Fluid dynamic research on polychaete worm, *Nereis diversicolor* and its biomimetic applications

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A thesis submitted for the degree of Doctor of Philosophy

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May 2012

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Acknowledgements

Throughout my adventures of my PhD study I have been fortunate to have been supported generously by many other people.

I would like to thank my first supervisor Professor Julian Vincent for his support and his kind words of encouragement. His insight into biomimetics and biological science provide many ideas and suggestions. His foresight and curiosity have provided the direction and motivation for this research.

I would like to thank my supervisor Dr. William Megill for his guidance over writing my thesis. His experience in swimming gives me many suggestions. I learned much about the scientific writing by his reviewing my draft several times. Without him I would not have finished this thesis.

The joint project ARTIC offered me an opportunity to work in the Laboratory for Aero & HydroDynamics of Delft University of Technology, The Netherlands, and to perform experiments there. I have learned much about fluid dynamics and the technology of particle image velocimetry. I would like the thank Dr. Ralph Lindken my supervisor there. He put a lot of effort in to let me come to Delft. He taught me the PIV technique from zero background and gave many suggestions and direction during performance of the experiments. Professor Jerry Westerweel gave me many guidance and knowledge in the fluid dynamics. Thanks to Dr. Breugem for the discussion and suggestion in CFD, and Dr. Poelma in the bio-fluid science. Thanks to Mr. Overmars for his supports in the experiments facility setup. Thanks to Norbert Warncke, U. Miessner and J. Hussong for the discussion and suggestion in my research. Thanks to everybody in the research groups in both Bath and Delft, not only for their help with research, but also for making my time very enjoyable.
Summary

This thesis is a study of the swimming locomotion of the polychaete worm, Nereis diversicolor. Previous research has shown that there are two distinct jet-like flow regions in the wake of a swimming polychaete worm (Hesselberg 2006). In the first section of this thesis, this flow pattern is studied in greater detail using a high resolution particle image velocimetry (PIV) technique. A small region close to the wave crest of the undulating worm is recorded and the fluid velocity vector fields are plotted. The close-up PIV results show how the jet-like fluid pattern is formed due to the action both of a single sweeping parapodium and to the interaction between adjacent parapodia, proving for the first time that Gray’s (1939) explanation of the propulsion mechanics is in fact correct.

The second part of this thesis is focused on the pumping action of the polychaete worm, a behaviour adopted by the worms to create a flow of nutrients through their burrows. Particle image velocimetry (PIV) experiments were performed on tethered polychaete worms, Nereis diversicolor. The tethered worms moved in a gait which was different from that of freely swimming ones. They used a much smaller body wave amplitude, pumping liquid with very high efficiency by cooperative movement of their body and parapodia.

In the third part of the thesis, a mechanical model was designed and built. The model consisted of a series of paddle units. Each paddle was driven by a servo motor. Breugem (2008) did a CFD simulation of the paddle model. Similar fluid patterns were generated by the physical model. Reversed flow was found at low Reynolds number (Re) and higher Re situations. The flow direction could be controlled by simply adjusting the beating frequency of paddles. The mechanical model is not sufficient to mimic the pumping locomotion of the worms due to absence of an undulatory movement. The pumping efficiency is low compared to pumping worms.
Chapter 1
Introduction
1. Introduction

1.1 Introduction and motivation

This thesis is a study of the fluid dynamics of locomotion in the polychaete worm, *Nereis diversicolor*, and the potential to apply its pumping mechanism to engineering uses.

*N. diversicolor* is a common species in Europe. Polychaetes belong to the phylum Annelida (Rouse and Fauchald 1997). Like all other species of Annelida, the polychaete *Nereis diversicolor* has a segmented body, and each segment has a pair of appendages known as parapodia. Separate sets of muscles independently control the movements of the body and parapodia (Smith 1957).

In one of the earliest studies of the locomotion of polychaete worms, *Nereis diversicolor*, Gray (1939) divided the locomotion of these worms into two gaits. At low speed, the worms crawl using only their parapodia. At higher speeds, or when swimming, they undulate their bodies in synchrony with their parapodia. This thesis will focus on the latter gait.

Taylor (1952) compared the locomotor behaviour of several animals which swim by undulatory movements including polychaete worms. He compared the animals’ swimming by so-called undulation movements. The animals were divided into two groups: smooth bodied animals including snakes and leeches, and rough bodied ones such as polychaete worms. He found that these two types of animals undulate their bodies to generate body waves in opposite directions. Rough animals like *Nereis diversicolor* generate body waves from tail to head, while the smooth animals generate theirs from head to tail. He explained theoretically how both kinds of animals could generate thrust force to propel themselves forwards.
To date there has only been one experimental study on the fluid dynamics of this system using Particle Image Velocimetry. Hesselberg (2006) used digital particle image velocimetry (DPIV) to show that two distinct jet-like flow regions are generated in the wake of the swimming worm, but he did not show the details of how the twin jet-region is formed. The flow pattern around the parapodia which plays the most important role for the swimming worms was not studied. One of the objectives of this thesis is to explore this research area.

Figure 1-1 The wake of a swimming Nereis diversicolor. Two jet-like flow regions are found on either side of the polychaete worm (Hesselberg 2006). Colours indicate the magnitude of the flow speed and arrows show DPIV points. The worm is shown in red and the black boxes around it show the extent of the mask required to conduct DPIV calculations.

Due to the special fluid pattern found in the swimming polychaete worms, two distinct jet regions are generated, which means a net flow can be created if the
worm is tethered. This would be a novel worm-inspired pumping mechanism. To study the pumping mechanism of the polychaete worms is another objective of my research. This work is funded by the European project ARTIC, which aimed to develop a micro-fluidic pump inspired by cilia. This kind of pumping system can be integrated in Lab-on-Chip devices.

Many pumping mechanisms are found in nature, such as ciliary suspension feeding and burrowing filter feeding (Foster-smith 1976; Strathmann and Bonar 1976; Riisgard 1991; Stamhuis and Videler 1998). A review paper about animals pumping in a tube system was published by Riisgard and Larsen (2005). Most of these pumping mechanisms work in low Reynolds number situations. Polychaete worms can generate a continuous flow in one direction as a pump. The second target of this thesis is to study the pumping mechanism of a tethered polychaete worm in its fast crawling locomotion.

To study the pumping mechanism in depth, a simplified mechanical model was built. DPIV experiments were carried out on the model to study its fluid dynamic performance. The second objective of building the model was to compare the result with Breugem’s (2008) computational fluid dynamics (CFD) simulation results.

So the overall objectives of my PhD research are:

To study the fluid dynamics of polychaete worms especially the flow around the parapodia.

To analyse the pumping mechanism of tethered worms in order to explore the method of how the fluid is delivered.

To investigate the feasibility of a novel pumping system inspired by the worms.
1.2 Chapter Preview

Chapter 2 presents the fluid dynamics research on freely swimming polychaete worms, *Nereis diversicolor*. The PIV and kinematic experimental setup are described first. PIV results which show the flow pattern are presented and discussed. Kinematic results of swimming worms are given, and the hydrodynamics of the worm is studied quantitatively.

The pumping mechanism of a tethered polychaete worm is discussed in Chapter 3. The experimental method of carrying out the measurement is described. The mechanism of how fluid is moved by the worm in its fast crawling locomotion is given from the PIV results.

Chapter 4 describes the design and construction of a physical paddle model and the PIV measurements carried out using the model. The experiments are done at various Reynolds numbers. The PIV results of the paddle model are compared with the results from a CFD simulation done by Breugem (2008). Finally the model is compared with pumping results from polychaete worms described in Chapter 4.

Finally, Chapter 5 presents the conclusion and future research directions.
Chapter 2
Fluid dynamics of freely swimming polychaete worms, *Nereis diversicolor*
2. Fluid dynamics of freely swimming polychaete worms, *Nereis diversicolor*

2.1 Introduction

*Hydrodynamics of aquatic locomotion*

More than 70% of the earth’s surface is covered by water. Organisms living under water choose swimming as key locomotion. Swimming is achieved by transferring momentum from part of the animal’s body to the surrounding fluid as thrust (Webb 1988). This is achieved in a variety of ways, from jet propulsion in simple animals such as jellyfish, to paddling in insects, to undulation in fish. The polychaete worm, *N. diversicolor*, swims by undulating its body and paddling using its parapodia (Clark 1976).

The Reynolds number (Re) is the most important dimensionless parameter in fluid mechanics and gives an indication of the situation experienced by swimming organisms. It is defined by Equation 2.1

$$Re = \frac{\rho UL}{\mu} = \frac{UL}{\nu}$$  \hspace{1cm} (2.1)

where $\rho$ is the density of the fluid, $U$ is the characteristic velocity of the object and fluid, $L$ is a characteristic length, $\mu$ and $\nu$ are dynamic viscosity and kinematic viscosity of the fluid.

<table>
<thead>
<tr>
<th>Organism/Scenario</th>
<th>Reynolds number</th>
</tr>
</thead>
<tbody>
<tr>
<td>A large whale swimming at 10 m/s</td>
<td>300,000,000</td>
</tr>
<tr>
<td>A tuna swimming at the same speed</td>
<td>30,000,000</td>
</tr>
<tr>
<td>A duck flying at 20 m/s</td>
<td>300,000</td>
</tr>
<tr>
<td>A large dragon fly going 7 m/s</td>
<td>30,000</td>
</tr>
<tr>
<td>A copepod in a speed burst of 0.2 m/s</td>
<td>300</td>
</tr>
<tr>
<td>Flapping wings of the smallest flying insects</td>
<td>30</td>
</tr>
<tr>
<td>An invertebrate larva, 0.3 mm long, at 1 mm/s</td>
<td>0.3</td>
</tr>
<tr>
<td>A sea urchin sperm advancing the species at 0.2 mm/s</td>
<td>0.03</td>
</tr>
<tr>
<td>A bacterium, swimming at 0.01 mm/s</td>
<td>0.00001</td>
</tr>
</tbody>
</table>

*Table 2-1 A spectrum of Re for organisms (Vogel 1994)*
The Re represents the ratio of inertial forces to viscous forces in the fluid. The inertial effects tend to keep an object moving at a constant velocity. The Re represents the ratio of inertial forces to viscous forces in the fluid. At very high Re, the inertia of the fluid dominates its behaviour, and turbulence is easily induced. At low Re, on the other hand, the viscosity dominates, and inertial effects all but vanish – any movements in the fluid are quickly damped out by the action of the internal friction forces between particles. The values of “high” and “low” are specific to the fluid and the geometry of the fluid/structure interaction – in a pipe of circular section.
2000 is the critical Reynolds number above which turbulence will occur.

An object moving through a flow will experience a hydrodynamic resistive force. At high Re, where inertia dominates, this drag will be a function of both shear forces in the boundary layer between the object and fluid, and the pressure gradient across the object, which creates a wake of disturbed fluid into which energy is lost. At very low Re, the resistance to movement is nearly all due to the viscosity of the fluid. In the transition region between these two states, the total hydrodynamic drag is a combination of both of these effects. Table 2-1 lists some characteristic Re of organisms from nature (Vogel 1994). The characteristic velocity (U) is the organism’s swimming velocity. The characteristic length (L) is the size of the organism. The density and viscosity are those of water. The Reynolds numbers range from $10^{-5}$ for a bacterium to very large value of $3 \times 10^8$ for a large swimming whale. Animals swimming in medium and high Re regimes normally have two types of locomotion, undulatory and oscillatory (Webb 1988). Figure 2-1 shows example animals which swim at the different Reynolds numbers.

In undulatory locomotion, animals undulate their body or part of it to generate thrust. These animals include most fish (Drucker and Lauder 1999; Muller, Smit et al. 2001; Muller, Stamhuis et al. 2002), eel (Gillis 1998; Tytell 2004; Tytell 2004), salamander (Gillis 1997), some aquatic and semi aquatic mammals (Fish 2000) and larvae (Wassersug and Hoff 1985). In oscillatory locomotion the animals oscillate appendages including pectoral fins of fish, legs and feet of amphibians, reptiles and mammals. A third class of swimmers are the jet-propelled animals such jellyfish (Colin and Costello 2002; Shorten, Davenport et al. 2005). For organisms living in low Reynolds number regimes where $Re \ll 1$ and the Inertia « Viscosity, the fluid will always be laminar, and so no vortices will shed making it impossible for these animals to propel themselves in the same way as those living in high Re regimes. Organisms in low Re rely on asymmetric movements of power and recovery strokes,
such as those shown in Figure 2-2.

![Figure 2-2](image)

*Figure 2-2. The centrelines of a beating cilium during its complete cycle including power and recovery strokes. After Fauci and Dillon (2005).*

As stated earlier, the model organism used in this research is the polychaete worm, *Nereis diversicolor*. It swims in a low Reynolds number regime (1000-2000 for swimming worms and Re=50 for the parapodia during power strokes), well below that of most fish. Not much research has been done on animals which swim at this Re. As with all the other species of Annelida, the polychaete *Nereis diversicolor* also has a segmented body and each segment has a pair of appendages, named parapodia. The body and parapodia have their own muscles which control the movement of each separately (Smith 1957).

**Ecology of polychaete worms.**

Polychaete worms of the family Nereididae are a common inhabitant of the north temperate zone on both sides of the Atlantic (Smith 1977). In Europe, these worms are found widely spread from northern Europe and the Baltic Sea to the Mediterranean, Black and Caspian Seas (Clay 1967). Due to their widespread distribution, these polychaete worms are used commercially as bait (Scaps 2002).
There are 12 species found in the UK (Chambers 1992). One of the species, *Nereis diversicolor*, is found in sandy or muddy bottom habitat in estuaries and in shallow coastal marine and brackish waters (Clay 1967). Polychaete worms can tolerate a great range of environmental conditions (Wolff 1973). They can survive very well up to two months withstanding salinities of up to twice that of normal seawater (Oglesby 1970). Most of their life-time worms inhabit U or Y-shaped burrows in sandy mud which they build themselves, see Figure 2-3 (Clay 1967; Trevor 1977; Davey 1994). The worm first buries its anterior segments by evertting its pharynx. When half of the body is buried, it starts to burrow by peristaltic wave movement of body (Trevor 1977). The burrow’s structure was described by Scaps (2002). The burrow is Y shaped (Figure 2-3). With the movement of worm’s body, water ventilation is achieved. It may subsist as a filter-feeder system (Harley 1950). Nutrition particles are ventilated in the burrow. Particle transport is influenced by sediment reworking of the burrow construction. Interaction between the sediment and water is increased by a factor of three by the burrowing construction of polychaete worms (Davey 1994; Scaps 2002).
Figure 2-3 Burrow structure of polychaete worms and its interaction with the environment. Water ventilation is achieved by the movement of worm body. (Scaps 2002)

Locomotion of polychaete worms

One of the earliest studies of the locomotion of polychaete worms (*Nereis diversicolor*) was done by Sir James Gray more than 70 years ago (Gray 1939). Based on the movements of polychaete worms’ body and parapodia, the locomotion gaits of worms can be classified into three gaits (see Figure 2-4). These can be described as slow crawling, fast crawling, and swimming (Gray 1939).
Foxon (1936) studied the crawling behaviour of polychaete worms using cinematographic techniques. He described the propulsion action of parapodia when polychaete worms move in their crawling gait. Except at the slowest speeds, the crawling locomotion of polychaete worms is achieved by coordinated movement of their body and parapodia (Gray 1939).

As mentioned in the first part of this section, undulation, oscillation and jet propulsion are the most used swimming locomotion in nature. Most organisms rely on one of these locomotion techniques, and some use two. Polychaete worms swim by undulating their bodies and oscillating their parapodia generating a paired jet wake (Hesselberg 2006).

Gray (1939) initially described the undulation kinematics of polychaete worms. Taylor (1952) studied the fluid dynamics of swimming worms from a theoretical basis. Hesselberg (2006) did some particle image velocimetry measurements, but his work was confined to a large scale view of the flow pattern of freely swimming polychaete worms. There have to date been no experimental studies of fluid flow on a micro scale around the worm which show how the fluid is moved and how the jet-like flow is maintained. The objective of this chapter is to fill this gap.

To study the kinematics of swimming worms, high-frequency video will be recorded. The recording will be analysed frame by frame using customized Matlab routines. A simulation model will be created to predict the kinematics of the swimming worm. The results both from experiments and simulation will be compared. Two dimensional DPIV experiments will be conducted. Using DPIV, the fluid dynamics of worms will be studied, especially the hydrodynamics of a single parapodium and the interaction between adjacent parapodia.
Figure 2-4 Three gaits of the polychaete worm, Nereis diversicolor. Top image is crawling gait, middle one is fast crawling gait, and the bottom one is the swimming gait. In crawling gait, only the parapodia are active. In both the fast crawling and swimming gaits, the worm’s body undulates to generate a wave in addition to the parapodia movement. The body wave amplitude is smaller and the wave speed is slower in fast crawling gait than in the swimming gait.
2.2 Experimental setup and data analyzing methods

2.2.1 Experimental setup

Figure 2-5 shows the two-dimensional DPIV setup used in this chapter. The system consisted of a high speed camera, a high frequency laser and a computer. The laser sheet illuminated a plane in which the worm swam. The flow velocity was evaluated by cross-correlation of two sequential images captured by the camera.

Alongside the DPIV, a second set up was used to obtain image sequences of the worm swimming (Figure 2-6). A light illuminated the field from the top. A diffuser board was used to generate uniform background illumination. A high speed camera was used to record swimming worms from below. A clear contour of the worm’s body was recorded.

*Figure 2-5. Experimental setup showing arrangement of high speed camera, tank, high frequency laser and computer. The light plane illuminates the fluid in which the worms swim.*
Figure 2-6. Experimental setup for visualization recording. The high-speed camera captured backlit images of the worm swimming in the horizontal plane in the aquarium.

Observations were made of the swimming of three individual polychaete worms, *Nereis diversicolor*, and data sets of two of those worms were analyzed in detail.

Worms were housed in artificial sea water (salinity 30ppt). The water was maintained in a temperature of 10 ±2°C. They were fed fish flakes twice weekly. Experiments were carried out in a room maintained at a temperature of 15°C. Worms were introduced to the room one hour before the experiments.

**Experimental set-up for recoding the flow pattern**

To record the flow pattern of *Nereis diversicolor*, individual worms were placed in an aquarium (length 50cm, width 25cm, depth 10cm) filled with artificial sea water
Neutrally buoyant fluorescent particles with a diameter in the range between 15 um to 20 um were added to the sea water in the tank. The scattered light from each particle is in the region of 2 to 6 pixels across the image. The size of the particles were sufficiently fine in the experiments. The fluorescent particles used in the experiments were made by Joe Katz’s group from USA in 2006. The particles were made by dissolving acrylics in a solvent. Then fluorescing dyes were mixed with the solution. Solid acrylic with imbedded fluorescing dye was generated by spraying the mixture into a heated chamber (Katz 1992). The particles had a 580-nm emission wavelength. A long-pass filter with a bandpass at 570nm was used to remove the background light. Only the light emitted from the particles could get through the filter. The particles were illuminated by a laser light sheet (0.5 mm thick), generated by a dual-cavity pulsed, high repetition rate, diode-pumped Nd:YLF laser (New Wave Pegasus). The wavelength was 527nm with 10mJ at 1kHz. The repetition rate of each cavity ranged from 1 to 10,000Hz. The laser sheet coincided with the mid plane of the worm’s body. Illuminated fluid with particles was recorded using a high speed camera (Photron high speed, CCD resolution 1024 pixels by 1024 pixels) equipped with a Nikon micro lens (105 mm), mounted normal to the laser sheet. An orange filter was fitted to the lens to allow only light from the fluorescent particles through to the camera, so as to avoid overwhelming the image with laser light reflected from the worm’s body. The whole system was synchronized by a timing unit connected to a computer. The software package Davis (Version 7.2.2, Lavision, Göttingen) was used to operate the system, including setting the recording frequency of the camera and storing image data.
Figure 2-7 Experimental arena. Free swimming Nereis diversicolor were introduced into the aquarium at the left-hand end. The 'Direction Gate' ensured that the worm swam past the recording window.

The size of the recording window was only 1.8cm by 1.8cm, which was very small compared to the worm’s body (12cm length), so following Hesselberg (2006), a gate was used to guide the worms to swim properly through the recording window (Figure 2-7). Before recording, the worm was placed behind the gate. On release it swam first through the gate and then through the recording window (green square shown in Figure 2-7). Only recordings in which worms swam straight through the recording window were retained for analysis.

**Evaluation and data processing**

Figure 2-8 shows the three steps of the DPIV data evaluation. Two subsequent images are chosen, with time delays chosen such that particles are displaced approximately 4-8 pixels between the two frames. In the Davis software, the Mask function is used to cut off the parts of the images which are not used in the cross-correlation. A mask contoured tightly around worm’s body was applied to reduce the reflection noise close to the worm’s body. Finally, the fluid velocity vectors are calculated using a cross-correlation algorithm.
The fluid velocity field in the wake of worm was calculated from consecutive video frames (image resolution: 1024 x 1024 pixels) using Davis 7.4. As the measurement noise produces several peaks in the correlation function, some might be higher than the right one. Therefore the search window needs to be restricted such that it only searches for small displacements. But to do that, a rough estimate for velocities is needed, and this is obtained from the PIV run on a coarser interrogation window. How many refinement steps are finally required depends on the quality of the PIV images and the velocity distributions; two or three passes are most common. In this case, a 3-pass cross-correlation method was used. In the first pass, an interrogation window of 32 x 32 pixels was used. Then, a smaller size window of 16 x 16 pixels was applied twice to achieve the final vector plot.

