Rostock. Meeresbiolog. Beitr. (1993)1

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A long-term study of Zooplankton succession in enclosures with special reference to *Eurytemora affinis* (Poppe), Calanoida, Copepoda

Introduction

The genuine brackish water copepod *Eurytemora affinis* (Poppe) is common in shallow estuarine waters of the southern Baltic and is found throughout the year. Monitoring studies lasting many years in the Darß-Zingst estuary {54°26'N,12°42'E) have revealed a stable pattern of seasonal fluctuation of *E.affinis* each year (HEERKLOSS et al. 1991). The time of the most vigorous development of this species is late spring, when its biomass reaches 3 mm^3/l (Fig.1). After the spring peak, the biomass declines within one or two weeks down to densities resembling those observed in winter. A second, less pronounced peak appears in late summer, and an autumn peak is also sometimes observed. Such a pattern of seasonal fluctuation has also been reported for other estuarine waters (CRONIN et al. 1962, JEFFRIES 1962, HERMAN et al. 1968, LEAH et ai 1978, MILLER 1983, CHRISTIANSEN 1988, HEERKLOSS et al. 1991). The causes of the fast decline of the *E.affinis* population after the spring peak are interesting fróm the viewpoint of modelling and prognosis. It seems improbable that food deficiency plays a role. With suspended particle concentrations of between 40 and 50 mg dry weight per litre (HEERKLOSS et al. 1984) at their disposal, the animals are well supplied with food. So far, no clear water phase has been observed in the Dars-Zingst estuary as a result of the copepods spring peak. Nor, apparently, is food quality a key factor. Besides nanophytoplankton, the species can exploit a variety of other food items: bacteria (BOAK & GOULDER 1983), protozoans (BERK et.al. 1977, BURCKHARDT & ARNDT 1987), detritus (HEINLE & FLEMER 1975, WOLTHUSEN 1982, HEERKLOSS et al. 1990).

The period of rapid decline following the copepod spring peak is accompanied by signs of physiological stress. Feeding activity, for instance, decreases (HEERKLOSS & RING 1989). Analysing the population dynamics at a station in the middle of the Darß-Zingst estuary (Zingster Strom), ARNDT (1985) found that the egg-number per female was reduced when the population declined in late spring. A similar result was reported by CHRISTIANSEN (1988) for the Schlei. However,

KHATIB (1989), who investigated two stations in the western part of the Darß-Zingst estuary (Saaler Bodden) was able to confirm this result for only one of them. Therefore, the reported reductions in the egg ratio could also be a result of selective predation on egg carrying females by visual predators. Predation pressure by fish larvae and the mysid *Neomysis integer* shows a pronounced increase during late spring (JANSEN et al. 1983, DEBUS & ARNDT 1984, FRANEK 1985, ARNDT 1986).

When trying to model the annual copepod biomass cycle in the Darß-Zingst estuary, VIETINGHOFF (1982) was forced to assume that some additional factor besides predation inhibits copepod growth during the decline phase following thespring peak. Since toxic effects of cyanobacteria on Zooplankton have been reported in literature (ARNOLD 1971, MILLS & WYATT 1974, LANPERT 1981), he assumed hypothetically that these were responsible for inhibitory effect on copepod growth. The assumption led to good curve fitting. Cyanobacteria, especially the species *Gomphosphaeria pusilla* (see Fig.1), become a dominant phytoplankton group in the Darß-Zingst estuary during June.

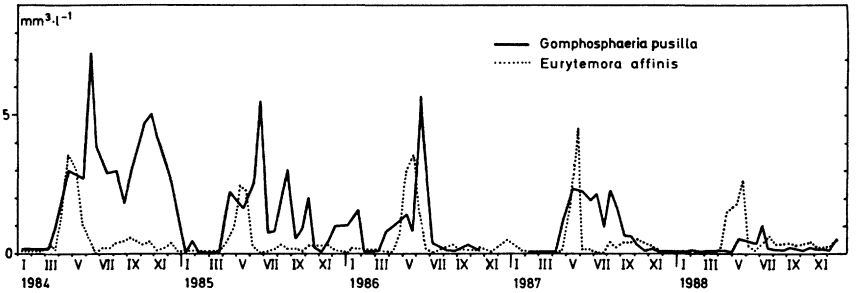

Fig. 1 Annual biomass cycle of *Eurytemora affinis* (Calanoida, Copepoda) and *Gomphosphaeria pusilla* (Cyanobacteria) at the station "Zingster Strom" in the middle of the Darß-Zingst estuary. Data for *E.affinis* in 1987 for the station Dierhagen (Saaler Bodden) from KHATIB (1989)

