Fluxes of Particulate Matter Across Benthic Boundaries: A Workshop Report

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FLUXES OF PARTICULATE MATTER ACROSS BENTHIC BOUNDARIES: A WORKSHOP REPORT

Edited by

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ABSTRACT

Wildish, D. J. (Ed.). 1986. Fluxes of particulate matter across benthic boundaries: a workshop report. Can. Tech. Rep. Fish. Aquat. Sci. 1458: iv + 19 p.

This report contains summaries of work presented by fourteen speakers at a benthic workshop of the above title, held at the St. Andrews Biological Station on 29-30 October 1985. Included are précis of questions addressed to each speaker, with their answers, which were tape recorded during the meeting. The addresses of all who attended the workshop are included for reference purposes. Some of the papers prepared for the workshop will be published in full in a special issue of Biological Oceanography at a later date.

RÉSUMÉ

Wildish, D. J. (Ed.). 1986. Fluxes of particulate matter across benthic boundaries: a workshop report. Can. Tech. Rep. Fish. Aquat. Sci. 1458: iv + 19 p.

Le présent rapport résume les exposés présentés par quatorze orateurs au cours d'un atelier sur le benthos qui avait lieu à la station biologique de St. Andrews les 29 et 30 octobre 1985. On y retrouve également un précis de questions adressées à chaque orateur, ainsi que des réponses, qui avaient été enregistrées au cours de la réunion. À titre documentaire, vous trouverez ci-joint l' adresse de toutes les personnes qui ont assisté à cet atelier. Certains de ces exposés seront publiés au complet dans un numéro spécial de la revue Biological Oceanography à une date ultérieure.

INTRODUCTION

by

D. J. Wildish

Although the title of this workshop report may seem to indicate a narrow subject within benthic science, the contributing authors have interpreted their canvas in a broad way. Thus, bioturbation and benthic metabolism are treated both from an experimental and theoretical viewpoint, while both laboratory and field experimental approaches to the biology of suspension feeders and sediment particle resuspension and transport processes are discussed. Two final presentations are concerned with ecosystem budgets, particularly the flux of organic matter between the pelagic and benthic environments.

Presented here are the summaries of each talk, written by the authors, and a précis of the discussion following each one. These were recorded during the meeting and an expurgated version prepared for publication by the editor. I regret the witticisms and other bon mots removed in this process. Some of the talks will appear as refereed papers in a special 1986 issue of Biological Oceanography and include those by Grant and Hargrave, Wildish and Lobsiger, Muschenheim et al., Brock and Kofoed, and Harding and Hargrave.

The Workshop was held at the Biological Station, St. Andrews on 29-30 October 1985 and was organized by Drs. B.T. Hargrave, J. Grant and D.J. Wildish in the format of an earlier benthic workshop (see D.J. Wildish (Ed.) 1984, Biology of the Sediment-Water Interface: Report of the St. Andrews Biological Station's 75th Anniversary Workshop. Can. Tech. Rep. Fish. Aquat. Sci. 1263: iv + 38 p). Addresses of all participants at the workshop are included in an Appendix.

BIOTURBATION, BENTHIC METABOLISM AND SEDIMENT ORGANIC MATTER

MATHEMATICAL MODELS OF BIOLOGICALLY INDUCED SEDIMENT MIXING

by

B. P. Boudreau

Currently, the (eddy-) diffusion analogy is the predominant model used to quantify bioturbation in aquatic sediments. This model requires that mixing events be random in space and time and on a small scale, i.e. local mixing. Infaunal organisms are capable, however, of reworking sediment in ways that are inadequately and even incorrectly described by diffusion. For example, head-down deposit (conveyor-belt) feeders induce a downward advection of sediment. The actual mixing of older reworked sediment with recently deposited material occurs in the immediate vicinity of the sediment-water interface. In addition, the size of burrowing macrofauna, which primarily dictates the scale of biological sediment transport, is often sufficiently large that the exchange of material must involve widely separated points within the column, i.e. nonlocal mixing.

A completely general model for biological mixing can be derived from simple mass conservation principles. The result is an integro-differential equation that accounts for mixing on all scales, both local and nonlocal. The model contains parameters which can be related clearly to the actual average biological behavior and physical properties of the organisms. Solutions for the model have been obtained for the distribution of a stable transient tracer and a steady-state decaying tracer in two important situations: for a collection of conveyor-belt feeders, and for symmetric nonlocal exchange within sediments.

Conveyor-belt mixing of an ingested steady-state decaying tracer produces profiles that are nearly identical to those of a diffusion model. If the tracer is selectively rejected by the deposit feeders, a maximum will develop near the base of the mixed layer. The discriminatory behavior of conveyor-belt feeders can lead to graded beds and lag deposits. Numerical calculations for a transient stable tracer show that this form of mixing is significantly less dissipative than diffusion. Consequently, at low to moderate injection rates, tracer fronts and waves are attenuated but not obliterated as they are with diffusion.

Symmetric nonlocal exchange means that the net transfer of total sediment between two given points is zero. The intensity of the exchange may, nevertheless, change both with distance from a given point and with distance from the sediment-water interface. The lower (deeper) portions of the tracer profiles generated by this form of mixing resemble those from the diffusion model, but unlike the latter, the distributions with nonlocal mixing are characterized by the development of sharp gradients adjacent to the sediment-water interface (i.e. a boundary layer). Like conveyor-belt mixing, nonlocal bioturbation is not as dispersive as biodiffusion. Fronts and waves of a stable transient tracer are attenuated at low to moderate mixing rates, which again suggests that sedimentary features such as laminae may be preserved in sediments which otherwise exhibit distinct evidence of bioturbation.

DISCUSSION

BARETTA How does your approach compara with the bio-advection model of Don Rice?

BOUDREAU The two models were developed independently, with my model being more general and Rice's applicable only to head-down, conveyor-belt deposit feeders.

BUTMAN Your model predictions differ most from the biodiffusion model at low input values. Have you determined experimentally realistic outputs for these values?

BOUDREAU Yes, the advective velocity can be determined physically in situ and it is best to do this outside the zone of biodeposition to avoid bioturbation effects. The biological parameters should be determined experimentally in the lab. Don Rhoads has estimated the latter by spreading carbonate on the sediment and seeing how long it takes for it to be recycled. Values for R_o for the case of head-down deposit feeders in Buzzards Bay vary from 4 to 10^6. The wide range depends on the macroinvertebrate density, with high values indicating intense sediment mixing.

BUTMAN Can you quantify the intensity of mixing?

BOUDREAU An R_o or E_x value ≥ 10 is very intense but to convert this to an animal density you would need to know the species involved and its reworking rate, etc.

WILDISH What was your purpose in constructing this model?

BOUDREAU To see how non-biodiffusion model tracer profiles are different from diffusional model profiles. The most fascinating result of the modelling was to suggest an explanation for observed physical phenomena such as the presence of shell fragments on top of clay.

BARETTA Shell fragments do indicate the depth to which biological mixing occurs. But what was the depth of your biologically reworked layer?

BOUDREAU In my model it is non-dimensionalized, but typically it would be between 4 to 10 cm.

BARETTA Yet many reworked sediments would be much deeper and there would be distinct seasonal effects.

BOUDREAU Yes, my model could handle the deeper reworked sediments but it applies to a steady state situation which integrates seasonal effects as an average. I didn't start with data and try to extract numbers, I started with the model and

predicted sediment physical profile data. So my model offers a new framework for those interested in fluxes within the sediment and it requires experimental testing in which the predictions are compared to observed profiles.

GRANT Can the model be used to predict a pore water profile?

BOUDREAU Yes, you can predict pore water irrigation from the radial average model which treats irrigation as a source or a sink in the sediment rather than a diffusion process.

WATLING What happens if you choose a benthic environment where there are two distinct community patches with reworking depths which are distinctly different, as occurs in the Gulf of Maine?

BOUDREAU You have to define the mixing functions in such a way that they account for the reworking depths of each of the community patches. This would usually be the maximum reworking depth at each station rather than infinity, which complicates the mathematics.

