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Marine snow microbial communities: scaling of abundances with aggregate size

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ABSTRACT: Marine aggregates are inhabited by diverse microbial communities, and the concentration of attached microbes typically exceeds concentrations in the ambient water by orders of magnitude. An extension of the classical Lotka-Volterra model, which includes 3 trophic levels (bacteria, flagellates, ciliates) and considers colonization, detachment, growth and predator-prey interactions on the surface of the particle, was used to examine the processes that govern abundances of attached micro-organisms. Effects of sinking on colonization rates as well as the fractal nature of natural aggregates were also taken into account. As input for the model, I used experimentally determined encounter and detachment rates, and density-dependent growth and grazing rates, as well as information on relevant properties of natural aggregates, all taken from the literature. The model reproduces the temporal development of attached populations of bacteria, flagellates, and ciliates, as observed in experimental systems, and also predicts steady-state abundances of attached micro-organisms that are close to those observed on field-collected aggregates. The model suggests that attached bacterial populations are controlled by flagellate grazing, while flagellate and ciliate populations are governed by colonization and detachment. The model also suggests that microbial populations are turned over rapidly (1 to 20 times d^{-1}) due to continued colonization and detachment. The model overpredicts somewhat the scaling of microbial abundances with aggregate size observed in field-collected aggregates. This may be because it disregards the aggregation/disaggregation dynamics of aggregates, as well as interspecific interactions between bacteria.

KEY WORDS: Microbial population dynamics · Colonization · Grazing rates · Detachment rates · Growth rates · Fluid dynamics

INTRODUCTION

Marine snow aggregates are inhabited by diverse microbial communities and the concentrations of micro-organisms in snow aggregates are typically several orders of magnitude higher than in the ambient water (Simon et al. 2002). The attached micro-organisms play a pivotal role in the remineralization of sinking aggregates in the water column (Ploug & Grossart 2000, Grossart & Ploug 2001) and, hence, for the recycling of elements in the upper ocean (Kiørboe 2001). The activity of attached micro-organisms is ultimately limited by their abundance, but the processes regulating the abundances of particle-attached microbial populations remain unresolved.

Several studies have quantified the abundances of microbes attached to marine snow, and a universal scaling of microbial abundances to the size of aquatic aggregates appears to exist. This is particularly evident for abundances of attached bacteria. Several studies have shown that the abundance of attached bacteria scale with the size (equivalent radius) of aggregates raised to a power ≤ 1, and that this weak scaling apparently applies to aggregates from strikingly different environments such as rivers (Zimmermann-Timm et al. 1998), coastal waters (Grossart et al. 2003a), and more open oceans (Alldredge & Gotschalk 1990, Alldredge 1998, data compilation in Kiørboe 2000), as well as to aggregates of diverse origin (Alldredge & Gotschalk 1990). The scaling of protist

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abundances (flagellates and ciliates) with aggregate size is less well described, but appears to be similar to that found for attached bacteria (Fig. 1). In contrast, the abundance of zooplankters attached to marine aggregates scale with squared aggregate size (Kiørboe 2000).

While the scaling of the abundance of attached zooplankton can be explained by the colonization mechanisms (Kiørboe & Thygesen 2001), the observed scaling of micro-organism abundances is not intuitive. Colonization of sinking aggregates by micro-organisms from the ambient water scales approximately with radius to the power of 1.5 (Kiørboe & Jackson 2001, Kiørboe et al. 2002). The food availability, expressed as either the carbon content, nitrogen content or dry mass of an aggregate (Alldredge 1998), or as the interstitial content of dissolved organics (Alldredge 2000), also scales approximately with size to the power of 1.5. Thus, microbial abundances are not governed in simple ways by either colonization rates or resource availability inside an aggregate. However, micro-organisms also interact with one another on the aggregate, and trophic interactions, in particular, may be intense (Artolozaga et al. 2002). It has long been recognized that pelagic microbial communities are regulated by growth and predator-prey interactions (Fenchel 1986), and such interactions may interplay with colonization and detachment to govern the dynamics of attached microbial communities (Kiørboe et al. 2003). The purpose of this study was to examine to what extent colonization, growth and trophic interactions on the aggregate surface can together account for the observed abundances of attached micro-organisms and the scaling of abundances with aggregate size. This was done by means of a modification of the classical Lotka-Volterra model, primarily using the mechanistic understanding and estimates of interaction coefficients achieved in experiments specifically designed to provide input for this model (Kiørboe et al. 2002, 2003), as well as information on the properties of natural aggregates (Alldredge & Gotschalk 1990, Alldredge 1998, 2000).

