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Characteristics, Dynamics and Importance of Aggregates in Rivers – An Invited Review

key words: suspended particulate matter, detritus, river, estuary, food web

Abstract

The current knowledge of micro- and macroaggregates in running waters as well as an assessment of their importance will be given in this overview. Micro- and macroscopic aggregates are an abundant component of running waters, considering both rivers and estuaries. They are composed of different kinds of organic and inorganic matter and elements, mainly from the aquatic but also from the terrestrial environment. Their production is determined by natural and anthropogenically influenced abiotic and biotic factors. Aggregate abundance, size and composition vary greatly along the longitudinal profile of running waters. Aggregates are actively or passively colonized by bacteria, protozoa (amoebae, ciliates and flagellates) and metazoa (copepods, nematodes, rotifers, veliger larvae) and they show higher loads of nutrients and organisms compared to the surrounding water. Detritus in running waters has been examined over a period of 100 years but investigations of single aggregates began only in 1996, after pioneering works in the marine field and in lakes. Since then studies have been focused on several aspects of aggregate formation, colonization, nutrient recycling and decomposition. Aggregates have been identified as foci of microbial activity. It has been shown that the significance of aggregate – associated organisms and processes varies both temporally and spatially and is also affected by the nutrient status of surrounding water. An important conclusion from recent studies is that the resuspension and sedimentation of aggregates connects pelagic and benthic food webs to an aquatic food web. It also underlines the importance of the microbial food web, with its fluxes among aggregate-associated pico- and nano-organisms, to organisms of higher trophic levels. Predators of higher trophic levels are only able to eat small-sized organisms if they are associated to aggregates.

1. Introduction

In this review only running waters of the order >3 with a mean drainage (MQ) of $>1 \text{ m}^3 \text{ sec}^{-1}$ and a width $>3 \text{ m}$ including the hydrological zones Epi-, Meta- and Hypopotamal (UHLMANN, 2001) will be taken into account. In the following paragraphs “river” is used to distinguish lotic freshwater environments from “estuaries”.

1.1. Definition

The word “aggregate” was established only recently as scientific term. Taking all environments into account, the marine as well as the limnetic, “*aggregate*” is defined as a *fragile, amorphous, macroscopic or microscopic particle consisting of organic and inorganic material*. Aggregates have different forms and sizes ($\geq 0.45 \mu\text{m}$) and three size classes are distinguished: 1) macroscopic aggregates $>150 \mu\text{m}$; 2) microaggregates $<150 \mu\text{m}$; and 3) submicron particles $<1 \mu\text{m}$ (Fig. 1; ALLDREDGE and SILVER, 1988; PERRET *et al.*, 1994).

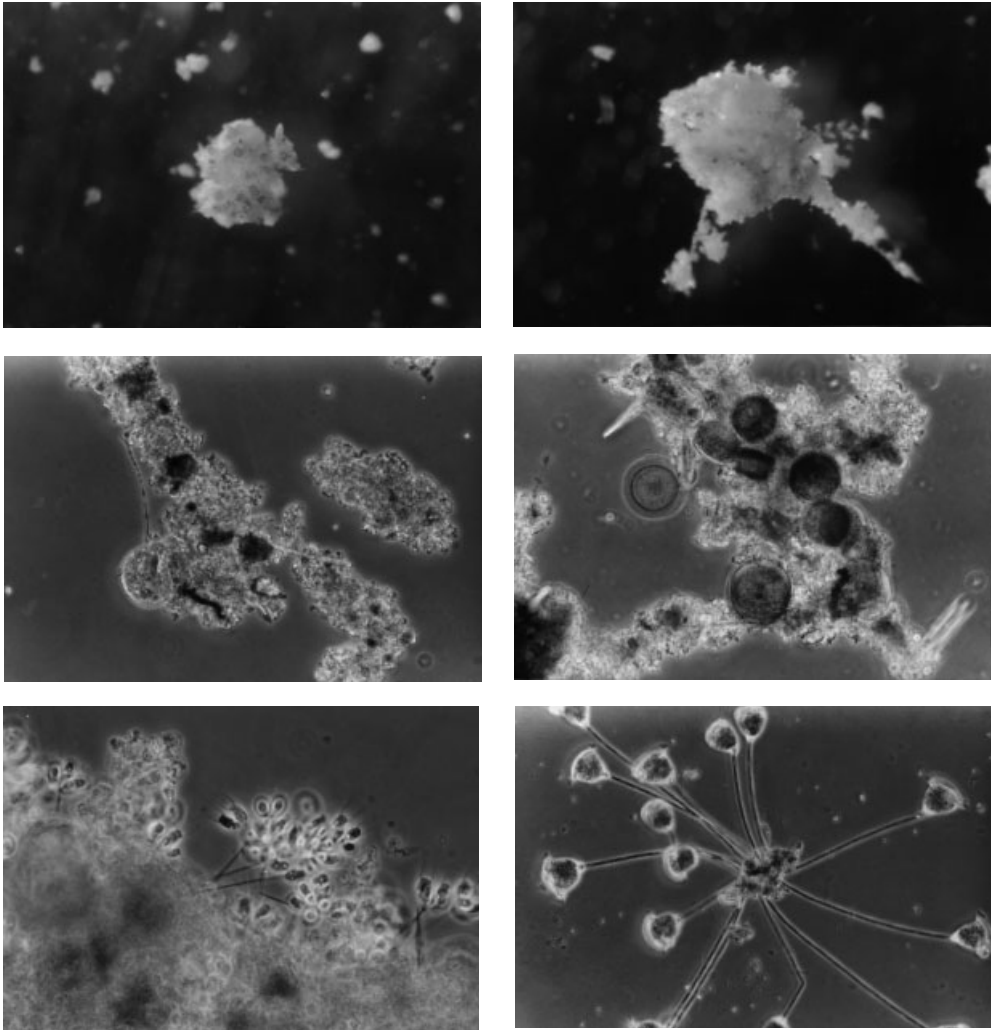


Figure 1. Typical riverine aggregates (photo 1 and photo 2; each scale 200 µm, photos: UTE WÖRNER), two different composed aggregates (photo 3 and photo 4; each scale 100 µm; photos: HEIKE ZIMMERMANN-TIMM) and protists associated with aggregates (photo 5 and photo 6; each scale 50 µm; photos: UTE WÖRNER).

1.2. Historical Comments

The interest in aggregates is relatively new (ALLDREDGE and SILVER, 1988), although there are many historical observations about suspended particulate matter, summarizing both information about aggregates, plankton and resuspended or eroded sediment particles, and their effects in rivers, estuaries and adjoining terrestrial environments.

In Antiquity, the interest was mainly restricted to the effects of large rivers carrying suspended sediment into the coastal sea, causing siltation in embayments and filling up shallow straits between some islands. One of the commercial results was the cultivation of river

basins, with the classical examples of the rivers Nile and Don (BERGER, 1903; FORBES, 1963).

During the Middle Ages, former informations were preserved but little was added except by the Arabian travelers, who passed on informations on south Asian rivers (MIQUEL, 1975, 1980). More than 5000 rivers were described in China. As water engineering flourished in China, practical knowledge on the behaviour of suspended matter was developed equally such as experience with extensive canalization, dike construction and silt precipitation.

In Europe, after the Middle Ages, the earlier observations made during Antiquity were continued by Leonardo da Vinci, who described the conditions of mud depositon at low current velocities and in lentic areas in plant roots along the river banks (LEONARDO DA VINCI, 1948).

The lack of quantitative data changed during the 19th century and many observations became available for many rivers. Measurements referring the current velocity, total discharge and water temperature were carried out. The latter was done because a relation between the settling velocity of particles in water and the viscosity of the water had been formulated by STOKES (1845). The methods of determination, however, were not very precise: one example for a quick estimate of transparency is the application of a white disk of 30 cm in diameter, developed by SECCHI (1865) and today commonly referred to a "Secchi disk".

It is important to note, that during the 19th century in particular biologists developed an interest in the turbidity of water, since they had realized its impact on light and its coupled influence on plankton growth (REYNOLDS, 1984) and phototropic movements of zooplankton (SOMMER and GLIWICZ, 1986). Considering results from the sea (SUZUKI and KATO, 1953) and different lakes (GROSSART and SIMON, 1993) scientists started to observe single aggregates in fluvial environments (ZIMMERMANN and KAUSCH, 1996). They were interested in the aggregate structure and composition, to better understand aggregate – associated processes and their interactions with the pelagic and benthic environment.

1.3. Characterization of Aggregates in Running Water

Aggregates are an ubiquitous phenomenon in running waters, including tidal estuaries and freshwater rivers. In most of the world's rivers the suspended particulate matter is dominated by material mobilised from the upstream drainage basin by erosion or by allochthonous or autochthonous organic material that is then transported through the river basin (Fig. 2; DEGENS and ITTEKOT, 1984; EISMA, 1993; ELLSWORTH, 1986; FINDLAY *et al.*, 1991; ITTEKOT, 1988; MILLIMAN and MEADE, 1983; VANNOTE *et al.*, 1980). In the global hydrological cycle, lotic systems are the major links between terrestrial and aquatic habitats, including surface and groundwater (JUNK *et al.*, 1989, WARD, 1989, WARD and STANFORD, 1983). Running waters are enormously diverse in size, ranging from small creeks to great rivers, and occur under widely different conditions of climate, vegetation, topography and geology. We also have to take into account the physiographic characteristics of the upstream drainage basin and the geomorphological and hydrological processes responsible for mobilising and transporting sediment within the basin (WALLING, 1996). The transport of suspended particulate matter to the sea, which includes aggregates and their components, has been described by EISMA (1993; Table 1).

I will first briefly summarize the main characteristics of aggregates in running waters, detailed explanations to the different aspects will be given in the following chapters:

Hydrographical regime (Fig. 3) – The hydrographical regime is particularly important in respect to current velocity, since increasing current velocity and discharge rate result in a large amount of aggregates in the water column (BERGER *et al.*, 1996; ZIMMERMANN, 1997). Most of the resuspended material are heavy particles (f.e. diatoms, mineral particles) requiring a relatively high current velocity to resuspend (Table 2), other particles are carried

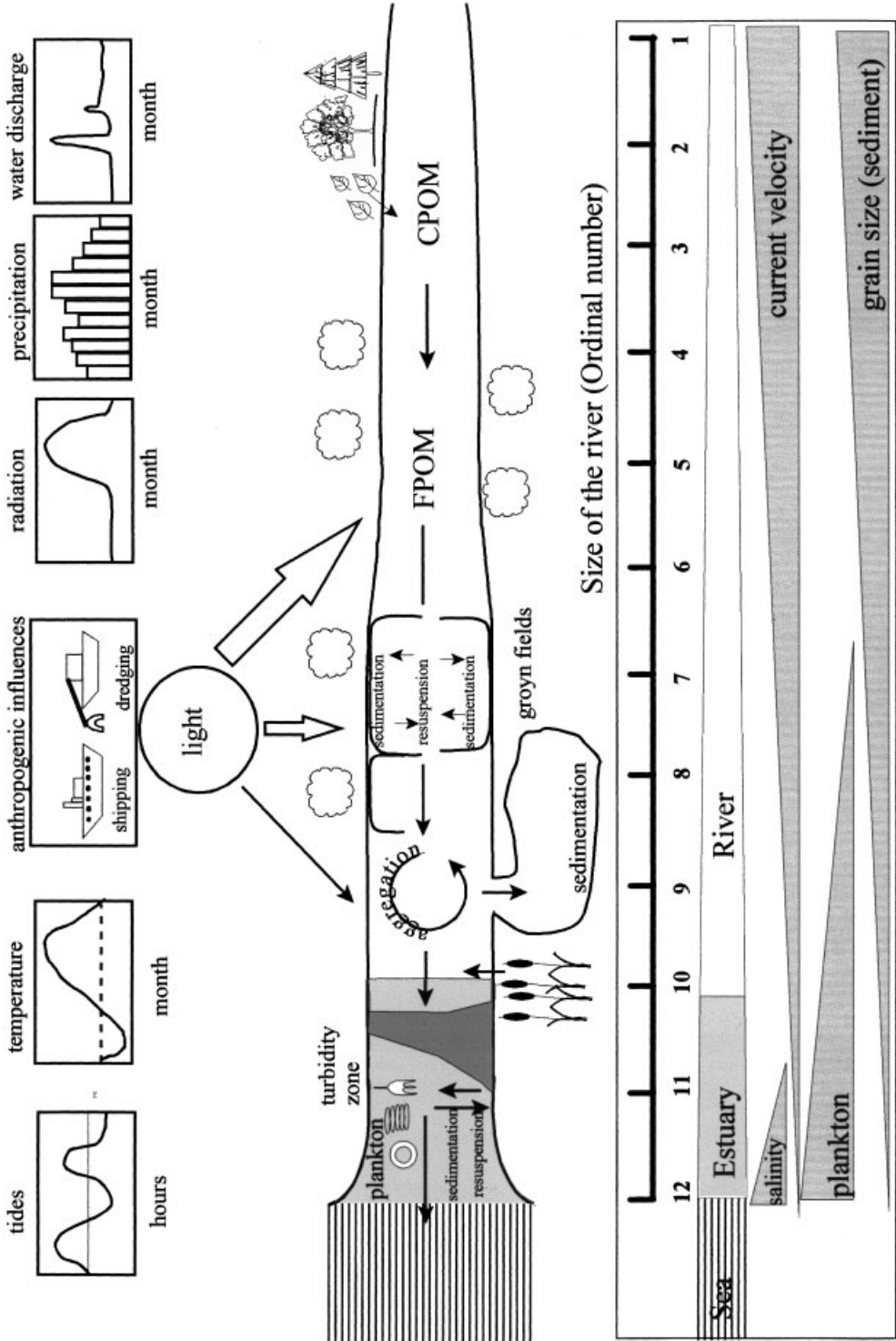


Figure 2. Generation of aggregates in the riverine and estuarine environment considering different biotic (benthic and planktonic materials), abiotic (tides, temperature, radiation, precipitation, water discharge) and anthropogenic factors (e.g. shipping, dredging). Downstream there is a decrease in current velocity and sediment grain size, but an increase in plankton abundance and salinity. Sediment water interactions by sedimentation (e.g. estuary, groyne field) and resuspension are typical for running waters. FPOM (fine particulate organic matter), CPOM (coarse particulate organic matter).

Table 1. Average sediment transport to the sea of 33 large rivers (after EISMA, 1993, with data from: ADMIRAAL and ZANTEN, 1988; FRIEDRICH and MÜLLER, 1984; T. GAUMERT, ARGE Elbe, pers. communication).

