DYNAMICS OF THE MAIN MESOZOOPLANKTON TAXA IN THE BORNHOLM BASIN (1988–1992)

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Abstract. Within the monitoring programme of the Helsinki Commission (HELCOM) the mesozooplankton of the Bornholm Basin (ICES subdivision 25, station BMP K2) was sampled by the WP-2 net (100μm) 5–8 times a year in 1988–1992. Abundance, biomass, secondary production and productivity (P/B) were given for mesozooplankton groups and copepod species. Environmental factors recorded were temperature, chlorophyll a and primary production.

Within copepods, the dominant species were *Temora longicornis* and *Pseudocalanus minutus* with yearly peak values of 40–50% of the monthly copepod numbers and biomasses. The annual production of *Temora longicornis* was highest (6.5g $C*m^{-2}*y^{-1}$). The biomass of all copepods was at its maximum in June (mean = 2.25g $C*m^{-2}$), especially in 1992 (3.65g $C*m^{-2}$). The differences between results from two methods used to calculate the production of copepods were greatest in June and July.

The cladocerans were only important in summer and the appendicularians only in spring. The productivity (P/B) of the appendicularians was highest of all mesozooplankton groups. Numbers and the biomass of the meroplankton were one or two orders of magnitude below the holoplanktic groups.

Key words: Baltic Sea, mesozooplankton, annual patterns, production

Introduction

Since the work of Apstein in 1906, the annual course in abundance or biomass of single mesozooplankton taxa of the Baltic Sea has been extensively surveyed. Knowledge about the annual patterns of abundance or biomass of the mesozooplankton are useful for fisheries scientists, because the mesozooplankton is important food for larval and adult fish. The conditions in the Bornholm Basin in the Southern Baltic are of particular interest, because that is the only spawning ground in the Baltic Sea for the Eastern Baltic cod (*Gadus morhua callarias*). In other potential spawning areas the oxygen conditions are insufficient (Plikshs *et al.*, 1993). Surveys of the Bornholm mesozooplankton for the years 1991–1993 have recently been reported by Krajewska-Soltys & Linkowski (1994).

This paper presents data of the Baltic Monitoring Programme (BMP) on mesozooplankton abundance in the Bornholm Basin for each of the years 1988–1992. Viitasalo (1992) also used BMP data to describe the annual courses in abundances of single copepod species or other taxa of the mesozooplankton, but from the Northern Baltic Proper. The BMP data about the Bornholm Basin were used as a background for investigations about the mesozooplankton vertical distribution not described in this paper (Dahmen, 1995). The vertical distribution was investigated by a 47µm net, whereas in the BMP the WP-2 net was used, so that a comparison of results by the two nets was possible.

Materials and methods

HELCOM methods

The Bornholm Sea is part of the Southern Baltic Proper with a maximum depth of 105 m. The Bornholm Basin is the central deeper part of the Bornholm Sea. The BMP mesozooplankton raw data were obtained according to the guidelines set by the Helsinki Commission (HELCOM, 1983, 1988):

> The monitoring station in the Bornholm Basin called BMP K2 is situated at the position 55°15.00´N 15°59,00´E and has a depth of 90 m. For sampling a WP-2 net was used with a mesh size of 100 µm, which was hauled vertically with a speed of about 0,5 $m*s^{-1}$. Sampling took place 5–8 times a year in 1988–1992. The depth intervals the water column was devided into were dependent on the water stratification, but for this publication the abundances were summed up over the whole water column. For subsampling the Kott whirling apparatus or the Folsom sample splitter were used. The volume of the subsample was chosen so, that at least 500 specimens were retained. The biomass was calculated as the sum of individual volumes. The list of individual volumes elaborated by the BMB working group on mesozooplankton biomass assessment (Hernroth ed., 1985) was used. For cladocerans, larvae of mollusks and polychaetes and for *Microsetella norvegica* the individual volumes were taken from Hernroth (1975).

The BMP zooplankton data were obtained from Poland for all five years, for 23 August 1988 from Finland and for 1991 and 1992 additionally from the Institut für Ostseeforschung Warnemünde in Germany.

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The values of chlorophyll a concentration and in situ – primary production were obtained also according to the HELCOM guidelines by the Institut für Ostseeforschung Warnemünde.

Evaluation of data

The wet weights were transformed to carbon contents by factors of 0.08 (rounded) for copepods, 0.06 for cladocerans, 0.1 for appendicularians and 0.08 for polychaetes and mollusks (Heerkloss & Vietinghoff, 1981; Schneider, 1989).

The secondary production was calculated for copepods according to a holistic approach (Huntley & Lopez, 1992) and by summarizing the production values of single species and their development stages (Edmondson & Winberg, 1971). The production of cladocerans was calculated with an equation formed for *Bosmina coregoni* (Kankaala *et al.*, 1984). For appendicularians a P/B value of 0.27 d^{-1} (rounded) set up for *Fritillaria pellucida* at 13.5°C (Fenaux, 1976) was adapted to other temperatures with the Q_{10} rule and a Q_{10} value of 2 (Ikeda, 1985). The production of rotifers was determined with a modified "increment summation" method (Pauli, 1991).

The production values for certain depth strata were calculated using the zooplankton abundance and the temperature of the respective depth. The values then were summed up to the production of the whole water column. The temperatures of September were averaged from the values of August and October. The averaged annual courses in biomass and production are based on years with a different distribution of sampling dates. That means that the mean values of the months refer to a different number of single values. The annual production was calculated assuming the production from December to February being zero and missing months having an interpolated production. Nauplii were not included in the abundance and production of single copepod genera, because the nauplii were not counted always by seperating genera. *Eurytemora affinis* and *Microsetella norvegica* were not considered for the copepod production and polychaetes and mollusks not for the mesozooplankton production.

Additionally horizontal tows were conducted using a net with a mesh size of 47 µm and a mouth diameter of 4 cm. The towing speed was 3 kn. The tows were concentrated at the lower depths with a depth interval of 5 to 10 m. The abundances of the single depth strata were integrated over the whole water column. The records were made on 13 October 1988, 13 July 1991 and 9 April 1992. More details are given by Dahmen (1995).

The annual courses in chlorophyll content (0–30 m) and primary production were averaged over the years 1988–1992 in the same manner like those of mesozooplankton biomass and production. Likewise the annual primary production was calculated from the daily values in the same way like the annual mesozooplankton production.

Results

Annual course of temperature

The temperature profiles measured by the BMP working groups in the Bornholm Basin in the years 1988–1992, are given in Fig. 1.

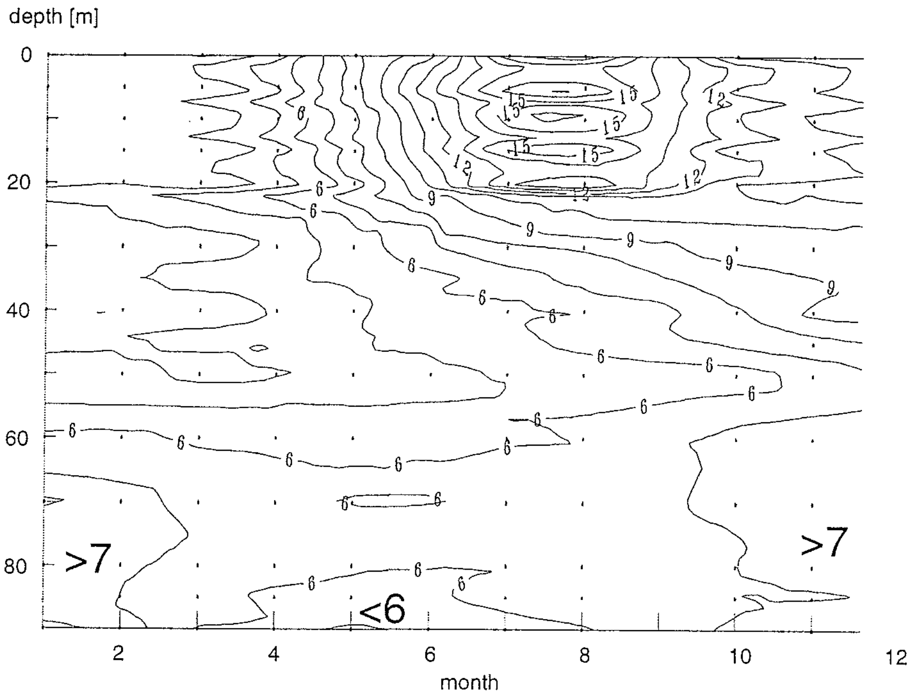

Figure 1. Annual course of the temperature in relation to depth, averaged over the years 1988–1992.

The summer thermocline is situated in 20m depth. In July and August the "mixed" layer shows a fine stratification. In the intermediate water the increase of temperature in spring and summer decreases with depth. The temperature of the deep water is highest in winter.

Abundance of the zooplankton

In the following the annual courses in abundance are described for the single mesozooplankton taxa and concerning the copepods additionally for the different stage groups.

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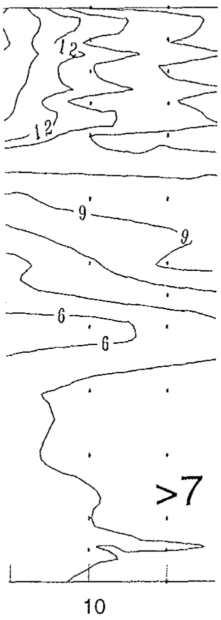

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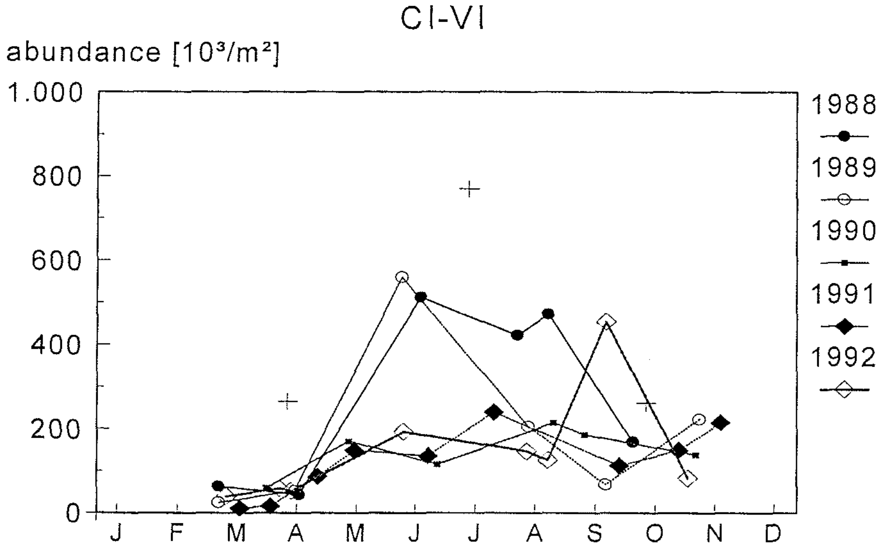
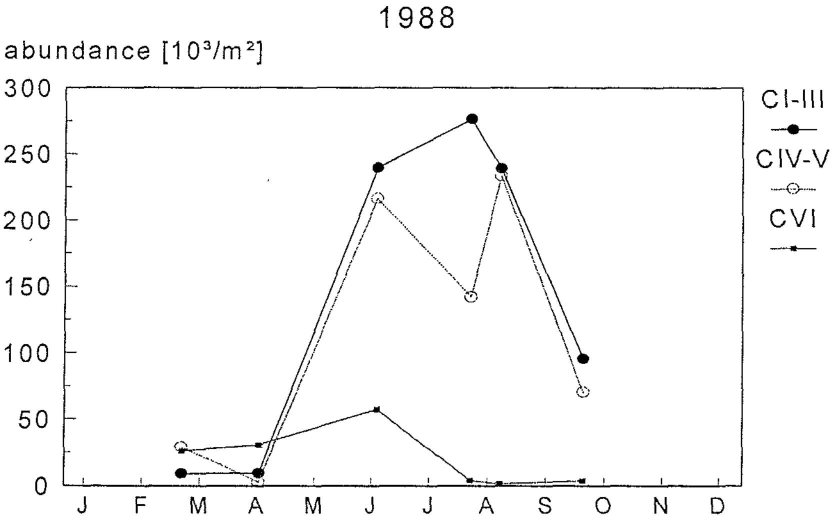
Pseudocalanus (Fig. 2) showed significant maxima not in all years.