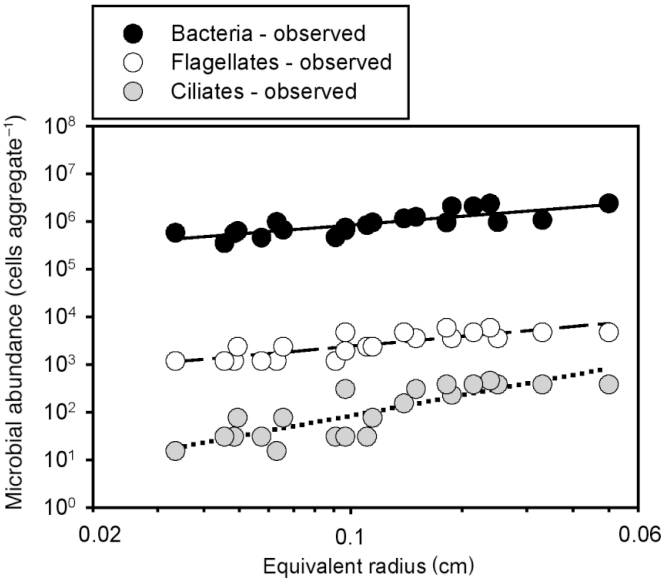

Fig. 1. Microbial abundances on field-collected marine snow aggregates as a function of the equivalent spherical radius of the aggregate. Data are from the Øresund, Denmark (Grossart et al. 2003). Log-log regressions of the form $\log y = a + b \times \log x$ are shown for bacteria ($a = 6.54$, $b = 0.62$, $R^2 = 0.65$), flagellates ($a = 4.06$, $b = 0.68$, $R^2 = 0.67$) and ciliates ($a = 3.34$, $b = 1.42$, $R^2 = 0.70$)

METHODS

The model. Microbes colonize and detach aggregates, they grow, and they feed upon each other. I consider sinking aggregates that are being colonized by populations of bacteria (B), heterotrophic flagellates (F), and ciliates (C), and assume that the flagellates graze on the bacteria, and that the ciliates graze on the flagellates. The rates of changes of each of these populations are governed by colonization, detachment, growth, and for the bacteria and flagellates also by grazing mortality:

$$\frac{dB}{dt} = \beta'_B B_A + \mu(B)B - \delta_B(t)B - p_F(B)FB \quad (1a)$$

$$\frac{dF}{dt} = \beta'_F F_A + a_F BF - \delta_F F - p_C(F)CF \quad (1b)$$

$$\frac{dC}{dt} = \beta'_C C_A + a_C FC - \delta_C C \quad (1c)$$

where t is time; B, F, and C are bacterial, flagellate and ciliate densities (no. cm^{-2}), respectively; β'_B, β'_F, and β'_C are the encounter rate kernels for bacteria, flagellates and ciliates, respectively, normalized by the surface area of the aggregate (cm min^{-1}); B_A, F_A, and C_A are the ambient microbial concentrations (no. cm^{-3}); μ is the specific bacterial growth rate (min^{-1}); p_F and p_C are the flagellate and ciliate grazing coefficients ('surface clearance rate', cm^2 min^{-1} protozoan^{-1}); $a_F = Y_F \times p_F$ and $a_C = Y_C \times p_C$, where Y_F and Y_C are the flagellate and ciliate growth yields, respectively (number of cell divisions per prey ingested); and δ_B, δ_F, and δ_C are the bacterial-, flagellate- and ciliate-specific detachment rates, respectively (min^{-1}) (see Table 1 for parameter definitions). Bacterial growth (μ) is density dependent, the grazing coefficients (p_F and p_C) depend on prey density, and bacterial detachment rate (δ_B) depends on the time that a bacterium has resided on the aggregate, all in accordance with experimental evidence (Kiørboe et al. 2003).

Table 1. List of symbols used and default values of input parameters for the model. Source is given where relevant