River	Mean sediment discharge (10^6 t y^{-1})	Average water discharge ($\text{km}^3 \text{ y}^{-1}$)	Average concentration (mg l^{-1})
Amazon	1000–1300 [1000–1300]	6300	190
Yellow River (Huang He)	1100 (100) [1200]	49	22040
Ganges-Brahmaputra	900–1200	970	1720
Chang Jiang	480	900	531
Irrawaddy	260 [260]	430	619
Magdalena	220	240	928
Mississippi	210 (400) [500]	580	362
Godavari	170	92	1140
Orinoco	150 (150) [150]	1100	136
Mekong	160	470	340
Purari/Fly	110	150	1040
Salween	~100	300	300
Mackenzie	100 (100) [100]	310	327
Parana/Uruguay	100	470	195
Zhu Jiang (Pearl)	80	300	228
Copper	70 (70) [70]	39	1770
Choshui	66	6	11000
Yukon	60 (60) [60]	195	308
Amur	52	325	160
Indus	50 [250]	240	208
Zaire	43	1250	34
Liao He	41	6	6833
Niger	40	190	210
Danube	40 [70]	210	190
Columbia	8	250	32
St. Lawrence	3	450	7
Rhine	3	482–950	1–120
Elbe	<1	669	58
Rivers that formerly discharged large sediment loads:			
Nile	0 [125]	0 [was 39]	
Other rivers that discharge large volumes of water:			
Ob	16	385	42
Zambesi	20	220	90
Yenesei	13	560	23
Lena	12	510	24
Columbia	8 [15]	250	32
St. Lawrence	3	450	7

() Presumed natural level; [] year 1980

through the water column by currents from former still or stagnant waters or material is eroded from the terrestrial environment. The high density of aggregates and other suspended particles in the water column increases the probability of particle contact in the water column, therefore an increase in the number and size of aggregates is likely. Under these conditions the changes in concentration of suspended material indicate that the highest con-

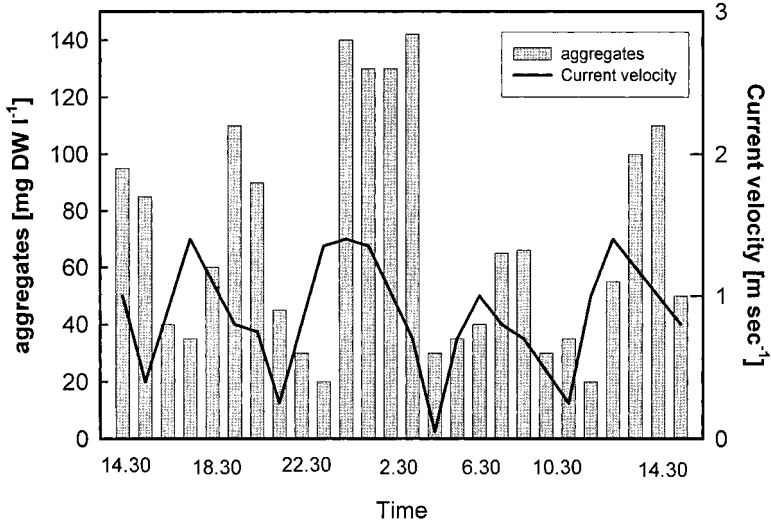


Figure 3. Interactions between current velocity and amount of suspended particulate matter in the Elbe Estuary near Brunsbüttel during two tides.

centrations of suspended matter occur a few days before the flood crest (Fig. 4), whereas later on the number of aggregates in the water column is reduced (Fig. 4), and the amount of praesediment, is low. In a tidally influenced system the maximum or minimum concentration of suspended particulate matter concentration follows with some delay (Fig. 3). In most cases the maximum or minimum concentration of suspended particulate matter was

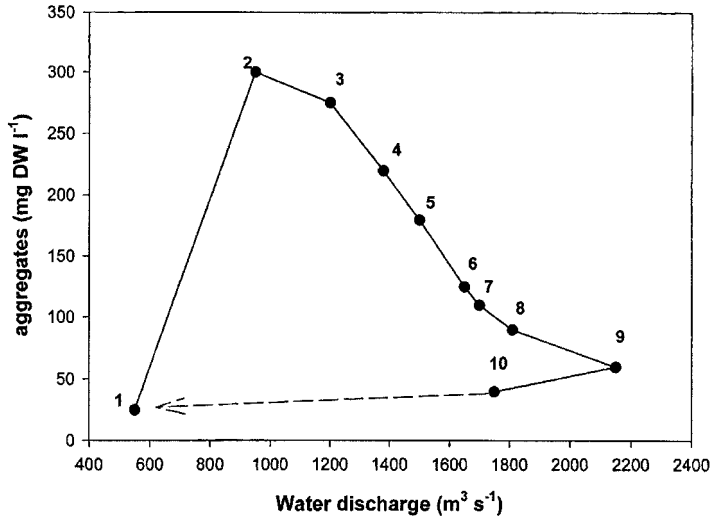


Figure 4. Suspended particulate matter and water discharge in the River Elbe near Magdeburg (after: SPOTT and GUHR 1996). The numbers 1 to 10 characterize the dates, when the measurements were done. 1: 27.02.1979, 2: 06.03.1979, 3: 07.03.1979, 4: 08.03.1979, 5: 09.03.1979, 6: 12.03.1979, 7: 13.03.1979, 8: 15.03.1979, 9: 20.03.1979, 10: 27.03.1979.

Table 2. Organisms predicted to resuspend in each of three ranges of tidal-current strength. HNF (Heterotrophic nanoflagellates).

$<0.5 \text{ m sec}^{-1}$	$0.5\text{--}1 \text{ m sec}^{-1}$	$1\text{--}1.5 \text{ m sec}^{-1}$
bacteria	bacteria	bacteria
HNF	HNF	HNF
Oligotrich ciliates	Oligotrich ciliates	Oligotrich ciliates
	Hypotrich ciliates	Hypotrich ciliates
	Scuticociliates	Scuticociliates
	Bacillariophyceae	Bacillariophyceae
Chlorophyceae	Chlorophyceae	Chlorophyceae
Cyanophyceae	Cyanophyceae	Cyanophyceae

measured 1 to 2 hours after the maximum or minimum current velocity. These findings are based on the density of the particles and their different settling behaviour. Those aggregates were of benthic and/or pelagic origin.

Waves (Figs. 2, 4) – Wave action influences the generation of aggregates in the water column of lotic systems (VAN LEUSSEN, 1996). Waves are very efficient in stirring up bottom sediment and can lead to suspension at much lower equivalent velocities than unidirectional currents. When surface waves stir up sediment from the bottom, there is considerable variation in particle concentration within each wave oscillation, which is related to wave phase, height above the bottom and the maximum oscillatory velocity. Much of the suspended matter transport occurs under the combined influence of currents and waves, particularly in estuaries, and it is determined by the roughness and morphology of the bottom. Detailed investigations on this topic are absent.

Shipping (Fig. 2) – High concentrations of suspended particulate matter are the result of disturbances and other processes related to ship movements up- and down-stream (KAUSCH, 1996, SPOTT and GUHR, 1996). One important aspect deals with the resuspension of benthic material caused by ships. Up to now no detailed investigations on this topic exists for rivers and estuaries.

Deepening (Fig. 2) – The deepening of the aquatic systems due to dredging or water injection also influences the sediment transport and the formation of “benthic aggregates” in rivers (JUNG, 1999). In both cases benthic material reaches the water column and may therefore be involved in the formation of aggregates.

Precipitation (Fig. 2) – Rain, or melting water from snow, increases the transport of particles into the water body (HAMM *et al.*, 1996). Similar evidence is available from the Vågåvatn delta in Norway where the influence of melting snow on the transport of high amounts of suspended particulate matter was emphasised (ELSTER *et al.*, 1996). In both cases particles from the terrestrial environment were transported into the running water, which caused high particle abundances in the water column. Rain and snow can also influence the water discharge.

Stagnation (Fig. 2) – Low amounts of aggregates are present at slack water, i.e. during the change of the tides, in estuarine environments (Fig. 3), in areas of still or stagnant water, between groynes in large rivers and other slow-flowing areas like the riverine meadows of the middle Elbe.

Transport (Table 3) – Dependent on the current velocity, horizontal transport of aggregates is typical for running waters. Water residence times in estuaries are influenced by interactions between the tides and the water flow. Dependent on the water discharge the residence time in estuaries is longer than in riverine environments (BERGEMANN *et al.*, 1996). For example, in the Elbe Estuary one particle needs around 1 week to be transported over 50 km at a water discharge rate of approximately $250 \text{ m}^3 \text{ s}^{-1}$. In the middle part of the Elbe influenced by the groyne field, water masses take for the same distance and at comparable

Table 3. Characterization of aggregates in the sea, in lakes, estuaries and rivers.

	Sea	Lake	Estuary	River
transport	vertical horizontal	vertical horizontal	horizontal vertical	horizontal vertical
amount	production	production	production erosion hydrographic regime	
size	$\leq 5000000 \mu\text{m}$	$1-10600 \mu\text{m}$	$\leq 5000 \mu\text{m}$	$\leq 1000 \mu\text{m}$
abundance	$0-489 \text{ l}^{-1}$	$0-100 \text{ l}^{-1}$	$\text{max. } 4.0 \cdot 10^3 \text{ l}^{-1}$	$\text{max. } 1.3 \cdot 10^8 \text{ l}^{-1}$
composition	pelagic materials exception: shallow waters		pelagic and benthic materials	
organic content	1 – more than 90%		often <1%	
settling velocity	1–400 m d⁻¹		1–665 m d⁻¹	1–22 m d⁻¹
sedimentation – resuspension	coastal area	shallow lakes	tides lotic systems	often groynes lotic systems

water discharge around 15 hours. Theoretical calculations showed that without groyne fields the same distance will be passed in around 20 hours. Riverine systems with groyne fields produce rapid transport of water masses and, consequently, lead to downstream transport of suspended particulate matter (EIDNER *et al.*, 1996).

Aggregate composition (Table 3) – The aggregates are formed by allochthonous and autochthonous material, which could be either of the pelagic, benthic or terrestrial environment (EISMA, 1993; KIES, 1995; ZIMMERMANN-TIMM, *et al.*, 1998). This is different from the situation in most lakes and in the sea, where aggregates are often dominated by pelagic material (see ALLDREDGE and SILVER, 1988; GROSSART and SIMON, 1993). During his study in the Elbe Estuary HOBURG (1997) observed an enormous input of terrestrial material caused by the transport of large water masses.

Organic content (Table 3) – The large input of benthic material, degraded by benthic microorganisms, often results in an organic content of less than 1% of the dry weight in riverine aggregates (DEGENS and ITTEKKOT, 1984). For the organic matter, a distinction can be made between labile organic material that is easily consumed by microbes and organic material which is refractory. ITTEKKOT (1988) found that up to 65% of the river – supplied organic matter reaching estuaries is refractory.

Aggregate size (Table 3) – It is important to note that riverine aggregates are usually smaller than “lake snow” or “marine snow”. They reach typical sizes of 5000 μm and smaller (see Table 4).

Sedimentation and resuspension (Table 3) – As explained above aggregates interact with resuspension and sedimentation processes in the pelagic and benthic environment. Aggregates and other suspended material can sink out of the flowing waters but during periods of high current velocities they may be resuspend (BERNAT *et al.*, 1996).

2. Sampling of Aggregates

2.1. *In situ* Collection of Aggregates

Investigations of suspended particulate matter have taken on new interest and vigour due to recent changes in the collecting methods and subsequent laboratory analysis. Collection and analysis are no longer carried out by concentration of settled material in sedimentation traps over different depths and time (KRAMER *et al.*, 1994), using equipment which separates particles with different settling velocities (DYER *et al.*, 1996; KERNER *et al.*, 1995), with enrichment by filtration (ETCHEBER and JOUANNEAU, 1980) and concentration of material by centrifugation (KRAMER *et al.*, 1994). All these techniques destroy the typical structure of fragile aggregates and produce a mere mass of organic and inorganic material.

While single aggregates in lakes and in the sea often were collected by scuba-diving, the high concentration of small particles which are more frequent in fast-flowing systems require other methods; one suitable method is to isolate single aggregates with wide-bore pipettes from a horizontal tube (ZIMMERMANN-TIMM, 1999). A refined technique is the optical study of abundance, size and form by camera systems (EISMA, 1993). In combination with computer assisted image analysis these methods yielded *in situ* size spectra of aggregates and their dynamics and have resulted in new insights into the formation, short – and long-term dynamics and fractal geometry of aggregates (CHEN and EISMA, 1995). It appears that there is no significant difference between size measurements of aggregates using image analysis and those obtained conventionally by a Coulter Counter (BILLIONES *et al.*, 1999 a; B. KARRASCH, UFZ Magdeburg (Germany), pers. com.).

Note, that chemical and biological investigations have to be done with suspended aggregates as described in PLOUG and JØRGENSEN (1999), because material that has already settled out may have different exchange processes than suspended particles (PLOUG *et al.*, 1999).

Aggregates, in particular the small aggregates from running waters, have also frequently been pooled, because single aggregates are often too small for reliable chemical or biological measurements. Such pooling tends to underestimate the true values, for example of production measurements, which can be explained by the operation of diffusion processes among the many particles in a pooled sample (GROSSART and PLOUG, 2000). Because of this fact up to now some measurements are limited to large aggregates; this may change in the near future after the development of more sensitive methods.

Fixation is another problem since it often destroys aggregate structure and stimulates the excretion of mucopolysaccharids before the associated organisms die. Fixation may also change the habit of many aggregate – associated protozoans or may lead to their disappearance, thus resulting in underestimation of their numbers in fixed samples (ZIMMERMANN-TIMM, 1999). I, therefore, recommend to perform studies on the abundance, size and composition of aggregates and their associated community with live material.

2.2. *Experimental Formation of Aggregates*

Studies on the experimental production of aggregates from riverine systems are scarce. WÖRNER and ZIMMERMANN-TIMM (2000) and WÖRNER *et al.* (2000) produced aggregates in glass bottles on a horizontal roller and a tilted tube roller to study the formation of different aggregates and their colonization by organisms (see chapter 4). Obviously the hydrodynamics in the bottles are somewhat different from *in situ* conditions. The results so far obtained using experimentally produced aggregates cannot be transferred directly to the natural environment where there are larger size classes and higher numbers of organisms than on aggregates formed in rolling tanks. This is possibly due to the formation of more compact

artificial aggregates, primarily containing pelagic materials (WÖRNER *et al.*, 2000). To better understand the processes of aggregate formation and colonization novel exposition equipment is needed.

