

Non-Flagellar Swimming in Marine *Synechococcus*

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Abstract

Certain marine unicellular cyanobacteria of the genus *Synechococcus* exhibit a unique type of swimming motility characterized by the absence of flagella and of any other obvious organelle of motility. Although the mechanism responsible for this phenomenon remains mysterious, recent advances have included the development of testable models as well as the identification of a cell-surface polypeptide that is required for the generation of thrust. These developments, as well as the future research directions they suggest, are discussed.

Introduction

Unicellular cyanobacteria of the genus *Synechococcus* occupy an important position at the base of the marine food web. They are among the most abundant photosynthetic organisms in oligotrophic open ocean regions, where they contribute significantly to primary production (Iturriaga and Mitchell, 1986; Waterbury *et al.*, 1986; Olson *et al.*, 1990). Waterbury *et al.* (1985) reported that several isolates of marine *Synechococcus* were capable of swimming. This discovery was remarkable for two reasons. First, unlike other motile cyanobacteria which move by gliding on surfaces, motile *Synechococcus* were unique in their ability to swim in liquids. Second, marine motile *Synechococcus* had neither flagella nor any other visible organelle of locomotion. Other prokaryotes that are able to swim in liquids do so by means of flagella which function as helical propellers driven by a biological rotary motor (Hazelbauer *et al.*, 1993; Macnab, 1996). To my knowledge, the ability to swim in the absence of flagella has not been since reported for any other bacterium and appears to be confined to certain *Synechococcus* species isolated from oligotrophic marine waters (Waterbury *et al.*, 1986).

The Problem

Cells of swimming *Synechococcus* are coccoid to rod-shaped and range in size from 0.7 to 0.9 μm in diameter and 1 to 2.5 μm in length (Waterbury *et al.*, 1985). Certain features of swimming in *Synechococcus* resemble flagellar swimming. Swimming speeds range from 5 to 25 $\mu\text{m}/\text{sec}$ (Waterbury *et al.*, 1985; Willey, 1988). Swimming cells rotate about their longitudinal axis as they translocate and

hence generate both torque and thrust. Like flagellated bacteria (Berg and Turner, 1979), *Synechococcus* cells are slowed down and ultimately immobilized by increasing medium viscosity (Willey, 1988). Cells that become fortuitously attached to the slide or coverslip will rotate about their point of attachment at an average rate of 1 revolution/sec. Cells can rotate either in the clockwise (CW) or the counterclockwise (CCW) direction but a rotating cell has never been observed to change the direction of rotation, which, as Willey has pointed out (Willey, 1988), suggests that the "motor" rotates in only one direction and does not switch. This further implies that *Synechococcus* cells may have a "front" and a "back" end and that the direction of rotation depends on which end of the cell is tethered (Willey, 1988). Unlike flagellated bacteria, no obvious patterns in swimming behavior, such as tumbles or reversals or stops, have been observed but cell shape appears to affect motility: more coccoid cells tend to swim in more looped or spiral paths while rod-shaped cells swim in straight paths (Willey, 1988).

Initial efforts were directed at visualizing the organelle or structure responsible for the generation of torque and thrust in *Synechococcus* and included transmission electron microscopy of negatively stained whole and thin-sectioned cells (Waterbury *et al.*, 1985; Willey, 1988), and freeze-fracture and etching which has been used to visualize membrane-embedded components of the rotary motor in flagellated bacteria (Coulton and Murray, 1978; Khan *et al.*, 1988; Willey, 1988). These studies did not reveal the presence of either flagella (external or periplasmic) or other identifiable structures that might be associated with the ability to swim and in fact, the envelope structures of motile strains did not appear to differ from those of nonmotile strains (Willey, 1988). Also, an examination of actively swimming cells by high-intensity darkfield microscopy, a technique which makes possible the visualization of single flagella (Macnab, 1976), did not reveal any (Willey, 1988). Furthermore, no motility-dependent amplitude spectra were seen in images of swimming *Synechococcus* (Willey, 1988). The method used can detect the rotation of even very short cellular projections (Lowe *et al.*, 1987; Willey, 1988). Shearing experiments, which are extremely effective at eliminating motility in flagellated bacteria, did not at all affect swimming in *Synechococcus* (Waterbury *et al.*, 1985; Willey, 1988).

