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ZOOPLANKTON PRODUCTION AND ITS CONSUMPTION BY PLANKTIVORES IN A BALTIC INLET

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ABSTRACT

Quantitative studies on the planktonic matter flux were carried out in the shallow eutrophic waters south of the Darss-Zingst Peninsula (southern Baltic, 3—9‰). Zooplankton production and P/B values were estimated by the egg ratio method (rotifer and cladoceran species) and cumulative growth method (copepods). Predation pressure on zooplankton was estimated for all important planktivores (*Neomysis integer*, fish juveniles, smelt and herring). A comparison between predation rates of planktivores and rates of zooplankton production indicated that planktivores had the most important impact on the dynamics of crustacean plankton. Short life times of adult copepods can be explained by high predation pressure during summer. Rotifer mortality could be only attributed to the consumption by planktivores. The same seems to be valid for protozooplankton.

The main components of the planktonic food web of the estuary are summarized. The only partial use of phytoplankton production by herbivorous zooplankters as well as the only partial use of zooplankton production by planktivores are discussed.

INTRODUCTION

In limnetic ecosystems the knowledge of interactions between planktivores and their zooplankton food organisms is already used to manipulate aquatic food webs as an additional possibility to limit the effects of eutrophication (cf. Shapiro et al., 1975, Benndorf et al. 1984) i.e. the development of carnivorous fishes as consumers of planktivores is encouraged in order to reduce the predation pressure on zooplankton and in this way increase zooplankton biomass which in turn intensively reduces phytoplankton biomass and its sedimentation. In estuarine and marine waters quantitative data on zooplankton — planktivore interactions on the ecosystem level as a basis for such purposes are

rather rare. This is especially due to the large area under study, the difficulties in routine sampling, the complex processes of water exchange and animal migration etc. To contribute to some quantitative estimates of interactions in the pelagic zone, a complex ecosystem analysis in the shallow Darss-Zingst estuary (cf. Vietinghoff, 1984), an eutrophic inlet with some similarities to other coastal inlets of the southern Baltic like Schleifjord and Vistula Lagoon, was used for quantitative studies on the relation between zooplankton production and feeding activity of planktivores.

MATERIAL AND METHODS

In this paper quantitative estimates are presented for the Barther Bodden as a major aim for ecosystem analysis of the Darss-Zingst estuary (southern Baltic; 54°25′ N, 12°45′ E). It has the area of 19.4 km² and the mean depth of 1.8 m. Salinity ranges normally from 3 to 7 with the mean of about 5.5‰. Primary production and seston contents are very high (for details see Heerkloss et al. 1984, Schiewer et al., 1986).

Zooplankton production was determined for 12 dominant species and for Synchaeta spp., which account for more than 95% of the total mesozooplankton production (cf. Table 1). Integrated sampling was performed weekly by means of a 5 1-Hydrobios-sampler and following concentration on a 56 µm sieve. Formalin-fixed samples were analysed for all developmental stages and sexes. Cohort analysis was carried out for copepods according to Rigler and Cooley (1974). For all zooplankton species (excluding Synchaeta) the egg types were differentiated and egg ratios determined. Production of copepods was estimated using the cumulative growth method (Edmondson, 1974; Uye, 1982) and temperature-dependent regressions for development time. Cladoceran and rotifer production was determined by the egg ratio method (Edmondson, 1974) by taking development times from the literature (cladocerans: Vijverberg, 1980; rotifers: Bottrell et al. 1976, generalized regression). For the quantitative estimation of seasonal changes in predation pressure on the separate zooplankton groups (copepods, cladocerans, rotifers), the available values for biomass, predation rates, and food selectivity of the dominant predators were summarized for different investigation periods. Data for biomass of the mysid Neomysis integer were taken from Arndt and Jansen (1986; and 1979, 1980), for fish juveniles in the shore region from Bast et al. (1980), Winkler et al. (1984) and Pribbernow et al. (1985) (years: 1979; 1981; 1983), and for pelagic fishes from Winkler and Debus (personal comm.) and Franek (1985) (years: 1983, 1984). For mysids the data for predation rates and food selectivity were obtained from Arndt and Jansen (1986), and Jansen et al. (1983), for fishes in the shore region from Debus and Arndt (1984) and Arndt et al. (1984), and for pelagic fishes from Franek (1985) and Arndt (1985).

