Biology of the Sediment-Water Interface: Report of the St. Andrews Biological Station's 75th Anniversary Benthic Workshop

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This report contains summaries of work presented by nine speakers at the St. Andrews Biological Station's 75th Anniversary Workshop held on December 8, 1983. Also included are précis of questions addressed to each speaker and their answers which were tape-recorded during the meeting. Over 45 persons attended the workshop and the addresses of this "invisible benthic college (N.E. American Chapter)" are included for reference.

RÉSUMÉ

Wildish, D. J. (Ed.). 1984. Biology of the sediment-water interface: Report of the St. Andrews Biological Station's 75th Anniversary Benthic Workshop. Can. Tech. Rep. Fish. Aquat. Sci. 1263: iv + 38 p.

Le présent rapport contient les résumés des travaux présentés par neuf chercheurs, lors du cercle d'étude tenu à l'occasion due 75e anniversaire de la station de biologie de St. Andrews, le 8 décembre 1983. On y trouve également les résumés des questions adressées à chacun des orateurs et de leurs réponses qui ont été enregistrées au cours de la réunion. Plus de 45 personnes ont assisté à ce cercle d'étude et les adresses des membres de ce groupe peu connu s'intéressant au milieu benthique (Chapitre de l'est de l'Amérique du Nord) sont incluses à titre de référence.

WELCOMING ADDRESS BY DR. R. H. COOK

It is my pleasure, as Director of the Biological Station, to welcome you to the 75th Anniversary Benthic Workshop.

The Biological Station was established in St. Andrews in 1908 and was the first marine fisheries research station in eastern Canada. The original wooden laboratory was destroyed by fire in 1932 and replaced by a brick building the following year. Numerous additions since that date have produced the mix of modern and traditional buildings we now occupy. Currently, plans are under way for a new multi-story brick building to replace many of the older wooden buildings on our campus. We look forward to these developments.

From the earliest times, the Biological Station has maintained close collaborative links with the University community. In our earlier years, all the scientific staff were university professors. In 1970, the Huntsman Marine Laboratory, an educational and research institute comprising a consortium of Eastern Canadian Universities, was established on properties adjacent to the Biological Station. We wish to take this opportunity to thank the HML Director, Dr. Tom Moon, for help in providing accommodation for some of the workshop participants. We hope your stay at Anderson House is a pleasant one.

One important feature of the research conducted at the Biological Station is concerned with the interaction between the fisheries resource and the aquatic environment. In many ways, studies on benthic biology manage to improve our understanding of this interaction. Benthic organisms are the principal food of groundfish, such as cod and haddock, and are also recognized to be good indicators of environmental disturbance, benthic organisms not being able to move away from the polluting source. Research on fish habitat, the biological effects of toxic chemicals, and fisheries ecology are topics of importance at the Biological Station.

The opportunity to organize this workshop is therefore most relevant to our research interests and, I hope, the opportunity for participants to meet and discuss the biology of the sediment-water interface during this workshop will be productive.

I would particularly like to greet out guests who have traveled far to be here today. I note that we have vistors from Yale University, University of Maryland, Guelph University, Dalhousie University, University of New Brunswick, and the Marine Ecology Laboratory, Bedford Institute of Oceanography. Visitors from Université Laval and Université de Montréal were prevented from attending by a snowstorm.

Without further ado, may I wish you success in your workshop efforts and hope that the presentations prove to be stimulating to all.

INTRODUCTION

by

D. J. Wildish

By way of introducing this workshop I will attempt to define the sediment-water interface and also provide a framework which may help to orient the reader to the abstracts and discussions which follow.

The marine environment has many zones of sharp physical discontinuity, for example, between the sea and air or between zones of differing salinity, referred to as the pycnocline. A characteristic discontinuity occurs on the sea bottom between sediment or bedrock and the sea water immediately above it.

The water-column limit of the sediment-water interface of the Continental Shelf is bounded by the upper limit from which benthic organisms can obtain food, respire, excrete, and/or void biogenic materials. In the majority of cases this will coincide with the upper limit of the turbulent, benthic boundary layer (Fig. 1). Within the boundary layer, the drag effects of currents passing over the rough sediment surface produce turbulent mixing which results in a well-mixed layer often of several meters thickness. The exact thickness of the well-mixed boundary layer will depend on the degree of sediment surface roughness and the tidal current velocity.

Because it is probably unusual to find a smooth natural sediment surface, laminar flow conditions will usually be absent and thus need not complicate our definition. Occasionally sea water above the sediment may lack any tidal current or wave energy and here anoxic conditions will be present, as in some deep fjords. In such conditions the redox discontinuity layer migrates above the sediment surface due to seasonal pulses of organic matter from natural or anthropogenic sources. This is followed by aerobic catabolism and chemical oxidation, resulting in oxygen depletion and mortality of aerobic organisms. Occasionally there may be no tidal but considerable wave energy, in which case the wave pulse near the bottom oscillates water particles backwards and forwards with a slight movement in the direction of wave propagation. Wave motion near the bottom depends on the depth of the water column; it is circular at the surface, then elliptical and finally flat in deeper water.

The sediment limit of the sediment-water interface is bounded simply by the penetration of macrofauna into the sediment. This may range from a few millimeters to over 3 m depth in the sediment. Macrofauna may burrow deeper than the redox discontinuity layer, where pumping activities maintain an aerobic microniche.

The sediment-water interface is known to be important for chemical fluxes and where physical energy, in the form of tidal currents and waves, is dissipated. It is also a zone of importance in primary and/or secondary production of the marine ecosystem and, for this reason, it is appropriate to define the sediment-water interface in terms of biological as well as physical factors involved in shaping the biology of the organisms that live there.

The subject matter covered by the nine workshop speakers falls into one of the following categories. Trophic pathways leading to macrobenthos, including sedimentation of planktonic organisms, lateral transport of organic matter by bedload transport, and erosion/redeposition processes. Experiments with suspension-feeding animals include field and laboratory approaches. The last theme, the provision of novel methods for the study of macrobenthos, is of critical importance if benthic biology is to develop as a meaningful subdiscipline of marine biology.

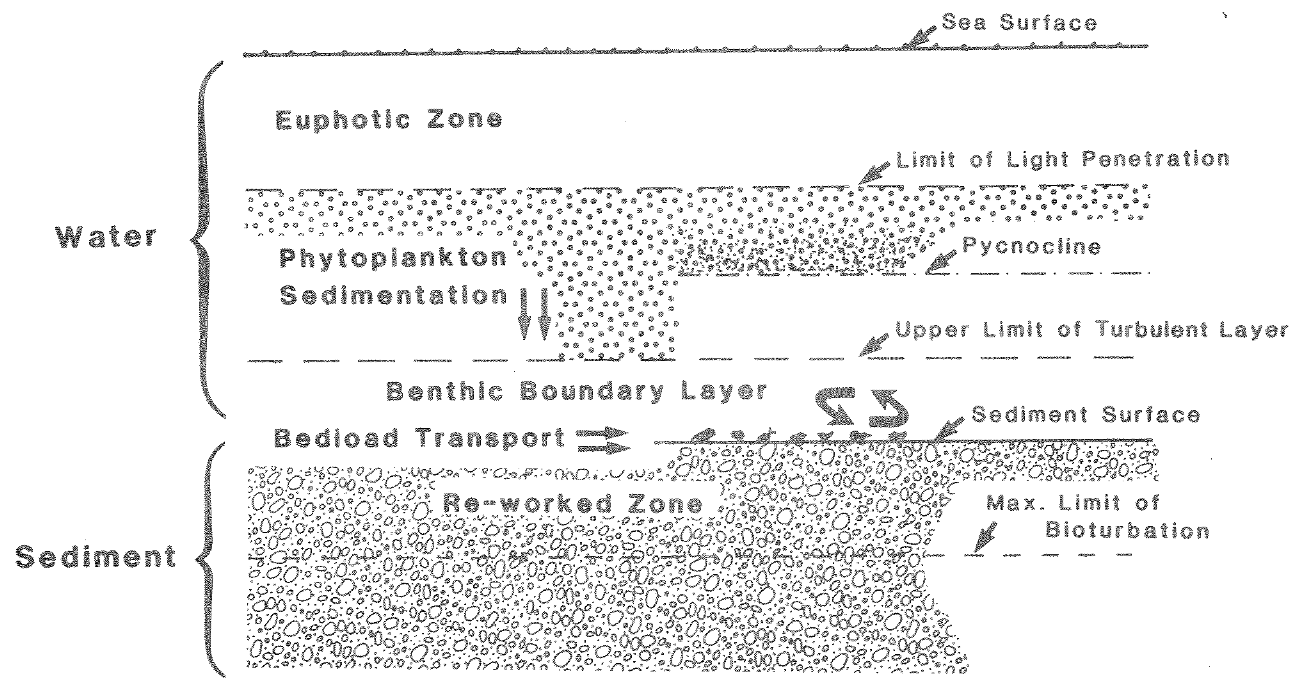

Fig. 1. Diagramatic representation of major physical features of the sediment-water interface.