EFFECTS OF EXPERIMENTAL ENRICHMENT WITH SPARTINA DETRITUS ON SEDIMENT COMMUNITY BIOMASS AND METABOLISM

by

P. Schwinghamer and P. Kepkay

Intertidal sediment collected from a silt flat in the Minas Basin (Bay of Fundy) was placed in laboratory aquaria and subjected to various experimental treatments to assess the effects of enrichment with detritus from Spartina alterniflora on the chemical fluxes across the sediment water interface and on community structure and dynamics within the sediment. Four aquaria enriched with Spartina demonstrated increased flux rates for dissolved oxygen, carbon dioxide, organic carbon, nitrates, and ammonia compared to the unenriched control aquarium. Increased bacterial biomass and activity accounted for most of the increased chemical flux. Meiofaunal biomass was not affected for the 29 d following enrichment during which the biomass levels were monitored. The growth of sediment micro-algae was inhibited by the addition of the detritus, possibly owing to antagonistic interactions with bacteria. The metabolic inhibitors sodium azide, sodium molybdate, and the nematocide fenamiphos, were added to three of the enriched aquaria to experimentally remove aerobic respiration, anaerobic sulfate reduction, and meiofaunal metabolism respectively, thus determining the importance of each to flux rate and biomass composition during detrital decomposition. The inhibitors were partially effective initially and apparently became less effective with time. The results indicated that care must be taken when interpreting the results of experiments in natural communities in terms of the effects of selective inhibitors. In other respects our experiments confirmed previous observations on the effects of Spartina detritus on the flux of materials between sediment and water column. In addition, we demonstrated the effects of this addition on the sediment biological community.

DISCUSSION

GRANT The bacterivorous grazers such as Protozoa and meiofauna did not seem to respond to the increased bacterial biomass caused by the Spartina enrichment?

SCHWINGHAMER No, although because the meiofauna were such a small proportion compared to the bacterial biomass this effect should not be expected to be large. Other evidence, such as lack of meiofaunal egg and juvenile production indicates that the meiofauna were not actively feeding.

WILDISH What are meiofaunal generation times?

SCHWINGHAMER Of the order of 5-10 generations per year with production of eggs in the spring and summer being very rapid.

WILDISH There were no cage effects?

SCHWINGHAMER I'm sure there was a cage effect. There was also an initial decrease in meiofauna which started at $1\frac{1}{2}$-2% of total biomass and decreased to 0.7% by the end of the experiment. The initial decrease may have been due to our handling of the mud. The poisons we used were quite effective with meiofauna. Fenamiphos was used to inhibit meiofaunal metabolism at a concentration which was 10x less than that required to inhibit bacteria in plate cultures.

WILDISH In my experience with insecticides, benthic diatoms, for example, rebound quickly from insecticide effects.

SCHWINGHAMER Yes, the bacteria seem to rebound from sodium azide treatment within a day.

WAINWRIGHT How did you separate the material fluxes from the water column and sediment?

SCHWINGHAMER The aquaria were closed during the observations and changes were observed in both water and sediment.

WAINWRIGHT You assume that the concentrations were in a steady state in the overlying water?

SCHWINGHAMER Yes.

KEIZER Do you have sufficient data to calculate the nitrogen fluxes?

SCHWINGHAMER Yes, but we have not yet done this.

THE COUPLING BETWEEN PARTICLE FLUX AND BENTHIC METABOLISM

by

J. Grant and B. T. Hargrave

A major question in the energetics of benthic communities is the extent to which benthic metabolism is fueled by deposition from the water column versus the standing stock of organic matter in the sediment. We used data from our own and published "starvation" experiments (the respiration

of cores supplied only filtered seawater) to examine (a) the decline in metabolism in the absence of particulate input and (b) the amount of utilizable organic carbon in the sediment column. At low temperatures (2°C), cores could hypothetically be maintained on sediment carbon for periods of years. At higher temperatures (15°C), the respiration of starved cores gradually declines, reaching 0 after about 50% of the carbon standing stock is consumed. We present various curves showing changes in respiration over time after particulate supply is stopped and suggest how the results can be used to assess the dependence of benthic community metabolism on particulate input from the water column.

DISCUSSION

BOUDREAU I wonder if your approach is really useful? Your use of total organic matter, when the reality is that there are many fractions each with different supply, decay and utilization rates, may bias your results and really reflect the sensitivity or resolution of the organic matter measures used.

GRANT Perhaps a more sensitive measure of organic matter could be used, such as protein. But because the chemistry and microbiology of organic matter breakdown is so complex and incompletely known, it is difficult to choose a suitable measure to follow decay processes. Total organic matter is a relatively conservative property of sediments and therefore not ideal for following decay. In addition, the measure is subject to error and contamination problems.

MAYER So your measure of organic matter is a composite of many fractions?

GRANT Yes, there are a variety of fractions and not a single pool from which organisms are feeding. The fractions are probably mixed and may be absorbed on the same sedimentary particle. It is difficult to know the nature of the fractions, how they are related, and whether they are independent or linearly additive. My approach is thus simplistic in regard to organic matter.

WILDISH Is there any correlation between the sediment types and the particulate organic carbon flux?

GRANT Yes, it depends critically on the sediment-hydrodynamic interaction and whether the sediment is a net depositional or erosional one, as well as the source of organic material. The traditional view of this is that it is the balance between supply and demand, with the demand function represented by organisms eating organic matter.

WILDISH The most efficient trophic group for processing particulate organic carbon are suspension-feeding animals?

GRANT Yes.

MAYER Why do you use only the top 1 cm of the sediment profile for estimating oxygen fluxes?

GRANT Because the redox potential discontinuity (RPD) is at 1 cm, so we considered that oxygen consumption was going on to that depth.

MAYER But oxygen often disappears well before the RPD.

GRANT Yes, there is not necessarily a linear change in oxygen consumption within the RPD layer, and much of the oxygen may disappear near the sediment interface. Anyway our techniques did not allow resolution of oxygen consumption within the upper 1 cm of sediment.

MAYER A result is that you may overestimate oxygen consumption.

BARETTA Another factor influencing oxygen demand is anoxic metabolism occurring beneath the RPD, which produces a chemical oxygen demand and must be considered.

GRANT Yes, we prepared a number of formalin-poisoned cores to give some estimate of chemical oxygen demand.

MAYER Could you do slurry experiments and thus get rid of some of these artifacts?

GRANT Perhaps if you did aerobic and anaerobic incubations separately. We tried to maintain the natural sediment column as much as possible.

SCHWINGHAMER The problem of measuring oxic respiration in enclosed microcosms is just as great as measuring total organic carbon. The degree of stirring can affect respiration measurements by 10 to 50 fold.

GRANT Yes, I agree on the importance of stirring and the difficulty of knowing how much stirring mimics the natural situation. The next logical step is to use a flume, where mixing by water flow over a natural sediment can be controlled and microelectrodes used to measure dissolved oxygen.

SCHWINGHAMER So your estimates for the labile fraction are inaccurate?

GRANT Insofar as our data are limited by the measurement problems discussed above.

SCHWINGHAMER I have one more question concerning the CO_2:O_2 ratio which you found to be 4. In a totally anaerobic sediment (surface Eh ~ -150 mV) I found CO_2 ratios to be $2\frac{1}{2}$ to $3\frac{1}{2}$. So you can't use the ratio to indicate anaerobic conditions which are dependent on the type of microbiology.

GRANT Our ratios were variable but we have measured them for each month during the year in subtidal conditions at this site.

BOUDREAU The question is whether the logarithmic curvilinear relationship between oxygen uptake and organic matter is due to the organic matter or the microbiological population effects associated with the decay process.

BROCK Bacterial species composition could be one way of indicating the type of degradation.

TOWARD A MEASURE OF ECOLOGICALLY LABILE ORGANIC MATTER IN SEDIMENTS

by

L. M. Mayer and L. L. Schick

Most measures of organic matter in marine sediments are analyses either of a major fraction of the organic matter, consisting mostly of refractory humified materials, or of specific biomarker compounds which can be used as tracers of biogeochemical processes. Neither result allows quantification of a major nutritional source pool for sediment heterotrophs. We present here a new method for measurement of proteinaceous material which is demonstrably composed of compounds that are largely available to these heterotrophs. This technique combines an enzymatic hydrolysis with detection using dye binding. Evidence for the lability of the protein measured is given by its relatively rapid loss during downcore burial, and its relatively good geographic correlation with water column and sediment chlorophyll in continental shelf sediments. Biomass comprises a small fraction of sedimentary protein thus measured. Using this measurement, we demonstrate that resuspended sediment contributes negligibly to protein in seston.

