FINAL REPORT
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Title: Coupling Behavior and Vertical Distribution of Pteropods in Coastal Waters using Data from the Video Plankton Recorder

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Abstract
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.

Overall Objective:
The objective of this project is to test, using both experimental manipulations and field observations, the hypothesis that the vertical distribution of the pteropod *Limacina retroversa* over its ontogeny is predictable as a function of light, temperature, salinity, food concentration, stratification and mixing intensity. First, a series of mesocosm experiments were conducted to determine the effects of each of these variables on swimming behavior and vertical position in the water column. Second, still images from the mesocosms using the mini-VPR were used to infer behavior of individual pteropods. Third, a random walk turbulence model with behavioral feed-back is providing coupling to the population level. And, fourth, the hypothesis is being tested in the field using both moored and towed VPR instrumentation in conjunction with the NSF-GLOBEC Georges Bank Program.

Progress To Date:

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 F3 generation of *Limacina* in culture. The key to culturing the larvae has been the use of large culture vessels (>12l), low food concentrations ($<10^3$ cells.ml), mixed algal diet (*Croomonas*, *Isochrysis*, *Hterocapsa*, and *Proocentrum*), and low mixing conditions. Additional field collections were completed during the 1999 GLOBEC field year. 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 were conducted using video image and image processing techniques. 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 move lower in the water column at night.

We have conducted several experiments where predators (*Clione* sp.) were added to the mesocosms while DVM was monitored. The hypothesis that *Limacina* will ignore food distributions near the surface in favor of avoiding predation during the daylight hours was unsubstantiated: *Limacina* continued its normal migration pattern in the presence of severe predation pressure by *Clione*. Since Clione is a mechanosensory predator and does not use vision, this result is not suprising, but does demonstrate that predation pressure in not necessarily the key factor controlling DVM.

Individual-Level Experiments:

Experiments were performed on individual pteropods to analyzed their swimming, sinking and feeding behavior, the kinematics of motion, and ecological energetics. Individual pteropods were 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.

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.

Field Distributions and Behavior:

In this component of the project, the still images of the VPR were used to infer an instantaneous behavior associated with parapodia position. We have finished the re-analysis of VPR 22 transect across Great South Channel (Gallager et al., 1996. Deep Sea Res. II. 43:1627-1663) 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.

Simulation modeling:

Both Dr. Hidekatsu Yamazaki and his wife Atsuko Yamazaki spent six weeks here in Woods Hole during the summer of 1997. 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.
The objectives for the third year of the program including the 6 mo extension are to:
1) Continue culturing *Limacina* in large vessels.
2) Continue mesocosm behavioral experiments focusing on food and thermal gradients as modulators of vertical excursion.
3) Complete and submit the following manuscripts:
Gallager, S.M. A kinematic analysis of swimming in the pteropod *Limacina retroversa.* to: J. Bio-Fluid Mechanics
Gallager, S.M. and P. Alatalo. Swimming and feeding in the Thecosomate pteropod *Limacina retroversa.* Mar. Biol.
Yamazaki, A. H. Yamazaki and S.M. Gallager. New approaches to coupled physical and behavioral simulation modeling in Zooplankton Ecology. To: Mar. Ecol. Progr. Ser.
Gallager, S.M. Behavior of individual zooplankton quantified over their meso-scale distributions To: Science
4) Complete coupling of physics and behavior in simulation models including using the Mellor-Yamada turbulent closure scheme to simulate turbulence.

Presentations citing this award:
1998 SM Gallager, H Yamazaki, A Yamazaki, P Alatalo. Scale translation in the plankton: Coupling behavior and vertical distribution on pteropods in coastal waters. OS41N-09

1998 SM Gallager, CS Davis, H Yamazaki, P Alatalo. Observations of plankton pancakes on Georges Bank: The roles of behavior, startification and microstructure. OS51H-09

1998 Van Keuren, JR, SM Gallager, RG Lough, LS Incze, E Caldarone, P Alatalo, EA Broughton, JP Manning. Interaction of hydrographic and biological conditions with growth and feeding of larval cod and haddock on Georges Bank's southern flank. OS21E-03 AGU, 1998.

1998 MC Benfield, PH Wiebe, DG Mountain, CS Davis, SM Gallager, CH Green, TK Stanton. Visulaizing fine-scale physical and biological structure: Results from optical, acoustical and environmental sensing. OS21E-09, AGU, 1998

1998 CS Davis, SM Gallager, X Tang, CJ Ashjian. Real-time visulatization of taxa-specific plankton distributions. OS21E-10, AGU, 1998

1998 CL Johnson, SM Gallager, CS Davis. Observations in 3-D of in situ copepods motion. OS21E-11, AGU 1998

1998 FT Thwaites, SM Gallager, CS Davis AM Bradley, A Girard. The Autonomous vertically profiling observatory (AVPPO). OS31A-16, AGU, 1998

1998 MR Dennett, DA Caron, A Michaels, SM Gallager, CS Davis. Colonial radiolarian abudance and biomass estimates in the upper 150 m of the Eastern Pacific and Western Atlantic using a mini-Video Plankton Recorder. OS41N-01, AGU, 1998

1998 CJ Ashjian, CS Davis, SM Gallager, P Alatalo. Distribution of plankton and particles across Georges Bank during 1994-1995 GLOBEC cruises: Results of cross-bank surveys using the Video Plankton Recorder (VPR). OS41D-07.

1998 RG Lough, LS Incze, SM Gallager, EA Broughton, JP Manning. Sampling strategy fro larval fish and their zooplankton prey in the tidal mixing front on Southern Geotrges Bank, May 1997. OS42H-01

1998 F Bar, C Lee, KH Brink, CS Davis, SM Gallager, M Berman. Observations of major warm water intrusion onto Georges Bank: Summer 1997 OS32C-08

Finances:
Funds for this project are 98% expended and a 6 mo extension has been requested to allow completion of the manuscripts stated above.

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13. Abstract
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.

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