3. Occurrence, Abundance, Mass, Size, Composition and Structure of Aggregates

The aggregate content of rivers has received little attention so far, even though high concentrations of suspended inorganic and organic particles are a characteristic feature of many running waters (FINDLAY *et al.*, 1991), and fluctuations in suspended matter influence several important biological and chemical processes in these systems (see chapter 6 and chapter 7).

3.1. Abundance and Mass of Aggregates

The abundance and mass of aggregates depend on several different factors, which determine the number of suspended dead or alive organic particles in an aquatic systems. An increase in the number of suspended particles includes also an increase in their encounter rate in the water column and because of this in aggregation (see chapter 4). The size and the stability of aggregates also depends on the availability of mucopolysaccharids, which glue the different particles together.

Productivity – The productivity of an aquatic environment, which is influenced by the trophic state and season, influences the amount of newly formed particles. A highly productive system is characterised by high primary production and, therefore contains many planktonic and benthic components, which are potential substrata for aggregates (UEHLINGER *et al.*, 1995). A productive system also contains relatively more detritus (UHLMANN, 2001), faecal pellets, and parts of macrophytes.

Input – The importance of allochthonous input (e.g. algae from lakes, reservoirs and tributaries, temporary ponds, macrophytes from the littoral, leaves), that also changes with season, should not be underestimated for the formation of aggregates (VANNOTE *et al.*, 1980; ZIMMERMANN-TIMM *et al.*, 1998).

Resuspension – High discharge rate, current velocity, waves, and various anthropogenic influences (e.g. dredging, water injection) may increase resuspension and erosion and may therefore, also increase the amount of material in the water column (BERNAT *et al.*, 1996; JUNG, 1999; SPOTT and GUHR, 1996).

In most cases the amount of suspended matter was measured after concentration on filters ($\geq 0.45 \mu\text{m}$) or by sampling of settled material collected by sediment traps (KRAMER *et al.*, 1994; DYER *et al.*, 1996; KERNER *et al.*, 1995; ETCHEBER and JOUANNEAU, 1980). Due to this sampling and analytic design, suspended particulate matter has traditionally been quantified as a mass parameter in mg l^{-1} . Consequently, there are more published mass measurements for large rivers than there are publications on abundances or size spectra. Dry weight measurements for large rivers are in the range of 10–100 mg l^{-1} (FINDLAY *et al.*, 1991; HOCH *et al.*, 1995; SCHMIDT, 1994). Compared to the lower River Rhine (Netherlands) and the Elbe Estuary (Germany) the dry weight of suspended particulate matter is between two and six times lower (ADMIRAAL and ZANTEN, 1988; ZIMMERMANN, 1997). Losses on heating are around 70% for Elbe Estuary sediments and after periods of high water discharge the amount of ash – free dry weight increased (HOCH *et al.*, 1995; ZIMMERMANN, 1997). BERGER *et al.* (1996) and ZIMMERMANN (1997) found that the concentration of suspended matter is correlated with discharge rates, but this holds true only before flood crests (Fig. 4). It was also shown, that dry weight and ash-free dry weight corresponded to the number of particles (BERGER *et al.*, 1996; ZIMMERMANN, 1997).

Aggregate abundances and size spectra are available only for the River Danube (BERGER *et al.*, 1996) and the lower and middle part of the Elbe (WÖRNER *et al.*, 2002; ZIMMERMANN, 1997). BERGER *et al.* (1996) reported 1.27×10^5 particles ml^{-1} for the River Danube but did not record dynamic aspects of aggregate abundances. Such data on seasonal and spatial dynamics are currently only available for the lower and the middle Elbe. In this river maxima in aggregate abundance with values up to 4000 aggregates l^{-1} were reached downstream near the salinity gradient between km 675 and km 707 in the Estuary (ZIMMERMANN, 1997). 1200 aggregates l^{-1} were found in the middle Elbe near Magdeburg where the River Saale contributes with high conductivity to the Elbe (WÖRNER *et al.*, 2002). Similar results were found by EINSTEIN and KRONE (1962), MIGNIOT (1968) and WHITEHOUSE *et al.* (1960). Maxima in aggregate abundance of the estuarine and the freshwater part of the River Elbe were observed during spring and summer (Fig. 5).

It seems, that aggregate abundances are higher in these systems than in lakes and in the sea due to high resuspension rates (Table 3). Highly dynamic change and abundance and size redistributions occur within tidal cycles (EISMA, 1993; EISMA and LI, 1993; MILLIGAN, 1995; ZIMMERMANN, 1997). This holds particularly true for the turbidity maximum occurring in tidally affected estuaries at salinities between 2 and PSU as an effect of the residual circulation (EISMA, 1993; CRUMP and BAROSS, 1996; GRABEMANN *et al.*, 1996; FÖRSTNER, 1996; CRUMP *et al.*, 1998). The Elbe turbidity maximum deposits about 1/11 of the mean yearly load of suspended particulate matter, whereas during the Weser turbidity maximum about 1/24 is stored (GRABEMANN *et al.*, 1996). Values of ~ 80000 t suspended matter were recorded for the turbidity maximum in the Elbe. These maxima often include dead organic material since many organisms die due to osmotic stress by the salinity gradient (KIES *et al.*, 1996; SPOONER, 1947). Most of the estuarine turbidity maxima show vertical gradients and these are visible especially after slack water, when high concentrations of suspended particulate matter appear a few decimeters above the river bed (EISMA, 1993). A detailed study was carried out in Chesapeake Bay during the tidal cycle about variation of current velocity and concentration of suspended sediment concentrations in the turbidity maximum. The results showed remarkable differences in the concentration of suspended sediment in the near bottom layer, whereas the surface layer had remained nearly unaffected by the change of the tides (SCHUBEL, 1969). However, no in – depth investigation of such gradients considering aggregates in estuaries and large rivers had been undertaken yet.

3.2. Aggregate Size

Organisms from the pelagic and benthic environment range in size from a few micrometers (*e.g.* picoplankton) to several millimeters (*e.g.* cyanobacterial filaments, crustaceans, macrophytes), depending on the system's trophic state, seasonal phase and geographic region. Aggregates in running waters occur in a size range between $0.45 \mu\text{m}$ and $\sim 5000 \mu\text{m}$. They can be of similar size to aquatic organisms or up to ten times bigger but can be smaller if broken down by mechanical disruption, consumption by detritivores or microbial decomposition. In rivers the main size influencing fact seems to be the mechanical disruption near the surface and in the water column (ARGAMAN and KAUFMAN, 1970; PARKER *et al.*, 1972), therefore most of the aggregates are microaggregates, with a size smaller than $150 \mu\text{m}$. Size spectra of aggregates in large rivers are rare. Large abundances of aggregates in the Elbe Estuary near the North Sea were described above, but larger size classes, up to $5000 \mu\text{m}$, were found upstream in limnetic reaches (Table 4). In the middle Elbe the size spectrum is different. Downstream, with the reduction of current velocity, the percentage of small particles ($25\text{--}50 \mu\text{m}$) decreases in favour of particles larger than $50 \mu\text{m}$ (WÖRNER *et al.*, 2002). BERGER *et al.*, (1996) found particles of $13\text{--}16 \mu\text{m}$ in the River Danube and the Danube Canal near Vienna (Austria). As described for other environments I also found that abun-

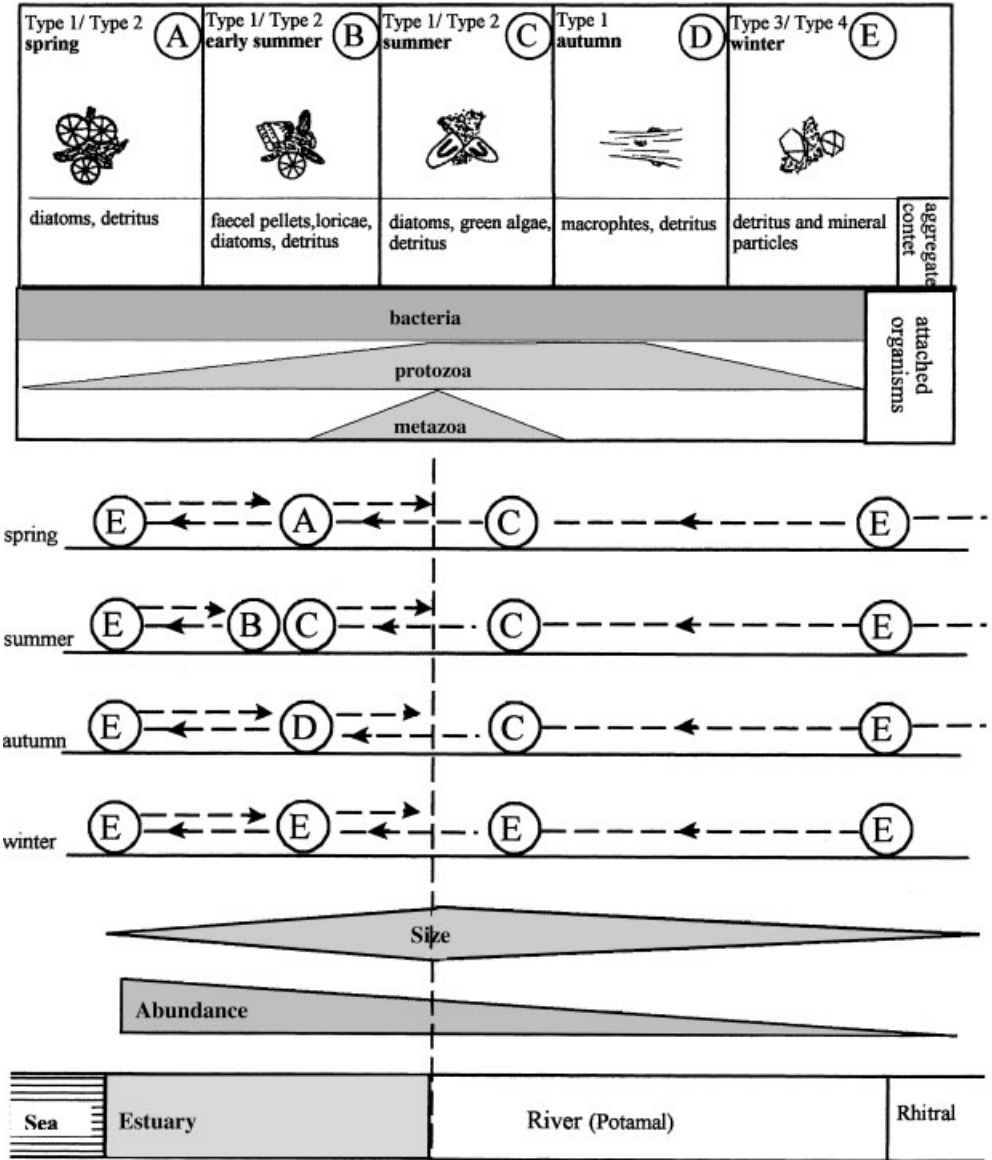


Figure 5. Different aggregate types, seasonal changes, aggregate content and attached organisms and their distribution in the riverine and estuarine environment. There is an increase in size between the river and the estuary and an increase in abundance downstream. See text for further explanation.

dance and size showed an inverse relation in the estuarine and riverine system. Moreover, it appeared that estuarine aggregates compared to riverine aggregates as well as aggregates from areas with high current velocity compared to such with low current velocity (e.g. stream and groyne field), reach larger size classes in environments with longer residence time.

The size spectra being available for riverine and estuarine particles indicate running water particles as smaller than lake and marine- "snow" (Table 3). Although macroaggregates are

Tab. 4. Aggregate size classes in different large rivers and estuaries.

River	Size [μm]	Author
Dan River (March to November)	0.45–25	KONDRATIEFF and SIMMONS (1985)
Danube River (July to December)	13	BERGER <i>et al.</i> (1996)
Danube Canal (July to December)	16	BERGER <i>et al.</i> (1996)
Elbe-Estuary near Hamburg:		ZIMMERMANN-TIMM <i>et al.</i> (1998, 2002)
spring	1100	
early summer	1250	
summer	1200	
autumn	200	
winter	100	
Elbe-Estuary around Glückstadt and downstream:		
spring to autumn	200	
winter	50	
Elbe		WÖRNER <i>et al.</i> (2002)
Geesthacht (km 583) June	max. 1000	
Damnatz (km 510) October	max. 375	
Schnackenburg (km 475) August	max. 375	
Havelberg (km 422) July	max. 500	
Magdeburg (km 317) April	max. 500	
Ria de Aveiro (January to December)	1–140	ALMEIDA and ALCANTARA (1992)
Saale		ZIMMERMANN-TIMM, BREITENBACH and GÄRTNER
Jena	max. 16240	

also found in estuarine waters, they are still smaller than those in lakes and in the sea due to much higher shear rates. These shear rates lead to disaggregation, and approx. 5000 μm is the maximum size described for estuarine environments (Tables 3, 4). In the Elbe Estuary the abundance of these large aggregates was between 20 and 4000 l^{-1} . Larger aggregates are probably formed only around slack tide (VAN LEUSEN, 1996) when the bed shear stress decreases below the critical level required for disaggregation. It is remarkable that the aggregate size decreases toward the sea (ZIMMERMANN, 1997). In the estuarine and riverine environment a pronounced seasonal variance occurs with smaller aggregates in fall and winter. The size of macroaggregates is positively related with phytoplankton biomass (ZIMMERMANN, 1997). But on a temporal and vertical scale, abundances of macroaggregates often lack behind phytoplankton growth, peaking at the end of diatom blooms. While diatom blooms in lakes and in the sea are often terminated by aggregation events (RIEBESELL, 1991a, 1991b) and sink out, we frequently find changes between sedimentation of algae incorporated into aggregates (*e.g.* *Actinocyclus normanii* (GREGORY EX GREVILLE) HUSTED 1957) and resuspension of single cells in estuaries and rivers (GÄTJE, 1992; ORTHEGA and STEEGE, 1995; WOLFSTEIN, 1996). It rarely happens that phytoplankton does accumulate on the ground (CHRISTIANSEN and HAAR, 1991). According to KIES *et al.* (1996) increasing salinity

produces more free living algae to be incorporated in aggregates. I can not support these findings. As explained above and in chapter 5, in the estuarine and riverine environment of the Elbe, the River Rhine and the Zaire River Estuary a decrease in aggregate size and can be found following an increase in salinity.

3.3. Aggregate Sinking Rate

Particles are suspended in the aquatic environment, if the hydrodynamic frictional forces are larger than the gravity. This is the case in running waters with turbulent and laminar currents (NEISS, 1994).

