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PHYTOPLANKTON PRODUCTION IN THE WESTERN BARENTS SEA 1949-1954

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During the years 1949-1954 the R. V. Ernest Holt has made several thousand plankton observations in that part of the Barents Sea covered in the course of her Arctic Fishery Investigations. Of these some three hundred have been taken by 50 m. hauls using the International Fine Net as well as a water bottle sampling for phytoplankton during 1953. This Fine Net and water bottle plankton has now been analysed; it is found to fall into a well defined pattern whose description and interpretation will be the object of the present paper.

Figure 1 shows the area covered by the Ernest Holt. There have been two main lines of plankton and hydrographic stations. The West Bear Island section runs from the island along the $74^{\circ} 24'$ parallel to longitude $13^{\circ} W$ while the southern section runs from Cape Bull (the southerly point of Bear Island) to Loppen on the Norwegian coast. A further three lines of stations running off the Spitzbergen bank into the deeper water to the north east of Bear Island have also been worked. Here the coverage is far less complete. The southern stations A-E were only sampled for phytoplankton in 1949 and 1950.

The hydrography of the area has been discussed by Lee (1952). The western section was designed to run from the Arctic water of the Bear Island current through an area of mixed water and out into the oceanic water of the West Spitzbergen Current. The southern section also starts in Arctic water near Bear Island and passing through a region of variable hydrography crosses the N. Cape branch of the oceanic current where it flows into the S. Barents Sea. The three eastern bank sections are also in water of variable composition and currents. A branch from the N. Cape Current flows northwards in the region of $73^{\circ} N. 30^{\circ} E.$, and circles round upon itself either becoming confused with the Arctic water flowing down off the Spitzbergen bank or else returning south with the Bear Island current. In this area, just off the bank, eddies are set up and the position corresponds to those edges of the Arctic water in the West Norwegian Sea described by Wiborg (1954) as being highly productive of zooplankton.

Though a general account of the phytoplankton species to be found in the west Barents Sea was given by Wulff (1916) there have been no detailed ecological studies in the area. The standard work on the phytoplankton of the Barents Sea was done by Kreps and Vjerbinskya (1931) and consisted of a nutrient, pH, oxygen and pigment survey along the Kola meridian at $33^{\circ} 30' E.$, and also at $38^{\circ} E.$ extending northwards from the Murman Coast as far as the ice edge. The sequence of nutrient depletion and pigment development they describe has been confirmed in terms of the changes in standing crops of phytoplankton in the Bear Island region some 300 miles to the west. The actual compositions of the arctic and oceanic floras near Bear Island together with the seasonal abundance of the constituent species, agrees well with other results from sub-arctic phytoplankton investigations, more especially those of Braarud and Neilson from the Denmark Strait and Iceland. The reasoning applied by Sverdrup (1953) in a recent paper on the "Conditions of Vernal Blooming of Phytoplankton" give an explanation of the timing and extent of the Bear Island phytoplankton production when adapted for this area.

Methods

The sampling error of the Fine Net, as compared with other standard techniques of phytoplankton estimation has been calculated by Steeman Nielson and also by Oushing (unpub.). The results from Fine Net hauls are subject to a variable error dependent both on the quantity and composition of the flora through which it passes, an error which may be very great when the species sampled are among the smaller phytoplanktons. Although this makes the Fine Net unsuitable for determining the true standing crop or exact composition of the phytoplankton it is considered, especially when compared with occasional water bottle samples, to give a sufficiently good guide to the relative variations as to justify its use (Corlett 1953). Water bottle samples taken from the Arctic water indicate that the diatoms are by far the most important constituents of the phytoplankton. There are more nannoplanktons and small diatoms in the oceanic water and a preliminary survey of the former indicates that they are relatively insignificant (Butcher, unpub.).

For detailed examination of the relationships between vertical stability of the water column and distribution of the phytoplankton water bottle samples from 1953 have been used.

The method of counting in the case of water bottles has been by an inverted microscope while Fine Net hauls have been counted by sub-sampling using a stempel pipette (Hensen's method). The former have been expressed as number of cells/litre and the latter as number of cells under a m^2 column of 50 metres depth. In both cases the spring diatom Chaetoceros sociale has been estimated as numbers of chains/sample owing to the very small size of its individual cells.

Results from these counts and the identification of the species fall into a consistent pattern from year to year. The trips of the "Holt" are irregular and the coverage sometimes poor owing to weather conditions so that in some years this pattern of phytoplankton production is clearer than in others. Besides this the blooming of diatoms may take place extremely rapidly and there must be numerous occasions when the time interval between consecutive cruises of approximately a month has caused us to miss a large scale production.

A monthly summary of the Fine Net and water bottle samples over the period of 6 years gives a picture as follows:-

Jan. Feb. Mar. The phytoplankton is generally poor over the whole region. Dinoflagellates and tintinnids outnumber the diatoms which are extremely scarce. The species of diatom that are found belong to the summer and autumn flowering types and only come in the deep water stations. On the bank there is almost no trace of spores or chains of the spring flowering arctic species which supports the view of Ussachev that these are brought down each year in the ice floes. (Ussachev, 1946), though there is also the possibility that they are on the bottom during winter.

April (Fig. 2) A large outburst of spring phytoplankton takes place on the Spitzbergen Bank. In nearly every instance high standing crops of diatoms are recorded from the shallow Arctic stations MX-BK6. At the same time the phytoplankton in the deep water stations of the West Spitzbergen current remains at its winter level. The stations that are just off the bank show a high standing crop only under certain hydrographic conditions - namely a shallow temperature inversion with cold arctic water of low salinity lying on top of warmer and more saline water. The water in which a spring flowering takes place seems associated with the edge of the ice pack or with ice floes blown S.W. by the prevailing winds during this month. The species which make up the spring flowering are all described by Lebour as arctic-neritic and in general correspond to those found in great quantities near the ice edge by Braarud and Nielsen. (Mostly Chaetoceros sociale, Thalassiosira and Fragilaria spp.) In the deep water stations of the West Spitzbergen and N. Cape currents there is no ice coverage and no transient incursions of melt water. There is also a homogenous water column far down below the euphotic zone which is perhaps the critical factor in delaying the flowering of the oceanic species. Observations taken in April 1952 with a Hensen 1 m. net in the region of Station A and extending westwards to the Norwegian coastal water, showed a large standing crop of phytoplankton was present. During this month there appears to be a flowering of diatoms in the coastal water to the south and near the ice edge to the north, but none in the oceanic water between. This observation agrees with the findings of Kreps and Verbjinskya.

May (Fig. 2) The spring outburst is still recorded from the east part of the Bank (St Bk I-6) where periods of stability and turbulence may be supposed to alternate but where the bottom is within the "critical" depth for the time of year. (An elaboration of this concept will be found under the section on radiation and stability.)

The standing crop of zooplankton in these arctic water stations is also low and a theoretical estimate of its grazing potential coupled with the standing crops and reproductive rates of the phytoplankton, indicates that the plants are not limited by grazing. This contrasts with the position in the mixed and oceanic water over the same period, when high standing crops of zooplankton and numbers of nauplii associate low standing crops of phytoplankton

with a grazing control, (i.e. in addition to the physical controls of radiation and stability.) That this is so is indicated by the very low quantities of phytoplankton that have been taken in the deep water stations during this month, even when a thermocline within the critical depth has become established.

June (Fig. 2) The quantities of phytoplankton recorded vary greatly for different years. The general indications are that radiation and stability no longer limit production, except where the ice is still present towards Hope Island, but that the rich standing crops previously noted on the Bear Island Bank have depleted the nutrients and have partly sunk and partly been grazed down.

Such flora that is recorded consists of oceanic species in the deep water dominated by Chaetoceros spp (more particularly C. compressus, C. Convolutus, C. lascinosus.) which is also found mixed with the remains of the spring flowering in the cold water stations. At stations M-P the temperature remains in the region of 2°C during June and the occasional large flowerings of chaetocerids always appear associated with water of 6-7°C. (Fig. 2) The Arctic water thus seems inimical to these oceanic forms.

The water to the N.E. of Bear Island always has low standing crops with a few chaetocerids and Rhizosolenia spp. present. However, the great number of copepod nauplii found here during this month indicates that there is a high productivity coupled with intense grazing. Occasional high standing crops are found along the southern section but the rarity with which these are encountered suggests that they are rapidly eaten down and only fortuitously sampled by the Ernest Holt. Along the outer stations of the west section there have never been good catches of phytoplankton during June but again this is doubtless due to the heavy grazing.

July (Fig. 2) A shallow thermocline at less than 25 m. coupled with 24 hours daylight provides at least two of the factors for rapid production of algae. Very large hauls were obtained on the southern section stations A, B and C during 1949 but on the whole July is poor in standing crops over the whole area. The work of Kreps and Vjerbinskya shows that the upper layers of both Arctic and Atlantic water have been depleted of nutrients by this month and the position is likely to be similar in the Bear Island region.

August (Fig. 2) The pattern of phyto production during autumn is, at least to some degree, the reverse of that we have traced during spring. Large flowerings of Rhizosolenia and Thalassiothrix are found in the deep oceanic water of the West Bear Island section and also in the southern stations, though the coverage here is extremely poor. Both these spp. have been found in quantity off the Bank north of Bear Island in the autumn. This poor coverage is due to the fact that the cod at this time are far to the north of Bear Island so that there has not always been time to sample the two fixed sections as the Holt proceeds to the area of the fishery. From the evidence available the autumn flowering seems specific to certain regions. The position is thus comparable with that described for Rhizosolenia styliiformis and Biddulphia sinensis in the North Sea by Wimpeny and Savage where huge crops of these diatoms are found year after year in the Smith's Knoll, Dogger bank and Scheldt areas.

Of the diatoms, Thalassiothrix longissima and Rhizosolenia spp. dominate the autumn phytoplankton. Very large standing crops of these diatoms are found off the bank to the south and west of Bear Island and also along the western edge of the Spitzbergen bank itself during August and September.

Besides the species mentioned above some of the summer flowering Chaetocerids persist into the autumn and a large outburst of Chaetoceros convolutus was found at the southern stations C and D in September 1949. The peak flowerings of these Chaetocerids are associated with oceanic water from 6-7°C.

Near Bear Island the autumn phytoplankton, such as it is, consists of a mixture of the Arctic neritic forms in small numbers which have remained from the spring production, together with varying quantities of the oceanic

water species which have drifted into the colder water from their main centres of reproduction off the bank.

September (Fig. 2) The amount of radiation available for phytoplankton production during this month is comparable with that in March, and after the equinox gales and cooling of the water begin to break up the summer stratification near the surface. These factors militate against the reproduction of algae and towards the end of the month phytoplankton hauls begin to decrease rapidly.

Off the bank the flowerings described above may persist well into September, but in the shallow water on the bank catches consist almost entirely of Ceratium arcticum, C. fusus and great numbers of the Tintinnopsis favella.

Nutrient observations from September 1949 show that along the southern section regeneration has taken place as compared with the July figures.

October There is a good coverage during this month of the bank and deep water sections reflecting the whereabouts of the cod during the same period. The Fine Net hauls are smaller than those of the previous month with dinoflagellates and tintinnids replacing the diatoms. The depth of the surface thermocline, where this is detectable, is greater than that found during September. The radiation is definitely limiting for plant production.

November and December These months reflect an increasing degree of vertical turbulence in the surface waters and an almost total lack of radiation. Phosphate values for November 1953 in the surface 10 m. along the West Bear Island section gave a mean value of 21.3 mg./m³ which is \approx to a winter level of 0.75 μ gm. atoms P/litre - somewhat higher than Harvey's estimate for the Channel maximum.

