extent the demand for extra time brought about by sample replication.

Fig 4



Although continuous pumping devices for taking samples from the photic zone have been previously described (Beers et al., 1967) there appears to be no satisfactory way of taking integrated samples from surface waters. To fill this need, an integrated sampling device was developed for the present programme (Figures 4, 5 & 6). This is a device supported by two side-angled floats (to keep it from the wake of the boat) and designed to scoop-up the top 5 cm of the water column as it is towed at a speed of 4 knots. Water continuously enters the sampler where it is mixed and a fraction is continuously pumped off with about 60 litres being collected over a distance of 1.5 Km. Full details are given in Section (e). Integrated samples were also pumped from several depths (down to 10 metres) using a 1 inch diameter vinyl tube, and again 60 litres of water was collected over the same distance (1.5 Km).

The sampling variance of this method was investigated to determine whether it provides a meaningful assessment of the standing crop in the area. Integrated surface samples were taken immediately after the collection of the seven discrete samples, between stations 2 and 3 and are, thus, directly comparable with them. The 'transect' across the Fairlie Channel from stations 2 to 3 (crossing station 1) was traversed seven times within an hour giving seven integrated surface samples of this 1.4 Km stretch of water. The standing crop was estimated from the phytoplankton counts with the following total number of (Chaetoceros) chains:

721, 746, 804, 726, 780, 801, 753 Mean = 763.

The Chi-squared value calculated for this series = 6.41 which means that the hypothesis of random distribution is not disproved.

The variance of the counts = 815 gives a standard deviation of 29.6. Thus the 95% confidence limits for six degrees of freedom are $\pm 2.45 \times 29.6$ or $763 \pm 10\%$. This is approximately the same as the error

Fig 5a

in the counting process which is about ±8%. Thus, using an integrated sampling method, a single sample may be taken which will reproducibly represent an area rather than just a single station.

d) Sampling Programme - August, 1972 to August, 1973

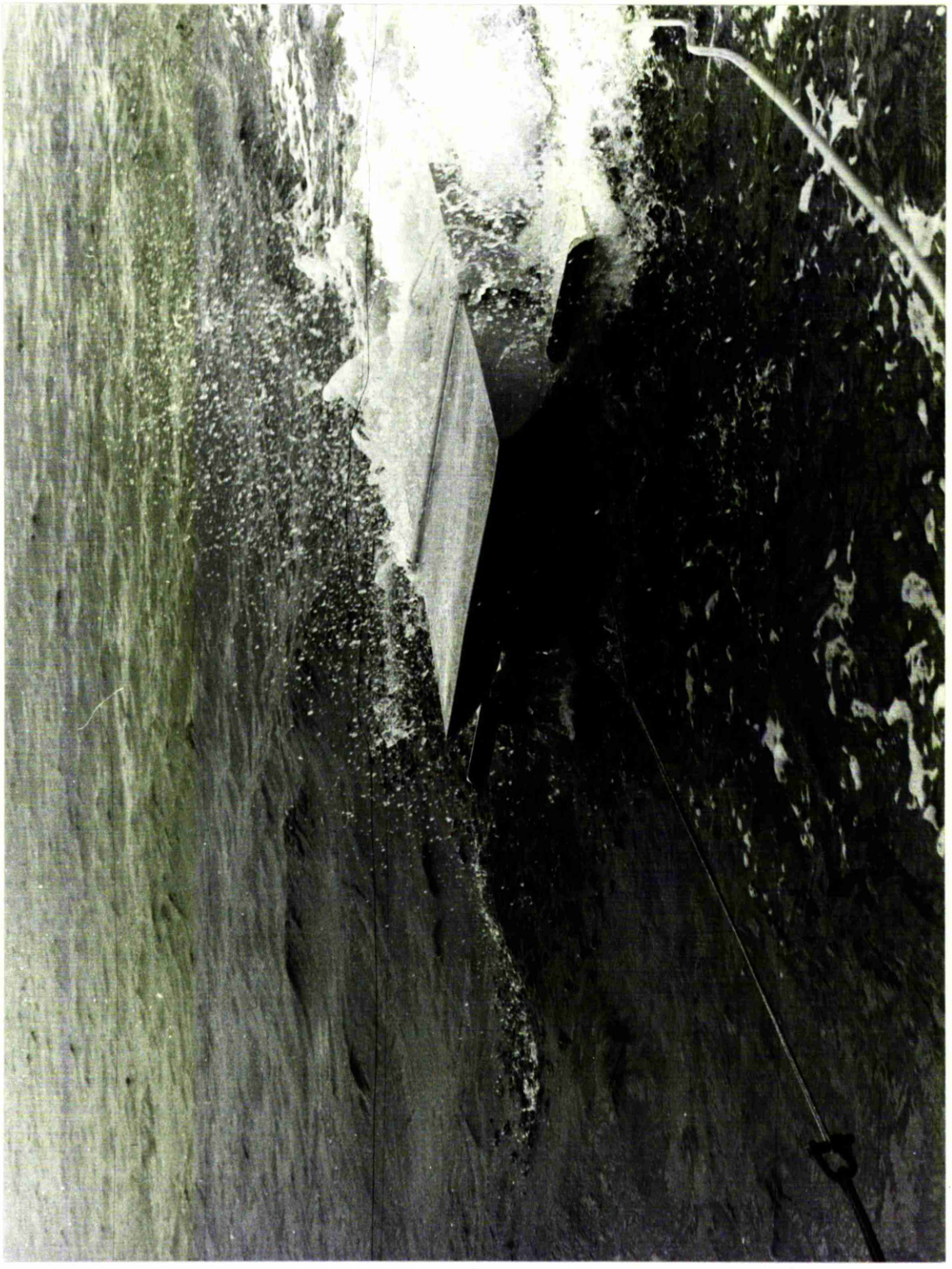
For the purpose of ascertaining the optimum sampling interval a programme of twice daily sampling at the surface and 3 m depth was undertaken during August, 1972 in the Fairlie Channel. Integrated samples were taken between 08.00 and 10.00 hours and from 15.00 - 17.00 hours. Persistant rhythms were found in standing crop and nutrients both showing changes of up to threefold between morning and afternoon.

On the basis of this study the same pattern of sampling was continued for an entire year (till August, 1973). The 'transect' across Fairlie Channel from Keppel Pier (station 2) to the Perch (station 3) was chosen as the main sampling area and was sampled twice daily from the R.V. Mizpah. Integrated samples were taken from 3 m depth twice per day and integrated surface samples were collected once per day (where practicable). Additional depths (1m, 10m, 20m) were sampled regularly.

e) Sampling Methods

The specially designed integrated surface sampler used during the present study is shown in diagrammatic form in Figure 4 and in the photographs in Figures 5 & 6. The side-tracking floats which support it were originally designed to support a side-tracking neuston net (Ben Yami, 1970). The surf-board-like floats keep the sampler to one side of the propeller wake of the boat, and it thus passes through water unaffected by passage of the boat. The metal frame, which supported a net in the original neuston net model, in this case provides the support for the surface sampler. This means that the bottom of the sampler

Fig 5b



is only just in contact with the water surface.

The intake scoop extends 5 cm beneath the water surface and is protected from any turbulence from the floats by the two large fins either side of it. As the sampler is towed at a speed of 3 knots the water is forced up the inclined slope (10 cm above water level) and into the reservoir at the back which holds around 10 litres. The water passing over the short is deflected downwards ensuring thorough mixing of the water sampled. The excess water flows continuously out through the stern.

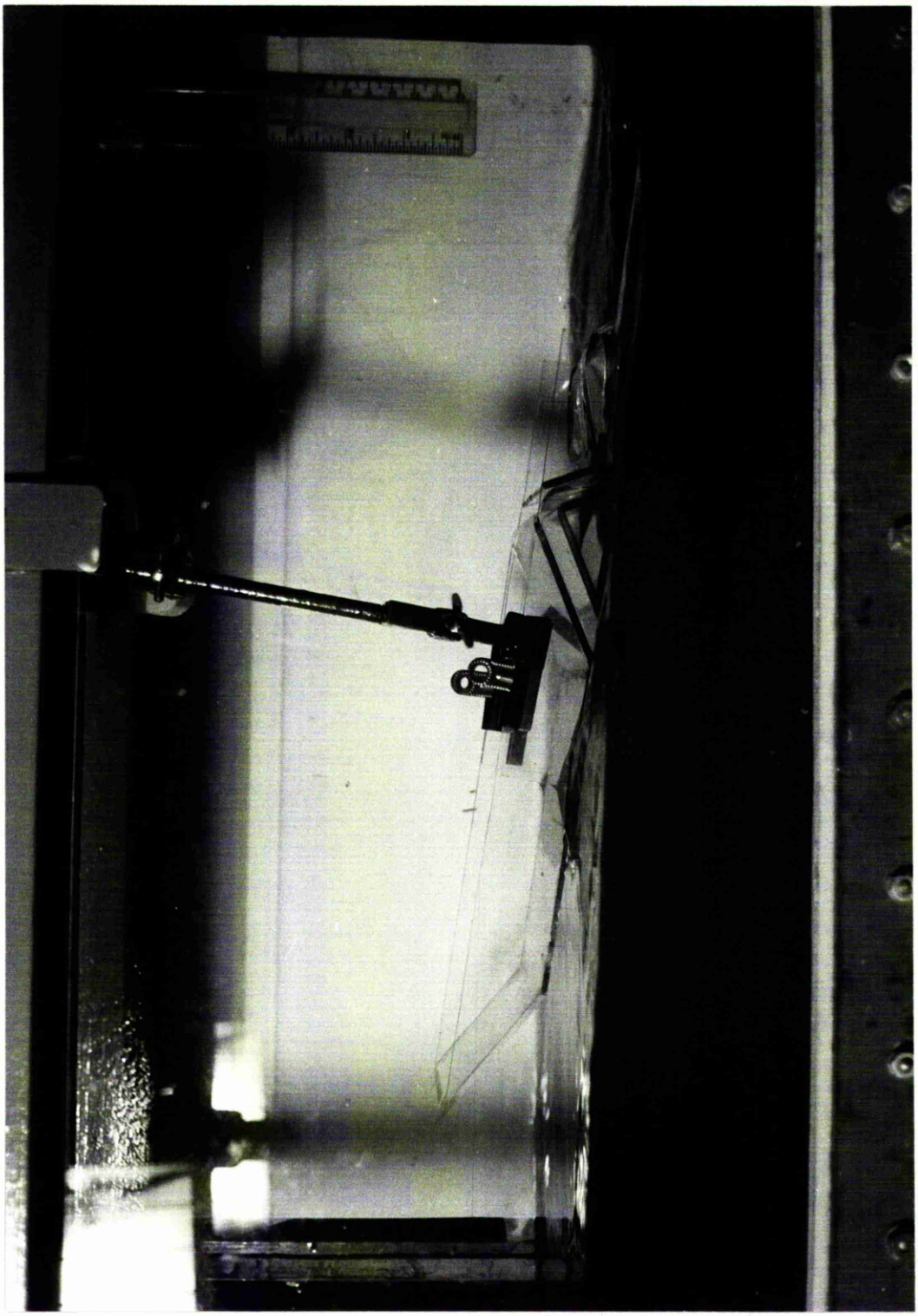
Samples are taken by continuously pumping-off a fraction of the water passing through it. The pump used was a 12V D.C. "Water Puppy" pump which was situated on-board the towing vessel. The connection to the sampler was via a half inch (1cm) diameter vinyl tube (15 metres in length) through which about 60 litres of water was pumped over a distance of 1.5 Km. This procedure took about 10 minutes. The 60 litre sample is collected in a large plastic container, mixed thoroughly and then sub-sampled (by syphon) into a 5 litre narrow-neck polythene bottle. Depth samples were taken using a one inch diameter vinyl tube (25 metres in length) attached to a steel towing cable. At a speed of 3 knots, 15 metres of cable were required to take the end of the tube down to 3 metres. A large depressor on the end of the cable kept the wire taut during sampling. A 60 litre sample was pumped over a distance of 1.5 Km, collected in a large plastic container and sub-sampled as previously described.

An investigation of the performance and efficiency of the surface-sampler was carried out at the beginning of July, 1972. During this period a great abundance of dinoflagellates (mainly Peridinium) accumulated in the calm surface waters. This was clearly shown from the integrated samples of the upper 5 cm where Peridinium was five-fold higher than in integrated samples from 1 m depth. Samples taken from the surface

in the normal way (by bucket), generally showed intermediate numbers, suggesting that the integrated sampler provides a more valid impression of the surface phytoplankton population.

The initial testing of the surface-sampler design was carried out on a perspex, 1/5th scale model, in the flow tank of the Department of Mechanical Engineering (Figure 6). This was followed by field trials with a full-scale plywood prototype. Once the design had proved feasible the actual sampler was constructed in fibre-glass. This material was chosen for its ability to withstand the stresses placed on it at sea and for the non-contaminating nature of the fibre-glass itself.

Fig 6



CHAPTER 4

CHAPTER 4

ANNUAL VARIATION OF PHYTOPLANKTON AND RELATED CHEMICAL AND PHYSICAL FACTORS

The results discussed in this section are based on the intensive programme of twice-daily sampling carried out in the Fairlie Channel from the beginning of August, 1972 until the end of August, 1973. Data for nutrients (nitrate, phosphate and silicate) in Figures 7, 8 and 9 have been plotted on a daily basis showing two curves, one for morning sampling (08.00 - 10.00 hours) and one for afternoon (15.00 - 17.00 hours) all at a depth of 3 metres. The various estimates of standing crop (total phytoplankton, chlorophyll *a*, and total particle volume) shown in Figures 17 and 18, and the quantitative annual distribution of the main phytoplankton (Figures 14, 15 and 16) have been plotted on a daily basis for morning samples only (08.00 - 10.00 hours).

The annual cycle of dissolved nutrients in temperate waters generally follow one another and result from the alternation of the seasons affecting the physical and biological state of the area. During the winter the falling air temperature causes cooling of surface waters followed by convectional mixing. This process is assisted by winter gales which caused turbulent mixing of nutrient-rich deep water and the nutrient-depleted surface water (Barnes, 1957). Thus the winter period is characterized by uniform high nutrient throughout the water column which is further influenced by the increased nutrient input from catchment area due to heavy winter rainfall. Nutrients do not become depleted till the spring when the rapid multiplication of phytoplankton removes nutrient from the surface waters. As the air temperature increases during the summer stable layering takes place, cutting off the productive upper layer from the supply of nutrients. Thus growth of diatoms during

the summer is generally nutrient limited and crops tend to be smaller than the spring peak.

The summer and autumn pulses of phytoplankton are probably a result of sudden increases in nutrient in the euphotic zone. These may be caused by the influx of nutrient from deep water, when mixing takes place due to occasional gales or by input from external sources such as drainage from the catchment area during short periods of heavy rainfall. The products of regeneration from decay which accumulate in deeper water during the summer are again brought to the surface during winter mixing.

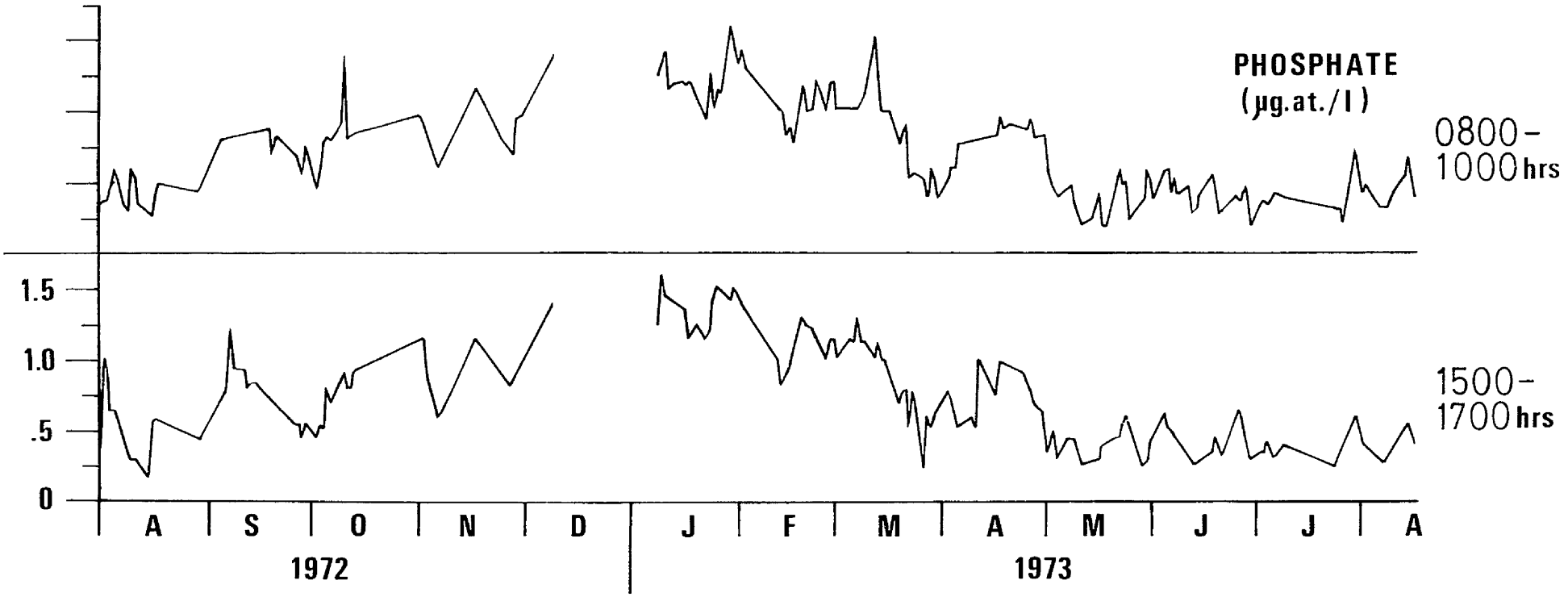
The quantitative aspect of this general pattern is subject to considerable variations between different regions although the overall picture is the same. Thus different bodies of water are often quantified by reference to their highest and lowest recorded nutrient values, which may give a limited guide to their productivity. For the spring diatom increase, which acts as a batch culture, the final crop is roughly proportional to the concentration of limiting nutrient (Fogg, 1967). In temperate coastal waters where the main constituent of the phytoplankton is generally diatoms the limiting factors are considered to be either nitrate (Barnes, 1957) or silicate (Marshall & Orr, 1930). Phosphate is not usually a limiting factor in marine waters (Corner & Davies, 1971).

The nutrient which is most fully documented in northern waters is phosphate for which a considerable amount of seasonal data are available from coastal locations. In the present survey (in Fairlie Channel) phosphate (Figure 7) generally exceeded 1.0µg at P/l from November till the middle of March, with a maximum of 1.6 in January. In the previous year (1972) a peak of 1.43 was recorded. These values are considerably higher than the only published figures for the Clyde Sea Area, given by Marshall & Orr (1927) from their studies on Loch Striven. They recorded a maximum phosphate level of 0.97µg at P/l in November and

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

3 METRES DEPTH Fig 7



indicated that this rise was due to turbulent mixing following the breakdown of stratification in the autumn. However, visits to the same loch during the present investigation showed maximum winter phosphate levels (again in November) of 1.63 throughout the loch. This high phosphate concentration was not associated with reduced salinity. Samples taken from the Gareloch, which suffers considerable pollution from the Clyde estuary, and samples from Loch Long, an adjacent unpolluted loch, showed markedly differing phosphate maxima. In Gareloch the winter levels generally lay around 2µg at P/l with a recorded maximum of 3.93 at the entrance to the estuary. In Loch Long phosphate values reached 0.82 in 1972 and 1.30 in 1973.

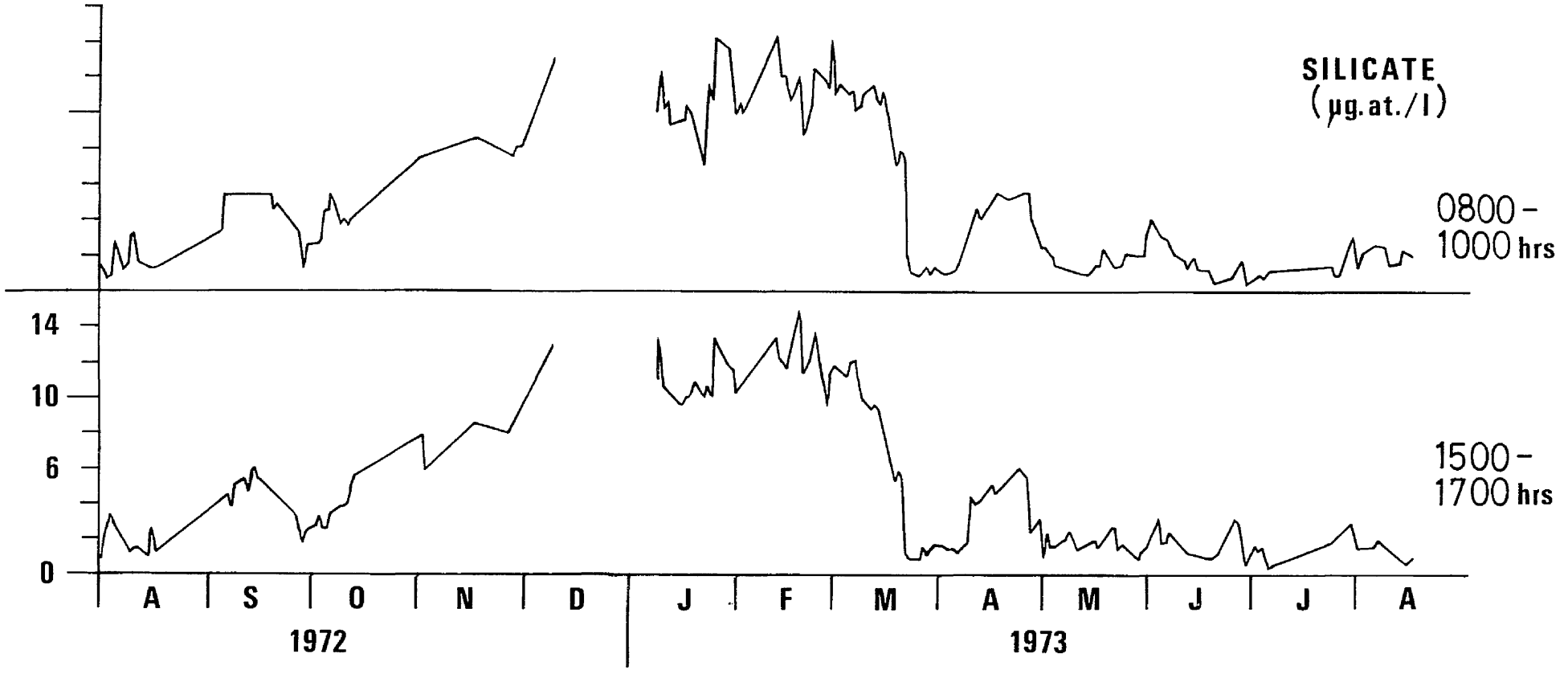
Unpublished figures for Loch Creran, a sea loch which lies to the north of the Clyde (Tett, 1974) showed a much smaller maximum. The peak recorded concentration in 1973 came in February reaching 0.53µg at P/l. The maximum abundance of phosphate to the north of Scotland (around the Shetlands) was given by Barnes (1957) as between 0.66 and 1.14µg at P/l. Cushing & Nicholson (1963) indicated a phosphate maximum for the North Sea of 0.75µg at P/l. This is close to the winter phosphate content of the Hardangerfjord (0.64)(Braarud, 1973) and the Trondheimsfjord (0.8)(Sakshaug & Myklestad, 1973). The only area where seasonal data has been collected over a long period of time is station E1 in the English Channel, which shows considerable variations in recorded maxima from year to year. In 1931, 1.28µg at P/l was recorded (Cooper, 1933), and 0.45 in 1961 (Armstrong, 1970). Values for the Welsh coast are fairly similar, 0.95µg at P/l for Cardigan Bay (Sykes, 1969) and 0.8µg at P/l for Menai Straits (Ewins & Spencer, 1967). It is clear that (during the period of the present survey at least) the Clyde Sea area is considerably richer in dissolved phosphate than any other coastal area.

In none of the areas discussed was phosphate recorded as being undetectable during the summer, and minimal values generally lay between

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

3 METRES DEPTH Fig 8



0.07 and 0.1µg at P/l. The lowest recorded phosphate level (0.2µg at P/l) was found in Fairlie Channel in 1973, which is similar to the minimum in Menai Straits (Ewins & Spencer, 1967), although in 1972 levels in the Clyde fell to 0.1µg at P/l.

The maximum recorded levels of nitrate in the Clyde Sea area appear to exceed the winter maximum for other areas around the coasts of Britain. The greatest recorded abundance of nitrate in Fairlie Channel in 1973 was 23.7µg at N/l at the end of January. In 1972 a peak of 14.3µg at N/l was recorded, although the actual maximum may have been missed due to the longer sampling interval. The greatest value found in the outer Firth in 1972 was 18µg at N/l at Garroch Head (station 8 in Figure 3), whereas the heavily polluted Gareloch gave an extreme value of 57.7µg at N/l at its opening to the estuary. Normal winter levels in this body of water lie between 15 and 25 and are related to lowered salinity; Ewins & Spencer (1967) considered that the enriched nitrate status of the Menai Straits was a consequence of nitrogen from run-off water and drainage. The winter maximum in Loch Long was 15.2µg at N/l in 1972 and 22.0 in 1973.

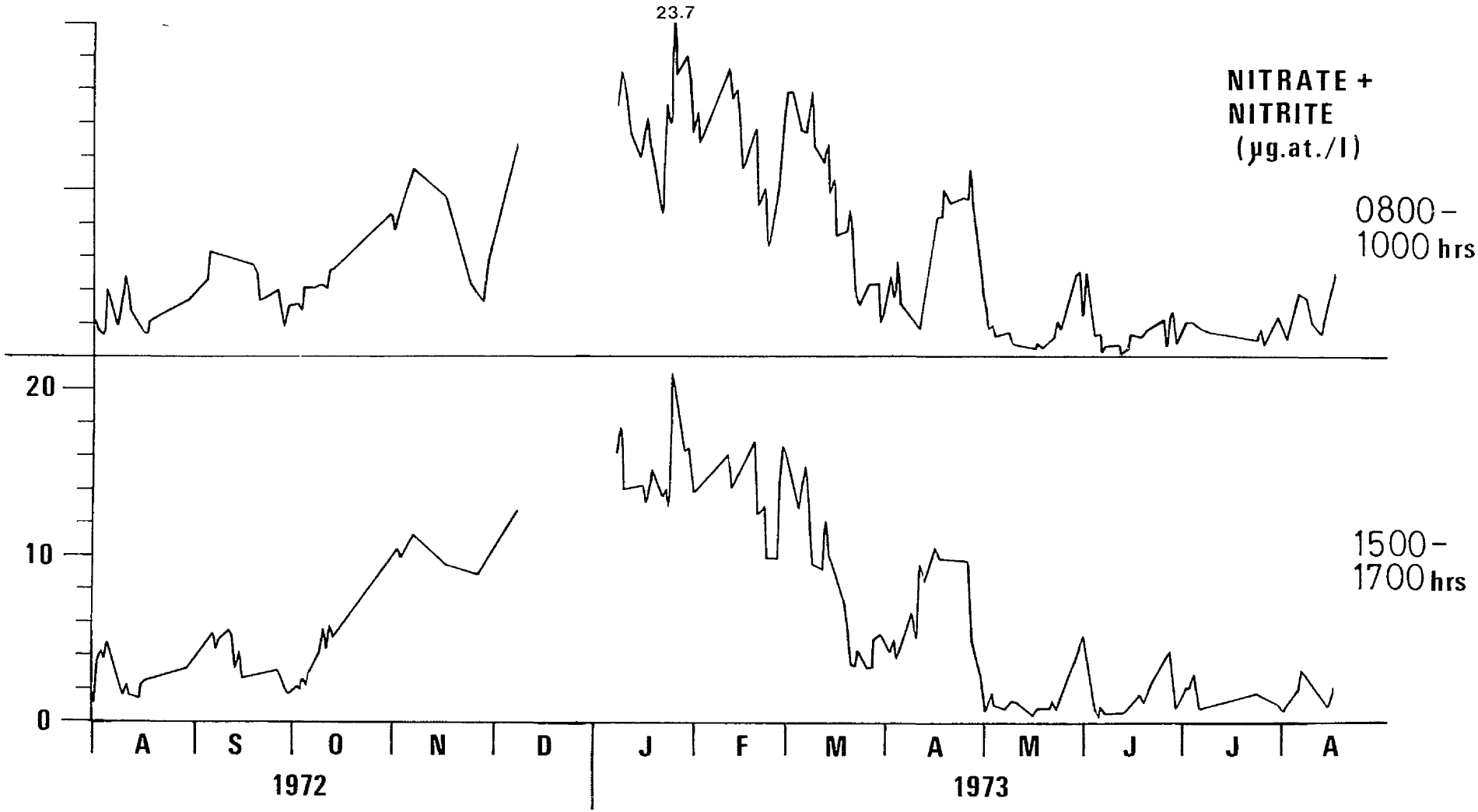
TABLE 2. Nitrate Nitrogen (µg at N/l) for surface waters from various localities

Locality	Maximum	Minimum	Author
Loch Creran (1973)	5.31	0.09	Tett (1974, unpublished)
North Sea	9	--	Cushing & Nicholson (1963)
Trondheimsfjord	6.6	0	Sakshaug *et al.* (1973)
English Channel 1925	6.0	<0.5	Cooper (1933)
1926	7.0	"	
1927	8.0	"	
1928	7.8	"	
1961-62	13	<0.5	Armstrong (1970)
Cardigan Bay	24*	0	Sykes (1969)
Menai Straits	16.5	<0.5	Ewins & Spencer (1967)

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

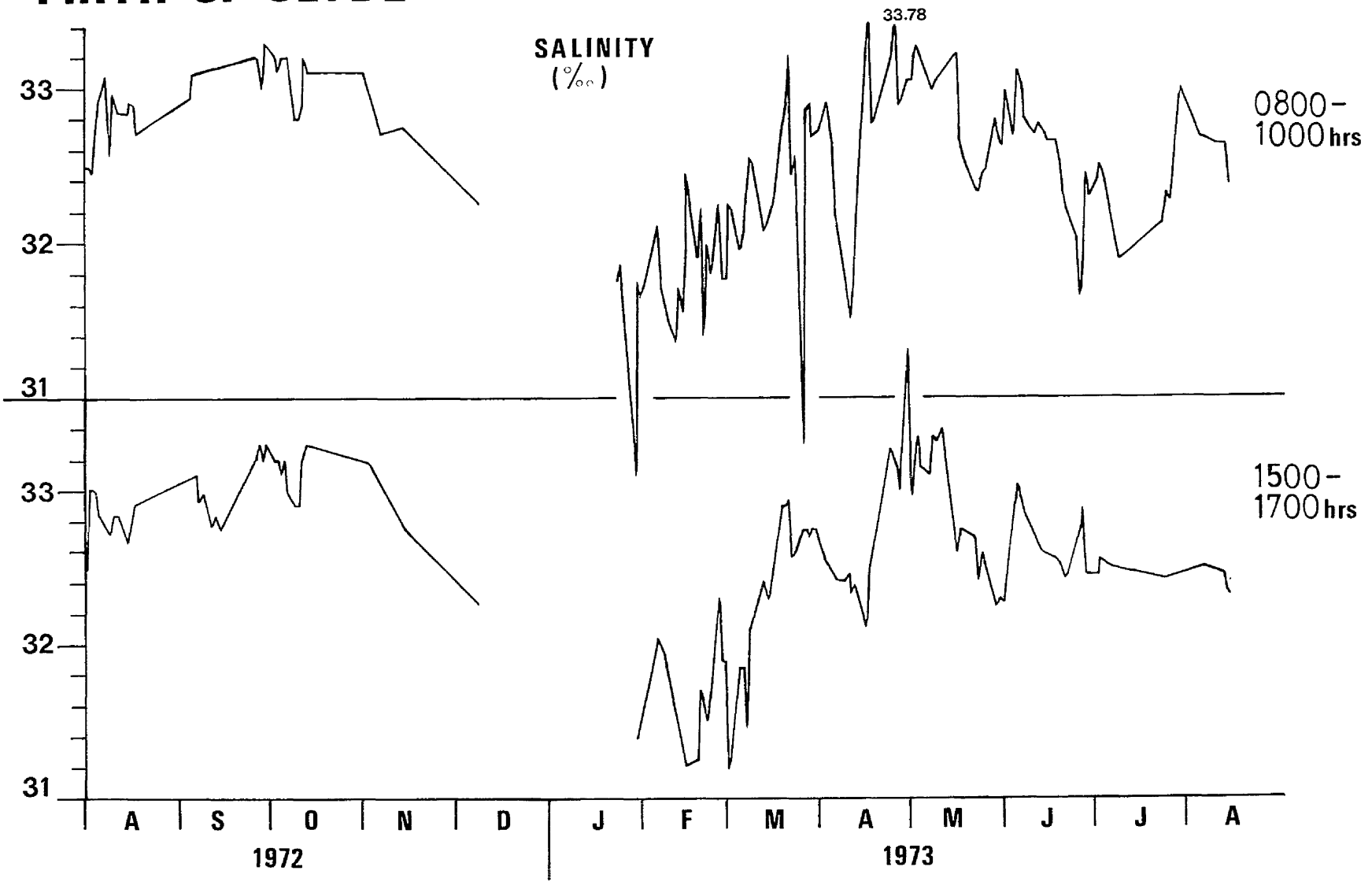
3 METRES DEPTH Fig 9



Although nitrate fell to undetectable levels in some areas, most maintained an equilibrium concentration below 0.5µg at N/l. This was also true for the Fairlie Channel where levels often fell below 0.5 during May and June in both years. However, as indicated by Ewins & Spencer (1967) an equilibrium nitrate concentration of 0.5µg at N/l is adequate to maintain an appreciable standing crop. The fairly constant ratio between nitrogen and phosphorus both in marine plankton and in the sea water has often been remarked on, with the average value being 15:1 by atoms (Corner & Davies, 1971). This ratio was found to hold in the Clyde during the winter, with an extreme range of 13 to 20:1. During the summer, however, considerable anomalies were found, with the ratio falling to 1:1 at the beginning of June. This is similar to the ratio recorded for Naragansett Bay (Pratt, 1965) which never exceeded 4:1 and generally lay below 1:1.

