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Author(s): Heike Zimmermann-Timm, Henry Holst, Stefan Muller

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# Seasonal Dynamics of Aggregates and their Typical Biocoenosis in the Elbe Estuary

HEIKE ZIMMERMANN-TIMM<sup>1</sup>

HENRY HOLST

STEFAN MÜLLER

*Institut für Hydrobiologie und Fischereiwissenschaft*

*Hydrobiologische Abteilung*

*Universität Hamburg*

*Zeiseweg 9*

*D-22765 Hamburg*

*Germany*

**ABSTRACT:** In 1995, an extensive investigation was carried out in the Elbe Estuary in Germany. Special attention was paid to organisms, including bacteria, amoebae, ciliates, flagellates, rotifers, larvae of *Dreissena polymorpha*, and nematodes, dispersed in the water column and associated firmly or loosely with different types of aggregates. The abundance, size, and colonization by microorganisms of the aggregates varied during the seasons. The largest aggregates were found during spring and summer, when diatoms, rotifers, and crustaceans were present. The most aggregates were encountered in spring and from summer to autumn. Most of the species observed during the study were more common in pelagic habitats than in benthic ones. However, the presence of ciliates in the groups Hypotrichida and Sessilida as well as flagellates in the groups Biosoecida, Cercomonadida, Choanoflagellida, Chrysomonadida, Kinetoplastida, and amoebae and some nematodes in the open water depends upon the availability of surfaces, because they are sessile or poor swimmers, and some flagellates and amoebae need to attach themselves to an object to feed. Most organisms were much more abundant in or on aggregates than in the surrounding water during spring and summer, which indicates that aggregates enhance the habitat and promote the development of the organisms. From spring through autumn, the structure of the community associated with the aggregates is influenced by the pelagic environment. The presence of the species in the benthic community was detected only during summer.

## Introduction

Much of the suspended organic and inorganic matter in aquatic systems exists as aggregates, which range from a few microns to many centimeters in size. An aggregate is fragile and amorphous in microstructure. It may occur in different forms and sizes (Allredge 1979; Allredge and Cox 1982; Fowler and Knauer 1986; Allredge and Silver 1988). Aggregates are ubiquitous in the ocean (Herndl 1988), lakes (Grossart and Simon 1993; Grossart 1995), and estuaries (Eisma 1992). Aggregates are rich in nutrients, particularly those containing carbon, which enhance their colonization and the subsequent growth of the organisms. Macroaggregates are characterized by their bacterial content, which is two or three orders of magnitude greater (determined numerically) than that in surrounding water (Caron et al. 1982; Müller-Niklas et al. 1994). Studies in marine and freshwater habitats have shown that aggregates play an important role in the flow of energy through mi-

crobial communities, as well as in horizontal (Berger et al. 1996) and vertical transport (Turley and Carstens 1991) of some elements in the aquatic community. The biological study has focused mainly on the bacterial community (Allredge and Youngbluth 1985; Allredge et al. 1986; Herndl 1988; Azam et al. 1993). The relation of protozoans and metazoans to aggregates remains almost unknown, but they are thought to play an important role in their transformation and decomposition (Lochte 1991; Turley 1991). Organisms feeding on loosely associated or attached bacteria are probably a major controlling factor of the bacterial assemblages in this habitat, and they thereby control the remineralization rates of the nutrients. On the other hand, they seem to contribute to the breakdown of macroaggregates by mechanical disruption and direct consumption of the particulate material (Pomeroy and Deibel 1980; Biddanda and Pomeroy 1988; Lochte 1991; Zimmermann and Kausch 1996). In order to obtain information about the role of organisms attached to aggregates, their behaviour must first be determined. However, the information reported about this topic still remains contradictory. According to some authors

<sup>1</sup> Corresponding author; tele: 0049-40-4123-6653; fax: 0049-40-4123-6696; e-mail: hz@rrz.uni-hamburg.de.

