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**LA THÈSE A ÉTÉ  
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Hydrodynamics and the Ecology  
of Suspension-Feeding Benthos

by

Dwight Keane Muschenheim

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Submitted in partial fulfillment of the requirements for  
the degree of Doctor of Philosophy.

at

Dalhousie University  
Halifax, Nova Scotia  
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This thesis is dedicated to my mother, Ronda Keane,  
Muschenheim, and to the memory of my father,  
Dr. Carl Muschenheim.

## Table of Contents

|   |     |
|---|-----|
| List of Figures.....                                  | vii |
| List of Tables.....                                   | ix  |
| Abstract.....   | x   |
| List of Symbols.....                                  | xi  |
| Acknowledgements.....                                 | xii |
| <br>  |     |
| Chapter 1) Introduction .....                         | 1   |
| Factors Affecting Food Availability                   |     |
| Velocity.....   | 7   |
| Seston Concentration.....                             | 9   |
| Flux.....   | 11  |
| Choice of a Model Suspension Feeder                   |     |
| <u>Spio setosa</u> .....                              | 12  |
| Thesis Organization.....                              | 18  |
| <br>  |     |
| Chapter 2) Flumes for Benthic Ecologists: Theory,     |     |
| Construction and Practice.....                        | 21  |
| Introduction.....                                     | 22  |
| Flume Design.....                                     | 26  |
| Entrance and Exit Conditions.....                     | 30  |
| Flume Geometry.....                                   | 32  |
| Working Section.....                                  | 34  |
| Flow Measurement.....                                 | 34  |
| Theory of Near-Bottom Flow.....                       | 34  |
| Methods.....  | 36  |
| Data Logging and Control.....                         | 42  |
| Other Velocity Methods.....                           | 47  |
| Suspended Sediments: Theory.....                      | 48  |
| Suspended Sediments: Methods.....                     | 49  |
| Suspended Sediments: Alternative Methods.....         | 53  |
| Alternative Flume Designs.....                        | 53  |
| Further Design Considerations.....                    | 54  |
| Flume Application .....                               | 56  |
| Summary and Conclusions.....                          | 57  |
| <br>  |     |
| Chapter 3) The Dynamics of Near-Bed Seston Flux       |     |
| and Suspension-Feeding Benthos.....                   | 60  |
| Introduction.....                                     | 61  |
| Suspension-Feeding Benthos.....                       | 63  |
| Model Development: Analytical.....                    | 65  |
| Velocity.....   | 66  |
| Concentration.....                                    | 66  |
| Model Development: Numerical.....                     | 68  |
| Methods: Laboratory Experiments.....                  | 74  |
| Methods: Natural Sediments.....                       | 78  |
| Methods: Field Studies.....                           | 79  |
| Results: Flume Flux Experiments.....                  | 81  |
| Results: Field Experiments - <u>Spio setosa</u> ..... | 90  |
| Results: Field Experiments - Ingested Particles.....  | 91  |

|   |     |
|---|-----|
| Results: Field Experiments - Plankton Camera.....   | 93  |
| Discussion.....   | 101 |
|   |     |
| Chapter 4) The Role of Hydrodynamic Sorting of Seston<br>in the Nutrition of a Benthic Suspension<br>Feeder, <u>Spio setosa</u><br>(Polychaeta: Spionidae)..... | 109 |
| Introduction.....   | 110 |
| Methods: Field Site.....  | 113 |
| Methods: <u>Spio setosa</u> .....   | 113 |
| Methods: Flume Experiments.....   | 117 |
| Results: Feeding Experiments.....   | 126 |
| Discussion.....   | 135 |
|   |     |
| Chapter 5) Summary and Conclusions .....  | 142 |
|   |     |
| Appendices.....   | 147 |
| Appendix I: Derivation of Logarithmic Velocity<br>Profile.....  | 148 |
| Appendix II: Permission to Use Copyrighted<br>Material.....   | 151 |
|   |     |
| References.....   | 153 |

List of Figures

Figure 1) Plan and side views of Dalhousie Flume.....28

Figure 2) Typical velocity profile: flume experiments...40

Figure 3) Reynolds apparatus for thermistor calibration in  
laminar pipe flow.....44

Figure 4) Data-logging and control systems.....46

Figure 5) Simultaneous profiles of velocity, seston  
concentration and flux.....52

Figure 6) Theoretical flux profile.....70

Figure 7) Parameter space plot: flux profile skewness...72

Figure 8) Seston sampling apparatus.....76

Figure 9) Model and experimental flux profiles.....83

Figure 10) Model and experimental determinations of relative  
flux.....87

Figure 11) Scanning electron micrographs of hydrodynamic  
sorting.....89

Figure 12) Plankton silhouette camera photographs.....95

Figure 13) Seston concentration tidal time series for  
particles  $>90 \mu\text{m}$ .....98

Figure 14) Seston concentration tidal time series, for  
particles greater than 300 $\mu$ m:.....100

Figure 15) Schematic of flume feeding experiments.....119

Figure 16) Settling tube experiment: Eastern Passage  
sediment.....123

Figure 17) Krone's method for determination of "effective  
settling velocity": Eastern Passage sediment.....125

List of Tables

Table 1) Organic/Inorganic particle ratios: ambient sediment  
vs. S. setosa gut.....92

Table 2) Particle Types: Eastern Passage sediments and S.  
setosa guts.....116

Table 3) Organic/Inorganic particle ratios: high flow rate  
flume feeding experiment.....127

Table 4) Organic/Inorganic particle ratios: low flow rate  
flume feeding experiment.....128

Table 5) Organic/Inorganic particle ratios: ambient sediment  
vs. S. setosa gut contents for summer and fall, 1985,  
at Eastern Passage.....131

### Abstract

Suspension-feeding benthic organisms depend on the horizontal transport of living and detrital particles for their food supply. Strong gradients in water velocity and seston concentration occur in the near-bed region; together they determine the flux of particles to benthic suspension feeders. Analysis of the equations predicting the vertical distribution of velocity, and concentration revealed variation in the height of near-bed flux maxima with changing flow conditions. Hydrodynamic sorting of seston particles creates gradients in seston quality in addition to the flux gradient.

Experiments in a 3-meter seawater flume, using sediments from Eastern Passage, N.S., revealed the same qualitative patterns predicted by the analytical model. Flume feeding experiments showed that hydrodynamic sorting in the near-bed region is important to a tube-building benthic suspension feeder, Spio setosa (Polychaeta: Spionidae). Worms feeding from 4 to 6 cm above the bed ingest a higher proportion of organic particles than those feeding from 0 to 2 cm.

