COUPLING BEHAVIOR AND VERTICAL DISTRIBUTION OF PTEROPODS IN COASTAL WATERS USING DATA FROM THE VIDEO PLANKTON RECORDER

Scott M. Gallager
Woods Hole Oceanographic Institution
Woods Hole, MA 02543
(508) 289-2783
sgallger@whoi.edu

N00014-96-1-0684

LONG TERM GOALS

A combination of empirical, theoretical, and field studies are being used to develop a method for making accurate short- term (hours-days) predictions of the abundance and distribution of zooplankton, *Limacina retroversa* (Pteropoda, Thecosomata), in the ocean. This snail occurs in large numbers in coastal waters, forming dense patches (many kilometers in length) that are acoustically and optically opaque due to the animal's hard shell. A new conceptual approach is being developed to obtain behavioral information on individual plankton over a large range of spatial scales (1 cm-100 km). Still images from the Video Plankton Recorder (VPR) are being used to link behavior at the micro-scale to vertical and horizontal distributions of plankton over much larger scales.

OBJECTIVES

The general hypothesis being tested is that the vertical distribution of the pteropod *Limacina retroversa* is predictable as a function of light, temperature, salinity, food concentration, stratification and mixing intensity. To accomplish this, the following objectives are being addressed:
1) To determine the effects of light intensity and phase, temperature, salinity, food concentration, stratification, and turbulence on the swimming behavior and vertical position of *Limacina*.
2) To develop a behavioral repertoire for Limacina relating body orientation, as viewed from a static image in the plankton, to a dynamic description of its instantaneous swimming behavior.
3) To couple objectives 1 and 2 through numerical modeling of pteropod behavior to allow projection of a pteropod population in space and time as a function of its behavioral responses to specific environmental characteristics.
4) To test the predictions of the numerical models with data collected on Georges Bank and the Southern New England Bight using both towed and moored Video Plankton Recorder instrumentation.

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APPROACH

Objective 1 is being addressed through a series of mesocosm experiments which are being conducted to determine the effect of each environmental variable on swimming behavior and vertical position in the water column. Objective 2 requires still images to be collected from mesocosms containing pteropods using the mini-VPR. The images are being used to develop a complete behavioral repertoire for *Limacina* which may be used to infer the behavior of individual pteropods from the field. Objective 3 focuses on the development of coupled 2-dimensional bio-physical model superimposing pteropod swimming characteristics on a background of multi-scale physical structure. The physical component uses a sophisticated turbulence closure technique while the biological component provides for multiple levels of behavioral feed-back as a function of environmental characteristics. An IBM (individual based model) approach is providing the coupling between individuals and the population level of statistics. The fourth objective addresses the need to test the hypotheses being generated against data collected from critical habitats: Georges Bank and the Southern New England Bight as part of the U.S. GLOBEC Northwest Atlantic program.

WORKED COMPLETED

Collection and Culture of Pteropods

All the experimental work being conducted in the laboratory requires a consistent supply of pteropods of a variety of developmental stages. This is being addressed through both field collections and laboratory culture programs. Pteropod collections were initiated in March 1996 with the help of numerous investigators in the US GLOBEC Georges Bank Program Broadscale cruises. Four collections of about 5,000 individuals each were made on the Southern Flank of Georges Bank providing sufficient material for lab work throughout the Spring months. Attempts to get *Limacina* into culture were made throughout the season, but survival of the larval stages was poor. During the 1997 GLOBEC field year (March-July) we made 7 independent collections of at least 10,000 adult pteropods each. Together with my Research Associate Phil Alatalo, I have completed numerous lab experiments and now have an F1 generation of *Limacina* in culture. The key to culture the larvae has been large culture vessels (>12l), low food concentrations (<10^3 cells.ml), mixed algal diet (*Croomonas*, *Isochrysis*, *Hterocapsa*, and *Proocentrum*), and low mixing conditions. We hope to keep *Limacina* in culture for years to come as a consistent supply of material for various experimental studies.

Population-Level Experiments:

Experiments on populations of pteropods in 4 m deep laboratory mesocosms are looking at responses to light, temperature, food concentration, salinity, stratification, and mixing intensity. Continuous observations of population diel vertical migration patterns over periods of weeks are being conducted using video image and image processing techniques.

Individual-Level Experiments:

Experiments are being performed on individual pteropods to analyzed their swimming, sinking and feeding behavior, the kinematics of motion, and ecological energetics. Individual pteropods are followed in a 4 m-deep tank for periods of up to eight hours while observing swimming/sinking speeds and parapodia positions and other behaviors. This information is essential as input into the IBM simulation models being developed below.

A complete data set has now been collected describing parapodia position and the instantaneous swimming behavior of an individual as a function of organism size. Based on the angle the parapodia makes with the gravity vector, we can now infer with 99% accuracy the swimming behavior (swimming or sinking) and the relative speed and direction. This information is critical for extracting behavioral information from the still VPR images described below.

