



## 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

frequency of cell motor switching is no higher than 100 Hz (Xie et al., 2015). Thus, for the sake of simplicity in the scale of  $10^{-7}$  m and  $10^{-9}$  s  $\dot{x}'(t)$ ,  $\dot{y}'(t)$ ,  $\dot{z}'(t)$  in Eqs. (5)–(7) can be considered as:

$$\begin{aligned}\dot{x}'(t) &= \Delta\dot{x}'(t) + \bar{x}'(t), \dot{y}'(t) = \Delta\dot{y}'(t) + \bar{y}'(t), \dot{z}'(t) \\ &= \Delta\dot{z}'(t) + \bar{z}'(t); \end{aligned} \quad (8)$$

$$\begin{aligned}h_{x'}\bar{x}' &= F + (m-m_m)g_{x'}, h_{y'}\bar{y}' = (m-m_m)g_{y'}, h_{z'}\bar{z}' \\ &= (m-m_m)g_{z'}; \end{aligned} \quad (9)$$

$$|\Delta\dot{x}'(t)| = \frac{D_{x'}}{d_{x'}}, |\dot{y}'(t)| = |\dot{z}'(t)| = \frac{D_{y',z'}}{d_{y',z'}}, \quad (10)$$

where  $\bar{x}'$ ,  $\bar{y}'$ ,  $\bar{z}'$  are the averaged velocities of the particles identically orientated with respect to coordinate axes  $X$ ,  $Y$ ,  $Z$  and to the action of cell motors;  $d_{x'}$  and  $d_{y',z'}$  are the dimensions of the particles along the axes  $X'$  and  $Y'$  or  $Z'$  correspondingly;  $D_{x'}$  and  $D_{y',z'}$  are coefficients of diffusion along the axis  $X'$  and  $Y'$  or  $Z'$  correspondingly.

Having considered Eqs. (8) and (9), let us transform Eqs. (5)–(7) in:

$$\begin{aligned}m\ddot{x}' + h_{x'}\Delta\dot{x}' &= A_{x'}(t), \quad m\ddot{y}' + h_{y'}\Delta\dot{y}' \\ &= A_{y'}(t), \quad m\ddot{z}' + h_{z'}\Delta\dot{z}' = A_{z'}(t). \end{aligned} \quad (11)$$

Eq. (11) permit us to consider the particle in a state of equilibrium only under the condition:

$$|\bar{x}'| < \frac{D_{x'}}{d_{x'}}, \quad |\bar{y}'| < \frac{D_{y,z'}}{d_{y,z'}}, \quad |\bar{z}'| < \frac{D_{y,z'}}{d_{y,z'}}, \quad (12)$$

when  $\dot{x}'(t)$ ,  $\dot{y}'(t)$ ,  $\dot{z}'(t)$  according to Eqs. (8) and (10) can change their sign independently from cell motor switching.

## 2.1. Time reversal transformation. Appearance of diffusional force

Let us obtain the sum of Eq. (11) for  $x'$  in points  $t = \tau$  and  $t = -\tau$ ;  $\tau \neq 0$ , where  $\tau$  is the time during which the particle does not switch its cell motor and translocates a certain distance which is not equal to zero. Then let us average this sum with respect to the ensemble of a multitude of identical systems as we have already done (Pundyak, 2014). Then, if the system is in a state of equilibrium, according to the laws of equipartition and the symmetry of movement under time reversal transformation, we obtain:

$$\Lambda \equiv \bar{A}_{x'} = 0.5(h_1 - h_2)\Delta\bar{x}', \quad (13)$$

where  $\Lambda$  is the averaged fluctuation force (let us call  $\Lambda$  diffusional force);  $\Delta\bar{x}'$  is the averaged diffusional velocity of such translocation;  $h_1$  and  $h_2$  are the averaged friction coefficients for a particle which moves in the same direction as the cell motor action and in the direction opposite to the cell motor action correspondingly. If the particle moves in a pure viscous medium with a speed not much higher than the speed of its Brownian motion (with low Reynolds number), then its  $h_1$  always equals  $h_2$  and so  $\Lambda = 0$  (Happel and Brenner,

1983). But what happens in the case of particles with strong AB collocated with particles of the same dimension but without AB? Let us posit that while moving in the same direction as the cell motor action, the particles with strong AB do not encounter any other particles (as a consequence of active escaping them). While moving in the direction opposite to the cell motor action (as a random fluctuation process), the particles can encounter only the particles without AB. In the latter case the rate of impulse losses of the particle is bigger than in the former case. Therefore, for such a model a situation may happen when  $h_1 \neq h_2$  and so  $\Lambda \neq 0$ .