Field studies revealed the importance of low-density organic seston in the diet of S. setosa. Variation in the abundance of flocculated aggregates and macrophyte detritus coincides with the natural seiche period of Halifax harbour. S. setosa's distribution and abundance are responses to hydrodynamic conditions on an intertidal sand flat.

### List of Symbols

|              |  |
|--------------|--|
| $a$          | reference height                               |
| $C_{a,z}$    | seston concentration at heights $a, z$         |
| $C_{o,i}$    | index of spionid tube regeneration: initial    |
| $d_{f,p}$    | diameter of filter fiber, suspended particle   |
| $F_z$        | horizontal seston flux at height $z$           |
| $I_{d,i}$    | index: direct interception, inertial impaction |
| $K_v$        | vertical eddy diffusivity                      |
| $P$          | $w_s / Ku^*$ (Rouse Number)                    |
| $Q_{o,i}$    | index of spionid tube regeneration: daily      |
| $R_{di}$     | $I_d / I_i$                                    |
| $u_z$        | streamwise velocity at height $z$              |
| $u^*$        | shear velocity = $(\tau_0 / \rho)^{1/2}$       |
| $V$          | velocity upstream of a filter fiber            |
| $w_s$        | particle fall velocity                         |
| $z$          | vertical coordinate, height above the bed      |
| $z_0$        | roughness length                               |
| $\alpha$     | significance level                             |
| $\gamma_1$   | skewness                                       |
| $K$          | von Karman's constant (=0.41)                  |
| $\rho_{p,w}$ | density of seston particle, seawater           |
| $\mu$        | dynamic viscosity                              |
| $\nu$        | kinematic viscosity                            |
| $\tau$       | shear stress                                   |
| $\tau_0$     | shear stress at the bed                        |

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Others have abetted my progress in more material ways. U.V. Bathmann made the SEM photographs in Chapter 3. Dr. K. Kranck provided the Benthos Instruments silhouette camera. D. Conrad and A. Ramard designed and built the control circuits (Chapter 2). B. Scofield and J. Grant assisted in construction of the flume (Chapter 2) and M. Snyder, L. Ogden, T. Milligan and C. Hopper assisted me in the field.

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CHAPTER 1

Introduction

Suspension-feeding invertebrates are ubiquitous components of marine benthic communities. The processes affecting the transport and capture of food particles by these organisms affect the trophic structure of marine ecosystems. With the publication of "Biology of Suspension Feeding", C.B. Jørgensen (1966) consolidated many years of diverse research into one conceptual fabric. His focus on commercially important bivalve species reflected the bulk of prior research efforts, yet he was careful to point out other primarily suspension-feeding groups. His list has since been expanded to include groups with, at least, a facultative ability to feed on suspended particles. He was also the first to make the important distinction between the "active" and "passive" modes of suspension feeding. Active suspension feeders expend metabolic energy to create local currents which carry food particles past the animals' feeding structures. This group includes lamellibranch bivalves, brachiopods, bryozoans, barnacles and chaetopterid polychaetes, as well as sponges (Vogel, 1981), alpheid shrimps (Gust and Harrison, 1981), and some Amphipoda (ampeliscids, Mills, 1967; corophiids, Miller, 1984). Passive suspension feeders create no such currents and rely solely on the horizontal transport of food particles by ambient water currents (Jørgensen, 1966; Warner, 1977; LaBarbera, 1984), although maintaining proper orientation of their feeding structures may have its own metabolic cost (Koehl, 1977). The organisms traditionally placed in this

category include actinians, corals, gorgonians, crinoids, serpulid polychaetes and some ophiuroids. Recently some groups, especially in the Polychaeta, previously thought to be exclusively deposit feeders, have been shown to be facultative suspension feeders. Notable among these are the terebellid (Caréy, 1983) and spionid polychaetes (Taghon et al., 1980; Dauer et al., 1981).

Jørgensen (1966) recognized the importance of the nature of the particles in suspension: "It is reasonable to discuss food conditions as a function of the habitat as characterized by the organic particulate matter in suspension.". Colloidal or flocculated organic matter and organic-mineral aggregates present as potentially rich a food source as do phytoplankton cells or organic detrital particles (Bowen, 1984). High concentrations of quartz, clay or other inorganic components, while providing surfaces for bacterial epiflora, are of little nutritive value and may clog the feeding structures of many suspension feeders. The ecological implications of this were presented by Rhoads and Young (1970), who suggested that substrate destabilization and resuspension by motile deposit feeders resulted in the exclusion of many suspension feeders from soft-bottom assemblages ("trophic group amensalism"). Wildish and Kristmanson (1979, 1984) proposed the alternative concept that flow speed and bottom roughness control the food supply, hence the distribution, of suspension feeders. Recently Genin et al. (1986) have demonstrated that this is

indeed the case with deep-sea corals. Rhoads et al. (1984) provided evidence of the richness of particles in the near-bed region, which they called the "Benthic Turbidity Zone" (BTZ), and emphasized its potential for bivalve aquaculture. Placing suspension feeders on racks slightly above bottom circumvents the amensalism process and provides bivalves with a rich and dense seston mixture which is a combination of particles resuspended from the bed as well as particles produced in the water column and settling to depth.

Exact knowledge of the type and quality of material available to, and ingested by, benthic suspension feeders is important to several marine disciplines. Application of Optimal Foraging Theory (OFT) to the marine realm holds the promise of producing explicit and testable ecological theories (Hughes, 1980; Townsend & Hughes, 1982). Before this is possible, specific knowledge of resources available to benthic organisms is necessary to complete the OFT equations (Jumars & Gallagher, 1982). This means characterizing both the particles in suspension near the bed and the particles actually ingested. Study of the transport of estuarine pollutants demands a knowledge of the steps affecting particle deposition, resuspension and ingestion by benthos. Dense assemblages of suspension feeders may deplete near-bed seston concentrations (Frechette, 1984; Wildish & Kristmanson, 1984) and will reduce deposition. Resuspension of polluted bottom sediments makes them available for ingestion by benthic suspension-feeders, while the rapid

settling of flocculated organic-mineral aggregates transports dissolved pollutants from the water column to the bed (Kranck, 1974; Bowen, 1984; Melack, 1985). The role of benthic suspension feeders, living in the ecotone between sediment and water column, in the bioaccumulation of estuarine pollutants has important implications for the transfer of these materials through estuarine trophic systems. My specific aim is to examine the fine vertical structure of seston in the near-bed region (0-10 cm.) and study the response of a suspension feeder to the physical factors determining this structure. A better appreciation of the physical milieu will advance our understanding of its role in foraging strategies of the benthos as a whole.