DISCUSSION

GRANT Would you agree that in looking at the correspondence of benthic biomass or activity to substrate organic matter, that the benthic communities seem food limited?

MAYER What I'm trying to do is relate the sediment protein value to the amount of nitrogen available to an organism. We have also started making elementary budgets for benthic animals which we couldn't do before because we weren't able to measure satisfactorily the sedimentary food.

GRANT Do you think the next step is to determine what controls the protein content of sediments?

MAYER Yes, that's something we are certainly getting into. Just how available is this protein we are measuring? We need to start doing some feeding experiments to determine the assimilation efficiencies of our measured protein by different animals.

WILDISH Could the high protein values you've been getting in the Gulf of Maine be correlated with the high macrobenthic production there?

MAYER Yes, it does seem to be.

SCHWINGHAMER Why did you choose Coomassie blue rather than something like DNFB?

MAYER The beauty of Coomassie blue is that it only reacts with polymers. It requires a polypeptide of between 7-20 amino acids in length.

SCHWINGHAMER I have found that there is a good correlation between bacterial biomass and percent organic carbon or percent clay in the sediment. You get a correlation of $p \geq 0.95$ when you look at a range of inshore to deep-sea sediments with this measure.

MAYER That's the old bacteria vs surface area or bacteria vs organic carbon correlation.

SCHWINGHAMER Yes. If you just look at bacteria vs organic carbon, it's very poor; the same with bacteria vs surface area. But combined, they produce a good correlation. Is there any evidence in your data as to whether surface area or carbon controls bacterial activity?

MAYER We have done correlations strictly against surface area but you see the same thing against carbon because surface area is so tightly coupled with carbon. So I don't think a multiple regression will help us that much.

SCHWINGHAMER I was using the data from various oligotrophic mud samples from the upper Bay of Fundy and eutrophic mud samples from Minas Basin.

MAYER You are mixing environments! We tend to stay within one environment when doing these regressions. Although we have a student who is researching the carbon vs grain size question.

BIOLOGY OF SUSPENSION FEEDERS

A TIME-LAPSE UNDERWATER PHOTOGRAPHIC STUDY OF STATION 82, S.W. BAY OF FUNDY

by

D. J. Wildish and U. Lobsiger

Extensive deposits of LaHave clay occur in the mouth of the Bay of Fundy. Benthic macrofauna present are highly diverse but relatively low in secondary, heterotrophic production. Sediment-water interface photographs at Station 82 indicate an equilibrium macrofaunal assemblage as determined by Rhoads and Germano (1982. Mar. Ecol. Prog. Ser. 8: 115-128), predominantly consisting of deposit-feeding animals. The redox potential discontinuity depth is 6-12 cm and there is a ~1 cm surface layer consisting mainly of fecal pellets.

Time-lapse photographs from Station 82 were obtained on four occasions during September 1985 with ~300 frames and 10- or 12-min time delays for each stereo-camera deployment. Epifaunal tubes partially identified included two species of polychaete, an amphipod tube (Haploops fundiensis), and many burrow openings. Analysis of sabellid polychaete tube #1 shows that the tubes follow changes of tidal current direction, thus acting like a spar buoy in relation to the currents. A conical, branchial crown is present at the top of the tube and is open for most of the tidal cycle. Species, such as the pink shrimp, ocean pout and mudstar, Ctenodiscus crispatus, forage in the area, making characteristic biogenic marks at the sediment surface.

DISCUSSION

BUTMAN When you have a sediment resuspension event, does it block visibility sufficiently to ruin your photographs?

WILDISH There were no storm-related sediment resuspension events at Station 82 (depth = 80-100 m) while the time-lapse stereo camera was there.

BUTMAN On Georges Bank where long-time series photographs have been made, storms completely block out the picture.

WILDISH Previously, I have sampled Station 82 with a grab every 2 mo for a 2-yr period. The results were used to describe production of the four dominant amphipods present (D. J. Wildish. 1984. Can. J. Zool. 62: 1027-1033), although a total of 26 amphipods were recorded. In January 1980, a de-populaton event occurred followed by a new build-up in amphipod density and addition of "new" species which replaced some of the earlier subdominants. The cause of these changes was unknown (D. J. Wildish and M. J. Dadswell. 1985. Proc. N.S. Inst. Sci. 35: 1-15), but could have been due to a storm-related sediment resuspension.

BUTMAN You don't feel that photography can replace conventional benthic grab sampling?

WILDISH No.

LOBSIGER With stereophotography you can look through a lot of particulates and can identify what's below and how far away it is.

BUTMAN Why is this so?

LOBSIGER In stereophotography, you are looking from two angles so that an area blocked from one camera view may be seen from the other camera. Wide-angle lenses also reduce light scattering. We can take close-ups of mud, which is difficult to illuminate because it has so little contrast.

UNKNOWN Will the analyses be tedious?

LOBSIGER Not if an automated or semi-automated analytical system is used. In an automated system, you view slides through a stereoscope, match the cursor lines, press some buttons and get your data -- there are three or four commercially available systems. A simpler, less accurate method involves digitizing after the coordinates have been traced with a cursor or pen.

BARETTA What are you going to measure?

LOBSIGER Size of organisms, in length, or volume. The precision is 0.2 mm in clean seawater at 30 cm above the sediment.

BARETTA What is the major advantage of this technique over others?

LOBSIGER That you can observe and measure animals in their natural environment without disturbing them.

WILDISH The major disadvantage is that you only see <10% of the macrofauna when the substrate happens to be a soft sediment.

LOBSIGER Underwater imaging must always be an auxillary technique, except in the few cases where no other method is possible as, for example, on subtidal rocky bottoms. In shallow water, it would be ideal to combine it with a T.V. camera which would allow you to choose a suitable patch for stereophotography.

NEAR-BOTTOM PARTICLE FLUXES AND SUSPENSION-FEEDING BENTHOS

by

D. K. Muschenheim, J. Grant and E. Mills

Benthic detritivores depend on advective processes to renew their food supply. Suspension feeders, in particular, rely on the horizontal flux of particulate organic matter in the near-bed region. In the benthic boundary layer, a zone of

substantial vertical gradients in both velocity and seston concentration, hydrodynamic conditions such as flow velocity and bottom roughness, as well as the nature of the particles themselves, determine the flux profile. Analytic and numerical simulations of these conditions have shown how the shear velocity (U*), bed roughness (Zo), and particle fall velocity (Ws), interact to place the maximum horizontal flux at the bed or higher up in the boundary layer. Experiments using natural sediments in a 3-m seawater flume at Dalhousie University show the same pattern and suggest that, as flow velocity increases, suspension feeders must reach higher off the bottom to optimize their energy intake. The hydrodynamic sorting that occurs as a function of the different fall velocities of the various particle fractions leads to qualitative differences in the type of material predominating at different heights above the bottom. Thus, the flux maximum may coincide with a maximum in suspended organic-mineral aggregates. The behavioral response of the polychaete, Spio setosa, to varying current and concentration regimes may reflect adaptation to take advantage of this hydrodynamic sorting.

DISCUSSION

SCHWINGHAMER So you basically counted numbers of discrete aggregates?

MUSCHENHEIM Yes, for each sample I counted 30 fields. I made sure I had counted at least 200 particles for each sample.

SCHWINGHAMER Was there a size difference between the aggregates in the worm gut and those suspended in the benthic boundary layer?

MUSCHENHEIM I don't know. It would be one way to determine whether or not organic mineral aggregate formation occurred internally. I think this can occur in the gut and so I tried to get to the material as soon as possible after the experiment.

UNKNOWN Did dissecting the worm aggregate the particles?

MUSCHENHEIM No, you still see individual sand grains in the gut as well as the aggregates.

BUTMAN In regard to the distribution of particles above the sediment interface in the BBL - they appear to peak at 1 cm height?

MUSCHENHEIM Particle distribution increased around the tubes which were 2 cm high and would reach up to 2 cm above the tubes.

BUTMAN Is the flow rough turbulent in field conditions?

MUSCHENHEIM No, the flow would most likely be smooth turbulent flow at high tide.

BUTMAN Are there significant waves? Do you see a ripple bed?

