



UNIVERSITY OF
LATVIA

Summary of
Doctoral Thesis

Māra Šmite

**DEVELOPMENT OF
EXPERIMENTAL,
MOTILITY-BASED METHODS
FOR THE QUANTITATIVE
CHARACTERIZATION OF
MAGNETOTACTIC BACTERIA**

Riga 2026



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Summary of the Doctoral Thesis

Submitted for the degree of Doctor of Physics and Astronomy
Subfield of Fluid and Gas Mechanics

Rīga, 2026

The Doctoral Thesis was developed at the Chair of Theoretical Physics, Department of Physics, Faculty of Science and Technology, University of Latvia from 2022 to 2026. It was developed within the Latvian Council of Science funded Fundamental and Applied Research Project "Advancement of methods for measuring the motility of microswimmers(A4Mswim)" Izp-2021/1-0470.

The thesis comprises of 10 chapters, which include introduction, main results and conclusions, bibliography, one appendix, and acknowledgments.

Form of the Thesis: a dissertation in Physics and Astronomy, subfield of Fluid and Gas mechanics.

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Defense of the Doctoral Thesis will take place at a public session of the Doctoral Committee of Physics, Astronomy and Mechanics of the University of Latvia on 02.10.2026 at 15:00 at UL House of Science in Jelgava Street 3, Riga.

The Doctoral Thesis and its Summary are available at the Library of the University of Latvia, Raina blvd. 19, Riga.

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ISBN 978-9934-36-639-0

ISBN 978-9934-36-640-6 (PDF)

ABSTRACT

Magnetotactic bacteria are single cell organisms that can be controlled using an external magnetic field. They are able to actively move and can be genetically modified, making them a promising model organism in micro-robotics, biophysics, and active matter research. However, quantitative characterization of the motion of magnetotactic bacteria remains challenging due to the many factors that can influence their trajectories.

The aim of the thesis is to develop experimental methods for the characterization of the magnetotactic bacteria motion and statistical analysis of the motion of bacterial ensemble. To achieve this, experimental protocols for visualization of the motion of bacteria in external magnetic field were developed, as well as open source methods for trajectory analysis were created, which allow to automatically determine statistics of cell size, speed and magnetic moment.

As a result, using newly developed methods, it was shown that in *Magnetospirillum gryphiswaldense* cells there is a direct correlation between cell size and its magnetic moment. A rich source of magnetotactic bacteria was found in the Ogre River in Latvia and the new methods were used to characterize the bacterial population. The developed methods will be used in further studies of magnetotactic bacteria and other magnetically controlled micro-systems.

Keywords: Magnetotactic bacteria, magnetic moment, active matter, bacteria motility

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ABBREVIATIONS

L distance between the U-turn branches

m magnetic moment

R effective radius of a microorganism

τ characteristic time

v velocity

AIC Akaike information criterion

CCW counterclockwise direction

CW clockwise direction

MF magnetic field

MSR-1 *Magnetospirillum gryphiswaldense*

MTB magnetotactic bacteria (singular/plural)

PDF probability density function

SS-5 *Magnetovirga frankeli*

TEM transmission electron microscopy

U-turn U-shaped trajectory a magnetic microorganism makes when the direction of applied magnetic field is reversed

1. INTRODUCTION

1.1. General introduction and motivation

Microscale motility is a fundamental research question in biological systems [1]. Many microorganisms rely on active motion to navigate their environment, search for nutrients, and adapt to changing conditions. Because these organisms operate at very small length scales, their motion occurs in a physical regime where viscous forces dominate over inertial forces.

As a result, the principles that govern the movement of microorganisms differ significantly from those observed in macroscopic systems [2]. Understanding the physical mechanisms that enable microorganisms to move and respond to external stimuli is therefore an important topic at the intersection of microbiology, physics, and biophysics [3].

Magnetotactic bacteria (MTB) represent a unique group of microorganisms that combine active motility with passive response to the magnetic field [4, 5]. These bacteria contain specialized intracellular organelles known as magnetosomes, which are membrane-bound [6, 7] magnetic nanoparticles arranged in chains inside the cell [8–10]. The magnetosome chain generates a permanent magnetic dipole moment that allows the bacteria to align with external magnetic fields, including the Earth’s geomagnetic field [11]. This magnetic alignment enables MTB to navigate efficiently along field lines and locate optimal environmental conditions in aquatic habitats [12–15].

In addition to their biological significance [16–20], magnetotactic bacteria are of considerable interest in the field of physics [21–23]. Their motion can be manipulated using externally applied magnetic fields, which allows us to study the interaction between magnetic torque, hydrodynamic forces, and bacterial propulsion mechanisms [24–26].

Experiments involving controlled magnetic fields provide insight into fundamental questions related to microscale locomotion, low Reynolds number hydrodynamics, and active matter systems [27]. MTB and magnetosomes have attracted interest as functional components in a range of applied contexts. Magnetosomes, because of their narrow size distribution, small size, and stable magnetic properties, have been investigated as biologically produced MNPs for applications such as magnetic resonance imaging contrast enhancement and magnetic hyperthermia. In comparison to chemically synthesized nanoparticles, magnetosomes offer a naturally optimized magnetic architecture, which has motivated efforts toward their extraction, functionalization, and large-scale production.

On the other hand, cells themselves have been studied as magnetically steerable microswimmers, where the intrinsic coupling between magnetic alignment and active propulsion enables remote control of cell orientation and tra-

jectories using an external magnetic field. This concept has been explored for applications in microrobotics, targeted transport, and collective phenomena such as swarming and microfluidic mixing [21, 28]. In these applications, MTB serve both as biological actuators and as model systems for studying magnetically guided motion at low Reynolds number, linking applied research with fundamental questions in active matter and microscale hydrodynamics.