Early studies of the behaviour and habits of benthic suspension feeders have been replaced by more mechanistic studies of the process of suspension feeding. The small-scale physics of particle capture were first reviewed by Rubenstein and Koehl (1977) and put in ecological context by Vogel (1981) and LaBarbera (1984). Of the five modes of particle capture outlined by Rubenstein and Koehl (1977), only two have been recognized to be of any importance to marine benthic suspension feeders. These are i) direct interception, in which only the relative diameters of the particle and the filter fiber affect capture efficiency, and ii) inertial impaction, in which the density difference between the particle and the fluid medium also exerts an effect. Particles of low density closely follow flow

streamlines and, as water is diverted around the filter fiber, so are the particles. Denser particles have greater inertia, are not as easily diverted, and are thus more likely to contact the fiber and be captured. The formulae presented by Rubenstein and Koehl (1977) for these two modes of particle capture are:

$$I_d = d_p/d_f \quad (1)$$

for direct interception, and

$$I_i = \frac{(\rho_p - \rho_w) d_p^2 V}{18 \mu d_f} \quad (2)$$

for inertial impaction, where  $d_p$  and  $d_f$  are the diameters of the particle and fiber,  $V$  is the fluid velocity,  $\mu$  is the molecular viscosity of the fluid and  $\rho_p$  and  $\rho_w$  are the specific gravities of the particle and fluid.

Combining equations (1) and (2) yields an expression for the relative importance of the two feeding modes:

$$R_{di} = \frac{I_d}{I_i} = \frac{18 \mu}{(\rho_p - \rho_w) d_p V} \quad (3)$$

equation (3) predicts that the role of inertial impaction increases with increasing particle diameter, greater particle specific gravity and increasing flow velocity.

These are physically controlled factors to which organisms must adjust. Large vertical gradients in each of these factors occur in the near-bed region and their effects on suspension-feeding benthos may be predicted by looking at their behaviour singly and together.

## Factors Affecting Food Availability

### Velocity

The reduction of water velocity in the near-bottom region, due to drag exerted by the seafloor, is appreciated by marine ecologists. What has only recently come into general view is the specific role of near-bed velocity gradients and how they exert stresses on sediments and organisms. The specific structure of the benthic boundary layer will be discussed in chapter 2 and a review of the derivation of the velocity profile is presented in Appendix I.

Reviews of the role of boundary layer flow in the ecology of marine benthos (McCave, 1974; Vogel, 1981; Nowell et al., 1982; Nowell & Jumars, 1984; Jumars & Nowell, 1984) have focussed largely on reciprocal interactions between deposit feeders and sediment transport. Jumars and Gallagher (1982) made the point that near-bed velocity gradients force benthic suspension feeders in the deep sea to feed relatively high off the bottom. Suspended sediment loads are so low that the metabolic costs of pumping water are not repaid, thus excluding active suspension feeders. Passive suspension feeders that successfully colonize deep-sea habitats usually have structures that allow them to extend many centimeters above bottom as adults. This brings them into faster flowing water, which transports particles at a greater rate. Jumars and Gallagher (1982) speculated that deep-sea suspension feeder populations may be limited by the

number of suitable larval colonization sites. Juvenile suspension feeders are not large enough to extend into sufficiently fast flow and need platforms (rocks, hummocks) on which to settle. Such platforms are exceedingly rare in the deep sea.

The interaction between boundary-layer flow, biogenic structures on the seafloor and benthic suspension feeders was first addressed by Carey (1983). His detailed study of flow around tubes of the terebellid polychaete, Lanice conchilega, showed that resuspended particles, advected vertically in the lee of the tube, could be captured by the suspension-feeding worm. Scour and resuspension at the base of the tube are due to a flow structure called the horseshoe vortex (Carey, 1983), wherein high-velocity fluid is deflected to the bed at the front of the tube and forms twin helical wakes in the tube's lee, much as in flow around wharf pilings (Niedoroda & Dalton, 1982). Recently, Eckman and Nowell (1984) have made detailed measurements of bed shear stresses around a worm tube and Paola (1983) has made similar measurements around larger benthic objects (mounds, ripples).

The shear stress at the bed is most commonly determined from velocity profiles measured in the boundary layer. The measured profile is fitted to the Karman-Prandtl logarithmic velocity profile, most simply expressed by:

$$u_z = \frac{u_*}{K} \ln \frac{z}{z_0} \quad (4)$$

The relevant parameters are  $z_0$ , which is called the "roughness length" and is the  $z$ -intercept, and  $u_*$ , called the "shear velocity", is a parameter describing the slope of the velocity profile and the shear-generated turbulence in the boundary layer. It is equivalent to  $(\tau_0 / \rho_w)^{1/2}$ , where  $\tau_0$  is the shear stress at the bed and  $\rho_w$  is the fluid density. A log-linear regression of the measured profile yields  $z_0$  (intercept) and  $u_*$  (slope), from which  $\tau_0$  is obtained. Although more complex formulations exist for depth-limited, stratified and high suspended load conditions, Anwar (1983) found that the simplest form of equation (4) could accurately describe the velocity profile of well-mixed estuaries. Stratified estuaries required an additional buoyancy term when the stratification extended into the boundary layer.

#### Seston Concentration

A consequence of the logarithmic velocity profile is that particles with a given fall velocity ( $w_s$ ) have their fall opposed by turbulent diffusion, (characterized by  $u_*$ ), in the boundary layer. Rouse (1937) first formulated an explicit equation to predict the vertical distribution of seston concentration (see chapter 2). Review and explanation of the derivation are presented in Vanoni (1946), Raudkivi (1976) and Middleton & Southard (1984). Laboratory tests of the Rouse equation (Vanoni, 1946) have shown it to work well for rapidly falling particles (medium and coarse sands), but

field tests (Sternberg et al., 1986) suggest that it may underestimate concentrations of light particles (silt, clay) in the near-bed region. This is most likely due to flocculation and enhanced settling of fine particles in estuaries (Kranck, 1984; Sternberg et al., 1986), although Sternberg et al.'s (1986) measurements were restricted to heights above 18 cm. and are thus of limited value in elucidating seston concentrations very close to the bed. Nonetheless, the Rouse formulation of seston concentration profiles remains a reasonable starting point for modelling natural conditions.