Field Distributions and Behavior:
In this component of the project, the still images of the VPR are being used to infer an instantaneous behavior associated with parapodia position. We have almost finished the re-analysis of VPR 22 transect across Great South Channel for zooplankton postures. Appendage and orientation of all zooplankton along that transect are being classified manually. In addition we have recently completed a series of cruises with the VPR to Georges Bank in which many pteropods were sighted. One particularly exciting study was done in June 1997 when a patch of copepods and pteropods were followed for a period of 48 hours while quantifying their horizontal and vertical distribution in real-time with computers on board ship. The more than 10,000,000 images extracted and processed for organism abundance during that study are now being re-processed for posture and orientation information. The data obtained from these field collected images will be combined with the kinematic studies outlined above to produce spatial maps of zooplankton behavior over the transect. The simulation models (below) will then be used to simulate and project those populations days into the future knowing the individuals responses to environmental gradients.

RESULTS

Population-Level Experiments:
In the absence of food (motile dinoflagellates), predators and strong mixing, *Limacina* appear to be reverse diel migrators moving to the surface 180 degrees out of phase with the light regime (up at the surface during the day and near the thermocline at night). When dinoflagellates are added, the pteropods continue to follow their prey to the surface during the day and lower in the water column at night.

We are preparing to conduct an experiment where predators will be added to the mesocosms while DVM is monitored. The hypothesis is that *Limacina* will ignore food distributions near the surface in favor of avoiding predation during the daylight hours. These experiments will continue throughout the following year.

Individual-Level Experiments:
High-speed video observations of the feeding process in juvenile and adult pteropods show clearly that phytoplankton prey are captured on the dorsal surface of the parapodia through interaction with cilia during the sinking phase when the parapodia are held dorsal to the shell. Captured cells are transported to the mouth through an extensive network of ciliated channels leading from the tips of the parapodia. Moreover, individual cells may be selected for ingestion following capture.

This description of feeding behavior is in direct contrast with the mucus web observations of feeding reported in the literature. We have never seen a mucus web in the laboratory or in VPR images from the field. Thus, there is more than one mode of feeding which may depend on local particulate conditions or other environmental characteristics.

The energetics of swimming/sinking, feeding, mating, etc. are being measured on individual pteropods as input to the simulation models described below. Tall but narrow polarographic respiration chambers allow individuals to behave reasonably normally as oxygen utilization and behavior is monitored. These data are being taken over a wide range of developmental stages (larvae-adult) and temperatures. One of our most recent and fascinating findings is that pteropods switch between muscular swimming by sculling with their parapodia to ciliated swimming when they hold their parapodia still. From the observer's perspective, when the pteropodia are held motionless above the shell, the animal can either sink like a rock at 2-3 $cm.s^{-1}$ or they may float around appearing to have attained neutral buoyancy. Close examination of the ciliation on the edge of the parapodia and the flow field resulting from the beating of these cilia shows that the cilia are responsible for holding the pteropods position in the water column, not a mucus web as stated in the literature.

Growth and developmental rates are being quantified from hatching through senescence using high-speed video microscopy, thick-section histology, and Scanning Electron Microscopy. SEM images are invaluable for describing the three-dimensional pattern of ciliation on the parapodia used during food collection and swimming.

Simulation modeling:
Dr. Hidekatsu Yamazaki spent two weeks in September 1996 in my laboratory working on a coupled bio-physical model of pteropod vertical distribution and turbulence. The results of these models were encouraging but lacked the behavioral response by the organisms we have grown to expect under specific environmental conditions. To follow up on this work, both Hidekatsu and his wife Atsuko Yamazaki spent six weeks here this summer. Atsuko is a computer engineer and numerical modeler. Together we developed an IBM simulation model for pteropods allowing internal state (hunger, energy levels, etc.) along with external food, light and temperature to govern swimming and sinking patterns. The results are very exciting- the models show very clear resemblance to the individual behaviors observed in our tanks in both frequency space and over time. Coupling the behavioral model now with the Ekman layer model for production of turbulence is the next phase of the program.

IMPACT

This study is providing a novel and powerful conceptual framework for viewing and understanding plankton dynamics across multiple temporal-spatial scales. With this concept of collecting behavioral data on plankton from static images, and then projecting that behavior in time and space to establish future population distributions, complete and accurate descriptions of population and community structure in the plankton may be possible. This will allow scientists for the first time to observe plankton behavior over extremely diverse scales, while allowing the Navy to better understand and predict ocean optical and acoustic scattering characteristics; The goal being to accurately differentiate between manmade and natural structures on scales of mm to km.

TRANSITIONS

This work is finding its way into more applied applications through its proposed use in the National Oceanic Partnership Program where we plan to install an Ocean Observatory in Massachusetts and Cape Cod Bays using a distributed network of the Moored Profiling VPR System. This will be used to measure plankton distributions instantaneously and make forecasts of plankton populations based on their instantaneous behavior. These predictions will be used in both commercial and military sectors to evaluate the potential for the presence of baleen whales and other large, planktivorous organisms.

RELATED PROJECTS

A closely related project is "Real-Time Quantification of Plankton Abundance, Size, and Taxonomic Composition Using the Video Plankton Recorder."
PIs: Cabell Davis, Scott Gallager and Xiaoou Tang.
This project is developing the real-time plankton identification tools critical to mapping plankton distributions over wide temporal-spatial scales.