CAN NATURAL BACTERIA TAKE ADVANTAGE OF INCREASED DISSOLVED SUBSTANCE FLUX OWING TO TURBULENCE?

F. Peters
Institut de Ciències del Mar, CMIMA (CSIC), Barcelona 08003, Catalunya, Spain
cesc@icm.csic.es

Abstract

The potential increase in nutrient flux towards bacteria owing to turbulent motion is insignificant under normal environmental turbulent conditions because of the small size of bacteria (Karp-Boss et al., 1996). However, after a chlorophyll production peak, which provides the necessary organic matter for bacteria to grow, it is observed that the bacterial community composition changes, and bacteria that tend to aggregate or become filamentous are favorably selected. I argue that this effective increase in size may account for some observations of increased bacterial activity under turbulent conditions.

Introduction

Bacteria are osmostrophic organisms. That is, they take up dissolved substances (I will call them "nutrients" in a generic way) from the surrounding medium for structural and energetic maintenance and growth. The velocity at which nutrients can be taken up depends on various passive and active processes, and will ultimately determine the rate of growth of bacteria. In most natural environment situations nutrient concentrations are relatively low so that the limiting step in the nutrient uptake process is the velocity at which nutrients can reach the bacterial cell surface, where the concentration is theoretically null. Any relative motion of the bacterial cells with respect to the surrounding medium will bring the far field concentration somewhat closer to the cell surface and hence increase the nutrient gradient to the cell and consequently the flux of nutrients to be incorporated (Fig. 1). The Sherwood number (Sh) is defined as the flux of a solute to the cell surface under a specified hydrodynamic condition with respect to the flux of that solute by molecular diffusion alone. Sh depends on the type of water motion relative to the cell, on the diffusivity of the nutrient and on microorganism size. Although no analytical solution has been obtained under turbulent motion, Karp-Boss et al. (1996) propose approximations derived from steady shear flow. Sh is close to one for bacteria in normal environmental energetic magnitudes. Thus, little enhancement in nutrient flux is expected under average mixing conditions and low molecular weight substances such as nitrate, ammonium, phosphate or glucose. On the contrary, larger osmostrophic organisms such as large phytoplankton can see the nutrient flux to the cells increased owing to average mixing. We have shown this difference to happen in
natural oceanic water samples, size-fractionated, and subjected to different levels of turbulence (Fig. 2). Radioactive phosphate is taken up at a higher velocity with increasing levels of turbulence for aquatic organisms larger than 10 µm, while organisms smaller than 2 µm do not show a consistent response of phosphate uptake to turbulence (Peters et al. 2004). We have also shown that turbulence increases the growth and maintenance of large phytoplankton cells compared to small phytoplankton cells (Peters et al. 2006).

Often times, whole oceanic water samples that are incubated in the laboratory will produce a growth peak that bacteria will respond to by increasing in numbers but also by increasing in cell size, as they consume dissolved organic matter produced by phytoplankton. It turns out that turbulence will favor different types of phytoplankton, in general larger diatoms, and that the associated bacterial assemblage will also change with respect to still water conditions (Pinhassi et al. 2004). It is also observed that, at least, some bacteria will cluster in aggregated or produce filamentous growth (Pinhassi et al. 2004). I argue that this may be a strategy to effectively increase in size and that the resultant association may then take advantage of the fluctuations in the surrounding nutrient field.

Methods

The equations applied (after Karp-Boss et al., 1996) are:

\[ Sh = 1 + 0.29 Pe^{1/2} \]  \hspace{1cm} (1)

for \( Pe \ll 1 \)

and

\[ Sh = 0.55 Pe^{1/3} \]  \hspace{1cm} (2)

for \( Pe \gg 1 \)

where the Péclet number is calculated as
\[ Pe = \frac{r^2}{D} \left( \frac{\varepsilon}{\nu} \right)^{\frac{1}{2}} \]  

(3)

where \( r \) is the radius of the cell, \( D \) is the diffusivity of the solute, \( \varepsilon \) is the turbulent kinetic energy dissipation rate and \( \nu \) is the kinematic viscosity.

