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Chemotaxis toward Nitrogenous Compounds by Swimming Strains of Marine *Synechococcus* spp.†

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Many of the open-ocean isolates of the marine unicellular cyanobacterium *Synechococcus* spp. are capable of swimming motility, whereas coastal isolates are nonmotile. Surprisingly, the motile strains do not display phototactic or photophobic responses to light, but they do demonstrate positive chemoresponses to several nitrogenous compounds. The chemotactic responses of *Synechococcus* strain WH8113 were investigated using blind-well chemotaxis chambers fitted with 3.0-μm-pore-size Nuclepore filters. One well of each chamber contained cells suspended in aged Sargasso Sea water, and the other well contained the potential chemoattractant in seawater. The number of cells that crossed the filter into the attractant-seawater mixture was measured by direct cell counts and compared with values obtained in chambers lacking gradients. Twenty-two compounds were tested, including sugars, amino acids, and simple nitrogenous substrates, at concentrations ranging from 10^{-5} to 10^{-10} M. Strain WH8113 responded positively only to ammonia, nitrate, β-alanine, glycine, and urea. Typically, there was a 1.5- to 2-fold increase in cell concentrations above control levels in chambers containing these compounds, which is comparable to results from similar experiments using enteric and photoheterotrophic bacteria. However, the threshold levels of 10^{-9} to 10^{-10} M found for *Synechococcus* spp. chemoresponses were lower by several orders of magnitude than those reported for other bacteria and fell within a range that could be ecologically significant in the oligotrophic oceans. The presence of chemotaxis in motile *Synechococcus* spp. supports the notion that regions of nutrient enrichment, such as the proposed microzones and patches, may play an important role in picoplankton nutrient dynamics.

Unicellular cyanobacteria of the genus *Synechococcus* (41) are prominent components of the picoplankton in the temperate and tropical oceans (19, 50). Many of the *Synechococcus* strains isolated from the oligotrophic open oceans are capable of swimming motility (50, 51). Swimming motility in cyanobacteria is rare, occurring only in marine *Synechococcus* spp., and is unusual because these cyanobacteria lack bacterial flagella or other visible organelles that might be associated with swimming (51). The study reported here examines the responses of swimming strains of *Synechococcus* spp. to light and chemical cues.

Under nutrient-depleted conditions, microorganisms expressing a variety of specifically adapted physiological and ecological strategies possess a selective advantage (12, 23, 27, 36, 37). The ability to respond to changes in light, oxygen, and nutrient concentrations permits motile microbes to position themselves in the regions best suited to their metabolic requirements (11, 29, 38). However, for motile marine bacteria, the nature and utility of any behavioral response is limited by the physical constraints of an environment dominated by large-scale mixing driven by wind and thermohaline processes (35).

In phototrophic microorganisms, motility is almost always associated with behavioral responses to light. Three types of photoresponses have been characterized (14). Photokinesis is the modification of the speed of motility in response to changes in light intensity. Phototaxis is described as movement towards (positive) or away from (negative) a light source. Photophobic responses are rapidly induced alterations in motility caused by sudden changes in light intensity. Although all three of these responses have been documented in gliding cyanobacteria (11), we have been unable to demonstrate either photophobic or phototactic responses in swimming strains of *Synechococcus*.

Chemosensory behavior has been documented in a number of microorganisms but has been studied most extensively in enteric bacteria. In cyanobacteria, a few gliding filamentous forms have been shown to respond positively to gradients of carbon dioxide, bicarbonate, and oxygen (30) and negatively to organic acids (17), sulfide (39), and fructose (40). In the marine environment, freshly enriched bacterial isolates have been shown to display chemotaxis to algal extracts (7), and a coastal pseudomonad was shown to be capable of chemotaxis in gradients of sugars and amino acids at concentrations as low as 10^{-8} M (13).