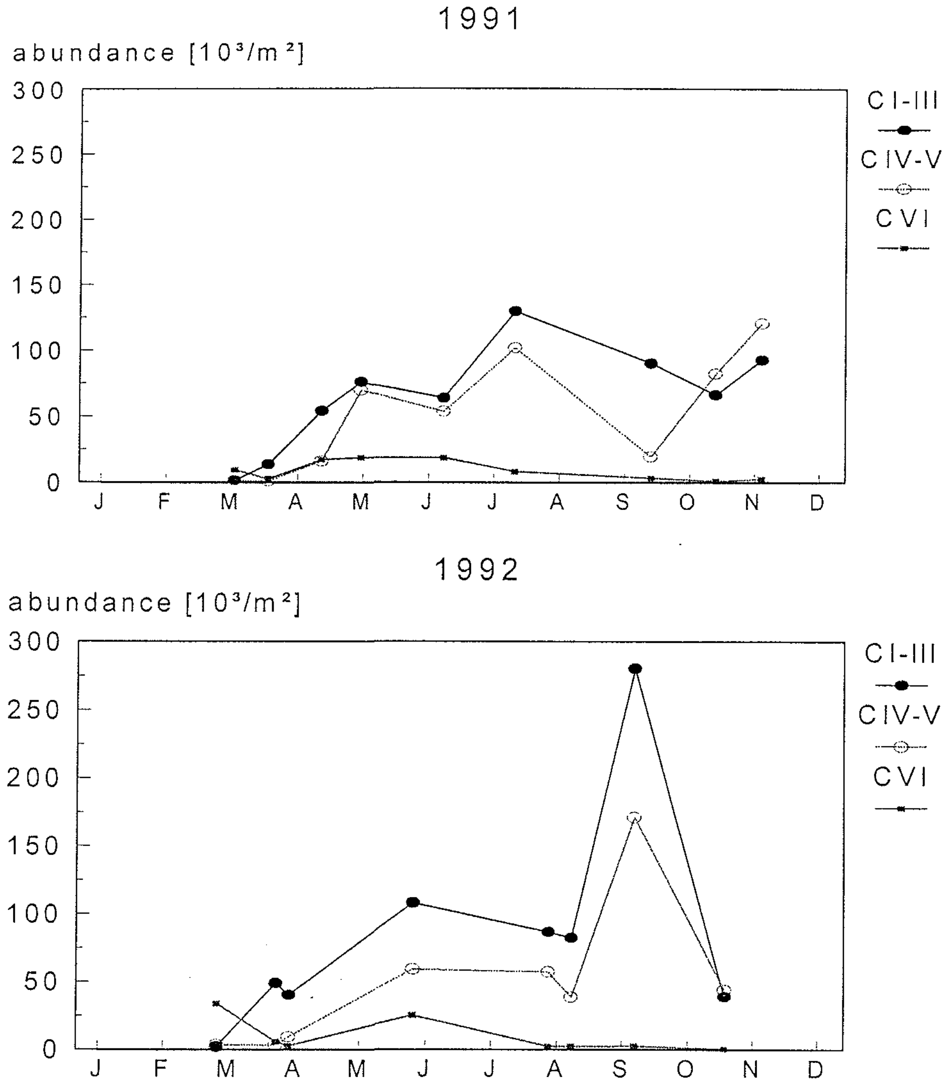
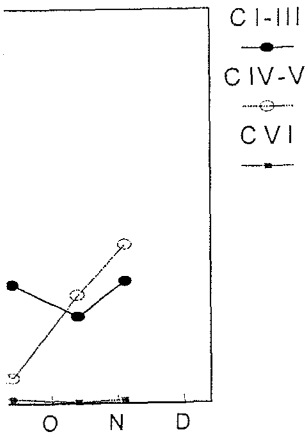
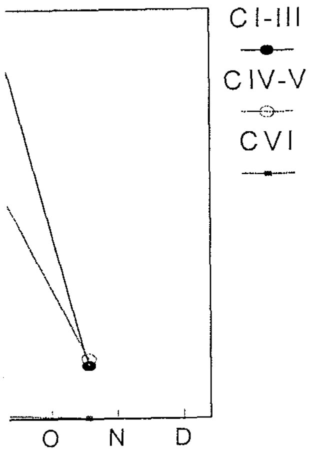


Figure 2. Annual course of *Pseudocalanus minutus*. The crosses in the first of the four diagrams mark abundances from own vertical recordings.

In 1990 and 1991 only abundance levels of $1–2*10^{5}$ Ind.$*m^{-2}$ occurred, while in the other years the maxima reached to numbers of more than $4*10^{5}$ Ind.$*m^{-2}$. According to the horizontal tows there was a higher maximum also in July 1991. It is not clear, whether the higher level in 1988 from June to August was one broad maximum or consisted of one maximum in spring and one in late summer.

In 1989 and 1991 a late maximum didn´t occur till november. For the years, in which the horizontal tows were conducted, the copepod genera were divided into





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age groups. The abundances of younger and older copepodites ran synchronous in all these years. The adults didn´t contribute to the second maximum in any year. The maximum in 1988 turned out to consist of two single maxima only for the older copepodites and not for the younger ones.

The spring maximum of *Acartia* (Fig. 3) occurred in May to June.

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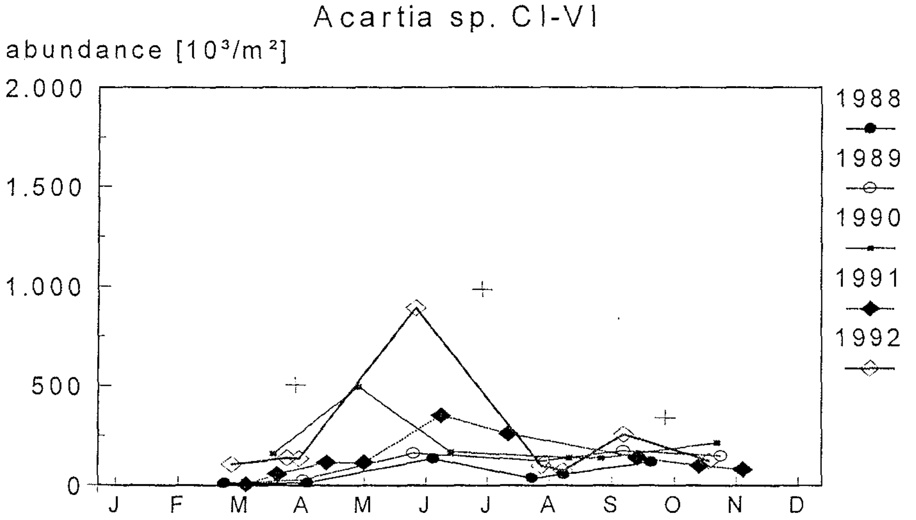

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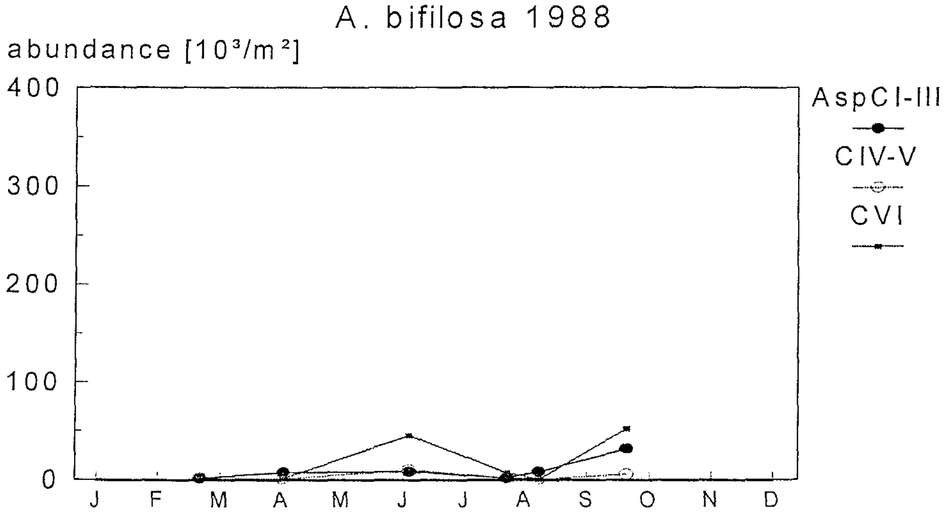


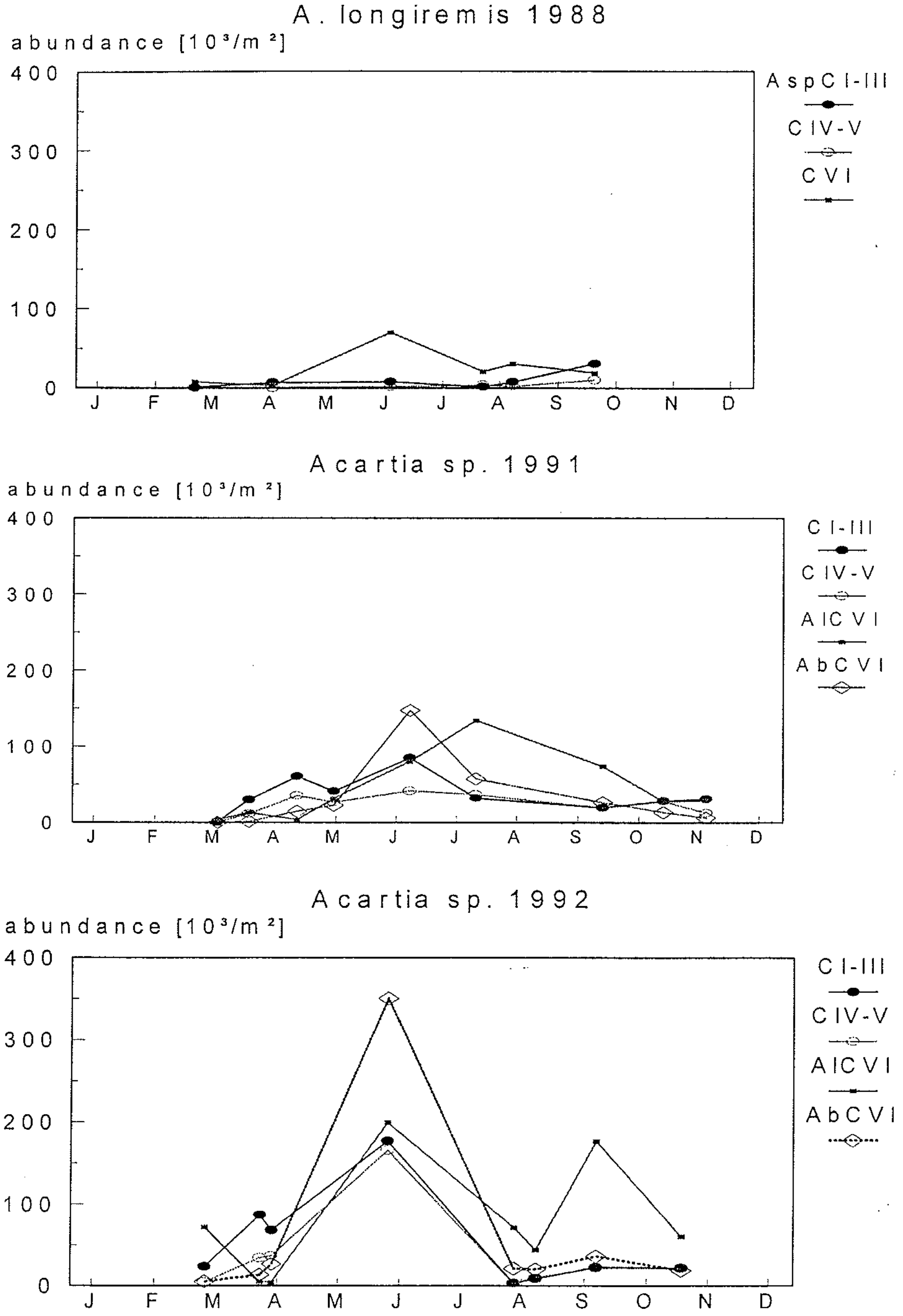
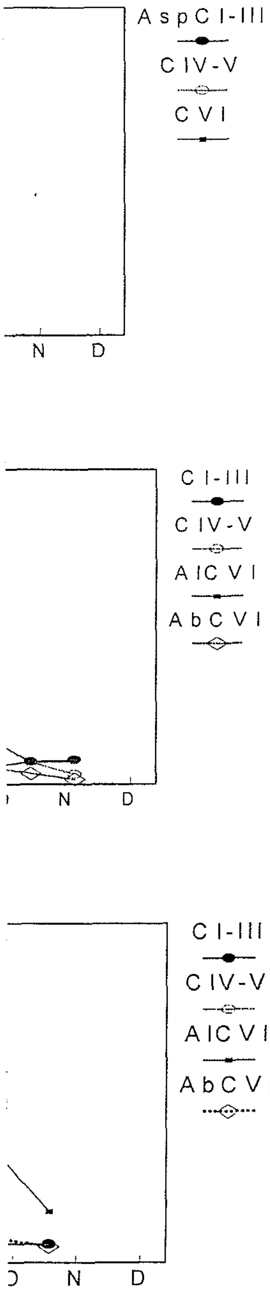