A post-processing algorithm was applied. Bilinear interpolation was applied to replace outlier vectors. Removed and replaced vectors outside the range of the RMS (Root mean square) value $\pm 3 \times SD$ of their neighbours. Approximately 4096 vectors were created in a 3.24 cm$^2$ plane.
Figure 2-8. Flow velocity calculation using two sequential high speed video images. Pairs of images were obtained of the fluorescent particles in the flow. Masks with the same shape as the worm’s body were applied. Finally, the fluid velocities were calculated by cross-correlating the unmasked areas of the two images.
2.2.2 Data analysis methods.

In the first part, the kinematics of the worm was analysed with a MATLAB (Version R2007b, The Mathworks Inc.) routine to generate information on parapodia moving velocity, waving angle and inter area between two adjacent parapodia.

**Angle and angular velocity of the parapodium**

Figure 2-9 is a diagrammatic view of the method for calculating the parapodium angle relative to ground. The angle is approximated as that of the line BD as shown in Figure 2-9 Step 2. Custom-written software in the Matlab programming language was developed to calculate the angle semi-automatically. It is called semi-automatic because the coordinates of points A, B and C (Figure 2-9) have to be selected by eye for each frame. Point D is the middle of line AC which is calculated based on the coordinates of A and C. In summary, two key steps are involved. Step one, the coordinates of three points, A, B and C are chosen for all frames. Step two, the middle line (BD) of parapodium is calculated based on the coordinates from the last step (Figure 2-9, Step1, Step2). The MATLAB routine is presented in Appendix 1.
The angular velocity of the parapodium during a power stroke was calculated by using the central time differencing scheme. The points of parapodia in the image were selected by eye and then their coordinates were digitized. So to reduce noise caused by digitization, the central time differencing scheme was used. Figure 2-10 shows the method used. $\alpha(n+1)$ and $\alpha(n-1)$ refer to the angle of parapodium at time step $T(n+1)$ and $T(n-1)$, respectively. Angular velocity is calculated by using a central time differencing scheme, see Equation 2.2. $T(n+1)$ and $T(n-1)$ refer to one time step after and before the $T(n)$ at which angular velocity is calculated. $\alpha(n+1)$ and $\alpha(n-1)$ are the angle of the parapodium at each time frame of $T(n+1)$ and $T(n-1)$. $dt$ is the time step, which was obtained from the video recording frequency.
\[ \omega_{T(n)} = \frac{\alpha_{T(n+1)} - \alpha_{T(n-1)}}{2 \cdot dt} \]  

(2.2)

**Figure 2-10. Geometry used to calculate the angular velocity of the parapodium.**

**Velocity analysis of the parapodium**

Figure 2-11 shows the method for calculating tip velocity of a moving parapodium relative to the ground. T and B refer to the tip and base of parapodium as shown in Figure 2-11 Step2. A similar calculation method is used to that discussed in Section 2.3.1.1. When the coordinates of the tip and base points of parapodium were determined, the velocity of the tip and base of a parapodium were calculated based on the coordinates using the following equation. The velocity in both X and Y component is presented in Figure 2-12. The Matlab routine is given in Appendix 1.

\[ V_{T(\beta)\alpha} = \frac{x_{T} / \cdot b(n+1) - x_{T} / \cdot b(n-1)}{2dt} ; V_{T(\beta)\gamma} = \frac{y_{T} / \cdot b(n+1) - y_{T} / \cdot b(n-1)}{2dt} \]  

(2.3)
Figure 2-11. Schematic drawing shows the steps used to calculate the parapodium tip velocity relative to the ground. In step 1, points A, B and C are selected by eye. The coordinators of parapodium’s tip T and base Ba are calculated in step 2.

Figure 2-12 Schematic showing tip and base velocities in both X and Y directions.
Inter area between adjacent parapodia analysis method

The diagramatic view of Figure 2-13 shows the method for calculating the area between two adjacent parapodia during their power stroke. The area is approximated as a polygon consisting of four points A, B, C and D as shown in Figure 2-13. Custom-written Matlab routines were developed to calculate the area semi-automatically. Firstly, the coordinates of the four points of each video frame were picked out by hand. The command in Matlab, `impixel`, was used. The coordinates were stored as arrays automatically. Secondly, the inter-area of each frame was generated based on the coordinate value. The command in Matlab, `polyarea`, was used to calculate the area based on the coordinates of the four points. The routine is presented in Appendix 1.

Figure 2-13. Area between two adjacent parapodia is calculated. Blue polygon highlights the area. Points A-D are selected manually, and an algorithm calculates the area of the polygon.
Secondly, the PIV data was analysed also by a MATLAB routine, including mean fluid velocity of jet region, fluid dynamics around a cycling parapodium, and mean velocity profile perpendicular to swimming direction.

**Analyzing method of the mean fluid velocity of jet region**

In this section, the fluid velocity of the jet region (see Figure 2-14) is studied. The picture gives a DPIV result of two subsequent video frames. The red outline is the body of a polychaete worm which swims through the window from right to left. In the white box the mean value of all DPIV vectors which give local fluid velocity information is calculated. First, the coordinates of the box boundary are defined. Then the average values of the fluid velocity in both X and Y directions are calculated by using the Matlab commands, *sum* and *mean*. The routine written in Matlab is presented in Appendix 2.

![Image description](image)

**Figure 2-14. A:** Description of the mean flow velocity. This picture shows a DPIV result of two subsequent video frames. The red outline is of the body of a polychaete worm which swam through the window from right to left. In the white box the mean value of all PIV vectors which give local fluid velocity information is calculated.
Fluid dynamics around a cycling parapodium

To study the fluid flow around a moving parapodium during its power stroke, a region was chosen (the white square in Figure 2-15) around the tip of a moving parapodium which moves with the parapodium. The coordinates of parapodium’s tip were picked by hand for each time step. Then based on these coordinates, the white square can be defined. The mean fluid velocity is calculated by averaging every vector velocity inside the white square in both X and Y directions. The Matlab routine is presented in Appendix 3.

Figure 2-15. Description of the target square which follows a parapodium as indicated in the figure. This picture shows a Digital Particle Image Velocimetry result of two subsequent video frames.
Mean velocity profile perpendicular to swimming direction

To study the fluid velocity as a function of position relative to the worm’s body, a DPIV result was chosen and the mean velocity of each row (see Figure 2-44) was calculated. The first step is the spatial averaging. The average fluid velocity of each row is calculated for every PIV frame. PIVMAT toolbox was used to read Davis file into Matlab. The second step is temporal averaging. The average fluid velocity over a stroke period of each row is calculated with its standard deviation. The Matlab script used to do these calculations is presented in Appendix 4.

2.2.3 Simulation modeling for kinematic study of the swimming worms.

The simulation is developed with Matlab/Simulink. The SimMechanics toolbox in Simulink provides the components such as body, joints and actuators to build the physical model of the worm.

The model consists of 28 body segments which generate one whole undulating wave of the swimming worm, as presented in Figure 2.16. Figure 2.17 gives the structure of each segment. Each segment has two parts. One part is the body section with two parapodia attached, one on each side of the body section.

One way to generate a traveling wave along a series of segments is to have the joints rotate sinusoidally with a phase shift between each joint. Figure 2.11 gives the geometry of two segments. $\theta$ is the joint angle, defined as:

$$\theta = \theta_{\text{max}} \star (\sin(2\pi ft + n \star \omega) + 1) \quad (2.4)$$

where $\theta_{\text{max}}$ is the maximum rotation angle of joint, $f$ is the frequency of travelling wave, $n$ is the segments index, is the phase angle offset of each joint and $t$ is time.
The phase offset can be calculated using:

\[ \phi = \frac{2 \pi}{N} \]

where N is the number of segments. For this simulation N = 28.

The axis in Figure 2.18 is perpendicular to the worm body. The parapodia wave around the axis. \( \phi \) is the angle between the parapodia and the axis. In the case where the parapodia have no actuator, they do not move actively, then \( \phi \) is equal to zero.

Figure 2-16. Simulink blocks of 28 segments of an undulating body wave.
Figure 2-17. The structure of each block shown in Figure 2.9.

Figure 2-18. Geometry of two segments. The red lines are the middle lines of simulation model, including the worm’s undulating body and parapodia as indicated in the figure. The joint between two segments is shown in the figure. $\theta$ is the rotation angle of one segment. $\phi$ is the rotation angle when the parapodia wave actively, otherwise the $\phi$ is equal to zero.
2.3 Results

2.3.1 Kinematic analysis of freely swimming worm

2.3.1.1 Simulation results of kinematics based on the simulation model

To study the effect of actively rowing parapodia, this section presents the simulation results in both cases. One snapshot of an undulating worm model is presented in Figure 2-19. The red lines refer to the middle line of worm body and parapodia. The top panel shows the structure while the parapodia row actively. The bottom panel shows the structure when the parapodia do not row.

Figure 2-20 shows the angular velocity of the parapodia during one undulation period. The red line in the figure refers to the case in which parapodia do not row actively. The blue line refers to the case of parapodia which row actively. In the actively rowing case, the parapodia reach the highest angular velocity at 4 rad/s, which is two times bigger than the angular velocity when parapodia do not row.

Figure 2-21 gives the sweeping angle of parapodia during one period in both cases. The parapodia sweep 170 degrees when they row actively. The sweep angle is just 70 degrees in the case of parapodia which do not row actively.

The tip velocity of parapodia is given in Figure 2-22. The blue line refers to the case where parapodia row actively. The red profile shows the result when parapodia do not row actively. The parapodia have higher tip velocity in the actively rowing situation.

The area between two adjacent parapodia is shown in Figure 2-23. Again, the blue profile refers to the case of parapodia actively rowing, and the red profile refers to the other case. The area varies from 1.5 mm$^2$ to 4.5 mm$^2$ when parapodia actively row. But in the other case, the area ranges from 3.3mm$^2$ to 3.7mm$^2$. 
Figure 2-19. Body structure comparison. The middle lines of worm’s body and parapodia are indicated in the figure. Top: The parapodia wave themselves, in an active rowing motion. They have a function similar to legs. Bottom: The parapodia do not move actively. They are driven by worm’s undulatory body.
Figure 2-20. Angular velocity of a parapodium during one undulating period. The red line is the profile in the case where the parapodia do not move actively. The blue line shows the velocity profile when parapodia wave themselves. Note the larger velocity amplitude in the active case.

Figure 2-21. Sweep angle of a parapodium during one undulation period. The red line is the profile in the case where parapodia do not move actively. The blue line shows the angle profile when parapodia wave themselves. Note the higher swept angle in the active case.
Figure 2-22. The parapodium’s tip velocity during one undulation period. Red and blue lines refer respectively to the passive and active cases. Note the asymmetry in the motion in both cases, with a higher velocity amplitude during the first part of the period, followed by a much slower return stroke. Note that in the active case, the velocity is higher during the initial power stroke, but not different in the return part of the stroke.

Figure 2-23. Area between two adjacent parapodia during one undulating period. As in other figures, the red curve is the passive case, and blue the active one. Note the very different area change patterns in the two cases.
2.3.1.2 Absolute angle and angular velocity during the power stroke of a parapodium.

Figure 2-24 shows three different positions of a moving parapodium during its power stroke, including starting from recovery stroke, middle position and end (start of next recovery stroke). Yellow lines indicate the absolute angle of parapodium relative to the ground. Red lines are the midline of the parapodium. Black arrows show the direction of movement of the parapodium.

![Diagram showing parapodium positions during power stroke](image)

**Figure 2-24. Schematic drawing of the parapodium position at different times (beginning, middle and end) during its power stroke. Black arc arrows indicate the direction of motion of the parapodium. Yellow arc lines show the parapodium’s absolute angle relative to the ground. Red lines highlight the midline of the parapodium.**

Figure 2-25 presents the absolute angle of a parapodium as a function of time during its power stroke period. The sequence lasts about 110 ms. 11 frames with time delay of 11.4 ms were used for the analysis. The data shows that the parapodium moves through an arc of about 140 degrees over the whole power stroke, from 20 to 160 degrees relative to the horizontal. Figure 2-26 presents simulation prediction results of the parapodium angle relative to ground during one whole period including the power stroke and recovery stroke. The first half profile gives the angle prediction.
during the power stroke which has the similar profile as experimental results refers to Figure 2-25. The profile is harmonic.

**Figure 2-25.** Parapodium angle relative to ground during its power stroke. The sampling rate is 88Hz. The parapodium goes through 120 degrees. The first half data are below the diagonal and the second half are above it, which is due to the varying waving speed of the parapodium.

**Figure 2-26.** Simulation prediction of the parapodium angle relative to ground during one whole period including the power stroke and recovery stroke.
Figure 2-27 shows the angular velocity of the parapodium during its power stroke. The following observations can be made. During the stroke, the angular velocity is not constant. It moves from beginning (Figure 2-24A) to crest position (Figure 2-24B) with an acceleration seen in Figure 2-27 from 0 to 60 ms. From the middle position (Figure 2-24B) to end of the stroke (Figure 2-24C) the parapodium is decelerating, (Figure 2-27) from 60 ms to 110 ms. Figure 2-28 shows the simulation prediction of the parapodium’s angular velocity relative to ground during one whole period including the power stroke and recovery stroke. The first half is the power stroke period and the other half is the recovery stroke period. The profile of the angular velocity is sinusoidal.

![Parapodium angular velocity during power stroke](image)

Figure 2-27. The angular velocity of a parapodium during its power stroke.
2.3.1.3 An individual parapodium's absolute tip/base velocities during its power stroke.

Figure 2-36 gives the simulation prediction of a parapodium’s tip velocity in the X-direction the worm’s swimming direction during one period including power and recovery stokes. Positive value in the figure refers to the the point moves in opposite direction as the worm's swimming direction.

The results in Figure 2-30 show the absolute tip and base velocity (in both X and Y directions) of a parapodium during its power stroke. The maximum velocity in the x direction is approximately 70mm/s. The tip velocity in the X direction is not constant, but rather reaches its maximum near the middle of its power stroke which is at the crest of the body wave. Tip velocity in the Y-direction is positive at the first half of the stroke and negative at the second half due to the circling movement of the parapodium and undulation of the worm’s body. At the beginning and end of the
power stroke, tip velocity in the Y-direction reaches its maximum of about ±85 mm/s. When the parapodium is at the position of the crest of the body wave, the tip velocity in the Y-direction is almost zero while the velocity in X-direction reaches its highest value, which is caused by the undulation movement of the worm’s body, as shown in Figure 2-30A & B.

Panels C & D in Figure 2-30 show the absolute base velocity (X and Y direction) of a parapodium during its power stroke. The base velocity of the parapodium in the X direction is given in Figure 2-30C. Negative X values refer to the swimming direction of the worm. The worm was continuously moving forward. All of the values are negative, indicating that the wave is travelling tail to head. The base velocity in the Y direction is just half that of the tip, as shown in Figure 2-30D. The base point is on the worm body and so follows the undulation movement of the worm. But the tip has another source, namely the oscillation of the parapodium. Comparing Figure 2-30A and C, it is clear that the x-direction tip velocity is always larger than that of the base, which explains why the parapodium produces a thrust force during the whole power stroke period.

The velocities of the tip (Figure 2-30A & B) and base (Figure 2-30C & D) are completely different. This result proves that parapodium is actively moved during the power stroke and is not only driven by the undulation of the worm’s body.

Compare with the first half period of Figure 2-29(from 0 to T/2) of and the Figure 2-30A, they have the similar profile.
Figure 2-29 Simulation prediction of a parapodium’s tip velocity in the X-direction the worm’s swimming direction during one period including power and recovery stokes.
2.3.1.4 Area between two adjacent parapodia during the power strokes

The parapodia move relative to each other forcing water to enter and exit the space between them. The area between the parapodia provides a measure of the volume of this water movement. Figure 2-31 presents the period during which space between two parapodia is studied. Three time-steps are shown in the picture: beginning, middle and end. Figure 2-32 shows the prediction of the area between two parapodia over one period based on the simulation model. The first half (0 to $3\pi/5$) presents the open and close period which has similar profile as experimental result shown in Figure 2-33. Data shown in Figure 2-33 is the area between the parapodia at each time-step over a power stroke period. The time step interval is about 11.4ms. During
the whole power stroke, 11 video frames were used in the analysis. The sequence lasts about 110 ms. The area between two adjacent parapodia ranges from 1mm$^2$ to 4.5mm$^2$. Secondly, it reaches a maximum value (i.e. the two parapodia are maximally separated) around the middle of the power stroke period, which is when the parapodia are at the crest of the worm’s body wave. By the beginning of the recovery stroke, these two parapodia were immediately next to each other.

Figure 2-31. Schematic drawing shows the area in beginning, middle and end of a power stroke. The right hand parapodium moves through its arc first and then it is followed by the left hand one. In the end, the left hand parapodium will catch up with the right hand one. The area between the parapodia increases from the beginning A, and reaches the maximum in the middle B, then decreases until the end C.

Figure 2-32. The simulation prediction of the area between two adjacent parapodia
during one period including power stroke and recovery stroke.

Figure 2-33. Area between two adjacent parapodia during power stroke.

To investigate the rate of change of area, a central time differencing scheme was used to calculate the change of speed:

\[
d\frac{\text{Area}}{dt} = \frac{\text{Area}_{(t+1)} - \text{Area}_{(t-1)}}{2dt}
\]  

(2.4)

where \( \text{Area}_{(t+1)} \) and \( \text{Area}_{(t-1)} \) are the area at time steps (t+1) and (t-1). The time step (dt) is equal to the sampling period, which is 11.4 ms.

The prediction of the area changing rate is presented in Figure 2-34. The rate of change of area is shown in Figure 2-35. It is obvious from the figure that the rate of change is not constant during the power stroke. At the beginning of the stroke (Figure 2-31 A), the rate of change of area is high. It goes through a minimum when the parapodia are fully opened (Figure 2-31. B), then increases again until the end of the stroke (Figure 2-31. C). The results show that in the beginning of the power
stroke two parapodia open with an acceleration. During the middle the area is almost constant. In the last part, the gap between the two parapodia accelerates to a close.

Figure 2-34. Simulation of rate of change of area between two adjacent parapodia during one period including power and recovery strokes.
2.3.2 Wake of the freely swimming worms

Two continuous jet-like flow region bands with significant velocity in the wake of a swimming polychaete worm, *Nereis diversicolor*, were found by Hesselberg (2006). A typical DPIV result from his work is reproduced in Figure 2-36 A. The red area is the swimming worm which swims from the top to bottom in the figure. Two distinct jet-like flow patterns moving in a direction opposite to that of the worm can be found on either side of the worm. Figure 2-36B shows the jet width as a function of distance from the body of the worm, and Figure 2-36 C presents the mean fluid velocity of the jet region. No distinct increase or decrease was found, indicating that the jet-fluid is quite steady and uniform.

A closer view of the flow pattern of the wake of a freely swimming worm is shown
in Figure 2-37 and Figure 2-38, in which a steadily swimming worm is moving from right to left through the recording window (18mm by 18mm in size). The fluid pattern in the wake is shown in the time series pictures. The white outline in the figures highlights the same parapodium in different video frames. The aim of the study is to analyze the flow around a parapodium to determine how the jet is formed. The situation after the previous wave crest of the worm is shown in Figure 2-37A: there is an obvious continuous backward flow relative to the worm’s direction of travel. In this flow region the average fluid speed is 32mm/s in the horizontal direction. The next crest of the body wave, shown in the sequence of frames, will pick up this backward fluid flow and keep it continuously moving. During the power stroke, parapodia move backward relative to the body of the worm and push fluid ahead of themselves, toward the tail end of the worm.
Figure 2-36.  A. The wake of a swimming Nereis diversicolor. Two jet-like flow regions are found on either side of the polychaete worm. Note the oversized, boxy mask which has been applied to the worm, which prevents detailed analysis of the interactions between the parapodia and the flow. Colours indicate the magnitude of the flow speed and arrows show DPIV pints. The worm is shown in red and the black boxes around it show the extent of the mask required to conduct DPIV calculations. B. The width of the right hand jet as a function of distance along the jet. C. The average speed of the left hand jet. (Hesselberg 2006)
Figure 2-37 Fluid flow along a steadily swimming worm during the first half of the power stroke of a parapodium. The white highlighted outline shows the same parapodium in each time-step during its power stroke. Yellow vectors indicate the magnitude and direction of the fluid flow velocity. The timing of each step is indicated on each frame. Frame A shows the beginning of the stroke. It is clear that fluid is sucked into the opening area between the parapodium and the one following it from the left, see frame B. When the parapodium moves through, flow is accelerated, see C & D.
Figure 2-38 Fluid flow along the body of a steadily swimming worm during the second half of the power stroke of a parapodium. The white highlighted contour shows the same parapodium in each time-step during the stroke. Yellow vectors indicate the magnitude and direction of the fluid flow. The timing of each step is indicated on each frame. At the end of the power stroke, this parapodium moves toward the previous one (right one in the figure). Fluid between the parapodia is ejected. Frame H is nearly the end of the stroke.
There was a high shear rate in the region around the edge of the jet, see the red rectangle in Figure 2-39. The velocity gradients in the jet edge create a high shear flow. As shown in the figure, on the top of the shear region is the quiet water. Below the shear region, there is the jet fluid.