In flagellated bacteria, torque and thrust are generated by the rotation of the flagellum. In the absence of such appendages how then might *Synechococcus* generate these forces? As pointed out by Pitta *et al.*, (Pitta and Berg, 1995; Pitta *et al.*, 1997) this leaves the cell body itself or the cell surface as the only structures with which to generate thrust.

Models

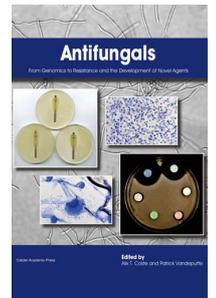
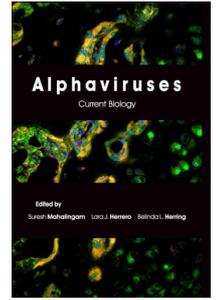
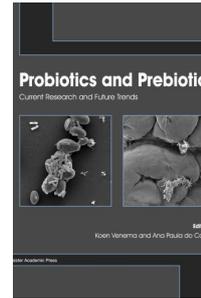
Two models have been proposed for how *Synechococcus* might swim without flagella. One of these has been tested experimentally. Pitta and Berg (1995) ruled out self-

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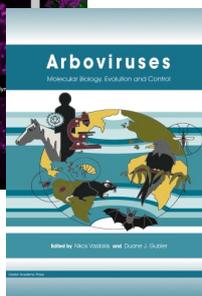
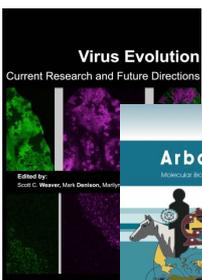
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electrophoresis as a possible propulsive mechanism by demonstrating that in a seawater-based medium, the electrophoretic mobility of *Synechococcus* was essentially 0. In such a model, a cell carries a fixed charge on its surface that is shielded by counterions in the medium. If the cell then pumps ions in at one end and pumps them out at the other end, an electric field will be set up in the external medium. In such a field, the external fluid layer containing the counterions would be driven over the cell surface like the treads of a tank and the cell would move in a direction opposite to the movement of the external fluid layer (Pitta and Berg, 1995). In a medium of high ionic strength such as seawater, a surface charge would be easily neutralized. Furthermore, because of the high conductivity of seawater, the cell would have to generate a very high current density, making self-electrophoresis for *Synechococcus* difficult, if not impossible in this environment (Pitta and Berg, 1995).

Ehlers *et al.* (1996) have proposed a model in which *Synechococcus* moves by generating traveling longitudinal or transverse surface waves, and have calculated that waves of 0.2 μm length, 0.02 μm amplitude and traveling at 160 $\mu\text{m}/\text{sec}$ would allow the cell to swim at speeds of 25 $\mu\text{m}/\text{sec}$. In this model, the waves are generated by the expansion and contraction of local regions of the outer membrane and create thrust such that the cell moves in the direction of the wave. The observed rotation of the cell body during swimming can be explained by waves that are not axially symmetric. Although there is yet no experimental evidence for this model, aspects of it are certainly testable. These waves are not expected to be visible by phase contrast microscopy but Ehlers *et al.* (1996) have pointed out that it should be possible to attach particles to the cell surface and observe their behavior. The particle will vibrate at the frequency of the wave if it attaches to a region of the cell that is contracting and expanding. According to this model there is no net flow of the cell membrane and in fact, Stone and Samuel (1996) have calculated that simple surface flow is unlikely to be propulsive. There is some evidence that the outer membrane does not flow. Willey (1988) observed that beads that became attached to the cell surface served as a fixed reference point as the cell rotated, suggesting that the cell surface does not flow in bulk or move in tracks as in the gliding bacterium *Cytophaga* (Lapidus and Berg, 1982). The generation of surface waves by the contraction of helically arranged fibrils has been proposed as a mechanism for gliding in the filamentous cyanobacterium *Oscillatoria* (Halfen and Castenholz, 1971). Although this hypothesis has not been proven, the presence of such a fibrillar array between the peptidoglycan and the outer membrane of *Oscillatoria* has recently been confirmed (Adams *et al.*, 1999). Although such an array has not been observed in marine *Synechococcus*, there may be other ways of generating contractions and expansions, such as localized swelling of the cell surface (Koch, 1990; Pitta *et al.*, 1997).