Of the sources of combined nitrogen available to phytoplankton nitrate is generally the most important inorganic source (Barnes, 1957). Although during the summer when nitrate becomes depleted ammonia (resulting from short term regeneration) may be extremely important in maintaining productivity (Dugdale & Goering, 1967). The levels of this nutrient for the Clyde Sea area have been analysed by the Clyde River Purification Board (unpublished) who show maximum winter values of 3.4µg at N/l, falling to less than 0.3µg at N/l in the summer. The other inorganic source of nitrogen, nitrite, is always present in very low amounts with a maximum of 0.33 and a minimum of 0.04µg at N/l.

Silicon exists in sea water as orthosilicates and is an essential part of the solid structure of the main primary producers in temperate waters, the diatoms (Armstrong, 1965). Frustules of the organisms may contain up to 30% of SiO_2 (Lewin & Guillard, 1963) and their growth and multiplication may exhaust supplies of silicate in a matter of days. The winter concentration of this nutrient in the Fairlie Channel was


FIRTH OF CLYDE
FAIRLIE CHANNEL STATION
3 METRES DEPTH
Fig 10
SALINITY
(‰)
33.78
0800-
1000 hrs
1500-
1700 hrs
33
32
31
33
32
31
A
S
O
N
D
J
F
M
A
M
J
J
A
1972
1973

similar in both 1972 and 1973 when respective maxima of 13.4 and 14.95µg at Si/l were recorded. Values reached 16 at Garroch Head (station 8).

Like nitrate, there is a complete absence of any seasonal data for silicate in the Clyde Sea area and it is useful to make comparison with other parts of this region. In 1972 silicate levels in Gareloch ranged from 40µg at Si/l at the mouth to 20µg at Si/l at the head of the loch, while in 1973 the recorded peak was 20µg at Si/l. In Loch Long the maximum abundance of silicate was 14µg at Si/l in 1972 and 20.4µg at Si/l in 1973, while a peak of 12.7µg at Si/l was recorded in Loch Striven in November, 1972. It appears that the distribution of silicate in these lochs was largely governed by the extent of dilution with fresh water. This phenomenon was also observed by Banaub & Burton (1970) who showed that in Southampton Water within the salinity range of 22 - 34‰ there was a linear relationship between amount of fresh water dilution and silicate concentration during the winter.

TABLE 3. Silicate (µg at Si/l) for coastal waters from various locations

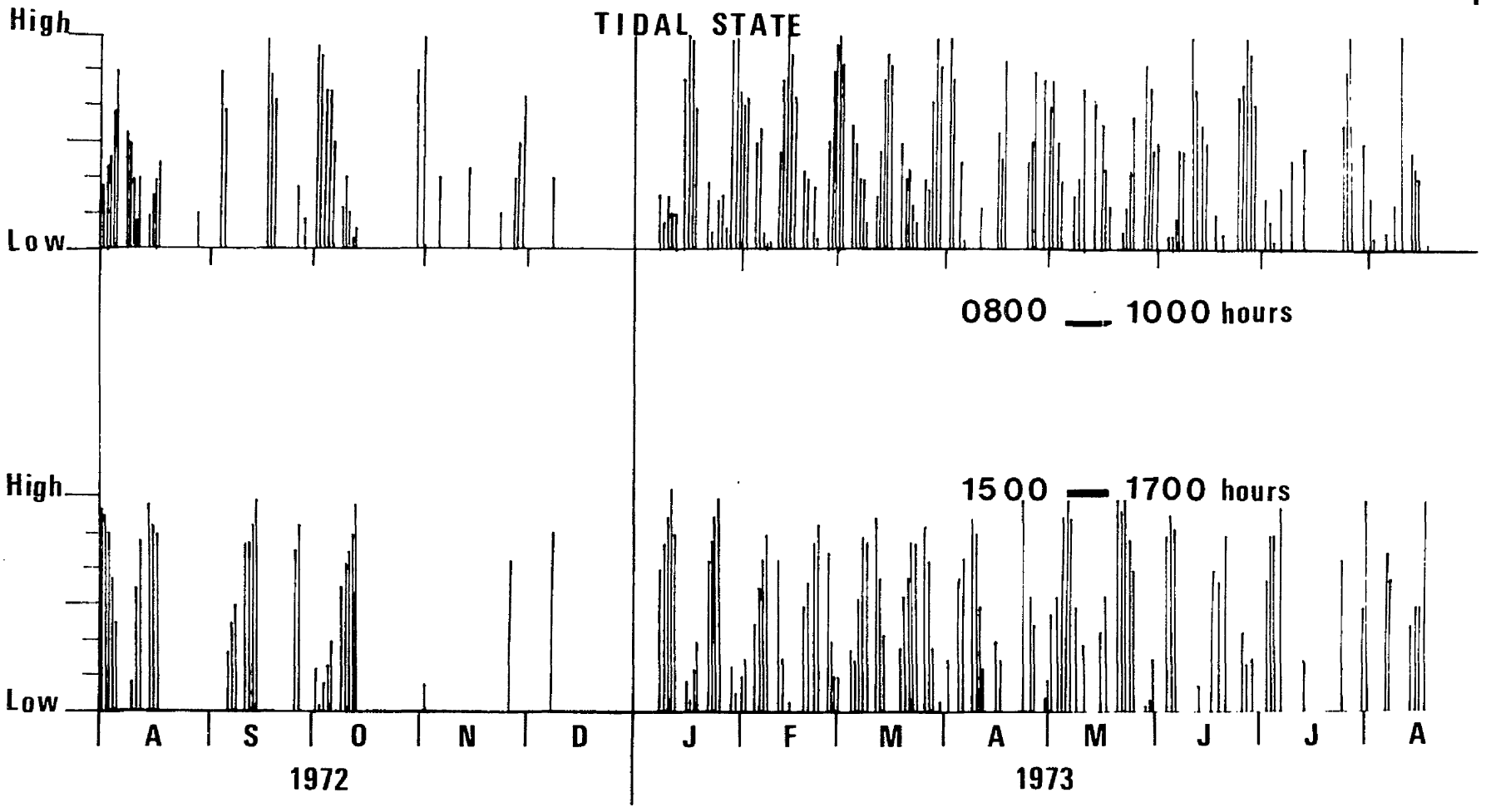
Locality	Maximum	Minimum	Author
Loch Creran (1973)	8.94	0.85	Tett (1974, unpublished)
North Sea	9	--	Cushing & Nicholson (1963)
Trondheimsfjord (1971)	>8	<1	Sakshaug et al. (1973)
English Channel (1924, 1927)	6.7	--	Cooper (1933)
(1928)	5	0.4	Cooper (1933)
(1931)	7.2		Cooper (1933)
(1932)	9.4		Cooper (1933)
(1957)	3.5	0.5	Armstrong (1959)
(1960-61)	3.0	0.5	Armstrong (1970)
Menai Straits	9	0.5	Ewins & Spencer (1967)
Cardigan Bay	12	--	Sykes (1969)

The minimum recorded levels of silicate in the Fairlie Channel lay between 0.4 and 0.5µg at Si/l in both years with values falling to 0.18µg at Si/l southwards from Garroch Head (station 11, Figure 3).

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

Fig 11



Loch Long and Gareloch fell to less than 1µg at Si/l in 1972 and 1973. Silicate shows a certain similicitude to both nitrate and phosphate, in never being reduced to undetectable levels in the summer and in having a larger winter maximum than other areas.

******

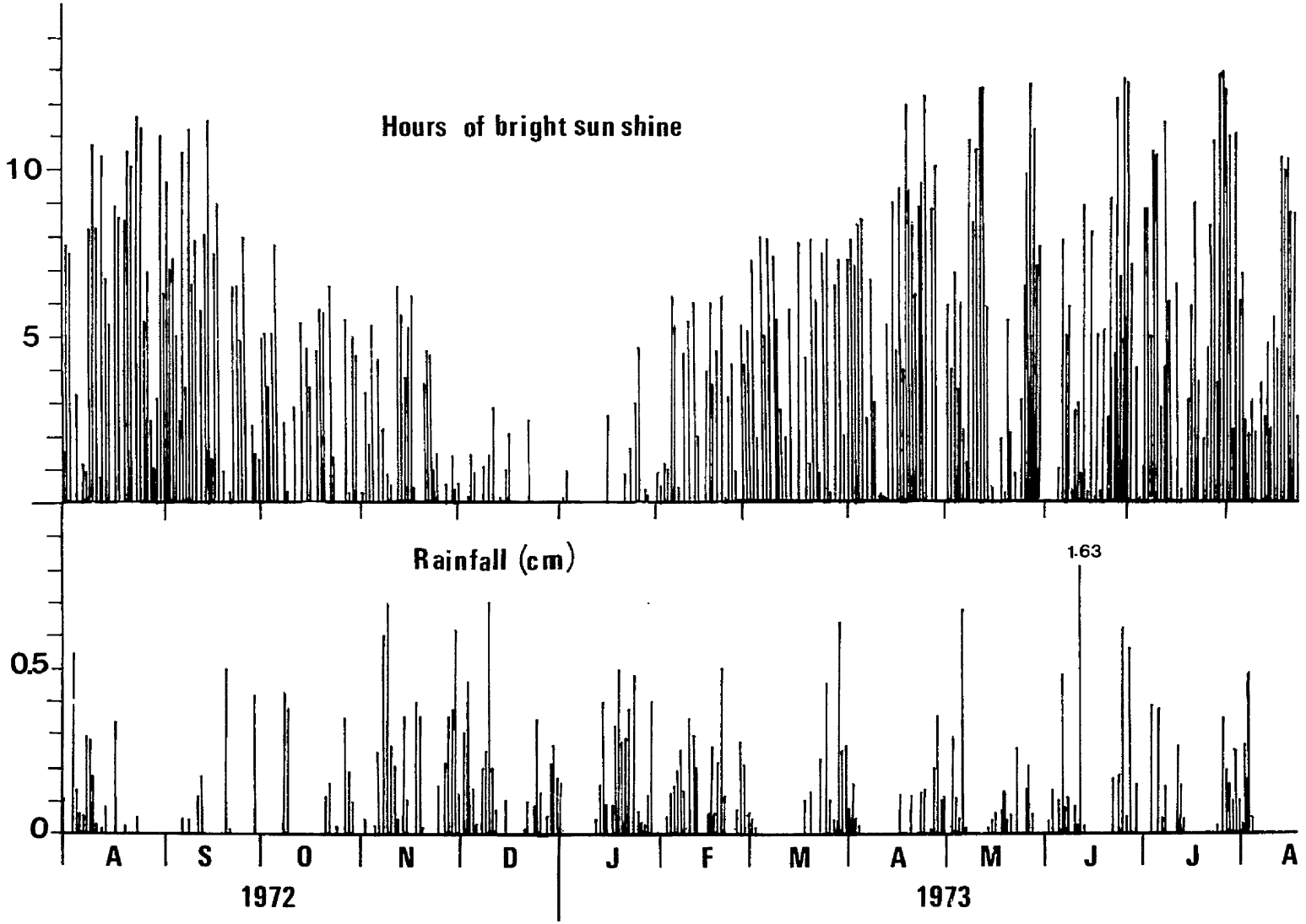
The seasonal patterns of distribution of phosphate, silicate and nitrate, shown in Figures 7, 8 and 9, are more detailed than curves available for any other area. In consequence, the detailed features of the curves, which require individual consideration, will be discussed in full, on a monthly and weekly basis in the next Chapter. Only the overall pattern of seasonal change will be discussed here. In general the year can be divided into two periods; first, a winter period (November to February) when the light regime and the environmental conditions are unsuitable for phytoplankton growth. During this period changes in nutrients are mainly due to non-biological environmental factors. The second period comprises the remainder of the year when the rise and fall of phytoplankton populations and other biological activity bring about rapid nutrient changes.

Figure 7 shows the seasonal cycle of phosphate in the Fairlie Channel. Fluctuating levels in August, 1972 rise to a maximum in September followed by a decline at the end of the month. This fall was short-lived and an irregular rise ensued reaching a maximum between January and February. For the entire winter period phosphate remained above 1µg at P/l followed by a marked reduction in early spring, 1973, associated with the spring diatom increase. Apart from the marked rise in April, levels fluctuated between 0.25 and 0.6µg at P/l during the spring and summer. The phosphate changes during the spring rise in diatoms in 1972 was similar but apparently occurred about a month later. The phosphate minimum was slightly less, 0.18µg at P/l, and no increase in levels occurred in

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

Fig 12



late spring.

Silicate (Figure 8) followed a regular seasonal pattern in the Fairlie Channel although Raymont (1963) found that its seasonal distribution in the English Channel was somewhat irregular. Low, fluctuating summer levels in August, 1972 gave way to a period of increase towards the latter half of the month reaching an early autumn maximum of around 6µg at Si/l. This agrees with Cooper (1933) who has recorded a marked regeneration in some years in August. This he attributed to the more rapid regeneration and cycling of this nutrient, due to the dissolution of dead diatom valves, both in surface and bottom waters.

The marked fall at the end of September accompanied the decline of phosphate and was similarly short-lived. The winter silicate rise started in October reaching its highest levels from December onwards (as does phosphate).

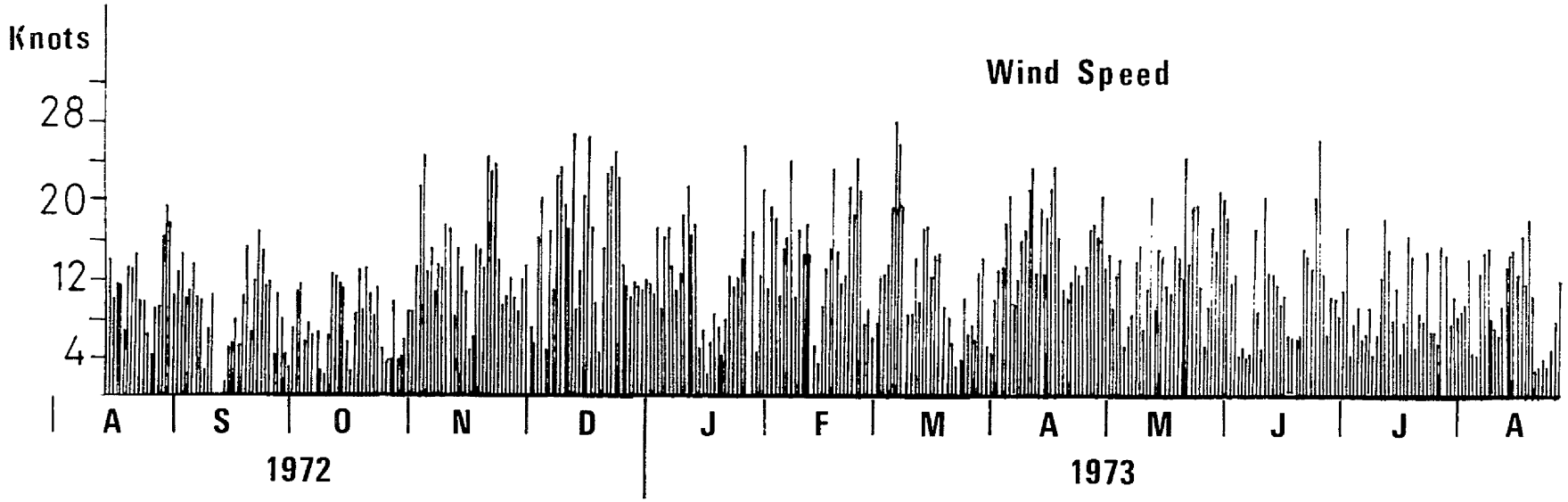
The dramatic fall in silicate levels in early spring (middle of March) caused by utilization of diatoms reduced this nutrient to very low levels (0.5µg at Si/l) in a matter of days. During the rest of the spring and summer, with the exception of the prominent rise in April, silicate levels remained below 4µg at Si/l with clear fluctuations. In the spring of 1972 silicate utilization appears to begin at the same time as in 1973. However, the rate of depletion was much slower with minimum levels (0.21) not being reached till the end of April. Silicate persisted at lower levels than in 1973 (less than 1) with only small rises (to around 2) in June.

Nitrate and nitrite (Figure 9) show a clear seasonal pattern although short-term fluctuations are considerable. Varying levels in August, 1972 give way to a steady rise in September along with the increase of phosphate and silicate. The subsequent depletion of all nutrients during the latter half of September accompanied the autumnal rise in phytoplankton. Nitrate levels thereafter increased, exceeding 10µg at N/l

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

Fig 13



by the end of November, although its maximum abundance was not recorded till February. This is two months later than when phosphate and silicate approached their highest winter levels and is in agreement with Barnes (1957) who indicates that nitrate shows a longer regeneration period than the other two nutrients.

A remarkable feature of the winter variation of nitrate is its wide range of fluctuations, with extreme values of 6 to 23.7. Periodic nitrate peaks appeared to be related to transient reductions in the salinity. During the vernal diatom increase nitrate fell to around 4µg at N/l. The winter irregularities gave way to a clear pattern during the late spring and summer, when levels fluctuated below 6 except for the prominent rise in April which was common to all nutrients. During spring, 1972 the fall in nitrate occurred in April reaching considerably lower levels (0.5µg at N/l) than in 1973. These low concentrations persisted till June.

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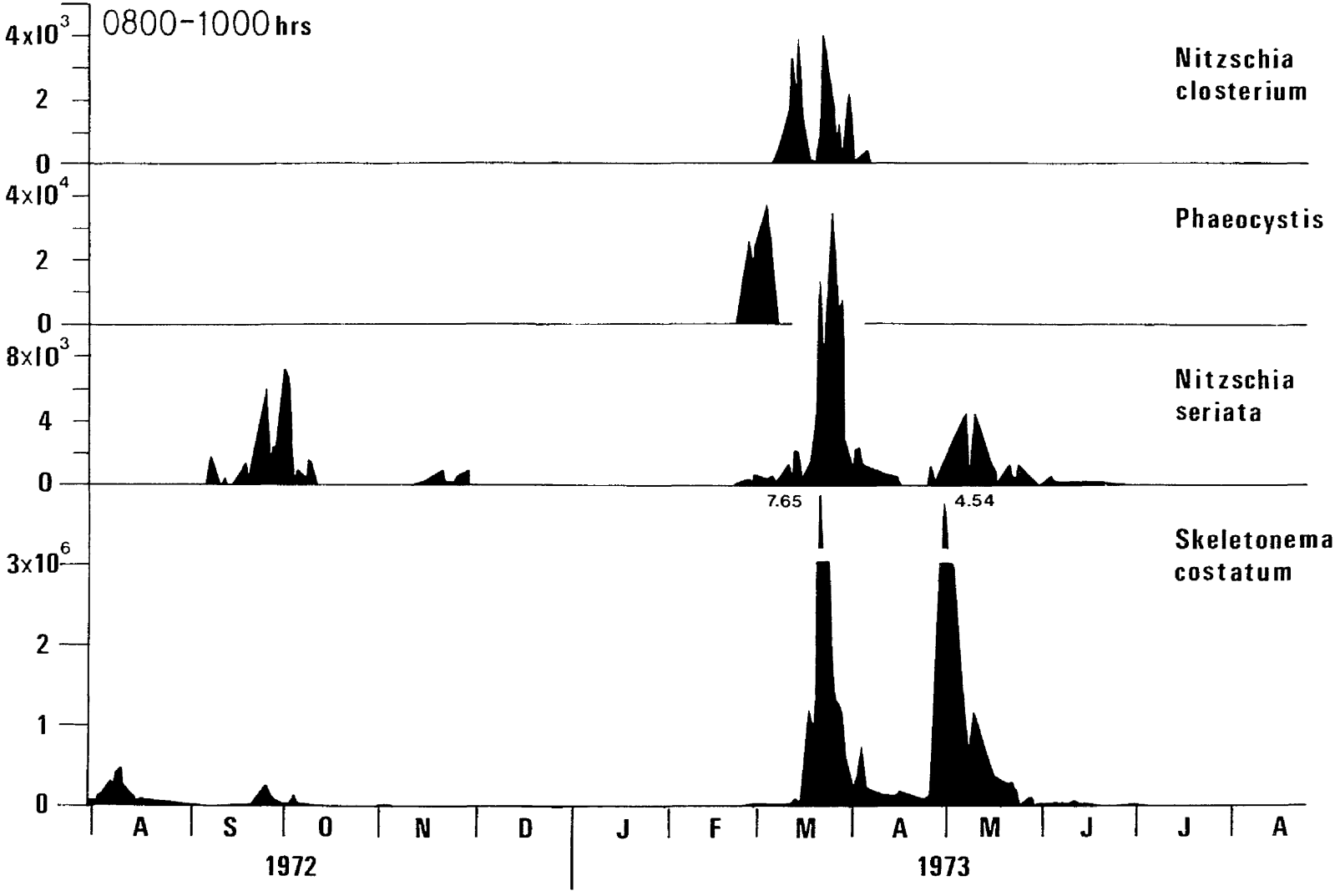
The rise and fall of the salinity curve (Figure 10) with its distinctive winter minimum is clearly related to the seasonal pattern of rainfall (Figure 12) and the influence of winds (Figure 13) on the movement of water masses (Barnes, 1961). Short term fluctuations may be related to the state of tide at the time of sampling (Figure 11) (Barnes & Goodley, 1958). During August, 1972 the salinity fluctuated between 32.5 and 33 rising to a maximum of 33.3 in October. This increase is probably associated with two factors, firstly the very high (20 knots) south-westerly winds in August which evidently introduced highly saline water into the lower Firth and secondly the extremely low rainfall throughout August, September and the first half of October. The turbulent mixing of nutrient-rich deep water with surface waters during this period was the probable cause of the rise in all nutrients observed in September

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

3 METRES DEPTH

Fig 14



and coincided with small total number of phytoplankton during the first half of September (Figure 17).

Following the salinity maximum in October, the amount of rainfall rapidly increased with November being particularly wet. The increased flow from the estuary resulted in a rapid reduction in salinity, falling to 32.2‰ at the end of the month. This was accompanied by very high (more than 20 knots) winds causing vertical mixing of the water column. The rapid enrichment of nutrients in surface waters is probably a consequence of both the nutrient rich deep water and the high nutrient load from the Clyde estuary. In general, anomalously low values of salinity corresponded with high nutrient levels. This is clearly seen at the end of January when salinity fell to its lowest recorded level, 30.4‰, which coincided with nitrate, phosphate and silicate peaks.

Following the low salinity levels of January and February an increase was clear in March, which was a month with little rainfall and slight winds. A maximum of 33.2‰ occurred at the middle of the month although salinity fell rapidly at the beginning of April (to 31.3‰) following a period of high rainfall. The subsequent increase in salinity was rapid with the annual maximum of 33.78‰ being recorded at the end of April. An overall fall in salinity occurred from May till July with periodic heavy rainfall being associated with transient salinity reductions. During the spring and summer period nutrient pulses were often associated with increased salinity. The annual variation of salinity for the Fairlie Channel given as the mean of the years 1949 - 1954 (Barnes, 1956) shows a maximum salinity in June of 32.98‰, while in this survey a maximum of 33.78‰ was found in April. The minimum salinity was recorded in January by Barnes, which is in agreement with the present findings.

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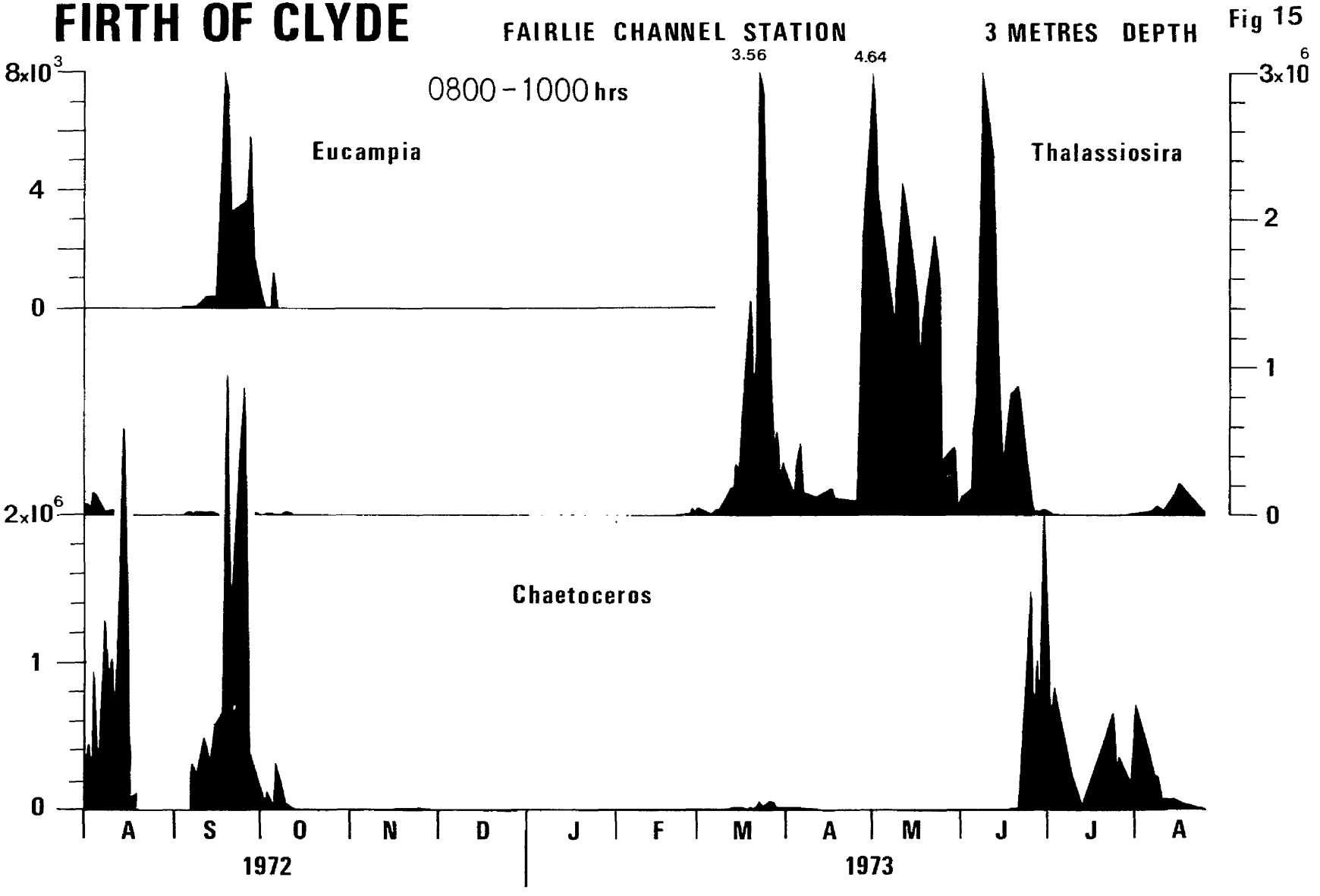

FIRTH OF CLYDE
FAIRLIE CHANNEL STATION
3 METRES DEPTH
Fig 15
0800 - 1000 hrs
3.56
4.64
8x10^3
4
0
Eucampia
Thalassiosira
3x10^6
2
1
0
2x10^6
Chaetoceros
1
0
A
S
O
N
D
J
F
M
A
M
J
J
A
1972
1973

The pattern of seasonal succession of phytoplankton studied in the Fairlie Channel (Figures 14, 15 and 16) shows a clear similarity to that described for Loch Striven in 1926 by Marshall & Orr (1927). In both 1972 and 1973 the dominant component of the spring diatom increase (S.D.I.) was Skeletonema costatum, the typical vernal diatom of the Clyde Sea area. This was accompanied by smaller amounts of Thalassiosira nordenskioldii, which constituted one-tenth of the total in 1972 and one-third in 1973. In the earlier year the S.D.I. occurred at the beginning of April, whereas in 1973 the increase was almost over by the end of March. The water temperature at the time of increase was 7.0°C. However, it has been shown that Skeletonema can reach great abundance in nature at any temperature between 2° and 9°C (Raymont, 1963) and is not temperature dependent.

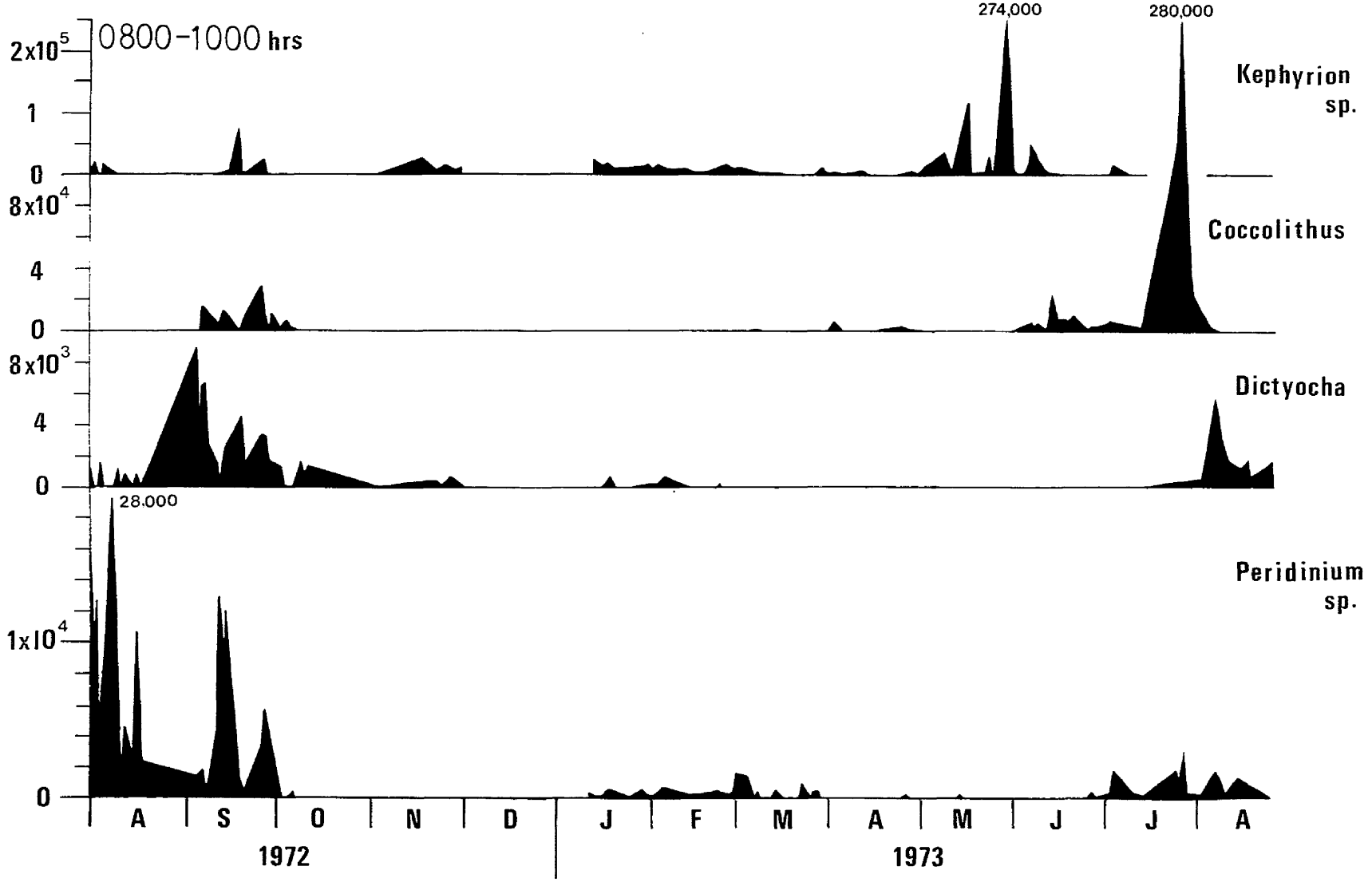
The complete predominance of Skeletonema reported on several occasions in Loch Striven (Marshall & Orr, 1930) was not found during the two years of the present survey. The accompanying diatoms were generally Thalassiosira, Nitzschia seriata and Nitzschia closterium (Phaeodactylum tricornatum), with the spring outburst being preceded by a small pulse of Phaeocystis pouchettii.