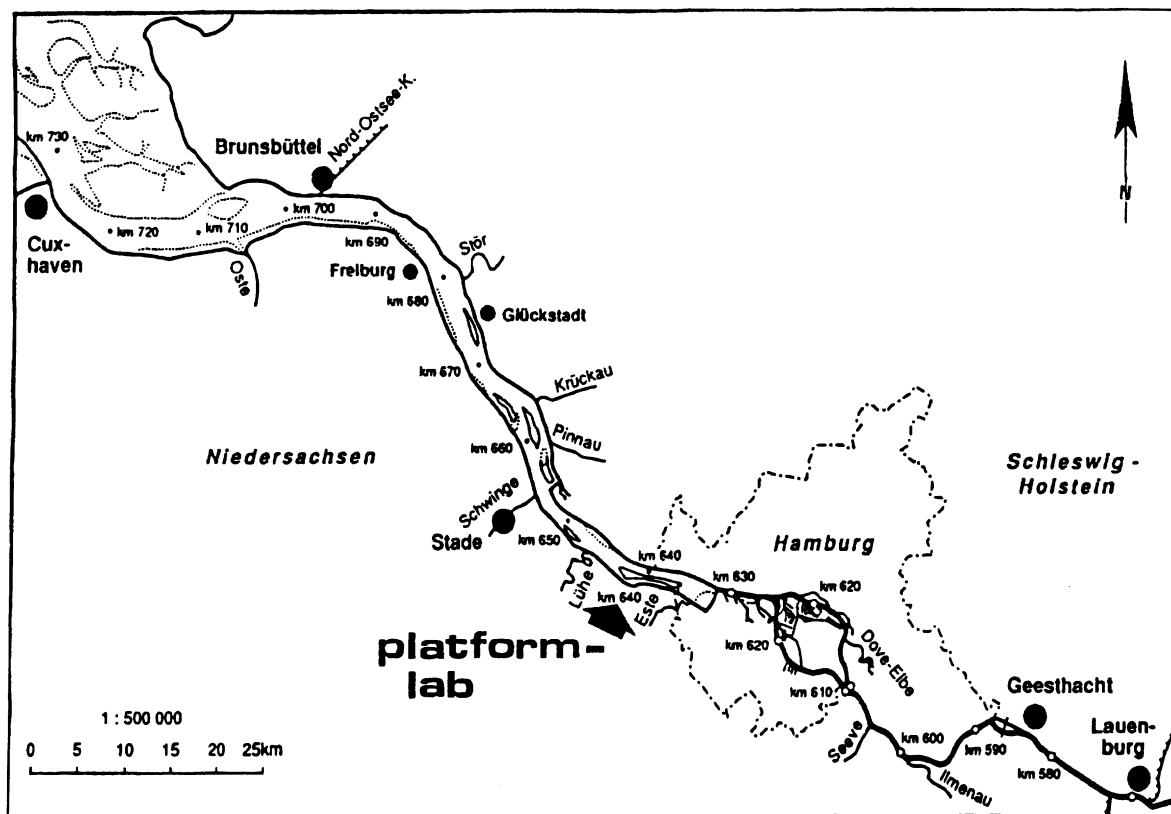


Fig. 1. Map of the Elbe Estuary showing the location of the platform lab in the Hahnöwer Nebelbe.

(Caron et al. 1982; Patterson and Fenchel 1990; Caron 1991) many of the species associate themselves with particles and are poorly adapted to life in the plankton, just as benthic species are. In contrast, other authors (Fenchel 1982) have observed the same species both in aggregates and in the surrounding water.

Using a special sampling technique (Zimmermann and Kausch 1996), we looked for the most representative colonists of aggregates, whenever and wherever they appeared. We noted where they occurred and how they behaved.

### Material and Methods

#### SAMPLING

Samples were taken from January through December 1995 from a research platform in the shallow, slow flowing Hahnöwer Nebelbe (Fig. 1) near Wedel, Germany. Water samples were taken from a depth of 1 m through a horizontal tube (HYDRO-BIOS, Kiel).

#### PLANKTON

To collect planktonic bacteria, amoebae, ciliates, and flagellates, samples were taken weekly and treated as described by Zimmermann and Kausch (1996).

The abundance of rotifers and *Dreissena polymorpha* larvae in 2.0-l samples, concentrated on a 30- $\mu$ m sieve and fixed with 4% formalin, was determined under an Uthermöhl inverted microscope at 100 $\times$  magnification (Holst 1996). Samples were taken weekly from January to June and biweekly from July to December.

The abundance of nematodes in 2.0-l samples from the open water were concentrated on a 30- $\mu$ m sieve, washed, and fixed with 4% formalin. The specimens were identified at 25 $\times$  magnification under a dissecting microscope. Samples were taken weekly from January through December.

#### AGGREGATES

The abundance and size of the aggregates were determined as described by Zimmermann and Kausch (1996).