MUSCHENHEIM No to the first question. You do, however, see a ripple effect in the sand, but it is formed by the tidal stream.

BUTMAN So you don't think there is a rough turbulent flow out there?

MUSCHENHEIM No, not usually. We are limited because of flume length to studying suspended particles in current speeds of 5-10 cm/s. This range is adequate to demonstrate a flux of organic material fairly high off the bed and another layer of organic particles fluxing just above the bed.

BUTMAN Regarding the values for shear velocity and 50% shear velocity that you cited. What criteria did you use for the cut off point for the literature data?

MUSCHENHEIM I used several. Most of the field measurements of shear velocity have been taken from velocity profile where U* = 0.035 to 0.05 of the free stream velocity.

BUTMAN Is that for smooth or rough turbulent flow?

MUSCHENHEIM It wasn't specified.

BUTMAN It would make a big difference since a rough turbulent flow forms a fully developed profile in less time than a smooth turbulent flow.

GRANT Rough turbulent flow doesn't occur with the slow velocities we use in the flume.

MUSCHENHEIM Yes, you would need a longer flume to develop a smooth turbulent flow.

WILDISH Did you observe any behavioral differences between Spio in the flume and those in the field?

MUSCHENHEIM They are more difficult to observe in the field because you can't keep them at eye level. We noticed in both the flume and the field that feeding commenced soon after they were submerged. The palps formed little helices at low current speeds and straightened at higher velocities.

WILDISH They do change their behavior as the current speed increases?

MUSCHENHEIM Yes, but they respond to the suspended flux level as well. If the current speed is increased but the suspended flux level is nil, they will withdraw their palps and stop feeding.

WAINWRIGHT From your experiments, it looked as though you had three layers of seston, a bottom mineral layer, then a large aggregate layer with a layer of small aggregates on top. Does this occur in nature as well?

MUSCHENHEIM It depends on the composition of the aggregate and what the relative organic and inorganic loads are. Ultimately, it will be the particle's mass/density that will determine its rate of descent and its reaction to shear flow. It may be that

once you get a large particle that has aggregated somehow and settles in a sheared flow that the shear forces may resuspend it and distribute it elsewhere.

THE IMPORTANCE OF TURBULENT DIFFUSION IN SUPPLYING PHYTOPLANKTON TO MUSSELS

by

M. Fréchette

The contribution of vertical turbulent diffusion in supplying phytoplankton to an intertidal Mytilus edulis L. population was estimated at different points of the fortnightly tidal cycle. Vertical diffusion of phytoplankton accounted for 43.5% of overall mussel consumption. It is suggested that strong vertical depletion of phytoplankton owing to low rates of vertical diffusive transport of phytoplankton may contribute in limiting bivalve beds in the direction of current flow.

DISCUSSION

BAILEY What was the depth at your study site?

FRÉCHETTE We were at a point where at the EHWS tides there was 2.5 m of water with a tidal rise and fall of 4.8 m.

BUTMAN The depth is critical because the log·layer is usually about 10% of the tidal BBL and if the water depth is reduced it will result in a reduction in the log·layer. The log·layer equation used in your model is thus appropriate for only about 1/10 of the water depth which is variable with tidal time. Your assumption that the log·layer is 50–100 cm deep at your station may frequently be wrong. Turbulent mixing is energetic in the log·layer but much less so above it.

FRÉCHETTE What I wanted to show is that turbulent diffusion is important for mussel feeding and you believe that my calculation of diffusion may be overestimated?

BUTMAN Yes, what you could do is to go through your data and determine depths throughout the tidal cycle. If you then apply a 10% criterion as the depth of the log·layer and compare each with your model prediction, you will see whether my criticism is a valid one.

WILDISH An interesting feature of this field data is in relation to a queston raised earlier by J. Grant regarding competition among macrofauna. The data provides an example of intraspecific competition among suspension feeders, which opposes the conventional wisdom on this subject.

BROCK There must be differences among suspension feeding bivalves - thus mytilids congregate in aggregated clumps, whereas many other bivalves, particularly infaunal ones, are more evenly distributed.

BARETTA But this doesn't really change intraspecific competition for food because individual suspension feeders which are downstream of the prevailing current may still face food (=seston) depletion in the BBL. The mussel bed may be in a better position than infaunal bivalves because its clumping behavior increases bottom roughness and hence turbulent supply of seston.

WILDISH Isn't the strategy of the mussel bed to create a rough bottom and therefore increase the turbulent mixing and seston supply available to downstream mussels?

BARETTA That turns it into a teleological discussion.

BUTMAN It seems to be a teleological argument because their body form is highly adaptive but it is unlikely that adaptive processes can make them increase turbulence.

WILDISH That's true, the selective advantage goes to those mussels able to reach the top of the clump -- they can feed on a richer seston supply and therefore presumably produce more larvae. But from the population point of view, it is obviously advantageous to the whole colony to increase roughness and therefore turbulent mixing. The Neo-Darwinian adaptation involved with this population advantage may be gregarious spat settlement.

BROCK In the case of infaunal, suspension-feeding bivalves, it does not matter where an animal is, whereas for a mussel it is better to be at the top of a clump.

BARETTA On the contrary, the current orientation over a tidal flat will decide where an infaunal bivalve should be to maximize feeding and growth. Hence, animals at the upstream end of the current flow will be favored over those downstream of it. This applies only if the density and path length involved are sufficient to cause seston depletion at some stages of the tide.

NEWELL Supposing mussel filtration rates were increased, how would this change your results?

FRÉCHETTE Difficult to say precisely, but if mussel density or filtration rates were increased, the depletion effect would appear faster. In the Wildish and Kristmanson (1979) model, filtration rate was treated as a constant (average pumping rate per individual times the proportional filtering efficiency) and only population density was variable within the model. I think perhaps the filtering rate should be made variable.

WILDISH The main purpose of our model was to focus attention on the population, rather than the physiology of one mussel. It is only from the viewpoint of the whole mussel bed that the seston depletion effect can be appreciated.

NEWELL If you examine a wild mussel bed, you will see that mussels at the edge are generally larger and with higher meat weights than those further in the bed. I have also commonly found that higher current areas support larger mussels.

BUTMAN What were the mussel clump sizes in your study?

FRÉCHETTE On the order of 5 cm high.

BUTMAN Are they oriented in any relationship with tidal current direction?

FRÉCHETTE No.

BUTMAN There should be a minimum length of the mussel bed for increased roughness to cause increased turbulence -- did you calculate that?

FRÉCHETTE No.

BARETTA How do the clumps come into existence? Is there a nucleus of a hard substrate for the first mussel spat to settle on? If the previous generation is successful, subsequent spat fall will encourage the clump to grow. If water currents or seston supply change or a predator comes along, the clump may fail. The clump has no control over its size, except at the time of spatfall.

BUTMAN The number of spat that settle and survive in a given area depends on an integration of processes in time that are peculiar to that area.

WILDISH Mytilids are gregarious or social settlers. The spat preferentially settle on the byssus threads of established mussels and as mentioned earlier this can lead to clump formation and have a selective advantage for the whole mussel bed (c.f. with the antagonistic spacing strategy employed by infaunal suspension feeders).

BUTMAN Yes, but the roughness scale must be larger than that of the natural sediment surface for this to be effective.

FRÉCHETTE The clumps have to be bigger than the other roughness elements. Thus, if the substrate is stony and the stones are larger than the mussel clumps, there is no roughness - induced increase in turbulent seston supply.

GRANT Many of the shells in a mussel bed are dead, although the shells remain in place. Thus, spat settlement is enhanced by a greater supply of seston due to roughness and the dead shells do not compete for food.

NEWELL Mussel clumps grow higher and higher above the substrate until ice scours them away. Clumps of mussels are frequently found in the intertidal zone at very high densities. If these individuals are replanted in the subtidal zone, you may see an up to a fivefold increase in production.

FRÉCHETTE This increased production response does not depend on placing them in the subtidal but on reducing the density.

GRANT Mussels also compete with macroalgae don't they?

FRÉCHETTE There was little present in the area where my field experiments were carried out. Seastars were a significant predator of mussels though.

PEER The horse mussel, Modiolus modiolus, builds substantial beds like the Mytilus ones. They bind the sediment together and form roughness elements similar to the blue mussel situation.