Figure 2-39 The velocity gradients in the edge of jet generated by the swimming worm show up with high shear rate. A high shear rate region is presented in the red rectangle. On top of the region, there is still water. And below the region, there is the jet.
2.3.3 PIV fluid velocity analysis

2.3.3.1 Mean fluid velocity of the jet region over a period

Figure 2-40 shows the mean fluid velocity and acceleration in the X and Y directions. The fluid is accelerated by the swimming worm starting from still. The mean velocity increased from 5mm/s to approximately 40 mm/s, Figure 2-40A. The speed did not increase constantly. From time 0s to 0.6s, fluid speed increased very quickly with large acceleration from 5mm/s to 35mm/s. After 0.6s until the worm swam out of the recording window, the velocity increased much more slowly between 35mm/s and 40mm/s which indicates that the flow became steady. After time 1.3s, the fluid was decelerated as the polychaete worm swam away from this recording area. The mean fluid velocity in Y direction is always negative, see Figure 2-40B, indicating that the flow was toward the worm. A flow jet was created by the swimming worm. Fluid flows toward the jet region, which was negative value of flow velocity in Y-coordinate. Figure 2-40C & D present the fluid acceleration in both the X and Y directions. The acceleration in both directions is wave-like, which corresponds to the undulatory of worm’s body.

Each peak show in Figure 2-41 B corresponds to an undulating wave of worm body. When one wave moved through the recording window, a peak of the mean flow velocity is achieved.
Figure 2-40 Flow velocity information of the white boxed region shown in Figure 2-41. The x-axis gives the time in seconds during the period the polychaete worm swam through the recording window and the y-axis gives the speed in each video frame with interval of 2.85 ms. A Mean flow velocity in X direction of the white boxed region. B Mean flow velocity in the Y direction of the white boxed region indicated in. C Acceleration of fluid in the X direction. B Acceleration of fluid in the Y direction.
2.3.3.2 Fluid analysis of an area following a cycling parapodium.

Figure 2-41 A: Description of the mean flow velocity. B: Mean flow velocity of white box indicated in frame A. Each peak shown in the figure corresponds to a body wave moving through the box.
the time in seconds during the power stroke which lasts about 120 ms. The highest fluid speed is approximately 98mm/s in the middle of the period. The position when the flow reached its maximum was the position where the parapodium was at the crest of the body wave. Mean flow velocity in the Y direction is given in Figure 2.42B. Mean flow velocity in the Y direction is negative (toward the worm) in the first half period (before time 0.7s) and positive (away from the worm) in the last half. During the middle point of power stroke period, when the parapodium is almost perpendicular to the worm body, the fluid only has X-component velocity. The Y-direction is zero. The data indicates that the fluid moves backward parallel relative to the worm’s swimming direction.
Figure 2-42. A gives flow velocity in the X direction in the moving white box of Figure 2-41. The x-axis gives the time in seconds during the power stroke and the y-axis gives the velocity in each video frame of the target area with an interval of 2.85 ms. Velocities are calculated with reference to the origin of the moving box. B Mean flow velocity in the Y direction in the white box of Figure 2-41. The x-axis gives the time in seconds during the power stroke and the y-axis gives the velocity in each video frame of the target area with an interval of 2.85 ms.
2.3.3.3 Compare the parapodium’s tip speed with flow velocity following the wave parapodium.

To study the relationship between the movement of the parapodium during its power stroke and the velocity of the surrounding fluid, the tip velocity of a parapodium and velocity of a region following the parapodium were processed. In Figure 2-43, the green line shows the mean flow velocity in a region which moved with the tip of a cycling parapodium, and the red line shows the tip velocity of the parapodium. Figure 2-43A gives the velocities in the X-direction. Their values are quite comparable, though the fluid velocity is larger than the parapodia’s tip velocity. This is because, due to the continuity of the fluid, the fluid velocity was not zero at the beginning of the parapodium’s power stroke. It was accelerated by the cycling parapodium. The fluid reached its highest velocity with a time lag compared with the parapodium’s tip speed. Figure 2-43B gives the velocities in the Y direction. The tip velocity is much higher than the fluid velocity in the Y direction, but the trend of these two is the same.
Figure 2-43. A. Comparison of the flow and parapodium tip velocity. The x-axis gives the time in seconds during the power stroke and the y-axis gives the mean fluid velocity and parapodium tip velocity in each video frame of the target area with an interval of 2.85 ms. The green line is mean flow velocity in the X direction. The red line is the parapodium tip velocity in the X direction. B. Comparison of the flow and parapodium’s tip velocity. The x-axis gives the time in seconds and the y-axis gives the mean fluid velocity and parapodium’s tip velocity in each video frame of the target area with an interval of 2.85 ms. The green line is mean flow velocity in the Y direction. The red line parapodium's tip velocity in the Y direction.
2.3.3.4 Mean velocity profile perpendicular to direction of travel

Figure 2-44 Right frame gives the mean velocity of the fluid in the X direction of each row with standard deviation during a stroke period. The average fluid velocity of each row is calculated for every PIV frame. PIVMAT toolbox was used to read Davis file into Matlab. The second step is temporal averaging. The average fluid velocity over a stroke period of each row is calculated with its standard deviation. The Matlab script used to do these calculations is presented in Appendix 4. The fluid has a high velocity near the worm’s body with a maximum of approximately 70 mm/s, and decreases with distance away from the body. The peak value is around the tip the parapodia, where the fluid velocity is faster than in other areas. From this point toward the worm’s body, fluid velocity is slower due to the drag from the body.

Figure 2-44. Left frame is a DPIV result of two subsequent video frames of a swimming polychaete worm. Right frame is the mean velocity in the X direction for each row of vectors. The x-axis gives the mean velocity of each row in mm/s with standard deviation and the y-axis gives the distance from worm body in mm.
2.4 Discussion and Summary

In this chapter I have described the kinematics and near-field fluid dynamics around the parapodia of freely swimming worms. Evidence is presented for a novel method of continuous jet-like propulsion in the errant polychaete Nereis diversicolor. All known instances of jet propulsion by aquatic animals involve a cycle with a propulsive phase ejecting water from a body cavity and a recovery phase where water slowly refills the cavity. This is periodic jet propulsion (Weihs 1977). This form of propulsion is found in jellyfish (Colin and Costello 2002; McHenry and Jed 2003), scallops (Cheng and DeMont 1996) and squids (Bartol et al 2001). Polychaete worms swim in a unique way using body undulation coupled with parapodia beating. This generates two distinct flow jet-like bands on either side of the worm’s body (Hesselberg 2006).

Clark (1976) suggested that water is sucked into the space between two adjacent parapodia when they start to open on the leading edge of the body wave and ejected out when they close at the back of the wave for the swimming in the Heteronereis life stage of Nereis. Heteronereis is a reproductive stage of the nereids. The Heteronereis swims much more actively than the nereids and can reach speeds of up to 5BL(Body length)/s, 10 times faster than the adult Nereis diversicolor (Hesselberg 2006). The interaction between parapodia might be a reason for this distinct swimming speed difference between different species of polychaetes as Clark assumed.

The kinematics results show that the parapodium moves in a direction opposite to that of the worm during its power stroke, when the parapodium is at the crest of the body wave exposed to the fluid. This shows that the worm experiences thrust during the power stroke. The parapodium reaches its maximum speed around the middle of the power stroke, position 3 at the crest of the body wave. Parapodia swept through an angle of about 140 degrees with a maximum angular velocity of 5 r/s. The absolute tip velocity relative to the ground can reach up to 70 mm/s at the middle of
the power stroke. The area between two parapodia varied during the power stroke, which gives the possibility of the suck and eject effect between inter-parapodia.

But unfortunately, in this study the clear suck and eject flow pattern between the inter-parapodia was not observed from the DPIV results. But the suck and eject flow was found in the pumping worm, which will be presented in Chapter 3.

It also might show that the parapodia do not mainly drag along individual masses of water as added mass, but that their main function literally is that they are oars that principally work as rotating flat plates that due to their high resistance perpendicular to the plate accelerate the water that they ‘bump into’ and thereby contribute to the velocity in the lateral jets. The parapodia act like a conveyor belt from a succession of appendages.

The undulatory movement of the worm’s body plays three main roles in the swimming mechanism. First, it drives the movement of the parapodia. The beat frequency of parapodia is increased by the undulation of the worm’s body. Second, parapodia touch each other during their recovery stroke due to the bending of the worm’s body. There is almost no space between parapodia, so they are not exposed to the fluid which means much less drag. The swimming efficiency is increased dramatically by this mechanism.

DPIV experiments have been performed by Hesselberg (2006) on polychaete worms. His work focused mainly on the large scale view of the worms. Two distinct jets in the wake of swimming worms were found. No significant widening and velocity decrease were found in the fluid jets. However, he did not study the flow around parapodia at the micro scale. The DPIV measurements around individual parapodia which are presented here are the first such measurements, and show that the jet is generated by the beating of parapodium and interaction between parapodia.

The DPIV measurements were two-dimensional, and no attempt was made to
quantify the fluid flow in the third dimension. It is possible that the flow into the third dimension may have been quite significant. Further work with a detailed three-dimensional DPIV system will be required to know for sure. However, the change in area between the parapodia was significant, and so fluid must have been sucked in and driven out. The existence of the twin jet-like wakes indicates that a significant proportion of the flow is directed caudally.

Fluorescent polymer particles were used to seed the water when during DPIV experiments. It is possible that the worms’ swimming locomotion could have been affected by the particles. However, in the experiments carried out here, the worms swam in water with particles and without, and no clear differences were observed in the behaviour of worms.
Chapter 3
Hydrodynamics of pumping polychaete worms, *Nereis diversicolor*
3. Hydrodynamics of pumping polychaete worms, *Nereis diversicolor*

3.1 Introduction

*Biomimetics*

The term Biomimetics was coined by Otto H. Schmitt (1969), where *bio* means life or biology and *mimetics* means imitate. The basic concept of the science is learning from nature. Several authors have defined the term (Franz 2000; Bar-Cohen 2003; Vincent 2006). A clear definition is given by Gleich (2009):

“*Biomimetics is the attempt to learn from nature; it deals with development of innovations on the basis of investigation of natural, evolutionarily optimized biological structures, functions, processes, and systems.*”

Life has existed on Earth for more than 3.8 billion years as evidenced by geological studies (Lowman 2002). After billions of years of evolution, nature has created enormously effective solutions. We can learn from them and apply them into engineering applications.

Biomimetics plays a very important role in robotics. People have tried to emulate organisms or even human beings since ancient Egypt and Greece (Cassell 2001). Holland (2003) states that the first biological inspired robots were designed and created by W. Grey Walter in 1949, Figure 3-2. The robots were called electromechanical tortoises.
Pumping mechanisms in Nature

There are a lot of pumping mechanisms in nature, such as suspension pumping, filter pumping, burrow pumping and pumping function achieved by locomotion of animals. Suspension feeding or filter feeding is a very common feeding method adopted by invertebrate organisms. There is a lot of literature on this research topic. Most suspension feeding is achieved by cooperative movements of an array of cilia (Jørgensen 1982). Hartmann et al (2007) presented the fluid patterns of the feeding mechanism of sessile protozoan *Opercularia asymmetrica*. Protozoans feed by beating cilia to generate a flow which transports particles to the oral cavity of the organism, as illustrated in Figure 3-2. The suspension feeding mechanism of mussel gill was studied by Jørgensen (1982). He found the beating cilia produced oscillatory currents which played an important role in the suspension feeding mechanism.

*Figure 3-1 Biomimetic tortoise built by Grey Walter (Michael Gasperi web source).*
Figure 3-2 PIV result of the velocity vector of the fluid generated by cilia after (Hartmann et al 2007). Fluid moves toward the protozoan.

**Burrow pumping**

Brown (1977) described the pumping mechanism of *Chaetopterus variopedatus* in a tube. *Chaetopterus* pumps water using a 3-piston pump mechanism (Figure 3-3). Figure 3-3 A shows the position of a worm in its tube. This mechanism achieved a continuous flow from left to right in the figure. During a segmental piston’s power stroke, it seals the tube and pushes fluid. The three pistons have a phase difference of 1/3. They move metachronally to generate a net flow in the tube.
Figure 3-3 A Chaetopterus pumps water in its tube, after (Brown 1977). B is the tip position of segmental piston during six consecutive strokes. C-H gives the pumping sequence by three segmental pistons. Black indicates recovery stroke segments. White indicates power strokes. This mechanism achieved a continuous flow from left to right in the figure. During a segmental piston’s power stroke, it seals the tube and pushes fluid. The three pistons have a phase difference of 1/3. They move in sequence to generate a net flow in the tube.
Stamhuis and Videler (1998) carried out DPIV experiments on the pumping mechanism of the tube-dwelling shrimp, *Callianassa subterranea*. They placed the shrimp inside an artificial transparent burrow. Laminar and steady flow was found inside the tube shown in the DPIV results, with a mean velocity of approximately 2 mm/s. The flow was accelerated by pleopods during their power stroke and was decelerated very little because of the reducing pleopods’ size during recovery stroke. A flow jet at the velocity of 18 mm/s was found under telson (tail of the shrimp) just behind the shrimp. Figure 3-4 shows a DPIV image of the flow behind a pumping shrimp, *Callianassa subterranea*, in an artificial burrow.

*Figure 3-4 Flow velocity vector diagram of a pumping shrimp, Callianassa subterranea (Stamhuis and Videler 1998a). The grey area is the shrimp body. It is placed in a tube whose upper and lower boundaries are shown in black. The higher fluid velocity (indicated in green, red and yellow) found on the lower part of the tube is caused by the movement of pleopods during their power stroke.*
The water-pumping mechanism of the amphipod, *Corophium volutator*, in its burrow was studied by Riisgård (2007). The three pleopods of the amphipod beat in a metachronal pattern to pump the fluid. At the beginning of power stroke, the burrow is sealed by the pleopod tip touching the wall to prevent any backward flow caused by the recovery stroke of the other two pleopods. During the power stroke, the pleopod beats through an angle of 60° with a mean tip velocity of 16.8 mm/s to push fluid forward. In the end, fluid ventilation is achieved.

The burrow feeding of lugworm *Arenicola marina* was described by Retraubun (1996). The lugworms have U shape burrows. The feeding is achieved by the headshafts of the burrows which are distinguished from the tailshafts by mounds of faecal casts and cone-shaped depressions forming funnels in the surface sediment. Riisgård and Larsen (2005) reviewed the burrowing pumping systems of zoobenthos focusing mainly on the water pumping and the fluid dynamics of flow generated by burrowing zoobenthos, aiming to study the type of pump and mechanisms involved, flow rate, pumping power and pumping pressure.

Objectives of this research

Part of this project is funded by the European project ARTIC whose objective is to develop a micro-pumping system inspired by cilia. By the asymmetric movements of cilia in their power stroke and recovery stroke, organisms can swim or fluid can be pumped (Barlow et al 1993). Polychaete worms can achieve similar results by oscillating parapodia in conjunction with undulation of their body. The objective of this chapter is to explore the pumping mechanism by polychaete worms.

The burrow pumping of the polychaete worms has been reported by researchers in the past. Harley (1950) showed the pumping mechanism of Nereids, *Nereis diversicolor*, for the first time. He described the filter-feeding of worms by
undulation of their bodies in a tube. Riisgard (1991) analyzed the pump mechanism quantitatively by measuring the pumping rate. Riisgard et al. (1992) used an infrared photo transducer device to analyze the pumping activity and found the high stroke frequency of worms was correlated with high pumping rate. They do not however discuss the mechanics or hydrodynamics of the worms’ pumping.

In chapter 2, I discussed the fluid dynamics of the freely swimming polychaete worms. Two distinct jet-like flow regions are found in the wake of the worms. We can consider this phenomenon in other way. If worms were tethered and moved in a similar locomotor pattern as they do when swimming, then the fluid should be pumped by the worms. The investigation of this phenomenon in this chapter will lead into the biomimetic applications in the next.
3.2 Material and methods

3.2.1 Experimental setup

The technique used in this chapter was the same as the 2-dimensional DPIV system described in Chapter 2. Worms were housed in artificial sea water (salinity of 30ppt). The water was maintained at a temperature of 10 °C. Worms were fed fish flakes twice weekly. Experiments were carried out in a room maintained at a temperature of 15 °C. Worms were introduced to the room one hour before the experiments.

Figure 3-5 The method of immobilising Nereis diversicolor. The top part of the figure is a schematic drawing of how the body of the worm was held. The green area is the video recording window. The insert shows the device used to tether the worm. The tail of the worm was clamped in the gap highlighted in the red circle. The dimension of the gap is just smaller than the worm’s body and so held the worm by slightly compressing its body near the tail.
To record the flow pattern around *N. diversicolor*, individual worms were placed in an aquarium (length 50cm, width 25cm, depth 10cm) filled with artificial sea water. The worm was carefully clamped by gripping its tail using the device shown in Figure 3-5. On the right-hand end of the device, a semicircular gap was made. The dimension of the gap was just smaller than the height of the worm’s tail, and held the worm by compressing its body slightly. They moved in a slow swimming gait, using a small amplitude body wave and slower wave speed than in the fast swimming locomotion discussed in Chapter 2. Worms can undulate their body naturally generating a wave from tail to head. The body wave first occurs at the anterior end of the worm (Gray 1939). Gray’s study suggested that if worms’ anterior end was clamped, they could not generate a body wave. I also tried to clamp their anterior end, but they failed to move as normal. In fast crawling (or slow swimming) gait, the worm body undulates with limited wave amplitude.

Figure 3-6 describes the steps followed in the analysis of the DPIV data. Fluid velocity fields in the wakes of the worms were calculated from consecutive video frames (image resolution: 1024 x 1024 pixels) using Davis 7.4. The recording frame rate was 351Hz. A sequential cross-correlation method was used with a first interrogation window size of 32 x32 pixels followed by two passes at 16 x 16 pixels (overlap of 50%). Vector post-processing was evaluated, which removed and replaced vectors bigger than 3 times RMS of their neighbours. Approximately 4096 vectors were created in a 3.24cm\(^2\) plane.
Figure 3-6. Calculation of flow velocities using two sequential high speed video images. Fluorescent particles were used, as seen in images in the top left panel. Masks were applied to remove the worm’s body from the analysis window. Finally, the fluid velocities were calculated by cross-correlation of the two images.

3.2.2 Data analysis methods

In the first part, the kinematics of the pumping worm was analysed with MATLAB (Version R2007b, The Mathworks Inc.) routine to generate information on inter area between two adjacent parapodia, waving angle / angular velocity and parapodia
velocity.

**Inter area between adjacent parapodia analysis method**

The same method is used as presented in Chapter 2, section 2.2.2. The area is approximated as a polygon consisting of four points A, B, C and D. Custom-written Matlab routines were developed to calculate the area semi-automatically, including choose four points by hand and calculation area automatics. The routine is presented in Appendix 5.

**Angle and angular velocity of the parapodium**

The parapodium beating angle and its angular velocity during its power stroke were calculated using the method described in Chapter 2, section 2.2.2. Firstly the midline of the parapodium is calculated from three points selected by eye. Then the angle of the line relative to the worm’s direction of motion is calculated. The Matlab routine used is presented in the Appendix 5. The angular velocity of the parapodium during a power stroke was calculated using the central time differencing scheme generating from the parapodia angle at each time frame.

**Velocity analysis of the parapodium**

The same calculation method is used as discussed in Chapter 2, Section 2.2.2. When the coordinates of the tip and base points of parapodium were choosed, then the velocity of the tip and base of a parapodium were calculated automatically. Secondly, the PIV data was analysed also by a MATLAB routine, incluing mean fluid velocity of jet region, fluid velocity around a cycling parapodium, and mean velocity profile perpendicular to swimming direction.

**Mean fluid velocity of jet region**

The mean fluid velocity in the jet region is calculated by averaging the PIV vector in the analysing area. The same method is presented in Chapter 2, section 2.2.2.
Jet width calculation method

The jet width refers to the size of the jet as presented in Figure 3-7. The width is counted from tip point of parapodium to the row with mean velocity less than a threshold value. The threshold value is defined as the one percent of the highest fluid velocity.

Figure 3-7. Fluid jet width, distance between the two red lines. Fluid moving in the X direction is considered as having been pumped.

Mean velocity profile perpendicular to swimming direction

The average fluid velocity of each row is calculated for every PIV frame. The second step is temporal averaging. The average fluid velocity over a stroke period of each row is calculated with its standard deviation. The same method is presented in Chapter2 section 2.2.2.

Fluid dynamics around a cycling parapodium

To investigate the flow pattern around a waving parapodium, a region was chosen around it, as shown in Figure 3-8. The region is moving with the tip of the parapodium. The area of the regions is approximately 5mm by 5 mm.
A region was chosen around the tip of a waving parapodium which moves with the parapodium. The coordinates of parapodium’s tip were picked by hand for each frame. Then based on the coordinates, the white square can be defined. The mean fluid velocity is calculated by averaging every vector velocity inside the white square in both X and Y directions.

![Region drawing]

*Figure 3-8. Schematic drawing of a region of interest around a beating parapodium. The region moves with the parapodium. t1 and t2 indicate two time frame during the stroke.*

**Mass flux calculating method**

Basically, there were two ways used to calculate the fluid mass. Firstly, the mass was calculated based on the geometry of inter-parapodia space. The result is shown in Fig 3-29B. Secondly, the mass was calculated based on the PIV results. The boundary fluid velocity was gained from the PIV fluid velocity vectors. Then according to the equation 3.2, the mass flux can be calculated.

Interaction of two adjacent parapodia plays a very important part in the pumping mechanism. The changing of the fluid mass contained between two adjacent parapodia is estimated by two methods. The first method is based on the geometry changing. The second one is calculated by the bound fluid velocity, see Figure 3-9. More details of calculation method can be found in Appendix 10.
Figure 3-9 Left schematic drawing shows how fluid is sucked in as the area between two parapodia increases. Right schematic drawing shows how fluid is ejected as the area between two parapodia decreases.