The phytoplankton consists almost entirely of Peridinians and Tintinnids but the quantities are extremely small - not, however, reaching their absolute minima until March. For November 1953 one or two chains of Chaetoceros convolutus and a few Rhizosolenia spp. were found in most section stations but at N and NX at this time there was no sign of initial overwintering population of those species which were to constitute the spring flowering of 1954. A discussion on the significance of this will be found under the section on Ice Effects.

The Composition of the Phytoplankton

Although some 17 species of dinoflagellate and 40 species of diatom have been observed from time to time in the Fine Net hauls, by far the bulk of the Bear Island phytoplankton consists of a few dominant species of diatom.

For the sake of convenience a somewhat arbitrary distinction has been made between those stations where a spring flowering occurs and those at which no such flowering has been found. A mean percentage composition of the diatom flora for the whole period 1949-1954 gives the following picture:-

DIATOMS % COMPOSITION (FROM NO. OF CELLS/SPP. PRESENT)

MEAN VALUES 1949-1954

Fine Net hauls at 50 m.

	APRIL-MAY	JUNE-JULY	AUGUST-SEPTEMBER
B	<i>Thalassiosira gravida</i> 40.54	<i>Thalassiosira gravida</i> 4.60	
A	<i>T. hyalina</i> 7.58	<i>T. nordenskioldii</i> 1.64	
N	<i>T. fallax</i> 2.95	<i>Chaetoceros convolutus</i> 15.37	} Little or no phyto- plankton (except for station P + Q whose % composition is the same as that shown below).
K	<i>Chaetoceros sociale</i> 4.41	<i>C. decipiens</i> 16.23	
	<i>Fragilaria oceania</i> 18.18	<i>C. lasciniosus</i> 4.77	
	<i>F. islandica</i> 4.31	<i>C. densus</i> 19.26	
T	<i>Achnanthes taeniata</i> 2.50		
A	<i>Bacteriosira fragilis</i> 7.21	<i>Nitzschia frigida</i> 2.63	
T	<i>Coscinosira polychorda</i> 2.90	<i>Fragilaria oceania</i> 0.68	
I	<i>Biddulphia aurita</i> 1.94	<i>Corethron criophilum</i> 2.80	
O	<i>Amphiphora hyperborea</i> 1.87	<i>Rhizosolenia hebetata</i> 16.13	
N	<i>Lauderia gracilis</i> 3.00	To 100% 5.89	
S	To 100% 2.61		
W.		<i>Chaetoceros convolutus</i> 33.69	<i>Chaetoceros convolutus</i> 27.60
S		<i>C. decipiens</i> 30.24	<i>C. decipiens</i> 5.26
P	Little or	<i>C. lasciniosus</i> 23.17	<i>C. atlanticus</i> 0.55
I	no	<i>C. densus</i> 0.53	<i>Thalassiothrix longissima</i> 32.71
T		<i>Nitzschia seriata</i> 1.00	<i>Rhizosolenia hebetata</i> 21.06
4.	Phytoplankton	<i>Corethron criophilum</i> 10.51	<i>R. styliformis</i> 0.16
S		To 100% 0.89	<i>R. alata</i> 10.00
T			To 100% 2.60
N			
S.			

The above table thus does not correspond to any one year but is generally true from year to year. As previously described, the species *Chaetoceros sociale* has been estimated as no. of chains/col. owing to the very small size of individual cells when compared with other diatoms observed. If counted as actual number of cells it would make up considerably more than the 4.41% of the spring flora shown, as the cell/chain number at this time varies between 7 and 12.

The numbers of dinoflagellates taken do not allow a reliable table to be drawn up as in the case of the diatoms, nor do they occur in sufficient quantities to make a valid distinction between the composition of the bank and deep water species. The commonest species on the bank appear to be Ceratium arcticum, C. intermedium, C. macroceros, Peridinium pellucida and P. depressum. In the West Spitzbergen current the highest numbers of dinoflagellates were taken during the autumn with the most abundant species being C. fusus, C. furca, C. macroceros, and to a lesser extent C. lineatum, C. tripos, Peridinium curtipes and Dinophysis norvegica.

Other flagellates recorded include Halosphaera viridis, Phaeocystis spp., occasionally in great numbers, and also silicoflagellates including Pontosphaera huxleyi.

It is of considerable interest to compare the dominant species found in the Bear Island region with those reported by other authors for the Norwegian Sea, the Fjords, Greenland, Iceland and the Denmark Strait. Braarud (1929) from the Denmark Strait finds the spring diatom outburst in Arctic water was an "Achnanthes-Fragilaria" or a "Thalassiosira" vegetation; later succeeded by "Detonula". The summer dominant in mixed Arctic-Atlantic water was the diatom Nitzschia delicatissima while the autumn flowering was dominated by Rhizosolenia alata.

Steeman Nielsen (1935) in his paper on the phytoplankton of the Faroes, Iceland, and E. Greenland records the spring diatoms were made up mostly of N. delicatissima and Fragilaria nana off the Faroes. In the coastal waters of Iceland a flora dominated by Skeletonema costatum, Thalassiosira gravida and T. nordenskioldii was found for May. In the oceanic water Nitzschia delicatissima continued to play an important role throughout the summer with Rhizosolenia faeroense increasing by August. For the Denmark strait region in June Nielsen records a diatom phytoplankton composed mainly of Chaetoceros debilis, C. contortus, C. lacinosus and C. furcellatus.

Gaarder (1938) working in the fjords of N. Norway finds a spring flora of arctic composition consisting mainly of Chaetoceros sociale and Fragilaria oceanica is replaced by a summer outburst of more southern origin such as Chaetoceros affinis and C. curvisetus.

Per Halldal (1953) in a study of phytoplankton taken from the Weather Ship M in the Norwegian Sea describes a similar summer and autumn flora as that found in the West Spitzbergen water at Bear Island. The major exception seems to be that whereas he found Fragilaria nana the dominant diatom throughout the whole flowering season it has not yet been found at Bear Island.

The Pattern of Flowering

The pattern of phytoplankton production in the Bear Island region with the sharp distinction between a spring arctic flora and a summer oceanic flora has also been recorded for other regions in the Arctic Oceans. As stated in its general form this pattern was most clearly shown by Kjepp and Verbinskya (1930) by chemical methods and as far as the present work is concerned their findings are fully corroborated by a quantitative estimation of the flora itself.

All the phytoplankton works cited above devote some space to an ecological consideration of the flora. There has been a gradual developing of the early ideas of Gran and Brandt in assessing the role of nutrients, temperature, stability, radiation and other factors and their relative importance in determining the timing and extent of phytoplankton production. Although any of these factors may be the limiting one for a particular flowering of algae, increasing emphasis has been laid on grazing and stability in recent papers. Development of hydrographical methods has allowed a more intimate study of the relations between radiation availability and thermal stratification. For example, the paper of Halldal's (see above) from the Norwegian Sea correlates the onset of phytoplankton production with the gradual stabilizing of the water column and the reduction of vertical transportation of algae out of the photic zone. He shows that, at Weather Ship M, it is this ecological factor which predominates in determining the commencement of an overall phytoplankton production.

The work with most bearing on the interpretation of the pattern described from the Ernest Holt is that of Sverdrup (1953) "On conditions for the vernal blooming of phytoplankton". This is concerned with the mutual interaction of increasing radiation, and thermal stratification in defining a "critical" depth the reaching of which determines the start of phytoplankton production in the spring. A method is described for working out this depth for a given area and this is applied to the understanding of production of phytoplankton and zooplankton in the spring at Weather Ship M.

The technique has been adapted for the Bear Island region. An examination of the critical depths and extent of vertical turbulence found by the Ernest Holt at the same time as the phytoplankton hauls were taken, gives the underlying explanation of the timing already described above. Besides the radiation and stability factor some consideration is given to the effects of ice coverage, as being particularly relevant to the area. Less can be said about nutrients and grazing but what is known of these contributes to establishing an explanation of the changing pattern of Fine Net and water-bottle phytoplankton throughout the year.

Ecology of Bear Island Phytoplankton

The method of presentation will be to deal with radiation, stability, ice, grazing and nutrients separately and then to summarize their interaction on the production of the phytoplankton. Selected water bottle stations will then be analysed in detail in the light of the ecological considerations previously deduced.

1. RADIATION

Radiation is perhaps the most important factor in the production of phytoplankton in the sea. At high latitudes, such as Bear Island, there is a complete change during the spring from total darkness to total daylight, and vice versa in the autumn.

The amount of radiation available together with the turbidity of the water defines the euphotic zone and compensation depths, hence governing the degree of stability necessary for production to take place. It also determines the reproductive rates of the diatoms within the euphotic zone. Ice coverage cuts out a large degree of the incident radiation and is of importance in limiting the productive areas during the season when radiation would be otherwise sufficient.

It has been thought worthwhile to make a detailed study of the quantity of radiation available in the west Barents Sea and the effects of ice and turbulence in limiting reproduction of algae.

The incident radiation at Bear Island was calculated from Mosby's formula:-

$$I_0 = .027 (1 - 0.075\bar{C}) \bar{L} \text{ gm. cal cm}^{-2} \text{ min}^{-1}$$

where I_0 = incident radiation, .027 = factor for atmos. turbid, \bar{C} = mean cloudiness \bar{L} = mean alt. of sun. The factor of .027 was obtained for a latitude of 70°N but would be approximately the same for Bear Island at 74°N . The mean cloudiness and altitude of the sun may be obtained from the meteorological tables and nautical tables respectively. The percentage of total energy available for photosynthesis is taken by Sverdrup to be 20%.

In determining the actual amount of energy entering the sea surface it is necessary to introduce a reduction factor for surface reflection. This varies both with the altitude of the sun and with the degree of cloudiness and cannot be readily ascertained. However, it is known that 9% of the surface energy is reflected for a totally overcast sky and as the Bear Island area has consistent cloud values greater than 7/10ths, this loss has been taken. The values obtained may thus be a little high.

From the energy entering the sea surface, and a knowledge of the extinction coefficient for green light in the area concerned (Wimpenny and

Corlett 1953, unpub.), the depth of compensation has been worked out. The method will be discussed in the section on stability. Assuming that $I_d = I_0 e^{-kd}$ (where I_d = energy at depth d , I_0 = incoming energy, k = ext. coeff.) the mean energy values in the photic zone have been obtained. (Fig. 3).

The final step was to equate a reproductive rate to these figures of available energy. The data used here was taken from Jenkins (1937). This has been adapted by Riley and a graph drawn between the number of divisions/day and the radiation in gm.cals/cm². Below 25 gm.cals./cm² day the relationship between reproductive rates and radiation is linear. This was also shown by Barker (1935). Jenkins used Coscinodiscus excentricus in her experiments and although the above relationships refer to the basic processes of photosynthesis in diatoms, differing degrees of efficiency of utilization between species occurs. This problem was studied by Lanskaya and Sibkov (1950) who showed that 3 Coscinodiscus spp., Rhizosolenia calcar-avis and Biddulphia mobiliensis each required a similar number of calories for a division while Ditylium Brightwelli needed only half this quantity. This should be borne in mind when the mean reproductive rates (obtained as indicated from Coscinodiscus excentricus) are applied to any other diatom species.

