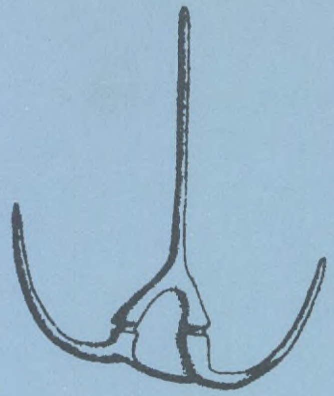
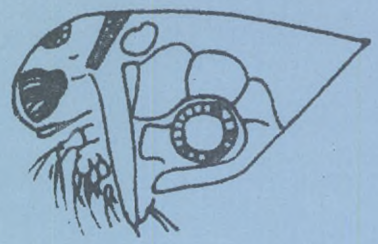
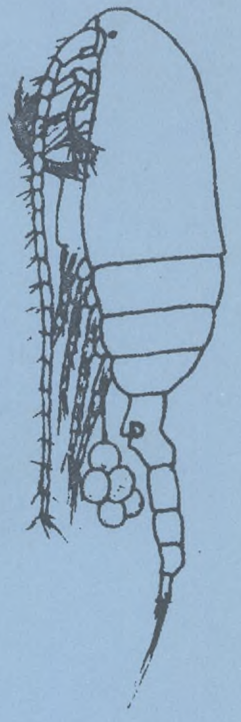
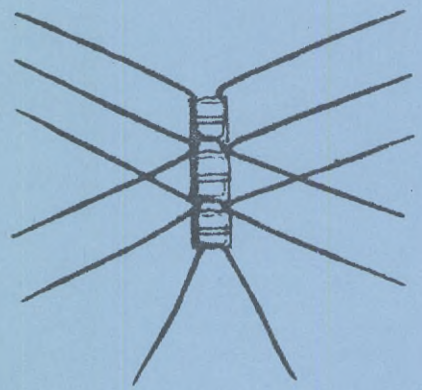
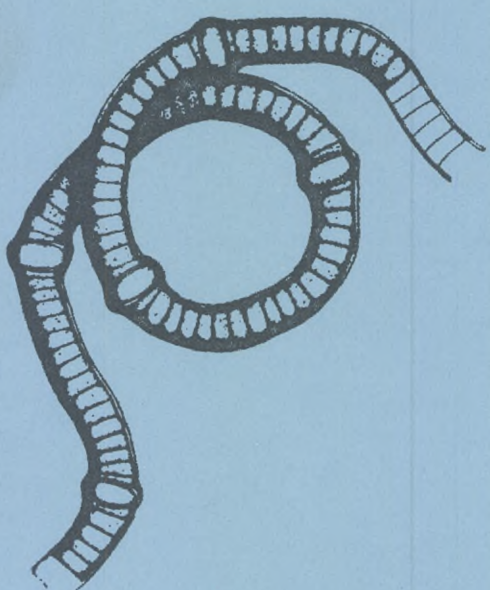
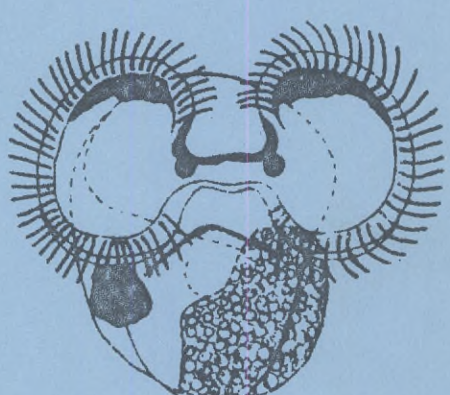

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Studies on the production of phytoplankton and zooplankton in the Baltic in 1975

by

Odd Lindahl

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ABSTRACT

Primary production, phytoplankton, chlorophyll a and zooplankton studies have been carried out at three off-shore stations in the Baltic in 1975. This is a continuation of an investigation which started in 1973. The stations were situated in the Hanö Bight, east of Gotland and in the Åland Sea. The sampling was carried out on 45 occasions.

The winter 1975 was comparatively mild, no ice was found in the investigated areas. 1975 will be rembered because of the very warm weather in July-August in the southern Scandinavia. As a result of the fine weather, surface water temperatures around 20 ^{o}C was found in August.

The primary production was measured with the ^{14}C-technique <u>in situ</u> using an incubation time of four hours. The measurements were carried out at ten depths and always around noon. The calculated annual primary production at the most southern station (the Hanö Bight) was 132 gC m^{-2}. East of Gotland an annual production of 96 gC m^{-2} was calculated, and in the Åland Sea (the most northern station) the annual primary production was found to be 67 gC m^{-2}. Compared with 1973-1974 this was a slight increase of the production in the Hanö Bight, while it was about the same production east of Gotland and in the Åland Sea.

The chlorophyll a values mainly varied between 10 - 30 mg m^{-2}, with slightly higher values in the north compared to the south. During the vernal bloom, some peak values of about 75 mg m^{-2} were found.

The phytoplankton biomass values were mainly in the magnitude 1 - 6 g m^{-2} (wwt). In general, higher values were found in the north compared to the south. However, during the vernal bloom some much higher values were sampled. The composition of the phytoplankton flora has also been investigated.

Zooplankton were regularly sampled at all three stations using vertical hauls with a Nansen-net. The mesh-size has

been 90 µm. The biomass values were in general lower than those usually found in the off-shore areas of the Baltic. The highest values were found in July east of Gotland (27 g m^{-2} wwt) and the lowest in the Åland Sea in May (1.6 g m^{-2} wwt). The dominant species in the Hanö Bight and east of Gotland were the copepods Acartia spp., Centropages hamatus, Pseudocalanus m. elongatus and Temora longicornis. During a short summer period very high abundances of Bosmina cor. maritima were found. In the Åland Sea the copepods Acartia spp. and Eurytemora sp. were responsible for more than 80 % of the total biomass during all months except June when the rotifer Synchaeta spp. was very abundant.

The zooplankton production has been calculated. The annual production in the Hanö Bight, east of Gotland and in the Åland Sea was estimated to 6.5, 7.0 and 8.5 gC m^{-2} respectively.

INTRODUCTION AND ACKNOWLEDGEMENTS

Since January 1973 the Institute of Marine Research in Lysekil, Sweden, has carried out a research programme for primary production studies in the Baltic proper and the Bothnian Sea. The field work for the programme was finished by the end of 1976. The aim of this investigation has been from the beginning to find adequate values for the primary production in four different off-shore areas in the Baltic. Later, zooplankton studies were also included. The measurements were carried out at four stations 10 - 20 nautical miles off the coast (fig. 1). The results are therefore considered representative for "off-shore" conditions in the Baltic.

The author would like to thank the crews of the rescue cruisers GRÄNGESBERG, ÖSTERGARN and K. A. WALLENBERG for their cooperative help on the many sampling occasions. I would also like to thank Mr Lars Edler, Mr Bo Eriksson and Mrs Brita Gornitzka for carrying out all the expeditions.

Further, I would like to thank the following persons, who have carried out different parts of the programme:
Dr Hans Ackefors, Lysekil, for being responsible for the whole investigation. He has also taken part in many valuable discussions, and has given comments to the concept of this paper. I am specially thankful to Dr Ackefors, who has spared no pains in the efforts to obtain financial support to the programme.
Mr Lars Edler, Lund, for performing the phytoplankton analyses and compiling the results. He has likewise taken part in valuable discussions, and has given comments to the concept of this paper.
Mr Lars Hernroth, Lysekil, for compiling the zooplankton results. He has as well given many good advices, and has taken part in several fruitful discussions.
Mrs Cornelia Sellei, Uppsala, for performing the zooplankton analyses.
Miss Ann-Christin Rudolphi, Lysekil, for typewriting and drawing the figures.

Two separate papers giving the results of 1973 and 1974 have been published (Ackefors & Lindahl 1975 a, 1975 b).

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METHODS AND MATERIAL

In this report only a summary of the methods and material used will be given. A more detailed description can be found in Ackefors & Lindahl (1975 a).

Station network and frequency of measurement

In table 1 the position of the stations and the number of measurements carried out at each station are listed.

Table 1. Station network and frequency of measurement.

Sta-tion No.	Position N	E	Distance from shore Nautical miles	Number of measurements 1973	1974	1975	1976
1	55°40'	15°20'	20	18	15	14	14
2	57°25'	19°15'	10	10	9	17	27
3	59°50'	19°35'	15	9	7	-	-
3'	60°20'	18°50'	10	-	-	14	22
4	63°25'	20°20'	15	12	11	4	-

Data collected

The following parameters were investigated using different sampling methods:

1. Primary production was measured in situ at ten depths.
2. Samples for determining the amount of chlorophyll a and the phytoplankton biomass were collected from 15 m to the surface.
3. Net samples for qualitative phytoplankton analysis were taken from 20 m to the surface.
4. Mesozooplankton were sampled from the whole vertical column.
5. Water temperature, salinity and pH (only at station 1 and 2) were measured.
6. Air temperature, cloud cover, wind direction and speed and secchi-disc values were recorded on different sampling occasions.
7. Irradiation was measured from a land based station close to each sampling area.

The author is well aware of the absence of nutrient-data in this investigation. However, it was impossible to solve the practical arrangements in order to obtain accurate chemical results, due to widespread investigation area.

Primary production

The primary production measurements were carried out *in situ* with the ^{14}C-technique, in nearly all respects according to Dybern *et al*. (1976). However, the methods were slightly modified due to practical reasons. Fixed incubation depths were used, with a single bottle at each sampling depth. The depths were 0, 1, 2, 3, 4, 6, 8, 10, 15 and 20 m. Four dark-bottles were used at 0, 4, 10 and 20 m depth. Primary production below 20 m depth was negligible.

An incubation time of four hours was used. The incubations were always carried out at the same time of day (9 am - 3 pm). It was then possible to compare different measurements without any transformations. However, it was necessary to transform the four hour values (mgC m^{-2} h^{-1}) into daily production (mgC m^{-2} d^{-1}). The factor used for this transformation was called the lightfactor (LF). $LF = \frac{I_d}{I_m}$, where I_d is the irradiation during the day and I_m the irradiation during the measurement.

The ampoules and filters used (Sartorius, pore size 0.2 µm) were bought at the Carbon 14 Central in Copenhagen. The Central has measured the radio-activity on the filters with the Geiger-Müller counting equipment. The author was aware of the fact that the GM-technique may be less accurate than the liquid scintillation technique, but decided not to change method during this investigation.

Chlorophyll

The water-samples were taken with a hose (15 m long) as an integral sample. The SCOR/UNESCO method was used when storing the samples and measuring the amount of chlorophyll (Carlberg 1972).

Phytoplankton biomass

The water-samples were taken as described above and were preserved in Keefe's solution. The phytoplankton was analysed according to the Utermöhl technique and the cell volume for each species was calculated (Utermöhl 1958). The density of the biomass was assumed to be 1 g cm^{-3}.

Phytoplankton flora

The samples were collected using a net with a mesh-size of 25 µm. Vertical hauls were taken down to a depth of 20 m. The samples were preserved in Keefe's solution.

Zooplankton

In 1975, all zooplankton samples were collected with a Nansen net (90 µm). The hauls were vertical and the towing speed was 0.5 m s^{-1}. At station 1 the sampling was carried out from 30 m to the surface, at station 2 from 55 m to the surface and at station 3' from 40 m to the surface.

The samples were preserved in 4 % formalin. Before analysis the samples were subsampled in a whirling apparatus (Kott 1953). In the subsamples all specimens were analysed to species and the copepodes were, in addition, determined to developmental stages. The biomass was calculated by adding all individual volumes (Ackefors 1972), assuming a density of 1 g cm^{-3}.

According to a recent investigation into the filtration efficiency of different nets (Hernroth unpubl.) it was found that the Nansen net has a poor capacity (only 50 %). The present results have therefore been compensated by a factor of 2. However, from the beginning of 1976 the Nansen net was replaced by a UNESCO WP 2 net.

An attempt to measure the zooplankton production has been made using the technique described by Winberg (1971). The P/B-coefficients used derive from Ciszewski (in print), Hernroth (unpubl.), Zawislak (1974) and Winberg (1971).

In order to illustrate the relative importance of herbivores, omnivores and carnivores throughout the year, a rough grouping has been made according to Petipa et al. (1970), Hillebrandt (1972) and Schnack (1975).