PELAGIC-BENTHIC COUPLING IN THE MARINE ENVIRONMENT

by

J. C. Roff

Present estimates of the proportion and component types of primary production exported from the pelagic to the benthic realm vary substantially and are subject to several biases. In a compilation of data consisting mostly of observations at lower latitudes, Suess (1980) indicated that only 10-25% of annual primary production is exported below a pycnocline. However, if all the production is grazed by one trophic level of consumers at 60% assimilation efficiency, the flux at the base of the euphotic zone should still exceed 30% of the annual primary production. For coastal temperate waters, grazing rate estimates vary from about 5 to 90% of production, with an annual mean around 30 to 50% (copepods only). Calculations based on energy density measurements from Emerald Bank data suggest that grazing by copepods is about 50% but, on the basis of nitrogen production and requirements, the total zooplankton community may graze $\gg$70% of production.

When annual primary production is seasonally highly modulated, the grazing zooplankton community does not closely "track" production, and much ungrazed algal material can escape directly to the benthos. Thus, at higher latitudes in continental shelf ecosystems, energy export from the pelagic community may be elevated. This would explain observed latitudinal gradients in the ratio of pelagic to benthic production (Petersen and Curtis 1980).

In coastal ecosystems where the pelagic particulate organic carbon (POC) contains detrital material of several origins, it is useful to partition carbon fluxes into macrophytic, microbial inclusive of phytoplankton, and fecal components. This has been accomplished, using an image analysis system comprising an inverted phase contrast microcope, TV camera and monitor, and sonic digitizer interfaced to an IBM-PC computer. Volumes of cells and fecal pellets and their carbon contents have been calculated for samples collected by sediment traps from the Beaufort Sea (Issungnak) and Bedford Basin. Collections from Barrow Strait (Resolute) are being processed.

Estimates of the relative contributions of phytoplankton and fecal material to downward flux may be heavily biased by sediment trap design. Devices with low aspect ratios undersample small particles. Resuspension of settled material also occurs, but may be quantifiable as a ratio of fecal pellets with and without peritrophic membranes.

Differences in pelagic-benthic coupling among tropical, temperate, and arctic ecosystems are not yet established, but certain generalizations may hold, viz:

(i) Both cellular and fecal POC fluxes may be highly variable seasonally. Cell flux dominates at times of high primary production. At times of heavy grazing the fecal component dominates.

(ii) Coprophagy is probably an extensive and important process.

(iii) Microzooplankton (Protozoa) grazing on nannoplankton must be significant; seasonal tintinnid fluxes can be very high.

(iv) Loss of nannoplankton to sedimentation is probably negligible due to negligible sinking rates.

(v) Community respiratory losses may be high at elevated temperatures.

REFERENCES

Petersen, G. H., and M. A. Curtis. 1980. Differences in energy flow through major components of subarctic, temperate and tropical marine shelf ecosystems. Dana 1: 53-64.

Suess, E. 1980. Particulate organic carbon flux in the oceans; surface productivity and oxygen utilization. Nature 288: 260-263.

DISCUSSION

RHOADS Do you find amorphous aggregates formed from dissolved organic matter (DOM) à la Riley and vascular plant debris among the particulate organic matter?

ROFF I have found amorphous aggregates, but not vascular plant debris. The reason for this is that my samples have been from offshore. I am sure if I looked in coastal areas, where intertidal or subtidal macrophyte production was high, that I would find vascular plant debris. Another POM species evident in my samples is zooplankton fecal pellets. You can still distinguish them even after the peritrophic membrane has been ruptured.

RHOADS The chemical nature of sediment organic matter is of interest as is the transition from DOM to POM.

ROFF Yes, there are two categories from coastal waters: labile and phenolic DOM with amounts up to ~ 5 mg/L at the time of spring bloom, and 1-3 mg/L at other times of the year. Very little is known of the interactions of the two chemical pools or of the DOM to POM transition. A further mystery is that POM from the deep sea is estimated by ^{14}C dating to be twice as old as the ocean from which the samples were taken.

WILDISH In the Arctic situation you describe, where a single sedimentation pulse of ice algae occurs, isn't this a good opportunity to relate the rate of benthic-pelagic coupling (i.e. processing of carbon by fauna)?

ROFF Yes.

NEWELL Do you think that the pulse of phytoplankton cells which are deposited in the autumn of temperate climates is actually available for benthic consumers or are the cells encysted and therefore, indigestible to them?

ROFF Dinoflagellates and chytrids are certainly encysting at that time and I would suspect that a proportion of them would be unavailable to consumers. The majority of the cells appear healthy whereas an empty frustule or part of a frustule is easily recognized. Alan, can encysted dinoflagellates pass through invertebrate guts without being digested?

WHITE There is no definitive evidence on this point, although I would suspect that they could.

NEWELL It would be useful to test the digestibility of phytoplankton which are consumed by representative invertebrate consumers.

ROFF Yes, but the probability is that most phytoplankton species can be digested by at least one of the consumer species.

GRANT Are Protozoa attracted to fecal pellets because they graze on attached bacterial microflora or because they use the pellets as a solid substrate?

ROFF There is argument at present as to whether the peritrophic membrane of fecal pellets is broken from the inside out or from the outside in, and hence it is unclear as to the origin of the microflora and microfauna which rapidly colonize the fecal pellet. In 100-200 m of water a fecal pellet sediments in less than 2 d.

GRANT Do mobile protozoans attached to the fecal pellet slow down its rate of sedimentation?

ROFF Yes, and I have tried to calculate how many cells it would take to keep a fecal pellet up in the water column if all the Protozoa were swimming. In temperate climates during fall the tintinnids encyst within the loricule and stop swimming, which tends to make them sink. The carbon calculations presented were made on the basis that if a lorica was found the cyst was also present even though it was not counted.

SCHWINGHAMER In the intertidal sediments of the Bay of Fundy live non-encysted tintinnids are found, but as you go further into the subtidal the sediments contain only encysted cells or loricules without the cyst.

ROFF In the near subtidal, many ciliates may also become trapped in benthic material.

GRANT Are there many Protozoa among the under-ice algae?

ROFF Incredible amounts in some places, for example, in an apontic community I have studied, oligotrich and hypotrich ciliates are active at -2°C in large numbers. There are no grazing estimates for these animals and I am convinced that production estimates made for the apontic community are too low.

LATERAL FLUX OF ORGANIC MATTER IN THE ESTUARINE ENVIRONMENT

by

J. Grant

Bedload movement of organic matter has often been invoked as a missing term to explain why budgets of benthic carbon supply and metabolism do not balance. Despite its apparent importance to benthic-pelagic coupling in coastal and oceanic ecosystems, the magnitude of this process has never been measured. Sedimentologists have estimated bulk sediment transport through various means, but no methodology exists for the associated movement of organic material. Vertical deposition into cylindrical sediment traps fails to account for lateral transport, particularly close to the bed where benthic organisms are likely to capture particles. Such traps measure deposition only to the sediment-water interface whereas detrital flux involves the upper few centimeters of the sediment column.

Once reaching the sediment-water interface, organic matter is incorporated into the bed in a variety of ways. Detritus may accumulate in ripple troughs and form flaser-like structures (i.e. mud laminations) which are buried by migrating ripples. Depending on shape and texture, detrital particles may also behave as individual mineral grains and be transported like sand under given flow conditions. However, because sand and detritus are often combined in organic-mineral aggregates, the distinction between discrete organic particles (e.g. fecal pellets, macrophyte fragments) and mineral grains (with their associated organic matrix) is often muddled. This problem is indicative of a third means by which detritus becomes part of the bed: mucus binding in exudates produced by microbes and metazoans. The role of biofilms in stabilizing sediments has received recent attention, but their ability to "scrub" particles from the water column has not been examined.

