Fluid Mechanical and Chemical Cues in Thin Layers: Role in Organizing Zooplankton Aggregations

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LONG-TERM GOALS

We are examining the physical and chemical conditions that are conducive to the formation of plankton aggregations to help address the prevalence and importance of thin layers in the world's oceans. The goal of the laboratory experiments is to define the mechanisms by which zooplankton are attracted to thin layers, and to determine the properties of thin layers that evoke orientation responses of copepods.

OBJECTIVES

A series of experimental treatments are planned to isolate the hydrodynamic and chemical signals that induce zooplankton orientation. The objectives include: 1) improving our understanding of formation and persistence of thin layers and zooplankton aggregations; 2) identifying the balance between physical forcing and biological responses in thin layer formation; 3) generating data on zooplankton responses that are required for individual-based models of aggregation to thin layer signals; 4) providing information to field studies about the range of physical measurements that must be performed in order to characterize thin layers and to evaluate their spatial and temporal persistence; and 5) helping to identify target field sites by determining the thresholds at which relevant signals induce aggregations.

APPROACH

The hypothesis to be tested is that fluid mechanical and chemical signals characterizing thin layers actively modify the behavior of zooplankton to attract them to these regions and result in significant accumulation of zooplankton near, or in, these features. A series of experimental treatments will isolate the chemical and hydrodynamic signals that induce zooplankton orientation. Copepods encountering newly developing thin layers experience only velocity gradients since phytoplankton haven't yet accumulated at the discontinuity. Experiment 1 subjects copepods only to velocity

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gradients that bracket natural conditions in thin layers. Phytoplankton exudates accumulate in developing thin layers to provide chemical cues in addition to velocity gradients. Experiment 2 assays copepod responses to combined velocity and chemical gradients. Since chemicals dissipate more slowly than momentum, chemical gradients may outlive the velocity gradients that create them. Experiment 3 examines copepod responses to chemical features in the absence of velocity gradients. Finally, the relative scaling of flow and odor gradients to animal size and motility may affect responses to thin layers by different organisms. We make high-resolution observations of orientation behavior of tethered copepods in experiment 4. We will employ controlled water jet stimuli that mimic spatial and temporal patterns deduced from experiments 1-3 to mediate orientation responses. Experiment 4 tests hypothesis generated in phases 1-3 regarding necessary cues, and allows us to examine how copepod responses to fluid mechanical and chemical cues varies with animals' size.

Yen (PI) is responsible for overall coordination of fluid mechanical, behavioral and sensory experiments. Webster (co-PI) is responsible for the design and implementation of flow and odor field analysis. Weissburg (co-PI) is responsible for the experiments on copepod mechanosensory orientation. Brock Woodson (graduate research assistant) has been performing the flow apparatus design and experimentation. Jason Brown (technician) has been developing the IR PIV instrumentation and software. David Fields (post-doc) and Jarad Mellard (graduate research assistant) will perform the jet stimulation experiments.

WORK COMPLETED

An important aspect of the laboratory experiments is coordination with field studies of Cowles et al. and others. Brock Woodson accompanied Cowles' group on a research cruise off the coast of Oregon from 21 June to 2 July 2003. Woodson assisted the monitoring of the microscale structure of a dye patch as it was mixed into the surface layer during upwelling. Observations and discussions during this cruise revealed that many occurrences of thin layers (or other biological structure) more closely resemble a planar jet than a mixing layer. Vertical profiles show correlated small-scale jumps in velocity, density, and fluorescence, quickly return to ambient levels over a few centimeters. *These discussions led to the redesign of the experimental apparatus used in our investigation to more closely mimic field conditions.* Additionally, Woodson was introduced to the challenges of oceanographic field research, including the limits of the techniques used to quantify observations, and attained a better understanding of the physical and biological processes associated with thin layers.