The influence of potential inhibiting factors on the population growth of *E.affinis* was also analysed by Ring et al. (1985), Ring (1987) and HEERKLOSS et al. (1990). They studied (1) the natural spring phytoplankton population for toxic effects, (2) the influence of temperature, pH-value and high concentrations of free ammonia on this species, and (3) whether mortality increases as a result of attached epizoic ciliates. Using the feeding rate as an indicator of vitality, RING (1987) showed that the animals adapt to the seasonal temperature cylce by a shift in their temperature optimum from 10° to 15°C. He showed that a temperature of 20°C is above-optimal. However, in his experiments the animals were acclimized to the experimental temperature for only 24 hours. This may have been too short, because HEERKLOSS et al. (1990), reporting on laboratory cultu-

res growing at various temperatures, observed no signs of stress in animals grown at 20°C. The correlation between generation time and temperature followed the Vant-Hoff rule between 5° and 20°C. It therefore seems unlikely that the higher temperatures typically occurring in shallow water areas in June contribute to the decline of the spring peak of *E.affinis.* With respect to cyanobacterian toxicity, RING (1987) found no indication that natural phytoplankton collected in early summer was toxic. On the other hand, his results indicated that high pH-values and epizoic ciliates play a role. He found that pH-values above 9 inhibited the feeding rate. Open water pH-values in the Darß-Zingst estuary rise to between 9 and 10 in June.

This paper presents data about the development of *E.affinis* in an enclosure experiment. They allow an evaluation of the relative importance of various factors that can be considered potential causes of the spring peak decline because the environmental factors influencing the population dynamics of this species are more defined in experimental compartments than in the open water. The experiment called KOLA 89/1 (Komplexes Laborexperiment) started in April 1989. Its original aim was to study the succession of the plankton community in 90-litre containers under controlled temperature and light conditions for only seven weeks. Owing to the stability of the population dynamics of *E.affinis* in the compartments, observation continued after the original experiment finished in May 1989. Zooplankton samples were collected, and a restricted data set was measured, once or twice a month for over 15 months. The results from three compartments will be presented here. Two were in a tempered cold room at 10°C, and the third was held at room temperature. It was possible to study the effects of food quality on the *E. affinis* population development besides the temperature because the successional paths of the phytoplankton and protozoan communities diverged in the different compartments. Since planktivorous predators were excluded from the compartments, the experiment represented an opportunity to study the food-zooplankton interaction on its own.

Material and methods

The compartments were prepared by filling cylindric plastic containers (height 75 cm, diameter 45 cm) with a 10 cm layer of sediment from a nearshore station in the central part of the Darß-Zingst estuary (Barther Bodden). The container was filled with 90 litres of water from the same location. After preincubation for one week to stabilize the sediment stratification, the experiment was started by changing the water which had been filtered through gauze with a mesh size of 200 *µm.* The water was destratified by aeration. The illumination from above (26.1 watt/m^2 at the water surface) was swiched on for 16 hours a day in summer (March - October) and 12 hours a day in winter (November - February). Originally there were four compartments, two serving as control enclosures and the two other being nutrient enriched by the addition of 120 ml 0.1 M $NaNO_3$. One set was run at 10°C and the other at 20°C. Only the results from three compartments are described here because *E.affinis* disappeared completely from the fourth after so-

me months when a clear water phase led to the elimination of almost all phytoplankton. The compartments considered here are

comp. I: control, 10°C,
comp.II: added nitrate, 10°C,
comp.III: control, room temperature.

