REVIEW

Microbial ecology of organic aggregates in aquatic ecosystems

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ABSTRACT: Macroscopic organic aggregates, which are >500 µm and known as marine and lake snow, are important components in the turnover, decomposition and sinking flux of both organic and inorganic matter and elements in aquatic ecosystems. They are composed of various organic and inorganic materials depending largely on the given system and environmental conditions. The systems include the pelagic limnetic, the neritic and oceanic marine region, as well as shallow turbid environments, e.g. rivers, the littoral zone of lakes, estuaries and tidally affected coastal areas with intense turbulence and a high load of suspended matter. Aggregate abundance and size vary greatly among these systems. Macroaggregates are heavily colonized by bacteria and other heterotrophic microbes and greatly enriched in organic and inorganic nutrients as compared to the surrounding water. During the last 15 yr, many studies have been carried out to examine various aspects of the formation of aggregates, their microbial colonization and decomposition, nutrient recycling and their significance for the sinking flux. They have been identified as hot-spots of the microbial decomposition of organic matter. Further, microaggregates, which are <5 to 500 µm in size and stained by different dyes, such as transparent exopolymer particles (TEP) and Coomassie blue-stained particles, have been discovered and shown also to be important in the formation and decomposition of macroaggregates. In this review we give an overview of the present state of the microbial ecology of macro- and microaggregates, including the mentioned points but highlighting in particular the recent findings on the bacterial colonization of aggregates using molecular tools, their microbial decomposition and mineralization, and the significance of protozoans and metazoans for the colonization and decomposition of macroaggregates. Today it is evident that not only the aggregates but also their surroundings are sites and hot-spots of microbial processes, with the plume of solutes leaking out of the aggregates and greatly extending the volume of the intense decomposition processes. This microheterogeneity has important implications for the spatial and temporal dynamics of the organic-matter field in aquatic ecosystems and for our understanding of how heterotrophic organisms are involved in the decomposition of organic matter. The significance of aggregate-associated microbial processes as key processes and also for the overall decomposition and flux of organic matter varies greatly among the various systems, and is greatly affected by the total amount of suspended particulate matter. A conclusion from the presented studies and results is that the significance of bacteria for the formation and decomposition of aggregates appears to be much greater than previously estimated. For a better understanding of the functioning of aquatic ecosystems it is of great importance to include aggregate-associated processes in ecosystem modeling approaches.

KEY WORDS: Aggregates · Transparent exopolymer particles · Particulate organic matter · Algae · Bacteria · Zooplankton · Sinking flux · Dissolved organic matter

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1. INTRODUCTION

One of the major topics in aquatic microbial ecology deals with the fate of particulate organic matter (POM) and the pathways by which it is (1) produced biologically or abiologically, (2) transferred within the food web or (3) transported downward as sinking POM through the water column, and decomposed and mineralized by microbes. POM interacts in various ways with colloidal and dissolved organic and inorganic materials, e.g. by adsorption or dissolution, and leads to the redistribution of elements, nutrients and specific compounds such as organic pollutants, heavy metals and radioisotopes in aquatic ecosystems. Operationally, the colloidal and dissolved material is separated from the particulate material by the fact that the latter is retained on filters with a pore size of 0.2 to 0.45 µm. The primary and most important process of POM formation is photoautotrophic fixation of CO_2 into biomass, in pelagic ecosystems usually by phytoplankton, but in coastal areas, shallow lakes, rivers and estuaries also by macrophytes, macroalgae and benthic microalgae. Hence, POM is initially living biomass of primary producers that, by various processes and after transfer steps in the food web, eventually turns into dead (detrital) POM often dominating the total POM. One important feature of organic particles is that they are densely colonized by various microbes, which often have key functions in the formation and decomposition of these detritus-dominated micropatches. The often very specific environmental conditions within these micropatches, distinctly different from the surrounding water, and the strikingly high activities of the particle-associated microbes, make them a unique and important subject in aquatic microbial ecology. Because many of these structures are composed of smaller primary components, they are actually composites of detrital particles rich in organic matter and thus are called organic aggregates. Their macroscopic forms, i.e. >500 µm, are known as marine snow and lake snow aggregates (Fig. 1). These terms, as well as microaggregates, i.e. those <500 µm, include not only the detrital organic matter but also the associated microbes as integral components.

POM is one important component of the total suspended matter, consisting of living biomass, detrital organic and inorganic matter. The general significance of suspended matter in marine, estuarine, lacustrine and riverine ecosystems has been reviewed recently (Eisma 1993, Wotton 1994) but the microbial ecology of organic aggregates only to a lesser extent (Alldredge & Silver 1988, Alldredge 1992, Kirchman 1993, Lampitt 1996, Kiørboe 2001). These reviews, except the most recent one by Kiørboe (2001), do not include the recent progress in analyzing their decomposition and turnover of various substrates, the structural composition of aggregate-associated bacterial communities by molecular methods, and interactions with the surrounding water. However, the significance of POM, its microbial decomposition and its role in recycling of nutrients have been acknowledged and studied for more than 30 yr (Johannes 1968, Melchiorri-Santollini & Hopton 1972, Eppley et al. 1977, Cole et al. 1984, Kirchman & Ducklow 1987). The overall, but also very specific, significance of organic aggregates for the cycling and flux of elements and energy in pelagic marine, and more recently in lacustrine and estuarine ecosystems, in the light and significance of the microbial loop has emerged more and more only during the last 10 to 20 yr. Inspired by new concepts of the significance of aggregate-associated bacteria for the cycling and decomposition of organic aggregates (Azam & Cho 1987, Cho & Azam 1988, Azam & Smith 1991, Smith et al. 1992, Grossart & Simon 1993) and by new technologies and methods to study the occurrence, size, spatio-temporal dynamics and microbial colonization of organic aggregates, research on this topic was boosted in the 1990s and led to the present knowledge in this field. In this review we focus on the formation and occurrence of organic aggregates and on heterotrophic processes of the associated microbes. Autotrophic processes are included only when appropriate.
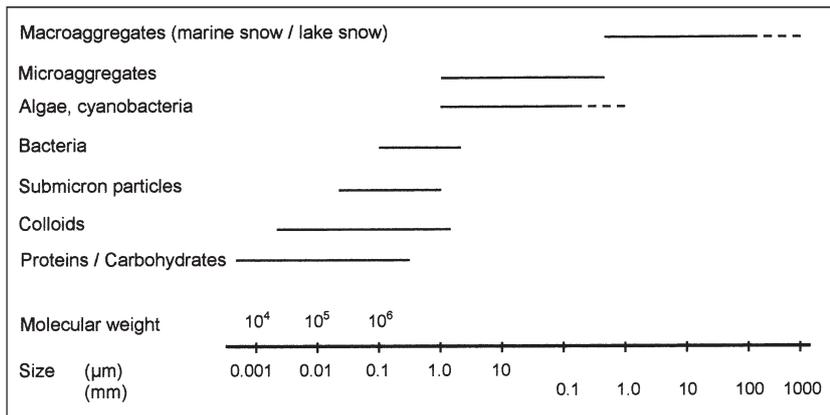

Fig. 1. Size spectra of the major particulate and dissolved organic constituents in aquatic systems

2. METHODS TO STUDY AGGREGATE ABUNDANCE AND FORMATION

2.1. *In situ* abundance

Aggregate abundance *in situ* has been studied by SCUBA divers' visual observations, and by various types of still camera systems, also moored to sediment trap devices (e.g. Honjo et al. 1984, Johnson & Wangersky 1985, Asper 1987, Alldredge & Silver 1988, Costello et al. 1989, Alldredge 1991). Later, remotely or automatically controlled underwater still- and video-camera systems were applied to record vertical and temporal dynamics of aggregates in various size classes (e.g. Walsh & Gardner 1992, Lampitt et al. 1993a,b, Milligan 1995, Lampitt 1996, Jackson et al. 1997, Pilskaln et al. 1998). In combination with computer-assisted image analysis, these methods made it possible to establish *in situ* size spectra of aggregates and their dynamics, and resulted in new insights into their formation and short and long term dynamics.

2.2. *In situ* collection of macroaggregates

Macroscopic aggregates are very fragile and easily collapse when sampled by classical sampling devices such as Niskin and GoFlo bottles and when transferred into other bottles for further investigations. Therefore, special care has to be taken to sample these aggregates for further experiments. Still the best and most careful sampling method in pelagic environments is by SCUBA diving and the collection of macroscopic aggregates *in situ* in open-ended plastic syringes or widely opened bottles (Alldredge & Gotschalk 1990, Alldredge 1991). Once collected, aggregates remain in the syringes until further processing aboard the ship. Often it is unavoidable that aggregates in the syringes become more compact than when freely floating in the water. This collection method, however, limits aggregate studies to the upper 20 to 50 m. For sampling deeper layers, submarines and large volume transparent bottles were used (Alldredge & Youngbluth 1985, Lampitt et al. 1993a, Turley & Mackie 1994, Lampitt 1996). From these large bottles, individual aggregates can be collected visually once the bottle is hauled back on deck.

Sediment traps have been used for many years to collect sinking POM which is dominated by macroaggregates. Even though the elemental and biopolymer composition of this material can be examined (e.g. Cowie & Hedges 1992, Haake et al. 1992, Wakeham & Lee 1993), the aggregate structure is destroyed due to the long (days to years) deployment periods. Traps, exposed for short periods of time (hours), however,

were successfully used to collect fresh aggregates for studies of their bacterial colonization in which the aggregate size structure can be neglected (Grossart & Simon 1998a, Schweitzer et al. 2001).

Horizontal tubes and wide-mouthed funnels have been used to collect highly abundant aggregates in a very turbid estuarine environment, allowing the collection and gentle concentration of aggregates for further investigations (Kerner & Krogmann 1994, Zimmermann 1997). Possible biases by further aggregation and restructuring of the size distribution during the concentration procedure need careful examination.

2.3. Experimental formation of aggregates

Formation of macroscopic organic aggregates was first examined experimentally by Shanks & Edmondson (1989) in plexiglass cylinders rolling horizontally. This method gave the basis for many experimental studies examining details of the formation of aggregates and their microbial colonization and decomposition. This device is supposed to mimic the collision by differential settling of aggregates *in situ* and has often been used in various sizes and modifications since its introduction (Gotschalk & Alldredge 1989, Riebesell et al. 1991, Weiss et al. 1996, Artolozaga et al. 1997, Grossart et al. 1997, 1998, Unanue et al. 1998a, Knoll et al. 2001). Because the hydrodynamics in the rolling cylinders are somewhat different from *in situ* conditions with enhanced shear during the start-up phase, Couette flocculators were suggested as a better means to mimic *in situ* hydrodynamics (Jackson 1994) and were used in several studies (e.g. Kiørboe & Hansen 1993, Drapeau et al. 1994). Aggregates are more difficult to collect in Couette flocculators, which limits the use of these devices. Vertically rotating glass syringes containing only 1 or a few macroaggregates were used to examine autotrophic and heterotrophic activities and colonization, and interactions with the surrounding water (Biddanda 1988, Biddanda & Pomeroy 1988, Gotschalk & Alldredge 1989, Grossart & Simon 1998b, Schweitzer et al. 2001).

3. OCCURRENCE OF ORGANIC AGGREGATES

3.1. Size, abundance and fractal dimension

In pelagic systems, phytoplankton primary production forms biological particles in the size range of 1 µm (picoplankton cells) to a few hundred micrometers, and in extreme cases a few millimeters (diatom chains) or centimeters (cyanobacterial filaments), depending

on the trophic state, seasonal phase and geographic region of the system. Yet, organic particles and aggregates occur in the size range of <1 µm to beyond 10 cm and thus cover a much wider range than biological particles—more than 6 orders of magnitude (Fig. 1), implying that many complex physical, chemical, biological and specific microbial processes are involved in the formation and decomposition of organic particles and aggregates. In systems dominated by macroalgae, macrophytes or allochthonous inputs, even larger particles are the primary sources of organic aggregates. Various processes contribute to the break-down of these large particles, such as mechanical disruption, consumption by detritovores, and microbial decomposition. There is a continuum in the size distribution but special types of aggregates often occur in distinct size classes, which often reflect their origin, significance and fate. Operationally, 3 size classes of organic aggregates are distinguished (Fig. 1): macroscopic aggregates >500 µm (macroaggregates, marine snow, lake snow), microscopic aggregates 1 to 500 µm (microaggregates), and submicron particles <1 µm, discovered a decade ago (Koike et al. 1990, Wells & Goldberg 1991). There is no evidence that submicron particles are involved in the formation or break-down of micro- and macroaggregates. The abundances of the smallest microparticles and largest aggregates range from <1 to >10^8 l^{-1} and are inversely related to size.

It has been shown that the structure of macro- and microaggregates is best described by fractal geometry (Logan & Wilkinson 1990, Kilps et al. 1994, Chen & Eisma 1995). Exceptions are abandoned larvacean houses, which are not formed by aggregation (Alldredge 1998). Fractal geometry means that the mass or number of component particles (N) and the characteristic length scale of the aggregate (l) are related according to the function $N \sim l^{Dn}$. 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 does the aggregate have an Euclidian geometry, e.g. $D_3 = 3$ for a sphere. Marine snow typically has a fractal dimension of D_3 between 1.3 and 2.1, which is much lower than that of inorganic colloidal aggregates and only slightly higher than that of activated sludge flocs (Logan & Wilkinson 1990, Logan & Kilps 1995, Jackson et al. 1997). D_1 and D_2 of aggregates in the shallow North Sea and the Elbe estuary, Germany, range between 1.01 and 1.14, and between 1.41 and 1.81, respectively (Chen & Eisma 1995), and D_2 of marine snow of various types in Californian coastal waters between 1.1 and 1.8 (Kilps et al. 1994). Fractal geometry allows estimation of the porosity of aggregates, i.e. pore volume, which is inversely related to the fractal dimension (Logan & Wilkinson 1990). The porosity is important in controlling the aggregate's sinking rate, the flux of water through the aggregate moving relative to the surrounding water, and the flux of nutrients and substrates to and from the microorganisms colonizing the aggregate's surface (Logan & Hunt 1987, Alldredge & Gotschalk 1988, Logan & Alldredge 1989, Ploug 2001).

3.2. Formation of organic aggregates

Aggregates are formed by a variety of physical, physico-chemical and biological processes. In particular, the former have been studied and reviewed quite extensively (e.g. O'Melia 1987, Eisma 1993, Johnson et al. 1994, Stumm et al. 1994). These reviews provide the basis for the outlines below. Biological factors and the significance of microorganisms in aggregation processes have attracted detailed interest only fairly recently. Generally, aggregation is a complex process controlled by 3 primary variables: (1) the particle concentration, density, size distribution and shape; (2) shear and differential settling velocities; and (3) the probability with which the particles stick together after collision. The sticking coefficient (α) describes the ratio of numbers of successful collisions/numbers of total collisions (McCave 1984). It varies considerably for different types of marine macroaggregates and ranges from <0.2 for non-sticky material to 0.60–0.88 for sticky phytodetrital aggregates (Alldredge & McGillivary 1991, Kiørboe et al. 1994, 1996, Waite et al. 1997). Interestingly, the stickiness of diatoms and aggregates appears to be highest during the transition from the exponential growth phase to the stationary phase and decreases again thereafter (Kiørboe et al. 1990, Kiørboe & Hansen 1993, Drapeau et al. 1994, Dam & Drapeau 1995). In contrast, Engel (2000) reported an increasing stickiness during the decline of an experimental diatom bloom and highest values at the end. Transparent exopolymer particles (TEP) have been identified as very important in controlling the sticking coefficient of diatoms and other organic particles (Alldredge et al. 1993, see Section 3.4.1). The following mechanisms causing collisions of suspended particles have been identified:

Brownian motion: Collision of particles due to random walk. It is only important for particles <8 µm because their movement is largely controlled by laminar flow and their diffusivity (Eisma 1993).

Shear: Particles in laminar or turbulent shear collide if the distances of their flow streamlines or eddies are smaller than the sum of the particle radii. It is important for the collision of particles >8 µm (Eisma 1993) and is the dominant mechanism at interfaces such as at discontinuity layers in the water column, in the bottom

nepheloid layer, or at tidal currents in estuaries and shallow seas. In pelagic systems, shear is one of the major factors controlling aggregation (Jackson 1990). At energy dissipation rates of 10^{-7} to $>10^{-4}$ m^2 s^{-3}, which can occur at the abovementioned discontinuity layers, the resulting shear may lead to disaggregation or size reduction of macroaggregates, depending on the physical strength and size of the aggregates (Alldredge et al. 1990, Riebesell 1991a, 1992, McIntyre et al. 1995).

Differential settling: Settling particles can overtake, and intercept, more slowly sinking particles. As with shear, particles collide if the distances of their flow streamlines are smaller than the sum of the particle radii. Usually, larger, more rapidly sinking particles scavenge smaller particles by this mechanism (Jackson 1990, Kepkay 1994). If the larger particle is surrounded by a diffusive boundary layer, the collision also depends on the diffusion rate of the smaller particle. This may be important for scavenging submicron particles and colloids. Differential settling is important for sinking particles in the water column and in slack water in tidally affected shallow seas and estuaries.

