Final Report for Period: 09/2009 - 08/2010
Submitted on: 09/07/2010

Principal Investigator: Weissburg, Marc J.
Organization: GA Tech Res Corp - GIT

Submitted By:
Weissburg, Marc - Principal Investigator

Title:
The hydrodynamics of benthic predation

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**Project Participants**

### Senior Personnel

**Name:** Weissburg, Marc  
**Worked for more than 160 Hours:** Yes  
**Contribution to Project:**

**Name:** Webster, Donald  
**Worked for more than 160 Hours:** Yes  
**Contribution to Project:**

### Post-doc

**Graduate Student**

**Name:** Smee, Delbert  
**Worked for more than 160 Hours:** Yes  
**Contribution to Project:**

**Name:** Ferner, Matt  
**Worked for more than 160 Hours:** Yes  
**Contribution to Project:**

**Name:** Delavan, Sarah  
**Worked for more than 160 Hours:** Yes  
**Contribution to Project:**

**Name:** Watts, Miranda  
**Worked for more than 160 Hours:** Yes  
**Contribution to Project:**

**Name:** Berry, W. Alex  
**Worked for more than 160 Hours:** Yes  
**Contribution to Project:**

**Name:** Hill, Jennifer
Undergraduate Student

Name: Coleman, Brandon
Worked for more than 160 Hours: Yes
Contribution to Project: Assisted in performing field measurements. CIRE Award winner.

Name: Hickey, Star
Worked for more than 160 Hours: No
Contribution to Project: Assisted in performing field measurements

Name: Lefivre, Morey
Worked for more than 160 Hours: Yes
Contribution to Project: Ms. Lefivre was employed as an undergraduate field assistant during the summer of 2008. She helped collect animals, set up field experiments on predation along oyster reefs, assisted with flow measurements and behavioral experiments.

Technician, Programmer

Other Participant

Research Experience for Undergraduates
Name: Moir, Flora
Worked for more than 160 Hours: Yes
Contribution to Project: Performed experiments on risk sensitivity in blue crabs as functions of animal size

Years of schooling completed: Sophomore
Home Institution: Other than Research Site
Home Institution if Other: SUNY Binghampton
Home Institution Highest Degree Granted (in fields supported by NSF): Doctoral Degree
Fiscal year(s) REU Participant supported: 2005
REU Funding: REU supplement

Name: Spellman, Tayna
Worked for more than 160 Hours: Yes
Contribution to Project: Performed experiments on risk sensitivity in blue crabs as functions of hunger level

Years of schooling completed: Junior
Home Institution: Other than Research Site
Home Institution if Other: Adelphi University
Home Institution Highest Degree Granted (in fields supported by NSF): Associate's Degree
Fiscal year(s) REU Participant supported: 2006
REU Funding: REU supplement

Name: Troyer, Rachel
Worked for more than 160 Hours: Yes
Contribution to Project:
Ms. Troyer developed a behavioral investigation examining the role of aversive chemical stimuli in mediating behavioral interactions among bivalves, and mud crabs, and specifically examined the role of flow in determining the strength of this interaction. This project was part of a site REU awarded to the School of Biology at Ga Tech.

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Organizational Partners

Skidaway Institute of Oceanography
SkIO has helped provide logistical support for lab and field work. We have employed SkIO undergraduate interns as part of our outreach efforts.

Other Collaborators or Contacts

Lee Smee, Assistant Professor at Texas A&M Corpus Cristi, continues to collaborate with us on field measurements of flow.

Activities and Findings

Research and Education Activities:
We have performed laboratory studies examining the relationship of turbulence to foraging success/odor perception in a number of invertebrate species. We have performed manipulative field experiments based on our laboratory results. These experiments manipulated turbulence using natural substrates and examined predation intensity in a variety of field conditions. These experiments also examined the relationship between prey perception of predator risk and flow regime. Most recently, we have examined how oysters reefs, an ecosystem engineer in these systems, may affect or participate in chemically-mediated interactions. These experiments focus on whether reefs act as large scale sources of chemical fluid mechanical cues that change behavior of reef consumers, and whether there is a chemically-mediated trophic cascade of blue crabs-intermediate predators-oysters, that affects oyster abundance. We have also measured ambient fluid flows in a variety of habitats to better understand relationships between perceptual abilities, flow properties and animal distribution and abundance.

