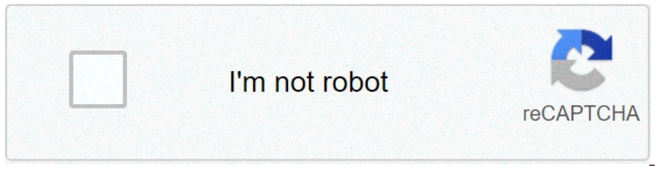

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Bacterial motility was recognized 300 years ago. Throughout this story, research on motility has led to progress in microbiology and physics. Thirty years ago, this union helped to run and to tumble chemotaxis the paradigm of the bacterial movement. This review highlights how this paradigm has expanded and changed, and highlights the following points. The absolute magnitude of the swimming speed is ecologically important because it helps determine the vulnerability to the Brownian movement, sensitivity to gradients, type of receptors used and the cost of movement, with some bacteria moving at 1 mm s−1. High costs for high speeds are offset by the benefit of resource transfer through submillimetre redox and other environmental gradients. Much of the environmental chemotax seems to be adapted to respond to micrometer gradients, rather than migration of centimeters. In such gradients, control of ion pumps is particularly important. Mobility, at least in the ocean, is highly intermittent and the speed is variable within a race. The subtleties in flaming physics provide a variety of reorientation mechanisms. Finally, while careful physical analysis has contributed to our current understanding of the bacterial movement, tactical bacteria are increasingly widely used as experimental and theoretical model systems in physics. Swimming is the most immediately evident behaviour of prokaryotes. He defined it as living entities in the first observations of van Leeuwenhoek (Ford, 1991). At the beginning of 1800, these observations of bacterial swimming contributed to the concept of a vital force for inanimate objects. Motility and thermal movement that became known as brown movement were not conceptually distinct. Einstein's work separated motility from the Brownian movement by identifying it as a physical expressiontemperature. However, 150 years later, Brownian motility and movement were merged again when Einstein's quantitative description for the Brownian movement was used forconstraints on Escherichia coli chemotaxis (Berg & Purcell, 1977; Berg, 1983). The documents gathered bacterial physics and motility and laid the foundations for a continuous understanding in both disciplines. This review examines recent developments in microbiology and physics that have expanded our concept of bacterial motility by a unique strategy, all-purpose to a diversified repertoire of specific responses in bacterial swimming that find heuristic value beyond microbiology. Classical studies underlined the qualitative importance of swimming for bacteria and presented them as the first microsensors of chemical gradients (Engelmann, 1883). The modern systematic study began with work on Adler's chemotax (1966), Berg & Brown (1972) and Macnab & Koshland (1972). In these canonical observations, E. coli responded to an attractive gradient with swimming periods of 1-s (races) punctuated by tumble in which cells randomly reorientated, producing a new direction of swimming. Reduced drop frequency in response to an attractive gradient led to migration to the gradient. The speed of migration has been of some percent of the speed of swimming, which is characteristic of a casual blamed walk. Inefficiency comes from the randomness of the puzzler and Brownian movement that rotates the ride. The implicit spread in the brown movement is at the heart of why bacteria move. A molecule moves through a bacterial cell of 1 μm in 0.5 ms, but through 1 mm in 1000 s because the travel time increases as the square of the distance. The movement is beneficial when nutrients are limited as it brings cells away from competing bacteria. The function of movement, therefore, is to find new environments and the function of chemotax is to ensure that those environments are high of nutrients or low of poison. Apply the racing paradigm andto non-enteric bacteria met the mixed success. Rhizobia show run and tumble chemotaxis with 1- to 2-s execution time and random reorientation by peritrichous peritrichous(Götz & Schmitt, 1987). However, for many bacteria that exist in environments where steep gradients are common, the run and tumble model is the starting reference to describe variations. The distinction between simple swimming and chemotax is significant. Bacteria can become highly motile without chemotaxes (Merrell et al,. 2002) and one of the most simple variations is swimming speed. The current range of fluid swimming speeds is 1–1000 μm s−1 (Marwan et al,. 1991; Fenchel & Thar, 2004) and both ends seem to represent physical limits. For the slower bacteria than about 1 μm s−1, the movement value can be lost as the nutrient spreads faster than the bacteria can find it. The fastest speeds must meet the physical limits of the maximum rotation rate of the motor and the length and number of flagella. If the speed is measured as the distance or lengths of the body per second is relevant for comparing the speed between the different sized bacteria. Thus, a 25 μm long bacteria that swims 600 μm s−1 moves 24 body lengths per second, while a 1-μm long bacteria that moves 450 μm s−1 moves 450 body lengths per second (Mitchell et al, 1995). The absolute value is used for calculating energy expenditure, comparing cell size and running length for diffusion and slope length, while normalized body-length speed is more relevant for determining and testing hypotheses on physical limits. The swimming speed and the length of the gradient determine the minimum size of the cell for chemotaxes (Dusenbery, 1998; Mitchell, 2002.) The bacteria have long been used as patterns of behavior due to their simplicity compared to animals (Berg, 1975; Segall et al, 1982; Marques et al,. 