RESULTS AND DISCUSSION

Values for seasonal changes in daily production are shown in Fig. 1. Annual means for daily P/B ratios and production for all investigated species are listed in Table 1. The only productive copepods of the Barther Bodden are Eurytemora affinis (Poppe) and Acartia tonsa Dana. In 1981 E. affinis reached the highest production of all mesozooplankters. In both years, 1981 and 1982, the species produced 11 generations, of which the third to the fifth were the most productive. The 11th generation overwinters and has a generation time in

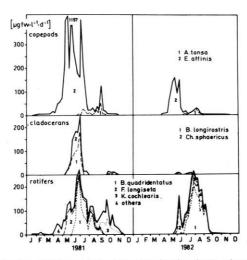


Fig. 1. Seasonal changes of daily zooplankton production in Barther Bodden (summarized to 3 zooplankton groups).

the field of about 92 days. Maxima in egg production occured in May and September. Generally, only 10—30% of eggs produced develop into copepodite stages. Mean daily P/B ratio was relatively high but similar to values reported by Heinle (1981) for the same species and lower when compared to the thermophile species A. tonsa. The latter species hatches from resting eggs in April/May when temperatures are above 10°C. About 8 to 9 generations are produced up to December. In autumn, when temperatures are below 15°C, the species begins to produce resting eggs, and below 10°C only resting eggs are to be found (for details see Arndt and Schnese, 1986).

The two cladoceran species, *Chydorus sphaericus* (O. F. Müller) and *Bosmina longirostris* (O. F. Müller), are typical limnetic forms. Their occurrence is strongly influenced by annual fluctuations of salinity conditions. For both species sexual forms were found very seldom. In Barther Bodden *Chydorus sphaericus* seems to reproduce only asexually. Resting eggs were produced by both species at the end of exponential growth phases.

During 1982 rotifers were the most productive mesozooplankters. Apart from some species of *Synchaeta* (Arndt et al., 1985) and *Brachionus plicatilis*

limnetic forms dominated (see Arndt et al., 1984). P/B values recorded for the most important species *Brachionus quadridentatus* Hermann were in the upper range of values reported for natural rotifer populations. Though it is possible that production of this species was a little bit overestimated by using generalized temperature-dependent development times, its productivity is still considered to be extraordinarily high. There are several characteristics indicating that this population is especially adapted to the conditions of this estuary when compared to limnetic populations of the same species (cf. Arndt, 1985).

Table 1. Estimations of mesozooplankton productivity (P/B), annual production and losses due to predation

	P/B mean (d ⁻¹)	Mean annual prod. (mg fw l ⁻¹ a ⁻¹)	Consumption by planktiv. (g fw m ⁻³ a ⁻¹)	(%)
Copepods				
Eurytemora affinis	0.20	16.8		1
Acartia tonsa	0.27	1.3		
Total		18.1	3.8	21.0
Cladocerans				
Bosmina longirostris	0.07	1.8	ť	
Chydorus sphaericus	0.10	2.2		
Total		4.0	1.8	45.0
Rotifers				
Brachionus quadridentatus	0.89	9.0		1
Filinia longiseta	0.41	4.7		
Keratella cochlearis	0.22	2.1	3	
K. quadrata	. 0.23	0.7		
B. calyciflorus	0.30	1.1		
B. angularis	0.46	0.4		
B. plicatilis	0.69	0.6	y F 4	
F. terminalis	0.21	0.5	* 1 m m m	
Synchaeta spp.	0.11*	2.4	4.	
Total		21.5	1.7	7.9

