RESEARCH ARTICLE

Bacterial motion in narrow capillaries

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One Sentence Summary: Bacteria swim in spirals and distorted circles in capillaries that are sufficiently narrow. These motions significantly influence their migration in porous environments.

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ABSTRACT

Motile bacteria often have to pass through small tortuous pores in soil or tissue of higher organisms. However, their motion in this prevalent type of niche is not fully understood. Here, we modeled it with narrow glass capillaries and identified a critical radius ($R_c$) for bacterial motion. Near the surface of capillaries narrower than that, the swimming trajectories are helices. In larger capillaries, they swim in distorted circles. Under non-slip condition, the peritrichous Escherichia coli swim in left-handed helices with an $R_c$ of $\sim 10$ $\mu$m near glass surface. However, slipping could occur in the fast monotrichous Pseudomonas fluorescens, when a speed threshold was exceeded, and thus both left-handed and right-handed helices were executed in glass capillaries. In the natural non-cylindrical pores, the near-surface trajectories would be spirals and twisted loops. Engaging in such motions reduces the bacterial migration rate. With a given pore size, the run length and the tumbling angle of the bacterium determine the probability and duration of their near-surface motion. Shear flow and chemotaxis potentially enhance it. Based on this observation, the puzzling previous observations on bacterial migration in porous environments can be interpreted.

Key words: porous environment; swimming bacteria; hydrodynamics; migration rate

INTRODUCTION

Flagellar rotation-mediated swimming is the most common strategy of bacterial motion (Berg 2003). The peritrichous flagella of Escherichia coli form a bundle that rotates counterclockwise (viewed behind the cell) to propel the cell and the cell body rotates clockwise to balance the drag load when they swim in a relatively straight line (called run). About once per second, some flagella reverse direction, causing the cell to turn erratically before resuming a run when the usual direction of rotation is restored (tumble) (Darnton et al., 2007). This alternating ‘run and tumble’ scenario is reminiscent of the random walk of particles in Brownian motion (Berg 1993). External stimuli suppress tumbles in the favorable direction, and hence bias bacterial dispersal (Berg 2003; Saragosti et al., 2011). Monotrichous bacteria such as Pseudomonas fluorescens swim faster and exhibit more sophisticated patterns (Xie et al., 2011; Ping, Birkenbeil and Monajembashi 2013; Son, Guasto and Stocker 2013), but the same random-walk principle applies (Ping 2012).

Most biodiversity on this planet is in soil, and 0.02–0.17% of those available surfaces are effectively colonized by bacteria (Crawford et al., 2005; Or et al., 2007). These environments are composed of tortuous pores usually less than 50 $\mu$m in dimension (Or et al., 2007). Similar environments include the small crevices in eroded rock and tiny body cavities in multicellular organisms (Egan, Thomas and Kjelleberg 2008; Ping 2012; Pointing and Belnap 2012; Stocker 2012). Understanding how bacteria migrate in such environments is important for bioremediation, infectious disease control and ecosystem...
maintenance (DiLuzio et al., 2005; Or et al., 2007). These environments are conceptually different from another type of porous medium, namely the meshwork formed by cross-linked polymers, which is outside the scope of this communication.

The presence of a rigid surface (wall) influences the motion of nearby swimming bacteria (termed the wall effect). They swim in circles near a flat surface (Frymier et al., 1995; Ping et al., 2013), because the hydrodynamic force on the rotating bacteria due to the wall effect constantly pushes cells perpendicularly to their direction of motion (Ramia, Tulloch and Phan-Thien 1993; Lauga et al., 2006). The same hydrodynamic interaction makes E. coli swim along the right-hand sidewall of small rectangular channels made of oxidized polydimethylsiloxane on an agar bottom (DiLuzio et al., 2005). If the channels are marginally wider than the bacteria, E. coli swim unidirectionally and the trajectories are punctuated with periodic stops and reversals (Männik et al., 2009).