2002). The key parameters of the bacterial movement are the absolute speed, the constancy of speed, the angle ofthe length of the gradient, cell size, receptor sensitivity and the extent to which casual walk can be biased. the values of these easily measurable parameters can be changed from the cells and the environment. This suggestsfield of application for change in motility and chemotactic strategies. exploring movement strategies usually requires recourse to computer modeling and laboratory testing. fenchel (2002) emphasizes that the measurement of bacterial shamid in the ocean is probably impossible, but that understanding is important because all metabolically active bacteria in the ocean seem to be motile. continues to underline that motility is probably even more useful in sediments and soils, where steep, complex and dynamic chemical gradients occur. the potential diversity and importance of motility in these systems has increased from recent theoretical and experimental demonstrations that at least some bacteria perceive chemical gradients on their body lengths, in contrast to the standard paradigm that says they can not (berg & brown, 1972; dusenbery, 1998; fenchel, 2002; overmann & schubert, 2002.) the number of emergent bacteria from the paradigm of the stroke and tumble chemotaxis This review summarizes the progress in motility grouped in methods and mechanics, individual behavior, group behavior and ecology. sections are designed to bring the reader from the cell surface to the ecosystem scale. an additional section describes motility in modern physics to illustrate its oo in the wider scientific environment. methods and mechanics instruments and techniques the modern study of bacterial chemotax began with microcapillary technique (adler, 1966) andrefinements continue. For example, methods have been developed that allow microscopy enumeration to replace plate meters (Meyer et al.,2002). The result isDirect cell counts can be used on volumes of some microliters. This technique is useful for finding new attractions. New sophisticated techniques are also available to study motility. Vigeant (2002) used the total internal reflection fluorescence aqueous microscope to describe motility near surfaces. They found three 'compartments' relevant to motility: Refuse fluid, bulk liquid near the surface and neighboring liquid. The size of the compartment varies with ion concentration, but in general, cells less than 10 nm from a surface become 'constraneous' and irreversibly attached to the surface. The cells slightly above 20 nm swim parallel and can escape the surface. Cells above 10 μm distance do not feel the surface. Where they are common, surfaces could be a reliable method of reorientation for bacteria. The cell form contributes to this. Spherical cells have a torque to the surface that induces rotation but does not cause hydrodynamic penetration. Asta-shaped cells have the same torque induced by the surface, but also have a balanced resistance induced by the shape. The two torches cause hydrodynamic incorporation and cause rod-shaped cells that swim parallel to the surface (Vigeant et al, 2002.) The cell aspect ratio determines if the torque balance, then the cell form is a determining factor of how motile cells react to surfaces. Chemla (1999) used a superconductive quantum interference device to study bacterial magnetotassi. In addition, they have created a microscope of magnetic fields of force similar to the Earth's magnetic field. They measured an average rate of rotation of the flagellator of 89.2±9.6 Hz, an average cell rotation rate of 25.9±0.2 Hz, and vibrational deviations andof 5.5±0.7° and 7.0±0.4° on populations of 10–100 million cells. Using non-mobile cells, they were able to measure rotational drag coefficient, size and average cell distribution around that average. These measurements are impossible to carry out simultaneously on 10–100 millionby light microscope. authors argue that non-magnetic motility can be analyzed by connecting magnetic particles to cells. The new techniques are only a way to advance the search for motility. the form of flagellar and the stress of the beam are known to respond to environmental change (calladine, 1978,) but the new varieties of scourge control continue to be discovered. the complex flagrant strand of rhizobium lupini is a new variant (scharf, 2002.) it is three flagrant subunits connected by interflageline bonds that are stuck in a right helical conformation. this is fundamental for scourge that only rotate clockwise and that tumbles due to the asynchronous deceleration of bundled filaments. filaments are stable from ph 4 to 9, but straighten to ph more extreme and high viscosity. scharf (2002) suggests that this answer prevents the engine stop. is not known if the flagella blocked runs the direct viscotaxis or ph taxi. however, changes in these conditions make it more frequent. the control of the orientation by modulation of the velocity of a single conformatively dynamic scourge was described in rhodobacter sphaeroides (armitage et al, 1999.) initially, r. sphaeroides was thought to turn for the brownian movement (armitage & macnab, 1987,) but this is now known to be wrong for this species. It can be an unlikely strategy for any species because it is only useful for the cells within a few cents of a micrometer of 0.75 μm (mitchell, 2002.) in any case, the observation of the turning with dynamic scourge conformation and the relationship that r. lupini reorients between 0° and 180° with two three filaments and between 0° to 90° with five filaments shows methods of reorientation as a fertile research area. modeling suggests that the integrity of the flaming beam is influenced by the single scourge creatingTurbulents (Trachtenberg et al., 2003). This is surprising because bacteria and their scourge are non-inertial devices, laminaries-flow only. Just.The flow is laminating for Reynolds numbers less than 1 and completely turbulent than 2000. On