Considering DYER (1989) and TEN BRINKE (1996) the settling rate increases as a function of particle diameter. This can be offset by a lower density of the aggregates as compared to the original constituent particles when the larger aggregates have a higher content of organic matter, e.g. by the inclusion of organic particles, and/or more water. KRONE (1978), RILEY (1970), KAJIHARA (1971), TAMBO and WATANABE (1979), HAWLEY (1982), MC CAVE (1984) and GIBBS (1985) have indicated that the density of aggregates decreases with increasing size.

Also important is the composition of aggregates, influencing their sinking velocity. The composition shows seasonal changes (Table 4). Aggregates consisting of many mucopolysaccharids, blue – greens, faecal pellets and detritus show smaller sinking rates than those, including diatoms or inorganic particles (Table 3; GROSSART *et al.*, 1997; ZIMMERMANN-TIMM *et al.*, 1998). This can be explained by the density of the different components: mineral particles (quartz, feldspars, clays) have a density of ca. 2.65, calcium carbonate 2.7, opal frustules ca. 1.8, and organic matter (mainly carbohydrates, humic and fulvic acids and fatty acids) ca. 1.3. The volume of enclosed water is usually not known. According to KOZERSKI *et al.* (1991) and PROCHNOW *et al.* (1996) seasonal differences in the settling velocity of the River Spree were apparently not important. These findings differ, however, from measurements in estuaries, lakes and the sea (ALLDREDGE and SILVER, 1988; GROSSART, 1995; WOLFSTEIN, 1996), where changes in the aggregate composition were visible in different settling velocities resulting in seasonal changes among them. For bigger particles with a density considerably higher than that of water, several different aspects contribute to the settling velocity: besides size, shape and density it is mainly the particles surface roughness. In laboratory measurements it was found that the settling velocity is related to the particle concentration and that after a critical concentration the velocity is reduced (MEHTA, 1989). The sinking rates of aggregates in the estuarine environment range between 1 and 665 m day⁻¹ (KINEKE *et al.*, 1989; VAN LEUSSEN and CORNELISSE, 1992; STERNBERG *et al.*, 1986; ZIMMERMANN-TIMM *et al.*, 2002) and in the riverine environment between 1 and ~22 m d⁻¹ (PUSCH *et al.*, 2001). Sinking rates determined *in situ* were lower than those determined in settling chambers (MEHTA, 1989) since net sinking rates *in situ* are affected by turbulences and orbital motions, which are most pronounced close to the water surface.

Settling aggregates in a turbulent flow have to pass the more turbulent near – bottom layer and having passed without breakup and reentrainment into the main flow, they settle into the viscous sublayer. In this sublayer the velocity gradient is more or less constant and the shear being controlled by the viscosity of the water. At a rough ground, the entrapment of flocs in the sublayer will be not constant, but as soon as enough aggregates have been deposited, the bottom roughness will be reduced and the thickness of the sublayer (which is in the order of 0.5–1.0 mm) increases two to five times (GUST, 1976) and the entrapment of aggregates is enhanced. A very rough bottom, such as gravel or coarse sand, may allow some entrapment of aggregates between the grains or stones where the sublayer is thicker. But it may not necessarily result in the development of a mud deposit, so that “muddy gravel” or “muddy coarse sand” can be found. This is an indication for a critical relation between flow

characteristics, bottom roughness, suspended matter concentration and average particle settling rate, which in turn determines whether deposition will occur, or whether the formation of a mud deposit is stopped in an early stage (EINSTEIN and KRONE, 1962; HUNT, 1986; MC CAVE, 1970; MC CAVE and SWIFT, 1976).

3.4. Composition of Aggregates

The composition of aggregates in running waters includes autochthon (chapter 3.4.1.) and allochthon material (chapter 3.4.2.), which reflects the particle spectrum in the water column, the sediment and the terrestrial environment (Table 3; WÖRNER *et al.*, 2002; ZIMMERMANN-TIMM *et al.*, 1998).

Estuarine and riverine aggregates may contain:

1. non-living geogenic components (quartz, feldspar, mica, clay minerals, etc.),
2. occasional anthropogenic components (*e.g.* flying ashes),
3. non-living biogenic material (biogenic opal, *i.e.* mineral-bound or water-suspended silic acid; biogenic calcite),
4. attached or associated organisms (algae, bacteria, fungi, protozoa and metazoa),
5. macrophytes, stem remains
6. detritus, dead and dying organic material (VELMIROV, 1991), whose origin cannot be classified visually.
7. faecal pellets, mainly produced by metazoans.

The components named in points 1–7 loosely united into aggregate particles (BÖCKELMANN *et al.*, 2000; KIES *et al.*, 1996; KOZERSKI *et al.*, 1991; PROCHNOW *et al.*, 1996; WÖRNER *et al.*, 2002; ZIMMERMANN-TIMM *et al.*, 1998), are held together by sticky, hydrated, matrix substances. As explained in chapter 3.4.1. these substances are produced mainly by algae and bacteria. They consist of acidified polysaccharides (KIØRBOE and HANSEN, 1993; KIES, 1995), which are suspended, and thus released from their producers, into the aquatic environment. Comparing the composition of “marine snow”, “lake snow” and aggregates from running waters it is obvious, that estuarine and riverine aggregates are build up by a large part of benthic material (Table 3).

Considering the aggregate composition, aggregate types can be distinguished in the longitudinal profile of running waters and during different seasons. First examinations in the riverine environment showed compared to lower reaches only small differences in the content of aggregates along the longitudinal profile of the middle Elbe (Table 5; WILTSHIRE *et al.*, 1996; WÖRNER *et al.*, 2002; ZIMMERMANN, 1997). It might be that the longer retention time of water in the estuary causes this change in composition (BERGEMANN *et al.*, 1996). The seasonal fluctuations are associated with aggregate types typical for spring, summer, autumn and winter aggregate types (BÖCKELMANN *et al.*, 2000; ZIMMERMANN-TIMM *et al.*, 1998).

Recent studies about “marine snow” and “lake snow” did not consider the composition of microaggregates. WÖRNER *et al.* (2002) were able to show, that microaggregates may not differ from macroaggregates in composition.

3.4.1. Autochthonous Material

As described above the primary productivity affects the supply of different organic material as building block of aggregates. A high primary production may be responsible for a high number of autotrophic organisms yielding in high numbers of both consumers and mineralizers.

Table 5. Different kinds of colonization of aggregate – associated organisms. Obligate associated organisms only live on aggregates, the others are facultatively associated.

Organisms	Aggregate	Interface	Pelagic Environment
Ciliophora			
<i>Acinertia uncinata</i> TUCOLESCO, 1962	+		
<i>Askenasia</i> sp.	+	+	+
<i>Aspidisca cicada</i> (MÜLLER, 1786) CLAP. & LACHM., 1858		+	
<i>Aspidisca</i> sp.	+	+	
<i>Balanion</i> sp.	+	+	+
<i>Carchesium polypinium</i> (LINNAEUS, 1758) EHRENBERG, 1830	+		
<i>Chilodonella uncinata</i> (EHRENBERG, 1838) STRAND, 1928	+	+	
<i>Cinetochilum margaritaceum</i> EHRENBERG, 1838	+	+	+
<i>Coleps hirtus</i> MUELLER, 1786, NITSCH, 1827	+	+	+
<i>Colpoda steinii</i> MAUPAS, 1883	+		
<i>Cyclidium glaucoma</i> MÜLLER, 1773	+		+
<i>Cyclidium citrullus</i> COHN, 1865	+	+	+
<i>Dendrosoma radians</i> EHRENBERG, 1837	+		
<i>Didinium</i> sp.	+	+	+
<i>Euplotes</i> sp.	+	+	
<i>Frontionia</i> sp.	+	+	
<i>Glaucoma scintillans</i> EHRENBERG, 1830	+	+	
<i>Halteria</i> sp.	+	+	
<i>Heliophrya rotunda</i> (HENTSCHEL, 1916) MATTHES, 1954	+		
<i>Litonotus</i> sp.	+	+	
<i>Lohmaniella</i> sp.	+	+	
<i>Paradileptus elephantinus</i> (ŠVEC, 1897)	+	+	+
<i>Stentor coeruleus</i> (PALLAS, 1766) EHRENBERG, 1831	+	+	+
<i>Strobilidium caudatum</i> (FROMENTEL, 1876) FOISSNER, 1987	+	+	+
<i>Strobilidium</i> sp.	+	+	+
<i>Strombidium</i> sp.	+	+	+
<i>Stylonichia mytilus</i> complex	+		
<i>Tachysoma pellationellum</i> (MÜLLER, 1773) BORROR, 1972	+		
<i>Tintinnidium fluviale</i> – <i>pusillum</i> complex	+	+	
<i>Tintinnidium</i> sp.	+	+	
<i>Tintinnopsis cylindrata</i> KOFOID and CAMPBELLI	+	+	
<i>Uronomea nigricans</i> (MÜLLER, 1786) FLORENTIN, 1901	+	+	
<i>Urotricha</i> sp.	+	+	
<i>Vorticella campanula</i> EHRENBERG, 1831	+		
<i>Vorticella convallaria</i> complex	+	+	
<i>Vorticella octava</i> complex	+	+	
<i>Vorticella picta</i> (EHRENBERG, 1831) EHRENBERG, 1838	+		
<i>Vorticella microstoma</i> -complex	+	+	
Flagellates			
<i>Anisoema</i> sp.	+		
<i>Bicosoeca</i> sp.	+	+	
<i>Bodo designis</i> SKUSA	+	+	

Table 5. Continued

Organisms	Aggregate	Interface	Pelagic Environment
<i>Bodo saltans</i> EHRENBERG, 1838	+	+	
<i>Bodo</i> sp.	+	+	
<i>Bodomorpha minima</i>	+	+	
<i>Cafeteria</i> sp.	+		
<i>Cercomanos</i> sp.	+	+	
<i>Ceratium</i> sp.	+	+	+
<i>Chrysamoeba</i> sp.	+		
<i>Codonosiga</i> sp.	+	+	+
Cryptomonadida	+		
<i>Diplophrys archeri</i> BARKER	+	+	+
<i>Euglena viridis</i> EHRENBERG, 1830	+		
<i>Goniomonas</i> sp.	+		
<i>Kentrosiga thienemanni</i> SCHILLER, 1953	+	+	
<i>Kittoksia</i> sp.	+		
<i>Monosiga ovata</i> KENT, 1890	+	+	
<i>Paraphysomonas</i> sp.	+		
<i>Peranema</i> sp.	+		
<i>Petalomonas</i> sp.	+		
<i>Protaspis</i> sp.	+	+	
<i>Pseudobodo</i> sp.	+	+	
<i>Rhynchomonas</i> sp.	+		
<i>Rhynchomonas nasuta</i> (STOKES, 1888). KLEBS, 1893	+		
<i>Spiromonas</i> sp.	+	+	+
<i>Spumella</i> sp.			
<i>Thaumatomastix setifera</i> LAUTERBORN, 1899	+		
<i>Thaumatomonas</i> sp.	+		
<i>Tetramitus</i> sp.	+		
Rhizopoda			
Amoebida			
Hartmanellidae	+		
<i>Nuclearia</i> sp.	+		
Vahlkampfiidae	+		
<i>Vanella</i> sp.	+		
Testacea			
<i>Cochliopodium</i> sp.	+		
Rotifers			
<i>Anuraeopsis fissa</i> (ROUSSELET, 1910)		+	+
<i>Keratella cochlearis</i> (GOSSE, 1851)		+	+
<i>Keratlia cochlearis</i> var. <i>tecta</i> (LAUTERBORN, 1900)		+	+
<i>Notholca squamula</i> (MÜLLER, 1786)		+	+
<i>Notholca acuminata</i> (EHRENBERG, 1832)		+	+
<i>Notholca labis</i> (GOSSE, 1887)		+	+
<i>Pompholyx sulcata</i> (HUDSON, 1885)		+	+
<i>Pompholyx triloba</i> (PEJLER, 1957)		+	+
<i>Trichocerca pusilla</i> (LAUTERBORN, 1898)		+	+
Mollusca			
<i>Dreissena polymorpha</i> (PALLAS, 1771)	+	+	+
Nematodes	+	+	+
Turbellaria			
<i>Haloplanella obtusituba</i> LUTHER, 1946	+		

Planktonic algae – An important autotrophic component are the algae, where we have to distinguish between planktonic and benthic forms. Studies on aggregates show, that compared to the surrounding water aggregates are often enriched with planktonic algae (about 20–30%; WOLFSTEIN, 1996). In fact algae, especially diatoms and colonies of blue greens, are important in the formation of aggregates and their biomass is positively correlated with aggregate size. Therefore a large amount of macroaggregates co-occurs during high abundance of these algae (KOZERSKI *et al.*, 1991; PROCHNOW *et al.*, 1996; ZIMMERMANN-TIMM *et al.*, 1998). The contribution of living planktonic algae to particulate organic carbon (POC) varies longitudinally, and seasonally in the Elbe estuary (Fig. 5). Maximum rates appear during late summer with a range from 1 to 69% of the aggregate POC built up of phytoplankton (WOLFSTEIN and KIES, 1995). In contrast, the Ems Estuary (Germany) where phytoplankton numbers are lower (especially diatoms; BRUNHOEBER, 1990), contains fewer exopolymeric substances and thus a low amount of organically formed aggregates can be found (GRESIKOWSKI *et al.*, 1996). Most of these algae use special strategies to bind to other particles: there are spines, which cause a mechanical connection (f.e. *Stephanodiscus* spp., *Scenedesmus* spp.; KJØRBOE *et al.*, 1990) and there are processes (dissolved and particular exopolymeric substances; BERNHARDT *et al.*, 1989; DECHO, 1990), which determine the stickiness. It is known, that the formation of mucopolysaccharids is depending on the physiological state of algae (MYKLESTAD *et al.*, 1989). Physiological stress such as increasing conductivity leads to an increase of the production of mucopolysaccharids (DECHO, 1990).

Microphytobenthos – Due to the current velocity near the bottom ($>0.05 \text{ m sec}^{-1}$) the amount of phytobenthic material increases in the water column. Beside this the percentage of eroded material depends on the phytobenthos composition: a high amount of diatoms is causing a high amount of mucopolysaccharids and thus increasing the stability of the sediments (DIERKS, 1995; HUMANN, 1995; MADSEN *et al.*, 1993).

Macrophytes – Microscopical studies (ZIMMERMANN-TIMM *et al.*, 1998) and one detailed study with chemical analysis (HOBERG, 1997; ZIMMERMANN-TIMM *et al.*, 2002) showed, that macrophytes from the littoral are also involved in the composition of aggregates. Microscopic and chemical analyses of estuarine aggregates in the Elbe, indicated that substantial amounts of their POC content consisted of macrophyte debris (more than 60% remain in the estuary), especially during autumn and winter, with lignin likely to reflect the microbial decomposition. In this case a comparison with other systems is difficult, however, since only one study has considered changes in the lignin content and cellulose composition of aggregates.

