



## ORIGINAL RESEARCH ARTICLE

# Possible means of overcoming sedimentation by motile sea-picoplankton cells

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**Summary** A model for overcoming the gravity by sea-picoplankton cells is proposed here. It is based on different means of escaping from potential predators used by cells of co-existing picoplankton species. These different means cause friction anisotropy of motile cells with strong antipredator behavior (AB). According to equations of stochastic movement used in this model for picoplankton cells with strong AB, collocated with high concentration of cells with weak or absent AB, the sedimentation can be considerably overcome.

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## 1. Introduction

Plankton microorganisms in wide range of sizes are extremely numerous in saline waters of seas and oceans. They are the key agents of global biogeochemical cycles (Strom, 2008) and their ecology is partly driven by their motility patterns, which

dictate their distributions and encounters with biotic and abiotic targets (Visser and Kiorboe, 2006). Many planktonic organisms are known to undergo diel vertical migrations (DVMs) up to tens of meters per day in the field (Smayda, 2010). DVM may allow individuals to avoid predation, for example by moving through haloclines (Bollens et al., 2012; Harvey and Menden-Deuer, 2012) and, in the case of phytoplankton, to balance daytime near-surface light exposure with nighttime nutrient uptake at depth (Cullen, 1985). Marine planktonic cells can undergo DVM in two ways: by gravitaxis or by gravikinesis (Eggersdorfer and Häder, 1991; Schuech and Menden-Deuer, 2014). The process of microorganisms' gravidependent spatial orientation is called gravitaxis (known historically as geotaxis). The motile microorganism's spatial orientating to move upwards and downwards is called negative and positive gravitaxis respectively (Roberts, 2006). Gravitaxis has two different aspects: biological and physical. The biological aspect of gravitaxis is

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expressed by the existence of certain cell receptors accepting gravistimulus and, through signaling chains, causing the change in the direction the cell moves (Hemmersbach and Häder, 1999). The physical aspect of gravitaxis is visible in the occurrence of hydrodynamic (Hagen et al., 2014; Roberts and Deacon, 2002) or density gradient (Kessler, 1985) torque which changes the orientation of the cell. The speed of some microorganisms depends on their orientation within the gravity field (excluding buoyancy of the whole cells). This phenomenon is called gravikinesis. So far, physiological mechanisms of gravikinesis have been well examined and described by Hemmersbach and Häder (1999) for example. Its physical aspect however has not yet been investigated and it might be expressed by an anisotropic interaction of the microorganisms with the water medium.

Many planktonic species are non-spherical, extended along their single axis and typically wider at the rear than at the front. Such an asymmetrical shape causes the above-mentioned torque orienting their fronts upward (Schuech and Menden-Deuer, 2014). Thus, it is natural to conclude that if these organisms need cell receptors for realizing DVM (Schuech and Menden-Deuer, 2014), then, for the simple overcoming of sedimentation, these organisms need only physical mechanisms, which are quite enough to direct the averaged locomotion force upwards. A considerable part of the biological diversity of motile picoplankton organisms (whose dimension varies from  $0.2 \times 10^{-6}$  to  $2 \times 10^{-6}$  m) consists of flagellar bacteria. The bacterial cell motor can switch the direction of its action. For example, this has been shown for the marine bacterium *Vibrio alginolyticus* (Xie et al., 2015). Therefore, cell asymmetry cannot play the part in their physical gravitaxis. Thus, a question can be raised: whether these organisms can overcome sedimentation without any special cellular mechanism for gravity perception, as it has been shown for asymmetric microplankton (Hemmersbach and Häder, 1999)? We have tried to answer this question positively taking into account antipredator behavior (AB) – the ability of picoplankton organisms to detect and escape their predators by outrunning them. ABs of different species vary considerably (Pernthaler, 2005). Analogical behavior has also been revealed for microplankton (Harvey and Menden-Deuer, 2012). As it has been shown, in presence of active predator the sexual and predatory activities of prey cells were inhibited (Harvey and Menden-Deuer, 2012). Thus, to simplify we excluded from our model predatory and sexual behaviors of the microorganisms facilitating the encounters between the cells. Although there are numerous picoplanktonic species in natural sea waters, for simplicity's sake we considered a collocation of only two species: those with strong and absent AB. The cells with strong AB always try to escape the others as potential predators. We have also taken into consideration the influence of thermal fluctuations on the movement of these tiny plankton microorganisms. Thus, the movement of a microorganism can be described by Langevin's equation, which considers random fluctuation force. Therefore its coordinate, velocity and acceleration depend on time randomly, too. However, when averaged, these quantities depend on time unambiguously. Such movement is called stochastic (Sklar, 1993). Let us show the possible result when an averaged fluctuation force, which acts on the cells with strong AB, is orientated upwards. By causing physical gravikinesis, described above, the averaged