the contrary, R. lupini scourgeella can get turbulence on the surface during their maximum rotation rate (Trachtenberg et al, 2003.) The sharp flagella and Archimedean screw contours are claimed to produce turbulence at a number of Reynolds of 0.26, which would push the beam's dispersion. The experimental verification of this theoretical work apparently unlikely would change the microfluidics and would cause a paradigm shift in fluid mechanics. The full implications of the turbulence generated by the scourge are not clear; but the consequences of speed change are clear in some species. Rhodobacter sphaeroids show a variety of swimming behaviors within and between individual cells (Armitage et al, 1999). The speeds were constant, oscillating or intermittent. Intermittent behavior combines the other two behaviors, where the speed is high with occasional sharp drops and short-term. The reverse intermittent was not observed, but it is possible and could be useful to pursue behavior (Barbara & Mitchell, 2003). The mapping was immediate, which occurred between two frames of films taken at about 25 frames s−1, or as a slow deceleration. Similarly, startup may be immediate or slow acceleration, which occur between milliseconds and seconds. A single cell can use all combinations. The Flagellar conformation changes at the same time as speed (Armitage et al, 1999.) This related link is supported by the mechanical consistency of flaming changes which are a narrow and high brightness coil that does not protrude the cell, a prop that pushes the cell and a straight form that pushes the cell. Transitional states exist that are curled at the end and straight to the base. The transition and the rolled statesthe cell and represent distinct rotation speed. Thus, excellent engine control is important for environmental bacteria. Chemosmosis and engine control The flagellar motor is 45 nm and embedded in the cytoplasmatic cytoplasmThe electrochemical gradients of H+ or Na+ generated through the cytoplasmic membrane drive the engine (Manson et al., 1977), making it a real molecular machine that converts electrochemical energy into mechanical work (Hirota & Imae, 1983). Bacillus subtilis, E. coli, Salmonella typhimurium, Streptococcus sp. and R. sphaeroides are the H+-driven type, while alcalophilic Bacillus YN-1 (Hirota & Imae, 1983) and some marine bacteria, such as Vibriemo alginolyticus, Vibrio limited information About 60% of the speed in some marine bacteria is due to engines dependent on Na+ (Asai et al., 2003). Sea water alkaline pH makes it difficult to establish a proton gradient directed towards the inside. Since a gradient Na+ is less interested in a H+ gradient for pH, it should be a distinct advantage in salini environments. Engine components continue to be investigated. For H+ engines, the integral proteins of the MotA and MotB membrane are essential for the determination and generation of the ion pair. They form a transmembrane proton channel anchored to a peptidoglycan layer. The Na+-driven motor in V. parahaemolyticus has four integral membrane proteins, PomA, PomB, MotX and MotY respectively. PomA and PomB are homologated in MotA and MotB respectively. Asai (2003) concluded that the transmembrane domains of PomA/B are essential for Na+ engines and that MotX/Y play the essential role of cell domain The presence of Na+- and H+-driven motors in a cell was first found in V. parahaemolyticus (Atsumi et al., 1992). The single sheath polar scourge used in a liquid medium is energized by Na+. The numerous side flagellas are excited by a gradient H+. These last scourges are synthesizedcells are on theor in viscous environments. The result is a morphotype of shaving, presumably used for movement along marine animals and other surfaces. Vibrio alginolyticus has a similar system (Kawagishi et al., 1995). The Halomonas marine sp. US201 and US172 also have two engines, but they only have one type of flagella (Kita-Tsukamoto et al., 2004). The Halomonas were isolated from different environments, including deep sea hydrothermal mouths (Kaye & Baross, 2004), polar waters (Reddy et al., 2003) and dairy food (Maoz et al., 2003). Although more work is needed, the dual system in Halomonas can give them functional versatility. The dark field laser microscope shows that E. coli flagella rotates up to 270 r s−1 (Kudo et al., 1990) and V. alginolyticus up to 1700 r s−1 (Magariyama et al., 1994). With a revolution of 1000 ions, the engine requires 5% of Na+ cytoplasm per second (Magariyama et al., 1994), making an efficient Na+ efflux indispensable. With the exception of the Bacillus alkalophile YN-1, all bacteria with Na+ engines have a primary sodium pump that establishes the electrochemical gradient Na+ as a moving sodium (smf) driving force directly from the respiratory chain (Tokuda & Unemoto, 1981; Tokuda & Kogure, 1989; Hase et al., 2001). We assume that biological functions, such as flagellar rotation and Na+ transport system, are evolved with primary pump systems. Swimming speeds are a linear function of the flaming rotation speed for V. alginolyticus and S. typhimurium (Magariyama et al., 1995). However, considering that the Ovobacter engines move at 1 mm s−1 (Fenchel & Thar, 2004), the rotation rate is well above 10 000 r s−1 or the swimming speed cannot be extrapolated from the rotation rate in some species. Environmental interface The rotation of the motor can be controlled by chemicals that reduce the proton gradientthe membrane (Minamino et al., 2003). High pH and low organic matter concentration of sea water canat high speeds of marine bacteria (Mitchell et al., 1995; Fenchel & Thar, 2004). Alternatively, the Aer gene products perceive intracellular energy levels rather than specific chemicals in the external environment (Rebbapragada et al., 1997). This allows you to maximize the energy available in the cell