Faecal pellets – Most of the observed faecal pellets are produced by metazoans, particularly by copepods, and these copepods follow peaks of centric diatoms. According to this correlation we find a high number of faecal pellets in aggregates during spring and summer, mainly in the estuarine environment, where phytoplankton is controlled by herbivorous crustaceans.

Mineral particles – Another typical component of aggregates are mineral particles, which were mainly found during high water discharges and remarkable current velocities. The input of mineral particles, rises up to 99% with water discharge. In Vågåvatn, 60–80% of the suspended sediments were composed of silt and clay but changes in the grain size of suspended sediments were poorly correlated with water discharge though showing considerable temporal and spatial changes (ELSTER *et al.*, 1996).

3.4.2. Allochthonous Material

Leaves, branches and wood - Leaves, branches and wood of the shorelands are also a typical substrate for aggregates. They all are important in small running waters with forest, but

of decreasing relevance with increasing width of the river. Young coarse material (>1 mm) has higher C : N rates than fine and already decomposed material (BOLING *et al.*, 1975, KING *et al.*, 1987; NAIMAN, 1983; WALLACE *et al.*, 1982). In running waters of the order 1 the POM input is around 307–534 g ash free dry weight m⁻² whereas in rivers of the order 6, this is between 15 and 17 g ash free dry weight m⁻². Taking this fact into account about 85–97% of the POC in large rivers are autochthon materials (CONNERS and NAIMAN, 1984) and allochthonous material is of less importance.

Terrestrial arthropods – Also the input of terrestrial arthropods, falling from trees into the water has been underestimated (NELSON, 1965). Occasional terrestrial insects were found in the potamal of the Elbe, but no investigation about their importance as aggregate building block as been undertaken so far.

Mineral particles – After heavy rainfall or thaw sediments originating from the terrestrial environment can occur in running waters. Before they sediment out they are suspended in the water column. To my knowledge investigations about suspended terrestrial and fluvial sediments are not available.

3.4.3. Elemental Composition of Aggregates

The elemental composition of aggregates has so far been reported only from macroaggregates since it has not yet been possible to analyse microaggregates because of their small size. Investigations from the estuarine environment showed, that the dry weight and POC of single aggregates are greater in the limnetic than in the seaward Elbe during spring and summer. Values of 15–51 ng POC aggregate⁻¹ were recorded in the estuary and the largest values were found in the limnetic reaches. The C:N ratio (w:w) ranges between 7:1 and 12:1 describing a positive function of aggregate size to the energy content of single aggregates lying between 1003 and 1375 J g⁻¹ dry weight. In the Elbe estuary lipids made up 2–3%, and proteins 10–30% of the ash-free dry weight of single aggregates from the limnetic environment in spring and winter. GRESIKOWSKY *et al.* (1996) showed with their measurements of protein and carbohydrate in the Ems that there are also spatial differences. The content was higher in the freshwater than in the brackish environment and higher at the bottom than at the surface.

The findings about the elemental composition indicate that aggregates are likely to be adequate food for aquatic animals (see chapter 7). However, the suspended particles differ in quality and low substrate quality is indicated by high respiration rates in combination with high ectoenzymatic activities (PLOUG *et al.*, 1999; see also chapter 6).

Only little information is available about the dominant biopolymers of aggregates although carbohydrates, proteins (or particulate combined amino acids, PCAA) and lipids constitute the majority of the aggregate – bound POM.

Examination of the exopolymeric substances, the “glue” holding aggregates together, showed that proteinaceous and lipid substances are only found within living or moribund cells. It is most likely that these substances become readily metabolized after algal cells have lysed. Hexoses, acid mucopolysaccharides and carboxyl groups were also found in estuarine aggregates. Many aggregates also contain sulfonated polysaccharides which are produced by diatoms (KIES *et al.*, 1996).

In some recent studies aggregate composition has been examined by epifluorescence microscopy after staining with compound specific dyes. In particular, fluorescent lectins examined by confocal laser scanning microscopy supported to detect details of aggregate composition including methyl α -D-mannopyranoside, D (+) mannose, D (+) galactose, α -methyl-D-mannopyranoside D (+) mannose, N-acetylneuraminic acid, D-glucuronic acid, L (-) fructose N-acetyl-D-glucosamine (NEU, 2000).

3.5. Aggregate Structure and Dimensions

Observations of the natural aggregate structure in the marine (TRENT *et al.*, 1978), estuarine (EISMA *et al.*, 1983; ZIMMERMANN-TIMM *et al.*, 1998) and limnetic environment (GROS-SART *et al.*, 1997; WÖRNER *et al.*, 2002) are limited. To understand the structure of aggregates, they were collected by EISMA *et al.* (1983) in the Ems Estuary and by WÖRNER *et al.* (2002) and ZIMMERMANN-TIMM *et al.* (1998) in the Elbe. The following types have been found:

Type 1 – Loose, apparently unstructured mixture of organic matter and mineral particles including biogenic particles such as diatom frustules and frustule fragments, green or blue – green algae, faecal pellets of copepods, loricae of tintinnids, parts of macrophytes and detritus ($>150\ \mu\text{m}$).

Type 2 – Compared to type 1, this type shows a more or less layered dense mixture but otherwise the same composition.

Type 3 – Densely packed layered mineral particles and detritus ($<150\ \mu\text{m}$), they are often spherical.

Type 4 – Only detritus densely packed (in most cases $<150\ \mu\text{m}$), they are often spherical.

The aggregates structure changes with the season (Fig. 5), indicating that type 1 and type 2 are visible from spring to autumn in the limnetic environment of our running waters, but a dominance of type 1 is visible in the estuary. Type 3 aggregates are visible during winter and autumn in the riverine and estuarine environment and during flood. Type 4 is suspended in the water column during the whole year with maximum concentrations during winter. Comparing aggregates in the longitudinal profile of running waters (Fig. 5) a dominance of type 1 and type 2 can be observed in the limnetic part and with increasing salinity particles of type 3 and 4 dominate the aggregate spectrum.

Information on the structure of particles in rivers of the order 3 and less are not available, but considering MINSHALL *et al.* (1985) and VANNOTE *et al.* (1990) I suspect more coarse and fine macrophyte fragments (SCHÖNBORN, 1992; LAMPERT and SOMMER, 1993).

The structure of aggregates in running waters has been described by fractal geometry (CHEN and EISMA, 1995): the mass or number of component particles (N) and the characteristic length scale of the aggregates (l) are related according to the function $N \sim l^{D_n}$ where D_n (D_1, D_2, D_3), a non-integer between 1 and 3, is the fractal dimension of the aggregate and a function of the perimeter ($P \sim D_1$), the area ($A \sim D_2$), or the volume ($V \sim D_3$). Only when D_n is an integer the aggregate has Euclidian geometry, e.g. $D_3 = 3$ for a sphere. Aggregates in the Elbe estuary have D_1 of 1.41 and D_2 of 1.81 (BILLIONES *et al.*, 1999 b; CHEN and EISMA, 1995). Fractal geometry allows estimation of aggregate porosity, *i.e.* inner surface area, which is inversely related to the fractal dimension.

Many aggregate – associated microorganisms, moving through the aggregate, are responsible for porosity (see chapter 5). For example: the ciliate *Stentor coeruleus* (PALLAS, 1766) EHRENBERG, 1831 is able to move its basal parts through the aggregates and to form hollow spaces. Something similar could be observed with metazoans like the rotifer *Keratella* spp. or some copepods. The formation of these pores is important in controlling the aggregates sinking rate, the water flux through the aggregate relative to the surrounding water and, in consequence, the flux of nutrients and substrates to and from microorganisms colonizing the aggregate surface.

4. Generation of Aggregates

The physical, chemical and biological processes that form aggregates from suspended organic and inorganic material have previously been described and reviewed for different marine and limnetic environments. Most of these processes are also important for riverine

systems (EISMA, 1993; JOHNSONS *et al.*, 1994; O'MELIA, 1987; STUMM *et al.*, 1994). The above mentioned authors emphasize that aggregation is a complex process that is controlled by three variables:

Particle concentration – The larger the abundance of microaggregates the more frequently they collide. It can be expected that at very low concentrations no flocculations occur because the collision frequency is too low. In the Mahaham river plume, aggregates were observed in concentrations as low as 0.1 to 0.3 mg suspended particulate matter l⁻¹ (EISMA, 1993).

Stickiness of particle surface – Organisms (e.g. bacteria and phytoplankton) exude organic substances (polymers) and produce mucus that acts as “glue” (SEKI, 1972; PAERL, 1973, 1974; ALLDREDGE, 1984; BIDDANDA, 1988).

Velocities – Such as means shear and differential settling velocities (DIERKS, 1995; PATERSON, 1994; WETZEL, 1983).

Probability of attachment – Probability of particles to coalesce once they have collided. Although adherence coefficients have been calculated for marine environments they are, however, not available for other systems (MCCAVE, 1984).

4.1. Physical and Chemical Processes

The following processes cause the collision of suspended particles:

Brownian motion – The movement and collision of particles smaller than 8 µm under the influence of heat energy induced motion of water molecules (EISMA, 1993; HUNT, 1980; MCCAVE, 1984).

Shear forces – The strength of laminar and turbulent shear determines the frequency and the push of particles. For a successful collision the distances of the flow streamlines have to be smaller than the sum of the particle radii. This mechanism is particularly important for particles ≥ 8 µm in the wind-influenced surface layers and in the water – sediment contact zone in riverine and estuarine systems. It is known that high energy dissipation rates of 10⁻⁷ to >10⁻⁴ m⁻² s⁻³ lead to disaggregation or size reduction of aggregates (ALLDREDGE *et al.*, 1990; EISMA, 1993; HUNT, 1980).

Differential settling – This mechanism is depending on aggregate composition (chapter 3.3.), size (chapter 3.2.) and abundance (chapter 3.1.) and results in the generation of larger particles during horizontal transport. Rapidly settling particles can overtake and intercept those sinking more slowly and as described for shear above will collide if the distances of their flow streamlines are smaller than the sum of the particle radii. Through this mechanism large and more rapidly sinking particles scavenge small particles (HUNT, 1980; JACKSON, 1990; LAL, 1980; KEPKAY, 1994; MCCAVE, 1984). Differential settling is important in the estuarine environment during slack tide (JUNG, 1999) and in slowly flowing areas, such as groyne fields and riverside meadows of large rivers.

Filtration – Theoretical studies of fluid dynamics have shown that highly porous aggregates may experience interstitial water flow when they are sinking. Smaller particles, nutrients and colloid particles are collected and included on this way. A high mucopolysaccharid content may limit advection through aggregates, however, (JOHNSON and WANGERSKY, 1985; LOGAN and ALLDREDGE, 1989; LOGAN and HUNT, 1987; STOLZENBACH, 1993) and, although this phenomenon has as yet been described only for marine environments, it may be important in estuaries during slack tide and on the slow flowing reaches of rivers.

Bubbling surface coagulation – Gas bubbles are released from sediments and rise through the water column until they burst or collapse. Particles concentrate at the border between gas and liquid are thus transported as aggregates through the water column (EISMA, 1993; JOHNSON *et al.*, 1986; MARI, 1999; MOPPER *et al.*, 1995; RILEY, 1963; ZHOU *et al.*, 1998). Experiments by JOHNSON and COOKE (1980) indicate that aggregates up to 32 µm in diameter

are formed by such bubbles. This phenomenon is also important in running waters, especially in zones with anaerobic sediments. It is an open question, whether bubbles formation by escaping organisms in rivers is important or not (EISMA, 1993).

More important is the formation of bubbles formed by waves breaking at the surface. It was described for the open sea, that they can move downwards to a maximum depth of 20 m (EISMA, 1993). Their influence in rivers, e.g. during ship passage, was not studied up to now. Information about the inclusion of bubbles in weirs and ship's propellers are also not available.

Precipitation, polymerisation and adsorption – Particles may gain material by the precipitation of dissolved organic and inorganic substances onto them, the polymerisation of such materials with existing particle components or by the adsorption of substances by the particle surface (JANNASCH, 1973; SIEBURTH, 1965). Several authors have noted that the addition or loss of dissolved organic matter from the aggregation is dependent on quality (EISMA, 1993; GERRITSEN and BRADLEY, 1987; GIBBS, 1983; JOHNSON *et al.*, 1994; ZUTIC and TOMAIC, 1988).

Surface properties – Particles or aggregates have attractive or repulsive surface properties, depending on size, composition and chemical coating. Most particles are negatively charged at the surface because the adsorbed organic material carries many carboxy or hydroxy groups (GIBBS, 1983; JOHNSON *et al.*, 1994; O'MELIA, 1987; STUMM *et al.*, 1994). In the marine environment different surface properties, depending on physiological state as well as microbial colonization, determine selective aggregation of diatoms during phytoplankton blooms (ALLDREDGE *et al.*, 1995; ALLDREDGE *et al.*, 1998; PASSOW *et al.*, 1994; RIEBESELL, 1991a, 1991b). In running waters the surface properties change with the seasons and along the longitudinal profile of the river. Downstream, where a large number of phytoplankton and bacteria can be found, the surface properties support the aggregate formation. The physiological state of the surface is affected by seasonal changes (e.g. temperature, nutrients) but also by waste, passing weirs or when reaching the salinity gradient in the estuarine environment.

Bridging with divalent cations – Positive cations act as chemical bridging agents enhancing the attraction and adhesive properties of electronegatively charged particles. They are important in mediating the aggregation of these particles and are also an important reason for aggregation in salty areas like estuaries or polluted rivers (EDZWALD, 1972; EISMA, 1993; SCHOFIELD and SAMSON, 1954; STUMM *et al.*, 1994; VON OLPHEN, 1963; WÖRNER *et al.*, 2000). In the River Rhine aggregation could be explained by pollution of the river with salts discharged from the potassium and coal mines (SANTEMA, 1953) but it became apparent that also other factors were involved (organisms, natural organic compounds, and cellulose fibers discharged from the paper industry). According to many authors (EISMA *et al.*, 1991; MEADE, 1972; MANHEIM *et al.*, 1972; FEUILLET and FLEISCHER, 1980) there is no clear evidence for salt – flocculation at the contact zone of fresh and salt water. GIBBS *et al.* (1989) concluded that a salinity effect occurred in the Grionde but this was based on only one freshwater sample. Investigations from the Elbe, Ems, Rhine and Zaire River Estuary support, however, this hypothesis; nevertheless laboratory studies on this topic are necessary (EISMA, 1993; ZIMMERMANN, 1997).