SPECIES-SPECIFIC IRRIGATORY EFFICIENCY OF CARDIUM (=CERASTODERMA) EDULE (L.) AND C. LAMARCKI (REEVE) RESPONDING TO DIFFERENT EXPERIMENTAL TEMPERATURES

by

V. Brock and L. Kofoed

Clearance rates and oxygen concentration were studied simultaneously for co-occurring individuals of the two closely related Cardium species at different temperatures. The bivalves acclimated to different temperatures in nature, were studied at different exposure temperatures in the laboratory. When acclimated to temperatures of 4-23°C, oxygen consumption increased at equal rate for both species at exposure temperatures throughout the range 2-20°C. At exposure temperatures 20-28°C, C. edule respired at a higher rate than C. lamarcki. Both species exhibited maximal respiration at 24°C. Oxygen consumption at a given exposure temperature was lower for both species when adapted to lower temperatures than to higher.

The clearance rate (mL H_2O µg dry $wt^{-1}hr^{-1}$) of suspended cells (2.5-10 µm) measured synchronously with oxygen consumption showed species-specific differences. Cardium edule filtered at a high rate in the temperature range 8-20°C and at a lower rate at temperatures lower than 8°C and higher than 20°C when adapted to these temperatures, while C. lamarcki filtered at a slow rate in the temperature range of 4-12°C and at a high rate in the range 16-28°C, when adapted to these temperatures. The irrigatory efficiency (mL H_2O μLO_2^{-1}) of C. edule was higher than that of C. lamarcki in the exposure temperature range 4-16°C while the irrigatory efficiency of C. lamarcki exceeded that of C. edule in the exposure range 16-28°C when the cockles were adapted to corresponding temperatures. The irrigatory efficiency at different temperatures for the two species is discussed in relation to their occurrence and growth in different habitats.

DISCUSSION

WILDISH Do you know anything about the physiological mechanisms behind the effect of temperature on cockle feeding?

BROCK No, we could not make an energy budget because we did not investigate and measure anaerobic processes occurring within the animal.

WILDISH How long were the incubations?

BROCK They lasted for 2 h and oxygen was never depleted to below one-half of the saturation.

WILDISH In studying sea scallops, Placopecten magellanicus, we have done similar experiments in a Blazka respirometer. The question we want to answer is whether there are physiological mechanisms, involving energy expenditure, behind the observation that adult scallop growth rates decline as flow rates increase above ~10 $cm \cdot s^{-1}$. Other hypotheses considered concurrently in these experiments are that assimilation efficiency decreases with increasing ration, and that ciliary action on the gills cannot overcome the higher drag forces at faster current speeds.

BROCK We thought that there might have been a difference in the energy output as eggs, but found no difference between C. edule and C. lamarcki. They also spawned almost simultaneously.

WILDISH Is there any possibility of interbreeding between the two Cardium species?

BROCK No, breeding tests showed that no fertile eggs were produced by cross-breeding. But the species are so alike when they occur in sympatry that you are forced to use biochemical methods to distinguish them.

BUTMAN Do they start out looking the same?

BROCK Yes, according to the literature, some C. lamarcki may grow byssus threads, but I have never seen this. A possible explanation is that they have been taxonomically confused with another small species of Cardium, which does have byssus.

BUTMAN What do you think of the study by Baggermann (Baggerman, B. 1953. Spatfall and transport of Cardium edule L. Arch. Neerl. Zool. 10: 315-342) on Cardium? He thought that growth and distribution was controlled by the flow regime. How do you think flow affects the cockle's clearance rates?

BROCK Baggermann's study was in an intertidal area and thus the cockles were temperature-stressed when the tide was out. C. edule is an efficient digger in sand but this must result in a significant energy expenditure compared to subtidal cockles where washout is less frequent.

BARETTA Does C. edule grow slower in intertidal areas than in subtidal ones?

BROCK This is a difficult question to answer satisfactorily, because many factors are involved in determining growth rates. I have found high Cardium growth rates in subtidal areas, at least as high as you find anywhere in the intertidal. Growth efficiency in the Wadden Sea is high in subtidal locations, but in the intertidal ones they seem to be less healthy.

WILDISH Are your growth measurements by shell length?

BROCK Yes.

WILDISH Because in sea scallop growth, tissue growth occurs at one time, and shell growth at another time of the year.

BROCK That's probably also true of cockles, but if you look at annual growth of several year-classes by interpreting the growth rings, you have a satisfactory growth measure. I should add that Mars (Mars, P. 1951. Essai d'interprétation des formes généralement groupées sans le nom de Cardium edule Linné. Bull. Mus. Hist. Nat. Marseille 11: 2-31) suggests that instead of the two species that are the subject of my talk, there are actually about 50 forms, all associated with particular locations.

SEDIMENT PARTICLE RESUSPENSION AND TRANSPORT PROCESSES

POTENTIAL BIOLOGICAL EFFECTS ON SEDIMENT TRANSPORT AND BOTTOM FLOWS IN COASTAL EMBAYMENTS

by

C. A. Butman and W. Grant

Accurate calculations of near-bottom flow, bottom friction and sediment transport require proper inclusion of a movable bed and biological effects on bottom sediments. Movable beds and biological processes affect predictions of roughness, length scales, sediment reference concentration, sediment fall velocity, and bottom shear stress. Movable-bed processes affect these parameters through bedform generation and dissipation due to near-bed transport. Biological processes can have both indirect and direct effects on these parameters by modifying sediment texture, grain-size distribution, cohesiveness and microtopography of the seabed. Ongoing studies of near-bed flows and benthic biology in a shallow (10-m depth), muddy region of a coastal embayment (Buzzards Bay, Massachusetts, U.S.A.) provide quantification for these effects. Observations suggest that potential biological effects on bottom flows and sediment transport differ between storm and non-storm conditions. Flow measurements at the site indicate that the mean currents during every day conditions are too weak to initiate motion of the silty sediments and surface waves are fetch-limited and normally do not penetrate to the sea bed. Under non-storm conditions, biological modification of bottom microtopography is a dominant effect on near-bottom velocity profiles. During storm conditions, mechanical reworking of sediments dominates a seabed microtopography; surface waves penetrate to the sea bed and resuspend and rework bottom sediments. Ripples have been observed on the sea bed following a typical storm event. Under storm conditions, biological effects on the vertical distribution of grain size and on sediment cohesion still can affect both the near-bed profiles and sediment transport.

The potential importance of biology on bottom flows and sediment transport is evaluated using benthic data from the study site and a boundary-layer model. The impact of biology on near-bed profiles during non-storm (no sediment transport) conditions is determined for all dominant biological induced microtopography scales observed at the study site; results differ depending on the size concentration of the bedforms. For the storm case, the nature and importance of biological effects on sediment transport may vary seasonally. During the spring, mechanical reworking of surface sediments appears to be dominant. Results from vertically sectioning (at 2-mm intervals) a field core collected in April suggest that sediments in the top 4 mm are reworked by storm flows. The observed bed sediment profile can be explained by the distribution of fall velocities present in the sediment. A fine sediment layer occurring from 4-6 mm from the sediment surface is apparently armored from the flow by the coarser sediments above it. The dominant (<90% by number) infaunal organism at the study site, Mediomastus ambiseta, a subsurface deposit-feeding worm, probably feeds below 10 mm in the sediment in the spring; preliminary evidence indicates that large adults dominate the population at this time of year and that depth of occurrence in the sediment is proportional to worm size. Thus, biological activities (i.e. mixing sediments through feeding) of this infaunal species may have a negligible effect on sediment transport in the spring except in severe storms where the armoring sand layer can be removed by mechanical processes. Larval settlement occurs during the summer months, when population numbers reach a maximum. These small individuals live and feed in the top few millimeters of sediment so that biological mixing of surface sediments may significantly alter the particle fraction that is available for transport in the late summer and fall. Samples are being collected in September to test this hypothesis.

DISCUSSION

GRANT — Is the difference in your summer and winter sediment distribution due to fecal pellets or actual mineral grain size?

BUTMAN — We have only measured the adult fecal pellets, so we don't know what size of pellets the larvae produce. The adult fecal pellets are much larger than the peak sediment size distribution but as you can see for September the adults are really a small proportion of the fauna. We would like to determine whether the fecal pellets break down instantly or are transported as pellets.

GRANT — Does the water content change?