Compartment III was not controlled by thermostat after June 1989, but ran at room temperature, which varied between 18°and 21°C (in January and February 1990 between 15°and 18°C). Zooplankton samples were collected by filtering 5 to 10 litres of water through gauze with a mesh size of 200 µm. Additionally, a one litre sample was filtered through a net with a mesh size of 20 µm to estimate microzooplankter abundance. Animals were washed into 20 ml water of the same salinity and fixed with formaldehyde to a final concentration of 4%. The microscopic counts were made in flat chambers. Abundances were converted to biomasses by using volume standards (c.f. HEERKLOSS et al. 1991). The turbidity (extinction at 720 nm), temperature, pH-value and salinity were measured when samples were collected. Counting results for the nanophytoplankton, picophytoplankton, heterotrophic nanoflagellates and ciliates for the first seven week period were taken from the data stock of the original experiment KOLA 89/1 (H.P.Spittler, R.Schumann pers.comm.). After the seventh week, numbers of individuals for these groups were quantified once a month by inspecting a live sample in a Kolkwitz chamber under an epifluorescence mikroscope.

The pH-value averaged 8.5 and never exceeded 9.0. It can be assumed, therefore, that the zooplankton was not pH-stressed during the experiment. The salinity was 8.5‰ at the beginning. Due to evaporation it increased to 11.0‰ in compartments I and II and to 14‰ in compartment III. This can be regarded as having no significant influence on the population dynamics of *E.affinis* because the species tolerates salinity fluctuations from 0.2 to 33‰ (JEFFRIES 1962, KATONA 1970).

Results and discussion

The succession of the Zooplankton in the different compartments and the variation in time of turbidity are shown in Fig. 2, 3 and 4. Estimates of the seston dry weight during the first week varied between 19 and 26 mg/l. Using these values as for reference, a rough estimate of the concentration of suspended particulate matter can be made by multiplying the extinction at 720 nm by the factor 4. Thus the seston content during bloom phases in comp.II was as high as 100 mg/l (Fig. 3, but during a clear water phase in comp.I it dropped to below 1 mg/l. The water placed in the experimental containers when the experiment began contained several nanophytoplankton species, and the chlorophyceans *Monoraphidium contortumand Tetrastrum trangulare* were the dominant species (Table 1). However, the phytoplankton changed drastically in both

qualitative and quantitative terms during the first seven weeks. The biomass started at a level of 5.2 to 5.4 mm^3/l and increased to 6.8 mm^3/l in comp.J and 15.4 mm^3/l in comp.II, but dropped to 0.35$mm^3/1$ in comp.III. The cyanobacteria species *Gomphosphaeria pusilla* appeared in comp.I and II, whereas the rather diluted phytoplankton of comp.III consisted mainly of *Scenedesmus spp.* and *Stephanodiscus hantzschii.*

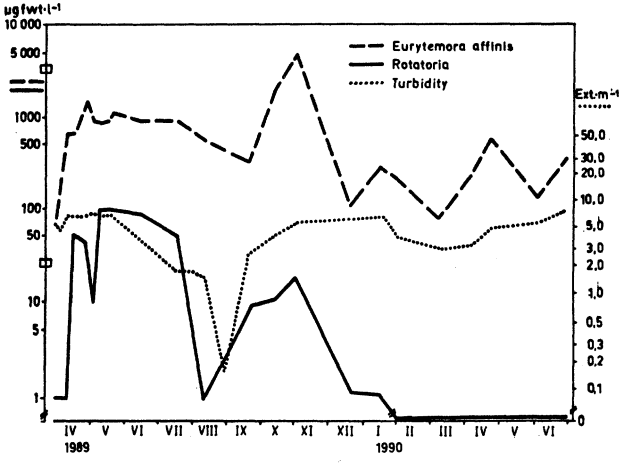

Fig. 2 Development of the biomass of *Eurytemora affinis* and rotifers and the time course of turbidity (extinction at 720 nm) in compartment I (without nutrient enrichment, 10°C)