To date, use of the Rouse equation in marine ecology has been limited to predicting whether particles of a given fall velocity will travel as suspended or bedload material in a flow of known  $u_*$ . This was applied by Nowell et al. (1981) to fecal pellets of the polychaete Amphicteis scaphobranchiata and used experimentally by Miller (1984) to ensure that corophiid amphipods fed in a uniform suspension in a small flume. Particles of very low fall velocity, two orders of magnitude less than the friction velocity, will generally be uniformly distributed (Jumars & Nowell, 1984). Any particles with fall velocities greater than  $0.1u_*$  will form vertical concentration gradients. Although relatively straightforward for well-sorted sediments, the prediction of seston concentration profiles is difficult for the poorly-sorted, highly organic sediments characteristic of estuaries. Krone (cited in McCave, 1979) devised the concept

of "effective settling velocity", which is estimated from a concentration profile in a flow of known  $u_*$  and may then be applied to other flow situations. This still does not overcome the problem that the seston is composed of diverse particle types which, in flow, will hydrodynamically sort to different heights. This problem is addressed in chapters 3 and 4.

Flux

Despite making use of material settling directly from the water column, passive suspension feeders depend primarily on material moving horizontally past their feeding structures (Jørgensen, 1966; Warner, 1977; Jumars & Gallagher, 1982; LaBarbera, 1984; Genin et al., 1986). Neither the seston concentration, nor the flow velocity alone are really appropriate to assess the particle supply to passive suspension feeders. The product of these two components, however, yields the horizontal flux of material. Measuring (preferably simultaneously) profiles of velocity and concentration allows one to calculate the flux profile. This was appreciated by Nowell and Jumars (1984), but they carried the suggestion no further. The fact that theoretical formulae are known for the velocity and concentration profiles in the benthic boundary layer means that a theoretical study of the flux profile is relatively straightforward. This is done in chapter 3 and applied to a benthic suspension-feeding polychaete in chapters 3 and 4.

## Choice of a Model Suspension Feeder

### Spio setosa

Although the potential for spionid polychaetes to intercept suspended particles has been known for some time, Taghon et al. (1980) first reported specific behavioural adaptations to facilitate suspension-feeding. Pseudopolydora kempii actively coiled its palps in response to higher flow rates or increased seston load. It showed an ability to switch from deposit- to suspension-feeding modes as conditions of flow and particle flux changed. Dauer et al. (1981) observed the feeding behaviour of several spionid species, including S. setosa. They reported detailed information on the progression of palp orientation, from sweeping the bed (deposit feeding) to the full coiling seen in suspension-feeding. Pseudopolydora (Taghon et al., 1980).

Dauer et al. (1981) also reported observations on the suspension-feeding activities of S. setosa. Its habit of constructing a conspicuous sand tube often isolates the worm from feeding at bed level, so that any deposit feeding it may do must be from the sides and top of the tube and not the bed surface. Dauer (1984) reported the feeding and particle selection behaviour of another spionid polychaete (Streblospio benedicti) and concluded that it performs post-capture selection of particles by means of ciliary currents in the buccal region. My observations of both S. setosa and Spiophanes sp. feeding under a dissecting microscope revealed no such selection of particles. The only particles

that these species rejected were physically too large to be ingested. Jørgensen's (1966) statement of non-selectivity in suspension feeders seems to hold for S. setosa: "...the composition of the ingested material is roughly similar to that of the suspended material in the surrounding waters."

Recent study of deposit-feeding benthos (Cammen, 1980; Taghon & Jumars, 1984) has shown many species to be less actively selective than previously supposed. These organisms adjust the quality of their ration by varying their ingestion rate in response to changing conditions.

Suspension feeders have another option for adjusting the nature of the ingested ration. Hydrodynamic sorting of suspended particles is a potential mechanism by which suspension feeders may feed selectively on one fraction of the seston. In the aquatic analogy of separating wheat from chaff, denser particles either settle out completely or form strong gradients of suspended load near the bed. In this case it is the "chaff", remaining uniformly suspended or forming gentle vertical gradients, that is of greatest interest to benthic detritivores. In estuaries this material is formed of flocculated aggregates, decomposing macrophyte fragments and small diatoms. Organisms which may suspension feed at some distance above the bed may be able to take advantage of the sorting and maximize their intake of organic particles.

As predicted by equation (2), the capture of denser particles is greater than that of light particles in a

complex suspension. From equation (3), the role of inertial impaction increases with increasing particle density or increasing flow velocity. In the benthic boundary layer these two factors oppose each other. Velocity increases with distance from the bed while particle density decreases. It is therefore hard to predict whether inertial impaction is more important than direct interception close to or far away from the bed. What is clear is that, in a complex suspension, dense particles are more easily captured than light particles. Any adaptation that allows an organism to feed in a region where the proportion of light (organic) particles is enhanced will gain an energetic advantage. It is possible that the tube of S. setosa allows the worm to do this.

Even though this thesis focuses on the role of near-bed seston fluxes in the nutrition of passive suspension feeders, the general patterns of near-bed flux affect all benthic suspension feeders. Active suspension feeders, bivalves especially, take an integrated ration from the lowest few centimeters. Macoma balthica, a supposed deposit feeder, actually obtains the majority of its ration from suspended material, in spite of spending less than 20% of its time suspension feeding (Hummel, 1985). Infaunal species, such as Mya arenaria, are faced with capturing bedload as well as suspended load material. Epifaunal species like Mytilus edulis often form hummocks which raise them above the bed, increase local turbulent mixing and

place the organism in a region of higher flux. Production of pseudofaeces by lamellibranch bivalves is an adaptation to feeding in an environment with high inorganic seston loads, but it can have a significant metabolic cost (Hughes, 1980).

Flux per se is not as important to active suspension feeders as it is to passive suspension feeders. The prodigious filtering capacities of many bivalves has long been documented (c.f. Rice and Smith, 1957: up to  $7 \text{ l hr}^{-1}$  by Mercenaria mercenaria) and makes them relatively independent of the ambient flow speed. However, the few documented instances of seston depletion by active suspension feeders (Wildish & Kristmanson, 1984; Fr chet te, 1984) suggest that their nutritional requirements are not completely independent of local flux conditions.