Symbol	Definition	Units	Default value	Source
A	Aggregate surface area	cm^2	Eq. (5)	
a_F	$Y_F \times p_F$	$cm^2\ min^{-1}$	–	
a_C	$Y_C \times p_C$	$cm^2\ min^{-1}$	–	
B	Bacterial density	cells cm^{-2}	–	
B^*	Threshold bacterial density	cells cm^{-2}	Eq. (7)	
B_A	Ambient bacterial concentration	cells cm^{-3}	10^6	
C	Ciliate density	cells cm^{-2}	–	
C_A	Ambient ciliate concentration	cells cm^{-3}	10	
D_B	Diffusivity of bacteria	$cm^2\ min^{-1}$	1.4×10^{-3}	Kiørboe et al. (2003)
D_C	Diffusivity of ciliates	$cm^2\ min^{-1}$	1.2×10^{-3}	T. Kiørboe et al. (unpubl.)
D_F	Diffusivity of flagellates	$cm^2\ min^{-1}$	5.9×10^{-3}	Kiørboe et al. (2003)
F	Flagellate density	cells cm^{-2}	–	
F_A	Ambient flagellate concentration	cells cm^{-3}	10^3	
p_C	Ciliate surface clearance rate	$cm^2\ min^{-1}$	Eq. (8)	
p_F	Flagellate surface clearance rate	$cm^2\ min^{-1}$	Eq. (8)	
r	Aggregate radius	cm	–	
Sh	Sherwood number	–	Eq. (3)	
u	Aggregate sinking velocity	cm s^{-1}	Eq. (4)	
Y_F	Flagellate growth yield	cells $cell^{-1}$	0.003	Fenchel (1986)
Y_C	Ciliate growth yield	cells $cell^{-1}$	0.003	Fenchel (1986)
α	Proportionality constant (Eq. 5)	$cm^{1/2}$	25	This study
β'_B	Normalized encounter rate kernel for bacteria	cm min^{-1}	Eq. (2)	
β'_C	Normalized encounter rate kernel for ciliates	cm min^{-1}	Eq. (2)	
β'_F	Normalized encounter rate kernel for flagellates	cm min^{-1}	Eq. (2)	
δ_B	Bacterial detachment rate	min^{-1}	2.3×10^{-2}	Kiørboe et al. (2003)
δ_C	Ciliate detachment rate	min^{-1}	6.4×10^{-4}	T. Kiørboe et al. (unpubl.)
δ_F	Flagellate detachment rate	min^{-1}	6.7×10^{-3}	Kiørboe et al. (2003)
γ	Proportionality constant (Eq. 7)	$min^{-1}\ cm^{-\lambda}$	1.9×10^3	Alldredge & Gotschalk (1990)
κ_C	Ciliate surface clearance at low prey density	$cm^2\ min^{-1}$	1.25×10^{-5}	This study
κ_F	Flagellate surface clearance at low prey density	$cm^2\ min^{-1}$	5×10^{-7}	Kiørboe et al. (2003)
λ	Exponent (Eq. 7)	–	1.34	Alldredge & Gotschalk (1990)
μ	Bacterial growth rate	min^{-1}	Eq. (6)	
μ_{Max}	Maximum bacterial growth rate	min^{-1}	1.39×10^{-3}	Kiørboe et al. (2003)
ν	Kinematic viscosity	$cm^2\ s^{-1}$	10^{-2}	
τ_C	Ciliate prey handling time	min	0.24	This study
τ_F	Flagellate prey handling time	min	0.24	Kiørboe et al. (2003)

Functional relations and parameter estimates. It is assumed that the sinking aggregate is spherical. Default parameter inputs are given in Table 1. Below I rationalize the functional relations assumed and the parameter choices.

Colonization-rate and encounter-rate kernel: Micro-organisms encounter sinking aggregates because the organisms swim, but encounters are further facilitated by the flow of water past and through the sinking aggregate. The enhancement of encounters due to flow past the aggregate may be significant, up to a factor of 20, and can be quantified by the Sherwood number (see Eq. 3). The enhancement due to flow through a porous aggregate is negligible (Kiørboe et al. 2001), small (up to factor of 2; Logan & Alldredge 1989), or modest (up to factor of 4; Ploug et al. 2002a), but is difficult to quantify and has consequently been ignored. It is assumed that the motility of the micro-organisms can be described as random walk and characterized by a diffusion coefficient (e.g. Berg 1993). The normalised encounter-rate kernels then become:

$$\beta' = 4\pi r D\,\mathrm{Sh}/A \quad (2)$$

where r is the radius of the aggregate, D is the diffusivity of the micro-organism (determined experimentally, Table 1), A is the aggregate surface area, and Sh is the Sherwood number (Kiørboe et al. 2001):

$$\mathrm{Sh} = 1 + 0.619\left(\frac{ur}{\nu}\right)^{0.412}\left(\frac{\nu}{D}\right)^{1/3} \quad (3)$$

where ν is the viscosity of the water (~10^{-2} $cm^2\ s^{-1}$) and u the sinking velocity of the aggregate (Alldredge & Gotschalk 1988):

$$u\,(\mathrm{cm\ s^{-1}}) = 0.13 r\,(\mathrm{cm})^{0.26} \quad (4)$$

For a solid sphere, $A = 4\pi r^2$. However, marine snow aggregates are porous, fractal structures with a surface area that can be larger than the surface area of the

circumscribing sphere. Because marine aggregates have porosities > 99% (e.g. Logan & Alldredge 1989), one can assume that the total surface area of the aggregate equals the surface area of the component particles (assuming negligible contact area between particles), which in turn implies that the total surface area scales with the solid mass of the aggregate. Alldredge has in several studies demonstrated that the mass of marine aggregates scales with the square root of the aggregate volume and, therefore, with equivalent radius raised to the power of 1.5 (e.g. Alldredge 1998). Thus, I will assume that:

$$A = \alpha r^{1.5} \quad (5)$$

The proportionality constant α is unknown. I shall as a default value assume $\alpha = 25\ \mathrm{cm}^{0.5}$. This implies that the surface areas of 0.1 to 1 cm radius aggregates are 2 to 6 times the surface area of the equivalent spheres. This is not inconsistent with intuition developed from looking at pictures of marine aggregates (Fig. 2), but such pictures also suggest that this factor is likely to vary widely.