Capillaries with well-defined diameters are simplified models for the tubular solid surfaces that bacteria may encounter. However, in the widely used capillary assay for bacterial chemotaxis, those capillaries are so large (internal radius 0.1 mm) that the surface is essentially flat for bacteria (Adler and Dahl 1967; Berg and Turner 1990). Berg and Turner (1990) showed that the circular motion of E. coli near the surfaces of capillary that are larger than 50 μm in diameter is responsible for trapping the cells in the capillary assay. It has also been reported that E. coli swim with reduced velocities in 6 μm and 3 μm capillaries compared to free-swimming (Liu and Papadopoulos 1995; Liu, Chen and Papadopoulos 1997), but hydrodynamic simulations predict that velocity would increase in such a narrow space (Ramia et al., 1993). To further understand this phenomenon, we systematically studied E. coli and P. fluorescens swimming in glass capillaries ranging from 5 to 50 μm in diameter, and discovered a critical radius that determines whether they swim in helices or in circles. Because the net displacement of helical and circular motion of bacteria is small compared to free-swimming, they potentially suppress bacterial dispersion. Their influence at the population level in natural environments is also discussed.

MATERIALS AND METHODS

Bacterial strain and growth condition

The smooth-swimming E. coli strain HCB437 (Frymier et al., 1995) is a gift of Howard C. Berg, the wild-type E. coli strain AW405 (Armstrong, Adler and Dahl 1967) a gift of Sandy Parkinson and the soil bacterium P. fluorescens SBW25 (Ping et al., 2013) a gift of Christian Kost. Seed cultures were prepared by growing in LB broth at 23 °C with agitation at 160 rpm to early stationary phase (OD_{600} = 1.2). 10 μl seed culture was diluted with 10 ml fresh LB medium and incubated at 23 °C with agitation to early exponential phase (OD_{600} = 0.4). Bacteria were then spun down at 10 000 g for 2 min and gently resuspended in chemotaxis medium (Hedblom and Adler 1980) to the original volume when applied to the flat chamber on diagnostic slides (Ping et al., 2013) and to different concentrations for filling capillaries (Table S1, Supporting Information).

Narrow glass capillaries

Narrow glass capillaries were generated by pulling the microcaps end-to-end disposable glass pipettes and Duran disposable glass micropipettes with ring mark (Hirschmann Laborgeräte GmbH and Co. KG., Eberstadt, Germany). The heating value of a Narishige PE-2 Microelectrode puller (Narishige Scientific Instrument Lab., Tokyo, Japan) equipped with 43mm Kanthal wire heater was set at 50.0, and the pulling values of the submagnet and the main magnet were 0.7 and 30.0, respectively. Pulling distance was controlled through sliding the pulling bar gently on the polished hypotenuse surface of a polyoxymethylene track that is a 3-cm-thick right triangle with two legs 10 and 20 cm long, respectively. The expected interior diameters of the narrow capillaries are listed in Table S1 (Supporting Information). After pulling, the end remnants of the glass pipettes (arms) were glued on a microscopic slide using semi-oxidized nail polisher (Fig. S1, Supporting Information). The precise diameter of the narrow capillaries was determined by focusing an upright Axio Imager Z1 microscope (Carl Zeiss Microscopy, Jena, Germany) equipped with 40× and 60× oil objective to the center of the narrow capillaries before taking movie clips (below).

Movie acquisition and analysis

Narrow capillaries larger than 15 μm in diameter were filled by gently pipetting the bacterial suspension through a Prot/Elec Protein Gel Loading Pipet Tip (Bio-Rad, Hercules, CA, USA) that was firmly pressed on the mouth of an arm. Narrow capillaries smaller than 15 μm were filled by dropping 20 μl suspension on one mouth, allowing it to be sucked in via the capillary effect. When the concave surface of the bacterial suspension reached the opposite arm, a drop of chemotaxis medium was applied to the opposite mouth so that an air bubble was formed in that arm. The capillary sucking force was balanced by the surface tension of the air bubble to stop the sucking (Fig. S1, Supporting Information). While the fluid inside the narrow capillary was still oscillating, the capillaries were immersed in a drop of optical oil and focused to the center for capillary size determination and to the top inner surface for movie acquisition. It is worth noting that when the depth of the field of view was less than the capillary radius, the center of the narrow capillary was out of focus in the movie recorded. To avoid oxygen depletion, movie clips were taken within 5 min when the fluid became stagnant. An AxioCam HSm High Speed Monochrome camera (Carl Zeiss MicroImaging GmbH, Göttingen, Germany) was used to record movie clips as described previously (Ping et al., 2013). Free-swimming and near-flat-surface motions in the chamber on diagnostic slide were recorded similarly. Movie clips were analyzed with the AxioVision 4.8 software provided by the manufacturer and Fiji ImageJ (Schindelin et al., 2012). The bacterial velocity tangential to the trajectory and the pitch of the trajectory were determined with a few images of bacteria swimming in the focal plane. The pitch sizes of the trajectories of wild-type cells were calculated by extrapolating the recorded arcs using formula $H = 2r \cdot r \cdot \tan(\phi)$, with $\phi$ as the gradient of the helix. The radii of the equivalent circles were calculated by setting the curvature of a circular trajectory equals to that of a helical trajectory, then yields the equation $r_\phi = (r_0^2 + H^2/4\pi^2)/r_0$, here $r_0$ and $H$ are the radius and the pitch of the helical path.