#### AGGREGATE-ASSOCIATED FAUNA

Particles were collected in a Pasteur pipette from the horizontal tube. Protozoans, nematodes, and *Dreissena polymorpha* larvae were counted on each aggregate using the live counting technique (Zimmermann and Kausch 1996). The organisms most typically associated with aggregates were identified according to their morphological characteristics

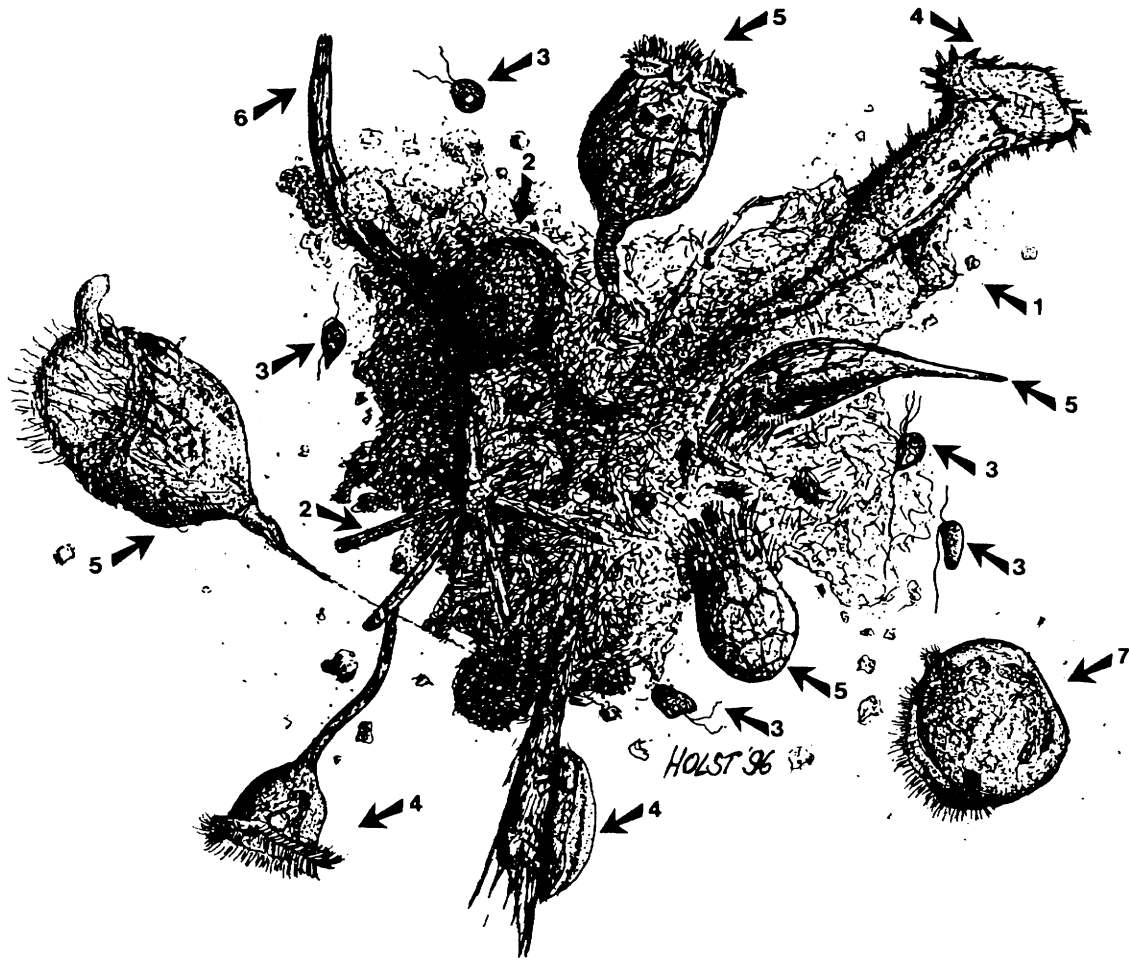


Fig. 2. Pattern of aggregate colonization during the whole year: 1 = bacteria-enriched environments, 2 = algae, 3 = flagellates, 4 = ciliates, 5 = rotifers, 6 = nematodes, 7 = *Dreissena polymorpha* larvae.

and behaviour, as observed under a light microscope. Three groups of organisms were identified: those organisms living in the aggregates, those on the surfaces, and others living in the open water. According to their occurrence, two groups were recognized: facultative and obligate aggregate-associated organisms. Organisms of benthic origin were associated obligately with aggregates. Bacteria were dislodged by ultrasonic vibration, and they were stained and counted on black filters (Zimmermann and Kausch 1996).

#### ADDITIONAL PARAMETERS

Temperature, oxygen concentration, salinity, conductivity, and current velocity were recorded simultaneously (G. Schymura, GKSS in Geesthacht, Germany, personal communication).

#### Results

During 1995, differences in the colonization of aggregates by organisms were observed in the shal-

low, slow flowing Hahnöwer Nebelbe near Hamburg. Bacteria, amoebae, ciliates, flagellates, rotifers, nematodes, and molluscs colonized the aggregates (Fig. 2). Only amoebae, nematodes, some ciliates, and most flagellates were obligate aggregate colonizers (Table 1).