BUTMAN — Yes. The top 2 cm of sediment in April weighs 15 g and in September it weighs 25 g; so predictably, the water content of sediments is less during physical reworking. An obvious project to do would be to subject the September distribution to simulated April conditions to see if we get a graded bed and do a similar study on the effect of September conditions on April distribution.

We still don't know anything about the reference concentration on the bed. Is the top 0-2 mm of sediment available to be transported or is it left on the bed during transport? This could be determined through flume studies where suspended sediments could be conveniently studied, or by recording near-bottom flows in the field.

PETT — What is the light penetration?

BUTMAN — Visibility is low due to resuspended sediments, a large phytoplankton population, and a lot of debris from the shore.

SCODITTI — You said the resuspended layer is just 1 mm?

BUTMAN — It is at least 1 mm but (according to our sediment distribution) it is not more than 4 mm.

SEDIMENT TO WATER FLUX OF PARTICULATE MATERIAL AND ASSOCIATED BACTERIA IN THE NEARSHORE ZONE OFF GEORGIA, U.S.A.: LABORATORY ESTIMATES

by

S. Wainwright

Water in the nearshore zone off Georgia is normally turbid, but is especially so at ebb tide and during storms. To assess what proportion of this excess turbidity is due to tidal and storm-related resuspension of bottom sediments, a flume was employed to simulate shear stresses which might occur during normal tidal and storm events. Preliminary results show that particulate concentration may reach 186 g dry wt m^{-2} during simulated storm events. As might be expected, finer sediments (muds and fine sands) contribute more to the seston than coarse sand sediment (4 to 9 times more in these experiments).

Sediment-associated bacteria also increased in the overlying water during flume runs. Sediment to water fluxes of bacteria ranged from 1.19 to 9.13 x 10^{12} m^{-2} during simulated storm events. However, while seston settled relatively rapidly after flume runs were stopped, many bacteria remained in suspension or, in one case, increased after the flume was stopped. This suggests that, on resuspension, sediments may release dissolved or nonfilterable nutrients capable of supporting planktonic bacterial communities after the bulk of the filterable seston has settled out.

The findings imply that bacteria-based planktonic food webs may be stimulated following resuspension events, either by the direct release of bacteria from sediments, by the release of nutrients from sediment which support planktonic bacterial communities, or both.

DISCUSSION

BUTMAN Do you have any problem with cross-phase circulation in your annulus flume?

WAINWRIGHT I'm sure that is a problem. I did a cursory transect across the flume with a velocity probe and there was quite a velocity gradient.

MUSCHENHEIM When you've resuspended some sediments, do you expect to get equilibrium between resuspension and settling throughout the annulus?

WAINWRIGHT I'm not sure that it has reached equilibrium. I've got several problems that I have to reach a compromise with. First, the experiment must reach an equilibrium between settling and resuspension. I also have to keep my times down because I don't want bacteria blooming in the water during the runs. So that leaves us with two problems at odds with each other.

WILDISH Do you feel that the bacteria come off before the heavy sediment material is separated?

WAINWRIGHT Yes. Looking at the cores before the run starts, you can see a fluffy layer on the surface. It's the first thing to come off, and there should then be a lag before the rest of the bacteria come off with the heavy particles.

GRANT Have you done a calculation to see what percentage of the bacterial population is resuspended from the sediment?

WAINWRIGHT I haven't done that yet. I suspect if I did let these runs go longer that the whole thing would behave like a sediment homogenizer and would knock the bacteria off the particles. I may eventually get more bacteria in the water column that are disassociated from particles.

SCODITTI How do you count bacterial numbers?

WAINWRIGHT Part of a 5-mL sample is diluted to get a countable result, stained with Acridine Orange, and then directly counted.

WATLING You could try looking at the seston with S.E.M. to see where the bacteria are.

WAINWRIGHT I know from my counts that 80% of the countable bacteria are associated with particles.

BUTMAN You might see a size-specific resuspension by doing counts with a Coulter counter.

MAYER Ratios of bacteria to seston, in your experiments are about 5 to 1 x 10^{11} bacteria/gram, which is really high for sediments.

SCHWINGHAMER But this is the light stuff that is coming off in 10 min. I imagine that what is resuspended is mostly organics, which is what the bacteria colonize.

MAYER I'm not sure that all those bacteria could be associated with sediment at all. I've only seen numbers like that in the literature associated with sewage sludge.

WAINWRIGHT I don't think I'm working in that!

SCHWINGHAMER A very good point raised with this kind of study is the quality of associations. Do you think you could avoid the problem of bacterial buildup by using poisons?

WAINWRIGHT I hate to poison my flume, but you're right, I could do something like that. One thing I'd like to do is run some settling experiments with bacteria-sized latex spheres, just assuming they behave like bacteria.

BUTMAN I think it's a good idea to use particles that are predictable. Each flume is different, so if you use particles dynamically similar to bacteria, then sample those particles over time, you'll find out where they go, and that tells you something about the physics of your flume.

WAINWRIGHT As a matter of fact, I do have some idea where they go because any sediment that doesn't stay in the water column settles out on the inside; it's like a stream meander.

GRANT Do you actually transport the sand, or any sediment with surface layer sediment transport?

WAINWRIGHT Yes, it goes all the way around and back the other side. I'm just assuming it reaches an equilibrium.

GRANT There's probably bedload transport of bacteria as well.

WAINWRIGHT That's true, but I don't think my flume is designed to test that.

ORGANIC MATTER ASSOCIATED WITH FLOCS IN SUSPENSION

by

K. Kranck

Suspended particulate matter in relatively turbid coastal waters including near-bottom suspension consists largely of mixtures of inorganic silicate mineral grains and detrital organic matter flocculated together into soft, low-density, fragile flocs. Their transport behavior is controlled by hydrodynamic flow conditions and, consequently, particle size characteristics reflect past and present current energy. The size distribution of the mineral grain component is described by a model assuming settling from a turbulent suspension. Settling from unflocculated suspensions causes progressive removal of particles from the coarse end of the mineral grain size range. Settling from flocculated suspensions results in removal of a representative proportion of all sizes. The relative magnitude of each type of settling can be estimated from the size spectra of the bottom sediment.

At the present time, it is not possible to predict the size characteristics and amount of organic matter associated with a given inorganic settling fraction. Several possible patterns describing the association between inorganic and organic matter are suggested by results of past studies in coastal environments. These will be discussed and experiments to test the models presented.

DISCUSSION

MUSCHENHEIM Your graph shows 50% organic matter in suspension, so presumably that's going to settle out quickly, and essentially you have an effect of combining organic and inorganic fractions forming floccules which deposit rapidly, thus scrubbing the water column. Yet, in superficial sediments, you do not see such high organic content. Do you think this is because it's being consumed as soon as it gets down there?

KRANCK Yes.

MUSCHENHEIM So is this a source of very organic rich material available to benthic organisms that no one has ever measured before?

KRANCK It is measured by volume, not by weight, so it is not that high.

BROCK Where were these samples taken?

KRANCK In three estuaries: the Miramichi, St. Lawrence, and the Saint John.

MAYER Theory predicts that you get the most collisions between large and small particles rather than particles of the same size; therefore, you should have the poorest sorting possible at a given particle suspension in the floc?

KRANCK Yes, I suspect there is some flocculation mechanism that favors poor sorting at a particular particle grain size distribution.

KEIZER Is there any evidence that the nature of the organic material has anything to do with the rate or extent of flocculation of material; for example, is there any evidence of seasonal variation in flocculation based on biological cycles?

KRANCK There is seasonal variation, but there are so many variables, it's hard to separate them. There is less inorganic matter in suspension in summer, but is it due to biological effects, or because there is so much organic matter in suspension in summer, that it has flocculated the inorganic matter so that it's all on the bottom?

BROCK It's also found on fecal pellets?

KRANCK Fecal pellets in most coastal areas are volumetrically not important to settling. In any case, fecal pellets would not change this distribution.

GRANT Do you find some sort of a peak mode or some common aggregate mode between different environments, based on the floc size? It seems that if you have a constant 50% organic/inorganic ratio, one would expect some sort of equilibrium of the flocs?

KRANCK We have not had a chance to look at floc size but a flume experiment indicates floc size is related to inorganic grain size. You would expect that, because flocculation continues up to a point where the individual aggregates settle out, they become larger than the largest unflocculated grains. They won't stay in suspension.