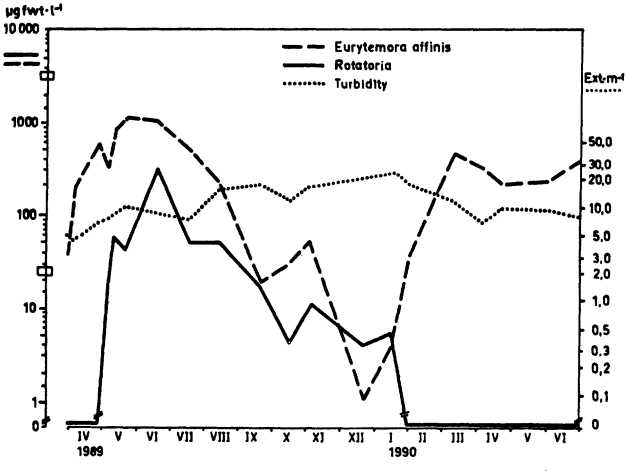

Fig. 3 Development of the biomass of *Eurytemora affinis* and rotifers and the time course of turbidity (extinction at 720 nm) in compartment II (nitrogen enriched, 10°C)

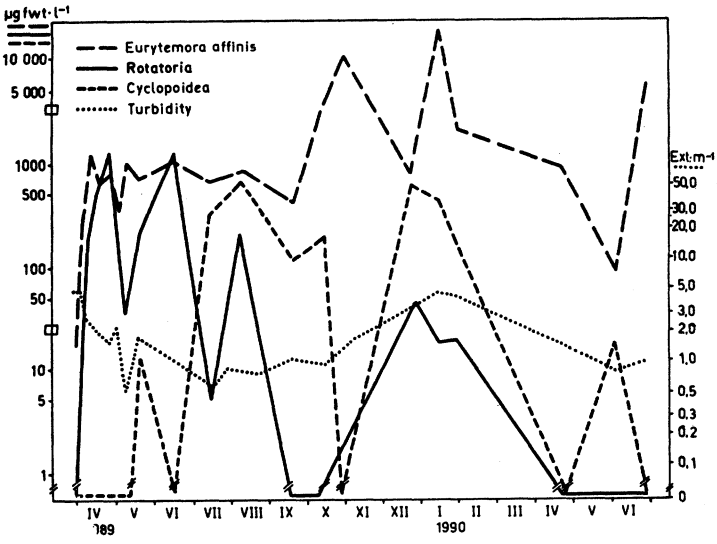

Fig. 4 Development of the biomass of *Eurytemora affinis*, rotifers and cyclopoids and the time course of turbidity (extinction at 720 nm) in compartment III (without nutrient enrichment, room temperature)

Table 1 Abundance of the dominant nanophytoplankton species in compartment II. Numbers are cells/ml or colonies/ml.

1 = *Gomphosphaeria pusilla*, about 30 cells/colony; 2 = *Merismopedia spp*, 16 cells/colony;
3 = *Oscillatoria limnetica*, trichom length 30 µm; 4 = *Scenedesmus spp.*;
5 = *Tetrastrum triangulare* 6 = *Monoraphidium contortum*;
7 = *Stephanodiscus hantzschii.*

DATA	1	2	3	4	5	6	7
89/29/03	0	550	0	1,950	11,650	14,250	1,800
89/17/04	0	450	0	1,900	4,200	18,500	340
89/05/05	2,900	550	0	1,200	3,500	19,500	275
89/18/05	6,100	950	0	775	1,000	22,750	200
89/20/09	19,000	0	0	230	0	5,550	1,210
89/12/10	120,000	240	0	0	0	1,350	180
89/01/11	105,000	0	0	0	0	0	0
90/01/02	125,000	0	0	0	0	0	0
90/08/03	43,000	0	0	90	0	9,000	0
90/05/04	59,000	0	0	50	0	1,850	0
90/03/05	81,000	0	75	0	0	22,000	0
90/31/05	43,000	0	7,500	0	0	33,800	0
90/24/06	50,100	0	36,000	0	0	50,000	0

The further succession in the nutrient enriched comp. II was characterized by the dominance of *Gomphosphaeria pusilla.* A dense bloom of this species developed, reaching a maximum with an abundance of 125,000 colonies per ml (= 60 mm3/l) in February 1990 and when it was almost the only nanophytoplankton species (Table 1). The *Gomphosphaeria* population then gradually declined. The chlorophycean species *Monoraphidium contortum* and the filamentous cyanobakterium *Oscillatoria limnetica* became more numerous. The biomasses of the picophytoplankton and the heterotrophic nanoflagellates in comp. II remained at a low level during the whole investigation period (as a rule below 0.5 mm^3/l), but large hypotrichous ciliates developed biomasses between 0.5 and 2.0 mm^3 /I.

