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A long-term investigation of the fauna, its biology and ecology

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Contents

Abstract

This paper is based on the results from a long-term zooplankton investigation in the Baltic proper in the years 1968—1972. Additional results, obtained by the authors in more recent investigations, have also been used in order to enrich the material with information not obtained in the principal investigation.

Seven standard plankton stations, covering seven sub-areas of the Baltic proper have been visited on average four to five times per year. All cruises have been made in connection with ordinary hydrographical expeditions which means that all zooplankton samples are accompanied by a complete list of hydrographical data.

The paper describes the zooplankton fauna of the Baltic proper which comprises about 40 regularly appearing species excluding the microzooplankton. The main part of the fauna in respect of biomass and production consists, however, of only 10—12 species. The most important were the cnidarian *Aurelia aurita*, the rotifers *Synchaeta* spp., the cladocerans *Bosmina coregoni maritima* and *Evadne nordmanni*, the copepods *Pseudocalanus minutus elongatus*, *Temora longicornis*, *Acartia bifilosa, A. longiremis* and *Centropages hamatus* and the larvacean *Fritillaria borealis*.

Species of less importance were the larvae of *Pleurobrachia pileus*, the cladocerans *Podon intermedius*, *P. leuckarti* and *Pleopsis polyphemodides* (the latter is abundant in coastal areas), the copepods *Eurytemora* sp. and *Oithona similis*, the larvae of gastropod species, *Mytilus edulis*, *Macoma baltica*, *Cardium glaucum*, *C. hauniense* and *Mya arenaria*, the chaetognath *Sagitta elegans baltica* and the larvacean *Oikopleura dioica*.

Occaisonal species were the cnidarians *Sarsia tubulosa* and *Cyanea capillata*, the rotifers *Keratella quadrata quadrata, K. qu. platei, K. cruciformis eichwaldi* and *K. cochlearis recurvispina*, the larvae of *Pygospio elegans* and *Balanus improvisus*, the copepods *Calanus finmarchicus*, *Limnocalanus macrurus* and *Cyclops* sp., the mysidaceans *Mysis relicta* and *M. mixta*, the amphipod *Hyperia galba* and the chaetognath *Sagitta setosa*.

All samples have been collected by vertical, fractionated hauls with a Nansen net. The mesh size was 0.160 mm in the years 1968—1971 and 0.090 mm in 1972. A correction of all results due to the poor filtering capacity of the Nansen net has been made. The additional results are mainly based on samples from the UNESCO WP 2 net.

All specimens have been analysed to species and the copepods also to developmental stages. The biomass has been calculated as the sum of all individual volumes.

The paper also describes the hydrography of the Baltic proper in general and presents the data for temperature, salinity and oxygen in the years 1968—1972. The relationship between the unique hydrography of the Baltic with its stable, brackish water contidions and the planktonfauna is discussed.

The regulating factors for the vertical and horizontal distribution of the fauna were found to be either temperature or salinity or a combination of these factors.

The seasonal variation in biomass values showed a rather good correlation with the temperature of the surface layer viz. the lowest biomass values (< 10 g m^{-2}) were usually found in March—April, an increase started in May—June and a maximum (30—60 g m^{-2}) was most often reached in August—September. There were great variations in biomass between the seven stations. The highest mean values (20—25 g m^{-2}) were found in the southern and south-eastern parts of the Baltic proper and the lowest (12—13 g m^{-2}) in the northern and south-western parts. Looking at the biomass values over the whole period of investigation, a remarkable stability has been found. There is no evidence of either increasing or decreasing trend.

The production of zooplankton has also been estimated. According to our calculations the production amounts to about 20 gC m^{-2} $year^{-1}$ (380 g wwt) in the southern Baltic proper and 10 gC m^{-2} $year^{-1}$ (190 g wwt) in the northern part.

The last part of the paper discusses the role of zooplankton in the energy flow of the whole pelagic ecosystem, i.e. from primary phytoplankton production to reproduction and recruitment of pelagic fishes.

Introduction

The Baltic, which is the largest brackish water area in the world, with stable salinity conditions, does, in many respects, provide rather unique conditions for its fauna and flora. The Baltic is influenced on one hand by the freshwater discharged from the rivers, and on the other hand by the inflow of salt water from the ocean entering through the Danish sounds. Due to the different density of these water masses a two-layer situation occurs, concisting of a light surface layer with very low salinity and a heavier deep layer with a higher salinity. A schematic picture of these layers is illustrated in fig. 1.

An ecological zooplankton investigation was started in this area in 1968 in order to follow the yearly fluctuations of the fauna in off-shore conditions. Later, the biomass and production studies came into focus. From 1972 onwards, both primary and secondary production were studied. A new, very comprehensive sampling program for secondary zooplankton production studies was started in 1975 in conjunction with primary production studies.

The present paper includes the results from a sampling program covering seven standard plankton stations, which were visited two to seven times a year from 1968 until 1972 (fig. 2). The paper also includes information from the sampling of a transsect between Gotland and the mainland of Sweden in 1972—1973 as well as results from dense sampling at two stations in the Baltic proper and one station in The Åland Sea in 1975—1976 (fig. 2). Preliminary results from the standard stations have been published previously (Ackefors & Hernroth 1970 a, b, 1971, 1973, 1975).

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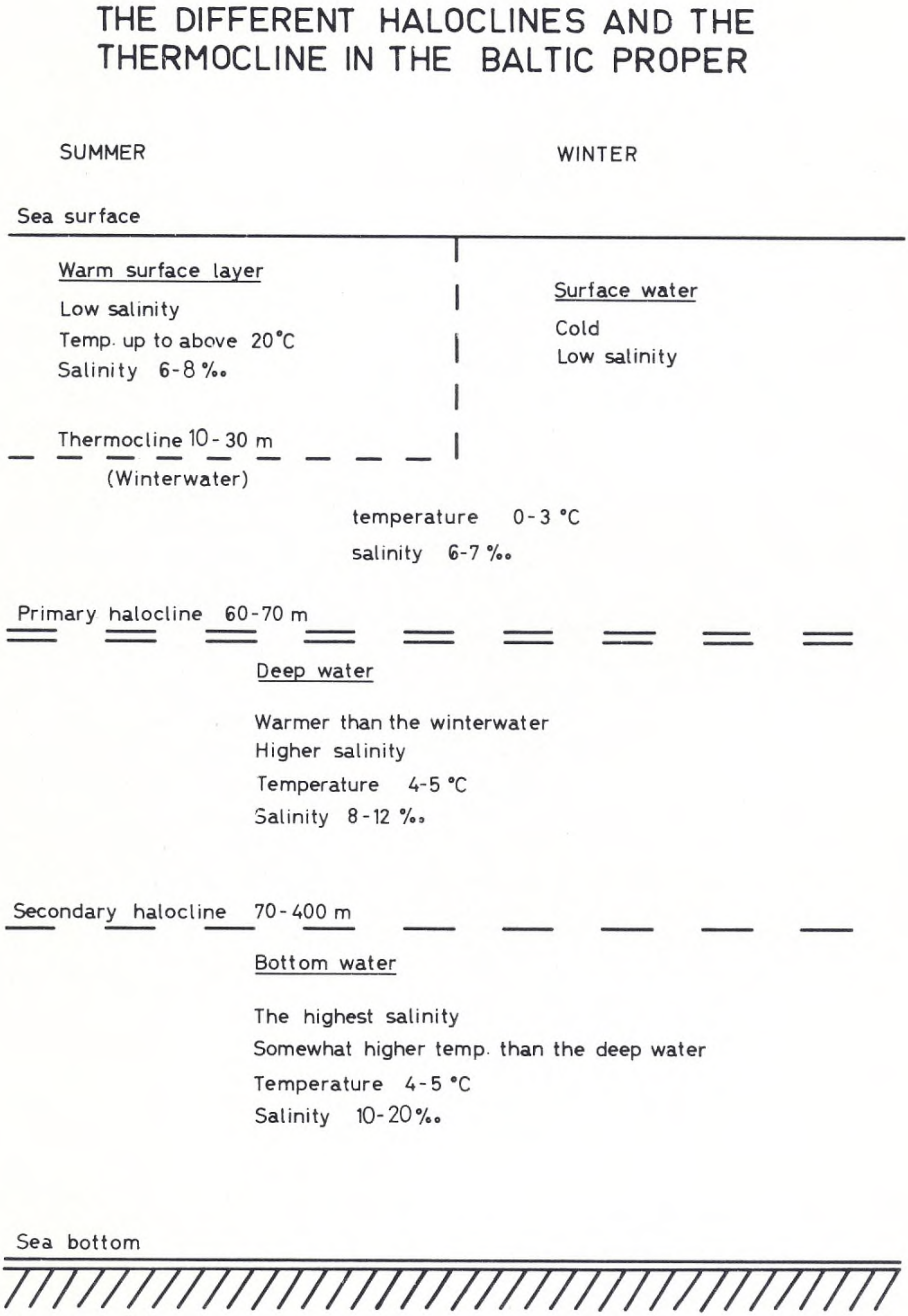

Fig. 1. The different water layers and pycnoclines in the Baltic proper. Slightly modified after Fonselius 1970.

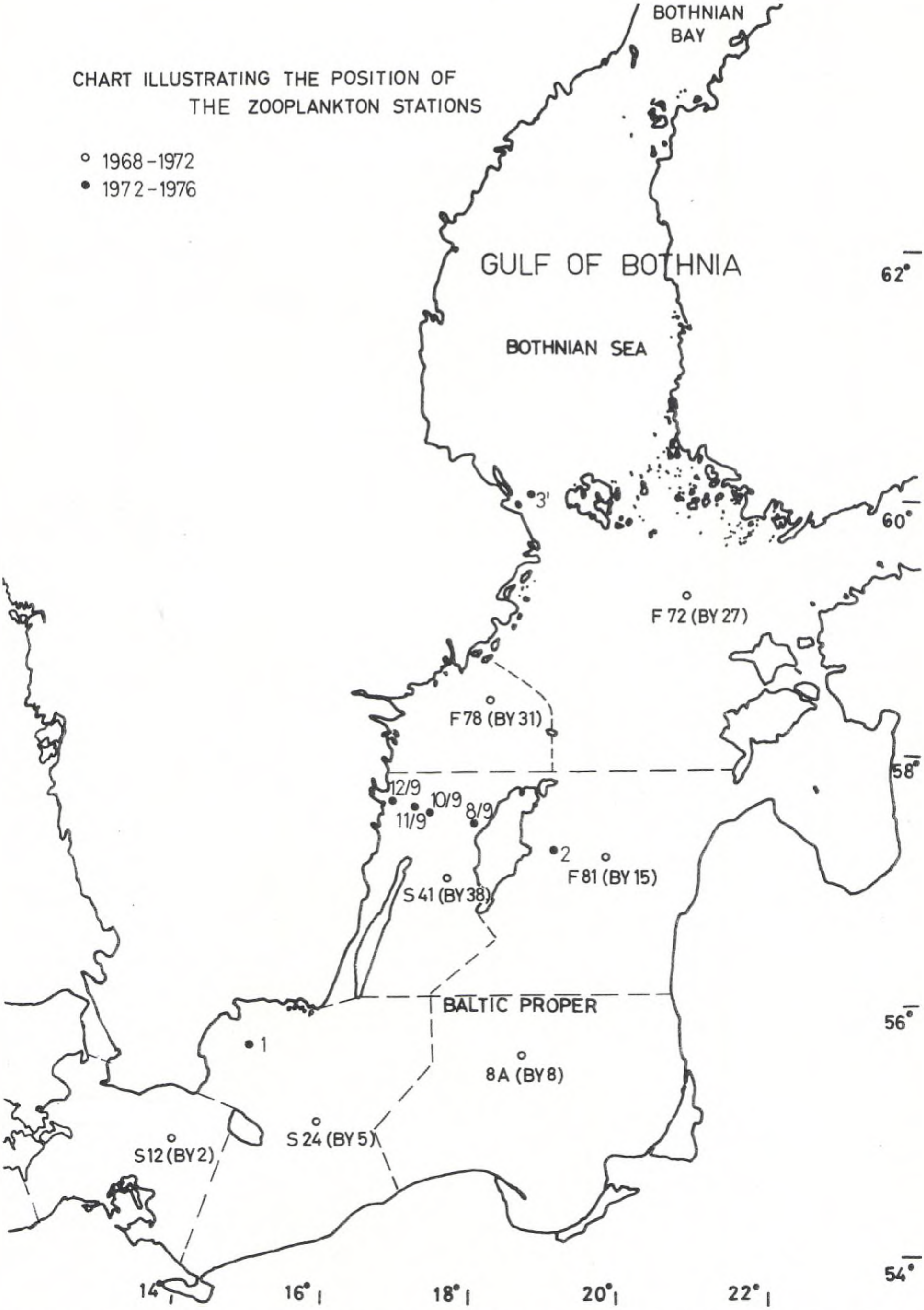

Fig. 2. Chart illustrating the position of seven standard zooplankton stations where sampling was performed 1968—1972. At the transsect (8/9—12/9) sampling was performed in 1972—1973 and at the other stations in 1975—1976.

Material and methods

This investigation has covered the Baltic proper including the Åland Sea (fig. 2). Due to differences in hydrography the Baltic proper can be divided into seven sub-areas (cf. Ackefors 1969 a), and for this investigation one plankton station was chosen in each of the seven areas. These stations are a part of the net of standard stations used by hydrographers since the beginning of this century.

During the period of investigation, 1968—1972, three to seven expeditions per year have been carried out on board the research vessels of the Fishery Board of Sweden.

Due to the difficulties involved in visiting off-shore stations frequently, gaps in the sampling have been inevitable. In order to compensate for this, the results from two more recent plankton investigations in the Baltic have to some extent been used.

The first investigation is one that was carried out in 1972—1973 along a transsect between the Island of Gotland and the Swedish mainland (stations 8/9—12/9), and the other investigation referred to is a large scale pelagic study, carried out at three off-shore stations (stations 1–3′) in the years 1975–1976. The latter stations were in some cases visited as often as 22 times per year.

The topography and hydrography of the Baltic proper have been dealt with by many authors, e.g. Fonselius (1962), Ackefors (1969 a). Therefore, only a very brief description will follow in this paper.

The Baltic proper can be characterized as a very large estuary which covers an area of 200,000 km². The area is shallow and the mean depth is about 60 m. In each of the seven subareas there are deep areas. The greatest depths are the Landsort Deep F78 (459 m) and the Gotland Deep F81 (249 m). The depths are connected by furrows along the bottom. Saline, heavy water can flow from west to east and then to the north along these furrows.

The hydrography is greatly influenced by the inflow of salt water from the Belts over the sill of Darss (18 m) at the entrance to the Baltic proper. The area is also influenced by the discharge of freshwater, mainly originating from the rivers entering the Gulf of Bothnia (north of the Baltic proper). The stable brackish water of 6—8‰ at the surface is characteristic for the area (fig. 1). The salinity increases only slightly towards the bottom. The halocline is located at approximately 40 m depth in the Arkona Sea and between 60 and 80 m depth in the rest of the Baltic proper. The bottom salinity below the secondary halocline is about 15—20‰ in the Arkona and Bornholm Basins and 10—12‰ in the other areas.

The oxygen conditions deteriorate very rapidly below the halocline. The oxygen concentration is less than 1—2 ml O_2/1 in many parts of the Baltic proper.

In the deep basins hydrogen sulphide develops now and then and the duration of these periods is dependent on the intervals between inflows of heavy saline water entering the Baltic through the Belts. This heavy, oxygen-rich water alters the conditions by forcing the hydrogen sulphide out of the basins.

In winter the temperature is low (0—3°C) and rather homogenous down towards the halocline (fig. 1). With increasing temperature in May—June a thermocline develops. This thermocline is normally very pronounced in the summer at a level between 10 and 30 m depth. The surface temperature reaches a maximum (16—20°C) in August. During autumn the surface temperature decreases, reaching 6—8° by the end of November.

Hydrographical measurements were made every 5 m down to the 20 m level and then every 10 m down to 100 m. From 100 m, normally every 25 m down to the bottom were investigated. The methods used have been described by e.g. Fonselius (1967). At the standard stations, temperature, salinity, oxygen, hydrogen sulphide, pH, nutrient salts, iron, silicium etc. were measured, and at the other stations only temperature, salinity and pH were measured.

Zooplankton samples were taken with Nansen nets with a diameter of 50 cm. The mesh size 0.16 mm was used 1968—1971 and 0.09 mm was used in 1972. In recent years we have used Unesco WP2-net with a mesh size of 0.09 mm (Unesco, 1968).

A comprehensive comparison between the two nets during all seasons was made in 1974—1975. The results from those investigations indicated that the efficiency of the Nansen net was only about 50 % (Hernroth, 1978). All the results in this paper have therefore been recalculated in order to make all of our investigations comparable. From 1976 we used only WP2-nets according to the agreements between the Baltic Marine Biologists. Recommendations for methods of zooplankton sampling and analyses were published in 1976 by Dybern *et al.*

The plankton samples were usually taken with fractionated hauls at the standard depths 25—0 m, 50—25 m, 100—50 m, 150—100 m, 200—150 m, 300—200 m and 400—300 m. Many samples were also taken according to hydrographical conditions, i.e. from the thermocline to the surface, from the halocline to the thermocline and from the bottom to the halocline.

The standard stations were sampled 2—7 times a year. Stations 1—3′ were sampled 9—22 times a year and the transsect (8/9—12/9) 8—10 times a year.

The samples were preserved in 4 % formalin. They were later subsampled with the modified whirling apparatus designed by Kott (1953). Most of the specimens were determined to species and the copepods to developmental stage. The biomass was calculated by using the individual volume method. The volume of each species and developmental stage has been determined earlier (Ackefors 1972). The density of zooplankton was considered to be 1 g cm^{-3} and the values could thus be converted into g wet weight (wwt). The medusae and all other macrozooplankton were excluded in the biomass calculations (cf. discussion p. 52).

