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1. REPORT DATE (DD-MM-YYYY) 13-02-2019	2. REPORT TYPE Final Report	3. DATES COVERED (From - To) 22-Sep-2015 - 21-Aug-2018
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6. AUTHORS	5d. PROJECT NUMBER
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7. PERFORMING ORGANIZATION NAMES AND ADDRESSES University of North Carolina - Chapel Hill 104 Airport Drive, CB 1350 Suite 2200 Chapel Hill, NC 27599 -1350	8. PERFORMING ORGANIZATION REPORT NUMBER
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13. SUPPLEMENTARY NOTES The views, opinions and/or findings contained in this report are those of the author(s) and should not be construed as an official Department of the Army position, policy or decision, unless so designated by other documentation.
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14. ABSTRACT
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15. SUBJECT TERMS
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a. REPORT UU	b. ABSTRACT UU	c. THIS PAGE UU	19b. TELEPHONE NUMBER 919-549-4254

# RPPR Final Report

## as of 13-Feb-2019

Agency Code:

Proposal Number: 67782MASR

Agreement Number: W911NF-15-2-0125

### INVESTIGATOR(S):

**Name:** Program Manager Virginia B. Pasour

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**Report Date:** 21-Nov-2018

Date Received: 13-Feb-2019

**Final Report** for Period Beginning 22-Sep-2015 and Ending 21-Aug-2018

**Title:** Mathematical Modeling of Macrophyte-flow Interactions and the Resulting Zooplankton

**Begin Performance Period:** 22-Sep-2015

**End Performance Period:** 21-Aug-2018

**Report Term:** 0-Other

Submitted By: Program Manager Virginia Pasour

Email: virginia.b.pasour.civ@mail.mil

Phone: (919) 549-4254

**Distribution Statement:** 1-Approved for public release; distribution is unlimited.

**STEM Degrees:** 2

**STEM Participants:** 6

**Major Goals:** The broad goal of this research project is to develop mathematical models, implement new numerical methods, and leverage existing state-of-the-art tools from computational and experimental fluid dynamics to understand the importance of aquatic plants in modifying the environment of small organisms. Such plants we will describe generally as macrophytes, which include sea grasses, submerged freshwater plants, and emergent vegetation. It is well known that the fluid dynamics within and around macrophyte beds have important ecological consequences on organisms, and these organisms also affect the hydrodynamics within these environments. Modeling flow within macrophyte beds is challenging due to the complex morphologies and material properties of these organisms. Flow properties can vary dramatically in space and time through such layers, and simplified models may not accurately capture mixing dynamics, particle paths, and other flow features important to zooplankton. Recent improvements in scientific computing have made numerical simulations of viscous and unsteady flows through complex and flexible structures feasible. The broad goals of this proposal are to develop new models of macrophytes and zooplankton and to incorporate these models with fluid-structure interaction simulations to reveal the properties of flows within these complex environments and to determine the impact on zooplankton distributions.

### Specific Objectives

The overall objectives of this project are as follows:

Aim 1: Determine how macrophyte height, flexibility, and density affect flow and mixing near the substrate using computational and experimental fluid dynamics.

Aim 2: Develop reduced order models that can be solved analytically to describe the flow through macrophyte beds and to test when such models are reasonable.

Aim 3: Determine how the presence of macrophytes enhance or reduce flow, the amount and mixing, and the distribution of zooplankton.

Specific subprojects are listed in Figure 1. The darker green boxes represent the main research thrusts, while the lighter green represent subprojects within each research area. The overarching goal of the project is to predict the resulting plankton distributions based on flow fields, presence of macrophytes, and plankton behavior. The main mathematical components of the project include 1) computational fluid dynamics to resolve the flow around the macrophytes, 2) the development of reduced order models of the flow, 3) the development of models of zooplankton movement, 4) simulations to determine the effect of zooplankton movement of flow, and experimental validation of the fluid and zooplankton models.

Figure 1. Project map highlighting how the various components of the project will be integrated to determine how

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**Accomplishments:** Given the relatively small amount of work at the mesoscale, we have focused on the effects of small (1 mm - 1 cm) scale vegetative and coral structures on flow. Such mesoscale structures and protective layers are replete throughout the natural world and provide protective layers for micro-organisms. For example, trichomes (the hairs or fine outgrowths on plants) can drastically alter both the average flow speed and profile near a leaf's surface, affecting the rates of nutrient and heat exchange. These layers can also affect the settlement and dispersal of microscopic plankton that live on vegetative structures and within coral reefs. Characterizing the flow profiles through such layers is therefore critical towards understanding the function and diversity of small branches, hairs, and bristles.