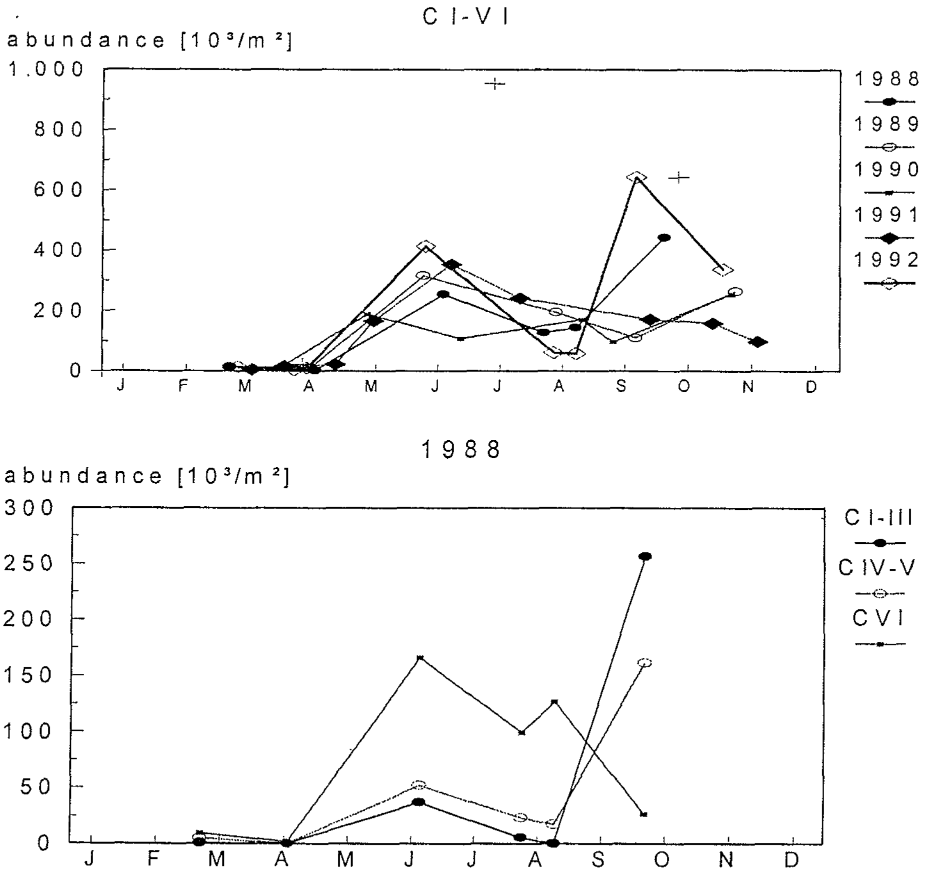
Figure 3. Annual course of *Acartia* sp. (Asp). Al = *Acartia longiremis*, Ab = *Acartia bifilosa*.



ı longiremis, Ab = Acartia

In 1988, 1989 and also 1991 marked maxima were missed because of the wide sampling intervals perhaps. In 1991 the low peak was possibly only the beginning of a maximum value, which followed a few days later and was detected by the horizontal tows. However, in April 1992 there was a difference between the abundance from the horizontal tows and the BMP value, although both values refer to nearly the same day. The BMP data show the increase of the abundance in that year to a later time. The maxima of *Acartia* in the years 1988, 1991 and 1992 in contrast to those of *Pseudocalanus* were made up by the adults. In 1988 the copepodites weren't significant until August. In 1991 the younger copepodites and in 1992 also the older copepodites contributed significantly to the spring maximum. The second maximum of *Acartia longiremis* adults in 1992 was notable.

The autumn maximum of *Temora* (Fig. 4) was expressed more clearly than that in June.



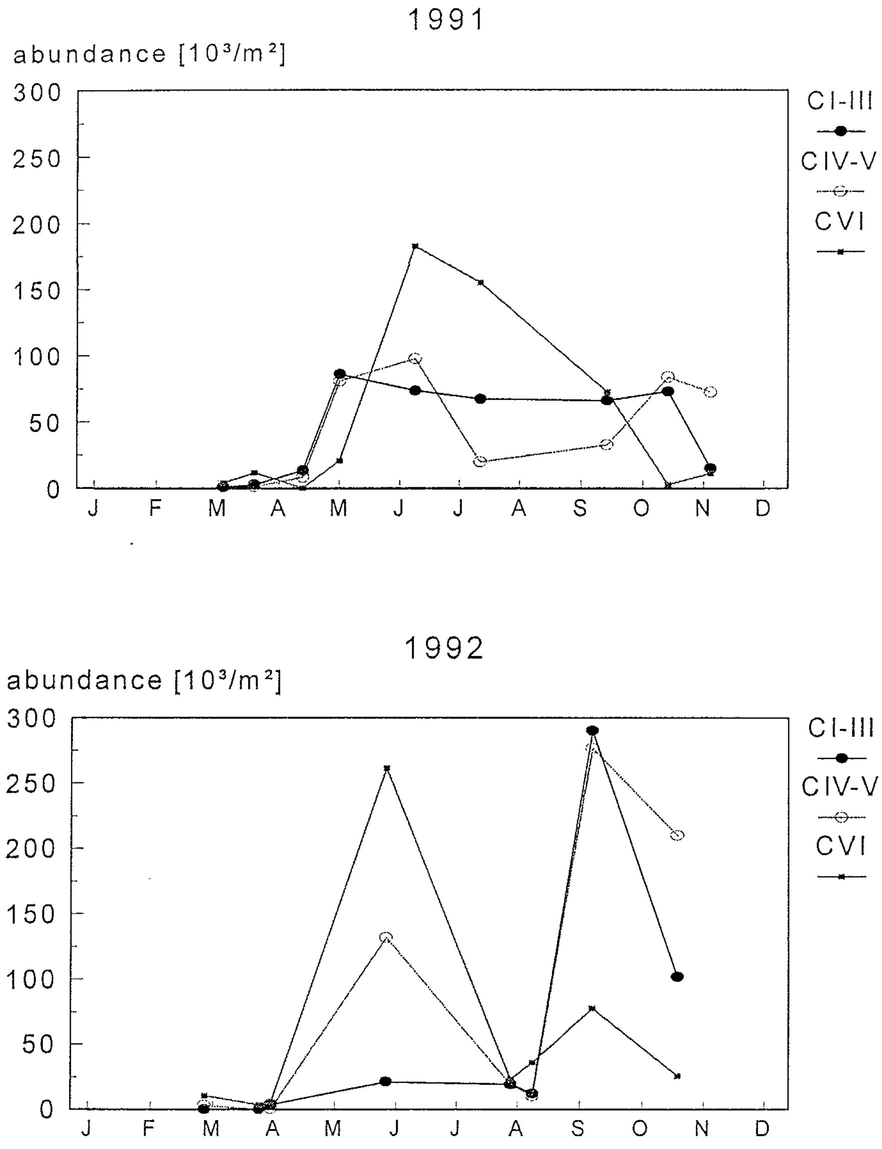
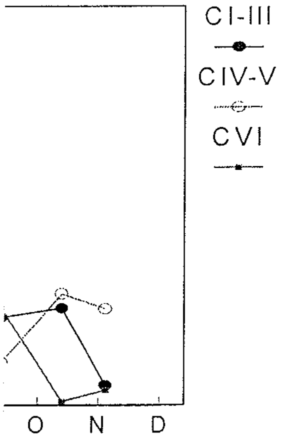
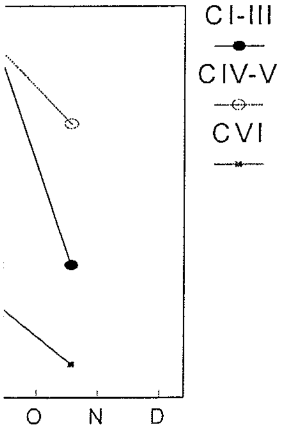


Figure 4. Annual course of *Temora longicornis*.

In the years, for which the species was divided into stage groups, the first maximum was dominated by adults, as it was the case for *Acartia*. In 1991 the autumn maximum existed only for the copepodites, while the decrease of abundance of the adults at the same time swallowed this second maximum considering the total abundance of *Temora*.





