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Bacteria as a food source for microzooplankton in the Schlei Fjord and Baltic Sea with special reference to ciliates*

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ABSTRACT: *In situ* investigations revealed that number and biomass of microzooplankton increased with eutrophication along the length of the Schlei Fjord (FRG). The same observation was made for total bacterial numbers and biomass. Microzooplankton of the Schlei and total bacterial numbers showed a minimum in winter and major periods of development in late summer/autumn and spring. Usually the microzooplankton biomass in the Schlei was greater than the bacterial biomass. In contrast, the bacterial biomass for 5 of 6 stations in the Baltic Sea surpassed that of the microzooplankton during summer. Number and biomass of microzooplankton in both bodies of water can mostly be attributed to protozoans of the 3 to 30 µm fraction. Determined with the aid of radioactively labelled bacterial cultures, the filtration rate of 'natural' microzooplankton populations exhibited a distinct dependency on microzooplanktonic biomass and water temperature. In March 1982 microzooplankton populations in the eutrophic Schlei Fjord filtered 5 to 58 % of the water per day. In the central Baltic Sea in August 1982 the rate was 70 % d^{-1} during the late stage of a decaying blue-green algae bloom. Laboratory experiments with *Uronema marinum* clearly showed that bacteria concentrations exert a considerable influence on the development of ciliates. Only when a limiting concentration of about 1 x 10^6 bacteria ml^{-1} is attained does a proliferation of ciliates commence. Hence, bacteria can represent an important food source for microzooplankton, especially in biotopes with a high bacterial number and biomass.

INTRODUCTION

Along with particulate organic material, heterotrophic aquatic bacteria chiefly utilize dissolved organic compounds for cellular energy requirements as well as for the formation of bacterial biomass. This bacterial biomass can be utilized by filtering organisms as a food source. Through this process dissolved organic material is introduced into the food web.

The major fraction of pelagic bacteria in the western Baltic Sea is free-living; attached bacteria generally account for less than 10 % of the total bacterial number (Zimmermann 1977). An enormous concentration of bacteria may, however, develop in microbiotopes such as the mucous sheaths of blue-green algae or in decaying phytoplankton blooms (Rieper 1976, Hoppe 1981).

Consumption of bacteria is primarily attributed to microzooplanktonic organisms. The term 'microzooplankton' refers to organisms less than 200 µm in size. It includes small metazoans, but for the most part comprises heterotrophic protozoans such as flagellates and ciliates (Beers & Stewart 1971, Takahashi & Hoskins 1978, Heinbokel & Beers 1979). The microzooplankton filters particles in the pico- and nanoplankton range especially effectively (Capriulo & Carpenter 1980), while for larger metazooplankton, bacterial nourishment is rather unimportant (Marshall 1973, Nival & Nival 1976).

Numerous studies have shown that ciliates and flagellates can be grown in cultures with different bacteria as nutrient (Fenchel 1968b, Hamilton & Preslan 1969, Lighthart 1969, Tezuka 1974, Ashby 1976, Berk et al. 1976, Haas & Webb 1979, Fenchel 1982a, Kracht 1982).

Laboratory experiments on the decomposition of plant material and detritus led to a typical succession of organisms, whereby protozoan development com-

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mences following a strong proliferation of bacteria. This effects a considerable reduction of the bacteria (Harrison & Mann 1975, Fenchel & Jørgensen 1977, Linley & Newell 1981, Stuart et al. 1981, Robertson et al. 1982). These experiments suggest a special importance of protozoans as consumers of bacteria also under natural conditions. Hence, it is necessary to obtain more information concerning the transfer of bacterial biomass to primary consumers (Rheinheimer 1981).

In light of these considerations, data on the abundance and distribution of microzooplanktonic organisms, especially ciliate fauna, were recorded and their biomass estimated. Concentrations and biomass of bacteria were calculated, and the filtration rates of 'natural' microzooplankton populations measured using a radioactively labelled bacterial culture. These investigations were conducted from June 1981 to October 1982 in the strongly eutrophic Schlei, a Baltic fjord polluted by municipal and rural sewage sources. A cruise to the central Baltic undertaken in August 1982 supplied data from an unpolluted brackish water area. The influence of bacterial concentrations on ciliate growth was studied in laboratory experiments with *Uronema marinum*.

MATERIALS AND METHODS

Area of investigation and sampling. The Schlei is one of 4 fjords of the Kiel Bight. A narrow, man-made opening of the Schlei permits the only exchange of water with the Baltic Sea. The fjord measures about 40 km from its outlet to the town of Schleswig. The salinity of the Schlei shows a sharp decline from the mouth region (14 to 20 ‰) to Schleswig (2 to 5 ‰). Eutrophication steadily increases from the fjord's mouth towards Schleswig (Rheinheimer 1970). High inorganic nutrient content leads to considerable phytoplankton blooms. In the period from summer to autumn the bloom is dominated by the mass development of *Microcystis*. Schlei Fjord studies were conducted at 5 stations between Kappeln and Schleswig and an additional station directly off the Schlei outlet (Fig. 1). Eleven samplings of the fjord were undertaken from June 1981 to October 1982.

The studies in the Baltic Sea were conducted from 16 to 21 August 1982 during a cruise by the Department of Marine Microbiology at the Institute of Marine Sciences in Kiel (Fig. 2). At the time of investigation warm summer temperatures of 15.6 to 17.9 °C were recorded in the upper 10 m for the Baltic stations. However, in the Fehmarn Belt and Arkona Basin a temperature reduction of 7 C° was recorded at 20 m depth. The high temperature decreased, relative to the surface temperature, only slightly in the Bornholm Basin and south of the Gotland Deep, and remained almost constant with depth in the Gotland Deep proper. In the central Baltic region, horizontal and vertical salinity differences remained relatively small (7.3 to 8.1 ‰). In contrast, the salinity in the Fehmarn Belt at 2 m depth was 18.4 ‰ and increased to 24.3 ‰ at 20 m depth.

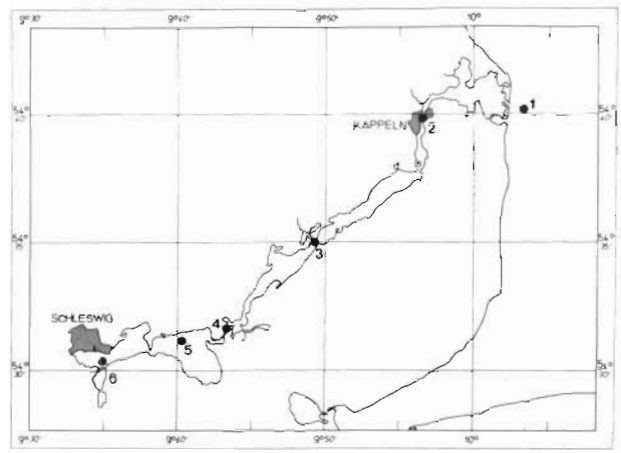

Fig. 1. Location of stations in Schlei Fjord. 1 Schleimünde: N 54°, 40,1′; E 10°, 3,4′; 2 Kappeln: N 54°, 39,6′; E 9°, 56,2′; 3 Lindaunis: N 54°, 35,0′; E 9°, 49,2′; 4 Missunde: N 54°, 31,7′; E 9°, 43,1′; 5 Große Breite: N 54°, 31,2′; E 9°, 40,2′; 6 Kleine Breite: N 54°, 30,5′; E 9°, 34,7′

ZoBell water samplers or 2 l containers constructed for sterile water sampling were employed for microbiological studies. Nansen samplers were used for other analyses. Samples were taken at a depth of 1 m in the Schlei and at 2, 10 and 20 m in the Baltic. The qualitative assessment of the phytoplankton standing stock was made with 20 µm and 50 µm plankton nets, trawled for several minutes. Usually, sampled materials were processed on board immediately following their retrieval. In a few cases, water samples obtained from a small pier were transported in insulated containers to the laboratory and processed there within 3 h.