Another way to estimate the mass is based on the fluid velocity on the boundary of a volume. The boundary fluid velocity of two parapodia is known, so the mass of fluid flow through (in and out) the boundary (See Figure 3-9) can be calculated as follows:

$$ \text{mass} = V_{\text{boundary}} \cdot t \cdot L_{\text{parapodium}} \cdot \rho $$  \hspace{1cm} (3.1)

where mass is the mass of the fluid, $V_{\text{boundary}}$ is the mean velocity of the fluid at the boundary calculated from the 2-dimensional DPIV data, $t$ is time, $L_{\text{parapodium}}$ is the length of the parapodium, and $\rho$ is the density of the fluid.

3.2.3 Simulation modeling for kinematic study of pumping polychaete worm

The same simulation model is used as presented in Chapter 2, section 2.2.3. Based on equation 2.4, the amplitude of the traveling wave along the worm’s body can be adjusted by varying the $\Theta_{\text{max}}$. The pumping worm has smaller waving amplitude. $\Theta_{\text{max}}$ is seted to 4 degree in this case. Based on the experimental film, one body wave has 12 segments, so $N=12$ for pumping simulation.
3.2.3 Simulation modeling for kinematic study of pumping polychaete worm

The same simulation model is used as presented in Chapter 2, section 2.2.3. Based on equation 2.4, the amplitude of the traveling wave along the worm’s body can be adjusted by varying the $\theta_{max}$. The pumping worm has smaller waving amplitude. $\theta_{max}$ is set to 4 degree in this case. Based on the experimental film, one body wave has 12 segments, so $N=12$ for pumping simulation.

3.3 Results

3.3.1 Kinematics analysis of the pumping worm

3.3.1.1 Simulation results of kinematics based on the simulation model

Compared with the kinematics of freely swimming locomotion, the tethered worm uses a smaller body undulatory amplitude, and a shorter wave length. Twelve body segments and 24 parapodia are involved in one body wave for this simulation.

Figure 3-10 shows the body structures of pumping simulation worm model. The red lines refer to the middle line of worm body and parapodia. Top frame of the figure gives the body structure when parapodia actively row. The bottom one gives the structure when parapodia do not move by themselves. The dramatic difference can be found between the two cases. The top frame matches video recording from experiments. Parapodia row clock-wise during power stroke along with the undulating of worm’s body. When a parapodium reaches its end position, it starts to swing back slowly. During the recovery stroke, due to the bending of the worm’s body, the parapodia contact each other and have nearly no influence on the surrounding fluid.

Figure 3-11 and Figure 3-12 present a parapodium’s angular velocity and sweeping
angle. The tip velocity of parapodia is given in Figure 3-13. And Figure 3-14 shows the area between two adjacent parapodia. All of the results are shown in both cases. The red profile refers to the situation without active parapodia movement. The blue profile refers to the case in which the parapodia actively row. Compared with the swimming case, active parapodia have much important effect. The active parapodia case has almost 4 times angular velocity than the other one.

![Diagram of parapodia waving actively and not waving](image)

**Figure 3-10** Simulation of body structure comparison of pumping worm. Top: The parapodia wave themselves. They have the similar function as legs. Bottom: The parapodia do not move actively. They are driven by worm’s undulatory body.
Figure 3-11  Angular velocity of a parapodium during one undulating period. Red line is the profile in the case of parapodia do not move actively. Blue line shows the velocity profile when parapodia wave themselves. As in the free-swimming case, the difference between active and passive is obvious.

Figure 3-12  Sweep angle a parapodium during one undulating period. Red line is the profile in the case of parapodia do not move actively. Blue line shows the angle profile when parapodia wave themselves.
Figure 3-13 The parapodium’s tip velocity during one undulating period. Red line is the profile in the case of parapodia do not move actively. Blue line shows the angle profile when parapodia wave themselves.

Figure 3-14 Area between two adjacent parapodia during one undulating period. Red line is the profile in the case of parapodia do not move actively. Blue line shows the angle profile when parapodia wave themselves.
### 3.3.1.2 Area between two adjacent parapodia

Interaction between two adjacent parapodia plays an important role in the pumping mechanism of worms. Figure 3-15 presents the prediction of area between two parapodia based on the simulation model. The result gives the area profile during one period. The profile is harmonic which includes opening and closing of the inter-parapodia structure. Figure 3-16 shows the interparapodial area changing over a so-called 'suck and eject' period. The whole sequence lasts about 400ms, including the separating and closing of the two parapodia. 36 frames with time delay of 11.4ms were analyzed for this result. The maximum area is 10.2 mm$^2$, when the two parapodia are fully separated. The maximum area is achieved when the parapodia move to the crest of worm’s body wave.

To investigate the rate of change of the interparapodial area, a central time differencing scheme was used to calculate the area changing rate. The time step is equal to the sampling period which is 11.4ms. Figure 3-17 gives the area changing rate during the suck and eject period.

In the beginning of the suction phase, the area changes very quickly, increasing from 2 mm$^2$ to 9 mm$^2$ during the period from 0ms to 110ms (Figure 3-16), at a changing rate of 20 mm$^2$/s to 60 mm$^2$/s (Figure 3-17). In the middle part, from time 110 ms to 230 ms, the area does not change appreciably, remaining in the range of 9 mm$^2$ to 10 mm$^2$ (Figure 3-16). The rate of change during this period is also small, no more than 10 mm$^2$/s. During the ejecting period, the area decreases again at a high rate of change. It decreases from 9 mm$^2$ to 2 mm$^2$ in about 120ms (Figure 3-16). The rate of change ranges from 10 mm$^2$/s to 60 mm$^2$/s (Figure 3-17).
Figure 3-15. The simulation prediction of the area between two adjacent parapodia during one period including power stroke and recovery stroke.

Figure 3-16. Area between two adjacent parapodia of each frame during a full 'suck and eject' motion.
3.3.1.3 Parapodium angle and angular velocity

Figure 3-18 presents simulation prediction results of the parapodium angle relative to ground during one whole period including the power stroke and recovery stroke. The parapodia sweep about 80 degrees in both power and recovery strokes. Figure 3-19 shows the parapodium angle during its power stroke period. The sequence lasts approximately 290ms, 25 frames with time delay of 11.4ms were analyzed and it was found that for one power stroke the parapodium beats through approximately 70 degrees, from 65 degrees to 135 degrees. Figure 3-20 gives the swept angle of five parapodia during their power strokes. The error-bar gives their standard deviation of four strokes of each parapodium.

Figure 3-20 gives the prediction of the parapodium’s angular velocity during one period including power and recovery stokes. The angular velocity of the circling parapodium is shown in Figure 3-21. From the results, the following conclusions
can be made. Firstly, the angular velocity is not constant. Secondly, the parapodium reaches its maximum velocity near the middle of its power stroke.

Figure 3-18. Simulation prediction of the parapodium angle relative to ground during one whole period including the power stroke and recovery stroke.
Figure 3-19. Parapodium angle relative to ground during its power stroke. The X-axis is the time in ms and the Y-axis is parapodium angle relative to ground in degrees.

Figure 3-20 Swept angle of five individual parapodia during their power stroke. The
data collected for each parapodium is the average of four successive power strokes. The variation is shown on top of each bar.

Figure 3-20. Simulation prediction of the parapodium angle relative to ground during one whole period including the power stroke and recovery stroke.
Figure 3-21. Parapodium’s angular velocity during its power stroke. The X-axis is the time in ms and the Y-axis is parapodium’s angular velocity relative to ground in rad/s. It reaches highest angular velocity around the middle of the power stroke.

3.3.1.4 Parapodium tip velocity during its power stroke

Figure 3-22 gives the simulation prediction of a parapodium’s tip velocity in the X-direction during one period including power and recovery stokes. Positive value in the figure refers to the the tip point moves in opposite direction as the worm’s moving direction. The profile is harmonic. Figure 3-23 shows the tip velocity of a parapodium during its power stroke. The maximum velocity of the tip in the X-direction is 39mm/s and occurs at the middle of the power stroke period. The velocity profile is the same as the freely swimming case, but the parapodia of pumping worms have much slower cycling velocity. The pumping worm’s
parapodia tip velocity is just approximately half of the swimming worms, which is 70mm/s.

Figure 3-22. *Simulation prediction of a parapodium’s tip velocity in the X-direction the worm’s swimming direction during one period including power and recovery stokes.*
Figure 3-23. Parapodium tip velocity relative to ground during a power stroke.

3.3.2 Fluid flow pattern generated by a pumping worm

Typical velocity vector maps of flow around a pumping polychaete worm are shown in Figure 3-24 (overview of the flow pattern) and Figure 3-25 (close-up view around parapodia). Figure 3-26 presents a schematic drawing of the fluid pattern of two adjacent parapodia during the pumping sequence.

Fluid is pumped backward continuously relative to the worm’s body by the cooperative movement of parapodia. The panels in Figure 3-24 are four frames during a parapodium’s power stroke. Figure 3-24 T1 is the snapshot of the moment the indicated parapodium begins to separate from the adjacent one. Figure 3-24 T4 is a snapshot of the two parapodia once they are fully separated. The worm swam from right to left. The fluid flow pattern is indicated by the vector map. Alongside the worm, a continuous flow is generated.

A pair of adjacent parapodia is the basic unit in this pumping mechanism. Fluid is
accelerated by beating parapodia during power stroke. Figure 3-25 presents sequential frames of two beating parapodia. When a parapodium beats, fluid around it is dragged by its trailing edge and pushed by the leading edge, see Figure 3-25 T2, T3, T6 and T7.

Figure 3-25 T4 and T8 clearly show the fluid is squeezed out between two closing parapodia. The fluid velocity is much higher than the surroundings. The red vectors indicate higher fluid velocity. The first stage (Figure 3-25 T1-T4 and Figure 3-26 T1-T4) lasts about 170 ms is the suction period during which the available space between a parapodium and the one following it is increasing. During this period liquid is sucked into this space. When the following parapodium starts to beat, the ejection period starts (Figure 3-25 T5-T8 and Figure 3-26 T5-T8). The liquid which was sucked into the interparapodial space is now squeezed out. Thus the liquid is projected posteriorly.

The undulation of the worm body increases the efficiency of this pumping mechanism. During the recovery stroke, due to the undulation of the body, the parapodia are pulled away from the main stream flow region and contact each other. At this point in the cycle the parapodia have no effect on the liquid. There is almost no back flow during the recovery stroke (DPIV data see Figure 3-27).

A benefit of this so called 'suck and eject' mechanism is that fluid can be delivered efficiently and continuously in one direction. The maximum speed of the liquid in the power stroke is about 20 mm/s. During the recovery stroke the minimum speed of the liquid is still about 15 mm/s.
Figure 3-24. (last two pages) Flow pattern from PIV velocity vector plot of a pumping polychaete worm. Vectors give the fluid velocity information. The images are four snapshots taken during a cycling parapodium’s power stroke.

Figure 3-25 (next page). Close-up view around two cycling parapodia during their power stroke. Vectors show the fluid velocity information. The eight images are snapshots of the whole suck and eject sequence which lasts approximately 400ms. The images clearly present the sequence of how the fluid is moved by the circling movement of the parapodium and the undulating movement of the worm’s body.
Figure 3.26. Schematic reconstruction of pumping sequence. T1-T4 is the suction period. T5-T8 shows the ejecting. Black arrows give the moving direction of parapodium. Blue arrows show the fluid pattern. The thicker blue arrows indicate higher fluid velocity. T1 shows the start of the parapodium 1 (p1). There is no space between two parapodia (p1 and p2). T2-T3 show that the fluid is sucked in the space between p1 and p2 due to the movement of p1. T4 presents the ending point of power
stroke of p1, the space between two parapodia reaches maximum. T5 gives the starting point of p2’s power stroke. T6-T7 show that the p2 moved toward p1 and the space between two parapodia is closing together. The fluid in the space is ejected out.

Figure 3-27 Flow pattern around parapodia during the recovery stroke. There is almost no backflow found during the recovery stroke. The fluid velocity is decreased around the recovering parapodium, but the change is small. The white contour indicates the same parapodium in each frame.
3.3.3 Pump mechanism analysis

3.3.3.1 Mean velocity over a body wave period.

To analyze the fluid flow velocity changing over time, the mean flow velocity of the region (the red rectangle in Figure 3-28) along the pumping worm was calculated. The calculation method is given in Appendix 6. Mean fluid velocity over a worm body wave period is shown in Figure 3-30. The figure shows the mean flow velocity during a parapodium stroke period. A parapodium stroke includes two parts, power and recovery stroke. As mentioned before, a power stroke lasts 0.27 seconds and recovery period is 2 seconds. The whole period is approximately 2.3 seconds. During this period, the flow velocity ranges from 7 mm/s to 9 mm/s. The mean value over the period is 7.9 mm/s, the red line in Figure 3-31.

The amount of liquid pumped can be estimated from the two dimensional DPIV data giving about 0.35 grams per wave period (duration about 2s). Figure 3-29 shows the quantity of water pumped over a four cycle period. Equation 3.2 was used to estimate the mass of the liquid pumped by the worm. The flow was assumed to be two-dimensional, and the height of the fluid jet region is equal to the height of the parapodia ($h_{\text{parapodium}}$). $V_{\text{mean}}$ is the mean fluid velocity during one body wave period, $T$. $\rho$ is the density of sea water. $L_{\text{jet}}$ is the width of jet region.

\[
m = V_{\text{mean}} \cdot T \cdot L_{\text{jet}} \cdot h_{\text{parapodium}} \cdot \rho \quad (3.2)
\]
Figure 3-28. Schematic drawing showing the region (red square) in which the fluid mean flow velocity is calculated over a whole parapodium stroke period or body wave period.

Figure 3-30. Results show the mean flow velocity, the red line is the mean value during the whole period. T indicates the period and T=2.3s. One whole period includes power stroke and recovery stroke of a parapodium.
Figure 3-31 Mean fluid velocity during a period of 10 seconds.

Figure 3-29. Pumped fluid during each full stroke period (including power stroke and recovery stroke) of parapodia.
3.3.3.2 Pumping fluid jet width

The jet-like fluid width generated by the pumping polychaete worms is calculated. The width of the jet is an indication of the influence on the fluid by pumping worms. The two red lines in Figure 3-33 present the boundary of the fluid jet. A total of 3600 recording frames which lasted about 10 seconds were analyzed. During this period, each parapodium beats four cycles (including power stroke and recovery stroke). Twelve parapodia were involved in one worm body wave length. The width of jet-like fluid region ranged from 6mm to 10mm, see Figure 3-30. The histogram shows that data is mainly in the region from 8 mm to 9 mm, which includes more than 70% of the frames.

![Fluid jet width profile](image)

**Figure 3-30.** Histogram of the distribution of the fluid jet width. The fluid jet was calculated from 3600 frames recording over an approximately ten second period. The histogram shows the jet width mainly in the range of 8mm to 9mm. The result shows that the width of fluid jet region is very constant.
3.3.3.3 Flow velocity analysis

Figure 3-34 presents the mean fluid velocity of each row with its standard deviation in the yellow box as a function of distance to the body of pumping worm. The data is calculated from one DPIV frame. The maximum velocity is 17.0±1.5 _mm/s (mean±S.D., n=64), which is achieved at row 13, about 4mm away from the worm’s body. According to the flow velocity profile, see picture below, flow velocity is 8mm/s at Row 0, then it increases to 15.5mm/s at Row 8 and then it decreases again. The highest flow velocity is achieved at approximately 2.5mm away from the worm. At row 4 the fluid velocity is zero which is 12 mm away from worm body. Figure 3-34 right frame gives the mean fluid velocity of each row averaging from 3600 DPIV frames.

![Flow velocity analysis](image)

*Figure 3-31. Mean fluid velocity of each row in the yellow rectangle (left frame) is calculated. Right frame gives mean flow velocity of each row averaging of 3600 DPIV frames as a function of distance with respect of the pumping worm.*
3.3.3.4 Velocities around a cycling parapodium

The fluid velocities in the X and Y directions in the region are shown in Figure 3-32. X and Y direction are indicated in Figure 3-35. Flow speed in the X direction in region is accelerated during the power stroke period.

![Mean Flow Velocity in X direction of region](image1)

![Mean Flow Velocity in Y direction of region](image2)

*Figure 3-32 Mean flow velocity of the box (See Figure 3-34) following a beating parapodium’s tip during its power stroke.*
3.3.3.5 Fluid mass changing relative to the opening and closing of two adjacent parapodia.

The upper frame A in Figure 3-33 shows the area changing between two adjacent parapodia during the whole open and close period. Figure 3-33 B the fluid mass calculated based on geometry changing which is the area (or volume=area*thickness of the parapodia), positive refers to increasing and negative refers to decreasing area. Figure 3-33 C presents the mass of fluid flow through the boundary during the same period calculated based on the 2-dimensional DPIV data. The boundary is defined as the line connecting the tips of the parapodia. A positive value means fluid is sucked the region between two parapodia and negative means fluid is ejected out.

When the inter-parapodial area is increasing, fluid flows into the region. By calculating the change of area in the recording frame, it is possible to calculate the quantity of fluid being sucked in. Positive values in Figure 3-33B mean that fluid flowed into the area. Likewise the mass of fluid ejected can be estimated. Negative values in Figure 3-33B indicate that fluid flowed out of the area.

Comparing the results of B and C in Figure 3-33, a big difference is apparent. The data in B is almost 10 times larger than that in C. This result suggests that there must be a third dimension to the flow.
Figure 3-33 A shows the area changing between two adjacent parapodia during the whole suck and eject period. B shows the fluid mass calculated based on geometry changing which is the area (or volume), positive refers to increasing and negative refers to decreasing. C presents the mass of fluid flow through the boundary during the same period calculated based on the 2-dimension D PIV data, see Figure 3-25. The boundary is defined as the line connecting the tips of the parapodia. Positive values indicate that fluid is sucked the region between two parapodia and negative values indicate that fluid is ejected out.
3.4 Discussion and conclusion

In this chapter we have explored the hydrodynamics of polychaete worms, *Nereis diversicolor*, in tethered fast crawling locomotion. Worms crawl by undulating their body while simultaneously ‘rowing’ with their parapodia. The movement is very similar to their swimming gait, but there are some key differences. First, the body wave speed is much slower. Second, the body wave length and amplitude are smaller.

The tethered worm can be considered as a pumping system. Every pair of adjacent parapodia acts like a pump unit of the system. The inter-parapodial volume increases and decreases continuously during the power stroke of each pair of parapodia. During the first half, the inter-parapodial volume increases, and water is sucked into the volume in the leading side. During the second half, water is ejected out as the inter-parapodial volume decreases. The direction of the ejected water is backward as the parapodia are on the trailing edge of the worm’s bending body.

As a parapodium starts its power stroke, the fluid closely associated with the parapodium is accelerated. The higher velocity flows are found around the tip of parapodium during the middle of the power stroke, see parapodium 1 in Figure 3-14 T3 and on the trailing edge of the parapodium at the end stage of the inter-parapodial ejection, see parapodium1 in Figure 3-14T8. Figure 3-12 gives the velocity of parapodium’s tip: it achieves the highest speed during the middle of power stroke which generates the higher flow velocity around it. When this parapodium starts to decelerate at the end of the power stroke, the parapodium behind it catches up and water in the inter-parapodial volume is accelerated, and a second higher flow is generated. The fluid is accelerated twice. First one, it is accelerated by beating parapodium and the second time, it accelerated by ejecting of two adjacent parapodia, see figure 3-14.
Parapodia work in pairs to further accelerate and direct the flow. As in free swimming, after about half the power stroke period of the first parapodium, the next one starts to accelerate. The water is kept in the inter-parapodial volume. During the second half of the power stroke, the first parapodium decelerates and the second one catches up. The fluid between the inter-parapodia is ejected out to the main flow region until the two parapodia attach together.

The DPIV results show that there is almost no back flow during the recovery stroke of the parapodia. The undulation of the worm’s body increases the efficiency of this pumping mechanism by pulling the parapodia away from the flow region.

The Reynolds number (Re) can be calculated for parapodia beating in water from the following equation

\[
Re = \frac{\rho \omega l^2}{\mu}
\]

(3.3)

where \(\omega\) is the angular velocity of the parapodia, \(l\) is the length of the parapodia, \(\rho\) is the density of the liquid and \(\mu\) is the dynamic viscosity. During the recovery stroke, a characteristic length \(l\) is difficult to choose since the parapodia contact each other. So only the Re during the power stroke is calculated. For parapodia with an average length of 4 mm, moving at a maximum angular velocity of 1.1 rad/s, the Re is 18. At other stages of the cycle, the parapodia are moving very slowly. It is apparent that viscous forces may be significant in this stage. The effect at larger scale and higher Re was not investigated here. A mechanical pump system similar to the pumping worm might be restricted to lower Re.

Stamhuis (1998) observed similar movements in the ventilation of its burrow by the tube-dwelling shrimp *C. subterranea*. The recovery stroke of the pleopod is not the converse of its power stroke. During the recovery stroke, the pleopods are pulled away from the main stream, and act like oars. Thus the net flow velocity is reduced
very little. Due to the undulation motion of the worm’s body, the parapodia are hardly interacting with fluid during recovery stroke, suggesting that the drag on the worm is reduced.

The hydrodynamics of the comb plates of the ctenophore *Pleurobrachia* were studied by Barlow *et al.* (1993). During the recovery stroke, the plates bend which reduces drag. Barlow *et al.* showed that the period of effective stroke of the comb plates is much shorter than the recovery stroke, which is quite similar to the action of the parapodia of the polychaete worm. They found that the reversal of flow did not extend significantly beyond the cilia, which means the recovery plates have little effect on the main stream flow. These animals reach the same results by different locomotion. Polychaete worms reduce drag of their parapodia during recovery stroke by undulation of their body.