There are differences in the content, size, and colonization of aggregates during the annual cycle. The seasonal pattern of aggregate colonization by protozoans and metazoans is shown in Fig. 3. We distinguished five types of aggregates during the year, which appeared during spring, early summer, summer, autumn, and winter. During spring, their typical content was diatoms; during early summer, faecal pellets of copepods, loricae of tintinnids, and some diatoms were abundant. In summer, detritus, was typical in autumn, macrophytes, while in winter, detritus with some mineral particles were the main components. Most aggregates were in the size range 50–1100  $\mu\text{m}$ , but several large ones

TABLE 1. Different kinds of colonization of aggregate-associated organisms in the shallow, slow flowing Hahnöver Nebenelbe near Hamburg. Considering pelagic and aggregate-associated organisms, aggregate colonizing forms are printed in bold type.

Organisms	Aggregate	Interface	Pelagic Environment
<b>Amoeba</b>			
<i>Vanella</i> sp.	+		
<i>Cochliopodium</i> sp.	+		
<b>Ciliates</b>			
<i>Askenasia</i> sp.		+	+
<i>Aspidisca cicada</i>	+	+	
<i>Aspidisca</i> sp.	+	+	
<i>Balanion</i> sp.		+	+
<i>Cinetochilum margaritaceum</i>		+	+
<i>Coleps hirtus</i>	+	+	+
<i>Cyclidium glaucoma</i>	+	+	+
<i>Cyclidium citrullus</i>	+	+	+
<i>Didinium</i> sp.		+	+
<i>Euplotes</i> sp.		+	
<i>Frontonia</i> sp.	+	+	
<i>Glaucoma scintillans</i>	+	+	
<i>Halteria</i> sp.	+	+	
<i>Litonotus</i> sp.	+	+	
<i>Lohmaniella</i> sp.	+	+	
<i>Paradileptus elephantinus</i>		+	+
<i>Stentor coeruleus</i>	+	+	+
<i>Strobilidium gyrans</i>		+	+
<i>Strobilidium</i> sp.		+	+
<i>Strombidium</i> sp.		+	+
<i>Tintinnidium cylindrata</i>	+	+	
<i>Tintinnidium fluviatile</i>	+	+	
<i>Tintinnidium</i> sp.	+	+	
<i>Uronema nigricans</i>	+	+	
<i>Urotricha</i> sp.	+	+	
<i>Vorticella convallaria</i>		+	
<i>Vorticella octava</i>		+	
<i>Vorticella microstoma</i>		+	
<b>Flagellates</b>			
<i>Bicosoeca</i> sp.		+	
<i>Bodo designis</i>	+	+	
<i>Bodo saltans</i>	+	+	
<i>Bodo</i> sp.	+	+	
<i>Bodomorpha minima</i>	+	+	
<i>Cercomonas</i> sp.	+	+	
<i>Ceratium</i> sp.		+	+
<i>Codonosiga</i> sp.	+	+	
<i>Cryptomonadida</i>		+	+
<i>Euglena viridis</i>		+	+
<i>Kentrosiga thienemanni</i>	+	+	
<i>Monosiga ovata</i>	+	+	
<i>Pseudobodo</i> sp.	+	+	
<i>Rhynchomonas</i> sp.	+	+	
<i>Spumella</i> sp.	+	+	+
<b>Rotifers</b>			
<i>Anuraeopsis fissa</i>		+	+
<i>Keratella cochlearis</i>		+	+
<i>Keratella cochlearis</i> var. <i>tecta</i>		+	+
<i>Notholca squamula</i>		+	+
<i>Notholca acuminata</i>		+	+
<i>Notholca labis</i>		+	+
<i>Pompholyx sulcata</i>		+	+
<i>Pompholyx triloba</i>		+	+
<i>Trichocerca pusilla</i>		+	+
<b>Mollusca</b>			
<i>Dreissena polymorpha</i>	+	+	+
<b>Nematodes</b>			
	+	+	

reached 5000  $\mu\text{m}$  (Figs. 3 and 4). The largest aggregates were found during spring and summer. In the Hahnöver Nebenelbe, the number of aggregates varied between 20 aggregates  $\text{l}^{-1}$  and 4000 aggregates  $\text{l}^{-1}$  (Fig. 4). Seasonal peaks were observed in April and May and in July.

The concentration of bacteria fluctuated remarkably (Fig. 4), with low densities occurring during winter. The total abundance of bacteria varied between  $6.2 \times 10^8 \text{ l}^{-1}$  and  $2.6 \times 10^{10} \text{ l}^{-1}$ . The variations in the abundance of dispersed and attached organisms showed the same trends, but the unattached bacteria did not show such pronounced changes. The abundance of unattached bacteria varied between  $5 \times 10^9 \text{ l}^{-1}$  and  $17 \times 10^9 \text{ l}^{-1}$ , while attached bacterial density varied from  $0.3 \times 10^6 \text{ aggregate}^{-1}$  ( $=1.7 \times 10^7 \text{ l}^{-1}$ ) to  $2.5 \times 10^6 \text{ aggregate}^{-1}$  ( $=2.6 \times 10^{10} \text{ l}^{-1}$ ). Attached bacteria accounted about 36% of the total during the year.