**Aim 1:** Determine how macrophyte height, flexibility, and density affect flow and mixing near the substrate using computational and experimental fluid dynamics.

We have used dynamically scaled physical models to study the flow profiles outside of arrays of cylinders that represent such filtering and protective layers. 3D numerical simulations using the Immersed Boundary Method were used to resolve the three-dimensional flows within the layers. Physical models using arrays of pins as well as 3D printed models were used to resolve the flow outside of these layers. The numerical results demonstrate three-dimensional flows into and out of the layer that are not described by the Brinkman model (discussed in Aim 2) and may be significant for biologically relevant volume fractions. The Brinkman model does, however, do a good job describing the flows outside of the layers as well as the spatially averaged flow within the layers. The results can be used to understand how variations in density and height of such structures can alter mixing and bulk flows.

Figure: Comparison of numerical simulation results to the theoretical model. Dots show the averaged x-component of the velocity as a function of height for different densities of macrophytes. The dashed black lines show the best fit Brinkman model.

Figure: Velocity vector fields taken along planes parallel to the direction of flow at  $Re = 1$ . Note the three-dimensionality of the flow that is not captured by the analytical model. These flows may be relevant to zooplankton.

**Aim 2:** Develop reduced order models that can be solved analytically to describe the flow through macrophyte beds and to test when such models are reasonable.

The computational and experimental results given in Aim 1 have been compared to theoretical results obtained by modeling the layer as a Brinkman medium matched to flow within and above the layer. More specifically, we compare the results of the spatially averaged flow in the physical and numerical models as a function of height to the 1D analytical model. We fit the data to the Brinkman model using nonlinear least squares to find the best choice of porosity. The 3D simulations and analytical results are consistent and give the same flow profiles for the x-component of the average velocity and height,  $z$ . Moreover, from finding the best fit porosity coefficient for the analytical model, it appears that, as the height of the tower increases, the porosity coefficient decreases. This is consistent with the results from the experiments, which showed that the best fit value of  $\alpha$  decreased as the height of the cylinders was increased. At this scale ( $0.1 < Re < 10$ ), the model does an excellent job describing average flow rates, though it does not capture vertical flow within the layer itself.

**Aim 3:** Determine how the presence of macrophytes enhance or reduce flow, the amount and mixing, and the distribution of zooplankton.

Christopher Strickland (ARO funded postdoctoral fellow now faculty at UTK) has developed a general framework for simulating the passive and active movement of plankton within a given flow field (which may be spatially and temporally varying). One part of the movement of plankton is passive: the organisms move at the local fluid velocity. A second component is active, the plankton can move either purely randomly with a prescribed effective diffusivity or with a bias that is based on local flow conditions or chemical gradients. Currently, the movement of the plankton does not alter the flow fields, but the flow fields do advect the plankton. The active movement of plankton is superimposed upon the background flow field. The agent based code is available on github at the site <https://github.com/mountainindust/Planktos>.

Figure: Theoretical positions of individual brine shrimp within and above a protective layer with background flow. The histograms show the number of brine shrimp within each spatial position.

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Simultaneously, graduate student Kemal Ozalp and a team of 7 undergraduates are measuring the flow fields around physical models of macrophytes, releasing brine shrimp within these layers. The effective diffusivity of the brine shrimp is measured in a quiescent fluid. The brine shrimp are then released as a point source in a protective layer immersed in a moving fluid. Kemal then tracks the spatially and temporally varying densities of brine shrimp within and outside of the layer. Please see the attached Appendix which details the experimental protocol developed by Kemal for this work.

Additional work in code and infrastructure development

Code development:

Miller and Pasour have been working with Nick Battista to develop and expand a 2D MATLAB and Python implementation of the immersed boundary method, `ib2d`. This software package allows the user to implement various elastic and porous models of 1D boundaries. Muscle and neural activation models are also available, and users can now easily incorporate electrostatic forces, chemical bonds, and massive boundaries. More information can be found here:

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Construction of large flow tank:

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Current and future work

**Aim 1:** Determine how macrophyte height, flexibility, and density affect flow and mixing near the substrate using computational and experimental fluid dynamics.