At the University of Bath, a group of undergraduate students built a system consisting of multiple paddles which can generate a flow function as a pump (Cummings 2004). But the interaction between adjacent parapodia and undulation of the body which are an essential aspect of this worm-like pumping mechanism were not considered in that system. An ideal engineering design of a worm-like pump system must have the same function as polychaete worms. The structure of the pump should be a series of plates with their base attached to an undulating body. The waving movement of the paddles is incorporated into the undulating movement of the underlying body.

When the worms swim freely, they do not contact the substrate (in this case the bottom of the tank), but in the fast crawling gait, worms are very close the substrate, and so the effect from the third dimension could be negligible. As in Chapter 2, fluorescent particles were used to visualize the flow. Tests were carried out with particles and without, and no distinct gait difference was found.
Chapter 4
Design of a mechanical paddle pumping system
4. Design of the mechanical paddle model

4.1 Introduction

*Physical models or robots for the study of biological systems.*

Many mechanical systems or robots have been built to study the movement of animals in swimming and flight. The advantage of a robotic system is that experiments can be exactly duplicated, and single parameter changes can be made, which greatly simplifies the analysis of experimental results.

Van den Berg (1997) built a flapping wing mechanism called Flapper to mimic the wing locomotion of a hovering hawk moth and carried out the visualization experiments using the robot. The structure of leading-edge vortex generated by the flapping robot was clearly observed. Figure 4-1 shows the mechanical system built by van den Berg and the leading-edge vortex generated by the flapping wing.

![Figure 4-1 Visualization experiment of a mechanical system called Flapper. Leading-edge vortex is generated by the flapping wing (van den Berg 1997).](image)

A robot fish called RoboTuna was built by Barrett et al (2000) to study the swimming efficiency of fishes. The fish-like model was attached to an overhead carriage.
equipped with force sensors. They found that the power consumed was much less when the robot propelled itself forward in a fish-like locomotion than when it was towed forward at the same speed. These results would have been almost impossible to achieve using real fish.

To study the fluid mechanical principles of the ribbon fin propulsion of knife fish, several authors have constructed mechanical ribbon fin systems. Sfakiotakis (2001) made a mechanical fin using eight parallel bellows actuators for the fin. Another knifefish fin robot was built by MacIver et al (2004). They used 13 servo motors to drive the fin. Kentaro et al.(2006) used ionic polymer-metal composite artificial muscles as the actuator to mimic a rajiform fin. They did a parameter study of the robot swimming speed at various control parameters, including the wave frequency and number of waves. The swimming velocity and efficiency varies much with respect to the two parameters. Lim and DeMont (2009) built a mechanical lobster to mimic the locomotion of American lobster, *Homarus americanus*. They programmed the mechanical lobster to move based on the kinematic data of real lobster. They carried out DPIV measurements on the model and found the interaction between adjacent pleopods helped to increase the thrust.

In nature, there are animals which move by pumping water using cooperative movements of their appendages. Barlow et al (1993) studied the kinematics and fluid pattern of the ctenophore *Pleurobrachia* which propel themselves by beating their comb plates. They found that the antiplectic (interaction of two adjacent plates) coordination of the plates played a major role in this movement, (see Figure 4-2). The polychaete worm, *Nereis diversicolor*, adds one more dimension, and coordinates the movement of its parapodia and body to move fluid, (see Figure 4-3).

As we have seen, both ctenophores and polychaete worms can deliver or pump fluid in one direction with very high efficiency. From a biomimetics point of view, we want to find the possibility of applying this kind of mechanism into a pump system.
Breugem (2008) used computational fluid dynamics (CFD) to study the flow induced by a series of plates and showed that fluid can be pumped by the cooperative movement of plates, see Figure 4-4. Immersed boundary method was used to do the simulation. The simulation was made in 2D. The CFD was done on discrete model of deforming porous wall. For the physical model, the laser created a light sheet in the middle of the paddles to reduce the effect from the top and bottom edges of paddles.

The governing equations of Breugem’s CFD model are derived for the volume-averaged flow through deforming porous walls, the paddles in this case. A volume-averaging equation is applied into the Navier-Stokes equations for incompressible flow. He assumed local uniform motion of solid phase and solid phase velocity introduced from subfilter-scale can be neglected and that the volume-averaged flow is well-behaved.

The flow geometry of the CFD model is described as follows. A series of staggered cylindrical elements are positioned in wall of a plane channel. Each cylinder rotates back and forth periodically. An angle phase shift is applied to neighbouring cylinders. So a travelling wave is formed along the tips of cylinders. To solve the Navier-Stokes equations, the volume-averaged velocity of the cylinder elements is obtained by making an approximation of the angular velocity of elements.

The Navier-Stokes equations are solved in a frame of reference which moves along with the travelling wave. So the geometry and position of cylinder elements is fixed in time.

To study this phenomenon, a mechanical model was built. The model consisted of a set of paddles arranged like dominoes in a straight line. The paddles move in such a way as to create travelling waves passing through their tips. The physical design including the mechanical parts, electronic control system and programming will be discussed in the following sections.
There were three main considerations of the experiments. Firstly, I wanted to study the flow pattern of the same paddle model at different Reynolds number cases and compare the experimental results with existing computational fluid dynamics (CFD) simulation results (Breugem 2008). Secondly, I wanted to do a parametric study of the paddle model. I studied the fluid velocity and flow pattern at variable travelling wave speeds, wave amplitudes and different liquids with variable viscosity. Thirdly, I wanted to compare the pumping mechanism of the paddle model with that of pumping polychaete worms.

Figure 4-2. Comb plates of Pleurobrachia beating at 27Hz. The frames are printed from video recording at 290 frames/s. (Barlow, Sleigh et al. 1993)
Figure 4-3. A shot frame from a video record at 350 frames/s of a slowly swimming polychaete worm, Nereis diversicolor.

Figure 4-4. CFD simulation results of a serial of paddles. After (Breugem 2008)

4.2 Model design

Mechanical structure

The model consisted of eight paddle units driven by servo motors to move in the form of a travelling wave. The model is used to mimic one side of a pumping polychaete worm. Every paddle has only a single rotational degree of freedom.
Parapodia of polychaete worms, in addition to rotating around their bases, move with the worm body. However, in this model, the undulation movement of the worm body is not included. A wall was placed on the inner side of the paddles to represent the worm’s body. Paddles were rectangular in shape, 4 cm long by 3 cm wide. Paddles were connected to servomotors by dual side screws.

Figure 4-5 shows the 3D layout of a set of paddles. Eight paddle units are involved in one wave. They are placed parallel to each other in a straight line. Figure 4-6 is a photograph of the paddle model which consists of 24 paddle units generating 3 waves.

![3D layout of paddles](image)

*Figure 4-5. A set of paddles which generate one travelling wave in the experiments. Black boxes represent servo motors.*
Controller

A servo controller unit (Lynxmotion SSC-32) was used to communicate between the computer and servo motors (Hitec HS-50). A user interface written in Visual Basic (Microsoft Corp) was used to communicate through the serial port with the servo controller. Angular positions for each paddle were sent out from the computer to the servo controller. Then the servo controller translated the signals into pulse wavelength modulation (PWM) signals which drove the servo motors to the desired positions.

Computer interface

A Visual Basic (VB) interface was used to control the model. The parameters which could be adjusted included the frequency and amplitude of the travelling wave. The paddles’ sweep speed defines the frequency of the travelling wave. The paddles’ sweep speed can be defined by the user. The paddles’ sweep angle defines the wave’s...
amplitude. The sweep angle of paddles can be set by users. The program was written such that the parameters could be varied over a large range of values, in order to compare the hydrodynamic behaviours of the paddle model in different parameters. The parameters include the sweep speed of the paddles, the frequency of the travelling wave and the amplitude of the wave. More details of the parameters studied will be presented in the next sections. Figure A-7 shows the visual basic window interface of the controller program. The vertical bars in the top part of the window indicate the real angle of each individual paddle. The text boxes just below them show the angle values. Two vertical bars are the parameter setting buttons. Frequency defines the wave frequency and amplitude button sets the wave amplitude. Four buttons on the right side give the functions of starting the paddle model, stop model, centering each paddle and exiting the program. The VB routine is presented in Appendix 11.

Figure 4-7. The main window of the controller user interface. Before measurements, the frequency and amplitude are set to define the movement of the paddles. Then press the START, paddles will start to move. The set of bars on the top present the angle of paddles.
4.3 Wave mechanisms

The objective of the design of the model is to use a series of paddles to generate a travelling wave along the tips of the paddles. Each paddle only has one degree of freedom. They rotate around an axis through their bases, perpendicular to the long axis of the model (see Figure 4-8). The travelling wave is created by a rotation movement of paddles with a phase offset between each paddle. Each servo motor axis is adjusted so that it is a set phase angle from the previous motor axis. This phase offset is defined by the number of paddles which are involved in one wavelength. Equation 4.1 below shows the method of calculating the phase advance angle:

\[
\omega = \frac{2 \pi}{N}
\]

where \(\omega\) is the angle offset, \(N\) is the number of paddles involved in one wavelength.

Figure 4-8 shows a wave which is generated by eight paddles with a phase offset of 45 degrees. \(\lambda\) is the travelling wave’s amplitude, which can be calculated based on the wave period. The period of the travelling wave is equal to the time required for the paddles to rotate through a complete circle. The angle of each paddle over one cycle period is given in Figure 4-9, where each colour refers to a paddle.
In this experiment, each wavelength has eight paddles. So the angle offset is calculated as:

$$\omega = \frac{2\pi}{8} = 0.7845 (45^\circ)$$

(4.2)

\[ \text{Figure 4-8. Top view of a set of rotation paddle. Green points refer to the rotation axis of the paddles. } \Theta \text{ is the rotated angle of a paddle. } \Theta_{\text{max}} \text{ indicates the maximum angle a paddle can rotate. } l \text{ is the length of a paddle. Paddle model generates a travelling wave, see the contour of the red dots. } \lambda \text{ is the travel wave amplitude.} \]

$$\lambda = \frac{1}{2} \cdot l \cdot (1 - \cos \theta_{\text{max}})$$

(4.3)

where \(l\) is the length of the paddle and \(\theta_{\text{max}}\) is the maximum rotation angle of paddles.

$$\theta = \theta_{\text{max}} \cdot (\sin(2\pi ft \cdot n \cdot \omega) + 1)$$

(4.4)

where \(\theta_{\text{max}}\) is the maximum rotation angle of the paddles, \(f\) is the frequency of travelling wave, \(n\) is the paddle index, \(\omega\) is the phase angle offset of each paddle (see Figure 4-8), and \(t\) is time.
Figure 4-9 Paddles’ angle over a whole cycle period. Each colour refers to a paddle. x-axis means the time and y-axis is the angle of paddles.

4.4 Experimental setup

Figure 4-10 gives a general overview of the experimental setup. The system consisted of a computer, a high speed camera, a high frequency laser and paddle model. The laser and camera were synchronized by the computer using the commercial software Davis. Neutrally buoyant fluorescent particles approximately 20 um in diameter were added to the liquid in the tank. The particles were illuminated by a laser light sheet (0.5 mm thick) generated by a green light high frequency Nd:YAG laser (wavelength 527 nm, power of each pulse 10mJ). The laser sheet was aimed at the middle plane of the paddles. Illuminated fluid with particles was recorded using a high speed camera (Photron High speed, CCD resolution 1024 pixels by 1024 pixels) equipped with a Nikon micro lens (105 mm), mounted normal
to the laser sheet. An orange filter was mounted on the front of the lens to block all but the light emitted by the fluorescent particles. The whole system was synchronized by a timing unit connected to a PC running the software package Davis (Version 7.2.2, LaVision, Inc) which set the recording frequency of the camera and stored image data.

Figure 4-11 shows the paddle model’s position in the aquarium. The goal was to study the pumping phenomenon in a channel, so there was a wall on either side of the model. One wave in the middle was recorded, (see the red rectangle in Figure 4-11). To simulate a continuous wave, three wave sets were generated by the paddle model. The other two paddle wave sets are on the left and right sides of the one being recorded.

The goal of this experiment is to study pumping in a low Reynolds number (Re) situation. In nature, comb plates of *Pleurobrachia pileus* have a Reynolds number of 9 during their power stroke (Barlow et al 1993). The parapodia of polychaete worms operate at a Reynolds number of 18. The size of the model paddles was 4cm by 3cm. In this case, to recreate a low Reynolds number situation it was necessary to increase the viscosity of the fluid. The fluid viscosity was changed by mixing glycerol into the water.

The Reynolds number is defined by

\[
Re = \frac{\rho V L}{\mu}
\]  

(4.5)

where \(\rho\) is the fluid density, \(V\) is the mean velocity, in this case, the mean velocity of the travelling wave, \(L\) is the characteristic dimension and \(\mu\) is the kinematic viscosity of the fluid. The same calculation algorithm is used as Breugem’s simulation study (Breugem 2008). As described in Figure 4-11 and in keeping with the conventions used in the study of pipe flow, the characteristic dimension \(L\), is the distance between the midline of the travelling wave and the wall. Figure 4-11 gives
the diagram drawing of the characteristic length $L$ which equals $(A + \lambda)$, where $\lambda$ is the wavelength of the travelling wave. $(A)$ is the distant between the paddle tip and the wall when the paddle’s angle is zero. $(V)$ is speed of the travelling wave which can be calculated by Equation 4.6.

$$V = \frac{\lambda}{t}$$  \hspace{1cm} (4.6)

**Figure 4-10.** Diagram of the PIV experimental setup. The system consisted of a computer, a high speed camera, a high frequency laser and paddle model. The laser and camera are synchronised by a computer using the commercial software Davis. The light sheet was aligned with the centre of the paddles.
4.5 Results

4.5.1 Flow pattern of the paddle model at different Reynolds numbers

4.5.1.1 Varying the Reynolds number by changing fluid viscosity.

The fluid viscosity is changed by mixing glycerol and water. Three samples of fluid at different viscosities are 0.1 Pa/s = 1xH₂O (Labelled as L1), 0.022 pas/s = 22xH₂O (Labelled as L2), and 0.001 Pa/s = 100xH₂O (Labelled as L3) which is the pure water, at a temperature of 20 °C. Paddles beat at frequency of 1/16. The Reynolds number can be calculated by Equation 4.5.

\[
\text{Re}(L1)=4; \text{Re}(L2)=20; \text{Re}(L3)=400;
\]

Figure 4-12 L1 shows the flow pattern of fluid L1 at a Reynolds number of 4. Vectors indicate fluid velocity. Two distinct vortices are found in the DPIV image. The left one in the figure is anticlockwise and the right one is clockwise. The latter is much stronger than the former, which produces a net flow from left to right in the image. Figure 4-13L1 shows the mean fluid velocity at each time step during one wave.
period. A net flow velocity is 0.25 mm/s, where a positive value means fluid moves from left to right.

Figure 4-12 L2 shows the flow pattern of fluid L2 at a Reynolds number of 20. Vectors indicate fluid velocity. In this DPIV figure, there are again two vortices. The left is again anticlockwise and the right clockwise, but the clockwise vortex is smaller compared with Figure 4-12. The mean flow velocity during one wave period in fluid L2 is shown in the Figure 4-12. The net flow in the L2 case is 0.04mm/s

Figure 4-12 L3 shows the flow pattern of fluid L3 at a Reynolds number of 400. Vectors indicate fluid velocity. The flow pattern is much different with L1. A clockwise vortex dominates the fluid. The anticlockwise vortex is almost invisible. This flow pattern produces a net flow moving from right to left, in the opposite direction compared with L1. Figure 4-13 L3 shows the mean fluid velocity of each time step during one wave period. A net flow velocity is -0.5 mm/s, with the negative value indicating that the fluid moves from right to left.

This is a very interesting phenomenon. The only difference between the experiments was that the Reynolds number of the fluid had been changed by using liquid with different viscosity. Every other parameter was kept the same, including using the same paddle model system, travelling wave period, and geometric structure.

Figure 4-12. (next page) The top frame is the fluid flow vector field of the pumping model in fluid L1 at a Reynolds number of 4. Two distinct vortices are present in the DPIV image. The left one in the figure is anticlockwise and the right one is clockwise and dominant. The middle frame is the fluid flow vector field for fluid L2 at a Reynolds number of 20. A similar fluid pattern is found as in L1, but the right becomes much weaker. The bottom frame presents the fluid flow vector field for fluid L3 at a Reynolds number of 400. The fluid pattern is totally different. The right vortex is almost invisible. Fluid moves from right to left.
Net flow velocity in X direction during one wave period

L1

Net flow velocity in X direction during one wave period

L2
4.5.1.2 Changing the Reynolds number by varying travelling wave speed

To investigate the findings in the last section, in this section the phenomenon is approached using a different method. Here the Reynolds number is changed by varying the travelling wave period and varying frequency and thereby paddle’s speed. The flow pattern of the paddle model of two travelling wave periods was studied. They are 16s (Labelled as W1) and 1.2s (Labelled as W2). The same liquid with viscosity of 0.1 Pa/s was used in both cases. The Reynolds number of the two cases was calculated using Equation 4.5 to be Re (W1)=3 and Re(W2)=40;
Figure 4-14 W1 shows the flow pattern of W1, Re=3. Figure 4-14 W2 gives the flow pattern of W2, Re=40. Two vortices are found in both cases. In Figure 4-14W1 the anticlockwise one is dominant, but in Figure 4-14W2 the clockwise one is dominant. The net flow generated in the two cases is of opposite sign, consistent with the observations in the previous section.

Figure 4-14. (next page) Top frame gives the DPIV image of the flow pattern of W1. Reynolds number is 3. Vectors indicate the local fluid velocity. Two distinct vortices are found in the DPIV image. The left one in the figure is anticlockwise and the right one is clockwise. The clockwise vortex is stronger than the other one. So it dominates the flow which produces a net flow moving from left to right. The lower panel presents the flow pattern of W2. Reynolds number is 40. Two distinct vortices are found in the PIV image. The left one in the figure is anticlockwise and the right one is clockwise. The anticlockwise vortex is stronger than the other one, so it dominates in the flow and produces a net flow moving from right to left.
4.5.2 Parameter study of the pumping phenomenon about the paddle model.

To study the relationship between the paddle model and the fluid moved by the model, a parameter study was conducted. The fluid was a mixture of water and glycerol, with a viscosity of 0.022 Pa/s. Using this fluid, it was possible to span a range of Reynolds numbers equivalent to those experienced by the real worm.

*Travelling wave period. at 1.2 seconds*

The Reynolds number can be calculated by equation 4.5. The characteristic velocity, V, in this case is the travelling wave speed V=0.1 m/s, where 0.12 is the travelling wave length. L is 0.0364 m. Density is 1120 kg/m$^3$. So Re=188.

Figure 4-15 gives the mean fluid velocity in both X-direction and Y-direction during a recording period of 4 seconds. During this period, three whole wave periods are included. The profile of the velocity is wave-like, ranging from 5 mm/s to 26 mm/s. The maximum velocity is almost five times the minimum one, which indicates that the fluid was accelerated and decelerated very heavily. The negative value means the flow direction is opposite to the travelling wave direction. The red line on the top frame shows the mean velocity during the period, the net flow velocity is -17 mm/s. The wave phase speed is 100 m/s which is six times the net flow velocity.
Figure 4-15. Mean flow velocity over a 4 second, 4 wave period. X-axis is the time and Y-axis is the fluid velocity in mm/s. The Reynolds number is 188. Top frame is the X-direction velocity and bottom frame is Y-direction velocity. The red line in the top frame shows the average flow in X direction. The net flow speed is -17 mm/s.
**Travelling wave period at 2.5 seconds.**

The Reynolds number can be calculated by equation 4.5. Again, the characteristic velocity, V, is equal to the travelling wave speed \( V=0.048\,\text{m/s} \), where 0.12 is the travelling wave length. \( L = 0.0364\,\text{m} \). Density is 1120 kg/m\(^3\). So \( \text{Re}=89 \).

Figure 4-16 gives the mean fluid velocity in both X-direction and Y-direction during a recording period of 10 seconds. During this period, three whole wave periods are included. The profile of the velocity is wave-like, ranging from -1.5\,\text{mm/s} to -9\,\text{mm/s}. The maximum velocity is almost five times the minimum one, which indicates that the fluid was accelerated and decelerated very heavily. The negative value means the flow direction is opposite to the travelling wave direction. The red line on the top frame shows the mean velocity during the period, the net flow velocity is -6.5\,\text{mm/s}. The wave phase speed is 48\,\text{mm/s} which is eight times fast than the net flow velocity.
Figure 4-16. Mean flow velocity over a 10 second, about 4 wave period. X-axis is the time and Y-axis is the fluid velocity in mm/s. The Reynolds number is 89. Top frame is the X-direction velocity and bottom frame is Y-direction velocity. The red line in the top frame shows the average flow in X direction. The net flow speed is -6.5mm/s.
**Travelling wave period at 5 seconds.**

The Reynolds number can be calculated by equation 4.5. V is equal to travelling wave speed \( V=0.024 \) m/s, where 0.12 is the travelling wave length. L is 0.0364 m. Density is 1120 kg/m\(^3\). So \( Re=44 \).