The results are expressed in Fig. 3. They show the very rapid increase in the theoretical reproductive rates obtaining in the euphotic zone as the hours of daylight lengthen during the spring. The graph is not smooth as mean cloud values have been taken which alter the gradient for each month. Both along the southern and western sections a current of cold water is meeting a warmer one and these are the sort of conditions where cloud may be expected to form. The actual cloud values used are from the Meteorological station at Bear Island and in the outer stations away from the cold water there may well be rather less cloud. However, the effect of cloud is two-fold; it cuts down the direct light but it also increases the diffuse light so that for low sun angles, such as we are dealing with early in the year, the cloudiness of the sky may actually increase the quantity of radiation entering the water. This is because reflection losses for low sun angles are greater than losses of diffuse light by reflection.

How nearly the actual reproduction rates approach the theoretical figures, in fact how far this "production potential" can be realized, depends of course on a number of other factors.

2. STABILITY

The most significant of these factors is likely to be the maintenance of the reproducing population within the euphotic zone. How far the population of algae remains in this zone depends on their buoyancy and on the vertical movement, or turbulence, of the water column. Healthy diatoms may be expected to maintain their positions in still water (Gross and Zeuthen, 1948) so that the important factor is the turnover of the actual masses of water in which they are suspended.

Vertical turbulence is mainly due to a cooling of the surface water increasing its density and causing it to sink, it is also due to wind action, currents, tides and upwelling of deeper waters. Where the surface waters are warm and less dense than the underlying ones, and other factors are not causing turbulence, a thermocline of varying sharpness will be formed. The presence of such a thermocline, indicated by density measurements taken from the Holt, has been assumed to indicate the depth of mixing of the surface water masses. In Sverdrup's paper a similar method is used, taking both temperature and salinity measurements and a continuous temperature record using a Mosby thermosonde. The degree of mixing within the thermocline has been assumed to be uniform, as indeed must be the case for the thermocline to remain constant for any length of time.

Sverdrup shows that the processes of photosynthesis and respiration may be considered in terms of the relative volumes of photosynthesising and respiring algae respectively. The former will depend on the light and will decrease logarithmically from the surface (always bearing in mind that reproductive rate is only proportional to radiation below a certain value) whereas respiration, that is, loss of synthesised material, may be taken as

uniform throughout the water column in which the algae are contained. Where the rate of photosynthesis equals the rate of respiration is the compensation depth and the limit of the euphotic zone. For overall production total photosynthesis > total respiration and this condition depends on the relative depths of euphotic zone and surface turbulence.

The critical depth is that depth where the total photosynthesis below unit surface and respiration are equal. The expression for the critical depth is defined by Sverdrup as follows:-

$$\begin{aligned} \text{where } D_{cr} &= \text{critical depth} & \bar{I}_e &= \text{energy at sea} \\ k &= \text{extinction coeff.} & I_c &= \text{energy at compensation depth} \\ D_{cr} &= I_e / I_{ck} \end{aligned}$$

The mean energy values have already been obtained (see section on radiation). The extinction coefficient is known as is the energy at the compensation depth (0.15 g. cal cm⁻² hour⁻¹ after Jenkins). Thus the critical depth for the increasing radiation values can be determined. Using an extinction coefficient between 0.075 and 0.1 the results are as follows (Fig. 4).

The compensation depth is obtained from the expression

$$D_c = \frac{\log_e k D_{cr}}{k}$$

and this has also been shown in Fig. 4. From the compensation depths the total energy in the euphotic zone has been obtained as described above.

The records for depths of thermocline for different months are somewhat incomplete but a summary of 49-54 results is tabulated before detailed examination of any one station is undertaken. The interpretation of hydrographic data in terms of stability of the water column is extremely difficult where no obvious thermocline or density change exists. In stations where a shallow gradient of salinity and temperature exists for several hundred metres no conclusions have been made regarding vertical turbulence. Though a number of such cases are found in spring the majority have well defined thermoclines or density changes corresponding to the depths shown in Table 2.

Table 2

Months	Nov.-Feb.	Mar.-Apr.	May	June	July-Oct.
Critical Depth	0-5 m.	30-140 m.	140-190m.	190-240m.	240-30m.
Depth of turbulence	75m. (or where bottom depth is within this complete vertical mixing).	50m. (or where bottom depth is within this complete vertical mixing). In cases where ice has been present recently inversions form at 10-25 m.	25 m.	25m.	30-60 m.
1. Bank Stations L-P					
2. Deep Water Stations Q-W J-A	> 200 m.	> 200m.	Variable, usually > 150 m.	25-75 m.	40-80 m.

The general inference is that on the bank during the months March - May the depth of the bottom, or the depth of the thermocline, either positive or an inversion due to ice melt water or surface cooling is well within the critical depth for the time of year. Off the bank, however, the position is reversed during these months with the depth of turbulence exceeding the critical depth.

There is a sharp formation of a thermocline between May-June within the critical depth in the deep water, and the theoretical assumption that little or no overall production can occur there until the latter month is fully borne out by the quantitative sampling.

This relationship is shown schematically in Figure 5 where data from the spring months of 1952 is used.

ICE

The effect of ice in the vicinity of the Bear Island bank is extremely important in governing production. The extent of the Barents Sea ice field varies from year to year but the March - April limits for 1953 are shown in Fig. 6 and this is typical for the period studied. These spring limits correspond to the yearly limits - spring being the "hydrographic midwinter" for the ice coverage.

There are two ways in which the ice may be expected to influence phytoplankton production. In the first case it will reduce the amount of radiation available to the flora below it thus reducing or delaying the flowering of the algae; in the second case it has been shown to liberate a number of the main spring species on melting to form an initial reproducing population in water otherwise largely bereft of plants, and also it forms, in melting, a shallow thermocline of low density melt water in which rapid flowering can occur. Ice coverage may also be thought of as insulating the water below it from thermal effects and wind action, hence reducing its turbulence.

The passage of radiation through ice has been most fully studied by Greenbank (1945) in a monograph on the effects of ice coverage on fish survival in American lakes. He showed that the degree of radiation able to penetrate ice depends very largely on its inclusions - bubbles, detritus, etc., and the depth of snow coverage. A selection of his figures, together with those of Croxton et al. (1937), Hard and Lundquist (1942) and Thames (1938) for transmission through ice is as follows:-

<u>Ice depth</u>	<u>Condition</u>	<u>% of incident radiation transmitted (all wavelengths)</u>
10"	Clear	67%
10"	Soft on top	14%
10"	Very cloudy	7.2%
24"	Partly cloudy	7.6%
<u>Snow depth</u>		
1"	} wet snow	10%
2"		4%
3"		5%

(DRY snow gave a further reduction of 4/5ths on the wet snow transmissions)

Observations made from the Ernest Holt on the west Barents Sea ice indicate that the normal depths range from 1-4 ft. depending on the type of ice and its age. The snow coverage, also varies greatly. However, the above figures are enough to show how a very small depth of ice, in any state other than absolute clarity, is more than sufficient to reduce the radiation to a limiting extent for photosynthesis. From the radiation figures for April the effect of 1-ft. of ice is to reduce the overall reproductive rate on the Bear Island bank to

less than 1/10th of its value in clear water for the same area.

Braarud (1935) took a series of stations into the edge of the Greenland icefield leading from loose ice into the continuous rafted variety. He found very rich phytoplankton where the ice had recently decayed and this melt water of low salinity gave a sharp temperature inversion in which the flowering occurred. The nutrients in this surface zone rapidly became limiting.

For evidence on the release of spores and phytoplanktonts into melt water the work of Ussachev (1946) is the most comprehensive. He investigated the flora frozen into the ice masses of the Kara Seas and Straits of Franz-Joseph-Land. Besides numerous diatoms there were few flagellates, peridians or other algae. Among the most frequent species of diatoms were:-

Thalassiosira nordenskioldii, T. gravida, Fragilaria oceanica,

Nitzschia frigida, Achnanthes taeniata

and less frequently

Fragilaria islandica and Navicula spp.

These species represent some of the main constituents of the Bear Island bank spring flowering and there can be little doubt as to their similar origin from the melting of the ice field. The presence of rich crops of phytoplankton in the immediate vicinity of ice has been known for a long time and a number of theories such as the presence of organic "leptopels" or high molecular water (due to Dunbar but recently discarded) have been advanced. For the east Barents Sea itself Jaschnov (1939) notes that very abundant phytoplankton was found at 75°30'N - 76°30' in June, which corresponds to the position of the ice at this time of year.

Ussachev suggests a method whereby the overwintering diatoms may be supposed to get into the ice and considers they come down from a northern centre of distribution with the advancing ice each winter. The west Barents Sea ice recedes up the Bank to Spitzbergen, Hope Island and further north to 80°N and more during the summer and autumn of each year; a similar advance of the spring phytoplankton has been noticed, or where differential grazing has obscured the picture a nucleus of copepod nauplii taken with the Fine Net can be traced moving northwards. (Fig. 7). This peak of copepod nauplii taken by the Fine Net and consists of juv. Calanus finmarchicus, Metridia longa, Metridia lucens, Microsetella norvegica, Pseudocalanus elongatus and other species, though for the purpose of this paper they have been lumped together to illustrate the northward trend.

Finally the hydrographic effects of ice in producing sharp gradients can be clearly seen in the detailed examination of a melt water station following.

The conclusions as to the effect of ice on production of the Bear Island Bank are thus that it acts in a deleterious manner by cutting down radiation, but is otherwise an essential factor in contributing to the spring flowering of the Arctic water, both in providing a nucleus of algae and stable hydrographic conditions in which they can reproduce. A further point is that large "growlers" and portions of decaying ice are continually drifting off the bank into deeper and warmer water during spring, and where this happens a local "Arctic" flowering occurs over the mixed or oceanic water. A number of such advances and melting of individual parts of the ice field will have the effect of "manuring" the mixed areas and maintaining stability at the crucial time when production is starting and this is a possible factor contributing to the whole productivity of regions where cold and warm water meet (as shown by Wiborg 1954).

TEMPERATURE

As Sverdrup (Sverdrup et al. 1942) points out, the effect of temperature on a flora is more to govern its composition than its quantity. Fig. 8 shows the temperature range of the main phytoplankton peaks around Bear

Island and in the West Spitzbergen Current from 1949-55. That the effect of temperature on the extent of these peaks is a secondary one is already implicit in the consideration of the preceding ecological factors as indicating their primary causes. However, the "preference" of certain species for various temperatures can be seen from the composition of these hauls. Gran and Braarud (1935) for the Gulf of Maine show Thalassiosira nordenskioldii to have a preference for 3°C. water, Chaetoceros debilis for 6°C., Chaetoceros compressus for 9°C. and C. constrictus for 12°C. The toleration of each of these species seems somewhat below these figures from the Bear Island data, and all of the spring flowering species (see Fig. 8) appear to flourish from -1° to 2°C.

GRAZING

An account of the zooplankton data collected by the Ernest Holt is in preparation. The picture which emerges - as far as the grazing factor is concerned - shows that there are not sufficient animals on the bank to graze down the spring population of phytoplankton (Grazing "potential" of the standing crops using Gauld's data have been compared with standing crops and reproductive rate of diatoms). The copepods which dominate the zooplankton communities return from the deep water off the continental shelf fairly well into the spring and gradually advance up on to the bank regions. The normal definition of a marine flora by grazing, so well established by Fleming (1939) and others does not occur until the summer in this region when the pattern of production and standing crops of phytoplankton is due to the underlying grazing effects of herbivores (pers. comm. Corlett).