Irradiation

The irradiation was measured between 300 - 2 500 nm by a Kipp & Zonen solarimeter of type CM 6 connected to a Kipp & Zonen integrator of type CC 1. A printer connected to the integrator gave the irradiation values hourly on papertape. When irradiation values were missing for one reason or another, values from the nearest irradiation station belonging to the Swedish Meteorological and Hydrological Institute (SMHI) were used. These stations were situated at Svalöv, Visby and Erken for stations 1 - 3' respectively (fig. 1).

RESULTS AND DISCUSSION

On 44 occasions different parameters were investigated at three off-shore stations: in the Hanö Bight, east of Gotland and in the Åland Sea (fig. 1). In the Sydostbrotten area between the Bothnian Sea and the Bothnian Bay, measurements were carried out in 1973-1974. This was also planned for 1975-1976, but due to practical problems only four measurements were made in 1974. Therefore the station was closed at the end of 1974.

All of the stations are situated at least 10 nm off the coast. The frequency of the separate measurements is evident from fig. 2. The figure also shows the frequency of measurements carried out in 1973, 1974 and 1976.

Temperature and salinity

The winter of 1975 was very mild in comparison with a normal winter. At no station ice was found at sea. The summer of 1975 was also much warmer than normal in Scandinavia. The isopleths of the water-temperature at the various stations are reproduced in figure 3. A maximum water-temperature of 22 ^{o}C was found in August at the Gotland station. Both at stations 1 and 2, the temperature of the surface water was above 18 ^{o}C for a long time during August-September. At station 3' the temperature at the surface was above 16 ^{o}C from the end of July until the end of August.

On most occasions the salinity was homogeneous from the surface to the 20 m level. There were, however, small differences between the sampling areas. The lowest and highest salinities found at station 1 were 7.0 ‰ and 8.0 ‰ respectively. The mean value for the salinity was 7.5 ‰. At station 2, the salinity fluctuated between 7.2 ‰ and 8.2 ‰ with a mean value of 7.8 ‰. In the Åland Sea, the salinity was in the range 5.5 - 6.1 ‰ with a mean value of 5.8 ‰ . The salinity conditions at stations 1 - 3' were almost the same as in 1973-1974.

Irradiation

In 1975, irradiation measurements were carried out at stations 1 and 2, i.e. at Hörvik and Herrvik. From October and onwards, registration of the irradiation was carried out at station 3', i.e. Öregrund. The above-mentioned lack of data and some other small gaps in the registration of the irradiation have been filled by data from the nearest SMHI solarimeter station.

The monthly, quarterly and yearly values, as well as the yearly mean values for irradiation in the three areas are evident in figure 4 and table 2. The differences between the annual means for the period 1961-1975 (SMHI, pers. comm.) and the 1975 values from this investigation are +7, +4 and +5 % for the different areas in a progression from south to north. SMHI states that a yearly difference from the annual mean of ±10 % is reasonable (SMHI, pers. comm.).

Primary production

Station 1, the Hanö Bight: 14 measurements were carried out in 1975 (table 3 and fig. 5). On the first measuring occasion of the year, at the beginning of February (February 4), a daily production of 23 mgC m^{-2} d^{-1} was found. This is, compared with earlier investigations, a typical winter-month value. However, at the end of February, the primary production started to increase, and a production of 132 mgC $m^{-2}d^{-1}$ was measured (February 28). One month later (March 27), a value of 222 mgC m^{-2} d^{-1} was found. The highest spring production value was found in April (April 17), and was calculated to be 756 mgC m^{-2} d^{-1}. After that, the production decreased as usual, probably due to the lack of nutrients. Accordingly, a production of only 164 mgC m^{-2} d^{-1} was measured in May (May 11). Two measurements, with a mean production of 393 mgC m^{-2} d^{-1}, were made in June. In July, August and September, five measurements were made. The calculated production on those occasions ranged between 614 and 923, with a mean value of 779 mgC m^{-2} d^{-1}. On a very dark day at the end of October (October 24), a production of 124 mgC m^{-2} d^{-1} was measured. The last measurement for the year was made in November (November 12), and the calculated primary production was as high as 223 mgC m^{-2} d^{-1}. Compared with previous experience this is a very high production value for this time of the year. When calculating the quarterly and annual production, three fictitious values were used (January 1; 30 mgC m^{-2} d^{-1}, December 1; 40 mgC m^{-2} d^{-1} and December 31; 30 mgC m^{-2} d^{-1}). The annual primary production was calculated to be 132 gC m^{-2}.

<u>Station 2, east of Gotland</u>: 16 measurements were made in 1975 (table 4 and fig. 5). The result of the primary production from the first measurement (January 9), has unfortunately been lost. From measurements made at the end of March (March 25), a production value of 137 mgC m^{-2} d^{-1} was found. Unfortunately, only one measurement was made in April. The production was 372 mgC m^{-2} d^{-1} (April 17). In May, three measurements were carried out, with a mean production of 555 mgC m^{-2} d^{-1}. There are, however, reasons to believe that the peak of the springbloom might have occurred in the second half of April (see page 13). One measurement in June (June 12) gave, as expected, a relatively low production value (180 mgC m^{-2} d^{-1}). In July and August altogether six measurements were made. These six measurements, together with one in the beginning of September varied between 348 and 549 mgC m^{-2} d^{-1} with a mean of 486. The measurements carried out in October, November and December gave typical production values for those months (October 22; 178 mgC m^{-2} d^{-1}, November 7; 126 mgC m^{-2} d^{-1} and December 18; 22 mgC m^{-2} d^{-1}). When calculating the quarterly and annual production, two fictitious values were used (January 1; 30 mgC m^{-2} d^{-1} and March 1; 40 mgC m^{-2} d^{-1}). The annual primary production was calculated to be 96 gC m^{-2}.

Station 3', the Åland Sea: Due to practical reasons this station was moved in January 1975, about 25 nm to the NNW compared with the position in 1973-1974. At this new position 14 measurements were made in 1975 (table 5 and fig. 5). At the time of the first measurement of the year at the end of February (February 26) the primary production was only 13 mgC m^{-2} d^{-1}. On the next measuring occasion (March 18), the production had increased to 89 mgC m^{-2} d^{-1}. During April two measurements were made (April 8 and April 22). The production on those occasions had values of 279 and 358 mgC m^{-2} d^{-1} respectively. The latter value was the highest found at this station during the spring of 1975. In May and June, a total of four measurements were made, with an average production value of 226 mgC m^{-2} d^{-1}. In contrast to the other stations, there was no early summer minimum this year. Unfortunately, very few measurements were made during the summer. On one occasion in July (July 22), the primary production was calculated to be 352 mgC m^{-2} d^{-1}. No measurements were made in August. In September, two measurements gave a mean production of 445 mgC m^{-2} d^{-1}. Two measurements in October gave an average production of 181 mgC m^{-2} d^{-1}. The last measurement of the year was made on a very dark day in November (November 11). The primary production on this occasion was only 16 mgC m^{-2} d^{-1}. When calculating the quarterly and annual production, three fictitious values were used (January 1, December 1 and December 31; 20 mgC m^{-2} d^{-1}). The annual primary production was calculated to be 67 gC m^{-2}.

Table 6. Quarterly and annual primary production in gC m^{-2} at stations 1 - 3' in 1975.

Station No.	I	II	III	IV	Total
1	9	36	73	14	132
2	6	38	42	10	96
3'	4	23	34	6	67

The contribution of the second quarter was 27 - 40 %. The most productive quarter of the year was the third, at all stations. This is the same situation as for 1973-1974. The production in July-September was estimated to be 44-55 % of the annual production. The production from the second and third quarters was hence 83 - 85 % of the annual production. The contribution to the annual production by the months January-March and October-December was thus comperatively small.

Table 7. Calculated annual primary production in gC m^{-2} at stations 1 - 4 in 1973 - 1975.

Station No.	1973	1974	1975
1	105	121	132
2	91	116	96
3	94	-	-
3'	-	-	67
4	71	70	-

At station 1 there seemed to be a tendency for increased primary production during the period 1973-1975. At station 2 no such tendency was found. The production oscillated around 100 gC m^{-2} $year^{-1}$. The 1973 value from station 3 should not be compared with the 1975 value from station 3', since the station was moved 25 nm in January 1975. This new area seems to be different from the earlier one. In 1974 no annual production could be calculated for station 3 as only seven measurements were made.

Chlorophyll a

At all stations, chlorophyll a was measured according to the SCOR/UNESCO method. In the beginning of 1975 the earlier used Millipore Cellotate filters were replaced by Whatman GF/C glass fiber filters. The filters were stored in a deep-freezer prior to analysis. The results are shown in tables 3 - 5 and in figure 6. The fluctuations in the chlorophyll a values expressed in mg m^{-2} were similar to the fluctuations in the primary production values at stations 2 and 3'. However, station 1 showed a somewhat different picture.

At station 1, the amount of chlorophyll a during spring was about 10 mg m^{-2}, except on one occasion (April 17), when a conspicuous peak value of 75 mg m^{-2} was found. From that occasion onwards and almost until the end of September, low values were found. The mean amount of chlorophyll a during this period was 6 mg m^{-2}. At the end of the year, much higher values were found (about 30 mg m^{-2}).

During the first two months of the year, low chlorophyll a values were found at station 2. In April and May, values of around 25 mg m^{-2} were found. Compared with station 1, the summer-values for chlorophyll a at station 2 were twice as high as at station 1, or about 20 mg m^{-2}. Due to a precipitate in the cell of the photometer it was impossible to measure the samples from the last quarter of the year.

At station 3' the amount of chlorophyll a increased on each measuring occasion until the spring bloom was over. A remarkable peak of 78 mg m^{-2} was found in April (April 22). After that, the values oscillated around 20 mg m^{-2} until the end of the summer. In September, higher values for chlorophyll a were found, with a peak value of 47 mg m^{-2}. On the last two measuring occasions of the year, a chlorophyll a content of about 20 mg m^{-2} was found.

Phytoplankton

The phytoplankton biomass and the composition of the flora on each sampling occasion are shown in figure 7 and tables 8 - 10.

At station 1 (table 8), low values for phytoplankton biomass were found during most of the year. In the periods January-March and September-December the biomass was less than 1 g m^{-2}. The highest value of the year was found during the vernal bloom in the middle of April. From May until August the biomass ranged from 1.0 - 2.6 g m^{-2}.

Diatoms were the dominant species until June. Only a few species were of great importance: Actinocyclus octinarius (February), Skeletonema costatum (March, April, May), Thalassiosira baltica and Chaetoceros danicus (April, May). The diatoms became less dominating in June and July when bluegreen algae became abundant. Gomphosphaeria sp. and Microcystis sp. were the most abundant species. In August and September, the flora was a mixture of diatoms and dinoflagellates (Dinophysis acuminata, D. norvegica and Ceratium tripos). There were also monads and flagellates. During October the diatoms decreased in number, and in November they were again dominant (Chaetoceros danicus).

Low phytoplankton biomass values were also found at station 2 (table 9). At the beginning and at the end of the year, the biomass was around 1 g m^{-2}. During spring, the biomass values increased and a peak value was found in the beginning of May. Large cells of Skeletonema costatum were recorded in the middle of April. In early May only small dying cells of the same species were found. These observations indicate that the maximum of the vernal bloom occurred between the two sampling occasions. The increasing numbers of Chaetoceros wighamii between the two samplings underline this assumption. From May onwards until November, the biomass values tended to fluctuate between 1.0 and 3.9 g m^{-2}.

Until April, the dominance of the diatoms was very marked. The succession of species was somewhat different compared to station 1: Actinocyclus octinarius (January), Thalassiosira baltica (March, April), Skeletonema costatum (April, May, June) and Chaetoceros wighamii (May). Most of the biomass during May and June consisted of dinoflagellates: Gonyaulax catenata (May), Dinophysis (May-June). At this time, the chrysophyceans Dinobryon balticum and Ebria tripartita were also important. The bluegreen algae Aphanizomenon flos-aquae and Nodularia spumigena made up most of the biomass in July and August. From August until October, large numbers of monads and flagellates were found (see also station 1). During this period a gradual decrease in the numbers of monads and flagellates took place. They were replaced first by small dinoflagellates and later on by increasing numbers of diatoms: Chaetoceros danicus (September-October) and

Actinocyclus octonarius (October-December).