Results

Hydrography

Temperature

As is obvious from fig. 3 the surface temperature in the Baltic proper follows a rather constant seasonal rhythm. There is a large difference between the minimum values in winter (0—2°C) and the maximum values in summer (20—22°C), but the general annual pattern is obviously very similar from one year to another. However, small differences were apparent from year to year and those differences may have been of biological significance. There was also a slight difference between the southern and the northern areas.

The water masses below the halocline were, on the contrary, not at all subject to such seasonal variations. Here the temperature conditions were very similar throughout the year. The seasonal changes in temperature and the location of the different thermoclines and haloclines in the Baltic proper are illustrated in fig. 1 (Fonselius 1970).

From fig. 3 it is obvious that the surface temperature was, in general, less than 4°C during January—April with minimum values (0—2°C) in March—April in the southern area and in February—April in the northern area. The temperature was rather homogenous down to the halocline and was 4—6°C below the halocline. There was a slight increase towards the bottom with maximum temperatures close to the bottom.

In late April or early May the temperature began to increase, and by June the surface temperature had reached 10—16°C. However, below depths of 5—10 m the water temperature was very low. At the most northerly station (F 72), the surface temperature did not rise to more than 6—8°C.

In the period July—September the surface water was comparatively warm, with temperatures above 15—16°C. A very pronounced thermocline had developed at a depth of 15—20 m. Below this level the water was usually very cold, or 2—4°C down to the halocline.

With decreasing temperatures in the surface water during autumn and due to convection, a rather homogenous temperature of 9—12°C was found down to a depth of 30—40 m. The temperature usually remained higher in the southern area than in the northern area. By the beginning of December the temperature had decreased to 4—7°C.

In general, there were small temperature variations from year to year. However, the minimum winter temperatures in 1969—1970 were slightly lower and the

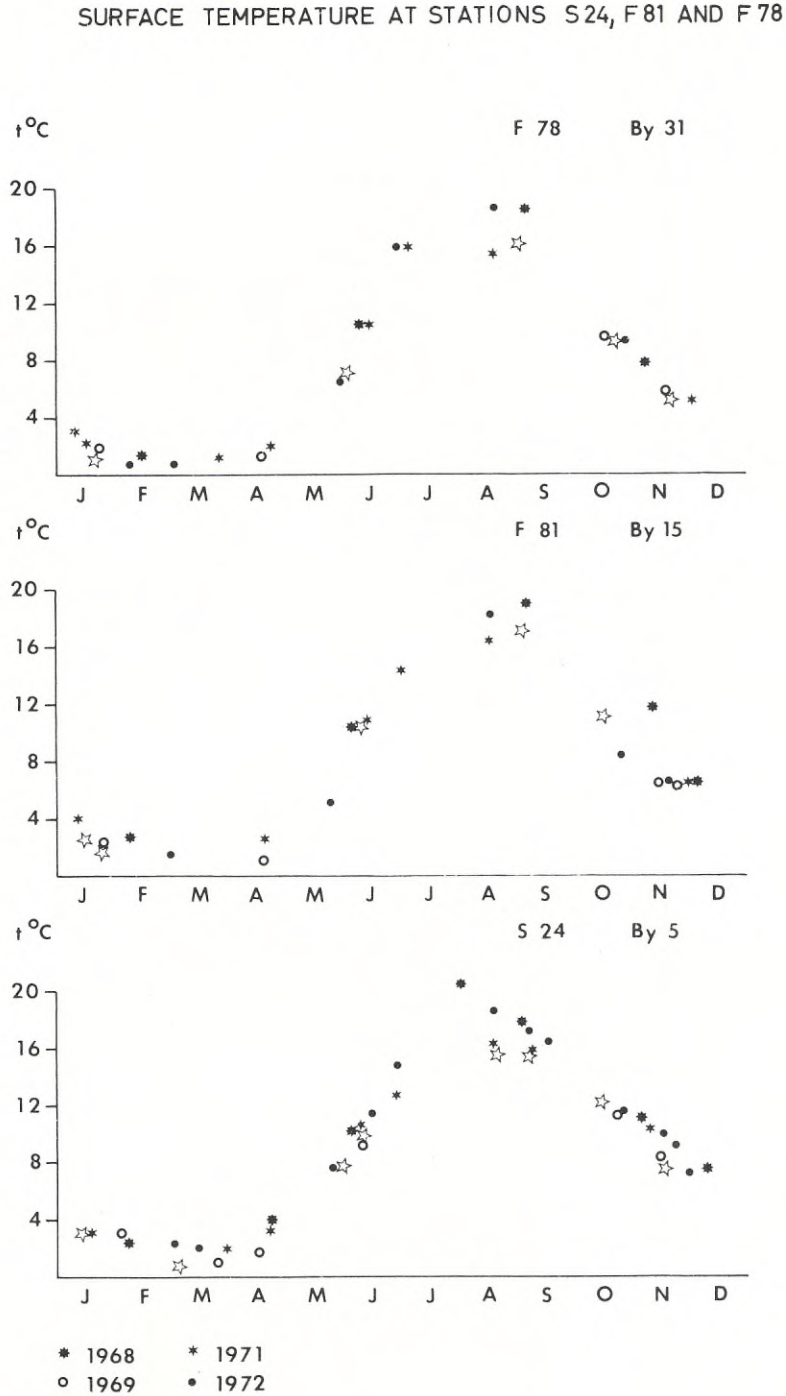

Fig. 3. Surface temperatures compiled for the various sampling occasions 1968—1972.

maximum summer temperatures in 1968 and 1972 were higher than in other years. There were obvious differences between the northern station F 72 and the southern stations. The minimum temperatures during the winters were less pronounced and the maximum temperatures during the summers more pronounced the more southerly the station.

Salinity

The surface salinity varied between 6 and 8 ‰, with the highest salinity in the Arkona Sea (S 12). The yearly fluctuation was about 1 ‰. From the surface to the halocline the salinity increased by 1—2 ‰. The halocline was found at a depth of 50—60 m in the Bornholm Sea (S 24) and at 60—70 m in the northern area. In the Arkona Sea the halocline was found at different depths from 15 m down to 40 m. Below the halocline, the salinity increased slightly near the bottom. In the Arkona and Bornholm Deeps the salinity fluctuated between 15 and 18 ‰. In the Gotland Deep (F 81) the salinity was about 13 ‰ and in the Landsort Deep (F 78) about 11 ‰. The salt-water inflows greatly influenced the bottom water in the deep basins (fig. 4b). However, only in the southern area was there an obvious increase in the salinity after an inflow. Both in 1968/1969 and in 1972 the salinity increase was about 2 ‰ in the Bornholm Basin.

Oxygen

The oxygen conditions from the surface down to the halocline were good, but below the halocline the oxygen concentrations decreased greatly. In the central and northern areas the oxygen concentration was less than 2 ml O_2 per liter. In the deep basins hydrogen sulphide was occasionally present in the bottom water (fig. 4b).

In the Arkona Basin (S 12), with a greatest depth of 48 m, the oxygen conditions were generally quite good (fig. 4a). In the Bornholm Basin (S 24), with greater depths, periods of very low oxygen concentrations alternated with periods of rather good conditions. In the latter part of 1968 hydrogen sulphide developed. A saline inflow at the end of the year changed the conditions conspicously. The salinity increased from 14.8 ‰ to 17 ‰ and the hydrogen sulphide was replaced by oxygen-rich water. In April 1969, the oxygen concentration was higher than 6 ml O_2 per liter. From then until the end of 1971, the oxygen concentrations and salinity decreased slowly, and finally, hydrogen sylphide developed again. This inflow has been described in detail by several authors, e.g. Fonselius (1970). A sudden inflow of bottom water changed the conditions in the beginning of 1972 and the oxygen concentration in the bottom water increased to about 6 ml O_2 per liter.

The oxygen concentrations in the other deep basins were also influenced by the inflows of salt water. The heavy saline water flows along the bottom from one basin to another and especially influenced are the areas south and east of Gotland. These areas might also be influenced by the flow of less saline water which glides over the heavy saline water in the Bornholm Deep (S 24). At station 8 A the differences in oxygen concentration were not so conspicuous, although it was quite obvious that the bottom water was greatly influenced by the inflow of salt water in 1969 and in 1972, which forced the old bottom water out of the basin. This was especially obvious on the two sampling occasions in 1972, when the oxygen concentration was higher in the bottom water than in water from a depth of 80 m. The concentration at that level was less than 1 ml O_2 per liter (Anon. 1969 a–1975 c).

The saline inflows in 1968 and in 1972 also influenced the bottom water in the Gotland Deep (F 81), although much later than in the Bornholm Deep (S 24). Sometime between April and November 1969 the bottom water was oxygenated (Nehring *et al.* 1971). In August 1972, the change had just begun. At that time the oxygen concentration was only 0.04 ml O_2 per liter. There was thus a time-lag of five months between the oxygenation of the two basins.

In the northern area, at station F 72 as well as in the Landsort Deep (F78), the bottom water was poorly oxygenated (fig. 4 b). At station F 72 hydrogen sulphide apeared in 1968—69 and in 1972. In the Landsort Deep (F 78), anoxic conditions appeared from the beginning of 1969 until the beginning of 1970, as well as in 1972. This was the first time that hydrogen sulphide was reported from the Landsort Deep. In the beginning of 1969 the hydrogen sulphide was present up to a depth of 300 m and in November the same year from the bottom up to the 125 m level. This means that anoxic conditions occurred in 70 % of the water column. Later, in January 1970, the hydrogen sulphide was restricted to the water mass between the bottom and a depth of 300 m.

Further to the south at station S 41, the oxygen concentration in the bottom water was very low. In every year there were periods when hydrogen sulphide appeared.

Zooplankton

CNIDARIA

Sarsia tubulosa (M SARS)
Juvenile specimens of *S. tubulosa* appeared occasionally in the southern Baltic proper as far to the east as station 8 A (fig. 2). The specimens were found in net hauls taken below the 20 m level down to 85 m. *S. tubulosa* was always found in March or April. On those occasions the temperature was around 2°C from the surface down to a depth of 50—70 m. Below this level the temperature increased to 4—5°C.

The lowest salinity in which the medusa appeared was about 8 ‰. The diameter of the specimens varied from 1 to 3 mm.

Aurelia aurita (L)
A. aurita was found all over the Baltic proper. Although large medusae were seen from the vessel on many cruises, very few of these were caught in the net.

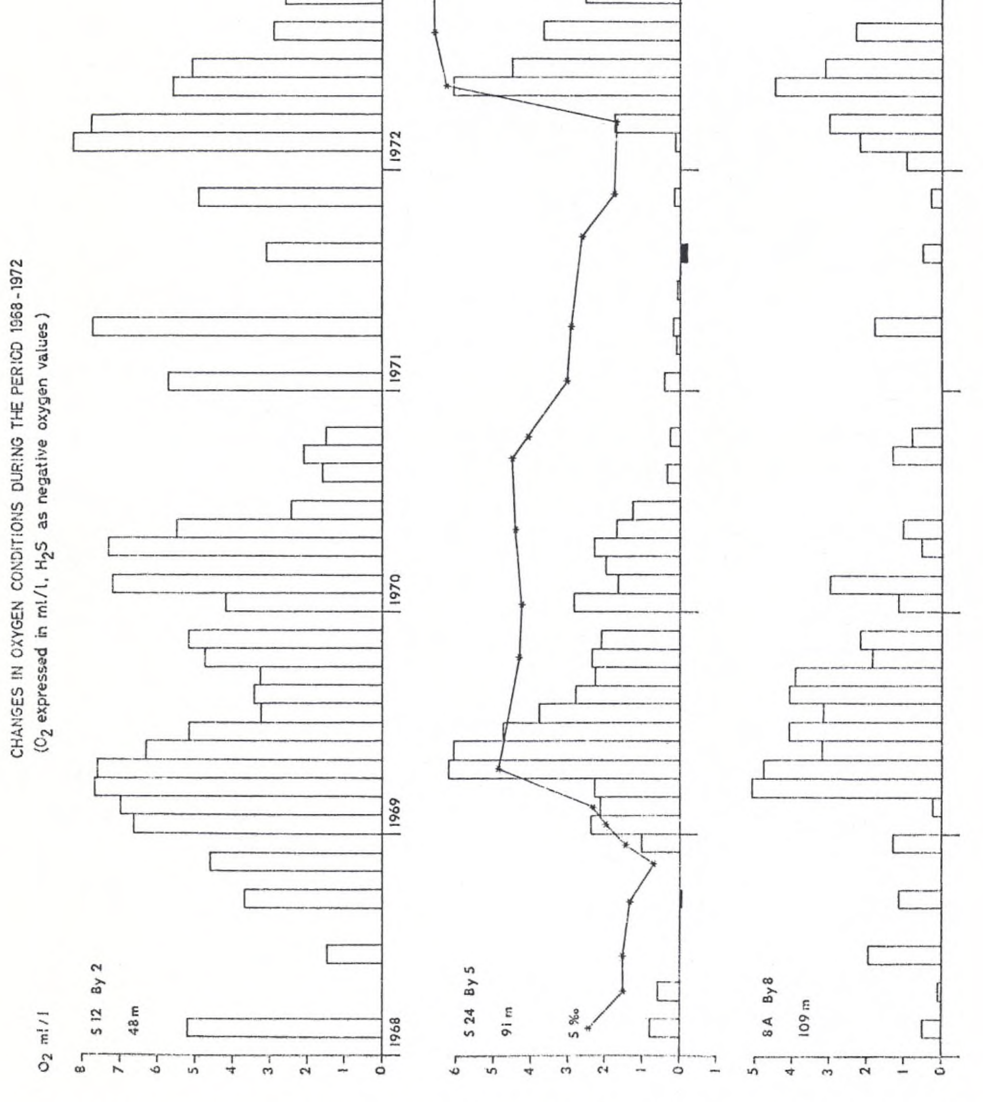

Fig. 4a. Changes in oxygen conditions during the period 1968—1972 at stations S 12, S 24 and 8 A (Anon., 1969 a—1975 c).

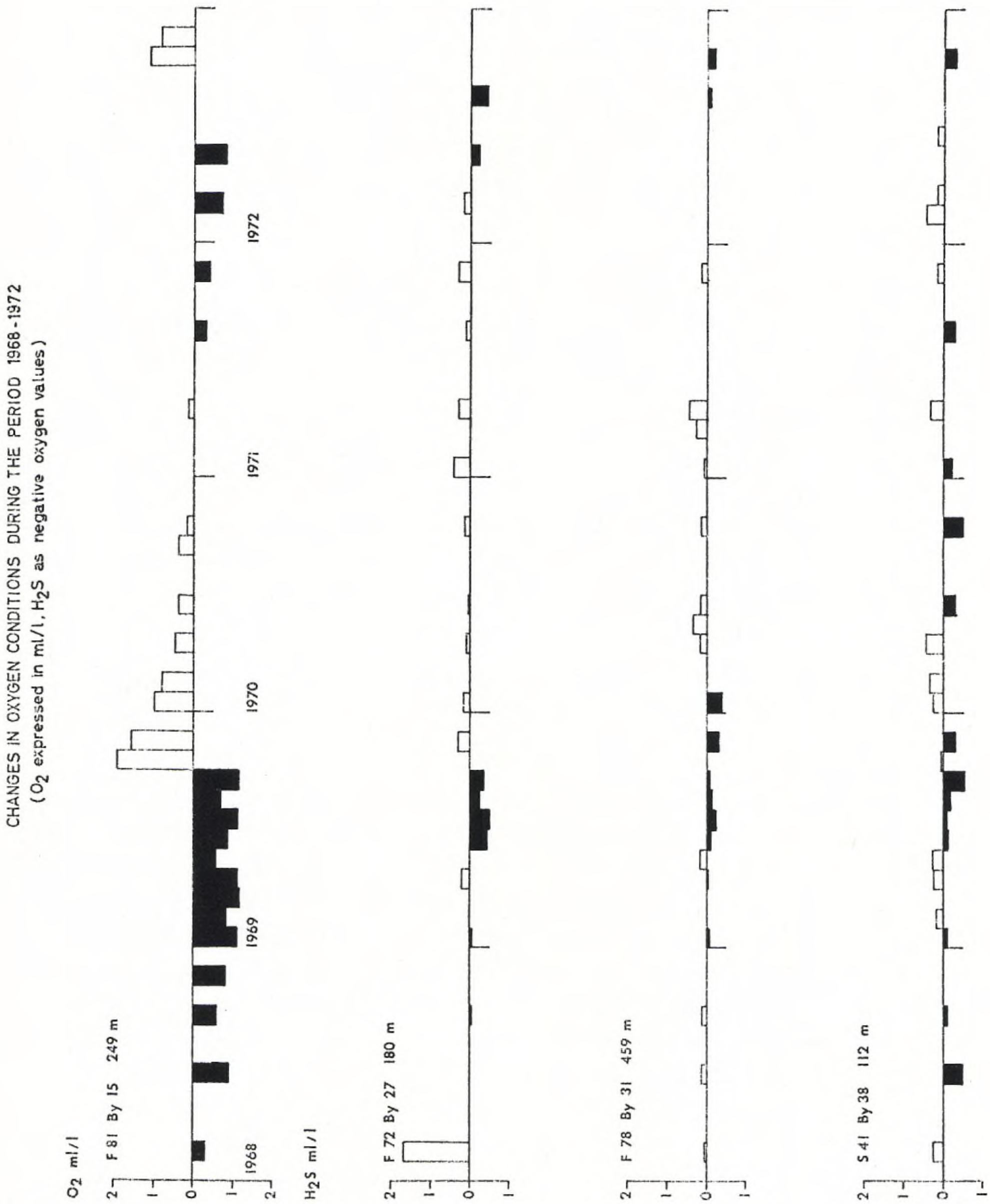

Fig. 4b. Changes in oxygen conditions during the period 1968—1972 at stations F 81, F 72, F 78 and S 41 (Anon., 1969 a—1975 c).