The total number of amoeboid species varied between  $17 \text{ l}^{-1}$  and  $34,000 \text{ l}^{-1}$  (Fig. 4). In the open water, this number varied between  $1 \times 10^3 \text{ l}^{-1}$  and  $11 \times 10^3 \text{ l}^{-1}$ . There were from 1–211 amoebae present on each aggregate ( $=17\text{--}24,000 \text{ l}^{-1}$ ). They were most abundant summer, when more than 55% were associated with aggregates. During the annual cycle, amoebae were the most important (41–82% of the aggregated associated zooplankton) aggregate-associated zooplankton (Fig. 5).

The abundance of ciliates (Fig. 4) was found to range from  $5 \times 10^3 \text{ l}^{-1}$  to  $25.07 \times 10^3 \text{ ciliates l}^{-1}$ . Abundance was greatest during spring and summer. Oligotrich ciliates dominated in spring, during summer there was a great diversity species, in autumn sessile forms dominated, and in winter large ciliates ( $>20 \mu\text{m}$ ) of different groups were present (Fig. 3). From 2% to 4% of ciliates were associated with aggregates during early summer, but the highest percentages, up to 19%, were reached in mid summer. Ciliates reached the highest percentage of aggregate-associated zooplankton in autumn (26% of the aggregate-associated zooplankton; Fig. 5).

Flagellates (Fig. 4) ranged in abundance from  $0.95 \times 10^6 \text{ l}^{-1}$  to  $6 \times 10^6 \text{ l}^{-1}$  in the open water, and there were 1–23 flagellates per aggregate ( $=15\text{--}2640 \text{ l}^{-1}$ ). During summer, only about 1% of the flagellates lived on aggregates. In autumn, sessile nanoflagellates were present (Fig. 3). Besides amoebae, the flagellates (13–31% of the aggregate-associated zooplankton) were the other important group of aggregate-associated zooplankton (Fig. 5) during the annual cycle.

Rotifers (Fig. 4) reached abundances between  $1 \text{ l}^{-1}$  and  $2000 \text{ l}^{-1}$ . During the summer and autumn, many rotifers seem to be associated with aggregates (3–4% of the zooplankton; Fig. 5).






	spring	early summer	summer	autumn	winter
scheme					
mean size	1100 µm	1250 µm	1200 µm	200 µm	100 µm
typical content	diatoms	faecal pellets of copepods, loricae of tintinnids, diatoms	detritus	macrophytes	minerals, detritus
attached organisms	oligotrich ciliates, some nanoflagellates, amoebae	oligotrich ciliates, nanoflagellates, rotifers, amoebae	amoebae, ciliates, flagellates, rotifers, nematodes, crustaceans, larvae of <i>Dreissena polymorpha</i>	sessile ciliates, sessile nanoflagellates, amoebae	large ciliates, some nanoflagellates, amoebae

Fig. 3. Seasonal changes in aggregate structure, size, content, and settlement by organisms.

Larvae of *Dreissena polymorpha* (Fig. 4) that developed during the summer reached abundances in the range of 1–220 individuals  $l^{-1}$ . During this season, 1–3 larvae were counted on each aggregate (Fig. 4); 3% of the aggregate-associated zooplankton were larvae of *Dreissena polymorpha* (Fig. 5).

Nematodes (Figs. 4 and 5) were also very abundant on aggregates during the summer. Nearly all nematodes were associated with aggregates.

With the exception of the amoeba *Vanella* sp., all obligate aggregate-associated organisms colonized the aggregates inside and their interface (Table 1). Holes of different sizes in the aggregates were structured by smaller ciliates, such as *Cyclidium* sp. and *Aspidisca* sp., and by nematodes. *Stentor coeruleus* moved its basal parts through different kinds of aggregates and formed hollow spaces. *Vannella* sp. had the ability to penetrate into very small spaces in aggregates as a sedentary form, feeding without pseudopodia. *Bodo* sp. and *Rhycomonas* sp. maintained contact with the substrate by employing their trailing flagella. Finally, the ciliates *Euplotes* sp. and *Aspidisca* sp. moved easily inside and on the surface of the aggregate using their cirri and created water currents with the membranelles in their adoral zones.