We continue to extend the mesoscale work at  $0.1 < Re < 10$  to higher Reynolds numbers ( $1,000 < Re < 100,000$ ) using turbulence models in OpenFOAM. OpenFOAM is an open source software library that supports a large variety of tools for computational fluid dynamics. Covering this large range of scales will allow us to describe how fluid physics changes from the scale of flow around individual trichomes/hairs to the scale of flow around large beds of seagrass and other macrophytes. This will also allow us to simulate the dispersal and movement of plankton across a large range of scales, from movement between macrophyte beds to settlement on a single leaf.

**Aim 2:** Develop reduced order models that can be solved analytically to describe the flow through macrophyte beds and to test when such models are reasonable.

The Brinkman model used at the mesoscale will be tested at the larger scales described above. We will also compare our spatially resolved numerical and experimental results to the simplified flows described by other models, such as those outlined in the reference below:

Lowe, R., Shavit, U., Falter, J. L., Koseff, J. R. and Monismith, S. G. (2008). Modeling flow in coral communities with and without waves: A synthesis of porous media and canopy flow approaches. *Limnol. Oceanogr.*, 53(6), 2668–2680.

**Aim 3:** Determine how the presence of macrophytes enhance or reduce flow, the amount and mixing, and the distribution of zooplankton.

The flow fields described above will be u

**Training Opportunities:** This project funded one mathematics postdoctoral fellow, Christopher Strickland. Dr. Strickland is now an Associate Professor at the University of Tennessee Knoxville.

Nick Battista (UNC mathematics graduate student), Kemal Ozalp, (UNC biology graduate student), and Michael Senter (UNC mathematics graduate student) also contributed to the project. Battista and Senter assisted with the development of immersed boundary and data analysis code. Kemal Ozalp assisted with the zooplankton and flow experiments. Nick Battista is now an Assistant Professor of Mathematics at the College of New Jersey.

Seven undergraduates have also worked on the experimental component of the project. This work will be incorporated into the mathematics honors thesis of Maddie Bray.

## RPPR Final Report as of 13-Feb-2019

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Miller, L. A. Plant Leaves Reconfigure into Cone Shapes to Reduce Drag and Flutter. The 68th Annual Meeting of the APS Division of Fluid Dynamics, Boston, MA, November 22-24, 2015.

Miller, L. A. Reconfiguration of broad leaves to reduce drag and flutter. Investigative Workshop Morphological Plant Models. National Institute for Mathematical and Biological Synthesis. Knoxville, TN, September 4, 2015.

### Symposia and workshops

Pasour along with Julia Samson (UNC Biology Graduate Student) and Brian White (UNC Marine Science Faculty) editing a volume for the Frontiers Research Topics Journal on the results from a symposium they organized at the 2017 ASLO Annual Meeting in Honolulu, Hawaii, February 26-March 3, 2017. The title of the symposium was "Canopies in aquatic ecosystems: integrating form, function, and biophysical processes."

Publications, submissions, and in-prep

## RPPR Final Report as of 13-Feb-2019

Battista, N. A. ‡, Strickland, C. S.\*, Miller, L. A. (2017). IB2d Reloaded: a more powerful Python and MATLAB implementation of the immersed boundary method. *Mathematical Methods in the Applied Sciences*, <https://doi.org/10.1002/mma.4708>, 1–26.

Christopher Strickland, Laura Miller, Arvind Santhanakrishnan, Christina Hamlet, Nicholas A. Battista and Virginia Pasour (2017). Three-Dimensional Low Reynolds Number Flows near Biological Filtering and Protective Layers. *Fluids*, 2(4), 62; <https://doi.org/10.3390/fluids2040062>

Strickland, C., Miller, L. A., Santhanakrishnan, A. et al. The fluid physics of long distance dispersal and its significance to ecology and epidemiology. In revision. Preprint available here: <https://drive.google.com/file/d/0B4mLG2SPb-tbUmVHZFI4UWFvSTQ/view?usp=sharing>

Strickland, C., Miller, L. A., and Pasour, V. A generalized framework for simulating plankton active and passive movement in flow. Planned submission in March 2019 for a special issue of *Biomimetics* (edited by George Lauder).

Miller, L. A., Strickland, C., Battista, N. and Pasour, V. A . Unsteady flow through flexible cylinders at intermediate Reynolds numbers: Applications to biological protective layers. Planned submission for April 2019 for a special issue of *Fluids*.