through the movement, without having to have a wide detection and processing system for any type of metabolize molecule. Similarly, sensitivity is improved by team-work chemoceptors forming clusters to cell poles (Ames et al., 2002), improving signal sensitivity. The distribution of receptors was considered irrelevant because the gradient detection through a body length was considered impossible (Berg & Purcell, 1977). The grouped receptors were the first clue that the body length detection was possible. For small free-swimming bacteria, spatial comparison on a body length is more sensitive than temporal comparison (Dusenbery, 1998). The theoretical limits of the lower dimensions are 0.29 and 0.32 μm for the detection of spatial and temporal chemicals. The challenge currently unexplored for experimenters is to measure lower size limits in real bacteria for the detection of space and time chemicals. Similarly, the minimum detectable length of the gradient for temporal detection was calculated as 100 μm (Dusenbery, 1998). However, it is now known that bacteria detect gradients of just 10 μm (Manson et al., 1977; Blackburn et al., 1998). If spatial or temporal detection is more advantageous depends on the molecule and length of the gradient. There are forecasts for ammonium, iron and many other compounds (Dusenbery, 1998), but experimental confirmation is required and information on sedimentary bacterial distributions and migrations. The confirmationthe above predictions began with experiments showing that an unidentified species perceives a chemical gradient on its body length (Thar & Kühl, 2003). These vibroid-shaped bacteria arebecause they progress along their short axis. The movement is similar to the propeller, but the rotation is not guided by a central tree, rather by flagella at the ends of the cell. The speed of rotation of the Flagellar beam is proportional to the concentration of environmental oxygen, which causes traces in the shape of U, long and helical klinotaxis of a few hundred micrometers. This is the real chemotaxis, where the direction of swimming and slope runs. This can only be possible for bacteria large enough to be negligibly influenced by the brown movement, although there is a report of small marine bacteria circulating mobile algae cells in what could be a version of helical klinotaxis (Barbara & Mitchell, 2003). In stable gradients, temporary attachment from mucous membrane wires is used to maintain the position. This intermittent attack presumably reduces motility costs and highlights the value of motility in finding unusual species in micronics. The behavior has been described before the cells have been identified or understood, but clearly the results provide an incentive to investigate other components of its microbiology and to search for other bacteria that perceive gradients on their body length. Individual behaviour Ultimately, the function of cell components must be seen in terms of behavior in individual bacteria. For E. coli, the mechanics of movement and chemotax are sufficiently well understood to support a book (Berg, 1983), but the selective use of only parts of the motility machinery can produce movement strategies that are counterintuitive. For example, motility is supposed to be chemotactic to be useful. However, Merrell (2002) has shown that hyperinfective cholera bacteria in the intestine are highly motile, but chemotax genes are repressed, which does not mateand chemotax, reducing retention time in the intestine, and increasing the probability of spreading the infection. Speed changes Motility decoupling from chemotax is a simple alteration. For other species, theand behavioral changes are complex. Photorhabdus temperata is mutalistic with pathogenic nematodes of the genus heterorhabditis. bacteria have primary and secondary forms that prefer oxy and anoxic environments. the primary form is mutile in both environments, but the secondary form is motile in anoxic conditions (hodgson et al,. 2003,) despite a previous relationship that was not (givaudan et al,. 1995.) this can reflect the differences in the conditions of culture, variation of tension and history. when the secondary module is transferred from anoxic to oxyche conditions remains motile, indicating that, once initiated, motility is maintained in a cell (hodgson et al,. 2003.) chemotax and motility are inhibited over 35°C. cells are not mobile without sodium, but potassium and magnesium replace sodium with a reduced rate marginally in the primary and marginal form. This is 75 mm. between 100 and 200 mm of potassium and magnesium concentrations, motility decreases (hodgson et al,. 2003.) the change of speed with salt concentration is consistent with the motility of ion pumps (mitchell & barbara, 1999.) a uniform response could be expected for organic signal molecules that are useful as energy sources and cell construction blocks. However, e. coli and, by inference, many other bacteria, have a biphasic response to signal molecules. leucine is a gradient attractor from 0–5-μM, but a repellent in gradient from 0–500-μM (khan & trentham, 2004.) is not known if there is a change of intermediate concentration in which there is no response. the biphasic response comes from double signals with the tar receptor, the signaling attraction, and the tsr receptor, signaling the repulsion. biphasic responses are important to consider where motility is investigated in a large number of species (johansen et al,.under identical conditions because each species is likely to respond biphatically toattracting concentrations. Johansen (2002) measured motility in 84 species and strains of marine bacteria. Swimming speeds ranged from 11 to 75 μm s−1 and accelerations from 80 to 189 μm s−2. Running times range from 0.11 to 0.32 s. The extremes were from unseen blocks, but it was not reported if they were recent