A new flume facility (Fig. 1) has been constructed at Georgia Tech to facilitate the proposed research. The apparatus creates thin layers in the laboratory via a planar jet flow into a stagnant environment. This is slight change from the mixing layer apparatus described in the proposal due to interaction (and discussion) with the *in situ* measurements (see above). Natural levels of strain rate, which vary from 0-0.1 s^{-1} in oceanic thin layers (e.g., Dekshenieks et al. 2001; Cowles, pers. comm), are targeted. We target a slightly larger range because the *in situ* measurements may be under-resolved. Shear layer thickness may vary from one to several centimeters in the flume, which is an order of magnitude larger than the plankton size.

The saltwater planar jet flows into a quiescent tank (25 cm span by 80 cm long) from a rectangular nozzle (25 cm span by 1 cm wide) at the end of a smooth contraction. The resulting flow is a three-layer configuration (stagnant upper and lower layers with flowing middle layer), which has several advantages. First, this flow arrangement resembles observed features in the ocean, where velocity (and density) jumps over centimeter scales are associated with biological activity. Second, this arrangement is more conducive for the planned laboratory experiments with copepods. Copepods will be aggregated in the lower stagnant layer, and then phototactically induced upward toward the moving layer. Animals demonstrating a positive response will aggregate in the shear layer, and repetitive turning will be observed. In the previously proposed mixing layer configuration, organisms passing into the upper moving layer would be swept downstream. For the new design, only organisms that remain in the core of the flowing layer for a significant period of time will be swept away. The new apparatus is also designed for the addition of chemical exudates for future experiments.

Figure 1. Photograph of new flume located in the temperature-controlled room.

Quantitative measurements of the flow and turbulence characteristics were obtained using Particle Image Velocimetry (PIV). This is a non-intrusive optical technique that measures fluid velocity by tracking the displacement of small tracer particles, which are illuminated by a sheet of a laser light. The evaluation of the PIV images consisted of correlation-based processing techniques to determine the displacement between two consecutive patterns of tracer particles (e.g. Webster et al. 2001). The particle displacement was combined with the image magnification and time delay between laser pulses to determine the local velocity. *In addition, in the past year we developed a PIV system that operates in the infra-red wavelengths. The purpose is to minimize the optical perturbation of the zooplankton and hence observe their natural behavior response to thin layer flows*. The system uses a pulsed IR laser (Oxford Lasers model HSI-500) and an IR sensitive camera (VDS Vosskühler CMC-1300). Preliminary tests indicate that under IR illumination, the animals were not disturbed and the cameras could detect the light scattered by the particles.

RESULTS

A sample velocity field for the new planar jet apparatus is shown in Fig. 2a. The layers below and above the jet core are nearly stationary, as planned. The planar jet velocity profile agrees extremely well with the theoretical laminar solution of Bickley (1937) for distances beyond 5 nozzle widths from the orifice (Figure 2b):

$$u = U \text{sech}^2 \left(\frac{Re^{1/2}}{2} \right) \eta$$

Where Re is the jet Reynolds number, U is the centerline velocity, and η is the non-dimensionalized y-coordinate.

Figure 2a additionally shows the strain rate field calculated from the velocity field. Strain rate magnitude varies between 0.0 and 1.5 s^{-1} for the sample shown, which agrees with the target range for thin layers. Furthermore, the preliminary results confirm that the velocity measurements can be accurately collected at the scale of individual organisms.