A visit made on 15th March, 1973 to Loch Striven, a week prior to the S.D.I. in the Fairlie Channel, showed that the spring increase had already reached its peak. Numbers of diatoms exceeded 13 million cells/litre in the upper 2 metres and the water was visibly brown. Nutrients were reduced to low levels, nitrate to 1.61µg at N/l, phosphate to 0.44µg at P/l and silicate to 1.27µg at Si/l. The domination of the diatom population by Thalassiosira nordenskioldii, which constituted more than 80% of the total is a phenomenon unusual for Loch Striven. However, Butler et al. (1970) recorded the predominance of Thalassiosira in the inner Firth in the S.D.I. of 1969. The spring increase in Loch Long and Gareloch in 1973 showed a similarity to Loch Striven in preceding

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

3 METRES DEPTH Fig 16



the outburst in the Firth of Clyde by about a week. However, the dominant phytoplankton in Loch Long was Skeletonema (66%) with lesser amounts of Thalassiosira. The Gareloch displayed a predominance of Thalassiosira with insignificant amounts of Skeletonema. In all bodies of water examined in spring, 1973, except for Gareloch, small numbers of Peridinium spp. were present reaching about 4000 cells/l.

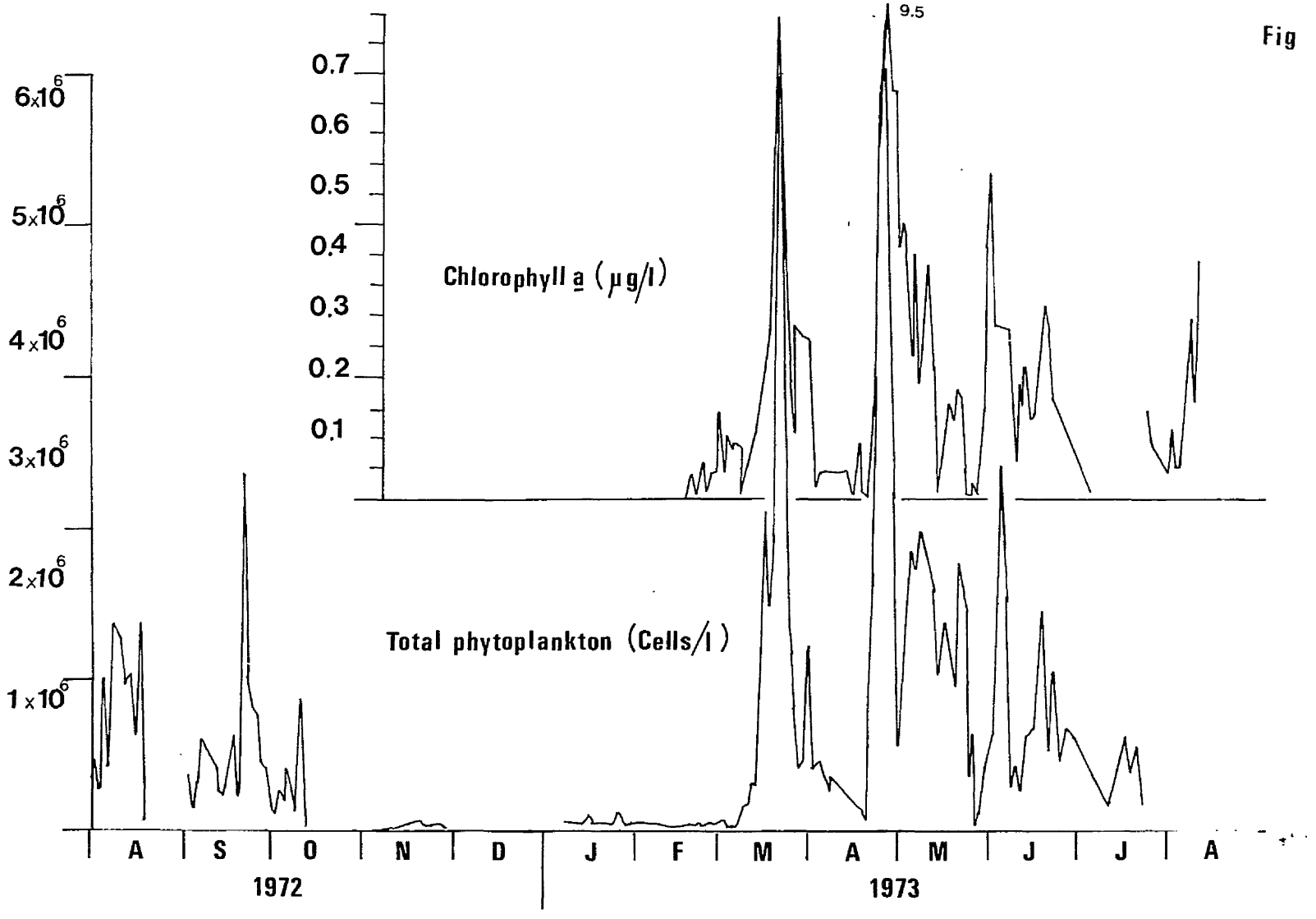
In Loch Etive, a sea loch to the north of the Clyde, the S.D.I. in 1970 and 1971 was dominated by Skeletonema which exceeded 95% of the total in both years. Other phytoplankton present were Thalassiosira nordenskioldii, T. rotula and Peridinium triquetra (which is frequently recorded in the Clyde). Comparable studies in Norway show a fairly similar picture. Jensen & Sakshaug (1973) showed that the spring population in Trondheimsfjord is dominated by Skeletonema with smaller numbers of Thalassiosira gravida and Chaetoceros debilis or C. sociale (species not found in the Clyde till later in the year). Small quantities of Nitzschia and Phaeocystis were also recorded. Hasle & Smayda (1971) observed a spring population of Thalassiosira nordenskioldii, Chaetoceros socialis and some Phaeocystis in the polluted Oslofjord. An extremely early S.D.I. was recorded by Braarud (1973) in Hardangerfjord where Skeletonema achieved complete domination in February.

Following the early spring diatom increase in the Clyde Sea area Thalassiosira, Skeletonema and Nitzschia seriata produced a second pulse during May, 1973. However, in 1972 Chaetoceros cinctum rapidly replaced the Skeletonema-Thalassiosira population to become the dominant organism at the beginning of May. A similar pattern of succession to 1972 was shown by Marshall & Orr (1927) for Loch Striven where the late spring population consisted of Skeletonema and Chaetoceros cinctum. The succession of Chaetoceros after the early spring population also occurs in Trondheimsfjord (Jensen & Sakshaug, 1973). In Loch Etive, as in the Clyde in 1973, the second spring pulse is again dominated by Skeletonema

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION 3 METRES DEPTH

Fig 17



(Wood, Tett & Edwards, 1973). This phenomenon has also been recorded in the Clyde Sea area (Marshall & Orr, 1927).

Following a third pulse of Thalossiosira in June in the Fairlie Channel (1973), the population became dominated by Chaetoceros cinctum. This is in agreement with the pattern of species succession described by Hasle & Smayda (1971) who showed that Chaetoceros usually succeeded Thalassiosira. As the water becomes warmer during the summer the population is characterized by increased numbers of flagellates and a more diverse species composition. The first flagellate to make its appearance in any numbers was Kephyrion sp., a chrysophycean species with a very small pale brown lorica (less than 5μ in length). This organism appeared in quantity in May in both years, and has not been previously recorded in such quantities from British coastal waters. Leadbetter (1974) has isolated similar Kephyrion spp. from the Mediterranean Sea.

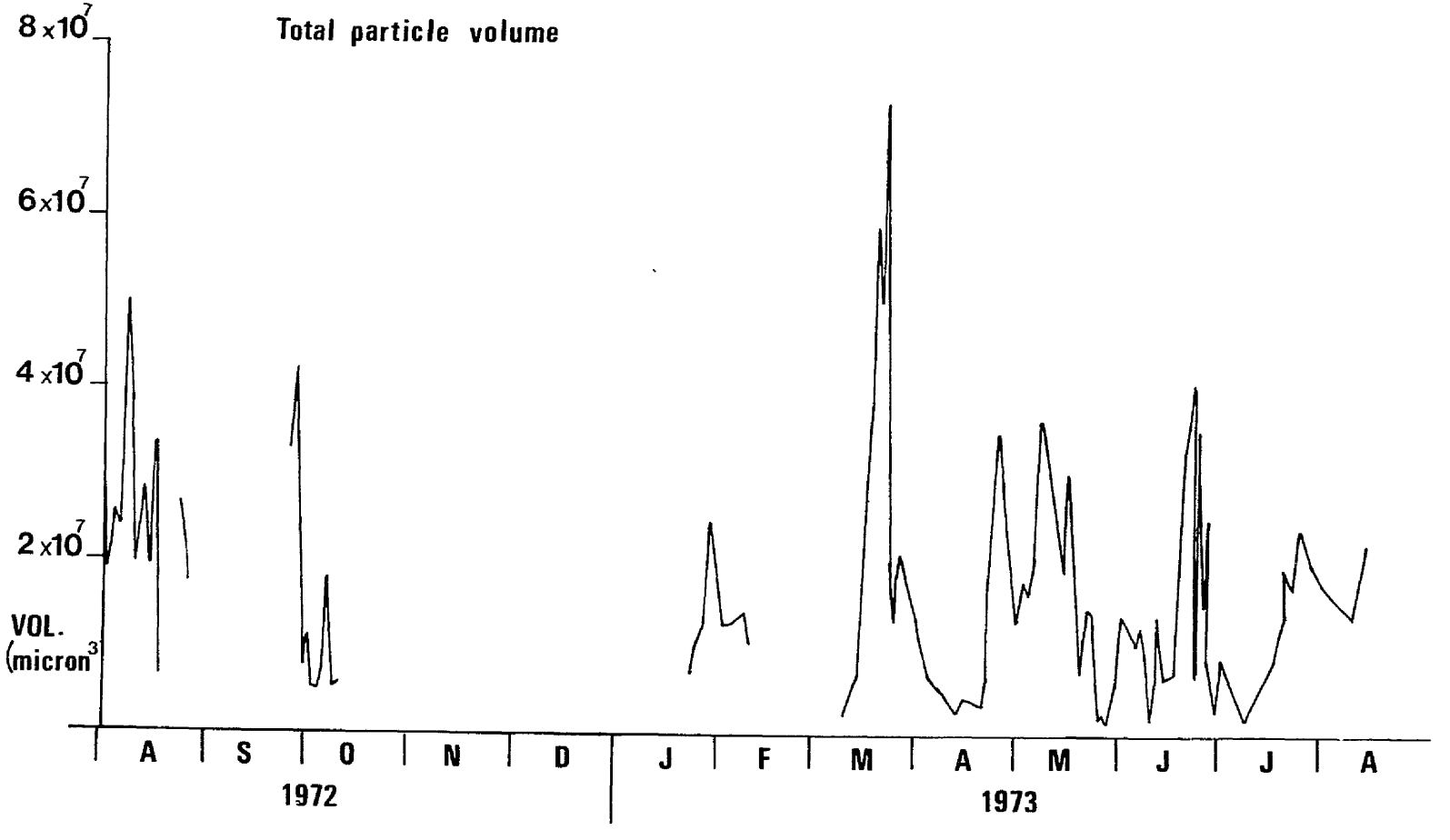
The coccolithophore, Coccolithus huxleyi, produced a pulse in late July, 1973, although it was not recorded in any abundance in 1972. This species has often been recorded from northern oceanic waters (Braarud, 1953) and from the North Sea (Round, 1970). Marshall (1924) recorded it from the stomach contents of Calanus taken from the Clyde, with maximum numbers in July. A great abundance of coccolithophores was noted in June by Nicoll (1971) in Loch Ewe where they reached sufficient numbers to colour the water a "milky green" colour. Hasle & Smayda (1971) described the very large populations of Coccolithus huxleyi in the Oslofjord as a manifestation of the polluted state of the water.

Dinoflagellates, notably the neritic species Peridinium triquetra occurred irregularly throughout the year and reached a summer maximum in both years. A large pulse occurred in July and August, 1972 while in 1973 a smaller increase was observed in July. The water during this period was warm (14 - 15°C). During August of both years Ceratium tripos

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

3 METRES DEPTH Fig 18



C. furca and Dinophysis sp. became common. Generally the latest recorded flagellate was the silicoflagellate Dictyocha speculum which occurred between August and September. Late summer also saw an increased diversity of Chaetoceros species with the appearance of C. diadema, C. breve, C. sociale and C. simplex.

The autumn diatom increase in 1972 consisted of Leptocylindricus danicus and Eucampia zodiacus with no increase in Skeletonema or Thalassiosira, although the species which usually accompanies them Nitzschia seriata increased. The autumn diatom increase in Loch Etive (Wood et al., 1973) consisted of Skeletonema and Leptocylindricus danicus in 1971, while Marshall & Orr (1927) showed that the autumn pulse in Loch Striven was due to a Leptocylindricus/Eucampia population.

The quantitative aspects of the changes in standing crop are shown in Figures 17 and 18 where three different estimates are given; total phytoplankton counts, chlorophyll a levels and total particle volume using a 'Coulter Counter'. It is evident that the three estimates closely parallel one another, each showing simultaneous pulses related to increasing biomass. The highest values for all three measurements came in early spring (23rd March) when the total cell count exceeded 11 million cells per litre. Chlorophyll reached 0.83µg/l and the total particle volume increased to 7.2×10^7 cubic microns (μ^3) per litre. This shows a close similarity to the vernal outburst in 1969 in which the maximum abundance of phytoplankton (mainly Thalassiosira) was 12.5 million cells/l with a chlorophyll a reading of 0.6µg/l (Butler et al., 1970). From a comparison with the small amount of quantitative data available it appears that the spring diatom increase of 1973 is much larger than the typical spring increase around the Cumbraes.

The maximum abundance of phytoplankton recorded in Loch Striven in 1973, 13 million cells per litre, was greater than that in the Fairlie Channel although it falls far short of the peak abundance for this loch

of 30 million cells/litre recorded in 1927 (Marshall & Orr, 1930). Wood et al. (1973) reported spring maxima in Loch Etive of 3 million cells/l in 1970 and 9 million in 1971. The spring productivity is of equal magnitude in the Norwegian fjords where Hasle & Smayda (1960) recorded a peak of 11.5 million cells/litre in Oslofjord while Jensen (1973) showed a pulse of 6.5 million in Trondheimsfjord.

The phytoplankton increase in the Clyde was accompanied by an increase in the amount of dissolved oxygen, rising from 94% at the beginning of March to 110% at the end of the month. pH displayed a simultaneous increase from 7.7 to 8.02 at the surface. Of the dissolved nutrients measured silicate fell by 11µg at Si/l, nitrate by 13µg at N/l and phosphate by 1µg at P/l. Ammonia (measured by C.R.P.B. at infrequent intervals) decreased from 3.4 to 1.8µg at N/l, while nitrite showed no overall change.

The late spring pulse reached a maximum of 11 million cells/litre towards the end of April. This was reflected in a large rise in chlorophyll a levels, to 0.81µg/l and a simultaneous increase in the total particle volume to $3.6 \times 10^7 \mu^3/l$. The presence of a second spring pulse of phytoplankton has previously been described for this region of the Clyde by Marshall & Orr (1927).

Two bursts of phytoplankton came in June, the first at the beginning of the month reaching about 3 million cells/l with a chlorophyll a reading of 0.5µg/l and a T.P.V. of $1.3 \times 10^7 \mu^3/l$. The second pulse towards the end of June slightly exceeded 2 million cells/l with a T.P.V. of $4 \times 10^7 \mu^3/l$. the chlorophyll peak, 0.66µg/l was greater than the first pulse and may have resulted from the changed species composition of the population. A further pulse at the end of July reached only 1.4 million with a T.P.V. of around $2 \times 10^7 \mu^3/l$. In general, in 1973, the magnitude of the spring increase was greatest with later pulses becoming successively smaller, till July. From August onwards the size

of the pulses may increase again. This is clearly shown in 1972 when the standing crop reached a maximum of 2 million cells/l in August with a T.P.V. of 3.4 while the autumn phytoplankton pulse (in September) rose to around 3 million cells/litre with a corresponding T.P.V. of $4.3 \times 10^7 \mu^3/l$

CHAPTER 5

CHAPTER 5

VARIATIONS IN THE PRODUCTION OF PHYTOPLANKTON IN SELECTED STUDY PERIODS AND ON SUCCESSIVE DAYS

Considerable day to day variations in the primary production of phytoplankton and in the population composition and biomass have been described by Spodniewska (1969). His short-term investigations on a daily basis indicate the potential of such studies, however the inability to distinguish periods of especial interest in advance make such work of limited use. In fertile coastal waters the generation time of the spring increase may be less than two days (Eppley and Strickland 1968) and the number of cells may increase 1000 to 10,000 fold in less than a week. The rapidity of such changes in primary production with populations reaching a peak and declining within two weeks and their uncertain period of occurrence necessitates continuous intensive sampling with samples taken at the shortest possible interval (a day or less). From this accumulated data selected study periods can be located at a later date and studied in detail in relation to other environmental parameters.

A further problem which is posed is that under the alternating light-dark cycle of the natural environment cell-division becomes synchronous. Jorgensen (1966) showed that under diurnally intermittant irradiation of 12 hours light and 12 hours dark cultures of Skeletonema costatum divide synchronously. Cell division was reported to commence in the middle of the light period. However there may be no general rule as cell division for some phytoplankton has been reported in the early hours of darkness (Riley and Chester 1971 and Eppley and Strickland 1968). If standing-crop estimates are made from chlorophyll determinations then the evidence of daily fluctuations in chlorophyll content per cell may have to be taken into consideration. Glooschenko et al (1972) have demonstrated such daily

fluctuations in cellular chlorophyll content in Skeletonema with peak concentrations at night. If, as seems likely, periodic variations affect natural populations samples for measurement of chlorophyll and cell numbers must be taken at the same time of day.

Selected study periods in which the most marked variations in phytoplankton and related parameters occurred have been chosen from the annual cycle, already described in the previous chapter. The data for these periods have been plotted as individual graphs for morning (0800-1000 hrs) and afternoon (1500-1700 hrs) samples. From this period a significant week has been chosen in which the data for a single depth (3 metres) has been plotted on a morning-afternoon and on a tidal basis. This type of representation allows consideration of the diurnal or tidal changes involved in biological, physical and chemical parameters. A number of depth profiles of both nutrients and phytoplankton (from the surface to 10m depth) have been plotted, accompanied by complete nutrient, oxygen, temperature and salinity profiles to the bottom of the channel (35 m).

i) March 1973

During March the early spring outburst of phytoplankton occurred with numbers rising from an initial sparse population (less than 10,000 cells/l) to exceed 14 million cells/l within a two week period. The dynamics of this increase for the two main constituents of the population, Skeletonema costatum and Thalassiosira nordenskioldii and for the major nutrients nitrate, phosphate and silicate are shown in Figure 19.

The change of season from winter to spring is indicated by the rising air temperature, increasing number of hours of bright sunshine (Fig. 12), increasing daylength and comparatively calmer weather(Fig. 13). In the Clyde Sea area in March 1973 meteorological data (obtained from hourly readings of wind speed and direction at Ardrossan) showed a windy period for the first 6 days of the month when mean daily velocities exceeded 13 knots with a maximum of 17.6 knots and the mean direction was west to south west. During this period the number of hours of bright sunshine per day was slightly less than four and the daylength was about 10.5 hours.

For the first week in March, and throughout the previous month, the predominant diatom was Thalassiosira which reached an average density of around 20,000 cells per litre by the first week in March. However, Skeletonema costatum only appeared occasionally and then in very small numbers (not exceeding 2,000 cells/litre). Chlorophyll a levels during this period were low (0.05µg/l) except for a sudden increase to 0.15µg/l from 5 to 8 March which was probably a consequence of the short appearance of the colonial alga Phaeocystis pouchettii. Nutrient concentrations in the water showed little difference from the high winter values recorded in February; silicate around 10µg at Si/l, phosphate around 1.0µg at P/l and nitrate at 15µg at N/l.

From March 7 till 15 winds became lighter (less than 10 knots) and variable in direction with the sea becoming calm from March 9. The number of hours of bright sunshine exceeded a daily average of 4 for the week with

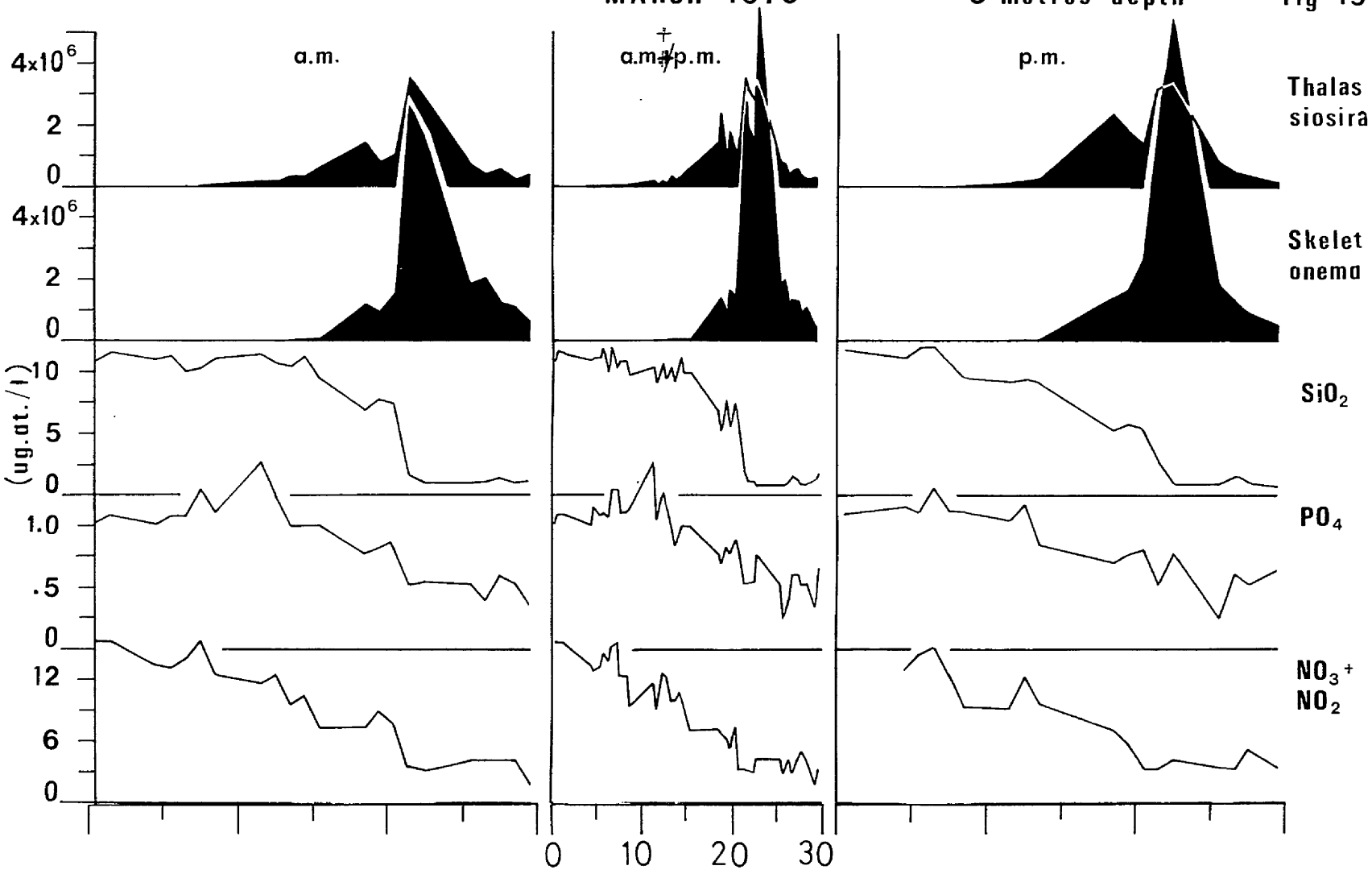
FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

MARCH 1973

3 metres depth

Fig 19



a maximum of 7.9 hours on 9 and 11 March. These two environmental parameters appear to influence the time of the initiation of the spring phytoplankton outburst. During this period Thalassiosira fluctuated in number between 30,000 to 100,000 cells per litre while Skeletonema made its first consistant appearance on March 9 when 2,000 cells/litre were recorded.

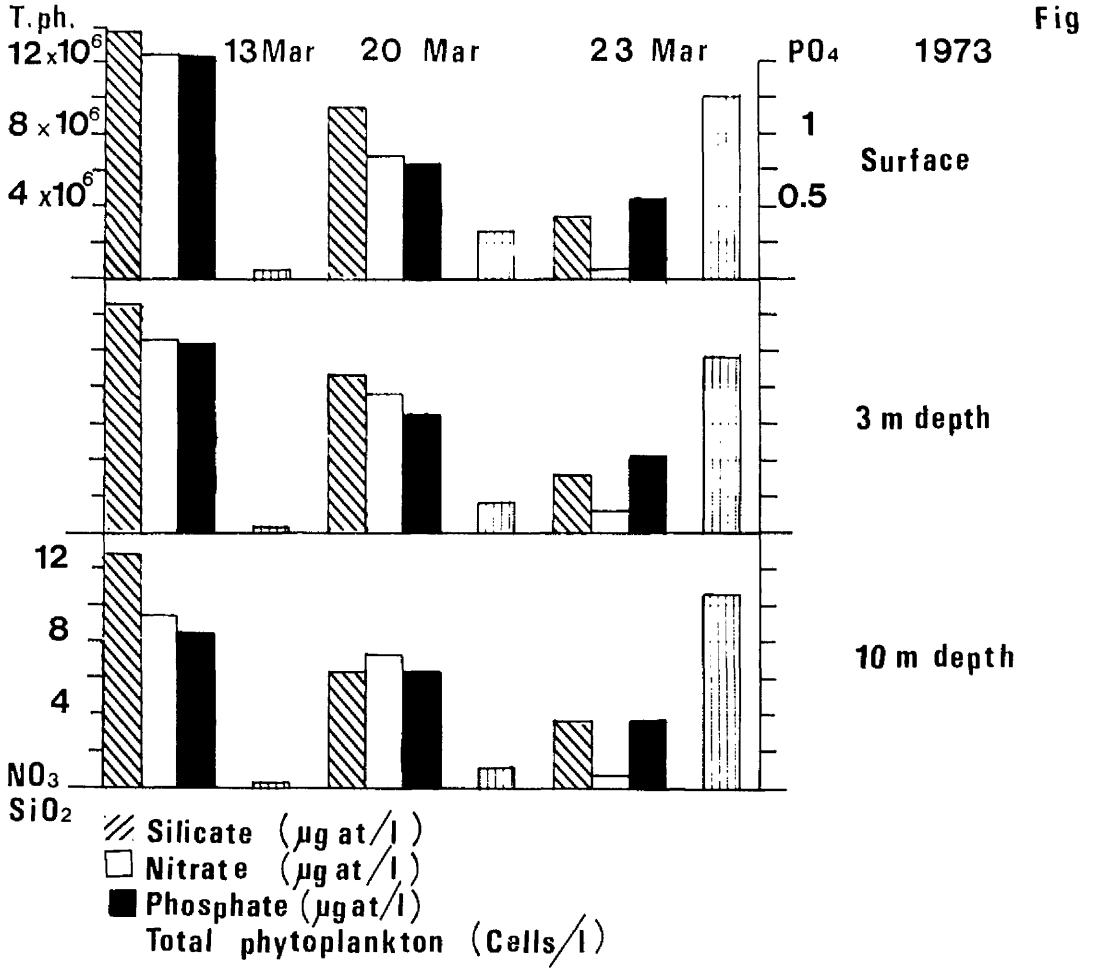
The commencement of the spring increase in the Clyde Sea area was taken by Marshall and Orr (1930) as being the time when the total phytoplankton population exceeds the arbitrary figure of 200,000 cells per litre. This number was reached on the morning of March 12, when Thalassiosira constituted 90% of the total. The chlorophyll a reading at this time was 0.07 µg/l and the total volume of suspended particles was 2.5×10^6 cubic microns. The calm period continued till March 16 when the total population 680,000 of which Thalassiosira constituted about 85%.

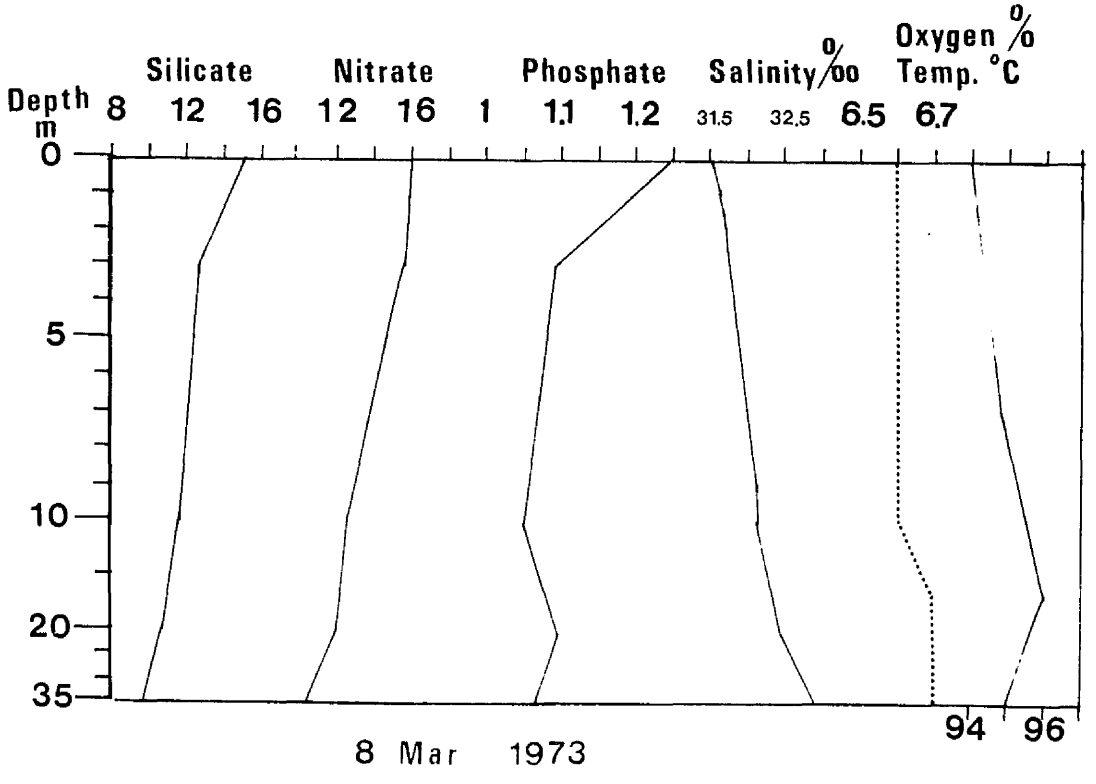
Over the following three days the number of Thalassiosira cells doubled while Skeletonema increased by ten-fold (to 1.18 million cells/l) giving a total population of 2.64 million cells/litre on the morning of March 19. The chlorophyll a level increased to 0.15 µg/l and the total particle volume showed a ten-fold rise to 2.72×10^7 cubic microns. Thalassiosira reached its maximum abundance of 3.4 million cells/l on the morning of March 23 while Skeletonema which had now increased to dominate the population did not reach its peak till the afternoon of the same day when 10.7 million cells/litre were recorded. Thus, the maximum abundance of phytoplankton in the early spring was found on the afternoon of March 23 when the total cell count just exceeded 14 million cells/litre, chlorophyll a readings reached 1.12 µg/l and the total particle volume exceeded 8×10^7 cubic microns. During the period of exponential growth the wind velocity increased, reaching a daily mean of 21 knots on March 24 while the number of hours of bright sunshine was nil on 19, 20 and 22 March. A similar phenomenon, with the growth kinetics of a diatom outburst being relatively independent of light changes

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

Fig 20





was also shown by Antia et al (1963) who studied a semi-natural population (including Skeletonema and Thalassiosira) isolated in a large volume plastic sphere.

By March 26 the spring pulse was almost dissipated with Thalassiosira declining to around 800,000 cells/litre and Skeletonema falling to 2 million cells/litre. Chlorophyll values declined to 0.5 µg/l on this date and the total particle volume fell to 2 x 10^7 cubic microns. For the remainder of the month winds exceeded a daily average of 15 knots reaching 23 knots on March 30. This period was characterized by a gradually declining diatom population.

The nutrient status of the water remained around its winter level during the first half of the month with the fluctuations being associated with purely physical factors. From the middle of the month as the phytoplankton abundance started to increase a gradual decline in nutrients was clear. Nitrate was the first nutrient to show a sustained fall, with a drop in concentration of 3 µg at N/l between March 14 to 15. No further depletion of this nutrient occurred till March 20 when a fall of 4 µg at N/l was recorded. Phosphate declined in a continuous but irregular fashion reaching its minimum level of 0.3 µg at P/l on March 26. The depletion of silicate occurred in two steps, firstly a gradual decline of 4 µg at Si/l between 16 and 19 March followed by a rapid fall from 9 to less than 1 µg at Si/l between the afternoon of 21 and the morning of 22. In both nutrient uptake periods the silicate depletion was seen to lag behind the uptake of nitrate. This phenomenon has also been described by Antia et al (1963) who showed that the uptake of silicate (for a semi-natural diatom population) lagged 2 to 5 days behind the uptake of nitrate.