blocks. The speed of swimming decreases with a growing concentration of nutrients (Mitchell et al., 1995; Khan & Trentham, 2004), and Johansen (2002) used the medium of Zobell at full resistance (Zobell, 1946). The implications for the interpretation of results are not clear because the sensitivity of nutrients has not been examined and the automatic monitoring system measured only a subset of possible bacterial speeds and turning angles. The work shows the diversity of motile marine bacteria. Methods to test the limits of bacterial motility are necessary if differences and extremes in motility should be discovered. The Niche position can be useful for motility assessment. Schmitt (2002) points out that E. coli is a specialist, while Sinorhizobium meliloti is a generalist. Sinorhizobium meliloti shows a more varied chemotax system than E. coli. The types of flaming filaments and their rotation differ among the species. Sinorhizobium meliloti has a right rigid filament for viscous swimming. Escherichia coli has flagellina monomer subunit, while S. meliloti has flagellina tetramerica subunit assembled as heterodimeri. The latter creates three helical strips that cause flagella only to rotate clockwise and directional control to be through modulation of the rotation rate. Thus, S. meliloti, R. spheroides and many marine bacteria (Mitchell et al., 1996) change the speed with the chemical signal. For S. meliloti, the reorientation is due to rotating engines at different speeds. Speed control mechanisms are unknown. Chemoattrants and receptorsof behavioral repertoire is becoming clear. Vibrio fischeri, a symbiotic species with bobtail squid, bobtail,N-acetylneuraminal acid chemotaptic (NANA), nucleosis and nucleotides, but not to the individual components of these compounds (DeLoney et al., 2003). The chemotax and breathing of the timidine in this species show the difficulty of esteeming growth by incorporation of the timidine. Chemotaxis a, and the metabolism of, NANA is consistent with taxis to drop, as it is produced by lowered surfaces. Nucleotides and nucleosis are released during symbiosis apoptosis. Concurrent complexity is indicated by 40+ chemoreceptor genes. Similarly, many species are chemotactic to many aromatic compounds (Parales & Harwood, 2002). The mechanisms are unknown. The number of chemoreceptor genes are unknown to Flavimonas oryzihabitans, but this bacterium is gas, oil and hexadecaneso chemotactic, and its chemoreceptors may be different as those in V. fischeri (Lanfranconi et al., 2003). There was a minimal microscopic description in this study. They were observed, 'changing the direction of swimming from a sudden short backward movement'. This describes reverse and running chemotaxes, perhaps a new variant. Chemotax was also referred to detergents and oxygen in negative controls, which suggests that chemotax was not an alkaline, but in the energy state. The detection of the energy state can be common in chemotaxes. The Aer and Tsr receptors are independent, but redundant and probably universal in holding a PAS domain (Stock, 1997). This underlines the importance of the aircraft. There is a trade-off between sampling and sensitivity (Johansen et al., 2002). The limits for each are not clear, but the experiments suggest that most bacteria are far from those limits. The drying rates reach 5 s−1 (Barbara & Mitchell, 2003; Fenchel & Thar, 2004) and the delayed responses in the rotation rate up to 100 s are reported (Chernova et2003). This indicates long-term response dynamics and represents a new field of research. Short-distance responses and rapid mobility are open for surveysthe discovery that bacteria trace microalgae swimming (Barbara & Mitchell, 2003). This is unusual in four ways: the bacteria remain within 10 μm of the alga; move ahead of the microalgae; turn in the direction that the microalgae is on the way; and bacteria accelerates and changes direction with the microalgae, sometimes using a circular orbital model without distinct turns. The direction-specific inverters and circular orbits are new behaviors and indicate new control mechanisms. It seems that there are at least seven distinct patterns of motility. In addition to the classic race and tumble chemotaxis, bacteria are able to perform and reverse, steering, location, tracking, orbiting, and running and stopping (Fig. 1). Guidance and localization are the only non-migration behaviors. Reorientation is tripping, reverse or extinguishing. Open in the new tabDownload slideMovement models for motile bacteria. (a) Running and tumble casual walk with a bias to the right. (b) Run and stop the casual walk with a bias to the right. The dotted line indicates that this method, while previously attributed to Rhodobacter's spurs, is not currently reported for any bacterial species. (c and d) Correct and reverse chemotaxes with right-hand prejudice for marine bacteria (Mitchell et al., 1995) and (e) fresh water bacteria (Mitchell et al., 1991). (f) Correct and arc, steering or, more formally, helical klinotaxi, with the ideal gradient a line/plane through the center. (g) Correct and reverse used to locate around a point source. (h) Correct and reverse the tracking followed by orbit of bacteria around a single algae cell. Increasing dark grey shading indicates an increasing attractive concentration. The energy cost of individual motion models can be calculated. Combining size, running length and minimum costfor each movement model shows where these models are more convenient (Fig. 2) (Mitchell, 2002). The model indicates that all moving organisms follow oneLaw (Fig. 3). The confirmation of this model requires the experimental determination of the energy cost of the bacterial movement. Open in the new tabDownload the slideDevice for possible running lengths. The main envelopes are shaded and bound by the maximum and minimum for