**Honors and Awards:** Nothing to Report

**Protocol Activity Status:**

**Technology Transfer:** Nothing to Report

### **PARTICIPANTS:**

**Participant Type:** PD/PI

**Participant:** Virginia Pasour

**Person Months Worked:** 12.00

Project Contribution:

International Collaboration:

International Travel:

National Academy Member: N

Other Collaborators:

**Funding Support:**

**Participant Type:** Co PD/PI

**Participant:** Laura Miller

**Person Months Worked:** 12.00

Project Contribution:

International Collaboration:

International Travel:

National Academy Member: N

Other Collaborators:

**Funding Support:**

**Participant Type:** Postdoctoral (scholar, fellow or other postdoctoral position)

**Participant:** Christopher Strickland

**Person Months Worked:** 12.00

Project Contribution:

International Collaboration:

International Travel:

National Academy Member: N

Other Collaborators:

**Funding Support:**

**RPPR Final Report**  
as of 13-Feb-2019

**Participant Type:** Graduate Student (research assistant)

**Participant:** Nick Battista

**Person Months Worked:** 4.00

**Funding Support:**

Project Contribution:

International Collaboration:

International Travel:

National Academy Member: N

Other Collaborators:

**Participant Type:** Graduate Student (research assistant)

**Participant:** Kemal Ozalp

**Person Months Worked:** 6.00

**Funding Support:**

Project Contribution:

International Collaboration:

International Travel:

National Academy Member: N

Other Collaborators:

**Participant Type:** Undergraduate Student

**Participant:** Maddie Braye

**Person Months Worked:** 4.00

**Funding Support:**

Project Contribution:

International Collaboration:

International Travel:

National Academy Member: N

Other Collaborators:

# **Project Report for ARO Staff Research Project “Mathematical Modeling of Macrophyte-flow Interactions and the Resulting Zooplankton Distributions”**

**PI: Virginia Pasour**

**co-PI: Laura Miller**

## **Major Goals**

The broad goal of this research project is to develop mathematical models, implement new numerical methods, and leverage existing state-of-the-art tools from computational and experimental fluid dynamics to understand the importance of aquatic plants in modifying the environment of small organisms. Such plants we will describe generally as macrophytes, which include sea grasses, submerged freshwater plants, and emergent vegetation. It is well known that the fluid dynamics within and around macrophyte beds have important ecological consequences on organisms, and these organisms also affect the hydrodynamics within these environments. Modeling flow within macrophyte beds is challenging due to the complex morphologies and material properties of these organisms. Flow properties can vary dramatically in space and time through such layers, and simplified models may not accurately capture mixing dynamics, particle paths, and other flow features important to zooplankton. Recent improvements in scientific computing have made numerical simulations of viscous and unsteady flows through complex and flexible structures feasible. The broad goals of this proposal are to develop new models of macrophytes and zooplankton and to incorporate these models with fluid-structure interaction simulations to reveal the properties of flows within these complex environments and to determine the impact on zooplankton distributions.

## **Specific Objectives**

The overall objectives of this project are as follows:

Aim 1: Determine how macrophyte height, flexibility, and density affect flow and mixing near the substrate using computational and experimental fluid dynamics.

Aim 2: Develop reduced order models that can be solved analytically to describe the flow through macrophyte beds and to test when such models are reasonable.

Aim 3: Determine how the presence of macrophytes enhance or reduce flow, the amount and mixing, and the distribution of zooplankton.

Specific subprojects are listed in Figure 1. The darker green boxes represent the main research thrusts, while the lighter green represent subprojects within each research area. The overarching goal of the project is to predict the resulting plankton distributions based on flow fields, presence of macrophytes, and plankton behavior. The main mathematical components of the project include 1) computational fluid dynamics to resolve the flow around the macrophytes, 2) the development of reduced order models of the flow, 3) the development of models of zooplankton movement, 4) simulations to determine the effect of zooplankton movement of flow, and experimental validation of the fluid and zooplankton models.

