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# POPULATION DYNAMICS AND PRODUCTION OF ESTUARINE PLANCTONIC ROTIFERS IN THE SOUTHERN BALTIC: *BRACHIONUS QUADRIDENTATUS* (HERMANN, 1783)

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Population dynamics and production of a natural population of *Brachionus quadridentatus* were studied by regular field sampling at a routine station in the shallow Darss-Zingst estuary (3–7‰ salinity), Southern Baltic, for two successive years. Investigations included observations of hatched resting eggs, abundance of amictic and mictic females, egg ratio, resting egg production, and mixis rate. Using egg development times from literature, instantaneous rates of growth, birth and death rates were estimated. Mixis rates increased with increasing productivity. The mean P/B value for the growth seasons was 0.89/d and the corresponding production was 9.0 mg wet weight/dm$^3$a. Significant parasitism by microsporidians was observed during one year when up to 12% of the females were infected during June/July. *B. quadridentatus* served as a food source for the rotifer *Asplanchna girodi*, the mysid *Neomysis integer*, and fish juveniles. Copepods could also be considered as predators. However, on an annual basis predators seemed to be of reduced importance and the population dynamics were governed mainly by autoregulative processes.

## INTRODUCTION

The monogonont rotifer *Brachionus quadridentatus* is known as a cosmopolitan species (cf. Pejler 1977) mainly from fresh water, but there are also records from brackish coastal and limnetic saline waters (Althaus 1957, Galliford 1946, Miracle and Vincente 1983). *B. quadridentatus* is morphologically a very diverse group (cf. Koste 1978). Generally, this species plays a minor role in the numerical composition of the rotifer fauna and is mostly found only as a member of benthic communities. However, in the coastal waters south of the Darss-Zingst peninsula, Southern Baltic, *B. quadridentatus* is the most productive member of the mesozooplankton community (Arndt et al. 1984; Arndt 1989). There are only a few detailed studies on population dynamics of estuarine rotifer populations. In this paper, an analysis of parameters of population dynamics and production of *B. quadridentatus* is presented from a two-year study in Barther Bodden (Southern Baltic).

## MATERIAL AND METHODS

The studies were carried out at the routine station Zingster Strom in Barther Bodden (see Fig. 1). The Barther Bodden is a shallow (mean depth of 1.8 m) inner coastal water body with a range of salinity generally from 3 to 7‰ and annual temperature ranges from −0.5 to 25°C. Long-term investigations showed that the station Zingster Strom is a suitable site for integrated sampling of the zooplankton of Barther