RESULTS AND DISCUSSION

To monitor bacterial motion in narrow capillaries, we first introduced the non-tumbling E. coli strain HCB437 to capillaries that are less than 12.5 μm in radius (Fig. 1A and B). These smooth-swimming cells could reach the surface if they originally swam with an angle to the capillary axis or be reoriented by rotational diffusion or hydrodynamic attraction (Berke et al., 2008). They
flow would force all of them to the surface causing, them to engage in helical motion (Movie S1, Supporting Information). Under such a condition, the pitch size of the trajectories decreased as the flow rate increased. Upon an end-on flow, bacteria quickly reoriented to face the flow. Similar reorientation in shear flow has also been observed near planer surface (Kaya and Koser 2012). This reorientation is due to rheotaxis (Marcos et al., 2012). The asymmetric drag load on cell bodies and on flagellar bundles caused by the flow field makes cells face the stream (Hill et al., 2007). The dissipative dynamics of bacteria in Poiseuille flow interacting with the nearby surface determines the stable helical trajectories (Zöttl and Stark 2012).

The cells of wild-type *E. coli* strain AW405 frequently run into the surface after a tumble, making the study of helical motion in static capillaries easier. However, these cells rarely completed a helical turn before tumbling away or changing the directions (Fig. 2A). In capillaries with diameter less than 10 μm in radius, the velocity tangential to the trajectory positively correlates with capillary size (Fig. 2B), while the pitch sizes of the trajectories negatively correlates with it (Fig. 2C). In capillaries broader than that, more and more bacteria began to swim in distorted circles near the inner surface (Movie S2, Supporting Information). For those still swimming in helices, the correlation disappeared. In capillaries larger than 12.5 μm in radius, circular motion became dominant. The pitch size and tangential velocity of the wild-type cells as well as their correlation with capillary size were very similar to those of the smooth-swimming cells (Table 1).

As the cell body rotates clockwise, the wall drag originating from a bottom surface counteracting the rotation creates a torque that pushes the cell body sideways; the lower portion of the helical flagellar bundle, which rotates counterclockwise, experiences a viscous drag in the opposite direction. Consequently, when viewed from above, the cells appear to be rolling to the right. This leads the cell swimming along the right-hand wall of a rectangular chamber (DiLuzio et al., 2005). In a cylindrical capillary, it would trace out a helical path due to the presence of continuously curving wall (Ping 2012). The helical arcs were thus back-transformed into the equivalent circles with the same curvature, so that the amount of torque required to generate the curvature remains unchanged (Fig. 2D). The radii of these equivalent circles were similar to those of the circular trajectories reported near flat surfaces (Lauga et al., 2006). The smallest radii of these equivalent circles is ~10 μm. This radius determines whether the bacterium swim in helices or in distorted circles, and is hereby called the critical radius (Rc). It is worth mentioning that the preference of *E. coli* swimming along the sidewall of the rectangular channels is controlled by the same mechanism. The preference was not observed in channels wider than 20 μm, similar to the diameter of the Rc capillary (DiLuzio et al., 2005).