The nanophytoplankton biomass in comp.I remained stable until the end of May 1989. The extinction curve in Fig. 2 shows that it then gradually declined. Finally, in early September, a clear water phase occurred. The phytopiankton that developed afterwards reached a biomass as high as that at the beginning of the experiment. The nanophytoplankton was almost fully replaced by coccoid and filamentous picoplankton species belonging to the cyanobacteria. In February 1990 this group reached a maximum level of 2.3×10^4 cells/ml. Heterotrophic nanoflagellates exhibited rather high and stable abundances during the period after the clear water phase. Their biomass was 1 mm^3/l at the beginning of the experiment, and their biomass levels were at least this high when samples were examined in October 1989 and February, March, April 1990.

The natural phytopiankton disappeared fairly rapidly in comp.III, although there was no genuine clear water phase (Fig. 4) . After a minimum in July, the extinction gradually increased and reached with 5 a level in January that was similar to that at the beginning of the experiment. Autotrophic nanoflagellates belonging mainly to the genus *Cryptomonas* contributed most to the suspended particulate matter from October 1989 to June 1990. The biomass levels of the picophytoplankton, heterotrophic nanoflagellates and ciliates were comparatively low during this period.

Eurytemora affinis was the main Zooplankton species in all compartments. The biomass of the rotifers, of which *Brachionus plicatilis* was the dominant species, originally equalled that of *E.affini,* but then decreased in relative terms. Considerable numbers of cyclopoid copepods were present in comp.III. Markers on the biomass scale in Fig. 2, 3 and 4 indicate the lowest and highest mean *E. affinis* biomasses calculated from long term monitoring programmes lasting several years in the Darß-Zingst estuary. The lower marker corresponds to the winter level. The upper marker shows the level during the spring peak. In comp.I and II the rotifers were unimportant, and cyclopoids appeared only sporadically. However, in the compartment running at room temperature rotifer biomass peaks of up to 1 mm^3/l were observed in April and June 1989. The rotifer biomass level remained rather low after September 1989, probably as a result of high grazing pressure by cyclopoids.

It can be seen from Fig. 2 and 4 that the *E.affinis* biomass of compartment I and III was high for almost the whole investigation period. Some biomass values even exceeded the maximum level observed in the field. Obviously, phytoflagellates and heterotrophicna noflagellates were a good food for *E.affinis* and served as a basis for a sustainable food chain. Because the two compartments differed in temperature, our results contradict the assumption that the copepod decline after the spring peak is caused by high temperature. On the contrary, it supports the conclusion drawn from earlier results obtained with laboratory cultures (HEERKLOSS et al. 1990) showing that temperature factor has to be excluded from the set of potential causes leading to the decline of the spring peak of *E.affinis.*

The results from comp. II seem to indicate that *Gomphosphaeria pusilla* has an inhibitory effect on *E. affinis.* This could be a factor that contributes to the spring decline. The *G.pusilla* biomass at the Zingster Strom in spring varied betweeen 5 and 10 mm^3/l from 1981 until 1988, which represents a considerable part of the total phytoplankton biomass. It must be remembered, however, that *G.pusilla* does not always develop blooms in spring. In 1988, its maximum biomass was only 1 mm^3/l, but the spring population decline of E. affinis took place in the same way as in other years. On the other hand, the fact that *E.affinis* declined in comp.II during a *G.pusilla* bloom, but recovered after January 1990 when the green alga *Monoraphidium contortum* developed besides *G.pusilla* (Table 1) does suggest the presense of an inhibitory effect. But this is not a result of selective food rejection by the animals. Feeding experiments with 1 4-C-labelled *G.pusilla* (unpubl.) showed that the feeding rate of adults and late copepodite stages is as high on this species as on other nanophytoplankton species. An additional pointer to a possible inhibitory effect of *G.pusilla* on *E.affinis* came from a further enclosure exporiment (KOLA 89/2), which started in October 1989. In this experiment, *G.pusilla* developed a bloom in one of the compartments running at 20° C, while *E.affinis* disappaered and was replaced by the copepod *Acartia tonsa.* Thus, there are definitely signs of an inhibitory effect of *G.pusilla* on *E.affinis,* but it is not clear wether this effect is adequate to explain the rather fast population decline of the copepods after the spring peak.