## 2.2. Evaluation of friction anisotropy

Let the averaged friction coefficient of a particle with strong AB, which moves in the direction of its cell motor action ( $h_1$ ) in consequence of escaping the other particles, be equal to the friction coefficient of a particle in a pure viscous medium  $h_0$ . Let us find the averaged friction coefficient of a particle with strong AB, which moves in the direction opposite to the cell motor action ( $h_2$ ). When the concentration of the particles without AB is relatively small (free volume is much bigger than common volume of these particles) and the both types of the particles are elastic, in the case of equipartition of directions and velocities of their movement,  $h_2$  is evaluated as:

$$h_1 \approx h_0; h_2 \approx h_0 + \frac{2}{\pi} \cdot d \cdot \sqrt[3]{C} \cdot \sqrt[3]{m \cdot k}; \quad h_0 = \psi \cdot \eta \cdot d, \quad (14)$$

where  $\eta$  is viscosity of the medium;  $\psi$  is shape coefficient (for spherical particles according to Stock's formula  $\psi = 3\pi$ );  $d$  is the averaged dimension of the particles;  $C$  is the concentration of the particles without AB;  $k$  is the stiffness coefficient of the whole cells. The cell wall of picoplankton is able to deform by thermal fluctuation of several angstroms approximately. So, according to the law of equipartition,  $k$  is near  $10^{-1}$  N m $^{-1}$ . The viscosity of seawater within the range of salinity  $S = 15-25$  g kg $^{-1}$  and temperature  $t = 20-30^\circ$ C is of order  $10^{-3}$  Pa s (Sharqawy et al., 2010). According to formula (14), friction anisotropy  $\xi$  may be described as:

$$\xi \equiv \frac{h_2 - h_1}{h_2 + h_1} \approx \frac{10^3 \cdot d^{3/2} \cdot \sqrt{C}}{1 + 10^3 \cdot d^{3/2} \cdot \sqrt{C}}. \quad (15)$$

The total concentration of picoplankton can reach  $10^{12}$  cells m $^{-3}$  (Denaro et al., 2013). So, the latter limit of concentrations can be applied in formula (15). Thus, we can construct a table, which shows the dependence of the friction anisotropy  $\xi$  of the picoplanktonic particles with strong AB on concentrations of the particles without AB (Table 1). As

**Table 1** The dependence of friction anisotropy  $\xi$  of the picoplanktonic particles with strong AB on the concentration ( $C$ ) of the particles without AB.

Concentration $C$ [cells m $^{-3}$ ]	$\xi$ for the particles of $10^{-6}$ [m] diameter	$\xi$ for the particles of $10^{-7}$ [m] diameter
$\sim 10^{12}$	$\sim 10^{-2}$	$\sim 10^{-3.5}$
$\sim 10^9$	$\sim 10^{-3}$	$\sim 10^{-4.5}$
$\sim 10^3$	$\sim 10^{-5}$	$\sim 10^{-6.5}$

the viscosity of seawater tends to decrease when the temperature increases (Sharqawy et al., 2010), then according to formulas (14) and (15)  $\xi$  is an increasing function of temperature.

### 2.3. Evaluation of diffusional force

Let us find  $\overline{\Delta \vec{x}'}(t)$  in formula (13) by averaging the diffusional velocities of the particle during its direct translocation throughout the distance that is equal to the particle dimension (with respect to the ensemble of all identical systems, which contain only the particles moving since  $t = 0$  till  $t = \tau$ ). This  $\overline{\Delta \vec{x}'}(t)$  is the result of averaging of  $\Delta \vec{x}'(\Delta x', \Delta y', \Delta z', t)$  in all points of coordinate space  $\Delta x', \Delta y', \Delta z'$  accessible to the particle for the time  $t$ . Coordinates  $\Delta x'(t), \Delta y'(t), \Delta z'(t)$  of the particle can be determined as:

$$\begin{aligned} \Delta x'(t) &= \Delta x'(0) + \int_0^t \Delta \dot{x}'(t) dt; \quad y'(t) \\ &= \Delta y'(0) + \int_0^t \Delta \dot{y}'(t) dt; \quad z'(t) \\ &= \Delta z'(0) + \int_0^t \Delta \dot{z}'(t) dt, \end{aligned} \quad (16)$$