Bacteriological parameters. Saprophyte counts were determined with the pour plate method using 2 modified ZoBell nutrient media 2216 E (Oppenheimer & ZoBell 1952) consisting of 0.5 % peptone, 0.1 % yeast extract and 1.5 % agar in tapwater (0 ‰ = ZL) and in brackish water (8 ‰ = ZB). The fluorescence microscopical assessment of the total bacterial number (TBN) was conducted according to Zimmermann et al. (1978). Bacterial biomass (BBM) was deduced from size categories and cell volumes as described by Rheinheimer (1977). The volume of bacteria with a specific weight of ca. 1 can be equated with mass (= wet weight). The dry weight of bacterial cells is assumed to be 20 % of the wet weight, and the carbon content comprises about 50 % of the dry weight (Schlegel 1981).

Microzooplankton. Living specimens of ciliates and heterotrophic flagellates were used. Qualitative investigations were designed to provide information on the major forms present. Quantitative investigations provided biomass estimates. A quick survey of the microzooplankton in a water sample was afforded by 20 µm and 55 µm plankton net samples. Due to the relatively high ciliate population density in the Schlei, counts were always made from unconcentrated water samples. Of each sample 80 ml were transferred to 100 ml bottles and maintained at 4 °C for a maximum of 4 h before preparation for analysis. In order to study less frequent larger forms, as well as the smallest more commonly occurring forms, volumes of 10 ml, 1ml and 100 µl to 10 µl were sorted out with a stereomicroscope (Wild M8) equipped with bright- and darkfield lighting. With the exception of the smallest volumes counting was carried out by removal of individual cells with a Pasteur pipette. The number of individuals in the subsamples from 10 ml to 100 µl varied between 1 and 150 organisms. Five parallel assessments resulting in a total of 50 to 100 individuals were conducted for the smallest volumes. Taxonomic identifications were made on the basis of Jørgensen (1927), Kahl (1934), Bick (1972), Borror (1973), Curds (1975), Matthes & Wenzel (1978) and Corliss (1979). Non-identifiable organisms were assigned to 2 size categories: (1.) 30 to 60 µm long ciliates; (2.) 3 to 30 µm size category containing ciliates and heterotrophic (fluorescence microscopically lacking chlorophyll) flagellates.

Biomass was determined volumetrically and expressed in µg C (after Strathmann 1967). Calculated from measurements of over 250 individual cells, average biomass was 138×10^{-6} µg C individual $^{-1}$ for the 3 to 30 µm fraction and 865×10^{-6} µg C indiv. $^{-1}$ for the 30 to 60 µm fraction. Biomass for the 3 to 30 µm fraction from the Baltic averaged 60×10^{-6} µg C indiv. $^{-1}$.

Filtration rate of 'natural' microzooplankton populations. Filtration rate, i. e. the quantity of water effectively cleared of food particles via filtering by a population per unit time, was determined with the aid of radioactively labelled bacteria. A 24 h old culture of *Vibrio* sp. grown at 20 °C in 300 ml of ZS-medium (same as ZB but without agar and with 24 ‰) was used for labelling. Following centrifugation (10 min, 5000 g) and resuspension in 100 ml of isotonic, particle-free (= 0.2 µm filtered) water (the process was repeated twice), 200 µCi (methyl-1', 2'-^{3}H)-thymidine (110 Ci mMol $^{-1}$) were added to the bacterial suspension. This was con-

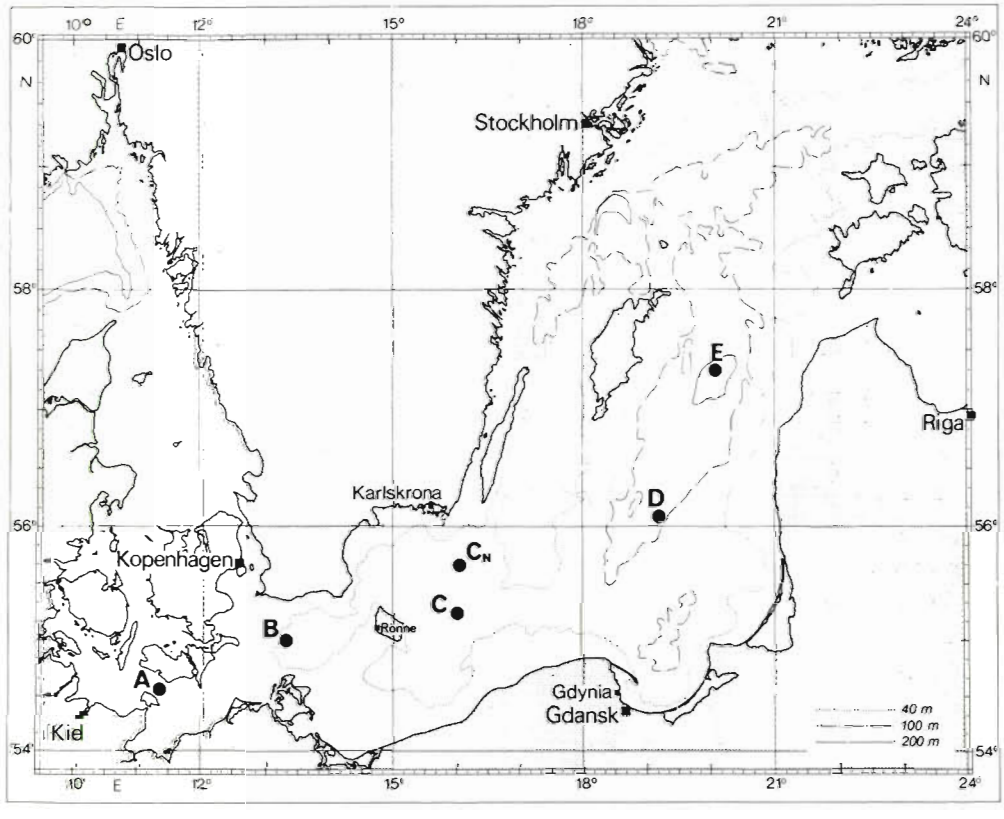

Fig. 2. Location of stations in the Baltic Sea. A Fehmarn Belt: N 54°, 32,3'; E 11°, 20'; B Arcona Basin: N 55°, 00'; E 13°, 18'; C Bornholm Basin: N 55°, 15'; E 15°, 59'; C_N: North of Bornholm: N 55°, 41,5'; E 16°, 01'; D: South of Gotland Deep: N 56°, 05'; E 19°, 10'; E Gotland Deep: N 57°, 20'; E 20°, 03'