Growth rates of attached micro-organisms: Kiørboe et al. (2003) found that the growth of bacteria attached to solid, stationary agar spheres is more or less constant until bacterial density exceeds a threshold value (B^*) and that it declines hyperbolically with bacterial density above this threshold:

$$\mu = \mu_{Max} \quad \text{for } B \le B^* \quad (6a)$$

$$\mu = \frac{\mu_{Max} B^*}{B} \quad \text{for } B > B^* \quad (6b)$$

This was interpreted as the result of resource limitation, which implies that there is a maximum rate at which cells can be produced on an aggregate. This maximum cell production rate is given by $\mu_{Max} B^* A$, where μ_{Max} is the maximum growth rate at low cell densities. The limiting resource can either be internal to the aggregate (i.e. the amount of dissolved or particulate organic material available to the bacteria), or it can be external (e.g. inorganic nutrients or oxygen delivered to the sinking aggregate from the ambient water). In the former case, total maximum cell production is expected to scale with internal resource availability and, therefore, with aggregate size to the power of ca. 1.5 (cf. above). In the latter case, maximum cell production depends on the delivery of molecules by advection and diffusion transport from the environment. By combining an expression for advective and diffusive transport of molecules towards the aggregate (similar to Eqs. 2 & 3, but without the area normalization) with estimates of size-dependent sinking velocity of aggregates (Eq. 4), one finds that the delivery rate of limiting elements from the surrounding environment also scales approximately with aggregate size raised to

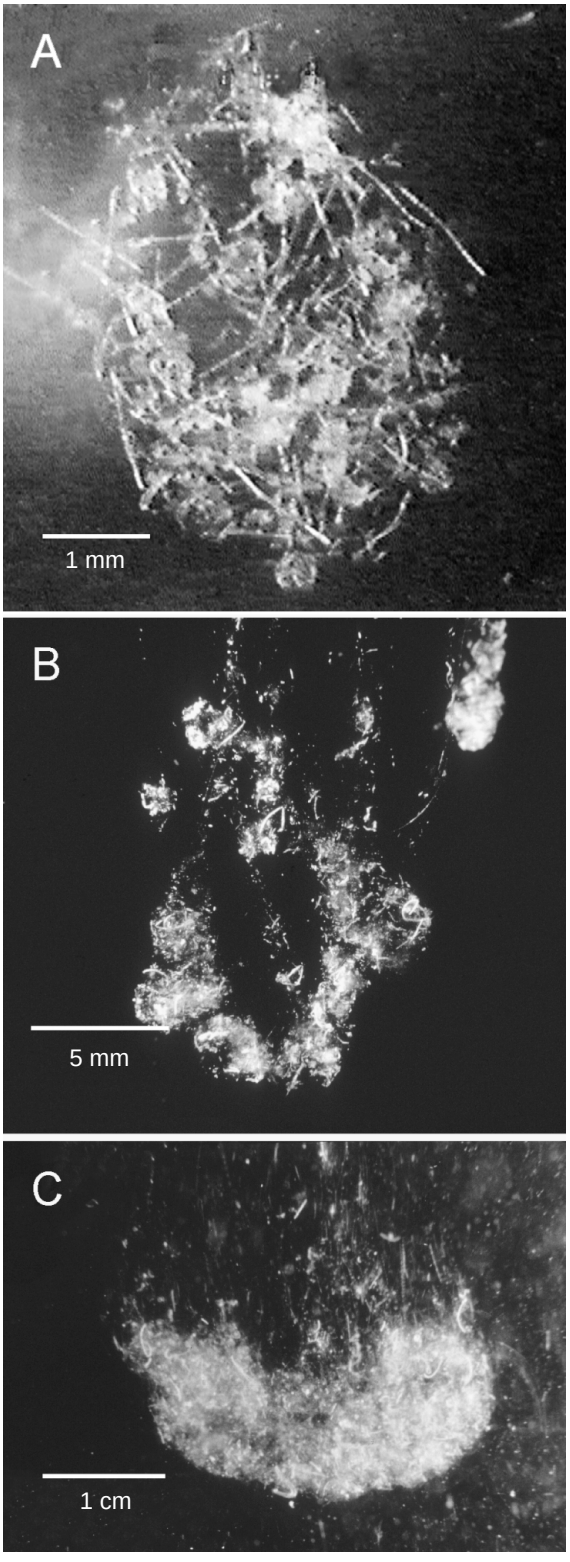

Fig. 2. *In situ* photographs of marine snow aggregates. (A) Diatom *Chaetoceros* sp. aggregate, Benguela upwelling current; (B) aggregate of mixed composition, off the Californian coast; (C) diatom aggregate, off the Californian coast. (B) and (C) are courtesy of Alice Alldredge

the power of 1.5 (Kiørboe et al. 2002). Thus, in either case, maximum cell production is expected to scale with aggregate size to the power of 1.5. Measurements of bacterial production rates in field-collected or man-made aggregates are, in fact, consistent with this expectation (see below in this section). Thus, the cell density at which bacterial growth rate becomes density dependent is given by:

$$\mu_{Max} B^{\star} A = \gamma r^{\lambda} \Rightarrow B^{\star} = \frac{\gamma r^{\lambda}}{\mu_{Max} A} \quad (7)$$

The proportionality constant (γ) estimated from measurements on field-collected or man-made marine aggregates varies widely between studies, 1.9×10^3 to 1.4×10^6 (when μ are in units of min^{-1} and B and $B^{\star}$ in units of cells cm^{-2}), while the exponent (λ) varies less, 1.34 to 1.82 (data combined from Alldredge & Gotschalk 1990 and Alldredge 1998, Ploug & Grossart 2000, Ploug et al. 2002b).