Magnetotactic bacteria are a special class of microorganisms in biology because they are only grouped together due to magnetosome production. There exists a great diversity in phylogenetics, morphology, and habitats [13, 29] within the MTB group, and there are also multicellular microorganisms [30–34] and even symbionts with magnetic properties [14, 15, 35]. Regardless of the species, almost all MTB have something in common: they use molecular motors and flagella to move, and magnetosomes to passively orient themselves in MF.

Based on their shape, MTB can have very different properties. The body of bacteria itself can have different shapes - sphere (coccus), rods (bacilli), curved rods (vibrio), helical (spirillum), and even ellipsoidal. This is important when creating mathematical models or simulations; different shapes will have different properties. In addition to this, MTB are able to detect various chemicals in the environment, most importantly oxygen levels in the media around them. The ability to sense oxygen and move towards or away from it as necessary is called aerotaxis, a type of chemotaxis [12, 36].

MTB can be divided in two types, depending on which pole of a magnet they will seek. MTB commonly found in the northern hemisphere are called north-seeking, and they will be attracted to the south pole of the magnet. Similarly, south-seeking MTB that are primarily found in the southern hemisphere will follow the north direction of the Earth’s MF lines [12, 37]. This confusing nomenclature stems from the fact that the geographic north pole of Earth is the magnetic south pole. In a MTB culture or an environmental sample, usually both types of behavior can be observed, with one being dominant. Some evidence has been found to suggest that MTB can switch magnetotactic polarity in response to pH gradients [38].

One of the most important physical parameters that describe MTB is the magnetic moment of the bacterium, which determines how strongly it responds to the external magnetic field. Accurate measurement of this parameter is essential for quantitative studies of bacterial navigation and for comparing different species or environmental populations [39–42]. Advances in digital image analysis have opened new possibilities for studying the behavior of microswimmers in a quantitative manner. Automated trajectory tracking and image-based analysis allow us to analyze large numbers of bacterial cells and extract key physical parameters such as swimming speed, trajectory curvature, and cell size.

The research presented in this thesis is motivated by the need to develop robust experimental and data analysis methods for the quantitative characteri-

zation of magnetotactic bacteria. The work focuses on automated image-based approaches for measuring bacterial magnetic moments and analyzing bacterial motility under controlled magnetic conditions. The thesis also investigates the behavior of magnetotactic bacteria in a rotating magnetic field and examines collective swarms as controllable microscale cargo carriers. This research aims to improve the understanding of magnetotactic bacteria by providing rigorous open experimental and open source data analysis methods that can be used to characterize MTB.

1.2. Scientific novelty

The scientific novelty of this thesis lies in the development of automated and experimental data analysis methods for the quantitative characterization of magnetotactic bacteria as magnetically controlled microswimmers. A fully automated image-based method was developed to determine the magnetic moment of magnetotactic bacteria by analyzing their motion in an alternating magnetic field. Unlike previous approaches that rely on semi-manual trajectory analysis, the proposed method enables efficient and reproducible analysis of a large number of bacterial trajectories, significantly improving the accuracy and throughput of magnetic moment measurements.

The new method is used to characterize a natural sample of MTB with an unknown number of populations, revealing the diversity in their physical properties. The thesis also investigates the motion of MTB in rotating magnetic field and examines the swarm dynamics of magnetotactic bacteria near surfaces.

1.3. Objective

The objective of this work is to develop and improve experimental and data-analysis methods for the quantitative characterization of microswimmer motility at low Reynolds number. The thesis addresses both artificial and biological microswimmers, with emphasis on magnetically controllable systems whose motion can be controlled or analyzed using external magnetic fields.

Microscale motility measurements are challenging because optical microscopy data are often affected by limited spatial and temporal resolution, weak object contrast, image noise, trajectory crossings, and the need for manual data processing. These factors limit the reproducibility, scalability, and statistical quality of the extracted motility parameters. As a result, the new methods provide practical tools for quantitative microswimmer characterization and are available to the broader scientific community.

Concrete objectives of the work were set within the framework of the funding project **FLPP project "Advancement of methods for measuring the motility of microswimmers (A4Mswim)"** lzp-2021/1-0470.

- 1. Improve methods for measuring the motility of magnetotactic bacteria.**

2. Determine motility statistical properties of natural ensemble of magnetotactic bacteria.

3. Assess the limits of particle image velocimetry using a magnetic filament swimmer.

1.4. Approbation of the results

Relevant publications

1. M. Smite, M. Birjukovs, P. Zvejnieks, I. Drikis, G. Kitenbergs, and A. Cēbers, Explicit analysis of magnetotactic bacteria motion reveals the length scaling of magnetic moments, *Biophysical Journal*, Volume 124, Issue 16, 2025, Pages 2583-2597 (2025), [43].
2. M. Smite, M. Birjukovs, M. Sirinelli-Kojadinovich, S. Grosse, A. Kokina, J. Liepins, D. Gudra, M. Lunge, D. Fridmanis, M. Posfai, A. Cēbers, D. Faivre, G. Kitenbergs. Image-based physical characterization of magnetotactic bacteria from an environmental sample. *Microbiology Spectrum* 0:e02563-25. [44]
3. M. Smite, G. Kitenbergs, and A. Cēbers, Optimized and validated flow field measurements around ferromagnetic microswimmers, short paper in *Proceedings of MARSS - Int. Conf. on Manipulation, Automation and Robotics at Small Scales - 2023 (IEEE, 2023)* pp. 10–11. [45]

Relevant international conferences attended by the thesis author

1. 13th International PAMIR Conference, 2024, talk "An Improved Method for Measuring Magnetic Moment of Magnetotactic Bacteria". M.Šmite, M.Birjukovs, G.Kitenbergs, A.Cēbers. Carry-Le-rouet, France.
2. 8th International Meeting on Magnetotactic Bacteria, 2024, talk "Magnetotactic bacteria diversity in the Ogre River". M.Šmite, M.Birjukovs, A.Cēbers, G.Kitenbergs. Bilbao, Spain.
3. MARSS: International Conference on Manipulation, Automation, and Robotics at Small Scales, 2023, talk "Optimized and validated flow field measurements around ferromagnetic microswimmers". M.Šmite, A.Stikuts, A.Cēbers, G.Kitenbergs. Abu-Dhabi, UAE.
4. 7th International Meeting on Magnetotactic Bacteria, 2022, poster "Continuous Tracking of a Motile SS-5 Bacterium In Rotating Magnetic Field". M.Šmite, A.Cēbers, G.Kitenbergs. Bayreuth, Germany.