Supporting the idea of an excessive production of spring phytoplankton much exceeding the grazing potential of the herbivore standing crop for the same months, is the large number of detritus feeders which are found on the bank or along its edges. The most important of these are the euphausiids which occur in great quantities; in the latter region on the bank itself Cucumaria frondosa has been reported at a density of 6 to a square metre. (Brotsky and Zenkewitch).

The very low temperatures in the Arctic water where the spring flowering is at its maximum are possibly prohibitive to the zooplankton though further evidence is required on this. That reproduction of copepods can take place near the ice edge has been shown already in Fig. 7, but again this may be when turbulence has disrupted the melt water thermocline and distributed the plants more evenly in the water column where they can be eaten.

NUTRIENTS

Nutrient observations taken by the Ernest Holt consist of phosphate measurements in 1949 and 1953. The full results will be included in future reports on the hydrography of the area and it will be sufficient for the purpose of this paper to extract any information indicating phosphate as a limiting factor for plant production.

During the July cruise 1949 no phosphate (measured as μ gm atoms P/litre₂₀) was detectable in the surface 50 m. at stations A, B, C, D where a large-scale flowering of phytoplankton was in process while at the surface 50 m. at other stations varied from 0.09 - 2.08 μ gm atoms P. The September values showed an increase for every station examined with more uniform values near the surface (0.32 - 1.18 μ gm atoms).

For 1953, winter values in the top 50 m. (measured as PO_4 mg/m³) were from 12-29 mg/m³ with the higher values in the shallow water stations. For the autumn of that year phosphate was entirely depleted in certain bank stations (October) near Hope Island though there was little phytoplankton there.

Phosphate may thus be limiting both on the bank and in deep water where a persistent crop of phytoplankton and thermocline have existed, but this is somewhat exceptional but there is not sufficient data to make valid conclusion about. Few phosphate values were taken in ice water flowerings but they show (for 1953) a very large reduction in the surface water which may have limited the extent of such flowerings. Braarud (1935) obtained zero values for phosphate in many of his ice water phytoplankton blooms.

Examination of selected stations

The ecological interpretation of the Bear Island phytoplankton production outlined above, more especially in its application to the spring flowering pattern, will now be applied in detail to selected stations.

During the spring we can classify three distinct types of station each with their characteristic hydrographic conditions and phytoplankton distribution.

First there are the stations in Arctic water, usually on the bank, where a shallow melt water layer limited by a strongly marked temperature inversion overlies warmer and more dense water. The typical profile shows high oxygen saturation, the thermocline corresponding to the phytoplankton production and low phosphate values. The majority of the phytoplankton itself is above the thermocline though after a period it may be supposed to limit itself in some way (i.e. utilization of nutrients) and become senescent and sink.

An example of this is St. 13, Cruise IV, 1953. The position is $75^{\circ}35'N.$, $32^{\circ}00'E.$, and the station was within visible distance of the ice field edge (Fig. 9).

Second are the stations, also in Arctic water, where no obvious thermocline exists but where the bottom is within the critical depth for the time of year and where a quantity of phytoplankton may be considered as fairly uniformly distributed throughout the water column. Such conditions are restricted to the shallow bank area and may well be a second stage in the development of a melt water station which has been subjected to turbulence. There is not sufficient evidence to show this but the composition of the flora, with the exception of a few neritic species, is very similar to that of a melt water station. An example is shown in Fig. 10.

Third are the stations in deeper water where no thermocline exists within the critical depth, where there is no flowering of phytoplankton and where no depletion of nutrient or oxygen saturation exists. Any station in deep water may be taken to illustrate this (Fig. 11). It will be seen that the phytoplankton taken is negligible and this is only to be expected, but it should be noticed that if the vertical turbulence extends down below 200 m., and the algae are uniformly distributed within this depth the sampling of the top 50 m. would only produce $\frac{1}{4}$ of the total population. However, even if the sample values are multiplied by a factor of this order the results still remain of a very low order of production.

These stations all relate to the spring flowering and a further example is taken for a deep water station showing ~~a high~~ production a little later in the year by which time the hydrographic conditions necessary have been fulfilled. (Fig. 12).

Discussion

Although the use of the Fine Net has limited the phytoplankton information which the Holt has obtained during her fishery investigations from 1949-1954, the overall timing and extent of the production is so marked, that the sampling technique has been adequate to show its general nature. Such water bottle samples that have been taken fully support the Fine Net results.

The picture that emerges from the phytoplankton counts and hydrographic data is perhaps not a new one, except in so far as Sverdrup's concept of a critical depth of turbulence (or degree of stability) has been shown to be a very important factor in understanding the detailed timing of the west Barents Sea flowering.

The recession of the ice and the production of algae which follows it each year is the most outstanding phenomena in the area investigated. This annual cycle of events followed, as we have seen, by the spawning of the copepods with the time lag which exists between the grazing control of the diatoms and their reproduction, must determine the whole richness of the area as a feeding ground for benthic life and fish. The abundance of

detritus feeders which live on the Bear Island Bank and extend north-west to Spitzbergen and north-east to Hope Island and beyond, may owe their great numbers to an excess of plant production in the Arctic and mixed water which sinks down through the water during the spring.

Though the Arctic algae themselves are adapted to low temperatures and only hold from reproduction by lack of radiation through the ice there can be no doubt that its withdrawal and the subsequent warming up of the bank water is important in controlling the northward movement of fishes on the edge of their temperature range, but that is outside the scope of this paper. The work done on the phytoplankton represents only a very small part of the whole biological and hydrographical investigation of the area carried out by the Holt.

The western section extends out into the West Spitzbergen current and beyond and here very rich oceanic phytoplankton has also been found from time to time, though the picture is much less consistent than that found on the bank. Harvey et al. have shown, with others, that the persistence of a standing crop of phytoplankton can only be explained as due to low grazing and that high standing crops of phytoplankton are normally transient phenomena. The successive years which we have found rich phytoplankton on the Bear Island bank indicate that it must last over a considerable number of weeks, and that the somewhat theoretical grazing potential calculated for the zooplankton present, really is correct in being only a fraction of the plant production for the same period.

The preparation of a more detailed examination of the flagellate population is in hand, also the identification of uncertain species of planktonts noticed during counting. The actual maximum quantities taken over the six years' work for the main diatom species in the Fine Net hauls is included at the end of this paper, together with the place of their occurrence and number of cells to a chain.

Summary

1. Fine Net hauls from 50 m. depth (using International net, 50 cm., 200 mesh) have been carried out over a period from 1949-1954 in the West Barents Sea and Bear Island bank region. Two main lines of stations are described.
2. The samples have been found to fall into a pattern of spring production in the Arctic water and near the ice pack with a diatom flora dominated by Thalassiosira spp., Fragilaria spp. and Chaetoceros sociale, and a later production in the oceanic water dominated by Chaetocerid spp. An autumn flora mainly composed of Rhizosolenia and Thalassiothrix species has been found in the warmer water.
3. A study has been made of the effect of radiation, ice coverage, vertical turbulence of the water column, and more briefly nutrients, temperature and grazing, in their interaction and effects on the timing and extent of the Bear Island phytoplankton. The concept of a critical depth to which turbulence may extend before it limits production has been taken from Sverdrup and applied to the Ernest Holt data. Values of incident radiation and extinction coefficients at Bear Island are given.
4. A northward wave of copepod nauplii production following the receding ice is shown.
5. Detailed examination of selected water bottle stations from 1953 is undertaken to illustrate the importance of the ecological factors previously described and finally
6. A suggestion is put forward to account for the richness of the West Barents Sea as a feeding ground for fish and other animals.

List of species maxima from Fine Net Hauls

Cells in 1 m.² column, 50 m. depth

<u>Diatoms</u>	<u>Year</u>	<u>Month</u>	<u>Station</u>	<u>Cells u.m.²</u>	<u>Cells/chain(av.)</u>
Melosira hyperborea Grun.	1949	5	M	188,000	4
Coscinodiscus radiatus Ehr.	1953	5	Bk1	1,650	-
C. sub-bulliens Jorg.	1953	5	Bk3	8,250	-
Thalassiosira Nordenskioldii Cl.	1952	4	P	490,000	13
T. gravida Cl.	1952	4	N	27,900,000	9
T. fallax Meun.	1954	5	Bk2	14,850,000	11
T. hyalina Grun.	1954	5	Bk4	99,000,000	11
T. bioculata Grun.	1953	5	Bk1	60,000	2
Coscinoscira polychorda Gran.	1950	5	Mx	984,000	3
Lauderia glacialis Grun.	1950	6	M	198,000	6
Bacteriosira fragilis Gran.	1953	5	Bk3	13,750,000	10
Skeletonema costatum Grei.	1953	5	M	40,000	8
Leptocylindrus danicus Cl.	1953	5	N	140,000	4
Corethron criophilum Cast.	1950	7	B	3,160,000	-
Rhizosolenia alata Brightw.	1952	8	V	34,000,000	-
R. setigera Brightw.	1949	6	M	4,500	-
R. styliformis Brightw.	1952	8	P	1,200,000	-
R. hebetata Bail.	1949	6	M	2,850,000	-
Chaetoceros atlanticus Cl.	1949	7	B	135,000	3
C. densus Cl.	1949	7	C	1,390,000	5
C. borealis Bail.	1954	8	K	25,000	5
C. convolutus Cast.	1949	7	C	58,000,000	2
C. concavicornis Mang.	1950	7	Q	473,000	1
C. danicus Cl.	1952	8	P	340,000	4
C. decipiens Cl.	1949	6	M	25,200,000	7
C. compressus Laud.	1952	8	Q	1,380,000	6
C. affinis Laud.	1950	7	G	1,320,000	4
C. laciniosus Schütt	1949	7	B	124,800,000	8
C. diadema Ehr.	1950	5	Mx	1,170,000	5
C. holsaticus Schütt	1953	5	Bk5	1,530,000	9
C. subtilis Cl.	1953	5	Bk3	165,000	5

<u>Diatoms (Cont'd)</u>	<u>Year</u>	<u>Month</u>	<u>Station</u>	<u>Cells u.m.²</u>	<u>Cells/chain(av.)</u>
<i>C. fragilis</i> Meun.	1950	7	G	750,000	5
<i>C. debilis</i> Cl.	1953	5	Bk2	1,344,000	12
<i>C. socialis</i> Laud.	1953	5	Bk2	230,000,000	10 ch/col
<i>Biddulphia aurita</i> Lyngb.	1952	4	Mx	588,000	3
<i>Fragilaria islandica</i> Grun.	1952	4	N	78,000,000	20
<i>F. oceanica</i> Cl.	1952	4	N	31,000,000	17
<i>Thalassiothrix longissima</i> Cl.	1953	9	R	10,000,000	-
<i>T. Nitzschoides</i> Grun.	1953	5	Bk2	150,000	5
<i>Achnanthes taeniata</i> Grun.	1953	5	Bk3	4,725,000	7
<i>Navicula pelagica</i> Cl.	1953	5	Bk3	180,000	12
<i>N. spp.</i>	1954	7	Nx	800,000	-
<i>Amphiphora hyperborea</i> Grun.	1953	5	Bk3	540,000	6
<i>Nitzschia closterium</i> Ehr.	1953		27	150,000	-
<i>N. frigida</i> Grun.	1949	6	M	300,000	20
<i>N. seriata</i> Cl.	1953	5	Bk4	40,000	7
<i>N. delicatissima</i> Cl.	1950	7	Q	1,120,000	4