the different methods of reorientation. The letters are per arc, s per stop and t per track. The tumble and reverse envelopes were calculated at the lower and higher limits. The a, s and t envelopes are estimated positions and shapes, and can overlay or extend beyond other envelopes. The thick black line at the bottom of the envelope is the point where the length of the ride is equal to the radius of the cell. The values below this line involve chemosensing on the body length, a possibility in some situations. After Mitchell (2002). Open in the new tabDownload slideProkaryotes indicating a possible universal law for the movement of organisms. The relationship between the mass of an organism and its energy use for movement. Solid circles and lines in the upper left are calculated costs for literature-based prokaryotes. The detained line is conjectural and the open circle is conjectural for the cost of the greatest motile bacteria known. The shady area is the transition to turbulence that Schmidt-Nielsen predicted would cause different alometric energy equations for microscopic and macroscopic organisms. The only equation for both is shown in the center. The four points for fish come from empirical measurements. There are no empirical determinations for energy use in prokaryotes, but they are clearly necessary. After Mitchell (2002). The group's behavior, in the wider sense of the bacteria moving together, was recognized by Engelmann (1883) and Adler (1966). Recent work on group behaviour reveals fundamental insights and diversity inbacterial. some effects are simple, with 50 μM football salts interrupting pseudomonas putida and pseudomonas farineescens swarming, but kcl and nacl havingHowever, group behaviour appears more complex in quorum systems. spontaneoo hyper-swimmer mutants of v. fischeri were poor to start symbiosis in bobtail squid (millikan & ruby, 2002,) despite their faster swimming, probably because of hyperflagellation. h strains had up to 16 flagella per cell while the wild type had two, the minimum number for reorientation of the dissociative beam. hyperswimmer strains are considered defective (millikan & ruby, 2002,) but the two distinct populations in the sacks of squabble symbiosis could mean that hyper-swimmers are a third population (visick & McFall-Ngai, 2000.) there are two reasons why hyper-swimmer bacteria can be distinct strains. first, the forms of hyper-swimmer spontanee have not converted into nature. Second, at about 100 μm s−1, Hyperswimmer was 150% faster than wild and all three spontaneous mutant types were within 2% of each other in speed (millikan & ruby, 2002.) further tests on hyperswimmer voltage are necessary. Although the three strains were identical in their movement, they showed differences in the formation of mucous membrane colonies, the inability to emagglutinate red blood cells and the inability to produce light. the speed of the hyper-swimmer strains arrived at a cost: They settled slowly, initially losing to the wild type, but capturing them in 48 hours. hyper-swimmer strains were not apparently able to migrate through the pores of the squid. group aggregation is necessary for the entry of pores. Hyper-swimmer aggregations were rare and small, about 15 cells, while wild-type aggregations were hundreds of cells. this is consistent with the work that is discussed below (park et al,. 2003a,) showing that groups have a mechanism to collapse in a pore that is not available for individuals or smallThe strains are distinct ecotypes, probably caused by a single change, such as overexpression scourge. Excessive expression of scourgette consumesso that it is overcome by the wild type, producing a natural experiment of type Lenski (Lenski et al., 1991). The work on V. fischeri gave an overview of the dynamics of the symbiosis and is completed by predictive models. Mazzag (2003) used 12 parameters measured in the Azospirillum brasilense movement to build a model using 16 variables. This model produced bands of position and width similar to their experiments, although they used a constant speed of 40 μm s−1 in the model, while the bacteria in the experiment swam 18 μm s−1 outside the band and 49 μm s−1 within the band. If the constant velocity results in band formation, the variable speed can indicate an energy saving mechanism. If the goal was to remain in the band, then a chemokinetic response, in which the bacteria slow down in the band and the speed out of the band would be expected. The observed behavior is better adapted to quickly cross the band. It is difficult to see how natural selection would favour spending less time at the 'optimal' concentration. Instead, you can select for the steepest gradient. Mazzag (2003) shows that an oxygen gradient has six distinct regions in 1 mm. These are areas where: (1) oxygen is high and there are no bacteria; (2) oxygen is decreasing, but it is high enough so that the bacteria are reversing; (3) oxygen is 'optimum' and bacteria are at maximum speed; (4) oxygen is low and most bacteria are reversed; (5) oxygen is unobservable with background concentrations of bacteria and (6) oxygen is zero and zero concentrations and bacteria. The presence of particles, multiple species and multiple signal compounds can produce many more regions and more complex chemical distributions and species on millimeters, but this remains untested. This work allows to predict the distance between the meniscus and the band (Mazzag et2003), and so it could show how pleasing bacteria groups. Brenner (1998) investigated on motility-driven motility-driventraining in search of long-range interactions in previous work (Budrene & Berg, 1995.) The results provide technical and conceptual information. For example, the oscillation speed decreases when the attractive concentration increases (Brenner et al., 1998). This is consistent with the previous work (Mitchell et al,. 