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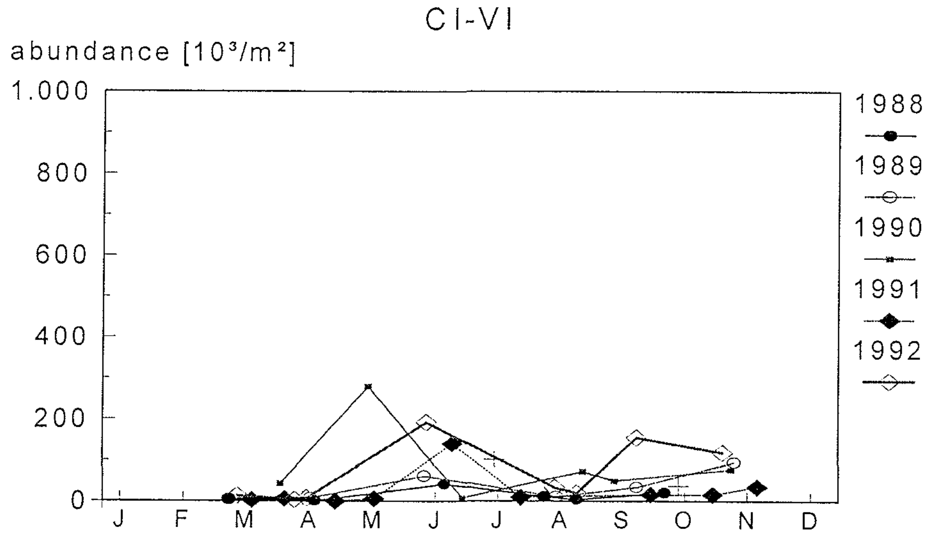
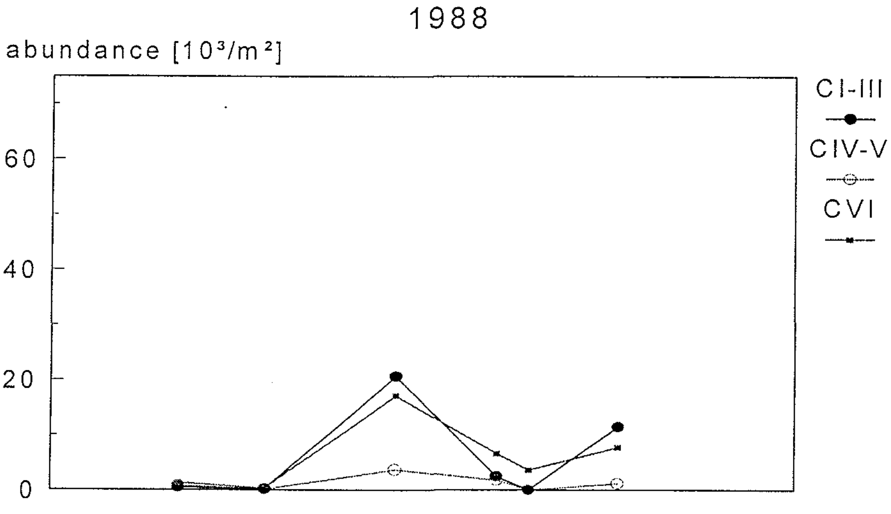
A distinct spring maximum of *Centropages* (Fig. 5) appeared only in 1990–1992.





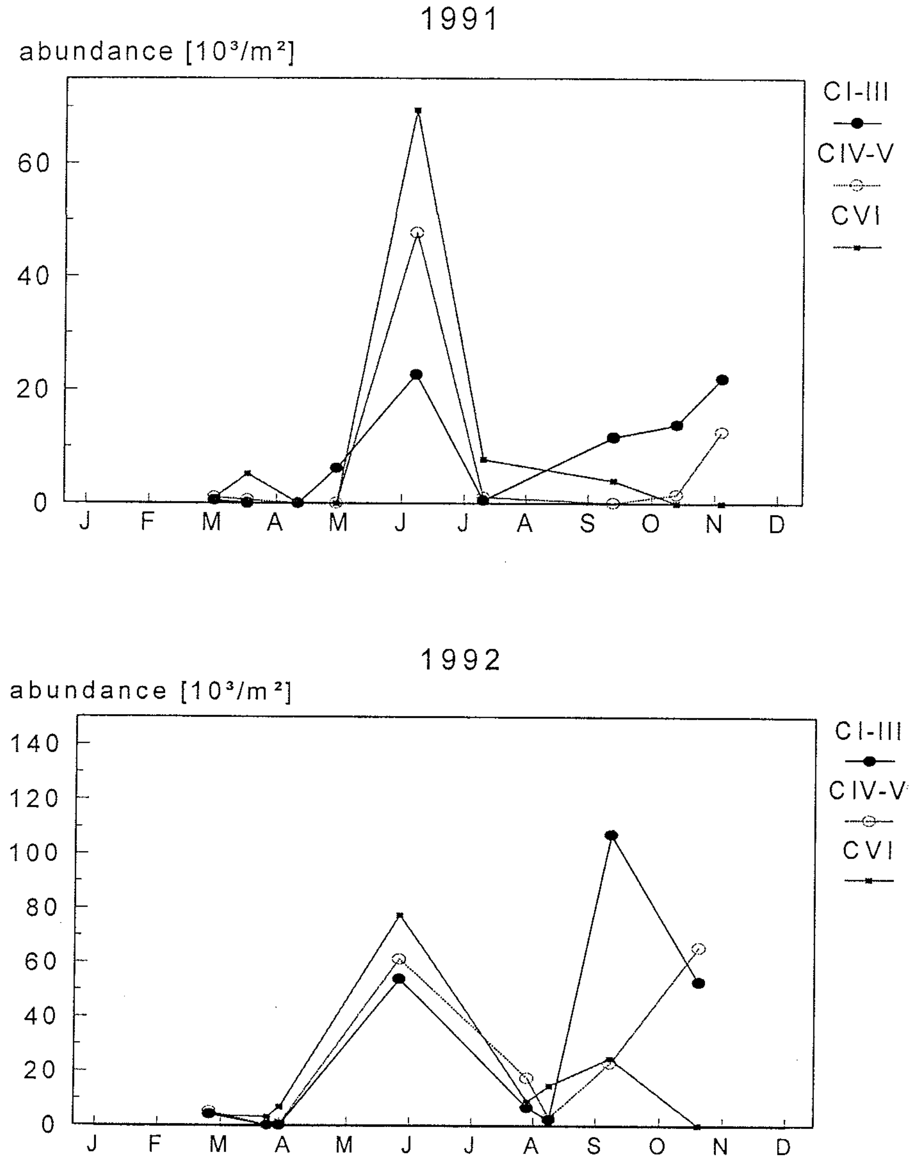
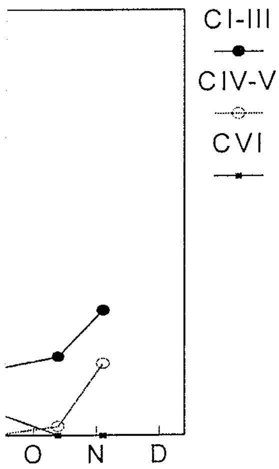
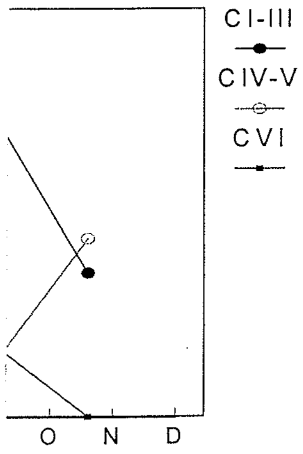


Figure 5. Annual course of *Cenropages hamatus*.

A second maximum was found 1989 and 1992. Looking at the age groups, a spring maximum becomes apparent also in 1988 and a second increase of the abundance was observed also 1988 and 1991, but only for copepodites. The succeeding of younger and older copepodites could be noticed 1991 and 1992.





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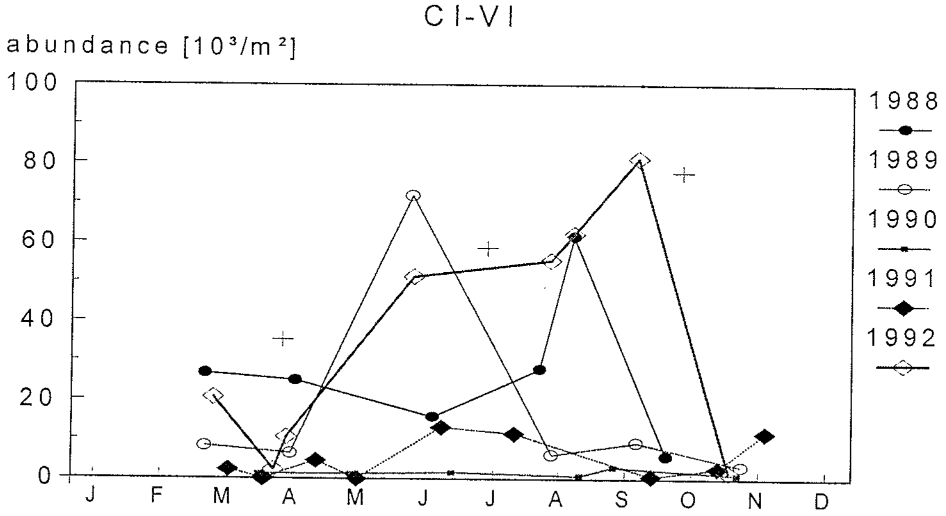
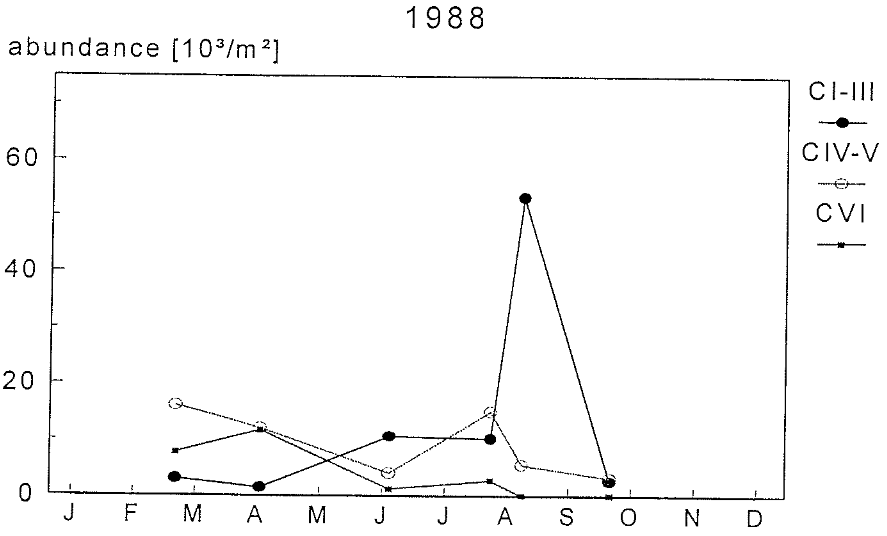
Oithona (Fig. 6) showed a distinct spring maximum in 1989 and, less clear, in 1991.