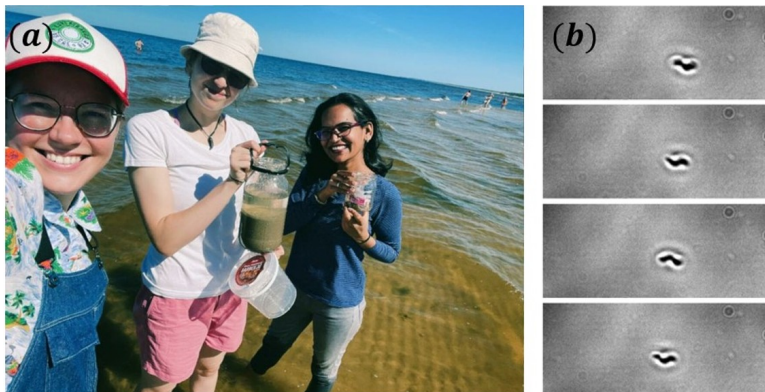
1.5. Structure of the thesis

The thesis consists of 97 pages, 9 chapters, and an appendix; 86 figures and 7 tables.

2. MAGNETOTACTIC BACTERIA AND WHERE TO FIND THEM

There are two ways to obtain MTB: extract them from a natural environment or cultivate them in a laboratory. Cultivation is an excellent way to obtain a single culture with known cell properties, while environmental samples can have a surprising diversity in MTB morphology, magnetosome shapes, and arrangement.

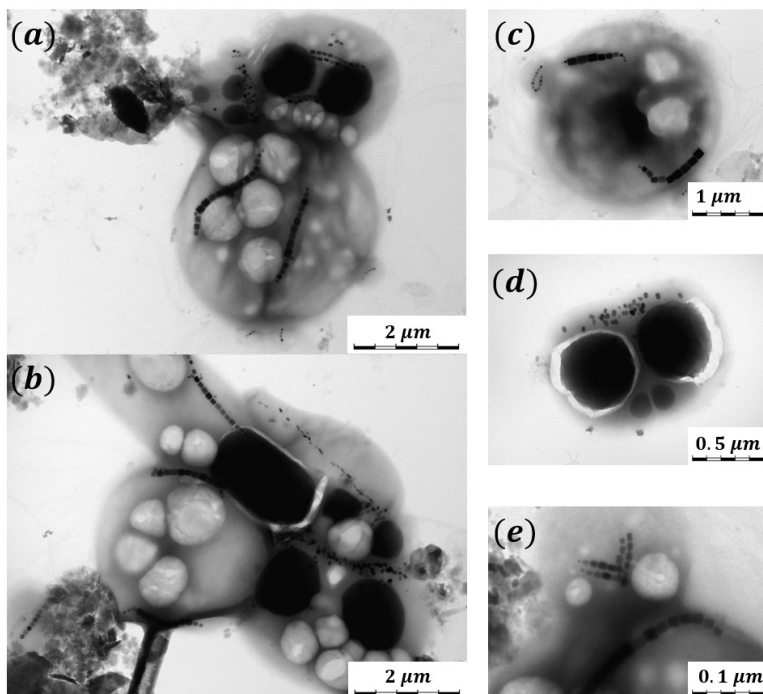
During the development of this thesis, the first MTB in Latvia were recorded Fig. 2.1. This led to a larger expedition, during which a MTB rich source was located in the Ogre River [44].



2.1. Figure: Collection of MTB in nature. a) Image from the expedition where the first MTB in Latvia were recorded, b) magnetic spirillum discovered in the expedition.

Transmission electron microscopy (TEM) images of the sample extracted from the Ogre River sediment revealed a surprising diversity in the morphologies of the cells and magnetosomes Fig. 2.2. There are cocci Fig. 2.2 b and c, cell clusters Fig. 2.2 a,b and possibly rods Fig. 2.2 d. Magnetosome diversity is also considerable - there are cubic, elongated prismatic and bullet shapes present, as well as different spatial arrangements.

This led us to assume that there will be considerable diversity in magnetic properties, cell motility, and morphologies. The methods used to characterize a natural sample using optical microscopy and MF are described in Chapter 4.



2.2. Figure: TEM images of diverse MTB discovered in Ogré River, a) Cocci with two chains and two double chains of magnetosomes, b) MTB cluster with multiple cell and magnetosome morphologies, c) coccus with a magnetosome double chain and a smaller bacterium attached, d) partially disordered magnetosome chain, e) a double chain of prismatic magnetosomes. TEM imaging by Damien Faivre.

When choosing the laboratory culture route, a precise recipe for cell medium and sterile techniques must be observed. *Magnetospirillum gryphiswaldense* (MSR-1) is a popular model organism used to study MTB. It has a corkscrew-shaped body and one flagellum at each pole [46].

The MSR-1 medium recipe was developed more than 20 years ago [47] and with some modifications was used to cultivate MSR-1 bacteria for the experiments described in this thesis.

Fig. 2.3 shows the medium recipe - the mix of chemicals and water where the bacteria will grow. MSR-1 is great for lab cultivation, a small amount of oxygen can be present in the culture, and the bacteria will still grow to be motile and magnetic. In comparison, the other MTB species researched in this work SS-

5, which are obligatory microaerophiles, are usually grown in semi solid medium which is trickier to make correctly.