An often neglected consideration in the above processes is that bedform migration is central to the horizontal movement of organic matter in non-cohesive sediments. Rates of ripple migration have occasionally been measured in flumes, but rarely determined in the field. Despite recent interest in microscale biogenic structure, ripples have been relatively ignored except for a few comparisons of sedimentary parameters and faunal abundance between crest and trough.

As an initial approach to lateral organic transport, I have recently completed a set of experiments designed to measure deposition and resuspension of organic carbon on sand bottoms. Trays of ashed sand were placed on a sheltered sand beach in Halifax Harbour, Nova Scotia. Ripples formed in the trays were identical to, and continuous with, those in the surrounding sediment. Within a single high tide, ashed sand gained a quantity of organic carbon equal to one-half of the ambient standing stock, although the rate of resuspension was very rapid over the next few days. Deposition was very much dependent on wind conditions and the resulting waves. These pulses of organic matter on short time scales (hours) could be exploited by animals with the ability to facultatively switch feeding modes, i.e. from deposit to suspension feeding.

In order to manipulate aspects of this intertidal environment, I will examine these processes in a laboratory flume. Of particular interest are the ways in which biotic factors such as microbial mats (Beggiatoa) affect fluxes between the sediment and the water column. I expect that this program of laboratory and continuing field work will elucidate the role of horizontal advection in coastal ecosystems.

DISCUSSION

RHOADS If you did the same experiment you described, but in a physically low energy area, one would get quite different results. When infaunal deposit feeders are present in sediments, there is a seasonal cycle of change in organic content. This is due to the pronounced summer activity of macrobenthos such as head down deposit feeders, e.g. maldanids, which manage to recycle the deeper carbon particles to the surface.

GRANT There were few macrofauna in my study area, although in adjacent high energy areas Arenicola, Mya, Gemma and Nereis may be present.

RHOADS What is the time scale for utilization of POM by macrofauna?

GRANT I was able to measure the flux of POM into experimental areas but not its utilization because of the lack of macrofauna. I am interested in the problem you raise and in particular the behavioral triggers which regulate changes to and from suspension feeding/deposit feeding. This transition is probably facultative in many species.

WILDISH Is the transfer of bedload material an indication of how much POM is coming into your trays?

GRANT Yes, but my method does not distinguish the source of the POM or the distance over which it has been transported.

NEWELL The POM which appeared in your trays was not necessarily evidence of bedload transport. For instance, wave action could cause considerable winnowing of fine POM from the sediment and the transport could be in water.

GRANT Where there are waves and oscillatory flow there is recycling of POM already present at that point. It does not matter whether the material is transported or recycled, because once it is in the water column it is available to suspension feeders. Resuspension may be important for processing of the POM which in water is exposed to an oxygen-rich environment where microbical activity may occur at an enhanced rate.

NEWELL The winnowing effect is important because in the water column POM is available as food to suspension feeders whereas material transported as bedload is not available to them.

GRANT There are incredible amounts of suspended POM just above the sediment. It would be useful to measure changes in the organic carbon content near the sediment during a tidal cycle, although the microscale sampling required could be a problem.

ROFF Resuspension rates are difficult to quantify in sediment traps near the sediment-water interface. The material collected includes fecal pellets both with and without a peritrophic membrane. Based on water depth, sinking rate of fecal pellets, the rate of peritrophic membrane breakdown (~ 20 d at 5°C), and the total amount of facal pellets in the sediment, it should be possible to calculate the resuspension rate. Fecal pellets sink at a rate which allows them to arrive at the bottom with an intact peritrophic membrane. Resuspended fecal pellets will include those without membranes. If you know the density and size of resuspended pellets and those collected in the sediment traps, it should be possible to calculate resuspension rate if you know the average lifetime of a fecal pellet.

GRANT That seems like a reasonable idea. There are numerous ways to measure resuspension rate. One I have tried in conjunction with Barry Hargrave is to emplace "pan's pipes" which are columns of small sediment traps, each of different height expecting different catches and rates of resuspension according to the length of the cylinder.

ROFF What kind of sediment trap did you use? The absolute size and height to diameter ratio of the trap would affect your catches.

GRANT This is certainly true for trapping of suspended particulates. Closer to the bed some people have used partially buried cylindrical sediment traps, but with these you would expect boundary layer flow disruption.

THE IMPORTANCE OF FOOD AVAILABILITY IN REGULATING REPRODUCTION IN ESTUARINE BIVALVE MOLLUSCS[1]

by

R. I. E. Newell

[1]Contribution #1479 from the Center for Estuarine and Environmental Studies

Many studies indicate that, although physical environmental factors are important in determining the overall distributional patterns of marine invertebrates, most species live well within their zone of physiological tolerance (Newell 1979). Instead, factors such as food availability and predation are important in governing their ecology, growth and fecundity, but these are less easily measured in the natural habitat.

The aim here is to indicate the ways in which food availability interacts with other factors to determine the ecology of three boreo-temperate suspension feeding bivalve molluscs, the cockle Cardium (=Cerastoderma) edule, the blue mussel Mytilus edulis, and the American oyster Crassostrea virginica. Some of the research outlined below has been described in more detail by Newell and Bayne (1980) and Newell et al. (1982). Each of these species has a variety of adaptations, both genetic and non-genetic, which coordinate reproductive events with the environment so as to maximize reproductive success (Bayne 1976). There is still only partial understanding of the complex interactions between exogenous (e.g. food availability, temperature, etc.) and endogenous (e.g. hormonal cycle, nutrient reserves, genotype, etc.) variables that ensure synchrony of gamete development within a population. This is of prime importance for dioecious species having external fertilization which requires synchronized liberation of gametes.

In Cardium edule there is a pronounced seasonal cycle of major physiological functions such as metabolic rate, feeding rate, carbohydrate storage, and reproductive condition, with minimum values in the winter and maximum values in the summer months (Newell and Bayne 1980). There was no direct correlation between the observed seasonal cycles and water temperature although, there were strong positive correlations between the reproductive condition and metabolic and feeding rates. However, the indirect influence of temperature and light levels in the spring on primary production and hence the effects on food available for gametogenesis and vitellogenesis remain to be elucidated.

For many years latitudinal differences in water temperature have been considered to exert a dominant influence on invertebrate reproductive patterns (Thorson 1946; Seed 1976). However, Newell et al. (1982) working on seven latitudinally separated populations of M. edulis on the East Coast of the United States found that differences in the timing of various phases of the gametogenic cycle could not be linked to latitude and hence water temperature per se. Indeed, two populations on Long Island, N.Y. (Stony Brook and Shinnecock) had the greatest temporal diferences in gametogenic cycle with summer reproduction maxima separated by a 3-mo interval. At Stony Brook, food is most abundant in the late spring and summer when mussel feeding rates are high and spawning occurs in April/May which is near the period of maximum food availability. They can obtain sufficient nutrients from the seston during this post-spawning period to accumulate a food reserve as is considered typical for the species (Gabbott 1976). In contrast, the Shinnecock population faces low levels of energy in the seston and unpredictable temporal peaks in energy availability during the same time of the year. The maximum seston energy levels were recorded during the winter when feeding rates are depressed. Thus, the high degree of synchrony in maximum gametogenic condition (and cyclicity) within the Stony Brook population reflects the timing and temporal variation in local food availability and the long period during the winter in which gametogenesis may proceed. In the Shinnecock population, maximum food availability occurs when the animals are not actively feeding and there is no chance to initiate a nutrient storage cycle. Subsequently, there is no pronounced spawning period, but rather a prolonged period of "dribble spawning" in which gametes are gradually released between July and October.

In an effort to understand the role of nutrition in regulating both fecundity and recruitment of the American oyster, Crassostrea virginica, I have initiated a field research program, in cooperation with Dr. Tom Jones, in two adjacent tributaries of the Chesapeake Bay with similar ambient temperature and salinity. Broad Creek has a high level of recruitment, but adult growth is relatively poor, whereas Tred Avon has comparatively poor recruitment but good adult growth. Currently we are studying how differences in the input of inorganic nutrients into these two systems affect primary production. Differences in the phytoplankton species may alter the biochemical composition, cell size, and even digestibility of the algae available to the suspension feeders. Differences in inorganic nutrients or light levels can alter the biochemical composition of even a single phytoplankton species (for review see Morris 1980). The size of the algal cell can also have a direct influence on the planktotrophic larva which can only ingest particles smaller than about 10 µm. It is imperative for their survival that there is a bloom of nannoplankton cells during the 3-wk period that the larvae are in the water column.