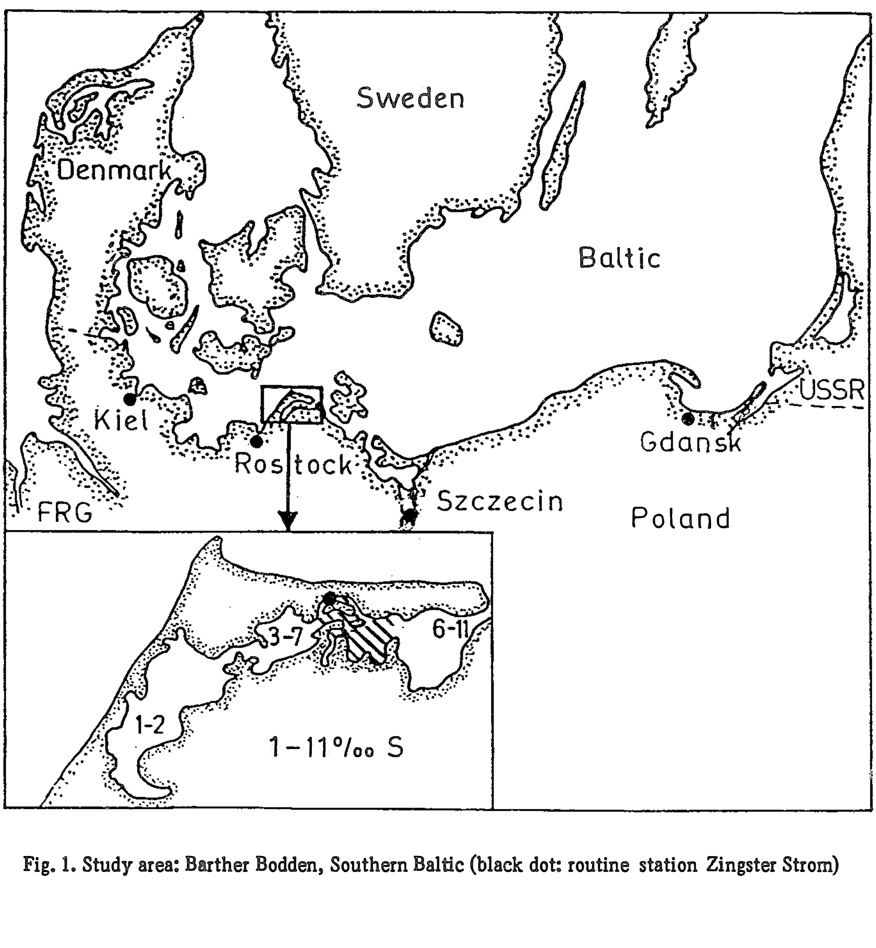


Fig. 1. Study area: Barther Bodden, Southern Baltic (black dot: routine station Zingster Strom)

Bodden due to continuous exchange processes of water masses between Barther Bodden and the western boddens (Arndt unpubl.).

Rotifer dynamics were investigated as described by Arndt (1988) by integrated sampling with a 5 l Hydrobios sampler at weekly intervals; 21 l of biotope water were filtered (> 56 µm) and preserved with 4% formaldehyde. Subsamples were searched for females and all types of eggs under a light microscope (160x magnification). The occurrence of males and covers of resting eggs (as an indication of hatching of resting eggs) were recorded only qualitatively. Experiments on the hatching of resting eggs were done with mud from the surface layer of sediment samples taken by means of an Ekman-grab in Zingster Strom on 21 January 1981 (4.1‰; −0.3°C). The sediment was diluted with biotope water exposed in petri dishes at 20°C to a light/dark cycle of 12 hours dishes were observed daily.

Parameters of population dynamics were estimated according to Edmondson (1965) and Paloheimo (1974) with the formulae $r = (\ln N_0 - \ln N_t)t$; $b = \ln(E+1)D$; $d = (b_0 + b_t) 2 - r$, with r as the instantaneous growth rate, b as the instantaneous birth rate, and d as the instantaneous death rate. No is the abundance of amictic females at time 0; $N_t$ is the abundance at time t; E is the egg ratio of subitaneous eggs per amictic female, and D is the development time of eggs, estimated according to Bottrell et al. (1976). The abundance of amitic females and the percentage of mictic females (mixis ratio in %) was calculated assuming the same mixis ratio for egg-bearing and non egg-bearing females. To reduce the influence of patchiness moving averages of abundances were used in calculations. Rotifer production (P) was estimated according to Edmondson (1974): P = E/DNW, where W is the individual biovolume of a female.