The role of chemotaxis in the marine environment is often considered at the ecological level of nutrient availability and recycling. There is strong evidence that within the euphotic zones of tropical and subtropical waters, the transport of biologically active nitrogen sources into the system, not the degree of light penetration, limits photosynthetic carbon fixation (15, 16, 24). Since soluble levels of nitrogenous nutrients are often below the limit of analytical detection (15, 16, 32), it has been suggested that chemotaxis allows motile marine microorganisms to exploit local sources of nutrient enrichment (2, 5, 6, 10, 20, 43). Fecal pellets (2), larger phytoplankters (5, 6), and amorphous particles of complex biological origin (termed microaggregates [20] or marine snow [10, 42, 43]) are potential sites for elevated nutrient concentrations and turnover rates. Indeed, the ammonia, nitrite, and nitrate concentrations associated with coastal microaggregates range from 3 to 300 times greater than concentrations in ambient seawater (42). The concentrations of photosynthetic and heterotrophic microbes attached to

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particles may exceed the concentrations of similar organisms in ambient seawater by as much as 4 orders of magnitude (10, 43). In addition, it has been postulated that some microbial communities within the oligotrophic marine environment are formed as clusters around microscale sources of sustained nutrient input, such as larger phytoplankton cells (5, 6, 20).

Using blind-well chemotaxis chambers, we have demonstrated that *Synechococcus* strain WH8113 exhibits positive chemotaxis in spatial gradients to a limited number of nitrogenous compounds, including ammonia, nitrate, urea, glycine, and β-alanine. Threshold values for the detection of these compounds were very low (10^{-9} to 10^{-10} M), in a range that could confer considerable ecological advantage to these cyanobacteria in nutrient-depleted oceanic waters.

MATERIALS AND METHODS

Bacterial strains and culture conditions. *Synechococcus* strains WH8103, WH8011, and WH8113 were used in the photoresponse experiments; *Synechococcus* strain WH8113 was used in the chemotaxis and amino acid uptake experiments. All cultures were grown in an excess of nitrate (medium SN) and incubated under conditions previously described (52).

Preparation of cell suspensions. Cells in the mid-logarithmic phase of growth were used without additional preparation for the photoresponse experiments. For chemotaxis and amino acid uptake assays, cells in the early to mid-logarithmic growth phase were harvested by centrifugation at 3,000 × *g* for 10 min at 4°C and washed a total of four times in 75% sterile Sargasso Sea water (SSW) made by diluting the seawater with double-distilled water. Cell densities for chemotaxis assays were then adjusted to 9.5×10^5 to 1.2×10^6 cells per ml as determined by direct cell counts (49). Cells used in determining the kinetics of amino acid uptake experiments were adjusted to densities of 5×10^9 to 1×10^{10} cells per ml (120 to 240 μg of protein per ml).

Photoresponse experiments. All photoresponse experiments were performed by examining wet mounts of cell suspensions by light microscopy (either phase-contrast or dark-field illumination) with a Zeiss inverted microscope (M35) with a Neofluar 100× objective and a 100-W halogen light source (47, 52). The potential for photophobic responses, photokinesis, and phototaxis was tested on cell suspensions examined in both white and green light. Cells were examined for photophobic responses by subjecting the cell suspensions to rapid decreases in light intensity by quickly reducing the voltage through the transmitted light source. Photokinetic responses were studied and were recorded on video tape in preparations examined with dark-field microscopy (52). Motility was then analyzed by computer-assisted motion analysis (Motion Analysis Corp., Santa Rosa, Calif.) as described by Sundberg et al. (47). Dark-field microscopy with a green filter over the field diaphragm in a darkened room was used to provide a discrete column of light illuminating only a portion of the microscope slide at levels sufficient to saturate photosynthesis. Experiments were conducted so that illuminated cells at one edge of the cover slip could be observed while those at the opposite edge were maintained in near darkness. Cells were recorded on video tape during direct continuous illumination and within seconds after incubation at reduced light intensities. This permitted the direct comparison between continuously illuminated cells and cells in the same preparation that had experienced incubation at very low light intensities.

Phototaxis was assessed in two ways. Cell suspensions were observed by phase-contrast microscopy in a sustained light gradient created by limiting the diameter of the light field and by dark-field illumination, as described above for the photokinetic experiments.

