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Formation and fate of marine snow: small-scale processes with large-scale implications*

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SUMMARY: Marine snow aggregates are believed to be the main vehicles for vertical material transport in the ocean. However, aggregates are also sites of elevated heterotrophic activity, which may rather cause enhanced retention of aggregated material in the upper ocean. Small-scale biological-physical interactions govern the formation and fate of marine snow. Aggregates may form by physical coagulation: fluid motion causes collisions between small primary particles (e.g. phytoplankton) that may then stick together to form aggregates with enhanced sinking velocities. Bacteria may subsequently solubilise and remineralise aggregated particles. Because the solubilization rate exceeds the remineralization rate, organic solutes leak out of sinking aggregates. The leaking solutes spread by diffusion and advection and form a chemical trail in the wake of the sinking aggregate that may guide small zooplankters to the aggregate. Also, suspended bacteria may enjoy the elevated concentration of organic solutes in the plume. I explore these small-scale formation and degradation processes by means of models, experiments and field observations. The larger scale implications for the structure and functioning of pelagic food chains of export vs. retention of material will be discussed.

Key words: food web structure, coagulation, vertical flux, remineralization, behaviour of heteretrophs.

INTRODUCTION

Vertical material fluxes in the ocean are believed to have influence on global climate by eventually leading to net burial of carbon in the seabed and, hence, potentially reduce atmospheric CO_2-content. Particles potentially sink, solutes don't. Thus, vertical material fluxes are primarily due to the sinking of particles. Zooplankton faecal pellets as well as marine snow aggregates are believed to be the main vehicles for vertical material transport in the ocean (Fowler and Knauer 1986). We are therefore interested in the mechanism(s) by which these rapidly sinking particles form, and in the dynamics governing their formation.

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Marine snow aggregates and faecal pellets are also subject to degradation. Aggregates may disintegrate physically (Alldredge *et al.*, 1990; Milligan and Hill, 1998), and they may be solubilized and remineralized by micro-organisms (Ploug *et al.*, 1999; Smith *et al.*, 1992) and zooplankton (Kiørboe, 2000). Likewise, faecal pellets may leak their contents of solute organics (Urban-Rich, 1999), and be consumed by zooplankters (Gonzales and Smetacek, 1994; Smetacek, 1980). Recent studies suggest that the degradation rates of aggregates and faecal pellets due to these processes can be very high, leading to an efficient retention of limiting elements in the upper ocean (Kiørboe, 2000). We are therefore also interested in exploring the mechanisms that govern large-particle degradation.

The sinking flux of material out of the euphotic zone, the export production, represents in a broad sense the balance between the formation and degeneration of rapidly sinking particles. However, the sinking flux is not *governed* by these processes, at least not in a simple fashion. Rather, the sinking of material out of the euphotic zone is governed by the rate at which the matter that limits production (be it nitrogen, phosphorus or iron) becomes available. Considered over sufficiently long time periods, and because mater does not accumulate in the euphotic zone, output (export) balances import. Therefore, the magnitude of the sinking flux is governed by the input of limiting elements to the euphotic zone. The significance of the processes that generate and destroy sinking particles in the euphotic zone is therefore primarily to influence the number of times nutrients are recycled, the magnitude of the pelagic biomass, and the structure of the pelagic food web.

In this article I will examine the small-scale processes that govern aggregate formation and degradation. My ambition is to approach a mechanistic understanding of the small-scale biological-physical interactions that govern aggregate dynamics. While my focus will be on the small-scale component processes I shall set the scene by first considering the larger-scale pelagic food web context of these processes.

FORMATION AND DEGENERATION OF SINKING PARTICLES AND PELAGIC FOOD WEB STRUCTURE

Consider an extremely simple (and simplified) pelagic ecosystem that consists only of phytoplankton (Fig. 1a). Limiting elements are made available through turbulent diffusion and entrainment across the pycnocline from below the euphotic zone and are taken up by the growing phytoplankton. The phytoplankton leaves the euphotic zone through aggregation and subsequent sinking. At steady state, the sinking flux balances nutrient input rate. What is the system biomass at steady state? Our constraint that $N_{Up} = N_{Down}$ implies that the concentration of phytoplankton will adjust exactly such that aggregation rate and, hence, sinking flux balances the input rate of limiting elements. Thus, the steady-state concentration of phytoplankton depends on the coagulation rate.

Consider next an alternative simplification (Fig. 1b), in which the phytoplankton is grazed by mesozooplankton, and vertical flux occurs only via sedimentation of zooplankton faecal pellets. In this scenario the zooplankton faecal pellet production rate and, hence, grazing rate and zooplankton biomass will at steady state adjust such that it balances the input rate of the limiting element. Note that this will be the case whether there is a microbial loop or not, or whether or not the zooplankton is grazed upon by planktivorous fish. The bottom line is that the zooplankton biomass adjusts to fit the flux, not vice versa (For the purpose of this simple analysis we ignore several complications, e.g., that the zooplankton may be food limited, and that assimilation efficiency may vary with feeding rate).

In a more realistic scenario, with two 'competing' settling mechanisms, marine snow aggregates and zooplankton faecal pellets, the 'need' for zooplankton will be less at steady state (Fig 1c). More generally, with increasing relative importance of settling mechanisms that are alternatives to zooplank-

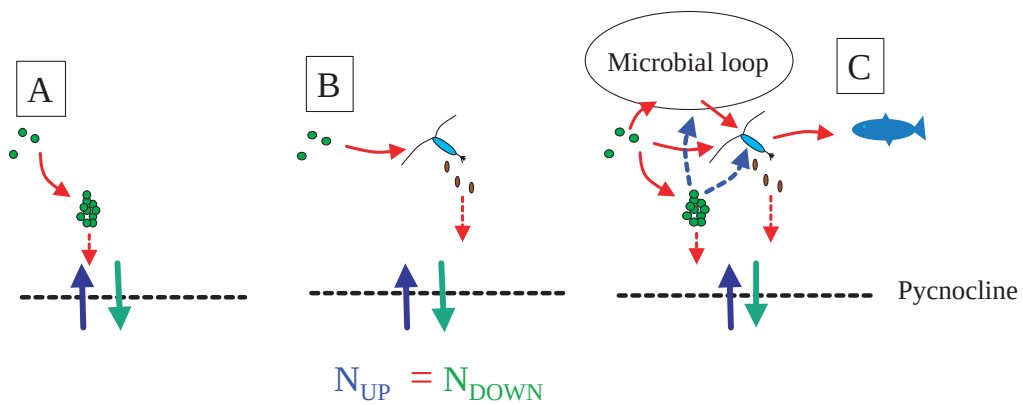

FIG. 1. – Schematics of euphotic zone pelagic food webs simplified to various extents. The main simplification and assumption made is that the downward flux of limiting elements (N_{Down}) equals the upward transport (N_{Up}) of the same elements if averaged over sufficiently long time. A: The pelagic biota consists of phytoplankton only, and the only sinking vehicle is phytoplankton aggregates. B: Sinking is only by zooplankton faecal pellets. In C sinking is both by aggregates and faecal pellets, and sinking aggregates are also being remineralised within the euphotic zone. See text for further explanation.