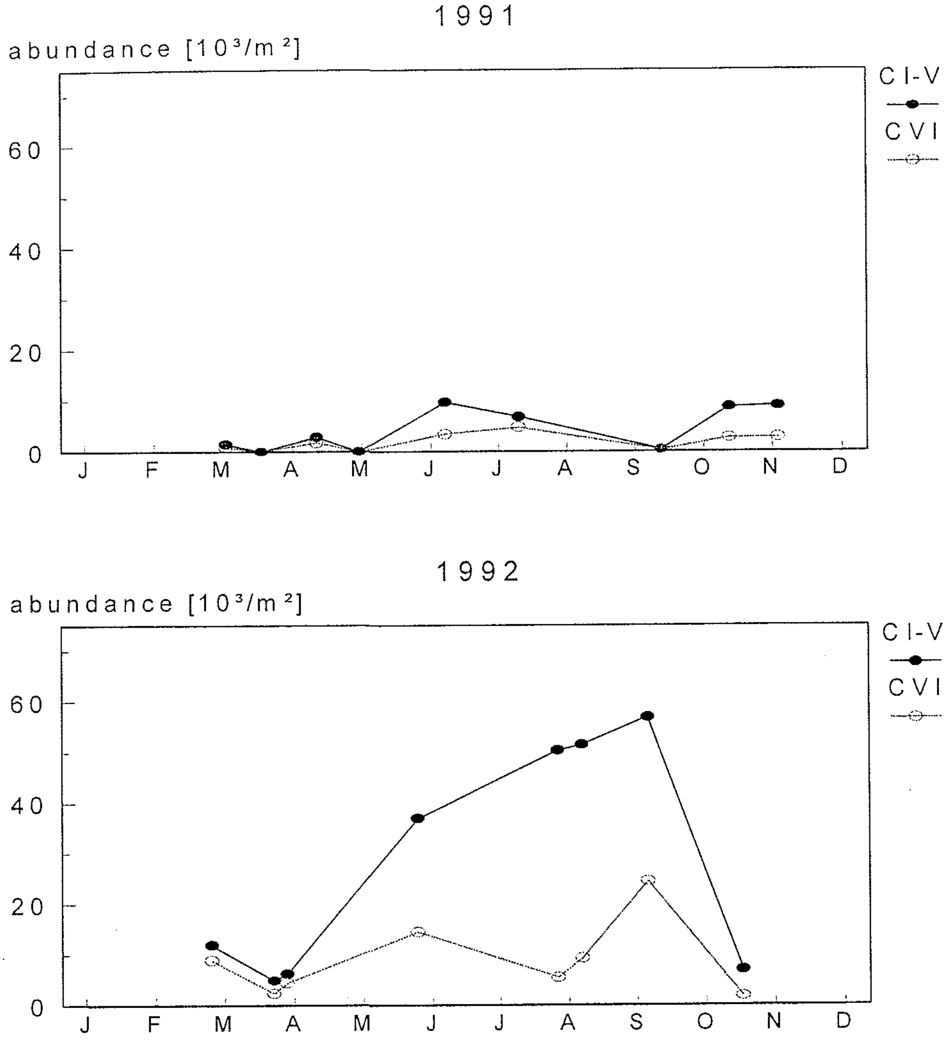
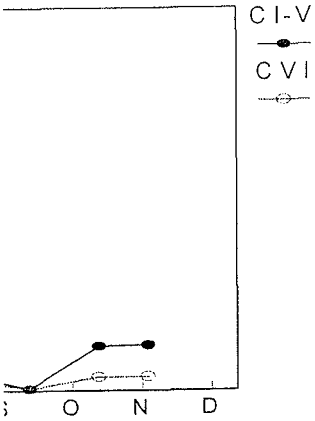
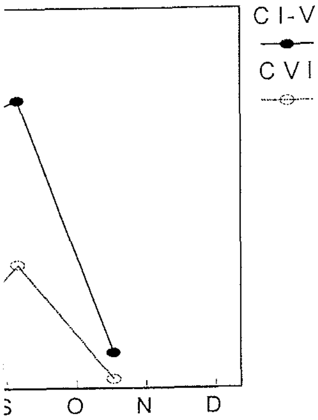


Figure 6. Annual course of *Oithona similis*.

The second maximum occurred at various times in the different years. The high abundance in the beginning of 1988 perhaps points to an early spring maximum, that was not sampled. Dividing the species in age groups the high winter abundance in 1988 can be attributed to the older stages, while the peak in late summer was only due to the younger copepodites. In 1992 a separation of the peaks in spring and autumn was possible for the adults, but not for the copepodites. The abundances detected by the horizontal tows were considerably higher and a coherence between the peak in summer 1988 and the data point in October, i.e. nearly two months later, cannot be assumed.





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Therefore the copepods generally showed two maxima per year. From 1988 to 1992 there was no year with constant very high or very low abundances (Fig. 7).

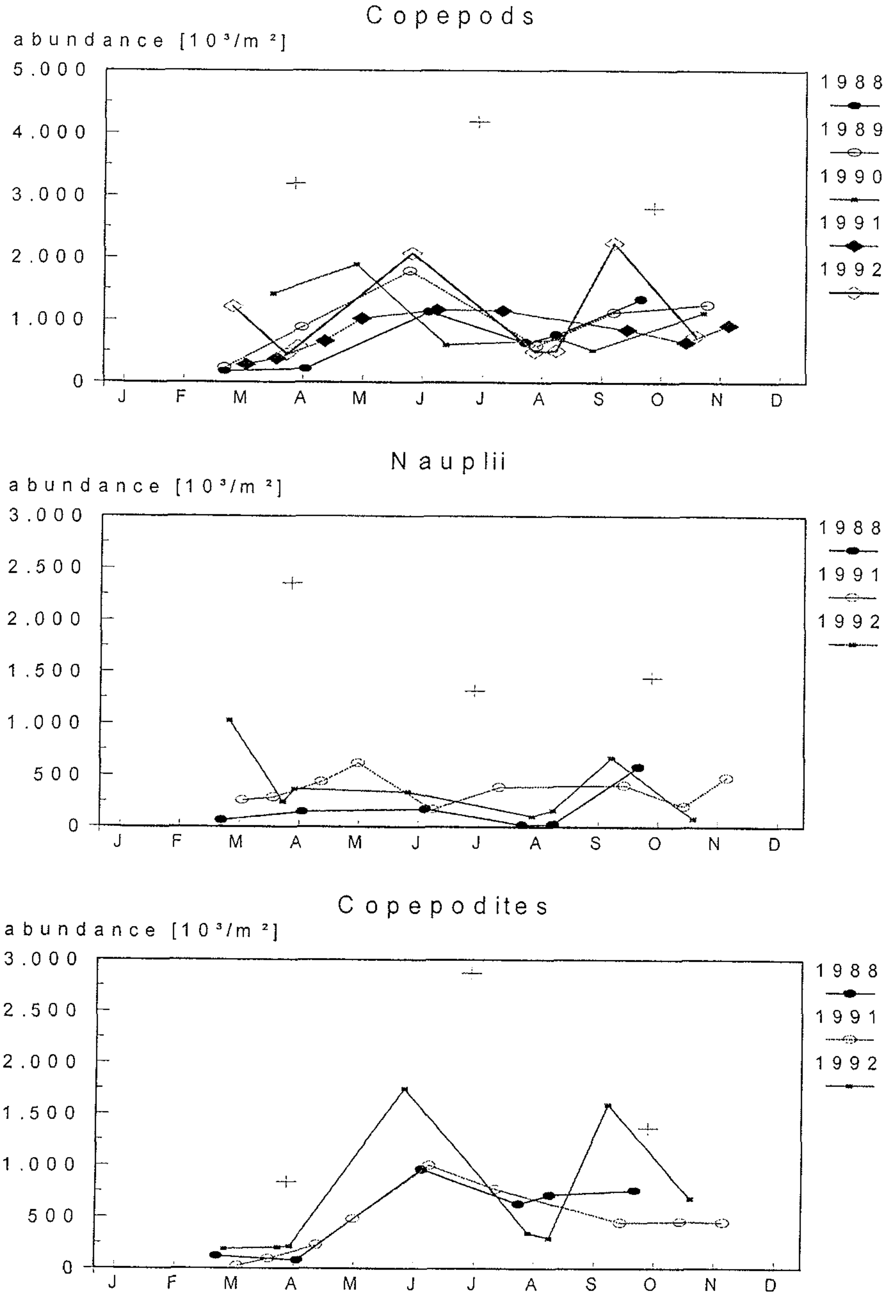
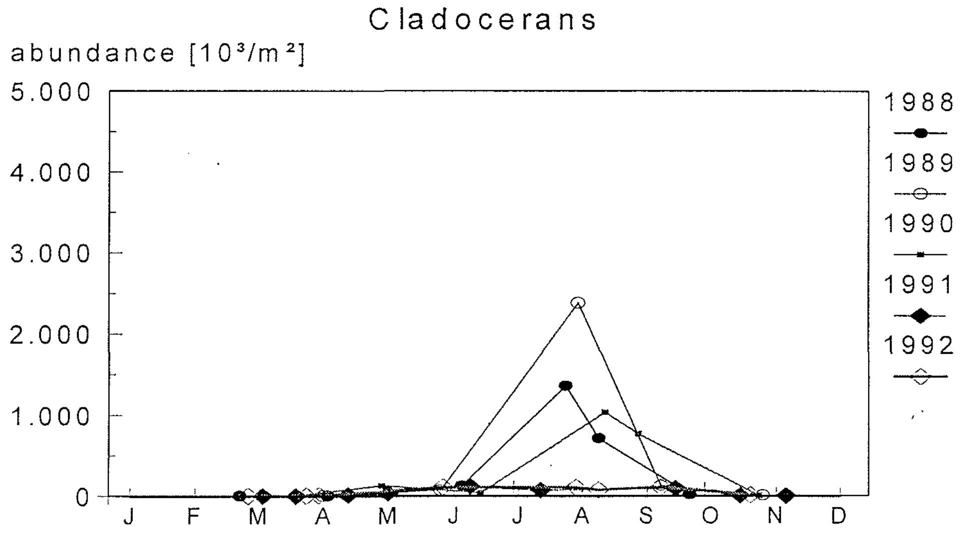


Figure 7. Annual course of all copepods.

The dominant copepods were *Temora longicornis* and *Pseudocalanus minutus* each having maximally 40–50% of the copepod numbers. The genus *Acartia* follows with 30–40%.

For the years, in which horizontal tows were conducted, the abundances for nauplii and copepodites were seperated. The BMP abundance of the nauplii generally was lower than that of the copepodites. The fact, that younger stages were not more abundant than the older ones in spite of more or less similar stage durations except for *Pseudocalanus*, can be observed also within the copepodite stages of *Temora* and *Acartia*. The abundances resulting from the horizontal tows were higher than those from the BMP data. This positive deviation of the values from the horizontal tows exists for all copepod genera, except for *Centropages*, and the appendicularians for at least one date of sampling. The deviations, which were similar for nauplii and copepodites, showed, that the low nauplii abundance compared with that of copepodites was not caused by a lower catchability of the WP–2 net for nauplii alone the mesh size being too great.

The cladocerans (Fig. 8) had a summer peak in 1988–1990. Until June they appeared only in low numbers. It is not clear, whether in 1991 and 1992 the maxima were missed or whether there were actually no cladocerans. The peaks in the other years may not be as broad as suggested by the sampling intervals, but in 1988 and 1990 the maxima extended still over two sampling dates.



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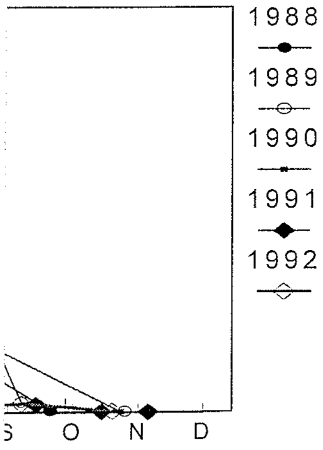