At station 3' (table 10) the phytoplankton biomass was considerably larger than at stations 1 and 2. Still another pattern for the succession and distribution of the algal groups was found at this station.

At the beginning and end of the year, the biomass values were less than 1.0 g m^{-2}. In the middle of March the biomass values began to increase and a peak value of 31.7 g m^{-2} was found in April. This is, so far, the largest biomass value found in the investigation. From May until September the biomass varied between 1.8 and 13.4 g m^{-2} with a mean of 5.6. At the end of the year, values below 1.0 g m^{-2} were found.

The dominance of diatoms during the first part of the year, observed further south in the Baltic, was not so obvious at station 3'. In February, about 50 % of the biomass was made up of monads and flagellates. In March however, they were replaced by diatoms: Thalassiosira baltica (March-May), Skeletonema costatum (April), Chaetoceros wighamii (May). The dinoflagellates were also important. The main difference, compared with the southerly stations, was the presence of high numbers of the dinoflagellate Gonyaulax catenata. During July and August, and at the beginning of September, the blue-green algae Aphanizomenon flos-aquae and Aphanocapsa sp. dominated. At the same time, Ebria tripartita had a second bloom, which is not common further south in the Baltic. As late as October and November Aphanizomenon flos-aquae was dominating the small biomass.

Zooplankton

a. Composition and biomass of the zooplankton fauna

From fig. 2 it is evident that zooplankton sampling was not carried out every month of the year. For all stations, the most incomplete sampling period is the winter. In this paper, it is therefore difficult to describe an annual cycle for species, biomass and production, but according to previous experience (Ackefors & Hernroth 1975), winter is the least important of the seasons. A significant improvement in the sampling frequency did, however, occur in 1976. This will hopefully help us in our efforts to describe the annual zooplankton cycle at the three stations.

Before the results are presented, it is necessary to point out some fundamental differences between phytoplankton and zooplankton investigations. In contrast to the phytoplankton which is mainly concentrated in the photic layer, the standing crop of zooplankton is usually found in the whole vertical column. The specimens are not randomly distributed; they are often stratified due to a specific tolerance level for temperature, salinity and light-conditions. It is therefore necessary to investigate not only the photic zone, but the whole vertical column. Since the Baltic proper contains two greatly differing water masses, separated by a halocline at the 50 - 60 m level, special attention must be payed to the depth of the stations. Consequently, the conditions found at a shallow station will be different from those at a deep station containing cold, salt water below the halocline. The composition of species, the biomass and the zooplankton production are therefore greatly dependant on the depth of the station, and this must be kept in mind when the results are discussed.

At station 1 in the Hanö Bight, the net hauls were made from a depth of 30 m to the surface. In 1975, the first sample was taken in the middle of April and the last in the middle of November. The biomass values were, in general, much smaller than the average values for the southern Baltic proper. This is simply a result of the shallowness, which during most months excludes those species that prefer cold water.

During April and May the biomass was approx. 3 g m^{-2} wwt (fig. 9). The dominant species were the copepods Pseudocalanus m. elongatus and Acartia spp., which together constituted 65 - 85 % of the total biomass.

Another species of significance was the appendicularian Fritillaria borealis acuta. Both P. m. elongatus and F.

b. acuta prefer cold water, and their appearance at station 1 was therefore restricted to the winter and spring seasons. The absence of the very important spring rotifer Synchaeta spp. is remarkable.

During the month of June the temperature rose considerably, and consequently, the numbers of P. m. elongatus rapidly decreased. Instead, a warm stenotherm copepod, Centropages hamatus, began to appear in great numbers. Together with Acartia spp., C. hamatus dominated the biomass. Other species were the copepods Pseudocalanus m. elongatus and Temora longicornis, the appendicularian Fritillaria borealis acuta, the cladocerans Evadne nordmanni and Podon leuckarti and a number of bivalve larvae. The biomass values in June varied from 7 - 8 g m^{-2} wwt. Two measurements were made in July, one in the beginning and one in the middle. The biomass values were slightly higher (9 - 11 g m^{-2} wwt), but no great changes in the fauna could be seen. Two later measurements, made in August and September, showed similar biomass values, but a marked change in species composition had taken place. As a result of the very high water temperature in August (20.2 ^{o}C), favourable conditions were created for a rapid increase in the numbers of Bosmina cor. maritima. In the beginning of August B. c. maritima was responsible for almost 50 % of the total biomass, and in late September 17 %. In addition to Bosmina, the three copepods Acartia spp., Centropages hamatus and Temora longicornis dominated the fauna. On the last two measuring occasions (October 24 and November 12) the biomass values had decreased to 5.2 and 2.6 g respectively. The major components of the fauna were Acartia spp. and Temora longicornis.

At station 2, east of Gotland, the biomass values were in general higher than at station 1. The reason for this is probably the greater depth at this station (55 m), which creates favourable conditions for the Pseudocalanus m. elongatus-population, even during the warm season. The abundance of Temora longicornis was also considerably greater at this station, especially during the warm season. Apart from these differences the fauna at station 2 was rather similar to that at station 1.

In the samples from April and May, the fauna was dominated by Acartia spp., Fritillaria borealis acuta and Pseudocalanus m. elongatus. This is the same as for station 1, and so was the biomass, which was about 3 g m^{-2} wwt in April and the beginning of May (fig. 10). In the middle of May the biomass was about 6 g. No sampling was carried out in June, but in July samples were taken on four occasions (July 2, 10, 18 and 30). The biomass values were then considerably higher (15, 27, 25 and 20 g resp.) and the increase was mainly caused by the copepods, especially Temora longicornis and Centropages hamatus.

On the two sampling occasions in August the surface temperature was very high (19 - 22 °C). The conditions for a rapid increase in the abundance of Bosmina cor. maritima were thus good. The maximum abundance of B. cor. maritima at station 2 was of the same magnitude as at station 1 (500 000 ind. m^{-2}) but the share of the total biomass was somewhat smaller (12 - 25 %) due to the larger total biomass at station 2. As was the case in July, the copepods were by far the most dominating group, especially Pseudocalanus m. elongatus and Temora longicornis.

On the next sampling occasion (September 2), the importance of Bosmina cor. maritima was, curiously enough, very small, although the water temperature was still high (19 °C). The total biomass was also surprisingly low, (6.7 g) but the decrease was not noticed among all species, only among the major copepods. However, a technical error in the sampling procedure is the most probable reason for the low values.

The low values from the sampling in November (3.7 g) were, however, expected. The water temperature was only 10 °C and most of the spring and summer species like Evadne nordmanni, Podon sp. and Centropages hamatus had lost their importance. The fauna was restricted to the copepods Pseudocalanus m. elongatus, Acartia spp. and Temora longicornis.

Station 3' in the Åland Sea is different from the other stations mainly because of the lower salinity. The mean salinity at station 3' was 5.8 ‰ compared to 7.5 at station 1 and 7.8 at station 2. The station was rather shallow (40 m) and combined, these factors create an unfavourable habitat for several important species. On the other hand, the low salinity makes it possible for brackish water species like Eurytemora sp. and Acartia bifilosa to play a more dominating role. The biomass values were thus of the same magnitude as those from station 2, despite the unfavourable conditions for several species. Compared with the other stations, the vernal increase in the water temperature occurred about one month later at station 3'. The biomass values from the samplings at the end of May and in the beginning and middle of June were consequently relatively small (1.6 - 4.7 g) (fig. 11).

In samples from the end of May, the copepods Acartia spp. and Eurytemora sp. dominated the biomass totally. However, on the next sampling occasion, only ten days later (June 5), the rotifer Synchaeta spp. was so abundant that it constituted 28 % of the total biomass. The temperature increased from 4.8 to 6.5 °C during the same period. In the middle of June the number of Synchaeta spp. was still high (450 000 ind. m^{-2}),and in addition, the numbers of Acartia spp. and Eurytemora had increased. A rapid rise in water temperature from 6.5 to 12 °C had taken place at the same time. By the end of July the biomass had increased almost four times (17.6 g) compared to the values from June. The rotifers were now of very little importance. The major increase in biomass was caused by Eurytemora sp. which reached its maximum abundance on this sampling occasion. However, Acartia spp. was still the dominant species. The cladocerans Evadne nordmanni, Podon leuckarti and Bosmina cor. maritima occurred, but in small numbers. Unfortunately, no samples were taken in August but in September sampling was carried out twice. On the first sampling occasion (September 2), the maximum biomass value for the year was recorded (20.9 g). Acartia spp. and Eurytemora sp. were very dominating (61 % and 25 % resp.) compared to e.g. Temora longicornis (4 %) and Bosmina cor. maritima (5 %). It is however, probable that the period of maximum abundance for B. cor. maritima was never found due to the absence of sampling in August. On the next sampling occasions (September 17 and October 1), the biomass was somewhat less (15.3 g and 19.4 g resp.) but the relative importance of the different species was still the same. By the middle of October the biomass had decreased drastically to only 6.0 g. All species were less abundant, except for the rotifer Synchaeta spp. which showed a distinct autumn peak (360 000 ind. m^{-2}). The last sampling occasion of the year was in the middle of November. The surface temperature was then only 6.8 ^{o}C and the biomass was accordingly low (4.3 g). The rotifers were then insignificant and so were the cladocerans. Acartia spp. and Eurytemora sp. were still by far the dominant species but both Pseudocalanus m. elongatus and Temora longicornis were also relatively important.

b. Zooplankton production

The intentions behind the zooplankton sampling in this "primary production"-project were primarily to investigate the seasonal cycle of the fauna, by taking advantage of the frequent measurements carried out for the primary production studies. In addition, due to the frequent measurements, an estimate of the zooplankton production could be made. This calculation (fig. 12), must be regarded as a relatively rough estimate, since some of the P/B coefficients are literature values calculated from rather different environments. Another limitation is the lack of values from the winter season. According to previous investigations however (Ackefors & Hernroth 1975), the contribution from the winter season is of minor importance compared to that of the other seasons.

The production has been calculated according to the method described by Winberg (1971). This method uses the ratio of production to biomass, the so called P/B coefficient. This coefficient is specific for each species, and is influenced by both water temperature and the developmental stage of the specimens. Consequently, the coefficient does not remain constant, but represents only a certain mean value, true for a defined period of time only.

At station 1, the total production from the middle of April until the middle of November was estimated to be 5.4 gC m^{-2} (104 g wwt). The maximum production (47 mgC m^{-2} d^{-1}) occurred during the period August 7th to September 22nd. The cladoceran Bosmina cor. maritima was, during this period, responsible for 64 % of the produced biomass, although its share of the standing crop was only 32 %. During the rest of the year, the copepods Acartia spp., Centropages hamatus, Temora longicornis and to some extent Pseudocalanus m. elongatus dominated the production.

At station 2, the total production from the middle of April until the beginning of November was calculated to be 5.8 gC m^{-2} (111 g wwt). However, there is reason to believe that this is an underestimation, due to the fact that both June and September-October are so poorly represented by samples. It is likely that samples from June would have contained a considerable number of rotifers, and since these have a rapid turnover rate, their contribution to the total production would have been important. The fact that no sampling was carried out during September and October has probably led to a substantial underestimation of the daily production. Earlier investigations have shown that the biomass values usually remain high during September and the beginning of October, and the decrease is not rapid until the end of October. A more likely total production has therefore been estimated to be 7 gC m^{-2} (135 g wwt). The main producers were the copepods Pseudocalanus m. elongatus, Acartia spp. and Temora longicornis. During August the influence of Bosmina cor. maritima was considerable due to its rapid turnover rate.

At station 3', the total production from the end of May until the middle of November was calculated to be 7.1 gC m^{-2} (136 g wwt). The maximum production occurred in August when a daily production of 64 mgC m^{-2} was found. The dominant producers throughout the year were Acartia spp. and Eurytemora sp. with occasional contributions from the rotifer Synchaeta spp. in June and October.

c. The feeding habits of the fauna

In an investigation like this, where more than one link in the food-web is being studied, it is challenging to look for an eventual relationship between the different components. In this investigation it was possible to make such an analysis only at station 2, since the number of zooplankton samples were too sparse at the other stations.