SCHWINGHAMER I noticed all the flocs seem to be formed around diatom clusters. Have you looked at this?

KRANCK Yes. In the Bay of Fundy, I noticed a lot of the flocs had diatoms.

WILDISH Where was the plankton camera sample from?

KRANCK I think the one I showed you was from Rotterdam Habour.

THE EFFECTS OF WIND ON THE PHYTOPLANKTON DYNAMICS OF THE LITTORAL ZONE IN A TIDE-DOMINATED ESTUARINE ENVIRONMENT

by

S. Demers, J. C. Therriault and Edwin Bourget

A number of biological and physical variables were measured for 148 consecutive days at a fixed station in the littoral zone of the lower St. Lawrence Estuary. The salinity time series showed strong fortnightly variations (neap-spring tidal cycle) which are believed to be linked to advective processes at the sampling station. Phytoplankton communities, however, did not exhibit any neap-spring tidal variations, suggesting a certain homogeneity in terms of cell number and species composition of water masses advected over the station. The seasonal pattern of variation of phytoplankton in the littoral zone was found to be similar to that observed off-shore in the pelagic zone of the St. Lawrence Estuary. On the shorter time scale, chlorophyll a concentrations in the littoral zone were found to be closely associated with the variations of the wind field, but no relationship could be found between phytoplankton biomass (cell numbers) and wind velocity. Therefore, the higher chlorophyll values observed resulted from mechanical resuspension of benthic diatoms due to wind mixing rather than to the growth activity of the phytoplankton. It was observed that wind velocity below 4 $m \cdot s^{-1}$ did not affect the resuspension of particulate matter in the water column. Over 4 $m \cdot s^{-1}$, the wind velocity increase was accompanied by a parallel increase in particulate matter concentration in the water column due to resuspension up to about 6 $m \cdot s^{-1}$ where a plateau of particulate matter concentrations was reached and no further increase could be observed. From these results, two conclusions are drawn: (1) wind velocity plays a significant role in secondary production by providing a constant food supply to the benthic and planktonic filter feeders, especially when plankton biomass normally used by these organisms is low; (2) resuspension due to wind increases energy transfer efficiency from one trophic level to another by recycling particulate matter which otherwise would remain unused by higher trophic levels.

DISCUSSION

BARETTA Why do you expect to find a diurnal component in your time series data? Your sampling was done at a fixed hour of the day and this was shifted through tidal time.

BOURGET Sampling was carried out four times a day, so I think we could distinguish a strong 12-h periodicity if there were one.

PETT How did you determine your sampling times?

BOURGET Initially on a tidal basis, but you then introduce biases in other parameters such as light intensity, so we finally decided on fixed times during the day.

SCHWINGHAMER The cycle correlated with wind in your data could be a spurious one caused by the recurring tidal cycle?

BOURGET Chlorophyll peaks showed up at 14 d at the time of spring tides and correlated with wind events are chlorophyll, particulate organic matter, cell numbers and nitrate.

NEWELL Did you notice peaks in silicate concentration associated with rainfall?

BOURGET I didn't study that.

GRANT How important do you think resuspension events are in providing nutrients for plant growth?

BOURGET Probably a major factor as far as phytoplankton is concerned in the littoral zone, but this does not apply to trace minerals also required by phytoplankters.

GRANT Do you think that it is settled phytoplankters that are being resuspended?

BOURGET No, we think that it is suspended benthic diatoms.

WILDISH Did you know at what depth that significant resuspension ceased?

BOURGET No.

BAILEY Did you run lag correlation analyses on your data, e.g. wind vs cell numbers?

BOURGET Yes, but the results were not conclusive.

SCHWINGHAMER Did you measure light accumulation?

BOURGET Our station was never light limited.

WAINWRIGHT You mentioned that the diatoms were not contributing much to primary production. Can you say which groups were the major primary producers?

BOURGET Yes, planktonic diatoms and chlorophytes rather than the microflagellates. But when wind events resuspended diatoms, the primary production values were not much increased.

ECOSYSTEM BUDGETS

A COMPARISON OF VERTICAL FLUX OF PARTICULATE MATTER BY SEDIMENTATION AND UPWARD ZOOPLANKTON MIGRATION

by

G. Harding and B. Hargrave

Particulate matter sedimentation and upward migration by zooplankton as dry matter, organic carbon and nitrogen were measured simultaneously in two experiments in St. Georges Bay, southern Gulf of St. Lawrence. Vertical transport of particulate matter by migrating zooplankton through the 30 m water column in August equalled or exceeded sedimentation. Zooplankton biomass was lower and particulate deposition was greater in the unstratified water column during April but upward transport of particulate matter by zooplankton migration was still a significant fraction of downward particle sedimentation.

DISCUSSION

BARETTA Your microzooplankton curve was quite irregular because of the subtraction term. Do you have any direct observations on the microzooplankton? Because we are having the same problem with this term.

HARDING No.

BARETTA Do you expect the chlorophyll/carbon ratio to be constant over the season?

HARDING No, not from what I've read.

KRANCK Did detritus get into your traps?

HARDING Yes, the traps facing up certainly caught detritus and on one occasion the ones facing down caught detritus. It is difficult to quantify with this type of trap, however, as the detritus sticks on the funnel giving a lower value than a cylinder would. In the future, we plan to use a large cylinder trap.

BARETTA Is there any glue available that could be applied to a plate to catch zooplankters drifting down on contact?

HARDING I don't know. Some species have dramatically large numbers of zooplankters moving up and nothing moving down.

BARETTA Just fom a mass balance viewpoint, is it intolerable?

HARDING Yes. B.T. Hargrave says he removes all the plankton from the samples so that is not a problem. However, I'm sure that there are microzooplankters that are producing those numbers.

BARETTA Did you use a transparent trap?

HARDING The light penetration through our traps was actually 20% so one might expect some effect due to shading. We set out two clear and two black traps to check whether shading would affect the upward movement and found there was no difference.

BUTMAN Utilization of an adhesive-type paper moving at a constant rate from roll to roll would even give a time series of falling particles. Preservation would be a problem; however, perhaps some kind of film like Sephadex would work?

WILDISH The Hardy continuous plankton recorders work like this don't they?

BARETTA But they move water and that is different; you would create problems due to passive gradients and movement in the water. It just doesn't work in a stationary situation.

GRANT The solution for the upwards facing trap has been to put a dense poison in the bottom so when things fall in, they can't swim out.

SCHWINGHAMER Using glycerine in the cylinder might be worth trying?

UNKNOWN But glycerine dissolves in water.

SCHWINGHAMER That's right but if you had it in the cylinder, the specific gravity would keep it there.

BUTMAN There would be no gradient.

SCHWINGHAMER But it would slowly effect quite a layer and I imagine it would blend with the water. But the specific gravity difference between glycerine and water is about 1.6 or so and it would take a long time for diffusion to create much of a mixture.

BARETTA Yes, but the problem would be that the zooplankters would just float in the glycerine. They would not sink through it. Wouldn't the glycerine also affect your carbon determination?

PELAGIC-BENTHIC INTERACTIONS IN THE CUMBERLAND BASIN ECOSYSTEM MODEL

by

P. Keizer, W. Ebenhoh and D. C. Gordon, Jr.

In the turbid waters of Cumberland Basin, the dynamics of suspended silt particles is a major forcing function for many biological processes. In the model, the transport, sedimentation and resuspension of silt is modeled in a simplistic manner to reproduce the sediment regime observed in the Basin. Biological variables which move in a manner similar to silt are handled by the same algorithm. Interactions between pelagic and benthic organisms are included in the model but the quantitative relationships are often tenuous. The uncertainty of these interactions severely limits the ability of models to accurately simulate ecosystems where these interactions are important.

DISCUSSION

WILDISH Is Cumberland ahead of Minas Basin in terms of the politics of potential power development?

KEIZER For the last 2 mo, yes. One of the major concerns with B-9 in Minas Basin is the effect on Logan Airport in Boston. There is no predicted increase in tidal amplitude in the lower part of the Gulf of Maine from the Cumberland Basin (A-8) site while there is from the large Cobequid Bay (B-9) site. Recent work by D. Dewolfe with Greenberg's model suggests that the effect on tidal range in the Gulf of Maine can be mitigated by changes in the operational strategy of the barrage. So there may be a switch back to B-9 as the favored site.