A strong correlation was found between the nauplian mortality and abundance of adults and copepodites. Fig. 5 demonstrates the inverse relation between the abundance and a coefficient C for nauplian survival. C is defined as

$$C(\%) = N_n \times 100/N_o$$

where N_o = individuals per litre of adults and copepodites

and N_n = individuals per litre of nauplian stages I, II and III divided by female individuals per litre.

The division of the nauplian number by female abundances served to standardize the nauplian number for recruitment by egg hatching. Fig. 5 shows that the number of early nauplian stages per female decreases as N_o increases. The obvious conclusion is that the copepodites and adults

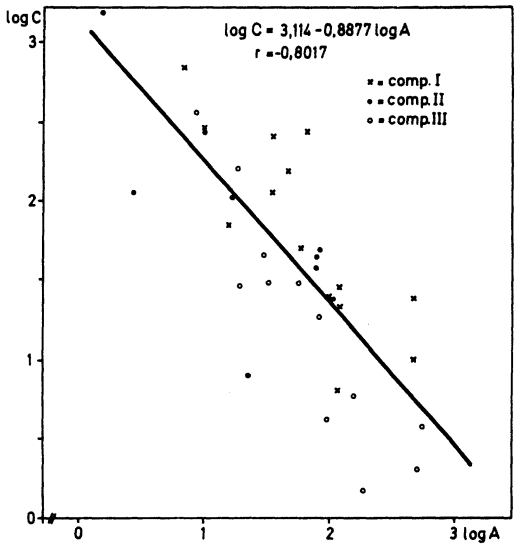

Fig. 5
Relation between the abundance of copepodites and adults of *Eurytemora affinis* and the survival coefficient C for the nauplian stages I, II and III

graze on the nauplians. Cannibalism on nauplians was observed also by HEERKLOSS et al. (1990) when nauplians hatched from egg-carrying females of *E. affinis* in small cultivation tubes and by LONDSDALE et al (1978) for *Acartia tonsa.* Cannibalism seems to be a mechanism regulating population size when the abundance becomes high, and it may explain the oscillation-like variations in *E.affinis* abundance in comp. I and III. As ARNDT (1985) has shown, the sex ratio changes in favour of the males when the population density becomes very high, and this may also contribute to the self-regulation of population size. It seems conceivable that cannibalism and the change in sex ratio can cause a fast population decline when the abundance surpasses some threshold value. If environmental factors such as pH-value, epizoans, planktivorous predation and composition of food cause an additional increase in mortality or decrease in natality, a rapid decline in population size to a very low level is understandable.

Summarizing the conclusions from the experiment, there are two questions to be answered separately: (1) which factors are responsible for the high rate of decline after the spring peak, and (2) why does the population remain small during summer. The explanation of the small population size in summer may lie in high mortality due to factors such as predation pressure and pH-value. These factors were excluded in our experiment, and this might be why the biomass was not as low as the observed in the open water in mid-summer even during periods of minimum density (e.g. in December 1989 in comp.I). The answer to the first question may lie in intraspscific control mechanisms. This would be in line with the findings of ARNDT (1985) and KHATIB (1989), who observed a high mortality among early nauplian stages for the third cohort of *E.affinis* in June.

Zusammenfassung

Kausalfaktoren der Populationsökologie des ästuarinen Copepoden *Eurytemora affinis* wurden an Hand von Zeitreihenergebnissen aus drei Mesokosmosexperimenten untersucht. Die Mesokosmen enthielten 90 Liter Biotopwasser und wurden im Labor unter konstanten Licht- und Temperaturbedingungen über einen Zeitraum von 12 Monaten gehältert. Nach anfänglichem Artenschwund bildete sich eine stabile Klimaxgemeinschaft des Planktons heraus. *E.affinis* wurde dabei zur dominierenden Komponente des Zooplanktons. Die Ergebnisse zeigten, daß die Blaualge *Gomphspheria pusilla* das Populationswachstum der Copepoden hemmend beeinflußt und daß die Moralitätsrate der Nauplien durch Cannibalismus erhöht wird.

Acknowledgement

We thank Mrs. Helga Albrecht for counting the Zooplankton samples and technical help.

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