In addition to the factors affecting primary production and the biochemical composition of the seston, we are studying the ingestion and storage of these materials by the adults. This involves measuring metabolic and feeding rates, absorption efficiency, nitrogen excretion of the adults, and the total accumulation of carbohydrates and lipids under ambient conditions. These parameters can then be linked to the reproductive cycle, total fecundity, and recruitment. Preliminary results indicate significant differences in the timing of primary production between these systems but no differences in the physiology of the adult oysters. This emphasizes the importance of measuring food availability when trying to understand the ecology of bivalve molluscs.

Additional research is still required into basic feeding mechanisms which have evolved to enable suspension and deposit-feeding invertebrates to maximize food intake from material that contains large quantities of non-nutritious mineral particles (see review in Saleuddin and Wilbur 1983). Recent work by Kiørboe and Møhlenberg (1981) indicated that 11 species of suspension-feeding bivalves could preferentially ingest algae from a mixture containing inorganic material and reject the inorganic particles as pseudofeces. Newell and Jordan (1983) found that the oyster Crassostrea virginica fed on natural seston could preferentially ingest organic particles, especially the more nutritious particles rich in nigrogen. Newell and Jordan (1983) explained how differential sorting of particles firmly bound in mucus (see Foster-Smith 1975) may occur on the labial palps by postulating that mucus viscosity is reduced by the mechanical action of the cilia. This explanation still needs further experimental work including the nature of the chemoreceptors on the labial palps.

In summary, food availability is of key importance in determining the growth, reproduction, and recruitment of bivalve molluscs. More research is required under field conditions into the importance of nutrition to all stages in the life cycle. In addition, laboratory research is required to elucidate the fundamental mechanisms that enable molluscs to maximize food intake when the seston comprises both non-nutritious inorganic particles and organic particles of differing nutritional quality.

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REFERENCES

Bayne, B. L. 1976. Aspects of reproduction in bivalve molluscs, p. 432-448. In M. Wiley (ed.) Estuarine Processes. Vol. I. Uses, stresses and adaptation to the estuary. Academic Press, New York.

Foster-Smith, R. L. 1975. The role of mucus in the mechanism of feeding in three filter-feeding bivalves. Proc. Malac. Soc. Lond. 41: 571-588.

Gabbott, P. A. 1976. Energy metabolism, p. 293-355. In B. L. Bayne (ed.) Marine mussels: Their ecology and physiology. Cambridge University Press, Cambridge.

Kiørboe, T., and G. Møhlenberg. 1981. Particle selection in suspension-feeding bivalves. Mar. Ecol. Prog. Ser. 5: 291-296.

Morris, I. 1980. The physiological ecology of phytoplankton. Blackwell Scientific Publications. 625 p.

Newell, R. C. 1979. Biology of intertidal animals. Marine Ecological Surveys, Faversham U.K. 781 p.

Newell, R. I. E., and B. L. Bayne. 1980. Seasonal changes in the physiology, reproductive condition and carbohydrate content of the cockle Cardium (=Cerastoderma) edule (Bivalvia:Cardiidae). Mar. Biol. 56: 11-19.

Newell, R. I. E., and S. J. Jordan. 1983. Preferential ingestion of organic material by the American oyster Crassostrea virginica. Mar. Ecol. Prog. Ser. 13: 47-53.

Newell, R. I. E., T. J. Hilbish, R. K. Koehn, and C. J. Newell. 1982. Temporal variation in the reproductive cycle of Mytilus edulis L. (Bivalvia, Mytilidae) from localities on the east coast of the United States. Biol. Bull. 162: 299-310.

Seed, R. 1976. Ecology, p. 13-65. In B. L. Bayne (ed.) Marine mussels: Their ecology and physiology. Cambridge University Press, Cambridge.

Saleuddin, A. S. M., and K. M. Wilbur. 1983. The mollusca: Physiology II. Academic Press, N. Y. 520 p.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates. Medd. Komr. Danmarks Fisker-og Havunders, Serie Plankton 4. 523 p.

DISCUSSION

RHOADS I understand from your talk that future research emphasis will not be on detrital sources of food for suspension-feeders, but on phytoplankton and factors controlling its supply.

NEWELL I have a Ph.D. student who is just starting to investigate the role of fungi and bacteria in the detritus cycle and the importance of detritus to the nutrition of bivalves.

RHOADS So you feel that detritus is important?

NEWELL Yes, I feel that detritus as a food supply for suspension feeders may be almost as important as phytoplankton. There is a large allochthonous input into the Tred Avon. During the summer this input may not be so important, but during the fall it is an important food supplement to suspension feeders. In the fall these animals are building up glycogen for the winter months. Larry Pomeroy has been suggesting this idea for a number of years.

ROFF The wet oxidation technique does not give an estimate of carbon that is available and can be digested by macrofauna. When you are comparing detrital based versus primary producer based systems, have you tried size fractionated ATP measurements?

NEWELL No, I haven't used ATP assays. In regard to the wet oxidation technique which is simply a chemical oxidation of any organic material present in the sample, you are right that it doesn't estimate what is available to the animal. I would stress that in an invertebrate feeding study you should measure energy content of the food and feces to determine what passes through undigested. There is evidence in the literature of enzyme induction in the invertebrate gut which is seasonally dependent on the kinds of foods available. I am currently measuring carbohydrate, protein, and lipid in food and feces. Probably lipid is the most important component to measure.

ROFF An encysted dinoflagellate may be full of lipid but is not digestible.

NEWELL In the oyster feeding rate experiments I discussed, the biochemical measures are made on seston, feces, and pseudofeces so, by subtraction, the amount of each component assimilated can be determined.

WILDISH How do you account for the possibility that an enteric microflora or rapid seeding of freshly deposited feces may occur and influence your biochemical indices?

NEWELL We try to collect the feces as soon as possible after production and freeze them immediately. The oysters process large amounts of seston and produce milligrams of biodeposits daily, so I don't think bacterial contamination will be significant.

WILDISH How did you obtain a representative sample of water containing seston which the oyster processes to obtain food?

NEWELL I used a high capacity pump with the inlet tube fixed at 0.5 m above the sediment-water interface, but I don't know whether it draws material from the resuspension zone that the oysters are utilizing.

WILDISH If your inlet tube is within a well developed turbulent layer, the sample should be representative of the sea water filtered by the oysters. However, this will also depend on the physical resuspension of sediment particles being constant over a significant path length before reaching the oyster.

UNKNOWN Do you think that the absorption of amino acids directly from sea water is trophically significant for suspension-feeders?

NEWELL Donald Monahan has shown to my satisfaction that both adult and larval bivalves can do this, but I do not believe that it is an important source for the adults. Why would bivalves have such well developed feeding adaptations such as gills, sorting surfaces and the enzyme-producing crystalline style if they relied primarily on dissolved amino acids? Monahan has shown that bivalves have a higher affinity for amino acids than bacteria such as *E. coli* but coliforms are adapted for very high substrate concentrations of amino acids and the best comparison, which has not yet been done, would be between bivalves and free-living, marine bacteria.

ROFF Did you investigate seasonal timing of phytoplankton bloom peaks in relation to the timing of bivalve reproduction?

NEWELL We are currently measuring primary production, the biochemical characteristics of seston, oyster feeding activity, reproduction condition, and stored nutrient content, at monthly intervals.

ROFF In embayments such as Chesapeake Bay, the spring diatom bloom occurs at any time between December and February and would correspond with early bivalve reproduction here, whereas on exposed Atlantic shores reproduction may be controlled by the predominant fall diatom peak.

NEWELL Yes, that is exactly the point I was trying to make. You have to consider local differences in food availability that will dominate any latitudinal effect claimed by the physiologists. Blake's work in Florida on scallops shows local differences in timing of reproduction which can be linked to differences in the food web.

GRANT Can glycogen content be used as an index of bivalve feeding conditions?