Energetics

As is the case for other types of prokaryotic motility, such as flagellar swimming and gliding, the source of energy for swimming in *Synechococcus* is not ATP (Willey *et al.*, 1987). Rather, the sodium motive force is likely to be the energy

source, suggesting that the device converting chemical into mechanical energy resides in the cytoplasmic membrane (Willey *et al.*, 1987). Recently, Pitta *et al.* (1997) showed that another ion, calcium, is also required for swimming. Although the role of calcium in *Synechococcus* motility is not yet understood, studies using inhibitors of voltage-gated calcium channels suggest that a calcium potential may be involved (Pitta *et al.*, 1997). These authors have suggested that calcium depolarization may serve as a way of generating a local swelling of the cell surface which could then be propagated along the cell body and hence may produce the waves postulated by Ehlers *et al.* (1996). Furthermore, calcium is required to maintain the structural integrity of the outer membrane. The specific requirements for sodium and calcium likely reflect *Synechococcus*' adaptation to its natural environment: seawater contains approximately 500 mM Na^+ and 10 mM Ca^{2+} and marine strains have elevated growth requirements for Na^+ , Cl^- , Mg^{2+} , and Ca^{2+} (Waterbury and Rippka, 1989).

SwmA

Recently, the development of tools for the genetic manipulation of *Synechococcus* has made it possible to address the problem at the molecular level (Brahamsha, 1996b). In the course of experiments designed to detect cell-surface components that may be involved in swimming, a major polypeptide of 130 kDa was identified whose decrease in abundance following brief proteinase K treatment of actively swimming cells coincided with the loss of motility (Brahamsha, 1996a). A survey of motile and non-motile marine *Synechococcus* indicated that a polypeptide of similar abundance and molecular weight was present in all of the motile strains tested but in none of the non-motiles. This polypeptide was designated SwmA and was purified from *Synechococcus* sp. strain WH8102 and shown to be associated with the outer membrane although it does not appear to be an integral outer membrane protein (Brahamsha, 1996a). Using recently developed tools for the genetic manipulation of marine *Synechococcus* (Brahamsha, 1996b) *swmA* was insertionally inactivated in *Synechococcus* WH8102. Insertional inactivation of *swmA* results in a loss of the ability to translocate, but cells can still rotate about a point of attachment (Brahamsha, 1996a) at wild-type rates (about 1 revolution per second) (B. Brahamsha, unpublished). This suggests that SwmA functions in the generation of thrust and that thrust and torque generation are genetically separable. Furthermore, these results suggest that at least one component of the cell surface is important for this type of motility.