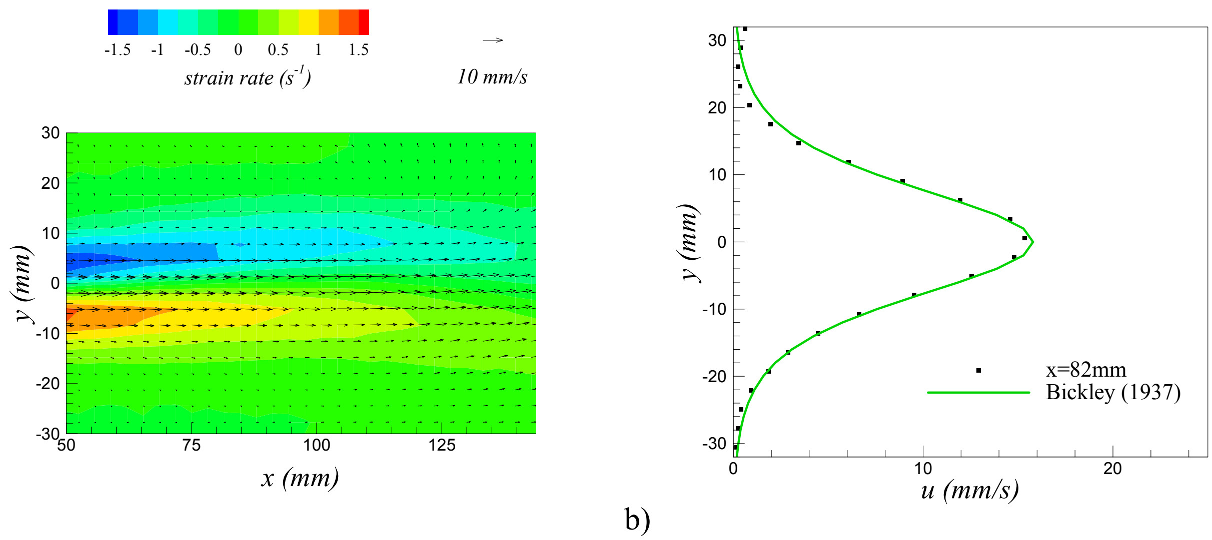

Figure 2. Sample velocity field and profile for the planar jet. a) Velocity field from 50-150 mm downstream of nozzle with strain rate contours; b) Sample profile at x = 82mm compared to theoretical Bickley jet.

IMPACT/APPLICATIONS

Determining the signal parameters that guide animals to thin layers, and the threshold levels of chemical and flow signals that induce aggregations, will improve our current understanding of formation and persistence of thin layers and zooplankton aggregations. Additionally, identifying the signals and thresholds at which relevant signals induce aggregations will help to target field sites that posses these characteristics. Once we understand if and how small-scale heterogeneity attracts plankton aggregations, we can begin to evaluate how grazers/predators influence the characteristics of these layers. Our experiments also will help establish the balance between physical forcing and biological responses in thin layer formation. When biological responses are a significant factor, individual based behavior models can be used in conjunction with Langrangian transport models to understand or predict aggregation to small-scale chemical and fluid structures (Yamazaki et al. 2002). Establishing the physical conditions under which zooplankton orient to fluid velocity or chemical gradients therefore will aid modeling efforts by outlining when these models must incorporate biological responses and active movement of individuals. Further, our experiments will supply data on movement velocities, turning rates and other response variables that are required for these individual-based models. Alternatively, determining when zooplankton responses are not the dominant driving force will establish a framework in which thin layers may be modeled via physical transport processes that affect organisms. Under these conditions, distributions of organisms can be modeled in a manner similar to other passive scalar quantities such as heat or chemical concentration (Osborn 1998). The relative simplicity of models that do not require explicit biological assumptions makes it critical that we establish when they can be reliably employed.

RELATED PROJECTS

The PIs have several projects that focus on the interdependence of copepod behavior, flow, turbulence, and mechanoreception. The measurement approach and techniques are similar among these projects. In addition, the observations and results of these projects reinforce and supplement the current project.

"A novel apparatus for simulating oceanic turbulence in the laboratory" PIs: Webster and Yen. Sponsor: NSF Ocean Technology and Interdisciplinary Coordination. August 2002 – July 2003

"Mechanoreception in marine copepods: coding complex fluid disturbances" PIs: Fields and Weissburg. Sponsor: NSF Integrative Biology and Neuroscience. Jan 2003 – Dec 2006.

"Dynamic similarity or size proportionality? Adaptations of a polar copepod" PIs: Yen, Weissburg, and Webster. Sponsor: NSF Polar Programs. March 2003 – Feb 2004.

"Collaborative research: Role of turbulence in structuring the vertical distributions of planktonic copepods in the western Gulf of Maine" PIs: Yen and Webster. Collaborators: Ann Bucklin and Jamie Pringle, Univ. of New Hampshire. Sponsor: NSF Biological Oceanography. Pending.

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