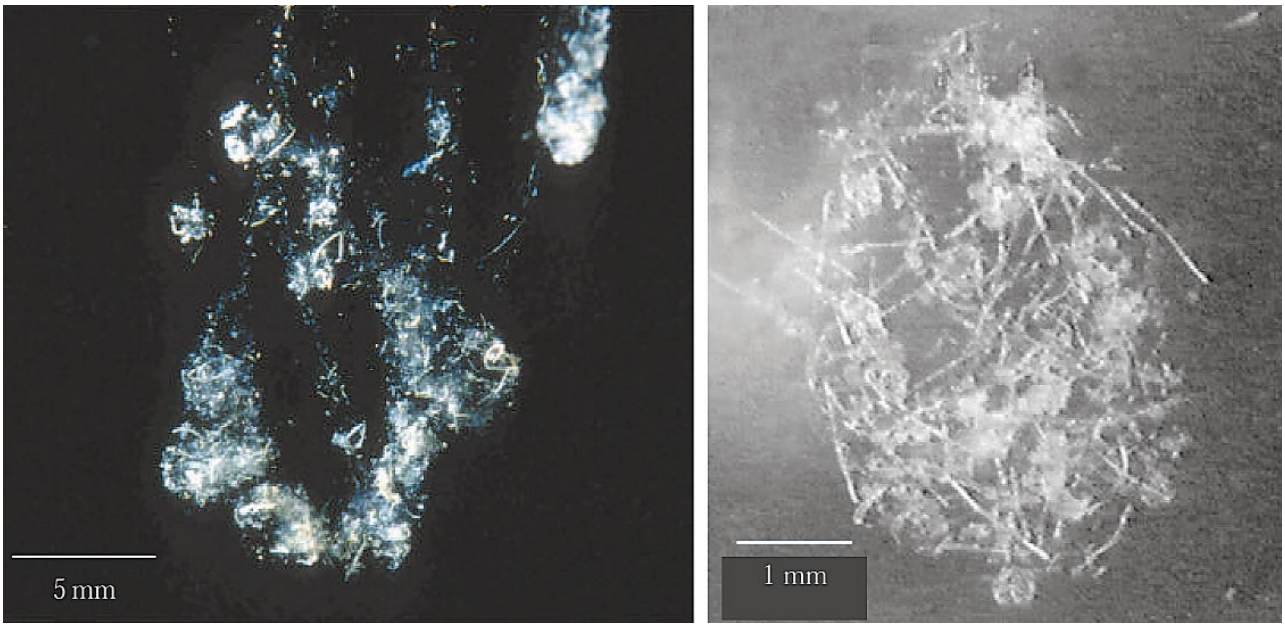

FIG. 2. – In situ micrographs of marine snow aggregates. A. Mixed diatom-faecal pellet aggregate. Individual faecal pellets are visible (by courtesy of Alice Alldredge). B. Diatom aggregate. Individual *Chaetoceros* chains can be seen.

ton faecal pellets, the less is the 'need' for zooplankton to drive the vertical flux, and the less the zooplankton biomass will be. In this scenario, thus, zooplankton biomass is determined by the rate at which marine snow form and sink!

Finally, in the most realistic scenario considered here we allow remineralization of sinking particles. Remineralization leads to retention of material in the upper ocean and, hence, to either increased zooplankton biomass or aggregate formation rate in order to maintain the balance between in- and output from the euphotic zone. To the extent that remineralization of sinking particles continues below the euphotic zone, the net burial rate of carbon in the deep ocean is reduced.

In the past, models of plankton processes have either focussed on aggregation processes –scenario 1– or food web interactions –scenario 2 . In most situations neither provide a complete or even adequate picture. It is only more recently that attempts have been made to combine aggregation and food web models to describe scenario 3 (Jackson, 2001).

While the above scenarios and the assumption of steady state may be challenged, the pictures painted here serve to illustrate that aggregation, sinking, and remineralization of sinking particles directly influence the structure of the pelagic food web, the biomass of the plankton biota, and the burial rate of carbon in the deep ocean. The purpose of this article is to describe and discuss the *mechanisms* and *dynamics* of aggregate formation and remineralization within this large context.

MECHANISMS OF MARINE SNOW FORMATION

Marine snow aggregates consist of all kinds of primary particles that are glued together in a 3-dimensional fractal pattern (Fig. 2): inorganic particles, detritus, phytoplankton, other micro-organisms, feeding webs, exuvia, etc. Aggregates form by a variety of processes and these can be separated in two groups: viz. physical coagulation and zooplankton-mediated aggregation.

Physical coagulation

Aggregation by physical coagulation requires that primary particles collide by some physical process and stick together upon collision. Coagulation theory dates back to Smoluchowski (1917), but has more recently been applied to describe aggregation of marine particles (McCave, 1984) and, specifically, phytoplankton aggregation (Jackson, 1990; Hill, 1992; Riebesel and Wolf-Gladrow, 1992). Laboratory experiments (Kiørboe *et al.*, 1990; Kiørboe and Hansen 1993, Drapeau *et al.*, 1994), mesocosm experiments (Dam and Drapeau, 1995; Jackson, 1995), and field observations (Kiørboe *et al.*, 1994, 1996, 1998) have all demon-

strated that coagulation theory at times provides an accurate description of phytoplankton aggregate formation (see Kiørboe, 1997).

Brownian motion, differences in sinking velocity between particles and fluid shear may all cause primary particles to collide. The collision frequency can be quantified by an encounter rate kernel, β. The encounter rate kernel has units of volume per time and is the imaginary volume of water within which an individual particle will encounter all other particles per unit time (equivalent to a clearance rate). β consists of additive components that are characteristic for each of the individual encounter processes. β is strongly dependent of the size of colliding particles; it scales with particle size to power 1, 2, and 3 for Brownian motion, differential settling and fluid shear, respectively. If we consider a suspension of equally sized particles, such as a phytoplankton bloom dominated by one species, occurring at concentration C, then the collision rate between primary particles becomes βC^2 (number of collisions per unit volume and time). If α is the probability that two particles will stick upon collision, then the rate at which aggregates consisting of two particles form is $\alpha\beta C^2$. After dimers have formed, these may collide with single cells or with one another to form trimers and quadramers, etc, and eventually larger sinking aggregates form. It turns out that, numerically, collisions between single cells by far dominate the process, and that $\alpha\beta C^2$ is a good first approximation of the aggregation rate and, hence, the sinking loss rate (Jackson and Lochmann, 1992). If we consider a phytoplankton bloom and ignore all other processes than growth and aggregation (sedimentation), thus resembling scenario 1 in Fig. 1A, then the change in phytoplankton concentration (C) is the difference between the growth and coagulation. Hence, in simplified form (Jackson, 1990):

$$\frac{dC}{dt} = \mu C - \alpha\beta C^2 \qquad (1)$$

where μ is the specific phytoplankton growth rate of the phytoplankton. At steady state phytoplankton growth will be balanced by aggregation and sedimentation such that

$$\hat{C} = \frac{\mu}{\alpha\beta} \qquad (2)$$

The situation described by this very simple model resembles the situation during a spring bloom in temperate neritic waters where zooplankton grazing can be ignored. In fact, the model has successfully been applied to such a situation and describes well both the phytoplankton population dynamics (Eq. 1, Fig. 3a), the steady state concentration of phytoplankton (Eq. 2, see Kiørboe *et al.*, 1994), as well as the temporal variation in sinking fluxes ($\sim\alpha\beta C^2$, Fig. 3b). This demonstrates that aggregate formation by physical coagulation may be a quantitatively important process that can account for important properties of pelagic systems including the vertical flux of phytoplankton.