Grazing rates and growth yield: The density-dependent ingestion and surface clearance rates of flagellates on bacteria attached to the surface of agar spheres were quantified by Kiørboe et al. (2003) and the observations fitted to a modified Holling disk equation of the form:

$$p_F = \frac{\kappa_F}{1 + \kappa_F \tau_F B} \quad (8)$$

where κ_F is the grazing coefficient of flagellates at an infinitesimal low prey density, and τ_F the 'handling time'. In their experiments, the flagellate grazers were small microflagellates (~5 µm diameter) typical of those found on marine snow (Patterson et al. 1993), whereas the bacteria were larger (~2 µm diameter) than those typical of marine aggregates (0.16 to 1.0 μm^3 volume or 0.7 to 1.2 µm diameter). Since maximum ingestion rate ($1/\tau_F$) is governed by the predator:prey volume ratio, I assumed a default τ_F-value $^1/_8$ of that found experimentally.

Ciliates grazing on attached flagellates are described in a similar fashion. I assume that typical snow ciliates are 25 µm in diameter (Ploug et al. 2002b), that the surface clearance rate scales with predator diameter squared (i.e. grazing coefficient of ciliates, $\kappa_{C,} = 25 \times \kappa_F$) and that maximum ingestion rate varies with predator:prey volume ratio, as assumed for the flagellates. With these estimated parameters, the maximum surface clearance of a 25 µm ciliate becomes 1.25×10^{-5} cm^2 min^{-1}, which is comparable to that estimated for *Euplotes* sp. of that size, 0.3×10^{-5} to 0.5×10^{-5} cm^2 min^{-1} (Lawrence & Snyder 1998).

A growth yield of 0.4 (growth in volume/ingested volume) is assumed for protozoan grazers (e.g. Fenchel 1986) and is converted to units of cells produced per cell ingested (Y_F and Y_C).

Detachment rates: Specific detachment rates have been determined experimentally for bacteria, flagellates and ciliates (Table 1). Bacteria, with time, become irreversibly attached to an aggregate as they become embedded in the exopolymeric substances they exude. I assume that bacteria become permanently attached at a specific rate equal to $^1/_{10}$ of the initial detachment rate; this is consistent with experimental observations (Kiørboe et al. 2003).

RESULTS AND DISCUSSION

The basic run with default parameters

The predicted accumulation of micro-organisms on aggregates shows an initial rapid colonization of bacteria, followed by flagellates, and later ciliates, and a subsequent slower increase towards steady-state abundances, which are reached within 0.5 to 1 d for bacteria and flagellates, and 2 to 3 d for ciliates (Fig. 3A,B). The temporal patterns are similar for small and large aggregates and there are no oscillations in abundances, except for an initial overshoot in the abundance of flagellates, particularly evident for small aggregates. A run with model parameters pertinent to the conditions of the experiments reported by Kiørboe et al. (2003) shows a similar temporal pattern and, in addition, a good correspondence to the observations (Fig. 3C). (The observations in Fig. 3C are independent of the observations used to provide parameter estimates for the model.)

At steady state, the microbial populations are turned over rapidly, mainly due to continuous and high colonization and departure rates of cells, while growth and mortality rates are modest (Table 2). Expressed relative to the magnitude of the attached population, bacteria, for example, colonize and detach at 17 and 14.5 d^{-1}, respectively, they experience a grazing mortality of 2.7 d^{-1}, and they have a very modest growth rate (0.2 d^{-1}). While the exact magnitudes of these rates depend on the specific parameter values, Table 2

Table 2. Simulated colonization, detachment, growth, and grazing mortality rates (d^{-1}) of bacteria, flagellates, and ciliates at steady state, expressed relative to the size of the attached populations. Values are for a 0.1 cm radius aggregate using default input parameters (see Table 1)

	Colonization rate	Detachment rate	Growth rate	Mortality rate
Bacteria	17.0	14.5	0.2	2.7
Flagellates	11.5	9.7	1.9	3.7
Ciliates	0.7	0.9	0.2	0