SwmA is an 835-aa glycosylated polypeptide and its sequence contains a number of Ca^{2+} -binding motifs including an EF hand loop and numerous repeats of a glycine and aspartate-rich motif that has been shown to function in Ca^{2+} binding in other proteins (Baumann *et al.*, 1993). Protein similarity searches have indicated that SwmA is similar to a number of functionally diverse cell surface-associated or secreted proteins such as an S-layer protein (Gilchrist *et al.*, 1992) and various hemolysin-like proteins (Glaser *et al.*, 1988). However, all of these proteins also contain multiple repeats of the Ca^{2+} -binding motif and the regions of similarity to SwmA are largely confined to regions that contain the Ca^{2+} binding patterns, hence SwmA is unlikely to be functionally related to any of these

(Brahamsha, 1996a). It has been suggested that calcium may play a role in the folding and stabilization of these proteins following secretion (Baumann *et al.*, 1993). It remains to be determined whether SwmA in fact binds calcium.

SwmA is also similar to oscillin, a 646-aa Ca²⁺-binding glycoprotein that forms an array of parallel fibrils on the surface of the gliding filamentous cyanobacterium *Phormidium uncinatum* (Hoiczky and Baumeister, 1997), as well as to HlyA, a 322-aa partial ORF of unknown function from the non-motile filamentous cyanobacterium *Anabaena* sp. strain PCC7120 (Brahamsha, 1996a). Both oscillin and HlyA also contain multiple repeats of the Ca²⁺-binding nonapeptide, and the regions of similarity to SwmA are for the most part confined to regions containing these repeats. These three cyanobacterial proteins have been proposed to be homologous on the basis of a stretch of similarity at their C-terminal 47 amino acids, a region that does not contain multiple repeats of the Ca²⁺-binding motif (Hoiczky and Baumeister, 1997). Although this is possible, this region does contain one copy of the nonapeptide within the parameters used by Hoiczky and Baumeister (1997) (GNLYFDTNG for oscillin, GALFFDVDG for HlyA, and GVLSFDADG for SwmA).

It has been suggested that SwmA and oscillin are functionally related (Hoiczky and Baumeister, 1997). This raises the intriguing proposition that swimming in *Synechococcus* and gliding in *Phormidium* share a common mechanism. However, although it has been proposed that oscillin is essential for gliding, this in fact has not yet been established since the non-gliding mutants that were studied lacked not only oscillin but also the S-layer underlying the oscillin fibrils and also did not produce slime (Hoiczky and Baumeister, 1997). Oscillin is proposed to play a passive role in gliding, with its helically arranged fibrils serving to guide the secreted slime. The interaction between the extruded slime, the surface of the cell and the solid substrate would then generate thrust (Hoiczky and Baumeister, 1997). Although this is a plausible scenario for gliding, swimming *Synechococcus* sp. do not produce extracellular slime, nor do they glide on solid surfaces (Waterbury *et al.*, 1985; Willey, 1988). Nevertheless, perhaps SwmA alters the cell surface's characteristics or shape in such a way that rotation of the cell body results in thrust. This might occur if SwmA were distributed in a helical manner around the cell, the way oscillin fibrils are arranged, although it is difficult to predict how large these fibrils or bundles of fibrils would need to be to give the cell an "effective" helical shape such that rotation, generated by some other component, would be accompanied by forward movement. There is at least one other example in a swimming bacterium where a mutation has uncoupled cell rotation from the generation of thrust: mutants of *E. coli* with straight, rather than helical flagella, still rotate their flagella, but cannot swim (Silverman and Simon, 1974). However, no obvious differences in cell shape between the wild type and the *swmA* mutant have been detected by electron microscopy (B. Brahamsha, unpublished). Polyclonal antiserum has been raised against SwmA and used in immunogold labelling of whole cells and of thin sections. The results have confirmed the biochemical evidence that SwmA is indeed localized at the cell surface and indicate that there do not appear to be localized concentrations, such as at a cell pole, for example. SwmA

appears to cover the entire surface of the cell (B. Brahamsha and S. Bakalis, unpublished). However, the techniques that were used to visualize SwmA may not have sufficiently preserved possible substructures and the use of cryotechniques such as the ones used to visualize oscillin (Hoiczky and Baumeister, 1995; Hoiczky and Baumeister, 1997) may be required. Efforts are under way to determine more precisely SwmA's arrangement on the cell surface (B. Brahamsha, unpublished).