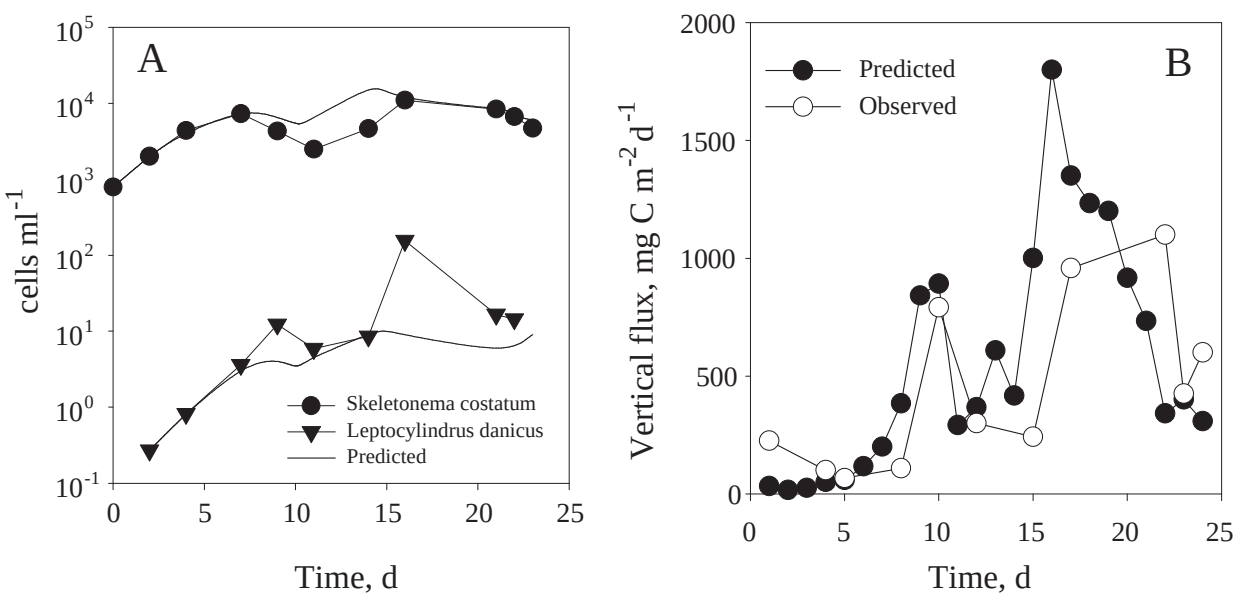

FIG. 3. – Observed and predicted temporal variation in the population sizes of two species of diatoms (A) and in the vertical flux of phytoplankton (B) in a Danish fjord. Predictions were made using eq. 1 and observations of phytoplankton growth rate, stickiness and ambient fluid shear as well as phytoplankton concentration and sizes. Data from Kiørboe *et al.* (1994) and Hansen *et al.* (1995).

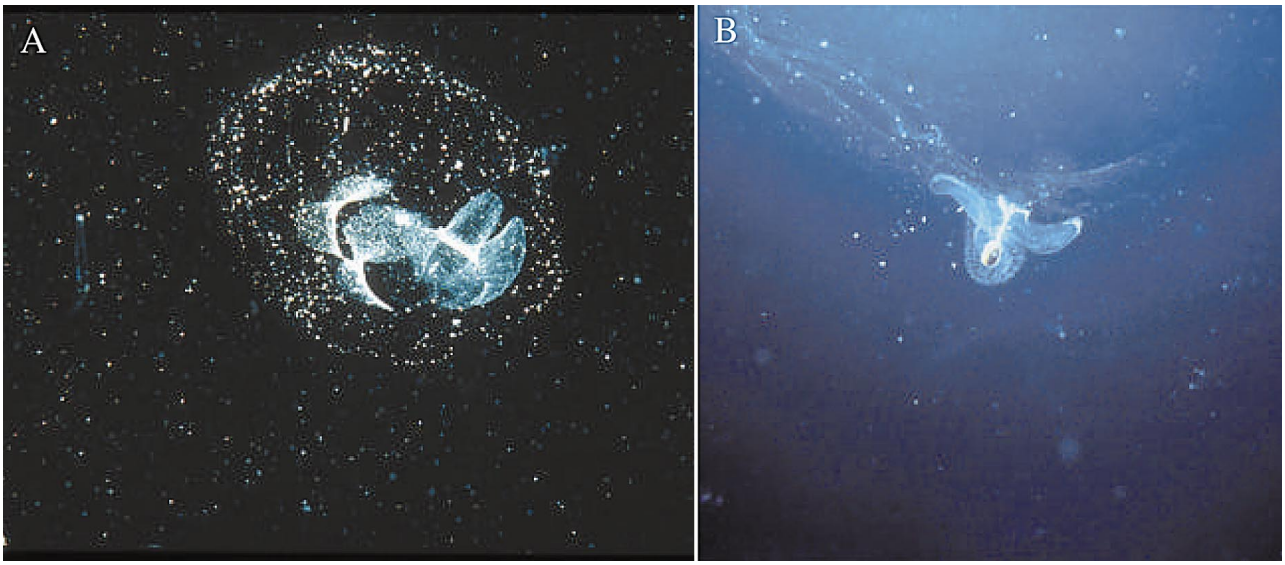

FIG. 4. – In situ photographs of a larvacean in its house (A) and of a pteropod (*Gleba chordata*) with its mucus feeding web (B) (both by courtesy of Alice Alldredge). Both of these zooplankton organisms are sources of marine snow, but the aggregation mechanisms differ. The larvacean strains particles from the ambient water, some of which are retained on an outer coarse filter. Houses with their load of particles are abandoned every few hours and are then marine snow aggregates. Few additional particles are scavenged as the house sinks. In contrast, pteropods collect sinking particles that intercept the blob of mucus secreted by the animal (flux feeding). Abandoned feeding webs are another important source of marine snow.

Zooplankton-mediated aggregation

Zooplankton faecal pellets can be considered aggregates of the primary particles that they contain. Zooplankton grazing is therefore an important and well-documented aggregation process that we need not consider in any further detail here. Mucus feeding webs are another source of marine snow (Fig. 4) that can be quantitatively very important (Hansen *et al.*, 1996). Larvaceans in particular seem to be an important source. These animals abandon their mucus houses frequently, and the particle-loaded house is a marine snow aggregate. Because larvaceans can be abundant this type of marine snow may drive the vertical material flux in some situations (e.g. Kiørboe *et al.*, 1996). Recently it has been demonstrated that giant larvaceans, occurring at mid-depth, may be quantitatively important and account for a substantial fraction of the vertical material flux (Silver *et al.*, 1998). Attachment of small particles to larvacean houses appear mainly to occur while the house is inhabited. The larvacean inside the house draws a water-current through a coarse outer filter on the house, and retains particles for consumption on a finer inner filter. Large particles screened by the outer filter remain attached when the house is abandoned, and some species of larvaceans also 'store' their faecal pellets inside the abandoned house. Scavenging of additional particles by the sinking house, on the other hand, appears to be of minor importance (Hansen *et al.*, 1996).

Fukuda and Koike (2000) suggested yet another zooplankton mediated mechanism of aggregate formation, which may be quantitatively important. They demonstrated how flagellates, *Paraphysomona imperforata*, that are attached to particles, generate an advective flow towards the host particle by means of their feeding current. Smaller particles entrained in this flow may collide with and subsequently stick to the host particle, hence leading to aggregation. There are likewise some ciliates, e.g. *Uronema filificum*, that attach to detritus particles and generate strong feeding currents (e.g. Fenchel and Blackburn 1999) that may similarly cause aggregation with smaller particles from the ambient water. In coastal shallow water aggregates may be inhabited by numerous nematodes. Shanks and Walters (1997) described how nematodes residing on aggregates may extend more than half of their body into the surrounding water, with the extending portion thrashing about vigorously. The extending body collects particles from the ambient water and, thus, adds to the host aggregate. Generally some of the protozoans and metazoans residing on aggregates may continuously add new material and, hence, lead to growth of the aggregate. The quantitative importance of this mechanism for aggregate formation remains unknown.