The ephyra larvae were found from April to June. The size increased during that period from 1—3 mm to 5—6 mm but even as late as in September small specimens of the size 7—12 mm were found. From August until November large medusae (80—150 mm) were seen from the vessel, but in our nets however, medusae larger than 80 mm in diameter were never caught. In October 1974, the number of large medusae reached such a density that it was impossible to take ordinary zooplankton samples in the Gotland Sea (west of Gotland). In the months of March—April 1976, we also met large concentrations of *A. aurita*. At least one specimen was caught in each net haul.

The vertical distribution of this medusae is not clear in detail from our sampling. We found *A. aurita* at most levels from the surface down to a depth of 150—200 m.

Cyanea capillata (L.)

C. capillata was found in the southern and eastern part of the Baltic proper up to station F 81 east of Gotland. The medusae appeared sparsely and only 1–2 specimens were caught on each expedition. The size of the specimens caught in the net varied from 3 to 40 mm in diameter.

Most of the specimens were found in net hauls below a depth of 50 m, except in February (1968) when one specimen was caught at the surface at station S 12. All individuals were thus found in cold water below 3—4°C. As the net hauls on some occasions crossed the halocline it is impossible to state whether the individuals appeared below or above this level. However, from net hauls taken below a depth of 100 m, it is obvious that some individuals appear below the halocline.

CTENOPHORA

Pleurobrachia pileus (O F MÜLLER)

Adult individuals of the ctenophore *P. pileus,* were not found during the cruises in 1968—1972. The larvae however, were sometimes rather frequent. The maximum abundance of larvae appeared from February to May. In February (1968) we found about 800 larvae per m^2 at station S 41 and the same number was found in May (1970) at station S 24. Single specimens were found from January to November all over the Baltic proper. The maximum abundance appeared in the middle and southern Baltic proper in net hauls from the 50—25 m level. The size of the larvae was 1—2 mm in diameter. They always appeared in cold water, and mainly in the salinity range of 6—8 ‰.

ROTATORIA

Keratella spp.

Specimens of the genus *Keratella* normally occur very sparsely off the coast in the

Baltic proper. In our investigations we found about 2,000—1,000 individuals of *K. quadrata quadrata* per m² on two occasions (station F 78 in the north and station S 12 in the south). On a few other occasions we found single specimens and on most occasions none. *Keratella* were generally found in the warm surface water and were most frequent in September, but single specimens were also found in October—November. Once, in September, single specimens were found of *K. qu. platei* (JÄGERSKIÖLD), *K. cruciformis eichwaldi* (LEVANDER) and *K. cochlearis recurvispina* (JÄGERSKIÖLD).

Synchaeta spp.

Six different species of the genus *Synchaeta* appear in the Baltic proper; viz. *S. baltica, S. curvata, S. fennica, S. gyrina S. monopus* and *S. triophthalma* (Berzins 1960). We have not distinguished between the species in our analyses, but *S. baltica* and *S. monopus* are probably the most common species.

Synchaeta spp. occur all over the Baltic proper (fig. 5). They are, however, only important from the end of May until July according to our observations. During that part of the year the biomass of the species may reach a level of 2 g per m², corresponding to a value of about 1 milj. individuals per m², as was the case in June and July 1972, at station F 81. During the rest of the year the species were sparse, but from fig. 5 it is evident that there might be a small maximum even in October—November.

The maximum abundance seems to be correlated with the temperature. In May when the temperature was below 8°C, *Synchaeta* spp. were not frequent. By the end of this period they had increased very rapidly in numbers and the maximum abundance occurred in the temperature range of 8—16°C in June—July. Above this temperature the population decreased rapidly. The small maximum in October—November appeared in the temperature range of 9—12°C. During the rest of the year the population was of little importance. The species were vertically distributed both above and below the thermocline. The maximum abundance occurred above the 50 m level.

POLYCHAETA

Pygospio elegans CLAPARÈDE

The larvae of this polychaete appeared every year at stations S 12 and S 24. Larvae were found from January until November. The maximum abundance occurred from January to May. During that time about 2,000 larvae per m² were found. The larvae appeared in all levels of the water column from surface to bottom, e.g. in February—March (1972) the maximum abundance appeared in the surface waters down to a depth of 20 m, and in May (1970) between a depth of 85 and 50 m. From our investigations, it is obvious that the larvae tolerate a salinity range of at least 8 ‰ to 17 ‰. During the summer however, they seemed to avoid the warm surface water.

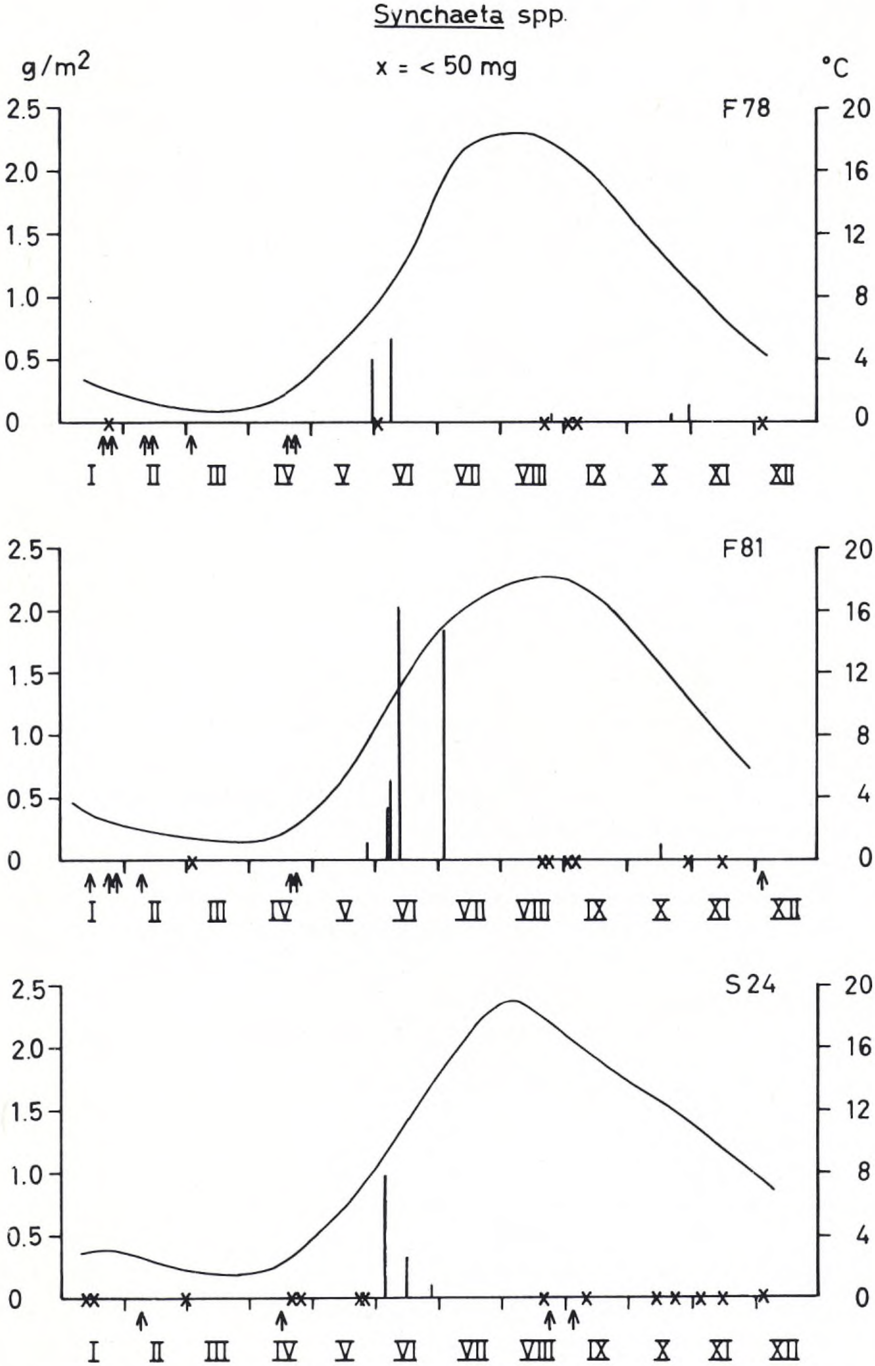

Fig. 5. The seasonal fluctuations of the biomass of *Synchaeta* spp., 1968—1972, in relation to the surface temperature at the stations F 78, F 81 and S 24. Arrows indicate that no specimens were found on that particular sampling occasion.

Harmothoe sarsi KINBERG

The larvae of *H. sarsi* are widespread all over the Baltic proper. All stages of development; trochophora, metatrochophora, nectochaeta and benthonic stages appeared in the samples. Putting the five year results together, we found larvae every month of the year. In general, the number of larvae was greater from April to October. On a few occasions, as many as 7,000—15,000 larvae per m² appeared. The greatest number of larvae were found mostly at stations S 24, 8 A and F 81, i.e. the southern and eastern part of the Baltic proper. Although the larvae were more numerous in the deeper hauls, specimens were also found in surface hauls (25—0 m). In general, no larvae occurred above the thermocline during the summer.

CLADOCERA

Bosmina coregoni maritima (P E MÜLLER)

B. cor. maritima began to appear in the samples in April when the surface temperature was about 2°C. The number of specimens was however, very small until the month of August. When the temperature rose to about 15°C the species became rather abundant all over the Baltic proper. In August and September it could be the dominant species, if the temperature was above 15°C. In 1968 the surface water was very warm (17—19°C) in most parts of the Baltic proper. The biomass of *Bosmina* reached 28 g (wwt) per m² of a total biomass of 64 g. If we compare four different years we get the following correlation between surface temperature (0—20 m), biomass and individuals per m² at station S 24 in August—September. The total biomass is in brackets.

	°C	g	milj. ind.
1968	17.6—16.2	28 (64)	2.8
1970	15.5—15.5	13 (37)	1.3
1971	15.7—15.2	5 (32)	0.5
1972	18.0—18.0	22 (82)	2.3

It is obvious from fig. 6 and the figures above that the species was important at temperatures higher than 15°C. However, there was a time lag of more than one month with temperatures above 15°C, before the species became frequent. The temperature usually exceeded 15°C by the beginning of July. In some years, however, there was a very short period prior to August—September with temperatures above 15°C in the northern and middle Baltic proper. This might explain the varying results at stations F 78 and F 81. *B. cor. maritima* was always very abundant at stations S 24 and F 78 when the temperature was in the range 17—19°C.

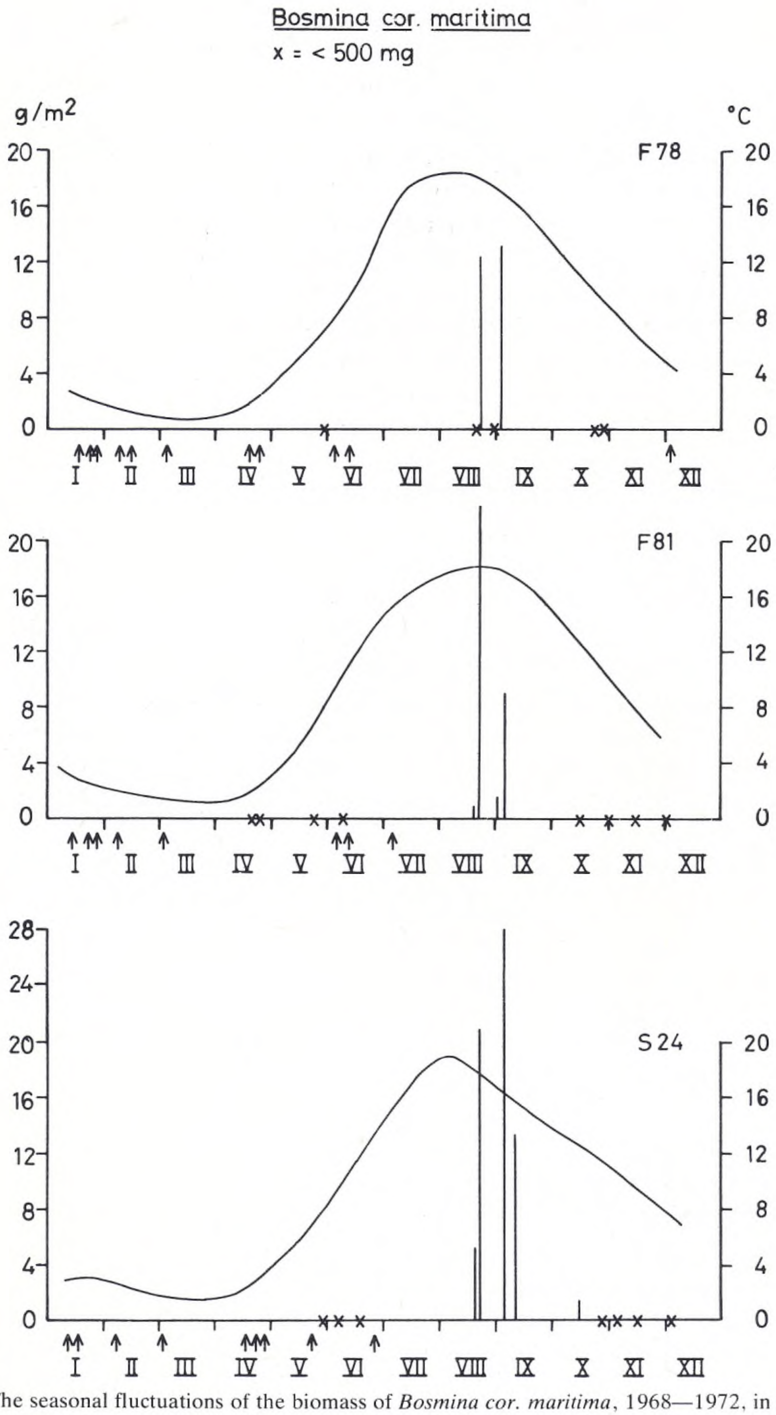

Fig. 6. The seasonal fluctuations of the biomass of *Bosmina cor. maritima*, 1968—1972, in relation to the surface temperature at the stations F 78, F 81 and S 24. Arrows indicate that no specimens were found on that particular sampling occasion.

After September the population decreased rapidly, and during the months of January—March the species was not found. From our stratified sampling, it is obvious that the greatest percentage of the population was found in the warm water above the thermocline. However, sometimes about 20 % of the population was found below the thermocline.

Podon intermedius LILLJEBORG

The population density of *P. intermedius* was very low all over the Baltic proper (fig. 7). The species began to appear in the samples in June at station S 24, when the surface temperature had reached a level of 8—9°C. In September the biomass amounted to 100 mg per m^2 in the northern and middle Baltic proper, and to 200 mg per m^2 in the southern Baltic proper. Thus, the number of individuals per m^2 was 5,000—6,000 and 10,000—12,000 respectively. The surface temperature was 16—17°C on those occasions. The population decreased in October, but as late as the middle of November the population amounted to 1,000—2,000 ind. per m^2 at stations S 24 and S 41. The temperature at the surface was still about 10°C on those occasions.

Podon leuckarti G O SARS

This species appeared from April until July. In 1968—1972 the species appeared in the southern area up to S 41 and F 81. However, in recent investigations (1975 and 1976), the species appeared as far to the north as station 3′ (the Åland Sea) from May until July.

P. leuckarti began to appear in April at a temperature of 4—5°C. In the Åland Sea the maximum abundance was 1,500 ind. per m^2 in early June (6.5°C), in the Gotland Sea (station 2) the same number appeared in July (15—16°C) and in the Hanö Bight (station 1) 3,500 ind. per m^2 appeared in June (14°C). The species disappeared simultaneously at the three stations by the end of July.

Pleopsis polyphemoides (LEUCKART)

(syn. *Podon polyphemoides*; cf. Gieskes 1971 a)

This species usually appeared very sparsely in our samples. From June until November a small number of specimens was occasionally found. In July 1972, no less than 9,600 ind. per m^2 were found. This corresponds to a biomass of 960 mg m^{-2}. The temperature was around 15°C down to a depth of 15 m. Later, in July 1975, *P. polyphemoides* was found on three successive sampling occasions in the temperature range of 15—16°C at station 2. The abundance was about 6,500 ind. per m^2. In August, when the temperature rose to 22°C, *P. polyphemoides* disappeared and was replaced by *Podon intermedius*. The vertical distribution of *P. polyphemoides* was mainly concentrated in the surface waters down to a depth of 20—25 m.