## RESULTS AND DISCUSSION

In Barther Bodden, two forms of *quadridentatus*-group (cf. Koste 1978) occur in plankton samples: the typical form *quadridentatus* and the form *brevispinus*. The ecological requirements of these forms seem to differ significantly. The *brevispinus* is rare in the brackish waters of the Darss-Zingst estuary and shows a preference for litoral limnetic habitats, whereas the typical form is widely distributed in the plankton of the estuary at salinities from 1–8 ‰. Even at 8‰, mass occurrence could be recorded for the typical form (Schwarz 1962). Its planktonic occurrence is in contrast to the behaviour of other populations (cf. Voigt 1904, Preissler 1977, Pourriot pers. comm.) and may be supported by the high rates of resupension in the shallow eutrophic estuary. Differences in ecology between both of the forms were also obvious during enclosure experiments (0.35 $m^3$) in Zingster Strom, when the *brevispinus* showed a mass development within a few days, while the typical form declined after organic enrichment in contrast to the opposite pattern of population development in the control enclosure (Arndt unpubl.). In Barther Bodden, the typical form is the most productive rotifer. The species occurred in plankton samples only from April to October, reaching maximum abundances during July and August. Significant numbers of hatched resting eggs were observed only at temperature above 10°C. Separate experiments using sediment samples from Zingster Strom revealed first hatching of resting eggs after 6 days of storage at 20°C. Nipkow (1961) included hatching of resting eggs from a two-years-old sediment layer from Lake Zürichsee after 5 days at 12–14°C. The polythermal behaviour of this species is an accordance with long-term investigations in the Darss-Zingst estuary and in Rugian coastal waters (Rentz 1940, Schwarz 1963) as well as in fresh water (Voigt 1904, Diffenbach and Sachse 1911).

## Population dynamics

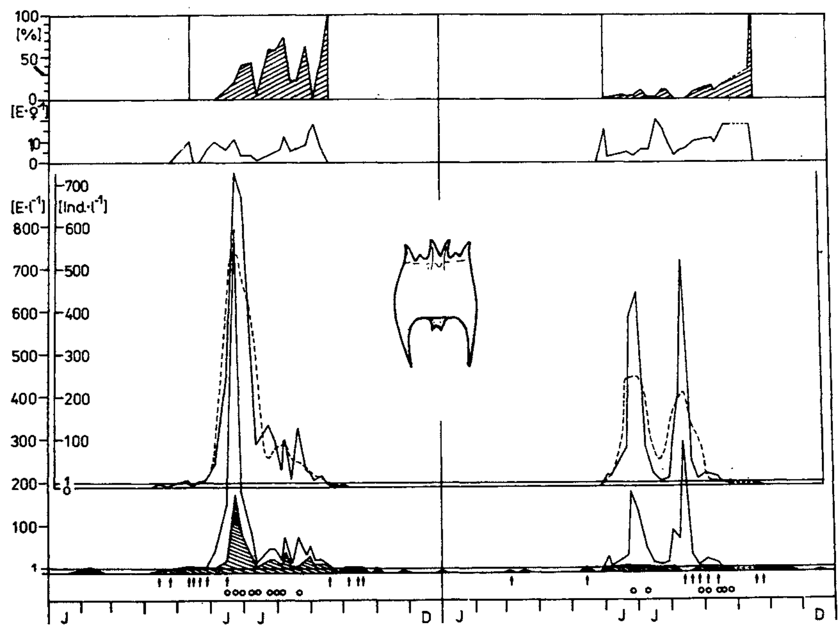


Fig. 2. Population dynamics of *Brachionus quadridentatus* in Barther Bodden during 1981 and 1982 (Mixis ratio as percentage of mictic females in relation to total number of females; egg ratio as subitaneous eggs per amictic female; abundance of all females, dashed line: moving averages; abundance of all female-eggs, hatched area: resting eggs; arrows indicate observations of hatched resting eggs in plankton samples; circles indicate occurrence of males)

Resting eggs hatched from the sediment in April/May when temperatures were above 10°C. Negative mortalities (Fig. 2) indicate significant recruitment from resting eggs in April/May and June. Very low death rates in September/October in connection with the observed hatching of resting eggs during this time point to an additional hatching period in autumn and probably in August, too. Egg ratios and birth rates were very high, but variable. Maximum birth rates were calculated to be up to 1.7/d. Though this value may be biased by underestimation of the egg development time using the generalized formula by Bottrell et al. (1976), the population development in th field shows the high productive potential of this population. Mictic females were present during nearly the whole growth season. Mixis ratios were variable within one season and between the two years. Mixis ratios seemed to increase with increasing productivity. A similar phenomenon has recently been described by Snell and Boyer (1988) for *B. plicatilis*. At the end of the growing season only mictic females were found.