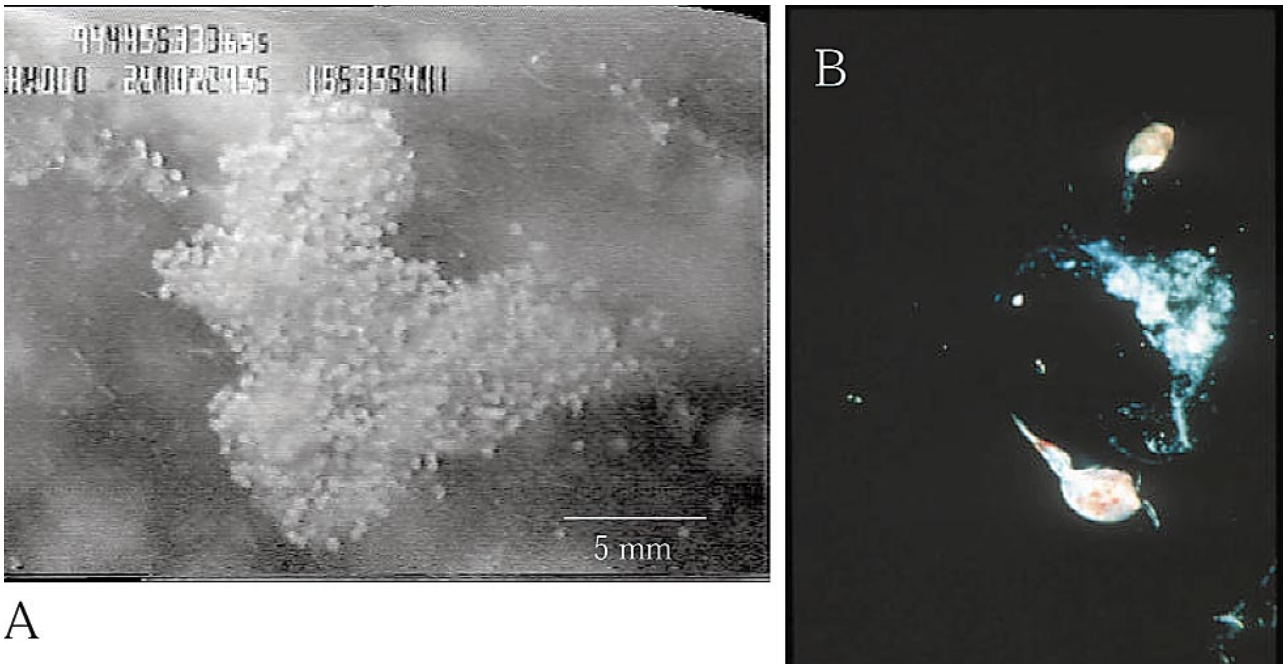

FIG. 5. – Heterotrophs feeding on aggregates. A: A diatom aggregate of the type shown in Fig. 2B has been colonized by the heterotrophic dinoflagellate *Noctiluca scintillans* (Tiselius and Kiørboe 1998). The flagellate feeds on the component diatoms, and in this particular situation diatom aggregation rate was exactly balanced by *N. scintillans* grazing, thus efficiently remeniralizing aggregated material within the upper ocean (Kiørboe *et al.* 1998). B: Copepods of the genus *Oncaea* colonize and feed on marine snow (by courtesy of Alice Alldredge).

MECHANISMS OF AGGREGATE DEGRADATION

Aggregates formed in the water column are also subject to degradation. Degradation can be due to physical disaggregation due to shear stress that tears aggregates apart (Milligan and Hill, 1998), but this process appears of limited importance at typical turbulent shear rates in the upper ocean (Alldredge *et al.*, 1990). Turbulent shear rather puts an upper limit to the size of aggregates (Jackson *et al.*, 1997). More important for aggregate degradation are biological processes. Aggregates may host a very rich and abundant flora and fauna and appear to be hot spots of heterotrophic activity in the water column (Alldredge and Silver, 1988; Kiørboe 2000).

Bacteria colonise and grow on marine snow aggregates. Their activity causes aggregates to solubilise and remineralise, apparently at high rates (Smith *et al.*, 1992; Ploug *et al.*, 1999). Bacteria typically occur on aggregates in concentrations that are 1-many orders of magnitude higher than in the ambient water (Alldredge and Silver, 1988) and they show higher per capita activities than free-living bacteria. Protozoans are also abundant inhabitants of aggregates (Fig. 5a), and they may feed on both bacteria and other particulate components of the aggregate (e.g., Caron, 1987, Tiselius and Kiørboe, 1998). Mesozooplankters also colonize aggregates and feed on their constituents (Fig. 5b) (Lampitt, 1992; Steinberg *et al.*, 1994; Kiørboe, 2000). Finally, fish and other macrophageous plankters may feed directly on intact aggregates (Larson and Shanks, 1996).

These biological processes cause a rapid turnover of aggregated material. Below I first consider the abundance of heterotrophs on aggregates and then provide some estimates of aggregate turnover rates due to their activity. I next explore the mechanisms by which heterotrophs colonize aggregates and finally consider the dynamics of the microbial populations inhabiting aggregate populations.

ABUNDANCE OF HETEROTROPHS ON AGGREGATES

Microorganisms: The abundance of microorganisms associated with an aggregate depends on the size of the aggregate, and maybe also on the availability of microbes in the ambient water. The relation between abundance, size and ambient concentration of micro-organisms appears, however, to vary between microbial groups as well as between studies (Fig. 6). I have here compiled studies that report simultaneous measurements of abundances of microorganisms on aggregates and in the ambient