Unwrapping a cylindrical surface containing a helix into a plane, the helix would be a straight line. The proposed torque due to wall effect near flat surfaces alone cannot lead to the observed helical trajectory, unless it is balanced by another torque (Fig. S2, Supporting Information). Furthermore, the measured correlation between trajectory pitch and capillary size was not strict, neither does the correlation between the tangential velocity and the capillary size (Fig. 2E). The pitch size and velocity depend on each other as well. In capillaries broader than 6.3 μm, faster cells tended to swim with smaller pitches compared to slower cells, but they tended to swim with larger pitches in narrower capillaries. Apparently, the curvature of the capillary surface imposes an additional torque on the swimming bacteria. Its magnitude was estimated by solving the Jeffery equation \( \nabla \Phi = 0 \) describing near-field lubrication for incompressible

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**Figure 1.** The helical trajectory of a non-tumbling *E. coli* cell in an 11.2 μm capillary. (A) Snapshots of cell movement every half a second. The bacterium is highlighted by white arrows. When the bacterium is out of focus, its putative positions are depicted as round-end rectangles. Because only a top segment of the cylinder was visible, about two-third of the trajectory was out of the observation field. Scale bar equals 10 μm. (B) The trajectory of the cell center recorded at 47 frames per second. (C) A diagram showing a cell swimming in a narrow capillary when viewed behind the cell. Rotation of the cell body and the flagellar bundle are depicted with curved arrows. The sideway forces due to wall effect are shown as double-line arrows.

exhibited smooth left-handed helical trajectories. The longest trajectory we tracked spanned four helical turns in a 5.2 μm capillary (~24 s). Near planar surfaces, cells swim in circles because the wall drag that counteracts the rotating cell body and the flagellar bundle generates a torque normal to the translational direction (Lauga et al., 2006). The same force operates in narrow capillaries: it tilts the cell body clockwise when viewed behind the cell (Fig. 1C), which was apparent especially when cells swam along the vertical sidewall (frames at 2.0 and 7.0 s, Fig. 1A).

In capillaries without flow, only a few smooth-swimming cells would reach the capillary surface. A head-on low-shear
Figure 2. The helical arcs traced by wild-type E. coli cells in narrow capillaries. (A) A swimming trajectory in a 3.5 μm capillary. Locations of the cell at every 20 ms are shown as white-filled black dots. Scale bar equals 10 μm. Tumbles are highlighted by white arrows. (B) The velocities tangential to the helical paths. TC, tumbled-once cells; NC, no-tumble cells. The NC data were fitted by linear regression. The vertical broken line denotes the critical radius. (C) The pitch sizes of the helical trajectories. (D) Radii of the equivalent circles (r_e) of the helical trajectories. (E) Scatter plot of velocity against pitch with linear-fitting curves. Capillary radii are shown on top of the panels. (F) The torque on the surface of rotating cell bodies that are 10, 20, 50, and 100 nm away from the capillary surface. The angular velocities at 10 Hz are shown as solid lines, and at 4 Hz dotted lines. The vertical gray line marks the capillary radius of 6.3 μm. (G) Iso-angular velocity lines on a capillary radius-separation distance plane when a curvature torque of 0.06 pN·μm was obtained. The angular velocities (Hz) were labeled beside each contour line.

Stokes flow ψ between two eccentric cylinders at low Reynolds number (Jeffery 1922). The profile was plotted in Fig. 2F (for details see Supporting Information). Like the torque due to wall effect, this torque counteracts the rotation of the cells. The torque varies little in capillaries broader than ~6.3 μm and becomes stronger in narrow capillaries (Fig. 2F). To minimize the Jeffery torque, the cells tend to stay away from the surface, thus suppressing the tilting of the cell induced by the torque due to wall effect (Fig. 2G). In sufficiently narrow capillaries, the increasingly strong Jeffery torque tends to push the cells swim along the capillary axis. The competition of these two torques makes faster cells swim with larger pitches in narrow capillaries than slower cells, but with smaller pitches in broader capillaries.

To verify the generality of helical motion in narrow capillaries, we also studied the soil bacterium P. fluorescens strain SBW25. Interestingly, Pseudomonas traced out both left-handed and right-handed helices (Fig. 3). The flagellum of P. fluorescens SBW25 is a right-handed helix that rotates clockwise (Ping et al., 2013), and hence would generate a right-handed helical trajectory if the boundary is non-slip. Linear regression analysis
verified that their right-handed helical motion is similar to those of E. coli (Table 1). Swift change in direction in helical motion due to tumbles like in E. coli was also observed (Fig. 3A).