Filtration: Theoretical studies of fluid dynamics have shown that highly porous aggregates may experience an interstitial water flow in the order of tenths to hundreds of μm s^{-1} when the aggregate is sinking (Logan & Hunt 1987, Logan & Alldredge 1989) such that nutrients, but also colloids or other particles, are collected by size exclusion (Stolzenbach 1993). Interstitial fluid flow through aggregates, however, has not been experimentally quantified due to insufficient spatial resolution and sensitivity of existing techniques. The high content of mucus and TEP within aggregates may in fact limit advection through aggregates. It is not known yet how important this mechanism is in aggregate formation. It may be important under certain conditions for passively capturing particles that do not actively form aggregates such as discarded larvacean houses, pteropod webs and non-sticky dinoflagellates (Alldredge & Silver 1988, Alldredge et al. 1998, Silver et al. 1998).

Biological capture: Zooplankton capture other particles by filtering food particles and thus aggregate such particles in the filtering apparatus or the gut. This process may contribute to structuring the composition of aggregates consisting of abandoned larvacean houses, pteropod webs and fecal pellets (Pomeroy & Deibel 1980, Lampitt et al. 1990, Bochdansky & Herndl 1992, Herndl 1992).

Whether the collisions are successful or not depends on the following factors:

Surface properties of the particle: A particle or aggregate has attractive or repulsive surface properties, depending on its size, composition and chemical coating. Most particles are negatively charged at the surface because of the adsorbed organic material with many carboxylic or hydroxylic compounds (Gibbs 1983, O'Melia 1987, Johnson et al. 1994, Stumm et al. 1994). In the presence of coatings of organic multilayers, particles may also exhibit hydrophobic attractive properties (Zutic & Tomaic 1988). Different surface properties of individual diatom species, depending also on their physiological state and the microbial colonization, lead to selective aggregation and removal of diatoms during phytoplankton blooms (Riebesell 1991b, Passow et al. 1994, Alldredge et al. 1995, 1998, Hansen et al. 1995, Hansen & Kiørboe 1997).

Bridging with divalent cations: Divalent cations such as Ca^{2+} and Mg^{2+} act as chemical bridging agents enhancing the attraction and sticking properties of electronegatively charged particles (Eisma 1993, Stumm et al. 1994). They are most important in mediating aggregation of electronegatively charged particles and are the main reason why aggregation is a positive function of salinity.

Mediation of coagulation and aggregation by dissolved organic matter: Dissolved organic matter (DOM) may enhance or reduce aggregation depending on its quality and concentration (Johnson et al. 1994). DOM, and in particular humic substances with a high negative charge, readily adsorb to particles but also reduce aggregation in the absence of cations such as Ca^{2+} and Mg^{2+} (e.g. Gerritsen & Bradley 1987, Zutic & Tomaic 1988, Eisma 1993). Therefore, aggregation can be expected to be negatively correlated with DOM concentration, if DOM is dominated by dissolved humics, and to be lowest in humic lakes. On the other hand, low concentrations of DOM enhance aggregation of inorganic particles exhibiting a positive surface charge when not coated by organic material (Gibbs 1983, Johnson et al. 1994). DOM of high molecular weight is more effective in surface-reactive properties than DOM of low molecular weight. Dissolved or particulate organic polymers produced by phytoplankton and bacteria have also been shown to be important in enhancing the formation of macroaggregates and in stabilizing the structure of aggregates (see Section 3.4.1).

There are also other processes resulting in aggregation:

Bubbling (surface coagulation) of DOM: Surface-reactive DOM, mainly polysaccharides, can be converted into particles through coagulation at the surfaces of gas bubbles when they burst or collapse (e.g. Johnson et al. 1986, Eisma 1993, Mopper et al. 1995, Zhou et al. 1998, Mari 1999). Even though this process has been studied quite extensively and occurs during the development of diatom blooms, it is not yet clear to what extent it contributes to the formation of aggregates. Presumably it is important under certain condi-

tions, such as at the sea surface, in the formation of TEP (see Section 3.4.1).

Spontaneous coagulation of DOM: DOM can form colloidal material, submicron particles and eventually also microaggregates due to spontaneous coagulation in the dissolved phase (Kepkay 1994, Chin et al. 1998, Mari & Burd 1998, Passow 2000). The occurrence of this process has been demonstrated convincingly but it is not yet known to what extent it contributes to the formation of aggregates. Most recent results suggest that it is important under certain conditions in the formation of TEP (Passow 2000, Section 3.4.1).

Biological processes may also directly result in and control the formation of aggregates by various mechanisms:

Larvaceans discarding their houses: Larvaceans discarding their houses with a clogged filtration apparatus directly generate macroaggregates because living and senescent algae, protozoans, bacteria and microaggregates are attached to these houses. In fact, abandoned larvacean houses are one of the most abundant types of marine snow in certain areas (Alldredge & Madin 1982, Alldredge & Silver 1988, Hansen et al. 1996, Silver et al. 1998).

Detached pteropod nets: Pteropods can lose their filter nets when they become clogged by various particles such as algal cells and microaggregates and thus directly produce macroaggregates in pelagic marine environments.

Defecation and molting of zooplankton: All marine and most lacustrine zooplankton produce fecal pellets, which consist of densely packed micro- or macroaggregates surrounded by a peritrophic membrane. These fecal pellets can stick to other aggregates or directly sink as individual particles to deeper layers in the water column, thus contributing substantially to the formation of sinking aggregates and sinking flux (e.g. Lampitt et al. 1990, Bochdansky & Herndl 1992, Turner 2002). Only herbivorous cladocerans in lakes, such as daphnids, do not produce fecal pellets and thus are differently involved in the formation of macroaggregates. This notion has implications for differences in the relationship between primary production and the sinking flux in marine and cladoceran-dominated lacustrine ecosystems (Aksnes & Wassmann 1993). However, due to the short generation time of their parthenogenetic generations (4 to 10 d), cladocerans can establish very high abundances for short periods of time and produce high amounts of molts and carcasses, which may dominate sinking macroaggregates in lakes for short periods of time (Grossart et al. 1997, Gries & Güde 1999). Holo- and meroplanktonic zooplankton may also contribute substantially to sinking macroaggregates in shallow bays (Shanks & Edmondson 1990, Shanks & Del Carmen 1997, Shanks & Walters 1997, see Section 4.1).

Mediation of aggregation by microbes: There is growing evidence demonstrating the direct significance of microorganisms in the formation of aggregates and that aggregation is a direct consequence of the activity of microorganisms: (1) Biddanda (1985) experimentally showed that the formation of marine macroaggregates was only possible in the presence of live microorganisms because no aggregation occurred when the samples were poisoned by mercury chloride or when bacteria were removed by filtration. (2) Paerl (1974) demonstrated by autoradiography that aggregate-associated bacteria take up DOM of low molecular weight from the surrounding water and convert it to fibrillar material gluing together microaggregates. Other authors also demonstrated the secretion of fibrillar material by bacteria, leading to strengthened aggregate structure (Leppard et al. 1979, Heissenberger et al. 1996). (3) Decho (1990), Alldredge et al. (1993) and thereafter many other authors showed that diatoms secrete large amounts of acidic mucopolysaccharides, named TEP, which are very important in and often control the formation of macroaggregates in pelagic ecosystems (see Section 3.4.1). Also, bacteria were recently shown to secrete large amounts of TEP and thus may directly control the formation of macroaggregates (Stoderegger & Herndl 1999). (4) Specific bacterial populations colonizing diatoms or living in their phycosphere (Bell & Mitchell 1972) obviously also control phytoplankton growth, mortality and secretion of polysaccharides, and thus may directly control the aggregate formation (Azam 1998, Brussaard & Riegman 1998, Guerrini et al. 1998, Azam et al. 1999, Grossart 1999, Herndl et al. 1999).

The net result of aggregation is a function of all the abovementioned parameters and processes, varying largely according to the type of aggregate, the environment and the organisms involved. There is growing evidence that phytoplankton and bacteria are often directly involved in and even may control aggregate formation. But also when aggregation may be a non-biological process, microorganisms indirectly affect it by secreting and consuming organic material, which leads to or prevents aggregation.

3.3. Macroscopic aggregates

Macroscopic aggregates were discovered in the 1950s by submarines and called marine snow due to their snowflake-like appearance when reflecting an underwater light beam (Fig. 2A; Suzuki & Kato 1953). They have been studied extensively in marine systems since then and more recently, to a lesser extent, also in lakes, rivers and estuaries (Fowler & Knauer 1986, Alldredge & Silver 1988, Alldredge & Gotschalk 1990,
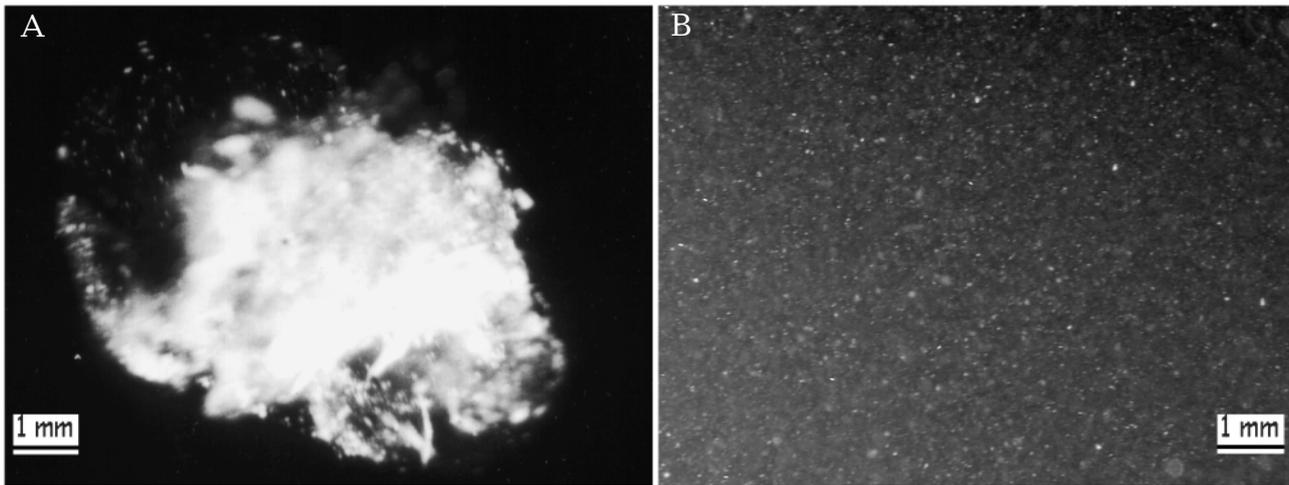
Fig. 2. *In situ* photograph of a marine snow aggregate (A) from a pelagic environment and (B) of microaggregates in a shallow turbid environment (photo M. Lunau)

Alldredge 1992, 1998, Herndl 1992, Grossart & Simon 1993, 1998a,b, Berger et al. 1996, Lampitt 1996, Grossart et al. 1997, 1998, Zimmermann 1997, Ploug et al. 1999, Grossart & Ploug 2000, Neu 2000). The term 'lake snow' was adopted from marine snow for limnetic macroaggregates (Grossart & Simon 1993) and most recently 'river snow' for riverine aggregates (Neu 2000). Coagulation theory has also been applied to aggregate formation (e.g. Jackson 1990, 1995, Hill 1992, Hansen et al. 1995). Today, the general ecological significance of macroaggregates is fairly well understood. In most oceanic and neritic environments and in the lakes studied so far, their size ranges between 300 and 500 µm to several centimeters, and their abundance between <1 and ~100 l^{-1} (Table 1). Macroaggregates in the pelagic zone of lakes appear to be smaller than those in pelagic marine environments. The largest aggregates of ~20 cm and of 1 to 4 m in size were reported from the mesopelagic zone off California (Steinberg et al. 1997) and from the Northern Adriatic Sea (Herndl 1992, Degobbis et al. 1999, Herndl et al. 1999), respectively. The large aggregates in the Northern Adriatic Sea exhibited a very dense structure, and their appearance was described as gel-like or as a false benthos (Kaltenböck & Herndl 1992). Diatom aggregates of ~20 cm in size were also observed in Danish coastal waters (H.-P. Grossart unpubl. results) and may be more abundant than assumed. Due to the fragile nature of these large aggregates they are very difficult to sample.

Across systems, the abundance of macroaggregates is positively related to phytoplankton biomass (Alldredge & Gotschalk 1990), but on a temporal and vertical scale, abundances of macroaggregates often lag behind phytoplankton growth and peak at the end of blooms, with highest numbers below the chlorophyll maximum (Alldredge & Gotschalk 1989, Riebesell 1991b, 1992, Lampitt et al. 1993a, Kiørboe et al. 1994, Alldredge et al. 1995, Grossart et al. 1997, Walsh et al. 1997, Becquevort & Smith 2001). In fact, diatom blooms often, but not always, are terminated by aggregation events and sink out of the mixed layer (Smetacek 1985, Kiørboe et al. 1994, 1996, 1998, Alldredge et al. 1995, Logan et al. 1995, Tiselius & Kuylenstierna 1996). Thus, macroaggregates dominate the sinking POM in marine as well as in lacustrine systems (Fowler & Knauer 1986, Asper 1987, Alldredge & Silver 1988, Riebesell 1991a, Walsh et al. 1997, Grossart & Simon 1998a, Pilskaln et al. 1998). Sinking rates of macroaggregates range from <5 to 200 m d^{-1} and are a positive function of their size (Alldredge et al. 1987, Asper 1987, Alldredge & Gotschalk 1988, 1989, Alldredge & Silver 1988, Grossart & Simon 1993, Kiørboe et al. 1994, Hansen et al. 1996, Pilskaln et al. 1998). Sinking rates determined *in situ*, however, were lower than those determined in settling chambers (Alldredge et al. 1987, Alldredge & Gotschalk 1988), presumably because aggregates become more compact when collected in syringes and transferred to the containers in which sinking rates are determined experimentally. Further, net sinking rates *in situ* are also the results of turbulent water movements and orbital motions, which are most pronounced close to the surface. In fact, aggregates can persist in the mixed layer longer than assumed from their sinking rates (McIntyre et al. 1995) and as reflected by the degradation state of the associated fecal pellets (Alldredge et al. 1987). At density discontinuity layers, sinking aggregates may accumulate because of a reduced excess density or enhanced shear rates (Alldredge & Crocker 1995, McIntyre et al.

Table 1. Abundances of macroaggregates and microaggregates in various aquatic environments. Macroaggregates were quantified visually, or by underwater (UW) photo- or videography. CSP: Coomassie-stained particles; DAPI: 4′,6-diamidino-2-phenylindole-stained particles; TEP: transparent exopolymer particles

Location	Depth (m)	Macroaggregates l^{-1}	Microaggregates l^{-1}	Type	Source
Southern California Bight	7–15	<1–8			Alldredge (1979)
Gulf of California	7–15	<1–3.7			Alldredge (1979)
Northern Atlantic	7–15	0.1–1.0			Alldredge et al. (1986)
Southern California Bight	7–15	1.4–4.0			Alldredge et al. (1986)
Subtropical NW Atlantic	120–530	<0.04			Alldredge & Youngbluth (1985)
Southern California Bight	7–15	0.2–1.7			Alldredge & Gotschalk (1990)
Monterey Bay	100–500	0.5–50[a]			Pilskaln et al. (1998)
Southern California Bight	7–15	<20–79.4			Graham et al. (2000)
Equatorial Pacific	0–80	10–55[a]			Walsh et al. (1997)
Equatorial Pacific	100–1000	2–15[a]			Walsh et al. (1997)
Northern Atlantic	270	<0.5–12[a]			Lampitt et al. (1993b)
Benguela upwelling	0–30	85–640[a]	5.5×10^6– 16×10^6	TEP	Kiørboe et al. (1998)
Coastal Atlantic	0–15	13.5–62.8			Shanks & Del Carmen (1997)
Coastal Pacific	0–15	1–11			Shanks & Del Carmen (1997)
Kattegat (North Sea)	0–50	<130			Tiselius & Kuylenstierna (1996)
North Sea, German Bight	0–30	425–5300[a]			Riebesell (1991a)
Elbe estuary	1	20–4000			Zimmermann (1997)
Baltic Sea (benthic boundary layer)	16–26	152–787			Jähmlich et al. (1999)
Lake Constance	5–25	<1–50			Grossart & Simon (1993)
Lake Constance	5–25	<1–50	$0.5 \times 10^2–1.5 \times 10^6$	TEP	Grossart et al. (1997)
Lake Constance	6–100		$3.1 \times 10^5–1.5 \times 10^6$	DAPI	Brachvogel et al. (2001)
Lake Constance	6–100		$7.1 \times 10^4–2.6 \times 10^6$	TEP	Brachvogel et al. (2001)
Lake Kinneret	15–35		$1.0 \times 10^5–7.0 \times 10^6$	TEP	Grossart et al. (1998)
Lake Kinneret	1–38		$4.4 \times 10^5–2.5 \times 10^7$	TEP	Berman & Viner-Mozzini (2001)
Lake Kinneret	1–38		$1.4 \times 10^5–1.2 \times 10^7$	CSP	Berman & Viner-Mozzini (2001)
Frederiksborg Slottsø	0.5		$0.84 \times 10^8–8.7 \times 10^8$	TEP	Worm & Søndergaard (1998b)
Southern California Bight	10		$2.8 \times 10^4–4.0 \times 10^5$	TEP	Alldredge et al. (1993)
Monterey Bay	5–100		$1.5 \times 10^5–4.9 \times 10^6$	TEP	Alldredge et al. (1993)
Monterey Bay	5–76		$2.5 \times 10^5–5.2 \times 10^6$	TEP	Passow & Alldredge (1994)
Southern California Bight	10		$2.5 \times 10^4–6.3 \times 10^5$	TEP	Passow & Alldredge (1994)
Subtropical NW Atlantic	300–1400		$2.0 \times 10^3–6.0 \times 10^3$	TEP	Passow & Alldredge (1994)
Kattegat (North Sea/Baltic Sea)	0–25		$3.0 \times 10^6–6.0 \times 10^7$	TEP	Mari & Kiørboe (1996)
Kattegat (North Sea/Baltic Sea)	0–30		$5.0 \times 10^7–3.8 \times 10^8$	TEP	Mari & Burd (1998)
Northern Adriatic Sea	0–15		$<1.0 \times 10^3–6.0 \times 10^5$	TEP	Schuster & Herndl (1995)
NW Mediterranean Sea	0–40		$1.0 \times 10^7–2.2 \times 10^8$	TEP	Mari et al. (2001)
NW Mediterranean Sea	0–75		$2.2 \pm 3.2 \times 10^6$	DAPI	Mostajir et al. (1995)
Scripps Pier, Southern California Bight	5		$2.0 \times 10^7–3.4 \times 10^7$	CSP	Long & Azam (1996)
Arabian Sea	0–1500		$2.0 \times 10^6–3.5 \times 10^7$	CSP	Long & Azam (1996)

[a]UW photography

1995). In fact, there is good evidence that the initial accumulation of mucilage at the density discontinuity layer in the northern Adriatic Sea is a result of this phenomenon (Alldredge 1999, Degobbis et al. 1999, Herndl et al. 1999) Aggregates dominated by cyanobacteria-derived material exhibit very low sinking rates or do not sink at all due to the very low excess density (Grossart et al. 1997). Macroaggregates with intensive primary production and entrapped oxygen gas bubbles may even move upward in the water column (Riebesell 1992, Herndl 1992). This may also occur when filamentous and gas vacuole-containing cyanobacteria are abundant (Capone et al. 1997, Stal et al. 1999).