tinuously shaken and incubated for 24 h. Repeated centrifugation removed unincorporated ^{3}H-thymidine from the solution. When necessary, a gradual adjustment to the station's salinity in steps of 5 ‰ S was made at this point. Finally, labelled bacteria were transferred to isotonic water and filtered twice through 3.0 µm polycarbonate filters (Nuclepore) in order to exclude bacterial agglomerates and to ensure distinct separation of the bacteria (<3.0 µm) from the microzooplankton (>3.0 µm) fraction in the subsequent feeding experiments. 100 ml bottles filled with 25 ml of the prefiltered (150 µm net) water sample and 200 µl of the ^{3}H-bacterial suspension served as experimental receptacles. The concentration of the radioactively labelled bacteria was about 40×10^6 ml^{-1}, and 6×10^6 ml^{-1} for investigations of the Schlei and Baltic samples, respectively. Each of 3 parallel samples was incubated in the dark at *in situ* temperature. Immediately after the start of the experiment and after 24 h (48 h for the station at Schleimünde) the samples were fixed with 500 µl of 37 % formalin. Control samples without microzooplankton were treated similarly with particle-free, filtered water from the respective station. Subsequent to fixation, all samples underwent filter-fractionation with a 3.0 µm polycarbonate filter (microzooplankton fraction) followed by a 0.2 µm membrane filter (bacterial fraction). Filters (25 mm in diameter) were transferred to scintillation vials containing 10 ml of scintillator (120 g naphthalene, 5.5 g Permablend III filled to 1 l with Dioxan). Radioactive microzooplankton excretion products and radioactive water resulting from bacterial respiration were measured in the <0.2 µm filtrate. Aquasol served as the scintillator for this procedure. Results were computed from dpm as corrected by the quench factor (established employing a ^{3}H-toluene standard). For further details see Gast (1983).

(1) Uptake (U_t) of radioactive bacteria by microzooplanktonic organisms present in the water sample (25 ml) during the time period, t:

$$U_t = \underbrace{(\text{dpm } 3\,\mu\text{m} + \text{dpm filtrate})}_{\text{water sample with microzooplankton}} - \underbrace{(\text{dpm } 3\,\mu\text{m} + \text{dpm filtrate})}_{\text{control without microzooplankton}} \quad (1)$$

where dpm = disintegrations min^{-1}; dpm 3 µm = radioactivity incorporated by microzooplankton; dpm filtrate = excreted or released radioactivity. (2) Calculation of the number (X_t) of ^{3}H-bacteria filtered by the microzooplankton present in the water sample (25 ml) during the time period, t

$$X_t = \frac{U_t}{B} \quad (2)$$

where B = dpm (^{3}H-bacterium)$^{-1}$. (3) Determination of filtration rate (F) of microzooplanktonic organisms present in the water sample (25 ml)

$$F = \frac{X_t}{C \times t} \times 25 \text{ ml} \quad (3)$$

where t = duration of experiment (h). C indicates average bacterial number in the receptacle over the time interval elapsed. Reduction in number of bacteria during the feeding experiment is considered to be linear, and the mean bacterial concentration at time t/2 is the basis for filtration-rate calculations.

Laboratory experiments with Uronema marinum *and* Vibrio *sp.* For these studies a 4 d-old *Uronema marinum* culture fed with bacteria (*Vibrio* sp.) on the first and third day was employed. Bacterial food suspension was prepared by growing *Vibrio* in a ZS-medium followed by repeated washing *via* centrifugation. The cultures were maintained under sterile conditions in 1 l Erlenmeyer flasks with cotton stoppers. The flasks were kept in the dark and filled with 300 ml particle-free, aged North Sea water (30 ‰), 10 ml ciliate culture and varying quantities of food organisms. The final concentrations were 0.60, 1.39, 6.40, 11.39, 58.65 and 89.09 $\times 10^6$ bacteria ml^{-1}. Control samples without food or without ciliates were also made. Ten ml subsamples were taken immediately following the start of experiment and at intervals during several days. The subsamples were fixed with 0.2 ml 37 % formalin. The bacterial number was determined with fluorescence microscopy. Ciliates were counted on Unipore filters of 0.4 µm pore size after staining in erythrosine.

RESULTS

Schlei Fjord investigations (summer 1981 to autumn 1982)

Development of saprophyte counts and total bacterial numbers along the length of the Schlei are presented in Fig. 3. Bacterial numbers in the Schlei outlet are always lowest and increase from the outer to inner strongly eutrophicated fjord regions. This increase is especially evident from Schleimünde to Missunde. The high bacterial counts in the inner Schlei may be in part due to an allochthonous input. A considerable input of organic nutrients, which promote autochthonous bacterial growth, may be the primary cause for the water's high content on bacteria.

The saprophyte counts disclose a population change parallel to falling salinity, whereby the component of marine and halophilic brackish water bacteria decreases in favour of halotolerant brackish water and freshwater forms (see also Rheinheimer 1970 and Rieper 1976). In this investigation bacterial numbers within the Schlei varied as follows:

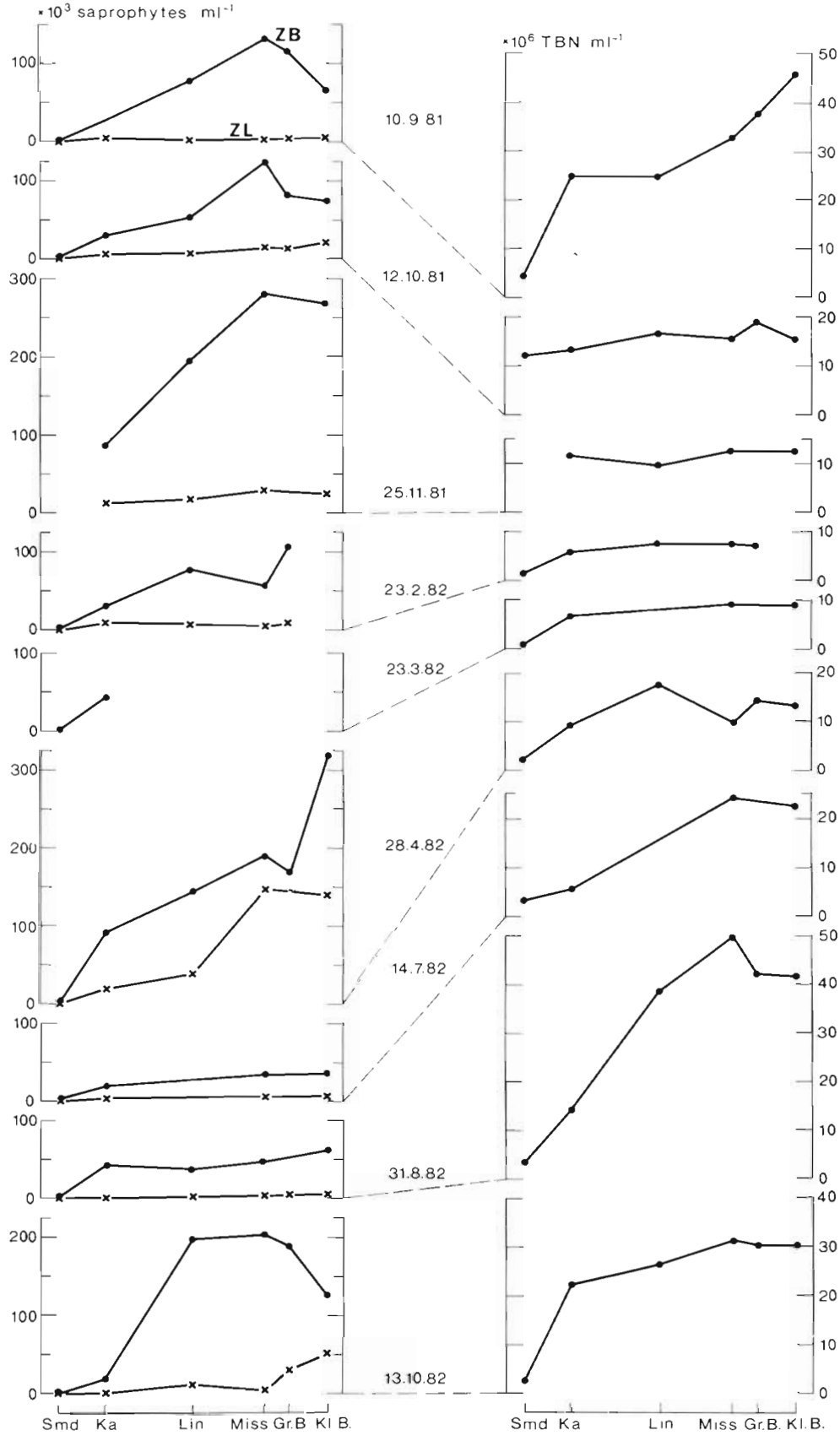

Fig. 3. Horizontal distribution of bacterial numbers in the Schlei. Saprophyte counts on ZB- (8‰) and ZL- (0‰) media (left) and total bacterial numbers (right). Schleimünde (Smd); Kappeln (Ka); Lindaunis (Lin); Missunde (Miss); Große Breite (Gr. B); Kleine Breite (Kl. B.)

Saprophytes on ZL: 0.5 to 150 × 10^3 ml^{-1}
Saprophytes on ZB: 20 to 320 × 10^3 ml^{-1}
Total bacterial numbers: 5 to 50 × 10^6 ml^{-1}.

Distinct seasonal changes in bacteriological parameters were also observed. Following breakdown of phytoplankton blooms in spring and autumn, saprophyte counts were high. They dropped in winter and exhibited a summer minimum. Total bacterial numbers were very high in late summer, remained at this level in autumn, and exhibited lowest values during the cold months.

Conditions for bacteria-consuming microzooplankton with respect to food sources become more favourable with increasing removal from the Schlei mouth towards the inner fjord.

The distribution of microzooplanktonic biomass (MZP-BM) along the length of the Schlei compared to bacterial biomass (BBM) is presented in Fig. 4. Shown together with total MZP-BM is the biomass of larger ciliates (>30 µm). The progression of total MZP-BM distinctly parallels that of BBM. However, MZP-BM is generally greater than BBM. The lowest biomass values in both cases were observed in the Schlei-mouth sampling station. The biomass of the microzooplankton increases rapidly with distance from the mouth and shows a slow increase as one moves further inwards. Investigations from 10 September 1981 present an exception. In this case a large increase in total MZP-BM from the middle to inner Schlei is observed due to the strong development of larger ciliates (>30 µm; 366 µg C l^{-1} of which *Tintinnidium fluviatile* comprises 303 µg C l^{-1}). The bulk of the microzooplankton is composed of smaller protozoans (3 to 30 µm), which on the average accounted for 92 % of total MZP-BM. In late summer/autumn and spring the Schlei MZP-BM attained high values. A minimum was observed in winter. In July 1982 the MZP-BM was likewise relatively low. Similar to MZP-BM, the BBM was significantly smaller in winter than in other seasons. MZP-BM in the Schlei ranged from 19 to 1162 µg C l^{-1} and BBM from 48 to 436 µg C l^{-1}.

Ciliates longer than 30 µm constitute only a minor component of the total number of microzooplankton. The numbers of Protozoa in the 3 to 30 µm fraction are commonly 2 to 3 orders of magnitude greater than the sum of the larger ciliates. Within the Schlei the population density of the 3 to 30 µm fraction ranged from 6500 to 84 000 cells (10 ml)$^{-1}$. The number of ciliates over 30 µm in length lay between a few specimens and 1400 cells (10 ml)$^{-1}$. Nevertheless, the latter also play an important role as consumers of bacteria. More than half of the species listed in Table 1 can at least partially cover their nutritional requirements from bacteria. A review of the comprehensive list of species compiled by Bock (1960) also reveals that bacteria-consuming ciliates play a significant role in the Schlei. The number of bacteriovorous ciliate species is especially large in the inner Schlei. Often encountered are *Tintinnidium fluviatile* and *Vorticella octava*. Both appear simultaneously during the *Microcystis* bloom. The mucous sheaths of these blue-green algae are usually well populated by bacteria. Live material reveals how numerous motile bacteria concentrate around *Microcystis* aggregates, penetrate the sheath and subsequently disappear, indicating that feeding conditions for bacteriovorous ciliates are especially favourable in the immediate environment of this microbiotope. *Microcystis* itself is apparently not used as a food source.

Freely suspended bacteria and bacteria attached to detritus particles represent a plentiful food source for consumers of bacteria throughout the year. Diatom-consuming *Strombidium* and *Strombilidium* are present all year round in the entire area of investigation. The outer Schlei and the Kiel Bight are the major zones of distribution of tintinnids (*Stenosomella, Helicostomella, Tintinnopsis* and *Coxliella*). Along with diatoms, armoured dinoflagellates, flagellates and bacteria can serve as a supplemental food source for these ciliates. In a mixed diet the preference of a particular source depends on the respective concentration and biomass of the individual components (Webb 1956). Most Schlei ciliate species are either bacteriophagous, herbivorous or exploit both types of food. Carnivorous ciliates are only represented by isolated specimens of *Litonotus* sp., *Lacrymaria* sp. and *Didinium* sp. Consumers of Schlei ciliates predominantly consist of rotifers.

Baltic Sea investigations (August 1982)

Total bacterial numbers ranging between 2.6 × 10^6 and 6.4 × 10^6 ml^{-1} were obtained at 0 to 20 m depths in the area investigated. Bacterial biomass was 40 to 140 µg C l^{-1}. Regional and vertical fluctuations in total bacterial number and bacterial biomass were relatively small (Fig. 5), whereas saprophyte counts demonstrated larger variations (297 to 1817 colony forming units ml^{-1}). The salinity of the ZB-medium (8 ‰) corresponds roughly to the surface water salinity of the Bornholm Basin. Hence, this medium offers better possibilities for the development of saprophytic bacteria from the Bornholm station than those of the more highly saline water of the Fehmarn Belt station.