According to Petipa *et al.*(1970), Hillebrandt (1972) and Schnack (1975), a rough separation of the zooplankton into feeding groups can be made. In this paper the separation has been made into herbivores, omnivores and carnivores. However, most authors have worked only with the older stages, which creates some uncertainty when classifying the young copepodites and nauplii of certain copepods. This rough separation of the fauna into major feeding groups will, however, give some indications of the relative importance of the different groups as well as the seasonal variation. From fig. 13 it is evident that the relative importance of the herbivores is greatest during April, May and June. This would seem likely, since there is a considerable amount of phytoplankton-biomass produced during April and May. The increase in the number of omnivores occur in the middle of May and a maximum is reached in mid-July. This increase is a result of the changing age-structure among the copepod populations. As the nauplii and young copepodites grow older, they often change from plain herbivores to mixed-food consumers (Petipa *et al.* 1970). This decreasing importance of the herbivores in June-July is surprisingly well correlated with the declining primary production that takes place in June. A new increase in the importance of the herbivores takes place during August. This is to a large extent caused by the herbivorous cladoceran *Bosmina cor. maritima*, which has its yearly maximum during this period. It is impossible to describe the situation during September and October, since no samples were taken during this period. In November however, the herbivores dominate. The reason for this is the appearance of the purely herbivorous copepod *Pseudocalanus m. elongatus* which at this time dominates the fauna.

The carnivores were obviously of very little importance (<7 %). The main carnivores in the Baltic are the rotifer *Synchaeta* spp., the cladocerans *Podon* spp. and *Evadne nordmanni*, the copepod *Oithona similis* and the medusae *Aurelia aurita*.

At station 2, none of these species were abundant in 1975. At other stations, several, and sometimes all of the above mentioned species can be abundant. This is, therefore, not a general description of the Baltic. It is, on the contrary, most probable that the carnivores play a much more important role.

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Table 2. Irradiation in mWh cm^{-2} at stations 1 - 3' in 1975.

MONTH	Station 1 (Hörvik)	Station 2 (Herrvik)	Station 3' (Öregrund)
January	1 127	1 126	814*
February	4 133	4 105	3 655*
March	7 619	6 981	6 909*
April	12 170	11 550	11 157*
May	16 317	16 308	15 856*
June	18 326	20 808	18 810*
July	17 508	18 437	18 237*
August	15 714	16 008	12 508*
September	8 742	9 427	7 970*
October	3 380	4 525	3 905
November	1 686	1 339	819
December	1 080	1 017	530
QUARTER			
I	12 879	12 212	11 378
II	46 813	48 666	45 823
III	41 964	43 872	38 715
IV	6 146	6 881	5 254
YEAR	107 802	111 631	101 170
ANNUAL MEAN	Svalöv	Visby	Erken
1961-1975	101 139	107 115	96 486
DIFFERENCE 1975	+ 7 %	+ 4 %	+ 5 %

* values from SMHI

Table 3. Irradiation, measured production, calculated production, chlorophyll a, phytoplankton biomass and zooplankton biomass.

Station 1, 1975

Date	Irradiation	Measured production	Calculated production	Chlorophyll a	Phytoplankton biomass	Zooplankton biomass
	mWh $cm^{-2}d^{-1}$	mgC $m^{-2}h^{-1}$ (0-20 m)	mgC $m^{-2}d^{-1}$ (0-20 m)	mg m^{-2} (0-15 m)	g m^{-2} wwt (0-15 m)	g m^{-2} wwt (0-30 m)
750204	23	4.2	23	3	0.4	-
750228	244	19.1	132	11	0.4	-
750327	281	25.5	222	15	1.6	-
750417	568	84.9	756	75	10.9	3.1
750511	377	21.3	164	6	1.9	2.8
750618	793	40.1	405	7	2.6	8.2
750626	609	44.2	380	1	1.8	7.6
750702	774	64.9	669	3	2.4	9.3
750714	394	81.0	923	13	1.5	11.4
750807	647	91.0	874	6	1.0	8.9
750831	493	97.2	817	5	0.9	-
750922	374	79.7*	614*	21	0.8	10.3
751024	21	22.2	124	36	0.7	5.2
751112	102	40.5	223	27	0.8	2.6

Calculated annual primary production: 132 gC m^{-2}

Calculated annual secondary production: 6.5 gC m^{-2}

*approximate value

Table 4. Irradiation, measured production, calculated production, chlorophyll a, phytoplankton biomass and zooplankton biomass.

Station 2, 1975

Date	Irradiation	Measured production	Calculated production	Chlorophyll a	Phytoplankton biomass	Zooplankton biomass
	$mWh\ cm^{-2}d^{-1}$	$mgC\ m^{-2}h^{-1}$ (0-20 m)	$mgC\ m^{-2}d^{-1}$ (0-20 m)	$mg\ m^{-2}$ (0-15 m)	$g\ m^{-2}$ wwt (0-15 m)	$g\ m^{-2}$ wwt (0-55 m)
750109	30	-	-	5	0.9	-
750325	266	20.8	137	10	0.2	-
750417	562	45.4	372	18	2.7	2.8
750506	707	61.0	586	41	4.2	3.1
750515	603	50.6	481	27	1.4	6.6
750528	724	60.4	598	30	1.0	-
750612	779	18.0	180	15	1.3	-
750702	812	47.3	497	23	1.5	15.5
750710	783	45.2	457	12	3.9	27.1
750718	767	53.8	549	21	3.3	25.3
750730	666	37.0	348	22	3.2	20.2
750808	647	57.2	549	25	2.9	17.2
750820	588	58.0	516	17	0.4	20.1
750902	480	58.0	487	24	2.0	6.7
751022	194	27.8	178	-	3.4	-
751107	46	23.4	126	-	3.1	3.7
751218	51	4.4	22	-	0.9	-

Calculated annual primary production: 96 $gC\ m^{-2}$

Calculated annual secondary production: 7.0 $gC\ m^{-2}$

Table 5. Irradiation, measured production, calculated production, chlorophyll a, phytoplankton biomass and zooplankton biomass.

Station 3', 1975

Date	Irradiation $mWh\ cm^{-2}d^{-1}$	Measured production $mgC\ m^{-2}h^{-1}$ (0-20 m)	Calculated production $mgC\ m^{-2}d^{-1}$ (0-20 m)	Chlorophyll a $mg\ m^{-2}$ (0-15 m)	Phytoplankton biomass $g\ m^{-2}$ wwt (0-15 m)	Zooplankton biomass $g\ m^{-2}$ wwt (0-40 m)
750226	178	1.7	13	8	0.8	0.1
750318	355	11.9	89	24	6.0	-
750408	380	35.3	279	37	6.7	-
750422	413	41.6	358	78	31.7	-
750507	593	25.4	229	24	13.4	-
750526	747	19.5	189	21	8.4	1.6
750605	439	25.6	292	21	4.5	3.2
750618	732	16.9	194	15	1.8	4.7
750722	452	35.9	352	26	2.4	17.6
750902	414	51.4	452	47	7.9	20.9
750917	296	43.7	437	27	4.4	15.3
751001	199	33.0	224	36	2.1	19.4
751016	96	16.8	138	20	0.1	6.0
751111	12	2.5	16	19	0.8	4.3

Calculated annual primary production: 67 $gC\ m^{-2}$

Calculated annual secondary production: 8.5 $gC\ m^{-2}$

Table 8. The components of the phytoplankton biomass expressed as percentage of the total. The total values are given as g m^{-2} (wwt).

Station 1, 1975

Date	Blue-green algae	Diatoms	Dinoflagellates	Chrysophyceans	Green algae	Monads and flagellates	Total
	%	%	%	%	%	%	g m^{-2} wwt
750204	0	94	0	0	2	4	0.4
750228	2	57	22	0	0	19	0.4
750327	56	42	0	0	0	2	1.6
750417	0	99	0	1	0	0	10.9
750511	1	90	1	6	0	2	1.9
750618	75	5	5	0	7	8	2.6
750626	67	5	0	0	22	6	1.8
750702	64	4	5	19	4	4	2.4
750714	61	3	9	13	2	12	1.5
750807	10	38	8	0	0	44	1.0
750831	7	18	6	0	0	69	0.9
750922	0	5	41	0	0	54	0.8
751024	10	17	51	1	0	21	0.7
751112	1	47	33	0	0	20	0.8

Table 9. The components of the phytoplankton biomass expressed as percentage of the total. The total values are given as g m^{-2} (wwt).

Station 2, 1975

Date	Blue-green algae	Diatoms	Dinoflagellates	Chrysophyceans	Green algae	Monads and flagellates	Total
	%	%	%	%	%	%	g m^{-2} wwt
750109	0	92	0	0	3	5	0.9
750325	3	74	3	0	0	20	0.2
750417	0	93	4	0	0	3	2.7
750506	2	39	53	3	1	2	4.2
750515	6	8	72	8	0	6	1.4
750528	15	0	37	38	2	8	1.0
750612	2	21	60	2	4	11	1.3
750702	17	25	19	17	6	16	1.5
750710	41	11	26	15	3	4	3.9
750718	57	6	13	12	9	3	3.3
750730	62	19	9	4	2	4	3.2
750808	84	3	5	0	0	8	2.9
750820	24	15	0	0	0	61	0.4
750902	3	25	33	0	3	36	2.0
751022	3	77	17	0	0	3	3.4
751107	7	70	19	0	0	4	3.1
751218	9	79	5	0	0	7	0.9

Table 10. The components of the phytoplankton biomass expressed as percentage of the total. The total values are given as g m^{-2} (wwt).

Station 3', 1975

Date	Blue-green algae	Diatoms	Dinoflagellates	Chrysophyceans	Green algae	Monads and flagellates	Total
	%	%	%	%	%	%	g m^{-2} wwt
750226	5	7	34	0	0	54	0.8
750318	0	50	40	4	0	6	6.0
750408	0	59	36	0	0	5	6.7
750422	0	46	30	17	0	7	31.7
750507	0	25	67	0	0	8	13.4
750526	0	34	50	0	0	16	8.4
750605	3	49	26	3	0	19	4.5
750618	30	33	6	1	0	30	1.8
750722	47	1	14	16	6	16	2.4
750902	64	16	4	4	2	10	7.9
750917	22	19	23	22	0	14	4.4
751001	17	15	43	0	0	25	2.1
751016	55	12	9	0	0	23	0.1
751111	54	17	2	4	0	23	0.8

Fig. 1

THE INVESTIGATION AREA IN THE BALTIC

Station	Position	
1	N 55° 40'	E 15° 20'
2	N 57° 25'	E 19° 15'
3	N 59° 50'	E 19° 35'
3'	N 60° 20'	E 18° 50'
4	N 63° 25'	E 20° 20'