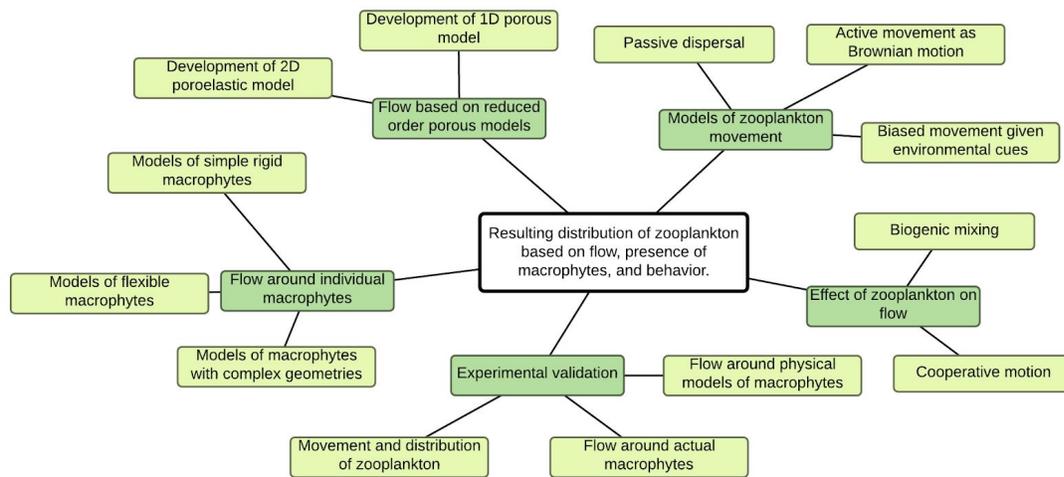


Figure 1. Project map highlighting how the various components of the project will be integrated to determine how flow, the presence of macrophytes, and behavior affect the distributions of zooplankton.

## Accomplishments

Given the relatively small amount of work at the mesoscale, we have focused on the effects of small (1 mm - 1 cm) scale vegetative and coral structures on flow. Such mesoscale structures and protective layers are replete throughout the natural world and provide protective layers for micro-organisms. For example, trichomes (the hairs or fine outgrowths on plants) can drastically alter both the average flow speed and profile near a leaf's surface, affecting the rates of nutrient and heat exchange. These layers can also affect the settlement and dispersal of microscopic plankton that live on vegetative structures and within coral reefs. Characterizing the flow profiles through such layers is therefore critical towards understanding the function and diversity of small branches, hairs, and bristles.

*Aim 1: Determine how macrophyte height, flexibility, and density affect flow and mixing near the substrate using computational and experimental fluid dynamics.*

We have used dynamically scaled physical models to study the flow profiles outside of arrays of cylinders that represent such filtering and protective layers. 3D numerical simulations using the Immersed Boundary Method were used to resolve the three-dimensional flows within the layers. Physical models using arrays of pins as well as 3D printed models were used to resolve the flow outside of these layers. The numerical results demonstrate three-dimensional flows into and out of the layer that are not described by the Brinkman model (discussed in Aim 2) and may be significant for biologically relevant volume fractions. The Brinkman model does, however, do a good job describing the flows outside of the layers as well as the spatially averaged flow within the layers. The results can be used to understand how variations in density and height of such structures can alter mixing and bulk flows.