After making the medium and ensuring that it is sterile, cells can be inoculated into it. Cells should be placed in an incubator at 29°C for two to four days, during which period they are ready to be used in motility experiments. Interestingly, cell length increases steadily with prolonged incubation time [48], therefore, the bacteria size distribution will change with time and multiple phenotypes will be observable in a sample.

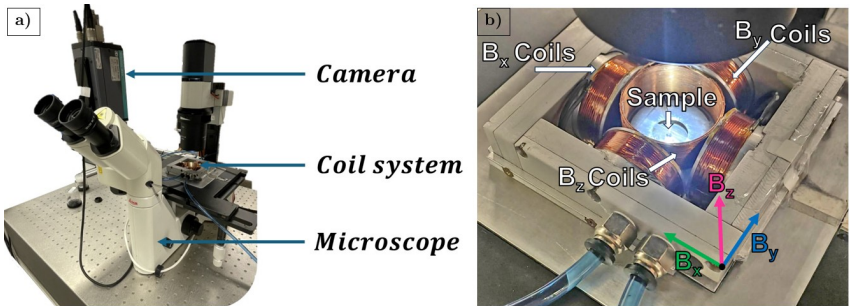
Ingredient	Concentration	Per 1l of medium
HEPES	1 Mol	10 ml
Lactate 60% -	2.5 ml	-
Soy peptone	-	3.0 g
Yeast extract	-	0.1 g
NaNO ₃	1 Mol	4 ml
KH ₂ PO ₄	100 g/l	1 ml
MgSO ₄ × 7H ₂ O	0.1 Mol	6 ml
Fe (III) citrate	10 mMol	5 ml
Modified Wolfe's mineral solution	-	1 ml
NaOH	1 Mol or 10 Mol	As necessary

2.3. Figure: MSR-1 Growth medium recipe

3. A FULLY AUTOMATED METHOD TO MEASURE CELL MAGNETIC MOMENT

A novel and fully automated method for determining the magnetic moment of magnetotactic bacteria is presented on the basis of their motion in externally applied magnetic fields [43]. The method is based on the classical U-turn approach, where bacteria reverse their swimming direction when the magnetic field switches, forming characteristic U-shaped trajectories. Unlike conventional time-based methods, which estimate the magnetic moment from the duration of the U-turn and are sensitive to noise and experimental limitations, the proposed approach directly analyzes the full geometry of the trajectory .

The experimental system is shown in Figure 3.1. It consists of an optical microscope, camera, and an electromagnetic coil system. Bacteria suspension is filled into glass capillary, which is then placed on the microscope stage, in the middle of the coils.



3.1. Figure: Experimental system used in MTB motility research. a) Optical microscope, b) electromagnetic coil system and the sample stage.

A new formula Eq. 3.1 was derived for magnetic moment calculation:

$$m = \frac{\pi \alpha \nu}{HL} \quad (3.1)$$

where α - rotational drag coefficient, ν - velocity, H - magnetic field strength, L - distance between branches of the U-turn.

Parameter L is found by fitting a shape function in Eq. 3.2 to the U-turn

$$y(x, L) = -\frac{L}{\pi} \ln \left(\sec \left(\frac{\pi x}{L} \right) \right) \quad (3.2)$$

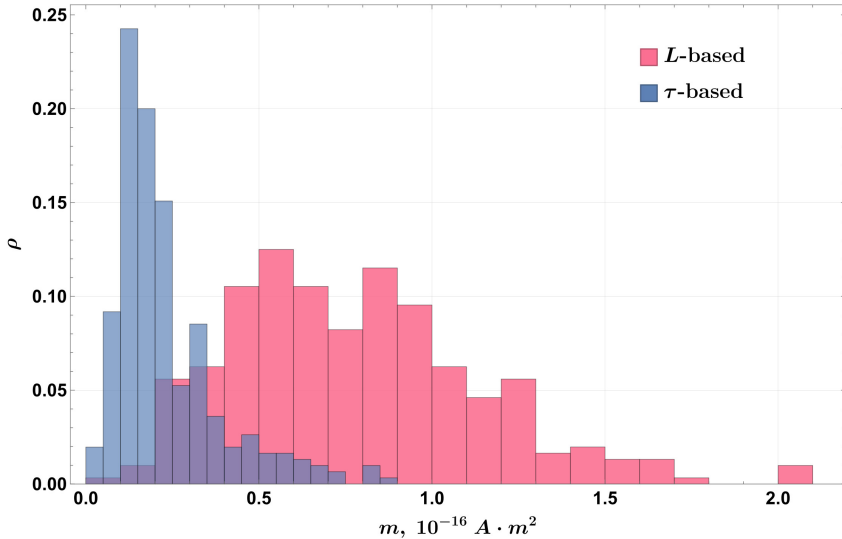
This model allows the magnetic moment to be calculated from the width of

the U-turn, together with experimentally measurable parameters such as bacterial velocity, cell size, and magnetic field strength.

The method was implemented as a fully automated analysis pipeline, including image processing, trajectory reconstruction, U-turn detection, and curve fitting, enabling efficient analysis of large datasets.

The approach was validated using *Magnetospirillum gryphiswaldense* (MSR-1) bacteria, where 18 thousand trajectories were analyzed. The same data set was analyzed using two methods: the m calculation based on the distance between branches (L-based method) and based on the time it takes the cell to complete a U-turn (τ -based). The method based on time used recorded magnetic field strength values that were matched to the respective trajectories to determine τ .