NEWELL Yes, but there are distinct differences between species in nutrient storage patterns; temporal differences in storage, for example, which depend on reproductive timing. If you have prior knowledge of reproductive cycles your suggestion might be possible. Even here I can envisage problems because some populations have two peaks of spawning if food availability is high enough. Such animals would over-winter with low glycogen reserves, whereas single spawners from poorer environments would overwinter with a higher glycogen reserve.

THE BENTHIC-PELAGIC INTERFACE: MUSSELS, PHYTOPLANKTON, AND THE BENTHIC BOUNDARY LAYER

by

M. Fréchette

Many non-quantitive field observations suggest that suspension-feeding animal growth is a function of tidal current velocity. Experimental attempts to test this hypothesis in the laboratory are nevertheless rare. Kirby-Smith (1972) attempted a growth experiment of this kind with the bay scallop, Argopecten irradians, in a multiple tube apparatus, but it is believed that it did not simulate benthic boundary layer conditions and had a complex flow pattern not represented by the bulk flow measurements made during the experiments.

Because of these difficulties with the Kirby-Smith growth tubes, an attempt was made to design a new apparatus suitable for measuring growth of suspension-feeding animals such as bivalve molluscs. The design criteria considered were:

- the hydrodynamic characteristics within the apparatus should resemble the benthic boundary layer as much as is practicable.
- the experimental animals should be supplied with a common source of water.
- the only experimental parameter that is required to be varied is the bulk tidal velocity over a range of 0 to 25 cm/sec.
- limitations on size (width) are imposed by the water pumping requirements of large facilities.

The final design chosen consisted of a flume of 5-m length, divided lengthwise into four 30-cm wide channels and fed from a common headbox. A pump of 2.5-HP capacity supplied natural sea water to the headtank at rates sufficient to induce a flow of 25 cm/sec with two channels blocked off. The apparatus allows comparative experiments at four current speeds. Direct comparisons between two consecutive runs of the experiment are not possible because of differences in quality and quantity of seston supplied to the common headbox of the apparatus. Because quality of seston may be dependent on species composition, a general measure of seston such as ATP content or plant pigment concentration is not possible.

Some limitations of the multi-channel flume in simulating the natural benthic boundary are:

- the flume boundary layer takes a significant length of the flume to develop whereas natural boundary layers are well developed, so that vertical mixing processes are more limited in the flume than in the benthic boundary layer.
- significant wall effects due to channel walls are absent in the sea.

REFERENCE

Kirby-Smith, W. W. 1972. Growth of the bay scallop: influence of experimental water currents. J. Exp. Mar. Biol. Ecol. 8: 7-17.

DISCUSSION

NEWELL What exactly is a hydrogen bubble probe? Have you thought of using a thermistor for measuring flow?

KRISTMANSON No, I haven't used a thermistor, but it is worth trying. The hydrogen bubble device is a platinum electrode on a support. It is connected to a D.C. source to make a circuit. The method I used was to tune the pulse frequency of the bubble sheet so that its trailing edge just reached a second wire 4 cm downstream as the next pulse was initiated. Knowing the pulse interval and distance between the wires the hydrogen bubble and therefore current speed could readily be calculated. The device can be moved up and down on its support so that the current within 1 cm of the sediment-water interface could be measured.

WILDISH The platinum wire must be very thin to obtain small hydrogen bubbles which do not float. A consequent operational problem was frequent platinum wire breakage.

KRISTMANSON The difficulty lies fundamentally in the low electrical resistance of sea water. The technique was designed for fresh water which has a high electrical resistance.

NEWELL Could you perhaps calibrate the flume with fresh water and thus get around the seawater problem?

KRISTMANSON Yes, that is what we did with the Mark I flume which I had in my lab in Fredericton. The Mark II flume has only been in use since October 1983 and is probably too large to transport to Fredericton.

WILDISH Another method potentially useful in measuring flow rates in the flume is the one suggested by Drew Carey (Can. J. Fish. Aquat. Sci. 40 Suppl. 1: 301) which is based on time-lapse photography of small, boiled, egg-white particles introduced to the inlet sea water.

NEWELL Have you tried using dye to visualize the flow patterns?

KRISTMANSON Yes, in the Mark I flume this was done in Fredericton. In turbulent flow the dye will delimit the developing boundary layer or mixing zone. In the laminar regions above this the dye shows up as nice straight lines. We still have further flow measurements to make in order to calibrate the Mark II model.

RHOADS Does the presence of animals in the flume change the flow patterns?

KRISTMANSON Yes, animals change the roughness and hence the flow. That is why it is important to make the flow measurements with the animals in situ.

ON GROWTH AND BEHAVIORAL EXPERIMENTS WITH SUSPENSION-FEEDING ANIMALS

by

D. J. Wildish

The purpose of these experiments was to test the hypothesis that tidal currents control the growth of suspension-feeding animals. A representative active suspension feeder, the blue mussel, Mytilus edulis (L), and representative passive suspension feeder, the sea scallop, Placopecten magellanicus (Gmelen 1791), were chosen for this purpose.

Two types of apparatus were used: the growth tubes of Kirby-Smith (1972) and the newly designed multiple-channel flume apparatus of Kristmanson and Wildish (1984). Preliminary observations were also made of scallop behavior in the multiple-channel flume.

BLUE MUSSEL GROWTH EXPERIMENTS

Two experiments with blue mussels were completed in the growth tube apparatus. In experiment 1, the effect of eight different current speeds in the range 0.1 to 3.9 cm/sec was tested at a single density of 364 mussels/ m^2 (mussels were selected so that mean wet weight/mussel = 2.80 g in each tube). Results showed that wet weight growth was a logarithmic function of current speed over the range tested. In experiment 2, the effect of density (91, 273, 455, and 909 mussels/m^2, with a mean wet weight of 2.53 g per mussel in each tube) at a slow (0.1 cm/sec) and fast (1.43 cm/sec) current speed was tested. Results indicated no effect of density at the faster current speed but a significant effect on growth at the slow current speed which was proportionately greater at higher densities. These results are consistent with documented effects of seston depletion in a flume turbulent boundary layer above a blue mussel bed (Wildish and Kristmanson 1984).

SEA SCALLOP GROWTH EXPERIMENTS

In the growth tube (experiment 1) shell-length increment of scallops was low and wet-biomass increment high although neither measure was affected by current speeds in the range 0.1 to 3.9 cm/sec. At the density of scallops used (91/m^2) and at the slowest current speed, there is evidence that shell growth was greater in the inlet end of the tube, indicating significant seston depletion. At a lower scallop density (16/m^2) in experiment 2, shell growth was similar over a current range of 1.9-10.1 cm/sec and there was no evidence of seston depletion at the outlet. However, wet-weight growth was inversely proportional to current speed, and this caused a significant drop in condition factor in scallops exposed to faster currents. Possible explanations for this could be that at higher ingested rations in higher current speeds food is rapidly passed through the gut, resulting in a drop in assimilation efficiency (see Griffiths and King 1979), or the ingested ration itself is reduced by closure of the valves (Foster-Smith 1975).

A very high current speed of 24.5 cm/sec (experiment 3) inhibited shell growth and resulted in negative biomass growth and loss of condition.

SEA SCALLOP BEHAVIOR IN THE FLUME

Field observations of the European scallop, Pecten maximus, by divers (Hartnoll 1967) indicate that the majority of the individuals are recessed in the sediment and move infrequently whereas those sitting on the sediment surface move much more frequently. Sea scallops in the multiple-channel flume in experiment 2 are equivalent to the latter group as they were unable to settle into the wooden substrate. In experiment 2, initiation of active movement was influenced by tidal velocity being 30 movements at 1.9 cm/sec and 53 movements at 10.1 cm/sec for the 24 individuals during the 33-d period of this experiment. Movement appears to be random either up- or downstream with a slight influence of passive carrying on distribution after swimming movements. At 24.5 cm/sec in experiment 3, the scallops are passively carried downstream by the current and block the outflow screen. The preferred settling position of scallops is in a wide upstream arc at all current speeds tested. This behavior ensures that individuals are in the best position to undertake passive filtering.

CONCLUSIONS

- Blue mussel growth is a function of tidal velocity as well as the concentration and quality of food particles. Experiments at higher current speeds and in a simulated benthic boundary layer are needed in order to determine the limiting tidal velocities and to investigate the nature of the physiological/behavioral mechanism involved.