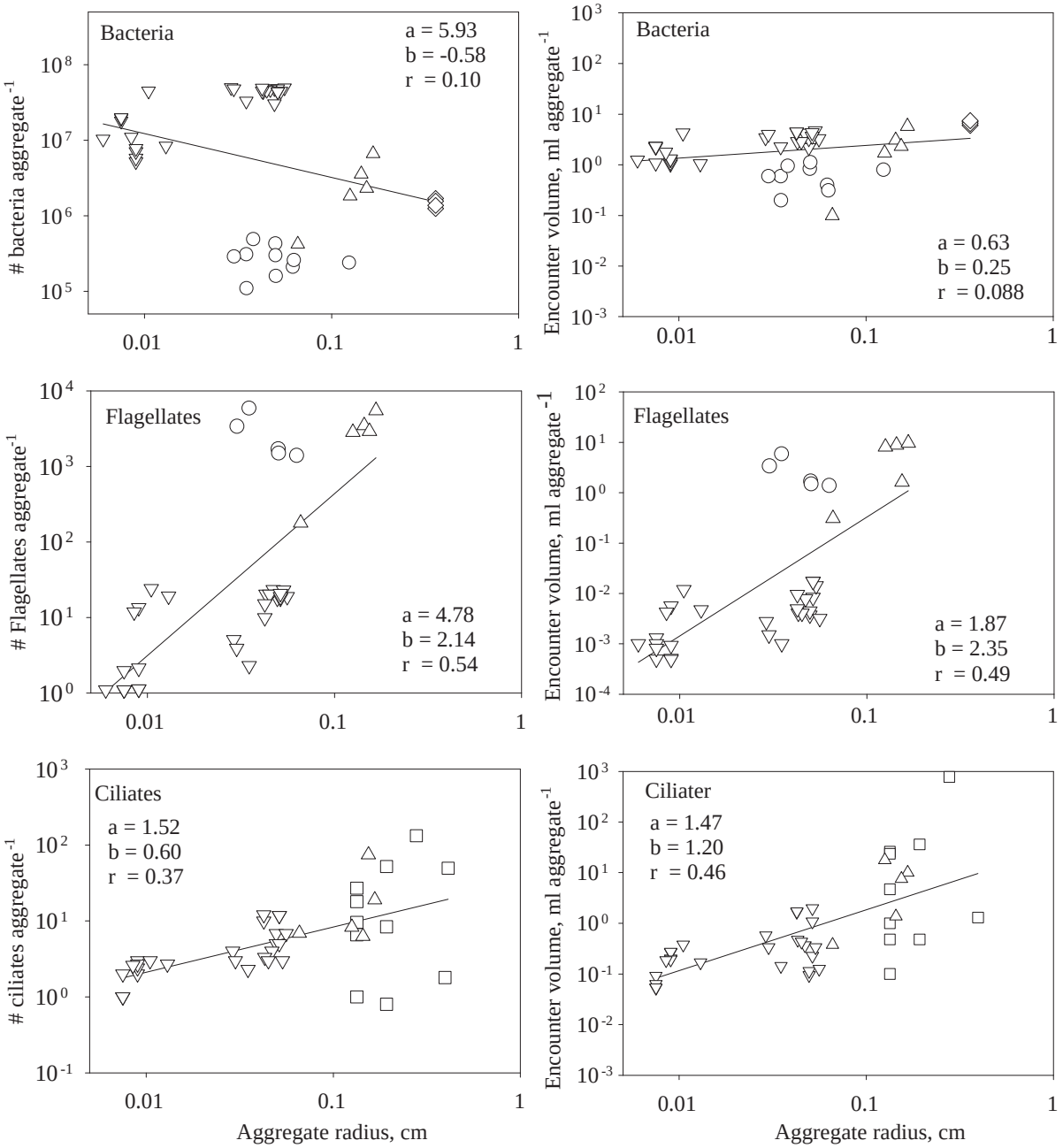

FIG. 6. – Abundances of bacteria, flagellates, and ciliates on aggregates collected *in situ*. In the right columns, abundances have been normalised by ambient concentrations. The normalised abundances (# aggregate^{-1}/# ml^{-1} = ml aggregate^{-1}) represent the equivalent volume of ambient water that contains the same number of organisms as the aggregate and has here been termed the encounter volume. Regression lines of the form logY=a + b logX, where X is aggregate radius (cm) and Y either absolute or normalised abundance have been shown. Data are derived from Alldredge *et al.* (1986), Davol and Silver (1986), Silver *et al.* (1978),Turley and Mackie (1984), and Zimmermann-Timm *et al.* (1998).

water. Bacteria seem to show the most consistent pattern between investigations: there are about 10^5-10^7 bacteria per aggregate, corresponding to the number of bacteria occurring in about 1 ml of ambient water (encounter volume = 1 ml = number of organisms per aggregate divided by ambient concentration = normalised abundance), and the abundance of bacteria on an aggregate appears to be almost independent of the size of the aggregate. Other studies find that the number of bacteria increases slightly with aggregate size. Both Kiørboe (2000) and Alldredge and Gotschalk (1990) found that bacterial abundances scale with aggregate radius raised to a power of about 3/4. The abundance of flagellates on aggregates varies substantially between studies. Flagellates can be either more or less enriched on aggregates than bacteria. However, overall flagellate abundance increases with aggre-

gate size, and considering all the studies together suggests that flagellate abundance scales with aggregate radius squared. Finally, the abundance of ciliates on average increases slightly with the size of an aggregate. The relatively characteristic abundances of microbes on aggregates and characteristic scaling with aggregate size suggest that the microbial populations are subject to some sort of population control. I consider this aspect later.

Mesozooplankters: Aggregates are visited or inhabited by numerous meso-zooplankton species that feed on aggregate constituents or on the microbes associated with the aggregate. Some apparently planktonic copepods, e.g. *Oncaea* spp, appear to be adapted to life on solid surfaces, such as those provided by aggregates, and these copepods may occur abundantly on aggregates. Other numerically important inhabitants include crustacean nauplii. In addition, several invertebrate larvae appear to use aggregates as sinking vehicles when they are ready to metamorphose and settle (Shanks and Carmen, 1997). There are only relatively few quantitative observations on abundances of meso-zooplankters on aggregates because sampling of aggregates with their inhabitant fauna intact requires diving and hand-collection. The available observations suggest that the number of attached meso-zooplankters increases with aggregate size and may reach several hundreds on the largest aggregates (Fig. 7a). If we, as above, normalise with ambient concentrations of organisms a clear scaling emerges: zooplankton abundance increases with the square of aggregate radius (Fig. 7b). The differences in the scaling of abundances of bacteria, flagellates, ciliates and meso-zooplankters suggest different accumulation mechanisms. We will return to this issue below.

AGGREGATE TURNOVER RATES

Leakage of DOM, bacterial remineralization of organic matter, and feeding on aggregated material and other activities by microbes, zooplankton and fish all contribute to aggregate degradation. Here we attempt some numbers. Ploug *et al.* (1999) and Ploug and Grossart (2000) measured carbon-specific respiration rates due to microorganisms of about 0.1 d^{-1} in natural and artificially made aggregates. This rate appears size-independent. Ploug and Grossart (2000) found that the microbial metabolism accounted for almost 80 % of the carbon loss rate in aggregates incubated in the laboratory. Others have found that the solubilization of particulate material in aggregates significantly exceeds the microbial remineralization rate and, therefore, that there is a substantial additional loss of material from aggregates in the form of leaking DOM (Cho and Azam, 1988; Smith *et al.*, 1992; Grossart and Simon 1998). Measurements reported by Smith *et al.* (1992) and Grossart and Simon (1998) suggest specific leakage rates on the order of 0.1-0.2 d^{-1} (Kiørboe and Thygesen, 2001), which is similar to losses due to microbial respiration. Grazing by colonizing meso-zooplankters may account for additional losses of similar magnitude (Kiørboe, 2000). Grazing on aggregates by fish and macrophageous zooplankters is difficult to estimate

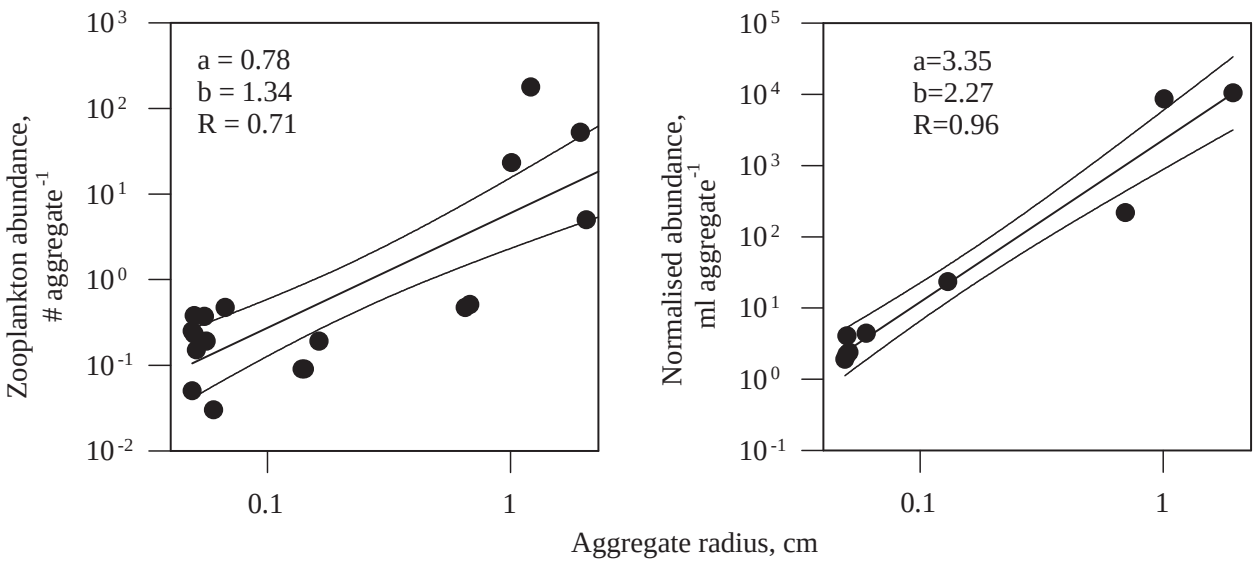

FIG. 7. – Absolute and normalised abundances of mesozooplankters on field-collected marine snow aggregates. Data compiled from the literature by Kiørboe (2000).

but is probably relatively minor. Disintegration of marine snow by swimming euphausids (Dilling *et al.*, 2000; Graham *et al.*, 2000) and due to the activity of other zooplankters (Stemmann *et al.*, 2000) may be significant. Disintegration is, of course, different from remineralization, but everything else being equal, disintegration leads to longer residence times and, hence, to further degradation of aggregates.