During summer, blue-green algae blooms can be observed frequently in the Baltic Sea. Even when a mass development of blue-greens was not encountered during our expedition, microscopical studies of the complex microbiotope of blue-green flocks at the sta-

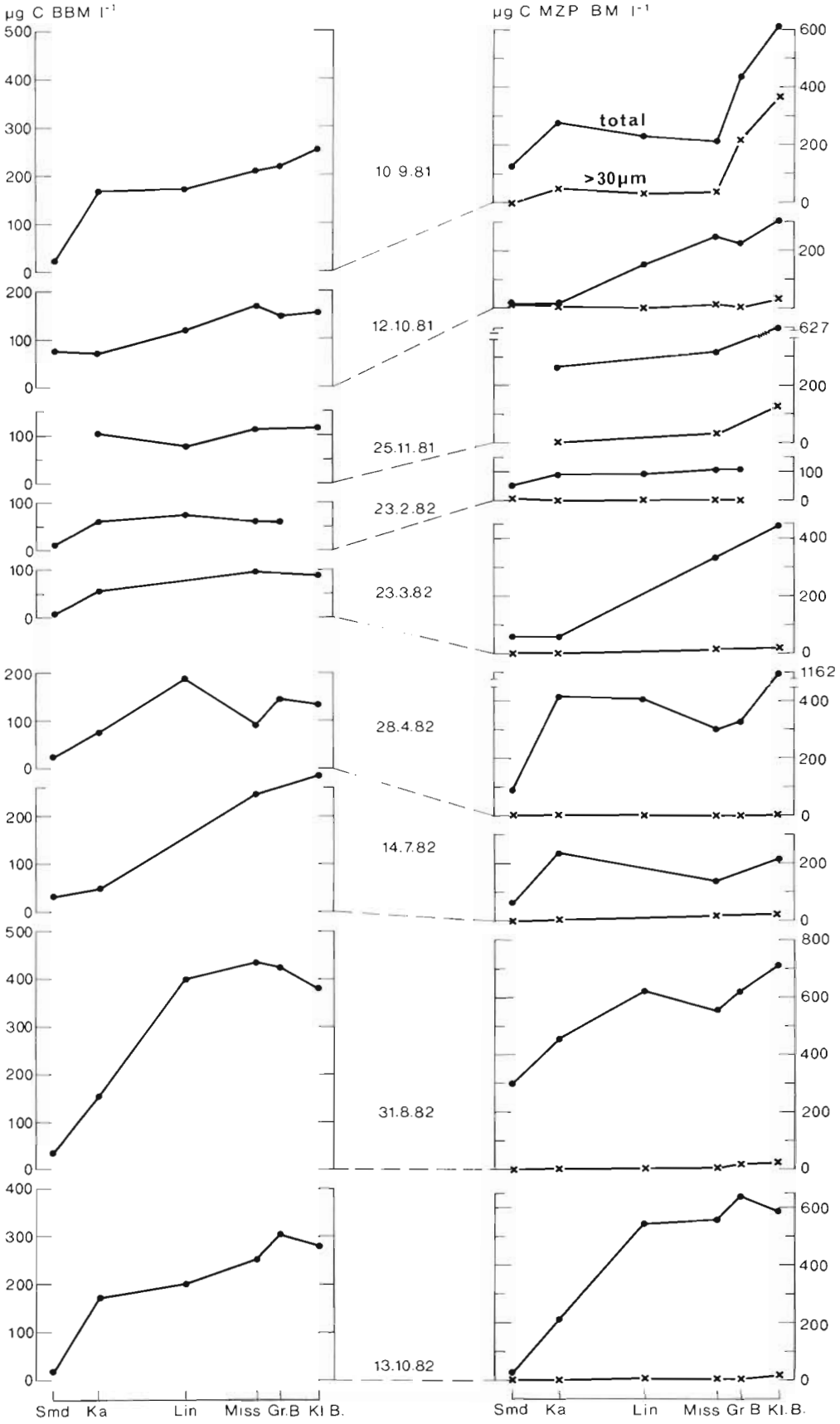

Fig. 4. Biomass of microzooplankton (total) and larger (>30 µm) ciliates (right), and bacterial biomass (BBM) (left) along the length of the Schlei. Stations as in legend to Fig. 3

Table 1. Ciliates found in the Schlei

Ciliates	Place of occurrence	Season				Frequency	Food source*
Prostomatida							
Prorodon sp.	Kleine Breite		su			+	Protophytes, histophages (2)
Coleps sp.	Kleine Breite		su			+	Small algae, ciliates, detr., histophages (4, 5, 6)
Tiarina sp.	Schleimünde, Kleine Breite			a		+	Bacteria, flagellates (7)
Haptorida							
Didinium sp.	Kappeln, Missunde, Kleine Breite	s		a		+	Ciliates (1, 5, 6)
Mesodinium pulex	Total Schlei	s	su	a	w	+++	Bacteria, small algae, detritus (5, 6)
Lacrymaria sp. large *Lacrymaria* sp. small	Schleimünde, Lindaunis, Missunde, Kleine Breite	s	su	a		++	Ciliates, detritus (1, 4, 5, 6, 9)
Pleurostomatida							
Litonotus sp.	Missunde		su			+	Protozoa (1, 4, 5, 6)
Scuticociliatida							
Cyclidium sp.	Missunde		su			+	Bacteria (5)
Peritrichida (Sessilia)							
Epistylis sp.	Kleine Breite			a		+	Bacteria (5, 9)
Vorticella octava	Lindaunis, Missunde, Große Breite, Kleine Breite		su	a		+++	Bacteria (5, 9)
Vorticella patellina	Kleine Breite	s				+	Bacteria (9)
Zoothamnium sp.	Kappeln, Lindaunis, Große Breite, Kleine Breite	s				+	?
Heterotrichida							
Stentor roeseli	Große Breite			a		+	Bacteria, flagellates, algae, ciliates (1, 5)
Spirostomum teres	Kappeln, Missunde, Kleine Breite	s	su	a		++	Bacteria, diatoms, algae, flagellates (4, 5)
Strombilidium sp.	Total Schlei	s	su	a	w	+++	Diatoms, detritus (1, 4, 8)
Strombidium sp.	Total Schlei	s	su	a	w	+++	Diatoms, detritus, bacteria, flagellates (1, 4, 7, 8)
Oligotrichida							
Stenosomella ventricosa	Schleimünde, Kappeln			a	w	+	Bacteria, flagellates
Stenosomella nucula	Schleimünde, Kappeln, Lindaunis			a	w	++	
Helicostomella subulata	Schleimünde			a	w	+	Diatoms, armoured dinoflagellates (3)
Tintinnopsis beroidea	Schleimünde, Kappeln, Lindaunis			a	w	+	
Coxliella helix	Schleimünde			a	w	+	
Tintinnidium fluviatile	(Kappeln), Lindaunis, Missunde, Große Breite, Kleine Breite	s	su	a		+++	Bacteria, diatoms, flagellates (5, 9)
Hypotrichida							
Oxitrichidae	Missunde, Kleine Breite	s	su			+	?
Euplotes sp. large *Euplotes* sp. small	Schleimünde, Kappeln, Große Breite, Kleine Breite	s	su	a		++	Bacteria, diatoms, detritus, algae (4, 5, 9)
Diophrys sp.	Kleine Breite		su			+	Bacteria, diatoms, detritus, algae (4, 7, 9)
Aspidisca sp.	Kappeln, Missunde, Große Breite, Kleine Breite		su	a		++	Bacteria, detritus (1, 2, 4, 5, 9)