$\overline{\Delta \vec{x}'}(\Delta x', \Delta y', \Delta z', t) = 0$  in all points of the coordinate space excluding the points of averaged trajectory of the particle. Thus, if the particle volume  $V_{par}$  is near the whole volume  $V_{acces}(t)$  accessible to the particle during time interval  $t$ , then analogically to Pundyak (2014) we obtain:

$$\overline{\Delta \vec{x}'}(t) = \frac{D_x}{d_x} \chi; \quad \chi(t) \approx \frac{V_{par}}{V_{acces}(t)}. \quad (17)$$

According to formulas (13) and (17):

$$\Lambda = \chi(t) \frac{D_x}{2d_x} (h_1 - h_2) = \chi(t) \frac{k_b T}{d_x} \xi. \quad (18)$$

If the locomotion or buoyant force is so high that according to Eq. (9)  $|\overline{\vec{x}'}| \geq D_x/h_x$ , then the condition (12) is invalid. Thus, in this case the system is not in equilibrium, therefore formula (18) is invalid and  $\Lambda = 0$ . Under the condition  $|\overline{\vec{x}'}| < D_x/h_x$ , the volume accessible to the particle moving in unbounded fluid, depends on  $t$  according to the law of diffusion,  $V_{acces}(0) = 0$ . Thus, having considered formula (17), we can calculate  $\chi(t)$  in formula (18):

$$\begin{aligned} \chi(t) &\approx \frac{d_x d_{y,z}^2}{(B_{x'} t^{0.5} + d_{x'})(B_{y',z'} t^{0.5} + d_{y',z'})^2}; \\ B_{x'} &\equiv \sqrt{D_{x'}}; \quad B_{y',z'} \equiv \sqrt{D_{y',z'}}. \end{aligned} \quad (19)$$

When the particle exists for a long time ( $t \rightarrow \infty$ ) in unbounded fluid, then according to formulas (18) and (19)  $\Lambda = 0$ . Although there is no report about AB of *V. alginolyticus*, let us consider our model particles with strong AB as having parameters of *V. alginolyticus*, which is well-studied (Xie et al., 2015). As it has been shown (Xie et al., 2015), averaged cell velocity of *V. alginolyticus* is about  $5.5 \times 10^{-5} \text{ m s}^{-1}$ . Its dimension is about  $2 \times 10^{-6} \text{ m}$  and its mass is about  $10^{-15} \text{ kg}$ . According to (9)  $F \sim k_b T/d$ . So, in our model we can consider the situation when  $|F| = k_b T/d$ . Then

$$|F| + |G| \geq \frac{k_b T}{d}; \quad |F| - |G| < \frac{k_b T}{d}; \quad G \equiv (m - m_m) g_{x'}, \quad (20)$$

where  $G$  is buoyant force. According to Eq. (9) and condition (20) if the particle moves downwards, then  $|\overline{\vec{x}'}| \geq D_x/h_x$ , and  $\Lambda = 0$ , but if the particle moves upwards, then  $|\overline{\vec{x}'}| < D_x/h_x$ , and  $\Lambda \neq 0$ . Let us posit that after the moving downwards, the particle starts to move upwards at  $t = 0$ . Thus, time  $t$  of such an upward movement can be considered as the time of the diffusional force acting in formulas (18) and (19). According to formulas (18) and (19) the diffusional force has considerable influence on the particles movement only if the time of their upward movement is short. The diffusional force acts only during upward movement of the particle (during downward movement  $|\overline{\vec{x}'}| > D_x/h_x$  and it equals zero) and always is directed upwards. In other words, although the orientation of a living microorganism within the depth of sea changes unceasingly, the averaged diffusional force is directed upwards constantly. To evaluate the influence of the diffusional force on the balancing of the particles let us average it with the respect to time and to spherical angle  $\alpha_x$ :

$$\begin{aligned} \overline{\Lambda}(\tau) &= \overline{\chi}(\tau) \frac{k_b T}{d_x} \overline{\Omega}(\alpha_m) \xi; \quad \overline{\chi}(\tau) \\ &= \frac{1}{\tau} \int_0^\tau \chi dt; \quad \overline{\Omega}(\alpha_m) \equiv \frac{1}{(\alpha_m)} \int_0^{\alpha_m} P \\ &\quad \times (\alpha) \cos(\alpha) \sin(\alpha) d\alpha, \end{aligned} \quad (21)$$