Blind-well chemotaxis chamber experiments. Blind-well chemotaxis chambers (NeuroProbe, Inc., Cabin John, Md.) were used to screen compounds that might elicit a chemotactic response in *Synechococcus* strain WH8113. Each clear acrylic chamber has a lower and upper well, with volumes of 200 and 800 μl, respectively, separated by a 13-mm-diameter polycarbonate filter with a uniform pore size of 3.0 μm (Nuclepore, Inc., Pleasanton, Calif.). A 165-μl portion of cell suspension was added to each lower well over which the polycarbonate filter was to be inserted without contacting the cell suspension. Each upper well was created by screwing the cap into place, and was filled with 835 μl of SSW containing the designated compound at the indicated concentration. A slight meniscus resulted by overfilling each upper well, preventing the introduction of air bubbles when chambers were sealed with Parafilm. Twenty-four chambers were clamped between two transparent acrylic sheets. The lower sheet acted as a tray to position the chambers, and the upper sheet was machined to hold 24 O-rings that completed the seals of the upper wells of the chambers. The experiment was started by inverting the tray of chambers and allowing simultaneous contact between cell suspensions and filters in all the chambers in a given tray.

Chambers were incubated at 25°C at 12 to 15 microeinsteins/m^2 per s for 65 min. A 65-min incubation period was chosen to maximize the difference between gradient and control chambers and to permit sufficient accumulation of cells in the upper chambers for accurate cell counts. Experiments were stopped by returning the chambers to an upright position, removing the upper acrylic sheet and Parafilm, and transferring the contents of each upper well to individually prelabeled tubes. The number of cells that crossed the filters into the upper wells was determined by direct microscopic counts with epifluorescence illumination (49).

When cells were suspended in the defined artificial seawater buffer used previously (52), more than 50% of the cell population was rendered nonmotile following the four washes by centrifugation required to obtain optimum and reproducible chemoresponses. Attempts to modify this buffer so that motility was preserved were unsuccessful. SSW collected in 1980 and aged at room temperature since then was sterilized by autoclaving in 750-ml portions. Cells suspended in this seawater retained the levels of motility observed prior to centrifugation. NH_4^+, NO_2^-, and NO_3^- concentrations in sterilized SSW were analyzed by the automated methods of Solorzano (45), Bendschneider and Robinson (8), and Wood et al. (53), respectively, and found to be at or below the limits of analytical detection (ca. 0.01 to 0.03 μg-atom of N per liter).

The establishment and stability of concentration gradients within the chambers were tested by introducing 1 mM $NaNO_2$ into the upper wells and colorimetrically measuring its concentration (46) in both upper and lower wells over 2 h. Regardless of the presence or absence of cells, the NO_2 concentration in the lower wells never exceeded 3 to 5 μM, indicating that the chambers could maintain steep concentration gradients throughout the experimental incubation period.

The optimum cell density for chamber experiments was determined by monitoring the response of cells to 10^{-5} M ammonia and nitrate after the lower wells were filled with 10^5

to 10^8 cells per ml. Cell suspensions with fewer than 5×10^5 cells per ml were impractical because accurate cell counts could not be obtained, and cell densities greater than 1×10^8 cells per ml tended to clog the filters. There was a linear relationship between cells crossing the filter and initial cell concentration when each lower well was filled with cell suspensions with densities ranging from 5×10^5 to 5×10^7 cells per ml. Greater initial cell densities did not result in an increase in the number of cells accumulating in the upper wells.

Two types of control chambers, both lacking chemical gradients, were employed. Cells in seawater control chambers were suspended in SSW, whereas the upper wells contained only SSW without added chemoeffector. Alternatively, chemoeffector was added at the same concentration to both the cell suspension and the upper well of each chamber.

Cellular uptake of amino acids. For each amino acid concentration tested, 1 ml of cell suspension was pipetted into an acid-washed 10-ml beaker and slowly mixed by gentle continuous shaking. To prevent light limitation due to high cell density, a circular cool white fluorescent lamp was positioned to generate an irradiance of 100 microeinsteins/m^2 per s (as determined with a Licor 2 π sensor) at the surface of the cell suspension. Each experiment was begun by labeling the cells with the designated concentration of [^{14}C]glycine (0.13 μCi/ml of cell suspension; specific activity, 114 mCi/mmol) or [^{14}C]alanine (0.17 μCi/ml of cell suspension; specific activity, 171 mCi/mmol). Following rapid yet thorough mixing (as established by methylene blue dye studies), 200-μl samples were rapidly collected by microcentrifugation through a 50-μl layer of silicone oil. The first portion was sampled within 15 to 25 s after the addition of label. The time of sampling was recorded, and when kinetics were calculated, 10 s was added to this time, since 10 s was required to separate cells from the surrounding medium by microcentrifugation. The amount of radioactivity in each pellet and that remaining in the supernatant were determined by standard scintillation counting techniques. Intracellular volumes and the amounts of extracellular matrix associated with the pellets were measured as previously described (52). Cellular protein concentration was determined by the method of Lowry et al. (28).