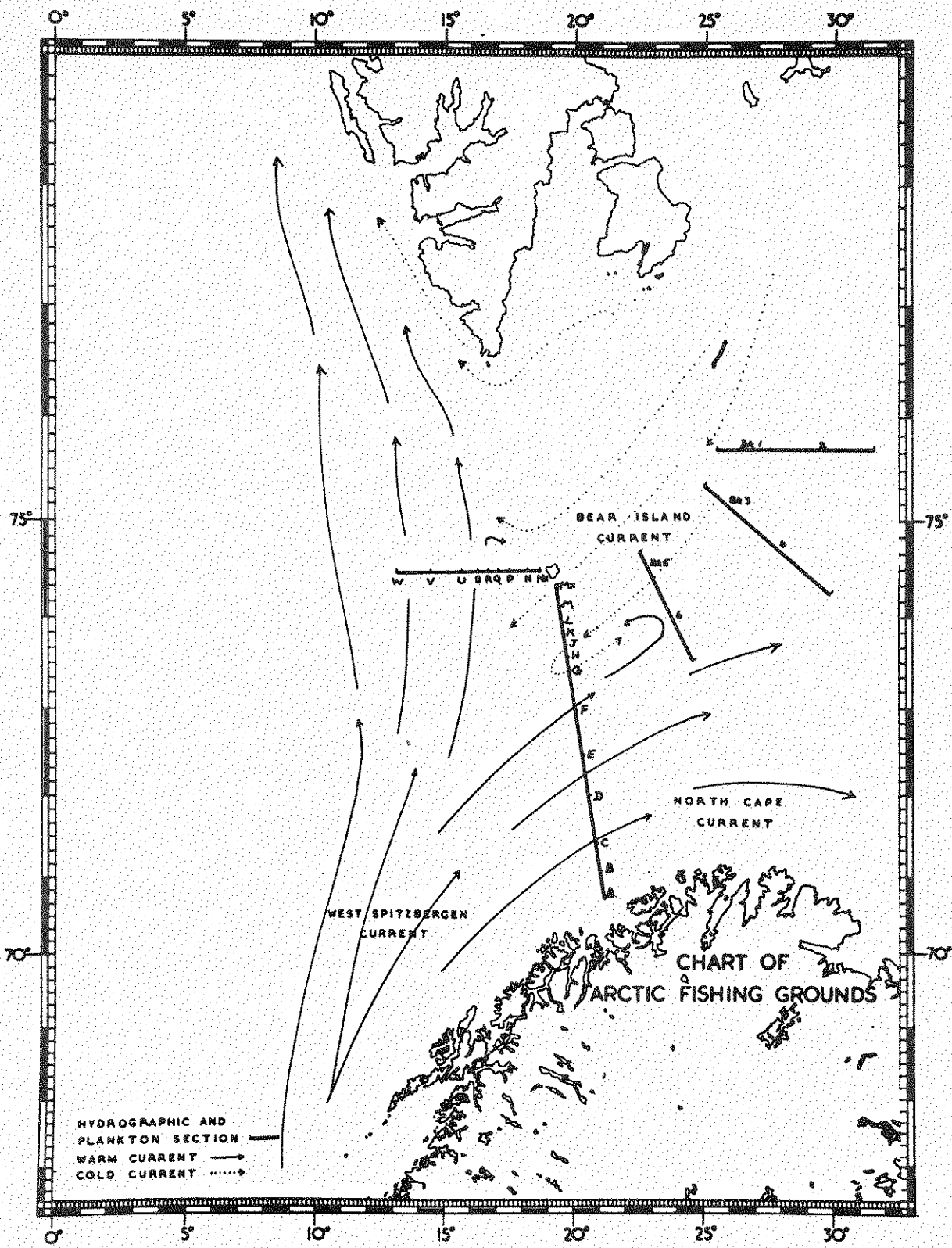
Dinoflagellates

<i>Dinophysis acuta</i> Ehr.	1949	9	C	1,500	-
<i>Peridinium depressum</i> Bail.	1952	6	P	280,000	-
<i>Peridinium curtipes</i> Jörg.	1950	10	G	27,500	-
<i>P. islandica</i> Paul.	1953	10	Bk3	37,500	-
<i>P. pellucida</i> Berg.	1950	10	G	1,000	-
<i>Ceratium furca</i> Ehr.	1950	10	S	10,800	-
<i>C. lineatum</i> Ehr.	1950	10	S	27,000	-
<i>C. fusus</i> Ehr.	1953	9	R	390,000	-
<i>C. tripos</i> Müll	1953	9	Q	165,000	-
<i>C. bucephalum</i> Cl.	1950	10	K	2,500	-
<i>C. macroceros</i> Ehr.	1950	10	U	147,000	-
<i>C. longipes</i> Bail.	1949	9	C	330,000	-
<i>C. arcticum</i> Ehr.	1953	8	Bk1	1,000,000	-
<i>C. intermedium</i> Paul.	1950	10	U	15,000	-

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GENERAL CURRENT SYSTEM IN WESTERN BARENTS SEA.
(48 1962)

FIG. 1.

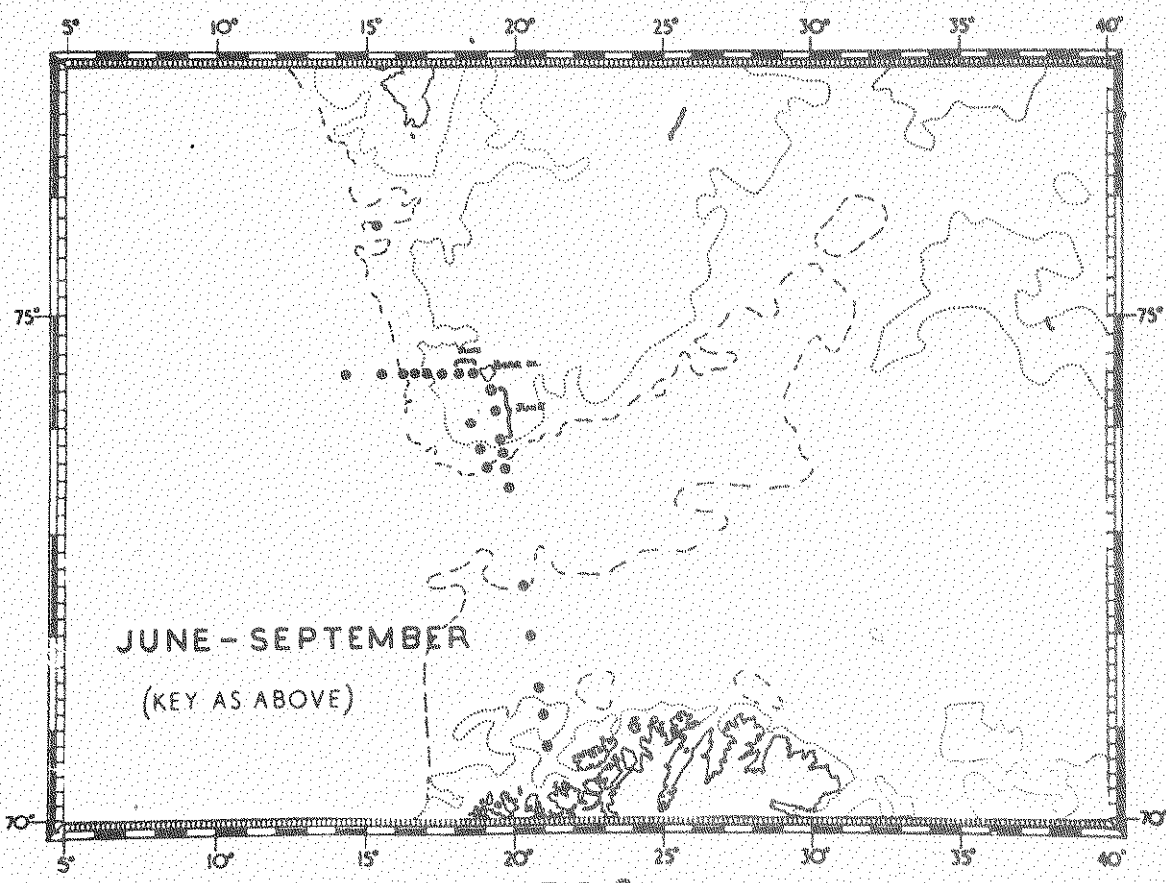
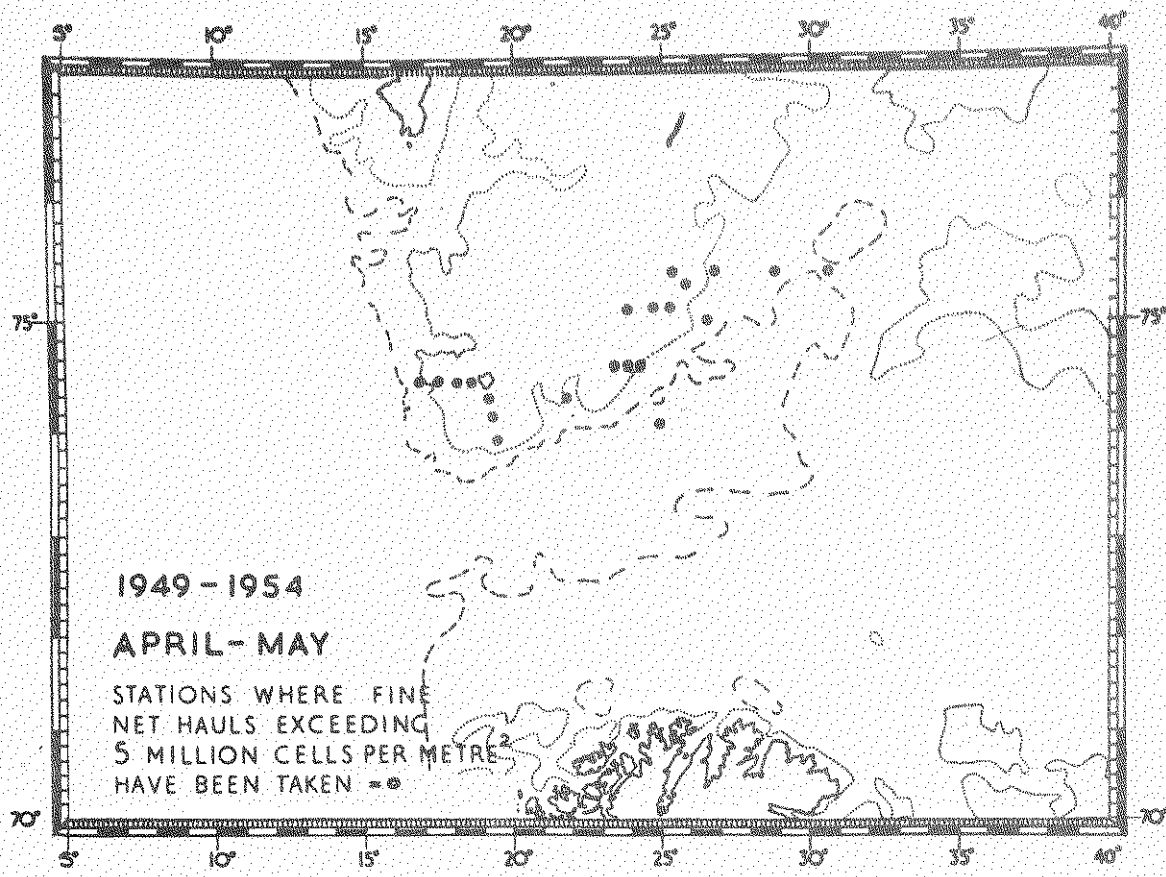