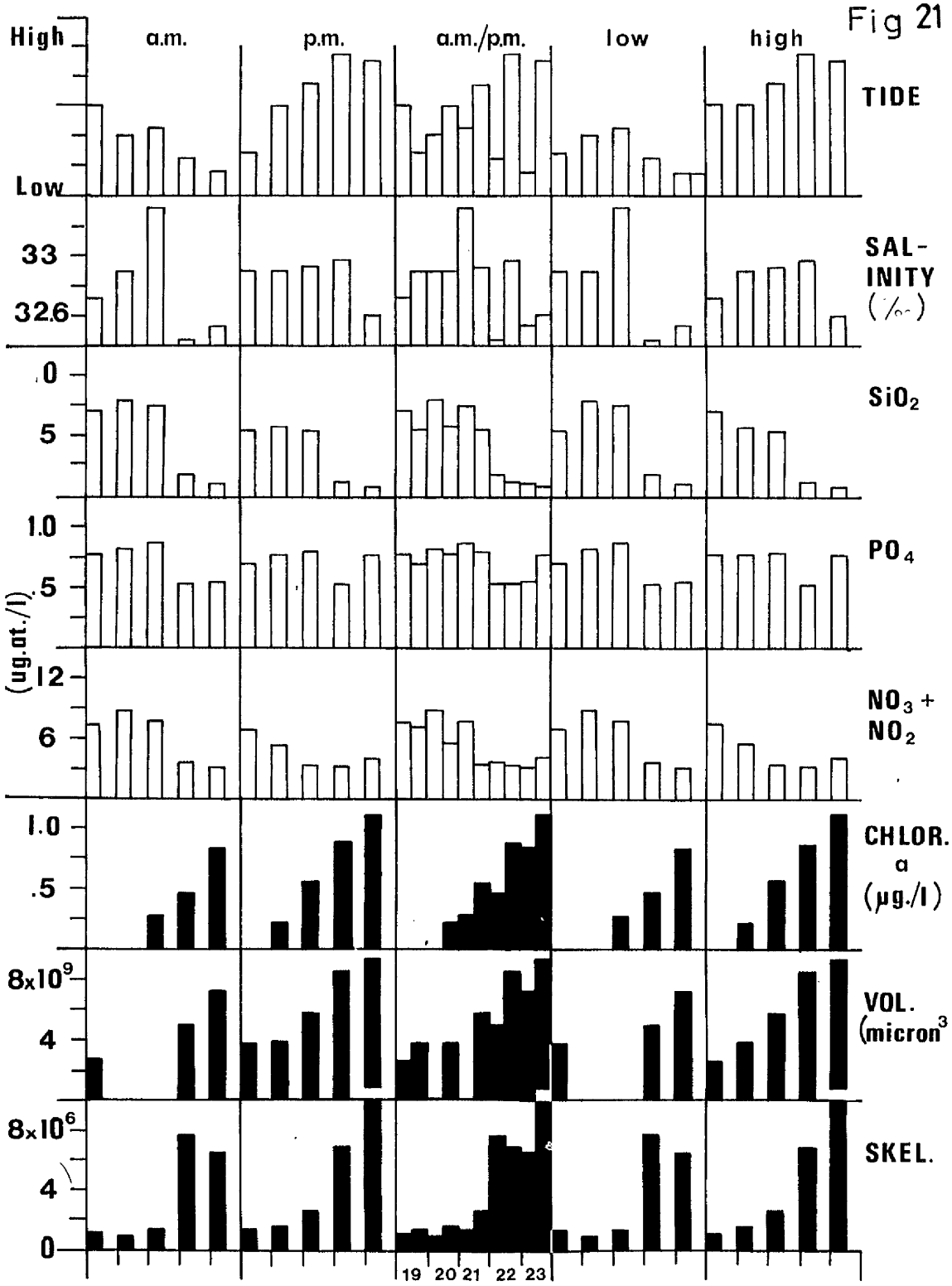
The period of phytoplankton production and nutrient decline was accompanied by comparatively calm weather (till March 20) while the amount of bright sunshine increased till 14. According to Sakshaug and Myklestad (1973) the spring diatom increase (in temperate waters) is triggered by a

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

19-23 MARCH 3 metres depth

Fig 21



certain threshold level in the amount of solar radiation. Marshall and Orr (1927) associated the spring increase (in Loch Striven) with increased stabilization of the water column due to falling salinity of the surface. A similar situation was recorded in the same loch during the present study; with a salinity range from 29‰ at the surface to 32.3‰ at a depth of 10 metres (on March 15). The situation in the Clyde at this time (Fig. 20) shows a continuous salinity gradient from 31.5‰ at the surface to 32.4‰ at the bottom (on March 8) with the water column being isothermal (6.6 - 6.7°C).

All measured nutrients showed a continuous gradient throughout the water column (Fig. 20) on March 8. Silicate fell from 15 (at the surface) to 10 ug at Si/l at the bottom, nitrate showed a gradient from 16 to 11 µg at N/l while phosphate ranged from 1.25 to 1.05 µg at P/l. The increased nutrient levels in the less saline surface waters may be a consequence of the additional nutrient load carried in the fresh water from the estuary. The bottom water, probably from the open sea is evidently unaffected by such influences.

The vertical distribution of phytoplankton and nutrients over the upper 10 m of the water column for March 13, 20, 23 (Fig. 20) shows the same phenomenon of increased nutrient levels (and decreased salinity) at the surface. However, on March 23 silicate was less at the surface than at 3 m or 10 m. From March 13 to 20 phytoplankton were most abundant at the surface whereas by March 23 (the peak of the spring diatom increase) numbers were marginally higher at 10 metres depth. On March 28 as the outburst declined, the cell density at 10 m (2.7 million cells/l) was twice that at 3 m.

From Figure 19 in which the morning and afternoon data for March have been separated (left and right graphs) and plotted on a continuous basis (middle graph), it is clear that the continuous data is more irregular. Data plotted on a morning or afternoon basis indicate the overall nutrient or phytoplankton changes which have occurred within a 24 hour period, however the timing of such changes cannot be determined. The continuous plot allows us to distinguish whether the variation occurs during the light or dark

period. A consideration of the phytoplankton curves in Figure 19 shows that the maximum abundance of Skeletonema from the morning data is 3 million cells per litre less than for afternoon samples. A clearer indication of biomass variations can be obtained from Figure 21 which shows the data for the period 19-23 March. These are plotted on a morning and afternoon basis (columns 1 and 2), a continuous basis (column 3) and on a tidal basis (columns 4 and 5).

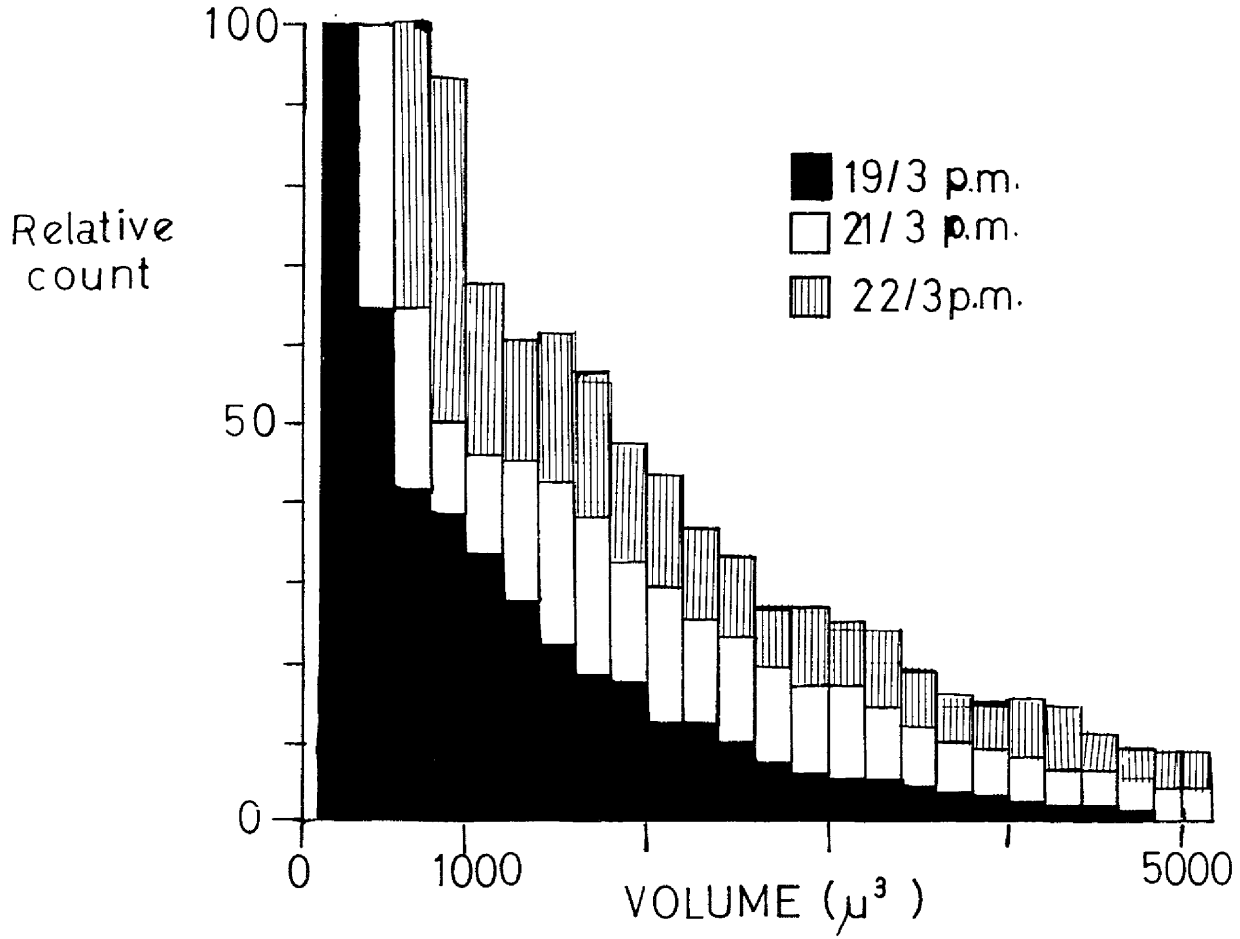
On most days during this period all estimates of standing crop were higher in the afternoon than in the morning of the same day. This pattern is unlikely to be a tidal phenomenon since salinity would also be expected to show similar regular fluctuations, which it did not. The most rapid increase in Skeletonema during week (4.2 to 11.3 million cells/l) occurred between the afternoon of March 21 to the morning of 22 following what was almost the sunniest day of the month (7.8 hours). This was accompanied by a marked decline of silicate and phosphate. By March 23 silicate had fallen below 1 µg at Si/l a level which may limit the further growth of diatom (Riley and Chester 1971). Neither nitrate nor phosphate were reduced to such low levels during the spring outburst. A falling off of the increase before the complete exhaustion of phosphate has been previously noted by Marshall and Orr (1927) and Sakshaug and Myklestad (1973). This period of exponential phytoplankton growth can be clearly followed using the coulter counter (Fig. 22) with threshold settings corresponding to increments of 200 μ^3. Not only does the number of particles increase dramatically, but there is also a gradual increase in the number of larger particles. According to Sheldon and Parsons (1967) this indicates the process of diatom chain lengthening and was confirmed by direct microscopic examination of average chain lengths during this period.

An interesting feature of the spring diatom increase was the initial domination of Thalassiosira which later gave way during the period of rapid growth to Skeletonema. This probably resulted from the much higher initial

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION **3 METRES DEPTH**

Fig 22



inoculum of Thalassiosira during February and early March which started to increase as soon as conditions became favourable. Skeletonema (which is a meromictic diatom - Fogg 1965) only appeared at the end of the first week in March and remained less abundant than Thalassiosira till 21 March. After this date, and under still favourable nutrient conditions, the much faster growth rate of Skeletonema (Lanskayo 1963) resulted in its eventual domination of the population at the culmination of the vernal outburst. Thus, in the Clyde Sea area, which one of these diatoms eventually gains dominance is probably a consequence of the balance between the initial inoculum of Thalassiosira and the prevailing nutrient conditions when Skeletonema first appears. The suggestion by Conover (1956) that the dominance of Thalassiosira is related to its adaptation to low temperatures does not seem to hold in the Clyde Sea area. In 1973 the water temperature in Fairlie Channel and Loch Striven was the same (7°C). Nevertheless, Thalassiosira preponderated in Loch Striven while Skeletonema predominated in the Channel.

The dissipation of the spring diatom increase came very rapidly after the maximum numbers had been reached and was probably a consequence of vertical mixing brought about by strong winds (exceeding 20 knots) on March 24. This resulted in cells being carried below the limit of the euphotic zone and by 26 March the total number of phytoplankton at 3 m depth had fallen to 2 million cells/litre. The only nutrient which showed a slight rise following the diatom outburst is nitrite which is known to be excreted by actively growing Skeletonema in culture (Corner and Davies 1971).

Thus, the spring increase in the Clyde in 1973 followed a period of increased solar radiation and began at the surface as the weather became calm and the water column stabilized. Diatoms were the main component of the population during this period and any nutrient changes which occurred might be related to their increase. The predominant species, Thalassiosira nordenskioldii and Skeletonema costatum were accompanied by pulses of Nitzschia seriata (frequently associated with Skeletonema) and Nitzschia closterium.

ii) April 1973

The beginning of April was characterized by similar nutrient levels to those at the end of March (Fig.23) with silicate just exceeding 1 µg at Si/l, phosphate fluctuating between 0.5 and 0.75 µg at P/l and nitrate varying between 3 and 6 µg at N/l. The total phytoplankton did not exceed 3 million cells/litre and was composed of equal amounts of Skeletonema and Thalassiosira. The depth profile for April 5 (Figure 24) shows that the population reached its maximum cell density at 3 metres where numbers were threefold higher than at the surface. Nutrients were generally higher at 10 m than at the surface with nitrate ranging from 6.7 to 11.4 µg at N/l, phosphate from 0.52 to 0.89 µg at P/l and silicate from 1.84 to 1.96 µg at Si/l. High winds mainly from the northwest at times exceeding 20 knots kept the water column isothermal at 7°C with uniform salinity (32.6‰). Further growth of diatoms at this time may have been limited to low silicate concentrations. However, it seems more likely that the vertical transport of cells below the compensation point accompanied by the rapid sinking of senescing cells may have been the causative factors.

The peculiar phenomenon observed between 10 and 11 April was a sudden nutrient upwelling. This followed the period of strong north-westerly winds and was accompanied by an abrupt rise in salinity levels from 31.5 to 33.4‰. This highly saline water was clearly the source of the nutrient enrichment and may have resulted from the wind-induced movements of water masses from the outer to the inner Firth. The salinity profile for the day following the increase (Fig. 24) shows a gradient from 32.7 at the surface to 33.7 at the bottom (35 m). High concentrations of silicate and phosphate were found at an intermediate depth (10 m) while the nitrate maximum was found at the surface. The temperature was about 1°C higher at the surface (8.15°C) than at the bottom, while oxygen levels were fairly high (101-103%) throughout the water column.

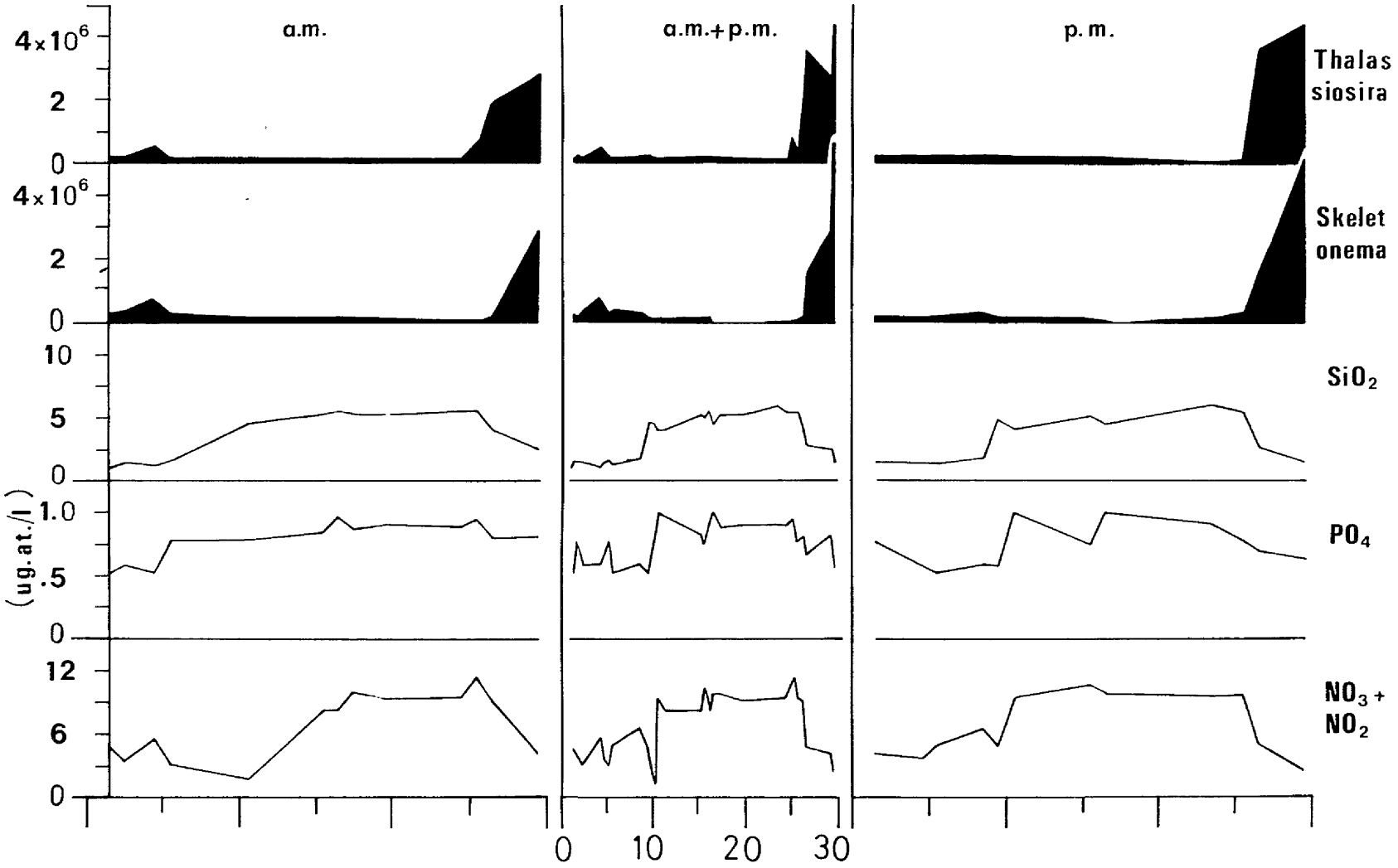
FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

APRIL 1973

3 metres depth

Fig 23



From the combined morning and afternoon data (Fig. 23) it is clear that silicate levels increased by the afternoon of April 10, whereas nitrate and phosphate did not show a rise till the afternoon of April 11. By reference to the annual cycles of nitrate (Fig. 9), silicate (Fig. 8) and phosphate (Fig. 7) it is clear that phosphate levels had returned to three-quarters of the winter value nitrate to two-thirds and silicate to half the mean winter concentration. The actual nutrient concentrations were 0.85 µg at P/l, 10 µg at N/l and 5 µg at Si/l. The nutrient increase was followed by a fall in cell numbers although the species composition did not change. Thalassiosira and Skeletonema were almost equal components of the total phytoplankton population (370,000 cells/l).

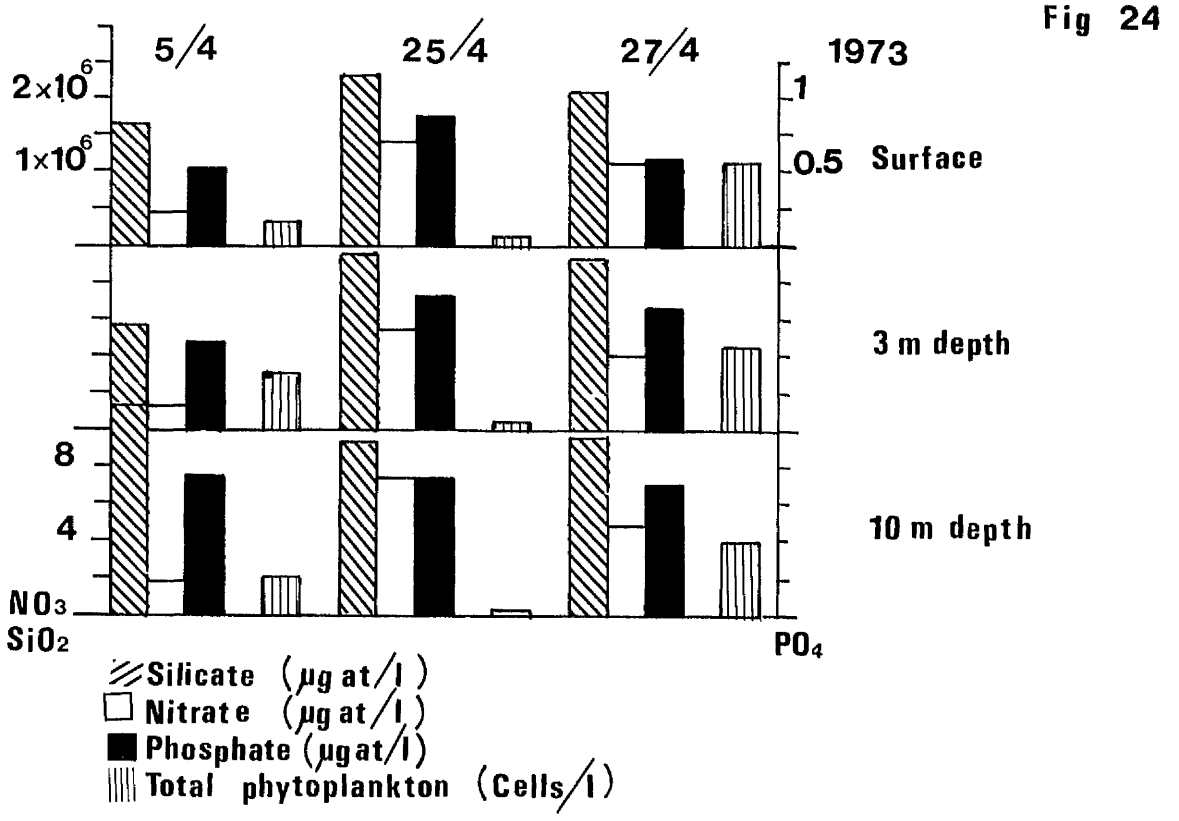
During the subsequent fortnight nutrients remained constant at these high levels, the amount of bright sunshine was variable and the weather was fairly calm. The undetectable phytoplankton activity when all measured physical and chemical factors appeared to be satisfactory is a puzzling feature. However, the simple answer to this problem probably lies in the abundance of zooplankton during this period in April. Approximate determinations from dry-weight of similar samples (collected by tow-net) show an eight-fold increase in zooplankton from the end of March to the beginning of April. Thus, although the early spring diatom increase was not reduced by grazing, the activity of zooplankton in the middle of April may have kept the population down when conditions for diatom growth appeared to be favourable. Most Skeletonema chains observed during this period were very short (around 2 cells per chain), with cell numbers falling from 100,000 per litre on 16 April to 18,000 on 25 April. However, Thalassiosira showed no overall change during this period, maintaining its numbers at about 100,000 cells/l. This differential reduction may be partly a function of the faster sinking rate of Skeletonema (0.3 - 1.35 metres/day) compared with Thalassiosira (0.5 - 0.7) (Smayda 1970).

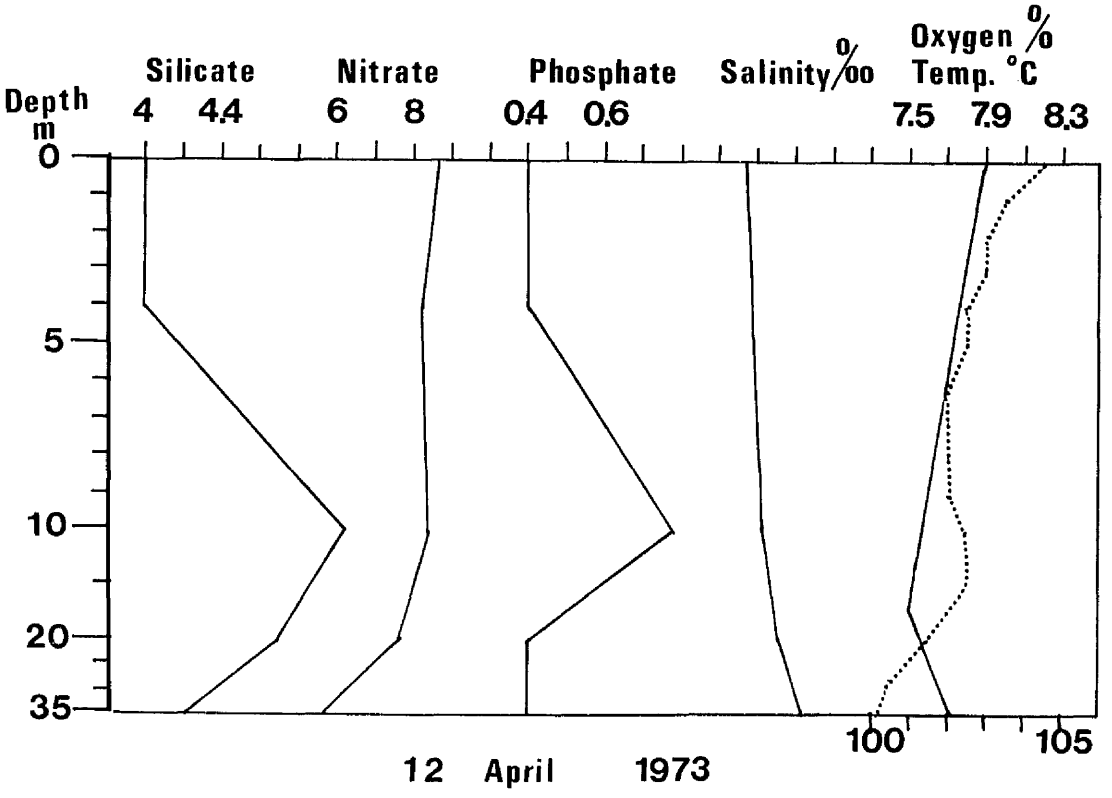
Between April 18 and 24, the number of hours of bright sunshine increased markedly, the wind lessened from 21 to 5 knots and a considerable decline in

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

Fig 24



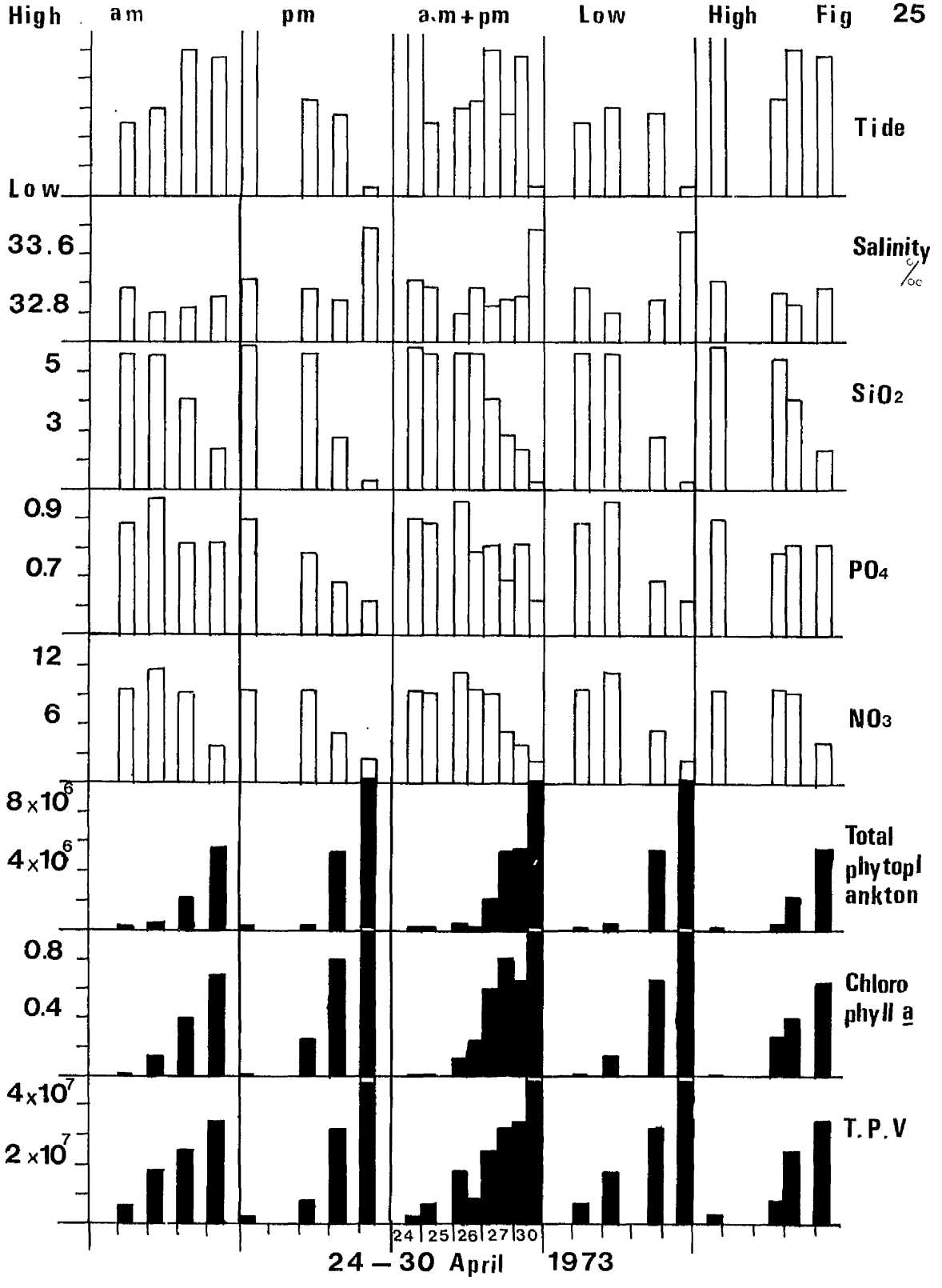


zooplankton abundance was evident. The accumulation of nutrients from the upwelling at the beginning of the month only now (after 24 April) gave rise to the expected diatom increase. As in the earlier phytoplankton pulse the population was composed of Skeletonema, Thalassiosira and Nitzschia seriata. However, Nitzschia closterium was conspicuously absent. At the commencement of the increase Thalassiosira was tenfold higher than Skeletonema, a similar situation to the one which prevailed before the early spring diatom increase. in March. Figure 23 clearly shows that the increase to 2 million cells/ litre on 27 April was almost entirely attributable to Thalassiosira which comprised 90% of the total. It was not until the afternoon of 30 April that Skeletonema (marginally) exceeded Thalassiosira. This is a further example of the competition between these two species for available nutrient. In this case Thalassiosira proliferated from a larger initial inoculum and reached 2 million cells per litre (on 27th) with a consequent halving of nutrient levels, before Skeletonema could establish itself. However, once established Skeletonema multiplies rapidly causing nutrient depletion in a short period. By the afternoon of 30 April Skeletonema exceeded the numbers of Thalassiosira with 5.6 and 4.4 million cells/litre respectively. Nutrients were reduced to levels below those found at the end of March; Nitrate to 2.62 ug at N/l, phosphate to 0.62 µg at P/l and silicate to 1.38 µg at Si/l.

The period of high phytoplankton productivity is shown in detail from April 24 to 30 in Figure 25. It is clear that the three estimates of standing-crop follow one another closely. No tidal rhythm was apparent in salinity, the highest (33.78‰) and the lowest (32.8‰) values were both found at low tide. Both silicate and nitrate show a regular decline whereas phosphate shows a rhythmic oscillation with an increase during the night. This may be due to the excretion of inorganic phosphate by zooplankton as they accumulate in surface waters during the night. Butler et al (1970) have shown, in the Clyde, that Calanus excretes up to 60% of its daily intake of particulate phosphorus more than 30% of which may be inorganic phosphate.

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION



The timing of the phytoplankton increase was variable, generally being during the night when Thalassiosira was dominant and during the day when Skeletonema became predominant. This fluctuating pattern is clear from all estimates of biomass. Nutrient depletion generally coincided with period of diatom multiplication. From the profiles (Fig. 24) it is clear that the increase was not confined to the surface but was uniform at all depths down to 10 metres.

Thus at the end of April 1973 there was a late spring diatom increase which is analogous in species composition to the early spring outburst. The maximum abundance was again found in the afternoon with the peak exceeding 10 million cells/l on April 30, of which Skeletonema constituted slightly more than 50%. This second spring outburst may be considered to result from the upwelling of nutrient enriched water into the euphotic zone. In general during this period zooplankton activity played an important role in regulating the standing crop.

iii) May 1973

During May the variation of all measured nutrients was extremely irregular in comparison with the previous months. This may be associated with two factors: firstly the severe nature of the weather during May in which the mean daily wind speed exceeded 20 knots on 4 occasions (1, 10, 19-21 and 30) with subsequent vertical mixing and secondly the generally low nutrient concentrations, on which even a small enriching influence would have an obvious effect. Despite the very low amount of bright sunshine recorded during this month (mean daily average of 4.8 hours compared with 6.7 in April) and the large number of completely overcast days, there was still a considerable amount of phytoplankton production. The two dominant organisms were Thalassiosira and Skeletonema as in the previous two months, although the latter species was not evident after the middle of the month.