- Experiments with sea scallops provide equivocal evidence because of problems with lack of substratum in the apparatus and/or choice of inappropriate tidal velocities.

- Because the Kirby-Smith growth tubes did not simulate boundary layer conditions, they are not considered suitable for measuring tidal velocity effects on growth of suspension-feeding animals.

- The combination of the many channels fed from a common source idea of Kirby-Smith in conjunction with open channels of adequate geometry enables simulation of relatively natural conditions and rigorous testing of varying tidal velocities up to ~ 25 cm/sec.

- Initiation of movement in "non-recessed" sea scallops is a function of tidal velocity and resting scallops are characteristically oriented with respect to current direction. The random movements appear to be part of an integrated behavioral response adaptively concerned with finding optimum growing conditions.

- A recurrent problem in this kind of work is the measurement of the food quality of seston for suspension-feeding animals.

- It is also the latter problem which prevents the use of the turbulent boundary layer model to be used as a predictor of suspension-feeding animal density or production.

REFERENCES

Foster-Smith, R. L. 1975. The effect of concentration of suspension and inert material on the assimilation of algae by three bivalves. J. Mar. Biol. Ass. 55: 411-418.

Griffiths, C. L., and J. A. King. 1979. Some relationships between size, food availability and energy balance in the ribbed mussel, Aulacomya ater. Mar. Biol. 51: 141-149.

Hartnoll, R. G. 1967. An investigation of the movement of the scallop. Helgoländer wiss. Meeresunters. 15: 523-533.

Kirby-Smith, W. W. 1972. Growth of the bay scallop: influence of experimental water currents. J. Exp. Mar. Biol. Ecol. 8: 7-17.

Kristmanson, D. D., and D. J. Wildish. 1984. A flume for measuring growth and behavioral characteristics of suspension-feeding animals in a simulated benthic boundary layer. (in preparation).

Wildish D. J., and D. D. Kristmanson. 1979. Tidal energy and sublittoral macrobenthic animals in estuaries. J. Fish. Res. Board Can. 36: 1197-1206.

1984. Importance to suspension-feeding animals of the benthic boundary layer. (submitted).

DISCUSSION

MUSCHENHEIM You called Placopecten a passive suspension feeder, yet they do produce currents by ciliary action on the gills. Hence they are not solely relying on tidal current energy.

WILDISH Yes, but I think passage of seston to sea scallops is dependent on tidal current energy as well as on the current created by the ciliary action on the gills of the sea scallop.

NEWELL So are you saying that there is no requirement for ciliary action in the sea scallops? That tidal currents could supply all the required energy for filtering, and in a static system that it couldn't feed?

WILDISH No, ciliary action is needed by scallops particularly if they must sort the particles before ingestion, as you suggested for other lamellibranchs. I believe that in a static system scallops would feed but not as well as those exposed to tidal currents, but this requires an experimental test.

NEWELL So the scallop feeding process is both an active and passive process from the point of view of the animal?

WILDISH Yes, I seem to have used a misleading categorization for the trophic differences between mussels and sea scallops. My aim was to bring out the essential differences between them. Mussel feeding currents produce a significant drag on currents and they can pull in seston from a few centimeters away, although within the turbulent boundary layer. Mussels are densely packed in suitable places and their annual population production per unit area is a function of tidal current speed. This contrasts with scallops in which the distribution is sparse, production does not appear to be a function of current speed, and they cannot pull in seston passing near them.

NEWELL I question the whole idea of mass transport limitation and depletion for species such as oysters and mussels. Where is the evidence for depletion?

WILDISH Wildish and Kristmanson have just completed experiments with blue and horse mussels which demonstrate that depletion can occur. Marcel Fréchette was planning to talk about intertidal blue mussels (see p. 14). He also observed depletion above a natural mussel bed at certain stages of the tide.

RHOADS It is clear from the very intensive mussel raft culture at Rias de Galicia, N.W. Spain that growth is always greatest on the up-current side of the rafts.

NEWELL In this work the densities of mussels were very high.

WILDISH In my experiments too, mussel densities were high, of the order of $1000-2000/m^2$. Although field densities, particularly of young mussels, could be much higher than this ($\sim$ 10,000 $mussels/m^2$).

NEWELL Mussels seem to be very poorly adapted, as far as food competition goes. Because they can only settle at metamorphosis on the byssus threads of other mussels, they practice gregarious settlement. This produces very dense beds, which seems to be counter-adaptive.

WILDISH To the contrary, I believe that the trophic strategy of mussels is to increase the turbulent supply of seston to the bed by increasing bed roughness. Current speed also affects turbulent supply of seston and many authors have indicated a correspondence between condition factor and tidal current speed.

GRANT Do you think that the hydrodynamic advantage of a dense mussel bed outweighs the disadvantage of depletion and what is the extent of the advantage in terms of enhanced capture of particles?

RHOADS In a thesis by Jennifer Smith at the University of Georgia, capture efficiency increased as the density of mussels increased. Using fibreglass model mussels of the same size and roughness as the live ones, she was able to measure the seston supply coefficients.

WILDISH If you increase the roughness you should increase the food supply available to suspension-feeders. This appears to be important to mussels; its application to sea scallops is another matter.

KRISTMANSON Two interacting factors are involved in answering Jon Grant's question. One is the turbulent mixing brought about by velocity and roughness of the sea bottom. The second is the relationship between seston concentration at which the population can just maintain itself, and the bulk seston concentration. If the latter is 1000 times the former there is no mass transfer limitation, but if the difference is small there may be mass transfer limitation and the rate of supply of seston can be increased by increasing velocity or roughness.

ROFF The direction of the required changes appears to be all wrong. Sea scallops ought to be gregarious and active pumpers.

KRISTMANSON Because scallops never form dense beds, this species is not utilizing roughness as a way of increasing seston supply.

ROFF Because mussels can draw seston from some distance above the sediment-water interface, there is an advantage to being gregarious whereas scallops which cannot pump in this way face a lower food supply.

WILDISH I dispute your first point: the mussel population creates a rough bottom to increase the depth of the boundary layer; turbulent mixing within this layer allows it all to be utilized. The scallop does not appear to use the same strategy: it recesses into the sediment, thus reducing roughness. It must use a different, but at present unknown strategy.

STUART In the case of mussels isn't predation important?

WILDISH The aim of my work was to evaluate tidal current speed as one factor controlling growth and production of mussels, but there are certainly a number of factors involved (see Wildish 1977, Helg. wiss. Meeresunters. 30: 445).

VOLCKAERT Is there any field evidence of a relationship between current speed and suspension-feeding animal density?

WILDISH Yes, for example Cooper and Marshall (1963). Chesapeake Sci. 4: 126, showed that in the bay scallop density was higher where currents were higher. The increased density was correlated with a lower condition factor, suggesting the possibility of food limitation. Our data (Wildish and Peer 1983. Can. J. Fish. Aquat. Sci. 40: 309) from the Bay of Fundy for horse mussels also shows a positive relation between current speed and production or density.

NEWELL There might be correlation between current speed and suspension-feeder density but is it due to food availability or because the sediment type is unsuitable in that area?

WILDISH I did try to bring this out in my talk that there are some areas where I would predict mussels would be present in large numbers, but in fact aren't, due to excess erosion at high current speeds and excess deposition at low current speeds.

A MODEL OF FACULTATIVE SUSPENSION-FEEDING BY SPIONID POLYCHAETES

by

D. K. Muschenheim

Numerous deposit-feeding infauna are also facultative suspension feeders under certain conditions of flow and particle concentrations. Studies of spionid and terebellid polychaetes have confirmed the importance of suspended matter concentrations in the feeding of these animals. There is little known, however, about the small-scale dynamics of particle motion, especially in relation to the types of particles available under different flow regimes, as well as their potential food quality.

A simple numerical model has been constructed to investigate potential enhancement of near-bed particle concentrations due to localized hydrodynamic effects of polychaete tubes. Upstream concentration gradients of various particle types given by the Rouse equation are introduced into a two-dimensional model of the downstream flow field. Input parameters include: particle fall velocity ($\overline{w}_s$), friction velocity (u_*), and free-stream velocity ($\overline{u}$). The output is in the form of concentration isopleths within 5 tube diameters both upstream and downstream of the worm tube. The model is non-dimensionalized in terms of tube diameter. Vertical particle advection in the lee of the tube is given as a function of free-stream velocity and downstream distance. The model was run, using literature values for fall velocity of several naturally occurring particle types, ranging from 0.001 (phytoplankton) to 5.1 cm/sec (polychaete fecal pellets).