However, about 80% of Pseudomonas trajectories were left-handed helices (Fig. 3B). They are not a consequence of backward swimming. The backward swimming of Pseudomonas is short and slow (Ping et al., 2013). Small distorted circles were traced out when they backed up near capillary surfaces (Fig. 3C). Furthermore, the tangential velocities of the left-handed helical motion did not correlate with pitch size (Fig. 3D), but were statistically indistinguishable from free-swimming (P = 0.1654, two-tailed Student’s t-test). The left-handed helical motion is a consequence of their high-speed swimming. Within a 12.6 μm capillary, the average tangential velocity of P. fluorescens SBW25 performing right-handed swimming was 46.9 ± 8.4 μm s⁻¹, and that of the left-handed swimming was 70.3 ± 13.3 μm s⁻¹. The Navié relation allows slip to occur at the boundary in thin-film lubrication when a critical shear force is exceeded (Salant and Fortier 2004). When slip occurs, the direction of the image system for a point force changes (Lauga et al., 2006), that leads to the opposite handedness.

We have demonstrated that bacteria perform helical and distorted circular motion in cylindrical capillaries, but in reality, natural porous environments like that in soil are tortuous networks (Fig. 4). Near such a surface, the trajectories of a bacterium that originally swimming in the x direction and tumble at time t would be either spirals or twisted loops depending on the space dimension D = √(y(t)² + z(t)²). It swim in a spiral if D < R; it would swim in a twisted loop if D > R. The net displacement of a spiral motion is much smaller than its arc length, and that for a circular motion is close to zero. Hence, engaging in near-surface motion (NSM) reduces the migration rate. The overall contribution of NSM to the migration rate depends on the probability of occurrence (P) given by equation (1) (for details see Supporting Information)

\[ P = \left(1 - \frac{2β}{π}\right) \frac{\sqrt{1 - D^2/R^2 - \cosα}}{1 - \cosα}. \]

Here α is the tumbling angle, and β is the idling angle, the angle between the swimming direction and the normal of the surface plane; R is the bacterial run length (Fig. 4). The time that a

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**Table 1.** Linear regression analysis on dependence of the pitch size and the tangential velocity of helical motion on the radius of the glass capillary.

<table>
<thead>
<tr>
<th>Bacterial strains</th>
<th>Trajectory handedness</th>
<th>Pitch size (μm)</th>
<th>Cell velocity (μm s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Intercept</td>
<td>Slope</td>
</tr>
<tr>
<td>E. coli HCB437</td>
<td>Left</td>
<td>65.46 ± 8.08</td>
<td>−2.28 ± 1.04</td>
</tr>
<tr>
<td>E. coli AW405</td>
<td>Left</td>
<td>59.67 ± 30.79</td>
<td>−3.04 ± 4.52</td>
</tr>
<tr>
<td>P. fluorescens SBW25</td>
<td>Right</td>
<td>70.77 ± 32.36</td>
<td>−2.58 ± 3.04</td>
</tr>
<tr>
<td>P. fluorescens SBW25</td>
<td>Left</td>
<td>75.19 ± 40.44</td>
<td>1.08 ± 3.46</td>
</tr>
</tbody>
</table>

The intercepts correspond to the values in an imaginary capillary whose diameter is 0; the sign of the slopes reveals whether the values increase or decrease as the capillary size increase.

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**Figure 3.** The helical motions of Pseudomonas in thin capillaries. Scale bar equals 20 μm. (A) A right-handed trajectory in a 12.7 μm capillary. Locations of the cell at every 20 ms are shown with white open dots. A turn is marked by an arrow. (B) A left-handed trajectory in an 4.4 μm capillary. Cell locations at every 29 ms are shown as black open triangles. (C) A cell backing up underneath the surface of a capillary. The center of the cell body in forward swimming is shown as white open dots. Two small counterclockwise circles are shown with white-filled black dots and with black dots. (D) Correlation of pitch sizes and tangential velocities of the left-handed helical motions in a 12.7 μm capillary.