In pelagic systems, numbers of macroaggregates generally decrease with depth, but the size does not. Due to the differential settling rates of aggregates of different sizes, larger aggregates accumulate with depth (Alldredge & Gotschalk 1989). Diurnal differences in the aggregate abundance with highest numbers during the day were reported from the mixed layer (Graham et al. 2000) as well as the upper mesopelagic zone (Lampitt et al. 1993b, Walsh et al. 1997), presumably due to the diurnal vertical migration of zooplankton affecting aggregation in various ways (see below). Possible effects of light-dependent formation of TEP and mucus by phytoplankton or enhanced microbial decomposition during the night need be examined in future studies.

In estuaries and tidally affected shallow seas, macroaggregates are usually smaller than in lakes and the open sea with a size of <2000 µm due to high shear rates leading to disaggregation (Chen et al. 1994, Chen & Eisma 1995, Riebesell 1991a, 1992, Zimmermann 1997, Zimmermann-Timm et al. 1998). In the Elbe estuary, pronounced seasonal variations with smaller aggregates in fall and winter and a continuously decreasing size toward the sea occur (Zimmermann 1997, Zimmermann-Timm et al. 1998). Abundances in these systems are much higher than in lakes and the open sea due to high resuspension rates (Table 1), and highly dynamic changes and redistributions in abundance and size occur within tidal cycles (Eisma 1993, Eisma & Li 1993, Milligan 1995, Zimmermann 1997). This is particularly true for the turbidity maximum, which is established in tidally affected estuaries at salinities between 2 and 6‰ and has great implications for physico-chemical and microbial transformation of dissolved and particulate matter (Eisma 1993, Crump & Baross 1996, Förstner 1996, Grabemann et al. 1996, Crump et al. 1998).

Also in the benthic boundary layer, macroaggregates have been observed even though very little information about their formation and composition is available. Preliminary results from the Baltic Sea show that their abundance is higher than in the pelagic zone (Table 1) and their size smaller (Jähmlich et al. 1999). Because high shear, intense resuspension and thus differential settling of particles occur, aggregate formation presumably is an important phenomenon in this environment, which needs be studied more intensively. According to reports on the fluff layer in the deep ocean, macroaggregates also play an important role in structuring the benthic boundary layer in this environment (Lochte & Turley 1988, Thiel et al. 1988, Thomsen & Graf 1994).

3.3.1. Composition

Macroaggregates are composed of component particles consisting of living, senescent and dead algae, mainly diatoms, but also of coccolithophorids, cysts of thecate dinoflagellates, filamentous cyanobacteria, phytodetritus, diatom frustules, bacteria, protozoans, zooplankton molts and carcasses, abandoned larvacean houses, pteropod webs, fecal pellets, macrophyte detritus, clay and silt minerals, calcite and other particles scavenged from the surrounding water (Alldredge & Silver 1988, Alldredge & Gotschalk 1990, Riebesell 1991b, Herndl 1992, Kaltenböck & Herndl 1992, Grossart & Simon 1993, Lampitt et al. 1993a, Zimmermann & Kausch 1996, Grossart et al. 1997, Alldredge et al. 1998, Kiørboe et al. 1998, Zimmermann-

Timm et al. 1998). Most typical in pelagic marine systems are macroaggregates composed of abandoned larvacean houses, fecal material, diatoms and miscellaneous unidentifiable materials in aging systems. Cysts of dinoflagellates and empty thecae obviously can be scavenged by diatom aggregates and make the aggregates extra dense and rich in organic matter but do not actively form macroaggregates (Alldredge et al. 1998). Algae often are highly enriched on aggregates as compared to the surrounding water (Table 2). Cyanobacterial colonies can be important components of macroaggregates in tropical marine systems (Capone et al. 1997), the Baltic Sea (Stal et al. 1999) and stratified lakes (Grossart et al. 1997, 1998, Worm & Søndergaard 1998a). In shallow seas and estuaries and in the littoral zone of lakes, macrophyte debris, resuspended minerals and organic particles are important in the formation and redistribution of macroaggregates (Eisma 1993, Eisma & Li 1993, Chen & Eisma 1995, Milligan 1995, Grossart et al. 1998). Macroaggregates harbor a rich community of heterotrophic microbes, predominantly bacteria, which contribute only a minor fraction to the organic carbon bound in macroaggregates but are most important for their decomposition and undergo a pronounced succession (see below). Usually, the composition of the macroaggregates reflects the particle spectrum in the water column, even though quantitative differences may also occur due to selective aggregation properties of the primary particles (see above).

The dry weight of pelagic marine and limnetic macroaggregates ranges from 3 to >200 µg per aggregate and is a positive function of the aggregate size (Alldredge & Gotschalk 1988, Alldredge 1998, Alldredge et al. 1998, Ploug & Grossart 2000). Organic carbon constitutes 10 to 40% of the total aggregate dry weight in marine and estuarine aggregates (Alldredge 1979, 1998, Eisma 1993) and up to 66% in limnetic aggregates, with highest percentages when cyanobacterial components are dominant (Grossart & Simon 1993, 1998b). Dissolved organic carbon (DOC) in the interstitial water of marine snow aggregates comprises 20% of the total organic carbon (particulate organic carbon [POC] + DOC) and is a non-negligible fraction of the organic carbon (Alldredge 2000). Dry weight, POC, DOC and particulate organic nitrogen (PON) significantly increase with the aggregate volume to the power of 0.49 to 0.54 (Alldredge 1998). The dry mass, however, occupies only <1% of the total aggregate volume and its relative proportion decreases with the aggregate size. This relationship reflects the fractal nature of macroscopic aggregates and their high porosity, which increases with the aggregate size (Alldredge & Gotschalk 1988, Logan & Alldredge 1989, Logan & Wilkinson 1990, Alldredge 1998). The C:N (w:w) ratio ranges between 5:1 and 20:1 and is a posi-

Table 2. Colonization of macroaggregates (agg) by various organisms and enrichment factors (EF) relative to the surrounding waters. EF were calculated as the abundances of organisms per volume aggregate divided by the abundances per volume surrounding water. na: not available

Organism	Location	Cells (ind.) agg^{-1}	EF	Source
Algae				
Phytoplankton <2 µm	NW Atlantic	na	19–43	Caron et al. (1986)
Phytoplankton 2–20 µm	NW Atlantic	na	7–67	Caron et al. (1986)
Phytoplankton >20 µm	NW Atlantic	na	13–700	Caron et al. (1986)
Diatoms	Monterey Bay	5.2×10^3	<27	Silver et al. (1978)
Diatoms	Monterey Bay	6.0×10^4–4.2×10^5	130–1.7×10^3	Silver et al. (1998)
Synecchococcus	Monterey Bay	1.9×10^6–5.4×10^6	45–160	Silver et al. (1998)
Diatoms	Southern California Bight	4.1×10^2–6.0×10^3	160–3.9×10^3	Alldredge et al. (1998)
Dinoflagellates	Southern California Bight	0.53×10^2–1.2×10^3	110–1.2×10^4	Alldredge et al. (1998)
Synecchococcus	NE Atlantic	1.0×10^4–2.5×10^4	1.0×10^3–7.6×10^3	Turley & Mackie (1994)
Zooplankton				
Harpacticoid copepods	Northern Adriatic Sea	0–250	3.5–10	Bochdansky & Herndl (1992)
Nauplii	Northern Adriatic Sea	0–1233	3.7–145	Bochdansky & Herndl (1992)
Polychaete larvae	Northern Adriatic Sea	30–3633	344–765	Bochdansky & Herndl (1992)
Juvenile turbellarians	Northern Adriatic Sea	0–1208	62–670	Bochdansky & Herndl (1992)
Calanoid copepods	Gulf of Mexico	0.1–32.9	0.9–1.9	Green & Dagg (1997)
Cyclopoid copepods	Gulf of Mexico	0.6–42	0.8–100	Green & Dagg (1997)
Harpacticoid copepods	Gulf of Mexico	0.2–14.3	18.5–57.1	Green & Dagg (1997)
Crustacean nauplii	Gulf of Mexico	1.6–72.7	100	Green & Dagg (1997)
Polychaete larvae	Gulf of Mexico	0.1–11.4	7.1–35.8	Green & Dagg (1997)
Molluscs	Gulf of Mexico	0.2–1.4	0.2–12.2	Green & Dagg (1997)
Salps	Gulf of Mexico	0.2–1.4	0.4–6.9	Green & Dagg (1997)
Larvaceans	Gulf of Mexico	0.1–26.2	8.2–35.1	Green & Dagg (1997)
Ascidians	Gulf of Mexico	1.0–4.1	0.45	Green & Dagg (1997)
Calanoid copepods	Coastal Atlantic	na	<3[b]	Shanks & Edmondson (1990)
Cyclopoid copepods	Coastal Atlantic	na	<3[b]	Shanks & Edmondson (1990)
Harpacticoid copepods	Coastal Atlantic	na	2–35[b]	Shanks & Edmondson (1990)
Crustacean nauplii	Coastal Atlantic	na	0.9–2[b]	Shanks & Edmondson (1990)
Nematodes	Coastal Atlantic	na	50–100[b]	Shanks & Edmondson (1990)
Polychaete larvae	Coastal Atlantic	na	3–20[b]	Shanks & Edmondson (1990)
Polychaetes	Coastal Atlantic	na	60–87[b]	Shanks & Edmondson (1990)
Polychaete larvae	Coastal Atlantic	<1	18–70[b]	Shanks & Del Carmen (1997)
Polychaete larvae	Coastal Pacific	<1	3–27[b]	Shanks & Del Carmen (1997)
Larvaceans	Coastal Atlantic/Pacific	na	2–3[b]	Shanks & Walters (1997)
Calanoid/cyclopoid copep.	Coastal Atlantic/Pacific	na	0.1–2[b]	Shanks & Walters (1997)
Harpacticoid copepods	Coastal Atlantic/Pacific	na	2–55[b]	Shanks & Walters (1997)
Copepod nauplii	Coastal Atlantic/Pacific	na	1–11[b]	Shanks & Walters (1997)
Nematodes	Coastal Atlantic/Pacific	na	8–88[b]	Shanks & Walters (1997)
Foraminifera	Coastal Atlantic	na	47[b]	Shanks & Walters (1997)
Bivalve veliger	Coastal Atlantic/Pacific	na	4.5–10[b]	Shanks & Walters (1997)
Gastropod veliger	Coastal Atlantic/Pacific	na	2–34[b]	Shanks & Walters (1997)
Anthozoan larvae	Coastal Pacific	na	2–32[b]	Shanks & Walters (1997)
Total copepods	Coastal Pacific	109.8 ± 28.4	197	Steinberg et al. (1994)
Calanoid copepods	Coastal Pacific	17.8 ± 7.6		Steinberg et al. (1994)
Cyclopoid copepods	Coastal Pacific	68.7 ± 20.0		Steinberg et al. (1994)
Harpacticoid copepods	Coastal Pacific	23.2 ± 11.3		Steinberg et al. (1994)
Protozoans				
Flagellates	NW Atlantic	na	17–520	Caron et al. (1986)
Flagellates	NE Atlantic	1.4×10^3–5.9×10^3	1.3×10^3–3.3×10^3	Turley & Mackie (1994)
Choanoflagellates	Northern Adriatic Sea	0.2×10^5–2.1×10^6[a]	2–253	Herndl (1988)
Monads	Northern Adriatic Sea	0.2×10^5–1.2×10^6[a]	1–290	Herndl (1988)
Ciliates	Monterey Bay	0–130	5–8.6×10^3	Silver et al. (1978)
Ciliates	Monterey Bay	1.5×10^3–1.7×10^4	30	Silver et al. (1998)
Sarcodines	Monterey Bay	220–230	220–380	Silver et al. (1998)
Flagellates	Elbe estuary	2–25	na	Zimmermann-Timm et al. (1998)
Ciliates	Elbe estuary	1–12	na	Zimmermann-Timm et al. (1998)
Amoebae	Elbe estuary	1–211	na	Zimmermann-Timm et al. (1998)

Table 2 (continued)

Organism	Location	Cells (ind.) agg^{-1}	EF	Source
Bacteria				
	Southern California Bight	1.3×10^6–1.7×10^6	30–37	Alldredge et al. (1986)
	NW Atlantic	1.8×10^6–2.8×10^6	20–55	Alldredge et al. (1986)
	Monterey Bay	4.2×10^5–6.7×10^6	83–300	Alldredge et al. (1986)
	Monterey Bay	3.2×10^8–5.4×10^8	0.6–16	Silver et al. (1998)
	NE Atlantic	2.5×10^5–4.3×10^5	400–5,700	Turley & Mackie (1994)
	Southern California Bight	0.1×10^6–1.7×10^6	na	Simon et al. (1990)
	Northern Adriatic Sea	1.3×10^6–$1.1 \times 10^{8\,a}$	2–133	Herndl (1988)
	Lake Constance	1.2×10^6–2.3×10^7	35–220	Grossart & Simon (1993)
	Elbe estuary	5.0×10^6–5.0×10^7	na	Zimmermann-Timm et al. (1998)

[a]per ml agg; [b]% on agg

Table 3. Dyes for staining specific biopolymeric components on aggregates. DTAF: 5-(4,6-dichlorotriazinyl)aminofluorescein; FITC: fluorescein isothiocyanate; TRITC: tetramethyl rhodamine isothiocyanate

Dye	Specificity	Source
Alcian Blue	Acidic polysacharides	Alldredge et al. (1993), Logan et al. (1994)
Coomassie Blue	Proteins	Long & Azam (1996)
Toluidine Blue	Proteoglycanes, acidic polysaccharides, polymers	Chayen et al. (1973)
DTAF	Polysaccharides	Schumann & Rentsch (1998)
FITC-/TRITC-labeled lectins	Specific bands of polysaccharides such as:	
Glycine max	*N*-acetyl-D-galactosamine	Grossart (1999)
Bandeiraea s. II	*N*-acetyl-D-glucosamine	Grossart (1999)
Wheat germ	*N*-acetyl-D-glucosamine, *N*-acetylneuraminic acid	Grossart (1999)
Concavaline A	Methyl α-D-mannopyranoside D (+) mannose	Grossart (1999), Neu (2000)
Abrin	D (+) galactose	Neu (2000)
Lentil	α-methyl-D-mannopyranoside D (+) mannose	Neu (2000)
Limulin	*N*-acetylneuraminic acid D-glucuronic acid	Neu (2000)
Lotus	L (-) fucose *N*-acetyl-D-glucosamine	Neu (2000)

tive function of the aggregate size except for larvacean houses, which are not formed by aggregation (Alldredge & Silver 1988, Grossart & Simon 1993, Müller-Niklas et al. 1994, Alldredge 1998, Grossart & Ploug 2000). Depending on the abundance, macroaggregates can contribute between <4 and ~30% to total POC in pelagic marine and lacustrine systems (Alldredge & Silver 1988, Riebesell 1991a, Alldredge et al. 1998, Grossart & Simon 1998b) but presumably much higher proportions in estuaries. Respective data, however, are not yet available.