The predator-prey relationship between blue crabs (Callinectes sapidus) and bivalve clams (Mercenaria mercenaria) is mediated by the transport of metabolites released by the prey (clams) and transported downstream as a passive scalar. Our hypothesis is that the clams alter their excurrent behavior according to the ambient flow conditions to promote mixing of their chemical scent with the surrounding fluid. This, in-turn, may alter the ability of the predator, blue crabs or whelks, to locate their clam prey. This study focuses on how the prey behavior contributes to the information available within the odorant plume. Clams may modify factors such as excurrent flow, flow unsteadiness, and siphon height and diameter. In addition, we are examining indirect interactions between various predator and prey species in the the community, particularly interactions between oysters and clams, and between blue crab and mud crab predators. Large aggregations of oyster reefs may act as attractants for foraging blue crabs, bringing them into locations where the encounter smaller clam aggregations and consume them. Blue crabs may interact chemically with smaller mud crabs to change patterns of activity, this affecting bivalve prey species. These issues are being examined with manipulative field experiments and focal behavioral studies in flumes and mesocosms.

Further, the excurrent siphon flow for bivalve clams (Mercenaria mercenaria) was measured using a Particle Image Velocimetry (PIV) system in order to evaluate hypotheses related to the unsteadiness of the velocity. Spectral, fractal, and lacunarity analyzes were employed to quantify the temporal patterns in the excurrent jet of the bivalve siphon. Experiments were conducted with varying stream velocity, clam size, and nearest neighbor distance. Experiments were also conduct with presence or absence of an upstream predator.

We developed a series of field methods to measure and analyze flow data from a variety of sites simultaneously to be able to better compare regional patterns of flow (and turbulence) within estuaries and map this on to biological patterns. ADV data were collected at a series of sites near Skidaway Institute of Oceanography in Wassaw Sound, Georgia during the summers of 2007, 2009, and 2010. A central challenge to the analysis and interpretation of these data is the ability to separate the kinetic energy and Reynolds shear stress associated with wave motion.
versus turbulence. We developed codes to perform this task as well as phase filtering of erroneous samples.

We designed and built two traversing mounting devices to deploy Acoustic Doppler Velocimeters (ADV) to measure vertical profiles of velocity under field conditions. Several substrates and conditions were tested (during Summer 2008) with and without the presence of clams such as mud alone, sand alone, mud next to oyster beds, and mud next to sea grass beds. These are conditions and substrates that are typical clam habitats in Wassaw Sound. The objective is to demonstrate whether the mean velocity and turbulence profiles differ with and without the presence of clams.

In addition, the ADV traversing/mount system was used to determine the boundary profiles in a laboratory flume at Skidaway Institute of Oceanography in order to compare boundary profiles in the flume with an active oyster reef, an inactive oyster reef, with no oyster reef but including oyster chemical cues, and without oyster reef. This will help interpret the experiments examining effects of oyster reefs on predation on other infaunal bivalves.

Findings:
Turbulence alters perceptual abilities of both marine consumers and their prey, generally diminishing the ability of animals to locate or identify sources of attractant or deterrent compounds. There appear to be distinct strategies among groups of organisms characterized by different sizes and motility; turbulence disrupts perception in small (clams) and or rapidly moving animals (crabs) whereas larger, slower animals ( gastropods, echinoderms) are less affected. Turbulence can be successfully altered locally and impacts foraging success of animals in the field. In the field, enhanced turbulence diminishes predation by crabs, but increases it in whelks suggesting turbulence is a niche dimension that allows resource partitioning via effects on perception. This is dependent on ambient flow regime as well as predator identity; rapidly mobile crab predators have a narrower range of turbulence in which they are effective predators compared to slow moving whelks.

Turbulence also reduces the ability of prey to sense predators. Prey exposed to predator odor in the field experience diminished predation, which is one of a handful of studies that successfully extrapolate lab behavioral measurements to consequences in the field. Local turbulence alters this signaling process in at least two different predator prey systems; prey are able to successfully respond to predation risk at longer distances when turbulence is low. Thus, turbulence alters information gathering by prey and may change the strength of indirect versus direct effects of predation.

