Nutritional Control of Bioturbation in Marine Sediments

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Award Number: N000140210653

LONG-TERM GOALS

We focus on the role played by food quality in controlling sediment mixing by benthic animals in coastal sediments. We hypothesize that a threshold level of food abundance controls whether or not significant mixing can occur, that this threshold is driven by protein concentrations, and regional differences in mixing among coastal regions may therefore be explained by differences in protein contents.

OBJECTIVES

1. Determine the threshold concentrations of sedimentary food at which marine benthic invertebrates can obtain nutrition and hence ingest sediments profitably.
2. Reassess feeding and movement modes of various deposit feeders to establish feeding patterns and movement patterns that can be put into bioturbation models.
3. Test if nutritional threshold concentrations control the styles, depth distributions and seasonality of bioturbation at two types of field sites representative of many coastal areas.

APPROACH

Our approach begins with laboratory studies of animal growth and feeding style in response to varying protein contents of sediments upon which they feed. We will work with a variety of feeding types of benthic invertebrates, providing sediments engineered to vary protein levels while minimizing artifacts due to particle selection. Ultrasound will be tested as a means for determining feeding modes and rates. This lab work will be supplemented by field surveys of mixing intensity in a temperate and a sub-tropical coastal region, which will use both spatial and temporal variations in food abundance to provide field tests of the results found in the laboratory component of the study. The chemical work on food engineering and analysis and measurement of various chemical parameters in the cores will be performed in L. Mayer's lab. P. Jumars' lab will be responsible for raising animals in the laboratory and assessing their growth, plus determination of biotic variables in field samplings. Bioturbation will

Report Documentation Page

Form Approved
OMB No. 0704-0188

1. REPORT DATE **30 SEP 2003**	2. REPORT TYPE	3. DATES COVERED **00-00-2003 to 00-00-2003**

4. TITLE AND SUBTITLE **Nutritional Control of Bioturbation in Marine Sediments**	5a. CONTRACT NUMBER
	5b. GRANT NUMBER
	5c. PROGRAM ELEMENT NUMBER
6. AUTHOR(S)	5d. PROJECT NUMBER
	5e. TASK NUMBER
	5f. WORK UNIT NUMBER
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) **Darling Marine Center, University of Maine,,Walpole,,ME,04573**	8. PERFORMING ORGANIZATION REPORT NUMBER
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)	10. SPONSOR/MONITOR'S ACRONYM(S)
	11. SPONSOR/MONITOR'S REPORT NUMBER(S)

12. DISTRIBUTION/AVAILABILITY STATEMENT
Approved for public release; distribution unlimited

13. SUPPLEMENTARY NOTES

14. ABSTRACT

15. SUBJECT TERMS

16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT	18. NUMBER OF PAGES	19a. NAME OF RESPONSIBLE PERSON
a. REPORT **unclassified**	b. ABSTRACT **unclassified**	c. THIS PAGE **unclassified**	**Same as Report (SAR)**	**5**	

Standard Form 298 (Rev. 8-98)
Prescribed by ANSI Std Z39-18

be assessed by both PI's, with help from D. Shull (Gordon College) and in collaboration with B. Boudreau (Dalhousie U.).

WORK COMPLETED

In laboratory testing of the threshold nutrient hypothesis (that a threshold nutrient level within the range found in nature limits deposit-feeder growth), most of the year was devoted to methods development. After switching to a more porous (electrophoresis) bead, we were able to attach sufficient protein. It took further refinement of the method to avoid toxic responses (covering of active molecules with amino acids and multiple rinses). Now that the methods for food preparation are in hand we have hired a postdoc, Eric Weissberger, to accelerate testing of the threshold hypothesis.

Field testing of the threshold hypothesis began by examining some nearshore sites as originally envisaged in the proposal. Downcore analysis showed that food contents are so high at depth, however, that nutritional thresholds obtained in the laboratory seem unlikely to be found in the field during the seasonal sampling. We have therefore moved to use offshore sites for the Gulf of Maine leg of this set of field tests. During the last year a multicorer was purchased for this project (Minimuc, Oktopus GmbH, Germany), but teething problems necessitated its return to the manufacturer for adjustments. The Gulf of Maine field samplings have only just begun, as a result. We have obtained preliminary sediment samples from the Gulf of Mexico, and analyzed their food content.

Because of problems quantifying selectivity, there are no published data for growth of surface deposit feeders as a function of ingested food quantity and quality. Eric Weissberger has initiated cultures of *Streblospio benedicti* for this purpose and is in the process of automating, through image analysis, volume estimates from digital photographs of specimens. From volume-weight regressions and before-after volume estimates on feeding regimens we will titer toward the threshold for zero growth. We postulate that in general the threshold will be higher for surface than subsurface deposit feeders at the same location as well as on average for the global ocean.