s Spring, su summer, a autumn, w winter
+ Isolated, ++ some, +++ numerous
* After (1) Aumann (1952), (2) Webb (1956), (3) Zeitzschel (1967), (4) Fenchel (1968a), (5) Bick (1972), (6) Matthes & Wenzel (1978), (7) Klekowski & Tumantseva (1981), (8) Smetacek (1981), (9) own observations

tions B – E could be undertaken employing the concentrated net samples. Among the dominating cyanophytes were *Nodularia spumigena, Aphanizomenon flos-aquae* and some specimens of *Anabaena baltica*. Diatoms (e. g. *Chaetoceros* species) were present in lesser numbers. Along with some extended strands of *Nodularia* without attached bacteria occurred numerous spiral-shaped *Nodularia* filaments, whose mucous

sheaths were heavily covered with bacteria. Many bacteria-consuming groups of Protozoa could be observed in these agglomerates: *Stentor, Vorticella,* flagellates, tintinnids and naked free-swimming ciliates. Considerable numbers of rotifers (*Keratella quadrata* and *K. cochlearis*) and suctorians, as well as isolated crustaceans were also present. Primarily dinoflagellates (species of *Ceratium* and *Prorocentrum*) were found in 55 µm net hauls in the Fehmarn belt. Ciliates over 30 µm in length (species of *Vorticella, Strombidium, Strombilidium,* etc.) appeared occasionally in unconcentrated water samples. The microzooplankton count was dominated by protozoans of the 3 to 30 µm fraction, whose density ranged from 1900 to 3800 cells $(10\ ml)^{-1}$ with the exception of the station north of Bornholm where a maximum of 12 000 cells $(10\ ml)^{-1}$ was demonstrated. Apart from the fact that the microzooplankton count at 20 m depth was smaller than that at 10 or 2 m, no distinct tendency was recognizable in the vertical distribution of microzooplankton at these depths (Fig. 6). The stations at Fehmarn Belt, Arkona Basin, Bornholm Basin, south of the Gotland Deep and the Gotland Deep provided MZP-BM values between 11.4 and 25.1 µg C l^{-1} with an average value of 17.1 µg C l^{-1}; these values lay considerably under that of the corresponding BBM with a value of 81.2 µg C l^{-1}. The situation was quite different north of Bornhom, where a maximal MZP-BM value of 73.8 µg C l^{-1} coincided with a remarkably low BBM of 39.4 µg C l^{-1}.

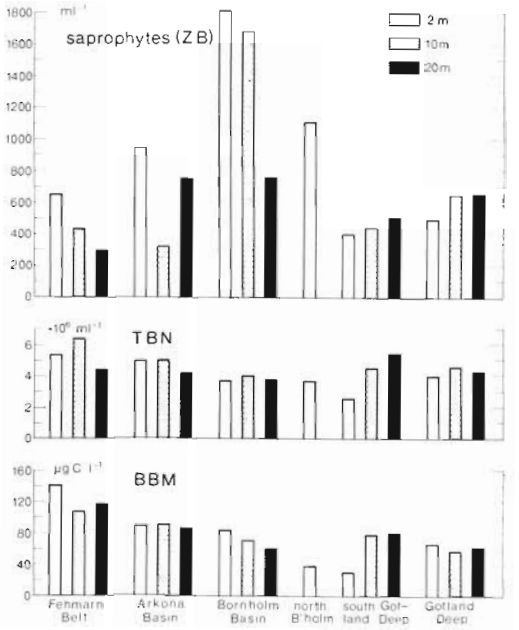

Fig. 5. Saprophyte count, total bacterial number (TBN) and bacterial biomass (BBM) at depths of 2, 10 and 20 m in August 1982, Baltic Sea

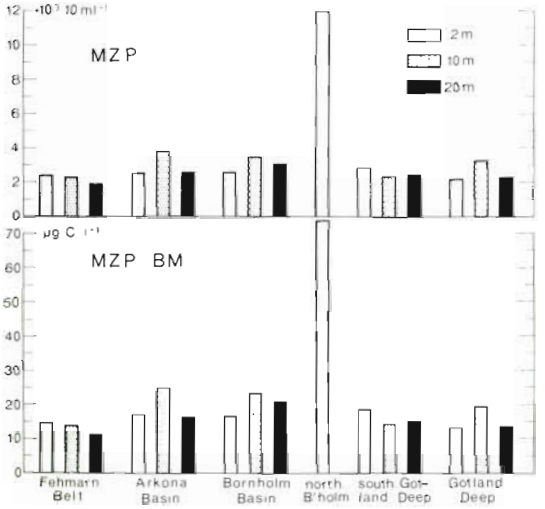

Fig. 6. Number (MZP) and biomass (MZP-BM) of the microzooplankton at depths of 2, 10 and 20 m in August 1982, Baltic Sea

Filtration rate of 'natural' microzooplankton populations

With the aid of a radioactively labelled bacterial culture, the filtration rate of 'natural' microzooplankton populations could be determined in spring for the Schlei (Schleimünde, Kappeln, Missunde, Kleine Breite) and in summer for the Baltic (north of Bornholm). Filtration rates of 25 ml samples of microzooplankton amounted to 0.055 to 0.600 ml h^{-1} at 5 °C in the Schlei and to 0.730 ml h^{-1} north of Bornholm at 18 °C; they were clearly dependent on the microzooplanktonic biomass (Table 2). Low filtration rates in samples from Schleimünde and Kappeln stations coincided with low microzooplanktonic biomass, and the surge in MZP-BM in the middle and inner Schlei resulted in a large rise in filtration rate. A comparison of these rates from microzooplankton populations of the Schlei and Baltic stations clearly indicates the influence of water temperature.

Laboratory experiments with *Uronema marinum*

The influence of bacterial concentrations on the development of *Uronema marinum* is presented in Fig. 7. In the control without bacteria the number of ciliates remains fairly constant. Ciliates nourished on bacteria produce a characteristic growth curve. For all but the smallest bacterial concentrations (0.6×10^6 bacterial cells ml^{-1}), the exponential (log) phase commences following a ca. 8 h initial (lag) phase. The duration of the log phase depends on bacterial concentration, i. e. the greater the food source, the shorter the duration.

The stationary phase and a more or less distinct death phase complete the sequence.

Uronema generation time is clearly shorter (g = 2.1 to 2.7 h) with high concentrations of bacteria (IV, V, VI) than with low concentrations (II, III) (g = 3.8 to 5.1 h). At the lowest bacterial concentration (0.6×10^6 cells ml^{-1}), no ciliate proliferation was observed within the first 24 h of experimentation. As demonstrated by the progression of bacterial counts (I Fig. 7), the bacterial number, however, increases within this time period to about 1×10^6 cells ml^{-1}. Apparently a proliferation of ciliates necessitates a preceding rise in *Vibrio* numbers. The bacterial count in arrangements III to VI distinctly sinks during the feeding experiments, whereby a concentration of 1×10^6 cells ml^{-1} is the lower limit. In the receptacle lacking ciliates, the bacterial number remains fairly constant, about the initial value of 15×10^6 cells ml^{-1}. No multiplication or lysis of bacterial cells was detectable. In contrast, with an initial concentration of 0.6×10^6 cells ml^{-1} there is an increase in bacterial cell number. Initial concentrations of 1.3×10^6 cells ml^{-1} remain relatively unchanged. However, since an obvious ciliate development occurs in this case, proliferation of bacteria is probably counterbalanced by grazing.