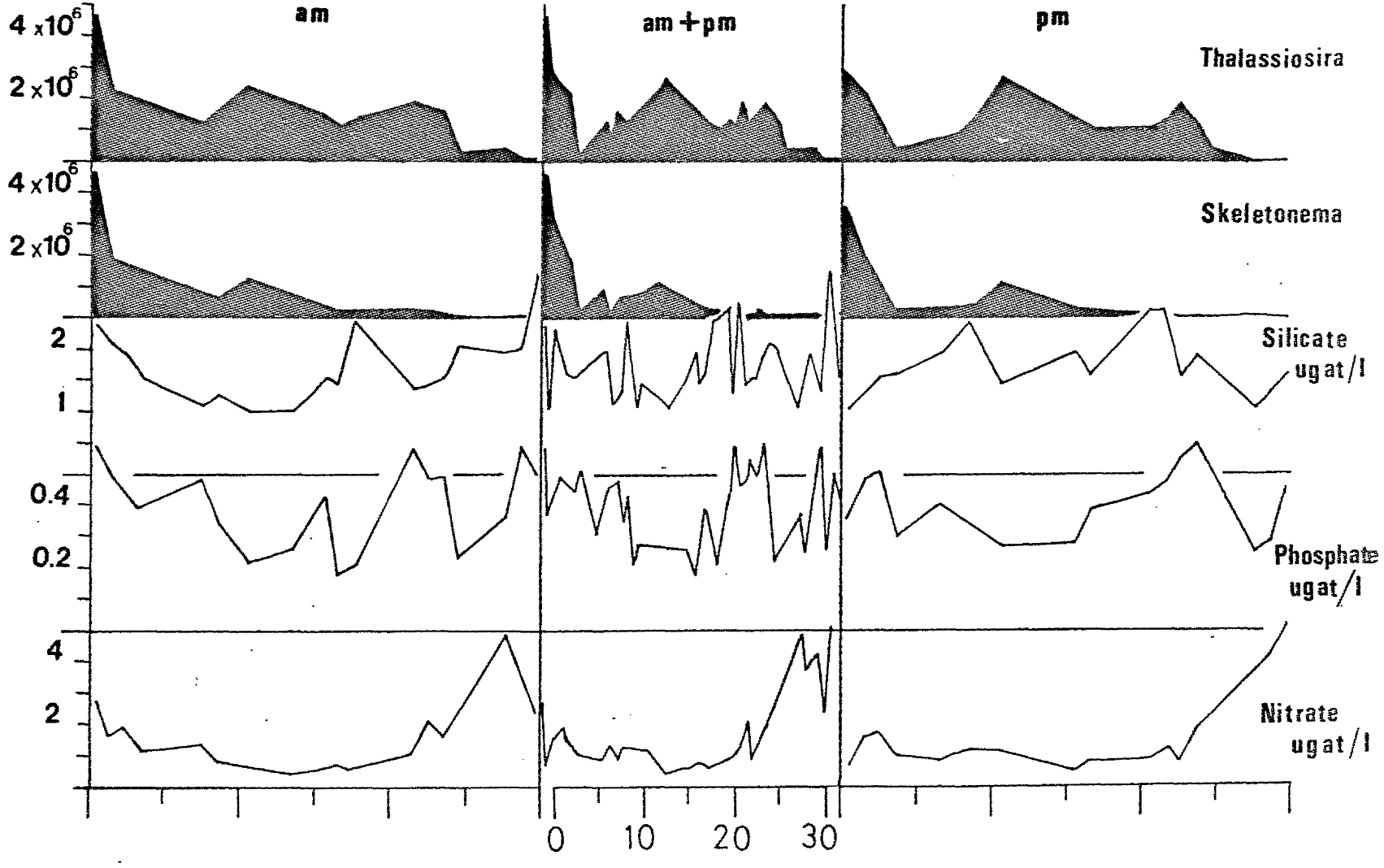
The late spring increase which reached a peak at the end of April showed a rapid decline between 1 and 2 May when very strong winds exceeded 20 knots. However, from an examination of the nutrient profiles on the afternoon of 2 May (Fig. 27) it is evident that the wind mixing did not affect more than the upper part of the water column, and all nutrients showed considerable statification. Nitrate displayed a gradient from the low value of 0.4 µg at N/l at the surface to 2.5 at the bottom, silicate from 1.21 to 3.5 µg at Si/l and phosphate 0.36 to 0.5 µg at P/l. Thus, low nutrient concentrations in the surface water, redistribution of the diatom population by vertical transport and the grazing pressure were probably all contributory factors to the dissipation of this late spring outburst. Although the total phytoplankton estimates were similar throughout the upper 10 metres Thalassiosira was more abundant at the surface whereas Skeletonema reached its highest cell density at 3 to 10 m depth. As in April it appears that Skeletonema becomes more rapidly reduced in numbers than Thalassiosira falling to 600,000 cells/litre by 10 May when the latter species still recorded 1.2 million cells/l.

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION
May 1973

3 METRES DEPTH

Fig 26



From 1 to 10 May nutrient levels fluctuated erratically with little overall change. Silicate varied between 1 to 2.5 µg at Si/l, nitrate from 1 to 2 µg at N/l and phosphate between 0.3 to 0.5 µg at P/l. An increase of Thalassiosira was evident on 8 May while Skeletonema did not show increased numbers till 10 May when both reached a simultaneous peak. This pattern was clear both for morning and afternoon samples and is similar to previous pulses of these two species (in March and April) in that Thalassiosira showed the earlier increase. A peculiar feature of this increase is that the nutrient levels at its initiation show little difference from those at the beginning of the month when the previous pulse declined. It is probably relevent here to bring in the estimates of zooplankton abundance which were high for the first 8 days of May and fell by more than 50% by 10 May, indicating a reduction in grazing pressure.

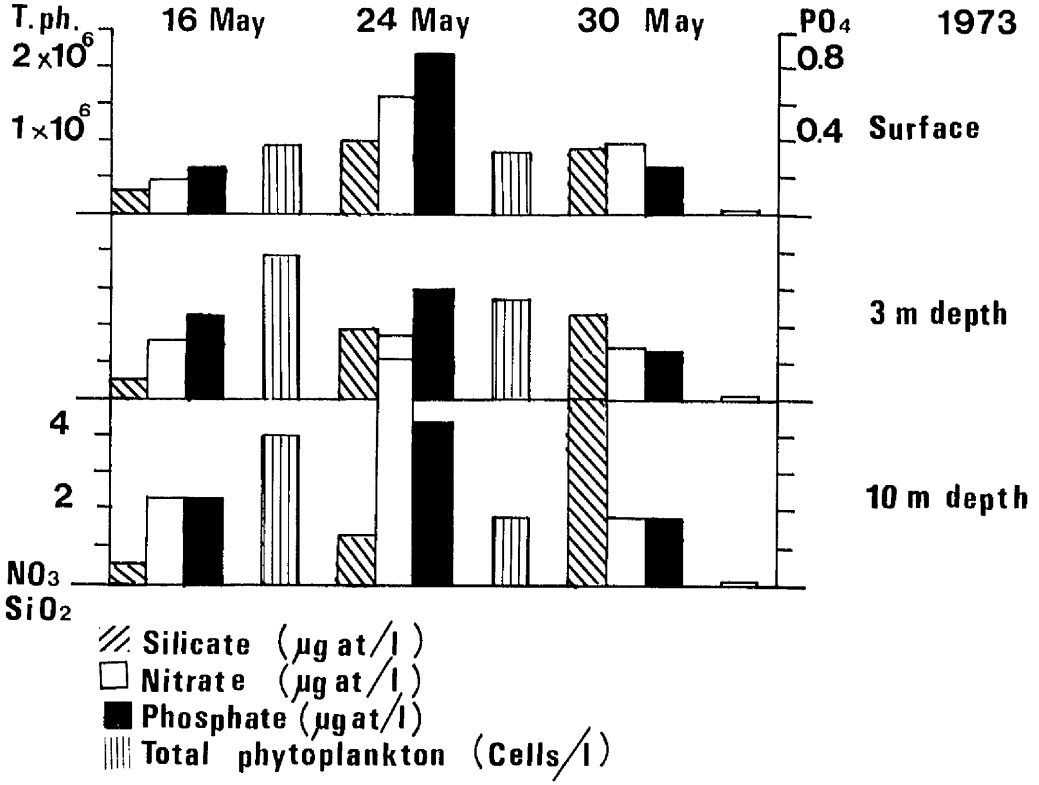
At the peak of this pulse (May 10) Thalassiosira reached 2.6 million cells per litre, for the first time (in 1973) exceeding the amount of Skeletonema (1.1 million cells/litre). The accompanying nutrient fall only encompassed silicate (2.4 to 1.1 µg at Si/l) and phosphate (0.48 to 0.2 µg at P/l) with nitrate levels showing no change. This might suggest that nitrate was not the only form of combined nitrogen available for utilization by diatoms at this time. The duration of this outburst was short with both organisms showing a simultaneous decline in numbers. It is possible that nutrient limitation was a contributory factor in the decline of this outburst although no measured nutrient reached undetectable levels. Riley and Chester (1971) suggested that 0.3 µg at P/l was a critical level for phosphate below which cell division becomes increasingly inhibited. For silicate Martin (1970) showed that 1.3 µg at Si/l could be a limiting level for particular diatom species. Both silicate and phosphate fell below these suggested levels in the present instance.

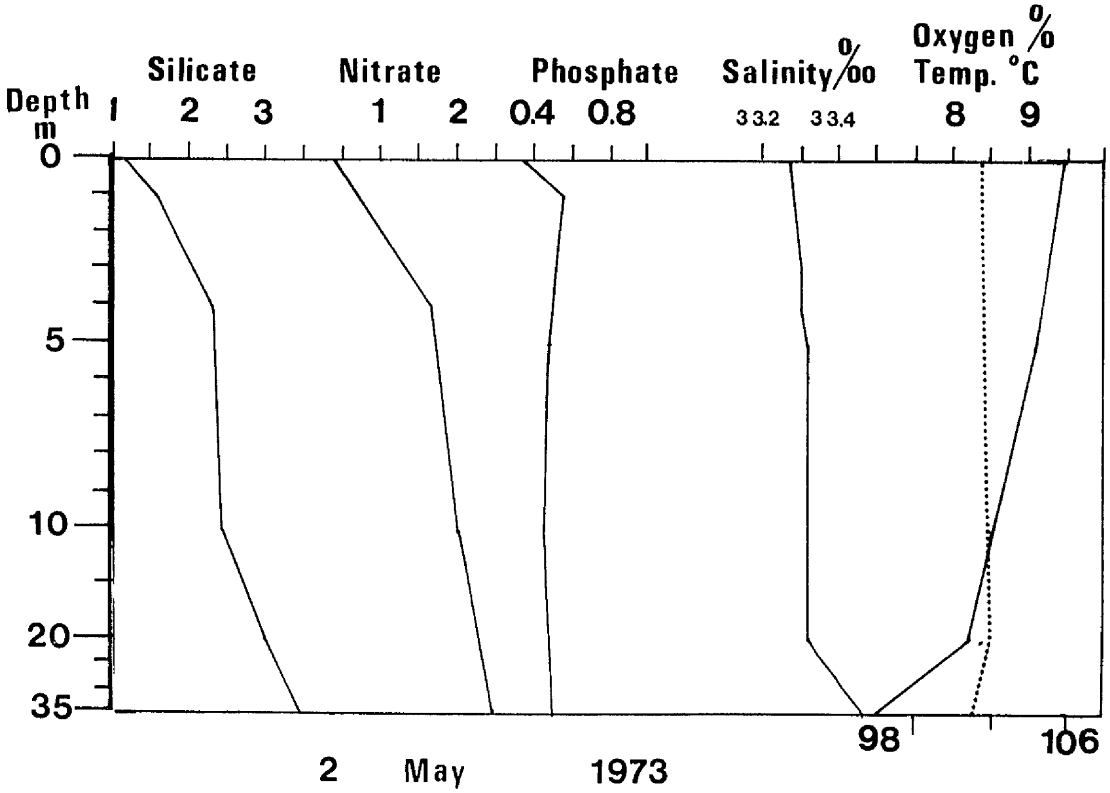
The vertical profiles for May 11 and 16 (Fig. 27) shows that the maximum abundance of phytoplankton was below the surface. This indicates

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

Fig 27





that under the fairly calm conditions prevailing, the population was sinking out of the euphotic zone. The relative numbers of Skeletonema and Thalassiosira at depth would suggest that Skeletonema was sinking faster. In fact by 17 May Skeletonema was reduced to about 300,000 at 3 m depth, whereas the number of Thalassiosira exceeded 1 million cells/l. The sinking rate of Skeletonema cells has been estimated (from a natural population) as around 1.4 metres/day (Marshall and Orr 1930). Once Skeletonema chains reach 10 m depth they begin to sink very quickly through the rest of the water column (Orr and Marshall 1969). The nutrient profile for May 16 (Fig. 27) shows that nitrate was evenly distributed between the surface and 10 m (around 0.5 µg at N/l) whereas silicate showed a gradient from 0.98 at the surface to 2.28 µg at Si/l at 10 m and phosphate 0.26 to 0.46 µg at P/l.

This reservoir of nutrients was brought to the surface between 18 to 21 May probably as a result of turbulent mixing from four days of high winds (exceeding a daily average of 20 knots). Thus silicate increased from 1.56 to 2.4 µg at Si/l, and phosphate from 0.2 to 0.6 µg at P/l., Nitrate, as expected, showed little change. However, after 24 May nitrate showed increased concentrations rising from 1 to around 5 µg at N/l on May 28. If these nutrients are solely the product of regeneration then the order of appearance, with nitrate showing slower regeneration than phosphate or silicate, follows the classic pattern (Barnes 1957, Riley and Chester 1971, Corner and Davies 1971). By reference to either the morning or afternoon curve in Fig. 26 it is clear that out of silicate and phosphate, the former is most rapidly recylcled as shown by Cooper, 1933.

Following the increase in silicate levels a further pulse of diatoms occurred, although this time Thalassiosira constituted more than 90% of the total. It appears that at the commencement of this increase the balance of the inoculum, with Thalassiosira being ten-fold more abundant than Skeletonema again favoured the former species. It is also possible that a chemical factor necessary for continued growth such as Vitamin B_{12} (Droop 1955)

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

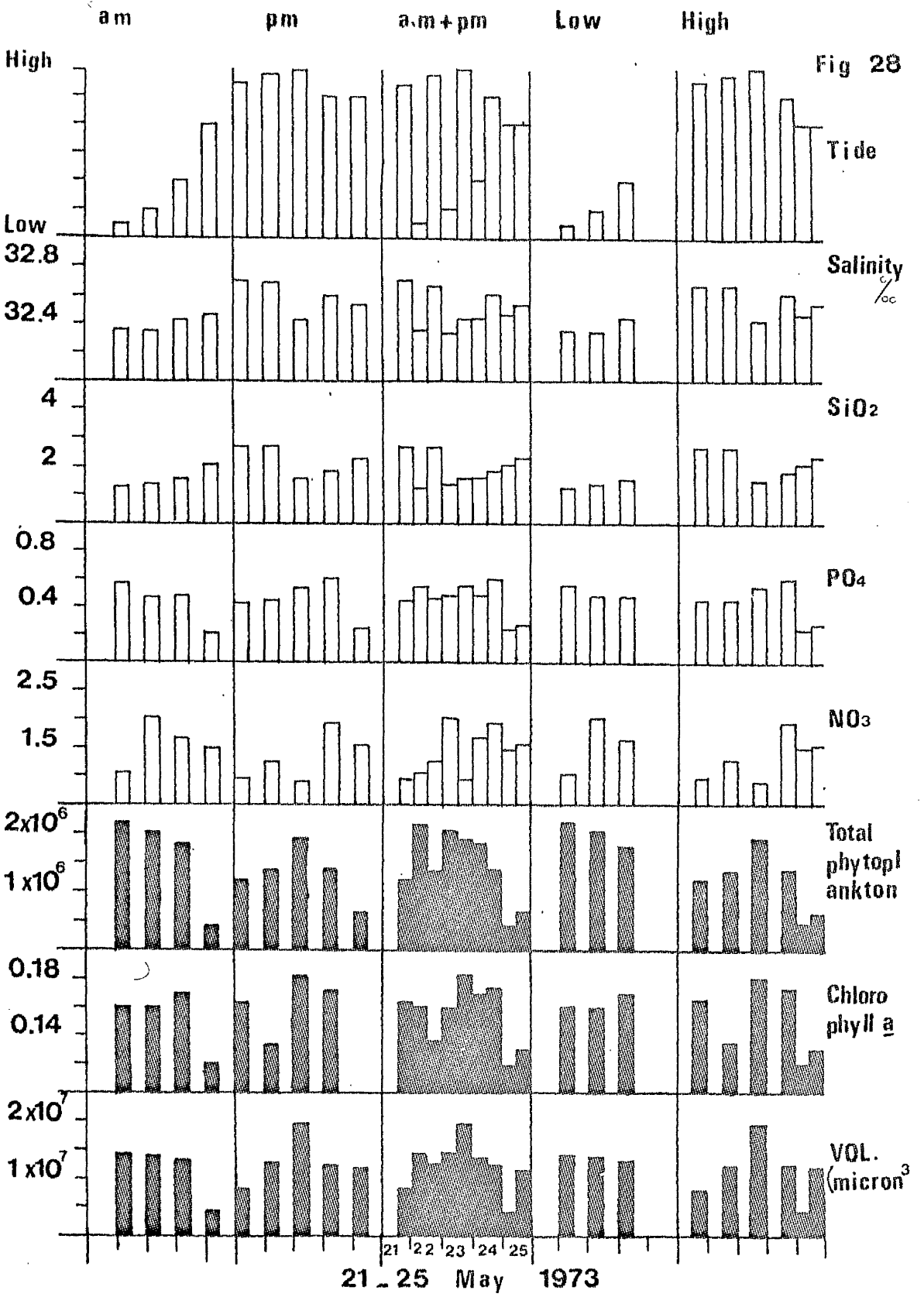


Fig 28

may be lacking or limiting at this time.

The period 21-25 May is represented in Fig. 28, which shows a clear rhythm in salinity, with higher levels at high tide (32.4 to 32.7‰) than at low tide (32.3 to 32.4‰). The only nutrient to show any relationship to the state of tide was silicate which was up to two-fold higher at high tide (reaching 2.7 µg/l). The total phytoplankton showed a very close correlation with the changes in total particle volume and chlorophyll a estimations. During this period the total phytoplankton doubled to 2.2.million cells/l. by the morning of May 22 while the afternoon maximum (1.9 million) was not reached till May 23. Any nutrient reduction which occurred in association with phytoplankton changes was short-lived, concentrations rising again within a day. This probably resulted from a continual supply of nutrients from deep water. The nutrient profile for 24 May (Fig. 27) shows extremely high concentrations of silicate (6.08 µg at Si/l) and phosphate (0.87 µg at P/l) below the surface, therefore any mixing would have been accompanied by nutrient redistribution with a consequent enrichment of surface waters. Nitrate however, did not show a gradient with depth till May 30 when a high concentration existed at 10 m (5 µg at N/l). Phytoplankton by this date was sparse at all depths.

The only other organisms present in any number during May was Kephyrion spp. This genus is a member of the Chrysophyceae and individuals are recognizable by their minute (less than 5µ) pale brown loricae. This genus has only once been described from British coastal waters (Lackey and Lackey 1963) who recorded Kephyrion ovum from qualitative samples taken near Plymouth. The present study gives the first record of the seasonal occurrence of Kephyrion in coastal waters and shows that the maximum abundance occurred at the end of May 1973 (and in 1972) with a peak of 250,000 cells/litre.

The month of May was thus dominated by Thalassiosira which formed

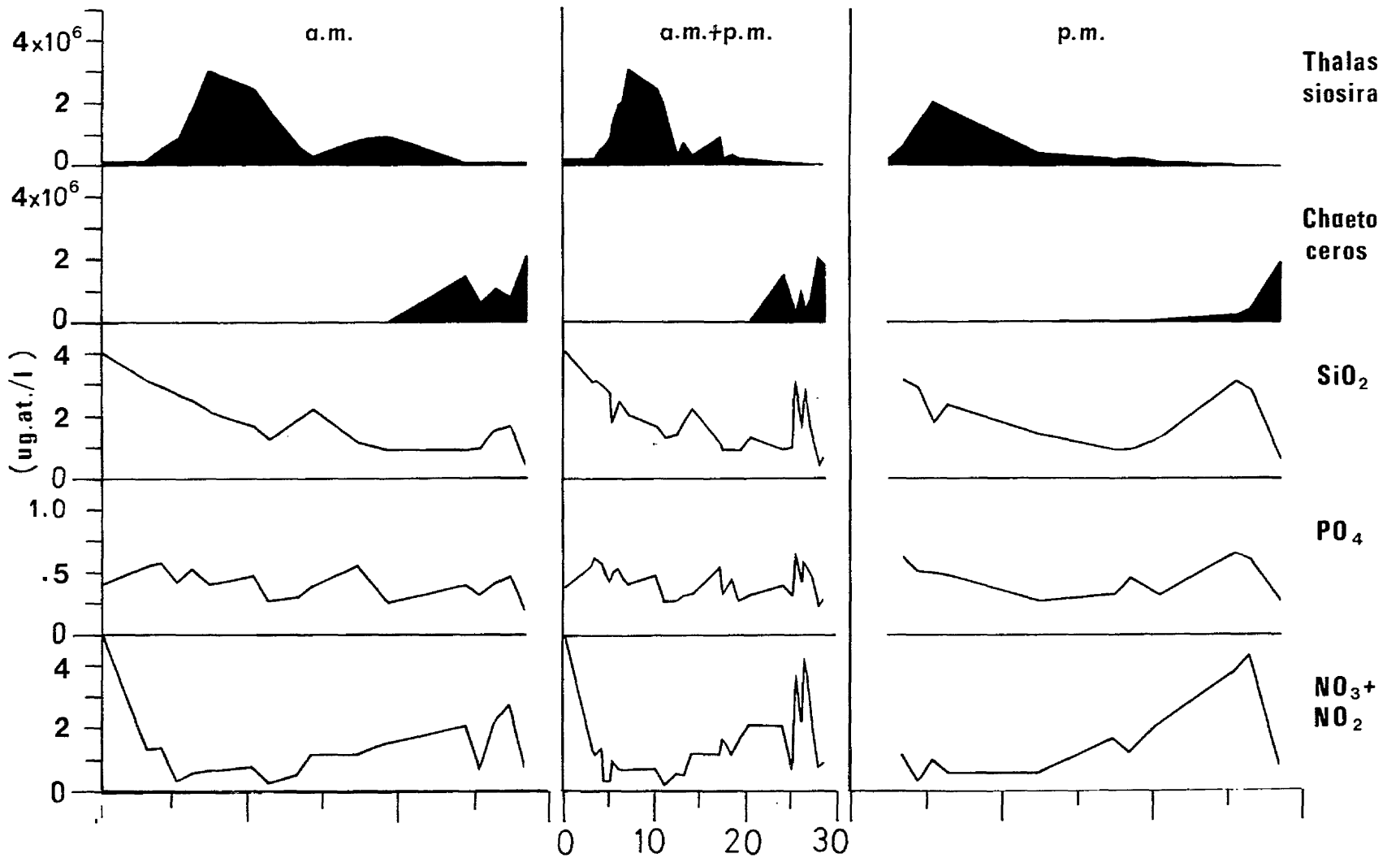
three pulses, each being successively smaller. The dissipation of each pulse resulted from a combination of zooplankton grazing, vertical mixing, sinking and nutrient limitation.

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

JUNE 1973

3 metres depth



iv) June 1973

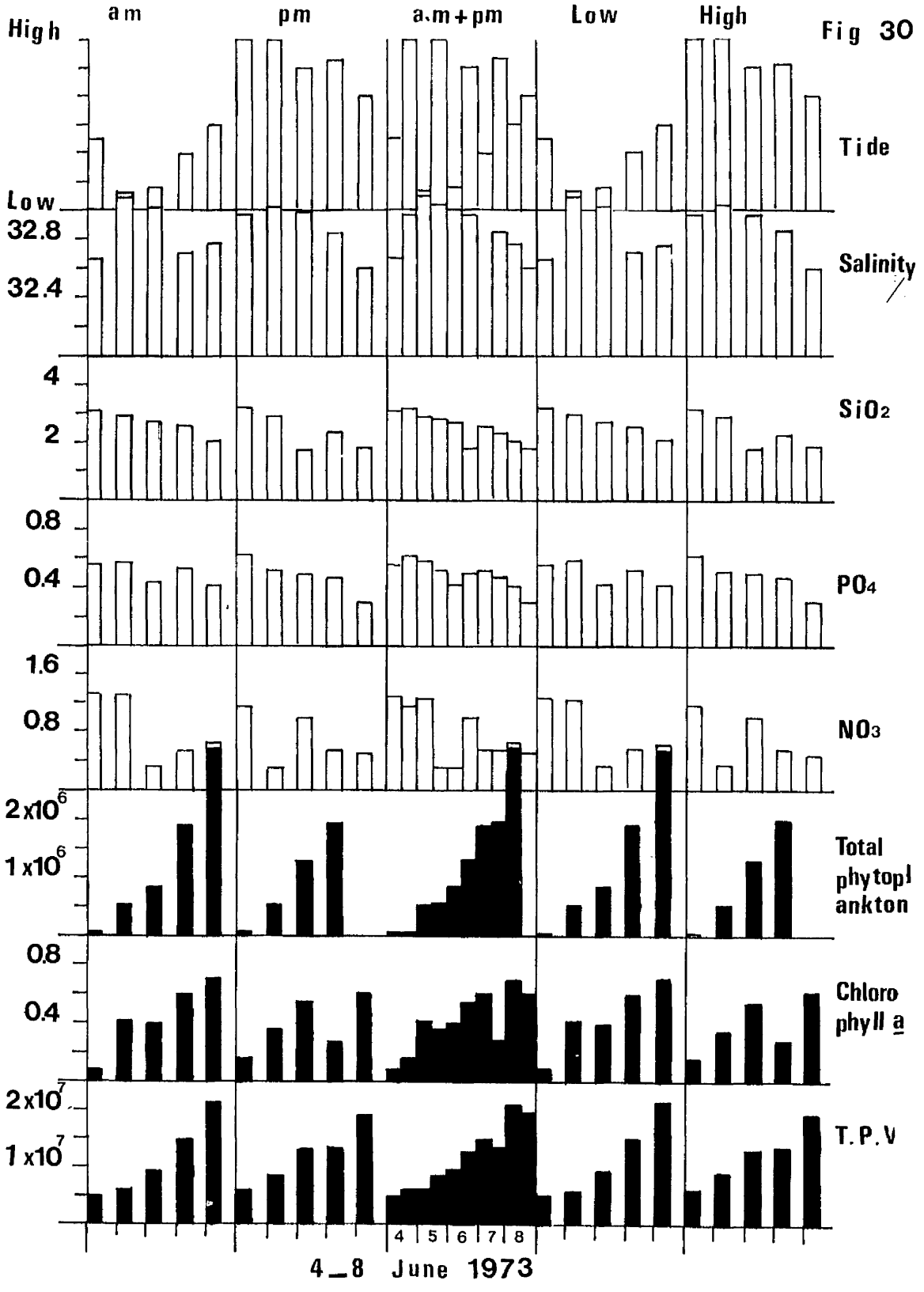
The upwelling of nutrients between the end of May and the beginning of June occurred simultaneously with a period of strong westerly winds, exceeding a daily mean of 20 knots (on May 30). Thus nutrient concentrations started at high levels at the beginning of the month with phosphate reaching 0.6 µg at P/l at 3 m (and 0.87 at the surface), silicate commenced at 4 µg at Si/l and nitrate at 5 µg at N/l (Fig. 29). These values are between half to two thirds of the nutrient levels following the upwelling in April. The mean daily amount of bright sunshine during June (5.6 hours) was less than that recorded for April, and must be considered to be extremely low considering that the maximum annual daylength (17.4 hours) is reached in this month.

The favourable physical and chemical conditions at the beginning of June, with relatively low zooplankton activity did not immediately stimulate the growth of phytoplankton but was followed by a lag phase of about 4 days in which numbers (of Thalassiosira) remained around 200,000 cells/l. Riley and Chester(1971) considered that "the combined effects of physical, chemical and hydrographic factors make it difficult to determine whether a lag phase occurs in the sea". However, several instances of the delayed increase of phytoplankton when growth conditions appear to be optimal can be seen from the present study (in March, April and May). Between 4-8 June diatom growth changed to the exponential phase culminating in a peak of about 3 million cells per litre, (almost pure Thalassiosira). The dynamic changes during this period can be more closely followed by reference to Figure 30 where the data is plotted on a daily and a tidal basis.

During the period June 4 to 8 there appears to be no relationship between the state of tide and any of the measured parameters, thus any changes can be considered to be a function of biological activity. As in the early spring, diatom outburst uptake of silicate seemed to lag behind the uptake of

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION



nitrate and phosphate both of which decreased considerably before any multiplication of diatoms occurred. This is in agreement with the findings of Lund (1965) who showed for fresh water diatoms that the silicate uptake did not take place till after the formation of the daughter cells. The overall uptake of silicate during the first Thalassiosira pulse in June was about 3 µg at Si/l compared with an uptake of 4 µg at Si/l in April when the maximum recorded standing crop was proportionally greater.

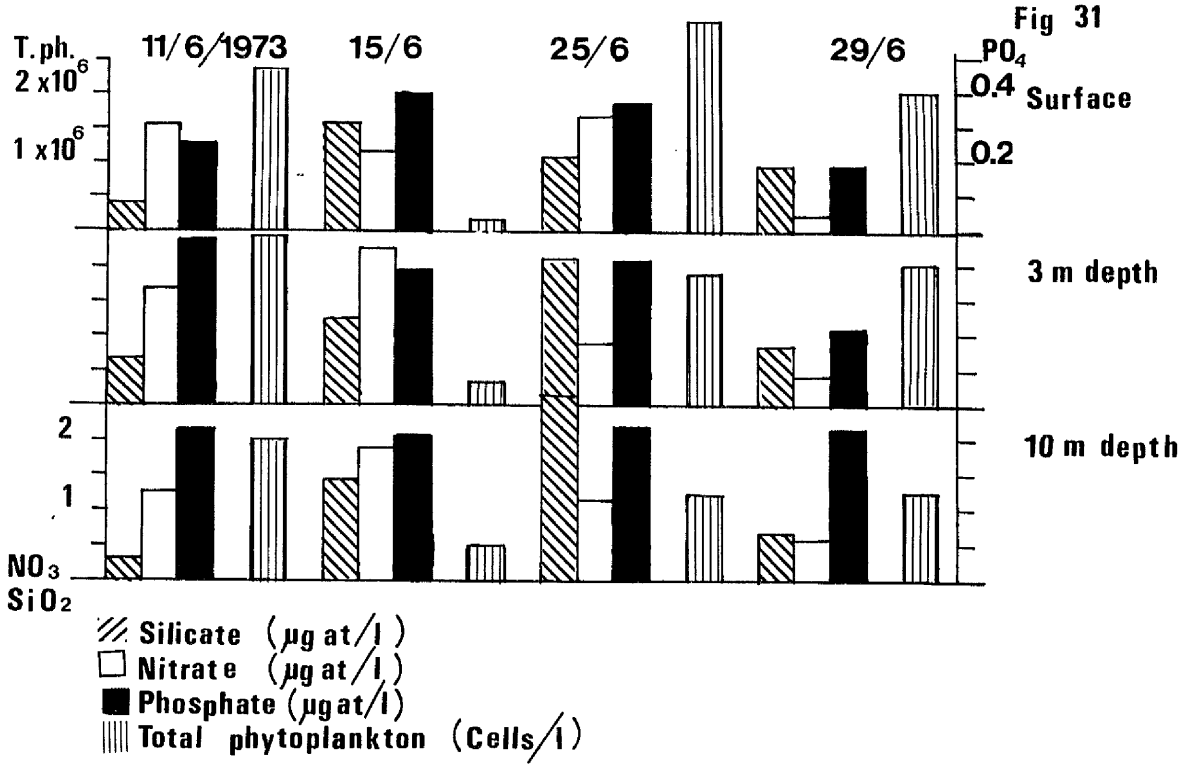
The most rapid rise in cell numbers occurred between 4 and 5 June when the cell density rose from 50,000 to 500,000 cells/litre. Cell numbers almost doubled on each of the three successive days reaching a peak of 3.2 million cells/litre on the morning of June 8. It is evident from the total phytoplankton data that cell multiplication occurred during the night throughout this period of rapid growth. Total particle volume estimates and chlorophyll values reached maximum levels on June 8 simultaneously with the maximum phytoplankton abundance; T.P.V. rose from 0.5 to 2.1 x 10^7 cubic microns while chlorophyll a increased from 0.08 to 0.7 µg/l. At the beginning of the increase (June 5) cell numbers were higher at the surface (1.2 million) than at 3 m depth (500,000) whereas by June 11 (Fig. 31) cells were evenly distributed throughout the water column. After June 5 the continued increase of Thalassiosira did not result in any further nitrate and phosphate reduction. However, on 6 and 7 June the nutrient levels at 10 m depth were considerably higher than at 3 m and surface. Consequently, in the absence of any temperature or salinity gradient, any tidal mixing would tend to bring these nutrients into the overlying waters.