Taken together, the solubilization, grazing, disintegration and other activities of heterotrophic organisms add up to substantial degradation rates of aggregates (cf. also Fig. 5a), particularly in the upper mixed layer, implying that a significant fraction of aggregated material is being remineralized in the upper ocean rather than being exported. For example, a degradation rate of 0.3 d^{-1} of aggregates sinking at 20 m d^{-1} implies a degradation rate of 0.015 m^{-1} (=specific degradation rate/sinking velocity) and that more than 80 % of the organic matter has been remineralized before the aggregate leaves a 50 m deep euphotic zone. Below the euphotic zone, degradation processes continue, albeit presumably at a lower rate, leading to a continuous decline in both the flux and the concentration of particles with depth. Typical decline rates are of order 0.0005 m^{-1} (Banse, 1990). This would correspond to a sinking velocity of 20 m d^{-1} and a degradation rate of 0.01 d^{-1}.

COLONIZATION OF AGGREGATES

The bacteria and the proto- and mesozooplankters inhabiting marine snow aggregates –or their ancestors– must have colonized the aggregate from the ambient water. There are different possible colonization mechanisms, and colonization can either be active or passive. Active colonization requires some kind of remote detection of aggregates, while passive colonization that the swimming organism randomly bumps into the aggregate and attach. I shall here consider the various potential mechanisms and examine how colonization rate scales with aggregate size. Because of their very different behaviours and perceptive capabilities I will treat microbes (mainly bacteria) and meso-zooplankters separately.

Copepods: Many of the zooplankters that colonize marine snow aggregates appear to reside on the aggregate for only a few minutes at the time (Alldredge, 1972; Shanks and Walters, 1997). Presumably they abandon the aggregate once they have filled their guts in order to reduce predation risk. Aggregates are high-risk environments because fish and other macrophageous planktivores may engulf the intact aggregate with its inhabitants. The high abundances of zooplankters on aggregates and the short residence times imply that encounter rates must be high. This, in turn, implies that zooplankters must be capable of actively colonize aggregates, i.e., detecting aggregates remotely. Kiørboe and Thygesen (2001) argued that copepods, for example, would be unable to use the hydrodynamic disturbance generated by a sinking aggregate because the cue is too weak. However, they should be able to detect aggregates chemically.

The bacterial populations residing on aggregates solubilise particulate material faster than they assimilate the solutes and dissolved organics thus leak out of sinking aggregates (Smith *et al.* 1992). A sinking aggregate therefore paints a chemical trail in its wake (Fig. 8a). Kiørboe and Thygesen (2001) suggested that horizontally swimming copepods may encounter the solute trail behind a sinking aggregate, and follow the trail to find the particle, much the same way that some male copepods encounter and follow pheromone trails of mates (e.g. Tsude and Miller, 1998). The solute distribution around a sinking aggregate can be accurately simulated in the laboratory (Fig. 8b), and some copepods are in fact able to follow amino acid trails generated that way (Fig. 9). Experiments conducted so far have not included copepods of the more relevant genus *Oncaea* due to difficulties of culturing these animals, but theoretical computations suggest that this encounter mechanism is sufficient to account for observed abundances of copepods on sinking marine snow aggregates (Kiørboe and Thygesen, 2001).

Microbes: Passive colonization of aggregates by direct interception of microbes depends on the motility of the microbes and on the scavenging of microorganisms by the sinking aggregate. Each of these processes can by quantified as encounter rate kernels, β_i, the imaginary volume of water from which the aggregate 'collects' microorganisms per unit time (independent of the mechanism). The kernels from the various encounter mechanisms are additive, such that $\beta = \Sigma\beta_i$. The encounter rate kernel for scavenging (differential sinking) is

$$\beta_{scavenging} = 0.5\ \pi a^2 U \qquad (3)$$

where U is the aggregate sinking velocity and a is the radius of the bacteria. Note that the kernel is independent of aggregate size – counterintuitive, yet true. The kernel for motility-colonization depends

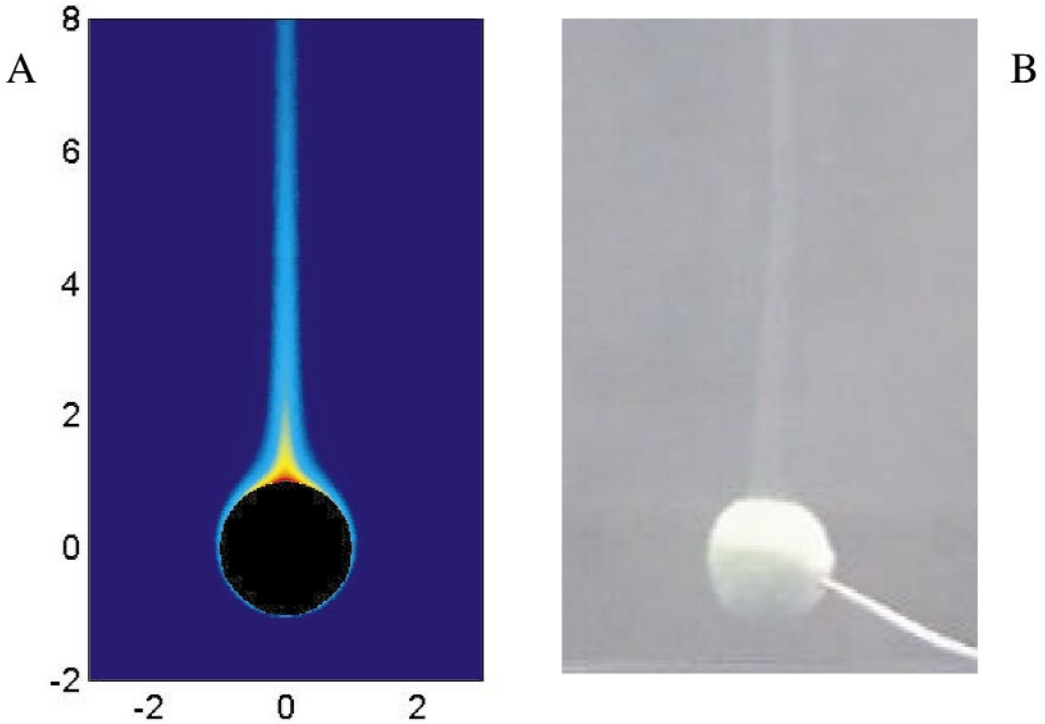

FIG. 8. – The elongated plume of leaking solutes trailing behind a sinking aggregate. A: The mathematical description of the concentration field is based on the assumption of a sinking rigid sphere and involves solving the Navier-Stokes' and advection-diffusion equations numerically (Kiørboe *et al.*, 2001). B: Physical model has been established in the laboratory by suspending a porous sphere in an upward directed flow. A fluorescent dye is slowly (~ 5 µl min^{-1}) pumped into the sphere and as the dye leaks out of the sphere it visualises the plume of any solute leaking out of the sphere. Sphere dimensions (~ 5 mm diameter) and flow velocities (0.1 cm s^{-1}) are representative of marine snow aggregates.