The flagellates *Pseudobodo* sp. and *Bicosoeca* sp. and the ciliate *Uronema* sp. developed near the aggregates. *Pseudobodo* sp. was observed in the surrounding water, with transient attachments to the aggregate surfaces. It fed on suspended prey by directing its anterior flagellum into the water surrounding it and using its posterior flagellum for transient attachment to the surface. *Bicosoeca* sp. was permanently attached to the particle surface by means of its lorica and fed on suspended prey

using its long anterior flagellum. *Uronema* sp. constantly swam in the surrounding water. Larvae of *Dreissena polymorpha* also swam constantly in the surrounding water and fed by filtering bacteria, which were more concentrated near the aggregates. Rotifers, such as *Anuraeopsis*, *Keratella*, and *Notholca*, showed similar behaviour. *Trichocerca* was able to attach to aggregates using special mucopolysaccharide stitches and grazed on picoplankton and nanoplankton concentrated near the aggregate surfaces.

### Discussion

Aggregates are a potentially important component of the estuarine environment (Eisma 1992). Their study involves many difficulties because aggregates are usually extremely fragile and easily disrupted by the usual sampling methods (Zimmermann and Kausch 1996). Information about the succession of aggregate-associated organisms is scarce (Zimmermann and Kausch 1996; Zimmermann 1997) and few investigations of bacteria and protozoans were conducted in laboratories or during studies of the marine environment.

The microbial succession on the aggregates was characterized by rapid bacterial growth followed by the appearance of nanoflagellates, ciliates, sarcodines, and later, during spring and summer, rotifers, nematodes, and *Dreissena polymorpha* larvae (Fig. 3). This pattern of colonization by protozoans has previously been described (Pomeroy and Deibel 1980; Pomeroy et al. 1984; Davoll and Silver 1986; Caron 1991; Zimmermann and Kausch 1996; Artoizaga et al. personal communication). However, investigations on the succession of metazoans on aggregates have not been conducted.