**Figure 4.** Diagram depicting a bacterium swimming in a solid space in porous environment. The dashed line shows an extrapolation of the preceding run. The tumbling angle is α. The potential distance that the bacterium can reach in a run is shown as a dotted arc. Gray arrows represent different types of instantaneous velocities.
bacterium spends in NSM is given by equation (2)

\[ T_n = \left( \frac{v^2}{b + t} - \frac{D_b}{(b + t) v_a \sin \alpha} \right) P \]  

(2)

with \( t_r \) as run time, and \( t_t \) as tumbling time. The instantaneous velocity of a bacterium swimming in such environments encompasses: velocity in NSM (\( v_{ns} = dL/dt \); that in surface-approaching motion (\( v_a \), decreases asymptotically) (Ramia et al., 1993); that of surface-parallel swimming (\( v_P \), slightly enhanced compared to free-swimming) (Ramia et al., 1993). The average velocity (one-dimension migration rate) is given by equation (3)

\[ \bar{v} = \frac{t}{t_r + t_t} \left[ v_P + v_a P + \frac{d_b (v_a - v_P P)}{v_a \sin \alpha} - \frac{v_P \pi P}{\pi - 2\beta} \right] \]  

(3)

We primarily verified this model by applying it to the narrow glass capillary discussed above (Table S2, Supporting Information). It has been reported that the speed of \( E. \) coli swimming in 3 \( \mu \)m capillaries was 11.4 \( \mu \)m s\(^{-1}\) and in 1.5 \( \mu \)m capillaries was 18.6 \( \mu \)m s\(^{-1}\) (Liu and Papadopoulos 1995; Liu et al., 1997), while the expected \( v_a \) in hydrodynamic simulation are 29.0 and 27.2 \( \mu \)m s\(^{-1}\), respectively. According to our measurements, the reported values correspond to \( v_a \) in the 3 \( \mu \)m capillary (11.7 \( \mu \)m s\(^{-1}\)) and \( v_a \) in the 1.5 \( \mu \)m capillary (17.3 \( \mu \)m s\(^{-1}\)). We obtained average speeds of 9.4 and 10.9 \( \mu \)m s\(^{-1}\) in these two kinds of capillaries. It is worthwhile to mention that circular motion is responsible for the retardation of bacteria in the classical capillary assay (Adler and Dahl 1967; Berg and Turner 1990). Although the values of \( P \) and \( T_n \) are very small in those glass pipettes, the high bacterial density and long incubation time ensures enough bacteria being trapped.

CONCLUSION

Because of potential applications in environmental and medical science, bacterial migration in porous environment has been the subject of some pioneer researches. Mechanisms such as collision frequency, temporary attachment etc. have been proposed to explain the varied migration rates at different tortuosity (Duffy, Ford and Cummings 1997; Liu, Ford and Smith 2011). These factors are indispensable; however, our experiment shows that NSM, especially spiral motion, constitutes a large portion of bacterial motion in narrow pores. Combining our model with the standard random-walk theory (Berg 1993), a good agreement with the en mass studies could be reached, for instance, although with same total porosity, the migration rate of \( E. \) coli in glass-bead columns and \( P. \) putida in sand columns decreased when grain size decreased. (Sharma and McInerney 1994; Barton and Ford 1995); when different interstitial flow rates were introduced, the migration rate of \( E. \) coli and \( P. \) putida in sand columns varies very little (Liu et al., 2011). Both observations can be attributed to the enhanced NSM. Nevertheless, the previously recognized factors were implicitly embedded in our general model.

This model is based on observation in isotropic medium. Chemotaxis only influences two factors, the run length and tumbling angle in our model (Berg 2003; Saragosti et al., 2011). Computer simulations predicted chemotaxis would enhance bacterial dispersion in porous environments (Duffy et al., 1997), but experimental data on \( P. \) putida in sand columns disagreed with it (Barton and Ford 1995), while that on \( A. \) brasilense and \( P. \) fluorescens in soil showed somewhat agreement (Bashan 1986).

Here, NSM is the major deferential factor in these systems. It is foreseeable that the travelling waves due to chemotaxis would be enhanced in narrow capillaries as well, since increasing run length at the leading edge and tumble frequency in periphery both enhance NSM (Mittal et al., 2003; Saragosti et al., 2011). Finally, the solid phase of porous environments is often also the source of nutrition. NSM might enable bacteria to stay longer and closer to resources and hence benefit the bacteria.

SUPPLEMENTARY DATA

Supplementary data is available at FEMSEC online.

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Conflict of interest statement. None declared.

REFERENCE