Chemicals. Radiolabeled amino acids were purchased from Amersham Radiochemicals, Arlington Heights, Ill., and [^{14}C]sorbitol and ^3H_2O used to measure intracellular volume were supplied by Dupont, NEN Research Products, Boston, Mass. All compounds used for chemotaxis chamber experiments were purchased from Sigma Chemical Co., St. Louis, Mo. Solutions of potential chemoeffectors in SSW were prepared on the day they were used.

RESULTS

Occurrence of motile *Synechococcus* spp. Our culture collection contains 98 strains of marine *Synechococcus* spp. isolated primarily from the North Atlantic Ocean, but also from the South Atlantic Ocean, Caribbean Sea, Gulf of Mexico, and Pacific Ocean. Of 83 offshore isolates (i.e., those found beyond the continental shelf), 27 (32%) were capable of swimming motility, whereas none of the nearshore isolates (15 strains) were motile.

Photoresponses. Cell suspensions of three motile *Synechococcus* strains were examined by light microscopy for potential phototactic, photokinetic, and photophobic reactions. No shock or photophobic responses could be demonstrated when cells were subjected to rapid changes in light intensity. Likewise, when cells were placed in a sustained light gradient, neither positive nor negative phototaxis was observed.

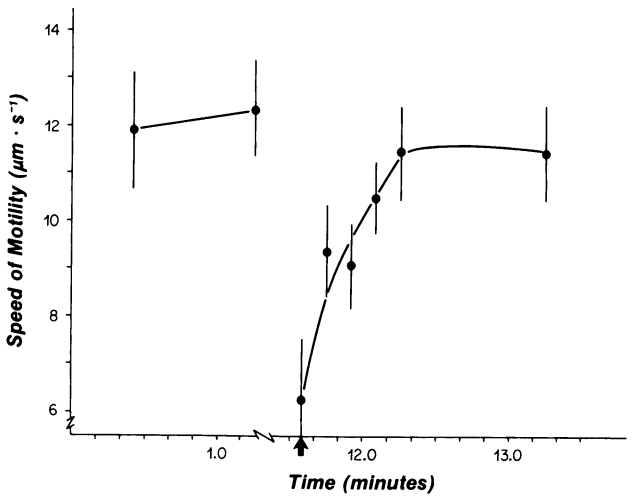

FIG. 1. Recovery of motility following low-light incubation was observed in wet mounts of cell suspensions in medium SN examined by dark-field video microscopy. For the first minute of incubation, cells were recorded in the area of focused light, where they were motile. The cell suspensions were then incubated for 10 min in near darkness and again examined in the focused-light field (arrow), where the recovery of swimming speed was recorded.

When cells were tested under dark-field illumination, photokinesis was observed following incubation in near darkness. Computer-assisted motion analysis of cells recorded on video tape after incubation for 10 min at severely limited light intensities revealed that the average speed of cell motility was reduced by about half, with recovery to preincubation swimming speeds occurring within 2 min of reillumination (Fig. 1). Photokinesis was not observed when cells were incubated at light levels greater than ca. 4 microeinsteins/m^2 per s. Cells incubated in complete darkness for as long as 12 h showed control levels of motility immediately upon reillumination (50).