The dominant biopolymers of macroaggregates are carbohydrates, proteins (or particulate combined amino acids [PCAA]) and lipids, constituting the majority of the aggregate-bound POM and also of the phytoplankton as the primary source of pelagic macroaggregates (Alldredge 1979). Surprisingly little information, however, is available about the biochemical composition of macroaggregates of different origin. PCAA was 0.20 to 1.13 µg per aggregate in selected marine snow samples from surface waters composed of larvacean houses and diatoms (Smith et al. 1992) and 0.14 to 0.47 µg per aggregate in lake snow samples

(Grossart & Simon 1998b). These values constituted 8 to 51% of the aggregate-bound POM, which were higher proportions than of total POM (Grossart & Simon 1998b). This notion indicates that macroaggregates may be of higher nutritive value as food for particle feeders than total POM, in particular when algae with a low C:N ratio constitute only minor proportions of total POM. In fact, macroaggregates are a food source for various animals (see below). The microscopic and chemical analysis of coastal sedimenting material and of riverine macroaggregates in the Elbe estuary, Germany, indicated that substantial amounts of their POC consisted of macrophyte debris and lignin fairly refractory to microbial decomposition, except during phytoplankton blooms (Cowie & Hedges 1992, Zimmermann-Timm et al. 1998).

The composition of aggregates often is examined qualitatively by brightfield or epifluorescence microscopy after staining with dyes specific for certain biochemical compounds (Table 3). The recent and ongoing introduction of highly intense fluorescent dyes such as 5-(4, 6-dichlorotriazynil)aminofluorescein (DTAF) and fluorescent lectins to detect specific poly-

saccharides will further help elucidate more details about the composition, fate and dynamics of organic micro- and macroaggregates (Schumann & Rentsch 1998, Grossart 1999, Neu 2000). Scanning (SEM) or transmission electron microscopy also has been used to examine the composition of micro- and macroaggregates (e.g. Paerl 1974, Leppard et al. 1979, Heissenberger et al. 1996, Grossart & Simon 1998b). It requires, however, fixing and drying of the specimen and thus may introduce artifacts. The introduction of confocal laser scanning microscopy (CLSM) provided new options to study the spatial organization of aggregates and, in combination with specific dyes and fluorescent lectins, allowed attractive and new important insights into the heterogeneous biochemical composition of aggregates (Caldwell et al. 1992, Manz et al. 1999, Neu 2000). In contrast to SEM it requires only little pre-treatment of the specimen and allows it to be examined when fully hydrated. The combination of CLSM and fluorescent *in situ* hybrization with rRNA-targeted oligonucleotides further provides attractive means to study the spatial distribution of bacterial populations colonizing aggregates (Wagner et al. 1994, Manz et al. 1999, see Section 4.4.1).

3.4. Microaggregates

Microaggregates often appear quite similar to macroaggregates when examined microscopically even though their composition is not as diverse. Certain classes of microaggregates such as TEP and protein-containing particles (see Section 3.4.2), which may also include non-aggregated particles, are dominated by specific biopolymers. The abundance of microaggregates, however, is higher than that of macroaggregates by several orders of magnitude (Table 1) and they often exhibit somewhat different spatio-temporal distributions from macroaggregates, indicating that they are differently involved in the processes of POM cycling, i.e. formation and decomposition of macroaggregates. Their abundance and size are inversely related (Riebesell 1991a, Li & Logan 1995, Mostajir et al. 1995, Long & Azam 1996, Mari & Burd 1998, Worm & Søndergaard 1998b, Brachvogel et al. 2001). Due to their high abundance, microaggregates collide much more frequently with macroaggregates than the latter with each other. This implies that they are subject to removal by macroaggregates provided they have a high sticking efficiency or are captured efficiently. Knoll et al. (2001) examined the formation of microaggregates during a limnetic diatom bloom in Lake Constance and found that they are formed freshly from senescent diatoms and that their size increased from 50 to 80 µm to >100 µm within 30 h.

These types of microaggregates, however, have only rarely been found *in situ*, presumably because of their high removal rate (Brachvogel et al. 2001). Azam et al. (1993), by examining the aggregation of marine diatoms, made similar observations of the initial formation of microaggregates and later of macroaggregates. Some types of microaggregates persist for quite a while and are not scavenged by macroaggregates, nor do they aggregate or sink, presumably because they have a low sticking efficiency and have a Reynolds number far below 1 (Drapeau & Dam 1995, Berman & Viner-Mozzini 2001, Brachvogel et al. 2001). In shallow turbid environments such as estuaries and tidally affected shallow seas with high hydrodynamic forcing, microaggregates exhibit the highest abundances and contain high amounts of resuspended inorganic particles (Fig. 2B). In the turbidity maximum of the Columbia River estuary on the Pacific NW coast of the USA, microaggregates in the size range 3 to 10 µm were associated with 87% of total bacterial production, thus demonstrating a key role of this size fraction in the estuarine carbon cycling (Crump & Baross 2000). Hence, microaggregates can be involved very differently in the cycling of organic matter, depending on the given system, the load of suspended matter and the quality of the POM. Due to the small size it has not been possible to determine the individual amount of organic carbon or nitrogen of natural microaggregates. Recently, however, new stains specific for various biopolymers were introduced (Table 3), which enabled the determination of the biopolymer composition of organic aggregates and led to the discovery of new classes of microparticles outlined below.

3.4.1. Transparent exopolymer particles

TEP were first described in 1993 from neritic waters off California (Alldredge et al. 1993). Thereafter they were found in many other environments including lakes and identified as a ubiquitous class of microparticles (Passow & Alldredge 1994, Passow et al. 1994, Logan et al. 1995, Schuster & Herndl 1995, Mari & Kiørboe 1996, Grossart et al. 1997, 1998, Kiørboe et al. 1998, Mari & Burd 1998, Worm & Søndergaard 1998b, Berman & Viner-Mozzini 2001, Brachvogel et al. 2001, Mari et al. 2001). TEP are stained bright blue by a simple technique with alcian blue (Alldredge et al. 1993, Logan et al. 1994). The abundance of TEP ranges from $<10^2$ to $>10^7$ l^{-1} (Table 1) and in general is positively correlated to phytoplankton biomass. The size varies between ~5 and >100 µm, and size-class distributions can change quite rapidly in particular during aggregation events. Such aggregation events may clear the water column of TEP and appear to be one of the most

important mechanisms to reduce their abundance (Logan et al. 1995, Mari & Kiørboe 1996). Several field and experimental studies showed that TEP is produced by diatoms during the exponential growth or stationary phase (Kiørboe & Hansen 1993, Passow & Alldredge 1994, 1995, Passow et al. 1994, Schuster & Herndl 1995, Engel 2000). The amount of TEP produced is species specific and depends on the growth conditions. In some cases acidic polysaccharides do not detach from the surface of phytoplankton cells such that they directly stick together and form macroaggregates, and TEP is produced only in the course of the microbial break-down of the aggregates, possibly also from colloidal material (Kiørboe & Hansen 1993, Hansen et al. 1995, Passow & Alldredge 1995, Grossart et al. 1997, Mari & Burd 1998, Engel 2000). TEP associated with diatom aggregates obviously reduces their excess density and thus their sinking rate (Alldredge 1999, Engel & Schartau 1999). Thecate dinoflagellates also produce large amounts of mucopolysaccharides, but this material is not TEP because it does not stain with alcian blue (Alldredge et al. 1998). The C:N ratio of TEP, formed from diatom exudates by bubbling, has been determined to be close to 7, which is surprisingly low (Mari 1999). Because the experiments were carried out with non-axenic algae, TEP was possibly colonized by bacteria, thus reducing the C:N ratio. In a field study in the northwestern Mediterranean Sea, the C:N ratio of TEP produced from DOM by bubbling ranged between 6.5 and 70 (Mari et al. 2001). Mean values before and after a phytoplankton summer bloom were 11.6 as compared to 37.7 during the bloom.

Bacteria, in particular when attached to surfaces like biofilms or macroaggregates, produce large amounts of exopolysaccharides as well (Decho 1990, Costerton et al. 1995, Heissenberger et al. 1996, Stoderegger & Herndl 1998). When freely suspended, they were also reported to produce TEP and thus may be an important source of these microaggregates under non-bloom conditions of phytoplankton (Stoderegger & Herndl 1999). The general significance of heterotrophic bacteria in the production and cycling of TEP, however, is not yet known. Because all experimental studies on the formation of TEP by phytoplankton were carried out with non-axenic cultures and because under *in situ* conditions phytoplankton are always associated with bacteria, it is possible that bacteria are much more actively involved in the formation of TEP than we assume. Bacteria in the phycosphere may control the production of TEP by algae by reducing the availability of inorganic phosphate to algae, resulting in enhanced rates of algal polysaccharide secretion (Guerrini et al. 1998, Azam et al. 1999, Grossart 1999). To specifically examine the role of bacteria in forming

TEP, comparative experiments with axenic and non-axenic algae need be carried out. It has been suggested and inferred from TEP size spectra and coagulation models that TEP is formed of colloidal precursors, thus representing a significant sink of dissolved carbohydrates (Kiørboe & Hansen 1993, Passow & Alldredge 1994, Mopper et al. 1995, Mari & Burd 1998). Recently, it has been shown experimentally that TEP are formed from colloidal precursor material and that formation rates vary according to the growth conditions of phytoplankton blooms (Zhou et al. 1998, Passow 2000, Mari et al. 2001).

TEP has attracted much interest because it was identified as important in the aggregation of diatom blooms. Interestingly, a class of microparticles with the properties found in TEP was hypothesized and predicted to exist shortly before the discovery of TEP (Hill 1992). Coagulation theory often could not properly predict aggregation events at the end of phytoplankton blooms without postulating the existence of a class of microparticles with properties as discovered with TEP. In fact, TEP must be considered to be one of the most important biological factors controlling the aggregation of phytoplankton blooms, leading to the formation of macroaggregates. One case study in coastal waters found that a diatom-dominated phytoplankton community did not develop a bloom with a terminating sedimentation event because the concentration of TEP remained surprisingly low (Kiørboe et al. 1996). Instead, most algae were sinking packaged in fecal pellets or as intact cells attached to larvacean houses. The specific roles of diatoms and in particular of bacteria in forming, cycling and degrading TEP are not yet comprehensively understood and need further work, which certainly will reveal more interesting details.

3.4.2. Coomassie blue-stained particles

Recently, a class of microparticles containing protein was discovered in the sea by staining water samples with Coomassie brilliant blue, a protein-specific dye (Long & Azam 1996). Their shape was quite variable and the size ranged from a few to >150 µm. Their abundance ranged from ~10^6 to 3.5×10^7 l^{-1} (Table 1) and decreased vertically, suggesting a positive relationship with phytoplankton biomass. Interestingly, in a few comparisons, the abundance was systematically higher than that of TEP determined in parallel samples. Due to the incompatible staining of particles by alcian blue and Coomassie brilliant blue, a direct comparison with respect to their content of acidic polysaccharides and proteins is not possible. In the only other study available, Berman & Viner-Mozzini (2001)

investigated these protein-containing particles in Lake Kinneret. They found abundances ranging from ~10^4 to ~10^7 l^{-1}, a close correlation of the abundance and area to the phytoplankton biomass and, in contrast to Long & Azam (1996), systematically lower numbers than of TEP. The general role, significance and fate of the protein-containing particles is not yet known. They may also be involved in the formation of macroaggregates but whether they exhibit a key function similar to that of TEP is at least questionable. Because protein is decomposed fairly rapidly, the microbial cycling of these particles may be higher than that of TEP (Grossart 1999). Further work is needed to better elucidate the origin and significance of these particles.

3.4.3. DAPI-stained particles

A class of microparticles that are stained yellow by DAPI (4′,6-diamidino-2-phenylindole), a DNA-specific fluorescent dye that stains double-stranded DNA blue and is normally used to stain and enumerate bacterial cells, has been described from Mediterranean waters (Mostajir et al. 1995). These particles occurred in the size range of 0.2 to 20 µm, with abundances around 2.2×10^7 l^{-1} (Table 1), and with an exponentially decreasing size-class distribution. There was a trend of decreasing numbers with depth in the size classes <5 µm but little variation with depth in the size classes 5 to 15 µm. Even though some covariations with chlorophyll were found and some changes in the distribution with stratification and mixing, nothing is known about their origin, fate and role in aggregation.

Somehow, comparable microaggregates, stained blue or yellow with DAPI, were found in Lake Constance, Germany (Brachvogel et al. 2001). They were studied in the size range 5 to >60 µm and exhibited abundances between 3.1×10^5 and 1.53×10^6 l^{-1} (Table 1) with highest numbers in the smallest size class (8 to 20 µm). They consisted predominantly of phytoplankton and zooplankton debris, diatom frustules and unidentifiable detrital components. The spatio-temporal patterns of these microaggregates differed from that of TEP, macroaggregates and diatoms, and exhibited some covariations with the biomass of chrysophytes and dinoflagellates. Brachvogel et al. (2001) suggest that they are the remains of detrital POM, either directly from senescent chrysophytes and dinoflagellates in surface waters, or from decomposed macroaggregates at greater depths. The conspicuous colonization by β-*Proteobacteria* and bacteria of the *Cytophaga/Flavobacteria* cluster but not by α-*Proteobacteria* substantiated the fact that these microaggregates are rather refractory remains of detrital POM and produced at the depth where they were

found (see Section 4.4.1.2). Further studies have to better elucidate the origin, significance and role of these microaggregates, and how they are involved in the formation or break-down of macroaggregates.

4. COLONIZATION OF AGGREGATES BY HETEROTROPHIC ORGANISMS

From the previous sections it is obvious that the occurrence and formation of organic aggregates is rather variable and dynamic, as are their origin, size and composition. They undergo pronounced changes and successions, and interact in various ways with the surrounding organisms, particles and dissolved material. These dynamics and interactions exhibit differences depending on the given environment, e.g. the pelagic zone of lakes and the sea, estuaries or rivers. A closer examination shows that these changes, in particular after aggregates are formed, are greatly influenced by the activities of the aggregate-associated heterotrophic organisms and in particular microbes, and are reflected in the colonization patterns of the aggregates. Hence, the understanding of these changes is only as good as our knowledge of the activities and composition of the microbial communities involved.

4.1. Metazoans

Since macroaggregates were identified as important microenvironments for the cycling and decomposition of organic matter in aquatic ecosystems, many studies were carried out to study their colonization by various heterotrophic organisms. Besides algae (see above), a great variety of metazoans was found on marine, riverine and estuarine aggregates (Table 2). Colonization of marine snow aggregates by metazoans was first reported by Alldredge (1972) but only during the last 10 yr was the colonization of aggregates by metazoans studied more extensively (Shanks & Edmondson 1990, Bochdansky & Herndl 1992, Steinberg et al. 1994, 1997, Green & Dagg 1997, Shanks & Del Carmen 1997, Shanks & Walters 1997, Zimmermann-Timm et al. 1998, Kiørboe 2000). Most metazoans on aggregates are enriched in numbers as compared to the surrounding water, and aggregates in coastal waters harbor a substantial fraction of all metazoans (Table 2). So far, little is known about the general significance of metazoans for the cycling and decomposition of aggregates. An examination of the behavior of zooplankton in the presence of aggregates showed that most animals visited and fed on aggregates for only a few minutes, but the behavior of individual taxa exhibited

pronounced differences (Green & Dagg 1997, Shanks & Del Carmen 1997, Shanks & Walters 1997, Kiørboe 2000). The abundance of zooplankton on aggregates integrated over time implies much higher enrichment factors than presented in Table 2, in the order of 10^2 to 10^4, 1 to 2 orders of magnitude higher than of protozoans and prokaryotes (Kiørboe 2000). These high enrichment factors cannot be explained by simple encounter rates or scavenging of zooplankton by sinking aggregates, and it has been proposed and shown that zooplankton detect sinking aggregates remotely by chemical clues due to the DOM plume leaking out (Kiørboe 2000, 2001, Kiørboe & Thygesen 2001). The swimming behavior of large zooplankton such as euphausiids can cause fragmentation of marine snow aggregates, whereas that of copepods and other smaller zooplankton cannot (Dilling & Alldredge 2000). Hence, the individual behavior of zooplankton in the surroundings of aggregates is important for their fate.

There is experimental evidence that zooplankton and juvenile fish and fish larvae actively feed on lake snow as well as marine snow and that the aggregate quality affects feeding and ingestion rates (Larson & Shanks 1996, Shanks & Walters 1996, 1997, Grossart et al. 1998, Dilling et al. 1998, Kamjunke & Mehner 2001, Kamjunke et al. 2002). The presence of TEP reduces ingestion of diatoms by euphausiids, but TEP are ingested as well as an alternative food source (Passow & Alldredge 2000). Coprophagy and coprorhexy need also to be considered as processes by which zooplankton interact with, disrupt or ingest aggregates dominated by fecal material (Lampitt et al. 1990). Feeding by macrozooplankton and fish on macroaggregates is a direct link between the microbial loop and the higher trophic levels of the food web, because these animals reach bacteria associated with aggregates which they cannot ingest as freely suspended picoplankton cells. Because bacteria can constitute up to 50% of the protein of macroaggregates (Simon et al. 1990), they can be a major aggregate-associated food source for macrozooplankton even though phytoplankton algae are usually a preferred food source. A first estimate by Kiørboe (2000) indicates that decomposition rates of marine snow by associated invertebrate zooplankton are of similar magnitude to that by bacterial activity. Hence, zooplankton may play a significant role in reducing the export production from the euphotic zone due to fragmentation, consumption and mineralization of aggregates (Banse 1990, Lampitt et al. 1990, Dilling et al. 1998, Dilling & Alldredge 2000, Graham et al. 2000, Kiørboe 2000). Further studies are needed to better elucidate the role of metazoans for the decomposition of organic aggregates.