Results show the potential for a twofold enhancement of particle concentration at the top of the tube. Increased fall velocity results in enhanced particle concentration. This is a direct consequence of the Rouse equation, which balances $\overline{w}_s$ and U_* in turbulent diffusion. The model, therefore, rests on assumptions (e.g. minimal particle-particle interactions) implicit in the Rouse profile. These assumptions may well fail to hold true so close to the bed.

To test this model and its assumptions a flume facility is nearing completion at Dalhousie University. A 3-m channel will be used to control growth of the turbulent boundary layer and a combination of direct and optical sampling techniques will be used to determine particle concentration profiles. Flow will be measured by a heated thermistor anemometer. Particle type and bulk concentration will be controlled by recirculation to a headtank.

Additional experiments will focus on spionid feeding under conditions of quiescent versus rapid flow, and the quality (C:N ratio) of food ingested under these different regimes. The aim is to produce an optimization model for the "switching" behavior between deposit- and suspension-feeding modes. Presumably this is a function of the amount of easily resuspended detritus with high organic content to the amount of suspended inorganic and refractory material. Such a "wheat-to-chaff" ratio may well be optimized at some intermediate flow velocity. The point (or range) in the tidal cycle where this parameter is optimized has important implications for the timing of feeding of many benthic organisms, as well as their demersal fish predators.

DISCUSSION

WILDISH Do you know what causes suspension-feeders to switch to deposit feeding?

MUSCHENHEIM Taghon and Jumars found that in spionids the switch was in response to a changed concentration of particles rather than current speed. I have observed spionids deposit feed and they seem responsive to the quality of particles available. Thus, as the sediment around their tube becomes depleted of POM they withdraw into it and await something better. If a pulse of detritus reaches them they respond by resuming feeding. I suspect that their response is triggered by a chemosensory cue. My aim is to develop an optimization model for predicting feeding behavior as a function of the quality of food. I assume that the lower density POM is more easily resuspended and laterally transported than inorganic sediment particles. Then at some point on the tidal current curve the spionid will decide whether the wheat (=POM) to chaff ratio is satisfactory for suspension feeding.

WILDISH Presumably the switching point is related to the energetic benefits of filter feeding versus deposit feeding?

MUSCHENHEIM Jumars and his group at Washington have been looking into the energetics of deposit feeding.

RHOADS Your model is based on the spionid tube as a roughness element. What happens if you have a much more densely packed tube bed, so that you encountered tubes every 2 or 3 diameters?

MUSCHENHEIM My model holds only for tube densities of less than 1/12 of the plan area. The hydrodynamic situation is one of a smooth flow with isolated roughness elements.

RHOADS Maybe there are different adaptive strategies for low density and high density tube fields.

GRANT Many people consider that the selection of food particles in suspension-feeding, tube-living polychaetes to be dependent on the properties of the particles. Do you think that particle selection is also a function of the hydrodynamic properties of the tube?

MUSCHENHEIM Adjustment of the height of the tube could have something to do with that.

GRANT Can tube height be adjusted by the worm?

MUSCHENHEIM Most polychates permanantly adjust the height of their tube depending on the local flow regime. The height achieved is a compromise between the advantage of protruding high into the boundary layer where seston supply is richer versus the possibility of the tube being eroded by the current.

Another polychaete has a collapsible mucus/sand grain tube held in place by the turgor of the worm's body when it is feeding. At rest the tube becomes collapsed on the sediment.

DEDUCING DYNAMICS FROM STRUCTURE USING *IN SITU* REMOTE IMAGING (REMOTS^{TM} SYSTEM)[1]

by

D. C. Rhoads

[1]A complete account of this work has been published in Mar. Ecol. Prog. Ser. 8: 115-128.

A benthic successional model allows interpretation of structures observed in sediment profile images. From these structures, temporal and spatial changes can be deduced in both benthic habitat and its associated fauna. The instrument used for in situ remote monitoring is the Rhoads-Cande profile photographic camera or its updated version, the video REMOTS (Remote Ecological Monitoring Of The Seafloor) system. Sediment profile imaging has been used to characterize an estuarine pollution gradient in Narragansett Bay, Rhode Island, and to monitor the 'August Effect' on benthic faunal dynamics in New Haven Harbor, Connecticut (USA). The ability of the profile camera to rapidly map patterns of seafloor disturbance and subsequent faunal change is described for a 1.5 mi^2 area near the Thimble Islands, Long Island Sound, Connecticut. I discuss the potential application of the REMOTS system for efficient monitoring of dredge-spoil activities and as a reconnaissance mapping tool for detecting change in benthic habitats in the region of outer continental shelf drilling fields.

DISCUSSION

ROFF What kind of evidence do you have for the existence of macrofaunally induced microbial gardens and what advantage does this have over surface decomposition?

RHOADS I have used a vertical array of capillary tubes containing aseptic frozen sediment and sea water or Agar sticks inserted in the sediment. They were removed in a time series to learn about microbial colonization rates. The numbers of bacterial cells produced per unit time are greater in a deeply, bioturbated sediment than in a pioneering one where all the macrofauna are present within a few millimeters of the sediment surface. Enhanced bacterial activity and turn-over rates in bioturbated sediments have also been demonstrated by ATP, dehydrogenase, and tritiated thymidine measurements. The more labile components of the organic matter input are metabolized rapidly at the sediment surface. The reason that macrofauna feed at depth is to metabolize, with the aid of microbial enzymes, the most refractory organic matter. Some of this organic matter remains and becomes buried. What is of interest to the geologist is the evolution of these infaunal systems because they did not exist before the Silurian when vascular plants first appeared and refractory vascular plant detritus entered the near-shore marine environment for the first time.

ROFF With marine macrophytes you would expect to find phenols and polyphenols.

RHOADS Yes, but the influence of these compounds on detritus feeders has not been determined yet. This work is just getting under way and one of the first things to do is to search for some morphological evidence of vascular plant detritus in feeding pockets (i.e. rejecta) using scanning electron microscopy.

WILDISH Is there any experimental evidence that capitellid polychaetes are attracted to anoxic sediments?

RHOADS Yes, *Capitella capitata* larvae are attracted by sulfides as shown in recent work by Carmela Cuomo (submitted to J. Biogeochem.)

WILDISH The kinds of climax, macrofaunal association found in high energy environments like the Bay of Fundy are quite different from the advective, bioturbating ones of low energy environments that you describe. I would expect that this would lead to different results with the sediment-water interface photographs.

RHOADS When you move from one biogeographic province to another or to a different hydrodynamic regime, you can expect differences and therefore the REMOTS technique has to be initially ground-truthed in the new area.

WILDISH The tidally impoverished macrofaunal association recently described (Wildish and Kristmanson 1979, J. Fish. Res. Board Can. 36: 1197, and Warwick and Uncles 1980, Mar. Ecol. Prog. Ser. 3: 9) is characterized by a few hardy deposit-feeders such as the sand dollar, *Echinarchnius parma*, which is morphologically adapted to resist erosion.

NEWELL There seemed to be a stage I succession on the most polluted dredge spoil material. Did that surprise you?

RHOADS It pleasantly surprised the U.S. Army Corps of Engineers.

ELNER Have you looked at the macrofaunal colonization of clean dumping spoil?

RHOADS Yes, in clean sedimentary material the redox potential discontinuity was depressed by bioturbational pumping at a rate of 300 µm/d compared to 200 µm/d in the most polluted 'black mayonnaise' spoil.

ELNER So the clean sand was colonized by macrofauna?

RHOADS The pioneering polychaete which appeared on the sand spoil was of the family Oweniidae whereas the 'black mayonnaise' colonizer was of the family Capitellidae.

ELNER I have followed a small experimental dump of 100 m^3 of silt/clay spoil in Halifax Harbour for over a year now. The spoil seems to be very poorly colonized by macrofauna, certainly not by the dramatic community changes that you described.

RHOADS One needs a 300-µm sieve in order to collect pioneers. They have been missed in many studies which used a 0.5- or 1.0-mm sieve mesh.