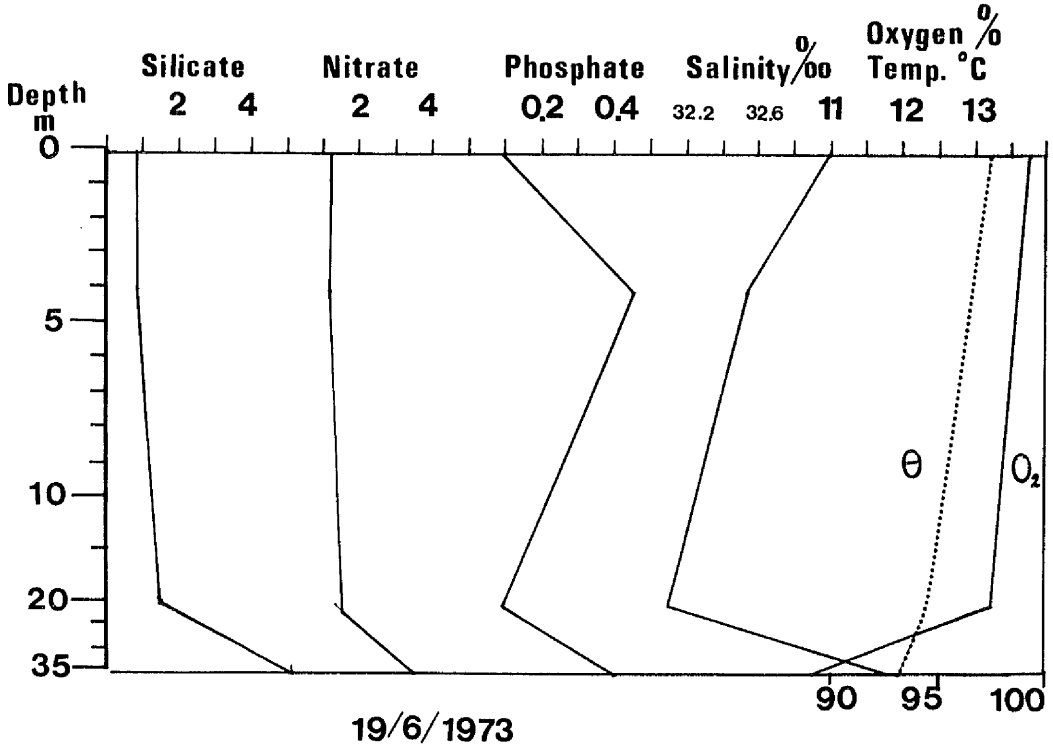
The gradual decline of this outburst from June 8 to 16 is probably a direct result of increased grazing activity. Zooplankton dry weight determinations increased four-fold from 1 to 9 June. Turbulent mixing from the strong winds on 12-13 June (exceeding 20 knots) may also have influenced the dissipation of this outburst. A small resurgence of nutrient levels which

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

Fig 31





19/6/1973

occurred by June 15, accompanied by a fall in grazing pressure, favoured a further small increase in Thalassiosira which tripled in number between 15 to 19 to reach 900,000 cells/l. The nutrient profile for June 15 (Fig. 31) shows that phosphate and nitrate were equally distributed with depth whereas silicate doubled from the surface (1.1 µg at Si/l) to 3 m (2.25 µg at Si/l).

The disappearance of Thalassiosira and its succession by Chaetoceros spp has been described for many temperate areas (Hasle and Smayda 1960, Raymont 1963, Jensen and Sakshaug 1973). Reasons for this succession, however, seem to be unknown. In the present case the explanation is two-fold; firstly the dissipation of the Thalassiosira outburst was a consequence of increased zooplankton activity which reached a peak as indicated by zooplankton (dry weight) between 18-19 June and secondly the establishment of stratification between 20-26 June (Fig. 32). The zone of temperature discontinuity began at a depth of 3 m, above which the temperature was constant at 13.5, and extended to 8 m where a temperature of 11.0 was recorded. Once cells of Thalassiosira sank below the bottom of the thermocline return to the surface was presented by the presence of the pycnocline, Chaetocerus on the other hand rapidly proliferated in the calm surface waters (where it remains in suspension probably by virtue of its fine silicerous spines and projections which aid flotation).

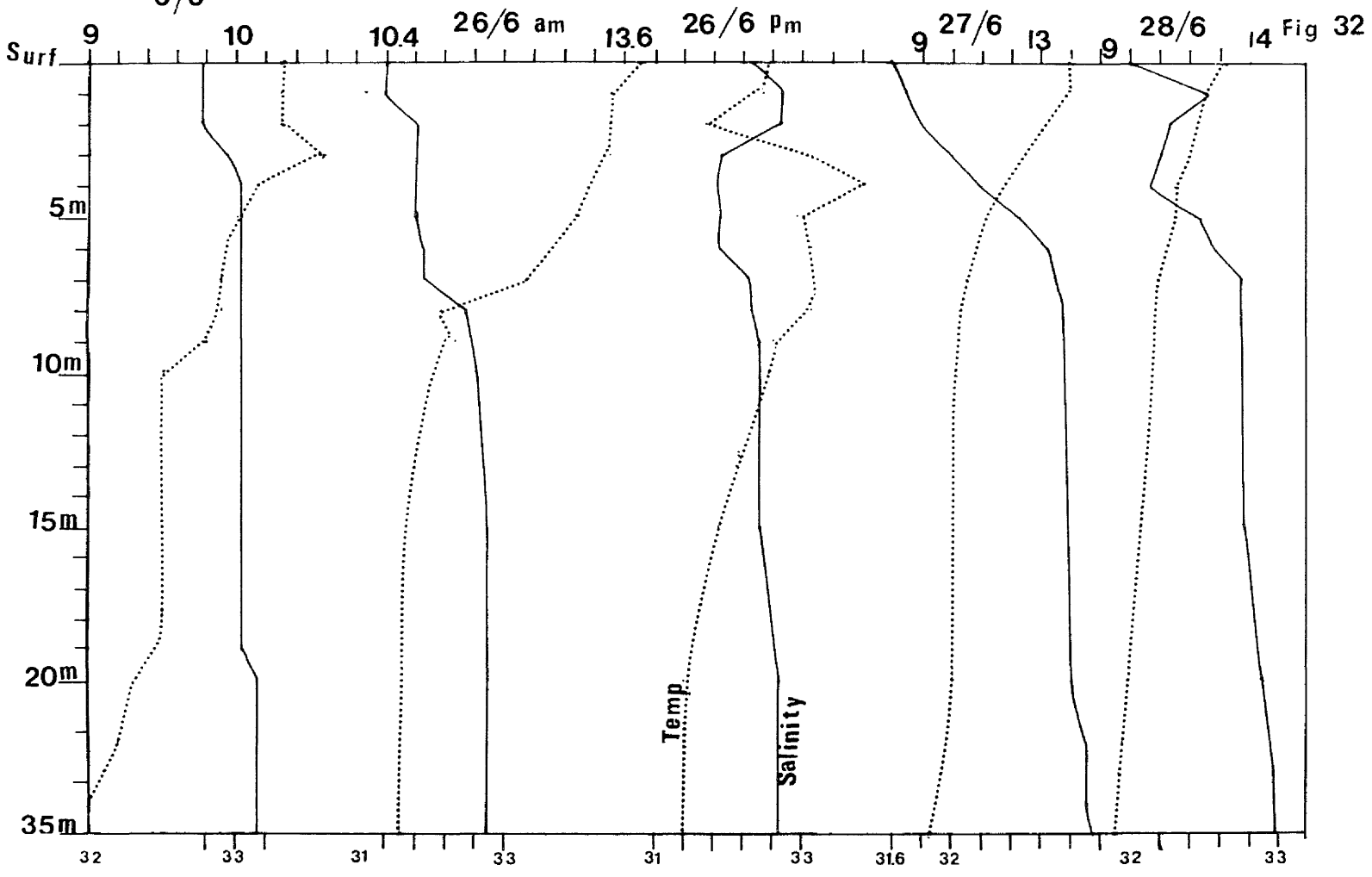
The intrusion of low salinity water below the surface on the afternoon of June 26 (Fig. 32) resulted in some vertical mixing bringing nutrient enrichment to the upper part of the water column. Silicate and nitrate, which were high at 25 metres on the morning of 26 (4.1 µg at N/l and 3.3 µg at Si/l), reached those values at 3 m depth on the afternoon of the same day. A distinct thermocline was re-established by 27 June and the proliferation of Chaetoceros which was temporarily halved by mixing continued under the enriched nutrient conditions.

The multiplication of Chaetoceros cells with numbers rising from around 10,000 to 2 million cells/litre within a week was accompanied by a rapid

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

Fig 32



fall in all nutrients at the surface and 3 m depth (see Fig. 31) although at 10 m no reduction in phosphate was evident (by June 29). The actual cell counts show that the increase began at the surface and gradually spread downwards; on 25th June numbers exceeded 3 million at the surface, were less than 2 million at 3 m depth and only 1.2 million at 10 m.

By the end of the month the nutrient concentration was generally low with silicate and nitrate concentrations of less than 1 µg at N/l and phosphate around 0.25 µg at P/l.

Although June had unusually dull weather a considerable amount of productivity was still evident. Thalassiosira nordenskioldii appeared in two pulses during the month and was succeeded by Chaetocerus cinctum which appeared as the water column became thermally stratified. Each phytoplankton pulse followed a period of nutrient upwelling. Towards the end of June species which are characteristic of warmer waters, Peridinium sp., Ceratium sp., and Coccolithus huxleyi first appeared in significant numbers (see Fig. 16).

v) Summer 1973

During July the water temperature increased, the epilimnion deepened and the strafification became more stable. The thermocline extended from 10 to 15 metres with a temperature gradient of about 3^{0}C. Nutrient levels during the first half of the month were generally low throughout the upper 10 m of the water column although a slight rise was occasionally evident in the vicinity of the thermocline. This can be clearly seen for July 6 and 9 in Fig. 34. During the first ten days of the month silicate ranged from 0.5 to 1 µg at Si/l throughout the epilimnion, phosphate from 0.25 to 0.4 µg ag P/l and nitrate from 0.9 to 2.3 µg at N/l. Below 10 m nutrients increased to 2.5 µg at silicate-silicon per litre, 0.9 µg at phosphate-phosphorous per litre and 2.5 µg at nitrate-nitrogen per litre. Therefore even if the water column became isothermal at this time the consequent nutrient redistribution would not lead to any great enrichment of surface waters .

Under the prevailing stratified conditions Chaetoceros sp predominated but was less than the maximal density recorded at the end of June (2 million cells/litre). The period 2-6 July is represented on a twice daily basis in Figure 33. Even under conditions of calm weather and long periods of bright sunshine the population showed no overall increase with the standing crop fluctuating between 300,000 and 800,000 cells/litre. Nutrient levels were similar to those preceding the Chaetoceros pulse in June and zooplankton were not abundant. Under these presumably favourable conditions for the growth of phytoplankton the lack of any overall changes is puzzling but may be related to the absence of some essential but unmeasured factor or factors.

Silicate levels appear to show a tidal rhythm with values exceeding 1.25 µg at Si/l at high tide and falling below 0.9 µg at /l at low tide. Nevertheless an overall decline was evident by the end of the week. Nitrate concentrations fell by half by July 6 whereas phosphate levels remained constant. Data from depth and surface samples showed that phytoplankton was

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

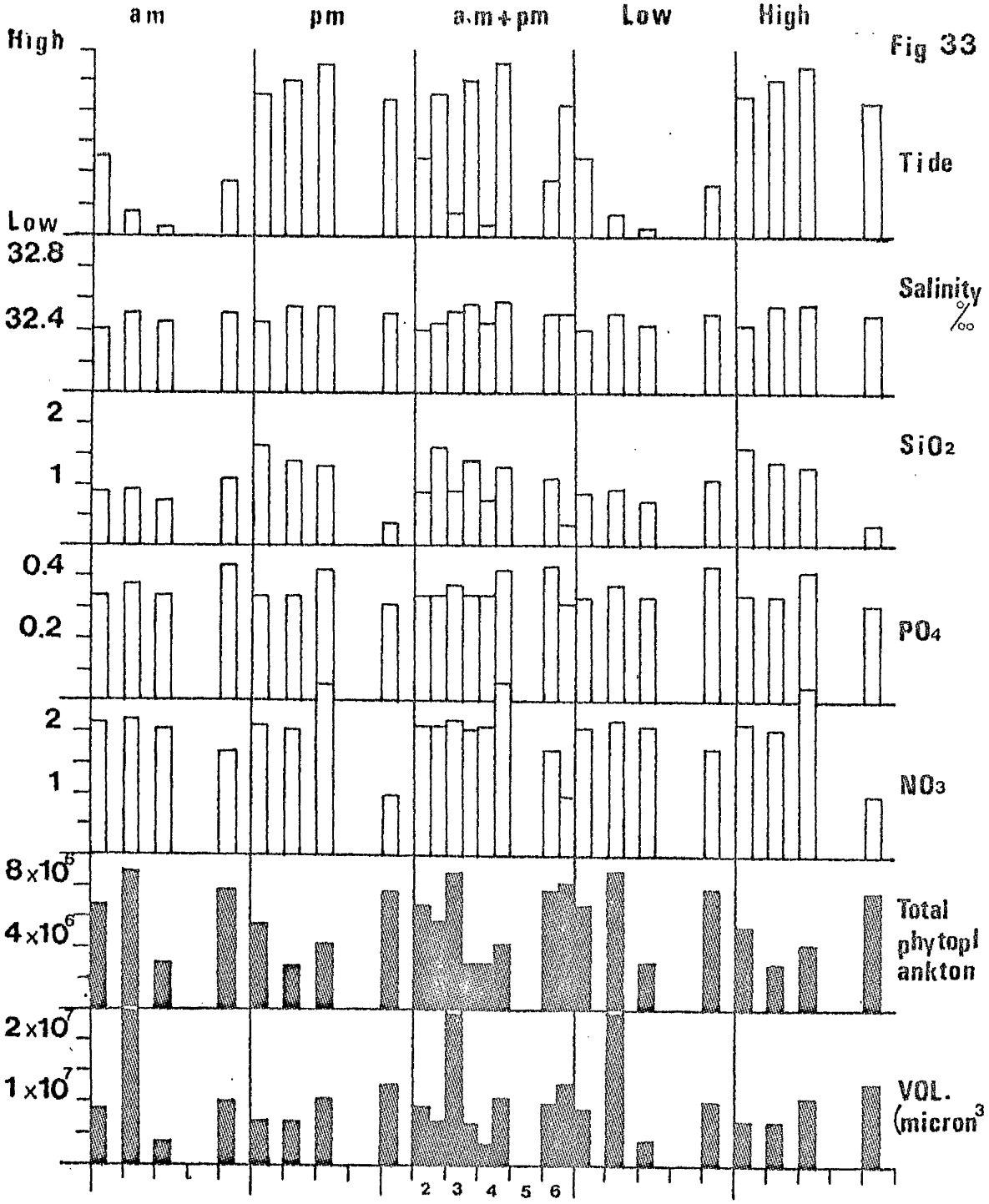


Fig 33

2_6 July 1973

either evenly distributed throughout the upper 10 metres or had highest numbers at the surface. By 9 July the standing crop was low (less than 250,000 cells/litre) at all depths although zooplankton were still not abundant and nutrient levels remained low. The fall in total phytoplankton numbers below 100,000 cells/l on July 13 was reflected in the very low total particle volume of less than $0.2 \times 10^7 \mu^3$.

By July 24 Chaetoceros numbers had again increased while nutrient values showed little change. Nitrate was uniform throughout the upper 10 metres at 1 ug at N/l, phosphate varied from 0.25 to 0.30 µg at P/l and silicate from 0.4 to 1.5 µg at Si/l. By July 25 (Fig. 34) nutrients at 3 and 10 m depth were almost twice the surface values, this was apparently due to depletion of surface nutrients rather than any supply from deeper water.

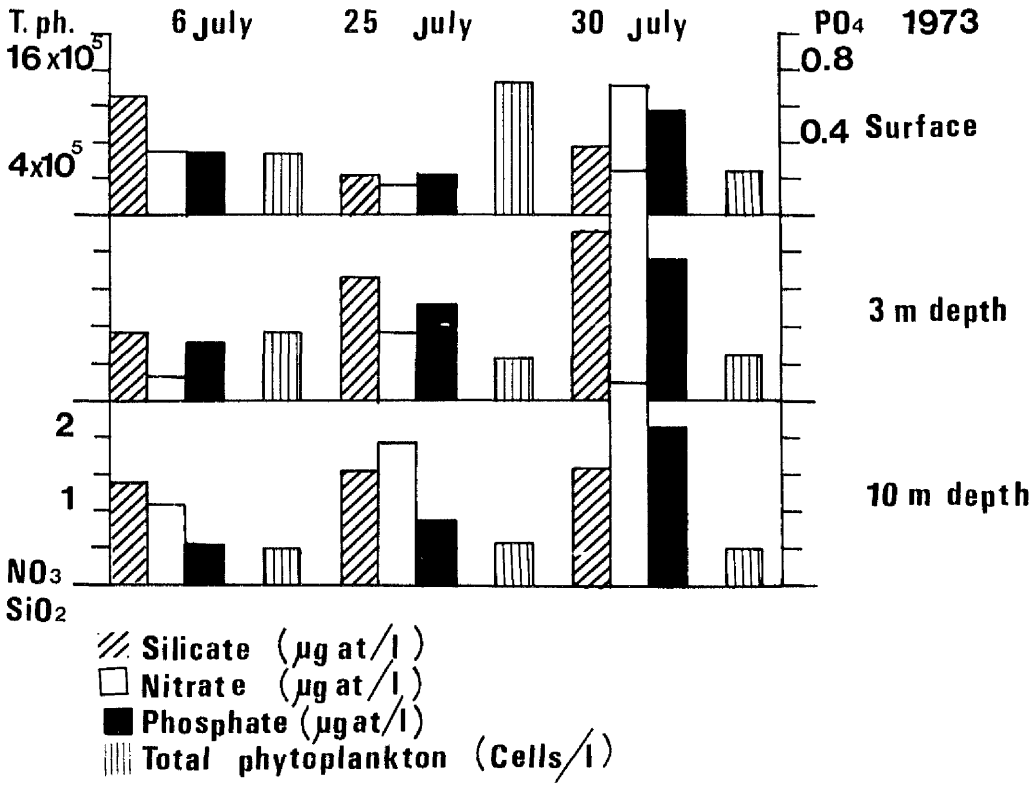
The standing crop which was dominated by Chaetoceros sp and Coccolithus huxleyi reached its maximum at the surface on the morning of July 25 following the sunniest day of the month (13 hours of bright sunshine). The total phytoplankton was 1.5 million cells/litre of which Coccolithus huxleyi contributed 524,000 cells. The outburst of this organism was evidently favoured by the nutrient depletion of the surface waters where concentrations of all nutrients fell to their annual minimum; nitrate - 0.56 µg at N/l, silicate 0.43 µg at Si/l and phosphate 0.22 µg at P/l. A consideration of the half-saturation growth constants for Coccolithus huxleyi and Chaetoceros gracilis given by Corner and Davies (1971) suggests that such a concentration of phosphate would support a much faster increase of C-huxleyi than Chaetoceros.

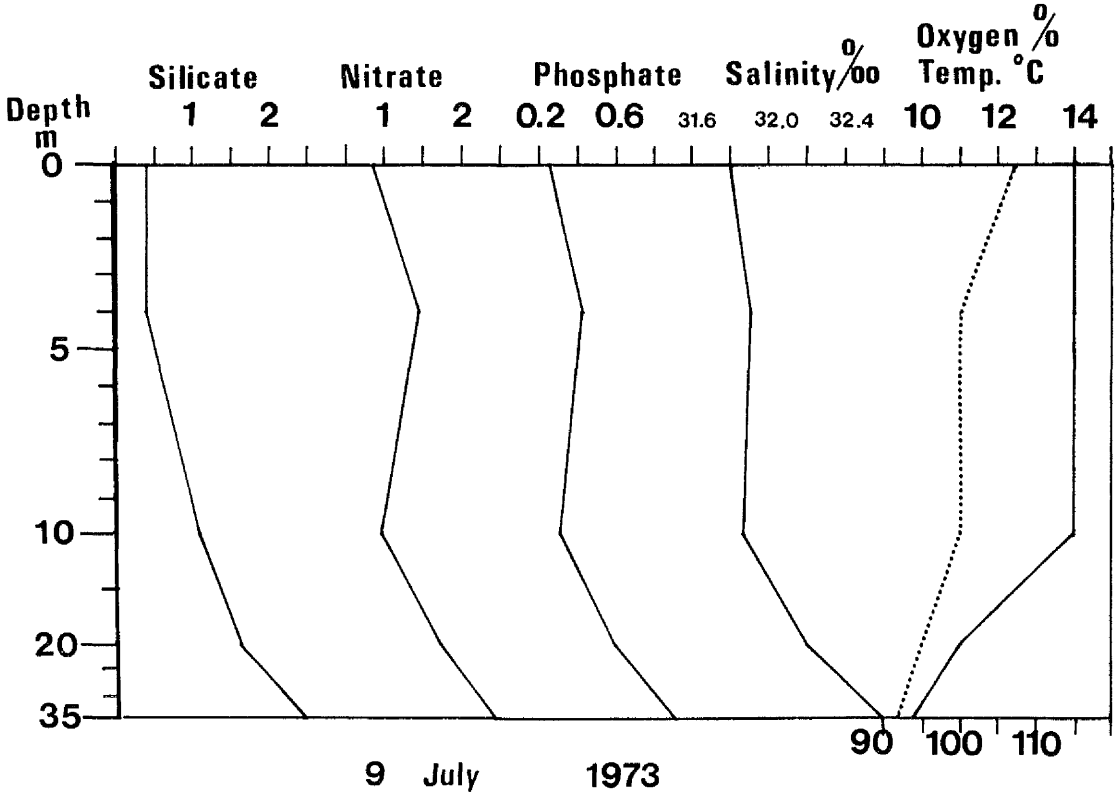
The "mass-occurrence" of coccolithophorids (reaching 1 million cells per litre) recorded by Hasle and Smayda (1960) in Oslo fjord was associated with a great abundance of dinoflagellates. However, during the present surveythe two organisms never reached great abundance simultaneously. From the present data it appears that Coccolithus huxleyi has a daily

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

Fig 34





rhythm of occurrence in surface waters, reaching maximum abundance in morning samples. The mass occurrence of this organism was transient, being confined to July 25 to 26. By July 30 nutrient levels were on the increase throughout the water column (Fig. 34), C. huxleyi had declined to 20,000 cells/l while Chaetoceros was increasing.

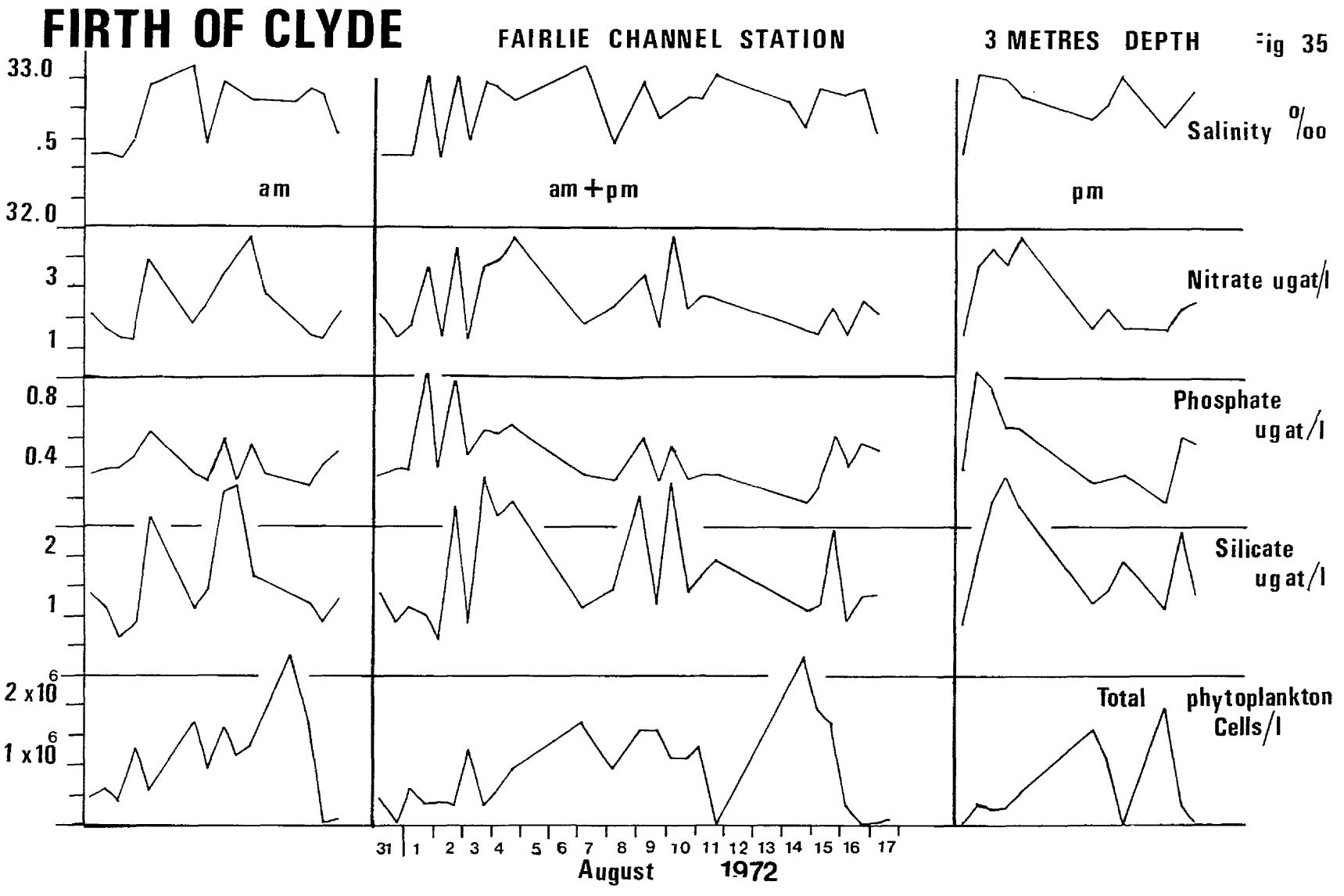
The following month, August 1973, is considered in detail in Chapter 6 since it covers the period leading up to the study of diurnal variation carried out on August 17. Thus in subsections (vi) and (vii) to follow the late summer and autumn period will be described from the 1972 data.

vi) Late summer 1972

A single feature stands out prominently in the day to day variations in August 1972 (Fig. 35), that is, the daily variations in salinity are reflected in the variations of the other measured parameters, nitrate, phosphate and silicate. The salinity variations are themselves a function of tidal changes with salinity being generally highest at high tide. Superimposed on the tidal changes are the biological changes which are nevertheless still detectable.

The salinity variation lag between 32.5 to 33.1‰ with the incoming more saline water evidently being richer in nutrients. The nutrient increase with depth, likewise is associated with increasing salinity (as on 1 August, see Fig. 37). The daily range of nutrient variation is extremely large at times. During the week 31 July to 4 August, nitrate content fluctuated regularly between 1.2 and 4.6 µg at N/l, silicate from 0.7 to 3.3 µg at Si/l and phosphate from 0.36 to 0.62 µg at P/l. These variations are consistent oscillations and indicate that there is a body of water oscillating to and fro across the sampling area, with the water present at a given high tide returning to that same position by the following high tide. The reduction in salinity at low tide is too small to account for the large nutrient reduction (up to four-fold). However, the low levels may be associated with the previous biological history of the water mass.

When the available data is plotted on a continuous basis, including both morning and afternoon samples the resultant pattern (Fig. 35) is irregular, but gives an accurate representation of the variation at this locality. When the data is plotted on a morning or afternoon basis only, the tidal rhythm is still superimposed. This represents an extreme example of the horizontal nutrient heterogeneity which may be recorded at a particular sampling area and emphasizes the problems of adequately representing such an area without an intensive sampling programme.


FIRTH OF CLYDE
FAIRLIE CHANNEL STATION
3 METRES DEPTH
Fig 35
33.0
.5
32.0
am
am + pm
pm
Salinity °/oo
3
1
Nitrate ugat/l
0.8
0.4
Phosphate ugat/l
2
1
Silicate ugat/l
2 x 10^6
1 x 10^6
Total phytoplankton Cells/l
31 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
August 1972

In contrast with the oscillating nutrient pattern for August the total phytoplankton curve (Fig. 35) is surprisingly regular. Three diatom species formed recognizable pulses during this period, Thalassiosira sp Skeletonema costatum and Chaetoceros spp. (Fig. 36) with the latter organism numerically dominant throughout this period. As previously described, the course of events when Skeletonema and Thalassiosira coexist appears to be influenced by the size of the initial inoculum. At the beginning of August Skeletonema was more abundant than Thalassiosira with roughly three-fold higher numbers (300,000 cells/litre). Both organisms increased concurrently with Thalassiosira reaching a maximum of 160,000 cells/l by August 4 by which time Skeletonema had risen to 280,000 cells/l.

During the period 4-7 August the nutrient decline was accompanied by a rapid fall in the abundance of Thalassiosira to 25,000 cells/litre. The rise in silicate levels by August 9 (to more than 3 µg at Si/l) possibly stimulated the further growth of Skeletonema, which increased to a peak abundance of 450,000 cells/litre on 10 August. This resulted in a rapid fall in silicate to 1.5 µg at Si/l. The final phytoplankton pulse in August (Chaetoceros sp) commenced as Skeletonema declined, with the cell density rising from the fluctuating population of around 1 million cells/litre during the previous week to a peak of 2.5 million cells/litre on 14 August. The nutrient reduction during this period was marginal. By the end of this period strong winds were recorded and the phytoplankton population had become reduced to low levels, with a total of less than 100,000 cells per litre.

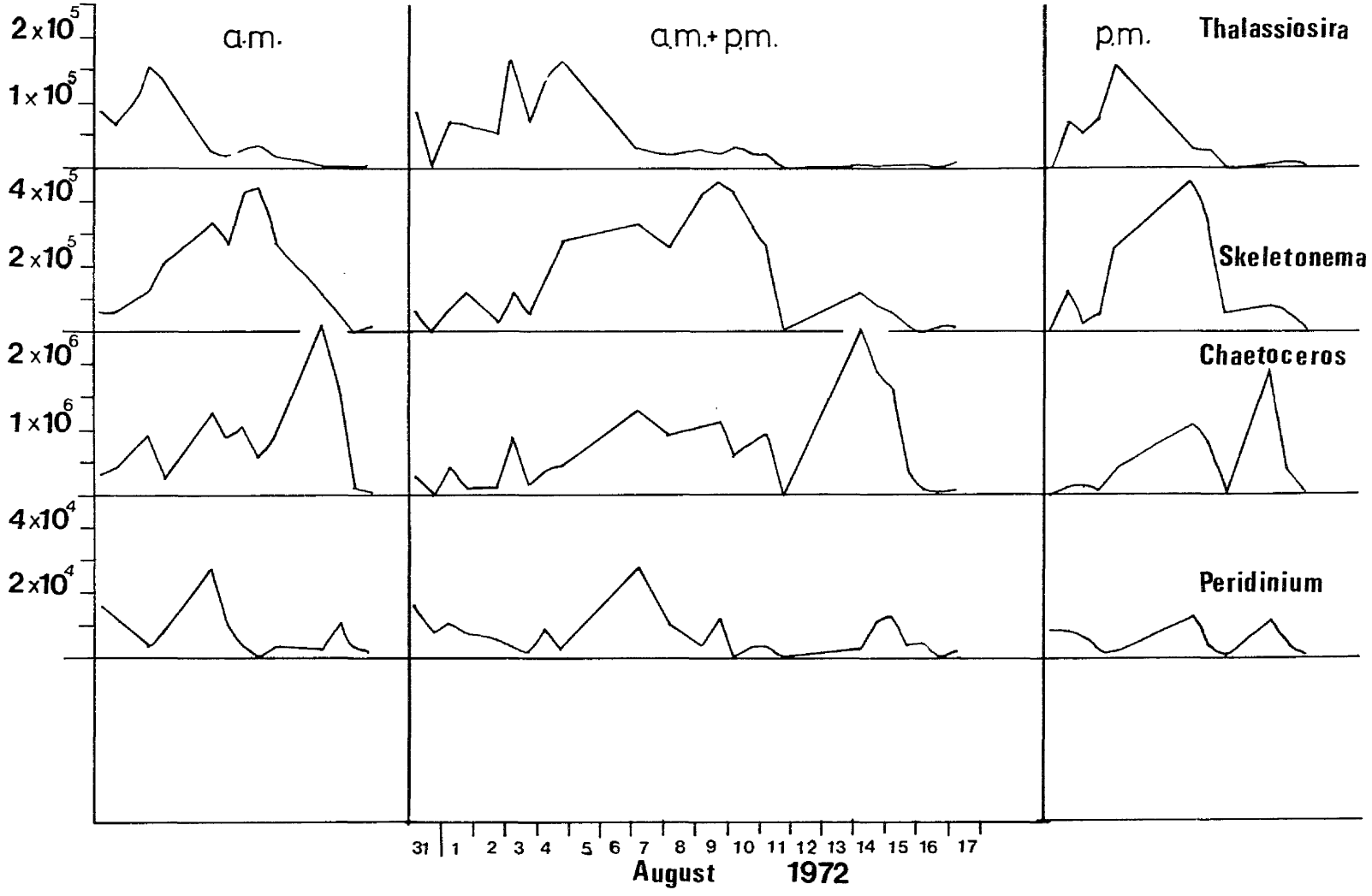
Depth profiles for August (Fig. 37) show that nutrient utilization extends at least to 10 m depth, with high concentrations only being found below 20 metres. On 29 August Silicate increased from 2 (at 20 m) to 5 µg at Si/l at the bottom, nitrate from 4.8 to 6.0 µg at N/l and phosphate from 0.6 to 1.0 µg at P/l. This indicates considerable nutrient regeneration at the bottom where the oxygen saturation was reduced to its lowest recorded level (67%).