Figure 4-17 gives the mean fluid velocity in both X-direction and Y-direction during a recording period of 24 seconds. During this period, three whole wave periods are included. The profile of the velocity is wave-like, ranging from -0.5mm/s to -3.5 mm/s. The maximum velocity is almost five times the minimum one, which indicates that the fluid was accelerated and decelerated very heavily. The negative value means the flow direction is opposite to the travelling wave direction. The red line on the top frame shows the mean velocity during the period, the net flow velocity is -1.85mm/s. The wave phase speed is 24mm/s which is 12 times faster than the net flow velocity.
Figure 4-17. Mean flow velocity over a 25 second, about 5 wave period. X-axis is the time and Y-axis is the fluid velocity in mm/s. The Reynold number is 44. Top frame is the X-direction velocity and bottom frame is Y-direction velocity. The red line in the top frame shows the average flow in X direction. The net flow speed is -1.8 mm/s.
Travelling wave period at 16 seconds.

The Reynolds number can be calculated by equation 4.5. \( V \) is equal to travelling wave speed \( V=0.0075 \text{ m/s} \), where 0.12 is the travelling wave length. \( L \) is 0.0364 m. Density is 1120 kg/m\(^3\). So Re=14.

Figure 4-18 gives the mean fluid velocity in both X-direction and Y-direction during a recording period of 24 seconds. During this period, three whole wave periods are included. The profile of the velocity is wave-like, ranging from 0.6mm/s to -0.6 mm/s. The maximum velocity is almost five times the minimum one, which indicates that the fluid was accelerated and decelerated very heavily. The negative value means the flow direction is opposite to the travelling wave direction. The red line on the top frame shows the mean velocity during the period, the net flow velocity is 0.05mm/s, the same direction as the travelling wave. The wave phase speed is 7.5mm/s which is 150 times the net flow velocity.
Figure 4-18 Mean flow velocity over a 25 second, about 1.5 wave period. X-axis is the time and Y-axis is the fluid velocity in mm/s. The Reynolds number is 14. Top frame is the X-direction velocity and bottom frame is Y-direction velocity. The red line in the top frame shows the average flow in X direction. The net flow speed is
0.05mm/s.

4.5.2.1 Mean fluid velocity as a function of wave speed.

Figure 4-19 summarises the results of this section, and presents the net flow at different travelling wave speeds. The relationship between the wave speed and net flow velocity is not linear. The net flow velocity is high at low wave period (i.e. high frequency), and drops off very quickly with increasing wave period (i.e. low frequency).

![Mean velocity as function of wave speed](image)

*Figure 4-19. Net flow velocity during one wave period as a function of Wave period. X-axis means the wave speed in mm/s. Y-axis means net flow velocity in mm/s.*

4.6 Conclusion and discussion

This chapter describes the fluid dynamics of a mechanical paddle model. The model consisted of a series of paddles. A traveling wave was generated by cooperative movement of the paddles. The model was studied in variable Reynolds number cases.
from 4 to 400. The most important finding in this research is the reversed flow direction generated by the same mechanism at different Re. The direction of jet generated by the two paddles at the crest of the traveling wave dominates the pumping fluid direction. At higher Re’s (400 in the case), the inertial force dominates the flow. The jet direction is opposite of the wave direction, as indicated in the Figure 4-20. In the low Re case (Re=1 in the CFD, Re=4 in the experiments), the viscous force is as important as the inertial force. The flow is in Strokes regime. The jet direction then goes in the same direction as the travelling wave (Figure 4-21).

Comparison of the experimental results with CFD simulation results (Breugem 2008).

Figure 4-20A gives Breugem’s (2008) CFD simulation result of fluid pattern at high Reynolds number (Re=100). The figure shows two vortices, one anticlockwise and the other clockwise. In this case, the anticlockwise vortex dominates which results in a pumped net flow moving from right to left. Figure 4-20B gives the experimental result of flow pattern generated by the paddle model. This is quite similar to the CFD result shown in Figure 4-20A. Two vortices, anticlockwise and clockwise, appear in the simulation, and the anticlockwise vortex dominates resulting a net flow movement from right to left.

Figure 4-21A is a CFD simulation of the fluid pattern at low Reynolds number (Re=1). The figure shows two vortices, one anticlockwise and the other clockwise. In this case, the clockwise vortex dominates which results in a pumped net flow movement from left to right. Figure 4-21B shows the experimentally obtained flow pattern generated by the paddle model. Again, the pattern is quite similar to the CFD model (Figure 4-21A). Two vortices, anticlockwise and clockwise are present, and the clockwise vortex dominates reducing a net flow movement from left to right. For the high Reynolds number case, Figure 4-20, there is not only a jet but also water
accelerated backwards (as indicated by the yellow arrow). But for the low Reynolds number case, Figure 4-21 there is mainly the sideways directed jet which does not contribute to propulsion.

Figure 4-20. A. CFD result at Re=100 (Breugem 2008). B. Experimental result at high Re=400. Strong jet flow is found in both of them, indicated by yellow arrows. The blue arrows show their flow pattern difference.
Figure 4-21. A. Flow velocity vectors plot of CFD result at Re=1. B is the Experimental Result at Low Re=4. Two vortices are found in both images, highlighted by yellow arrows and blue ones.
Comparison of the paddle model with pumping polychaete worms.

In the real worm, water is pumped continuously in one direction by the cooperative movement of worm’s parapodia, see Figure 3-26. There is almost no back flow resulted by parapodia in the recovery stroke. In the paddle model, however, the flow pattern is very different. A strong back flow can be seen in the DPIV results, (see Figure 4-12), at Reynolds numbers from 4 to 400.

For the pumping polychaete worms, the mean cycling velocity of their parapodia of 20 mm/s can generate a net flow at 10mm/s, the ratio between the two parameters is 2:1. But for the paddle model, the best ratio is 6:1 which shows a much lower efficiency.

The reason for the low efficiency of the mechanical model is likely the absence of the undulation movement of the paddles. The undulatory body movement of a worm helps them to hide the parapodia from the flow during the recovery stroke, as shown in Figures 4-20 and 4-21. Parapodia are close to each other and absent from the flow region during their recovery stroke, so the fluid will be dragged much less, and hence the pumping efficiency is greatly improved.
Chapter 5
Conclusion and future study
5. Conclusion and future study

5.1 Conclusion

In this thesis I have explored the hydrodynamics of polychaete worms, *Nereis diversicolor*, both in freely swimming locomotion and in tethered pumping motion. The interaction between adjacent parapodia of a polychaete worm generates a net flow in one direction, which thrusts the swimming worm forward. This unique mechanism could also work as a nature-inspired pumping system.

The first part of the research follows on from Hesselberg (2006), who found two distinct jet-like flow patterns in the wake of a freely swimming *Nereis diversicolor*. This thesis has extended that research by focusing on the micro-scale hydrodynamics around the parapodia. During the power stroke, they reach their maximum wave speed when they are perpendicular to the worm’s body wave. DPIV data also shows the flow has the highest velocity around the waving parapodia at that time. During the recovery stroke, as the parapodia are closed together due to the undulation movement of the worm’s body, and hardly interact with the free fluid which as a system in total reduced the drag and improves efficiency. From the DPIV results almost no back flow is found during the recovery stroke of the parapodia.

To explore the biomimetic aspect of the unique swimming mechanism of these polychaete worms, I studied the system as a pumping system. The worm was tethered and its swimming action functioned as a pump. The tethered worms moved in a gait similar to that of freely swimming worms which move by undulating their body while synchronously rowing with their parapodia. The tethered worms use a much smaller body wave amplitude and a larger wave period. The result is that the maximum volume between two parapodia is approximately twice that of the free swimming case. The continuous jet-like flow pattern generated by the tethered worm is qualititatively similar to that of swimming worms, but there are important fine scale differences. Fluid is pumped uniformly in a direction opposite to the direction
of motion of the worm, but the pulsatile suck and eject flow is clearly observed. Vortices were found around oscillating parapodium in the tethered case, and not in the free swimming case. The Re calculated based on the movement and dimension of the parapodia of pumping worms is about one fifth of that of free swimming ones. The Re of pumping worms ranges from 20 to 40. For this case, it is clear that the viscous force of the fluid is not negligible. A pulsation flow pattern can be seen in the DPIV images. But for the swimming worms, the inertial force is more than 100 times larger than viscous force, and hence the viscous force can be neglected.

A mechanical model was designed, constructed and studied in a range of Re (4 to 400) fluid. The results proved that periodic movement of a series of rigid paddles can generate a uni-directional flow. Compared with the pumping polychaete worms, however, the flow generated by the paddle model is not constant. This is due to the absence of the undulation movement of the paddles which reduces the efficiency of the pumping system. Vortices were observed around the paddle model at low Re which is similar to the vortices found in pumping worms. At Re=400, there were no vortices in the DPIV images around the paddle model, again similar to the freely swimming worms. Another very interesting finding of the model is the flow reversal at the different Re conditions. The results compare well with Wim-paul’s numerical simulations (unpublished paper).

Figure 5-1 gives the fluid patterns of the swimming worm and paddle model (Re=400). The top frame is the PIV result of the swimming worm. The bottom frame is flow pattern of the paddle model. The similarity of them is that both of them are at relatively high Re. The fluid is inertia-dominated flow. The flow is continuous, the result of shedding water mass. Figure 5-2 shows the flow patterns of pumping worm and paddle model (Re=4). Both of them are at relatively low Re. The average Re of the parapodium of the pumping worm is about 18 during power stroke. The viscous force can not be neglected for both cases. The distinct separation flow pattern is
presented for the paddle model. Also, the suck and eject effecion between parapodia is observed for the pumping worm, as the added mass of the fluid. In the beginning of the power stroke at very low Re, the velocity of the water close to the parapodium increases as added mass effiction. Then the water accelerated is stay constant and shed into the jet region, as the parapodium’s velocity of rowing increases. The Re increases, the inertial plays more important role keeping water mantle remais moving. This presents that the worm uses the physics of both low Re and high Re.
Figure 5-1 Flow pattern comparison. Top view: PIV result of the swimming worm. Bottom view: PIV result of the Paddle model at Re=400.
Figure 5-2 Flow pattern comparison. Top view: PIV result of the pumping worm. Bottom view: PIV result of the Paddle model at Re=4.

5.2 Future study

Undulation of the worms’ body plays a very important role in the both swimming and pumping movement. Because the body undulates, parapodia extend and separate
during their power stroke and close together during recovery stroke. During the recovery stroke, parapodia are absent from the fluid which reduces the drag. The mechanical model discussed in chapter 4 did not include the undulation movement of the paddles. In the future study, it is suggested that an advanced mechanical model which takes undulation movement account in should be built.

Figure 5.3 shows the structure of artificial cilia (red paddles) pumping system and the DPIV results of it (Hussong 2010) which is the key achievement of the European project ARTIC. The artificial cilia were actuated by an external magnetic field. An inhomogeneous magnetic field induced a time-averaged net flow due to an asymmetric beat cycle of each cilia and phase lag between beating cilia. But strong flow oscillation was found (Hussong 2010) which reduced the pumping efficiency dramatically.

There was almost no reverse flow observed in the pumping worm’s DPIV results as showed in Chapter 3. The micro-pumping system of ARTIC project can be adjusted by giving the base the undulatory movement as shown in Figure 5.4. The base material could be flexible polymers filled with magnetic particles. So a traveling wave can be created by applying an external magnetic field on the base. An increase of the pumping efficiency would be expected using this design.

Another finding is the flow reversal discussed in Chapter 4. By adjust the beating frequency of the paddles, the pumping flow direction can be controlled by the same pump mechanism. It is worth exploring the potential applications in the micro-fluid pumping system based on this phenomenon.
Figure 5.3 The structure of artificial cilia micro pumping system (Top) after (Balardi 2010). DPIV images of the artificial cilia in action (Bottom) after (Hussong 2010).

Figure 5.4 Micro-pumping system design inspired by polychaete worms. The base of the paddle can undulate to generate a wave along the base. The base can be driven by a magnetic or electric field.
6. Literature


Cummings, B. (2004). A biomimetic pump based on the fast-swimming locomotive
mechanism of Nereis diversicolor. Department of Mechanical Engineering, University of Bath.