Another component of the work, in collaboration with B. Boudreau of Dalhousie, is to develop and test automata descriptions of deposit-feeder behavior. In order to help with this task, through the graces of the University of Rhode Island and the Office of Naval Research, we acquired the ALOKA SSD-500 Ultrasound System previously used under ONR funding by Webb and Miller (2000). We were unable to achieve consistent results with known, buried targets and therefore asked Van Holliday of BAE SYSTEMS to evaluate the unit. His assessment was that because of human safety considerations, the sound intensity produced by this and other medical or veterinary units is low, explaining the generally poor capability to resolve targets below the sediment-water interface. The ALOKA unit apparently is tuned (by differencing) to be sensitive to target motion, so it may be more useful in this mode for testing some specific hypotheses about the rules that bioturbating burrowers follow, but will not be as useful as we had hoped for characterizing burrow geometries.

NSF-sponsored work on effects of unsteady flows on phytoplankton (Koehl *et al.* 2003) has sensitized us to unsteady processes, and the collaboration with B. Boudreau led us to question previous understanding of the fundamental mechanics of burrowing, especially in cohesive sediments. In particular, the mechanics of bubble shape and migration recently illuminated by Johnson *et al.* (2002) and Gardiner *et al.* (2003) appear to have striking analogies in both shapes of burrowers and mechanisms of burrowing as we have begun to reinterpret them: Clams are wedges, burrowing amphipods are bubble shaped, and the diverse anchor mechanism of burrowers in general may serve to focus energy at a crack, which the animal then moves easily through. This interpretation is vastly different from the current paradigm in which an anchor resists the sharp foot or anterior thrust into the sediments, and allows it to deform them plastically. We suspect that an incorrect or at least not universally applicable paradigm is responsible for the assessment that burrowing is the most expensive of all means of animal locomotion per body length moved (Hunter and Elder 1989).

For many years we have used seawater gelatin to demonstrate burrowing without realizing that its mechanical properties quite accurately mimic those of many cohesive sediments (Johnson and Boudreau, unpublished field measurements). We have just put together this observation with the photoelastic behavior of gelatin to begin to measure directly the stresses applied to sediments in burrowing by infauna. Stressed regions of the gelatin affect the transmission of polarized light in proportion to the magnitude of the imposed stresses. For a related application that explains the approach, see Fell et al. (1995)

RESULTS

We can now make protein-coated beads with contents as high as 10%, without inducing toxic responses in benthic invertebrates.

Evaluation by Van Holliday (BAE SYSTEMS) of the ALOKA ultrasound unit makes us less optimistic that commercial medical or veterinary ultrasound units will be useful for quantifying infaunal behaviors, so we have shifted focus to other means to provide constraints on automata and other kinds of bioturbation models. Namely, we are working to incorporate realistic physical constraints on both the behavior of the animals and the behavior of the sediments as they are influenced by animals. To date from measurements of pressure in model animals we have verified that the opening of a clam shell and radial expansion of soft-bodied burrowers take relatively little force to create a propagating crack perpendicular to the expansion direction. We have recorded photoelastic interference fringes from real animals burrowing in seawater gelatin and are carrying out the necessary calibrations and material-properties models to convert these stress observations to forces produced and work done by the animals.

No data are yet available from offshore Gulf of Maine sediment samplings. Abundant capitellid fecal pellets imply strong feeding activity in the September sampling or else very long half lives of the pellets. The food content of nearshore sediments (measured as enzymatically hydrolysable amino acids) from the Gulf of Mexico was strikingly low (as hypothesized), giving promise that the Gulf of Maine-Gulf of Mexico comparison will prove quite instructive.

IMPACT/APPLICATIONS

Should a threshold food level prove to be important in controlling bioturbation, then macrofaunal mixing of marine sediments, both temporally and spatially, will become somewhat more predictable. The nature of the mixing process, and its impact on particle movement within the sediment column, will also become more predictable from an understanding of local species composition, production and detrital processing. Understanding the mechanics of burrowing and feeding is expected not only to increase this predictability of animal behavior and its consequences for stratigraphic interpretation but also its consequences for acoustic propagation in sediments.

RELATED PROJECTS

We are aware that David Wethey and Sally Woodin of the University of South Carolina, together with Roberta Marinelli of the University of Maryland, are planning repeated ultrasound scans in an intertidal environment in order to obtain information about animal activities below the sediment-water interface, e.g., frequency of movement. We have been sharing the information noted in this report about the ALOKA unit and intend to continue to collaborate with this group and encourage their efforts.

We have reciprocated working visits with Bernie Boudreau's (Dalhousie) laboratory. Bernie Boudreau (Dalhousie) visited us in June to discuss automata rules for deposit feeders, and Kelly Dorgan, a graduate student working on this grant, visited Dalhousie in August to participate in field measurements of the linear elastic (stress, strain and fracture) properties of natural muds with Bruce Johnson and Bernie Boudreau. These visits have led to the confluence of both analytic (mechanical) and empirical (ultrasound and other observational) approaches in our work toward biologically and physically credible automata rules.

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