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

3 METRES DEPTH

Fig 36



Dinoflagellates became common during August particularly Peridinium sp which showed its greatest abundance in surface waters. Here, densities of up to 44,000 cells/litre were recorded. A diurnal rhythm in migration of this organism was clear over the upper 3 metres only, with up to four-fold higher densities in the morning than in the afternoon of the same day. This is shown in the following table of Peridinium counts for August 1972:

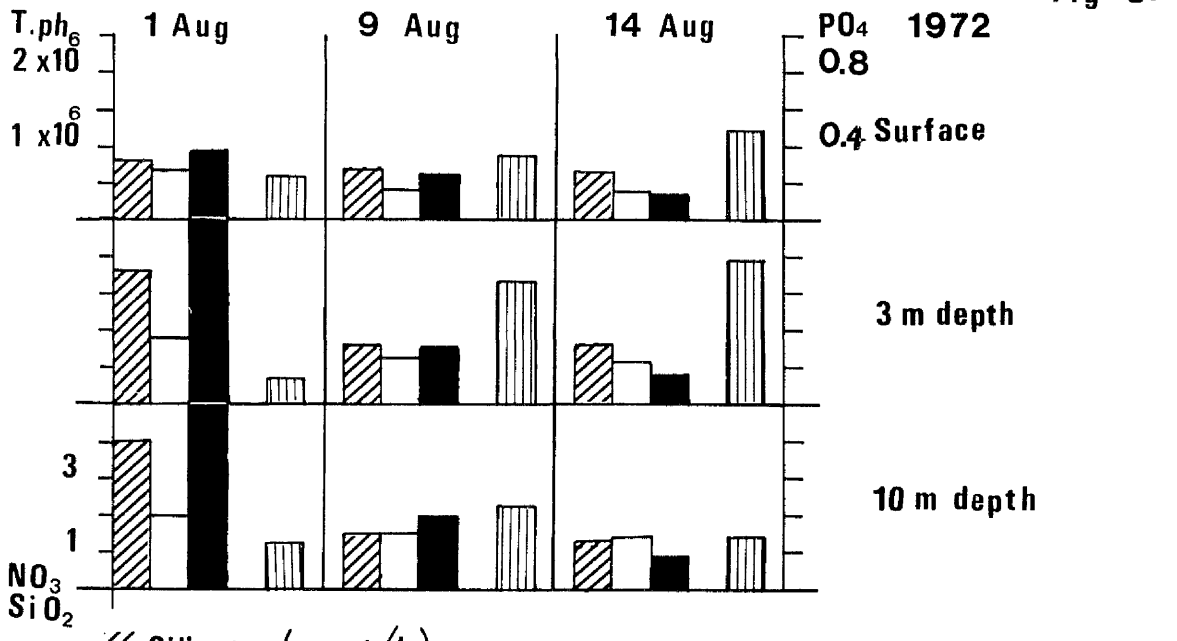
Time	1972 August 1	2	Date 3	4
0800-1000 hrs	31,200 cells/l	12,700 cells/l	4,000 cells/l	8,100 cells/l
1500-1700 hrs	8,400 cells/l	6,300 cells/l	2,800 cells/l	2,800 cells/l

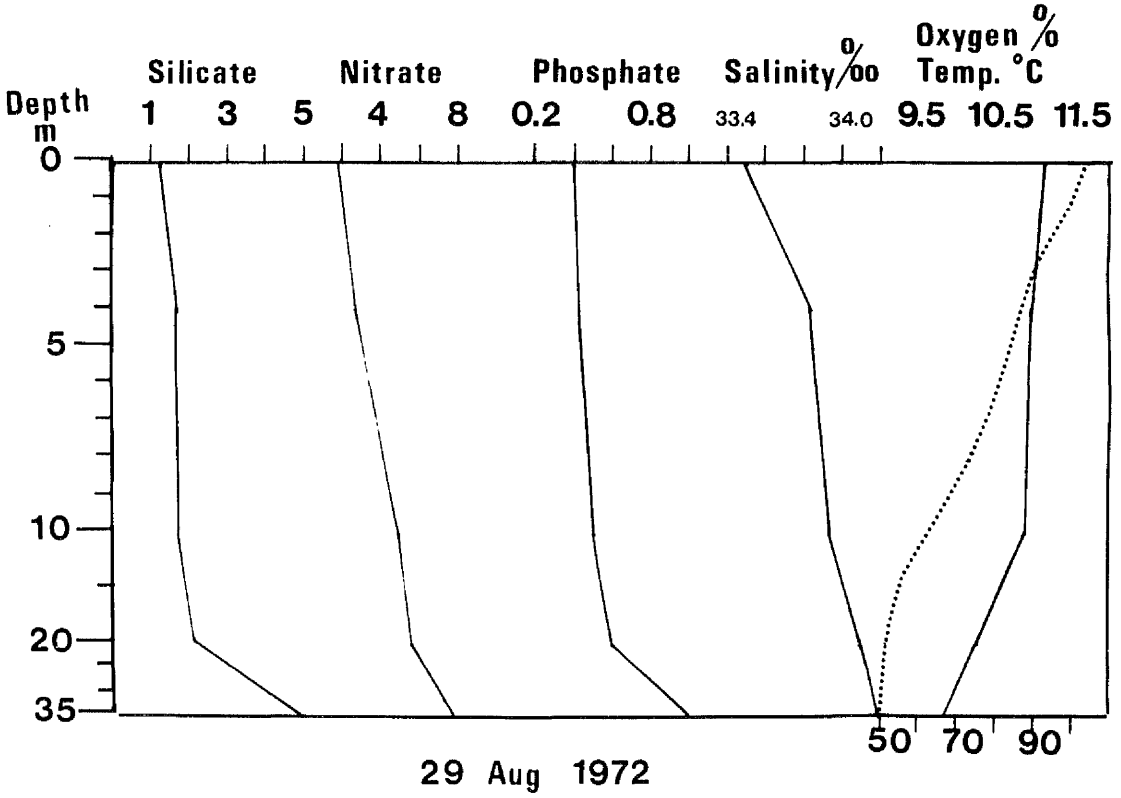
3 m depth

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

Fig 37





vii) Autumn period 1972

The autumnal phytoplankton increase was recorded during September (1972) and was composed almost entirely of the diatoms Leptocylindricus danicus and Eucampia zodiacus (Fig. 15). Between the end of August and September 4 nutrient levels almost doubled with nitrate around 5 µg at N/l, phosphate around 0.8 µg at P/l and silicate between 4 and 5 µg at Si/l. These increased nutrient levels probably stimulated the autumnal outburst, which commenced during the first week of September. From 4 to 15 September the standing crop fluctuated between 200,000 to 500,000 cells/l with Leptocylindricus comprising more than 95% of the total. Following this lag phase a fourfold increase took place between 18 to 18 September with the phytoplankton total reaching 2.95 million cells/l. This increase was accompanied by a pulse of Eucampia which reached reached a peak of 8,000 chains/l on 18 September. The depletion in nutrients (which was not evident till after this date) was about 4 µg at /l for nitrate and silicate and around 0.3 µg at P/l for phosphate.

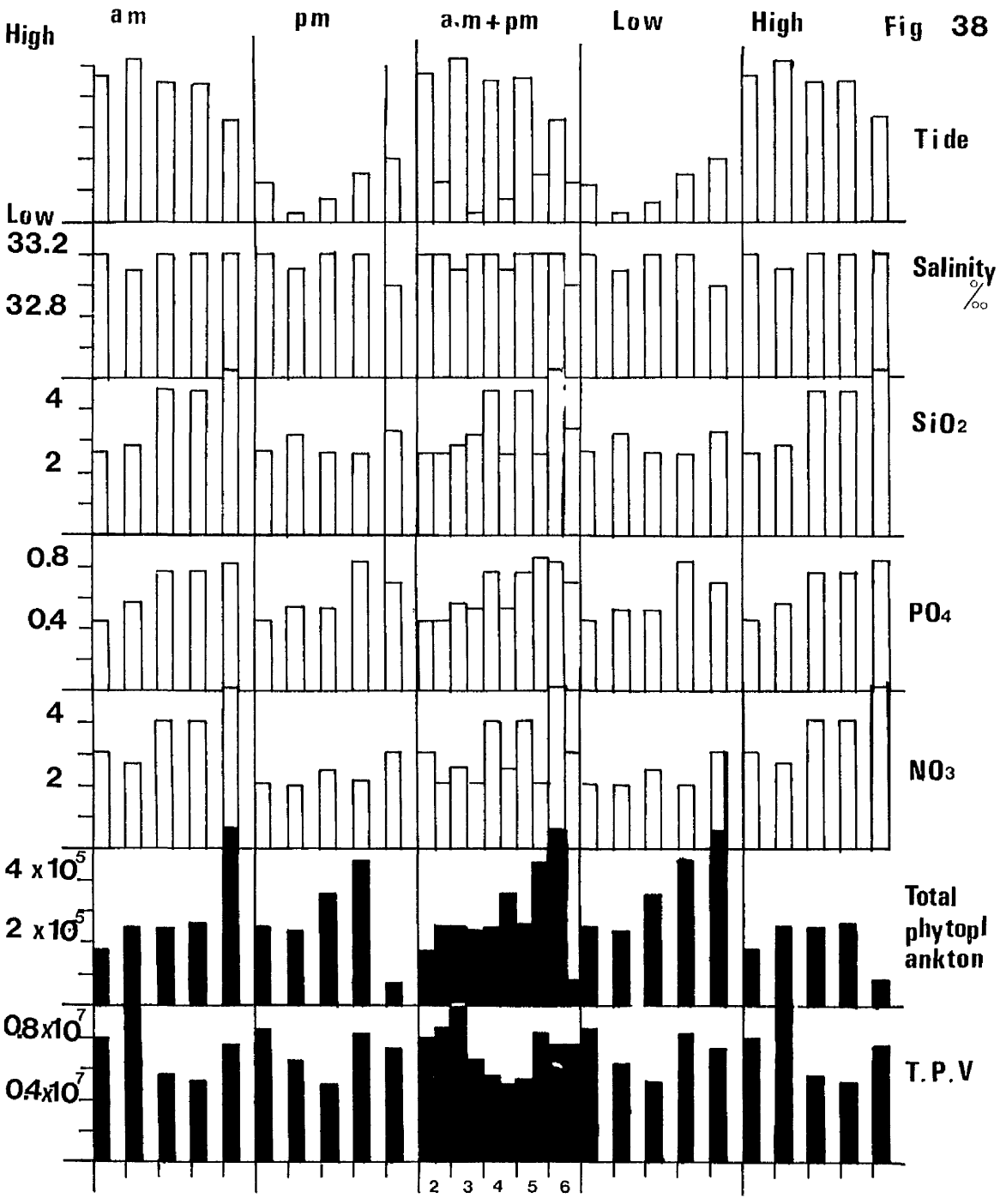
Both Leptocylindricus and Eucampia decreased to half by 20 September and were reduced to fairly low density (186,000 cells/l and 1,800 chains/l respectively) on September 26. On this date Skeletonema was the main organism of the population although it had been scarce in the preceding week. Out of a total standing crop of 840,000 cells/l, about 45% was Skeletonema, which was accompanied by Thalassiosira sp. and Nitzschia seriata. By 27 September the standing crop of all species had declined, (to 920,000 cells/l) falling to 600,000 at the end of the month. The only flagellate which was common during September was the silicoflagellate Dictyocha speculum which reached its maximum abundance of 8,900 cells/l on 4 September (the highest number of this species recorded in 1972 or 1973).

The standing crop at the beginning of October was low (170,000 cells/l). The composition of this population was similar to that in September, except for the disappearance of Eucampia. The small phytoplankton pulse which occurred

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

Fig 38



2_6 Oct 1972

during this month can be considered to be a continuation of the autumnal outburst which began in the middle of September. The period of this diatom increase, 2-6 October is represented in Fig. 38.

Two features are particularly clear during this period, firstly there is a doubling in nutrient concentration between 2 to 6 October and secondly there is a daily tidal rhythm in the concentration of all measured nutrients. The rise in silicate levels was from 2.5 on October 2 to 5.2 µg at Si/l on October 6, phosphate from 0.42 to 0.81 µg at P/l and nitrate 3 to 5.1 ug at N/l. The origin of this increase is unlikely to be from vertical mixing since there is still a temperature gradient present and no strong winds occurred during this period. It seems likely that the nutrient enrichment was a consequence of spring tides which reached their maximum range (2.9 metres on 6 October. Although no tidal oscillations in salinity were found, the nutrient enrichment on each incoming tide is clear.

The rising nutrient levels stimulated the small phytoplankton outburst which reached a peak of 570,000 cells per litre on 6 October. Leptocylindricus again constituted more than 60% of the total with small amounts of Skeletonema and Thalassiosira. Since the magnitude of the pulse was small there was no obvious nutrient depletion. By October 11 the outburst was over and the phytoplankton total had fallen to less than 100,000 cells/l. This was the last phytoplankton pulse in 1972, further growth evidently being limited by the rapidly declining day-length (9 hours at the end of October).

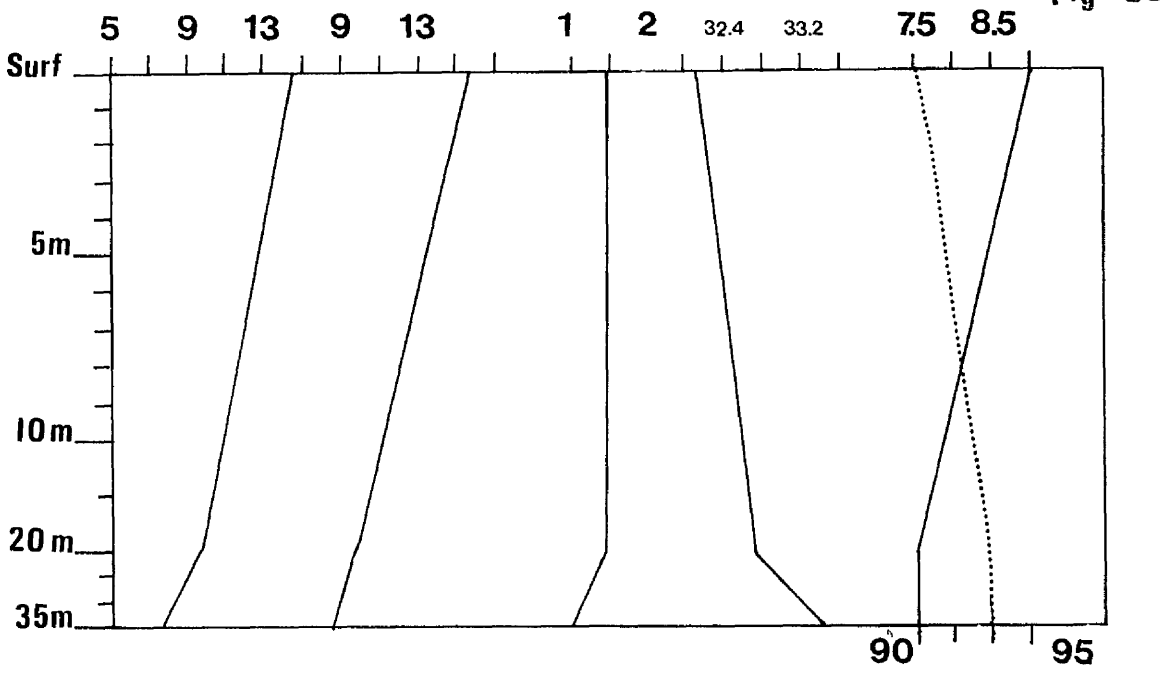
Following the decline of the phytoplankton, physical influences prevailed. By the end of October, following the breakdown of stratification by strong winds, nutrients had risen to half their mean winter values.

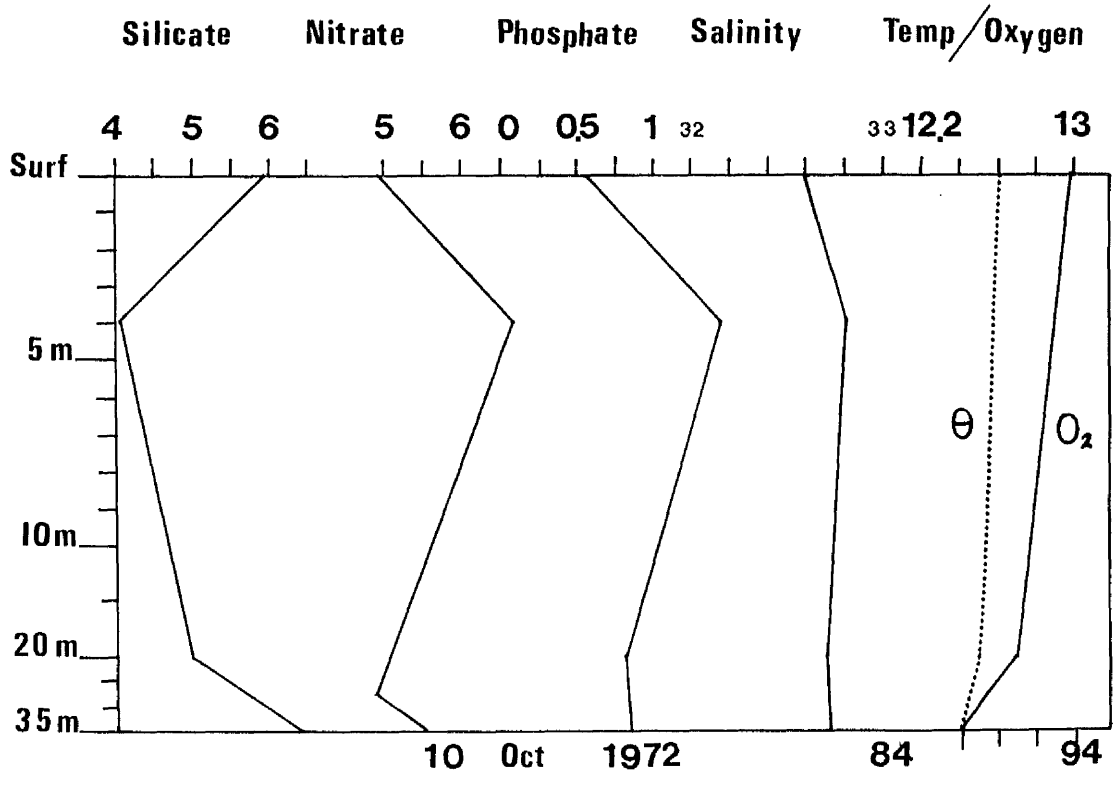
FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

8 Dec 1972

Fig 39





Winter Period 1972-1973

The winter period began in November with very strong winds, heavy periods of rainfall and rapidly declining day-length. The water column was isothermal with a temperature around 11°C (on November 7). Salinity at the surface began to fall from November 5 due to heavy periods of rain, and all nutrients showed a corresponding rise. Nitrate increased from 7.54 µg at N/l on 1st to 11.2 on 7th, silicate from 7.5 to 8.0 µg at Si/l and phosphate from 0.96 to 1.4 µg at P/l. The salinity decline (at the surface) was from 33.10 to 32.60‰. Nutrient concentrations were less at the bottom (35 metres) where the salinity was highest. The diatom population at this time was sparse and was frequently dominated by non-planktonic species particularly Naviculoid diatoms.

The largest rise in nutrients occurred between November 30 and December 8 when nitrate increased to 13 µg at N/l, phosphate to 1.4 µg at P/l and silicate to 14.5 µg at Si/l, (Figure 39). On this date temperature increased with depth (from 7.5 to 8.4°C) whereas salinity increased from 32.1 at the surface to 33.4‰ at the bottom. The highest nutrient levels are associated with reduced salinity indicating the influence of the high nutrient content of the inflowing fresh water. These nutrient levels were approaching the mean winter level and further variations in nutrient concentrations (during January and February) were associated with rainfall.

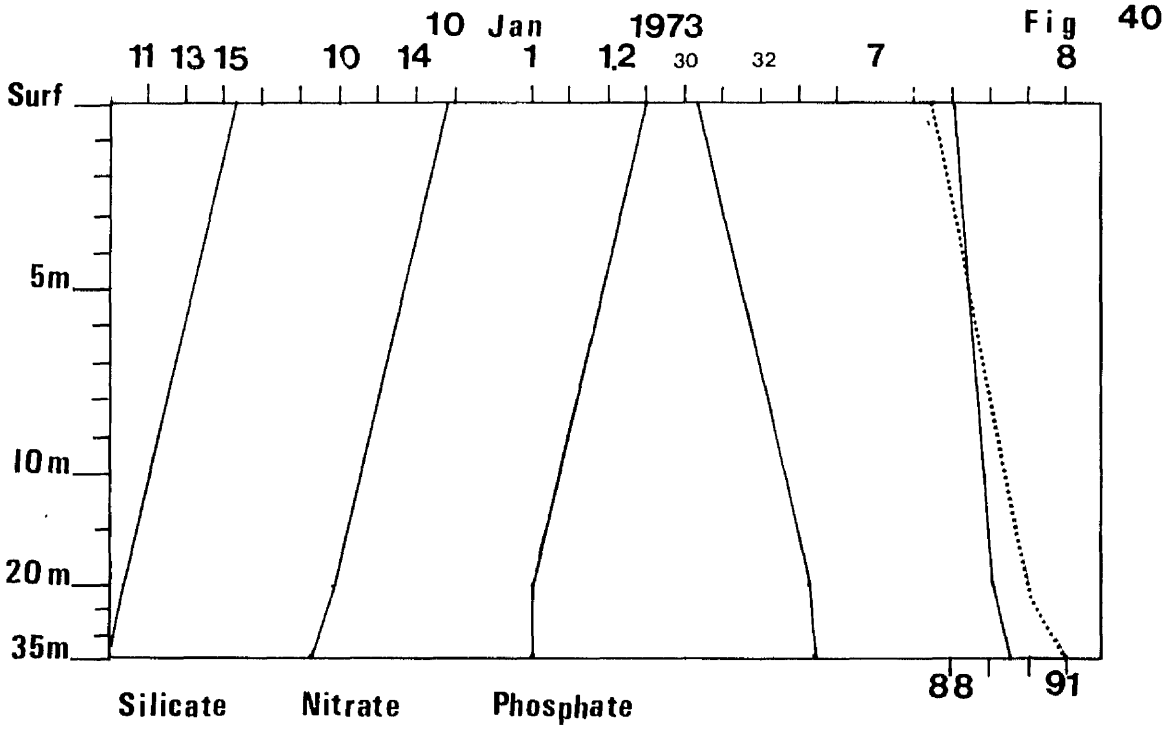
The relationship between rainfall, salinity and nutrient content of the water is clearest for nitrate and silicate. Maximum concentrations of these nutrients occurred around 25 January, 20 February and 1 March, coinciding with salinity depressions. Each reduction in salinity followed (or accompanied) a period of heavy rainfall.

Profiles for this period (Fig. 40) show one common feature, that the nutrients levels are consistently less at the bottom. These nutrient levels are evidently those of the incoming more saline water (from the

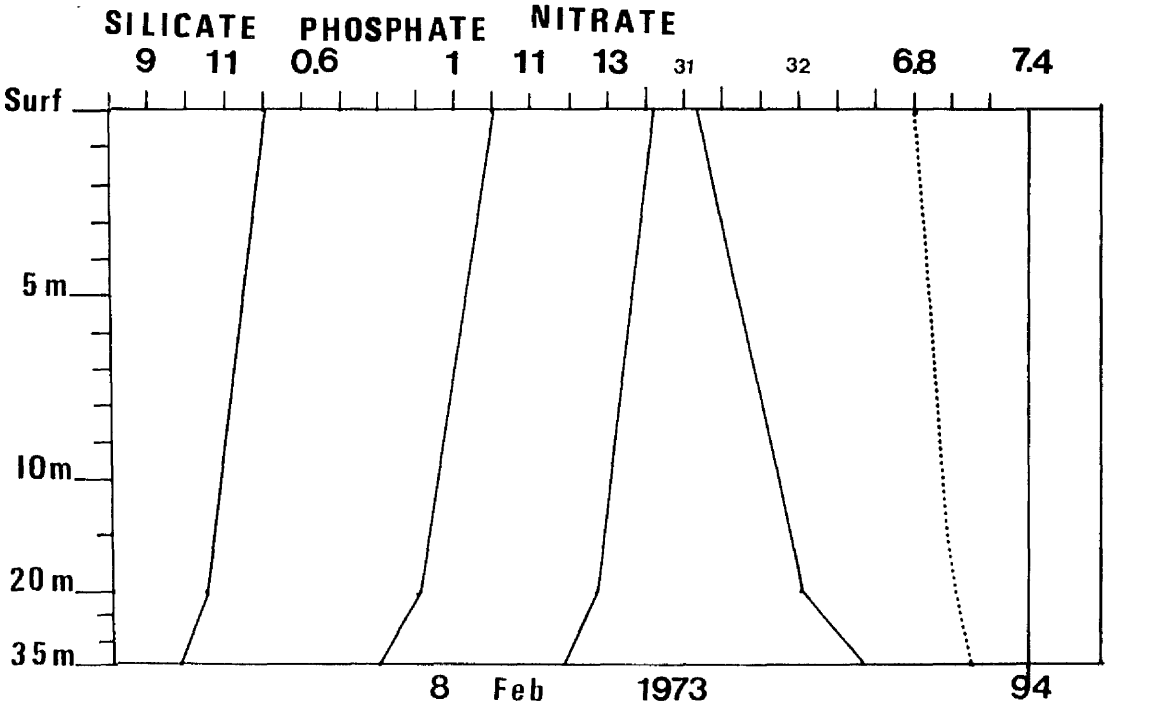
FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

Fig 40



Salinity Temp/Oxygen



North Channel). The temperature of this bottom water is generally warmer than the surface water, for instance on January 7 the increase is from 7.3 at the surface to 8.0°C at the bottom. The maximum concentration of all nutrients occurs towards the end of January and are as follows: nitrate 23.7 µg at N/l, phosphate 1.6 µg at P/l, and silicate 15 µg at Si/l. pH values during this period vary from 7.75 to 8.15.

The phytoplankton standing crop during this period is sparse, generally fluctuating between 30,000 to 60,000 cells/l. Apart from non-planktonic forms only Thalassiosira sp was common and Skeletonema was completely absent. Chlorophyll a values never exceeded 0.05 µg/l during this period and were often undetectable.

CHAPTER 6

CHAPTER 6

DIURNAL VARIATION

The existence of diurnal fluctuations in natural phytoplankton populations has been recognised by many workers. Diurnal variations have been recorded in photosynthetic assimilation rates (from carbon 14 uptake) chlorophyll a content and phytoplankton numbers. Periodicities related to the 24 hour day-night period have been observed both for marine and fresh-water communities. These rhythms have generally been detected from samples taken (usually from the surface only) at regular intervals. The shortest sampling interval was taken by Kramer et al (1970) who took samples from Lake Erie at intervals of 20 minutes. However, the usual sampling period for such studies is 2 to 4 hours.

Regular daily variations in the carbon 14 uptake of phytoplankton populations from Pacific surface water were reported by Doty and Oguri (1957). Samples were taken twice daily (in the morning and afternoon) with the maximum photosynthetic assimilation occurring in the morning. Although no direct estimates of standing crop were made they discounted the possibility of periodic zooplankton grazing or vertical migration of flagellates into surface waters. More detailed experiments by Newhouse et al (1967) demonstrated that the photosynthetic standing crop was maximum at 1600 hours decreasing to a minimum at 0600 to 0800 hours. Lorenzen (1963) found a chlorophyll a maximum in temperate coastal waters at mid-day coinciding with the daily maximum of phosphate and the minimum levels of nitrate. On the other hand Gloschenko et al (1972) found that chlorophyll a exhibited a diel periodicity in Oregon coastal waters with maximum surface concentrations around midnight. The highest concentration at 25 m depth was found in the late afternoon or evening.

Malone (1971) showed a differentiation between nanoplankton and net plankton from tropical oligatrophic surface waters, in the time of maximum carbon 14 incorporation. Nanoplankton had a morning maximum in photosynthetic assimilation whereas net plankton showed an afternoon maximum. This he attributed to a differential response to low nutrient regions under which nanoplankton were able to photosynthesize more efficiently, thus attaining an earlier maximum than net plankton. Evidence from fresh water studies by Kramer et al (1970) showed that chlorophyll reached maximum abundance in surface waters around 1800 hours although the maximum phytoplankton density occurred at 1200 hours. The timing of the daily maximum standing crop of phytoplankton is thus very variable and may occur at almost any time of the day.

Wood and Corcoran (1966) in their studies on the diurnal variation of phytoplankton in tropical and sub-tropical oceans demonstrated clear periodicities in the mean chlorophyll a level and phytoplankton counts (averaged over the entire water column). The number of organisms and chlorophyll a levels showed no constant relationship but always decreased at night and increased to a day-time maximum. This fluctuation was attributed to zooplankton grazing as it was most pronounced in areas where the deep-scattering layer showed pronounced vertical migration. They also postulated from their data that the reproduction of phytoplankton organisms is more rapid than is generally conceded. For a mixed population of coccolithophores and dinoflagellates a net generation time of 8 hours was suggested, and 4 hours for a population of Chaetoceros and Asterionella. The actual multiplication rates were considered to be even higher since the recorded rates are net and do not allow for grazing to be taken into account.

Hasle (1954) showed that the large accumulation of dinoflagellates (mainly Peridinium spp) in surface waters of the Oslo fjord was due to phototactic diurnal migration. The time of maximum abundance was variable but always occurred during the day time. Persistent vertical migration

rhythms have also been reported from intertidal populations (Brown et al 1972) with diatoms and flagellates reaching a maximum at the surface at 1000 hours. Doty and Oguri (1957) considered that a further cause for rhythmic variations in cell numbers may be the time of cell division, with the onset of reproductive activities occurring in the evening.

The nature of the present annual study allows us to detect diurnal variation on a twice daily basis for long periods but the dynamic phenomena which occur on an hourly basis are missed. The aim of this 24 hour study is to ascertain the extent and time period of the major biological and chemical variables in the Clyde. Two periods were chosen for study, one on July 13, 1973, and the other on August 17. During this period stratification would be expected under the prevailing calm conditions with a possibility of observing the influence of occasional wind mixing on the thermal structure of the water column. This would allow an assessment of the role played by the lower part of the water column in supplying nutrients to the overlying waters.

Organization and sampling programme for the study of diurnal variation

For the purposes of a study of diurnal variation in the Clyde two 24 hour sampling programmes were undertaken with the assistance of seven other people. The intensive sampling programme continued from 0000 hrs on both occasions to 0000 hrs the following night, although the first study on July 13 (see Tables 4 and 5) was abandoned at 1500 hours due to equipment malfunction. The 'transect' from Keppel pier (station 2) to the Perch (station 3) across Fairlie Channel was chosen for its proximity to the shore laboratory at the University Marine Biological Station. Integrated, pumped samples, were taken from surface, 1 m and 3 m depths while additional samples of 60 litres were pumped from 10 and 20 metres at station (1) - mid channel. Samples were taken at two-hourly intervals starting at 0000 hrs and were accompanied by vertical profiles of temperature, salinity and oxygen.

Each series of samples were returned immediately to the laboratory where 1 litre sub-samples for chemical analysis were frozen and filtration for chlorophyll a determination and phytoplankton estimation were made. The organization of manpower in the field, for sample collection, the handling of samples and filtration in the laboratory required strict integration of individual contributions to the overall programme.

Acknowledgements

I would like to offer my sincere thanks to Prof. N. Millott for putting the facilities of the Marine Biological Station at Millport at my disposal and for the use of the R.V. Mizpah for two complete 24 hour periods. I would also like to express my gratitude to Mr. B. K. Maulood for his indispensable help throughout the two operations. I would like to thank the following people who also gave assistance, Messrs. J. Clokie, S. Gorzula, J. Flanagan, I. Wilkie, and the boat crew: Messrs. R. McBay, C. McLoughlin and K. Cameron.