where  $\tau$  is the time of upward movement of the particle;  $\alpha_m$  is the minimal value of spherical angle  $\alpha_x$  (mentioned under Eq. (4) in Section 2) at which inequality (12) is valid;  $P(\alpha)$  is possibility of the particle to move in the direction determined by the angle  $\alpha_x$ . Let us consider the case of equal distribution of movement directions. According to condition (20)  $\alpha_m = \pi/2$ . Therefore according to formula (21)  $\overline{\Omega}(\alpha_m) = 1/\pi$ . The time scale of ballistic movement of *V. alginolyticus* is within  $10^{-1} \text{ s}$  (Xie et al., 2015). Therefore according to formulas (19) and (21) at the room temperature the quantity  $\overline{\chi}(\tau)$  is near 1 and depends on temperature weakly. Cells of *V. alginolyticus* are of  $2 \times 10^{-6} \text{ m}$  diameter (Xie et al., 2015). If the concentration of the particles without AB equals  $10^{12} \text{ cells m}^{-3}$ , which was observed in natural sea blooms (Denaro et al., 2013), according to Table 1 and formula (21)  $\overline{\Lambda} \approx 10^{-17} \text{ N}$ . Considering that *V. alginolyticus* can be denser than water by approximately several percent, the buoyant force for its cells is near  $10^{-16} \text{ N}$ . Thus, for motile picoplanktonic cells with strong AB collocated with the cells of similar dimensions without AB there may occur upward directed diffusional force, which is considerable when compared with buoyant force. As it has been mentioned above just after the Table 1 (Section 2.2) and clarified in this paragraph, according to formula (21) the diffusional force is an increasing function of temperature.

### 3. Discussion

Latter calculations support our hypothesis that physical gravikinesis can occur in bacterial plankton. However our model is also suitable for eukaryotic motile plankton of the same dimensions. Let us evaluate the possible role of the diffusional force for marine protists in wide range of sizes by

**Table 2** Comparison the diffusional force with buoyant force for marine motile protists cells of different dimensions.

Organisms	Dimension (d), [m]	Buoyant force (B), [N]	$\bar{A}_{\max}$ , [N]	$\bar{A}_{\max}/B$
Microplankton	$\geq 10^{-5}$	$\geq 10^{-13}$	$< 10^{-16}$	$< 10^{-3}$
	$\geq 2 \times 10^{-6}$	$\geq 8 \times 10^{-16}$	$< 10^{-15}$	$< 1$
Picoplankton	$\leq 2 \times 10^{-6}$	$\leq 8 \times 10^{-16}$	$> 10^{-15}$	$> 1$
	$\sim 10^{-7}$	$\sim 10^{-19}$	$\sim 10^{-14}$	$\sim 10^5$

calculating theoretically its maximal value according to formula (21), when  $\bar{\chi} \rightarrow 1$ ;  $\xi \rightarrow 1$ :

$$\bar{A}_{\max} = \frac{k_b T}{\pi \cdot d_x}. \quad (22)$$

According to formula (22) and considering that plankton microorganisms are denser by no less than 1% compared to water, we can construct the following Table 2 for sea motile microorganisms classed by size.

According to the Table 2 only for picoplanktonic organisms the diffusional force may have a considerable value in comparison with buoyant force. Also, according to the Table 1, this can be applied to the organisms of  $10^{-7}$  m dimensions, even if collocated with not very high ( $10^9$ – $10^8$  cells  $m^{-3}$ ) concentrations of cells without AB. Thus, we can say, that picoplanktonic organisms with AB can overcome sedimentation without any special physiological mechanisms at high, but only natural, concentrations of collocated cells without AB. Our model shows clearly the gravity-overcoming possibility of picoplanktonic organisms with the strategy of outrunning predators. In other words, we are dealing with physical gravikinesis. Thus, we can conclude that, though poorly studied in the world of motile picoplankton, the strategy of outrunning predators can also serve as an adaptation to overcome sedimentation. This finding may stimulate further research in this field.

#### 4. Conclusions

1. While in a state of equilibrium, sedimentation of motile particles with strong AB, collocated with particles without AB, decreases as a result of friction anisotropy.
2. The sedimentation may be overcome if the particles' dimensions are about  $10^{-7}$  m and the concentration of the particles without AB is equal to or bigger than  $10^8$  cells  $m^{-3}$ .
3. Outrunning as an antipredator strategy of motile picoplankton sea organisms can cause the gravikinesis of a physical nature.

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