FIG. 2

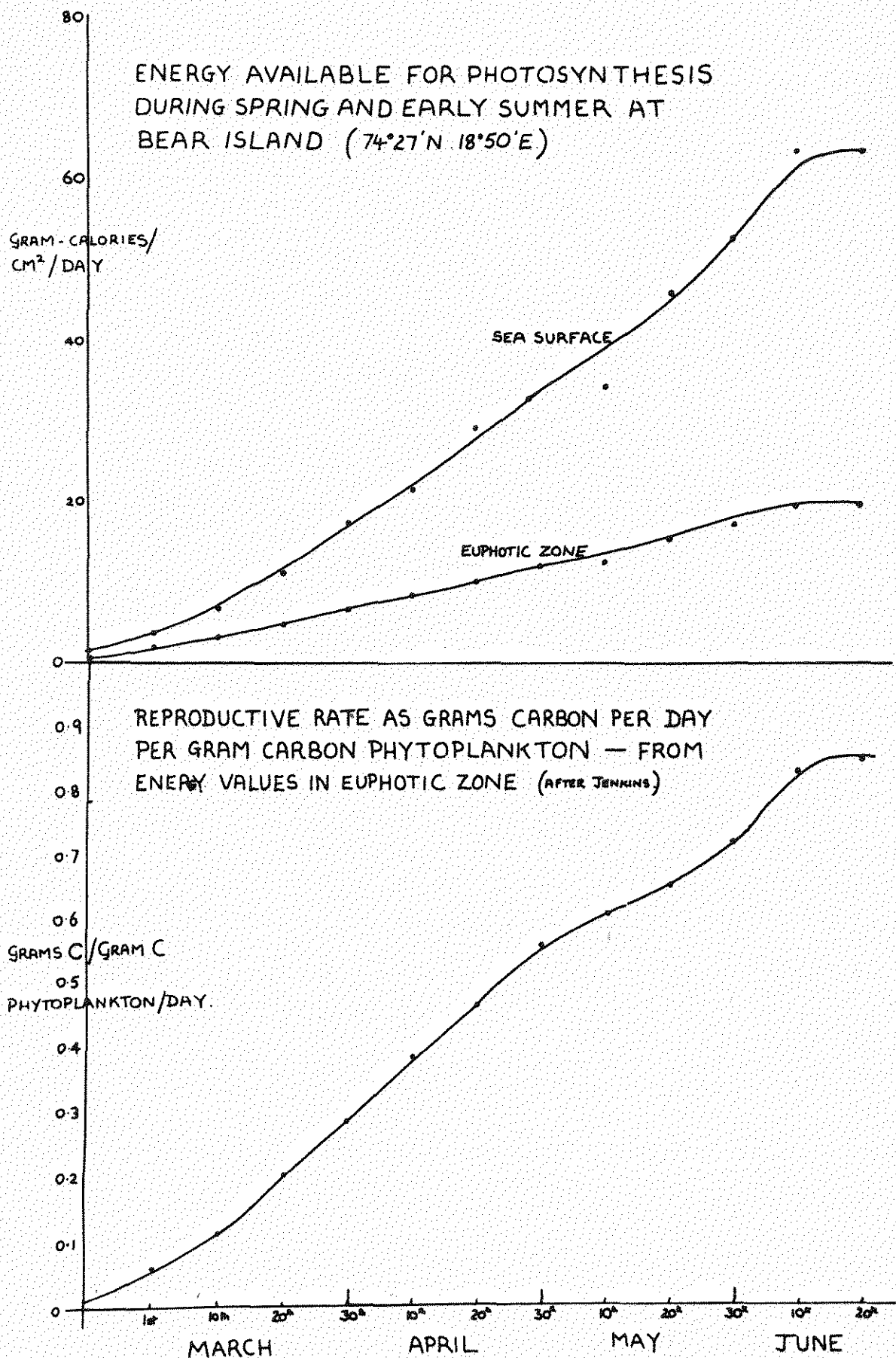


FIG. 3.

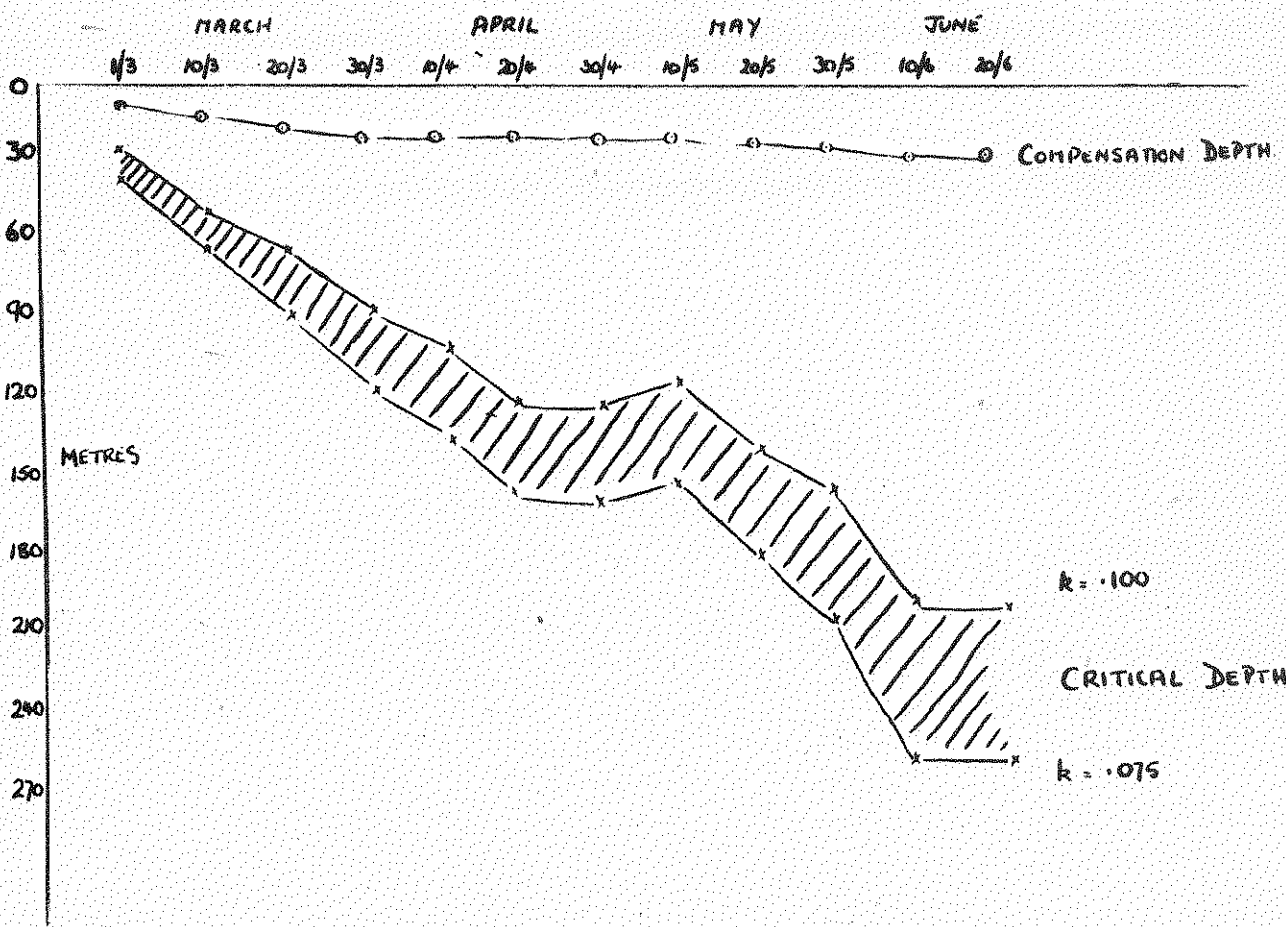


FIG. 4.

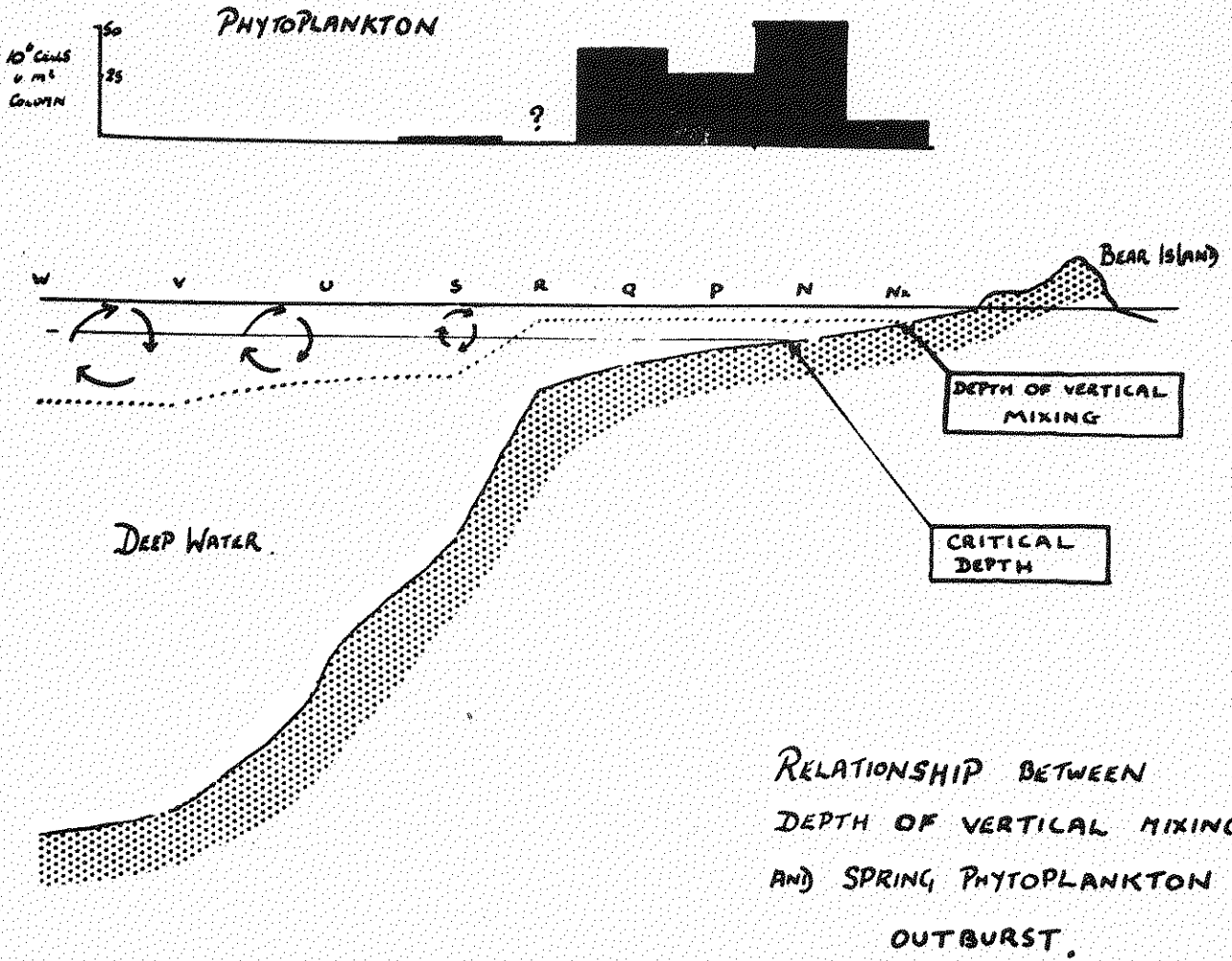


FIG. 5.