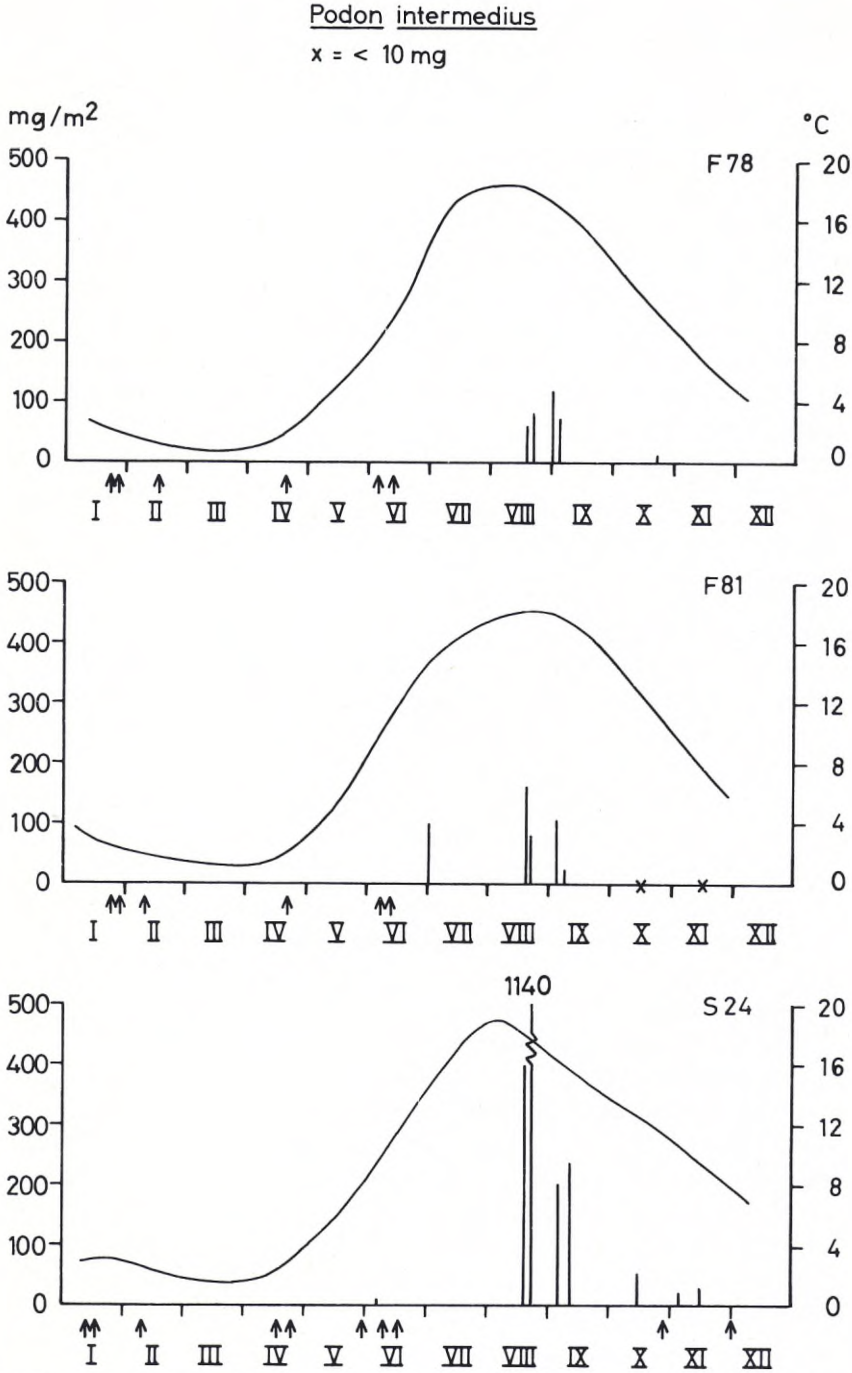

Fig. 7. The seasonal fluctuations of the biomass of *Podon intermedius*, 1968—1972, in relation to the surface temperature at the stations F 78, F 81 and S 24. Arrows indicate that no specimens were found on that particular sampling occasion.

Evadne nordmanni LOVÉN
Specimens of *Evadne nordmanni* may appear occasionally in every month of the year. From April—May the species appeared regularly all over the Baltic proper (fig. 8). From the middle or the end of May until November it is of great importance, especially in the southern Baltic proper. The population density decreased from south to north.

The greatest density appeared in May—June but the species may be important until October at station S 24. The highest density was correlated with the temperature range of 6—12°C and the highest abundance in the autumn appeared in the range of 12—17°C. At station F 81 the abundance was lower and rather even from June to September. A similar distribution pattern appeared at station F 78 in the north. The maximum biomass in May—June in the south reached 1,000—2,000 mg per m² (100,000—200,000 ind.), while the corresponding biomass in the north amounted to about 10 % of those figures.

The largest proportion of the population appeared in the surface waters, but as much as 25 % of the population may be present in the cold water below 25 m depth.

COPEPODA

Calanoida

Calanus finmarchicus S.L. (GUNNERUS)
In October 1970, single specimens of *C. finmarchicus* S.L. were found at station S 12 in a net haul from a depth of 45—25 m. The salinity close to the bottom was 18 ‰.

Limnocalanus macrurus (SARS)
(syn. *L. grimaldii* (DE GUERNE)
The population of *Limnocalanus* in the Baltic is not considered to be a different species from those populations which appear in fresh waters. According to the law of priority, the species in the Baltic should be called *L. macrurus* (Pejler 1965). By tradition, the species is called *L. grimaldii.*

The species appeared very sparsely in the Baltic proper during 1968—1972. Single specimens were found as far south as station S 24. However, even at the northern-most station, F 72, the species appeared very sparsely. The maximum density was 500 ind. per m². Normally the abundance was less than 50 ind. per m².

Acartia bifilosa (GIESBRECHT) and *A. longiremis* (LILLJEBORG)
The nauplii and the copepodite stages, except stage VI (adult) were grouped together in the analyses of the two species.

The two species are widespread all over the Baltic proper. According to our analyses of the adult males and females, *A. bifilosa* was more abundant than *A. longiremis* in the northern Baltic proper, while *A. longiremis* is more abundant in

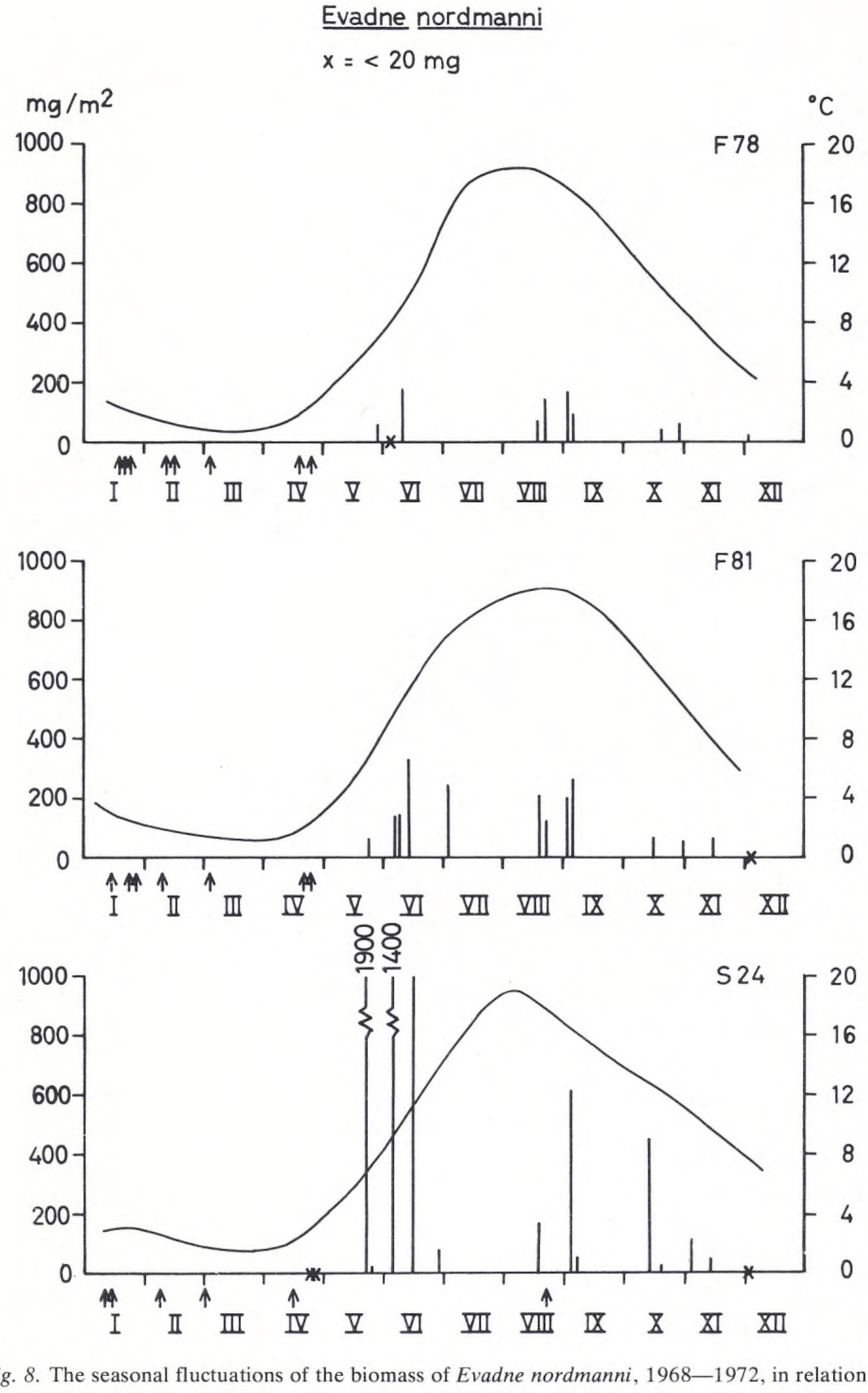

Fig. 8. The seasonal fluctuations of the biomass of *Evadne nordmanni*, 1968—1972, in relation to the surface temperature at the stations F 78, F 81 and S 24. Arrows indicate that no specimens were found on that particular sampling occasion.

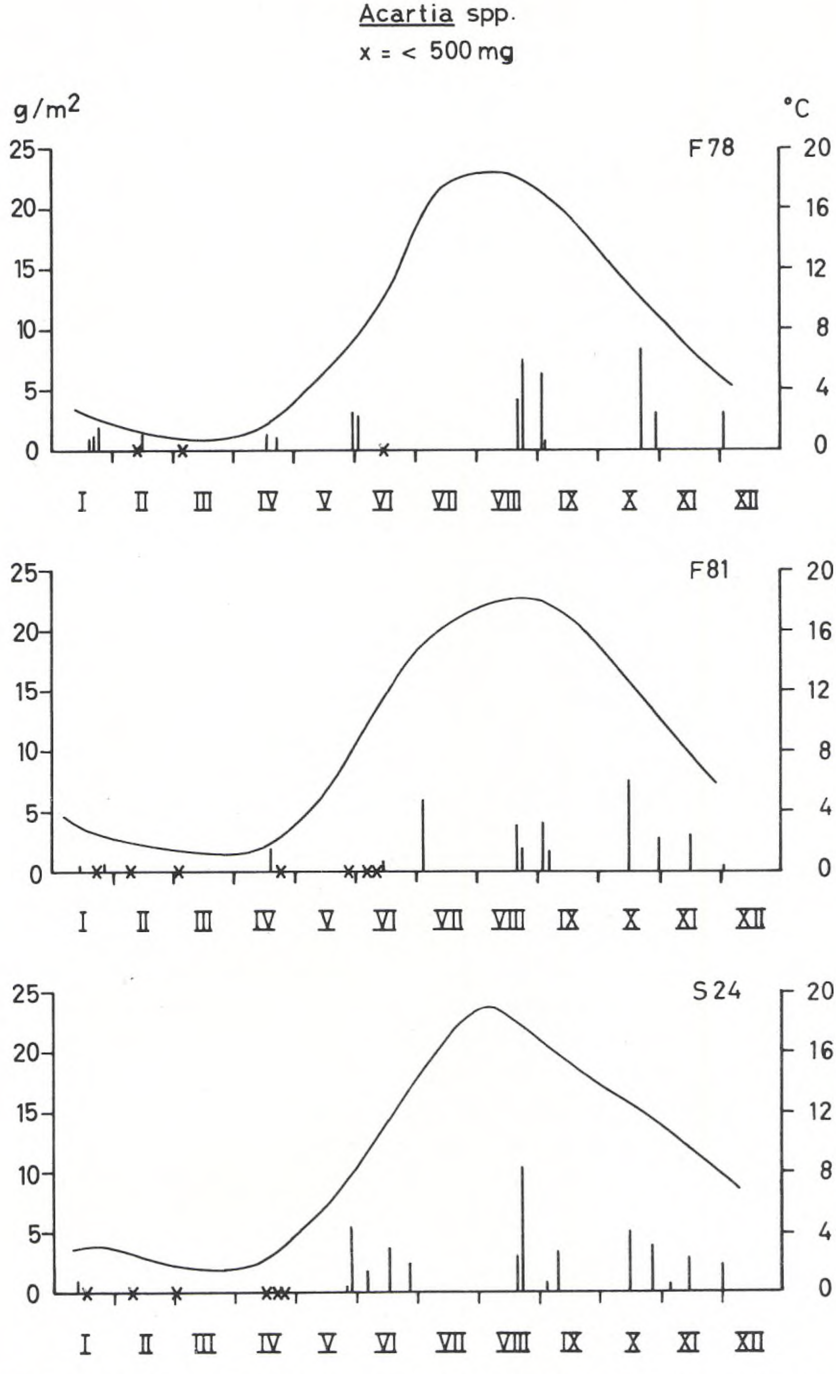

Fig. 9. The seasonal fluctuations of the biomass of *Acartia* spp., 1968—1972, in relation to the surface temperature at the stations F 78, F 81 and S 24. Arrows indicate that no specimens were found on that particular sampling occasion.

the south. The biomass of the two species together was relatively high during the second part of the year, when values of around 5 g per m^2 were recorded (fig. 9). During the rest of the year, the biomass values were generally less than 2.5 g per m^2, and at the beginning of the year, the biomass was less than 500 mg on many sampling occasions.

The species seemed to breed all year around in the Baltic proper. Nauplii were found on nearly all sampling occasions. In the northern Baltic proper, the maximum abundance of nauplii occurred in February—March (170,000 nauplii per m^2) and in November (110,000 nauplii per m^2). The first generation developed into C. I—III in April and was fully matured in May—June. At low temperatures the development is probably very slow. Later in the year, it is difficult to distinguish between different generations due to the more rapid development in the warm water. Although there were ralatively few nauplii from April until October, experience from the other stations indicates that the nauplii may be abundant during spring and summer. The last generation of the year, which is born in October—November may overwinter mainly as C. I—III in the northern Baltic proper, or as adults in the other parts.

In the southern Baltic proper there seems to be a rather similar spawning pattern. However, it is obvious that there was a great concentration of nauplii in May—June as well. During the second part of the year, the adults, including C. IV—V, dominated the population.

The vertical distribution was different for the adults of the two species. Males and females of *A. bifilosa* occurred mainly in the net hauls from 25 m to the surface, especially during summer. Net hauls in August—September from the thermocline to the surface contained many more adults than the deeper net hauls. In spring, and in the beginning of summer, before the surface water reached a temperature of 10°C, there were sometimes small differences between the net hauls from various depths. The adults were abundant down to at least 50—60 m. The females of *A. longiremis* were, on the other hand, very often more common in net hauls from 50 to 25 m depth than close to the surface. Both males and females avoided the warm surface water in the period July—October. The younger and older copepodite stages, as well as nauplii of both species were always more abundant in net hauls from 25 m to the surface than in deeper net hauls. The older stages (C. IV—V) may be rather abundant in the net hauls from a depth of 50 to 25 m as well.

Eurytemora sp.

Eurytemora sp. appeared abundantly only in the northern Baltic proper (fig. 10). The maximum abundance occurred in August—September when the temperature was above 16°C

The biomass amounted to 5—6 g per m^2 at station F 78 and 6—7 g at station F 72. Further to the south the biomass decreased rapidly east of Gotland. West of Gotland however, the population may be large. Analyses from the plankton station

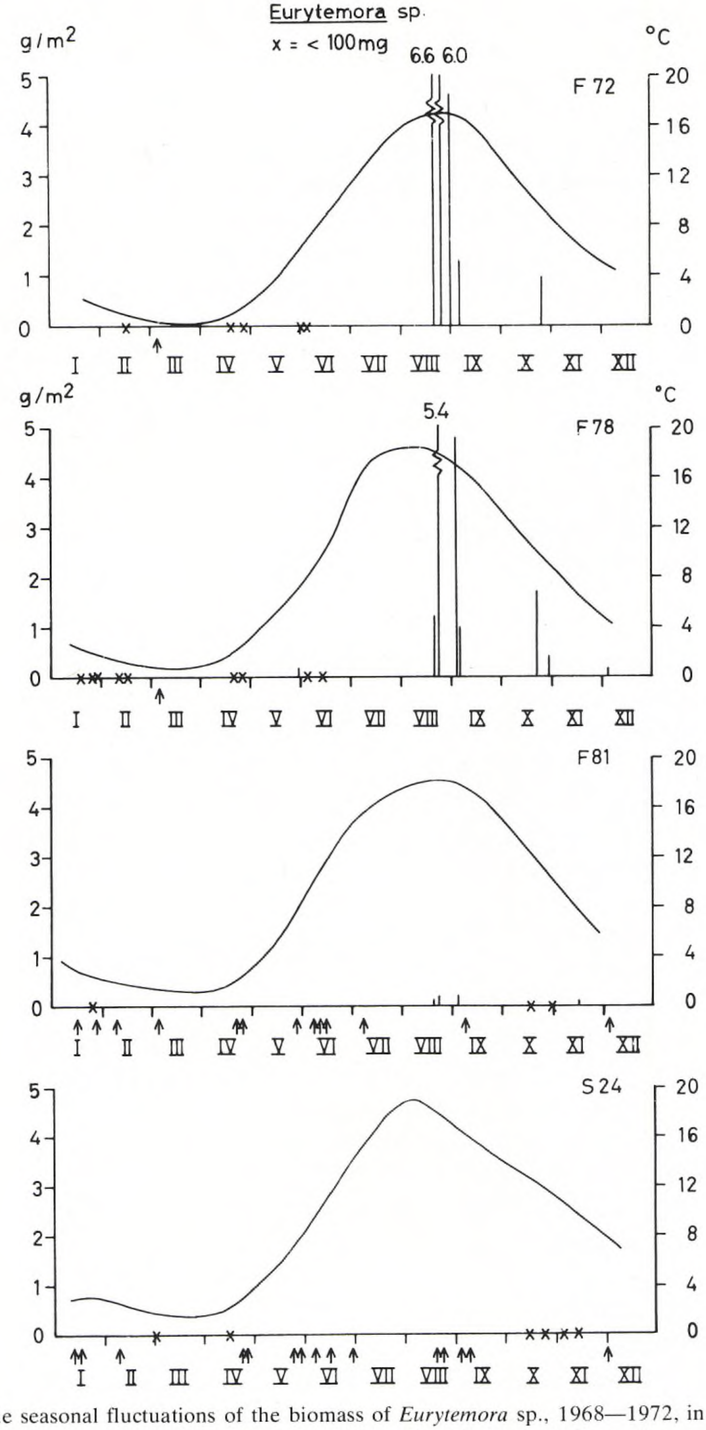

Fig. 10. The seasonal fluctuations of the biomass of *Eurytemora* sp., 1968—1972, in relation to the surface temperature at the stations F 72, F 78, F 81 and S 24. Arrows indicate that no specimens were found on that particular sampling occasion.