The effect of seston flux on suspension feeders differs slightly between the estuarine, shelf and deep-sea environments. Passive suspension feeders form a much larger percentage of deep-sea assemblages. Jumars & Gallagher (1982) attribute this to very low seston concentrations (one to two orders of magnitude less than in estuaries) which do not repay the metabolic costs of actively pumping water. Deep-sea suspension feeders are commonly stalked and reach many centimeters above the seabed. This raises them into a region of substantially higher flow rates than at the bed and, presumably, higher flux rates. If the bulk of material in suspension is composed of slowly settling organic particles, the flux profile will track the velocity profile

and increase in roughly logarithmic fashion from the seabed. The presence of many tall, fragile, stalked forms in the deep sea (c.f. Heezen & Hollister, 1971) is suggestive of low bed stress, slow flow and little resuspension of material. Resuspension certainly does occur, but in periodic events or "benthic storms" (Richardson et al., 1981).

Coastal and shelf ecosystems have higher seston input and are subject to wave effects. Both factors result in much more material, especially organic material, available in suspension. Surface waves exert effects to a depth equivalent to half their wavelength and thus are important even at ~~continental~~ shelf depths (Grant & Madsen, 1986). Wave effects are much more evident in shallow water, where their effect on the bed is often seen as symmetrical ripples. Combining wave and current effects in simple flumes is difficult, if not impossible, so it is best to isolate factors and not try to completely re-create natural conditions.

The capacity of estuaries for flocculation of organic and inorganic particles was first reviewed by Postma (1967) and later by McCave (1979). The incorporation of estuarine pollutants into flocculated aggregates (Kranck, 1974; Bowen, 1984) provides a specific mechanism for rapidly transferring pollutants to the bed or near-bed region. Many pollutants are incorporated into large, fast settling flocs and quickly make their way into the sediments. Unless resuspended, this material remains within the domain of deposit feeders.

Lighter, fragile flocs either settle slowly or are broken up and resuspended in the higher shear of the boundary layer. The position of benthic suspension feeders at this interface means that they are ideally situated to feed on a food source which is energetically rich (Bowen, 1984; Rhoads et al., 1984), but which also may carry a high pollutant burden. Organisms such as spionid polychaetes, which may either suspension or deposit feed, as flow conditions determine (Taghon et al., 1980), will ingest high amounts of flocculated material. Their tendency to deposit feed at low flow velocities means that they pick up recently deposited flocs, which settle rapidly at slack water. S. setosa's demonstrable preference for organic-mineral aggregates (OMA's, see chapter 4) indicates that this material forms a large proportion of its diet. The role of these organisms in estuarine food webs deserves further investigation.

The primary causes of resuspension in estuaries are currents, waves and bioturbation. The importance of each depends on local conditions but, in general, physical factors dominate in shallow water, especially intertidally (Grant, 1983). The principal forcing mechanism in estuaries is wind stress, resulting in distinct seasonal patterns in the amount (Anderson & Mayer, 1984; Cloern & Nichols, 1985) and quality (Somiat et al., 1984) of material in suspension. Resuspension plays an important role in the redistribution of organic matter after significant input events (e.g. sedimentation of a phytoplankton bloom), although the

trophic significance of this process changes as the nitrogen content of the supply declines (Graf et al., 1983). Periodic (or continual) resuspension of bottom sediments makes the equilibrium assumptions of the Rouse equation somewhat tenuous. The added complication of internal boundary layer formation in the lee of individual structures on the bed (Paola, 1983; Paola et al., 1986) further complicates the picture. If rotational current effects of tidal embayments are also to be considered, the question of small-scale seston flux measurements becomes experimentally intractable. Thus the aim of my experiments is not to provide a laboratory simulation of the field conditions, but rather to isolate specific hydrodynamic factors and estimate their potential effect in the field.

### **Thesis Organization**

The experimental portion of the thesis relies heavily on new techniques in the use of a laboratory flume, an important tool in experimental marine benthic ecology. A detailed understanding of the structure of boundary-layer flow and its reproduction in the flume is essential to obtain meaningful experimental results. Chapter 2 gives a review of boundary-layer theory and its prediction of velocity and seston concentration profiles. I review various flume designs and measurement systems and give a detailed description of the flume used in this work. A detailed derivation of the Karman-Prandtl formulation of the velocity profile is presented in Appendix I.

The principle aim of this thesis is to use three approaches to investigate the role of the near-bed particle flux in the nutrition of a benthic suspension feeder. The first approach is analytical; it is presented in chapter 3. Theoretical analysis of the velocity and suspended sediment equations is used to model vertical flux profiles in the near-bed region and to predict the patterns of horizontal flux of different particle types. These predictions are tested, in the second approach, by laboratory flume experiments. Natural suspensions of seston in controlled flow are sampled to provide vertical profiles of gradients in flux. The final investigation addresses the nature of particles actually ingested by a benthic suspension feeder, S. setosa, feeding at different heights above the bed. The flume provides the controlled flow and seston concentration for these experiments, which are presented in chapter 4.

Field investigation of seston concentrations available to S. setosa and particles actually ingested provides the connection between the theoretical and laboratory work and its relevance in estuarine conditions. The importance of hydrodynamic sorting in the nutrition of S. setosa is indicated by the agreement between the field and laboratory results. Relevant field results are presented in both chapters 3 and 4.

Chapter 5 summarizes the results presented in chapters 3 and 4. Although the analysis is applied only to one organism, a passive suspension feeder (S. setosa), the

implications of the results extend to suspension feeders in general, passive and active.

CHAPTER 2

Flumes for Benthic Ecologists:  
Theory, Construction and Practice

(C)

## Introduction

The flow of water over the bottom distributes sediments and food particles for benthic animals. Both the morphology of these animals and their means of acquiring food are adaptive responses to the fluid medium in motion (Rubenstein & Koehl, 1977; Vogel, 1981; Nowell & Jumars, 1984).

Increasing attention has been paid to the role of horizontal advection in supplying food to benthic organisms (Miller et al, 1984; Wildish & Kristmanson, 1984; Grant, 1985); this requires knowledge of the horizontal transport rates of organic detrital materials. Due to the inherent variation in size and density of naturally occurring organic-mineral aggregates, it is impossible to obtain calculated settling velocities from theory, and measured settling velocities can only be approximations with poorly sorted sediments.