Turbulence does not act as a refuge under all conditions, as been previously supposed. Small levels of turbulence actually benefit some foragers as it appears to both increase the transmittance of olfactory signals and also decrease prey perceptual ability more so than predators. Thus, field analysis of predation intensity versus turbulence reveal a hump shaped function, for some predators.

Field experiments indicate predation around larger aggregations of oysters is non-random, peaking at a small distance from the edge, suggesting oysters reefs may negatively affect burrowing bivalves indirectly by acting as a large scale attractant. Flume experiments suggest this is due to chemicals released by oysters or associated fauna, which may counteract the increased mixing associated with oysters beds. Interestingly, the impact of oyster reef chemical and physical structure is predator specific, based upon our results from the summer of 2010. Slow moving animals that time average chemical signals are not dramatically affected, again confirming that turbulence interacts with foraging mode and that turbulence represents a niche dimension along which predators can partition the habitat even when foraging for similar prey.

We also have evidence that blue crab chemical scent diminishes activity or smaller (but important) foraging mud crabs; blue crabs may directly predate on bivalves, but indirectly diminish predation by other consumers, thus setting the stage for complicated three-way direct and indirect interactions among the guild of crab predators. In fact, our most recent field experiments in the summer of 2010 indicate this trophic cascade works in the field, which is one of the few demonstrations of behaviorally driven cascades in near shore systems. Preliminary analysis of our 2009 experiment indicates this trophic cascade may also suppress foraging by very small predators on newly settled oysters.

A fractal analysis and a lacunarity analysis of the excurrent jet velocity time records found that clams alter their jet excurrent velocity unsteadiness according to the horizontal crossflow velocity. This behavioral change may contribute to the differences in the turbulence characteristics in the field experiment. Another result from the laboratory experiments is that the effect of clam patch density on the feeding activity was dependent on the size of the organism. This size/density dependent relationship suggests that predation by blue crabs dominates the system since larger clams are no longer susceptible to blue crab predation, whereas clams of all sizes are susceptible to whelk predation. Finally, clams increase the randomness of their excurrent jet velocity values when predator cues are located in the upstream flume flow. This suggests that the presence of predators elicits clam behavior that promotes the mixing and dilution of their chemical metabolites.

For the field ADV data collected in Summer 2007, burst-average velocity statistics, turbulent kinetic energy (TKE), Reynolds shear stress, and turbulence intensity (TI) were computed for each data set. Because multiple sites were monitored over multiple days, it was possible to examine the variation spatially and temporally. Large variability in turbulent characteristics was observed at different sites on the same day as well as...
within the same site over different days. Tidal influences were apparent as turbulent characteristics often reached absolute maximum values during the incoming or outgoing tides, and sites on the whole were less energetic at high tide when flowrates should be at a minimum. No consistent trends were observed in relationships between the sites. In some cases, sites located on Wassaw sound directly had lower TKE and Reynolds shear stress than those located further upstream, where sites would be expected to be less energetic. The findings emphasize the importance of applying data filtration to raw ADV data, suggest an order of magnitude of wave contributions in a particular tidal ecosystem, and demonstrate the inherent variability of turbulent characteristics. The high levels of variability are consistent with the complex predator-prey interactions that have been observed in the Wassaw Sound ecosystem. The findings also illustrate the importance of calculating multiple turbulence parameters for a site, due to the lack of observed relationships between TKE, TI, and Reynolds shear stress. Preliminary analysis of the ADV data collected in Summer 2009, indicate a strong correlation between tidal range and mean horizontal velocity and between wind speed and TKE.

Training and Development:
Graduate students get training in sensory, behavioral, and field ecology. Specific skills include video-motion analysis of behavioral and kinematic data, design and implementation of manipulative field experiments, the use of advanced flow instrumentation (Acoustic Doppler Velocimeter [ADV], Acoustic Doppler Profiler [ADP], Laser Doppler Velocimeter [LDV], Particle Image Velocimetry [PIV]) for collection and analysis of flow in laboratory and field settings. Participants work in an interdisciplinary environment along side oceanographers, ecologists, and fluid dynamicists. They have participated in interdisciplinary teaching (e.g. lab courses in biological applications of fluid flow) and mentored undergraduate students.