10/9 between Gotland and the mainland of Sweden indicated that biomass values may reach 12 g per m^2. In the northern area the species can be important until October although the temperature at that time of the year has decreased to 8—12°C.

At station 3′ (Åland Sea) the biomass increased rapidly from 0.5 g in June to about 4 g in July. During that time the temperature rose from 12 to 18°C. The biomass remained high until the beginning of October even when the temperature had decreased to about 11°C. However, later in the autumn when the temperature was in the range 6—8°C, the population decreased rapidly.

The abundance of different developmental stages showed that nauplii occurred from May until November. At station 3′ the nauplii were very abundant from June until the middle of October. Copepodite stages I—III and IV—V were most numerous from July until November, and the adults from July until September. Off the coast at station F 78 the copepodite stages IV—V were the dominant stages from December until March.

The vertical distribution of this species was concentrated mainly in the surface water above a depth of 20 m.

Centropages hamatus (LILLJEBORG)

Centropages hamatus was found on all sampling occasions over the whole Baltic proper (fig. 11). The population was very small at the beginning of the year. In the south, the population increased in April, in the middle part of the investigation area in May—June and at the most northern stations in August. The maximum density occurred in August—September with values around 9 g per m^2. From April until November the biomass was generally in the range of 1—2 g per m^2 in the southern Baltic proper. In general, the biomass values decreased from south to north. The temporal occurrence was more restricted in the northern area compared with areas in the middle and southern Baltic proper.

The nauplii appeared from May—June until November. The highest density of nauplii was found from July until October. *C. hamatus* overwintered mainly in the copepodite stages IV—V. The adult stage was most frequent in May—June and August—September. In the south it was also frequent in November. This indicates that there may be three generations during the year.

The largest proportion of the population appeared in the upper 25 m, although on some occasions it may be rather abundant at lower levels. During the summer, the species avoided the warm water close to the surface during the day—time. At night however, the largest proportion of the population appeared above the thermocline.

Pseudocalanus minutus elongatus (BOECK)

Pseudocalanus m. elongatus and *Temora longicornis* are the most important species in the Baltic proper. The former species was abundant during the whole year (fig. 12). In the southern Baltic proper the maximum biomass was in the range 17—31.5

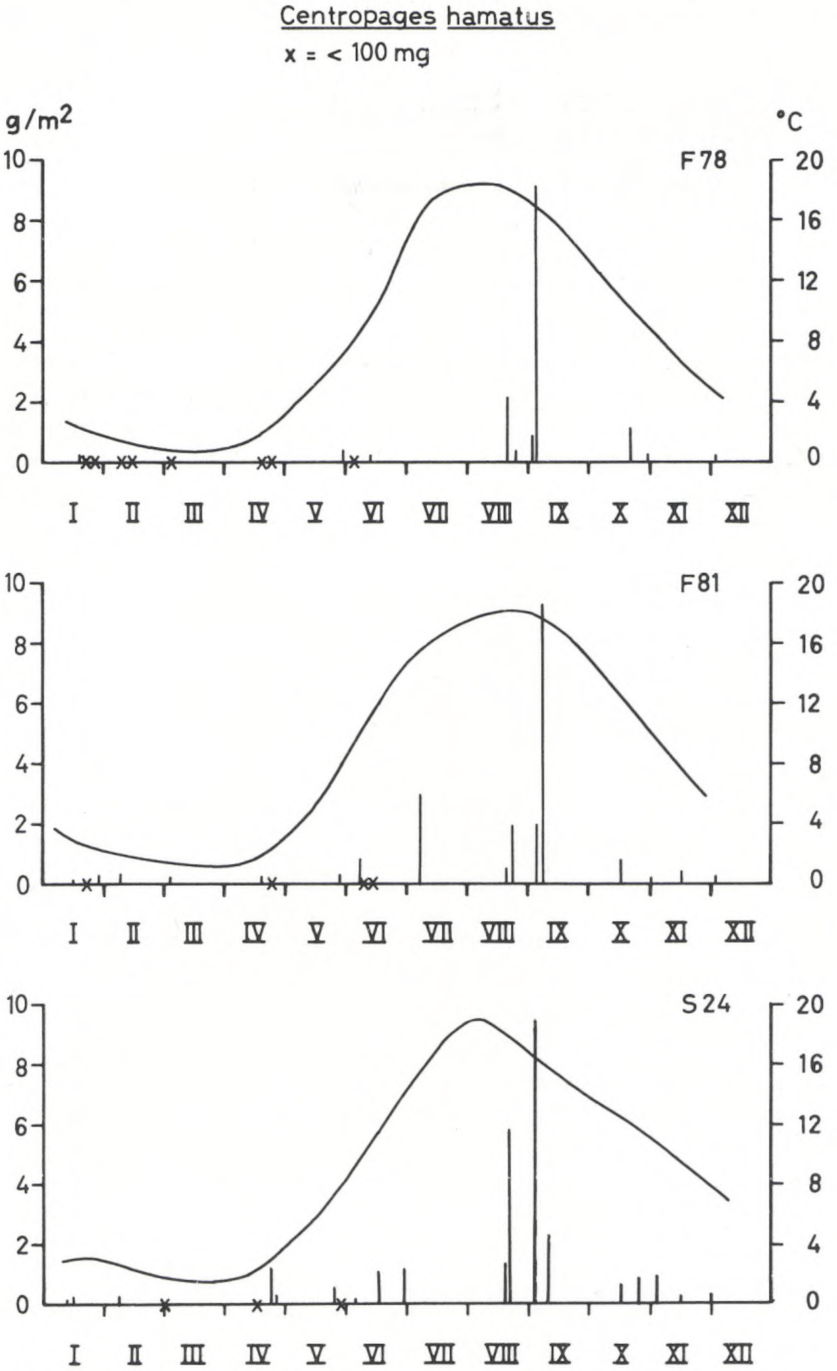

Fig. 11. The seasonal fluctuations of the biomass of *Centropages hamatus*, 1968—1972, in relation to the surface temperature at the stations F 78, F 81 and S 24. Arrows indicate that no specimens were found on that particular sampling occasion.

g per m², in the middle area 12.5—23.5 g per m² and in the northern area 5.0—9.5 g per m². As is obvious from fig. 12 the size of the population was very large on many sampling occasions during the year. The maximum values were observed mainly from May until September. The biomass was also very high during other parts of the year, e.g. most values (except the maximum values) were 4—10 g in the southern and middle area and 2.5—5 g in the northern. As far as concerns the biomass, this species is the most important one in the Baltic proper. High abundances were found all through the year.

The nauplii appeared on many occasions during the whole year. The main concentration was in April—June. In the most southern part of the Baltic proper, a high density of nauplii was also found in February and August. The maximum density of nauplii in the three different areas was from south to north: 800,000, 500,000 and 300,000 ind. per m². Copepodids I—III were numerous from May until November. The older copepodids (C. IV—V) were most abundant from July until March. The species overwintered nearly exclusively as C. IV—V. From February until May—June the adult stage was rather abundant, while their absence was almost total during the rest of the year.

Among the adults, females were much more abundant than males, which in fact were very rare on most sampling occasions.

The vertical distribution was different in the cold seasons, compared to the warm seasons. In winter the distribution was quite even down to 100 m with the exception of C. IV—V which were slightly more concentrated below the 50 m level.

In June when the water temperature had reached a level of 8—10°C the main concentration of nauplii was in the upper 50 m layer, the C. I—III between 50 and 25 m, the C. IV—V as well as the adults in the 100 to 50 m level. In September, when the surface water temperature was in the range 15—18°C the main concentration of C. I—III generally appeared below the 25 m level. The C. IV—V and adults were found at deeper levels. The same distribution occurred in October when the temperature at the surface had dropped to 10—12°C.

The great concentration of specimens below the halocline in water with an oxygen concentration of less than 2 ml O_2/l was conspicuous. E.g. in October 1970, when the thermocline was located at around the 35 m depth in the Landsort Deep (F 78), both the C. I—III and C. IV—V were concentrated below the 50 m level in the cold water with a salinity of 10‰. The oxygen concentration was less than 2 ml O_2/l in the whole water column below the 55 m level (at 50 m about 4 ml O_2/l).

Temora longicornis P MÜLLER

Temora longicornis is one of the most important species in the Baltic proper. It is frequent over the whole area. The species was more abundant in the southern area than in the northern area (fig.13). The maximum biomass, which occurred from July until September, was 11.5—16.5 g at station S 24, 10.0—14.5 g at station F 81 and 7.5—10.0 g per m² at station F 78. During the first months of the year, the species was of particular importance only in the middle and southern part of the

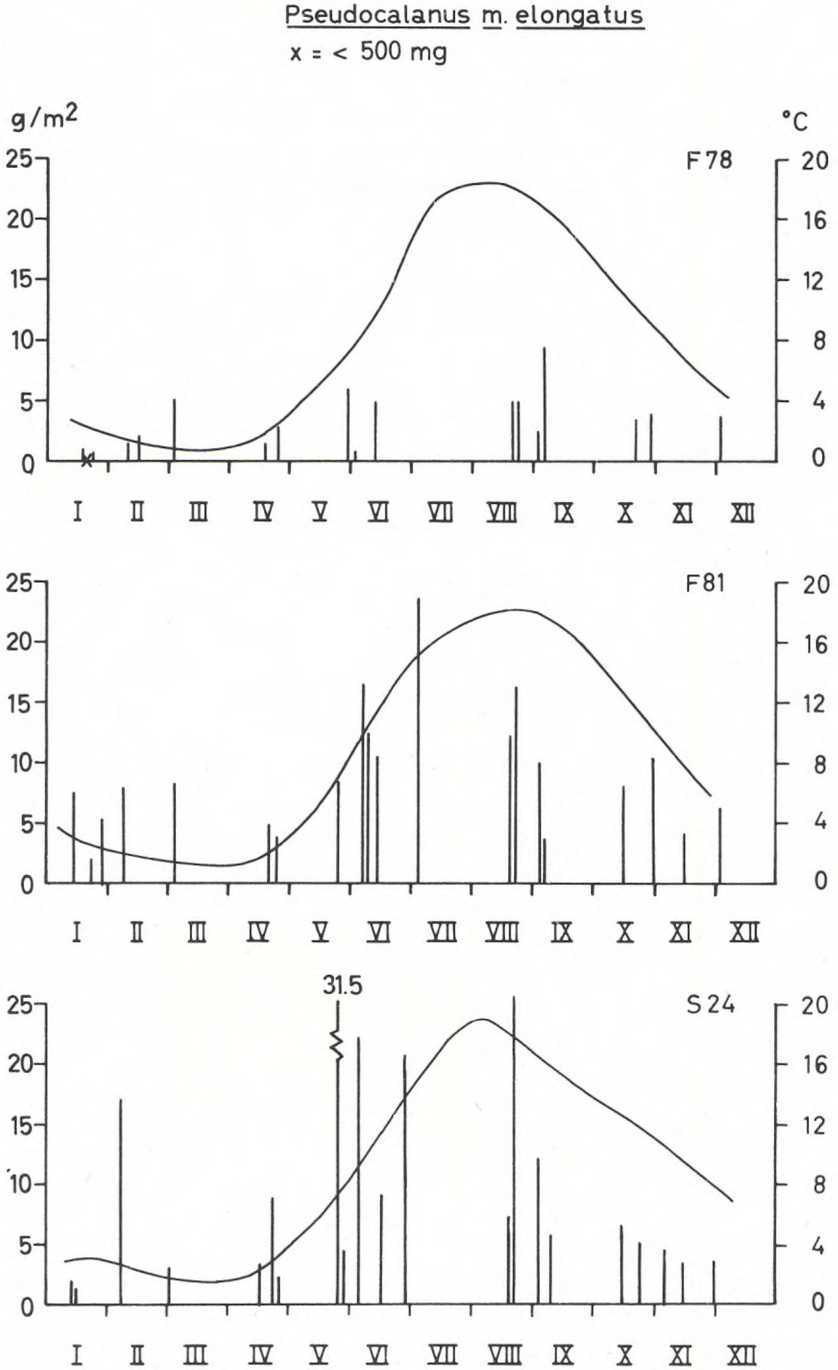

Fig. 12. The seasonal fluctuations of the biomass of *Pseudocalanus m. elongatus*, 1968—1972, in relation to the surface temperature at the stations F 78, F 81 and S 24. Arrows indicate that no specimens were found on that particular sampling occasion.

Baltic proper. In the south, the population began to increase in April. The maximum occurred in July—September. After September, the population decreased slowly, and in January—February it was still rather important in the middle and southern area of the Baltic proper. The biomass reached a minimum during a period of about one month in the south, and three months in the north.

The nauplii occurred mainly from May until November. The greatest concentration of nauplii was found in May—June and in September—November. In May—June, the abundance was on many sampling occasions 100,000—1,200,000 nauplii per m^2. In the autumn, the corresponding values were 50,000—150,00 nauplii per m^2. The occurrence of copepodite stages I—III coincided with the occurrence of nauplii. There was a time-lag in May—June, when the water was rather cold, between the occurrence of nauplius stages and C. I–III.

The relative abundance of C. IV—V and the adults was greatest during the first part of the year. The overwintering specimens were mainly C. IV—V. The greatest number of adults however, occurred in July—September when 50,000—200,000 adults per m^2 were found on many sampling occasions.

The present results indicate that there were two main spawning periods, one in May—June and one in August—September. However, nauplii were found in all months except January, which implies a very long spawning period, with more than two generations per year.

The vertical distribution seemed to vary according to the time of year and the time of day. In winter, the older copepodite stages and adults were vertically more homogenously distributed than during spring, summer and autumn. In January, no pronounced vertical migration occurred. In May—June, when the surface water was 8—10°C, all the developmental stages were usually found to be more numerous in the net hauls from 25 m to the surface than from 50 to 25 m depth, both day and night. In August—October, when a well marked thermocline had developed, the greatest concentration of specimens was found in the net hauls from 25 m depth to the surface, but only at night. During the day-time an accumulation of individuals was observed in net hauls taken just below the thermocline. Thus, diel migration was very marked during the warm season.

Cyclopoida

Cyclops sp.

Single specimens of *Cyclops* sp. were found at the northernmost stations.

Oithona similis CLAUS

This species was concentrated in the deep basins of the southern Baltic proper, mainly in the Bornholm Deep (S 24). On many sampling occasions a small number of specimens also appeared at stations S 12, 8 A and F 81. On two occasions single specimens were found as far to the north as F 78 and F 72. The greatest concen-

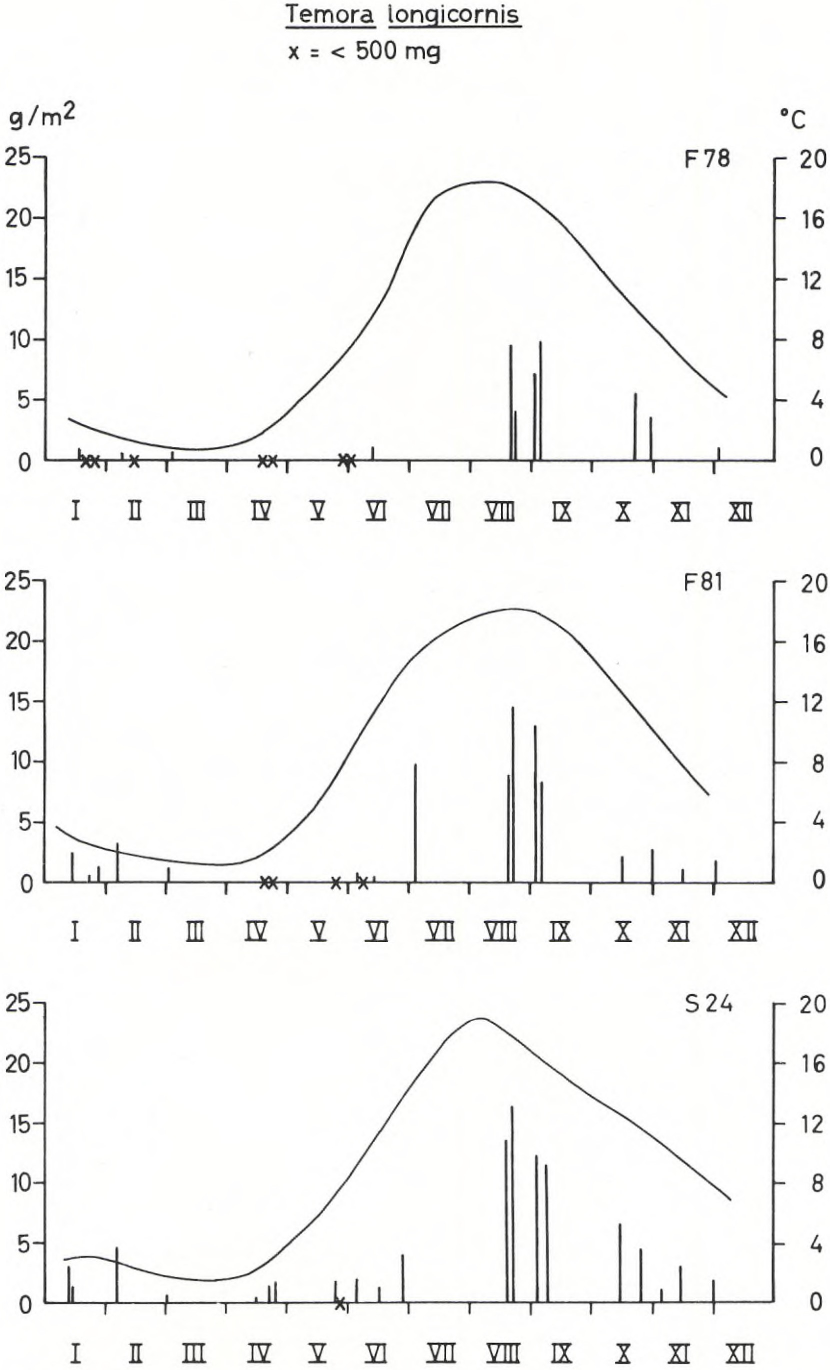

Fig. 13. The seasonal fluctuations of the biomass of *Temora longicornis*, 1968—1972, in relation to the surface temperature at the stations F 78, F 81 and S 24. Arrows indicate that no specimens were found on that particular sampling occasion.

tration of *O. similis* always occurred in the deep water close to the bottom, where the salinity was high. The maximum density was 160,000 ind. m^{-2} at station S 24 corresponding to a biomass of 470 mg. At the other stations in the southern Baltic the density was much less.