Studies with laboratory flumes have been used to isolate flow effects and elucidate relationships that could not be detected in field studies or by theoretical approaches. For example, Wildish and Kristmanson (1979, 1984) showed strong correlations between the rate of seston input and the growth of suspension-feeding bivalves. Carey (1983) showed that local scour due to the hydrodynamic effects of worm tubes provided a source of resuspended food particles. Looking more directly at the horizontal transport of such particles, Fisher et al. (1979) measured critical erosion velocities for organic detrital particles from streams and found them to adhere well to the standard

Shields "competency" criterion, formulated for well-sorted inorganic sediments. Grant et al. (1982) used the same criterion as a measure of the way biological processes modified non-cohesive sediments. Results, presented below, on the horizontal flux of suspended organic material show that a substantial gradient exists very close to the seafloor (Chapter 3). The conditions that determine whether the flux maximum occurs at the boundary or a few centimeters above will have important implications for foraging in suspension- and deposit-feeding benthos. Other modelling and experimental efforts have attempted to determine how the food supply to deposit-feeders is mediated by the local hydrodynamic regime (Jumars & Nowell, 1984; Miller et al., 1984).

In addition to the effects of flow on feeding and food supply, benthic organisms have a role in determining the stability of the seabed. This effect has been studied in a flume by Neumann et al. (1970) in tropical sediments, Rhoads et al. (1978) using natural sediments from Long Island Sound and by Young & Southard (1978) using Buzzards Bay sediments. Later work (Eckman et al., 1981; Nowell et al., 1981; Grant, 1983; Taghon et al., 1984; Eckman & Nowell, 1984) has been directed at separating direct biological effects from biologically mediated hydrodynamic effects on sediment stability. The ability to quantify biological effects on the physical environment in terms of roughening of the bed and the binding of sediments, has allowed ecological information

to become relevant to more applied disciplines, such as engineering geology and fluid mechanics.

Several technological factors have increased the number of recent flume studies. Relatively inexpensive means of measuring flow at fine scales have been presented in the biological literature (LaBarbera & Vogel, 1976; Vogel, 1981). As in other disciplines, the advent of micro-computers and appropriate software has made the logging and processing of large sets of data accessible to investigators who otherwise would not have the means to undertake this research.

Despite the experimental appeal of laboratory flumes, direct measurement of both bedload and suspended load in sediment transport studies has been a difficult problem. Bedload motion and particle flux have been experimentally examined from a sedimentological perspective for nearly a century since the work of Deacon (1894, cited in Gilbert & Murphy, 1914). Studies of the distribution of suspended load started later, with the theoretical formulation of Rouse (1937) and experiments by Vanoni (1946) and others. These investigations concern themselves primarily with the transport of well-sorted, non-cohesive inorganic sediments and therefore omit the components of greatest interest to students of the benthos, the organic and organic-mineral aggregates in natural sediments.

To be able to manipulate natural sediments and organisms for this type of study requires equipment with

special capabilities. These include the ability to (a) simulate natural near-bottom flow conditions while maintaining organisms in life position (b) observe flow over intact sediment samples with undisturbed organic aggregates and films (c) introduce and rapidly mix particles into suspension and (d) allow access for measurement and manipulation. The laboratory situation is ideal, because in the field the structure of flows and their organic particle load are difficult to characterize, especially in unsteady flows (e.g. over tidal flats) or on scales of interest to biologists (mm to cm).

My concern here is with laboratory flow channels intended to control water flow and the boundary layer processes relevant to benthic animals. The ecological literature includes many contributions dealing with flow, its measurement and the implications of water motion near a boundary, but the details of flume design and operation are dealt with only in a cursory way. Although flumes and flow tanks are obviously adaptable to ecological problems, details of the technology are scattered through a complex literature. The only reference specifically on flumes (Williams, 1971) is directed at sedimentologists and is not generally available. Flumes have often been used to study the behaviour of stream insects (Peckarsky, 1983) but these experiments are not concerned with boundary layer phenomena. To the marine ecologist aspiring to operate a flume, the prospect of approaching a diverse and specialized technical

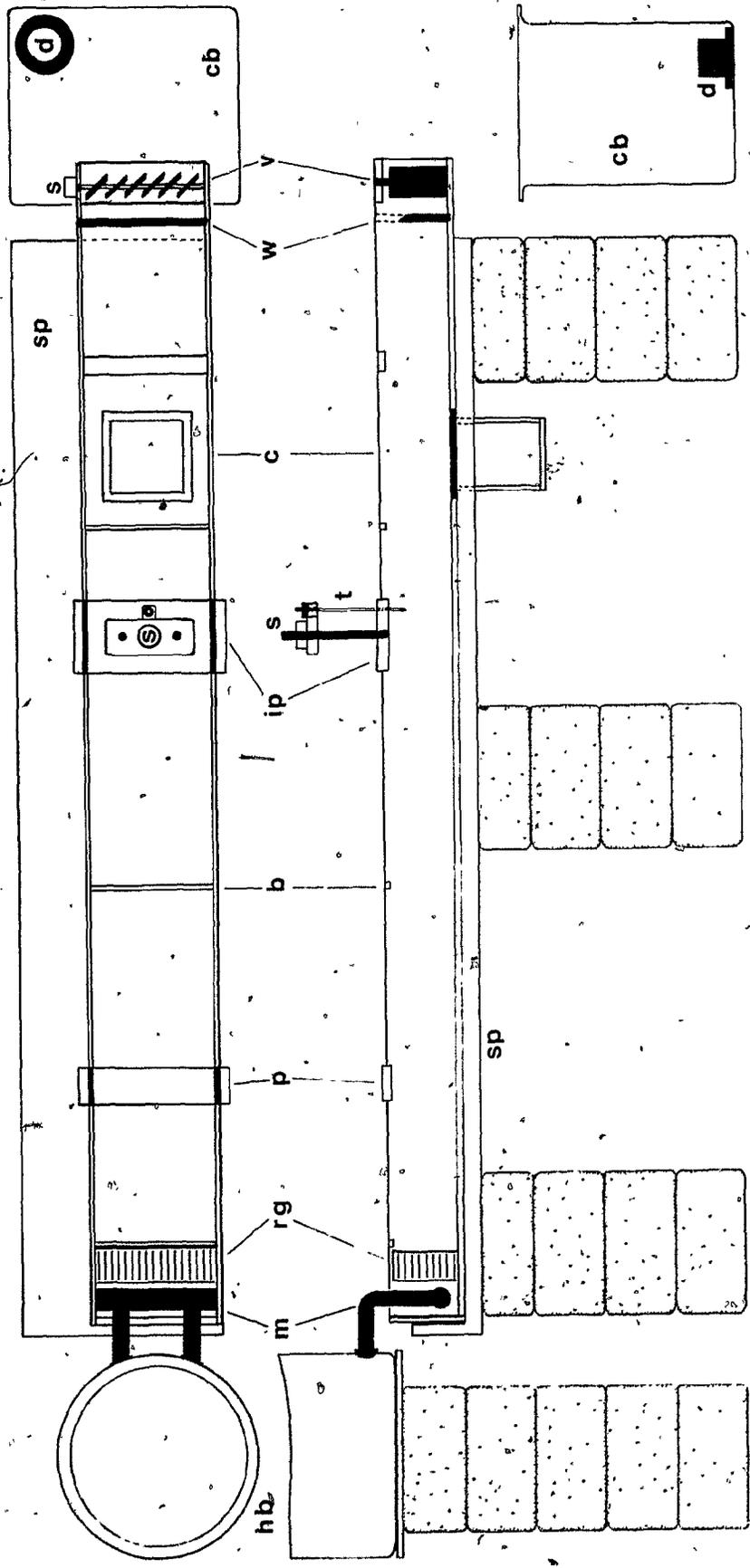
literature can be daunting. The purpose of this chapter is to provide constructive information on flume design, operation, instrumentation, methods, and measurement from a benthic ecologist's perspective. I present a newly installed flume at Dalhousie University as an example of a method that has great promise for experimental benthic ecology and that has already yielded significant results.