WATLING I personally have been a skeptic of the entire environmental effect argument. I believe in the heuristic value of models as you have presented it but it always seems the information transfer between the biologist and the modeler has been highly filtered. The obvious result is benthic deposit feeders shown as a box. At least you're one step ahead of other modelers that use benthic biota as a single box. But not all deposit feeders, as we have learned in the past few days, are using the same sources of carbon. The first step in refining models would be to take a functional group approach as you've done but subdivide even further so as to to include carbon sources. This would give more meaningful results for functional groups.

KEIZER I would like to comment on your point that these models are black boxes to biologists. I think that the modeling approach is a major advancement in attacking ecosystem problems. This model was not developed by modelers, but by biologists. They used software packages to handle the integrations and selected the time steps necessary for a reasonable rate of change for variables. The model is designed as a series of subroutines. If, for example, you were intrested in deposit feeders, you could extract one subroutine, work with it and then run it against the rest of the model without major difficulty.

WATLING What about energy transfer? If, for example, there were three subdivisions among deposit feeders, then energy tranfer from deposit feeders is coming from each of the three subdivisions. Also, bottom feeding fish could be subdivided and only one subdivision of fish could be interacting with one subdivision of deposit feeders. There isn't a total link between one box and the other but, in fact, it's parts of boxes going to parts of other boxes.

KEIZER That is true and there is a constant fight between people trying to disaggregate or aggregate the model beyond its present form. You have to reach a happy medium. A good example is the herbivore state variable in the present model which includes microzooplankton. How and who eats what presents the problem of how much of that state variable is microzooplankton or larger herbivores. One of the controlling factors has to be the state of our knowledge. If we have enough information to clearly assign all the parameters necessary for a new state variable, then its worth doing. If we are guessing the parameters, then we really don't get any more information back out. You can only get out of a model what you put into it.

WATLING That's right but my argument would be that if a model is going to be useful to the biologist who is trying to generate some of the numbers, it makes more sense to know what additional parameters to measure to produce a realistic number.

KEIZER Yes, and the model can tell you that.

BARETTA To make a working ecosystem model, it is necessary to have for a highly aggregated model, energy fluxes that are at least in the right order of magnitude before subdividing the functional groups into species you know about. I think it is usual to start with a highly aggregated model, get the fluxes as accurate as possible from field data and then start disaggregating.

KEIZER In our case, the flux measurements weren't obtained from species and specific physiological measurements. They are aggregated fluxes so these aggregated boxes are more appropriate to fluxes than disaggregated boxes.

SCHWINGHAMER It doesn't make sense to have a split between head-down and head-up deposit feeders, for example.

KEIZER Although some of the information generated by our workshop certainly adds to our understanding, I don't think we have enough to model it as a separate state variable and get reasonable feedback. This model, the physical part of it, is specific to Cumberland Basin; the biology isn't necessarily specific to Cumberland Basin. By changing the physical parameters in the model, you should be able to use this model for some other coastal environments. This is one of the strengths of the model. You can superimpose the Bristol Channel - Severn Estuary model on it and vice versa. The first run of the Cumberland Basin model was done with Dutch biology and I actually think looked better then, than after running for 2 1/2 yr. We had some discussions last spring in Holland about generic models. It's a nice concept and I think it is something that we will work towards. Basically, instead of including the environment, you include the entire suite of forcing functions and processes. Hopefully, as the model goes from one environment to the other, then the forcing

function that is important will switch as the controlling and environmental factors change. That seems a long way down the road but it is something which I think will evolve.

GRANT Do you wish you had done the model before you had started the field research in the Bay of Fundy?

KEIZER Definitely, although it would have been very difficult. We are in the process now of intializing an ecosystem study of the Scotian Shelf. We plan to adapt a model of the Grand Banks, although the first thing we have to know, is the physics of the system.

SCHWINGHAMER Another thing worth finding out, is the availability of detrital carbon.

KEIZER Yes. There is a whole picture about bioavailability that dates back to the early seventies with people talking about hydrocarbon pollution and the big buzzword then was the bioavailabilty of hydrocarbons. I think it is still as appropriate now. We really don't know what portion of the total carbon impact is actually available to the biota. We have a good measure of in situ production, we have a good estimate of transport in from the boundaries, but we really don't know how much is readily available to the organisms and how things are turned over.

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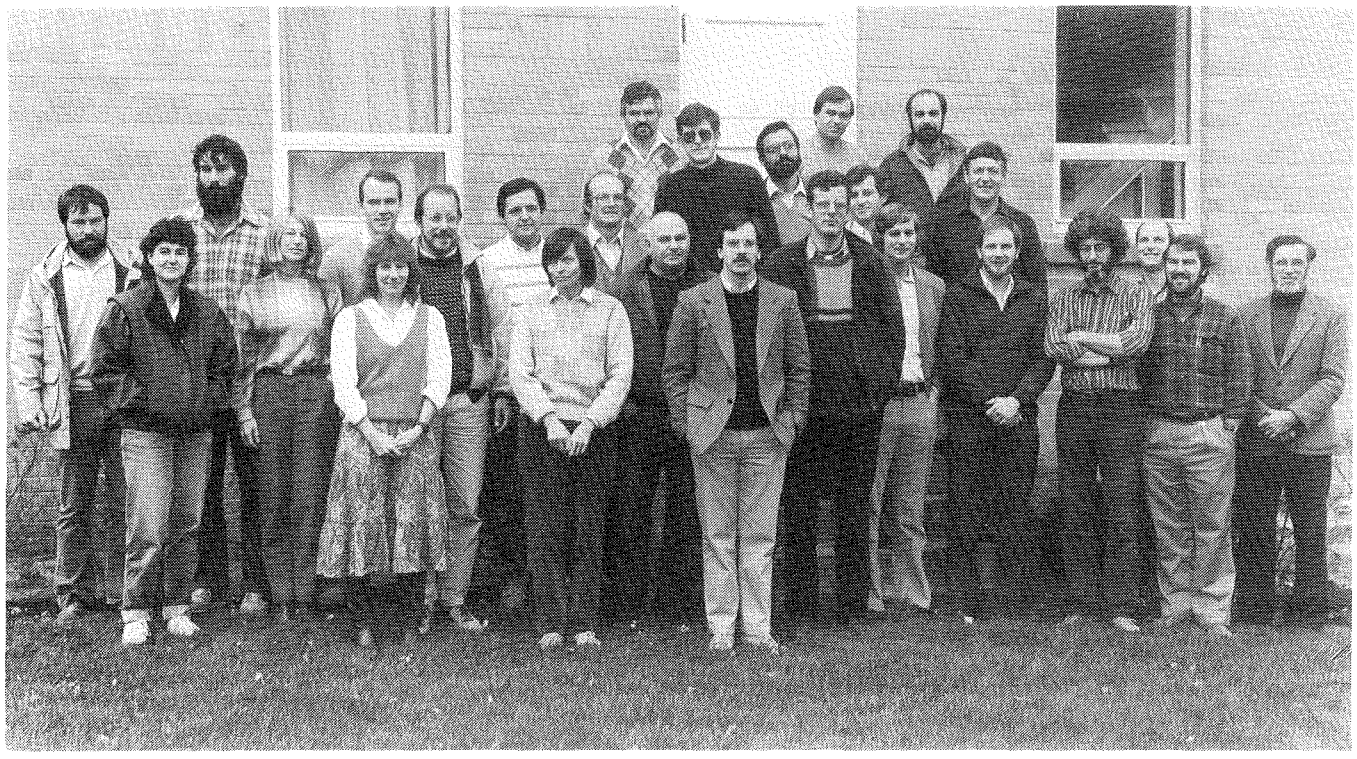

BENTHIC WORKSHOP

October 29-30, 1985
Biological Station, St. Andrews, N. B.

Fig. 1. Workshop participants. From left to right:

Front row
Decoste, Brock, Butman, Kranck, Boudreau, Baretta, Pett, Fréchette, Walting, Peer.

Second row
Martin, Frost, Bailey, Grant, Newell, Harding, Wilson, Waiwright, Mayer

Steps
Lobsiger, Keizer, Scoditti, Schwinghamer, Bourget, Muschenheim, Wildish

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