Harpacticoida

Single specimens were found in net hauls taken close to the bottom. Some finds from stations 8 A and F 81 were defined as *Ectinosoma curticorne.*

CIRRIPEDIA

Balanus improvisus DARWIN

Very few nauplii of *Balanus improvisus* were found. On only two occasions, in April 1969 and August 1971, nauplii appeared in the samples at S 12 and F 72 respectively.

MYSIDACEA

Specimens of *Mysis relicta* LOVÈN were found in February 1968, at station F 81 in a net haul from a depth of 100—50 m. In October 1970, single specimens of *M. mixta* appeared in samples from 100—50 m and in samples from below a depth of 100 m at station F 81.

AMPHIPODA

Hyperia galba MONTAGY

Hyperia galba appeared occasionally in January, February and April at stations F 81 and F 72 in samples taken below the 100 m level.

ACARI

Single specimens of unidentified mites were found in June 1968, in net hauls below the 250 m level at the Landsort Deep (F 78). The following year, single specimens were found in January in net hauls from 100—50 m depth as well as in net hauls from 50—25 m depth.

GASTROPODA

Gastropod larvae occurred from August until November. The greatest density was always found in August—September. The maximum density varied from 2,000 ind. in the south to about 500 ind. per m^2 in the north.

LAMELLIBRANCHIATA

Mytilus edulis (L.)

Larvae of *M. edulis* were found all over the Baltic proper. The greatest density was found from August to October, expecially in the southern Baltic proper. In November the density was low. From December until the end of February occasional specimens appeared. No larvae appeared in the samples from March—April. The maximum biomass was about 50 mg (13,000 ind.) per m^2 in the south and 2.5 mg (600 ind.) per m^2 in the north. The vertical distribution differed greatly on the various sampling occasions.

Macoma baltica (L.) *Cardium glaucum* Bruguière *C. hauniense* Petersen & Russel *Mya arenaria* (L.)

The four species were grouped together when the samples were analysed. The greatest density of larvae appeared in the period from May until August. From September to January the density was lower, and during February—April only occasional specimens appeared. The abundance of larvae decreased from west to east and from south to north.

CHAETOGNATHA

Sagitta elegans baltica (RITTER-ZAHONY)

S.e. baltica appeared regularly in the bottom water of the Bornholm Deep (S 24). The species was also very important in the Arkona Deep (S 12), where the greatest density appeared in November 1968. No less than 3,000 ind. per m^2 were caught, amounting to about 70 g (wwt). On a few occasions, *S. e. baltica* was also found at stations 8 A and F 81.

S. e. baltica always appeared in the samples from the deepest net hauls. The horizontal distribution of this species in thus correlated with the most saline water along the deepest parts of the basins in the southern and middle parts of the Baltic proper. The distribution indicated that the lowest salinity tolerated by this species was 10—12‰.

Sagitta setosa (MÜLLER)
On two occasions single specimens were found in net hauls taken at station S 12 in the Arkona Sea. The salinity of the bottom water was 15—17‰.

COPELATA

Oikopleura dioica (FOL)
This species appeared at station S 12 in September, October and November 1968—1969. On one occasion, a single specimen appeared at station S 41. The maximum density in November 1968 was 11,700 ind. per m².

Fritillaria borealis (LOHM)
F. borealis was rather evenly distributed over the whole Baltic proper. The greatest density was found from April until June—July (fig. 14), but even during the rest of the year the population may be rather large. The greatest abundance was observed in May 1972, at station 8 A. At that time about 350,000 ind. per m², with a biomass of 3.5 g, were found. Generally, the differences between various parts of the Baltic proper seemed to be small.

The biomass fluctuated between 200 and 1,000 mg per m² in April—June in the south, and in May—July in the north. There was a minimum in August, September and October with biomass values of less than 200 mg per m². A new maximum occurred from November until January (including February—March in the north) with many values higher than 200 mg. per m².

The species did not appear in the warm surface water during the summer. During the rest of the year, a great part of the population was found above the 25 m level.

The horizontal variation of species in the Baltic proper

The southern area of the Baltic proper was dominated by euryhaline marine copepods, i.e. *Acartia longiremis, Centropages hamatus, Temora longicornis* and *Psedocalanus minutus elongatus* (table 1). At certain times of the year *Aurelia aurita, Synchaeta* spp., *Bosmina coregoni maritima, Evadne nordmanni* and *Fritillaria borealis* were also very important. In the Bornholm Basin the biomass of *Sagitta elegans baltica* was high. The number of specimens was only moderatly high, but the individual volume of *Sagitta* is very large compared to other zooplankton species. Certain marine species were restricted to the more saline bottom water of the southern Baltic proper, viz. *Pygospio elegans* (larvae), *Oikopleura dioica, Oithona similis* and *Cyanea capillata*, which appeared mainly in the deep basins of the southern area (cf. tables 2 and 3).

The middle area, mainly represented by the station S 41, 8/9—12/9, F 81 and station 2, was also dominated by the copepods. However, the brackish water species, *Acartia bifilosa*, was as common as (or more abundant than) the marine

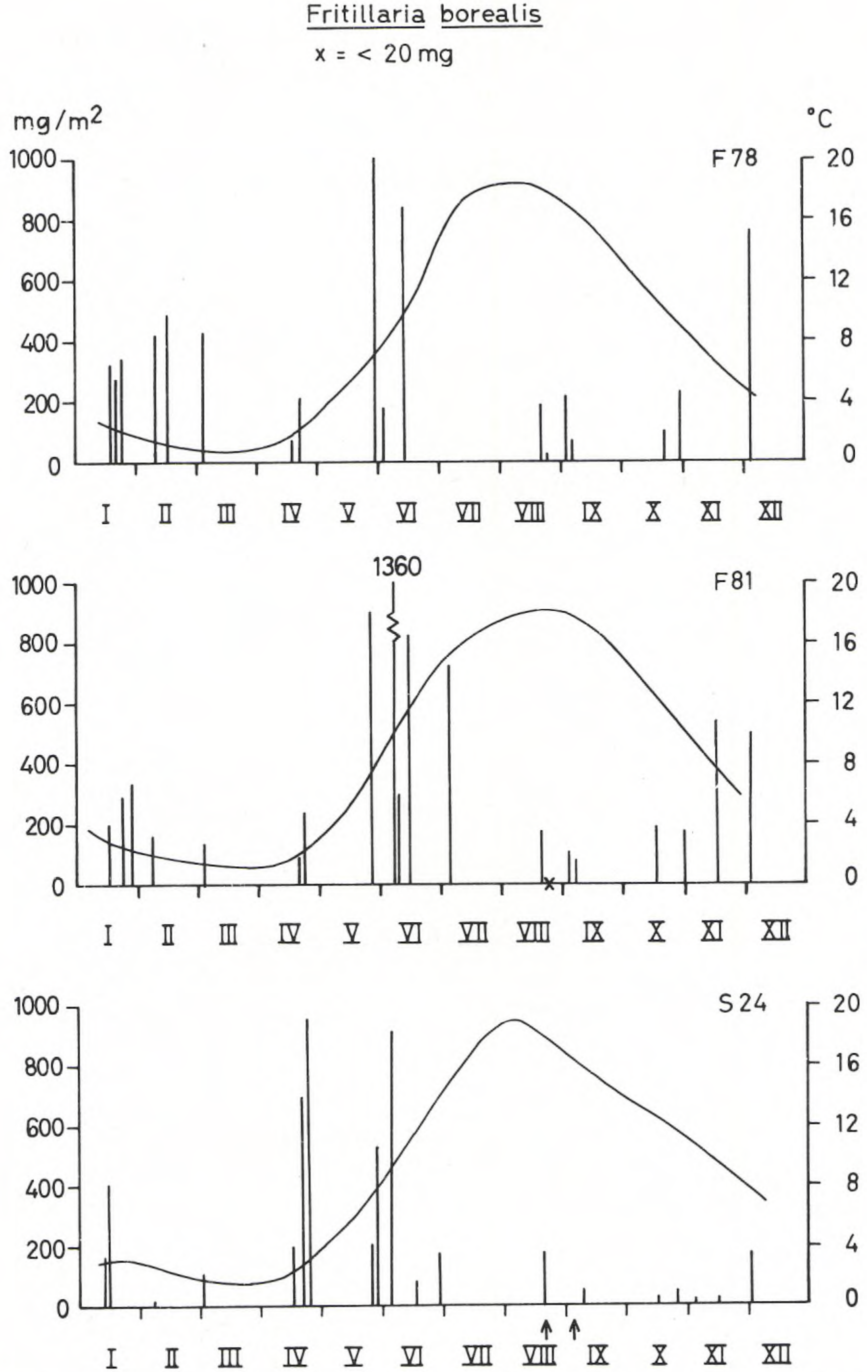

Fig. 14. The seasonal fluctuations of the biomass of *Fritillaria borealis*, 1968—1972, in relation to the surface temperature at the stations F 78, F 81 and S 24. Arrows indicate that no specimens were found on that particular sampling occasion.

Table 1.
The distribution of zooplankton in the northern (N), middle (M) and southern (s) part of the Baltic proper according to the investigations in 1968—1972.

	Abundant			Common			Sparse			Occasional		
	N	M	S	N	M	S	N	M	S	N	M	S
Sarsia tubulosa												X
Aurelia aurita		(X)	(X)	X	X	X						
Cyanea capillata								(X)	(X)		X	X
Pleurobrachia pileus (larvae)								X	X	X		
Keratella quadrata quadrata							(X)	(X)	(X)	X	X	X
K. qu. platei										X		
K. cruciformis eichwaldi										X		
K. cochlearis recurvispina												X
Synchaeta spp.	X	X	X									
Pygospio elegans (larvae)									X			
Harmothoe sarsi (larvae)				X	X	X						
Bosmina coregoni maritima	X	X	X									
Podon intermedius				X	X	X						
P. leuckarti						X	X	X				
Pleopsis polyphemoides	(X)	(X)										X
Evadne nordmanni			X	X	X							
Calanus finmarchicus S.L.												X
Limnocalanus macrurus							X				X	
Acartia bifilosa	X	(X)			X	X						
Acartia longiremis		(X)	X	X	X							
Eurytemora sp.	X				X				X			
Centropages hamatus	X	X	X									
Temora longicornis	X	X	X									
Pseudocalanus m. elongatus	X	X	X									
Oithona similis									X	X	X	
Gastropoda (larvae)							X	X	X			
Mytilus edulis						X	X	X				
Macoma baltica							X	X	X			
Cardium glaucum							X	X	X			
C. hauniense							X	X	X			
Mya arenaria							X	X	X			
Oikopleura dioica									(X)			
Fritillaria borealis	X	X	X									
Sagitta elegans baltica						(X)						
Sagitta setosa												X

species *A. longiremis*. West of Gotland another brackish water species, *Eurytemora* sp. was sometimes rather abundant. Other important species were *A. aurita* *Synchaeta* spp., *B. cor. maritima*, *E. nordmanni* and *F. borealis*. In general however, the populations were smaller compared with those in the southern area. *Pleopsis polyphemoides* was important during a short period in July.

The northern area was dominated by the same copepods as was found in the middle area, but in addition, *Eurytemora* sp. and *A. bifilosa* were very abundant. *A. longiremis* was, however, of less importance. As far north as the Åland Sea (station 3′) the population of *C. hamatus* was very small. The dominant copepods in the northern Baltic proper were thus *A. bifilosa*, *Eurytemora* sp., *C. hamatus*, *T. longicornis* and *P. m. elongatus*.

Synchaeta spp., *B. cor. maritima* and *F. borealis* were sometimes important species in the northern area. Occasional specimens of brackish or freshwater species like *Keratella* spp. and *Limnocalanus macrurus* could also appear.

Other species, regularly appearing in the whole Baltic proper, but of minor importance were *Harmothoe sarsi* (larvae), *Podon intermedius, P. leuckarti, Mytilus edulis* (larvae) and gastropod larvae.

The seasonal variation of biomass and total number of individuals

The mean biomass for two-monthly periods as well as the yearly means from a five year period for different standard stations in the Baltic proper are given in fig. 15 and the corresponding values of the total number individuals per m^2 are given in fig. 16.

The biomass differed in the various areas of the Baltic proper. In the southern area the yearly means for biomass at stations S 24 and 8 A were twice as high as in the northern area and in the Arkona Sea (S 12). The mean was 24 g m^{-2} (wwt) in the Bornholm Sea (S 24), and in the eastern part of the southern Baltic proper (8 A) slightly lower. In the middle area the biomass was 17 g west of Gotland (S 41) and 18.5 g east of Gotland (F 81). At the northern-most stations the corresponding values were 13 g (F 78) and 12.5 g (F 72). In the Arkona Sea (S 12) the biomass was only 13 g which is about 50 % of the value in the Bornholm Sea.

In general, the monthly means for biomass were low from the beginning of the year until the end of April. Most of the values were less than 10 g m^{-2}. In January—February the range was from 1.6 g (F 72) to 11.3 g (S 24). The biomass was also low in March—April. The differences between the areas were however, smaller during this period. The range was only 3.3—7.1 g. For some stations, the smallest biomass of the year was recorded in March or April. The biomass increased considerably in May—June, especially in the southern and middle Baltic proper (12.5—25.3). The total number of individuals increased even more during the same period (fig. 16). The reason is that the number of copepod nauplii and younger copepodite stages was very large, but they did not contribute very much to the biomass. In the northern stations the biomass increased comparatively little

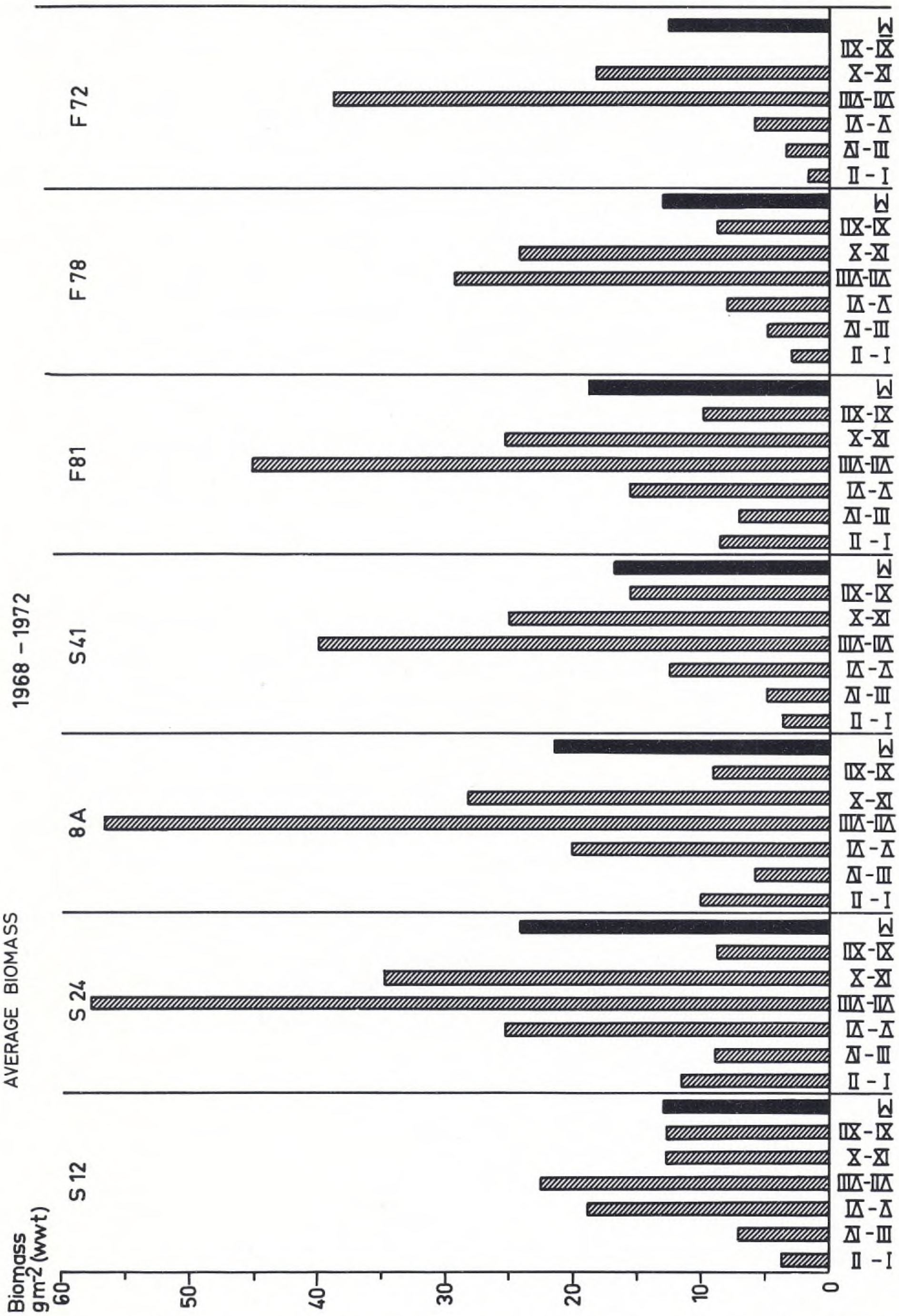

Fig. 15. The mean biomass for two-monthly periods and the yearly mean from a five year period for the seven standard stations (cf. fig. 2). The medusae and all other macrozooplankton were not included in the biomass values reproduced in this figure.