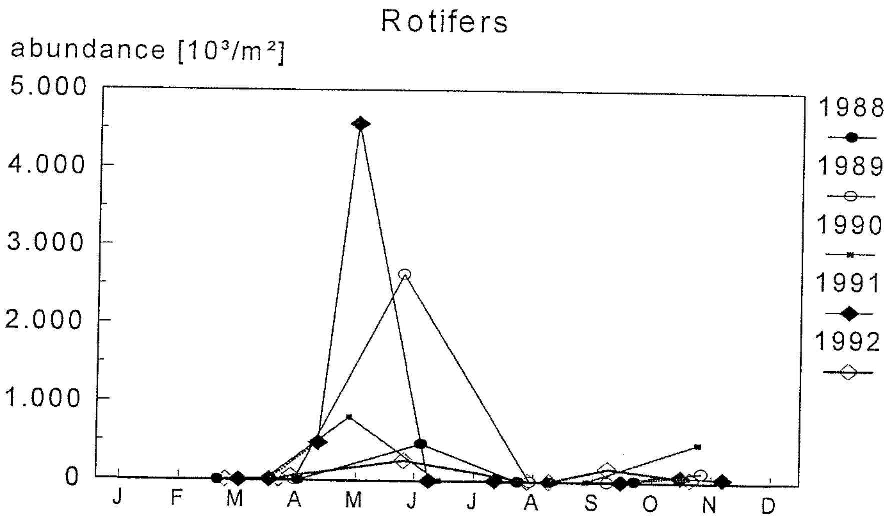
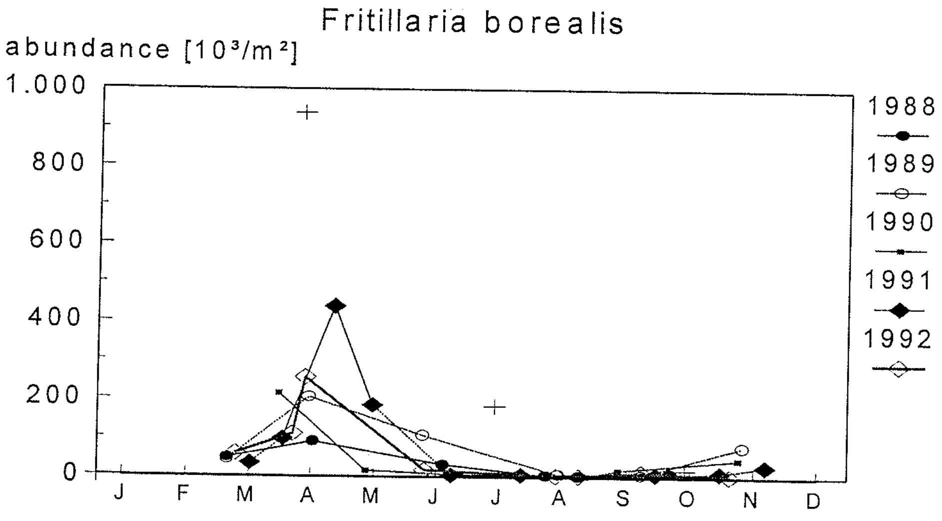
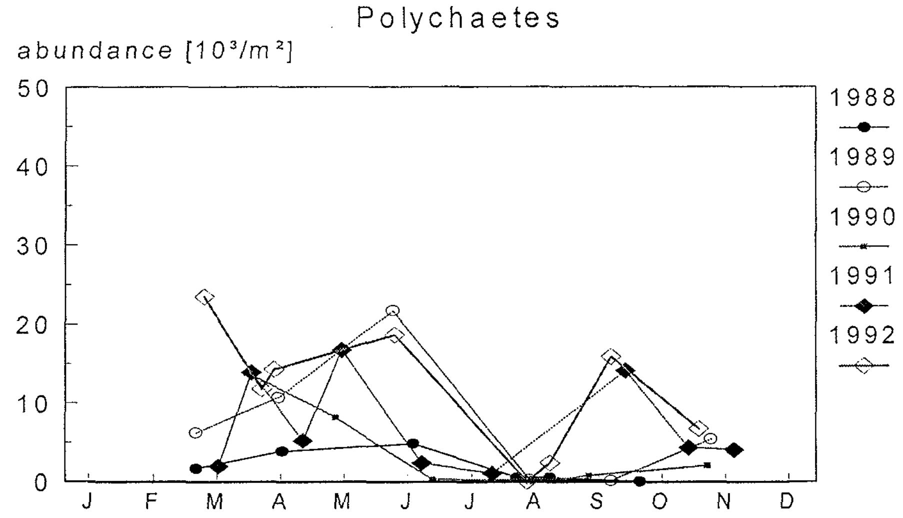


Figure 8. Annual course of cladocerans and rotifers.

Concerning the rotifers (Fig. 8) the BMP data were not quantitative. They always have their maximum in May or June with high abundances relative to copepods.

The peak of *Fritillaria borealis* (Fig. 9) was always in April, but in 1989 *F.borealis* occurred even in June. In April 1992 the horizontal tows with the 47 µm nets resulted in much higher abundances than caught by the WP-2 net. A possible reason for that was the smaller mesh size.





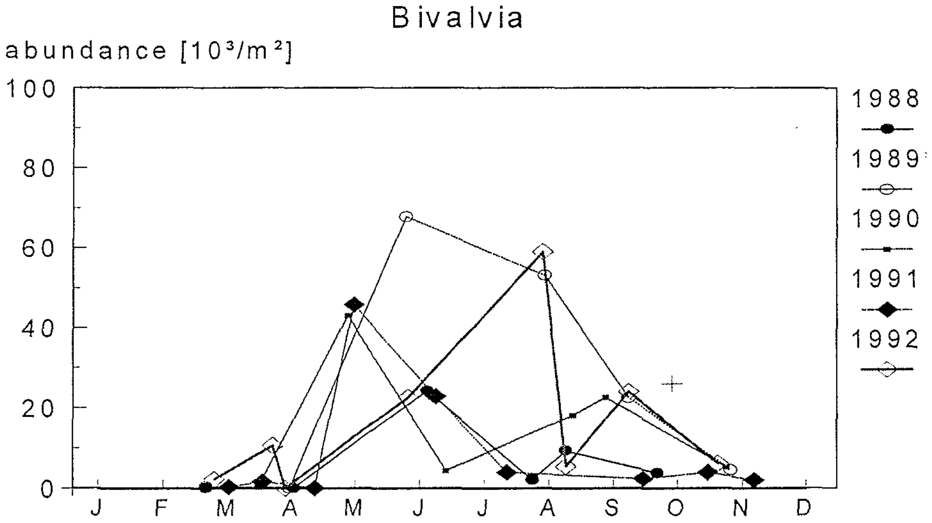
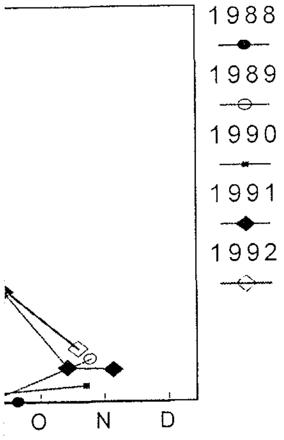
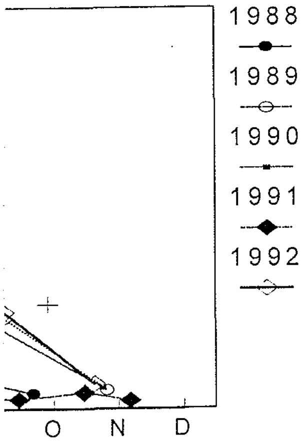


Figure 9. Annual course of *Fritillaria borealis*, the polychaetes and the larvae of molluscs.

The polychaetes (Fig. 9) generally showed low abundances. In 1988 there was no maximum. In 1991 and 1992 the spring maximum lasted for a longer time and in autumn of these two years there was also a marked one.





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The mussel larvae (Fig. 9) occurred in low abundances, too. They showed a highly variable annual pattern. Higher concentrations can be expected from April to September in principle.

Zooplankton biomass and production

The annual courses in biomass and production are means of the years 1988–1992 for each month. The means refer to six single values in maximum, the mean of July only to one and the means of May and October to two single values. The biomass of all copepods was at its maximum in June (mean = 2.25 g C*m^{-2}), especially in 1992 (3.65g C*m^{-2}) (Fig. 10).

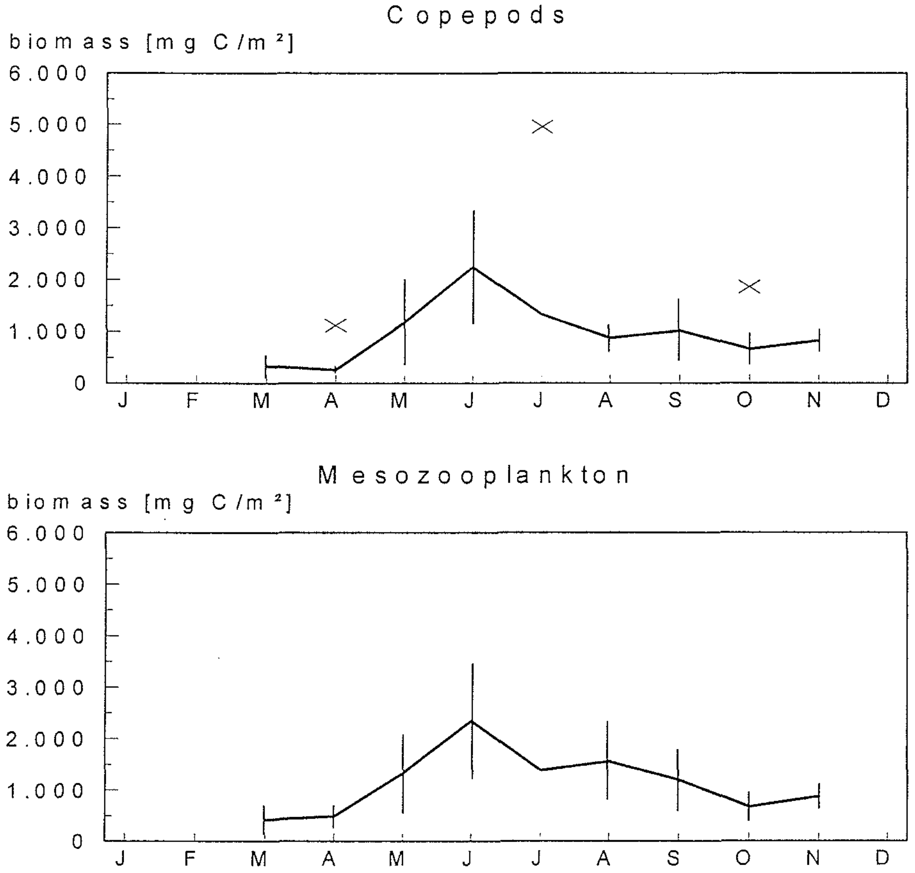

Figure 10. Annual course in biomass of copepods and of the whole mesozooplankton averaged over the years 1988–1992. The bars indicate standard deviations. The three crosses indicate the BIOMOC data.

The autumn peak of the copepods is not visible in terms of biomass. The biomass data resulting from the horizontal tows were, like abundances, much higher than those from the BMP data. The annual course of the mesozooplankton (Fig. 10) hardly differed from the one of the copepods, in August because of the cladocerans and in April because of *Fritillaria.*

The results in calculating the production of copepods according to Edmondson & Winberg (1971) and Huntley & Lopez (1992) showed the greatest differences in summer (Fig. 11). For the first method Eurytemora, Microsetella and the nauplii and the males of the remaining copepods were not taken into account. The method according to Huntley & Lopez (1992) refers more directly to the biomass of all the copepods. That results in a greater similarity of the annual course in copepod biomass with the annual course in production calculated using this method.