4.2. Fungi

Fungi are the primary decomposers of leaf litter and other macrophyte-derived detrital material in streams and rivers (e.g. Bärlocher 1992), and in the marine environment (e.g. Fell & Newell 1998). Therefore, they presumably also colonize micro- and macroaggregates in these ecosystems rich in macrophyte-derived organic matter. However, to our knowledge, nothing is known about the colonization of aggregates by fungi, which is a great gap in our understanding of the microbial ecology and decomposition of aggregates.

4.3. Protozoans

Protozoans such as heterotrophic flagellates, ciliates, sarcodines and amoebae have been found to colonize micro- and macroaggregates, and are highly enriched as compared to the surrounding water (Table 2). The protozoan community on aggregates exhibits differences from that in the surrounding water, because of the strikingly different environmental conditions, which obviously select more for benthic and biofilm-associated forms (Silver et al. 1978, Caron 1991, Rogerson & Laybourn-Parry 1992, Artolozaga et al. 1997, Zimmermann-Timm et al. 1998). Occasionally, nearly all flagellates and ciliates are found on aggregates and very few freely suspended in the water (Silver et al. 1978). It has been hypothesized that particles may be instrumental for the growth and survival of some species of flagellates and ciliates in the pelagic environment by grazing on particle-associated bacteria (Caron et al. 1982, 1986). Protozoans feed on aggregate-associated bacteria and algae. It has been shown that feeding by *Noctiluca scintillans* on diatom aggregates can be so intense that it prevents loss of aggregates due to sinking (Tiselius & Kiørboe 1998). Several studies showed that the population dynamics of protozoans follow that of bacteria and that they are important in regenerating ammonium and primary amines, which are released into the surrounding water (Pomeroy et al. 1984, Biddanda & Pomeroy 1988, Gotschalk & Alldredge 1989, Artolozaga et al. 1997, Grossart & Simon 1998a, Grossart & Ploug 2001). Hence, an important function appears to be remineralization of the aggregate-associated nitrogen and phosphorus, predominantly by grazing of bacteria. Interactions between protozoans and bacteria on aggregates, however, are still poorly studied. Recently, Ploug & Grossart (2000) showed that bacterial growth on aggregates can be balanced by bacterivory of protozoans. A further indication of intense bacterial grazing by protozoans is the occurrence of high abundances of aggregate-associated filamentous bacteria, which are known to be a

phenotypic response to protozoan grazing (Jürgens & Güde 1994, Grossart & Simon 1998b, Grossart & Ploug 2000).

4.4. Prokaryotes

Prokaryotes, predominantly *Bacteria*, have been found on nearly all types of aggregates studied so far, including marine, lacustrine, riverine, and estuarine macro- and microaggregates. Microaggregates without any bacterial colonization were also reported (Berger et al. 1996, Long & Azam 1996, Zimmermann 1997, Brachvogel et al. 2001). Inorganic components such as calcite and clay particles are not usually colonized. The bacterial cells usually are not uniformly distributed on aggregates but often form microcolonies and occur in filamentous structures (e.g. Logan et al. 1994, Grossart & Simon 1998b, Grossart & Ploug 2000). The number of bacteria per aggregate is positively correlated to the aggregate size, ranging between <100 per aggregate on the smallest microaggregates (Passow & Alldredge 1994, Berger et al. 1996, Brachvogel et al. 2001, Knoll et al. 2001) and >10^6 bacteria per aggregate on macroaggregates of a few to >10 mm, respectively (Table 2). Bacteria on aggregates are enriched as compared to the abundances of free-living bacteria in the surrounding water (Table 2). Enrichment factors decrease with increasing aggregate size (e.g. Alldredge et al. 1986, Davoll & Silver 1986, Herndl 1988, Alldredge & Gotschalk 1990, Turley & Mackie 1994, Ploug et al. 1999, Kiørboe 2000, Ploug & Grossart 2000). The bacterial abundance on aggregates is not proportional to the aggregate volume (Alldredge & Gotschalk 1990, Ploug et al. 1999, Ploug & Grossart 2000), and the number of bacteria per unit surface area is inversely related to the aggregate size, at least partially due to the fractal nature of the aggregates. Grossart & Simon (1993, 1998b) found that in Lake Constance the total number of aggregate-associated bacteria increased with depth, due to an increasing aggregate size. Grossart & Simon (1998b) and Herndl (1988) described a morphological succession of the bacterial community on aggregates with increasing age, indicating that aggregates undergo different decompositional stages.

The relative proportion of aggregate-associated bacteria to total bacterial numbers varies greatly, depending mainly on the abundance of aggregates. In most pelagic environments they constitute <10% and often <5% of total bacterial numbers (e.g. Alldredge & Gotschalk 1990, Grossart & Simon 1998b, Turley & Stutt 2000). In riverine and estuarine systems, however, they may constitute as much as 90% of total bacterial numbers and production (Bell & Albright 1981, Bent & Goulder 1981, Zimmermann & Kausch 1996, Zimmermann 1997, Crump & Baross 2000). In most environments, even with high amounts of suspended matter, the relative proportion of particle-associated bacteria is lower than that of free-living bacteria (Kirchman 1993, Berger et al. 1996, Crump & Baross 1996, Crump et al. 1998). Interestingly, it has been estimated that the number of bacteria colonizing TEP in pelagic marine environments equals 5 to 40% and in some cases 60% of the total bacterial numbers, suggesting that if TEP are not visualized by alcian blue many of these bacteria are enumerated as being free-living (Alldredge et al. 1993, Passow & Alldredge 1994, Mari & Kiørboe 1996, Worm & Søndergaard 1998b).

Bacteria on aggregates are often bigger than free-living bacteria in the surrounding water, ranging between 0.01 and 1.0 µm^3 or 30 to >100 fg per cell (Alldredge et al. 1986, Simon 1987, Herndl 1988, Alldredge & Gotschalk 1990, Simon et al. 1990). This is presumably due to the more favorable nutritive conditions than those in the surrounding water.

4.4.1. Structural composition of aggregate-associated bacterial communities

A very important question to better understand the specific roles and functions of bacterial communities on aggregates concerns their structural composition. Due to the application of various molecular techniques, including the establishment of procaryotic clone libraries on the basis of sequencing the polymerase chain reaction (PCR)-amplified 16S rRNA gene or fragments of it, and fluorescence *in situ* hybridization with rRNA-targeted oligonucleotide probes of various specificity (FISH), fairly detailed and important information on the community structure of aggregate-associated bacterial communities has become available.

It must be kept in mind, though, that all the information about the structure of bacterial communities based on phylogenetic relationships does not reveal any trait of their physiological properties, except for a few phylogenetic clusters, such as the sulfate reducers (subcluster of δ-*Proteobacteria*) or the ammonium oxidizers (subcluster of β-*Proteobacteria*). This drawback calls for a combination of phylogenetic and physiological analyses of bacterial communities. Due to very recent and ongoing methodological developments, the tools have become more and more available to perform such combined studies. Applying probes for specific aggregate-associated populations or physiological groups such as sulfate-reducing bacteria (SRB) (Grossart & Ploug 2000), methanogens or ammonium oxidizers, and combining them with substrate-specific fluores-

cent dyes and CLSM, or combining them with microautoradiography (Lee et al. 1999, Ouverney & Fuhrman 1999, Cottrell & Kirchman 2000) will result in new and exciting insights into the composition, the physiological activity and the spatial organization of aggregate-associated microbial communities.

4.4.1.1. Marine environments

On the basis of terminal restriction fragment length polymorphism or fully or partially sequenced clone libraries of the 16S rRNA gene, the diversity of marine snow- and particle-associated bacterial communities as compared to free-living bacterial communities in the surrounding water has been studied in various marine environments and an estuary. A high diversity was found on marine snow with dominant phylotypes of the *Cytophaga/Flavobacteria* cluster, and α- and γ-*Proteobacteria* (DeLong et al. 1993, Rath et al. 1998, Moeseneder et al. 2001). In contrast to these results, Acinas et al. (1999), in western Mediterranean waters, found only a low diversity in particle-associated bacterial communities with phylotypes belonging to the γ-*Proteobacteria*, and a higher diversity in free-living bacterial communities with phylotypes also from other phylogenetic lineages. In the same marine environment, Phillips et al. (1999) examined the composition of the ammonium-oxidizing bacterial community. They found that all particle-associated ammonium oxidizers belonged to the *Nitrosomonas* cluster whereas free-living ammonium oxidizers belonged to the *Nitrosospira* cluster. Hence, this notion demonstrates that the same chemolithotrophic metabolism is performed by genetically distinctly different clusters in each habitat, obviously reflecting the different adaptational properties of the members of these clusters to the given environmental conditions. Bidle & Azam (2001) analyzed the bacterial community on aggregates of diatom detritus by denaturing gradient gel electrophoresis of PCR-amplified 16S rDNA fragments and found distinct temporal colonization patterns with a dominance of γ-*Proteobacteria* and *Sphingobacteria/Flavobacteria*.

The results mentioned above only give information on the qualitative composition of bacterial communities but no quantitative data. Quantitative information is provided by analysis with FISH (Amann et al. 1995). Following this approach, members of the *Cytophaga/Flavobacteria* cluster were found to constitute around 30% of the DAPI-stainable cells on marine snow in the Southern California Bight (Ploug et al. 1999). Bacteria of this cluster, together with γ-*Proteobacteria*, were also dominant on naturally derived marine snow aggregates of various age in the polar frontal zone of the Southern Ocean, whereas α-*Proteobacteria* constituted much lower proportions (Fig. 3). Only in 1 case were α-*Proteobacteria* more important than γ-*Proteobacteria*, but cells of the *Cytophaga/Flavobacteria* cluster could not be enumerated in this and the other experiments in which no numbers of this cluster are shown. Bacteria of
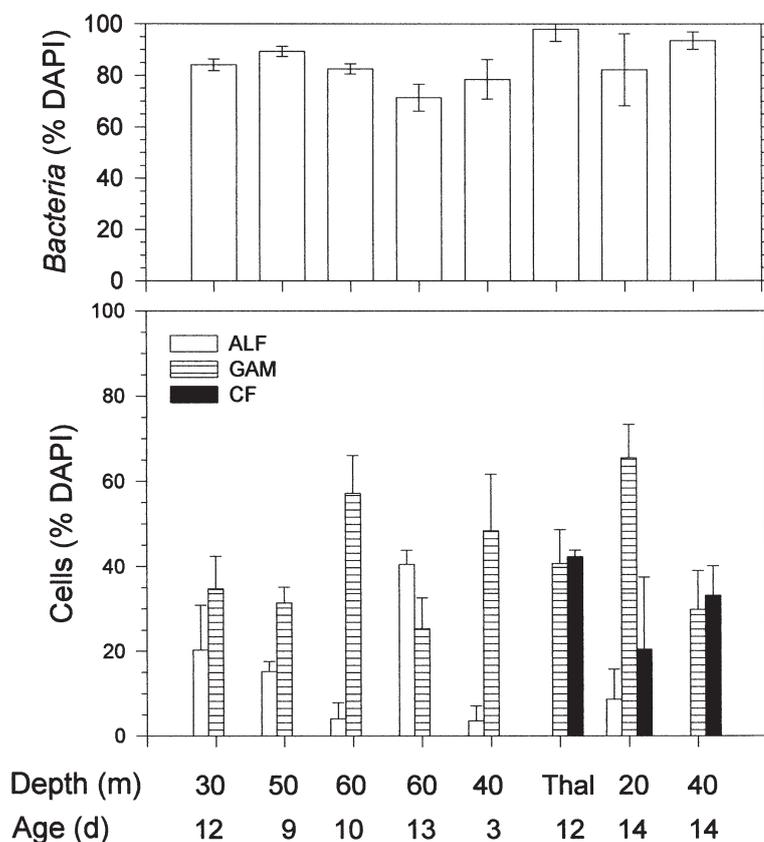

Fig. 3. Composition of the bacterial community on macroaggregates at the Polar Front in the Southern Ocean. Upper panel: *Bacteria*; lower panel: α-*Proteobacteria*, γ-*Proteobacteria*, *Cytophaga/Flavobacteria*. Hybridization with fluorescent oligonucleotides specific for *Bacteria* (EUB338), α-*Proteobacteria* (ALF1b), γ-*Proteobacteria* (GAM42a) and *Cytophaga/Flavobacteria* (CF319) was done as described by Weiss et al. (1996). On the 5 samples from the left, numbers of CF319-labelled cells could not be enumerated. The macroaggregates were formed in rolling tanks of natural samples from various locations and depths and incubated over time under ambient light and temperature conditions. In one experiment aggregates were formed from *Thalassiothrix* sp. (Thal), which were collected by a net tow. Experiments were carried out in December 1995 and January 1996 on board RV 'Polarstern'. DAPI: 4′,6-diamidino-2-phenylindole

all 3 phylogenetic lineages together constituted the great majority of the bacterial community and constituted >80% of the DAPI-stainable cells on the aggregates on which cells of the *Cytophaga/Flavobacteria* cluster were enumerated. The bacterial community on marine snow in the polar frontal zone was quite different from that in the surrounding water, which was largely dominated by cells of the *Cytophaga/Flavobacteria* cluster and comprised only very low proportions of *Proteobacteria* (Simon et al. 1999). A conclusion from the data so far available is that bacteria of the *Cytophaga/Flavobacteria* cluster, together with γ-*Proteobacteria*, appear to be dominant colonizers of marine snow aggregates. Bacteria of the former cluster are known to be able to degrade polymers including complex polysaccharides, which are important structural components of macroaggregates (see above, Reichenbach 1992).

4.4.1.2. Lakes

The structure of bacterial communities on lake snow aggregates is strikingly different from that on marine snow even though the functional properties of the bacterial communities on both types of aggregates are rather similar (see below). Detailed studies in Lake Constance revealed that the bacterial communities on natural lake snow in the upper 25 m are dominated by β-*Proteobacteria*, which constitute 20 to 60% of the DAPI-stainable cells (Weiss et al. 1996, Grossart & Simon 1998b, Schweitzer et al. 2001). Applying 3 probes highly specific for the β-*Proteobacteria Duganella zoogloeoides* (formerly *Zoogloea ramigera*), *Acidovorax facilis* and *Hydrogenophaga palleroni*, Schweitzer et al. (2001) detected between 42 and 70% of all β-*Proteobacteria*. α-*Proteobacteria* were also abundant on natural lake snow of an age of <2 d but usually did not exceed the abundance of β-*Proteobacteria*. By applying 2 probes highly specific for clusters of α-*Proteobacteria* closely related to *Sphingomonas* spp. and *Brevundimonas diminuta* 16 to 60% of all α-*Proteobacteria* were detected. These findings demonstrate that the aggregate-associated bacterial community in Lake Constance was dominated by surprisingly few species, even though nearly 200 clones were detected on aggregates (Huber 1997). This may reflect the close adaptation of a specialized bacterial community to the unique environmental conditions on aggregates. These specific populations already existed on microaggregates of an age of a few hours, which suggests that the seeding bacteria were already present on senescent algae prior to and during aggregation (Knoll et al. 2001). In support of this assumption, bac-

teria of these specific populations were never detected among the free-living bacteria (W. Zwisler & M. Simon unpubl. results). These seeding populations obviously include non-motile and gliding bacteria such as *D. zoogloeoides* (Dugan et al. 1992) and *Cytophaga* spp. (Reichenbach 1992), which presumably cannot actively approach the aggregates by chemotactic behavior such as many other motile bacteria (see below). The bacteria on aggregates detected by the highly specific probes or their close relatives are well known to colonize activated sludge flocs and thus indicate conspicuous similarities between these microenvironments (Wagner et al. 1993, 1994). γ-*Proteobacteria* were of no particular significance on lake snow in Lake Constance except on zooplankton debris and on phytodetrital aggregates composed of *Dinobryon* spp. (Brachvogel et al. 2001). Usually, they constituted <15% and often <5% of the DAPI-stainable cells. On aggregates of an age of >4 d, occurring below 30 m and on the sediment surface at 110 m, the relative proportion of β-*Proteobacteria* increased even more, but bacteria of the *Cytophaga/Flavobacteria* cluster occurred to increasing proportions of up to 15% (Schweitzer et al. 2001). These colonization patterns suggest that on the sinking aggregates the labile organic matter became increasingly decomposed, whereas the more refractory material resisted degradation. Interestingly, cells of the *Cytophaga/Flavobacteria* cluster always constituted higher proportions among the free-living bacterial communities (Zwisler & Simon 2002). Brachvogel et al. (2001) examined the bacterial colonization of microaggregates stained by DAPI (see above) and found that β-*Proteobacteria* and cells of the *Cytophaga/Flavobacteria* cluster dominated on these types of aggregates, constituting together 49 to 93% of *Bacteria*, which comprised 44 to 55% of the DAPI-stainable cells. α-*Proteobacteria* were not detected at all on microaggregates. In line with the abovementioned results, these colonization patterns indicate that DAPI-stainable microaggregates were late decompositional stages of phytodetrital aggregates.

The examination of naturally derived macroaggregates by FISH revealed that in Lake Kinneret, Israel, the composition of the aggregate-associated bacterial community was rather similar to that in Lake Constance (B. Schweitzer & M. Simon unpubl. results). β-*Proteobacteria* and *Cytophaga/Flavobacteria* dominated as well, and *Duganella zoogloeoides* and *Acidovorax facilis* constituted substantial proportions of this *Proteobacteria* subclass. Hence, these colonization patterns appear to be a general pattern on lake snow aggregates.