^{*} Assumed value

The available data on zooplankton consumption by planktivores allowed us to construct a figure of its mean seasonal changes (Fig. 2). Though the data were not always recorded during the same time as were values of zooplankton production, they seem to represent the general pattern. According to this estimation *Neomysis integer* is the most important consumer of mesozooplankton though studies by Debus (pers. comm.) and Franek (1985) indicated that during certain periods the fishes of the pelagic region like smelt and juveniles of herring; perch and smelt are able to consume similar or higher amounts of zooplankton when compared to mysids. With regard to food selection (selection for copepods, cladocerans, and rotifers was determined), consumption rates of planktivores were determined for the main zooplankton groups. As is

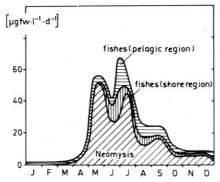


Fig. 2. Estimated mean seasonal changes of zooplankton consumption by planktivores (Neomysis = N. integer; fishes of the shore region = sticklebacks and juveniles of cyprinids, percids, and gobiids; fishes of the pelagic region = smelt, herring, and juveniles of other fishes).

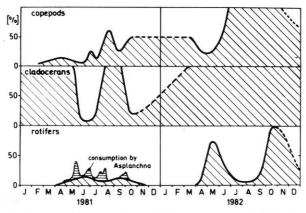


Fig. 3. Seasonal changes in the percentage of daily production of different zooplankton groups consumed by planktivores.

shown in Table 1, a significant part of total crustacean production, especially that of the cladocerans, is being consumed. Whereas rotifer consumption is not much of importance. A more precise insight into the mesozooplankton — planktivore interaction gives a comparison of production and consumption on a seasonal basis. In Fig. 3 the values of more than 100% were not shown since production and consumption were not determined for the same period. The remarkable influence of planktivores on the dynamics of copepods is clearly to be seen especially during the summer months. This result is marked by the fact that the mean life time of adult *Eurytemora* for 1981 and 1982 was 3.5 and 1.8 days, respectively, and for *Acartia* 7.0 and 2.6 days, respectively. All values lie far below the possible life span expectancy. Furthermore, life times in 1982, the year with estimated higher predation pressure, were much lower. Cladocerans are constantly much more under the control of predators. They are the prefered food item of all visually feeding predators of the inlet. This explaines our

experience that the cladocerans can only reach high abundances if abiotic (e.g. salinity) and food conditions allow for an exponential growth before or after intensive planktivore predation. Contrary to this rotifers were not under a remarkable influence of predators especially during the productive warmer season. In 1981 the omnivorous rotifer *Asplanchna girondi* was an additional predator. Rotifer populations hatched from resting eggs and grew exponentially by increasing mixis rates and reducing birth rates at the end of the log-phase (for details see Arndt, 1985). These results suggest that rotifer dynamics is mainly under the control of autoregulative processes.

One component of the zooplankton, the protozooplankton have, up to the last years largely been excluded from quantitative studies of zooplankton — planktivore interactions. Preliminary results for the Barther Bodden (cf. Arndt, 1986) indicated that ciliates contribute to a significant part of the total zooplankton production especially during summer. Recent results (Burckhardt, 1986; Arndt unpubl.; Burckhardt and Arndt, in press) showed that prior to the beginning of the phytoplankton bloom in spring the ciliates serve as an important food source for mesozooplankton, especially for *Synchaeta spp.* and *Eurytemora affinis*. During this period mesozooplankton seemed to have a remarkable effect on ciliate dynamics but during the high productive summer months predation pressure of mesozooplankton on ciliates seemed to be of minor importance. At this time omnivorous ciliates can have a temporary significant influence on ciliate dynamics (Arndt, in prep.). The frequent occurrence of cysts supports the hypothesis that during summer ciliate dynamics is like those of rotifers, governed by the processes of autoregulation.