1995.) Four routes have been found that lead to the aggregation: (1) constant expansion; (2) stable at a concentration threshold; (3) spontaneously unstable and (4) increasingly unstable. The following path depends on motility parameters, the attractive primary concentration and the presence of secondary attraction. The aggregates act as if they had zero, one, two or three dimensions. The meaning of this for environmental microbiology is that there are two possible origins for an aggregation: (1) is the creation of a gradient in response to a gradient (Mazzag et al,. 2003) or (2) is the residue of a past interaction aggregation (Brenner et al,. 1998). In particular, bacterial aggregations are intrinsically three-dimensional at the beginning and subsequently collapse in lower dimensions (Brenner et al., 1998). Only the lower dimensions can be accurately shaped. These are two new mechanisms (Brenner et al,. 1998; Mazzag et al,. 2003) for the migration of the band described and modeled in the 1960s and 1970s (Fig. 4a.) One model emphasizes the environmental spatial structure (Mazzag et al,. 2003), while the other emphasizes the chemotax (Brenner et al,. 1998.) Open in the new tabSload slideExamples of collective behavior. (a) A band of bacteria that create a gradient by consuming attractive (gray.) b) The bacteria that undergo a collapse of the quorum perceive the excretion and absorption of the attractor. (c) The bacterial groups collapse in a dead end. d) Heterogeneity within a group of bacteria has collapsed into a quorum attractor. Park (2003a) combinesspace and chemotactic behaviour to describe a system similar to the quorum sensitization in E. coli which is based on glycine and could be asystem for all chemotactic bacteria. Escherichia coli shows complex cluster dynamics in a random labyrinth of 100 μm long walls. The maze was a photolithographic simulation of complex topologies, such as sediments. The accumulation is a two-phase process. First, 'travelling waves' or, in the language of microbiology, chemotactic bands are formed (Fig. 4a). The behavior of the group is described with the physics of the waves. The second step occurs in complex topologies, where the wave collapses in a neighboring topology (Fig. 4). The collapse is not due to a chemoattrating, but is the result of nutrient depletion and subsequent excretion of glycine (Park et al., 2003a). This suggests that under stress bacteria are sought and confined. The bacteria can group into local populations on agar plates at high succinate concentrations (Budrene & Berg, 1995). Park (2003a) found a similar grouping or collapse as described above. The tsr gene controls this behavior as shown by the loss of clustering on tsr deletion, but its retention on tar or aer deletion. In addition, 1-mM l-serine deleted clustering, but 1-mM l-asparatate does not, again indicating tsr control. Also the cloamphenicol stopped grouping, showing the importance of expression and gene growth. The stationary phase cells had no glycine excretion and no collective behavior. During the coupling, the walls act as waveguides, or in this case collective behaviour guides (Park et al., 2003a). The microbiological meaning is that individual bacteria are not specifically looking for small spaces, but only as a group can and emerge this behavior. A significant implication of paper is that traditional homoserin quorum detection systems are special cases of a general phenomenon of communication with amino acids. This highlights the importancemotility for discovery in microbiology. glycine clustering is a non-linear and positive feedback system. therefore, the aggregation occurs when other models predict dispersion. Dispersion.the phenomenon is transient with a constant of 22 minutes (Park et al. 2003a.) The smaller the ratio of the opening area to the volume, the lower the critical bacterial concentration for collapse. Thus, the geometry of the pore influences and could check that the bacteria enter the room. The band's dynamics in a labyrinth do not end with collapse, as they have an internal dynamic structure (Park et al,. 2003b.) This structure has not been studied in detail, but groups of 10 μm indicate that bacteria do not work at the limit of their grouping capacity when they invade spaces such as light organs of squid. This could explain why there are distinct populations in distinct places within light organs. This is a mature area for the investigation. Ecology of the movement Individual and group swim for clean experiments. However, the prevalence and the range of behaviors in the environment are still uncertain. Environmental nutrient concentrations are invariably low and sporadic. The bacteria can be shaped 'almost perfectly' for motility, but this is largely based on cultures (Murray & Jumars, 2002.) Motility is a forage strategy to overcome the crowd in sediment, but the spread means that the crowd occurs when bacteria cover 0.1% of a surface. In sediments, attacked bacteria can overcome the limitation of nutrients by excreting protein enzymes (Vetter et al. 1998.) However, group behavior in density that cause nutrient limitations helps to find nutrient sources. Group behavior models provide information on optimization issues involving online distribution and cooperative computing challenges (Liu & Passino, 2002). Banding produces social forages, where more individuals respond to gradients with a low signal-noise ratio. Bacteria are the simplest of social precursorswith local clonal populations not competitors, the selective advantage is high. The size of the sedimentation grain alters the efficiency of migration, decreasing 20 times as the size of the grain is reduced byto 80 μm (barton & ford, 1995.) experiments that imitate the smallest gaps relevant to motility find that e. in a capillary bath of 6 μm in a direction, unable to turn due to their scourge (liu & papadopoulos, 1995.) in a capillary of 3 μm, the geometric restriction precludes the passage and the turn (liu et al, 1996.) the result is clusters of two and three cells that form and are maintained. clusters moved 15 instead of 18 μm s−1, but they gained the advantage of reverse direction in the capillary. a couple of cells is as small as possible group and reverse direction is among the simplest behaviors, but coupling to reverse could be a necessary and widespread method to explore restricted environments. escherichia coli has been used (liu et al,. 