Schweitzer et al. (2001) and Knoll et al. (2001) experimentally examined the colonization of naturally

derived lake snow aggregates and found a succession from an initially rather equal coexistence of α- and β-*Proteobacteria* to a dominance of the latter within 2 d and decreasing proportions of α-*Proteobacteria*. Concurrently, there was a transition from a consumption of dissolved amino acids by aggregate-associated bacteria to a release into the surrounding water (Schweitzer et al. 2001). After 2 to 3 d, bacteria of the *Cytophaga/Flavobacteria* cluster occurred on the aggregates with increasing proportions of up to 20%. These colonization patterns are similar to those found in the vertical distribution of bacterial communities on natural lake snow (see above) and reflect the decomposition process of the aggregates during sinking.

4.4.1.3. Rivers and estuaries

In a study analyzing the bacterial community on aggregates in the River Elbe, Germany (using FISH), Böckelmann et al. (2000) showed that it was largely dominated by β-*Proteobacteria* constituting ~50% of total DAPI-stainable cells. α- and γ-*Proteobacteria* were of lower significance and constituted 5 to 25% and 15 to 30%, respectively. Cells of the *Cytophaga/Flavobacteria* cluster made up not more than 15% of the DAPI-stainable cells from summer to winter but 40% in spring. Planktomycetes and SRB were also detected but usually constituted <10% except in fall, when the SRB fraction reached 18%. Using group-specific oligonucleotide probes, we examined the composition of the bacterial community on macroaggregates in the salinity gradient of the Elbe estuary in May and October (Fig. 4). In the limnetic section, β-*Proteobacteria* and cells of the *Cytophaga/Flavobacteria* cluster largely dominated, constituting 20 to 40% and 25 to 36% of the DAPI-stainable cells, respectively, in May, and 18 to 45% and 20%, respectively, in October. α- and γ-*Proteobacteria* were of minor significance even though the former occasionally comprised 13% of the DAPI-stainable cells. These colonization patterns are rather similar to that of aggregate-associated bacteria found by Böckelmann et al. (2000) in a section of the River Elbe further upstream. They are also similar to patterns found in Lake Constance, even though the proportion of the *Cytophaga/Flavobacteria* cluster is greater, presumably because more refractory organic matter (macrophyte debris) is present in the River Elbe (Zimmermann-Timm et al. 1998).

The composition of the aggregate-associated bacterial community in the brackish and marine section of the Elbe estuary, however, was strikingly different from that in the limnetic section. γ-*Proteobacteria* largely dominated whereas β-*Proteobacteria* constituted not more than 12% (Fig. 4). Obviously, β-*Proteobacteria* cannot cope with the increase in salinity and do not grow any further, so that marine γ-*Proteobacteria* replace them. Further studies are needed to elucidate the closer phylogenetic affiliation of these marine aggregate-associated bacteria. In other studies the lack of β-*Proteobacteria* in the marine environment has also been described (Glöckner et al. 1999, Simon et al. 1999) but not yet their strong decrease in a salinity gradient toward the sea.
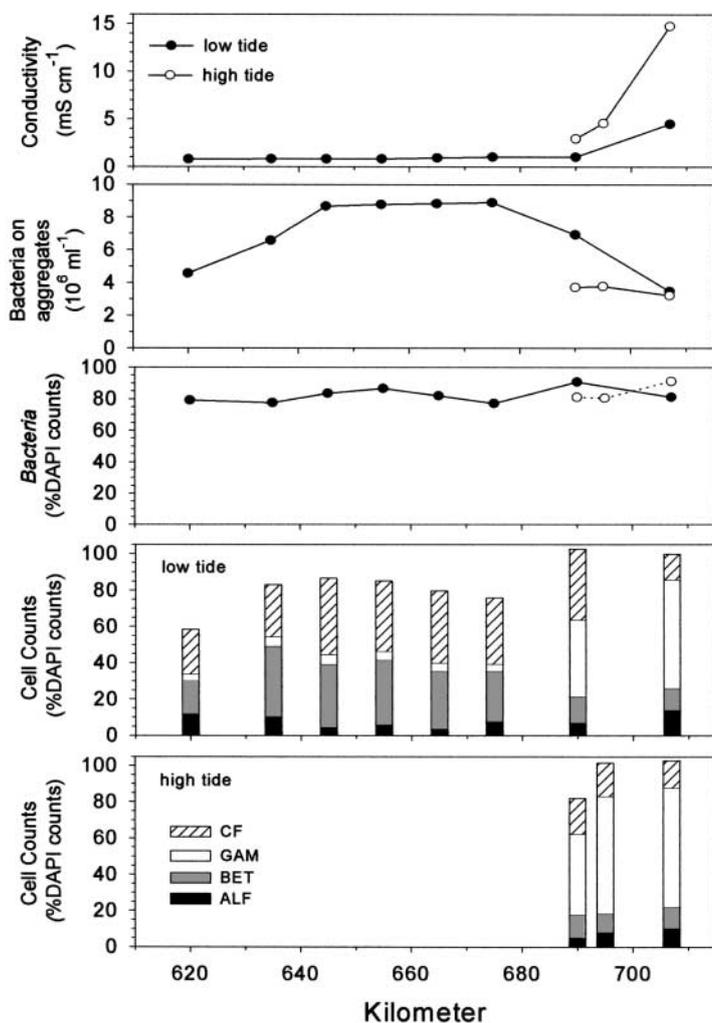

Fig. 4. Conductivity, total numbers of aggregate-associated bacteria, percentages of *Bacteria* (EUB338) and α-(ALF1b), β-(BET42a) and γ-*Proteobacteria* (GAM42a), and *Cytophaga/Flavobacteria* cluster (CF319) at low and high tide in May 1997 along the salinity gradient of the Elbe estuary. Hybridization was done as described in Schweitzer et al. (2001)

In the Columbia River estuary, in the Pacific Northwest of the USA, a specific bacterial community on particles in the turbidity maximum dominated by phylotypes of the *Cytophaga/Flavobacteria* cluster and the α-, γ- and δ-*Proteobacteria* was found (Crump et al. 1999). The composition of this community was substantially different from that in the surrounding water but also from that on particles in the limnetic section of the estuary and the adjacent coastal ocean. Differences between the community composition of particle-attached and free-living bacteria were also found in Chesapeake Bay, USA (Bidle & Fletcher 1995).

Differences among the particle-associated bacterial communities in the Sacramento River, California, its estuarine turbidity maximum and the oligohaline reach of San Francisco Bay, were reported by Hollibaugh et al. (2000). These authors compared banding patterns of PCR-amplified 16S rDNA fragments separated by denaturing gradient gel electrophoresis. Differences between particle-associated and free-living bacterial communities were found to be minor, but they may have been overshadowed by an insufficient separation of the 2 fractions of the highly turbid water by filtration through 1.0 µm filters.

Fig. 5. Loss processes and microbial decomposition pathways of macroscopicorganic aggregates. POM: Particulate organic matter

5. MICROBIAL ACTIVITIES, SUBSTRATE TURNOVER AND AGGREGATE DECOMPOSITION

POM solubilization, substrate hydrolysis and uptake, biomass production, respiration and substrate release into the surrounding water are the major microbial, and predominantly bacterial, processes by which organic aggregates are decomposed (Fig. 5). Their relative significance varies among different types of aggregates, and ongoing research is continuously revealing important details of these processes to better understand the overall decomposition of aggregates, but also to identify very specific traits.

5.1. The aggregates' chemical microenvironment and solute exchange with the surrounding water

The application of microsensors and the development of a specially designed vertical flow system, in which individual macroaggregates are stabilized in the water by an upward directed flow opposing sinking, has made it possible to examine their chemical microenvironment, and thus mass transfer and microbial growth conditions in sinking macroaggregates (Ploug et al. 1997, Ploug & Jørgensen 1999, Ploug 2001). Comparisons of measured gradients of flow and solutes in the vicinity of aggregates in this flow system with those predicted from mass transfer theory revealed a close reproduction of the natural flow and diffusion field in the vicinity of sinking aggregates (Kiørboe et al. 2001, Ploug 2001). These authors demonstrated from theoretical considerations as well as from experiments that mass transfer to impermeable model particles and to aggregates is 4- to 20-fold facilitated as compared to non-moving aggregates, depending on aggregate size and sinking velocity, due to the exchange of water in the vicinity of sinking aggregates. The impact of flow on the exchange of solutes between an aggregate and the surrounding water may be even higher if the aggregates are porous and several millimeters to centimeters large. From theoretical considerations it has been shown that fluid flow within centimeter-large aggregates can increase the solute fluxes 2-fold from the surrounding water to cells in the interior of the aggregates, compared to that to free-living cells (Logan & Hunt 1987, Logan & Alldredge 1989). Fluid flow velocities within macroaggregates have so far not been directly quantified because the techniques for such measurements are still under development. However, it was demonstrated recently that the bacterial production is up to 10-fold higher in sinking aggregates than in aggregates incubated under static conditions (see next section). Fluid flow around sinking aggregates thus is highly important for

the chemical microenvironment and growth conditions of the aggregate-associated bacteria and other micro-organisms. The diffusion-limited oxygen supply and the oxidation potential of organic matter in millimeter-large aggregates in the pelagic environment is at least 1 order of magnitude higher than the diffusion-limited oxygen supply in sediments with similar volumetric respiration rates because of the large surface-to-volume ratio of suspended aggregates (Ploug & Jørgensen 1999).

5.2. Bacterial production

Rates of bacterial biomass production by the thymidine (Fuhrman & Azam 1980) and leucine methods (Kirchman et al. 1985, Simon & Azam 1989) have been measured on a variety of aggregates in marine as well as in limnetic systems (Table 4). Generally, they are positively correlated to the aggregate size (Alldredge & Gotschalk 1990, Grossart & Ploug 2000). Most of the cell-specific incorporation rates of thymidine or leucine or calculated bacterial growth rates were only slightly higher or in the same range as rates of free-living bacteria. Only in a few cases were significantly enhanced rates of aggregate-associated bacteria found (Alldredge & Gotschalk 1990, Simon et al. 1990, Smith et al. 1995, Grossart & Simon 1998b). Hence, estimated turnover times of aggregate-associated POC on the basis of bacterial biomass production are in the range of months to years and thus unrealistically long (Karl et al. 1988, Simon et al. 1990, Smith et al. 1992, Grossart & Simon 1993, 1998b). In combination with findings of

a high carbon demand of free-living bacteria in the mesopelagic zone (Cho & Azam 1988, Simon et al. 1992), they inspired studies to examine the solubilization and release of dissolved substrates from aggregates into the surrounding water. In fact, high solubilization rates and a net release of labile substrates into the surrounding water, exceeding greatly the carbon demand of aggregate-associated bacteria, were found in several studies that could explain rapid decomposition rates of aggregate-associated POM (Smith et al. 1992, Hoppe et al. 1993, Grossart & Simon 1998a,b).

Aggregate- or particle-associated bacterial biomass production as a proportion of total bacterial production in various ecosystems is highly variable and depends predominantly on the concentration of aggregates and suspended particles. In oligo- and mesotrophic pelagic marine and limnetic systems, it is usually <14% and only occasionally substantially higher, whereas in more eutrophic and estuarine systems with higher concentrations of aggregates it may exceed 30% (Table 4). In the Northern Adriatic Sea, Müller-Niklas et al. (1994) also found that aggregate-associated bacterial production exceeded that in the surrounding water.

Recent measurements of production rates by aggregate-associated bacteria led to a reconsideration of the relative significance of the aggregate-associated POC channeled into biomass production of the aggregate-associated bacteria and being released into the surrounding water. By incubating aggregates spiked with radiolabeled leucine and thymidine on a plankton wheel, where they were thus permanently suspended, bacterial production rates were up to 1 order of magni-

Table 4. Rates of bacterial biomass production (BP) and respiration on aggregates (agg) and aggregate-associated BP as percentage of total BP. nd: not determined

Location	Depth (m)	Bacterial production (ng C agg^{-1} h^{-1})	(% of total BP)	Respiration (ng C agg^{-1} h^{-1})	Source
Subtropical Atlantic	120–530	0.5–78.1	<0.39	nd	Alldredge & Youngbluth (1985)
NW Atlantic	7–15	0.23–13.8	2.3–26.0	nd	Alldredge et al. (1986)
Southern California Bight	7–15	0.68–8.03	1.3–13.4	nd	Alldredge et al. (1986)
Southern California Bight	7–15	<0.1–1.25	0.2–3.5	nd	Simon et al. (1990)
Southern California Bight	7–15	0.1–2.3	0.2–10.9	nd	Alldredge & Gotschalk (1990)
NE Atlantic	0–100	0.01–0.22	1.8–3.4	nd	Turley & Mackie (1994)
NW Mediterranean Sea	40–450	1.0–5.08	2.8–48.3	nd	Turley & Stutt (2000)
Lake Constance	5–25	<0.1–1.55	2–30	nd	Grossart & Simon (1993)
Lake Constance	5–25	<0.1–1.08	<1–13.9	nd	Grossart & Simon (1998b)
Frederiksborg Slottsø	0.5	200–3770[a]	9–70	nd	Worm & Søndergaard (1998a)
Columbia River estuary	0–13	400–2000[b]	13–53	nd	Crump & Baross (1996)
Marine diatom aggregates	nd	6.3–187.5	nd	10.4–167	Ploug & Grossart (2000)
Riverine detrital aggregates	nd	<0.1–20.0	nd	1.0–89.6	Grossart & Ploug (2000)
Marine detrital aggregates	0–20	nd		0.3–150	Ploug et al. (1999)
Marine diatom aggregates	0–10	nd	nd	3.6–120	Ploug (2001)

[a]>20 μm fraction (l^{-1} h^{-1}); [b]>10 μm fraction (l^{-1} h^{-1})

tude higher than in non-suspended samples (Ploug & Grossart 1999, Grossart & Ploug 2000, Ploug & Grossart 2000). Traditionally, these measurements were carried out with pooled aggregates, which settled to the bottom of the test tubes (Alldredge et al. 1986, Alldredge & Gotschalk 1990, Simon et al. 1990, Smith et al. 1992, Grossart & Simon 1993, 1998b, Müller-Niklas et al. 1994). Examination of the oxygen gradient on the bottom of the test tube between the surrounding water and the center of the aggregate by a microelectrode revealed that a diffusive boundary layer had been established, which prevented a proper oxygen supply and rapid diffusion of the radiolabel to the inner parts of the aggregates (Ploug & Grossart 1999). Oxygen concentrations are up to 9-fold higher within 2 mm large sinking aggregates than in aggregates settling onto a solid surface, e.g. of an incubation vial or a sediment trap (Ploug & Jørgensen 1999). Hence, the unfavorable conditions lead to strongly reduced and thus biased production rates, which can be prevented by incubating the aggregates in test tubes rotating on a plankton wheel or a roller table. The production rates measured under these conditions may be somewhat higher than under *in situ* conditions because the oxygen supply *in situ* may not always be so favorable. They may also at least partially explain the notion that cell-specific thymidine incorporation rates are inversely related to the bacterial abundance normalized to microgram of aggregate (Alldredge & Gotschalk 1990). The conclusion from these experiments is that the heterotrophic bacteria on the aggregates utilize a substantially higher portion of the aggregate-associated POC than previously assumed, in particular amino-acid carbon (Grossart & Ploug 2001). This calls for a reexamination of the role of aggregate-associated bacteria for the cycling of aggregate-associated and total POC.

5.3. Respiration

In the studies in which carbon turnover by aggregate-associated bacteria has been determined, respiration has not been measured and bacterial growth efficiencies, if considered, were assumed according to published values of free-living bacteria or estimated indirectly (Smith et al. 1995, Grossart et al. 1998). Respiration of aggregate-associated microbes, though, can be determined from oxygen measured by a highly sensitive micro-Winkler technique (Parparov et al. 1998) or by oxygen microelectrodes (Alldredge & Cohen 1987, Ploug et al. 1997). The oxygen gradients around aggregates are proportional to the community respiration rates when mass transfer within aggregates occurs by molecular diffusion

(Ploug et al. 1997). Microelectrodes have been used to directly measure community respiration rates on marine snow from surface waters of the Southern California Bight, on riverine aggregates and on diatom aggregates (Table 4). In general, they were in the same range as, or slightly higher than, bacterial biomass production rates. On marine snow, respiration comprised $75 \pm 21\%$ of the gross photosynthesis, even at light intensities >500 µE m^{-2} s^{-1}, thus emphasizing the dominance of heterotrophic processes on these aggregates. Generally, respiration was positively correlated with aggregate size but inversely correlated if respiration was normalized to aggregate volume, or per bacterium (Ploug et al. 1999, Ploug 2001). On riverine and naturally derived diatom aggregates, respiration rates were positively correlated to POC content and respiration was higher on aggregates of an age of 5 to 14 d as compared to 1 to 5 d (Grossart & Ploug 2000, Ploug & Grossart 2000). These authors calculated that the turnover of the aggregate-associated POC by respiratory losses was substantially higher than on the basis of just bacterial biomass production, thus indicating that respiration is an important pathway of aggregate decomposition, to which more attention should be addressed than previously.