Spontaneous coagulation of dissolved organic matter – Spontaneous coagulation from the dissolved phase can form colloidal material, submicron particles and eventually also micro-aggregates (CHIN *et al.*, 1998; KEPKAY, 1994; MARI and BURD, 1998; PASSOW, 2000). These processes have, however, only been described for the marine environment and their role in other systems is unclear.

4.2. Biological Processes

Mucopolysaccharids – Many authors (e.g. ALLDREDGE *et al.*, 1993; AVNIMELECH *et al.*, 1982; DECHO, 1990; RILEY, 1963; RILEY, 1970; STODEREGGER and HERNDL, 1999) showed, that diatoms and bacteria secrete large amounts of slime (polysaccharids and other polymers) on submerged surfaces which enhance the stickiness of the particle surfaces. This phenomenon was also observed for large rivers and estuaries, especially during typical riverine diatom blooms (KIES, 1995; WÖRNER *et al.*, 2000; WÖRNER *et al.*, 2002; ZIMMERMANN-TIMM *et al.*, 1998).

Biological capture – Zooplankton capture food particles and thus aggregating such particles in the filtering apparatus or cell mouth. These processes also help to structure the composition of aggregates in different environments (see chapter 2.3.; LAMPITT *et al.*, 1993; NYGAARD, 1995; Wörner *et al.*, 2000).

Defecation of zooplankton – In all aquatic environments zooplankton produce faecal pellets which consist of densely packed micro- or macroaggregates surrounded by a peritrophic membrane. These faecal pellets can stick to other aggregates or directly sink to the sediment (LAMPITT *et al.*, 1993; WÖRNER *et al.*, 2000; ZIMMERMANN-TIMM *et al.*, 1998).

Moult of zooplankton – The exuviae and dead bodies of zooplankton as well as the loricae of tintinnids are occasionally important components of aggregates in running waters. Some exuvial structures (e.g. spines) can favour coagulation (ZIMMERMANN-TIMM *et al.*, 1998).

Bacterial aggregates – To minimize grazing pressure by bacterivorous protozoa aggregation of bacteria is well known in both lakes and the marine environment (JÜRGENS and GÜDE, 1994). Investigations in running waters are scarce (K. JÜRGENS, MPI Plön (Germany), personal communication).

5. Colonization of Aggregates through...

Micro- and macroaggregates in lotic systems are colonized by bacteria, protozoa and metazoa (ALMEIDA and ALCANTARA, 1992; KONDRATIEFF and SIMMONS, 1985; PALUMBO *et al.*, 1984; WÖRNER *et al.*, 2000; ZIMMERMANN and KAUSCH, 1996). The colonization of aggregates can be active or passive. Active colonization requires organisms moving directly towards the aggregate. Such movement has been observed in nature and under experimental conditions for protozoa (KAKUSCHKE, 1999), rotifers, copepods and the veliger larvae of *Dreissena polymorpha* (ZIMMERMANN-TIMM *et al.*, 1998). Passive colonization of aggregates proceeds for a number of different reasons: Organisms are occasionally resuspended from the sediment in highly turbulent areas, or they derive from the pelagic environment under turbulent conditions or during processes with high sedimentation rates.

To characterise colonization two types of organisms have to be distinguished: obligately and facultatively associated organisms (Table 5). Obligately associated organisms need a substrate in order to be able to move and to feed. Many flagellates and amoeba fall into this group and they leave the aggregates after more than 60 sec. Facultatively associated organisms are associated to a particle for only a short time (≤ 60 sec), they take attached organisms as food, leave the aggregate and swim actively to the next (ZIMMERMANN-TIMM *et al.*, 1998).

The colonization of particles by organisms can vary and has been attributed to the following characteristics:

Physical characteristics:

Salinity – The number and the composition of aggregate – associated assemblages were obvious in different salinity gradients. A decline in the number of organisms per aggregate was proven along a gradient from the freshwater to the salty environment. After conduc-

tivity concentrations had 2- to 10-fold increased (starting point was around $200 \mu\text{S cm}^{-1}$) bacteria (SCHWEIZER, 1998) and protozoa (WÖRNER *et al.*, 2002; ZIMMERMANN, 1997) showed a reduction in the colonization of about 50%.

Moreover, both groups showed changes in the composition. In the limnetic environment the bacterial structure was dominated by β -Proteobacteria and cells of the *Cytophaga*/Flavobacteria whereas in an environment with higher conductivity γ -Proteobacteria were abundant (SCHWEIZER, 1998). Those γ -Proteobacteria are also known from the marine environment. Concerning protozoa in the salty environment changes in the composition were observed due to an increase of flagellates of both groups Biosocida/Thaumatomonadida and oligotrich ciliates.

These statements were based on observations of the natural environment, including variations of other parameters (e.g. increase of aggregate number due to increase of salinity). Further investigations under controlled experimental conditions are necessary. The fact that in salty environments nearly all protozoa (about 95%) were associated with aggregates with a developed mucopolysaccharide matrix may indicate, that these organisms (Ciliates: Hymenostomata and Hypotrichia; Flagellates: Kinetoplastida and Thaumatomonadida) are able to survive the salt stress inside aggregates. But as mentioned above we need more results to support this observation.

Temperature – The effect of temperature is indirect since an increase of temperature in the lotic system is followed by an increase of the number of planktonic organisms in the aquatic environment. These living or dead organisms are a potentially valuable substrate for the generation of aggregates and therefore aggregate abundance and aggregate size increase (WÖRNER *et al.*, 2000; ZIMMERMANN, 1997; ZIMMERMANN and KAUSCH, 1996).

Light – The attachment of mobile phototrophic organisms (autotrophic/mixotrophic flagellates or mixotrophic ciliates) is low. Hence, they are only found sporadically on the aggregate surface but never inside (ZIMMERMANN-TIMM *et al.*, 1998). Specific investigations about the luminous intensity in aggregates are not available, so light limitation as well as missing structures to attach may be reason for the above mentioned observations.

Turbulence – In the region near the bottom, covering 10–20% of the water depth, about 80% of the turbulent energy is produced outside the viscous sublayer. Here the strongest shear and lift forces occur (MEHTA and PARTHENIADES, 1975). The turbulent conditions often result in a large number of benthic organisms in the water column. With current velocities around 0.5 m sec^{-1} and more, the number of bacteria, ciliates, flagellates and algae increases in the water column (Table 2). The resuspended heterotrophic benthic organisms can only survive in the water column if attached to particles as they need a substrate on which to move and feed (WÖRNER *et al.*, 2000; ZIMMERMANN-TIMM *et al.*, 1998).

Chemical characteristics:

Nutrients – ARTOLOZEGA *et al.* (1997) and CARON (1991) described that “marine snow” is colonized by organisms because it is nutrient enriched compared to the surrounding water. Up to now there are no informations available about nutrient concentrations in aggregates of running waters. Concerning spatial differences in aggregate colonisation it seems that colonization of aggregates is higher in areas with lower nutrient concentrations in the water column (WÖRNER *et al.*, 2002). Similar observations were obtained for seasonal differences in the estuarine environment. During winter only a few small aggregates (type 3 and type 4) with low energetic content (about $1000 \text{ J g dry weight}^{-1}$) and low abundances of aggregate-associated organisms were present. A similar situation could be observed in the turbidity zone of the estuarine environment during all seasons (ZIMMERMANN, 1997).

Evidence from marine environments indicates that the number of organisms decreases with aggregate age (ARTOLOZEGA *et al.*, 1997; HERNDL, 1988). Laboratory experiments carried out by PLOUG *et al.* (in press) showed, however, that the number of associated organisms does not decrease with age but that aggregates become substrate limited and the

attached organisms showed low activity (see also chapter 6). In the lenitic zone of estuaries and rivers this phenomenon does not occur because sedimentation and resuspension, especially in the estuarine environment, causes the continual restructuring of aggregates. As a result, although it is possible to distinguish between large and small aggregates, the age of aggregates cannot be determined. BERGER *et al.* (1996); ZIMMERMANN-TIMM *et al.* (1998) and WÖRNER *et al.* (2000) found that scantily colonized and uncolonized particles consisted mainly of the aggregate type 3 and type 4.

Biological characteristics:

Substrate Quality – Field observations and laboratory experiments showed, that turbidity, or more precisely, the number of large aggregates ($\geq 100 \mu\text{m}$), which are rich in organic materials, especially type 1 and type 2, apparently stimulates colonization by bacteria, protozoa and metazoa. As described in chapter 3.1. we find a high amount of large aggregates in highly productive systems with a high primary production. It was shown, that a large amount of attached algae is positively correlated with aggregate size and with large numbers of bacteria. These large numbers of bacteria attract a variety of protozoa, and sometimes also metazoa (BERGER *et al.*, 1996; WÖRNER *et al.*, 2000; ZIMMERMANN, 1997).

Grazing on aggregates – The structure on the aggregate-associated assemblage has an enormous impact on the community composition. Grazing by attached organisms can, for example, increase or suppress aggregate – associated populations. Food web studies within aggregates of running waters are not available but studies from the pelagic environment point out that grazing by metazoans can suppress protozoan growth and due to this we have a different biomass and structure of bacteria than without any impact by metazoa on protozoan populations (GÜDE, 1989; JÜRGENS *et al.*, 1997).

Aggregate grazing – Grazing on aggregate attached organisms through the pelagic community can change the associated community, this resulting in a dominance of grazing resistant organisms (WÖRNER *et al.*, 2000). Large numbers of calanoid copepods suspended in the water column of the River Elbe, and grazing on aggregates, release aggregate – associated protozoa into the pelagic environment. Laboratory and field studies revealed, that only those protozoa are associated to aggregates if calanoid copepods are absent. Further studies have to explain, whether chemical communication causes this reaction. Finally, the aggregate community is known to influence interactions between the aggregate and the surrounding water. Our understanding of these processes is, however, only as good as our knowledge of the composition and activity of the aggregate-associated assemblage (see also chapter 6).

5.1. Bacteria

Inorganic components such as calcite and clay particles are usually not colonized (BERGER *et al.*, 1996; ZIMMERMANN, 1997). Although up to half of all microaggregates are uncolonised by bacteria, both micro- as well as macroaggregates from rivers and estuaries can be colonized (BERGER *et al.*, 1996; CRUMP and BAROSS, 2000; CRUMP *et al.*, 1998; ZIMMERMANN, 1997). Bacteria are, in fact, often the first colonizers of newly formed aggregates. Working in the lab with uncolonized aggregates we found the first bacteria associated to aggregates within a few minutes ($<5 \text{ min}$); flagellates, however, appeared around 1 h later (WÖRNER *et al.*, 2000). The bacterial cells are not usually uniformly distributed on aggregates but often form microcolonies and occur in filamentous structures (K. JÜRGENS, MPI Plön, (Germany), pers. com., GROSSART and PLOUG, 2000; WÖRNER and ZIMMERMANN-TIMM, 2000). Newly formed phytoaggregates are colonized by coccidial and rod forms $< 0.5 \mu\text{m}$, whereas older aggregates are colonized by filaments larger than $0.5 \mu\text{m}$. Similar to other environments the bacterial cells on aggregates of rivers and estuaries are often

bigger than those living free in the pelagic environment (K. JÜRGENS, MPI Plön, (Germany), pers. com., ZIMMERMANN and KAUSCH, 1996).

Between $3 \cdot 10^7$ and $5 \cdot 10^7$ bacteria per aggregate were counted (BERGER *et al.*, 1996; WÖRNER *et al.*, 2002; ZIMMERMANN, 1997) with the highest numbers found during spring and summer. These loads were low compared to laboratory studies where aggregates could carry much larger numbers, up to $13.8 \cdot 10^9$ bacteria aggregate⁻¹ (WÖRNER *et al.*, 2000, see also chapter 3.2.). Several authors described for “marine snow” and “lake snow” bacterial abundances in the order of 10^5 to 10^7 aggregate⁻¹, whereas values around 10^7 aggregate⁻¹ are rare and they were only sometimes observed for surface water and the deep sea (ALLDREDGE and SILVER, 1988; GROSSART and SIMON, 1993; GROSSART *et al.*, 1997). Sometimes the number of bacteria per aggregate shows a positive correlation to aggregate size (ZIMMERMANN, 1997) but studies in other aquatic systems indicate that with decreasing particle size, microbial biomass and activity might increase (ALMEIDA and ALCANTARA, 1992; BERGER *et al.*, 1996; KONDRATIEFF and SIMMONS, 1985; WALLACE *et al.*, 1982).

Bacteria on aggregates are enriched as compared to the abundance of free-living bacteria in the surrounding water. The abundance of attached bacteria varies between factor 11 and 40 whereas free-living bacteria vary only between 2 and 8 (BERGER *et al.*, 1996; DE RUYTER VAN STEVENINCK *et al.*, 1992; DUCKLOW, 1982; KONDRATIEFF and SIMMONS, 1985; ZIMMERMANN, 1997).

The relative proportion of aggregate-associated bacteria to total bacterial numbers varies greatly, mainly depending on the abundance of aggregates. In riverine and estuarine systems, they may constitute between 14 and 90% of total bacterial abundance or production (BELL and ALBRIGHT, 1981; BENT and GOULDER, 1981; BERGER *et al.*, 1996; CRUMP and BAROSS, 2000; WÖRNER *et al.*, 2000; WÖRNER *et al.*, 2002; ZIMMERMANN, 1975; ZIMMERMANN, 1997). Molecular techniques have helped to understand the phylogenetic structure of bacterial communities but this reveals little of their physiological properties. Only in a few cases a physiological role can be ascribed to phylogenetic clusters, such as the sulfate reducers (subclusters of α -Proteobacteria) or the ammonium oxidizers (subclusters of β -Proteobacteria). Studies based on molecular techniques in lotic systems are rare. Three studies in the estuarine environment underline changes in assemblage composition at the turbidity zone and in areas of different salinity (CRUMP *et al.*, 1999; HOLLIBAUGH *et al.*, 2000; SCHWEIZER, 1998). In the Columbia Estuary, USA, a specific bacterial community was found on particles at the turbidity maximum and this was dominated by phylotypes of the *Cytophaga*/Flavobacteria cluster, and the α -, β - and γ -Proteobacteria. The composition of this community was substantially different from that in the surrounding water but also from that on particles in the limnetic and coastal section (CRUMP *et al.*, 1999). In the Sacramento River and its estuarine environment there were minor differences between particle-associated and free-living bacteria (HOLLIBAUGH *et al.*, 2000), but this conclusion may be an artifact of the separation method. As described above SCHWEIZER (1998) showed in a field study, using group-specific oligonucleotide probes, differences within the proteobacteria along the salinity gradient for the first time.