NEWELL Do you have any recommendations about how to go about dumping to minimize environmental disturbance?

RHOADS I have written some recommendations (Rhoads et al. 1978, Disturbance and Production of the estuarine seafloor. Am. Sci. 66: 577) on this subject. I suggest capping contaminated spoil with clean sand and avoid disturbing with another disposal operation for at least 1 yr, because with this distrubance frequency a pioneer macrofauna will attain peak production. If you dump at a frequency much less than 1 yr there will be a time delay before it reaches its maximum production rate again. This view utilizes Odum's concept of a pulse stability.

WILDISH You would presumably have preferred to see the dumping occur on the sandy areas of Long Island Sound?

RHOADS The spoil material went to two sites; one uncapped, which is the story I presented in my talk, and the other to an area where it was capped. In the latter case, which I did not mention, the contaminated 'black mayonnaise' spoil was covered with up to 5 cm of sand very successfully. Two disposal strategies can be used: containment within a capped mound, which is what has been done since 1973 in Long Island Sound, or dispersion which involves placing the spoil on a net erosional bottom and from where it is washed away and dispersed. The choice in a particular case may be dictated by the quality of the spoil material. Relatively clean material may be appropriate for dispersal over an extended period of time.

QUANTITATIVE PHOTOGRAPHY IN BENTHIC STUDIES - TIME-SERIES AND STEREOGRAPHIC TECHNIQUES

by

U. Lobsiger

Benthic investigations are among the most common applications of underwater photography. Cameras mounted on sleds, suspended from hydrowires, or attached to rigidly moored structures are used to visually document life on the ocean floor. Photographs can be used for descriptive interpretation or, if a number of physical constraints are taken into account, they allow a quantitative image evaluation.

The transmission of light in sea water is influenced by attenuation, due to absorption and scattering. In the case of artificial object illumination, these processes diminish the picture quality. The geometric arrangement between camera, object and flash, and the choice of flash output and film type determine the image clarity. Optimal combinations for specific waters yield minimal contrast worsening and contour spreading. The refraction effects associated with the transfer of light from the object space in water to the image space in air (the film plane in the camera, enclosed in a pressure housing), can be compensated for by a number of measures. We are now testing fully water-corrected optics (90 degrees diagonal wide-angle lens ELCAN C 240, by Ernst Leitz Canada), to evaluate their suitability for photogrammetric applications.

Time-series images with intervals from seconds to hours yield information about the behavior of benthic animals and, in a qualitative sense, about productivity and energy relationships. During a winter survey of an Arctic inlet, considerable lateral and vertical movement of brittlestars has been documented. During a more recent investigation of epibenthos in the Browns Bank area, sediment transport of a sandy substrate was observed within the span of a few minutes.

The methods of stereographic photography of underwater phenomena are largely derived from aerial photography techniqes. The theoretical background is briefly sketched and examples of the evaluation of small scale features are presented. A proposed camera system for quantitative sterophotography with long-term deployment capabilities and versatile electronic control options is discussed.

DISCUSSION

MUSCHENHEIM Is the amount of resolution limited by the amount of overlap present in serial photogrammetry?

LOBSIGER Yes, and this is dependent on the specific lenses and the stereocomparator or digitizer system that is used. For the Leitz lenses and digitizer system I am using the basal height ratio is 0.6. The vertical resolution at 60 cm above the sediment and with a field of view of 0.6 x 0.45 m should be 1-3 mm.

MUSCHENHEIM Is lateral resolution independent of separation?

LOBSIGER The lateral resolution depends on the lens properties. The lenses I am using were designed by Leitz for the U.S. Navy to reduce aberration in sea water, particularly the edge distortion present in deep-sea photographs. My company is the first to use these commercially and we have lens series numbers 49 and 50.

WILDISH So you think that the system you are designing will provide useful biological information for, say, a tube-living amphipod of 8-mm length?

LOBSIGER Yes, that is within the capability of this system. However, the practical results depend on a number of factors in addition to those mentioned above, for example, film type; it may not be possible to use color film; and lens type; it may be necessary to use a macro-type lens only available in 70 mm size, for the closeup work. All of the factors must be just right together to produce high quality closeup photographs of use in benthic biology.

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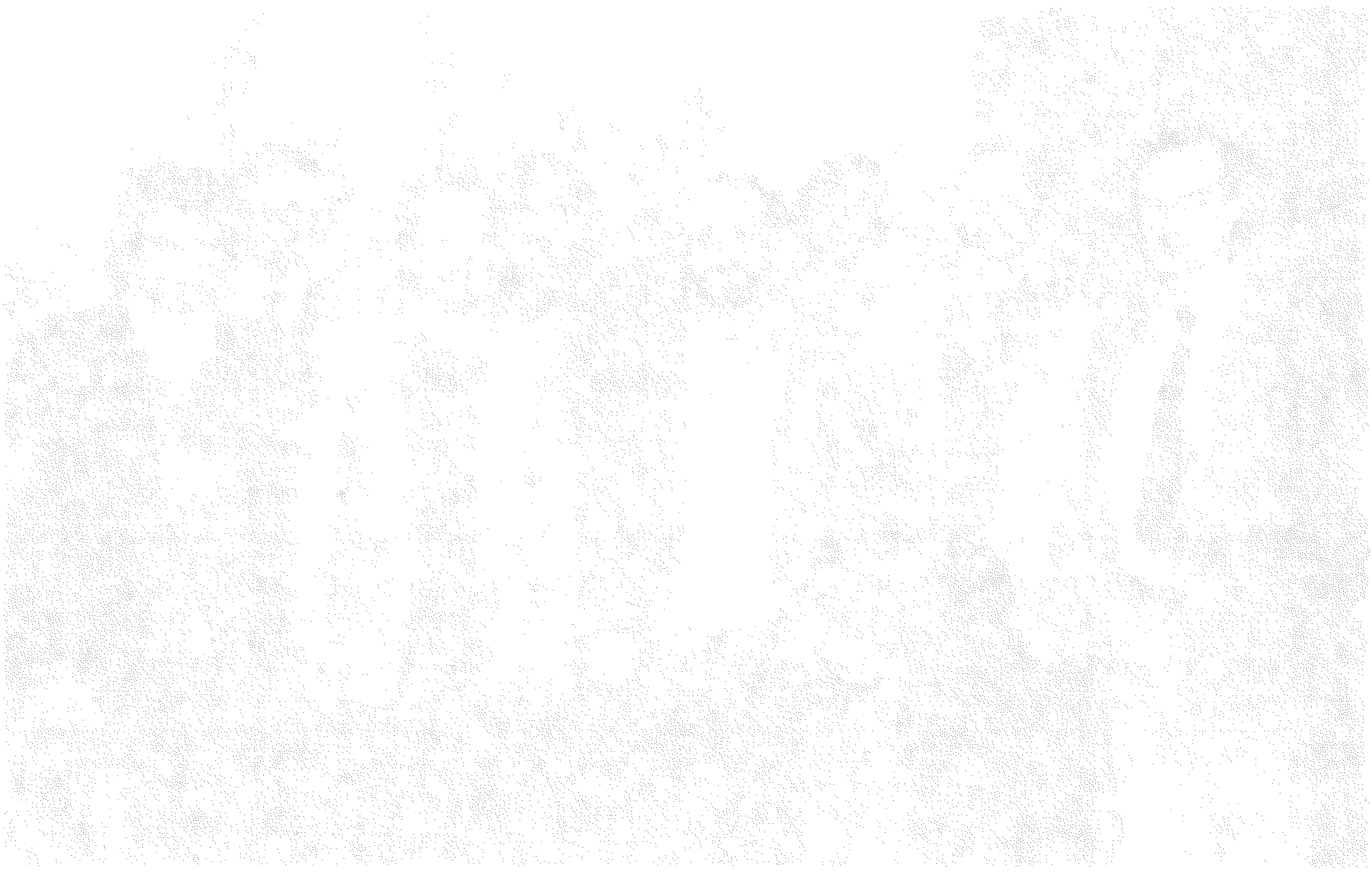
Fig. 2. Speakers at the St. Andrews Biological Station's 75th Anniversary Benthic Workshop. From left to right: Roff, Rhoads, Newell, Muschenheim, Wildish, Grant, Kristmanson and Lobsiger.



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