The graduate students involved in this project have used their skills to advance their academic careers. Ferner is currently at San Francisco Bay National Estuarine Research Reserve (S.F. State University), Smee is now an Assistant Professor in interdisciplinary marine sciences at Texas A&M- Corpus Christi, Delavan is currently a Post-doc at in Dept of Civil & Natural Resources Engineering, University of Canterbury, Christchurch, New Zealand. Berry is teaching math and science in Guyana for the 2010-2011 academic year. Watts and Hill are current Ph.D. students. Graduate students also have received training in organizational skills required to run conferences and symposia as a result of our outreach efforts.

Outreach Activities:
Our work has been featured in in-house tours at SkIO, where the public is invited to learn about marine science. We have also participated in the design and development of an exhibit, 'Crabs' that opened May 2005 at the Shedd Aquarium in Chicago, providing images and video from our work on chemosensation in crustaceans. We worked with Alice Kamps (exhibit writer and developer) to help develop this theme. In 2008 our research was featured in a Discovery Science Channel program titled 'Weird Connections' specifically focusing on our ability to 'visualize' odorant plumes. The research has also been highlighted for K-12 students visiting the Environmental Fluid Mechanics Laboratory on the main Georgia Tech campus. We are participating in a large scale data management proposal submitted by the GA Tech library and several collaborating institutions, with the goal of developing methods to catalogue, archive and make available complex digital data sets.

Weissburg was the primary organizer for the 2007 Benthic Ecology Meetings held at the campus of the Georgia Institute of Technology. Weissburg and Webster organized a topical session for 2005 ASLO Aquatic Sciences Meeting entitled, ‘TS28 - Beyond the Mean: Effects of Instantaneous Turbulent Events on Organismal Processes.’

In 2007, we hosted a high school teacher and student group from the GIFT program, which is designed to introduce high school students and teachers to research. They designed a project on olfactory signaling.

Journal Publications


Books or Other One-time Publications

Collection: M.S. Thesis
Bibliography: School of Civil & Environmental Engineering, Georgia Institute of Technology

Collection: Ph.D. Thesis
Bibliography: School of Civil and Environmental Engineering, Georgia Institute of Technology

Collection: Ph.D. Thesis
Bibliography: School of Biology, Georgia Institute of Technology

Collection: Ph.D. Thesis
Bibliography: School of Biology, Georgia Institute of Technology

Bibliography: DFD10 Meeting of The American Physical Society, Long Beach, CA, November 2010.

S.K. Delavan and D.R. Webster, "Clam Excurrent Siphon Velocity Patterns According to External Environmental Cues", (2010). Conference Proceedings, Published
Bibliography: 2010 Ocean Sciences Meeting, Portland, OR, February 2010

S.K. Delavan and D.R. Webster, "Field Boundary Layer Characteristics as Modified by Clams in Habitats of Varying Survival Rates", (2010).
Contributions within Discipline:
Our findings establish that flow environment has consequences for the ability of animals to find prey or avoid predators. We are further examining the effect of other aspects, such as the distribution of turbulence in time and space, on predatory activities. Such studies are the first direct evidence that patterns of predation in the field are partially determined by the impact of flow on chemical signals. Since different animals have different perceptual abilities, the flow environment may allow competitors to partition resources based on how turbulence affects odor signaling, shift the effects of predation from indirect to direct effects, or provide prey with a refuge where they are largely undetectable. Understanding these effects will help relate organismal distribution and abundance to physical processes in near shore communities. In fact, our recent finding that predation is non-linearly related to flow suggests that, like potentially lethal physical stresses, stressors affecting sensory processes may modify local predatory interactions. This relates sensory ecology to well-defined concepts in community ecology.

Our recent focus on oyster reefs as an important modulator of turbulent plumes will increase our understanding of oysters as key species in estuarine environments.