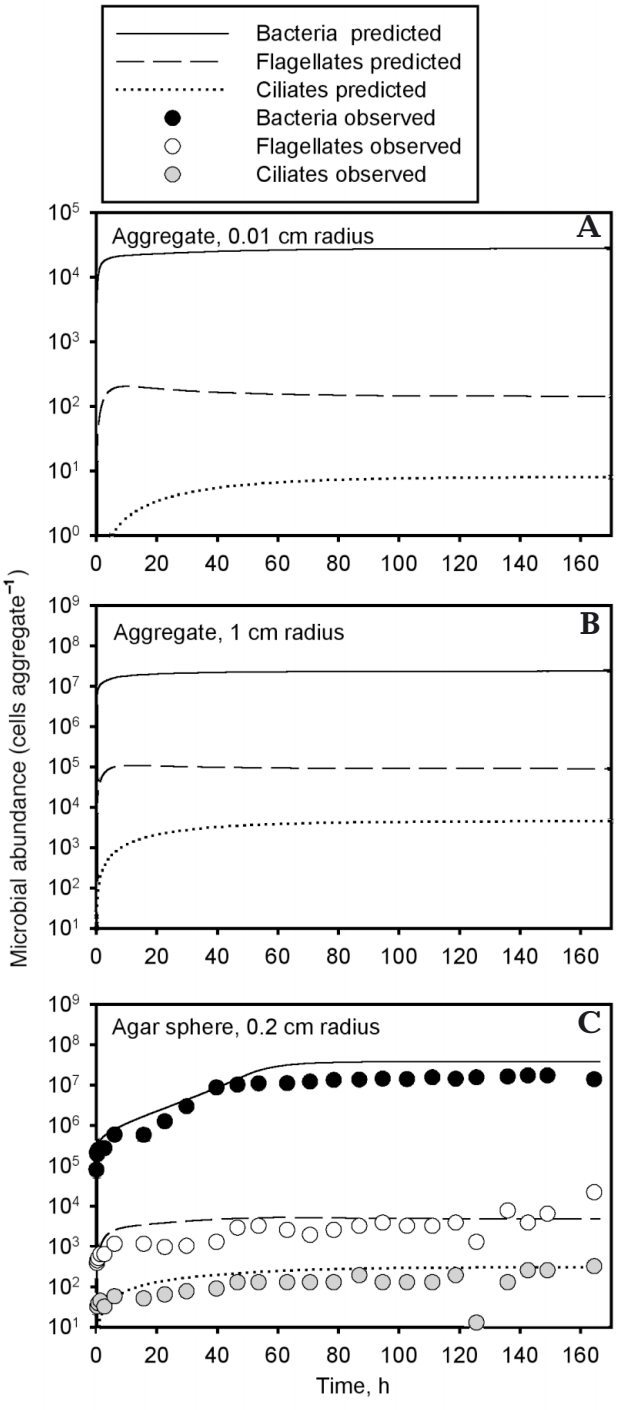

Fig. 3. (A,B) Predicted temporal development of micro-organism abundances on 0.01 and 1 cm radius aggregates. Default parameters (see Table 1) were used as input. (C) Predicted and observed population dynamics of bacteria, flagellates and ciliates attached to a solid, non-sinking sphere of 0.2 cm radius. Observations are from Kiørboe et al. (2003). The simulation uses the default parameters in Table 1, with the following exceptions that were pertinent to the particular experiment: (1) $A = 0.5$ cm^2 (= surface area of 0.4 cm sphere), (2) $B^* = 1.8 \times 10^7$ cells cm^{-2}, (3) $B_A = 1.5 \times 10^6$ cells cm^{-3}, (4) $C_A = 20$ cells cm^{-3}, (5) $F_A = 500$ cells cm^{-3}, (6) $\kappa_C = 0.5 \times 10^6$ cm^2 min^{-1}, (7) $\tau_C = 1.93$ min, (8) $\tau_F = 1.93$ min

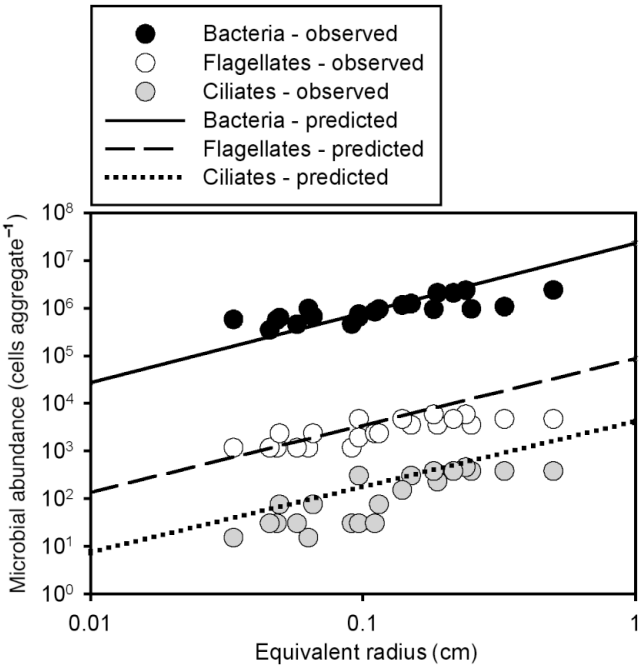

Fig. 4. Simulated steady-state abundances of microbes on aggregates as a function of aggregate size. Default parameters (Table 1) were used in the computation

suggests that there is a significant exchange between attached and freely suspended populations of bacteria, flagellates, and ciliates, and that marine snow microbial communities cannot be considered as isolated entities.