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7. Appendix

Appendix 1. Matlab routine for kinematic analysis of freely swimming worms.

```matlab
close all; clear all; clc;

%% parameters
f=351;
si=3;
dt=(1/f)*4; % in second
ow=18.66; % size of observation window in mm
p2mm=ow/1024; % unit pixel length in mm

%% set directory
filefolder=fullfile('C:\Ruitao\Sync\Research\Matlab\', 'Raw data');
vectors_rimg=dir(fullfile(filefolder,'B*****.tif')); % read the raw images
filenames_rimg={vectors_rimg.name}';
numims=numel(filenames_rimg);

%% load pics
for b=1:numims
    I(:,:,b)= imread(filenames_rimg{b});
end

%% Choose pixels
X=zeros(6,numims);Y=zeros(6,numims);
for c=1:numims
    [x,y,p]=impixel(double(I(:,:,c))./5);
    X(1:length(x),c)=round(x);
    Y(1:length(y),c)=-round(y);
end

%% Calc para angle
for na=1:numims
    if X(2,na)<X(5,na)
        xb(na)=X(2,na)+(X(5,na)-X(2,na))/2;
    else
        xb(na)=X(5,na)+(X(2,na)-X(5,na))/2;
    end
    if X(3,na)<X(4,na)
        xt(na)=X(3,na)+(X(4,na)-X(3,na))/2;
    else
        xt(na)=X(4,na)+(X(3,na)-X(4,na))/2;
    end
    if Y(2,na)<Y(5,na)
        yb(na)=Y(2,na)+(Y(5,na)-Y(2,na))/2;
    else
        yb(na)=Y(5,na)+(Y(2,na)-Y(5,na))/2;
    end
```

```
yb(na)=Y(5,na)+(Y(2,na)-Y(5,na))/2;
end
if Y(3,na)<Y(4,na)
    yt(na)=Y(3,na)+(Y(4,na)-Y(3,na))/2;
else
    yt(na)=Y(4,na)+(X(3,na)-X(4,na))/2;
end
end
angle=asin((abs(yt-yb))./sqrt((xb-xt).^2+(yb-yt).^2)); %use asin to calc angle
angle_deg=rad2deg(angle); %para angle relative to ground of each time step
for a1=1:numims
    if a1==1
        angle_deg_np=angle_deg(a1);
    elseif angle_deg(a1)<angle_deg(a1-1)
        angle_deg_np=180-angle_deg(a1);
    else
        angle_deg_np=angle_deg(a1);
    end
    angle_deg_n(a1)=angle_deg_np;
end
tangle=0:dt*1000:(numims-1)*dt*1000; %time step in ms
ap=polyfit(anglex,angle_deg_n,2);
pangle_poly=polyval(ap,anglex);
danglex=1:numims;
dap=polyfit(danglex,w,5);
w_poly=polyval(dap,danglex);
end % central time differencing scheme is used, angular velocity in rad/s
w_mean=sum(w)/length(w); %calc the average angular velocity

for d=1:numims
    if d==1
        wp=(angle_deg_n(d+1)-angle_deg_n(d))/dt;
    elseif d==numims
        wp=(angle_deg_n(d)-angle_deg_n(d-1))/dt;
    else
        wp=(angle_deg_n(d+1)-angle_deg_n(d-1))/(2*dt);
    end
    w(d)=wp/360;
end % central time differencing scheme is used, angular velocity in rad/s
for e=1:numims
    if e==1
        vtxp=((xt(e+1)-xt(e))/dt)*p2mm; %tip velocity in x direction in mm/s
        vtyp=((yt(e+1)-yt(e))/dt)*p2mm; %tip velocity in y direction
        vbxp=((xb(e+1)-xb(e))/dt)*p2mm; %base velocity in x direction
        vbyp=((yb(e+1)-yb(e))/dt)*p2mm; %base velocity in y direction
    elseif e==numims
        vtxp=((xt(e)-xt(e-1))/dt)*p2mm; %tip velocity in x direction
        vtyp=((yt(e)-yt(e-1))/dt)*p2mm; %tip velocity in y direction
        vbxp=((xb(e)-xb(e-1))/dt)*p2mm; %base velocity in x direction
        vbyp=((yb(e)-yb(e-1))/dt)*p2mm; %base velocity in y direction
    else
        vtxp=((xt(e+1)-xt(e-1))/(2*dt))*p2mm; %tip velocity in x direction
        vtyp=((yt(e+1)-yt(e-1))/(2*dt))*p2mm; %tip velocity in y direction
        vbxp=((xb(e+1)-xb(e-1))/(2*dt))*p2mm; %base velocity in x direction
        vbyp=((yb(e+1)-yb(e-1))/(2*dt))*p2mm; %base velocity in y direction
    end
    vtx(e)=vtxp;vty(e)=vtyp;vbx(e)=vbxp;vby(e)=vbyp;
end % central time differencing scheme is used
% Tip relative velocity
vtxr=vtx+vbx;
% tip x-velocity polyfit%
vtux=1:numims;
vtap=polyfit(vtux,vtx,4);
vtx_poly=polyval(vtap,vtux);
vtx_mean=sum(vtx)/length(vtx); %calc the average tip velocity in x direction of one power stroke
vty_mean=sum(vty)/length(vty); %calc the average tip velocity in y direction of one power stroke
vbx_mean=sum(vbx)/length(vbx); %calc the average base velocity in x direction of one power stroke
vby_mean=sum(vby)/length(vby); %calc the average base velocity in y direction of one power stroke
%for plot
nv=0:dt*1000:(numims-1)*dt*1000;
% Calc area
for f=1:numims
    parea(f)=polyarea(X([1:3],f).*p2mm,Y([1:3],f).*p2mm); %area of opening and closing in mm^2
end
nparea=0:dt*1000:(numims-1)*dt*1000; %time step in ms
% area polyfit%
areax=1:numims;
ap=polyfit(areax,parea,4);
parea_poly=polyval(ap,areax);
% area changing
for f1=1:numims
if f1==1
dparea(f1)=parea(f1+1)-parea(f1);
elseif f1==numims
    dparea(f1)=parea(f1)-parea(f1-1);
else
    dparea(f1)=(parea(f1+1)-parea(f1-1))/2;
end
end
dparea=abs(dparea);

%%area change polyfit%%
dareax=1:numims;
dap=polyfit(dareax,dparea,5);
dparea_poly=polyval(dap,dareax);

%% Calc Reynolds number
for h=1:numims
    lparap=(sqrt((xt(h)-xb(h))^2+(yt(h)-yb(h))^2))*p2mm; %parapodium length in mm
    pRe(h)= lpara*vtx(h);  %((vtx(h)^2+vty(h)^2)^0.5);
    lpara(h)=lparap;
end
mRe=sum(pRe)/length(pRe); %mean Re over a stroke

%% Calc Parapodium length

%% Plot
figure; plot(npangle,angle_deg_n,'rs','MarkerFaceColor','g','MarkerSize',5); hold on; plot(npangle,angle_poly);hold off;title('Parapodium angle relative to ground'); xlabel('Time(ms)'); ylabel('Angle(degree)');
figure; plot(npangle,w,'rs','MarkerFaceColor','g','MarkerSize',5); hold on; plot(npangle,w_poly);hold off; title('Parapodium angular velocity'); xlabel('Time step'); ylabel('W(rad/s)');
figure; plot(nv,vtx,'--rs','MarkerFaceColor','g','MarkerSize',5);title('Parapodium tip velocity in x'); xlabel('Time step'); ylabel('Velocity(mm/s)');
figure; plot(nv,vty,'--rs','MarkerFaceColor','g','MarkerSize',5);title('Parapodium base velocity in x'); xlabel('Time step'); ylabel('Velocity(mm/s)');
figure; plot(nv,vbx,'--rs','MarkerFaceColor','g','MarkerSize',5);title('Parapodium tip relative velocity in x'); xlabel('Time step'); ylabel('Velocity(mm/s)');
figure; plot(nv,vby,'--rs','MarkerFaceColor','g','MarkerSize',5);title('Parapodium tip relative velocity in x'); xlabel('Time step'); ylabel('Velocity(mm/s)');
figure; plot(nparea,parea,'rs','MarkerFaceColor','g','MarkerSize',5); hold on; plot(nparea,parea_poly);hold off; title('Area between two adjacent parapodia'); xlabel('Time(ms)'); ylabel('Area(mm^2)');
figure; plot(nparea,dparea,'--rs','LineWidth',2, 'MarkerFaceColor','g','MarkerSize',5); title('Area Changing between two adjacent parapodia'); xlabel('Time(ms)'); ylabel('Area(mm^2/s)');
Appendix 2 Matlab routine of calculating Mean velocity over a period of a freely swimming polychaete worms.

clear; close all; clc;

%% set directory
filefolder=fullfile('F:\Research\PIV data\Worm\Freely swimming\PIV\Data set for analyze\Vectors\','Vectors_No9_free_swimming_1');
vectors_vect=dir(fullfile(filefolder,'B*****.VC7')); % read the vectors data
filenames_vect={vectors_vect.name}';

numims=numel(filenames_vect);

%% load vector files
for a=1:numims
    vf(a) = loadvec(filenames_vect{a});
end

%% set region to be analyzed
rvx=[1:64];
rvy=[16:42];
f=351; %recording frequency
dt=1/f;
pl=18.66/1024; %length of each pixel in mm
vsz=18.66/64;
p2mmv=pl*f;

%Mean Velocity
for b=1:1

    subvx=(vf(b).vx(rvx,rvy).*p2mmv); %only consider the x velocity
    subvy=(vf(b).vy(rvx,rvy).*p2mmv); %only consider the y velocity
    sumvx=sum(sum(subvx)); %sum up the velocity of each grid
    sumvy=sum(sum(subvy)); %sum up the velocity of each grid
    avx(b)=mean(mean(subvx)); % calc the average velocity
    avy(b)=mean(mean(subvy)); % calc the average velocity
end

%Deviation of velocity---a
for d=1:1

    if d<12
        davx1=(avx(d+1)-avx(d))/dt;
    elseif d>numims-12
        davx1=(avx(d)-avx(d-1))/dt;
    else
        davx1=(avx(d+11)-avx(d-11))/(22*dt);
    end
    davx(d)=davx1;
end
%polyfit

e=1:numims;
dap=polyfit(e,davx,15);
davx_poly=polyval(dap,e);

%% PLOT
	nvx=0:dt:(numims-1)*dt; %time step in s
figure(1)
plot(nvx, avx,'-bd','LineWidth',1,...
     'MarkerEdgeColor','k',...
     'MarkerFaceColor','g',...
     'MarkerSize',3);title(['Mean velocity in x
direction']);XLABEL('Time(s)');YLABEL('veloctiy(mm/s)');
figure(2)
plot(nvx, avy,'-bd','LineWidth',1,...
     'MarkerEdgeColor','k',...
     'MarkerFaceColor','g',...
     'MarkerSize',3);title(['Mean velocity in y
direction']);XLABEL('Time(s)');YLABEL('veloctiy(mm/s)');

figure(3)
plot(nvx, davx,'bd','LineWidth',1,...
     'MarkerEdgeColor','k',...
     'MarkerFaceColor','g',...
     'MarkerSize',3);title(['Dv/Dt']);XLABEL('Time(s)');YLABEL('Dv/Dt(mm^2/s)');

% hold on;plot(nvx, davx_poly)

Appendix 3 Matlab routine for calculating Region following parapodium and parapodium’s tip velocity of freely swimming polychate worms.

close all; clear all; clc;

%% set directory

filefolder=fullfile('C:\Ruitao\Files from IBM\PHD in Bath\Thesis\Sync\Writting\Paper Journal of experimental biology\MATLAB\', 'process data');
vectors_rimg=dir(fullfile(filefolder,'B0****.tif')); % read the raw images
vectors_vect=dir(fullfile(filefolder,'B0****.VC7')); % read the vectors data
filenames_rimg={vectors_rimg.name}';
filenames_vect={vectors_vect.name}';
numims=numel(filenames_vect);
numims_img=numel(filenames_rimg);

%% parameters
psz=18.66/1024; %pixel size in mm
fz=351; %frequency
dt=1/351;
nic=3; %every nic image/vc7 chosen for analyze
dt1=3/351;
p2mm=18.66/1024;
p2mmv=psz*fz; %pixel displacement to velocity in mm/s
sx=4;sy=8; %set region size

% load vector files
for a=1:numims
    vf(a) = loadvec(filenames_vect{a});
end

% load pics
for b=1:numims_img
    I(:,:,b)= imread(filenames_rimg{b});
end

% Choose pixels
X=zeros(1,numims);Y=zeros(1,numims);
for c=1:numims
    [x,y,p]=impixel(double(I(:,:,c))./50);
    X(1:length(x),c)=round((x/1024)*64);
    Y(1:length(y),c)=round((y/1024)*64);
end

% Calc mean fluid in the chosen region
for d=1:numims
    rx=X(d)-sx:X(d)+sx;
    ry=Y(d)-sy:Y(d);

    rvx=vf(d).vx(rx,ry);
    rvy=vf(d).vy(rx,ry);

    srvx(d)=mean(mean(rvx))*p2mmv;
    srvy(d)=mean(mean(rvy))*p2mmv;
end

xt=X.*1024/64;yt=Y.*1024/64;

% Para tip velocity
for e=1:numims
    if e==1
        vtpx=((xt(e+1)-xt(e))/dt)*p2mm; %tip velocity in x direction in mm/s
        vtyp=((yt(e+1)-yt(e))/dt)*p2mm; %tip velocity in y direction
    elseif e==numims

vtxp=((xt(e)-xt(e-1))/dt)*p2mm; %tip velocity in x direction
vtyp=((yt(e)-yt(e-1))/dt)*p2mm; %tip velocity in y direction
else
vtxp=((xt(e+1)-xt(e-1))/(2*dt))*p2mm; %tip velocity in x direction
vtyp=((yt(e+1)-yt(e-1))/(2*dt))*p2mm; %tip velocity in y direction
end
vtx(e)=vtxp;vty(e)=vtyp;
end

%% set coordinate
nt=0:dt1:(numims-1)*dt1;

%% plot
figure(1)
plot(nt,srvx,'--gd','LineWidth',2,...
    'MarkerEdgeColor','k',...
    'MarkerFaceColor','g',...
    'MarkerSize',10); title(['Mean flow velocity vx in region']);
xlabel('timestep(s)');ylabel('Velocity(mm/s)');

figure(2)
plot(nt,srvy,'--gd','LineWidth',2,...
    'MarkerEdgeColor','k',...
    'MarkerFaceColor','g',...
    'MarkerSize',10); title(['Mean flow velocity vy in region']);
xlabel('timestep(s)');ylabel('Velocity(mm/s)');

figure(3)
plot(nt,vtx,'--gd','LineWidth',2,...
    'MarkerEdgeColor','k',...
    'MarkerFaceColor','g',...
    'MarkerSize',10); title(['Parapodium Tip velocity tvx in region']);
xlabel('timestep(s)');ylabel('Velocity(mm/s)');

figure(4)
plot(nt,vty,'--gd','LineWidth',2,...
    'MarkerEdgeColor','k',...
    'MarkerFaceColor','g',...
    'MarkerSize',10); title(['Parapodium Tip velocity tvy in region']);
xlabel('timestep(s)');ylabel('Velocity(mm/s)');

figure(5)
plot(nt,srvx,'--gd','LineWidth',2,...
    'MarkerEdgeColor','k',...
    'MarkerFaceColor','g',...
'MarkerSize',10);
hold on; plot(nt,vtx,'--rd','LineWidth',2,...
 'MarkerEdgeColor','k','...
 'MarkerFaceColor','g','...
 'MarkerSize',10); title(['Parapodium Tip velocity tvx in region(Red) and Flow Velocity(Green)']); xlabel('timestep(s)');ylabel('Velocity(mm/s)');

figure(6)
plot(nt,srvy,'--gd','LineWidth',2,...
 'MarkerEdgeColor','k','...
 'MarkerFaceColor','g','...
 'MarkerSize',10);
hold on; plot(nt,vty,'--rd','LineWidth',2,...
 'MarkerEdgeColor','k','...
 'MarkerFaceColor','g','...
 'MarkerSize',10); title(['Parapodium Tip velocity tvy in region(Red) and Flow Velocity(Green)']); xlabel('timestep(s)');ylabel('Velocity(mm/s)');

**Appendix 4  Matlab routine of calculating Mean velocity of each row counting from worm body of freely swimming polychaete worms.**

clear all; close all; clc;

%% set folder
filefolder=fullfile('F:\Research\PIV data\Worm\Freely swimming\PIV\Data set for analyze\Vectors\Vectors_No9_free_swimming_1');

vectors_vect=dir(fullfile(filefolder,'B00460.VC7')); % read the vectors data
filenames_vect={vectors_vect.name}';
numims=numel(filenames_vect);

%% Parameters
f=351; %recording frequence
dt=1/f;
pl=18.66/1024; %length of each pixel in mm
vsz=18.66/64;
p2mmv=pl*f;

%% load vector data
for vdata=1:numims
    v(vdata)=loadvec(filenames_vect{vdata});
end

%% calc mean x-velocity of each row
for a=1:47
    mvxr1=mean(v.vx(:,a).*p2mmv); % mean vx of row a
    mvxr(48-a)=mvxr1;
for a=1:47
    mvyr1=mean(v.vy(:,a).*p2mmv); % mean vx of row a
    mvyr(48-a)=mvyr1;
end

%% Plot
nt=0:vsz:vsz*(47-1);
figure(1)
plot(mvxr,nt,'-bd','LineWidth',1,...
     'MarkerEdgeColor','k','...
     'MarkerFaceColor','g','...
     'MarkerSize',3); title(['Mean V elocity in X diretion of each row']);xlabel('V elocity(mm/s)');ylabel('Distance(mm)');
figure(2)
plot(mvyr,nt,'-bd','LineWidth',1,...
     'MarkerEdgeColor','k','...
     'MarkerFaceColor','g','...
     'MarkerSize',3); title(['Mean V elocity in y diretion of each row']);xlabel('V elocity(mm/s)');ylabel('Distance(mm)');

Appendix 5 Matlab routine of analyzing the Kinematics of pumping polychaete worms.

close all; clear all; clc;

%% parameters
f=351;
si=3;
dt=(1/f)*3; %in second
ow=18.66; % size of observation window in mm
p2mm=ow/1024; %unit pixel length in mm

%% set directory
filefolder=fullfile('C:\Ruitao\Sync\Reseach\Matlab\','Raw data');
vectors_rimg=dir(fullfile(filefolder,'B*****.tif')); % read the raw images
filenames_rimg={vectors_rimg.name}';
numims=numel(filenames_rimg);

%% load pics
for b=1:numims
    I(:,:,b)= imread(filenames_rimg{b});
end

%% Choose pixels
X=zeros(6,numims);Y=zeros(6,numims);
for c=1:numims
    [x,y,p]=impixel(double(I(:,:,c))./20);
X(1:length(x),c)=round(x);
Y(1:length(y),c)=-round(y);
end

%%% Calc para angle
for na=1:numims
    if X(2,na)<X(5,na)
        xb(na)=X(2,na)+(X(5,na)-X(2,na))/2;
    else
        xb(na)=X(5,na)-(X(2,na)-X(5,na))/2;
    end
    if X(3,na)<X(4,na)
        xt(na)=X(3,na)+(X(4,na)-X(3,na))/2;
    else
        xt(na)=X(4,na)-(X(3,na)-X(4,na))/2;
    end
    if Y(2,na)<Y(5,na)
        yb(na)=Y(2,na)+(Y(5,na)-Y(2,na))/2;
    else
        yb(na)=Y(5,na)-(Y(2,na)-Y(5,na))/2;
    end
    if Y(3,na)<Y(4,na)
        yt(na)=Y(3,na)+(Y(4,na)-Y(3,na))/2;
    else
        yt(na)=Y(4,na)-(Y(3,na)-Y(4,na))/2;
    end
    angle=asin((abs(yt-yb))/sqrt((xb-xt).^2+(yb-yt).^2)); %use asin to calc angle
end

angle_deg=rad2deg(angle); %para angle relative to ground of each time step
for a1=1:(numims-1)
    if a1==1
        angle_deg_n(a1)=angle_deg(a1);
    elseif angle_deg(a1+1)<angle_deg(a1)
        angle_deg_n(a1)=180-angle_deg(a1+1);
    else
        angle_deg_n(a1)=angle_deg(a1+1);
    end
end
npangle=0:(4/351)*1000:(numims-1)*(4/351)*1000; %time step in ms
%angle polyfit%
anglex=1:numims;
ap=polyfit(anglex,angle_deg_n,a);
pangle_poly=polyval(ap,anglex);

%% Calc para angular velcoity w
for d=1:numims
    if d==1
        wp=(angle_deg_n(d+1)-angle_deg_n(d))/dt;
    elseif d==numims
        wp=(angle_deg_n(d)-angle_deg_n(d-1))/dt;
    else
        wp=(angle_deg_n(d+1)-angle_deg_n(d-1))/(2*dt);
    end
    w(d)=wp/360;
end % central time differencing scheme is used, angular velocity in rad/s
w_mean=sum(w)/length(w); %calc the average angular velocity

%%angular velocity polyfit%%
danglex=1:numims;
dap=polyfit(danglex,w,5);
w_poly=polyval(dap,danglex);

%%Calc velocity%%
for e=1:numims
    if e==1
        vtxp=abs((xt(e+1)-xt(e))/dt)*p2mm; %tip velocity in x direction in mm/s
        vtyp=(yt(e+1)-yt(e))/dt*p2mm; %tip velocity in y direction
        vbxp=abs((xb(e+1)-xb(e))/dt)*p2mm; %base velocity in x direction
        vbyp=abs((yb(e+1)-yb(e))/dt)*p2mm; %base velocity in y direction
    elseif e==numims
        vtxp=abs((xt(e)-xt(e-1))/dt)*p2mm; %tip velocity in x direction
        vtyp=(yt(e)-yt(e-1))/dt*p2mm; %tip velocity in y direction
        vbxp=abs((xb(e)-xb(e-1))/dt)*p2mm; %base velocity in x direction
        vbyp=abs((yb(e)-yb(e-1))/dt)*p2mm; %base velocity in y direction
    else
        vtxp=abs((xt(e+1)-xt(e-1))/(2*dt))*p2mm; %tip velocity in x direction
        vtyp=(yt(e+1)-yt(e-1))/(2*dt)*p2mm; %tip velocity in y direction
        vbxp=abs((xb(e+1)-xb(e-1))/(2*dt))*p2mm; %base velocity in x direction
        vbyp=abs((yb(e+1)-yb(e-1))/(2*dt))*p2mm; %base velocity in y direction
    end
    vtx(e)=vtxp;vty(e)=vtyp;vbx(e)=vbxp;vby(e)=vbyp;
end % central time differencing scheme is used

%%tip x-velocity polyfit%%
vtnx=1:numims;
vtap=polyfit(vtnx,vtx,2);
vtx_poly=polyval(vtap,vtnx);
vtx_mean = sum(vtx)/length(vtx); %calc the average tip velocity in x direction of one power stroke 
vty_mean = sum(vty)/length(vty); %calc the average tip velocity in y direction of one power stroke 
vbx_mean = sum(vbx)/length(vbx); %calc the average base velocity in x direction of one power stroke 
vby_mean = sum(vby)/length(vby); %calc the average base velocity in y direction of one power stroke 

%% Calc area 
for f=1:numims 
    parea(f)=polyarea(X([1:3],f).*p2mm,Y([1:3],f).*p2mm); %area of opening and closing in mm^2 
end 
narea=0:(4/351)*1000:(numims-1)*(4/351)*1000; %time step in ms 

%% area polyfit%% 
areax=1:numims; 
ap=polyfit(areax,parea,4); 
parea_poly=polyval(ap,areax); 

%%area changing 
for f1=1:numims 
    if f1==1 
        dparea(f1)=parea(f1+1)-parea(f1); 
    elseif f1==numims 
        dparea(f1)=parea(f1)-parea(f1-1); 
    else 
        dparea(f1)=(parea(f1+1)-parea(f1-1))/2; 
    end 
end 
dparea=abs(dparea)./(4/351); 

%%area change polyfit%% 
dareax=1:numims; 
dap=polyfit(dareax,dparea,5); 
dparea_poly=polyval(dap,dareax); 

%% Calc Reynolds number 
for h=1:numims 
    lparap=(sqrt((xt(h)-xb(h))^2+(yt(h)-yb(h))^2))*p2mm; %parapodium length in mm 
    pRe(h)= lparap*vtx(h);%((vtx(h)^2+vty(h)^2)^0.5); 
    lpara(h)=lparap; 
end 
mRe=sum(pRe)/length(pRe); %mean Re over a stroke 

figure; plot(npangle,angle_deg_n,'rs','MarkerFaceColor','g','MarkerSize',5); hold on; plot(npangle, pangle_poly);hold off;title('Parapodium angle relative to ground'); xlabel('Time(ms)'); ylabel('Angle(degree)'); 

figure; plot(npangle,w,'rs','MarkerFaceColor','g','MarkerSize',5); hold on; plot(npangle, w_poly);hold off; title('Parapodium angular velocity'); xlabel('Time step'); ylabel('W(rad/s)');
Appendix 6. Mean flow velocities and pump water estimation

clc; close all; clear all; clc;

%%% parameters
psz=18.9/1024; %pixel size in mm
vsz=18.9/64; %vector size in mm
fz=351; %frequency
dt=4/fz;
p2mmv=psz*fz; %pixel displacement to velocity in mm/s
sx=10; syu=5; syd=3; %set region size
density=0.001; %density of water in g/mm^3
parah=3; %the height of parapodium is 3mm

%%% Set directionary
filefolder=fullfile('C:\Ruitao\Research\Data\Research\data2\2009.01.12\vecytor_01_12');
vectors_rimg=dir(fullfile(filefolder,'B0****.tif')); % read the raw images
vectors_vect=dir(fullfile(filefolder,'B0****.VC7')); % read the vectors data
filenames_rimg={vectors_rimg.name}';
filenames_vect={vectors_vect.name}';
umims=numel(filenames_rimg);
umims_img=numel(filenames_rimg);

%%% load vector files
for a=1:numims
v(a) = loadvec(filenames_vect{a});
end

%%% load pics
for b=1:numims_img
I(:,:,b)= imread(filenames_rimg{b});
end

%% Choose pixels
[x,y,p]=impixel(double(I)./50);
X=round((x/1024)*64);
Y=round((y/1024)*64); % set the reference X,Y coordinates

%% set wave period
per1=[50:850]; per2=[850:1650]; per3=[1650:2450]; per4=[2450:3250];