Response to spatial chemical gradients. Twenty-two different chemical compounds were screened in spatial gradients established in blind-well chemotaxis chambers. These included sodium acetate, D-fructose, D-glucose, D-ribose, sucrose, potassium phosphate (monobasic), vitamin B_{12}, thiamine, urea, sodium nitrite, sodium nitrate, ammonium chloride, methylamine, trimethylamine, and those amino acids thought to be most important in bacterial chemotaxis (L-cysteine and L-methionine) and *Synechococcus* spp. nitrogen metabolism (glycine, alanine, sodium glutamate, L-glutamate, L-glutamine, and L-aspartic acid). All compounds were tested on at least three separate occasions, at concentrations ranging from 10^{-5} to 10^{-10} M in 10-fold increments (except vitamin B_{12} and thiamine, which were tested at 0.1, 1.0, and 10.0 μg/ml). Only ammonia, nitrate, urea, glycine, and β-alanine produced a positive chemoresponse (relative to responses in control chambers) in *Synechococcus* strain WH8113, as measured by a reproducible increase in the number of cells swimming through the filter separating each cell suspension (lower well) from each chemoattractant (upper well) (Fig. 2).

In each case, following a 65-min incubation period, 3.5 to 4.2% of the cells in the seawater control chambers passed through the filters from the lower to the upper wells. When

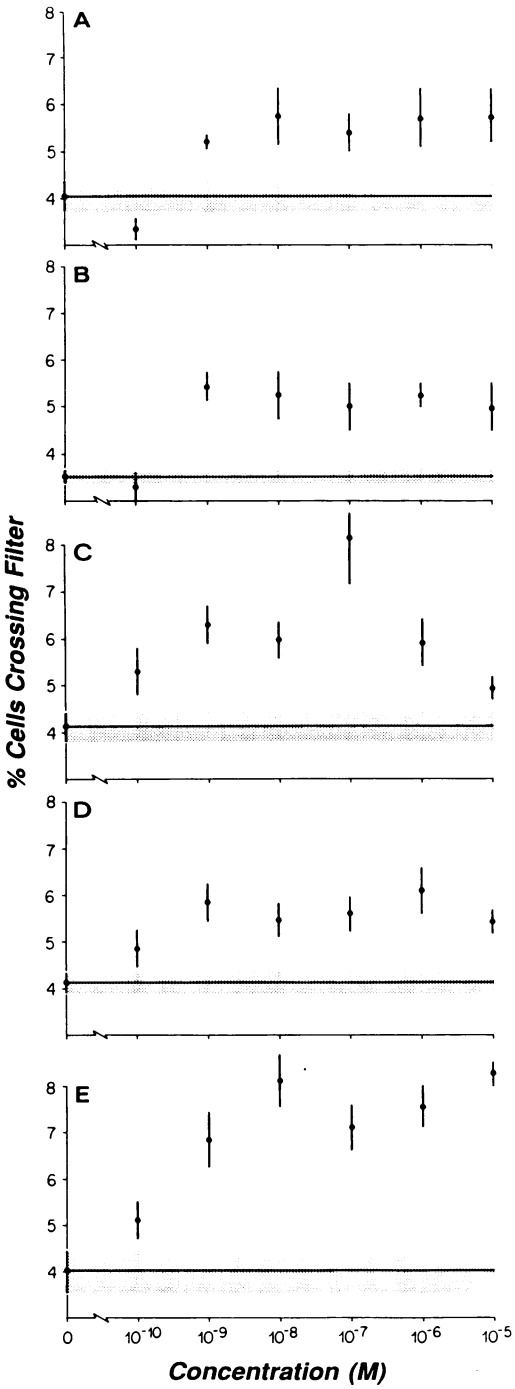

FIG. 2. Chemotactic responses of cell suspensions of *Synechococcus* strain WH8113 to various concentrations of simple nitrogenous compounds. The magnitude of response was measured as the percentage of cells crossing the filters in the chemotaxis chambers from the seawater-cell suspensions to seawater enriched with NH_4Cl (A), $NaNO_3$ (B), urea, (C), glycine (D), or β-alanine (E). Each point represents the mean of four separate experiments, each containing triplicate chambers for all concentrations tested. The bars indicate standard errors of the means. The horizontal lines represent the means, and the stippled areas represent the standard errors of seawater control experiments.

a positive response was elicited, between 5 and 8% of the cells from the lower wells crossed the filters and accumulated in the upper wells (Fig. 2).

