

ANNUAL PROGRESS REPORT
Year 1, 1 May 1996 to 30 September 1996

ONR Grant Number: N00014-96-1-0684

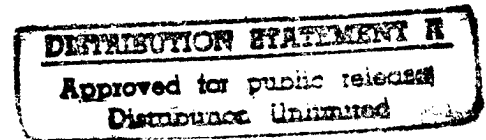
Title: Coupling Behavior and Vertical Distribution of Pteropods in Coastal Waters using Data from the Video Plankton Recorder

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PIs Institution: Woods Hole Oceanographic Institution

Funds related to this report: \$86,205

Total funds over 3 years: \$327,205



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 proposal 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 are being 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 are being 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 Broad-scale 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 (<10³ cells.ml), mixed algal diet (*Croomonas*, *Isochrysis*, *Heterocapsa*, 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. 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:

Experiments are being performed on individual pteropods to analyze 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.

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 parapodia are held motionless above the shell, the animal can either sink like a rock at $2-3 \text{ cm}\cdot\text{s}^{-1}$ 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 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 (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:

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.

Objectives for Years 2 and 3:

- 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) Present the following paper at the 1998 AGU/ASLO meeting in San Diego:
Gallager, S.M., A. Yamazaki, H. Yamazaki and P. Alatalo. New insights into zooplankton behavior through a combination of laboratory experiments, field observations, and simulation modeling
- 5) Complete coupling of physics and behavior in simulation models including using the Mellor-Yamada turbulent closure scheme to simulate turbulence.

Finances:

Funds for the first year of this project are exhausted at the time of this writing, I do not anticipate any problems since funding for the second year has arrived. In addition, I am still interested in working with investigators from an NRL laboratory to supplement this reasearch. No positive contacts have been made, however.

REPORT DOCUMENTATION PAGE			Form Approved OMB No. 0704-0188	
<small>Public reporting burden for this collection of information is estimated to average 1 hour per response, including the time for reviewing instructions, searching existing data sources, gathering and maintaining the data needed, and completing and reviewing the collection of information. Send comments regarding this burden estimate or any other aspect of this collection of information, including suggestions for reducing this burden, to Washington Headquarters Services, Directorate for Information Operations and Reports, 1215 Jefferson Davis Highway, Suite 1204, Arlington, VA 22202-4302, and to the Office of Management and Budget, Paperwork Reduction Project (0704-0188), Washington, DC 20503.</small>				
1. AGENCY USE ONLY (Leave blank)	2. REPORT DATE	3. REPORT TYPE AND DATES COVERED		
		Progress 5/1/96 - 4/30/97		
4. TITLE AND SUBTITLE			5. FUNDING NUMBERS	
COUPLING BEHAVIOR AND VERTICAL DISTRIBUTION OF PTEROPODS IN COASTAL WATERS USING DATA FROM			N00014-96-1-0684	
6. AUTHOR(S)				
THE VIDEO PLANKTON RECORDER				
Scott M. Gallager				
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES)			8. PERFORMING ORGANIZATION REPORT NUMBER	
WOODS HOLE OCEANOGRAPHIC INSTITUTION WOODS HOLE, MA 02543			WHOI Proposal No. 9897	
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)			10. SPONSORING/MONITORING AGENCY REPORT NUMBER	
ONR, Ballston Tower One 800 N. Quincy Street Arlington, VA 22217-5660				
11. SUPPLEMENTARY NOTES				
12a. DISTRIBUTION / AVAILABILITY STATEMENT			12b. DISTRIBUTION CODE	
APPROVED FOR PUBLIC RELEASE				
13. ABSTRACT (Maximum 200 words)				
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14. SUBJECT TERMS			15. NUMBER OF PAGES	
			16. PRICE CODE	
17. SECURITY CLASSIFICATION OF REPORT	18. SECURITY CLASSIFICATION OF THIS PAGE	19. SECURITY CLASSIFICATION OF ABSTRACT	20. LIMITATION OF ABSTRACT	

NSN 7540-01-280-5500

Standard Form 298 (Rev. 2-89)
Prescribed by ANSI Std. Z39-18
298-102