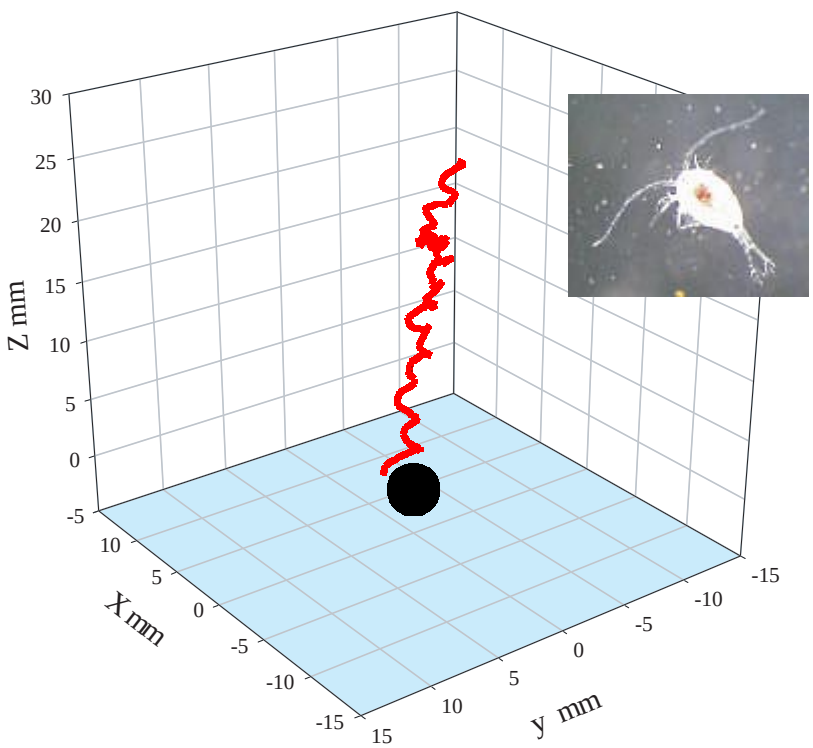

FIG. 9. – The copepod *Temora longicornis* tracking amino acid trail. A *T. longicornis* released in the experimental set-up described in Fig. 8B, where the dye has been replaced by a mixture of amino acids, may encounter the elongated plume and track it to reach the particle. The swimming copepod was filmed simultaneously by two video cameras that viewed the experimental arena at right angles, thus allowing a reconstruction of the 3-dimensional swimming track.

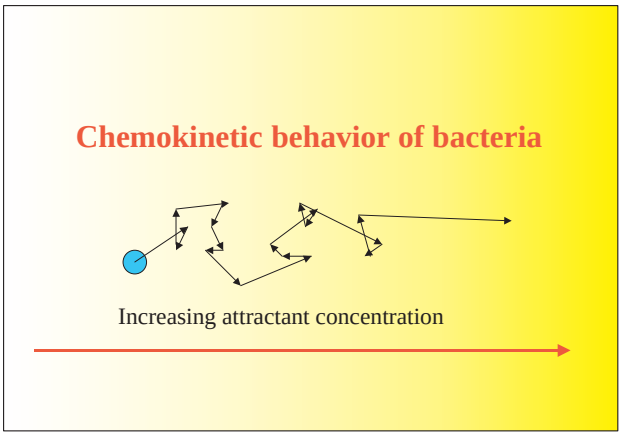

FIG. 10. – Chemokinetic behaviour of motile bacteria. A 'run-tumble' swimming mode has been described for bacteria and other micro-organisms: straight swimming 'runs' are interrupted by 'tumbles', where the organism changes to a new, random direction. Such a swimming mode can be characterised as random walk, and the motility quantified by means of a diffusion coefficient. Chemokinetic behaviour may imply that the probability of tumbling decreases if the organism experiences increasing concentration of attractant molecules during a run, and *vice versa*. Such behaviour will result in a net movement towards the region of high attractant concentration.

on the motility behaviour of the colonizer. We will here consider only the simple case in which the motility can be described as random walk (or biased random walk), which is a good approximation for many micro-organisms. For example, many bacteria swim in a run-and-tumble mode, i.e., they swim in straight lines, 'runs', interrupted at random intervals by 'tumbles' where they change swimming direction randomly (Fig. 10). For this kind of swimming behaviour, the motility can be quantified by a diffusion coefficient (Berg 1993):

$$D\frac{v^2\tau}{6} \qquad (4)$$

where v is the swimming velocity and τ the average run length (time). D for bacteria swimming at 100 μm s^{-1} and tumbling at 1-s intervals is ca. $10^{-5}cm^2s^{-1}$, which is similar to molecular diffusion. Now the kernel for motility-colonization can be estimated as

$$\beta_{motility} = 4\pi DrSh \qquad (5)$$

where r is aggregate radius, and Sh is the Sherwood number. The Sherwood number is the ratio of total to diffusive transport of microorganisms to the aggregate. It is equal to 1 if the aggregate does not move, and > 1 if the aggregate sinks. Kiørboe *et al.* (2001) estimated Sh numerically and found that a good approximation is

$$Sh = 1 + 0.619Re^{0.412}(\nu/D)^{1/3} \qquad (6)$$

where Re (=rU/ν) is the Reynolds number and ν the kinematic viscosity (~10^{-2} cm^2 s^{-1} for seawater). This relation is only valid for $0.1 < Re < 20$ and $30 < Pe < 50000$, where the Peclet number $Pe = rU/D$. A comparison of β-values for the two colonization mechanisms demonstrates that colonization is entirely dominated by motility (Fig. 11), and we can thus ignore scavenging in the following considerations.

Many microorganisms, including many bacteria, have chemokinetic swimming behaviour (Mitchell *et al.*, 1996). Some bacteria, for example, modify the duration of the straight runs between tumbles in response to chemical gradients: if the bacterium during a run senses an increasing concentration of attractant molecules, then on average its run length increases. This behaviour leads to the bacteria aggregating in regions of high concentrations of attractant molecules (Fig. 10), such as amino acids. This can be described as biased random walk and may further increase the rate at which microorganisms colonize marine snow: the plume of DOM surrounding the sinking aggregate may guide bacteria with chemosensory capabilities towards the aggregate.

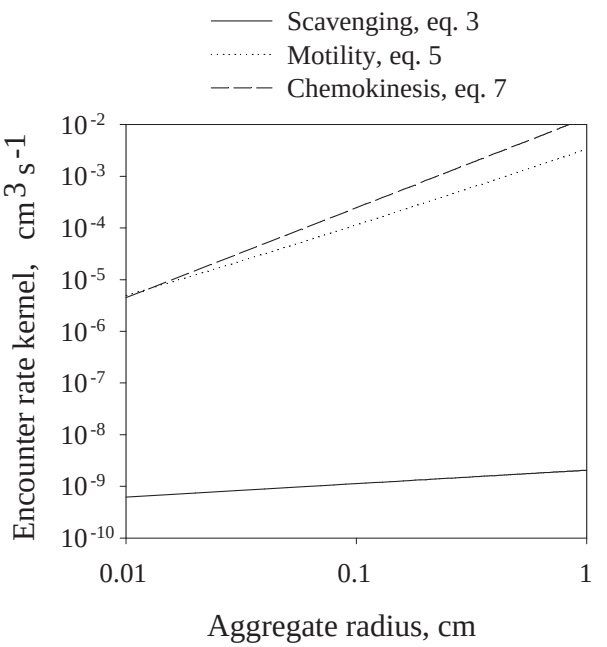

FIG. 11. – Encounter rate kernels for various bacterial colonization mechanisms as a function of aggregate size. Scavenging plays an insignificant role, and chemokinetic behaviour does not enhance colonization rates substantially. The main assumptions made regarding the aggregate are that their sinking velocity, U (cm s^{-1}), varies with aggregate radius, r (cm), as $U = 0.13r^{0.26}$, and that amino acids leak out of sinking aggregates at a rate Q (mol s^{-1}) given by $Q = 10^{-12}r^{1.5}$ (see Kiørboe *et al.*, 2001 and Kiørboe and Thygesen, 2001). The bacteria are assumed to swim at 100 μm s^{-1} and tumble at a frequency of 1 s^{-1}. Assumptions regarding chemokinetic behaviour are specified in Kiørboe and Jackson (2001).