### Flume Design

I will use the Dalhousie seawater flume and its instrumentation to illustrate critical aspects of design and operation. Its design is simple, with basic similarities to many flumes now in use, and is compared with other configurations to evaluate their relative strengths and weaknesses.

The flume used for the present study (Fig. 1) is a flow-through channel (non-recirculating) with a 3-meter long working channel, constructed from 1/2" acrylic sheet (plexiglas). Channel width is 35 cm and maximum flow depth is 20 cm. The walls are joined to the flume bed with plexiglas solvent (dichloromethane) and caulked with a thin bead of silicon cement. Cross braces add to the support of the walls (Fig. 1). One-inch thick laminated particleboard, resting on cinder-blocks, supports the flume and provides a down-channel slope of between 1-2°. A grid of 1 cm squares placed beneath the clear flume floor aids in instrument positioning and examination of flow characteristics. An opening in the flume floor accepts a flush-mounted 25x25 cm

Figure 1: Plan and side views of the Dalhousie flume, showing the headbox (hb), manifold (m), rectifier grid (rg), moveable platform (p), channel brace (b), instrument platform (ip) with profiling stepping motor (s) and thermistor probe (t). This platform is also moveable, but is generally used in the working section of the channel. The corewell and corebox (c) are located 75 cm upstream of the sharp-edged weir plate (w) and stepping motor (s) controlled weir vanes (v). Also shown are the flume support (sp), catch basin (cb) and drain (d). Not shown are the flow control valves on the manifold and the constant head overflow pipe between the headbox and catch basin. The total channel length is 325 cm.



acrylic corebox which is used to maintain benthic organisms and sediments in the controlled flow.

From a biological point of view, it is critical that the flume materials not be toxic to organisms, that the walls of the working section be clear for observation and photography, and that the channel be open and accessible for measurements and manipulation. For the first two considerations clear acrylic sheet is the material of choice, although wooden channels with glass windows have also been used. Obvious benefits are smoothness, visibility, strength and ease of construction, especially sealing. The ease of drilling and tapping acrylic makes machining easier and allows for better fit than with other materials. Wooden flumes have also been used successfully, offering benefits in cost, but are difficult to seal, and require the mounting of glass or acrylic windows flush with the inner channel surface. Lastly, moveable instrument platforms should span the channel and at least one wall of the flume should be flush with the support to permit photography at bed-level.

Filtered seawater for the flume comes from Dalhousie's Aquatron (Balch, 1978) at a constant delivery rate of  $450 \text{ l min}^{-1}$ . This is sufficient to maintain a constant flow rate of  $30 \text{ cm s}^{-1}$  at 7 cm depth and obviates the recirculation of flume water, greatly simplifying flume design and construction. Aquatron water is filtered through sand beds before entering a 500 l capacity head-tank with an overflow pipe to maintain static pressure upstream (Fig. 1). The

inflow to the tank can be fitted with a  $62\mu\text{m}$  plankton net to remove additional particles. Water exits the head-tank through a twin-valved ABS plastic manifold, into the flume turbulence chamber. A flow-through flume which receives filtered seawater is critical in organic resuspension or deposition experiments because the flume water supply does not contribute to the particle load.

#### Entrance and exit conditions

Both the entrance and exit conditions are important to development of the flow. At the entrance the primary concern is to dissipate the large-scale turbulence produced by the pumping (or other) water supply system. The pumped water is introduced through a perforated manifold into a combination of baffle elements, called rectifier grids, just before the entrance. Flow in the flume is rectified by several thicknesses of nylon furnace baffling and a 10cm thickness of laminated industrial lighting diffuser. Any installation requires time and testing to develop an efficient combination for a variety of flow conditions. The objective is to force the flow into the channel with a uniform velocity distribution in both the lateral and vertical dimensions, allowing the boundary layer to grow with distance downstream. This can be checked using flow visualization (see below).

The exit conditions, along with supply rate and channel tilt, determine the depth of flow. The flume contains both a

simple slotted weir bracket and an articulating vaned weir, operated by a stepping motor, which allows precise positioning and good position-holding torque (Fig. 1). The vanes can be rotated in small increments. Accurate control of flow is essential when determining critical erosion velocity of sediment and detritus.

Fluid engineering texts (e.g. Roberson & Crowe, 1980; Streeter & Wylie, 1979) present equations for the calculation of flow depth for specific channel and flow characteristics. If relatively slow but deep flow is desired, it will be necessary to impede the flow at the exit. The simplest way is to use a sharp-edged weir spanning the channel, as in the Dalhousie flume, producing a "backwater effect". This forces the water to back up and flow over the weir edge, with disruption of flow streamlines for some distance up-channel. In addition, there will be a water surface "dropdown" extending upstream. Engineering texts recommend making flow measurements at least 5 weir depths upstream (Streeter & Wylie, 1979) to ensure unaltered flow. If a slotted bracket is cut into the channel walls, weirs of different heights can be inserted to maintain a specific depth of flow. A variety of alternate designs, such as articulating vanes, perforated plates or variable width slots have also been used in place of weirs. In any case, one should allow enough channel length so that measurements can be made in a fully developed boundary layer sufficiently far upstream of the exit conditions to avoid

their effects.