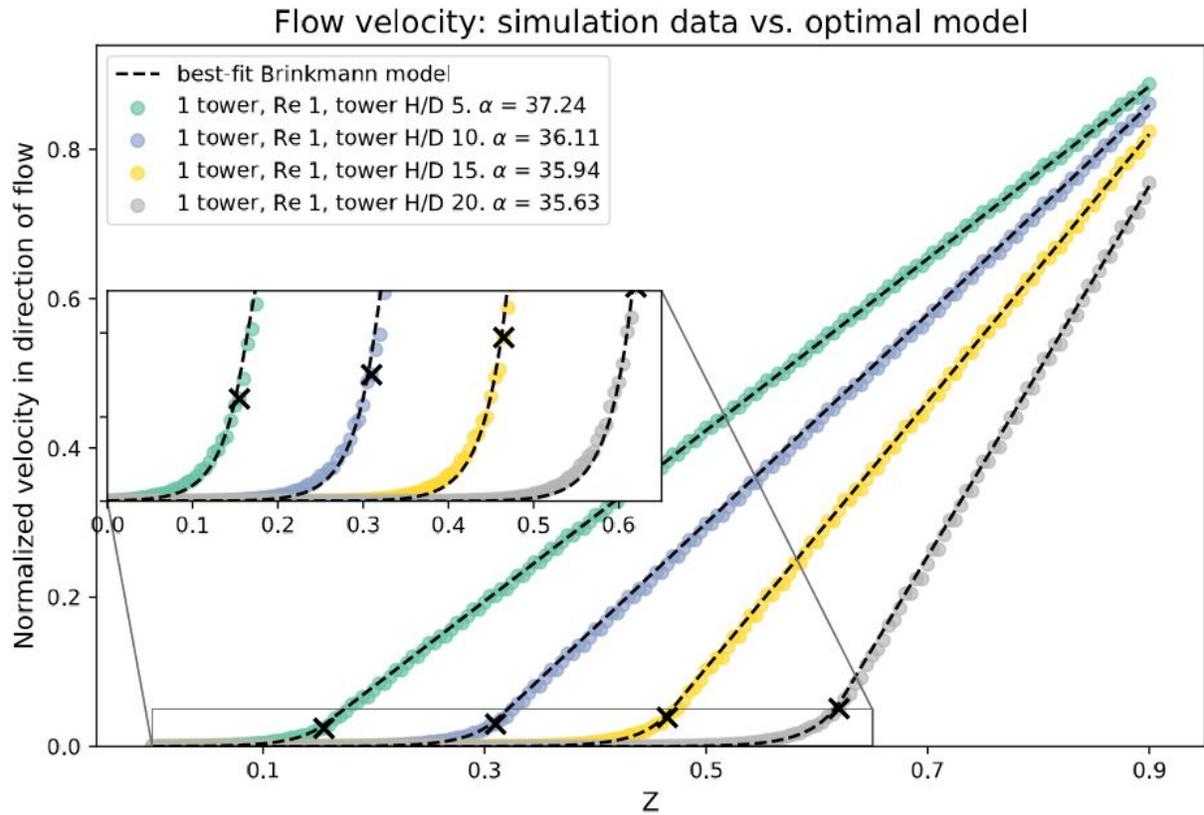


Figure: Comparison of numerical simulation results to the theoretical model. Dots show the averaged x-component of the velocity as a function of height for different densities of macrophytes. The dashed black lines show the best fit Brinkman model.

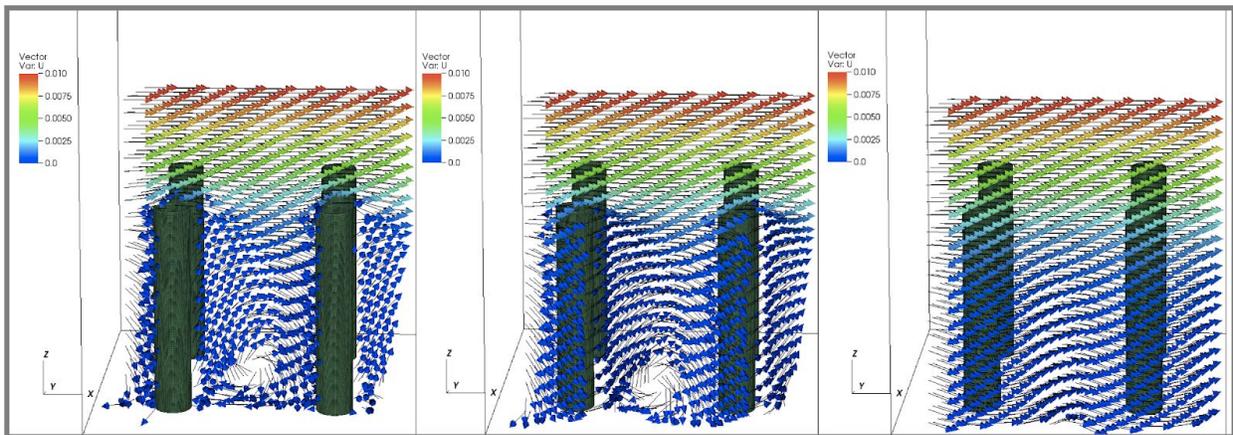


Figure: Velocity vector fields taken along planes parallel to the direction of flow at  $Re = 1$ . Note the three-dimensionality of the flow that is not captured by the analytical model. These flows may be relevant to zooplankton.