Observations at one sampling point in the riverine environment by BÖCKELMANN *et al.* (2000) showed for the first time that the bacterial aggregate community changed over the course of the year. This change was characterized by great bacterial diversity in spring and a reduction of the total bacterial cell counts in autumn and winter. During all seasons β -Proteobacteria constituted the numerically most important bacterial group forming up to 54% of the total cell number. They were represented by small, rod-shaped, bacteria with characteristic inclusion bodies. The percentage of γ -Proteobacteria was around 25% in spring and 14% in autumn, with filamentous or colony forming forms. The numbers of α -Proteobacteria peaked at 24% in spring, comparing to 4% in summer. In contrast, the relative abundance ranged from 2% for the order Planctomycetales to 36% for *Cytophaga*/Flavobacteria. In spring the community had been characterized by a high abundance of *Cytophagae*, which

seem to be typical in running waters (CRUMP *et al.*, 1999; KENZAKA *et al.*, 1998; LEFF, 1994; MANZ *et al.*, 1999; SCHWEIZER, 1998). The autumn and winter communities are quite similar and the decrease in bacterial cell counts in these seasons might be caused by the lack of nutrients and the low temperature.

Long term (14 days) observations of aggregates under experimental conditions revealed that bacterial numbers remained more or less constant and did not reflect changes in bacterial activity, there were, nevertheless, significant changes in the community structure (GROSSART and PLOUG, 2000). Older aggregates were strongly dominated by filamentous γ -Proteobacteria and Cytophaga, whereas percentages of α - as well as β -Proteobacteria decreased. Cytophaga are known to hydrolyse a variety of refractory compounds such as chitin and other polysaccharides, indicating the great potential of aggregate-associated bacteria to degrade highly polymeric substrates (DELONG *et al.*, 1993; RATH *et al.*, 1998).

Physiological studies, most in estuarine environments, have also contributed to our knowledge to the structure and processing in the aggregate assemblages of lotic systems. Nitrifying bacteria add up to 5–10% of the total bacterial community (GRESIKOWSKI *et al.*, 1996) and as much as 60% of these bacteria are aggregate – associated (SCHÄFER and HARMS, 1996). The concentration of inorganic N – compounds of the particulates can be 100 to 1000 times higher than that of the water column indicating that the aggregates have a much better supply of nutrients (GRESIKOWSKI *et al.*, 1996). Of the total bacterial activity, 90% could be ascribed to attached nitrifiers and, as water temperature and nitrifying activity increased, the amounts of aggregate – fixed ammonia and nitrite decreased (GRESIKOWSKI *et al.*, 1996). Most attached *Nitrosomonas euopea* cells were found on aggregates with high settling velocity (SCHÄFER and HARMS, 1996).

In an estuarine study up to 60% of the aggregates were colonized by the H₂S oxidizing bacterium *Beggiatoa leptomitiformis* and this species reached abundances of $0.3\text{--}0.71 \cdot 10^6$ bacteria ml⁻¹ with higher values on aggregates (WÖRNER and ZIMMERMANN-TIMM, 2000). This finding indicates that the aerobically living *Beggiatoa* originate their energy sources from anoxic zones in aggregates (see also chapter 6).

5.2. Fungi

Fungi are primary decomposers of leaf litter and other macrophyte-derived detrital material in streams and rivers (BÄRLOCHER, 1992) and thus it is likely that they colonize micro- and macroaggregates in these ecosystems being rich in macrophyte-derived organic matter. It is therefore surprising that only one study of fungal colonisation of aggregates has come to my notice (HINCK, 2001). This study was done in the estuarine environment and it shows that Phycomycetes (Thraustochytridiaceae and Chytridiaceae) and Eumycetes were associated to aggregates. It was shown, that Phycomycetes dominated in the water column where they can include nutrients on the osmotrophic pathway. Considering this result, the importance of aggregate associated fungi for matter fluxes within aggregates is low. But it might be, that the high nutrient concentrations in the estuarine environment cause this unexpected phenomenon. Further studies in more oligotrophic systems are necessary.

5.3. Protozoa

Protozoans such as amoebae, ciliates, flagellates and heliozoans have been found to colonize micro- and macroaggregates in rivers and estuaries (ROGERSON and LAYBORN-PARRY, 1992a; ROGERSON and LAYBORN-PARRY, 1992 b; WÖRNER *et al.*, 2000; WÖRNER *et al.*, 2002; ZIMMERMANN and KAUSCH, 1996) although only in the Elbe the colonization of single river-

ine aggregates has been studied (WÖRNER *et al.*, 2000; WÖRNER *et al.*, 2002; ZIMMERMANN and KAUSCH, 1996). Comparing aggregate colonization by protozoans and bacteria it is remarkable that only aggregates $\geq 100 \mu\text{m}$ are colonized by protozoa (WÖRNER *et al.*, 2000, ZIMMERMANN, 1997). Aggregate composition also plays a role since, in addition to the organic content, chlorophyll *a* determines the association of protozoa to aggregates (ZIMMERMANN, 1997). Due to this, spring and summer aggregates, in most cases aggregate type 1 and 2, are good substrates for protozoa (WÖRNER *et al.*, 2000; WÖRNER *et al.*, 2002; ZIMMERMANN, 1997; ZIMMERMANN *et al.*, 1998). WÖRNER *et al.* (2002) showed in the Elbe that the lower the nutrient status of the pelagic environment the higher the concentrations of organisms are on aggregates. High pelagic nutrient status on the other hand results in more suspended than aggregate-associated organisms.

Laboratory studies of seasonal succession with material from the estuarine environment (WÖRNER *et al.*, 2000) showed that bacterivorous flagellates (choanoflagellates and small euglenids) were the first protozoans to colonize aggregates with a rich bacterial community. Small ciliates $\leq 20 \mu\text{m}$, that consume bacteria, flagellates or small algae, follow later with the occasionally additional appearance of amoebae $< 30 \mu\text{m}$ and heliozoans. Colonization by carnivorous or omnivorous ciliates and by metazoans like small rotifers are rare in nature since the aggregates in rivers and streams are too small (ZIMMERMANN-TIMM *et al.*, 1998). However, colonization by these organisms is possible as was shown for larger aggregates ($> 100 \mu\text{m}$) created in laboratory experiments.

Aggregate-associated amoebae reached abundances of 211 individuals per aggregate or, equivalently, 24000 per litre. They reached high numbers during the summer after high current velocities and up to 55% of them were associated with the surface or the pores of aggregates. The dominant genera were *Vannella* sp. and *Cochliopodium* sp. (ZIMMERMANN-TIMM *et al.*, 1998).

In the Elbe Estuary, the only location where single colonized aggregates have yet been studied, colonizing forms of ciliates were found on single aggregates attached to the surface and pores (ZIMMERMANN-TIMM *et al.*, 1998). The animals were found throughout the year with a peak of peritrich ciliates (*e.g.* *Vorticella convallaria* complex, *Vorticella octava* complex, *Vorticella microstoma* complex) in autumn. In the aggregates holes of variable sizes were occupied by smaller associated ciliates, such as *Cyclidium* sp. and *Aspidisca* sp.. *Stentor coeruleus* (PALLAS, 1766) EHRENBERG, 1831 moved its basal parts through the aggregates and formed hollow spaces.

Up to 23 flagellates were attached to a single aggregate, translating to up to 2640 flagellates per litre and including obligate (*e.g.* *Bicosoeca* sp., *Bodo* sp., *Bodomorpha minima* HOLLANDE 1942, *Cercomonas* sp., *Codosiga* sp., *Rhynchomonas* sp., *Spumella* sp.) and facultative (*e.g.* *Ceratium* sp., *Cryptomonas* sp.) associated forms. Aggregate colonization by flagellates was compared to amoeba and ciliates – high during the whole year but increased with the grazing pressure on aggregates by metazoans and high current velocities.

The dense population of protozoa on aggregates appears to result from their ability to detect aggregates due to their higher nutrient status from the distance (KAKUSCHKE, 1999).

Interactions between protozoa and bacteria on aggregates from running waters are poorly studied. For the estuarine environment K. JÜRGENS (MPI Plön (Germany) pers. com.) could show, that the abundance of filamentous bacteria increases with increasing number of aggregate-associated flagellates. Nothing is yet known on the remineralization of aggregate-associated N and P by bacterial grazing in rivers and estuaries.

5.4. Metazoa

Aggregate-associated metazoa such as rotifers, nematodes, turbellarians, veliger larvae of *Dreissena polymorpha* have been described on single riverine aggregates for the first time

only recently (ZIMMERMANN and KAUSCH, 1996). Their findings have been confirmed by further studies (HOLST, 1996; WÖRNER *et al.*, 2000; ZIMMERMANN-TIMM *et al.*, 1998). All these studies underlined that metazoa only colonized aggregates larger than 2000 μm , which are rare in the natural environment.

On aggregates most metazoans appear in greater numbers compared to the surrounding water (about 1000 individuals l^{-1}). Since most of these metazoans are associated only over a short period (<30 sec), it is difficult to give exact data on aggregate-associated organisms. Only nematodes resuspended from the benthic environment and in need of a substrate are easier assessable. There were up to 10 individuals aggregate⁻¹ or 600 individuals l^{-1} . The metazoans derive from the pelagic or benthic environment and show different attachment strategies. Rotifers, like *Anuraeropsis fissa* GOSSE 1851, *Trichocerca pusilla* LAUTERBORN 1898, *Keratella cochlearis cochlearis* (GOSSE 1851) and *Notholca squamula* (MÜLLER 1786) touch aggregates and will feed on associated bacteria and protozoa only for a few minutes. The behaviour of individual taxa exhibits pronounced differences (HOLST, 1996; ZIMMERMANN-TIMM *et al.*, 1998); *Pompholyx sulcata* (HUDSON 1885), for example, can attach itself to the surface with mucopolysaccharids whereas *Brachionus* spp. uses their foot.

The swimming behaviour of zooplankton such as rotifers and sometimes copepods can cause the fragmentation of aggregates by dislodging the material mechanically with their limbs. Nauplius larvae and other small plankters occasionally die in sticky aggregates because they are unable to free themselves (FABRICIUS and WOLANSKI, 2000; HOLST, 1996; see chapter 7). It was also observed, that sticky aggregates reduce the ingestion rates of filtering zooplankters (BERNAT *et al.* 1996; see chapter 7).

Until now, little is known about the general significance of metazoans for the cycling and decomposition of aggregates. For future studies about aggregates in running waters it will be interesting to investigate aggregate-eating zooplankters (chapter 7) as well as their role as decomposers.

6. Activity of Aggregates

The production and growth of associated organisms, as well as respiration and anoxic processes lead to the activity on aggregates. Activity on aggregates varies between different types of aggregates in systems marked by different abiotic and biotic conditions. Current research is continuously revealing important details of this activity and therefore contributing to a better understanding, not only to the overall process of aggregate decomposition but also to very specific traits.

6.1. Bacterial Production

The rate of bacterial biomass production in some estuarine and riverine environments has been measured using radioactively labelled thymidine (CRUMP and BAROSS, 1996; GROSSART and PLOUG, 2000; SCHWEIZER, 1998) but most of investigations were carried out on pooled aggregates or non-suspended samples and their relevance to the natural situation is therefore doubtful. Recently bacterial production rates have been more representatively determined for suspended aggregates and were up to ten times the rates in non-suspended samples (GROSSART and PLOUG, 2000). This means, that variations in the exposition of the aggregates can underestimate aggregate-associated production values. Even so, the proportional contribution of aggregate-associated biomass production to total bacterial production is highly variable and depends predominantly on aggregate concentration and composition. In contrast to measurements in marine, lacustrine and riverine systems, bacterial production on estuarine aggregates seems to be 10 to 50 times higher than in the surrounding water (CRUMP

and BAROSS, 1996; SCHWEIZER, 1998). However, within the salinity gradient of the estuarine environment, a higher production was found in the limnetic than in the marine areas.

GROSSART and PLOUG (2000) showed that bacterial production in the River Weser is positively correlated with aggregate size, unsurprisingly since colonization by aggregate-associated organisms increased with aggregate size as described in other studies (PLOUG *et al.*, in press, ZIMMERMANN, 1997). The last named authors proved that bacterial production and respiration (chapter 6.2.) on aggregates depend on the associated community and the substrate composition of aggregates. High growth efficiencies of aggregate-associated bacteria, especially during the first days of colonization, suggest that aggregates are sites of high bacterial growth where a rapid and efficient transfer of organic matter into bacterial biomass takes place (PLOUG and GROSSART, 1999). Considering these new results it seems, that microorganisms on aggregates utilize a higher proportion of available organic carbon than usually assumed.

The only study currently available on bacterial growth efficiency on riverine aggregates presupposes that protozoans do not dominate on the aggregates and that productivity is entirely bacterial (GROSSART and PLOUG, 2000). The authors calculated a highly variable growth efficiency with high values of 0.4–0.5 in fresh aggregates and decreasing to 0.05 in 14 day old aggregates. “Young” (1–3 day old) riverine aggregates show relatively high bacterial growth efficiency in experiments (GROSSART and PLOUG, 2000; PLOUG *et al.* in press) but there was no correlation between respiration and the particulate organic carbon or particulate organic nitrogen content of the same aggregate. Newly formed aggregates present a relatively uniform quality of substrate which can be processed quickly and efficiently by the attached organisms. The substrates available for free living bacteria in different aquatic systems are far more variable. Bacterial efficiency on older aggregates (7–14 days) was half that on younger aggregates. The results showed that the abundance of associated bacteria was high, the production was then substrate limited and the relatively low respiration was correlated to POC and PON content of the same aggregates. Substrate limited β -proteobacteria and *Cytophaga* (LOBET-BROSSA *et al.*, 1998) were found on these older aggregates but the reason for their occurrence is their ability to hydrolyse proteins, polysaccharides and chitin (DELONG *et al.*, 1993) as well as their mobility.

These data indicate that growth efficiencies of aggregate-associated bacteria tend to range at the higher end for free-living bacterial communities. These calculations can only be considered as a first assessment and additional measurements of efficiencies are needed, taking other associated organisms into consideration.

6.2. Respiration

Most of the data available on respiration originate (as described in chapter 6.1.) from activity measurements carried out by pooling several aggregates in one sample with a few milliliters of sterile-filtered, surrounding water in order to limit the variability among individual aggregates. These measurements in lotic systems are open to considerable doubt because sedimentation and pooling significantly affect the diffusion field during incubation (PLOUG and GROSSART, 1999).