5.4. Growth efficiency of aggregate-associated bacteria

When respiration on aggregates is predominantly due to bacteria, provided that protozoans do not particularly dominate, combined measurements of bacterial biomass production and respiration on the same aggregate allow an estimate of bacterial growth efficiencies of aggregate-associated bacteria. The few measurements carried out so far show that the growth efficiency is highly variable, with highest values of 0.4 to 0.5 in fresh aggregates and values decreasing to 0.05 in aggregates of an age of 14 d (Grossart & Ploug 2000). These data indicate that growth efficiencies of bacteria associated with aggregates rich in labile organic matter are at the higher end of values found in free-living bacterial communities and similar to those of bacteria growing on labile substrates (Del Giorgio & Cole 1998). In contrast, the few published growth efficiencies of aggregate-associated bacteria estimated indirectly by correlating bacterial biomass production with respiration (Parparov et al. 1998) and budgeting bacterial biomass production with primary production and carbon losses on aggregates (Smith et al. 1995) ranged between 0.09 and 0.17, and thus were at the lower end of values for free-living bacteria (Del Giorgio & Cole 1998).

5.5. Bacterial turnover of aggregate-associated organic matter

It has been well established for >15 yr that particle-associated bacteria exhibit higher cell-specific uptake rates of free amino acids and monosaccharides than free-living bacteria, which implies that the former are metabolically more active (for review see Kirchman & Ducklow 1987, Kirchman 1993). Detailed studies, however, on the turnover of labile substrates on aggregates, including hydrolysis, uptake and release, and determining total turnover rates of aggregate-associated carbon and nitrogen, only started about 10 yr ago, after Cho & Azam (1988) and Azam & Smith (1991) had postulated that microbial decomposition rates of aggregate-bound organic matter must be much higher than estimated on the basis of biomass production of aggregate-associated bacteria alone (see Section 5.2).

Several studies found that bacteria associated with marine and limnetic macroaggregates exhibit significantly higher potential ectoenzymatic hydrolysis rates per cell of aminopeptidase, phosphatase and glucosidases, implying that labile biopolymers on aggregates are hydrolyzed faster than in the surrounding water (Karner & Herndl 1992, Smith et al. 1992, 1995, Agis et al. 1998, Grossart & Simon 1998b, Unanue et al. 1998b, Worm & Søndergaard 1998a). Due to decomposition, solubilization and varying bacterial communities on aggregates, hydrolysis rates of these bacteria, though, are rather variable and, in particular on more decomposed and thus aged aggregates, are reduced and may be lower than those of their free-living counterparts (Müller-Niklas et al. 1994, Agis et al. 1998, Grossart & Simon 1998b, Unanue et al. 1998b, Grossart & Ploug 2001). Usually, per cell hydrolysis rates of aminopeptidase are higher than of α- and β-glucosidase, but also decrease faster over time or depth, implying that protein is decomposed more rapidly than polysaccharides (Smith et al. 1995, Grossart & Simon 1998a, Simon et al. 2000). A preferential decomposition of organic nitrogen as compared to POC was observed by Grossart & Ploug (2001). These authors found a more rapid decrease of PCAA relative to total POC and enhanced uptake rates of amino acids relative to glucose on aggregates incubated in rolling tanks.

The rapid bacterial decomposition of PCAA and proteins has important implications for the decomposition of aggregates dominated by diatoms. Bidle & Azam (1999, 2001) demonstrated that dissolution of silica frustules in aggregates of diatom detritus takes place only when they are colonized by bacteria because they hydrolyze the protein matrix of the frustules. Individual bacterial species with different aminopeptidase activities exhibit different hydrolysis rates. Hence,

bacteria associated with diatom aggregates mediate a rapid recycling and enhance concentrations of silica within these aggregates (Brzezinski et al. 1997).

As a result of the high hydrolytic activities of aggregate-associated bacteria, and high metabolic activities of bacterial grazers, concentrations of DOC, dissolved free (DFAA) and combined amino acids (DCAA) and inorganic nutrients (phosphate, ammonium, nitrate, silicate) are significantly higher in the pore water of the aggregates than in the surrounding water (Table 5). Compared with DCAA, DFAA are relatively more enriched on aggregates than in the surrounding water (Table 5; Grossart & Simon 1998b), which is a further indication of the enhanced aminopeptidase activity of aggregate-associated bacteria. The high nutrient concentration in the pore water of aggregates, and the spatially tight coexistence of organisms within the aggregate matrix, enhanced nutrient recycling and uptake of the hydrolysis products by the aggregate-associated bacteria and algae and enhanced growth and biomass production rates (Gotschalk & Alldredge 1989, Alldredge & Gotschalk 1990, Ploug & Grossart 1999, Grossart & Ploug 2000, 2001). Besides recycling within aggregates, the highly enriched labile DOM and inorganic nutrients may also be partly released into the surrounding water. The finding that bacterial growth and production rates on aggregates often were not enhanced as compared to the surrounding water (see above) and that DCAA hydrolysis rates substantially exceeded the carbon and nitrogen demand of aggregate-associated bacteria led to the concept of an uncoupled hydrolysis and uptake of aggregate-associated organic matter by the associated bacteria and its subsequent predominant utilization by free-living bacteria in the surrounding water (Azam & Smith 1991). This concept was strongly supported by the measured net release of DFAA and DCAA from aggregates into the surrounding water (Smith et al. 1992, Grossart & Simon 1998a,b, Grossart & Ploug 2001, Schweitzer et al. 2001). Even though measured on various types of aggregates in marine and limnetic environments, DCAA release rates were relatively constant (0.32 to 2.25 nmol agg^{-1} h^{-1}). Please note that the respective data in Grossart & Simon (1998b) correctly range between 0.45 and 2.25 nmol agg^{-1} h^{-1} and thus are lower than those published in the original paper. Aggregates, however, do not always act as a source of dissolved amino acids but can also be a sink, as observed by Schweitzer et al. (2001) with fresh lake snow aggregates and by Grossart & Simon (1998a) with aged lake snow aggregates.

Recent model calculations and experiments, with a new approach simulating the release of DOM by sinking aggregates, indicate that the released compounds leave a plume with a strong spatial gradient behind the

Table 5. Enrichment factors (EF) of dissolved inorganic and organic nutrients on marine snow relative to the surrounding water. DOC: dissolved organic carbon; DFCHO: dissolved free monosaccharides; DTCHO: dissolved total carbohydrates; DFAA: dissolved free amino acids; DCAA: dissolved combined amino acids

Nutrient	Concentration (µM)		EF	Source
Location	Aggregates	Bulk water		
Phosphate				
Californian coastal Pacific	0.3–84	0.4–1.3	0.2–67	Shanks & Trent (1979)
Southern Californian Bight	0.04–21.7	0.01–0.4	<1–180	Alldredge & Gotschalk (1990)
Northern Adriatic Sea	2.92 ± 5.78	0.1 ± 0.19	22	Kaltenböck & Herndl (1992)
Lake Constance	72–318	<0.1	720–3180	Grossart & Simon (1993)
Nitrate				
Californian coastal Pacific	0.4–308	0.6–12.6	11–24	Shanks & Trent (1979)
Southern Californian Bight	0.1–73	0.1–5.2	<1–108.5	Alldredge & Gotschalk (1990)
Northern Adriatic Sea	3.84 ± 3.44	1.56 ± 1.91	2.5	Kaltenböck & Herndl (1992)
Ammonium				
Californian coastal Pacific	1–483	0.1–2.2	3–860	Shanks & Trent (1979)
Southern Californian Bight	0.2–25	0.1–0.4	5–55	Alldredge & Gotschalk (1990)
Northern Adriatic Sea	4.03 ± 4.38	1.07 ± 1.35	1.9	Kaltenböck & Herndl (1992)
Silicate				
Monterey Bay	7.0–305	3.6–10.2	1.0–48	Brzezinski et al. (1997)
DOC				
Northern Adriatic Sea	1217.5	85	14.3	Herndl (1992)
Coastal NW-Pacific	742–11 700	108–150	16–78	Alldredge (2000)
Southern Californian Bight	2430–2640	108–117	22	Alldredge (2000)
DFCHO				
Northern Adriatic Sea	6.16	1.26–6.66	0.53–1.47	Herndl (1992)
DTCHO				
Northern Adriatic Sea	11.6–31.0	14.4	2.2	Herndl (1992)
DFAA				
Northern Adriatic Sea	0.49–0.54	0.25–0.56	0.96–1.96	Herndl (1992)
Northern Adriatic Sea	0.61–27.2	0.20	3.0–134	Kaltenböck & Herndl (1992)
Lake Constance	0.15–0.72	0.01–0.21	1.6–25.0	Grossart & Simon (1998b)
DCAA				
Lake Constance	2.3–49.9	2.0–9.5	0.9–11.1	Grossart & Simon (1998b)

aggregates, which can extend to several centimeters (Kiørboe 2001, Kiørboe et al. 2001). The volume with enhanced substrate concentration can be 10- to 100-fold larger than the volume of the aggregate itself. Sinking aggregates and their associated microbial processes thus create pronounced heterogeneities of nutrients in the bulk water, which may affect nutrient recycling and colonization processes by chemotactic microorganisms and remote chemosensoric detection by meso- and macrozooplankton (Kiørboe 2001, Kiørboe & Jackson 2001, Kiørboe & Thygesen 2001, Kiørboe et al. 2001).

Even though production rates and respiratory carbon losses of aggregate-associated bacteria obviously are higher than assumed previously (see Section 5.2), the notion of a direct release of amino acids (see above), ammonium (Pomeroy et al. 1984) and DOM (Berman et al. 1999) strongly supports the validity of the concept that aggregates act as metabolically highly active bioreactors, leading to the decomposition and solubilization of the aggregate-bound POM by associated

microbes, but also by bacteria in the surrounding water, which decompose the released dissolved substrates. Recent experimental studies with laboratory-made aggregates examining the time course of aminopeptidase, α- and β-glucosidase activities, and leucine and glucose uptake by aggregate-associated and free-living bacteria further support this concept (Agis et al. 1998, Unanue et al. 1998b). These authors found that ratios of aminopeptidase/bacterial production, aminopeptidase/leucine uptake and β-glucosidase/glucose uptake by free-living bacteria were initially rather low and increased later than those by aggregate-associated bacteria. Further, concentrations of DFAA in the surrounding water increased over time and covaried with the ratio of aminopeptidase/leucine uptake by aggregate-associated bacteria and thus implied intense DCAA hydrolysis.

Measurements of concentration dynamics of dissolved amino acids in the surrounding water of freshly formed lake snow aggregates, however, showed that a net release of amino acids usually occurs with aggre-

gates of an age of at least 2 d (Schweitzer et al. 2001). These authors observed that the release phase was usually preceded by a period in which aggregate-associated bacteria consumed amino acids from the surrounding water. Hence, it is obvious that fresh aggregates in the mixed layer can also act primarily as a sink for labile DOM such as amino acids, convert it rather effectively into bacterial biomass due to a high growth efficiency (see above) and transport it, as a fraction of total aggregate-associated POM, to deeper layers, where a substantial proportion is reconverted to DOM and serves to support the growth of the free-living bacterial community.

So far, only very few studies have been carried out to directly compare the relative significance of bacterial production, respiration and solubilization for the overall decomposition of aggregates. In one study, which simultaneously measured bacterial production, respiration, net release of amino acids and ectoenzymatic activity on individual diatom aggregates, bacterial production and mineralization were found to be the major decomposition pathways for carbon and nitrogen (Grossart & Ploug 2001). A direct comparison of respiration and solubilization of organic matter of lake snow aggregates of various origins showed that both processes were highly variable, such that in some cases respiration dominated and in others solubilization dominated (Berman et al. 1999). More studies are needed to better understand under which conditions either of the processes mentioned is favored or suppressed.

5.6. Anoxic processes of aggregate-associated prokaryotic populations

Methanogens, and ammonium-oxidizing and nitrifying bacteria have been detected on and isolated from oceanic particulate matter, fecal pellets and zooplankton (Oremland 1979, Bianchi et al. 1992, Marty 1993, Phillips et al. 1999), and anoxic macroaggregates colonized by methanogens have been suggested as a source for the observed supersaturation of methane in the ocean (Karl & Tilbrook 1994). The production of CO_2 and ammonium within aggregates can promote growth of nitrifying bacteria, as has been observed in the mesopelagic zone in the North Pacific (Karl & Tilbrook 1984), and aggregates can be significant sites of ammonium oxidation by nitrifying bacteria in estuaries with high ambient ammonium concentrations (Kerner & Gramm 1995, Stehr et al. 1995, Schäfer & Harms 1996). The efficient mass transfer even to impermeable sinking aggregates and the high porosity of macroaggregates, however, imply that sinking aggregates are rarely anoxic in the natural environ-

ment. In non-sinking fecal pellets, i.e. not exposed to any water flow, anoxic microzones have been found by Alldredge & Cohen (1987). Concentration gradients of oxygen not reaching anoxia, however, do develop within sinking aggregates when microbial activities are high (see above). Even the diffusion-limited oxygen supply from the ambient water at air saturation can theoretically oxidize all aggregate-associated POC to CO_2 within 1 d, in 0.1 to 10 mm large sinking aggregates (Ploug et al. 1997). Such high metabolic rates are rarely observed in aggregates, and anoxic aggregates are therefore most likely to occur in the oxygen minimum zone in the ocean (Shanks & Reeder 1993, Ploug et al. 1997, 1999, Ploug 2001).

A conclusion from the mentioned observations is that anoxic processes may occur on certain types of macroaggregates under special environmental conditions but in general appear to be an ephemeral phenomenon and therefore presumably do not play a major role in the aggregate-associated decomposition of organic matter.

6. BACTERIA-BACTERIA AND BACTERIA-ALGAE INTERACTIONS

From the previous sections it is evident that aggregate-associated bacteria colonize highly specific microenvironments, which can be regarded as hotspots of microbial activities and turnover of POM in various aquatic systems. An important question in this context concerns the way bacteria first colonize algae, or micro- or macroaggregates. As very specific bacterial populations develop on aggregates (see above), they must first sense their potential colonization site and be able to get into close contact with it. This process can only be successful if such bacteria are motile or if they already inhabit the precursor component particles. Recent studies on bacterial motility demonstrate that various marine bacteria have specific flagellin genes (Winstanley & Morgan 1997), and that natural assemblages of marine bacteria exhibit high-speed motility and large accelerations after enrichment with nutrients (Mitchell et al. 1995, Fenchel 2001, Grossart et al. 2001, Kiørboe & Jackson 2001). Both characteristics are prerequisites for the chemotactic behavior and active interactions between bacteria and particulate colonization sites such as phytoplankton cells and suspended aggregates.

Bacteria can be loosely or tightly associated with phytoplankton (ZoBell 1941, Sieburth 1968, Caldwell & Caldwell 1978), leading to a multitude of possible interactions between these organisms in aquatic ecosystems (see review by Cole 1982). Symbiotic interactions between phytoplankton and heterotrophic bacteria led

Bell & Mitchell (1972) to formulate the concept of the 'phycosphere': chemotactic bacteria benefit from extracellular polymers, mainly polysaccharides, which are released by the algae, whereas the algae benefit from the nutrients remineralized by the associated microbes (Golterman 1972), vitamins (Pringsheim 1912, Haines & Guillard 1974) and other growth factors (Paerl & Pinckney 1996). Bacteria in the phycosphere can be free-living, be directly attached to algal surfaces or live inside algal cells (Kochert & Olson 1970, Kodama et al. 1990, Rausch de Traubenberg & Lassus 1991). It has been shown that marine bacteria accumulate around phytoplankton-derived detritus, resulting in increased microbial activities in the 'detritosphere' (Biddanda & Pomeroy 1988). Recent theoretical models of chemotactic behavior of marine bacteria support the hypothesis that bacteria, clustering around phytoplankton or macroaggregates, greatly benefit from increased concentrations of nutrients in the close vicinity of otherwise nutrient-poor environments (Blackburn et al. 1997, 1998, Kiørboe & Jackson 2001). New approaches to studying the release of dissolved substrates, e.g. amino acids, from marine snow, show that sinking organic aggregates are followed by a plume of released DOM, which extends the aggregate length and enlarges its volume many times (Kiørboe et al. 2001). Such plumes of potential bacterial substrates, e.g. amino acids and oligopeptides, can be detected by chemotactic bacteria and lead to intense clustering of motile bacteria around these nutrient point sources (Kiørboe 2001, H. P. Grossart & F. Azam unpubl. results). Larger organisms such as copepods may sense these nutrient point sources as well (Kiørboe & Thygesen 2001).

Phytoplankton and heterotrophic bacteria, however, do not always benefit from each other (see review Cole 1982, Imai et al. 1993). It has been shown that heterotrophic bacteria can be repelled by exudates of the algae, e.g. antibiotics (Steemann-Nielsen 1955, Sieburth 1968), which has been interpreted as a mechanism by which living phytoplankton can prevent bacterial colonization of their cell surface. It has been further shown that a former symbiotic relationship between phytoplankton and heterotrophic bacteria can turn into a parasitic one when the alga becomes stressed, e.g. by missing vitamins (Grossart 1999). Different species of attached bacteria may also compete for space and nutrients on the aggregate surface, e.g. outcompeting each other by increased growth rates or the production of growth- or motility-inhibiting secondary metabolites (Kawano et al. 1997, Burchard & Sorongon 1998, Long & Azam 2001). Further studies on specific bacteria-bacteria and bacteria-algae interactions are needed and will lead to a more precise understanding of the microbial colonization and decomposition of aggregates.