For \( 0.01 < Pe < 100 \), I averaged the following two equations that were obtained numerically by interpolation (Karp-Boss et al. 1996).

\[ Sh = 1.014 + 0.15 Pe^{1/2} \]  

(4)

and

\[ Sh = 0.955 + 0.344 Pe^{1/3} \]  

(5)

The solutes computed were phosphate with a \( D \) of \( 6 \cdot 10^{-10} \) m\(^2\) s\(^{-1}\) and the protein bovine serum albumin (MW 65000) with a \( D \) of ca. \( 6 \cdot 10^{-11} \) m\(^2\) s\(^{-1}\). A baseline reference \( Sh \) was computed for a 0.5 µm bacterium swimming at a velocity \( U \) of 30 µm s\(^{-1}\) with the equation in Karp-Boss et al. (1996)

\[ Sh = 1 + 0.5 Pe + 0.5 Pe^2 + \ln(Pe) + O(Pe^2) \]  

(6)

and \( Pe \)

\[ Pe = \frac{U r}{D} \]  

(7)

**Results**

The computations show that increasing the effective cell size by bacteria aggregating or forming filaments \( Sh \) may increase tremendously. For a turbulence level of 10^-7 m\(^2\) s\(^{-3}\) and using phosphate as a solute a 0.5 µm bacterium will have an \( Sh \) of 1.002, while a 5 µm aggregate will show an \( Sh \) of 1.02 and a 50 µm aggregate of 1.02, a 20% increase in the flux of the nutrient owing to turbulence. Higher turbulence values will logically show larger flux increases. Also, substances will lower diffusivity such as high molecular weight organic matter compounds used by bacteria present a further increased flux (Fig. 4).

**Discussion**

It is difficult to translate the predicted increases in the flux of solutes from the Sherwood number calculations into actual solute uptake or worse even growth or metabolism, since there are uncertainties and uncontrolled factors. First, the Sherwood number solutions for turbulence are just approximations from steady shear flow. We might expect that fully developed turbulence could even produce slightly larger effects. Also there is no solution for swimming bacteria in a turbulent field.
when it seems that most natural bacteria swim. There is also a question of diffusion being the limiting step. At high nutrient concentrations the actual uptake of the solutes could limit the process and hydrodynamic motion relative to the cell should not alleviate this limitation. For diffusion not being limiting, the concentration of the nutrient should be well above the half-saturation constant for uptake ($K_M$) of that solute. A wide range of $K_M$ is reported for bacteria for different solutes and growth conditions from nmol l$^{-1}$ to mmol l$^{-1}$ and even higher. Even under theoretically very high nutrient concentrations where diffusion should not be limiting, stirring of culture flasks is commonly used to enhance bacterial growth. Thus, taking into account all the uncertainties, it is surprising that the 400% enhanced physiology observed in mixing conditions (4.5·10$^{-3}$ m$^2$ s$^{-1}$) using wastewater organic matter strength solute concentration (Bergstedt et al. 2004) can be explained if 50 µm aggregates are considered.

If we add the fact that a fraction of phytoplankton exudates and other dissolved organic matter that serve as solutes for natural bacteria may have a high molecular weight, and hence a low diffusivity, under mixing we may expect increases in the flux of dissolved substances toward the bacterial aggregates of several times with respect to still water.

**Conclusions**

In the ocean, and aquatic systems in general, bacteria are key organisms that serve as food for other trophic levels, that compete with phytoplankton for available nutrients and that process large quantities of organic matter with implications in the global biogeochemical cycle of carbon and other substances. At times and/or situations of availability of high concentrations of dissolved organic matter and other nutrients (coastal zones, phytoplankton post-bloom conditions, etc.) turbulence may favor a

**Figure 4. Calculation of the Sherwood number for different hydrodynamic conditions.**

Lines are continuous (a 0.5 µm bacterium swimming at 30 µm s$^{-1}$ and not depending on external flow), discontinuous thin (a 0.5 µm bacterium subject to external flow), discontinuous medium thick (a 5 µm bacterial aggregate subject to external flow) and discontinuous thick (a 50 µm bacterial aggregate subject to external flow). The solute is phosphate (left panel) and bovine serum albumin (right panel).
faster turnover of substances when bacteria aggregate, a process that is also likely to be turbulence/shear driven. Turbulence is inherent to aquatic systems and especially to the oceanic upper mixed layer and coastal systems and is slowly becoming perceived as the "normal" condition as opposed to an exceptional or even impossible "still water" situation. Surely though, it is in engineering applications, where a turbulence/mixing treatment may be optionally extremely high, where these results may be more significant. Waste water treatment, industrial production of different substances in reaction tanks and aquaculture facilities are clear target applications for a turbulence optimization of organic matter reactivity.

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References