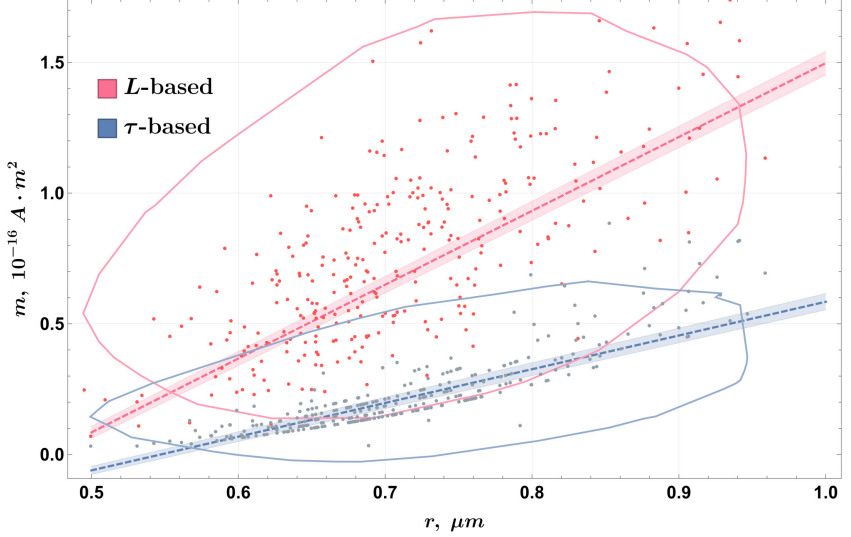
The resulting histograms in Fig. 3.2 show that the magnetic moment is on the order of $10^{-16} \text{ A} \cdot \text{m}^2$. There is a clear difference in the magnetic moment distribution dependent on the calculation method. The τ -based measurement method yields systematically lower m values, and the probability distribution of m is skewed towards larger values, more so than in the case of estimates based on L.



3.2. Figure: MSR-1 magnetic moment m probability ρ histograms for m calculated using the proposed U-turn shape function, coloured pink, and the τ time based approach. Freedman-Diaconis binning [43].

and scales linearly with the bacterial size, indicating that larger cells exhibit a stronger magnetic response.

Compared to the traditional time-based method, the proposed approach provides higher precision and avoids discretization artifacts, as seen in Fig. 3.3, while also allowing more comprehensive statistical analysis of bacterial populations.



3.3. Figure: Magnetic moment m versus MTB effective radius r : linear fits and $q = 0.95$ uncertainty regions for m calculated using the proposed U-turn shape function Eq.3.2 and U-turn analysis algorithm [43], colored pink, and using the τ -based method, colored blue [43].

In general, the developed method provides an open access automated tool for the quantitative characterization of MTB magnetic moment. Using the new method, we have shown that there is a direct positive correlation between cell size and magnetic moment.

4. PHYSICAL CHARACTERIZATION OF MTB FROM AN ENVIRONMENTAL SAMPLE

In Chapter 2, it was mentioned how, during this thesis, a sample containing considerable MTB diversity was extracted from the Ogre River. In addition to TEM imaging, environmental samples were analyzed using automated image-based analysis methods, including the previously described U-turn method [43]. Using the experimental system in Fig. 3.1, the cell suspension containing MTB from the Ogre River was subjected to constant and alternating magnetic fields, thus obtaining data on cell velocity, size, and magnetic moment. Image-based methods were used together with TEM imaging and genetic analysis, to characterize population structure in the sample.

The MTB of the Ogre River were viable for 2 days after removal from the sediment, and optical microscopy experiments were performed when the MTB were able to be extracted. Therefore, the populations observed in Day 1 and Day 2 are labeled accordingly. In Fig. 4.1 the correlation between bacteria velocity v and effective radius r is shown.

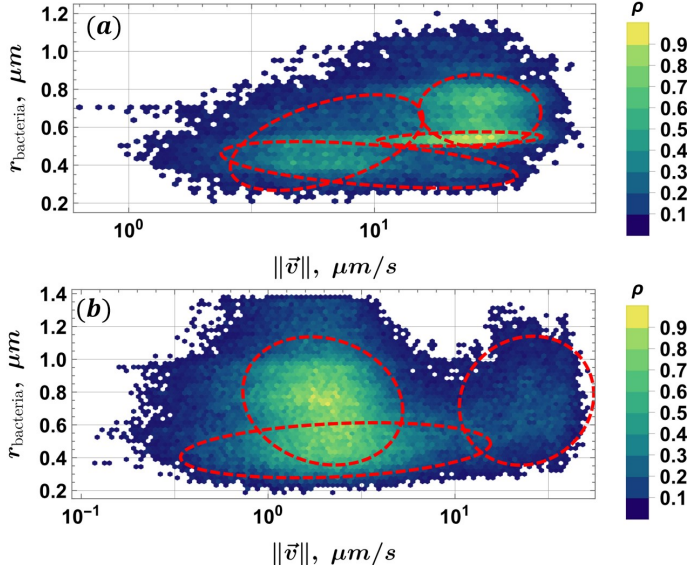
The results reveal significant diversity in both motility and magnetic behavior within environmental populations. Multiple subpopulations of bacteria with distinct physical properties were identified Fig. 4.1, based on cell size and velocity. Using the Akaike information criterion (AIC) [49] optimal number of Gaussians that characterize the sample with an unknown number of populations is found. As a result, on day 1, four populations can be observed, but on day 2 only three populations are present.

Additionally, the natural sample was subjected to an alternating magnetic field Fig. 4.2, and the cell populations were characterized based on the correlation between their magnetic moment and radius Fig. 4.3. This method found three populations present in the sample.

In summary, a pipeline for cell velocimetry is introduced which uses a static magnetic field and a method to classify cell populations based on their magnetic moment using a modified U-turn method [43], where cell behavior is studied in an alternating magnetic field.

This study demonstrates that image-based analysis methods provide a powerful, fast, and robust tool set for the analysis of MTB populations in a complex environmental sample.