△ Ordinary solarimeter stations

□ SMHI -"- -"-

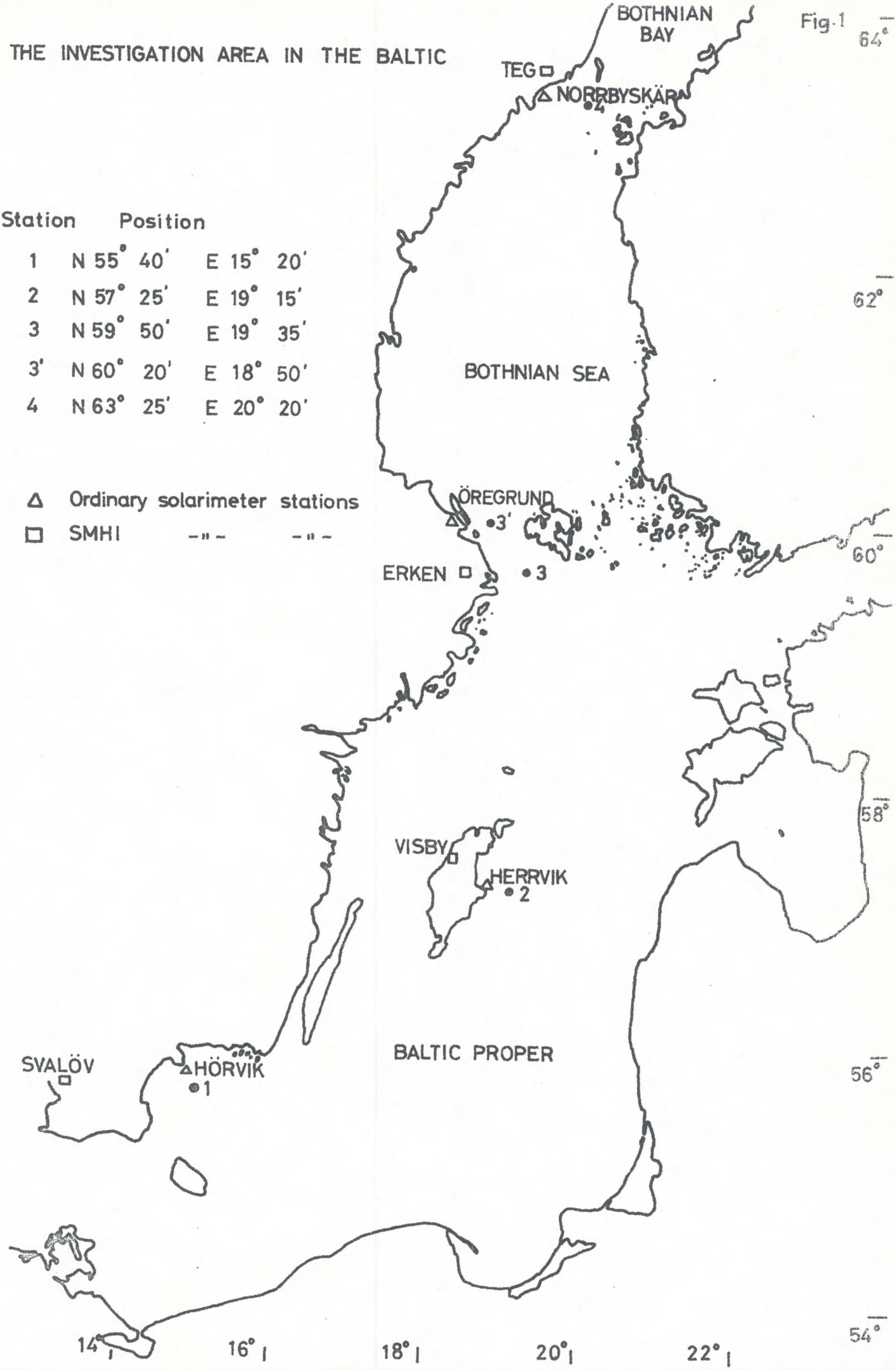
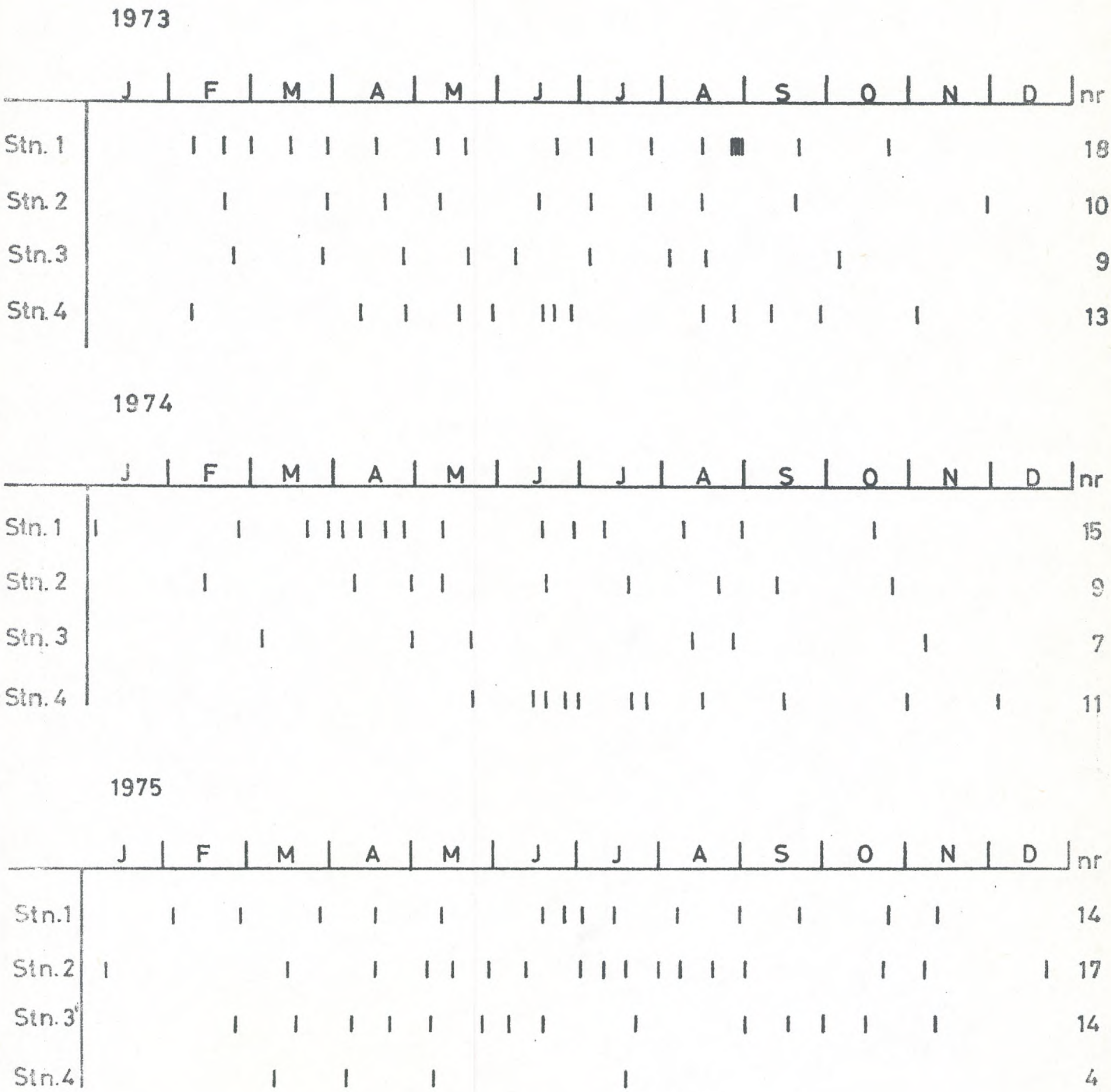
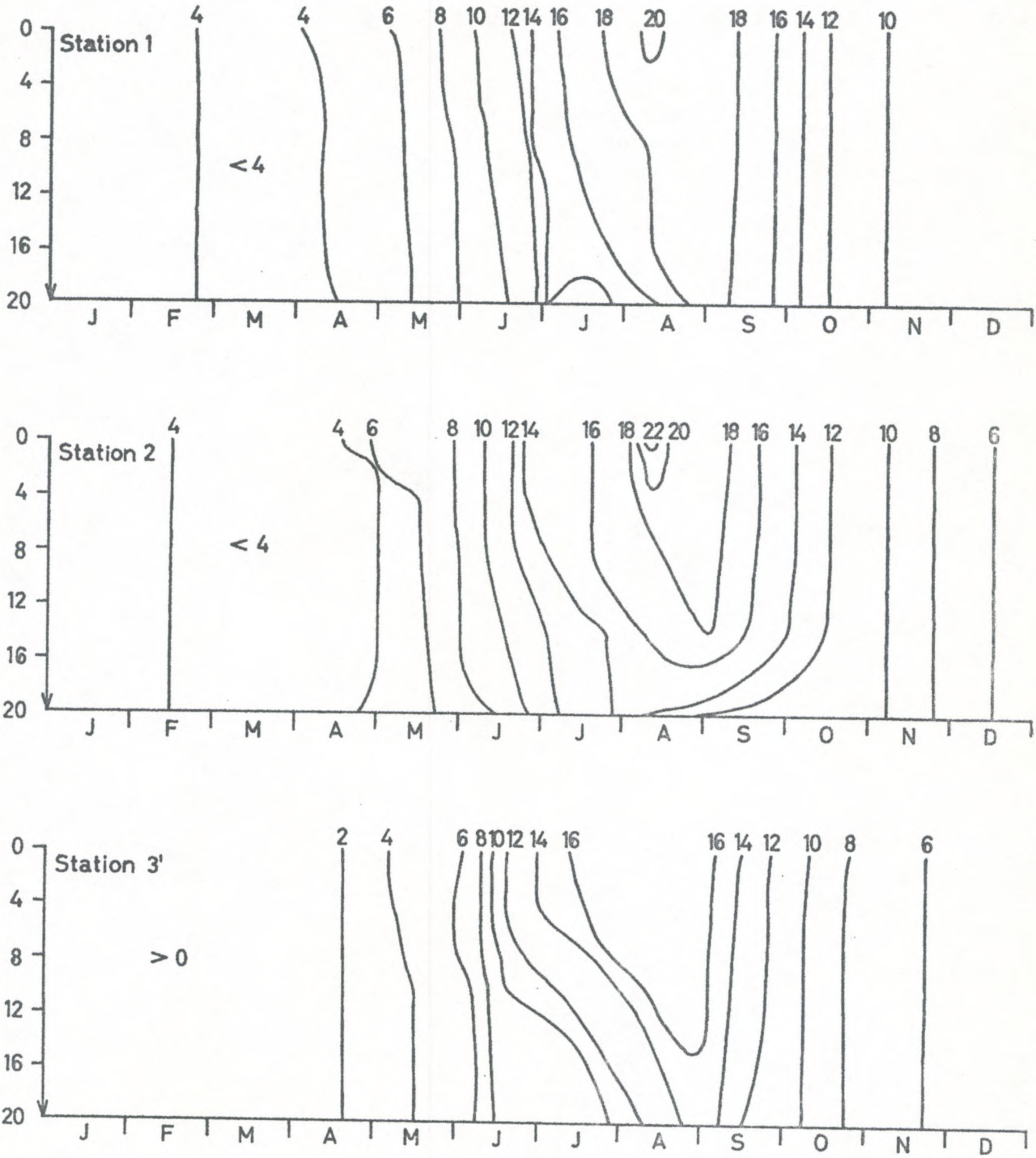