*Aim 2: Develop reduced order models that can be solved analytically to describe the flow through macrophyte beds and to test when such models are reasonable.*

The computational and experimental results given in Aim 1 have been compared to theoretical results obtained by modeling the layer as a Brinkman medium matched to flow within and above the layer. More specifically, we compare the results of the spatially averaged flow in the physical and numerical models as a function of height to the 1D analytical model. We fit the data to the Brinkman model using nonlinear least squares to find the best choice of porosity. The 3D simulations and analytical results are consistent and give the same flow profiles for the x-component of the average velocity and height,  $z$ . Moreover, from finding the best fit porosity coefficient for the analytical model, it appears that, as the height of the tower increases, the porosity coefficient decreases. This is consistent with the results from the experiments, which showed that the best fit value of  $\alpha$  decreased as the height of the cylinders was increased. At this scale ( $0.1 < Re < 10$ ), the model does an excellent job describing average flow rates, though it does not capture vertical flow within the layer itself.

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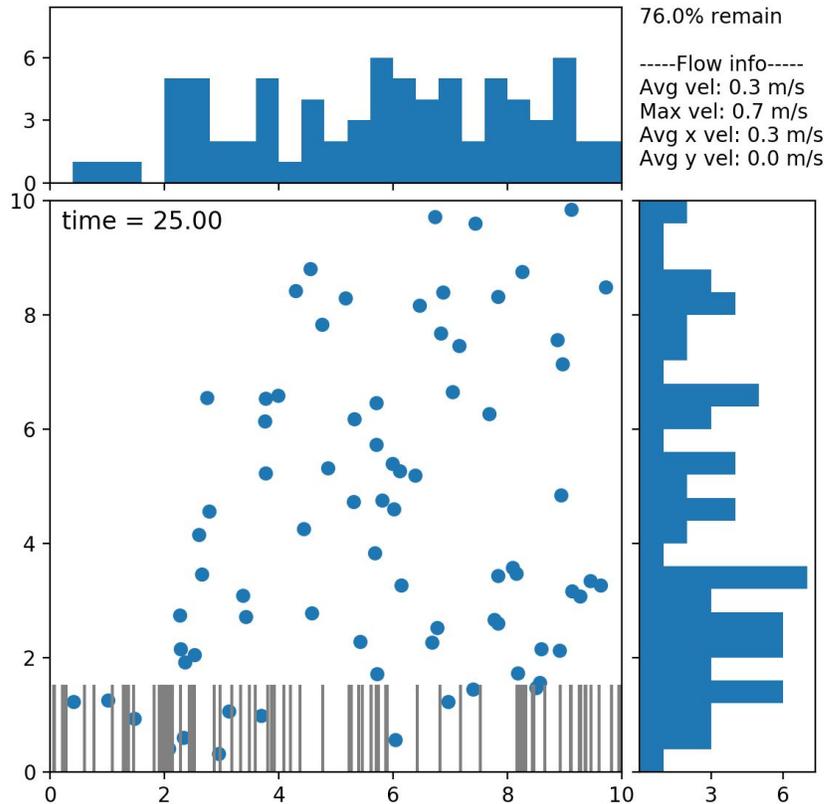


Figure: Theoretical positions of individual brine shrimp within and above a protective layer with background flow. The histograms show the number of brine shrimp within each spatial position.

Simultaneously, graduate student Kemal Ozalp and a team of 7 undergraduates are measuring the flow fields around physical models of macrophytes, releasing brine shrimp within these layers. The effective diffusivity of the brine shrimp is measured in a quiescent fluid. The brine shrimp are then released as a point source in a protective layer immersed in a moving fluid. Kemal then tracks the spatially and temporally varying densities of brine shrimp within and outside of the layer. Please see the attached Appendix which details the experimental protocol developed by Kemal for this work.

### ***Additional work in code and infrastructure development***

#### Code development:

Miller and Pasour have been working with Nick Battista to develop and expand a 2D MATLAB and Python implementation of the immersed boundary method, *ib2d*. This software package allows the user to implement various elastic and porous models of 1D boundaries. Muscle and neural activation models are also available, and users can now easily incorporate electrostatic forces, chemical bonds, and massive boundaries. More information can be found here:

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### **Training Opportunities**

This project funded one mathematics postdoctoral fellow, Christopher Strickland. Dr. Strickland is now an Associate Professor at the University of Tennessee Knoxville.

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Miller, L. A. Using Computational Fluid Dynamics to Understand Organism Form, Function, and Behavior. GALCIT Colloquium, Caltech, Pasadena, CA, September 30, 2016.

Miller, L. A. Plant Leaves Reconfigure into Cone Shapes to Reduce Drag and Flutter. The 68th Annual Meeting of the APS Division of Fluid Dynamics, Boston, MA, November 22-24, 2015.