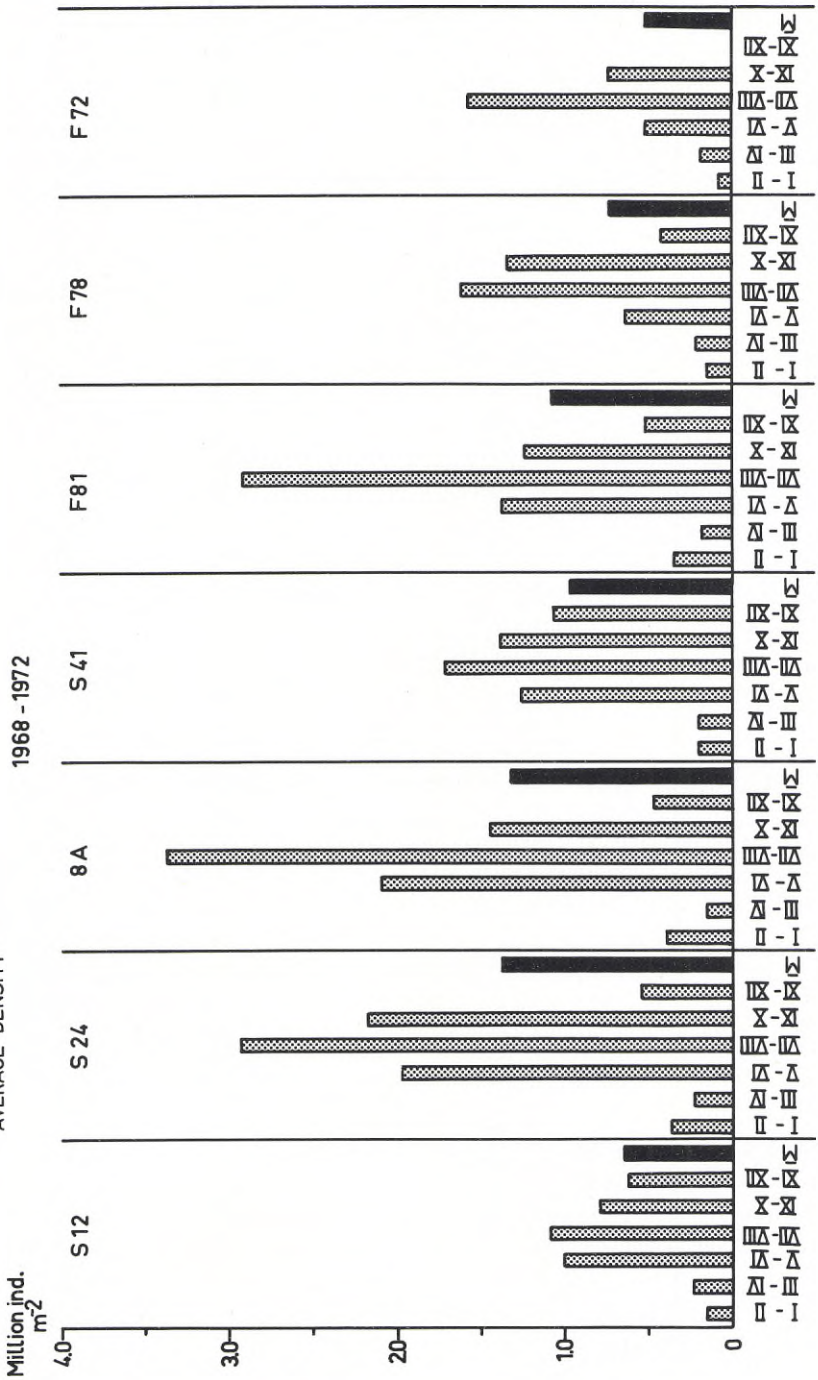

Fig. 16. The mean number of individuals for two-monthly periods and the yearly mean from a five year period for the seven standard stations (cf. fig. 2).

during this period. In general the biomass increased greatly in July—August; 2—3 times in the south and 3—6 times in the north. During this period the biomass values varied from 58 g m^{-2} at station S 24 in the southern area to 30—38 g at the most northern stations. The Arkona Sea also reached its maximum biomass at this time although the mean value was not higher than 22.6 g. As is obvious from fig. 16 the total number of individuals increased only 0.5—1 times in the southern and middle area (excluding S 12) during the same period. At the northern stations the increase was 1.5—3 times. The moderate increase in the number of individuals during the period in comparison with the high increase in biomass, can be explained by a decreased spawning activity among the copepods and a rapid growth increment for copepodites. The high number of *Bosmina coregoni maritima* in August contributed greatly to the maintaining of a high number of individuals in the sea. Without *Bosmina*, the mean number of individuals would have dropped drastically. The highest mean values were 2.8—3.4 million ind. per m^2. The mean value for all stations during July—August was 2.1 million ind. per m^2.

In September—October the mean biomass values were still rather high, although the values for September—October decreased by 17—50 % in comparison with the previous period. A similar decrease in the number of individuals was obvious at most stations. The range was 0.7—2.2 million ind. per m^2. Later in November—December the biomass values varied from 8.7 to 15.6 g per m^2 and the total number of individuals varied from 0.4 to 1.1 million per m^2 in the different areas.

The seasonal variation of important species and their contribution to the biomass

The biomass did not drop on any occasion below 1 g m^{-2} (wwt) in any part of the Baltic proper. Except at station F 72, the mean value was 3 g or more during the least productive period of the year (fig. 15). The reason for this was that *Pseudocalanus minutus elongatus* contributed on the average at least 2.5 g each month of the year (table 3). *Temora longicornis* was also important but the biomass of this species amounted to 2.5 g or more only for a restricted period of the year (August—October in the north and April—February in the south) (cf. discussion about production p. 53).

The largest proportion of the biomass thus consisted of *P. m. elongatus* in the beginning of the year. Later, in February—March, *T. longicornis* made an important contribution to the biomass in the southern and middle part of the Baltic proper. In April, the two above-mentioned species and *Fritillaria borealis* accounted for the largest proportion of the biomass. The same three species were also important in May, in addition to *Acartia* spp., *Synchaeta* spp. and *Evadne nordmanni*. In June—July, all the copepods except *Eurytemora* sp. (table 3) were important. Other species of significance were *Synchaeta* spp., *Podon leuckarti, Evadne nordmanni* and *Fritillaria borealis*. In July, *Pleopsis polyphemoides* could to some extent be important in the northern and middle area. In August, most species in table 1 were important. The copepod *Eurytemora* sp. then became an important fraction of the biomass at the northern stations. This was also true for *Bosmina coregoni maritima* which was very important, especially in the southern area. During August, the annual maximum for larvae of gastropods and *Mytilus edulis* usually occurred. In September, the plankton fauna was dominated by the copepods, the cladocerans *B. c. maritima, P. intermedius, E. nordmanni* and the larvae of *M. edulis*. In October, when the temperature had dropped to 10—12°C, the copepods dominated the plankton fauna completely. As it is obvious from table 3, *Acartia* spp. and *P. m. elongatus* were important in all areas until the end of the year. *T. longicornis* was also abundant, except in the northern area, while the populations of *C. hamatus* and *Eurytemora* sp. decreased after October—November (tables 2 and 3).

Table 2.
The maximum biomass and density of some important species in the northern (N), middle (M) and southern (S) parts of the Baltic proper (copepods excluded).

	Month	Biomass mg m^{-2} N	Biomass mg m^{-2} M	Biomass mg m^{-2} S	Individuals m^{-2} N	Individuals m^{-2} M	Individuals m^{-2} S
Synchaeta spp.	May–Jul	650	2 000	1 000	280 000	1 000 000	480 000
Bosmina cor. maritima	Aug–Sep	13 600	22 600	28 000	1 360 000	2 300 000	2 800 000
Podon intermedius	Sep	100	100	200	6 000	6 000	12 000
Podon leuckarti	Jun–Jul	15	15	35	1 500	1 500	3 500
Pleopsis polyphemoides	Jul	?	920	?	?	92 000	?
Evadne nordmanni	May–Sep	200	300	2 000	20 000	30 000	200 000
Gastropoda (larvae)	Aug				500	1 000	2 000
Mytilus edulis (larvae)	Aug–Oct	2,5	2,5	50	650	650	13 000
Sagitta elegans baltica	All months		11 500	70 000		500	3 000
Fritillaria borealis	Apr–Jul	1 000	1 400	3 700	100 000	140 000	370 000

Table 3.
The maximum and the usual range of biomass for the most important copepods of the northern (N), middle (M) and southern (S) parts of the Baltic proper.

	maximum biomass mg m^{-2} (wwt) N	maximum biomass mg m^{-2} (wwt) M	maximum biomass mg m^{-2} (wwt) S	Month	Usual range of biomass mg m^{-2}(wwt) N	Usual range of biomass mg m^{-2}(wwt) M	Usual range of biomass mg m^{-2}(wwt) S	Month
Acartia spp.	6 000–8 500	5 200–7 500	10 500	Aug–Oct	2 500–5 000	2 500–5 000	2 500–5 000	May–Dec
Eurytemora sp.	4 800–6 600	200	–	Aug–Sep	1 000–2 000	–	–	Aug–Oct
Centropages hamatus	2 300–9 100	3 000–9 300	5 800–9 400	Jul–Sep	1 000–2 000	1 000–2 000	1 000 2 000	Jun–Nov
Temora longicornis	7 500–10 000	10 000–14 500	11 500–16 500	Jul–Sep	2 500–5 000	2 500	2 500 5 000	Aug–Oct, Jul–Feb, Apr–Feb (N) (M) (S)
Pseudocalanus minutus elongatus	5 000–9 500	12 500–23 500	17 000–31 500	May–Sep	2 500–5 000	5 000–10 000	4 000–10 000	All months

Discussion

Environment and fauna

In many sea areas temperature is the master factor, affecting both the physiology and the ecology of zooplankton. Temperature influences physiological factors such as mortality, survival, metabolic rate, feeding rate, embryonic development and ecological features such as community structure, diapause and energy flow. In general this is true also for the Baltic proper. However, in a body of brackish water the salinity may also be a very important factor. Brackish water of 6—8 ‰ creates critical conditions for many zooplankton species. The stenohaline species are excluded due to their requirement for high salinity, and many euryhaline species live in the lower range of their salinity tolerance (cf. Remane 1940). There are, however, a few marine species which can tolerate a salinity as low as 2 ‰ (Ackefors 1969 a). This means that the salinity in certain cases is the master factor, but that in general it is the combined effect of temperature and salinity that regulates the fauna (cf. Kinne 1963, 1964 a,b).

The low oxygen concentration in the deep basins and the periodical development of hydrogen sulphide may have had a drastic effect upon the life in the Baltic Sea and especially upon the benthic fauna (Shurin 1962). This implies that in particular areas and levels of the water column the oxygen conditions are of decisive importance for the community. The effects of temperature, salinity and oxygen or a combination of two or three of these factors are decisive in an area like the Baltic, where many species live in the lower range of their tolerance limits. This is to some extent clear from the analyses of field samples, and might be more thoroughly explained by laboratory experiments. The influence of biotic factors such as food supply and competition may be difficult to distinguish from the influence of such abiotic factors as e.g. salinity, without comprehensive laboratory experiments. The lack of information concerning microzooplankton ($<200\,\mu m$) is embarrasing when certain results have to be explained.

On the other hand, the growing knowledge of the phytoplankton flora, gained in recent years, is of utmost importance for the understanding of the biocenosis of the Baltic.

Temperature

Temperature affects most processes in the plankton community, directly or indirectly. As is obvious from our results, the biomass of most species increased with increasing temperature. The maximum was reached simultaneously with the highest temperature in August, or slightly afterwards, in September. The mean values for a two-months-period indicate that the maximum total biomass occurred in July—August (fig. 15). Corresponding mean values for June—July and August—September (not published) indicate that the latter period was the most productive one. Following the yearly cycle, it is obvious that the biomass was in the range 1.5—11.5 g per m^2 (wwt) during the first four months of the year, when the surface temperature was less than 4°C. Most of the biomass consisted of two species, which prefer cold water all the year around, viz. *Pseudocalanus m. elongatus* and *Fritillaria borealis* (cf. figs. 12 and 14). In May—June, when the temperature rose from 4 to 12°C, the mean values for the biomass were in the range 6—25 g per m^2 (wwt). In addition to the above-mentioned species, *Synchaeta* spp. and *Evadne nordmanni* were also important. Beyond all comparison, *P. m. elongatus* was still the most important species. On certain occasions, the biomass of this species alone exceeded 20 g m^{-2} (fig. 12). During the warm season, July—September, the cladoceran *Bosmina cor. maritima* (fig. 6) and the copepods *Acartia* spp. (fig. 9), *Eurytemora* sp. (fig. 10), *Centropages hamatus* (fig. 11) and *Temora longicornis* (fig. 13) were very abundant and contributed greatly to the total biomass. *P. m. elongatus* remained the most important species. In July—August the biomass amounted to 23—58 g per m^2 and in September—October to 13—35 g per m^2. At the end of the year when the temperature was in the range 12—4°C, all copepods except *Eurytemora* sp. and *Centropages hamatus* were important and the biomass was in the range 9—12 g per m^2.

With reference to the seasonal variations in biomass, the following conclusions may be drawn regarding their optimum temperatures. The optimum temperature in this case implies the greatest abundance in relation to the surface temperature. This is, of course, only a rough estimate, since the depths reached by the surface net hauls (25—0 m) as well as the deep net hauls were, in spring, summer and autumn, at levels with much lower temperatures than the surface.

Some species appeared abundantly in a broad temperature range, the so called eurytherm species. In the Baltic proper this is the case for *Aurelia aurita, Synchaeta* spp., *Evadne nordmanni, Podon leuckarti* and *Acartia bifilosa*, which were most frequent in a temperature range of 6 to 16°C. *Pleopsis polyphemoides* is a stenotherm species which appears most abundantly in the temperature range of 15—16°C. Many other species were also stenotherm, although they appeared abundantly at slightly higher temperatures than 15—16°C, viz. *Keratella* spp., *Bosmina cor. maritima, Podon intermedius, Eurytemora* sp., *Centropages hamatus* and *Temora longicornis.*

Some species preferred the cold water all the year around. They were never found above the thermocline in summer, but in other seasons they also appeared in surface waters. The most important species were *Pseudocalanus m. elongatus* and *Fritillaria borealis.* Other cold stenotherm species were the larvae of *Pleurobrachia pileus, Limnocalanus macrurus, Mysis relicta* and *Mysis mixta.* The last three species, in addition to *Halitholus cirratus* are glacial relicts. The relicts may also occur in deep lakes in the Baltic area (Segerstråle 1956, 1962).

The optimum temperature may be different in various marine areas. In the North Atlantic the optimum temperature for *E. nordmanni* was 13.5°C (Gieskes 1971 b); in the Gulf of Lion (Mediterranean Sea) 19°C (Thiriot & Vives 1969); in the Gulf of Trieste (Mediterranean Sea) 13.7°C (Specchi *et al.* 1974) and in the Inland Sea of Japan 15°C (Onbé 1974). According to our results, the species was most frequent in May—June in a temperature range of 8—12°C, but it was also important at higher temperatures. This indicates that the optimum temperatures are quite different in various areas due to the influence of both abiotic and biotic factors. On the other hand, a detailed ecological investigation of the vertical distribution may give more precise information about where in the water column, and thus in what temperature the maximum density of specimens occurs. *P. polyphemoides* was most abundant, when the surface temperature was 12—17°C in a coastal area of the Baltic proper (Ackefors 1969 a). The greatest accumulation was, however, in the thermocline where the temperature was about 7—8°C (Ackefors 1969 b). Later laboratory experiments showed that the preferred temperature was about 8°C (Ackefors & Rosén 1970).

The seasonal variation in surface temperature greatly influences the vertical distribution as well as the diel migration. Cold stenotherm species such as *P. m. elongatus* and *F. borealis* did not occur above the thermocline in summer. Euryhaline marine species such as *T. longicornis and C. hamatus* appeared below the thermocline during the daytime, but at dusk they migrated upwards through the thermocline and appeared as far up as the warm surface water during the night (Ackefors unpubl.). There were differences in the vertical distribution of the copepods during winter and summer, indicating that they were more homogeneously distributed in the water column during the cold season. In spring, summer and autum the older copepodite stages generally appeared at deeper levels in comparison with younger copepodite stages and nauplii. The present results seem to indicate that there is no diel migration in winter. The migration seems to start simultaneously with the forming of a thermocline in May—June.

The reproduction of some zooplankton species is greatly affected by the seasonal variation in temperature. Rotifers, cladocerans and some copepods overwinter mainly as winter "resting" eggs. While the presence of dormant eggs among rotifers and cladocerans has long been quite well-known, it was only recently described in a marine copepod in laboratory and field studies (Zillioux & Gonzales 1972).

The rotifers, such as *Synchaeta* spp. develop three types of eggs during their reproduction cycle; thin shelled amictic and mictic eggs, and mictic thick shelled eggs. The latter type probably accumulate on the bottom in connection with the low maximum abundance during the autumn. Although single individuals were found during the whole winter in the southern Baltic proper, the very rapid growth of the population in May—June must be caused at first by the hatching of resting eggs. This is correlated with the temperature interval of 8—12°C.

The cladocerans also overwinter using resting eggs. Purasjoki (1958) found that the first individuals of *B. cor. maritima* may hatch in spring, when the temperature is still below 1°C. We found single specimens in April, but the population did not increase very rapidly until the end of August. The rapid growth of the population in the open sea at temperatures higher than 15°C was probably caused mainly by parthenogenetic propagation. The population can grow very fast as the turnover rate is only five days at this water temperature (Zawislak 1972).

P. intermedius, P. leuckarti and *P. polyphemoides* overwinter with resting eggs. With increasing temperature during the summer these cladocerans replaced each other in the fauna. The population maximum appeared at the following surface temperatures: *P. leuckarti* (6.5—16°C), *P. polyphemoides (15—16*°C), *P. intermedius* (16—17°C).