Fig.2

MEASUREMENTS CARRIED OUT IN 1973, 1974 AND 1975



TEMPERATURE (°C) 0-20 M IN THE BALTIC 1975 Fig. 3



IRRADIATION ON THE BALTIC IN 1975

Fig. 4

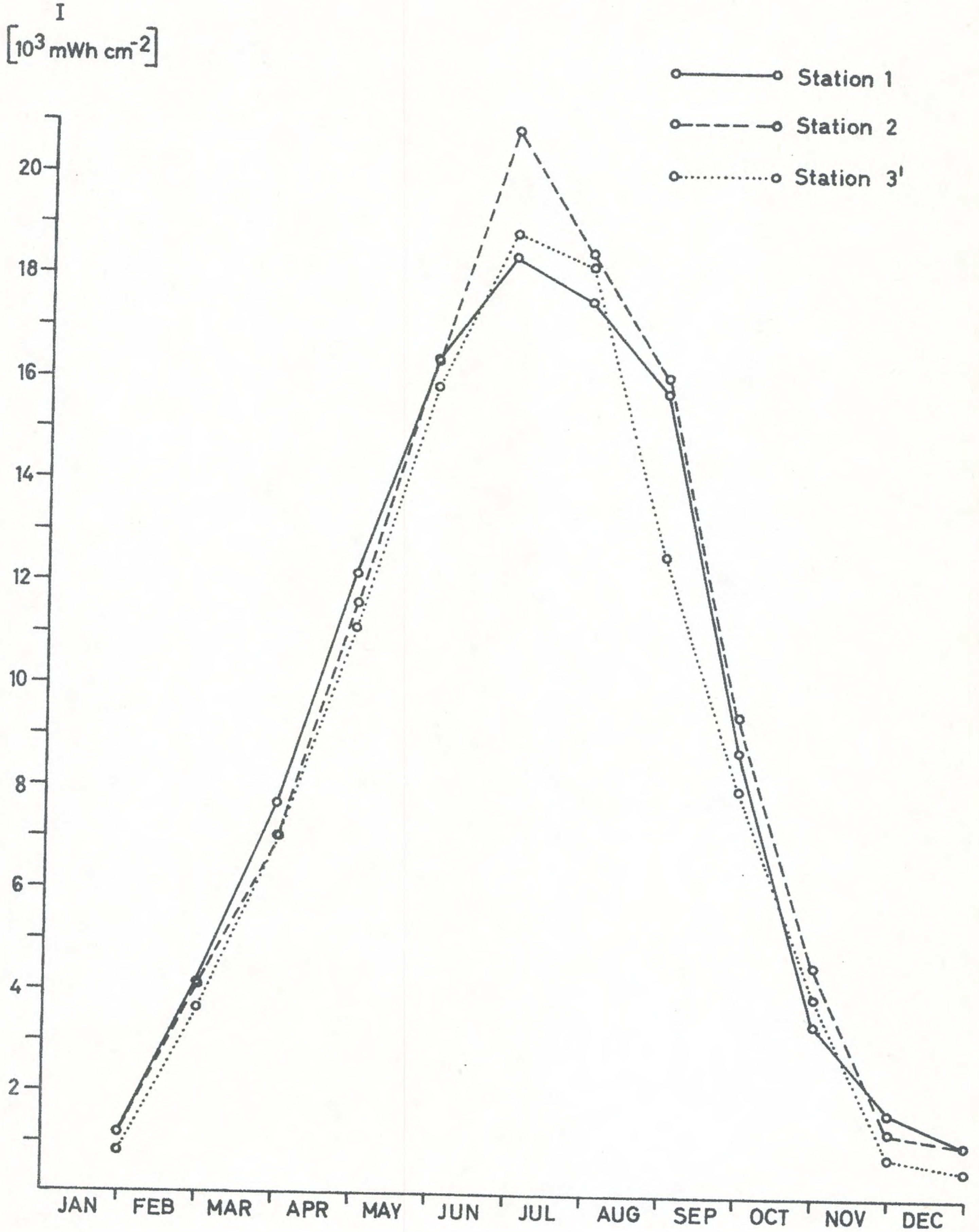


Fig. 5

PRIMARY PRODUCTION 0 -20 M IN THE BALTIC
1975

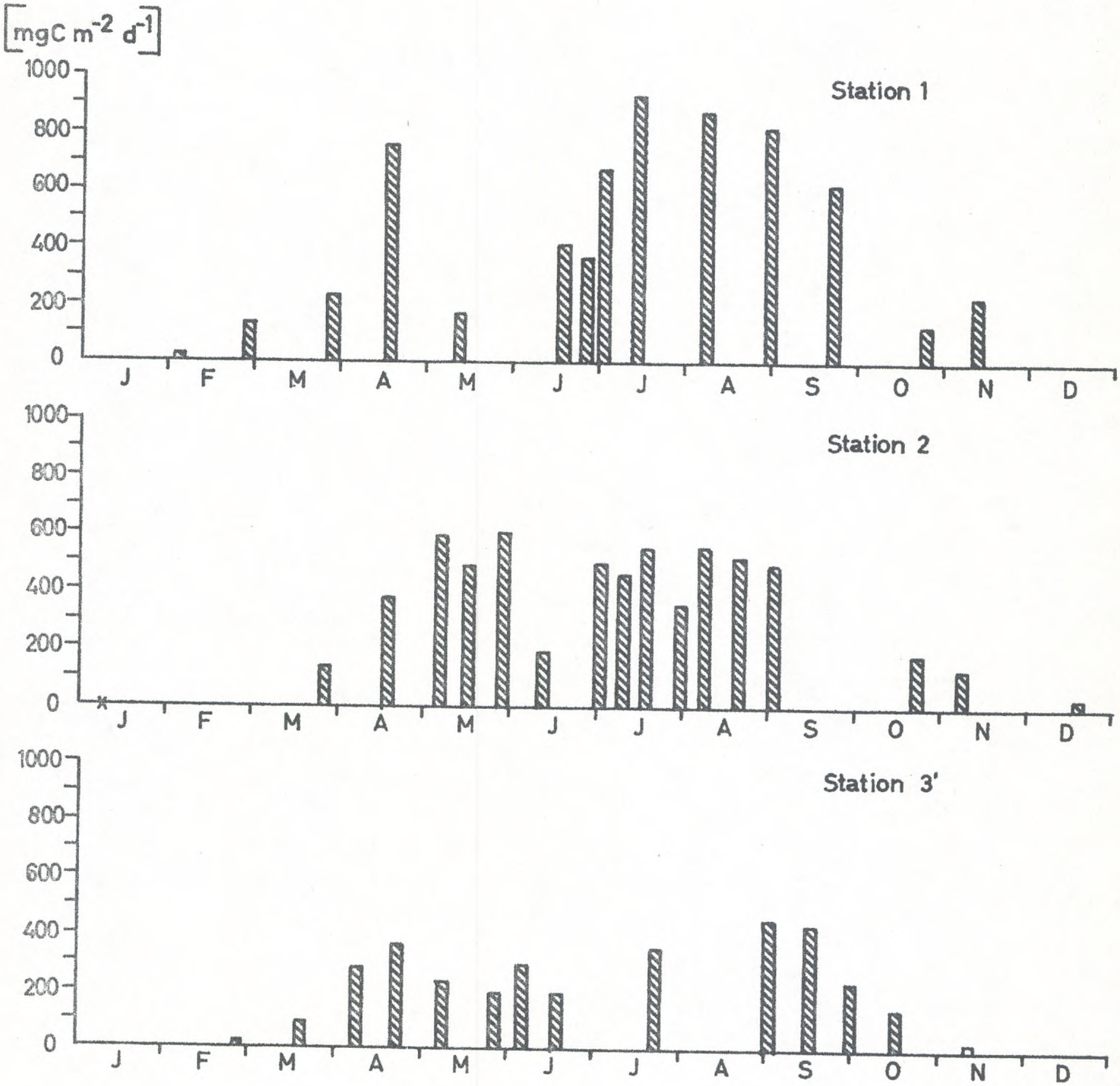
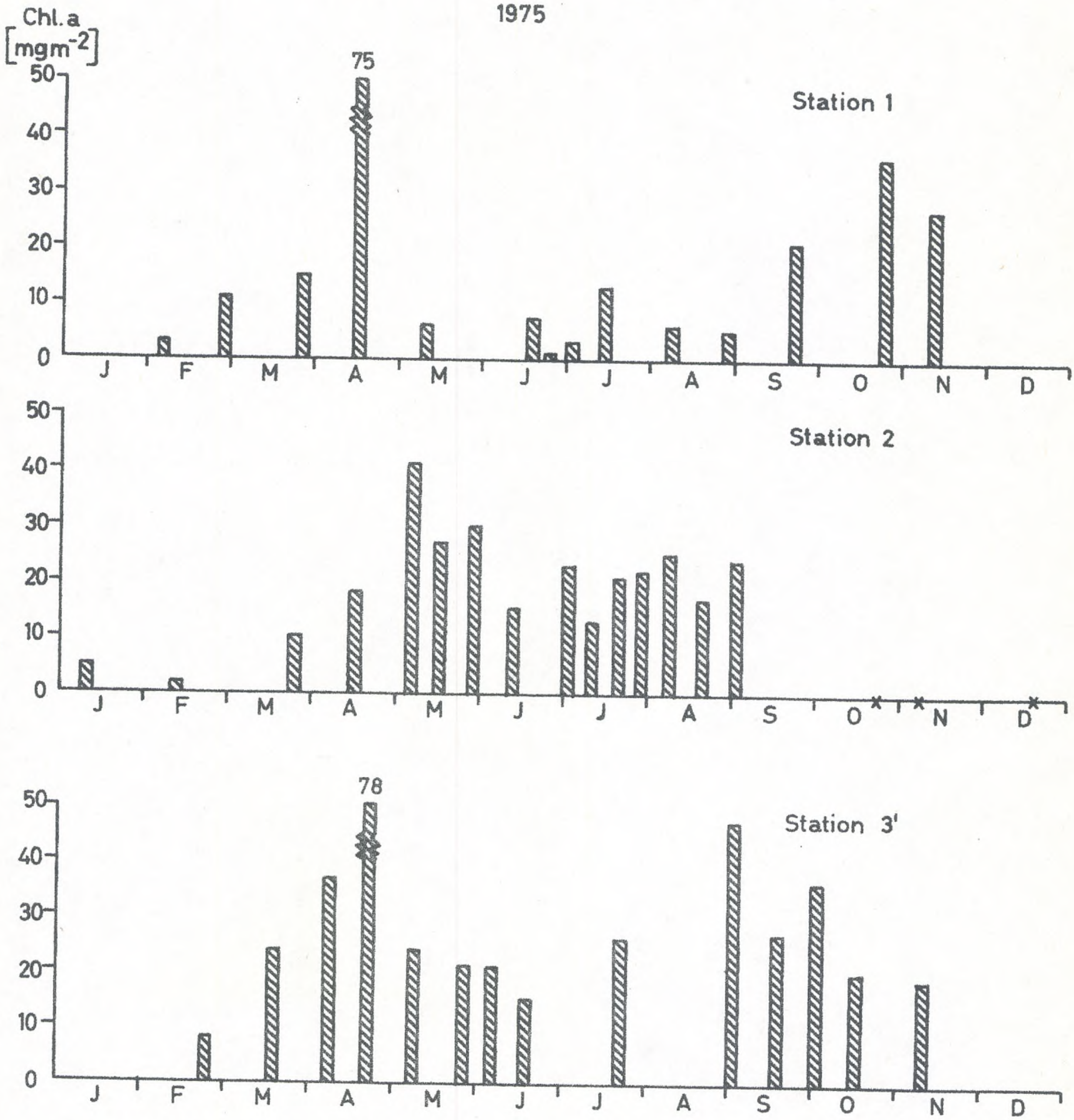