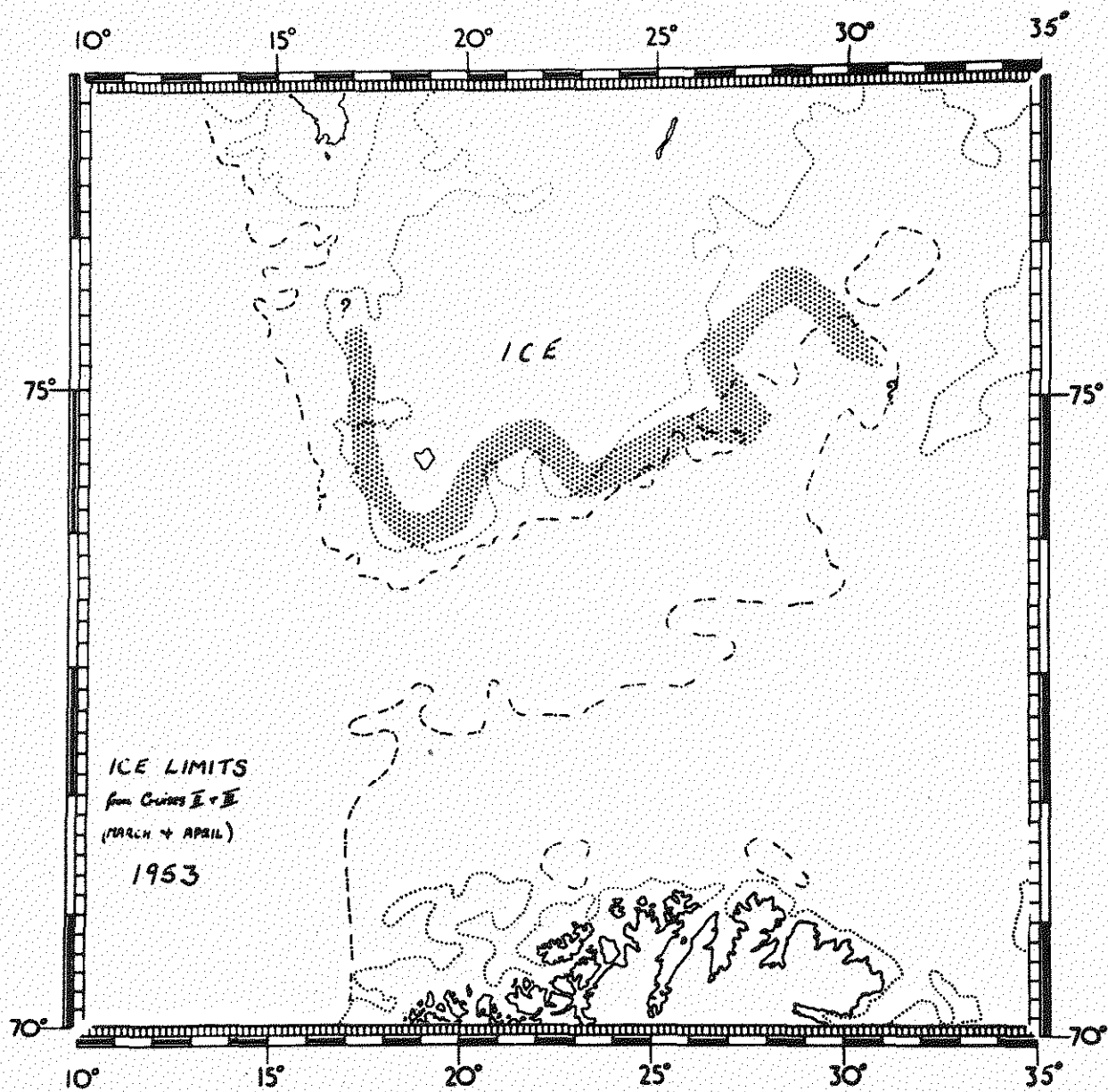


FIG. 6.

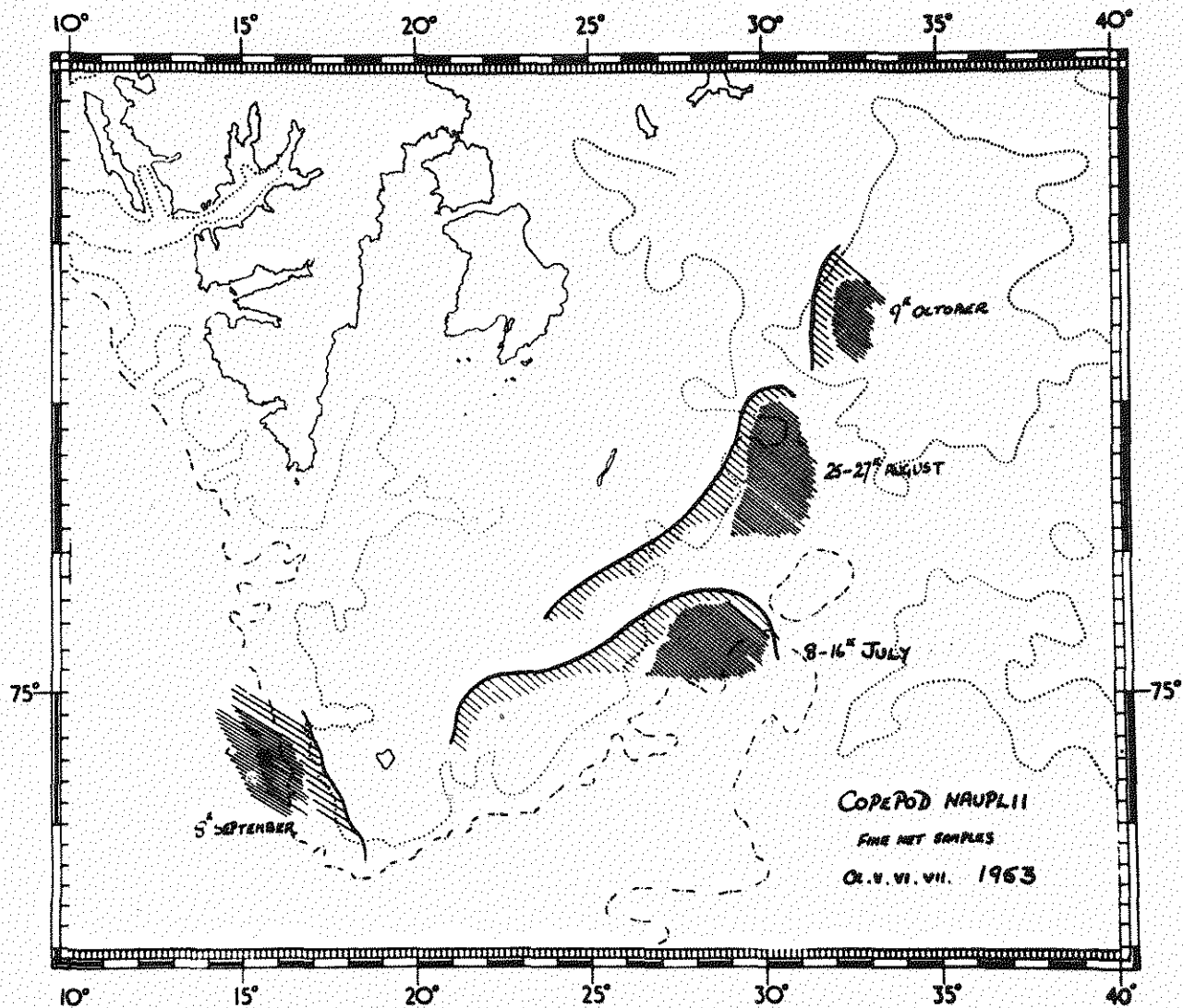


FIG. 7.

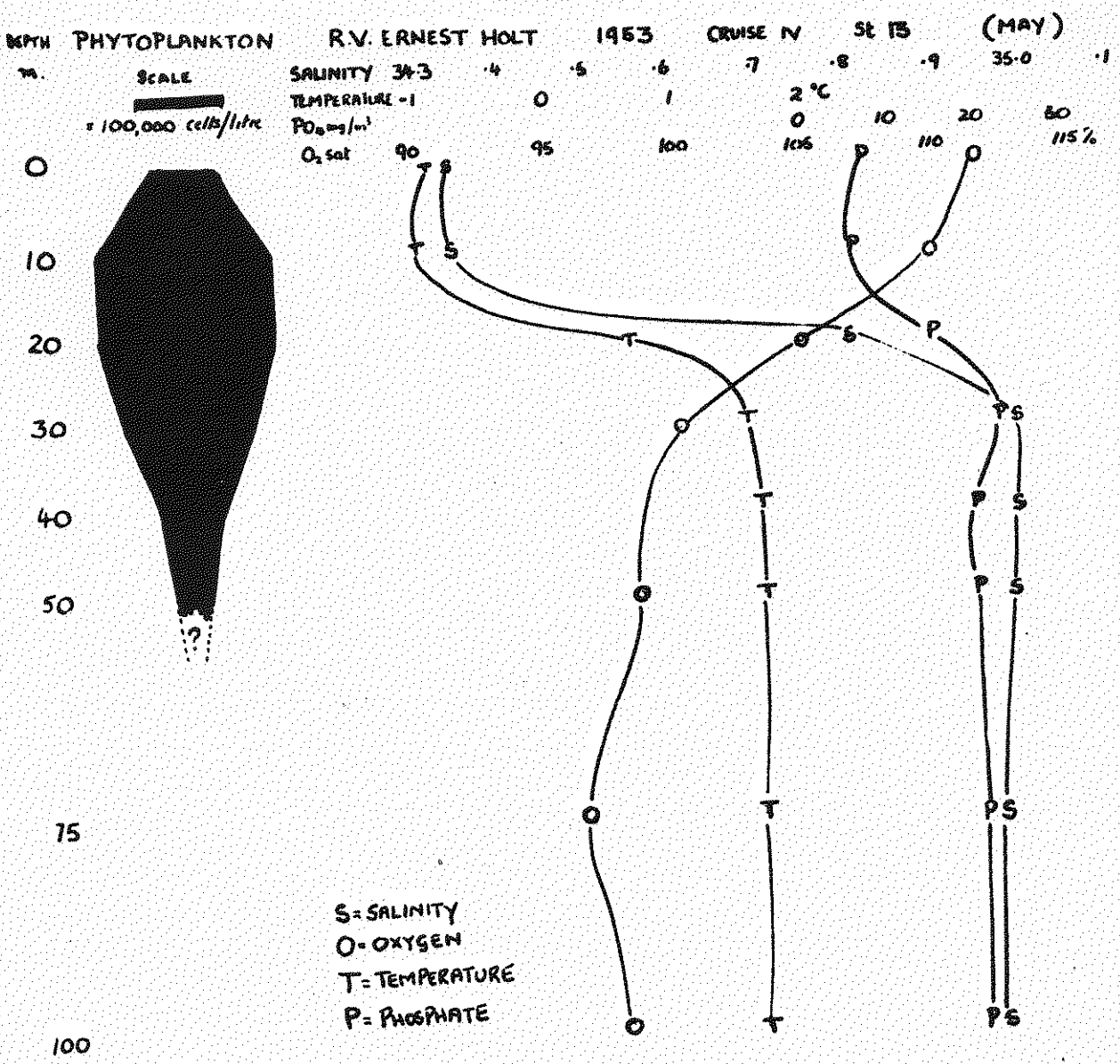


FIG. 9.