Predicted steady-state abundances of attached micro-organisms as a function of aggregate size are of the same order as those observed (Fig. 4). The predicted scaling with aggregate size is similar to the observed scaling for ciliates, but the predicted slopes are somewhat steeper than those observed for flagellates and bacteria (Table 3).

Sensitivity analysis

I examined the effect of parameter values and underlying assumptions by varying input parameters one by one, typically by a factor of 0.1 to 10 times the default values, and by changing the assumed functional relationships. Predicted steady-state abundances of attached micro-organisms varied with input parameters (Table 3) However, the slopes of log-log regressions of steady-state microbial abundances versus aggregate size predicted by the model were mostly robust to such changes in parameter values, and varied by less than 10% of the slope predicted using the default parameter values (Table 3).

Likewise, the predicted scaling of microbial abundances was insensitive to changes in assumed functional relations. I attempted, for example, to dramatically change the assumed growth regulation of attached bacteria. Because the aggregate content of dissolved organics scales with aggregate radius to the power of 1.5 (Alldredge 2000), the concentration scales with radius to the power of –1.5, i.e. it declines with aggregate size. Assuming a dependency of bacterial growth on DOM concentration, employing Michaelis Menten kinetics does not change the predicted scaling. In fact, the scaling of microbial abundances is insensitive to whether one assumes that bacteria always grow at their maximum rate, or do not grow at all. It is also insensitive to the assumed magnitude of the maximum growth rate. Likewise, the predicted scaling is insensitive to major changes in aggregate compactness (α), functional response and intensity of both flagellate and ciliate grazing (τ, κ), ambient concentrations of micro-organisms (B_A, F_A, C_A), and the rates at which they detach from aggregates (δ). The assumed relation between aggregate sinking rate and size (Eq. 4) may overpredict sinking velocities (e.g. Asper 1987, Pilskaln et al. 1998), but even assuming that the aggregates do not sink at all (i.e. Sh = 1) does not affect the predicted scaling for bacteria, but reduces the slopes for protozoans to ~1.

This lack of sensitivity of the scaling of bacterial abundance with aggregate size is due to the bacterial populations in the model being controlled by flagellate grazing. If the intensity of flagellate grazing is decreased sufficiently, the bacterial populations will escape grazing control and keep increasing infinitely. When checked by grazing, the bacterial population will reach a density (number per surface area) which is constant and independent of aggregate size; for our default run with the model, this density is ca. 10^6 bacteria cm^{-2}. The flagellate population, in contrast, is not controlled by ciliate grazing, despite the significant grazing mortality suggested by the default run of the model (Table 2); even if ciliate grazing pressure is set at zero, flagellates will enter steady state, and the scaling of their abundance with aggregate size remains largely unaffected. Thus, ciliate and flagellate populations are mainly governed by the balance between colonization and detachment, while the bacterial populations are checked by grazing. As a consequence, flagellate and ciliate abundances scale with colonization rate, while bacterial abundance scales with aggregate surface area.

The only parameter that materially changes the predicted scaling of bacterial abundance with aggregate size is the fractal dimension of the aggregate. This is because bacterial density is constant and the fractal dimension describes the scaling of surface area with

Table 3. Sensitivity analyses. Slopes of log-log regression of abundances of attached microbes as a function of aggregate size, and abundance of microbes attached to a 0.1 cm radius aggregate as observed in field-collected aggregates, and as predicted by the model using default input parameters (see Table 1 for definitions), or input parameters varied one by one. Most input parameters were varied between 0.1 and 10× their default value (represented by 0.1–10× in table); the fractal dimension of the aggregate were varied between 1 and 2 (represented by 1–2 in table); and the Sherwood number was fixed at 1 (aggregates do not sink) in the sensitivity analysis. B = bacteria, F = flagellates, C = ciliates