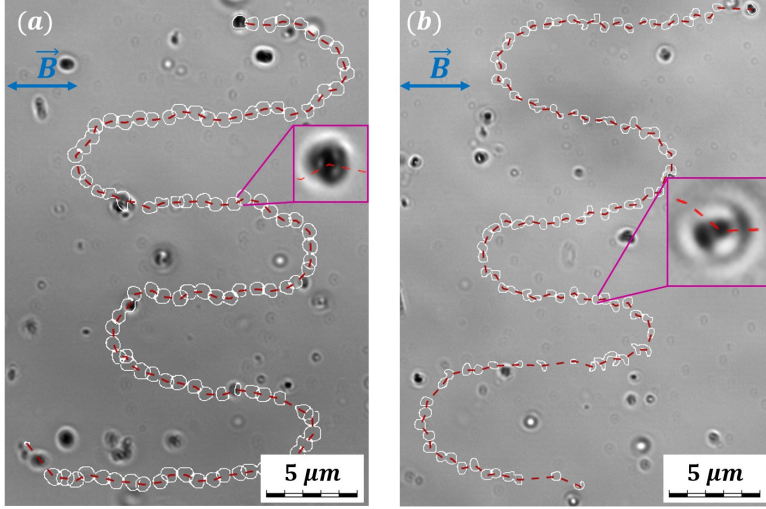
This approach enables large-scale quantitative characterization of environmental samples and contributes to a deeper understanding of the diversity and physical behavior of magnetotactic microorganisms. It can be used as a first step in characterizing an environmental sample - as the methods are faster than tradi-



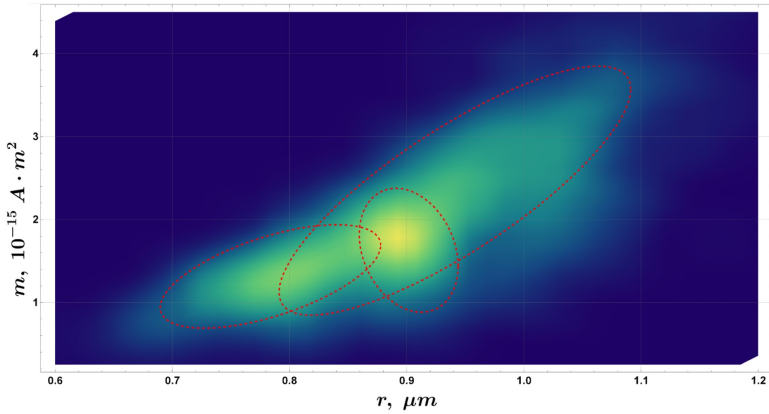
4.1. Figure: Relative frequency histograms for MTB effective radii r_{bacteria} and velocity magnitude $\vec{v}$ in the $\log_{10}$ scale, (a) Day 1 and (b) Day 2. Freedman-Diaconis binning. Dashed ellipses denote populations determined using the AIC-constrained multi-Gaussian fit, and the color coding indicates the relative frequency [44].

tionally used TEM and genetic sequencing, therefore providing an opportunity to rapidly determine population structure.

Overall, subjecting MTB to alternating MF provides insight into the dynamics of magnetotactic bacteria in time-dependent magnetic fields. The findings demonstrate that alternating MF can be used to determine the physical properties of bacteria and control their motion, which is relevant for applications in micro-manipulation and the study of active matter.



4.2. Figure: Bacteria making U-turns in alternating magnetic field, a) a coccus and b) diplococcus [44].



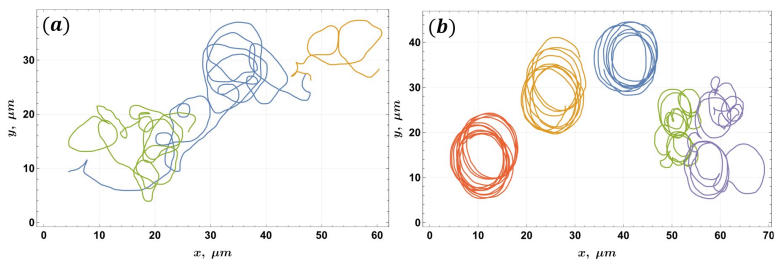
4.3. Figure: Magnetic moment m versus MTB effective radius r : a smooth density histogram (Sheather-Jones bandwidth estimator, Epanechnikov kernel). Dashed ellipses represent AIC-constrained multi-Gaussian fits showing 3 significant populations present in the sample [43]

5. MOTILITY OF *MAGNETOVIRGA FRANKELI* SS-5 IN ROTATING MAGNETIC FIELD

The motility of a novel MTB species [20, 50, 51] in the rotating magnetic field SS-5 has been briefly investigated as a result of collaboration with the Aix-Marseille Institute of Biosciences and Biotechnology.

SS-5 cells are rod-shaped, $2 - 3 \mu\text{m}$ long, and $1 \mu\text{m}$ wide. Cells possess a single flagellum that is typically 3-4 times longer than the cell body [51]. Unlike static or reversing magnetic fields, the rotating field imposes a continuously changing magnetic torque on the bacterium [26], leading to complex swimming trajectories Fig. 5.1.

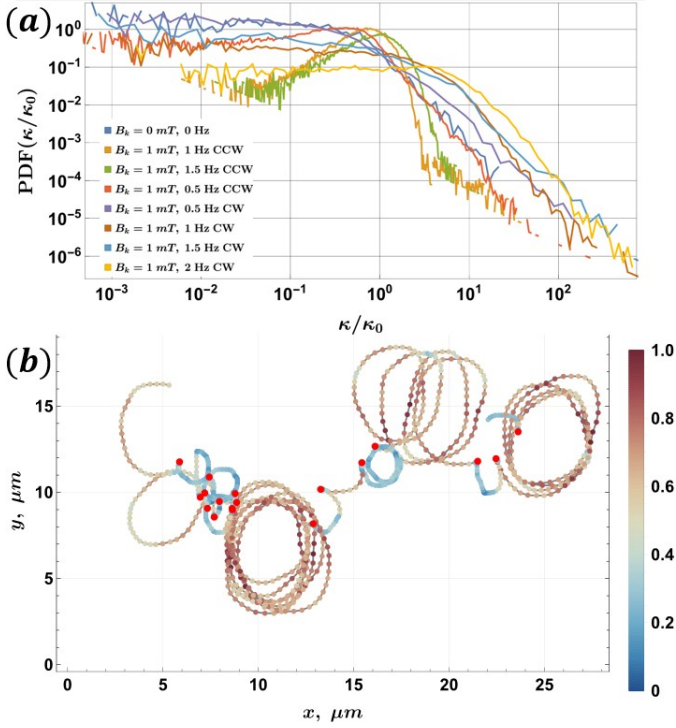
Experiments were performed using optical microscopy combined with a controlled magnetic field system capable of generating rotating fields with adjustable frequency. The trajectories of individual bacteria were recorded and analyzed using image-based tracking methods.