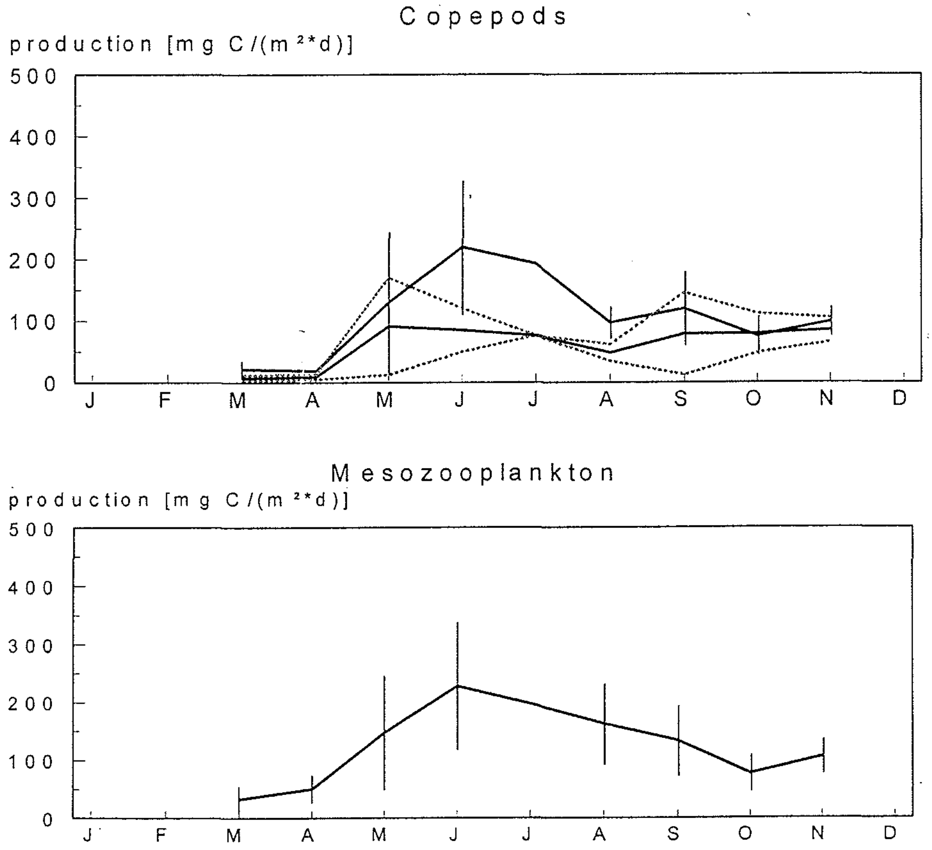

Figure 11. Annual course in copepod production and the production of the more dominant groups of the mesozooplankton averaged over the years 1988–1992. The standard deviation of the generally higher copepod production according to HUNTLEY & LOPEZ (1992) is shown by bars, that of the copepod production according to EDMONDSON & WINBERG (1971) by dashed lines.

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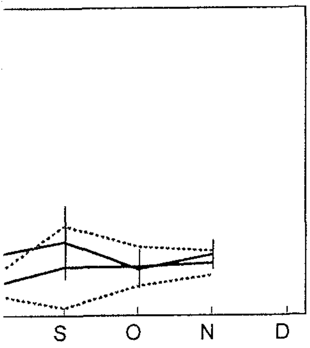

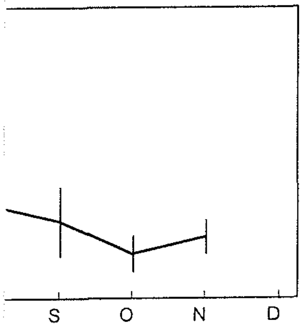

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The production of the mesozooplankton (Fig. 11) comprises copepods, cladocerans and appendicularians. In this context the production of copepods was calculated according to Huntley & Lopez (1992). Further groups showed a negligible contribution to the annual production and were not considered in the calculation, even when in May 1991 the rotifers contributed to 22.5% to the total metazooplankton production. The contribution of the cladocerans and appendicularians to the annual course in mesozooplankton production was comparable with that to the annual course in biomass. Values of annual production and contributions of non-copepod groups are given in Tab. 1.

Table 1

Average annual production for the years 1988–1992.

taxon	production +/– stddev [g C*m^{-2}*y^{-1}]	contribution [%]
Pseudocalanus[1]	4,32	
Acartia	3,64	
Temora	6,50	
Centropages	2,25	
Oithona	0,06	
copepodites[2]	16,42 +/– 3,84	
copepods[3]	29,95 +/– 6,03	84,83
cladocerans	3,17 +/– 2,61	8,98
Fritillaria	2,18 +/– 0,92	6,19
total	35,30 +/– 5,86	
(phytoplankton	222,10 +/– 33,09)	

[1] For the genera of copepods the production according to EDMONDSON & WINBERG (1971) refers only to the copepodites.

[2] according to EDMONDSON & WINBERG (1971)

[3] The production according to HUNTLEY & LOPEZ (1992) includes nauplii and males.

The productivity, i.e. the daily P/B ratio, should have a similar annual course like the average temperature of the water column, because production was calculated only from biomass and temperature (Fig. 12). The differences between the annual course of the average temperature and the P/B ratio must therefore be attributed to the vertical distribution of the zooplankton. So the relative mistake in the determination of production is shown, which would occur, if the WP-2 net would have been towed from bottom to surface without interruption. The average temperature was taken from one value for each depth, whereas the P/B refers mainly to the mode depth of zooplankton and the temperature there. Therefore the greater difference between the average temperature and the P/B value since August indicated an increase of the preferred depth of the zooplankton at that time.

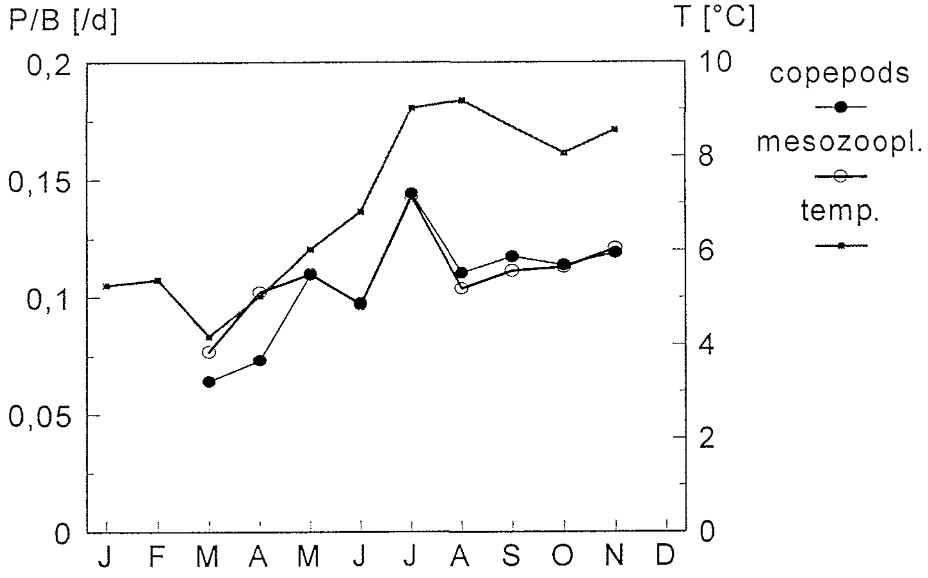
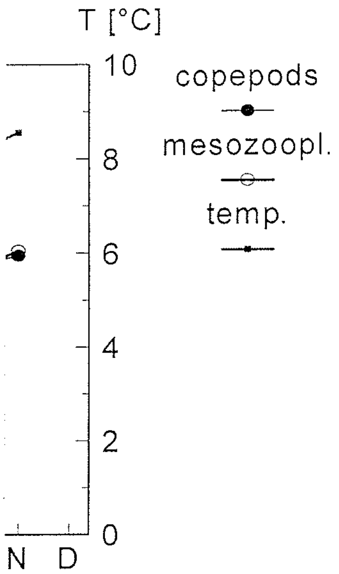


Figure 12. Annual course in the average productivity of the years 1988–1992 in comparison with the temperature averaged over these years and over the water column.

The little difference between the productivity of the copepods and that of the whole mesozooplankton can be attributed to the productivity of the remaining zooplankton groups. The P/B value of the cladocerans at a given temperature is lower than that of copepods, but that was hardly shown in the annual course in mesozooplankton productivity. The P/B values for cladocerans reached from 0.0146 d^{-1} in April to 0.0976 d^{-1} in July. The P/B value of *Fritillaria* was considerably higher than that of copepods and resulted in a greater productivity difference between copepods and the mesozooplankton in April, at the time of the *Fritillaria* maximum. The P/B value of *Fritillaria* reached from 0.109 d^{-1} in October to 0.199 d^{-1} in August. The extreme values of the copepods were 0.0166d^{-1} for *Temora* in March and 0.235d^{-1} for *Centropages* in November. *Temora* and *Centropages* hardly differ in their development time at a given temperature. Therefore these extreme values are to be attributed to the temperature distribution. The temperature of the mode depth of *Temora* in March and of *Centropages* in November staying in both cases in the upper water column was below 3°C or above 9.5°C respectively. So the highest P/B value was not discovered in summer. The reason for that was, that the high summer temperatures were limited to a thin surface layer and the copepod concentration was below this.



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Phytoplankton stock and production

The annual course in the chlorophyll a content of the water column (0–30 m) averaged over the years 1988–1992 showed its maximum in autumn. In June and September there were no chlorophyll a measurements. A spring bloom was not recognizable in the averaged annual course, neither in the courses of the single years (Fig. 13). The autumn maximum of the average annual course referred to the years 1988 and 1989. The deviations of own chlorophyll a measurements carried out in connection with the horizontal tows and in the same manner like the BMP measurements were small.

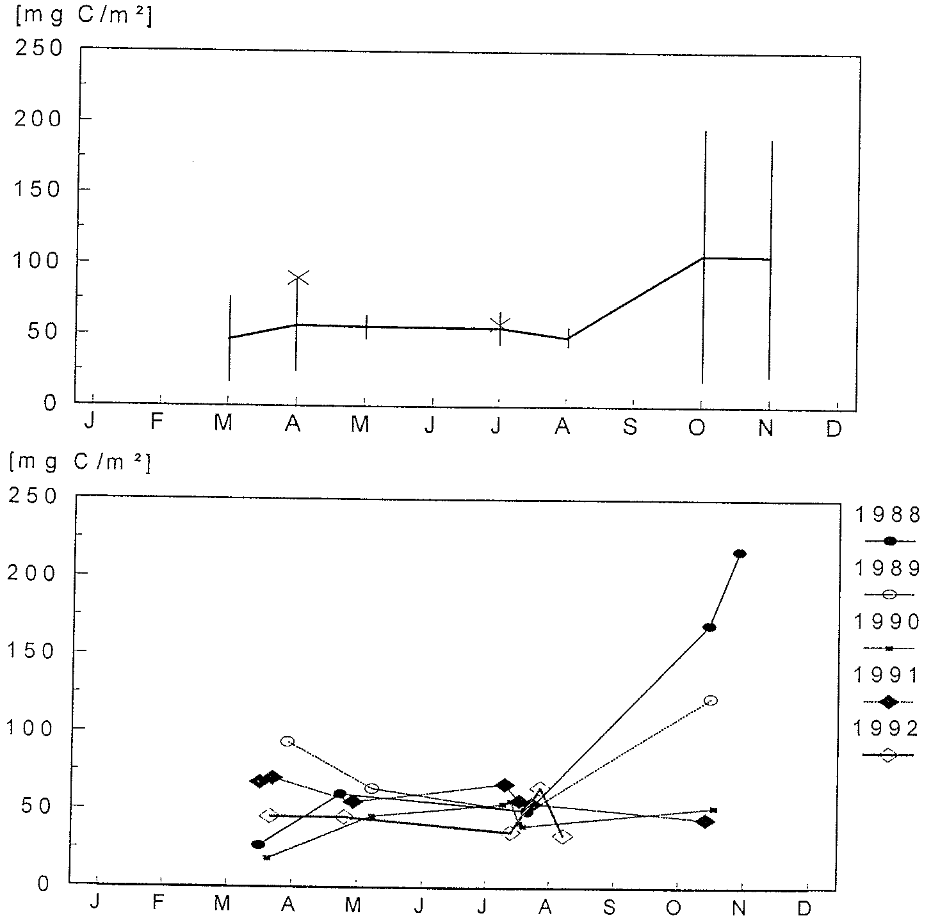

Figure 13. Annual course in the chlorophyll a content of the water column (above the mean with standard deviation and below the course of each year). Crosses in the above diagram indicate the values from own water samples, which were taken parallel to the BIOMOC hauls.