Alternatively, could SwmA be involved in a contractile mechanism that would generate the traveling waves proposed by Ehlers *et al.* (1996)? The fact that SwmA mutants still rotate is not necessarily inconsistent with this model. SwmA could affect certain properties of the waves, such as their amplitude for example. Could SwmA's putative Ca²⁺-binding sites be involved in a contractile mechanism? Calcium is required for swimming in *Synechococcus* (Pitta *et al.*, 1997) and the calcium analog terbium inhibits motility in the presence of calcium in a competitive fashion. Swimming speeds decrease linearly with increasing terbium which led Pitta *et al.* (1997) to suggest that there may be multiple force generators that act independently and that are inhibited in an all or none fashion. Does SwmA bind terbium? It is of course possible that SwmA physically interacts with another protein or proteins to generate thrust. Efforts are underway to identify proteins which might interact with SwmA (B. Brahamsha, unpublished).

If swimming in *Synechococcus* is anywhere as complex as two other types of prokaryotic motility, flagellar swimming and gliding, many genes and gene products will be involved. For instance, in *E. coli*, in addition to genes whose products are required for chemotaxis, there are over 40 genes involved in the synthesis and assembly of a functional flagellum (Macnab, 1996). In *M. xanthus*, about 70 loci have been identified which control the gliding movement of individual cells and groups of cells (Hartzell and Youderian, 1995). SwmA is clearly not the only protein involved in swimming. For example, what is the torque generator and what are its components? What are the components involved in transducing the sodium motive force into mechanical energy? Mutant screens are currently underway to identify some of these players. (B. Brahamsha, unpublished). A gene has been identified which is required for the expression of SwmA and may be involved in its glycosylation (B. Brahamsha, in preparation).

Ecological Implications

Why do some marine *Synechococcus* swim? Unlike some gliding cyanobacteria, marine *Synechococcus* appear to exhibit neither phototactic nor photophobic responses (Willey and Waterbury, 1989). Willey and Waterbury (1989) calculated that a cell swimming at 25 $\mu\text{m}/\text{sec}$ in a straight line would cover a distance of only 2 m in 24 hrs. Such a distance in the euphotic zone of oligotrophic waters would result in negligible differences in either light quantity or quality and hence phototactic or phobic responses would confer no advantage. Motile strains of marine *Synechococcus* are not usually found in nutrient-rich coastal regions but rather in oligotrophic regions of the world's oceans where nitrogen is often limiting (Waterbury *et al.*, 1986). Willey and Waterbury (1989) have shown that at least one motile strain of *Synechococcus* (WH8113)

is chemotactic toward nitrogenous compounds such as ammonia, nitrate, β -alanine, glycine, and urea at ecologically relevant concentrations. They have suggested that for organisms living in oligotrophic environments, the ability to detect and seek out patches of nutrient enrichment, such as larger phytoplankton cells or microaggregates (marine snow), may represent an ecological advantage. Indeed, such marine microaggregates are heavily colonized by bacteria and have been shown to be the site of a number of hydrolytic activities, including proteolysis (Smith *et al.*, 1992). It is possible that the resulting surrounding gradients of nitrogenous compounds are detected by motile *Synechococcus* species. Recent work has shown that such patches could serve to attract swarms of bacteria (Blackburn *et al.*, 1998). How cells of *Synechococcus* might modulate their swimming behavior to respond to chemical gradients remains to be determined. Unlike flagellated swimming bacteria, no behaviors such as tumbles or reversals have been observed in marine *Synechococcus*.

This brief review has raised more questions than it has answered, not the least of which is still how does *Synechococcus* manage to swim without flagella. It is hoped that the use of molecular tools to identify components of the motility machinery coupled with the testing of proposed models will yield further insights into this fascinating problem.

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