Sexual reproduction occurs especially when the population has already reached its maximum density. This reproductive strategy should support the maintanance of strains which are especially adapted (cf. King 1980) to these brackish water conditions

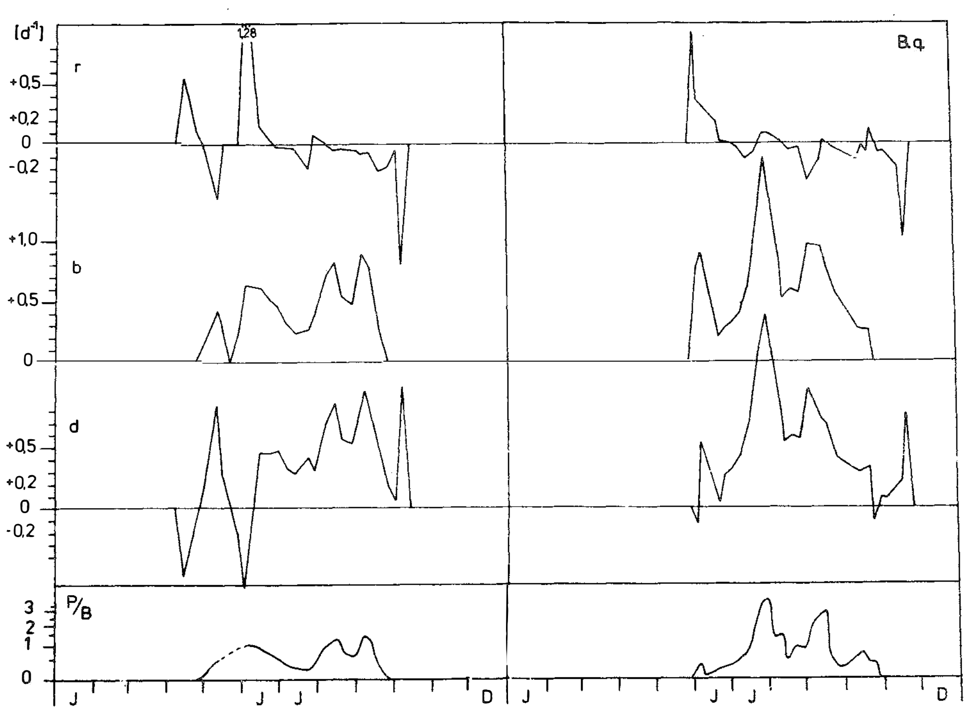


Fig. 3. Growth rate (r), birth rate (b), death rate (d), and productivity (P/B) of *B. quadridentatus* in Barther Bodden, 1981 and 1982

At least during 1982, two distinct periods of population development and sexual reproduction indicate the succession of possibly two different strains, as found for *Asplanchna* by King (1980). Similar observations were made also for other brachionid populations of the Darss-Zingst estuary (cf. Arndt 1985); however, genetic investigations are necessary to test if the hypothesis regarding the succession of several strains proves right.

The productivity of *B. quadridentatus* was highest among all metazooplankters of the Barther Bodden (Arndt 1989) and lies in the range of values recorded in laboratory cultures (cf. Preisser and Spittler unpubl.). The mean P/B ratio for both growth seasons was estimated to be about 0.89/d and the annual production was about 9 mg fresh weight/dm$^3$. According to these high values, the *B. quadridentatus* population should be optimally adapted to the brackish water conditions in Barther Bodden.

### Influence of abiotic factors

The temperature should have the most important influence on the dynamics of this polythermal species. Population growth was only possible above temperatures of 10–15°C. Maxima in egg production corresponded to maxima in water temperatures. Higher temperatures during the summer of 1982 should be the reason for the higher productivity during that year.

Salinities in the range at least up to 7‰ are tolerated by this population. There are no significant differences between the productivity of this species in Barther Bodden at about 5‰ compared to the results of Khatib (1989) from the inner part of the estuary at 1–2‰.