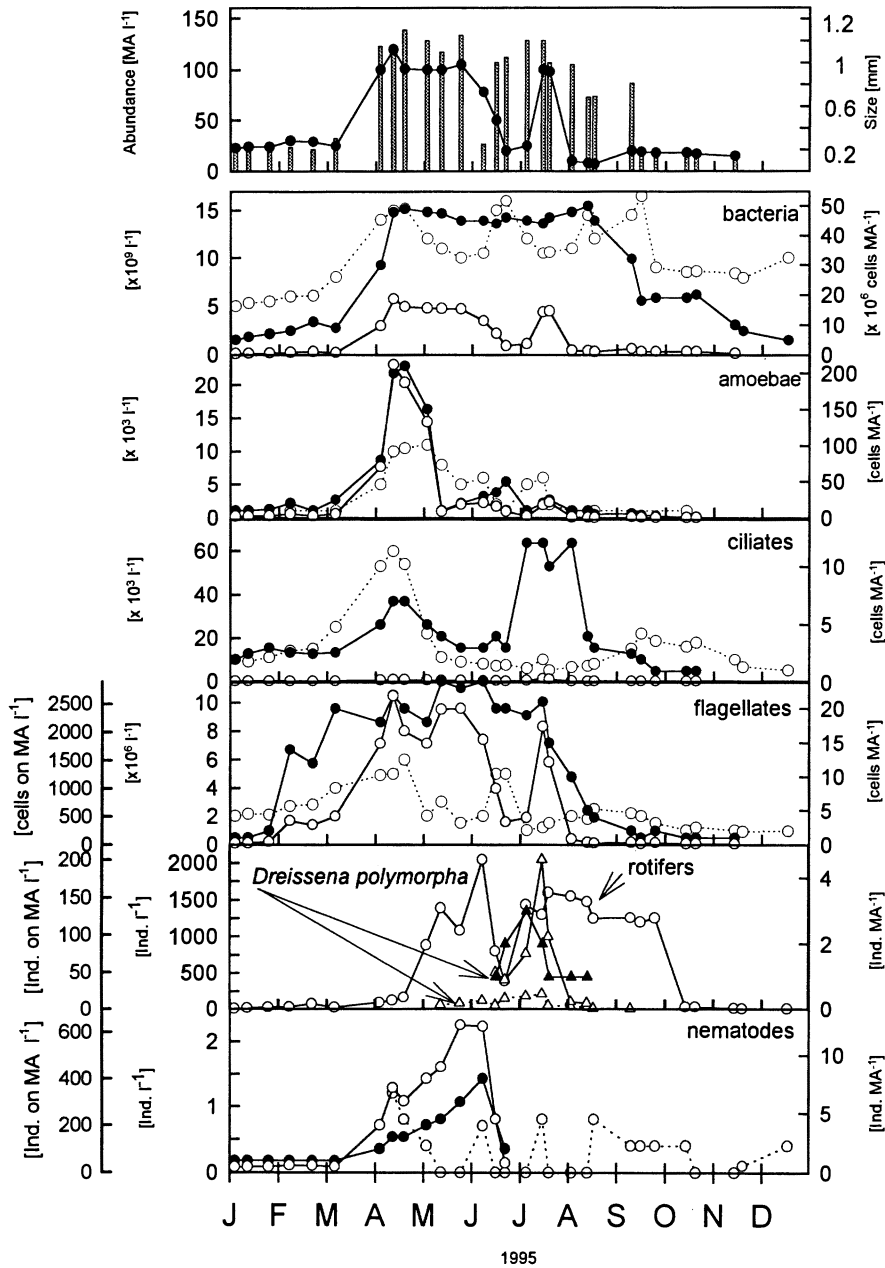


Fig. 4. Seasonal changes in macroaggregate (MA) abundance [aggregate  $l^{-1}$ ] and size [ $\mu m$ ]. Numbers of bacteria, amoebae, ciliates, flagellates, rotifers, larvae of *Dreissena polymorpha*, and nematodes in the water of the Elbe (dotted lines and open circles or open triangles) and on aggregates (lines and solid circles and solid triangles) between January and December 1995. Values are shown as individuals per liter or per aggregate. The number of aggregate-associated organisms (lines and open circles or open triangles) is shown as individuals per liter.

Heterotrophic nanoflagellates (Fig. 4) were the first protozoans to appear on the aggregates. They may be the pioneer organisms because they are more abundant than other protists in the water, possibly due to their ability to grow and reproduce when food is not abundant (Caron 1991). Although ciliates appear later, they seem to play a pivotal role (Fig. 4). Rotifers that graze on bacteria,

nanociliates, nanoflagellates, or whole aggregates, as well as the bacterivorous larvae of *Dreissena polymorpha* that are associated with the aggregates, have not been previously investigated. They developed during summer, when the organisms associated with the aggregates were very abundant (Fig. 4). Nematodes, observable during summer (Fig. 4) as components of aggregates, were described for

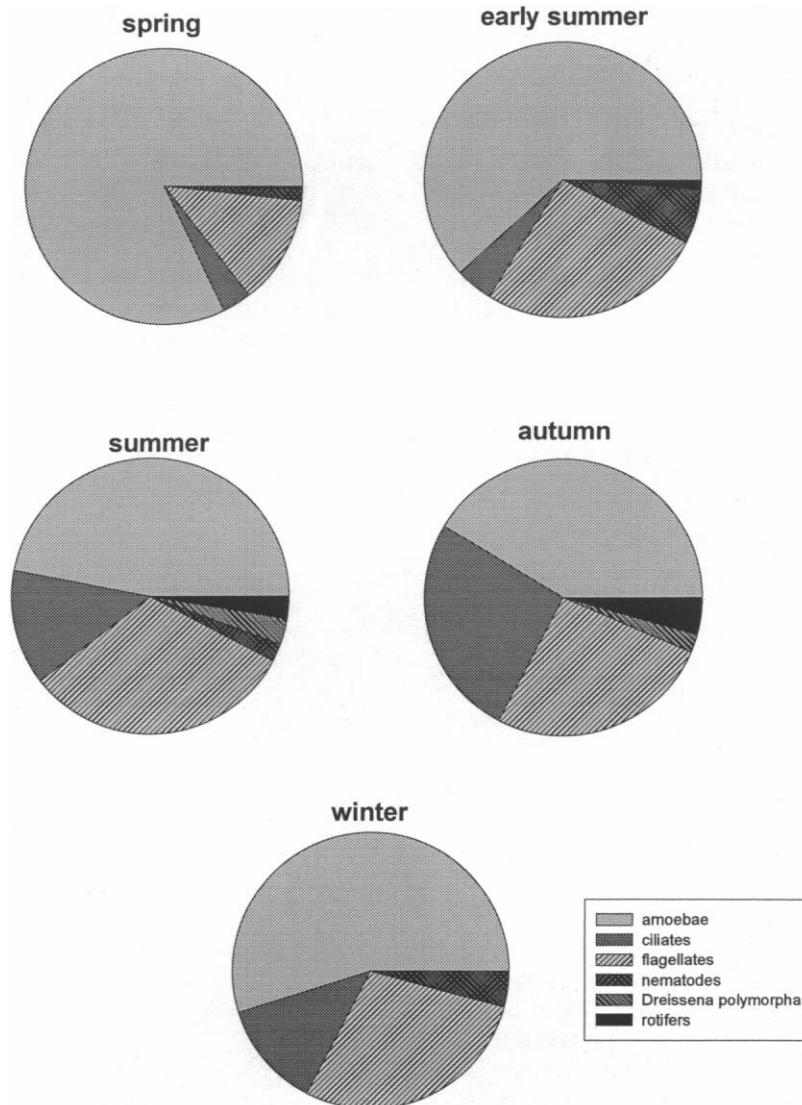


Fig. 5. Seasonal variations in the species composition [in percent] on or in the aggregates from the Elbe.

the first time on marine snow by Shanks and Edmondson (1989).