6.3. Microzones on Aggregates

The large number of active aggregate-associated organisms (ZIMMERMANN, 1997; ZIMMERMANN and KAUSCH, 1996; ZIMMERMANN-TIMM *et al.*, 1998) and the demonstrated presence of methanogens, sulfate reducers, ammonium-oxidizing and nitrifying bacteria on aggregates in experimental systems, where the aggregates were settled (KERNER and GRAM,

1995; STEHR *et al.*, 1995; WÖRNER and ZIMMERMANN-TIMM, 2000), could be taken as a sign of anoxic processes on aggregates. But PLOUG *et al.* (1997) showed that anoxic suspended aggregates are rare. Anoxia would be likely if aggregates had low porosity and if ambient dissolved oxygen was low but anoxic aggregates seem to be only an ephemeral phenomenon (PLOUG *et al.*, 1997) and therefore presumably do not play a major role in the aggregate-associated decomposition of organic matter.

Maybe the resuspension of sedimented material (*e.g.* after slack tide or during high current velocities) could be an explanation for these bacterial groups in suspended estuarine aggregates.

7. Importance of Aggregates for the Riverine Matter Flux

Riverine aggregates differ in time and space during horizontal and vertical transport. Nevertheless our scarce knowledge of riverine aggregates we are able to recognize that different aggregates influence the structure and function of lotic systems in diverse ways.

7.1. Aggregates as Food-Source

Aggregates could be expected to be an important food resource since microaggregate concentrations are up to 100 times higher than those of suspended auto- and heterotrophic food. However they differ in size, form, composition, colonization or nutritional value.

Aquatic organisms, planktonic protozoa, and metazoa, as well as fish, are able to use whole riverine aggregates as food or to graze selectively on aggregate-associated organisms (HOLST, 1996; ZIMMERMANN-TIMM, submitted; ZIMMERMANN-TIMM and BARKMANN, submitted; ZIMMERMANN-TIMM *et al.*, submitted). Investigation of *Neomysis integer* stomach contents during two tides in the Elbe near Brunsbüttel in June demonstrated that they had consumed crustaceans, rotifers, algae, mineral particles and detritus. In some cases up to 90% of the stomach content was composed of detritus giving credence to the idea that mysidaceans use aggregates, originating from the turbulent near bottom layer (see chapter 3.3.) and suspended sediments as food (B. KÖPCKE, University of Hamburg, pers. com.).

Further experiments in the field and in the laboratory were necessary to show that pelagic organisms are able to actively ingest single riverine aggregates (ZIMMERMANN-TIMM, submitted; ZIMMERMANN-TIMM *et al.*, submitted). Experiments with different types of suspended food (aggregates, algae, macrophytes and protozoa) being offered showed that the ciliate *Tintinnidium fluviatile* selected for aggregates and algae in contrast to macrophytes and flagellates of the same sizes. Macrophytes are in most cases not utilized as food, they are consumed as detritus and DOM (dissolved organic matter) within the microbial loop (SCHWOERBEL, 1999). On the other hand experiments with *Palaemon longirostris* showed that the consumption of the aggregates is governed by several aspects: whether the organisms feeding on aggregates are adult or juvenile, the temperature, the quality of the aggregates and availability of other edible particles (ZIMMERMANN-TIMM *et al.*, submitted). Adult organisms select plankton for aggregates and if plankton is not available they feed on aggregates but mostly macroaggregates. Juvenile *Palaemon longirostris* species use plankton and microaggregates as food. If the temperature is low (≤ 10 °C) they start filtering microaggregates since the chance to encounter an aggregate in the aquatic environment is more likely and requires less energy than to catch plankton (relationship aggregates:plankton is about 10:1). Ciliates can distinguish between different types of aggregates: they prefer aggregates of the type 2 over aggregate type 3 and type 4 (ZIMMERMANN-TIMM, submitted). The food quality of the aggregates can be characterized by their composition and for the first time the energy content of single estuarine aggregates was determined (ZIMMERMANN-TIMM

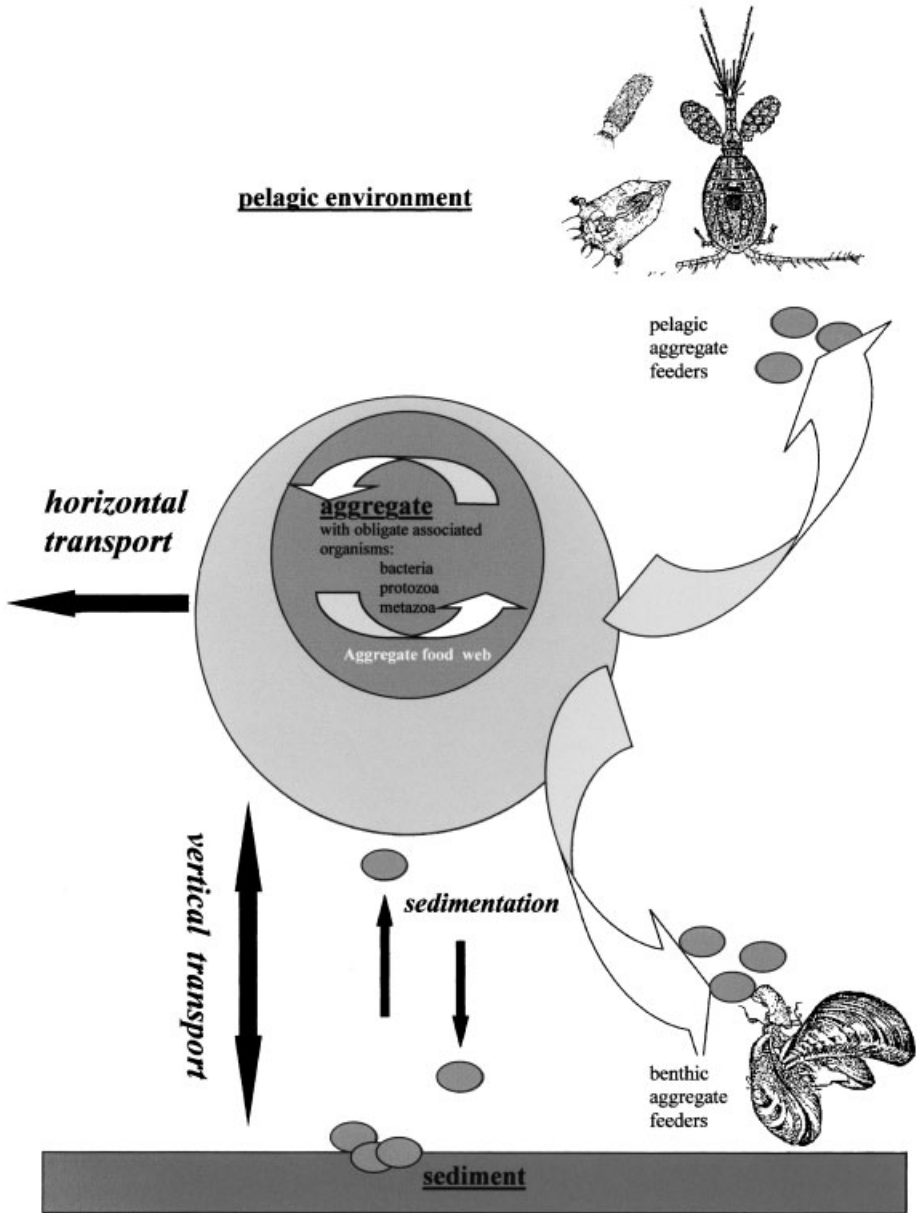


Figure 6. The importance of aggregates in large running waters.

et al., submitted). Aggregates contained 1000 and 1400 J g dry weight⁻¹ although, of course, not all measurable energy can be used such as food such as chitin and cellulose, for example, which can only be consumed by specialists.

By consuming aggregates, small and large raptorial feeders (*e.g.* crustaceans and fish) also ingest the associated pico- and nanoplankton and in consequence there is a link between the microbial to macrobial food webs. The sedimentation of pelagic aggregates means food for

the benthic organism community and the resuspension of benthic materials supplies pelagic organisms with “benthic aggregates”. Due to the changes between sedimentation and resuspension of estuarine and riverine particles and associated organisms we should name this an aquatic food web (Fig. 6). Nevertheless, it should be emphasised that filter feeding organisms can be inhibited by high concentrations of aggregates (BERNAT *et al.*, 1996; KOENINGS *et al.*, 1990). We observed the escape of aggregate-associated organisms (e.g. several protozoa) particularly when certain types of aggregate-feeding calanoid copepods (e.g. *Eurytemora affinis*) were present. It is possible that chemical communication between the associated protozoans and copepods revealed this behaviour (ZIMMERMANN-TIMM and MÜLLER, submitted) but further investigations on this topic are necessary.

It should be stressed the fact, that aggregates as long term food support growth and production of riverine protozoa and metazoa (ZIMMERMANN-TIMM, submitted; ZIMMERMANN-TIMM *et al.*, submitted).

7.2. Aggregates as Refuge

Aggregates with their sticky mucopolysaccharide matrix signify important places of refuge for many organisms:

Size – Small organisms (e.g. pico- and nanoplankton) associated with aggregates are not easy to handle by plankton feeders, being generally adapted to feed only on small particles ($\leq 50 \mu\text{m}$; see also LAMPERT, 1985; JÜRGENS *et al.*, 1997).

Chemical stress – It is assumed, that most of the aggregates with a developed polysaccharide matrix act as refuges during situations with chemical stress because the matrix stabilizes conditions within the aggregate. In alternating salinity concentrations (e.g. increase from $200 \mu\text{S cm}^{-1}$ to $600 \mu\text{S cm}^{-1}$) up to 98% of the pelagic protozoans (mostly Hymenostomata and Hypotrichida) were associated with aggregates. They possibly would be unable to survive in the surrounding water but they can persist for longer inside the aggregate. When conductivity concentrations 2- to 10 fold increased bacteria (SCHWEIZER, 1998) and protozoa (WÖRNER *et al.*, 2002; ZIMMERMANN, 1997) were following with a reduction in the colonization of about 50%.

Aggregates can adsorb and desorb dissolved organic matter (DOM; BAIER *et al.*, 1989; WEISS *et al.*, 1996), thus leading to a micro-spatial accumulation of nutrients (PEDROS-ALIO and BROCK, 1983). Aggregates bind and concentrate cations and anions (COSTERTON *et al.*, 1995; DECHO and LOPEZ, 1993) and, therefore, higher concentrations of these components occur on particles than in the pelagic environment and also leading to a lower toxicity in the surrounding water (KARBE and WESTENDORF, 1996).

Mechanical stress – When a high concentration of single mineral particles occurs in the water column 60–80% of fragile organisms (mainly protozoans) are associated with aggregates. Living in such a particle they are able to escape mechanical damage imposed by the mineral particles in the water column. Further investigations on this topic are necessary.

Mineralization – Aggregates and their associated organisms can absorb organic substances and mineralize them thus removing them from the water. They consequently act like filtration beds in sewage treatment plants and the result is cleared water.

7.3. Transport and Distribution

Aggregates with actively or passively associated organisms (see chapter 4; KAKUSCHKE, 1999) are also vehicles for the transport or distribution of associated organisms through the water column. Vertical transportation, sedimentation, as well as horizontal transport, mainly triggered by the water flow, yields to a wide distribution of aggregate associated

organisms. In addition, the resuspension of material by wind or water discharge and the erosion of terrestrial material can favour a passive colonization of particles and their transport. Eggs and other resting stages of planktonic and benthic organisms can be transported with the aggregates to another environment with more optimal abiotic and biotic conditions and thus providing the chance of colonizing a new habitat.

7.4. Negative Effects Caused by Aggregates

So far the role of aggregates has been presented in a positive context but there may be as well negative effects on aquatic organisms.

Sticky mucopolysaccharids – Organisms that come closer to aggregates with high mucopolysaccharid content may stick together and their efforts to escape simply increases their adhesion. This has been observed for rotifers and copepods in the Elbe estuary (HOLST, 1996) and elsewhere for nauplia-larvae which stick together and then die (FABRICIUS and WOLANSKI, 2000).

Reduction of feeding rates of planktonic organisms – High concentrations of aggregates reduced the filtration rate of *Eurytemora affinis* in an estuarine environment. This could be explained by high current velocities ($\sim 1.5 \text{ m sec}^{-1}$) causing a high amount of aggregates in the water column. When there was approx. 80% settling during slack tide the feeding rates of *Eurytemora affinis* on *Chlorella* sp. could increase from 50 to 400 $\mu\text{l individual}^{-1} \text{ h}^{-1}$ (BERNAT *et al.*, 1996).

Suppression of autotrophic production – High concentrations of aggregates effect high turbidity and can therefore suppress the autotrophic production. Interactions between turbidity and autotrophic production have been mainly studied by LÖHR (1985) and he found, that the turbidity can be equalized by the turbulence, bringing suspended and aggregate associated algae to the surface before they settle again (HORNBERGER *et al.*, 1976; JEWSON and WOOD, 1975; KOWALCZEWSKI and LACK, 1971).

Mechanical stress – Provided aggregates are mainly composed of mineral particles, they are also able to cause damage as well as mechanical stress to suspended planktonic organisms. Only hard-shelled organisms (e.g. *Brachionus* spp., *Keratella* spp., tintinnids) can survive these conditions. Further studies on this topic are necessary but microscopical observations underline this statement (HOLST *et al.*, 1998; ZIMMERMANN-TIMM *et al.*, 1998).

Nutrient limitation – As shown in chapter 6 aggregate associated organisms can be limited by nutrients (e.g. carbon) if diffusion with the surrounding water is impeded (PLOUG *et al.*, in press), thus leading to starvation and death of these organisms. Here high numbers of bacteria were found with low activity rates, in this case with low respiration.

Toxicity – Aggregates can absorb anions and cations (chapter 7.2.) and concentrate them on their surface (COSTERTON *et al.*, 1995; DECHO and LOPEZ, 1993). Depending on the identity of the concentrated ions, toxicity can raise with the consequence of enhanced mortality rates of the organisms. Up to now no detailed statements on this topic are available.

8. Conclusions

Our current knowledge of aggregates from running waters, their occurrence and composition, allows to begin to understand aggregate formation and their colonization by organisms. However further work is necessary: investigations of aggregate-associated processes, of the fluxes and interactions between aggregates and sediment as well as aggregates and the surrounding pelagic environment. It is also important to emphasize the role of aggregates as food and their following interactions with pelagic and benthic organisms leading to a link between the microbial and macrobial food webs. For a better understanding of aggre-

gates in running waters further measurements in systems with different turbulence regimes are essential. With completion of our knowledge aggregates should be included in food web and carbon cycling models.

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