Miller, L. A. Reconfiguration of broad leaves to reduce drag and flutter. Investigative Workshop Morphological Plant Models. National Institute for Mathematical and Biological Synthesis. Knoxville, TN, September 4, 2015.

Symposia and workshops

Pasour along with Julia Samson (UNC Biology Graduate Student) and Brian White (UNC Marine Science Faculty) editing a volume for the Frontiers Research Topics Journal on the results from a symposium they organized at the 2017 ASLO Annual Meeting in Honolulu, Hawaii, February 26-March 3, 2017. The title of the symposium was “Canopies in aquatic ecosystems: integrating form, function, and biophysical processes.”

Publications, submissions, and in-prep

Battista, N. A. ‡, Strickland, C. S.\*, Miller, L. A. (2017). IB2d Reloaded: a more powerful Python and MATLAB implementation of the immersed boundary method. *Mathematical Methods in the Applied Sciences*, <https://doi.org/10.1002/mma.4708>, 1–26.

Christopher Strickland, Laura Miller, Arvind Santhanakrishnan, Christina Hamlet, Nicholas A. Battista and Virginia Pasour (2017). Three-Dimensional Low Reynolds Number Flows near Biological Filtering and Protective Layers. *Fluids*, 2(4), 62; <https://doi.org/10.3390/fluids2040062>

Strickland, C., Miller, L. A., Santhanakrishnan, A. et al. The fluid physics of long distance dispersal and its significance to ecology and epidemiology. In revision. Preprint available here: <https://drive.google.com/file/d/0B4mLG2SPb-tbUmVHZFI4UWFvSTQ/view?usp=sharing>

Strickland, C., Miller, L. A., and Pasour, V. A generalized framework for simulating plankton active and passive movement in flow. Planned submission in March 2019 for a special issue of *Biomimetics* (edited by George Lauder).

Miller, L. A., Strickland, C., Battista, N. and Pasour, V. A . Unsteady flow through flexible cylinders at intermediate *Reynolds numbers*: Applications to biological protective layers. Planned submission for April 2019 for a special issue of *Fluids*.

### **Current and future work**

*Aim 1: Determine how macrophyte height, flexibility, and density affect flow and mixing near the substrate using computational and experimental fluid dynamics.*

We continue to extend the mesoscale work at  $0.1 < Re < 10$  to higher Reynolds numbers ( $1,000 < Re < 100,000$ ) using turbulence models in OpenFOAM. OpenFOAM is an open source software library that supports a large variety of tools for computational fluid dynamics. Covering this large range of scales will allow us to describe how fluid physics changes from the scale of flow around individual trichomes/hairs to the scale of flow around large beds of seagrass and other macrophytes. This will also allow us to simulate the dispersal and movement of plankton across a large range of scales, from movement between macrophyte beds to settlement on a single leaf.

*Aim 2: Develop reduced order models that can be solved analytically to describe the flow through macrophyte beds and to test when such models are reasonable.*

The Brinkman model used at the mesoscale will be tested at the larger scales described above. We will also compare our spatially resolved numerical and experimental results to the simplified flows described by other models, such as those outlined in the reference below:

Lowe, R., Shavit, U., Falter, J. L., Koseff, J. R. and Monismith, S. G. (2008). Modeling flow in coral communities with and without waves: A synthesis of porous media and canopy flow approaches. *Limnol. Oceanogr.*, 53(6), 2668–2680.

*Aim 3: Determine how the presence of macrophytes enhance or reduce flow, the amount and mixing, and the distribution of zooplankton.*

The flow fields described above will be used to simulate the dispersal of plankton within and above macrophyte beds using the agent based framework developed by Strickland called *Planktos*. We will extend our current work to model the behavior and movement of snail larvae and take advantage of existing data for validation.

Reidenbach, M. A., J. R. Koseff, and M. A. R. Koehl (2009) Hydrodynamic forces on larvae affect their settlement on coral reefs in turbulent, wave driven flow. *Limnol. Oceanogr.* 54: 318-330.

doi:10.4319/lo.2009.54.1.0318

Koehl, M. A. R., J. A. Strother, M. A. Reidenbach, J. R. Koseff, and M. G. Hadfield (2007)

Individual-based model of larval transport to coral reefs in turbulent, wave-driven flow: Behavioral responses to dissolved settlement inducer. *Mar. Ecol. Prog. Ser.* 335: 1-18. doi:10.3354/meps335001