This experiment clearly showed that ciliate production depends on the available amount of bacteria, i. e. the greater the food supply, the higher the ciliate yield.

DISCUSSION

In order to obtain a better understanding of the role of bacteria as food source for primary consumers, quantitative and qualitative studies of microzooplankton with special reference to ciliate fauna were undertaken along with assessments of bacteriological parameters. The investigations were conducted in the Schlei Fjord from June 1981 to October 1982 and on a cruise in the Baltic in August 1982.

In both bodies of water, microzooplankton number and biomass were dominated by small protozoans, i. e. ciliates and flagellates, 3 to 30 µm in length. The ratios of microzooplankton to bacterial biomasses in the Schlei were clearly different from those found in the Baltic proper. Whereas the microzooplankton biomass

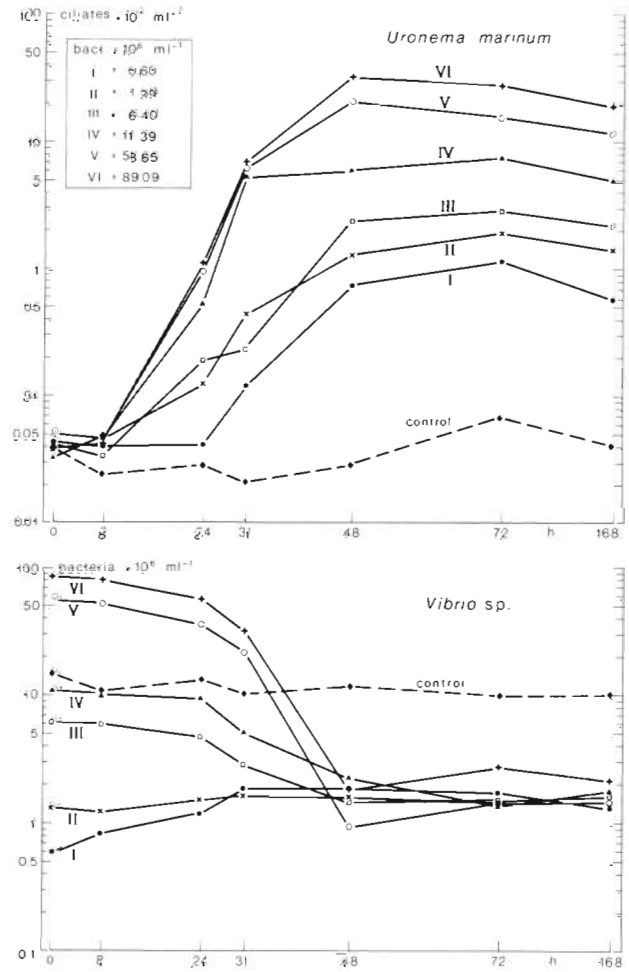

Fig. 7. Influence of bacterial concentration (*Vibrio* sp.) on the development of *Uronema marinum*. Above: development of ciliate numbers; below: development of bacterial numbers. Dotted lines: control samples without bacteria (above), without ciliates (below)

Table 2. Filtration rate and feeding rate of 'natural' microzooplankton populations. BBM: Bacterial biomass; MZP-BM: Microzooplankton biomass

Station	Date	Temp. (°C)	Filtration rate* (ml h^{-1})	Filtered vol. d^{-1} (%)	Feeding rate (µg C BBM l^{-1} d^{-1})	MZP-BM (µg C l^{-1})	BBM (µg C l^{-1})
Schleimünde	23. 3. '82	5	0.084	8.1	0.7	59.8	8.5
Kappeln	23. 3. '82	5	0.055	5.3	3.0	57.6	56.3
Missunde	23. 3. '82	5	0.465	44.6	42.4	334.8	95.1
Kleine Breite	23. 3. '82	5	0.600	57.6	51.3	446.4	89.0
North of Bornholm	18. 8. '82	18	0.730	70.1	27.6	73.8	39.4

* Of microzooplankton (< 150 µm in length) in 25 ml

in 5 of 6 stations from the Baltic was less than the bacterial biomass, with few exceptions the fjord's biomass of the microzooplankton distinctly surpassed that of bacteria.

The most important factor amongst parameters influencing ciliate populations is their food source, especially since ciliates possess a broad spectrum of tolerance to physical and chemical conditions (e. g. Noland 1925, Noland & Gojdics 1967, Fenchel 1968a). According to Fauré-Fremiet (1967), the influence of abiotic factors is more likely to be indirect in view of the stronger dependency of food organisms on physical and chemical environmental conditions.

Rieper & Flotow (1981) carried out some feeding experiments with *Uronema* sp. and different species of bacteria. They showed that *Uronema* grew better with 'List 7' and a mixture of oil-degrading bacteria than with *Serratia* sp. 'List 7', identified as *Vibrio* sp. by Rieper (pers. comm.), was used in the present investigations.

Laboratory studies with *Uronema marinum* disclosed that the concentration of the bacterial food source has a significant effect on ciliate development. Hence, the proliferation of ciliates required a minimal concentration of about 1×10^6 bacteria ml^{-1}. During feeding experiments the bacterial concentration sank occasionally slightly below this limiting value. Tezuka (1974) reported that the survival minimum for the much larger *Paramecium caudatum* corresponded to 1×10^7 bacteria ml^{-1}. A critical bacterial density of $\leqq 10^6 - 10^7$ bacteria ml^{-1} was calculated for *U. nigricans* by Berk et al. (1976), below which growth of the ciliates no longer occurred. Taylor (1978) found minimal concentrations of 7×10^6 bacteria ml^{-1} for *Colpidium campylum* and 4×10^6 for *C. colpoda*. These investigations were based on experiments utilizing culture bacteria, whose cell volumes greatly exceeded those of 'natural' bacteria. For example, the median volume of cultured *Vibrio* sp. is 1.15 μm^3, while the median volume for bacteria commonly occurring in the Baltic and Schlei is ca. 0.1 to 0.2 μm^3.

The limiting concentration of 1×10^6 bacteria ml^{-1} using *Vibrio* sp. corresponds to a biomass of 115 μg C l^{-1}. A comparison of these results with *in situ* conditions shows that although the bacterial concentration of 1×10^6 bacteria ml^{-1} was surpassed throughout the whole period of investigation in the Schlei (1.4 to 49.8 x 10^6 bacteria ml^{-1}), values greater than 100 μg C l^{-1} were only detected in the central and inner Schlei (maximum: 436 μg C l^{-1}) and in the Fehmarn Belt. In general, a bacterial biomass of 20 μg C l^{-1} is seldom surpassed in the Baltic proper (Zimmermann 1977, Meyer-Reil et al. 1979, Hoppe 1981). Fenchel (1980) calculated a required minimal content on organic material of 0.2 to 7 mg dry weight l^{-1} (corresponding to 100 to 3500 μg bacterial carbon l^{-1}) for bacteriovorous ciliates.