fluctuation force can theoretically influence picoplankton to overcome sedimentation entirely.

## 2. Model description

Let us consider the movement of a microscopic particle in a viscous medium under the influence of gravity. The particle undergoes locomotion force  $F$  directed along the axis of symmetry of the particle ( $X'$ ). Movement orientation of the particle randomly changes sharply. It also changes so as to prevent from encounter with a particle that has been detected further on the way. Such movement can be described as:

$$m\ddot{x} + h_x(\alpha)\dot{x} - (m - m_m)g - F_x(t) = A_x(t), \quad (1)$$

$$m\ddot{y} + h_y(\alpha)\dot{y} - F_y(t) = A_y(t), \quad (2)$$

$$m\ddot{z} + h_z(\alpha)\dot{z} - F_z(t) = A_z(t), \quad (3)$$

$$\mu\ddot{\alpha} + \gamma\dot{\alpha} - \Phi_\alpha(t) = H_\alpha(t), \quad (4)$$

where  $x$ ,  $y$ ,  $z$  are coordinates of the mass centrum of the particle;  $\alpha$  is the vector of orientation of spherical angles:  $\vec{\alpha} = (\alpha_x, \alpha_y, \alpha_z)$ ;  $g$  is gravity centrifugation;  $m$  and  $m_m$  are the particle mass and the mass of the medium of the same volume correspondingly;  $\mu$  is the mass moment of the particle;  $h_x(\alpha)$ ,  $h_y(\alpha)$ ,  $h_z(\alpha)$  are friction coefficients of the particle;  $\gamma$  is the moment of friction coefficient;  $F_x(t)$ ,  $F_y(t)$ ,  $F_z(t)$  are projections of the locomotion force  $F$  on the coordinate axes;  $\Phi_\alpha(t)$  is the moment of the force, which periodically changes the orientation of the particle sharply;  $A_x(t)$ ,  $A_y(t)$ ,  $A_z(t)$  are projections of fluctuation force on coordinate axes;  $H_\alpha(t)$  is the vector of the moment of fluctuation force.

For the sake of simplicity we can also describe the translational movement of the particle in an orthogonal coordinate system bounded with the axis ( $X'$ ), along which the locomotion force always acts, as:

$$m\ddot{x}' + h_{x'}\dot{x}' - (m - m_m)g_{x'} - F = A_{x'}(t), \quad (5)$$

$$m\ddot{y}' + h_{y'}\dot{y}' - (m - m_m)g_{y'} = A_{y'}(t), \quad (6)$$

$$m\ddot{z}' + h_{z'}\dot{z}' - (m - m_m)g_{z'} = A_{z'}(t), \quad (7)$$

where  $x'$ ,  $y'$ ,  $z'$  are the new coordinates of the particle;  $g_{x'}$ ,  $g_{y'}$ ,  $g_{z'}$  are the projections of gravity acceleration on axes  $X'$ ,  $Y'$ ,  $Z'$  correspondingly;  $h_{x'}$ ,  $h_{y'}$ ,  $h_{z'}$  are the friction coefficients of the particle, which moves along the new axes.

Considering the stochastic character of Eqs. (1)–(7) and the fact that relaxation time of water is shorter than the time needed for a considerable change in the spatial position of a microscopic particle, we can neglect sharp changes in  $x'$ ,  $|x'|$ ,  $y'$ ,  $y'$ ,  $z'$ ,  $z'$  during such changing of  $\alpha$ ,  $\dot{\alpha}$ ,  $\Phi(t)$  (Sklar, 1993). We can also neglect changes of the locomotion force considering that  $|F| = \text{const}$  (prokaryotic cells switch their cell motors periodically). As it has been shown for *V. alginolyticus* the

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