E. nordmanni was the only cladoceran which was found in every month of the year. From the end of May until November it was of great importance, i.e. in the temperature range of 8—20°C.

Fish & Johnson (1937) found evidence that the first spring nauplii of some neritic copepods developed from winter eggs. Subsequently, many authors suggested that winter egg dormancy might explain the winter survival of some neritic marine copepods. Zillioux & Gonzales (1972) proved the existence of winter egg dormancy for *Acartia tonsa* in field and laboratory studies. Later, other authors described the same phenomenon for other marine calanoid copepods, e.g. Kasahara *et al.* (1974), Grice & Lawson (1976). It is likely that at least one copepod, *A. bifilosa*, owerwinters with resting eggs in the Baltic. In the northern Baltic proper, where *A. bifilosa* is much more abundant than *A. longiremis*, very few adults appeared in winter. The sudden increase in numbers of nauplii in February—March, with densities of 10^5—10^6 nauplii per m^2 was probably caused by the hatching of winter eggs of *A. bifilosa.*

In the Baltic proper we found a successive maximum abundance of nauplii of the various copepod species to be correlated with increasing temperature during spring: *Acartia* spp. in March—April (0—4°C), *P. m. elongatus* in April—May (4—8°C), *T. longicornis* in May—June (6—10°C), *C. hamatus* in May—June (8—10°C) and *Eurytemora* sp. in June (8—10°C).

Salinity

The low and stable salinity in the Baltic proper models a specific habitat with a mixture of marine, brackish water and freshwater organisms. The marine species live in a hypo-osmotic milieu in the lower range of their tolerance limits, and the freshwater species in a hyper-osmotic milieu in the upper range of their tolerance limits. The salinity range of 6—8 ‰ is critical for both groups of organisms (cf. Remane 1940). This means that the number of marine and freshwater species are very much reduced in the Baltic proper. As there are very few brackish water species, the total number of zooplankton species is limited. Only three endemic brackish water species appear in the Baltic, viz. *Bosmina coregoni maritima, Keratella quadrata platei* and *K. cochlearis recurvispina,* which is explained by the fact that the Baltic is a young sea seen from the geological point of wiew (Segerstråle 1957 and 1962). The low salinity affects the physiological processes of the euryhaline marine organisms which have established populations in the Baltic. Those organisms are either osmo-regulators (homeoosmotic species) or osmo-conformers (poikilosmotic species) (cf. Kinne 1964 a, b). At a certain salinity level the amount of energy used for maintaining an acceptable internal ion concentration is so great, that they are outnumbered by organisms better adapted to these salinity conditions.

The salinity tolerance limits for different species greatly influence their horizontal and vertical distribution. In the deep basins of the southern Baltic, the occasional appearance of marine species is to be expected in connection with salt water inflows from the Belt Sea (cf. Mankowski 1951 a, b, 1962). In our investigations we have found single specimens of *Sarsia tubulosa, Cyanea capillata* and *Calanus finmarchicus S.L.* There are also marine species which are present permanently and propagate in the deep basins of the southern Baltic proper where the salinity exceeds 14—15‰, e.g. *Oithona similis* and *Sagitta elegans baltica*. Both species constituted very important populations in the Bornholm Deep during the years 1968—1972. Single specimens of the former species also appeared occasionally in the bottom water of the northern Baltic proper, while the latter appeared as far to the north as the Gotland Deep. A third group of organisms with an even broader range of salinity tolerance consisted of three species; the larvae of *Pleurobrachia pileus, Pseudocalanus m. elongatus* and *Fritillaria borealis*. They appeared in the whole Baltic proper in salinities as low as 6‰, but only in water with a temperature lower than 10°C. The explanation is probably that regulation of the body fluid in euryhaline marine organisms is often faciliated when the organisms live in cold water (Pantin in Schlieper 1958). A fourth group of organisms consists of those euryhaline marine organisms which live and propagate in waters with salinities as low as 6‰, while also appearing in warm water. The cnidarian *Aurelia aurita,* the copepods *Temora longicornis, Centropages hamatus* and the cladoceran *Podon leuckarti* are the most important species belonging to this group. A fifth group of marine species appeared in salinities as low as 2‰, the so called holeurysaline species (cf. Ackefors 1969 a). They are represented by the cladocerans *Evadne nordmanni*, *Pleopsis polyphemoides* and *Podon intermedius*.

The brackish water species *Bosmina coregoni maritima* appeared abundantly in the Baltic proper. In laboratory experiments the species tolerated the salinity range 2.5—7.5‰ very well. The survival in 10 and 12.5‰ was poor while 15‰ was lethal (Ackefors 1971 a). The presence of *B. cor. maritima* in extremely low salinities and nearly freshwater conditions is reported by Halme (1958), and in salinities slightly higher than 10‰ by Waldmann (1959). *Eurytemora* sp. appeared in small numbers in the southern Baltic proper in salinities of about 7–8‰, while the population in 6—7‰ salinity in the northern Baltic was very large. Analyses of a large number of samples from the Baltic proper and the Åland Sea indicate that the species was probably outnumbered by other copepods due to competition in the central and southern Baltic proper. This means that the salinity *per se* does not seem to limit an abundance in the southern Baltic proper. The other brackish water species as *Keratella* spp. and *Limnocalanus macrurus* appeared only occasionally in the northern Baltic proper, indicating a narrower salinity tolerance with the upper range around 6 ‰.

The occasional appearance of *Cyclops* sp. indicates that single specimens of freshwater species may appear in salinities up to 6—7 ‰. The incidence of spawning is restricted to salinities less than 6 ‰ (cf. Lindquist 1959).

Generalizing about the above-mentioned species in relation to salinity tolerance it is quite obvious that the plankton community in the Baltic proper consists of five groups of marine organisms and two groups of brackish water and freshwater organisms. The low salinity in the Baltic proper restricts the number of species in comparison with other areas west of Sweden (Zenkevitch 1963). On the other hand, the number of specimens of the various species is generally higher than in other areas. The capacity of each species to adapt itself to the brackish water conditions is decisive for the size of the population. The number of specimens of each species is thus determined by genetical selection or non-genetical adaptation evolved during the historical development of the Baltic proper.

The small salinity increase (0.5—1 ‰) in the Baltic proper since the middle of the thirties has had great biological consequences. This has been stated by many authors (cf. Ackefors 1969 a). The brackish water species *Acartia bifilosa* and *Eurytemora* sp. are nowadays less important in the middle Baltic proper west of Gotland, and the euryhaline marine copepods *Temora longicornis* and *Pseudocalanus m. elongatus* are more important than in the 1920's (cf. Hessle & Vallin 1934, Ackefors 1969 a). In the Bothnian Sea, Lindquist (1959) found that *T. longicornis* was rather common, which was not the case earlier.

Oxygen

The appearance of *Pseudocalanus m. elongatus* below the halocline (50—70 m depth) in oxygen concentrations of less than 2 ml O_2/l was conspicuous. An accumulation of plankton at levels with low oxygen concentrations has also been reported from other marine areas (Longhurst 1967). However, the conditions in brackish water with low oxygen concentrations are even more adverse than in marine waters. The oxygen consumption of euryhaline marine organisms increases with decreasing salinities due to the increasing metabolic rate. This might explain the low number of organisms of species other than *P. m. elongatus* below the halocline. Large numbers of *Harmothoe sarsi* larvae were malformed in areas with poor oxygen conditions. This seems to be a regular phenomenon in the Baltic proper (cf. Ackefors 1969 a, 1971 b). The alternating periods of adequate and deficient oxygen conditions with the development of hydrogen sulphide in the bottom water of the deep basins during the period 1968—1972 (figs. 4 a, b) have certainly influenced the bottom fauna (cf. Shurin 1962), as well as the nutrient content of the water (cf. Fonselius 1967). From the present results it is, however, impossible to draw any conclusions about changes, e.g. in the production of larvae of the bottom invertebrates. Nor is it possible to see any evidence of increasing productivity after the salt water inflows in 1968 and in 1972. After such inflows, the nutrientrich bottom water is forced out of the basins and the surface layers are supplied with nutrient salts, which increases the productivity of the water.

The dynamics of the plankton flora and fauna

The zooplankton community consists of herbivorous, omnivorous and carnivorous species. There are comparatively few species adapted to the low salinity brackish water conditions, due to physiological reasons mentioned above. Seen from a geological point of view, the Baltic is a young sea, and the immigration of faunal and floral components is closely connected with the events following the last glacial period. The alternation between epochs of salt and freshwater has resulted in a mixture of freshwater, brackish water and marine species (Segerstråle 1957, 1965). The selection of species that has evolved therefore forms a unique biocoenosis in the Baltic area.

During winter, the primary production has a value of about 30 mgC per m^2 and day and the phytoplankton biomass is in the order of 0.1 g per m^2 (wwt). The flora is dominated by the diatoms (Ackefors & Lindahl 1975 a, b). The zooplankton community consists mainly of *Pseudocalanus m. elongatus*, *Temora longicornis* and *Fritillaria borealis*. Most of the zooplankton biomass, which is in the order of 2—10 g per m^2, consists of *P. m. elongatus*. It is likely that there is very little energy flow within the plankton community at this time of the year. Individuals of *P. m. elongatus*, which overwinter mainly as C. IV—V, utilize their storage of fat during this season.

From the end of February onwards, primary production increases, and a large phytoplankton biomass accumulates during March—May, which is, to a small extent, utilized by the zooplankton community. The primary production reaches maximum levels of 1,000 mgC per m^2 and day and the phytoplankton biomass exceeds 10 g per m^2, especially in the northern area. From March until June the nauplii and adults of the various copepod species dominate the fauna. The nauplii attain their maximum abundance during this period. The proliferation of *Acartia* nauplii starts at the end of February and successive hatching of overwintering eggs and spawning occurs until June for the various species. The nauplii probably consume to some extent small phytoplankton such as the monads, which are very abundant. However, the bulk of the phytoplankton is not utilized by the zooplankton or the pelagic fish larvae. This is evident from looking at the accumulated biomass of diatoms in particular. The result is a continous flow of phytoplankton towards the bottom, supporting the bottom fauna. The main diet of the bottom invertebrates during spring is therefore likely to be phytoplankton. This energy flow will induce the spawning of some invertebrates. For example, the main spawning period for *Harmothoe sarsi* in the Kiel Bight and at Tvärminne coincides with the spring phytoplankton maximum (Sarvala 1971).

In early summer the primary production drops to 200—500 mgC per m^2 day and the phytoplankton biomass, which consists mainly of diatoms and monads, is small, or 1—2 g per m^2. The zooplankton biomass is mostly in the order of 5—25 g per m^2 with low values in the north and high values in the south. The bulk of the biomass consists of herbivorous, omnivorous and carnivorous copepods. The percentage of carnivorous organisms increases during this period of the year. The rotifers *Synchaeta* spp. and the cladocerans *Evadne nordmanni, Podon leuckarti* and *Pleopsis polyphemoides* attain their maximum abundance. *Synchaeta* spp. and *E. nordmanni* attain biomasses of up to 2 g per m^2. The importance of some species of the genus *Synchaeta* is probably very great, as the turnover rate is rapid and consequently the production very high. The growth of the *Synchaeta* populations seems to be dependent on the production of ciliates, which in their turn are dependent on pelagic bacteria (Hagström, Hernroth, Larsson pers. comm.). From this time onwards the top carnivore *Aurelia aurita* is very abundant. Due to an unsatisfactory sampling technique for this medusa we have not included this species in our biomass calculations. It is quite evident, however, that there is a great energy flow directed towards *A. aurita* during the whole summer and autumn, which has to be taken into consideration when estimating the total energy budget for the pelagic ecosystem of the Baltic proper.

In late summer and in the beginning of autumn primary production increases to 500–700 mgC per m^2 and day. Grazing by the zooplankton is extensive and consequently, the phytoplankton biomass is small. The zooplankton biomass reaches levels of 60 g per m^2, which may to a great extent consist of the herbivorous cladoceran *Bosmina coregoni maritima.* Even if this cladoceran constituted only about 30 % of the biomass, it accounted for 60 % of the production during a few weeks in August—September. The primary production during the third quarter was calculated to be 40—60 % of the yearly production by Ackefors & Lindahl (1975 a, b). As the phytoplankton biomass values are low, is is quite obvious that the effect of grazing by *Bosmina* as well as the herbivorous copepods is very great. The phytoplankton flora is dominated by the blue-green algae, the diatoms and the monads, the first group of phytoplankton not being utilized by the zooplankton. The energy flow from the pelagic ecosystem towards the bottom at this time of the year will therefore mainly be accounted for by blue-green algae and dead or ageing zooplankton.

During summer the diversity of the zooplankton community is at its greatest. The larvae of bivalves, gastropods and polychetes appear in the water, but they do not play an important role. There are rather few bottom invertebrates in the Baltic and the abundance of pelagic larvae is very low. Therefore *B. cor. maritima* and the copepods are the most important components of the plankton community during summer (cf. tables 2 and 3).

During autumn the importance of all the species, including the copepods, decreases. The populations of the warm stenotherm copepods *C. hamatus* and *Eurytemora* sp. decrease rapidly after September—October. *P. m. elongatus, T. longicornis* and *Acartia* spp. are still important in October—November. The primary production values decreases to less than 200—300 mgC per m^2. The relative importance of diatoms and monads increases. Due to a reduced grazing activity the phytoplankton biomass tends to increase, and the zooplankton biomass is in the order of 10—15 g per m^2. The overwintering zooplankton fauna consists mainly of *P. m elongatus,* and to a lesser extent of *T. longicornis* and *F. borealis.*

The production of food and its utilization by the pelagic fishes

The commercial fish catches consist mainly of three species in the Baltic proper, viz. herring, sprat and cod. The yearly catches of the pelagic fishes, herring and sprat, amount to about 500,000 tons. The catches of cod amount to about 200,000 tons. This implies that about 70 % of the catches consist of pelagic fishes. Those fishes are to a large extent dependent on the production of zooplankton.

Most of the herring catch consists of spring spawners (Anon. 1976). They spawn in May—June, which is also the spawning time for sprat and cod in the southern Baltic proper. Further to the north, the spawning of sprat takes place in June—July. According to Ojaveer & Simm (1975) the survival of herring larvae after they begin exogenous feeding is largely dependant on the availability of copepod nauplii and C. I—III. This is a period of maximum abundance for the relevant stages of *Centropages hamatus* and *Temora longicornis* in off-shore conditions, while *Eurytemora* sp. may be very important in coastal areas (cf. Hernroth in print). The spawning time of spring-spawning herring in the Gulf of Riga was regulated by temperature conditions and so was the production of *Eurytemora hirundoides* (Ojaveer & Simm 1975). Due to this fact, the peak production of *E. hirundoides* usually coincides with the maximum spawning activity of herring. If the intensity of zooplankton production is low the survival of the herring larvae is impaired. Aneer (1975) investigated the stomach contents of spring-spawning adult herring in the Askö area. He found that planktonic crustaceans were of considerable importance as a food item in April—June in 1971 and that they dominated the diet from January until August in 1972. The lower fat content of the herring in a certain period in 1970/71 was probably due to the absence or scarcity of zooplankton in the stomachs of the herring.

Popiel (1951) investigated the feeding habits and diet of herring in the Gulf of Gdansk. He found that younger herring feed to a large extent on copepods. The percentage of copepods consumed decreases as the herring become older. In the smallest size class (10—14 cm) the copepods made up 85 % of the diet while in the largest size class (> 25 cm) the corresponding value was 14 %. In off-shore conditions *Pseudocalanus m. elongatus* constituted most of the stomach contents, and in coastal areas *T. longicornis* was the main food-item. In accordance with Aneer (1975) he also found that the copepods dominated at certain times of the year. In his area they were the major component of the diet in May—June, but they also made a certain contribution in the intensive feeding period from July to December. At that time of the year, fish larvae and Mysidacea were more important than copepods. The greatest food supply for planktonic feeding fishes off the coast is available in late summer or early autumn according to our results. This can be correlated with the yearly fluctuation of the fat content in sprat. The highest fat content in the adult sprats from the Bay of Gdansk was found in late autumn October—November (Elwertowski & Maciejczyk 1964).

In the Pomeranian Bay, Wiktor (1967) investigated the feeding habits of larvae and fry of autumn-spawning herring. She found that in the stomachs of larvae of 35 mm or less, *Neomysis* and microzooplankton dominated. (Microzooplankton in this case includes copepods and cladocerans.) In winter the main food item was copepods, and in summer cladocerans. She also found that rotifers and veliger larvae were important food items in May—June.

According to our analyses of the zooplankton production in various parts of the Baltic, the values may amount to about 20 gC per m^2 and year in the southern Baltic proper and 10 gC m^{-2} $year^{-1}$ in the northern Baltic proper. In those years in which favourable conditions occur, nearly half of the production in the southern Baltic consists of *Bosmina coregoni maritima.* If this is not the case, the total zooplankton production will be much less. The high production of *B. cor. maritima* is always restricted to a short period of about six weeks in August—September, when the temperature is above 15°C.

The primary production is estimated to be about 120 gC m^{-2} $year^{-1}$ in the southern Baltic proper, and about 90—110 gC m^{-2} $year^{-1}$ in the middle Baltic proper (Ackefors & Lindahl 1975 a, b). The highest production occurs in the third quarter of the year.

According to our present knowledge we can now roughly state that the primary phytoplankton production is at least 100 gC m^{-2} $year^{-1}$, the secondary zooplankton production is in the order of 10—20 gC m^{-2} $year^{-1}$ and the fish production is in the order of 1 gCm^{-2} $year^{-1}$ in the Baltic proper. A lot of detailed investigations are necessary before we can elucidate the energy flow within the pelagic ecosystem. Biochemical investigations of important species with respect to respiration, metabolic rate, excretory nitrogen etc. and more detailed investigations into the food web, starting with bacteria and microzooplankton seem to be the most important tasks in the future if a more comprehensive knowledge of the Baltic ecosystem is to be attained.

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