Parameter:	**–**	**–**	**α**	**Fractal dimension**	**μ**	**τ_F**	**τ_C**	**κ_F**	**κ_C**
Parameter range:	Observed	Default parameters	0.1–10×	1–2	0–μ_{Max}	0.1–10×	0.1–10×	0.1–10×	0.1–10×
Slope B	0.62	1.46	1.38–1.52	1.16–1.42	1.46–1.60	1.47–1.41	1.47–1.39	1.49–1.45	1.48–1.39
Slope F	0.68	1.4	1.47–1.36	1.32–1.79	1.40–1.45	1.40–1.44	1.39–1.50	1.40–1.41	1.36–1.47
Slope C	1.42	1.37	1.38–1.41	1.45–1.29	1.37–1.39	1.38–1.35	1.40–1.33	1.38–1.36	1.4–1.4
# $B\times10^5$	8.4	7.9	7.8–37.9	15.8–7.7	7.7–18.2	8.0–8.0	7.5–18.5	52.2–2.3	6.3–38.7
# $F\times10^3$	2.4	3.5	6.9–4.5	4.2–1.6	3.4–4.1	3.1–6.8	3.8–1.3	3.3–4.4	4.9–0.7
# $C\times10^2$	0.8	1.6	2.7–1.4	1.5–2.2	1.8–1.9	1.7–2.7	1.4–1.22	1.8–2.0	1.4–2.6
Parameter:	**B_A**	**F_A**	**C_A**	**Sh**	**δ_B**	**δ_F**	**δ_C**		
Parameter range:	0.1–10×	0.1–10×	0.1–10×	1	0.1–10×	0.1–10×	0.1–10×		
Slope B	1.47–1.41	1.48–1.40	1.48–1.44	1.5	1.42–1.46	1.41–1.56	1.39–1.48		
Slope F	1.40–1.44	1.40–1.49	1.37–1.44	1.05	1.45–1.40	1.47–1.36	1.48–1.37		
Slope C	1.38–1.35	1.40–1.33	1.33–1.40	0.95	1.41–1.38	1.38–1.41	1.38–1.41		
# $B\times10^5$	1.09–7.5	39.1–3.8v	6.4–21.7	4.6	25.9–0.1	5.1–72.9	38.9–6.3		
# $F\times10^3$	3.1–6.8	0.67–12.3	4.8–1.1	1.1	1.4–3.0	7.1–0.5	0.7–4.9		
# $C\times10^2$	1.7–2.6	1.4–11.0	0.2–14.4	0.3	15.1–1.7	2.8–1.4	25.7–0.1		

aggregate size. Hence, bacterial abundance scales approximately with the fractal dimension of the aggregate.

Conclusions and future directions

Using rates and interaction coefficients determined experimentally, and properties of marine snow aggregates described in field studies, the simple model presented here is capable of predicting approximate bulk abundances of micro-organisms attached to particles, in both laboratory experiments (Fig. 3c) and field-collected aggregates (Fig. 4). Thus, simple considerations of hydrodynamics, attachment/detachment, growth and predator-prey interaction probably capture the quantitatively most significant processes determining the abundance of attached microbes. Important suggestions of the model exercise are that attached bacterial populations are grazer controlled, and that attached microbial populations are turned over rapidly due to a continuous exchange between attached populations and free populations in the ambient water. The latter finds some observational and experimental support, at least for bacteria (Jacobsen & Azam 1984, Friedrich et al. 1999, Batty et al. 2000), while the former needs more solid testing; so far only 2 studies have quantified flagellate grazing on bacteria attached to suspended particles (Artolozaga et al. 2002, Kiørboe et al. 2003).

The model is less efficient in describing the scaling of microbial abundances with aggregate size (Fig. 4), and one has to invoke additional mechanisms to account for the exact scaling. A number of potentially important processes that may contribute to the discrepancy between observed and predicted scaling have been disregarded in the above considerations. For example, the model assumes that attached organisms are evenly distributed over the entire aggregate surface. However, diffusing organisms may be able to penetrate only to a certain depth in the aggregate before they attach, and with increasing aggregate size this may cause increasing differences in organism densities between deep and superficial surfaces of the aggregate. As long as the flagellates are capable of checking bacterial populations, this should not influence the scaling properties, however. Another potential problem is that the model ignores the dynamics of the aggregates themselves. Aggregates form and disintegrate continuously, and they have size-dependent residence times in the water column because they sink at size-dependent rates. Sinking on its own has a limited effect on scaling (examined by considering microbial abundances after a time period equal to the size-dependent average residence time in the upper mixed layer, rather than steady-state abundances), while aggregate dynamics may have a substantial effect. However, it is unclear how the aggregation/disaggregation dynamics integrated over the entire particle size spectrum would change scaling relations. One argument that such interactions may play a limited role is that the scaling relation observed for field-collected aggregates is independent of aggregate origin, and applies also to aggregates that are not formed by coagulation, e.g. larvacean houses and fecal pellets (Alldredge & Gotschalk 1990).

The model also ignores inter-specific interactions among bacteria. Quorum-sensing type molecules are produced by some marine snow bacteria (Gram et al. 2002), and particle-associated bacteria show particularly strong antagonistic effects (Long & Azam 2001). The presence of one type of bacteria on an aggregate may severely reduce the attachment probability of others (Grossart et al. 2003b), and detachment rates may also be affected. Such interactions likely have strong effects at the species level, but may also influence the scaling of abundances. Since the number of bacterial species on an aggregate will increase with the absolute number of resident bacteria, such negative effects on attachment and emigration probabilities may increase with aggregate size. This would lead to a weaker scaling than predicted by the present model. There is a need to develop our understanding of inter- and intraspecific interactions among bacteria in a way that allows us to describe the significance of such interactions in shaping attached microbial communities, regulating their activity, and achieving mechanistic insights in the processes governing the remineralization of marine aggregates.

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