Though zooplankton — planktivore interrelationship and its consequences in limnetic waters were much more precisely understood (e.g. Zaret, 1980) than in marine waters, the knowledge of the latter case has increased much during the last decades. In most quantitative studies available up to now from marine waters, close interactions have been found (e.g. Greve, 1981; Möller, 1980). Unfortunately protozoans and rotifers have seldom been incorporated in such studies.

CONCLUSIONS

We have observed that the Barther Bodden crustacean zooplankton is significantly influenced by planktivores whereas only a minor part of the production of rotifers and probably also of ciliated protozoans is used by higher trophic levels. Zooplankton — planktivore interactions are one side of the food web. Another important question is, which effect do zooplankters have on primary production. This is the key question when one would like to disrupt the close connection between phytoplankton sedimentation and benthic respiration found in this area (Yap et al., 1986). In Figure 4 the zooplankton feeding rates estimated by using specific feeding rates (Heerkloss et al., 1984;

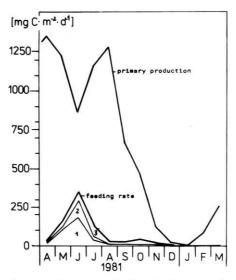


Fig. 4. Comparison of seasonal changes of phytoplankton production (from Börner, 1984) and the calculated feeding rates of zooplankton (1 = copepods; 2 = cladocerans; 3 = rotifers).

Heerkloss and Schnese — unpubl.), are compared with values of primary production (Börner, 1984) for the period 1981—1982. Only in late spring zooplankton is able to have a remarkable influence on phytoplankton. At this time zooplankters consume about one third of primary production and as can be shown by mesocosm experiments (Krummhaar, 1983; Heerkloss, personal comm.) zooplankters can have a significant influence on phytoplankton composition. But already one month later herbivores again seem to have no significant influence on phytoplankton development. In this period microconsumers (the important protozoans are not incorporated in Fig. 4) use, according to the literature, small detritus and bacteria as a significant part of their food. The majority of phytoplankton production is believed to be respired at the sediment surface and it is likely that a part of the benthic bacteria and degraded material is used by microconsumers in the plankton after resuspension.

One could speculate that a reduction of predation pressure by planktivores during summer could enable the copepods to maintain their influence on phytoplankton. However fact that dominating *Eurytemora affinis* is sensitive to increased temperature and pH-values (Ring, 1987) and enclosure experiments without predators also revealed a summer decrease of *Eurytemora* (Schiewer et al., 1986). Estuarine waters with salinities around 6—6‰ unfortunately lack such efficient filter feeders like the limnetic daphnids. The introduction of additional seston consumers like silver carps (Schnese, 1978) and *Mytilus edulis* (Arndt and Böttcher, personal comm.) revealed not satisfactory results due to low growth rates and high mortality during short periods of extremely low salinities.

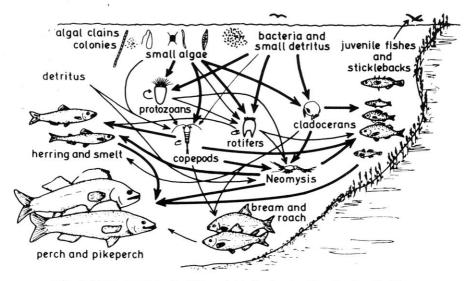


Fig. 5. Main components of the pelagic food web of the Barther Bodden.

Another problem is the complexity of interactions in the pelagic zone. Fig. 5 represents a summary of qualitative studies. For purposes of water management the most important zooplankton consumer which has to be reduced by carnivores is *Neomysis integer*. But this species is an important food item of both the planktivorous fishes and the piscivorous perch and pike-perch which also have important interactions. On the other hand, several groups (like mysids, copepods, and omnivorous rotifers) consume food items of at least three trophic levels. One gets an impression of the stability of estuarine ecosystem with its low diversity but very complex interactions when one tries to change its structure in a specific direction.

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