The minimum concentration at which positive chemotaxis was first detected was extremely low. Threshold values of 10^{-9} M were required for reproducible responses to ammonia and nitrate, whereas those for urea, glycine, and β-alanine fell between 10^{-9} and 10^{-10} M. Once above these threshold levels, there was no significant difference in the relative magnitudes of response over the ranges of concentrations tested. However, when concentrations greater than 10^{-5} M were tested for ammonia and nitrate, measurable positive responses were sharply eliminated at 10^{-2} M.

Control experiments using two types of nongradient controls demonstrated that cells did not respond chemotactically when both chambers contained either SSW or SSW with the same chemoeffector concentration (Fig. 3).

The magnitude and threshold values required to elicit chemoresponses were not altered by nitrogen starvation. The chemotactic responses shown by cells grown in medium SN, washed, and suspended in the same medium without combined nitrogen for about one doubling (24 h) did not significantly differ from the responses of cells harvested directly from high-nitrate medium. In addition, the magnitude of the chemoresponses relative to the seawater control values was not altered by cell age, as tested by comparing cells in the early to mid-logarithmic phase of growth with those in the early stationary phase of growth. However, the absolute number of cells swimming through the filters was diminished in chambers containing the older cells, presumably because there was a lower percentage of motile cells in the older cultures (51).

Cellular transport of amino acids. Although chemotaxis to a specific chemoeffector and its metabolism need not be coupled (33), an effective strategy for survival in an oligotrophic environment might be to augment chemosensory behavior with a high cellular transport or metabolic affinity for a chemoattractant. To test this hypothesis and to determine if the motile *Synechococcus* strain WH8113 was capable of glycine and β-alanine transport, the kinetics of [^{14}C]glycine and [^{14}C]β-alanine transport were measured. The apparent K_ms for glycine and β-alanine transport were about 1 μM and between 10 and 15 μM, respectively. The V_{max}s for glycine and β-alanine transport were 7.5 and 25.0 nmol/mg of protein per min, respectively. Although these amino acids were actively transported by *Synechococcus* strain WH8113, the affinity of *Synechococcus* spp. for these compounds was not higher than that reported for *Escherichia coli* (26), suggesting that enhanced transport and chemotaxis are not coupled in this cyanobacterium.

DISCUSSION

Previous studies of gliding filamentous cyanobacteria have shown that photoresponses are important both physiologically and ecologically (11, 18, 21, 22, 34). This is not the case for swimming strains of marine *Synechococcus* spp. Rapid changes in light intensity did not elicit photophobic responses, and phototaxis was not observed when cells were placed in sustained light gradients.

Photokinesis at photosynthetically limiting light intensities was the only observed light-induced change in motility (Fig. 1). Since cells incubated at low light intensities cannot meet the energetic needs of motility through photosynthesis or glycogen catabolism, an obligate dark reaction in cyanobacteria (44), this response is of energetic rather than behavioral