Ciliates with specialized feeding behavior also influence the structure of the community associated with the aggregates. They affect the decomposition rates by consuming the abundant small protists and also by grazing on bacteria (Silver et al. 1984).

Within aggregates, most protists were specifically adapted to inhabiting the surfaces. All of them grazed on attached bacteria but employed different feeding mechanisms. Caron (1987) showed that *Bodo* sp. and *Rhynchomonas* sp. moved and fed effectively when in contact with a surface but were poor swimmers and were inefficient feeding on suspended bacteria. On the other hand, *Vannella* sp. had the ability to penetrate into very small spac-

es in aggregates as a sedentary form feeding without pseudopodia, although it also appears as a nonfeeding floating form with pseudopodia (Arndt 1993). *Euplotes* sp. and *Aspidisca* sp. move easily inside and on the surface of the aggregate using their cirri and create water currents with the membranelles in their adoral zones to remove attached bacteria.

The flagellates *Pseudobodo* sp. and *Bicosoeca* sp. and the ciliate *Uronema* sp. benefitted from higher concentrations of suspended bacteria that developed near the aggregate (Zimmermann 1997, unpublished data). *Uronema* sp. constantly swam in the surrounding water and is a filter-feeder. For an opportunistic ciliate adapted to exploit transitory patches of abundant bacteria (Fenchel 1980; Sie-

burth 1984) these enriched environments can be ideal sites for growth and feeding.

According to Davoll and Silver (1986), aggregates are environments in the open water that support populations with a set of features suitable for both pelagic and benthic systems. However, most of the species observed during this study were more common in open water habitats than in benthic ones. Nevertheless, the presence of *Bodo*, *Rhynchomonas*, *Bicosoeca*, *Vorticella*, and nematodes in the plankton undoubtedly depends upon the availability of surfaces in the open water (Caron 1991). *Pseudobodo* also needs a point of attachment in order to feed. The floating and a feeding form of *Vannella* appear to be adapted to exploit open water and enriched detrital aggregates (Patterson and Fenchel 1990). *Coleps*, *Cyclidium*, *Euplotes*, and *Uronema* are ciliates that also have been found in aggregates (Caron et al. 1982; Davoll and Silver 1986). They employ very different survival and feeding strategies. *Euplotes* is a poor swimmer and is more typical in the benthic environment, while *Coleps*, *Cyclidium* and *Uronema* move rapidly and are more common in pelagic systems. *Aspidisca* is a benthic protist, but it has also been encountered in the water column, always associated with surfaces (Lee et al. 1985). Other studies have also indicated the aggregates host protists that feed on bacteria and are not common in the planktonic environment. Most of the ciliates and all rotifers are typical pelagic species (Table 1).

The importance of aggregates for the enhancement of growth of the organisms has been shown in the literature (Caron et al. 1986; Alldredge and Silver 1988; Turley and Mackie 1994). We observed a greater abundance of bacteria and protozoans on the aggregates than in the surrounding water (Fig. 4). For flagellates, the percentage on aggregates was low (about 1%), while those for amoebae and ciliates ranged from 1.7% to nearly 100%.

In the opinion of Artolozaga et al. (personal communication) and Caron (1991), when nutrients are scarcer, the aggregates become more important as sites for organisms. Our investigations in the Hahnöver Nebenelbe do not confirm these results. During winter (Zimmermann unpublished data), the aggregates are not abundant, are small in size and not enriched with organic material, and they are not a good food source in the pelagic environment, even though food is scarce. Similar results were observed in the turbid zone of the Elbe Estuary, a habitat characterized by extreme abiotic conditions (Zimmermann 1997; Zimmermann et al. unpublished data). Similarly, enrichment decreased as the aggregates became smaller and as their inorganic particle content increased. Herndl (1988) and Artolozaga et al. (personal communi-

cation) believed also that the enrichment tended to decrease as the aggregates became older, probably due to a release of organic nutrients from the aggregates into the surrounding water and a subsequent increase in free-living bacterial abundance. It seems that the conditions in an estuary are different. The effect of the tides causes changes in sedimentation and resuspension of the particles. Considering this phenomenon and the fact that in the productive zone during spring and summer there is abundant organic material and many exopolmer-forming organisms, large numbers of new aggregates can be continually produced. This and the dwelling of the estuarine water caused by the tides, produce changes in the estuarine aggregates show during the productive seasons in the limnetic zone. The aggregates do not become old and lose their nutrients.

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