7. VIRUSES

In the recent past, viruses were identified as an integral component of aquatic ecosystems, causing substantial proportions of the phytoplankton and bacterioplankton mortality (see review by Wommack & Colwell 2000). However, there is very little information available on the significance of virus infection on aggregate-associated bacteria and nothing on algal infection. Proctor & Fuhrman (1991) reported that in aggregated POM collected in sediment traps deployed in the northeastern Pacific, between 30 and 140 m depth, 0.7 to 3.7 % of the bacteria were visibly infected by viruses. In POM collected in a sediment trap deployed at 400 m, they did not find any infected bacteria. These proportions of infected bacteria are similar to values in free-living planktonic bacteria (Wommack & Colwell 2000). Hence, these observations indicate that virus infection of bacteria in marine snow aggregates is of similar significance to bacterial mortality as in free-living bacterial communities.

We examined numbers of bacteria and virus-like particles in lake snow aggregates formed in rolling tanks from Lake Constance water and incubated for up to 144 h (Fig. 6). The numbers of bacteria per aggregate increased over time in the experiments in May and August but not in June. Numbers of virus-like particles, counted by an epifluorescence standard method (Hennes & Suttle 1995), in the May experiment also continuously increased and covaried with bacterial numbers. In the June experiment virus-like particles decreased from initially high numbers until 23 h and covaried with bacterial numbers. In the experiment in August, numbers of virus-like particles peaked after 2 d but did not covary with bacterial numbers. Ratios of virus/bacteria generally followed dynamics of virus-like particles and ranged between 0.3 and 8.5 with a mean of 4.7 ± 2.3. In the experiments in May and August they were closely correlated to virus numbers (r^2 = 0.71 and 0.89, p < 0.01). These ratios are in the same range as values reported from studies on dynamics of viruses and free-living bacteria (Wommack & Colwell 2000) and imply that virus infection of bacteria and virus-induced bacterial mortality on aggregates is similar to that in free-living bacterial communities, confirming the results of Proctor & Fuhrman (1991) for marine snow aggregates. The rapid decreases we found suggest that viruses are readily decomposed in aggregates, possibly by the highly active bacterial aminopeptidases of the protein capsid (see above). Hence, large aggregates presumably are not a vehicle for free viruses to deep water layers and the bottom sediment. Only infected bacteria may bring viruses to these deep environments.

8. THE SIGNIFICANCE OF ORGANIC AGGREGATES TO THE FLUX AND CYCLING OF POM

From the presented information it is evident that organic aggregates and associated microorganisms are involved in many ways in the decomposition, cycling and flux of POM, DOM and inorganic nutrients in aquatic ecosystems. Major differences occur between pelagic marine and limnetic systems, with rather weak hydrodynamic forcing, and shallow and turbid marine, estuarine, riverine and lacustrine systems with strong and highly variable hydrodynamic forcing. The general aggregate-related microbial processes are rather similar in the various systems, even though the origin, size and composition of the aggregates and the major groups of microorganisms colonizing and decomposing them, and their quantitative significance for the overall POM cycling, may exhibit pronounced differences. In the following, and as a synopsis of this review, we want to highlight the major and most important features and the special significance of aggregate-related processes in the systems mentioned.

8.1. Pelagic marine and limnetic systems

A synopsis of formation and decomposition processes of marine and lake snow aggregates in pelagic systems with low hydrodynamic forcing is given in Fig. 7. Macroaggregates in these systems are rather large, 500 μm to >10 mm, but in lakes they are smaller than in marine systems, presumably due to the lower bridging potential of divalent cations in the latter. De novo production can originate from various sources, including abandoned larvacean houses, pteropod webs and gelatinous phytoplankton such as *Phaeocystis* in marine systems and colony-forming cyanobacteria in lakes. Biologically and chemically mediated physical aggregation may include a large variety of component particles but phytoplankton often dominates. However, only a small proportion of the phytoplankton and primary production is usually in aggregated form.

The role of bacteria in aggregation still needs further studies, but bacteria may be of higher importance in producing TEP or controlling TEP production by diatoms than assumed, and may also directly control aggregation. The aggregate abundance in pelagic
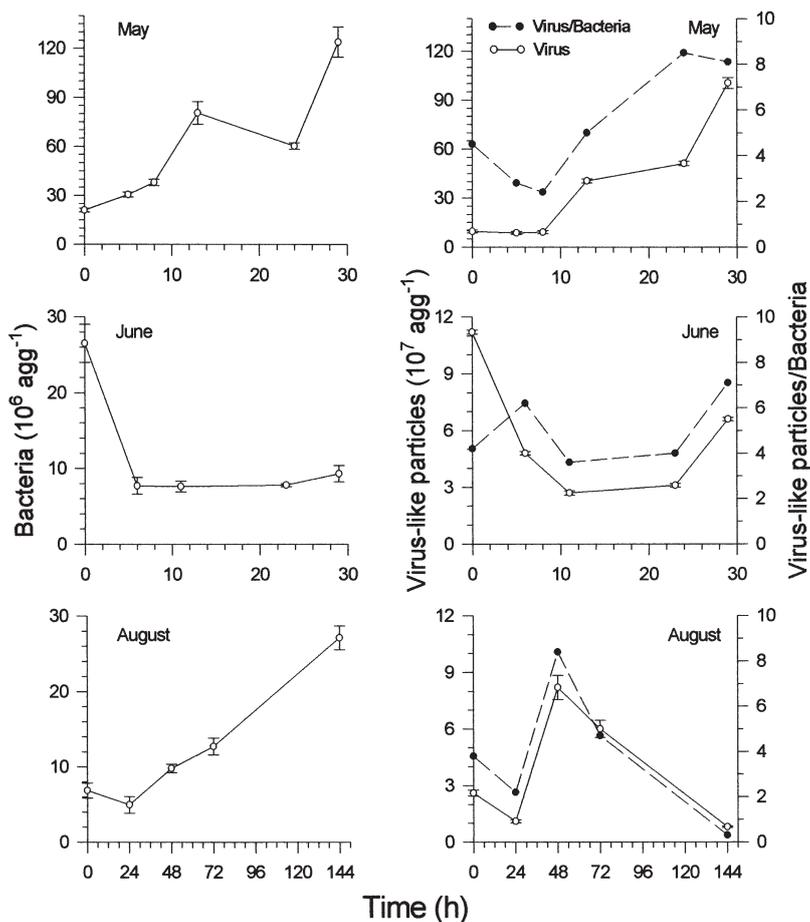

Fig 6. Time courses of numbers of bacteria and virus-like particles (VLP), and the ratio of VLP/bacteria on aggregates formed from Lake Constance water in rolling tanks and incubated at ambient light and temperature conditions. Results of experiments in May 1996 (top), June 1995 (middle) and August 1996 (bottom) are shown. Note the different scales for bacteria, virus-like particles and time

systems is rather low (<130 l^{-1}) and hence aggregate-associated microbial processes appear to be of relatively low overall importance. However, it must be kept in mind that macroaggregates are surrounded by a phycosphere and a plume of nutrients and microbes, extending their size considerably and also affecting microbial and zooplankton-related processes in the surrounding water (Fig. 5; Azam & Long 2001, Kiørboe 2001). Because of this microheterogeneity and the total space that is occupied by aggregate-related processes, their overall significance presumably is much greater than assumed from traditional measurements and is still underestimated. The aggregate-associated microbial community exhibits pronounced differences from that in the surrounding water. On lake snow aggregates, bacteria are dominated by α- and in particular by β-*Proteobacteria*, and cells of the *Cytophaga/Flavobacteria* cluster constitute increasing
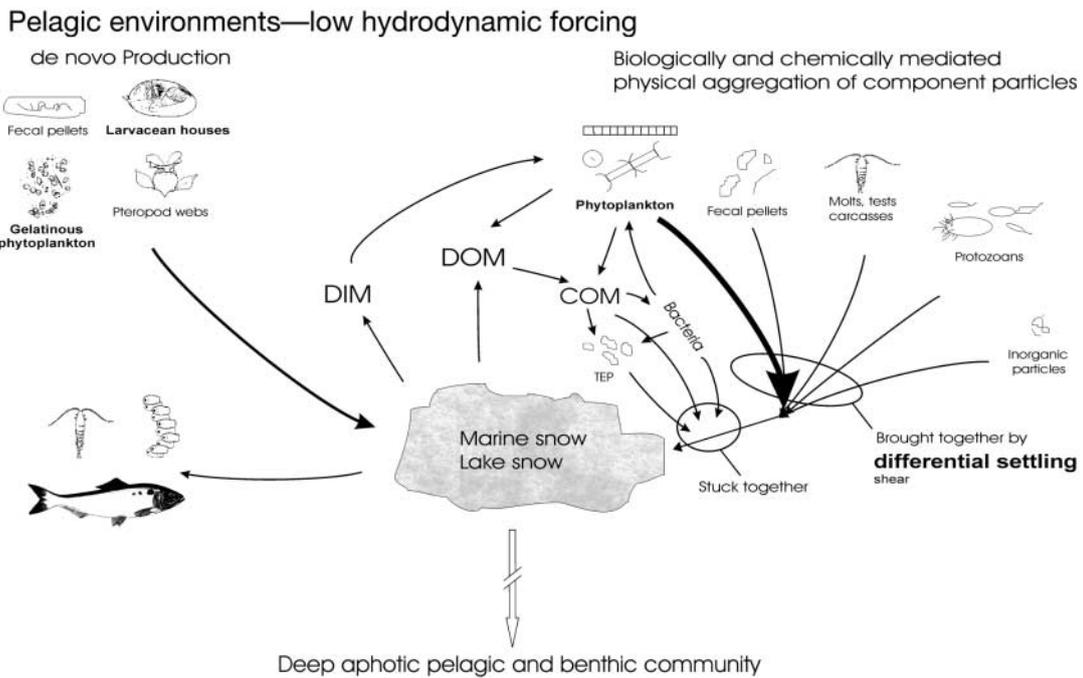
Pelagic environments—low hydrodynamic forcing

Fig. 7. Formation and loss processes of macroscopic organic aggregates in pelagic ecosystems with low hydrodynamic forcing (modified from Alldredge & Silver 1988). The size of the arrows and letters reflects the relative significance of the respective pathway. For microbial decomposition pathways see Fig. 5. DIM: dissolved inorganic matter; DOM: dissolved organic matter; COM: colloidal organic matter
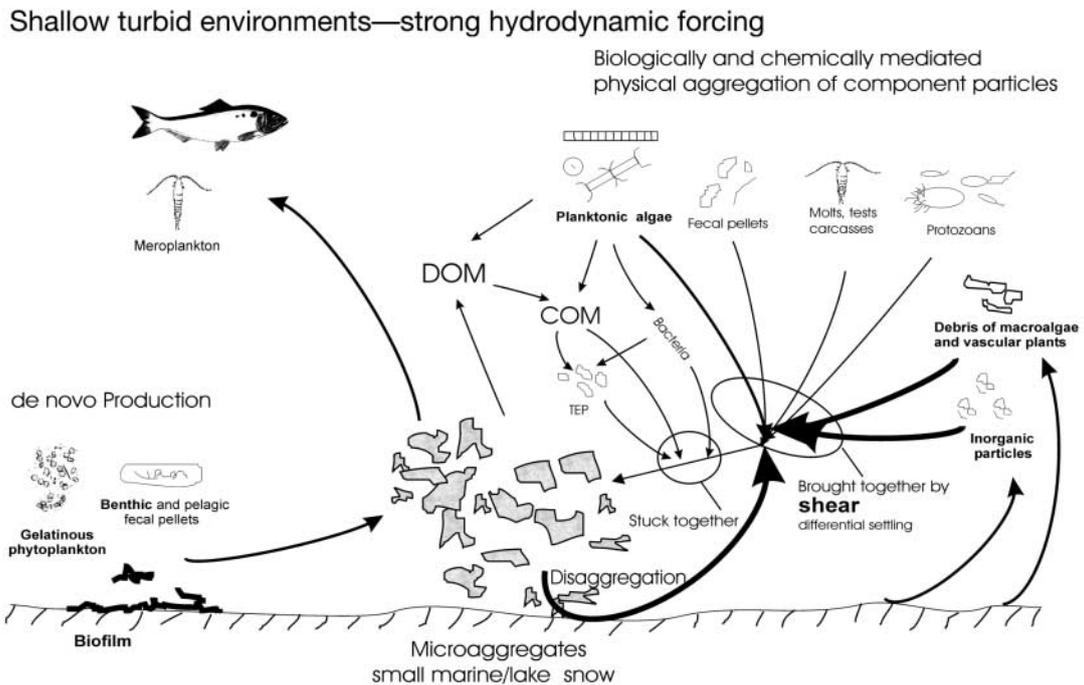
Shallow turbid environments—strong hydrodynamic forcing

Fig. 8. Formation and loss processes of macroscopic and microscopic organic aggregates in shallow turbid ecosystems with strong hydrodynamic forcing. The size of the arrows and letters reflects the relative significance of the respective pathway. For microbial decomposition pathways see Fig. 5, definitions as in Fig. 7

proportions on aged aggregates with increasing fractions of refractory organic compounds. On marine snow, γ-*Proteobacteria* and cells of the *Cytophaga/Flavobacteria* cluster appear to be the major bacterial colonizers, but nothing is known about the temporal succession.

Even though, from a quantitative perspective, macroaggregate-associated decomposition processes appear to be of minor importance as compared to the total POM decomposition, macroaggregates have to be considered as hot-spots and thus of key importance for the whole pelagic ecosystem. Nutrients limiting the growth of phytoplankton and bacteria, such as inorganic nitrogen, phosphorus and silica, are highly enriched and recycled very rapidly in aggregates, thus also supplying free-living phyto- and bacterioplankton with regenerated nutrients (Fig. 5), and possibly controlling aggregation of phytoplankton (Fig. 7). Macroaggregates dominate the sinking flux of POM in pelagic ecosystems and thus are of key importance in supplying nutrients and energy to the pelagic and benthic biota in deep aphotic layers.

8.2. Shallow turbid marine, estuarine and limnetic systems

Aggregate formation in shallow turbid systems with high hydrodynamic forcing exhibits pronounced differences from pelagic systems with low hydrodynamic forcing (Fig. 8). Generally, the suspended matter load in these systems is much higher than in pelagic systems including also the proportion of primary production in aggregated form. De novo production originates from gelatinous phytoplankton, and pelagic and benthic fecal pellets, but also from benthic biofilms disrupted and resuspended by high shear and turbulence. Biologically and chemically mediated physical aggregation includes a large variety of component particles, not only from the water column but also resuspended from the sediment. In addition to those from the water column, benthic algae, debris of macroalgae and vascular plants, and high amounts of resuspended inorganic particles constitute major aggregate fractions. The dominant physical process causing aggregation of the component particles is collision by turbulent shear of rather high intensity, not allowing large aggregates to persist for longer periods, but disrupting them again such that microaggregates dominate. Differential settling is only important for short periods of time with low wind-induced shear, or at slack water in tidally affected systems. Resuspension of sediment components and intense restructuring of the aggregates because of the high hydrodynamic activities are major features of these systems.

Biological activities on biofilms and of the zoobenthos are also important for aggregate dynamics in shallow turbid systems including the nepheloid layer. The aggregates in these systems are colonized, consumed and repackaged by various metazooplankton and protozoans, including high proportions of benthic and meroplanktonic forms. The aggregate-associated bacterial community in shallow turbid limnetic systems is dominated by β-*Proteobacteria* and cells of the *Cytophaga/Flavobacteria* cluster, thus reflecting the dominance of rather refractory material in the aggregate-associated POM. In marine systems, γ-*Proteobacteria* and cells of the *Cytophaga/Flavobacteria* cluster obviously dominate, even though further studies are needed to confirm the existing preliminary results. Microbial decomposition processes on aggregates in general are similar to pelagic systems, but their overall significance with respect to total POM decomposition is much more important and may even be dominant. To better understand their relative importance, more studies examining these processes are needed. From the information presented in this review it is obvious that aggregate-associated microbial decomposition processes are highly significant in these systems and lead to solubilizing and mineralizing the POM, thus exporting its components as DOM and inorganic nutrients from estuaries and tidally affected shallow coastal areas to the coastal sea, or from the littoral to the pelagic zone of lakes. Aggregate consumption by the zoobenthos, meroplankton and fish appears to be highly significant, showing that this detrital and microbial food source supplies high amounts of energy and nutrients to higher trophic levels.

9. CONCLUSIONS

Today, the microbial ecology of organic aggregates in marine and limnetic systems appears to be rather well understood, and the major processes forming and decomposing aggregates have been identified and studied in detail. Further work, in particular on specific details with respect to the role of bacteria in forming aggregates and interacting with algae, will certainly improve our understanding of the microbial ecology of organic aggregates and their significance in cycling of nutrients and elements, and the flux of energy in aquatic ecosystems more so. Only very recently have aggregate-associated processes been included in food web and carbon cycling models of pelagic systems (Jackson 2001). The results of this first modeling assay suggest that aggregation of phytoplankton strongly affects the relative partitioning of zooplankton grazing and sedimentation of primary production. Such approaches need to be elaborated and tested much

more and to be applied to other aquatic ecosystems. The inclusion of organic aggregates in food web models and concepts is urgently needed for a more comprehensive understanding of these systems, and will give us a much better and more realistic understanding of ecosystem functioning in limnetic, as well as marine systems, from selected local systems to a global scale.

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