5.1. Figure: Examples of SS-5 movement in a capillary, the colors denote a single trajectory; (a) cell movement without magnetic field, (b) cell trajectories in rotating MF (1 mT, 0.5 Hz).

Fig. 5.1 a) illustrates an example trajectory of a cell moving without an external magnetic field, and b) shows cell trajectories when a rotating field is applied. The red, orange, and blue trajectories demonstrate bacteria that prefer to move synchronously with the MF. The green and violet trajectories demonstrate bacteria that perform multiple switching events - they change the swimming trajectory multiple times, as opposed to swimming in a continuous loop.

Cell curvature, velocity, and switching events were analyzed from 73 bacteria tracks. This was done for MF rotating with a frequency of 1 Hz, with different field strength and rotation direction (clockwise and counter-clockwise). It was observed that the frequency of reversal events increased significantly for the counter-clockwise MF rotation direction.



5.2. Figure: SS-5 bacteria trajectory curvature data. a) Probability density function of curvature versus magnetic field frequency, trajectory curvature normalized with regards to cell size κ_0 b) visualization of a cell trajectory in rotating MF (1 Hz, 1 mT, CW). Velocity is color coded from slowest colored blue, to highest colored red. The points denote switch of the rotational direction.

A trend of increasing trajectory curvature with increasing frequency is observed in Fig. ?? a) for both MF rotation directions, it is curious that this effect is much clearer in the counter-clockwise MF case, where the ranges of observed trajectory curvature are dramatically broader. To help visualize the MTB behavior described with the PDF, in Fig. 5.2 b) an example trajectory is provided. The cell velocity is color coded from the slowest (blue) to the fastest (red), and the red dots denote a sharp change in trajectory.

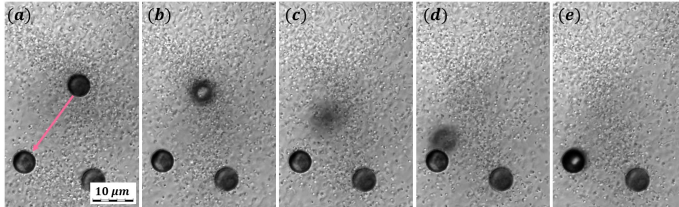
6. RESEARCH OF OTHER MICROSWIMMERS

In addition to researching MTB on single cell level, collective cell movement was considered, as well as a synthetic microswimmer.

MTB form collective structures under applied magnetic fields, enabling controlled microscale motion [28]. In this work, swarm formation and dynamics were experimentally investigated using *Magnetospirillum gryphiswaldense* (MSR-1) bacteria. Under a magnetic field applied perpendicular to the observation plane, as well as bacteria aggregate into stable clusters near the surface. Additional magnetic field components induce directed motion and rotation of these swarms.

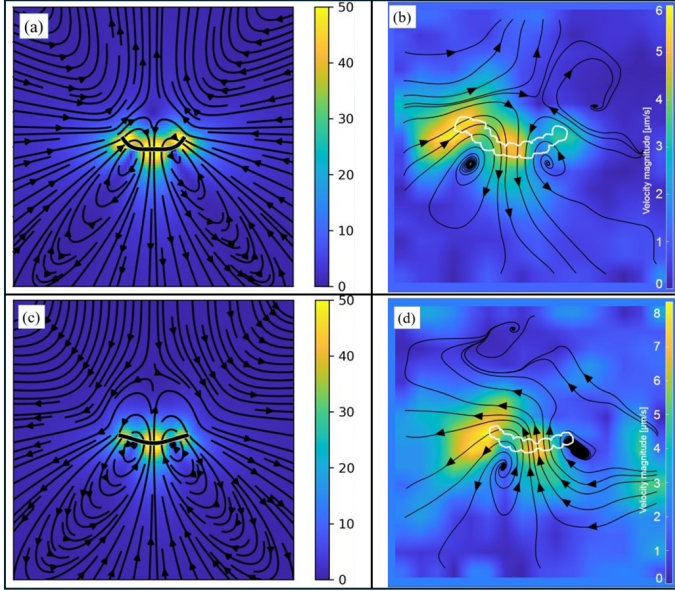
Experiments show that swarm size and behavior depend on magnetic field conditions, with swarms emerging from initially formed aerotactic bands. The motion of swarms follows a well-defined direction relative to the applied fields.

As a proof of concept, it was demonstrated that a bacterial swarm can lift, transport, and reposition a ferromagnetic bead Fig. 6.1. These results highlight the potential of MTB swarms as controllable systems for microscale manipulation and transport.



6.1. Figure: MTB swarm lifting and moving a ferromagnetic bead; (a) aerotactic band reaches a ferromagnetic bead; (b) the bead gets lifted due to swarm hydrodynamic interactions; (c) the bead moves with the swarm; (d) when a bead is close enough to the another, magnetic interaction ensures that the upper bead gets attracted to the bottom one; (e) both beads stay in place.