Results and Discussion

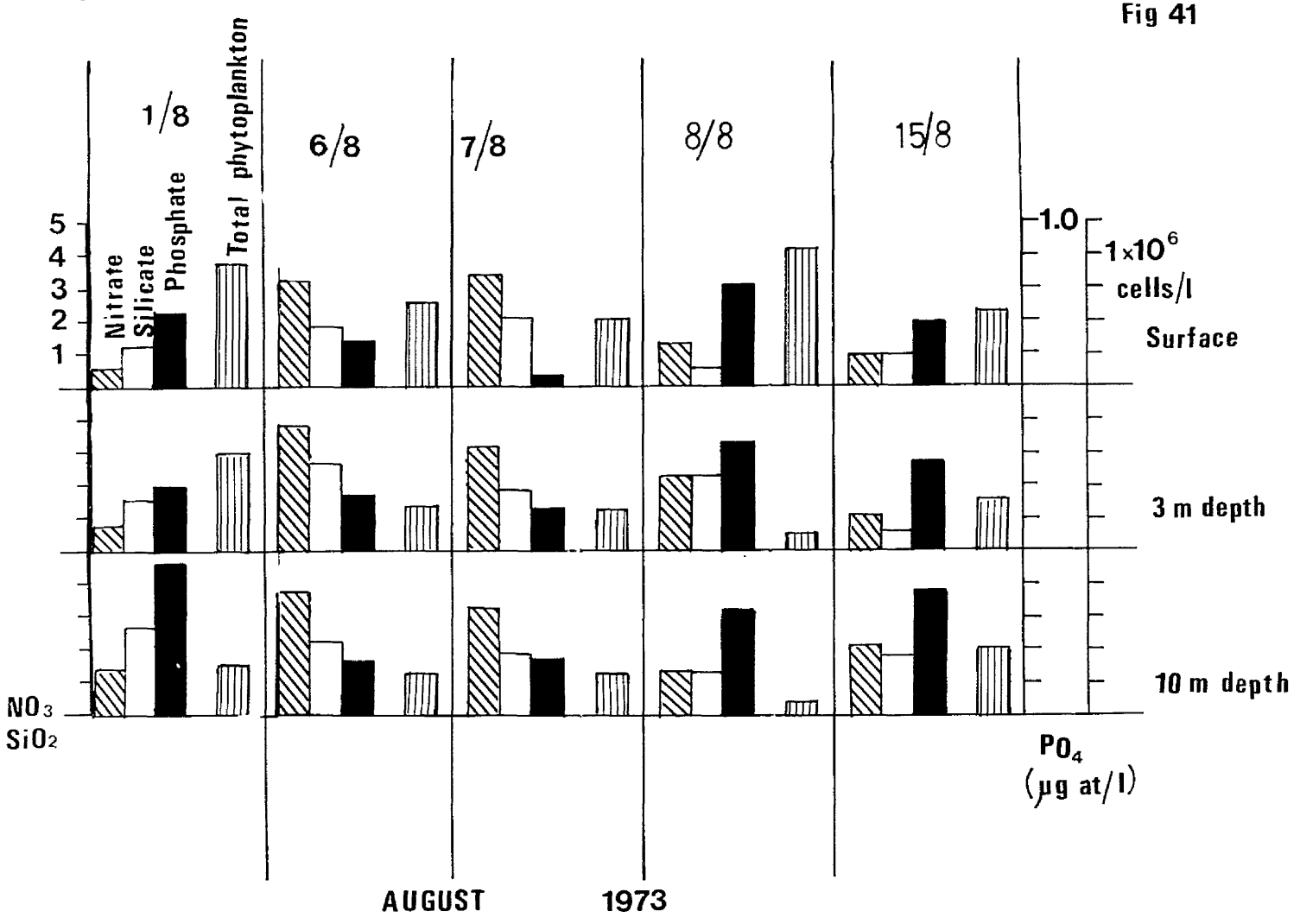
Before discussing the only completed diurnal variation study on 17 August, it may be useful to describe in detail the period leading up to this study (Fig. 41). The first 16 days of the month were generally calm with the 6 days prior to the diurnal study being particularly sunny and warm, in fact the water temperature reached its annual maximum of 16.8°C on the afternoon of August 14.

At the beginning of August, the standing crop throughout the upper 10 metres was fairly large (around 700,000 cells/l) with a chlorophyll a level of 0.15 µg/l. This declined to 500,000 cells/l at the surface on 6 August of which more than 90% was Chaetoceros spp, the standing crop at 3 metres was half that at the surface. Silicate and nitrate both displayed increases in the upper 3 metres whereas phosphate levels declined. By August 7 little change was evident except that phosphate was on the

FIRTH OF CLYDE

FAIRLIE CHANNEL STATION

Fig 41



increase at 10 m depth.

On August 10 and 13 the standing crop reached its maximum abundance at the surface increasing from 227,000 on the 10th to 994,000 on the 13th. Of this total, Chaetoceros spp constituted 50‰ and Thalassiosira represented 43‰, the latter diatom having proliferated by 20-fold in 3 days. Phytoplankton were still confined to the surface on the morning of August 14 where cell density (1 million cells/l) was 10-fold higher than the population at 3 m depth. Silicate and nitrate both showed depletion whereas phosphate showed little change. The domination of the populations was now taken over by Thalassiosira which constituted 61‰ of the total. By the afternoon of August 14 the population began to sink with cell density at 3 m being twice that at the surface. The decline was evident at all depths on 15 August and phosphate showed signs of depletion. By August 16 a total of 316,000 cells/l was recorded at 3 m depth of which two-thirds was Thalassiosira. Thus the diurnal variation study on August 17 took place during a period of population decline, with Thalassiosira and Chaetoceros being the dominant diatoms.

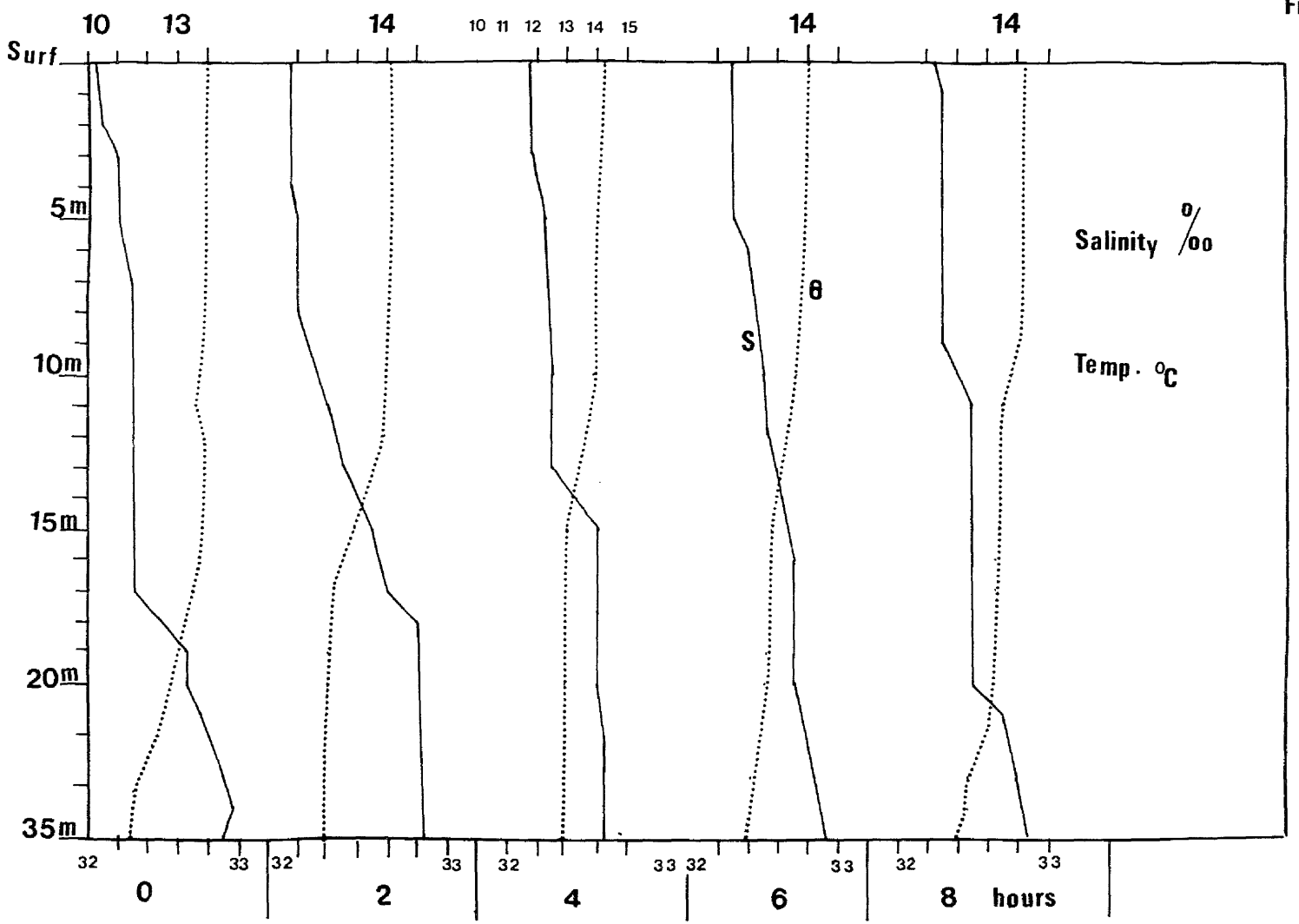
The weather conditions over the 24 hour sampling period were generally overcast and with light rain. Winds rapidly increased on the evening of the 16th rising from a daily wind speed of around 3 to 4 knots to exceed 10 knots on 17 August. The water mass was clearly stratified (Figs. 42 and 43) for the duration of the experiment. The position of the thermocline fluctuated dramatically during this period with the overlying layer varying in depth between 2 metres and 15 metres. At midday the thermocline was temporarily destroyed, only to be re-established 2 hours later. The temperature discontinuity was generally associated with a fairly short pycnocline having a gradient not exceeding 0.4‰. The position of this density gradient fluctuated in accordance with the upward or downward movement of the thermocline. Salinity at the surface fell to 32‰ while salinity at the bottom was generally around 33‰. The layer above the thermocline was around 14°C while the temperature reading at the bottom was about

DIURNAL VARIATION

17 AUGUST 1973

FAIRLIE CHANNEL STATION

Fig 42



12°C.

Measured nutrients (nitrate, phosphate and silicate) Figs. 44 and 45, showed distinct concentration gradients over the water column, all reaching their maximum abundance at the bottom. Fluctuations in nutrient levels were generally greater at 3 m and 10 m depth than at the surface or bottom. For example silicate levels varied from 0.9 to 3.2 µg at Si/l at 3 m depth whereas at the surface the variation was 0.5 to 2.2 µg at Si/l. Phosphate displayed concentrations at the surface ranging from 0.2 to 0.45 µg at P/l while at 3 m and 10 m the phosphate content reached 0.9 µg at P/l and fell below 0.4.

The timing of the maximum and minimum nutrient levels during a 24 hour period varied according to depth and the nutrient in question. At the surface all nutrients reached their daily maxima at 1400 hours with the following concentrations: nitrate 3.7 µg at N/l, silicate 2.2 µg at Si/l and phosphate 0.5 µg at P/l. Minimum surface concentrations were recorded for nitrate (1.1 ug at N/l)and phosphate (0.22 µg at P/l) at 1800 hours. The lowest silicate concentration (less than 1 µg at Si/l) occurred throughout the water column at 0800 hours. Averaged over the water column there were 2 maxima for all nutrients, one in the early morning around 0600 hours and one in the early afternoon at 1400 hours. Minima occurred at 0800 hours and 1800 hours. The afternoon maximum was higher than that of the morning. If these data are compared with the times of high and low water (High tide - 0258 and 1524 hours and low tide - 0827 and 2038 hours) then any tidal influence on the results can be discounted.

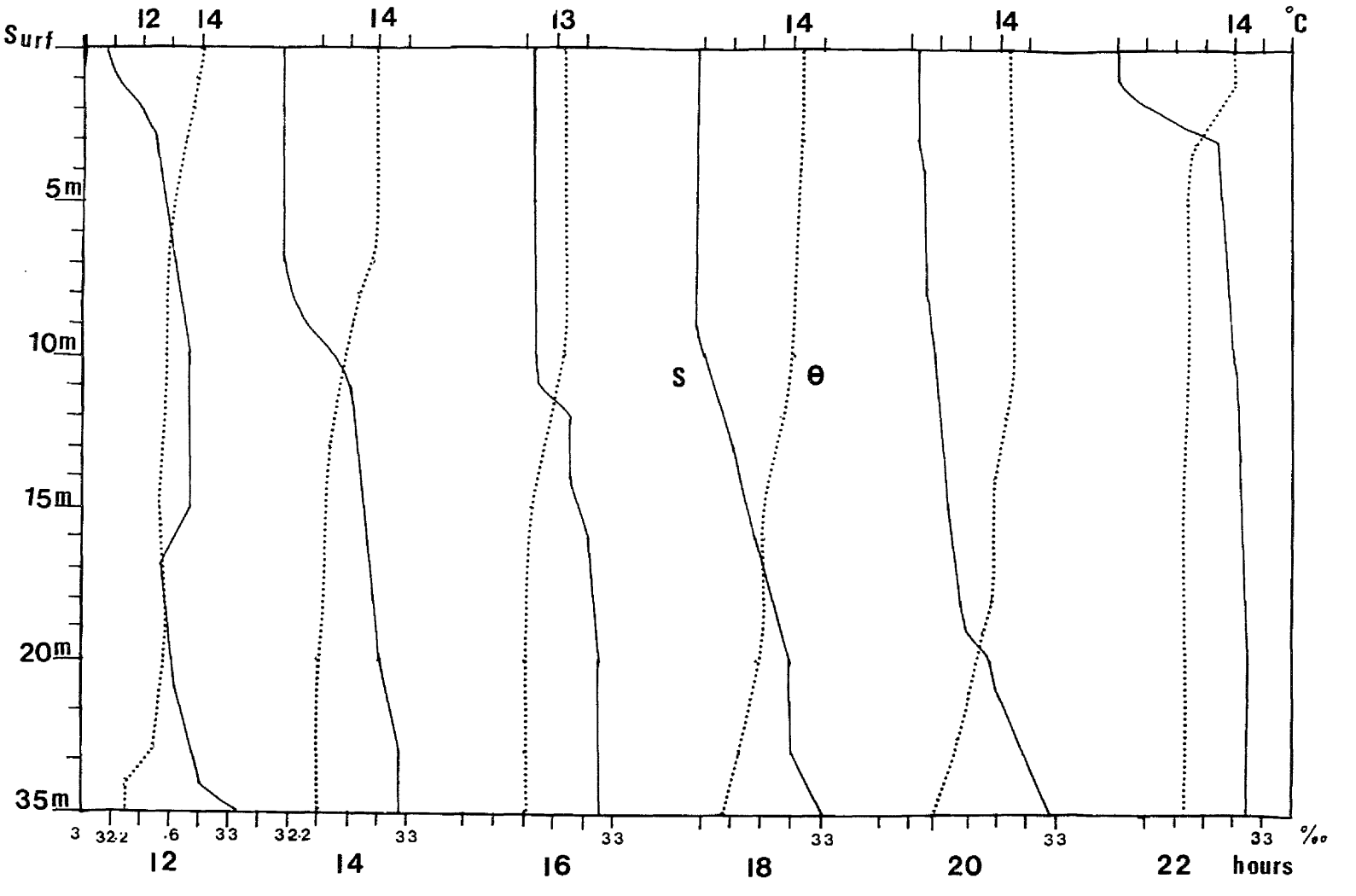
The observed nutrient fluctuations during this study appear to be a consequence of changes in the position of the steep density gradient (pycnocline) within the water column. Any upward or downward movement of the pycnocline will be accompanied by (potential) changes in the vertical distribution of nutrients.

From the profiles of salinity and temperature readings at 2-hourly

DIURNAL VARIATION

17 AUGUST 1973 FAIRLIE CHANNEL STATION

Fig 43



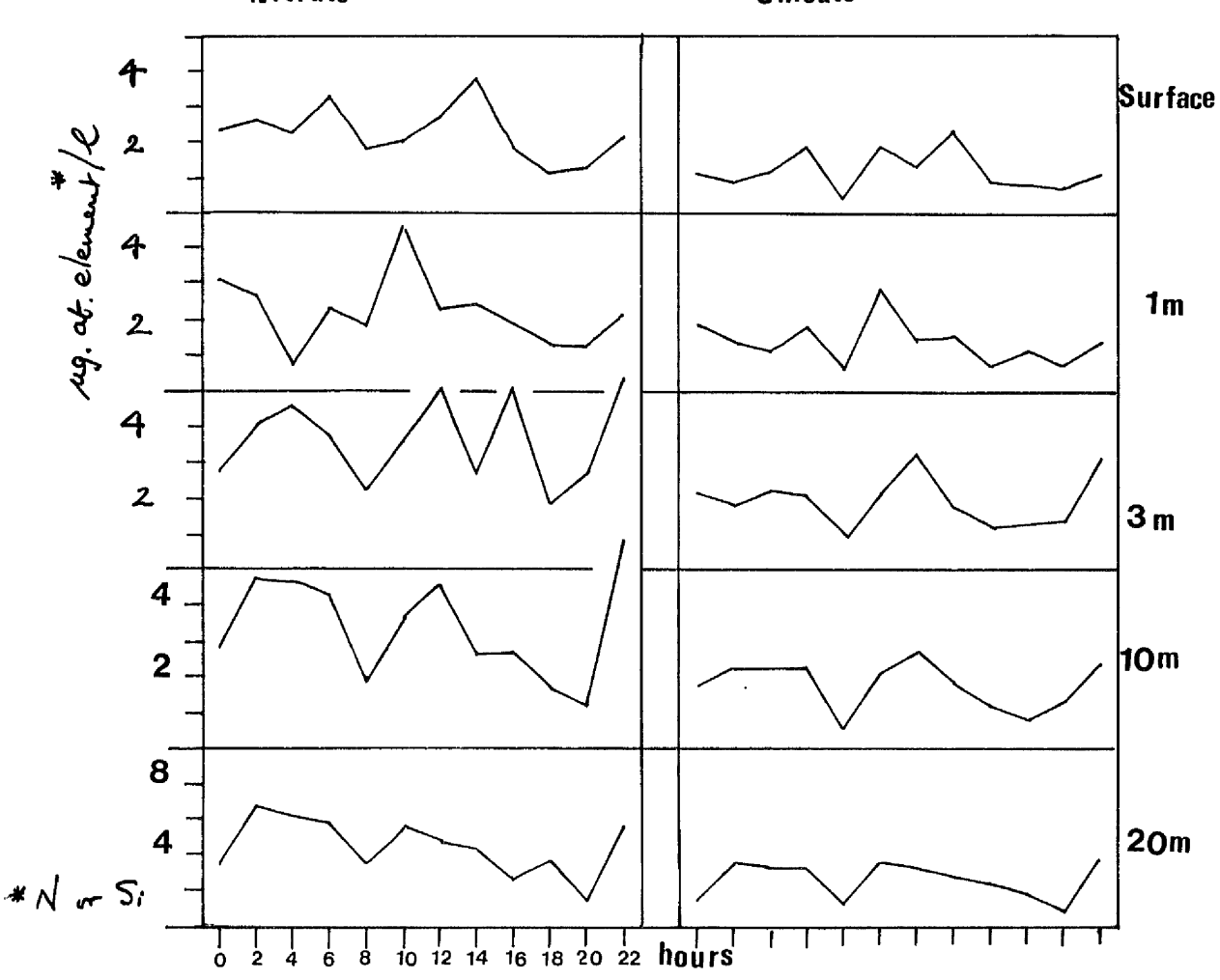
intervals throughout the 24 hour sampling period (Figs. 42 and 43) the vertical movement of the thermal and salinity gradients can be followed. At 0000 hours the pycnocline occurred between 17 to 20 metres, consequently samples taken at 20 m depth showed only slight enrichment compared with surface samples. By 0200 hours the pycnocline was 5 m nearer the surface resulting in an enrichment of all nutrients at 20 metres depth. The continued upward rise of the pycnocline resulted in a sustained nutrient increase in the overlying water, not reaching the surface till 0600 hours. At this time no clear thermal discontinuity existed, instead a continuous temperature gradient from surface to bottom was set up. The pattern of events can be clearly followed in the case of nitrate (Fig. 44). The increase in this nutrient first occurred below 10 m depth at 0200 hours reaching 3 m at 0400 hours, finally reaching the surface at 0600 hours.

The changes in the vertical position of the pycnocline and its formation and break-down (Figs. 42, 43) thus influence the vertical distribution of nutrients in the water column. During the 24 hour period the pycnocline was destroyed or almost reached the surface on 3 occasions, 0600 hours, 1200 hours and 2200 hours. These times correspond fairly closely with the timing of maximum abundance of nutrients over the upper 20 metres of the water column. They do <u>not</u> correspond with the state of tide.

During this 24 hour period the movement of the pycnocline appears to be <u>diurnal</u> rather than tidal. At midnight the pycnocline was at its greatest depth (17 m) gradually rising towards the surface over the next 6 hours. Between 0600 hours to 1200 hours the position of the pycnocline fluctuated between the surface and 10 m. During the afternoon and evening the pycnocline sank reaching 20 metres at 2000 hours. Similar diurnal variation in the position of the thermocline, with the thermal discontinuity moving towards the surface during the day was found in a freshwater loch by Maulood (personal communication).

DIURNAL VARIATION 17 AUGUST 1973

Fig 44



Thus the breakdown of stratification at 0600 hours and 1200 hours is followed (within two hours) by nutrient increases throughout the water column. The only peculiarity in the described pattern is the sudden rise of the pycnocline (to lie just below 1 metre depth) at the end of the sampling period (2200 hours). This was accompanied by an abrupt rise in all nutrients below a depth of 1 metre. The magnitude of these increases was remarkable with nitrate rising from 1.3 to 5.8 µg at N/l (at 10 m depth) within 2 hours and phosphate increasing from 0.42 to 0.94 µg at P/l over the same period. The rapidity and scale of these increases indicates that nutrient upwelling in this locality may be of very great importance in preventing nutrient depletion of surface waters even during periods of stratification.

As already mentioned, the phytoplankton population during this period was on the decline. This is clearly reflected in the chlorophyll a curve (Fig. 45) which shows an overall decline from 0.4 µg/l to 0.3 ug/l at the surface. However at 20 m depth the opposite picture was found with chlorophyll a increasing from 0.15 to 0.25 µg/l. This is probably a consequence of the sinking population (of Chaetoceros) falling below the limit of the thermocline.

The retarding influence of the pycnocline on the sinking population is clearly shown between 1400 to 2000 hours. During this period, chlorophyll a concentrations were generally greatest in the zone of thermal discontinuity (between 3 and 10 metres depth). Any breakdown of the pycnocline removes the retarding influence of a density gradient and cells sink rapidly from the photic zone. This phenomenon is clear at 20 m depth where pulses of chlorophyll a were recorded simultaneously with the breakdown of stratification at 0600 and 1200 hours.

Summary.

1. The pycnocline shows a diurnal oscillation moving upwards during the day and downwards at night.
2. Increases in key chemical parameters are related to transient breakdowns of the thermocline.

DIURNAL VARIATION

17 AUGUST 1973

Fig 45

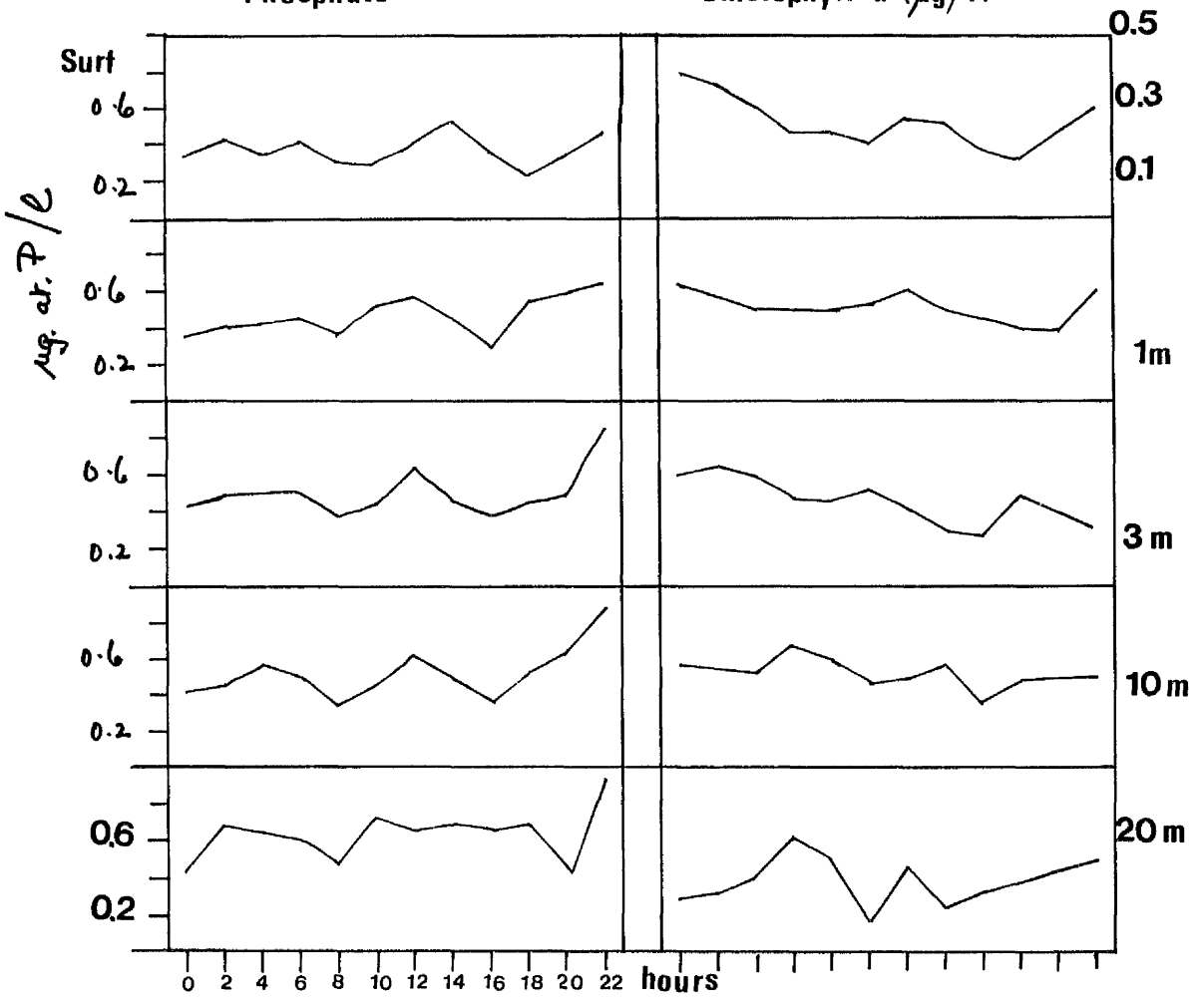


TABLE 4

Diurnal Variation in Fairlie Channel July 13, 1973

Sampling Time	Depth	Salinity (‰)	Temperature (°C)	Oxygen Saturation (%)	pH	Zooplankton dry weight (g)
0030	Surface	31.85	13.6	109%	8.0	0.285
	1 m	31.9	13.9	[redacted] 108%	7.88 [redacted]	[redacted]
	3 m	32.0	12.8	109%	8.0	
	10 m	32.06	12.4	100%	8.0	
	20 m	32.85	9.8	94%	7.95	
0230	Surface	31.9	13.6	110%	8.05	0.68
	1 m	31.9	13.6	112%	8.05	
	3 m	31.95	13.3	114%	7.99	
	10 m	32.7	11.2	94%	7.9	
	20 m	32.8	9.6	89%	7.87	
0430	Surface	31.9	14.3	109%	8.0	0.47
	1 m	31.9	14.0	107%	7.95	
	3 m	31.9	13.95	110%	7.9	
	10 m	32.04	13.95	110%	7.9	
	20 m	32.63	11.45	94%	7.9	
0630	Surface	31.9	13.9	103%	8.0	0.325
	1 m	31.9	12.6	113%	8.0	
	3 m	31.9	13.6	105%	7.91	
	10 m	31.95	12.1	90%	7.91	
	20 m	32.68	11.3	92%	7.8	
0830	Surface	32.85	13.1	98%	7.88	0.115
	1 m	32.05	12.8	102%	7.9	
	3 m	32.35	12.8	101%	7.86	
	10 m	32.75	12.8	100%	7.82	
	20 m	32.95	11	83%	7.81	

TABLE 5

Sampling Time	Depth	Salinity (%)	Tempera-ture (°C)	Oxygen Saturation (%)	pH	Zooplankton dry weight (g)
1030	Surface	32.15	12.8	98	7.8	0.35
	1 m	32.15	12.5	98	7.9	
	3 m	32.45	12.0	93	7.8	
	10 m	32.45	11.3	88	7.8	
	20 m	33.0	10.6	80	7.8	
1230	Surface	32.0	13.4	103	7.98	0.28
	1 m	32.25	12.9	106	7.94	
	3 m	32.3	12.9	95	7.9	
	10 m	32.85	11.1	89	7.9	
	20 m	33.05	10.6	85	8.0	
1430	Surface	32.0	13.6	100%	7.8	0.31
	1 m	32.1	13.1	103%	7.9	
	3 m	32.1	13.0	98%	7.9	
	10 m	32.7	11.6	89%	7.9	
	20 m	33.1	10.8	85%	7.9	
Discontinued due to equipment malfunction	Surface					
	1 m					
	3 m					
	10 m					
	20 m					
	Surface					
	1 m					
	3 m					
	10 m					
	20 m					

3. The source of nutrient to surface waters is from the deep water.
4. Large variations in nutrient levels and chlorophyll a values can be expected within a time period of two hours.
5. The observed variations are diurnal rather than tidal in origin.
6. Sinking phytoplankton cells accumulate at the pycnocline.

CHAPTER 7

CHAPTER 7

CONCLUSIONS

1. The various estimates of phytoplankton standing crop; total particle volume chlorophyll a measurement and actual cell counts showed a close relationship to one another particularly at times of high productivity.
2. The early spring diatom outburst in 1973 had a duration of less than two weeks.
3. The maximum numbers of phytoplankton (14 million cells/l) occurred on the afternoon of March 23, 1973. If samples had only been taken on the morning of this day, the spring outburst would have been underestimated by 4.5 million cells/l.
4. The spring outburst was probably dissipated by turbulent mixing from strong winds and may have been limited by depletion of silicate.
5. Competition appears to exist between *Skeletonema costatum* and *Thalassiosira nordenskioldii*, the outcome of which is probably determined by the following factors:
   a) The size of the initial inoculum of each species at the commencement of the outburst.
   b) The relative rate of multiplication of the two species.
   c) Difference in sinking rates of the two organisms.
   d) The concentration of key nutrients at the commencement of the increase.
6. The nutrient increase in April 1973 may be related to strong westerly winds bringing in enriched highly saline water from the outer Firth.
7. The lack of any phytoplankton increase following the period of nutrient upwelling in April, when all measured parameters appeared favourable, may be related to the greater abundance of zooplankton at this time.

8. The increase in phosphate during the night is possibly related to excretion of inorganic phosphorus by zooplankton which accumulate in surface waters at this time.

9. Probably, for the first time from field evidence it has been shown that Thalassiosira has its period of multiplication during the night while Skeletonema increases during the day.

10. The rapid reduction in Skeletonema numbers following a peak might be a result of its faster sinking rate.

11. Other forms of combined nitrogen (ammonia, nitrite and organic nitrogen) apart from nitrate may be utilized by phytoplankton particularly during periods of increase (particularly May 1973).

12. Three distinct pulses of Thalassiosira occurred in a single month (May) all but the last one accompanied by Skeletonema.

13. As in other coastal areas warm water species such as Peridinium, Ceratium and Coccolithus appeared during the summer.

14. The seasonal succession of dominant species in the Clyde Sea area in 1973 (till August) was Skeletonema costatum succeeded by Thalassiosira nordenskioldii succeeded by Chaetoceros cinctum.

15. Stratification in the Fairlie Channel lasts from late June till October.

16. Peridinium sp and Coccolithus huxleyi regularly show greater abundance in surface waters in the morning than in the afternoon.

17. Nutrient enrichment of surface waters during the summer was associated with the upwelling of highly saline waters. Transient nutrient rise during the winter were coincided with sudden reduction in salinity.

18. The Autumn flora in the Clyde appears to be dominated by Leptocylindricus danicus and Eucampia zodiacus.

19. The peak at the Spring diatom outburst around the Cumbraes occurred on March 23 (1973) whereas in more sheltered sea lochs the increase was up to a week earlier.

20. In 1972 and 1973 the spring diatom increase in the Fairlie Channel was dominated by Skeletonema costatum whereas in Loch Striven in 1973 Thalassiosira nordenskioldii predominated.

21. The horizontal distribution of nutrients in the Fairlie Channel was heterogeneous and Phytoplankton occurred in patches.

22. The dissipation of most outbursts was associated with higher numbers at successive depths indicating that the population was sinking from the productive zone.

23. Tidal oscillations in nutrient and salinity were observed on occasions.

24. Chaetocerus cinctum appear to flourish under stratified conditions.

25. A device for taking integrated surface samples has been devised, which provides reproducible samples from surface waters (upper 5 cm).

26. The Clyde Sea area has a higher nutrient status during the winter than many other coastal waters in Britain. This may be related to continuous enrichment from the estuarine inflow.

27. This program of continuous (twice daily) sampling indicates the presence of successive pulses of phytoplankton from the first spring peak onwards, each being smaller than the preceding one.

28. Due to the rapidly changing nature of the phytoplankton and the nutrient in the Clyde Sea area samples taken on a fortnightly or weekly basis would have given a completely erroneous picture of events. This may also be true for other coastal areas. A similar sampling program would be advisable for areas in which short term variation might be expected.

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