In the light of these considerations, a sufficiently large bacterial biomass permitting the maintenance or development of planktonic ciliate populations can only be expected in strongly eutrophic coastal regions or in microbiotopes with high bacterial activity. Such microbiotopes are provided by the summer blue-green algae blooms occurring in the central and northeastern Baltic. According to a calculation by Hoppe (1981), a *Nodularia* flock of 1 cm in length and 0.5 cm in diameter contains at least 7.5×10^8 bacteria, which presents an enormous enrichment of bacteria as compared with the surrounding water mass. Thus, it is not surprising that together with other microzooplanktonic organisms, numerous ciliates are encountered in blue-green algae agglomerates. A frequent bacteriovorous ciliate in this microbiotope is *Vorticella* (see also Bursa 1963), which apparently requires both a substrate for attachment and sufficient bacterial biomass. Coinciding with the Schlei *Microcystis* bloom from summer to autumn are *Tintinnidium fluviatile* and *Vorticella octava*. The *Microcystis* colonies possess a mucous sheath heavily colonized by bacteria and this offers favourable feeding conditions for bacteria-consuming ciliates.

In conjunction with the discussed limiting concentrations of bacterial number and biomass for the nutrition of ciliates, the question arises: To what degree do ciliates depend on bacteria as an exclusive food source? Table 1 demonstrates that most forms exploit a fairly broad spectrum of nutritional sources; they can consume flagellates and small algae as well as bacteria. The sum of the biomass of available foods is decisive for ciliate development under conditions of supplemental bacterial nourishment. Some species, however, apparently feed only on bacteria. Few species are carnivorous and independent of bacteria as food sources.

Ciliate production was dependent on the amount of bacteria available; the larger the food source (*Vibrio* sp.), the greater the yield (*Uronema marinum*). This experimental result agrees fundamentally with *in situ* observations along the profile of the Schlei. Hence, the biomass of microzooplankters accordingly rose with increasing bacterial biomass from Schleimünde to Schleswig. With respect to seasonal aspects, however, the data for bacterial and microzooplanktonic biomass did not clearly run parallel to one another. For example, in September, October and November a rise in microzooplanktonic biomass at Missunde was coupled with a reduction in bacterial biomass. Quite possibly, the grazing effect by the bacteriovorous microzooplankton outweighed bacterial production at this time. Experimental evidence for this assumption was given by v. d. Ende (1973) and Ashby (1976): in studies with

continuous cultures of ciliates and bacteria a steadily declining amplitude of countercurrent oscillations for both components was observed.

Food uptake apparently influences the generation time of ciliates. The generation time of *Uronema marinum* is distinctly shorter (g = 2.1 to 2.7 h) when coupled with high bacterial concentrations (11 to 89 × 10^6 ml^{-1}) than with low bacterial concentrations (>1 to 6 × 10^6 ml^{-1}; g = 3.8 to 5.1 h). Kracht (1982) reported that the generation time of *Colpoda cucullus* increases when the bacterial concentration is less than 4 × 10^8 *Escherichia coli* ml^{-1}. According to Banse (1982), ciliates can only take advantage of their high reproductive potential in patches with high nutrient concentrations.

In situ studies and laboratory experiments revealed that bacterial populations can exert a significant influence on the development of microzooplanktonic organisms and, in turn, bacteria are held in a state of physiological equilibrium by grazing (Johannes 1965, Barsdate et al. 1974, Harrison & Mann 1975, Fenchel & Jørgensen 1977). An additional mechanism of regulation was indicated by Legner (1973), who found that the metabolities of ciliates may stimulate bacterial proliferation.

For the study of the interaction between bacteria and bacteriovorous microzooplankters it is interesting to calculate the microzooplankton-induced reduction of bacteria and compare this with data on bacterial production. If the filtration rate of the 25 ml microzooplankton population is known, then the percent water volume per day filtered to a particle-free state by the microzooplankton can be calculated. Providing the standing stock of bacterial biomass has been determined, one can further calculate feeding rates in µg bacterial carbon $l^{-1}d^{-1}$. One must, of course, assume that 'natural' bacteria are filtered in the same manner as are tritium-labelled cultured bacteria. Spring feeding rates of 0.7 to 51.3 µg bacterial carbon $l^{-1}d^{-1}$ were measured in the Schlei. During the summer in the Baltic a reduction of 27.6 µg C $l^{-1}d^{-1}$ in bacterial biomass occurred as a result of microzooplankton grazing. Schlei bacterial production measured by Hoppe (unpubl.) according to the method of Fuhrman & Azam (1980) was as follows:

Schleimünde:	0.03 to 0.18 µg C $l^{-1}d^{-1}$
Kappeln:	1.21 to 7.88 µg C $l^{-1}d^{-1}$
Missunde:	5.11 to 33.21 µg C $l^{-1}d^{-1}$

Even though a direct comparison of Schlei bacterial production and reduction by microzooplankton grazing is not possible due to seasonal dissimilarities in data, both parameters obviously are of the same order of magnitude.

Hoppe (unpubl.) measured a bacterial production of 0.47 to 3.04 µg C $l^{-1}d^{-1}$ for the station lying north of Bornholm. This value lies far below the microzooplankton feeding rate of the same water sample. Bauerfeind (1983) calculated from turnover times for glucose and natural substrate concentrations bacterial production for the central Baltic in May 1982 ranging from 5.4 to 54 µg C $l^{-1}d^{-1}$. Employing data on the frequency of dividing cells, Hagström et al. (1979) obtained a daily Baltic bacterial production of 10 µg C l^{-1}. A smaller production of 1.0 to 5.7 µg C $l^{-1}d^{-1}$ in the Kiel Bight from July to October was determined by Meyer-Reil (1977) with a 'flow system'. Azam et al. (1983) assume a bacterial production of 2 to 250 µg C $l^{-1}d^{-1}$ for coastal waters. These references show that there is a relatively wide range in bacterial production for different aquatic sites and seasons. Accordingly, microzooplankton production will also fluctuate within a certain range.

In terms of number and biomass the major component of microzooplankton populations comprised small protozoans, including 3 to 30 µm long ciliates and flagellates. A bacteriovorous mode of feeding is also well known for flagellates (Lighthart 1969, Haas & Webb 1979). Applying laboratory data from flagellate cultures and data of naturally occurring microflagellate abundances, Fenchel (1982b) calculated filtration rates of 12 to 67 % of the Limfjord water per day. This value lies somewhat below that of the summer filtration rate of Baltic microzooplankton (70 % d^{-1}) determined in this paper. Fenchel (1982b) presumes that heterotrophic microflagellates are the major consumers of bacteria in the marine pelagic system. It remains to be clarified, what proportion of the 3 to 30 µm long protozoan fraction is actually represented by microflagellates.

In areas of higher bacterial concentration, e. g. in the strongly eutrophic Schlei and in microbiotopes of blue-green algae agglomerates, ciliates of over 30 µm in length can play an important role as consumers of bacteria.

Our investigations have demonstrated that bacteria can represent an important food source for microzooplankters. Moreover, due to their high reproductive potential, microzooplankton organisms can respond almost immediately to favourable environmental conditions and, thus, effect a rapid introduction of bacterial biomass to the food web.

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