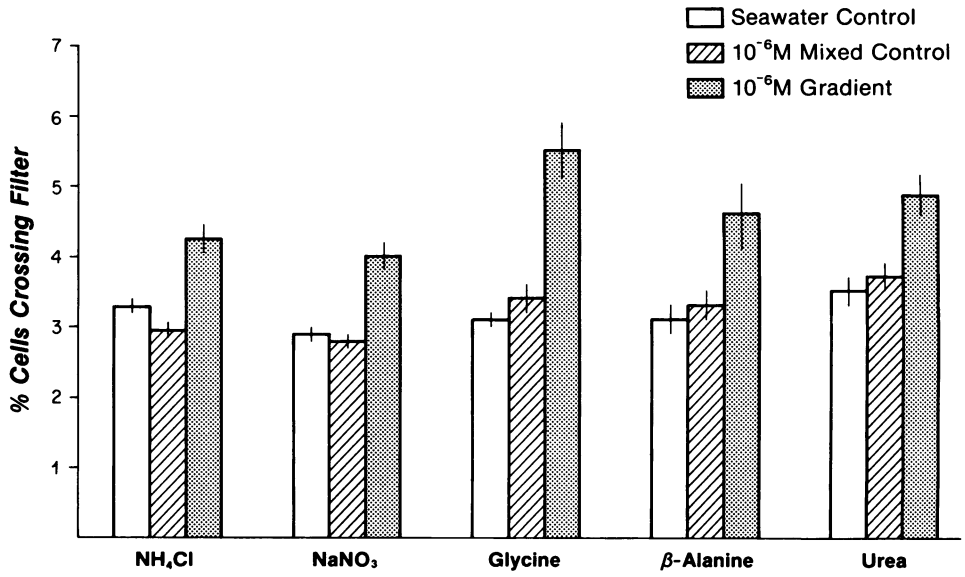

FIG. 3. Chemotactic responses of cell suspensions of *Synechococcus* strain WH8113 in three experimental setups. In seawater controls, both upper and lower wells contained SSW; in mixed controls, both upper and lower wells contained SSW augmented with 10^{-6} M chemoeffector; and in gradients, the lower wells contained cells suspended in SSW and the upper wells contained SSW plus 10^{-6} M chemoeffector. Results are expressed as the percentage of cells crossing the filters from lower to upper wells. Bars represent standard errors of the means.

or ecological relevance. It can be considered analogous to the inhibition of motility resulting from a decrease in the magnitude of the sodium-motive force to less than the energetic threshold needed to drive motility (52). However, cells maintained in absolute darkness exhibited control levels of motility immediately upon reillumination, indicating that glycogen reserves were capable of meeting the energetic requirements for motility in the dark.

The lack of photoresponses in swimming strains of marine *Synechococcus* spp. correlates well with the ecology of this cyanobacterium. Hypothetically, if *Synechococcus* spp. cells were to swim in a straight line at 25 μm/s, they would travel only 2 m in 24 h, a distance of almost no consequence with respect to either quantity or quality of light in the euphotic zones of the oligotrophic oceans. In addition, any behavioral responses to light would be negated by the physical mixing processes within the water column. Thus, it is much more likely that motility in marine *Synechococcus* spp. functions in responses to stimuli over much shorter distances (e.g., millimeters to centimeters).

Instead of responding to light, motile *Synechococcus* strain WH8113 displayed positive chemotaxis toward ammonia, nitrate, urea, glycine, and β-alanine when cells were placed in spatial gradients established in blind-well chemotaxis chambers (Fig. 2). The cell responses observed in two types of control experiments demonstrated that cells were capable of chemotaxis only when gradients of chemoeffector were present. Control chambers with the same concentrations of chemoeffector in both the cell suspensions and upper wells failed to elicit chemoresponses (Fig. 3). In addition, the lack of chemotaxis when cells were tested in higher concentration gradients (e.g., 10^{-2} M) of ammonia and nitrate also illustrated that it was not the presence of the compound per se to which the cells responded, but its gradient. Under these conditions, cellular receptor capacity was presumably saturated; thus, no gradient could be detected (1, 4).

The minimum concentration of attractant in each upper well required to elicit a chemotactic response in *Synechococcus* strain WH8113 was extremely low, ranging from 0.1 to 1.0 nM. However, the actual concentration to which the cells responded was certainly less than reported, since the attractant concentration could not be measured in the lower wells.

Experimental results suggested that the ability of a cell to respond to a chemical gradient was unrelated to growth phase and was expressed constitutively. This is supported by the maintenance of *Synechococcus* spp. isolates in rich batch culture for more than 5 years without noticeable changes in levels of motility. In addition, attempts to induce stronger chemotactic responses in gradients of ammonia, nitrate, or glycine following nitrogen starvation were unsuccessful.

The percentage of cells that accumulated in the attractant-containing upper wells was similar to the level of responses measured in other bacteria (3, 4, 25) (Fig. 4). However, the percentage of cyanobacteria crossing into the upper wells during control experiments was higher (4%) than that reported in experiments using other bacteria (2.5 to 3%) (Fig. 4). Possible explanations for this include differences in interspecific swimming speeds, patterns of motility, and variations in experimental procedures, including lengths of incubation, cell-to-filter pore size ratios, and growth phases of the microbes when tested.

The five nitrogenous compounds to which *Synechococcus* strain WH8113 responded corresponded well with the presence and potential importance of these nutrients in seawater. Calculations based on the assimilation rates of [^{15}N]nitrate (15), [^{15}N]ammonia (16), and [^{14}C]urea (31) by open-ocean and coastal clones of marine phytoplankton suggest that these three nitrogen sources could account for all the nitrogen needed to maintain measured rates of carbon fixation and the observed C/N ratios. Furthermore, glycine and β-alanine have been reported to be among the amino acids present in highest relative abundance in SSW, as recently determined by shipboard measurement of dissolved free amino acids with high-pressure liquid chromatography (48).