Our new examinations of multi-species interactions (e.g. blue crabs, mud crabs, bivalve prey) are an important step in scaling up our understanding of predatory dynamics from individuals to communities. Multi-species investigations of the impact of chemical signals are rare, despite evidence that multiple taxa may use a single cue to modulate different behaviors. Thus, a full understanding of chemically-mediated
processes in marine environments are unlikely to result from studies examine only predator-prey pairs. Our studies examining these multiple species interactions, and the influence of flow on chemical signaling, may result in a more complete view of the structure of estuarine communities.

We have also made a large step by performing manipulative experiments in the field that modify local turbulence. This builds on the long-standing tradition of using experimental studies of marine habitats to advance ecology. Our experiments show that modifications of the physical habitat can be performed, quantified and related to effects on organisms and their interactions. These experiments also provide information on boundary layer fluid flow properties in inter- and subtidal regions. Few data sets are available, in spite of the fact that these are important habitats for many animals, and that that the physical environment exerts strong effects on their survival.

Our data also providing flow measurements over several tidal scales across regions of the marsh system will allow us and other investigators to make more accurate linkages between organisms, ecological processes and the flow environment. There have been remarkably few flow measurements in these inter and subtidal communities and, to the best of our knowledge, none that are as comprehensive in space and time.

Contributions to Other Disciplines:
Efforts to understand the role of turbulence occur in a variety of terrestrial systems as well as for aquatic consumers and their prey. Very few of the studies in other systems have successfully examined the relationship between flow, odor perception and ecological interactions in the field, thus, our work may provide insight and guidance for investigations in other habitats. In particular, the role of indirect vs. direct effects is a critical issue in a variety of systems. Our data suggest that indirect effects are context-dependent, and may not be as far-reaching as assumed from previous investigations in which the physical environment is not considered. Finally, our current focus on multiple species interactions may provide models for how perceptual ability, and its modulation by the physical environment, allows for context dependency of species interactions.

In addition, there have very few studies of boundary layer dynamics (using either engineering or oceanographic approaches) in the intertidal or subtidal channels where our work occurs. Our investigations supply a motivation for other efforts to examine mixing processes in these complex environments. Since these habitats contain a number of threatened, economically important or key species, our work may also provide insights into management and conservation by identifying areas where animals may successfully find resources or avoid being consumed.

Lastly, our studies of orientation and navigation of organisms is contributing the development of sensory processing algorithms that can guide autonomous vehicles towards dangerous odor sources (e.g. pollution sources). This has considerable application in many areas.

Contributions to Human Resource Development:
We have participated in both undergraduate and graduate training in an interdisciplinary environment. We have also contributed directly to the REU and IGERT programs offered at Georgia Tech, and participated in training undergraduate interns at SkIO some of whom (SIRE Interns) are from underrepresented groups. These students have acquired skills in fluid dynamics, behavior, and field ecology, and been part of a multidisciplinary team. Undergraduate students have had the opportunity to present findings at national meetings, and have published their work in major research journals. Graduate students supported by this grant have entered the academic work force and are engaged in further research and training as post-doctoral associates and faculty. The participation of our graduate students in the GIFT program has contributed to developing curricular materials for basic biology and science classes, and we are helping to expose high school students to research so that they appreciate its societal value.

Contributions to Resources for Research and Education:
We have contributed physical and intellectual resources to our graduate and undergraduate training programs. Results from our studies have been incorporated into two exciting courses here at Georgia Tech (Fluid Mechanics of Organisms, and Biological Applications of Fluid Mechanics Lab), where we use our research experience to design laboratory exercises and lecture modules. This cross-disciplinary work is used to educate biology, chemistry, and engineering students. We have also incorporated this work into a summer field course. Instrumentation associated with this grant is used in both undergraduate and graduate courses, the summer REU program and the training of high school students and teachers. We have collaborations and contacts gained during this study to develop a local group that was successful in securing funding to upgrade the GA Tech Marine Laboratory at Priest Landing, and which will provide instrumentation for researchers at SkIO and other local institutions.

Contributions Beyond Science and Engineering:

Conference Proceedings
Categories for which nothing is reported:

Any Web/Internet Site
Any Product
Contributions: To Any Beyond Science and Engineering
Any Conference