1996,) therefore the prevalence of cell behaviour coupled as a strategy with respect to the turn altering the rotation rate is unknown. in narrow spaces, for diameters of less than 6 μm, motion models pass from a diffuser to a propagative wave (chen et al, 1998.) the length of the scourge and the cell determines the cut. this suggests that porosity selects for the length of scourge, the number of scourge and the size of the cell. clean walls make the glass microcapillars an unrealistic confined environment. motility modeling in a capillary with sticky walls indicates that bacterial distributions are controlled by the channel radius square ratio to the diffusion of motility-driven (bonilla & cushman, 2002.) four underlying mechanisms influence bacterial distributions in these circumstances: Bacterial-paretic interactions with dozens of nanometers, hydrodynamic interactions up to a few bacterial rays, and convection and motility over the dozens of micrometers. dynamics become non-linear with sticky walls and therefore difficult or impossible to predict.makes empirical studies on micro- and macro-scale (Mitchell et al., 1991; Barbara & Mitchell, 1996). Motion containment walls, butgradients, damp directional and turbulent flow, and then increase the effectiveness of chemotaxes. Where turbulence dominates movement and gradients are transient, research focuses on cell detection and response times. Kiørboe & Jackson (2001) model run and tumble vs. perform and reverse research strategies for bacteria that chase marine snow particles from 0.02 to 1.5 cm. These particles are rare, a few per cubic meter, but are important for the generation of nutrients and the heterogeneity of the habitat. As long as a bacteria can remain in the chemical pen behind a particle depends on physical constraints, research model, chemical sensitivity, signal integration time, swimming speed and initial position compared to the particle (Kiørboe & Jackson, 2001). It is presumed that the plume has a total average amino acid concentration of 30 nM. Zero was assumed for the bottom concentration. The selected swimming speeds were 10 and 100 μm s−1. The shorter length of the stroke with the highest sensitivity produced the largest rate of colonization of particles. However, only bacteria moving 100 μm s−1 have improved their time of residence. The resulting increase in nutrients from two to three times was considered modest (Kiørboe & Jackson, 2001). However, an increase of 1% of growth capacity gives a significant competitive advantage (Lenski et al., 1991), therefore also a factor of 2 probably has a remarkable selective and ecological significance. The type of research strategy has made no difference at the rate of colonization or enhancement of nutrients. This is in contrast with other experimental models and results (Manson et al., 1977; Luchsinger et al., 1999), but is probably due to differences in the size of the marker and the detailed implementation of the models and experiments. The improvement of absorption depended onfrom the size of the marine snow and it was a 20-fold improvement for a particle of 0.02-cm-radius, but twice improvement for a particle of 1.5-cm-radi (Kiørboe & Jackson, 2001), while the previous work considered particles that weresmaller (Manson et al., 1977; Luchsinger et al., 1999). The conclusion is that chemotax potentially increases bacterial growth rates from 0.1 to 0.5 days from 1 to 10 days−1 (Kiørboe & Jackson, 2001). To pursue plums to be advantageous they must be met quite frequently to have an ecological impact or a result in colonization. Predictions of marine aggregate colonization rates based on bacterial-motility parameters and research models show that mute bacteria quickly colonize aggregates while non-fatal bacteria do not (Kiørboe et al., 2002). The flow increases colonization. Chemotactic strains colonize preferential aggregates rich in organic. The work indicates that bacteria spend about 3 hours on an aggregate, making 'visit' a more accurate word than 'colonization'. The meeting rate is less than once a day, but in the model it is enough to explain all their food needs. Field observations were clearly different from patterns, and indicated that competition and predators can be more important than colonization to influence the dynamics of the marine bacterial population. A confusing factor in the bacterial motility present in the environment, but absent in cultures initially is the limitation of nutrients. For bacteria in the environment, motility is energetically expensive (Mitchell, 2002) and as such should be used with patrimony. Grossart (2001) faced this problem by carrying out a study of 10 months of percent of motile bacteria at Pier Scripps. The motility range was 5-25% in autumn and winter, and 40-70% in spring and summer. The bacteria did not swim continuously or at constant speed. Many bacteria swim less than 20% of the time. Motility also showed a distinct eel pattern, apparently only related to variations in the concentrationorganic particulate. The fraction of motile bacteria abruptly increased at the end of blooms, and increased motility was associated with increased colonization of living and dead deathsRemoval of particulate matter has decreased per cent of motile cells. The small cells