The average primary production (Fig. 14) in each month was based on the same number of measurements like the average chlorophyll a concentration.

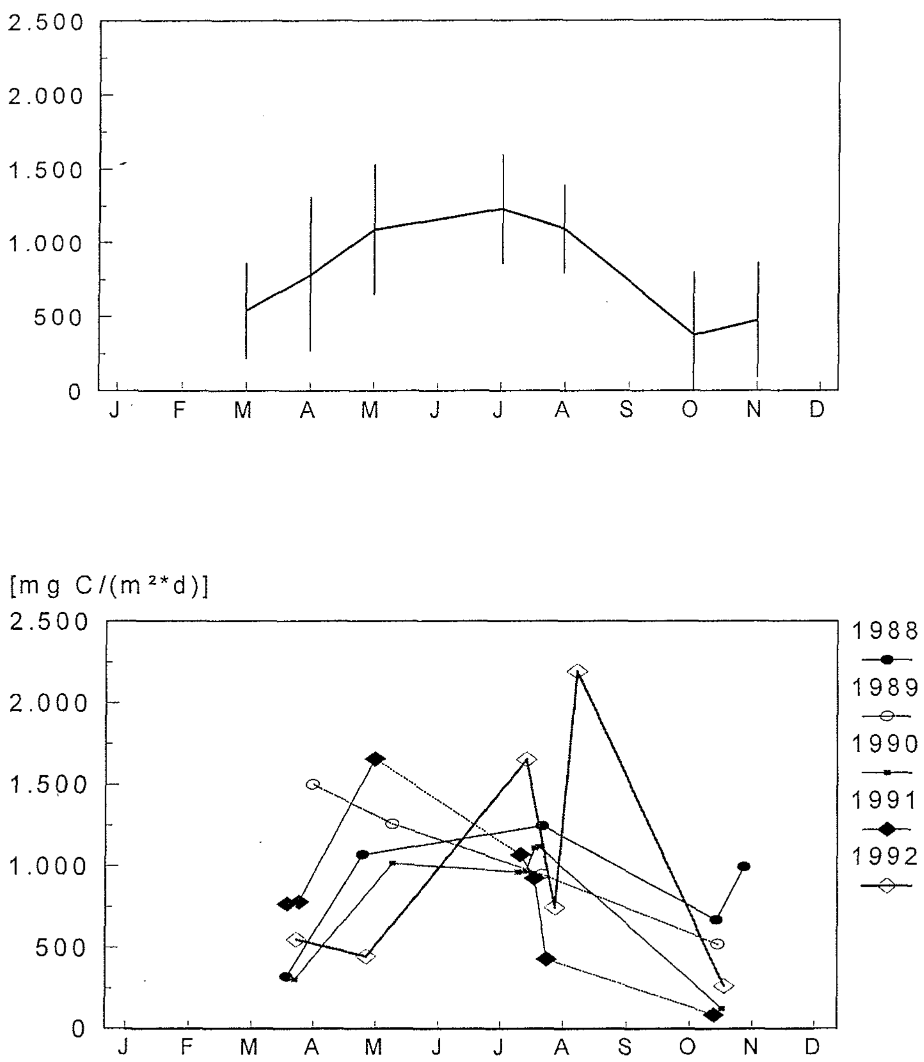

Figure 14. Annual course in primary production.

The maximum primary production was in July. The annual course in primary production of 1989 and 1991 deviated fundamentally from the one of the mean values. In these years a steady decrease from a maximum in April or May respectively until autumn occurred.

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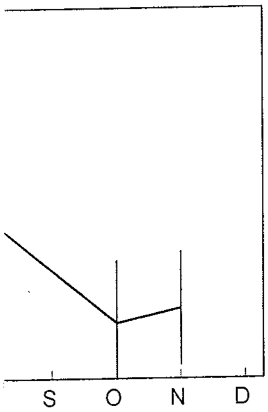

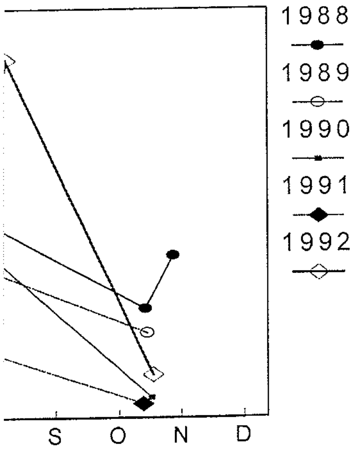

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The annual primary production amounted to 222 g C*m–2*y–1 (see also tab. 1). The annual potential production of the mesozooplankton was 10–16% of the annual primary production according to the method used to calculate the copepod production.

Discussion

The higher abundances from the horizontal tows showed a lower catch efficiency of the WP-2 net not only for nauplii, but even for copepodites. Postel et al. (1991) showed, that reducing the mesh size to 56 µm provides the four fold quantity of nauplii, whereas the number of the catched copepodites remains the same. Conversely Kankaala (1984) emphasized the bad quantitative properties of the WP-2 net just for adult copepods as a consequence of net avoidance. Møhlenberg (1987) proved the lower catchability of the WP-2 net relative to a net pump for all copepod stages, the mesh size of the net pump being the same. He saw the cause for that in the quick clogging of the WP-2 net.

The diagrams given previously show, that for drawing up a satisfactory course for the year the number of recordings in the frame of the BMP is not high enough. First following the generations, of which all the copepod species of the Baltic have several ones in one year, was not possible with the BMP data. Secondly it is not certain, that the annual maximum in the average biomass of copepods or the mesozooplankton respectively was in June indeed. The maximum could have been in July as well, because in 1991, the only year, in which sampling took place in this month, the mesozooplankton abundance could have been exceptionally low.

Generally all the copepod species show nearly the same annual course, what can be regarded as a result of the common environment, especially temperature and chlorophyll content. Species-specific differences in the answer to this environment couldn´t be detected. The interannual variability can be attributed at least in part to the low sampling activity.

The growth model of Huntley & Lopez (1992) with the constants used is suitable only for the calculation of production of copepod communities, not of single species and not of other zooplankton groups. The temperature is the only variable of the weight specific growth rate, not the species and not the body weight. According to Huntley & Lopez (1992) the accuracy of the determination of production is greatly dependant on the accuracy of the determination of the underlying biomass. The calculation according to Edmondson & Winberg (1971) with the constants of McLaren (1978) and McLaren *et al.* (1989) on the other hand assumes different development rates for the copepod species and for nauplii and copepodites. The food concentrations within the spectrum occurring in situ are said not to play a significant role for the growth rate compared with the temperature (Huntley & Lopez, 1992). The daily vertical migration is not considered for the calculation of production.

The annual mesozooplankton production values in the Baltic determined so far came to values between 1.5–4 g C*m–2*y–1 for the Bothnian Sea (Ackefors et al., 1978; Kankaala, 1987) and 39 g C*m–2*y–1 for Kiel Bight (Martens, 1976). The results of the determination of production at a given position depend on the sampling method, the method used to determine production and even more so on the size of the zooplankton stock in the respective year and the sampling frequency over the year. The position is relevant, when the water depth is very low, such as for Greifswald Bay (Heerkloss *et al.*, 1990) or in the Hanö Bight (Lindahl, 1977). The position is important for production also with regard to the trophic conditions, which vary with the latitude (Hernroth & Ackefors, 1979) and with the distance from coast. An annual course in mesozooplankton production in the Baltic was given only by Lindahl (1977) for the Åland Sea and the Eastern Gotland Sea. According to him the annual maximum in the Åland Sea lay in August and in the Gotland Sea in the end of August and September. He attributed these maxima to the *Bosmina* maximum. In contrast to that the *Bosmina* maximum in the BMP recordings just filled the copepod minimum in August, because in some years the *Bosmina* maximum may have been partially or totally missed. The production maximum according to the BMP recordings lying in June had to be attributed to all the copepod species equally. The contribution of the single copepod species to production in June is nearly the same as in the other months, because all these species, besides interannual variations, show nearly the same annual course, as already mentioned. The differences in the own values of the mesozooplankton production especially in June and July according to the method used to calculate it can largely be attributed to a single fact. The method according to Edmondson & Winberg (1971) in contrast to the other method doesn´t ascribe any productivity to the males (see also Huang *et al.*, 1993; Kiørboe & Johansen, 1986) showing high biomasses just in summer. By comparison *Eurytemora*, *Microsetella* and the nauplii of the remaining copepods showed only little producing biomass. The contribution of nauplii is taken up in detail by Dahmen (1995). In case of doubt the values according to Edmondson & Winberg (1971) should be preferred, because they are minimum indices and they were calculated more precisely, i.e. by differentiating between species and between stages.

The copepod species, which is called *Pseudocalanus minutus* within the BMP and in this article, actually is *P. acuspes* according to Frost (1989). That has consequences for the values of daily and annual production, because McLaren *et al.* (1989) succeeded in distinguishing the *Pseudocalanus* species with regard to the development times. So the annual production of *P. acuspes* amounted to 5.89 instead of 4.32 g C*m^{-2}*d^{-1} and the productivity of *P. acuspes* is 36% higher than that of *P. minutus* under the conditions in the Bornholm Basin. Taking into account the errors in determining biomass by net hauls the deviation in annual ily vertical migration is not

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production of the genus *Pseudocalanus* connected with the uncertainty about the species is considered to be low.

One condition for the first copepod abundance maximum is the spring bloom. A spring bloom was not recognizable in the averaged annual course in the chlorophyll a content of the water column (Fig. 13). According to Ackefors & Lindahl (1979) and Renk *et al.* (1988) however in the Bornholm Basin a spring bloom occurs in April. Following the diagram for single years the highest chlorophyll a concentrations in spring were measured in 1989. In comparison with the other years in 1989 the measurement was carried out at the latest in April, i.e. 13 April. The next measurements didn't take place until May in all the years. So the spring bloom in this area presumably occurs in the second half of April and the high chlorophyll a concentration in April 1989 marked the beginning of the spring bloom. However the absence of the spring bloom in the diagrams was probably not caused by missing it each year. The local climatic and hydrographic conditions might have prevented a spring bloom also in certain years by delaying a stratification of the water column. So nutrients at the surface were not assimilated in few days, but in a prolongated time interval. Under these circumstances, the highest potential concentration of chlorophyll a didn´t appear. The prevention of a phytoplankton bloom in the presence of nutrients by hydrographic conditions is already known for some HNLC areas (e.g. Thomas, 1979).

The transfer efficiency (SP/PP) of 10 to 16% corresponded with other results from the Baltic. They range from 10% (Hernroth & Ackefors, 1979) over 21% (Martens, 1976) to 30% (Ackefors et al., 1978), most of the results lying between 10 and 15%. Lower values than 10% were given by Leppänen & Bruun (1988) and Heerkloss *et al.* (1990), but they described special situations, i.e. a limited time interval instead of a whole year. The annual primary production value of 222 g $C*m^{-2}*y^{-1}$ is higher than those given by Ackefors & Lindahl (1979) for the Hanö Bight of only 154–194 g $C*m^{-2}*y^{-1}$ and by Renk *et al.* (1988) for the Bornholm Basin as a mean value for the years 1966–1986 of 88.76 g $C*m^{-2}*y^{-1}$. The limited sampling activity led to great uncertainties, especially because only one station was sampled. The values of annual primary production and, as mentioned above, mesozooplankton production therefore are only useful for a rough guide. One has to keep in mind that the transfer efficiency describes the relation between two trophic levels. The calculated mesozooplankton production however was not equal to the secondary production, because it didn´t contain the microzooplankton production and because copepods feeding sometimes on ciliates are also tertiary producers (for example Gifford & Dagg, 1991). Ryther (1969) established the connection between the transfer efficiency and the length of the food chain.

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