Finally, synthetic micro-swimmers/mixers were considered – magnetic filaments actuated by an applied magnetic field [52]. Here, in order to validate the numerical model developed to describe and predict their shape dynamics and induced flow field, micro particle image velocimetry (μ PIV) measurements were performed [53]. Using these experiments, it was shown that the numerical models capture the relevant fluid-structure interactions and hydrodynamic effects, and the experimentally obtained flow fields match numerical predictions quite well, as seen in Fig. 6.2. Additionally, we observe that rotating flexible ferromagnetic



6.2. Figure: Flow fields around magnetic microswimmers in infinite fluid determined numerically (left) and experimentally with (right) for a micro-swimmer in bending position (a-b) and in relaxation position (c-d).

filaments, as opposed to rigid straight rods, suck in the fluid in the rotation plane and push it out along the axis of rotation, which is the result of the bent tips of the filament. This kind of 3D flow is useful for micro-mixing.

Our measurements indicate that rotating filaments hover above the bottom, and the hovering height increases with the increase of the rotation frequency. This height greatly influences the velocity field around the filament. Fitting the numerically calculated velocity field of a straight rotating rod to the experimentally measured velocity fields allows one to determine this height. From a physics point of view, the height above the bottom influences the drag force that the filament experiences. This in turn has an effect on the shape of the filament. Decreasing the height increases the drag, which increases the bending of the tips. This has the same effect as increasing the frequency of the field. If the height above the bottom is taken into account, the elastic rod model can reasonably accurately calculate both the shapes and the velocity fields around rotating ferromagnetic filaments.

SUMMARY

This thesis presents a comprehensive study of magnetotactic bacteria as magnetically controlled microswimmers that combine experiments and automated image analysis methods to investigate their physical properties and motility behavior. The work focuses on developing robust and scalable approaches for quantitative characterization of magnetotactic bacteria at both the single-cell and population levels.

A major contribution of this research is the development of an automated image-based method to calculate the cell magnetic moment. A fully automated implementation of the U-turn method was introduced for determining the magnetic moment based on the trajectory shape a bacterium makes in an alternating magnetic field. This approach improves the efficiency, accuracy, and reproducibility of the measurements compared to traditional semi manual methods, enabling the analysis of large datasets and revealing statistical variability within bacterial populations. The results demonstrate that the magnetic moment scales with the size of the bacteria.

The developed method was then applied to environmental samples, where heterogeneous populations of magnetotactic bacteria were analyzed. The results show a wide distribution of physical properties, including swimming velocity, morphology, and magnetic moment, indicating the presence of multiple subpopulations with distinct characteristics. These findings highlight the importance of automated approaches for studying natural bacterial communities, where variability plays a key role in understanding biological function.

The thesis investigates *Magnetovirga frankelii* (SS-5) bacteria behavior under a rotating magnetic field. The results reveal a correlation between the applied MF direction and the trajectory switching events.

Furthermore, collective behaviors such as swarm formation were examined, providing insight into emergent dynamics in systems of interacting microswimmers.

Finally, the work contributes to the development of experimental techniques for studying microscale hydrodynamics, including methods for measuring flow fields around magnetic microswimmers. These approaches expand the experimental toolkit available for investigating active matter systems.

Overall, this thesis advances the understanding of magnetotactic bacteria by providing new methods for their quantitative characterization and by revealing key relationships between their physical properties and motility behavior. The results contribute to the broader field of active matter and magnetic microswimmers, and the developed methodologies can be applied to a wide range of systems in biophysics and soft matter research.

CONCLUSIONS

- Magnetotactic bacteria can be extracted from natural sources or cultured in the laboratory. Natural sources can provide a diverse sample with multiple populations, while cultivation ensures a single population with known properties and the ability to reproduce a sample.
- A new method that uses the distance between the U-turn branches to calculate the cell magnetic moment shows that there is a direct correlation between cell size and magnetic moment in MSR-1.
- A new MTB rich site was found in the Ogře River. Natural samples can possess multiple populations with an unknown number of species that can be resolved using image-based data analysis techniques. TEM imaging and gene sequencing give additional context to the MTB diversity of the sample.
- In an external magnetic field, MTB swarms are formed under confinement. A bacteria swarm is demonstrated to be capable of lifting and moving a ferromagnetic bead to another site.
- SS-5 is a novel MTB species with a single flagellum. SS-5 bacteria velocity in an external rotating MF depends on the direction of the field rotation

THESES

In *Magnetospirillum gryphiswaldense* the magnetic moment scales with the cell size.

By analyzing the motion of magnetotactic bacteria in applied magnetic field, it is possible to precisely determine the cell magnetic moments.

Natural samples can contain multiple magnetotactic bacteria species, which can be resolved by the developed U-turn method.

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ADDITIONAL INFORMATION

The two first author publications that were published during this thesis were included in the Latvian Academy of Sciences Achievements in science 2025 award that was given to author collective for our work on theoretical models and new research methods for controllable active matter ensembles.

ACKNOWLEDGMENTS

I would like to express my gratitude to my supervisors, Dr. habil. phys. **Andrejs Čēbers** and Dr. phys. **Guntars Kitenbergs**, for providing the opportunity to carry out this research, their guidance and critical insight throughout this work.

I am grateful to my colleagues at the University of Latvia, especially **Mihails Birjukovs**, **Lāsma Puķina-Slava** and **Bhagyashri Dada Shinde** for valuable discussions, technical assistance, and for creating a welcoming research environment.

I also thank the collaborators at Bioscience and biotechnology Institute of Aix-Marseille **Mila Sirinelli-Kojadinovic**, **Sandrine Grosse**, **Emilie Gachon** and **Damien Faivre** for introducing me to the wonderful world of microbiology.

Important credit goes to **Sintija Siliņa** for being great in helping navigate the administrative side of the studies.

Finally, I wish to thank my **family** and closest friends, **Sanda**, **Dagnija** and **Ennī**, as well as **Elizabeth Harris** for listening to me and supporting me during the years devoted to this work.

This research was supported by the **FLPP project “Advancement of methods for measuring the motility of microswimmers (A4Mswim)”** (lzp-2021/1-0470).

Financial support from the **University of Latvia** is gratefully acknowledged.