Fig. 6

CHLOROPHYLL a 0-15 M IN THE BALTIC

1975



x sample missing

PHYTOPLANKTON BIOMASS 0-15 M IN THE BALTIC 1975

Fig. 7

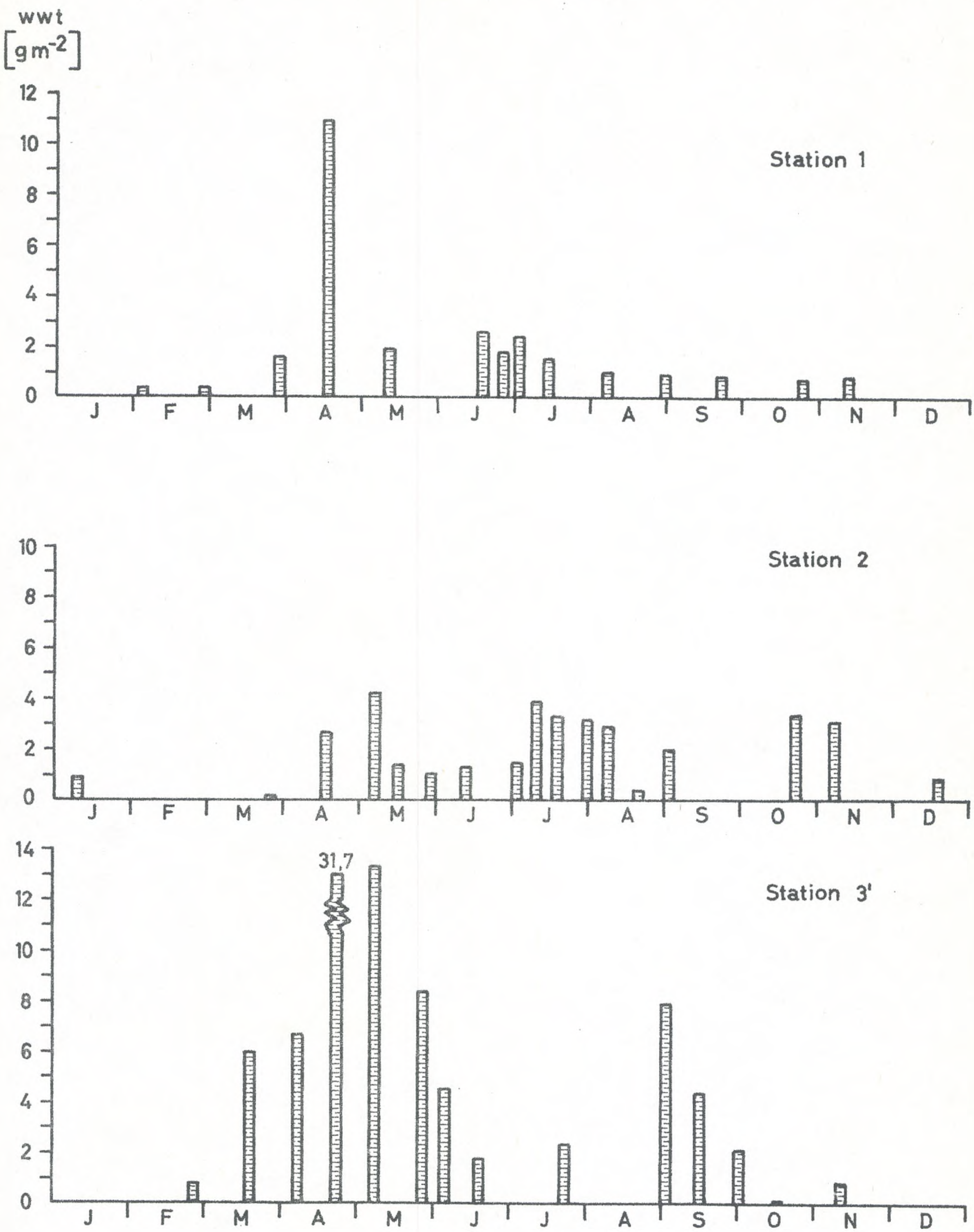


Fig. 8

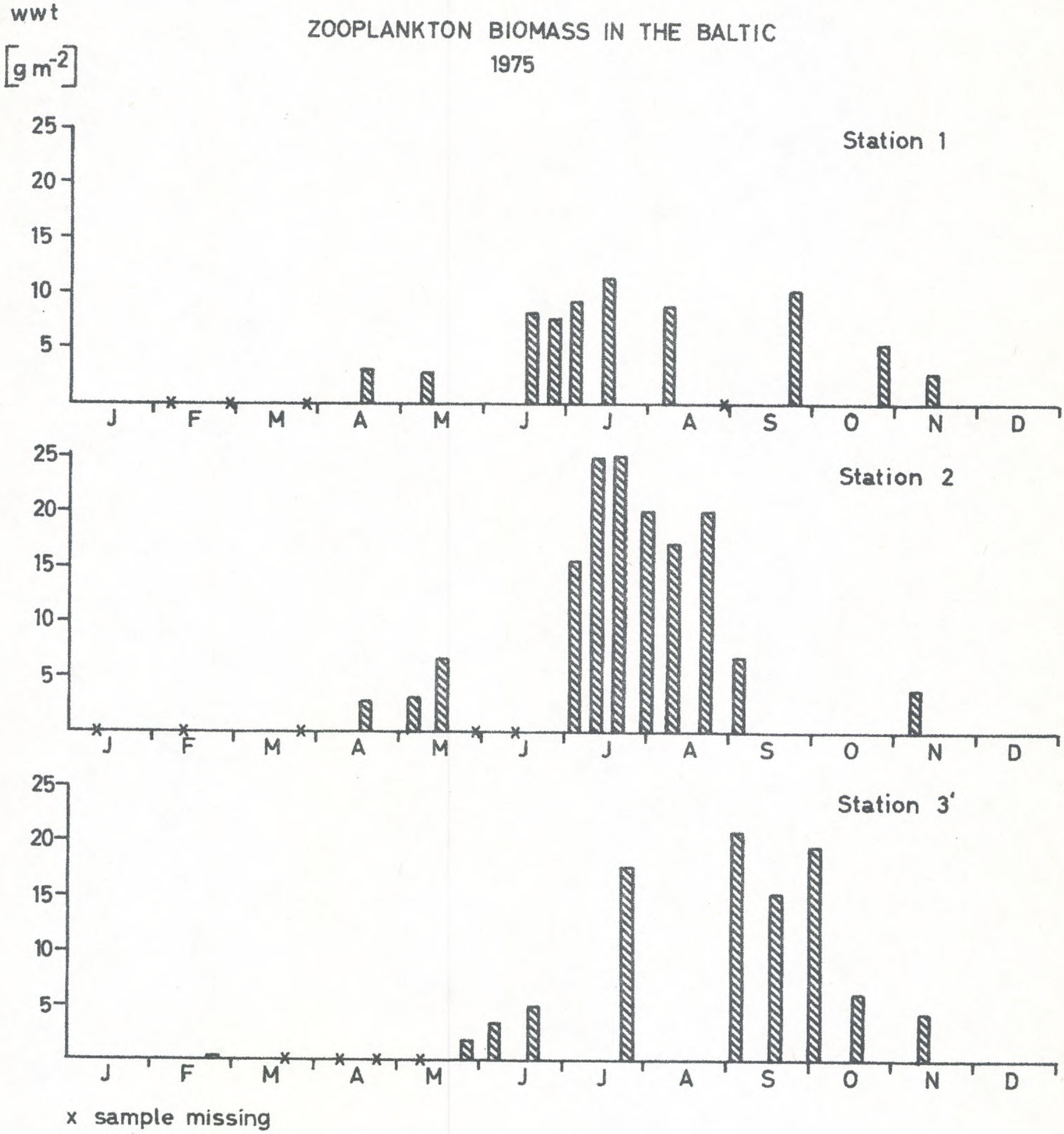

wwt
[g m-2]
ZOOPLANKTON BIOMASS IN THE BALTIC
1975
25
20
15
10
5
Station 1
J F M A M J J A S O N D
Station 2
J F M A M J J A S O N D
Station 3'
J F M A M J J A S O N D
x sample missing

Fig. 9

BIOMASS AND RELATIVE IMPORTANCE OF DIFFERENT SPECIES AT STATION 1

1975

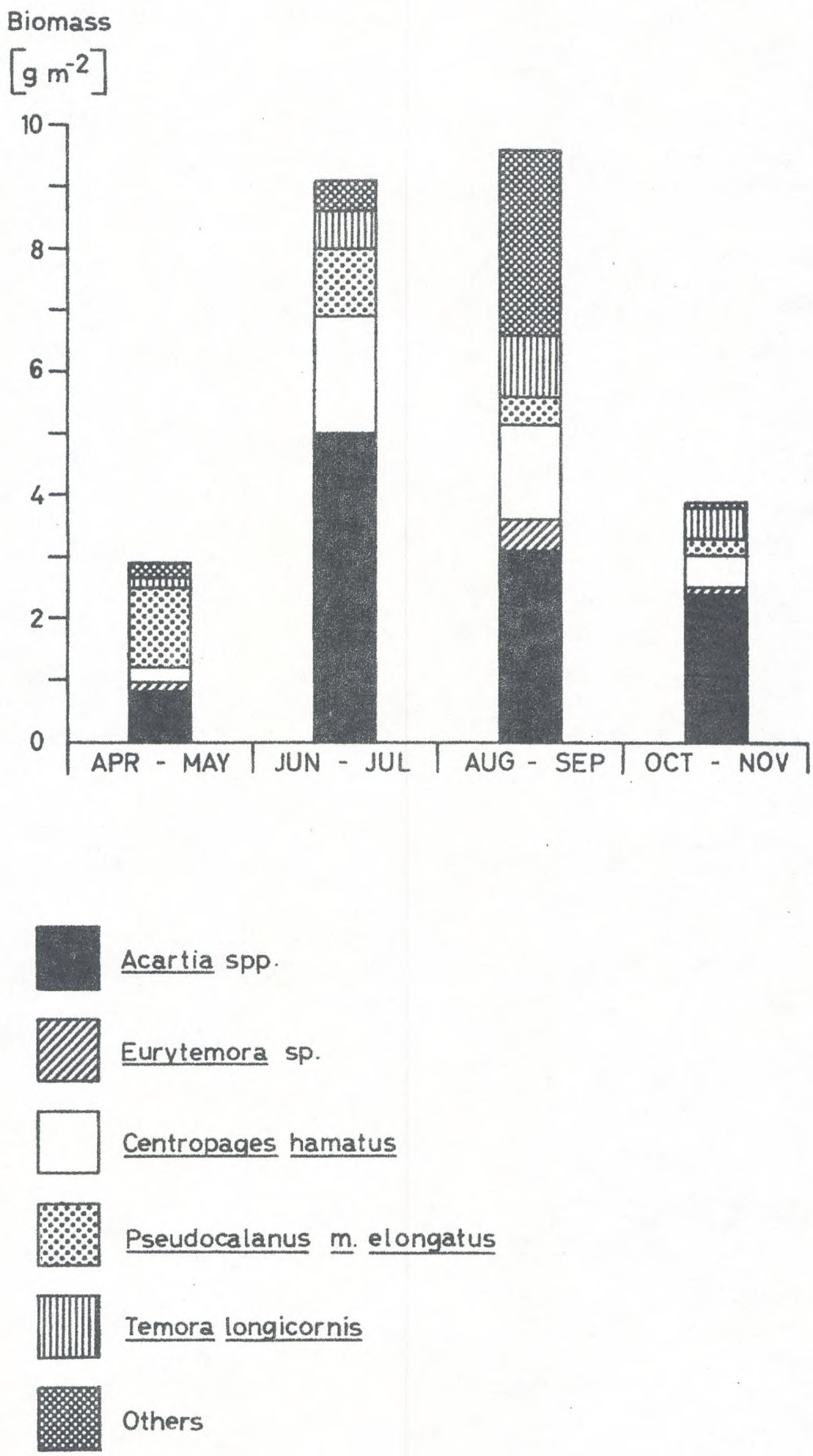
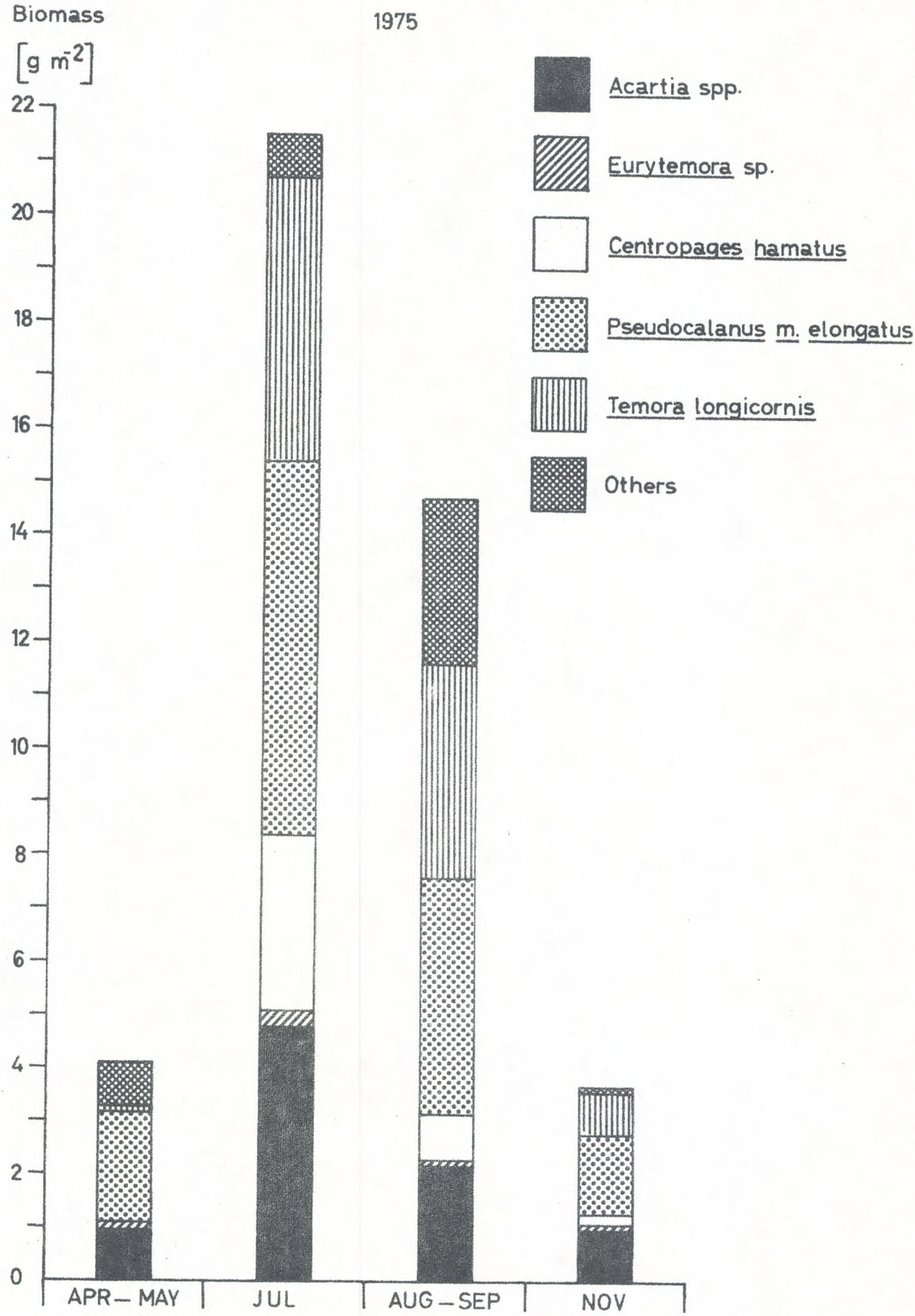