We have simulated colonization rates of bacteria with chemokinetic behaviour assuming a swimming velocity of 100 μm s^{-1} and a tumbling frequency of 1 s^{-1} and optimal chemosensory capabilities (Kiørboe and Jackson, 2001). Simulated colonization rate, quantified as an encounter rate kernel, scales with aggregate size as:

$$\beta_{Chemokinesis,\ cm3\ s\text{-}1} = 0.01365 r_{cm}^{1.74} \qquad (7)$$

Chemokinetic behaviour improves colonization rates a little, but not dramatically (Fig. 11). Microorganisms other than bacteria may likewise colonize aggregates because they swim and due to chemosensory behaviour. This can be described in a similar manner.

DYNAMICS OF MICROBIAL POPULATIONS ON AGGREGATES

The abundance of bacteria, other microorganisms, and small zooplankters scale very differently with aggregate size, suggesting that there are dramatically different accumulation mechanisms. We can distinguish between at least two different components, viz., colonization and population dynamics. For mesozooplankton, only colonization is of importance while for microbes, both colonization and population dynamics are important.

Once on the aggregate, the microorganisms grow and are being eaten. If we for simplicity assume that the dynamics of the bacterial population on an aggregate is governed only by bacterial colonization, growth, and by predator-prey interactions between bacteria and flagellates, then we can describe the interactions by a modification of the classical Lotka-Volterra equations:

$$\begin{aligned} \frac{dB}{dt} &= \beta B_S + \mu B - pBF \\ \frac{dF}{dt} &= aBF - mF \end{aligned} \qquad (8)$$

where B and F are bacterial abundances on the aggregate, B_s (volume^{-1}) is ambient bacterial concentration, β (volume·T^{-1}) is the colonization rate as estimated by equation 6 or 7 above, μ(T^{-1}) is the specific growth rate of the bacteria, p is the specific grazing coefficient (T^{-1}) (such that pF is the specific mortality rate of bacteria due to flagellate grazing), a(T^{-1}) is p times the growth yield, and m(T^{-1}) is the mortality rate of the flagellates. The steady state solution to these equations is:

$$\begin{aligned} \hat{B} &= \frac{m}{a} \\ \hat{F} &= \frac{a\beta^* B_S}{pm} - \frac{\mu}{p} \end{aligned} \qquad (9)$$

The steady state solution suggests that the numbers of bacteria residing on an aggregate is constant and independent of colonization rate and aggregate size, whereas the flagellate abundance depends on bacterial colonization rate and, hence, increases with aggregate size. While cyclic oscillations of bacterial and flagellate populations may be more likely than steady state, it can be shown that average population sizes equal equilibrium population sizes (cf. Pielou, 1969). These predictions in fact bear some relation to the observation that bacterial abundance is independent –or nearly independent– of aggregate size, while flagellate abundances increase with aggregate size (Fig. 6). Obviously, however, this model is too simple because other groups, such as ciliates, may be quantitatively important grazers on flagellates and possibly bacteria, and because microorganisms other than bacteria may colonize the aggregate. Also, aggregation is a continuous process and this may further complicate scaling relations. Yet, this simple model may be used as a starting point for more elaborate models.

FUTURE WORK

I have argued that the balance between sinking and remineralisation rates of aggregates are important for structuring the pelagic food web and in determining pelagic biomasses. The larger the fractional loss rate of limiting elements is, the smaller will the pelagic biomass be –and *vice versa*, remineralisation of aggregates and retardation of vertical flux help conserve matter in the upper ocean. Heterotrophs are important for degrading aggregates, and bacteria appear to play a central role. Not only do the bacteria contribute directly to aggregate remineralization, but their solubilization of particulate material leads to leakage of DOM, which generates solute signals that attract other bacteria and other heterotrophs, which, in turn, further enhance remineralization rates. Also, the solutes leaking out of sinking aggregates may constitute a quantitatively important source of DOM for free-living bacteria and the solute plume surrounding the sinking aggregate an important growth habitat for bacteria (Kiør-

boe and Jackson, 2001). Thus, it becomes critical to understand both how the abundance and the activity of aggregate-associated bacteria are regulated.

Some of the considerations above may be used to guide future observations and experiments that address this question of *regulation*. For example, we may ask whether local growth or colonisation from ambient water is the most important for the accumulation of bacteria. To address this, we equate the two accumulation terms in Eq. 8, i.e., $\beta B_s = \mu B^*$, and solve for $B^* = \mu / \beta B_s$, the bacterial abundance at which growth is as important as colonization. For example, assuming $\mu = 2\ d^{-1}$ and $B_s = 10^6\ cm^{-3}$ and that β can be described by equation 7, suggests that B* is about 10^6 for 0.01 cm radius aggregates and increasing to almost 10^9 for 1 cm aggregates. Since observed bacterial abundances on aggregates are on order 10^6 aggregate^{-1} (Fig. 6), this exercise suggests that colonization is more – or much more - important than growth in accounting for bacteria on aggregates. However, not all suspended bacteria are motile, and not all motile bacteria will necessarily colonise an encountered aggregate. For example, Fenchel (2001) found that about 20 % of pelagic bacteria are motile. Bacteria approaching a surface may show exploratory swimming behaviour and decide to leave rather than attach, and some attached bacteria may detach again (own unpublished observations). Therefore, bacterial composition on aggregates differs from that in the ambient water (e.g. Caron *et al.*, 1982), and growth is more important than this analysis suggests. However, the scaling of B* with aggregate size (increases with radius$^{1.74}$, cf. Eq. 7) demonstrates that we need worry more about colonization processes for large aggregates, and more about growth dynamics for small aggregates when attempting to describe bacterial dynamics on marine aggregates. Obviously, this is a topic area, which needs be addressed experimentally.

Bacteria attached to aggregates solubilze particulate material by means of ectoenzymes (Smith *et al.*, 1992). Do the bacteria regulate ectoenzyme production? This would seem sensible, since ectoenzyme production would be cost with no return when the bacteria are in the free-living phase. If they regulate enzyme release, how do they do it? Likewise, how do bacteria decide whether or not to attach to an encountered particle? Chemical communication between bacteria, 'quorum sensing', would offer a means for bacteria to regulate their activities. Many bacteria are known to release signal molecules at low rates, and to respond to the concentration of such molecules (Eberl, 1998). Release of ectoenzymes, for example, would make particularly sense when bacteria are many together on an aggregate and can collaborate in solubilizing particulate material, and quorum sensing has in fact been demonstrated to play such a role in some systems (Givskov *et al.*, 1997). On the other hand bacteria may also compete for space and resources on an aggregate, and chemical warfare between species is another possible means by which bacterial abundances and activities on aggregates are regulated. These kinds of processes may be further complicated by the fact that aggregates sink, because the flow of water past the aggregate may change concentrations of both signal and warfare molecules (cf. Schmidt and Jumars, 2001).

While this is all of a somewhat speculative nature my prediction is that there is a very rich research avenue here to explore in the future. And that the study of these key small-scale processes will help us address the larger issues of ocean biogeochemistry in a more competent manner.

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