ry=1:Y;
for c=1:numims
    vxm(c)=mean(mean(v(c).vx(:,ry).*p2mmv));
    vym(c)=mean(mean(v(c).vy(:,ry).*p2mmv));
end
mean_vx=mean(vxm(800:1600));

%% Pump water
pumpw1=sum(vxm(per1).*parah*(Y/64*18.9)*dt*density); % pump water in gram
pumpw2=sum(vxm(per2).*parah*(Y/64*18.9)*dt*density);
pumpw3=sum(vxm(per3).*parah*(Y/64*18.9)*dt*density);
pumpw4=sum(vxm(per4).*parah*(Y/64*18.9)*dt*density);
pumpw=[pumpw1,pumpw2,pumpw3,pumpw4];

plot(vxm(800:10:1600),'--bd','LineWidth',1,...
    'MarkerEdgeColor','k',...
    'MarkerFaceColor','g',...
    'MarkerSize',3); ylim([0 10]);
hold on;
plot(1:80,mean_vx,'--rd','LineWidth',2,...
    'MarkerEdgeColor','r',...
    'MarkerFaceColor','g',...
    'MarkerSize',3); hold off; title({'Mean Velocity over a body wave period'});
xlabel('time'); ylabel('Velocity(mm/s)');
plot(pumpw,'--bd','LineWidth',1,...
    'MarkerEdgeColor','k',...
    'MarkerFaceColor','g',...
    'MarkerSize',8); xlim([1 4]); ylim([0 3]); title({'Pump water of each period'}); xlabel('Period number'); ylabel('Water (gram)');

**Appendix 7 Matlab routine for calculating fluid Jet width**

clear all; close all; clc;
% set parameters
rr=351; %SET THE recording rate
ws=18.66; % recording window size in mm
dt=1/rr;

%set the threshold value for jet height

tn=80; %set the range in y on which calc.

%calc d(w)/dt=(d(t+jra)-d(t))/(jra*dt)

%set folder

filefolder=fullfile('F:\Research\PIV data\Worm\Freely swimming\PIV\Data set for analyze\Vectors\','Vectors_No9_free_swimming_1');

vectors_vect=dir(fullfile(filefolder,'B0****.VC7')); % read the vectors data

filenames_vect=(vectors_vect.name);

%load vector data

numims=numel(filenames_vect);

vectors_data=

for vdata=1:numims
    v(vdata)=loadvec(filenames_vect{vdata});
end

%wave1=[40:820];wave2=[820:1600];wave3=[1600:2380];wave4=[2380:3160]; %set the one para stroke range

%calc sum x-velocity of each row

for a=1:numims
    for b=ry
        svxrp=sum(v(a).vx([1:64],b)); % sum of vx of row b
        svxr(b)=svxrp;
    end
    svxrt(a,:)=svxr; % matrix of vx of each row of each picture
end

%Calc jet height

for d=1:numims
    jhp=0;
    for c=ry
        if svxrt(d,c)>tn
            jhp=jhp+1;
        end
    end
    jh(d)=(jhp/64)*ws; %width in mm
end

%first deviation of jet height (polyfit)

for d=1:numims-jra-1
    if d==1
        djhp=(jh(d+jra)-jh(d))/(jra*dt);
    elseif d==numims
        djhp=(jh(d)-jh(d-1))/dt;
    else
        djhp=(jh(d+jra)-jh(d))/dt;
    end
%     djhp=(jh(d+jra)-jh(d))/(jra*dt);
%     djh(d)=djhp;
end

djh=1:length(djh);
dap=polyfit(ndjh,djh,20);
djht=polyval(dap,ndjh);

%% Plot
close all;
nt=0:5*dt:(numims-1)*dt;
n1=0:5*dt:(numims-jra-2)*dt;
figure(1);
plot(nt,jh(1:5:numims),'-bd','LineWidth',1,...
     'MarkerEdgeColor','k','...
     'MarkerFaceColor','g','...
     'MarkerSize',2); ylim([0 13]);
title(["Width of Flow Jet over time"]);xlabel('Time step(s)');ylabel('Jet Width(mm)');
figure(2);hist(jh);
title(["Distribution of Jet Width" ]);xlabel('Width(mm)');ylabel('Distribution');
figure(3);plot(nt1,djh(1:5:numims-jra-1),'bd','LineWidth',1,...
     'MarkerEdgeColor','k','...
     'MarkerFaceColor','g',...
     'MarkerSize',2); hold on; plot(nt1,djht(1:5:numims-jra-1));hold off;
title(["First derivative of jet width with its polyfit" ]);xlabel('Time step(s)');ylabel('derivative of jet width');

Appendix 8. Matlab routine of the velocity analysis of an area following a cycling parapodium.

close all; clear all; clc;

  %% set directory
  filefolder=fullfile('C:\Ruitao\Sync\Research\Matlab\', 'Raw data');
  vectors_rimg=dir(fullfile(filefolder,'B0****.tif')); % read the raw images
  vectors_vect=dir(fullfile(filefolder,'B0****.VC7')); % read the vectors data
  filenames_rimg={vectors_rimg.name}';
  filenames_vect={vectors_vect.name}';
  numims=numel(filenames_vect);
  numims_img=numel(filenames_rimg);
  %% parameters
  psz=18.9/1024; %pixel size in mm
vsz=18.9/64; %vector size in mm
fz=351; %frequency
p2mmv=psz*fz; %pixel displacement to velocity in mm/s
sx=10; syu=5; syd=3; %set region size

%% load vector files
for a=1:numims
    vf(a) = loadvec(filenames_vect{a});
end

%% load pics
for b=1:numims_img
    I(:,:,b)= imread(filenames_rimg{b});
end

%% Choose pixels
X=zeros(1,numims);Y=zeros(1,numims);
for c=1:numims
    [x,y,p]=impixel(double(I(:,:,c))./50);
    X(1:length(x),c)=round((x/1024)*64);
    Y(1:length(y),c)=round((y/1024)*64);
end

%% Calc
for d=1:numims
    r1x=X(d)-sx:X(d);
    r1y= Y(d)-syu:Y(d)+syd;%set region 1
    r2x=X(d):X(d)+sx;
    r2y= Y(d)-syu:Y(d)+syd;%set region 2

    r1vx=vf(d).vx(r1x,r1y);
    r1vy=vf(d).vy(r1x,r1y);
    r2vx=vf(d).vx(r2x,r2y);
    r2vy=vf(d).vy(r2x,r2y);

    sr1vx(d)=mean(mean(r1vx))*p2mmv;
    sr1vy(d)=mean(mean(r1vy))*p2mmv;
    sr2vx(d)=mean(mean(r2vx))*p2mmv;
    sr2vy(d)=mean(mean(r2vy))*p2mmv;% mean velocity in the region 1 & 2
end

e=1; % choose which picture
for ax=X(e)-sx:X(e)+sx
    r1y= Y(d)-sy:Y(d);
    pvx(ax)=mean(vf(e).vx(ax,r1y))*p2mmv;
\[ \text{pvy(ax)} = \text{mean} (v(t(e)).vy(ax,t1y)) \times p2mmv; \]

\[ \text{pxc} = 0 \times \text{vsz} : 1 \times \text{vsz} : (sx \times 2) \times \text{vsz}; \% \text{set the coordinate for plot in mm} \]

\[ \% \% \text{ plot} \]

\[ \text{figure} \]

\[ \text{subplot}(2,1,1); \text{plot}(sr1vx,'--gd','LineWidth',2,... 'MarkerEdgeColor','k',.... 'MarkerFaceColor','g',.... 'MarkerSize',10); \text{title}(['\text{Sum vx in region 1}']); \text{xlabel}('timestep');\text{ylabel}('svx'); \]

\[ \text{subplot}(2,1,2); \text{plot}(sr1vy,'--gd','LineWidth',2,... 'MarkerEdgeColor','k',.... 'MarkerFaceColor','g',.... 'MarkerSize',10); \text{title}(['\text{Sum vy in region 1}']); \text{xlabel}('timestep');\text{ylabel}('svy'); \]

\[ \text{figure} \]

\[ \text{subplot}(2,1,1); \text{plot}(sr2vx,'--gd','LineWidth',2,... 'MarkerEdgeColor','k',.... 'MarkerFaceColor','g',.... 'MarkerSize',10); \text{title}(['\text{Sum vx in region 2}']); \text{xlabel}('timestep');\text{ylabel}('svx'); \]

\[ \text{subplot}(2,1,2); \text{plot}(sr2vy,'--gd','LineWidth',2,... 'MarkerEdgeColor','k',.... 'MarkerFaceColor','g',.... 'MarkerSize',10); \text{title}(['\text{Sum vy in region 2}']); \text{xlabel}('timestep');\text{ylabel}('svy'); \]

\[ \text{figure} \]

\[ \text{subplot}(2,1,1); \text{plot}(pxc,pvx(X(e)-sx:X(e)+sx),'--gd','LineWidth',2,... 'MarkerEdgeColor','k',.... 'MarkerFaceColor','g',.... 'MarkerSize',10); \text{title}(['\text{Position as a function of position}']); \text{xlabel}('Position(mm)');\text{ylabel}('Velocity in X(mm/s)'); \]

\[ \text{subplot}(2,1,2); \text{plot}(pxc,pvy(X(e)-sx:X(e)+sx),'--gd','LineWidth',2,... 'MarkerEdgeColor','k',.... 'MarkerFaceColor','g',.... 'MarkerSize',10); \text{xlabel}('Position(mm)');\text{ylabel}('Velocity in Y(mm/s)'); \]

**Appendix 9. Matlab routine of fluid acceleration of pumping polychaete worms.**

\[ \text{clc; close all; clear all;clc; } \]

\[ \% \% \text{ parameters} \]

\[ \text{psz} = 18.9/1024; \% \text{pixel size in mm} \]

\[ \text{vsz} = 18.9/64; \% \text{vector size in mm} \]

\[ \text{fz} = 351; \% \text{frequency} \]

\[ \text{dt} = 4/\text{fz}; \]

\[ \text{p2mmv} = \text{psz} \times \text{fz}; \% \text{pixel displacement to velocity in mm/s} \]
sx=10; syu=5; syd=3; % set region size

% Set directory
filefolder = fullfile('C:\\Ruitao\\Sync\\Research\\Matlab\\', 'Raw data');

vectors_rimg = dir(fullfile(filefolder, 'B0****.tif')); % read the raw images
vectors_vect = dir(fullfile(filefolder, 'B0****.VC7')); % read the vectors data

filenames_rimg = {vectors_rimg.name}';
filenames_vect = {vectors_vect.name}';

numims = numel(filenames_vect);
numims_img = numel(filenames_rimg);

% load vector files
for a = 1:numims
    v(a) = loadvec(filenames_vect{a});
end

% load pics
for b = 1:numims_img
    I(:,:,b) = imread(filenames_rimg{b});
end

% Choose pixels
[x, y, p] = impixel(double(I)./50);
X = round((x/1024)*64);
Y = round((y/1024)*64); % set the reference X, Y coordinates

% Calc
% Set the interested region in which data processed
rx = X - sx: X + sx;
ry = Y - syu: Y + syd;

% Calc a
for nt = 1:numims
    if nt == 1
        partax = (v(nt+1).vx(rx, ry) - v(nt).vx(rx, ry)) * p2mmv/dt; % in x direction at time t for edge data
        partay = (v(nt+1).vy(rx, ry) - v(nt).vy(rx, ry)) * p2mmv/dt; % in y direction at time t
    elseif nt == numims
        partax = (v(nt).vx(rx, ry) - v(nt-1).vx(rx, ry)) * p2mmv/dt; % in x direction at time t for edge data
        partay = (v(nt).vy(rx, ry) - v(nt-1).vy(rx, ry)) * p2mmv/dt; % in y direction at time t
    else
        partax = (v(nt+1).vx(rx, ry) - v(nt-1).vx(rx, ry)) * p2mmv/(2*dt); % in x direction at time t for rest
        partay = (v(nt+1).vy(rx, ry) - v(nt-1).vy(rx, ry)) * p2mmv/(2*dt); % in y direction at time t
    end
end

% gradient(v)*v
[dux duy] = gradient(v(nt).vx(rx, ry)*p2mmv); %, v(nt).x(rx)*psz, v(nt).y(ry)*psz);
[dvx dvy] = gradient(v(nt).vy(rx, ry)*p2mmv); %, v(nt).x(rx)*psz, v(nt).y(ry)*psz);

partbx = dux.*v(nt).vx(rx, ry)*p2mmv + duy.*v(nt).vy(rx, ry)*p2mmv; % zeros(64, 64);
partby=dvx.*v(nt).vx(rx,ry)*p2mmv+dvy.*v(nt).vy(rx,ry)*p2mmv;%zeros(64,64);

%%%acceleration%%%
acrtx(nt)=mean(mean(partax+partby)); %in mm^2/s
acrty(nt)=mean(mean(partay+partby)); %in mm^2/s
end
macrtx=mean(acrtx);
macrty=mean(acrty);
figure;
pxc=0:1*4/fz*1000:(numims-1)*4/fz*1000; %define the x-coordinate, time in mm
subplot(2,1,1); plot(pxc,acrtx,'--gd','LineWidth',2,...
    'MarkerEdgeColor','k',....
    'MarkerFaceColor','g',....
    'MarkerSize',10); title(['X-direction Acceleration in region around cycling para']);
xlabel('Time(ms)');ylabel('Acceleration(mm^2/s)');
subplot(2,1,2); plot(acrty,'--gd','LineWidth',2,...
    'MarkerEdgeColor','k',....
    'MarkerFaceColor','g',....
    'MarkerSize',10); title(['Y-direction Acceleration in region around cycling para']);
xlabel('Time(ms)');ylabel('Acceleration(mm^2/s)');

Appendix 10. Study of area changing between two adjacent parapodia and mass of water

close all; clear all; clc;
% set directory
filefolder=fullfile('C:\Ruitao\Sync\Research\Matlab\','Raw data');
vectors_rimg=dir(fullfile(filefolder,'B0****.tif')); % read the raw images
vectors_vect=dir(fullfile(filefolder,'B0****.VC7')); % read the vectors data
filenames_rimg={vectors_rimg.name}';
filenames_vect={vectors_vect.name}';
umims=numel(filenames_vect);
umims_img=numel(filenames_rimg);
% parameters
psz=18.9/1024/1000; %pixel size in m
vsz=18.9/64/1000; %vector size in m
fz=351; %frequency
dt=(1/fz)*5; %dt in s
p2mmv=psz*fz; %pixel displacement to velocity in mm/s
sx=8;syu=4; syd=3;%set region size
density=1000; %density of water in kg/m^3
ga=10; %m/s^2
% high of para in meter
parah = 5 / 1000;

% load vector files
for a = 1:numims
    vf(a) = loadvec(filenames_vect{a});
end

% load pics
for b = 1:numims_img
    I(:, :, b) = imread(filenames_rimg{b});
end

% Choose pixels
X = zeros(6, numims); Y = zeros(6, numims);
for c = 1:numims
    [x, y, p] = impixel(double(I(:, :, c))./5);
    X(1:length(x), c) = round((x/1024)*64);
    Y(1:length(y), c) = round((y/1024)*64);
end

% calc closed area
px_area = Y([2:5], :).*vsz; py_area = X([2:5], :).*vsz; % poly boundary of closing area
px_inlet = Y([1 2 5 6], :); py_inlet = X([1 2 5 6], :); % define inlet boundary
for d = 1:numims
    area(d) = polyarea(px_area(:, d), py_area(:, d)); % calc area of poly in mm^2
    angle_inlet = asin((Y(5, d) - Y(2, d))/(X(2, d) - X(5, d))); % calc inlet boundary angle
    l_inlet = sqrt((Y(5, d) - Y(2, d))^2 + (X(2, d) - X(5, d))^2)*vsz; % calc inlet length
    vfvx = vf(d).vx.*p2mmv;
    vnx_inlet = roipoly(vfvx, px_inlet(:, d), py_inlet(:, d)); % define mask poly
    vnewx_inlet = vfvx.*vnx_inlet; % delete elements outside mask
    naa = 0;
    for d1 = 1:64
        for d2 = 1:64
            if vnewx_inlet(d1, d2) ~= 0
                naa = naa + 1;
            else
                nna = nna;
            end
        end
    end
    avnewx_inlet = sum(sum(vnewx_inlet))/naa; % mean velocity in x in the closing area
    vfvy = vf(d).vy.*p2mmv;
    vny_inlet = roipoly(vfvy, px_inlet(:, d), py_inlet(:, d)); % define mask poly
    vnewy_inlet = vfvy.*vny_inlet; % delete elements outside mask
    nna = 0;
    for d1 = 1:64
        for d2 = 1:64
            if vnewy_inlet(d1, d2) ~= 0
                naa = naa + 1;
            else
                nna = nna;
            end
        end
    end
    avnewy_inlet = sum(sum(vnewy_inlet))/naa; % mean velocity in y in the closing area

end
\( \text{avnewy}_{\text{inlet}}(d) = \frac{\text{sum(\text{sum(vnewy}_{\text{inlet}}))}}{\text{naa}}; \) % mean velocity in y in the closing area

\( \text{vinlet} = \text{avnewx}_{\text{inlet}} \times \sin(\text{angle}_{\text{inlet}}) + \text{avnewy}_{\text{inlet}} \times \cos(\text{angle}_{\text{inlet}}); \) % mean inlet boundary velocity

\( \text{m}_{\text{water}}(d) = \text{vinlet}(d) \times \text{dt*1\_inlet} \times \text{density} \times \text{ga} \times \text{parah} \times 1000; \) % fluid through boundary

end

nplot = 0:dt*1000:(\text{numims}-1)*dt*1000; % for plot the x coordinate
% calc mass of fluid by area changing in g
for e = 1:numims
    if e == 1
        \( \text{darea}(e) = (\text{area}(e+1) - \text{area}(e)) \times \text{density} \times \text{ga} \times \text{parah} \times 1000; \) % for edge data
    elseif e == numims
        \( \text{darea}(e) = (\text{area}(e) - \text{area}(e-1)) \times \text{density} \times \text{ga} \times \text{parah} \times 1000; \) % for edge data
    else
        \( \text{darea}(e) = (\text{area}(e+1) - \text{area}(e-1)) \times \text{density}/2 \times \text{ga} \times \text{parah} \times 1000; \) % for edge data
    end
end

%%mwater polyfit%%
\( \text{mwaterx} = 1: \text{numims}; \)
\( \text{mwaterp} = \text{polyfit}(\text{mwaterx}, \text{m}_{\text{water}}, 5); \)
\( \text{mwater\_poly} = \text{polyval}(\text{mwaterp}, \text{mwaterx}); \)

%%area polyfit%%
\( \text{areax} = 1: \text{numims}; \)
\( \text{areap} = \text{polyfit}(\text{areax}, \text{area}, 4); \)
\( \text{area\_poly} = \text{polyval}(\text{areap}, \text{areax}); \)

%%darea polyfit%%
\( \text{dareax} = 1: \text{numims}; \)
\( \text{dareap} = \text{polyfit}(\text{dareax}, \text{darea}, 4); \)
\( \text{darea\_poly} = \text{polyval}(\text{dareap}, \text{darea}); \)

%% plot
\( \text{figure} \)
\( \text{subplot}(2,1,1); \) plot(nplot,\( \text{area} \times 1000 \times 1000, 'rd', 'MarkerFaceColor', 'g', 'MarkerSize', 5); hold on;
\( \text{plot}(\text{nplot}, \text{area\_poly} \times 1000 \times 1000); \) hold off; title(['Area']);
\( \text{xlabel('timestep(ms)'); ylabel('Area(mm^2)');} \)
\( \text{subplot}(2,1,2); \) plot(nplot,\( \text{m}_{\text{water}}', 'rd', 'MarkerFaceColor', 'g', 'MarkerSize', 5); hold on;
\( \text{plot}(\text{nplot}, \text{mwater\_poly}); \) hold off; title(['Fluid through boundary']);
\( \text{xlabel('timestep(ms)'); ylabel('Mass(g)');} \)
\( \text{figure} \)
\( \text{subplot}(2,1,1); \) plot(nplot,\( \text{darea}, 'rd', 'MarkerFaceColor', 'g', 'MarkerSize', 5); hold on;
\( \text{plot}(\text{nplot}, \text{darea\_poly}); \) hold off; title(['Fluid mass by area changing']);
\( \text{xlabel('timestep(ms)'); ylabel('Mass(g)');} \)
\( \text{subplot}(2,1,2); \) plot(nplot,\( \text{m}_{\text{water}}, 'rd', 'MarkerFaceColor', 'g', 'MarkerSize', 5); hold on;
\( \text{plot}(\text{nplot}, \text{mwater\_poly}); \) hold off;
Appendix 11 Mechanical model controller software

Visual Basic interface.

Figure A-1. The main window of the controller user interface. Before measurements, the frequency and amplitude are set to define the movement of the paddles. Then press the START, paddles will start to move. The set of bars on the top present the angle of paddles.

Figure A- shows the visual basic window interface of the controller program. The vertical bars in the top part of the window indicate the real angle of each individual paddle. The text boxes just below them show the angle values. Two vertical bars are the parameter setting buttons. Frequency defines the wave frequency and amplitude button sets the wave amplitude. Four buttons on the right side give the functions of starting the paddle model, stop model, centering each paddle and exiting the program.

Visual Basic routine of controlling the paddle model system.

Dim n As Double
Dim I As Double
Dim d As Double
Dim nr As Double
Dim cs As Double
Dim Amplitude As Double
Dim pc As Double
Dim dd As Double
Dim dd1 As Double
Dim cc As Double
Dim f As Double
Const Pi = 3.14159265358979
Dim S As Double 'section number
Private Sub Command1_Click()
    Timer1.Enabled = True
End Sub

Private Sub Command2_Click()
    If MSComm1.PortOpen = True Then
        MSComm1.PortOpen = False
    End If
End
End Sub

Private Sub Command3_Click()
    Timer1.Enabled = False
End Sub

Private Sub Command4_Click()
    'centre
    Timer1.Enabled = False

    For dd = 0 To 32
        MSComm1.Output = "#" & dd & "A" & "90" & "!
    Next dd

    For dd1 = 0 To 7
        VScroll1(dd1).Value = Str(90)
        Text1(dd1).Text = Str(90)
    Next dd1
End Sub

Private Sub Form_Load()
    MSComm1.Settings = "115200,n,8,1"
    MSComm1.CommPort = 4
    MSComm1.PortOpen = True
    Timer1.Enabled = False
    Timer1.Interval = 10
    S = 8 'set paddle numbers
    n = 0
    Amplitude = 0
    f = 1 / 500
    nr = 500 'set the step n range
    pc = 90 'set centre position
Text2.Text = Str(0)
Text3.Text = Str(0)
'For cc = 8 To 32
'MSCOMM1.Output = "#" & cc & "A" & "90" & "!"
'Next cc
End Sub

Private Sub HScroll1_Change()
Amplitude = HScroll1.Value
Text2.Text = Str(HScroll1.Value)
End Sub

Private Sub HScroll2_Change()
Timer1.Interval = HScroll2.Value
Text3.Text = Str(HScroll2.Value)
End Sub

Private Sub Timer1_Timer()
'tstep = 5
tstep = 1
If n <= nr Then
'1
  J2 = Round(pc - Amplitude * Sin(2 * f * Pi * n) - Amplitude, 1)
  VScroll1(0).Value = Str(J2)
  Text1(0).Text = Str(J2)
  MSComm1.Output = "#08A" & J2 & "!" 'paddle 1
  MSComm1.Output = "#16A" & J2 & "!" 'paddle 9
  MSComm1.Output = "#24A" & J2 & "!" 'paddle 17
'2
  J3 = Round(pc - Amplitude * Sin(2 * f * Pi * n + (2 * Pi) / S) - Amplitude, 1)
  VScroll1(1).Value = Str(J3)
  Text1(1).Text = Str(J3)
  MSComm1.Output = "#09A" & J3 & "!"
  MSComm1.Output = "#17A" & J3 & "!"
  MSComm1.Output = "#25A" & J3 & "!"
'3
  J4 = Round(pc - Amplitude * Sin(2 * f * Pi * n + 2 * (2 * Pi) / S) - Amplitude, 1)
  VScroll1(2).Value = Str(J4)
  Text1(2).Text = Str(J4)
  MSComm1.Output = "#10A" & J4 & "!"
  MSComm1.Output = "#18A" & J4 & "!"
  MSComm1.Output = "#26A" & J4 & "!"
'4
J5 = Round(pc - Amplitude * Sin(2 * f * Pi * n + 3 * (2 * Pi) / S) - Amplitude, 1)
VScroll1(3).Value = Str(J5)
Text1(3).Text = Str(J5)
MSCmm1.Output = "#11A" & J5 & "!"
MSComm1.Output = "#19A" & J5 & "!"
MSComm1.Output = "#27A" & J5 & "!"
'5
J6 = Round(pc - Amplitude * Sin(2 * f * Pi * n + 4 * (2 * Pi) / S) - Amplitude, 1)
VScroll1(4).Value = Str(J6)
Text1(4).Text = Str(J6)
MSComm1.Output = "#00A" & J6 & "!"
MSComm1.Output = "#01A" & J6 & "!"
MSComm1.Output = "#02A" & J6 & "!"
'6
J7 = Round(pc - Amplitude * Sin(2 * f * Pi * n + 5 * (2 * Pi) / S) - Amplitude, 1)
VScroll1(5).Value = Str(J7)
Text1(5).Text = Str(J7)
MSComm1.Output = "#13A" & J7 & "!"
MSComm1.Output = "#21A" & J7 & "!"
MSComm1.Output = "#29A" & J7 & "!"
'7
J8 = Round(pc - Amplitude * Sin(2 * f * Pi * n + 6 * (2 * Pi) / S) - Amplitude, 1)
VScroll1(6).Value = Str(J8)
Text1(6).Text = Str(J8)
MSComm1.Output = "#14A" & J8 & "!"
MSComm1.Output = "#22A" & J8 & "!"
MSComm1.Output = "#30A" & J8 & "!"
'8
J9 = Round(pc - Amplitude * Sin(2 * f * Pi * n + 7 * (2 * Pi) / S) - Amplitude, 1)
VScroll1(7).Value = Str(J9)
Text1(7).Text = Str(J9)
MSComm1.Output = "#15A" & J9 & "!"
MSComm1.Output = "#23A" & J9 & "!"
MSComm1.Output = "#31A" & J9 & "!"
n = n + tstep
Else
n = 0
End If
End Sub