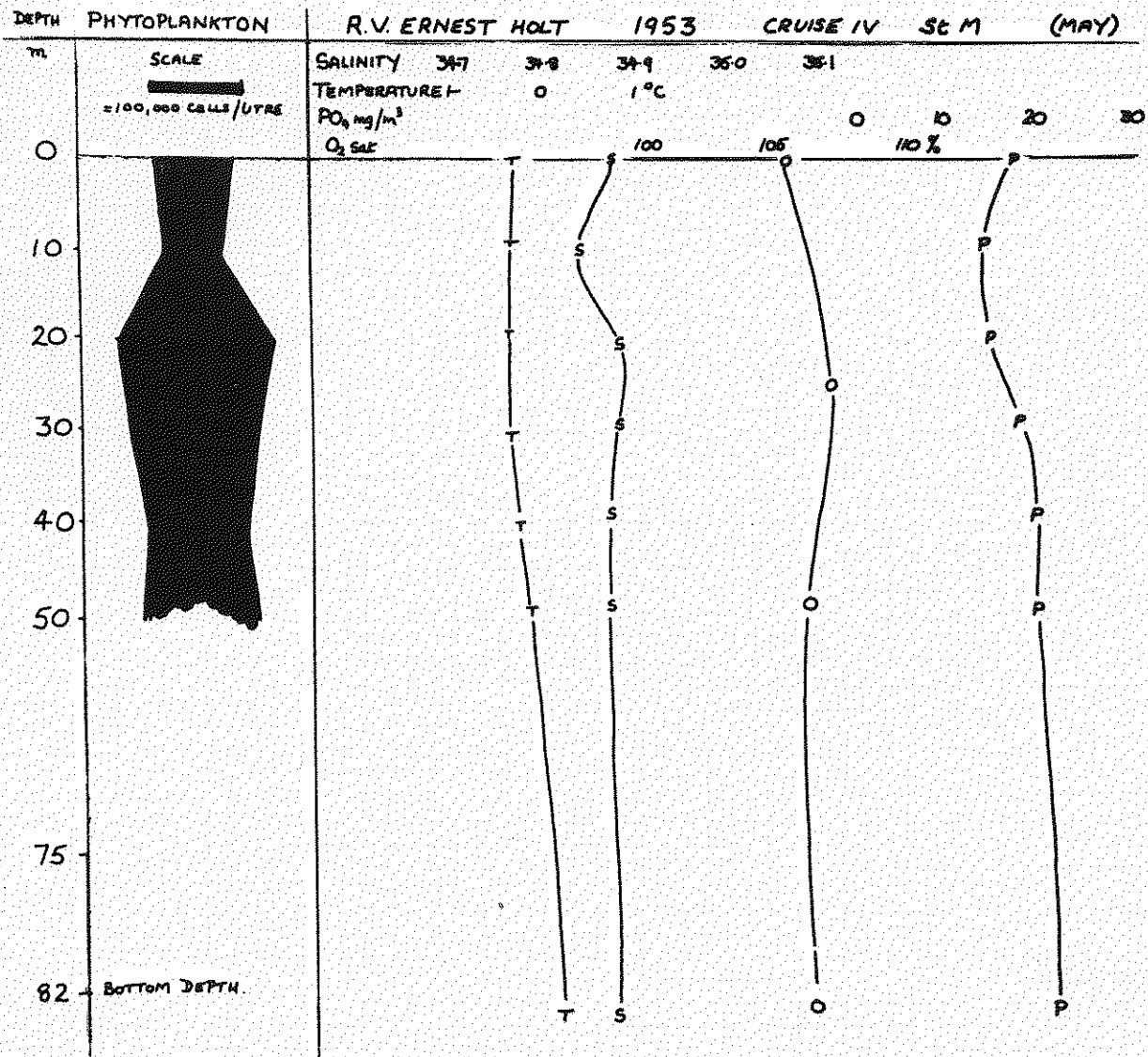


FIG. 10.

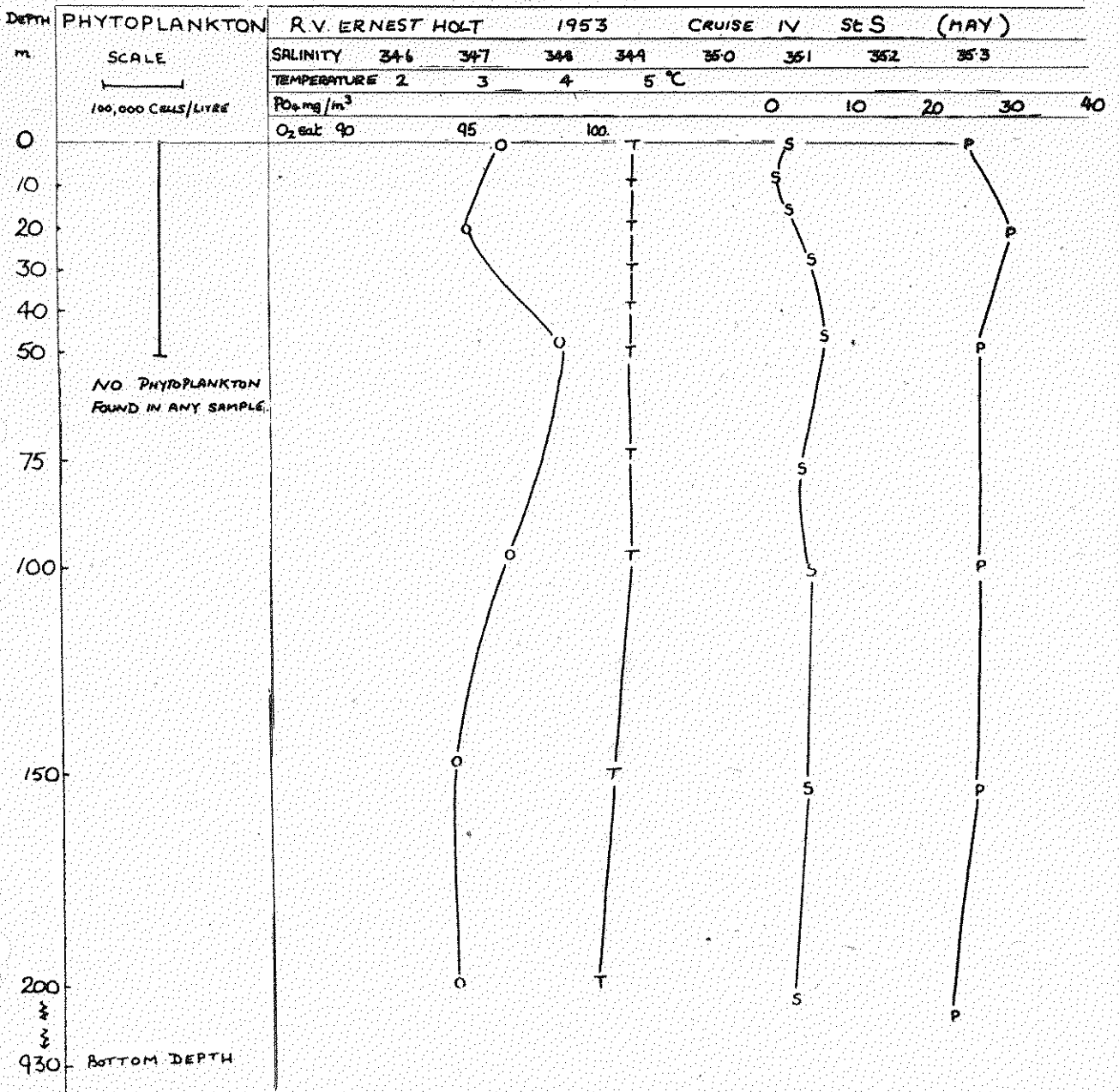


FIG. II.

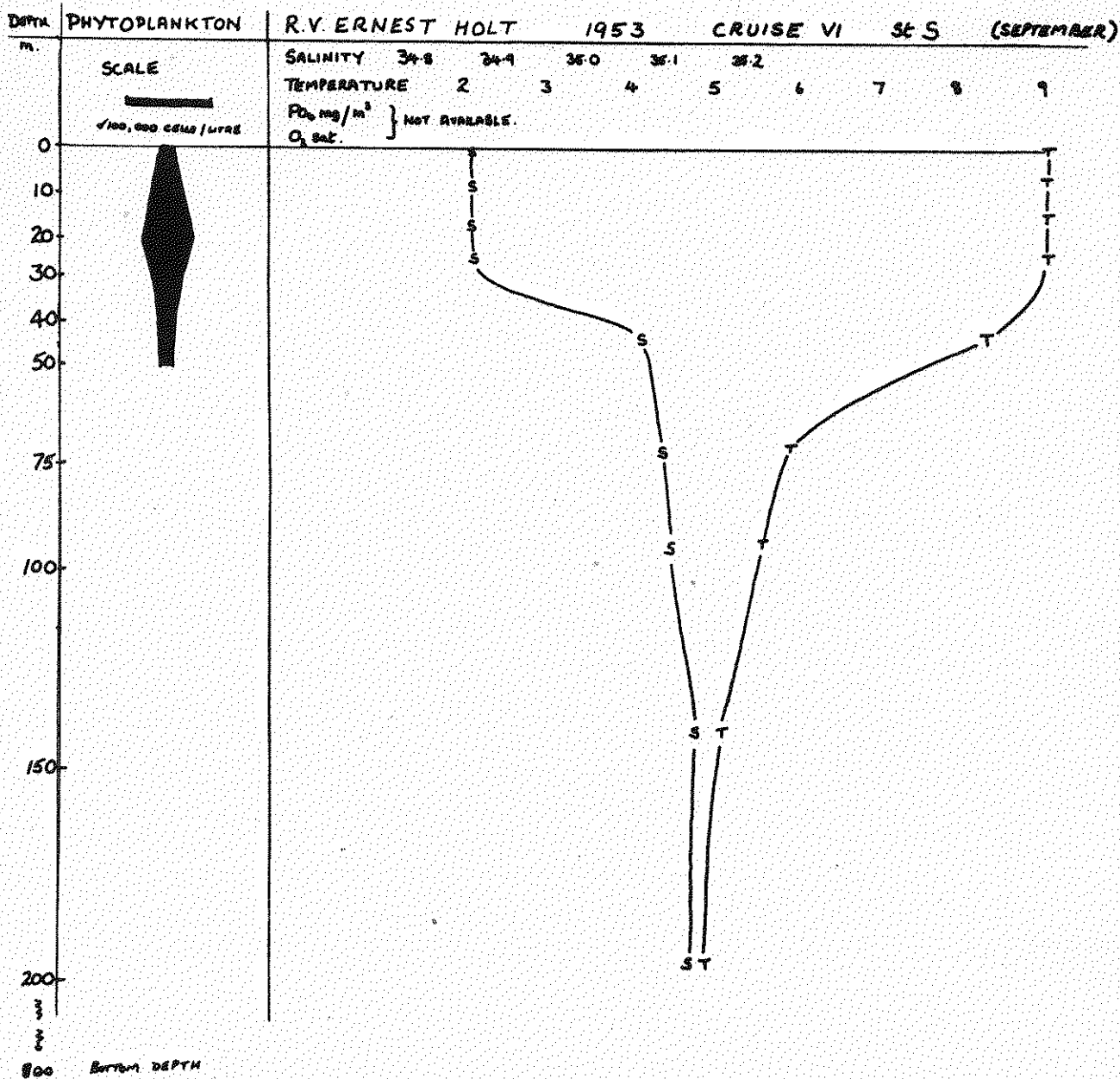


FIG. 12.