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The effect of tethering on the clearance rate of suspension-feeding plankton

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Many planktonic suspension feeders are attached to particles or tethered by gravity when feeding. It is commonly accepted that the feeding flows of tethered suspension feeders are stronger than those of their freely swimming counterparts. However, recent flow simulations indicate the opposite, and the cause of the opposing conclusions is not clear. To explore the effect of tethering on suspension feeding, we use a low-Reynolds-number flow model. We find that it is favorable to be freely swimming instead of tethered since the resulting feeding flow past the cell body is stronger, leading to a higher clearance rate. Our result underscores the significance of the near-field flow in shaping planktonic feeding modes, and it suggests that organisms tether for reasons that are not directly fluid dynamical (e.g., to stay near surfaces where the concentration of bacterial prey is high).

Marine zooplankton feed in a nutritionally dilute environment, and many organisms ranging from unicellular flagellates to millimeter-sized copepods live on suspended prey. To enhance their prey encounter rate, suspension feeders often create a feeding flow by the beating of flagella, cilia, or appendages (1). Many species are nonmotile when feeding, either by direct attachment to a surface (many unicellular organisms) or due to gravitational tethering (many copepods). Based on experiments and theory, several authors have suggested that tethering leads to more efficient feeding flows (2–7). In contrast, recent computational studies of the choanoflagellate Salpingoeca rosetta found that freely swimming individuals have a higher clearance rate than those tethered (8, 9). The cause of this apparent discrepancy is not evident, and the issue is important to the understanding of adaptations of key organisms at the base of marine food webs, including heterotrophic flagellates that are the main consumers of bacteria and cyanobacteria. Here, we quantify the effect of tethering on the feeding flow of a model flagellate, and we show that under general assumptions free swimming is superior to tethering in terms of clearance rate.

We consider a flagellate with a single flagellum. Our model is based on the solution of Stokes equations for the low-Reynolds-number flow due to a point force next to a no-slip sphere representing the cell body (10–13). The point force, $F$, represents the force from the flagellum on the water and the thrust, $T = -F$, the force from the water on the flagellum (Fig. 1A). The point force gives rise to the flow:

$$v_0 = \frac{G \cdot F}{8 \pi \mu}$$

where $\mu$ is the viscosity and $G$ the Green function tensor (10, 12). The flow results in a force on the cell body, $K$, that is opposite to $T$ and smaller in magnitude:

$$K = \left(3 \frac{a}{2} - \frac{a^3}{2 L^3}\right) T,$$

where $a$ denotes the radius of the cell body and $L$ the distance from its center to the position of the thrust (10, 12). In the tethered situation (Fig. 1B), an external force holds the cell body fixed in an infinite fluid domain, and the flow is given by Eq. 1. In the case of free swimming (Fig. 1A), the flagellum pulls the cell body through the water with a velocity, $U$, such that the drag, $D = -6 \pi \mu \frac{a}{L} U$, makes the net force on the flagellate vanish, $T + K + D = 0$ (11, 12). The flow is therefore the superposition, $v_0 + v_T$, where $v_T$ is the flow due to the towed cell body (Fig. 1C).

Depending on the detailed morphology, prey may be intercepted on the flagellum, directly on the cell body, or on tentacles extending from it (4). Here we consider an annular encounter zone of outer radius, $R$, in the equator plane (Fig. 1A). The clearance rate, $Q$, is the flow rate through the annulus:

$$Q = -2 \pi \int_a^R v_z \ r \ dr,$$

where $v_z$ is defined relative to the cell body. Both the magnitude of $v_z$ and $Q$ are larger by at least a factor of 3 for the freely swimming flagellate compared with the tethered counterpart (Fig. 2). The velocity profiles are normalized by the swimming speed:

$$U = \left(1 - \frac{3 a}{2 L} + \frac{a^3}{2 L^3}\right) U_\infty,$$

where the highest swimming speed, $U_\infty = F/(6 \pi \mu a)$, is obtained when $T$ acts far from the cell body and $K$ in Eq. 2 vanishes (12, 13). In free swimming, $Q$ approaches the ballistic clearance rate, $Q_\text{ballistic} = \pi R^2 U$, when $R \gg a$ and the influence of the cell body is insignificant (Fig. 2B). In the tethered case, the Stokeslet due to the force $F - K$ describes the far field flow. The clearance rate for a Stokeslet flow through a circular encounter zone is known (4), and using Eqs. 2 and 4 we obtain

$$Q_\text{Stokeslet} = \left(1 - \frac{3 a}{2 L} + \frac{a^3}{2 L^3}\right) \frac{F R}{4 \mu} = \frac{3}{2} \pi a R U.$$

The approximation works well when $R \gg a$, but it fails qualitatively and overestimates the clearance rate in the tethered case by more than 50% when $R/a < 5$ (Fig. 2B).

In contrast to the commonly accepted view (2–7), we find that tethering decreases rather than increases the clearance rate, consistent with the recent computational studies of tethered and freely swimming choanoflagellates (8, 9). The commonly accepted view builds theoretically on the fact that...
$Q_{\text{Stokeslet}} > Q_{\text{ballistic}}$ when $R/a < 3/2$ (5, 7). However, $Q_{\text{ballistic}}$ and $Q_{\text{Stokeslet}}$ represent models that ignore the effect of the cell body, and the two expressions are only applicable when $R \gg a$ (Fig. 2B). The clearance rate depends on the flow-generating apparatus and the structures on which prey are intercepted. We chose for simplicity an annular encounter zone, and a different choice should not change our qualitative result. Another simplification is that the flagellate is tethered in an infinite fluid domain as if it were gravitationally tethered like a copepod. Actual flagellates tether to surfaces, and including a surface would lower the clearance rate in the tethered situation (4, 8, 9). Furthermore, we assumed that the flagellum generates the same force in the tethered and the freely swimming case.

The flow past the beating organelles may be higher in the tethered than in the freely swimming case (14), but in most suspension-feeding plankton the clearance rate is proportional to the flow past the organism rather than the flow experienced by the beating organelle. In copepods, for example, the beating feeding appendages generate the feeding flow while also scanning the encounter zone, but it is the flow through the encounter zone, not past the nonfiltering appendages, that governs the volume of water scanned for prey (1). It is similarly the flow through the collar filter of a choanoflagellate that decides its clearance rate, not the flow experienced by the beating flagellum (8, 9). Our presumption is that our qualitative conclusion is correct as long as our key assumptions are satisfied, and that it is therefore valid for a large class of ecologically significant zooplankton. This suggests that the reason for attachment of heterotrophic flagellates is not fluid-dynamical; it may rather be the lower predator encounter risk of a nonmotile organism or the significantly elevated concentrations of bacterial prey near surfaces of, for example, marine snow, that are considered to be microbial hot spots (15).

Data Availability. There are no data underlying this work.

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Fig. 1. (A) Model of a freely swimming flagellate (gray) with the forces on the organism (blue), its velocity (green), and the annular encounter zone (magenta). The radius of the cell body is $a$, and the thrust, $T$, acts at a distance $L = 4a$ from the center of the cell body. (B and C) The velocity field relative to the cell body when the flagellate is tethered (B) and freely swimming (C). The point force on the water, $F$, is the red vector and the velocity, $U$, the green vector.

Fig. 2. Flow velocities and clearance rates when the model flagellate is tethered (dashed red line) and freely swimming (solid blue line). (A) The velocity component $v_z$ relative to the cell body in the equator plane as function of the radial coordinate, $r$, and (B) the clearance rate, $Q$, as function of the outer radius, $R$, of the annular encounter zone (Fig. 1A). The clearance rate, $Q$, is normalized by $Q_{\text{ballistic}} = \pi R^2 U$ (dashed-dotted green line), and the approximation $Q_{\text{Stokeslet}}$ is shown for comparison (dotted black line).
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Andersen and Kiørboe