### Influence of biotic factors

The food concentration seems to play a very important role for the population development of *B. quadridentatus.* In the coastal waters around Rügen only in the highly eurotrophic Darss-Zingst estuary with phytoplankton summer biovolumes of 40–50 mm$^3$/dm$^3$ and abundances of up to 1000 ind./dm$^3$ were found. Only little is known regarding the preferred food items of this species. Spittler (1976) found that particles in the size range of less than 1 µm up to 17 µm can be consumed. Preisser and Spittler unpubl. showed that *Chlorella* and also detritus of macrophytes can serve as a food source.

Correlation analysis (Spearman rank correlation) between the birth rate of *B. quadridentatus* during 1981 and 1982 and the biomass of potential planktonic food particles revealed highly significant correlations ($p < 0.001$) regarding the seston content, the bacterial biomass, the total biovolume of phytoplankton, the diatom *Stephanodiscus hantzschii,* and the blue-greens *Oscillatoria limnetica* and *Lyngbya contorta* (Arndt 1985). Observations on cultures revealed that *B. quadridentatus* is able to feed on filamentous bluegreens by biting off one end of the alga with the mastax. A similar observation was made by Starkweather (1981) for *B. calyciflorus.* In feeding experiments using cultures of *Chlorella* sp., *Scenedesmus quadricauda,* and beker's yeast, *B. quadridentatus* consumed all these organisms (Arndt unpubl.). One can conclude that *B. quadridentatus* should be able to make use of the high primary production of this estuary.

The high productivity presents the question of the fate of the rotifer production. Gut content analysis of potential rotifer predators during 1981 ans 1982 revealed that juveniles of bream (*Abramis brama*), roach (*Rutilus rutilus*), three-spined stickleback (*Gasterosteus aculeatus*), nine-spined stickleback (*Pungitius pungitius*), smelt (*Osmerus eperlanus*), and herring (*Clupea harengus*), as well as mysids (*Neomysis integer*) and omnivorous rotifers (*Asplanchna girodi*) fed on *Branchionus quadridentatus.* On an annual basis, only about 8% of the total rotifer production are consumed by planktivores, especially invertebrates (cf. Arndt 1989). During June/July 1981, *Asplanchna* selectively fed on *B. quadridentatus*; however, its estimated feeding rate could explain a daily loss of only about 20% of the production of *B. quadridentatus* (Arndt 1985). Up to now, the impact of calanoid copepods has not been considered as a source of rotifer mortality in the coastal waters of the Southern Baltic. However, our recent data indicate that the dominant calanoid copepod *Eurytemora affinis* is able to feed on large ciliates which are of the same size as rotifers (Burckhardt and Arndt 1987, Arndt et al. unpubl.). Recent experiments on limnetic calanoid copepods formerly classified as "herbrivorous" have shown that some are able to feed on rotifers (e.g. Williamson 1987). In early summer, when *Eurytemora* reaches very high abundances in the Darss-Zingst estuary, rotifers always occur only in low numbers in the plankton. Thus, the delayed development of rotifers, including *B. quadridentatus,* in summer, may be a result of interference with copepods. Parasitism was found to be an additional source of martality of *B. quadridentatus* especially in 1981. In June/July 1981, up to 12% of females were infected with sporophores of microsporidians as described by Budde (1927) for other planktonic rotier species. Some females were completely filled with sporophores. However, some infected females did still continue to produce eggs, making it difficult to estimate the real impact of parasites.

To summarize, one may explain the high production of the *B. quadridentatus* population by the following factors: high rates of resuspension in the shallow waters allow an occupation of the whole water column by this littoral species. The shallowness of the area of study makes it possible for warm temperatures to extend down to the bottom (during summer often above 20°C) supporting the development of this polythermal species. High concentrations of phytoplankton, bacteria and detritus obviously offer the required food concentrations and can be used by the rotifers. The reproductive strategy ensures the maintanance of well adapted strains in the estuary. Effective filter-feeders like cladocerans are excluded as competitors by strong predation pressure by planktivores as well as high salinities (cf. Arndt 1989). The loss of rotifer production due to predation should be of minor importance.

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