Fig. 10

BIOMASS AND RELATIVE IMPORTANCE OF DIFFERENT SPECIES AT STATION 2

1975



BIOMASS AND RELATIVE IMPORTANCE OF DIFFERENT SPECIES AT STATION 3

1975

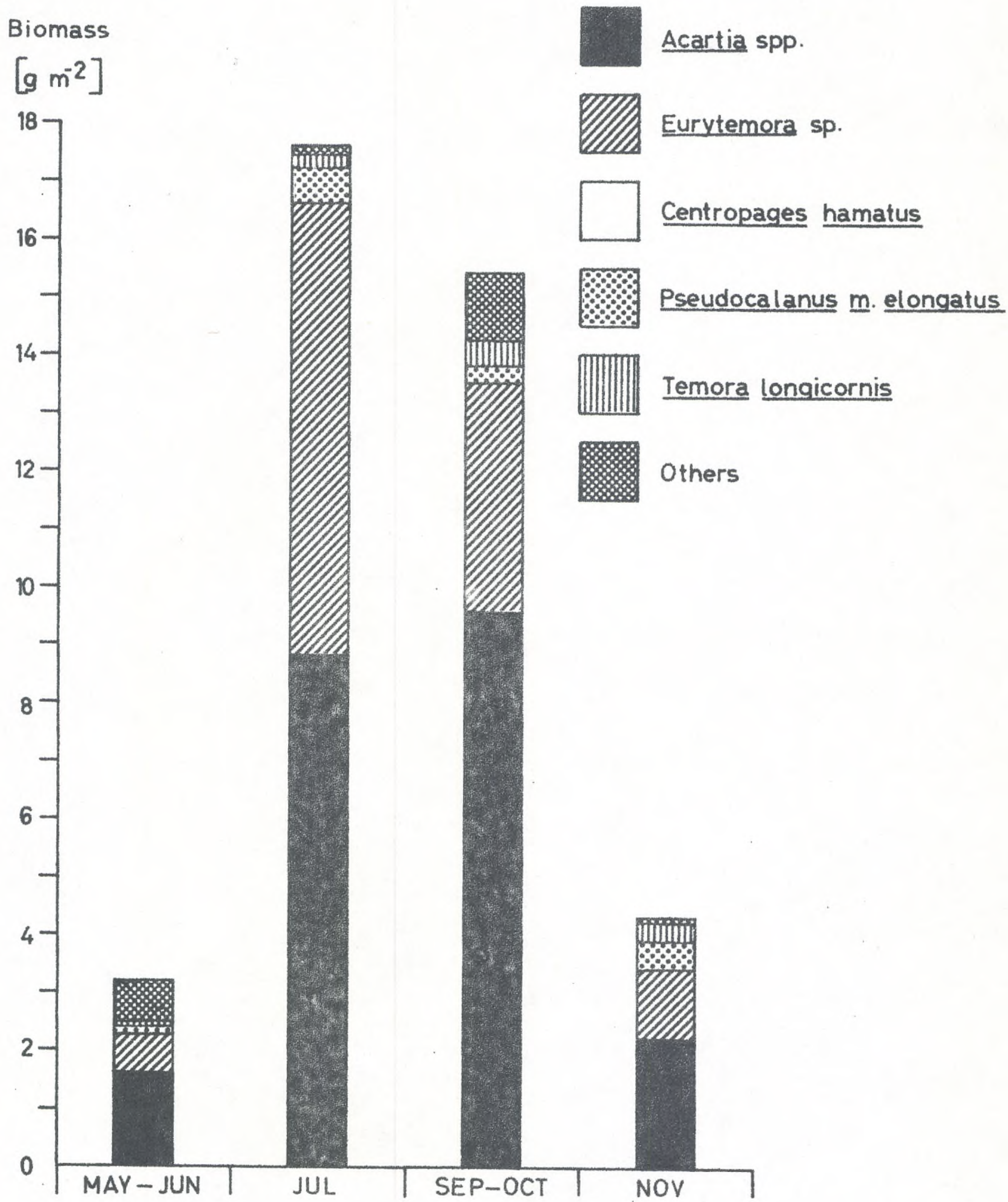
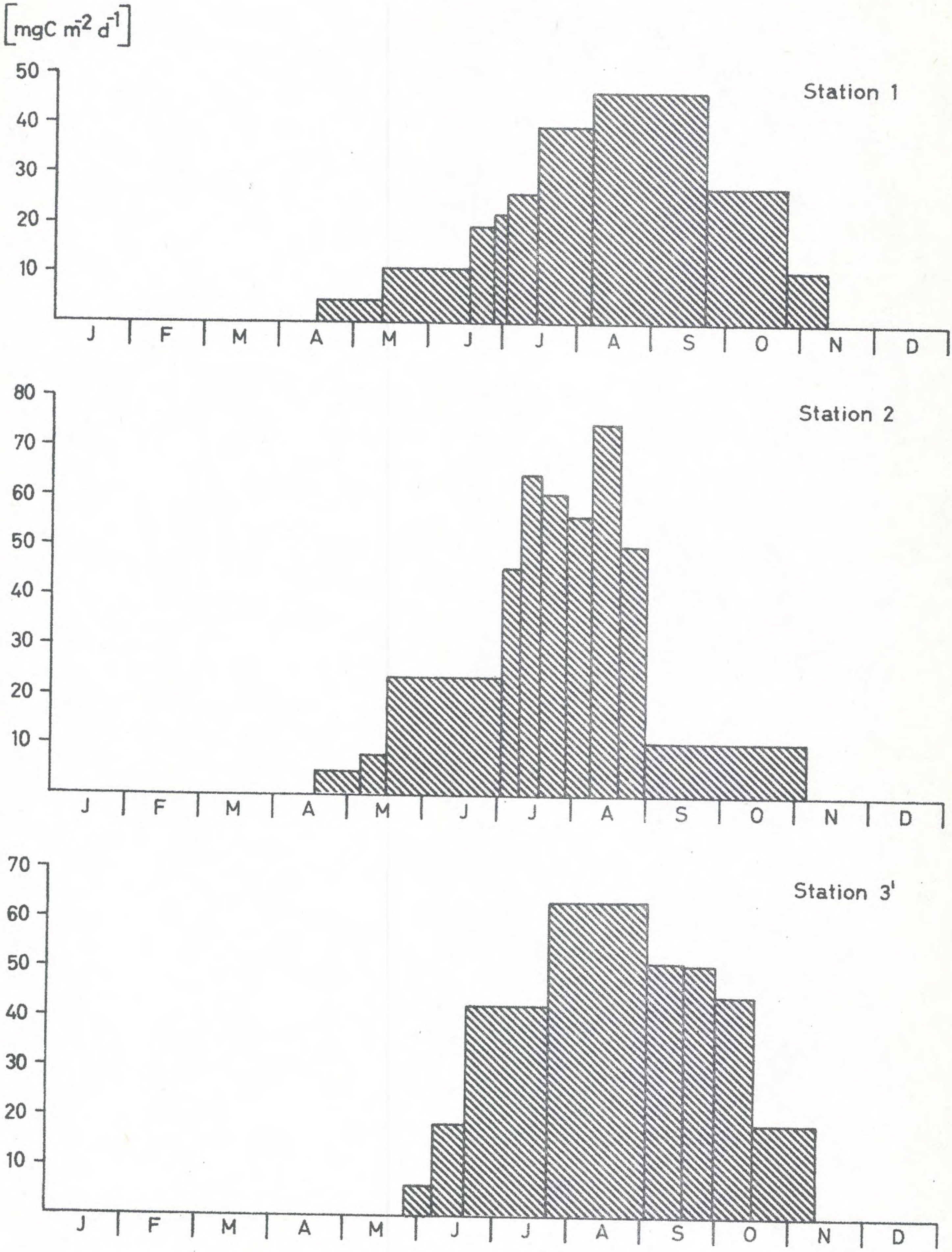


Fig. 12

ZOOPLANKTON PRODUCTION

1975



RELATIVE IMPORTANCE OF HERBIVORES, OMNIVORES AND CARNIVORES AT STATION 2

1975

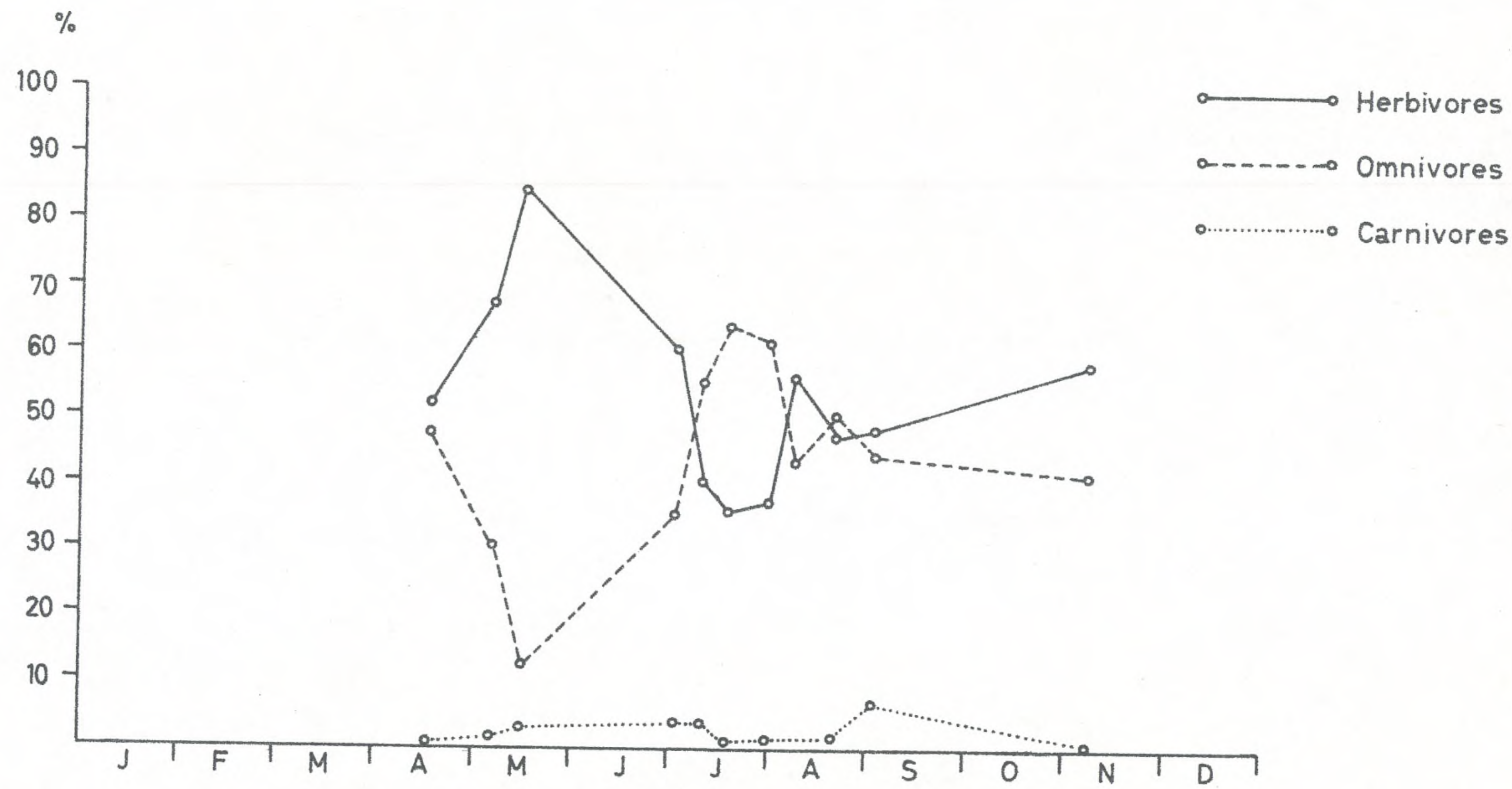


Fig. 13