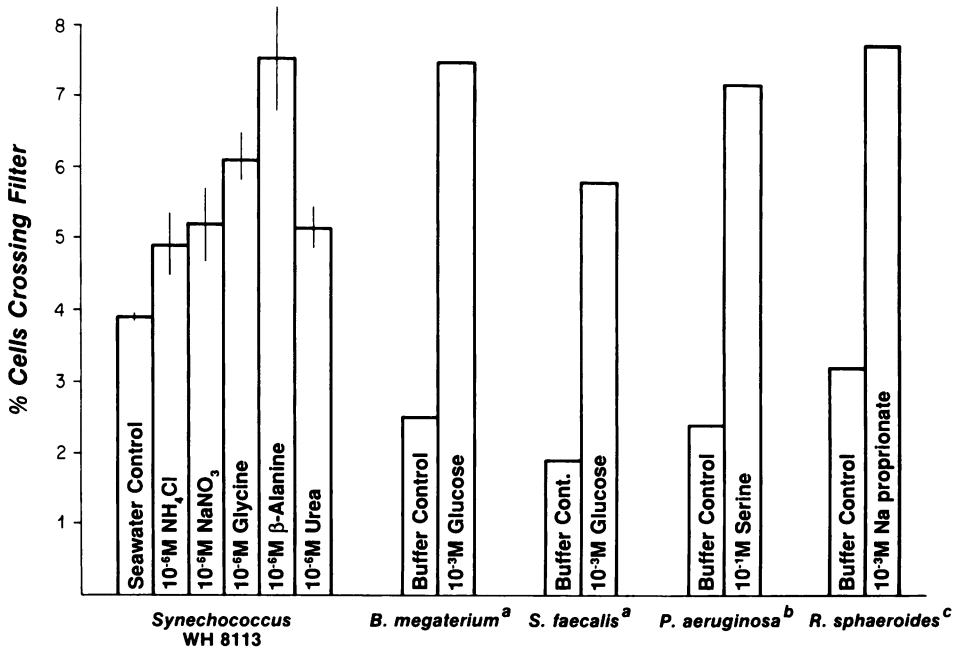

FIG. 4. Comparisons, by the same method, of the magnitude of chemotactic responses of *Synechococcus* strain WH8113 to those of other bacteria. a, Reference 4; b, reference 3; c, reference 25. Bars represent standard errors of the means.

Given that the utility of swimming motility in *Synechococcus* spp. is confined to a scale of millimeters to centimeters, it is reasonable to assert that this motility provides these strains with the ability to exploit local microenvironments of nitrogen enrichment, presumably conferring an ecological advantage. The relationship among motility, chemotaxis, and an inferred ecological advantage has been studied in mixed cultures of motile chemotactic heterotrophic bacteria which demonstrate a survival advantage over nonmotile strains of the same bacteria when essential metabolites are limiting (36). As a result of the low Reynolds number inherent to bacteria the size of *Synechococcus* spp., it has been calculated (9, 27, 38) that swimming through a dilute homogeneous liquid cannot enhance nutrient uptake. On the other hand, it is agreed that chemotaxis can augment nutrient uptake by increasing the number of encounters between a cell and the sites of nutrient enrichment.

The existence and role of zones of micronutrients around either microaggregates or larger phytoplankters have been widely theorized (2, 5, 6, 10, 20, 42, 43), although actual verification has been difficult. The finding that at least one swimming strain of *Synechococcus* spp. was capable of responding to gradients of simple nitrogenous compounds at concentrations of ecological significance helps support the notion that microscale nutrient dynamics may be important in maintaining microbial communities in the nutrient-depleted oceans. In addition, the finding that 32% of the open-ocean isolates of *Synechococcus* spp. were capable of swimming motility whereas isolates from relatively rich coastal waters were nonmotile indicates that motility in this cyanobacterium is functionally important in the oligotrophic open oceans.

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