#### Flume geometry

In addition to the control of flow velocity, an important concern in designing a flume is boundary layer development. For the range of velocities anticipated there must be sufficient length of channel to develop a boundary layer of workable thickness. Vogel (1981) has emphasized the inverse relationship between the Reynolds number and boundary layer thickness; both he and Schlichting (1967) present formulae for this calculation as a function of downstream distance from the leading edge (flume entrance). Nowell and Jumars (1984) have discussed the implications of this for ecological work such as settling plate experiments.

In straight channels the flow is usually driven by the energy available from the water height differential between the upstream and downstream ends. This differential is often augmented by tilting the flume. For critical measurements of bed shear stress the ideal condition is for the flow to be driven by tilting so that the water depth, thus the pressure distribution, is equal along the length of the channel. This point is not of sufficient importance to biologists to warrant the trouble involved. What is to be avoided is "adverse slope", where the channel exit is above the entrance (Chow, 1959).

The fact that boundary layers develop on both the channel floor and sidewalls means that to avoid flow artifacts, channel width and wall smoothness are crucial

concerns. Calculation of wall boundary layer thickness is not straightforward, due to interactions with the bottom and the free surface. Recommendations for the ratio of flume width to boundary layer thickness (or flow depth if the boundary layer intersects the free surface) vary from 3 to greater than 10. Nowell and Jumars (1984) suggest that the ratio must be greater than 7, although most workers seem to take 5 as a minimum value. The only systematic study of flume wall effects (Williams, 1970) concluded that width had very little effect on the relationship between bulk flow and net sediment transport, but that narrow flumes produced significant artifacts in bedforms. He did not address the effect of width on the shape of the velocity profile. The 35cm width of the Dalhousie flume allows a maximum flow depth of  $>5$ cm for most work, while the 20 cm wall height allows greater depth at slower flows. Narrower flumes, especially smooth-walled ones, can still be of use but one must ensure that the bottom boundary layer has developed in an unimpeded fashion (e.g. Eckman & Nowell, 1984). Some workers (Wildish & Kristmanson, 1979, 1984) have flared the channel walls with distance downstream to provide more free bottom area, but this presents problems due to flow deceleration; the bed shear stress will change constantly down channel because the boundary layer never reaches equilibrium. This was of little concern in their work, but it should be avoided in work involving sediment transport.

### Working section

The primary concern of a benthic ecologist using flumes is to be able to maintain organisms or place intact field cores in a controlled flow. Rhoads et al. (1978) used an ingenious arrangement in a small closed-channel flume, whereby part of the channel was a removable, diver-deployed corebox. The working section of the flume constructed for the present study consists of a 25 X 25cm corewell (Fig. 1), positioned 2.25m downchannel (far enough upstream of the exit to experience undisturbed flow), which accepts an 18 X 18cm boxcore. In the field, the boxcore is inserted into the sediment, the surrounding sediment excavated, and a bottom plate secured in place with elastic bands. The corewell in the flume has an adjustable false bottom to accommodate variation in core height. Once the boxcore is in the corewell, the flume can be filled slowly allowing gentle filling of the core. At this point the sides of the box can be removed leaving an undisturbed sediment sample. This technique is ideal for work with ripples, tubes, fecal mounds, etc. The grain roughness characteristics of the core can be simulated by spreading a thin layer of ashed sediment upstream. For other studies the corewell can be covered with an acrylic plate, converting the channel into a planar bed.

### Flow measurement

#### The Theory of Near-Bottom Flow

There are two fundamental consequences of living at a solid-fluid boundary that differentiate the benthos from the

plankton. The first is the presence of a substratum providing physical support and sedimented detrital particles serving as a concentrated food source. The second is the existence of a near-bottom velocity gradient, the "boundary layer", where the drag of the bottom retards the fluid for some distance above the substratum. The velocity diminishes to zero at the substratum. Within the boundary layer, the differential velocity produces a shearing force or shear stress which resuspends and transports sediments and organisms. Differential re-deposition of particles results from hydrodynamic sorting of organic-rich and inorganic sediments. The near-bottom water chemistry, microbial environment and pore-water conditions (Berner, 1974; Jumars & Nowell, 1984; Jorgensen & Reysbech, 1985) will also reflect the effect of this shear on the bottom. The relationship between bottom shear stress and near-bottom velocity gradients is outlined in the derivation of the logarithmic velocity profile (equation 4, Chapter 1) in Appendix I.

Roughness of the boundary plays an important role in determining the shape of the velocity profile. If the bed is flat and of uniform grain size, the  $z_0$  term typically represents only roughness that affects the flow through skin friction drag, e.g. viscous forces around sand grains. This is also the easiest situation to handle in flumes. As the "roughness elements" (such as pebbles, fecal mounds, worm tubes, etc.) get larger, and farther apart they start to affect the velocity profile through form drag in addition to

skin friction. This will also be reflected in the value of  $z_0$  and the observed profile will actually be a composite of the two effects (Arya, 1975; Chriss & Caldwell, 1982; Nowell & Jumars, 1984). This complicates the calculation of bed shear stress, as it is theoretically due to skin friction alone. Local flow effects become more complex as the diversity of roughness increases, with flow separation, horseshoe vortices (Niedoroda & Dalton, 1982) and internal boundary layers (Paola, 1983, Paola et al., 1986) forming in the lee of objects. For the details of these flow patterns see Taylor and Dyer (1971) Middleton and Southard (1978), Paola (1983) and Eckman and Nowell (1984). Although individual roughness elements direct flow toward the bed and promote scour near them (Eckman et al., 1981; Eckman & Nowell, 1984), their main effect on the mean flow is turbulence farther from the bed. At certain numerical densities the interaction of the turbulent wakes of individual roughness elements causes new flow patterns to emerge (Nowell & Church, 1979).

### Methods

In the course of my flume studies, several simple, inexpensive approaches to sampling and calibration problems were developed. Some have since been superseded by more technical approaches, but the value of simplicity makes them worth considering. The simplest and most intuitively satisfying approach to quantifying fluid flow is to add dye

or discrete particles to the water and follow their paths along streaklines. The assumptions in this Lagrangian approach are that the particles have the same momentum as the fluid and, if they are small, that they are nearly neutrally buoyant. If highly turbulent flow is required, turbulent diffusion will make the markers difficult to follow in addition to requiring many more measurements to extract a reliable mean value. Several dyes (red food colour, potassium permanganate, fluorescein) have been used effectively in flow visualization but care must be taken to match the buoyancy characteristics of the dye and the fluid. Dilute solutions (or suspensions), maintained at flume water temperature are most effective.

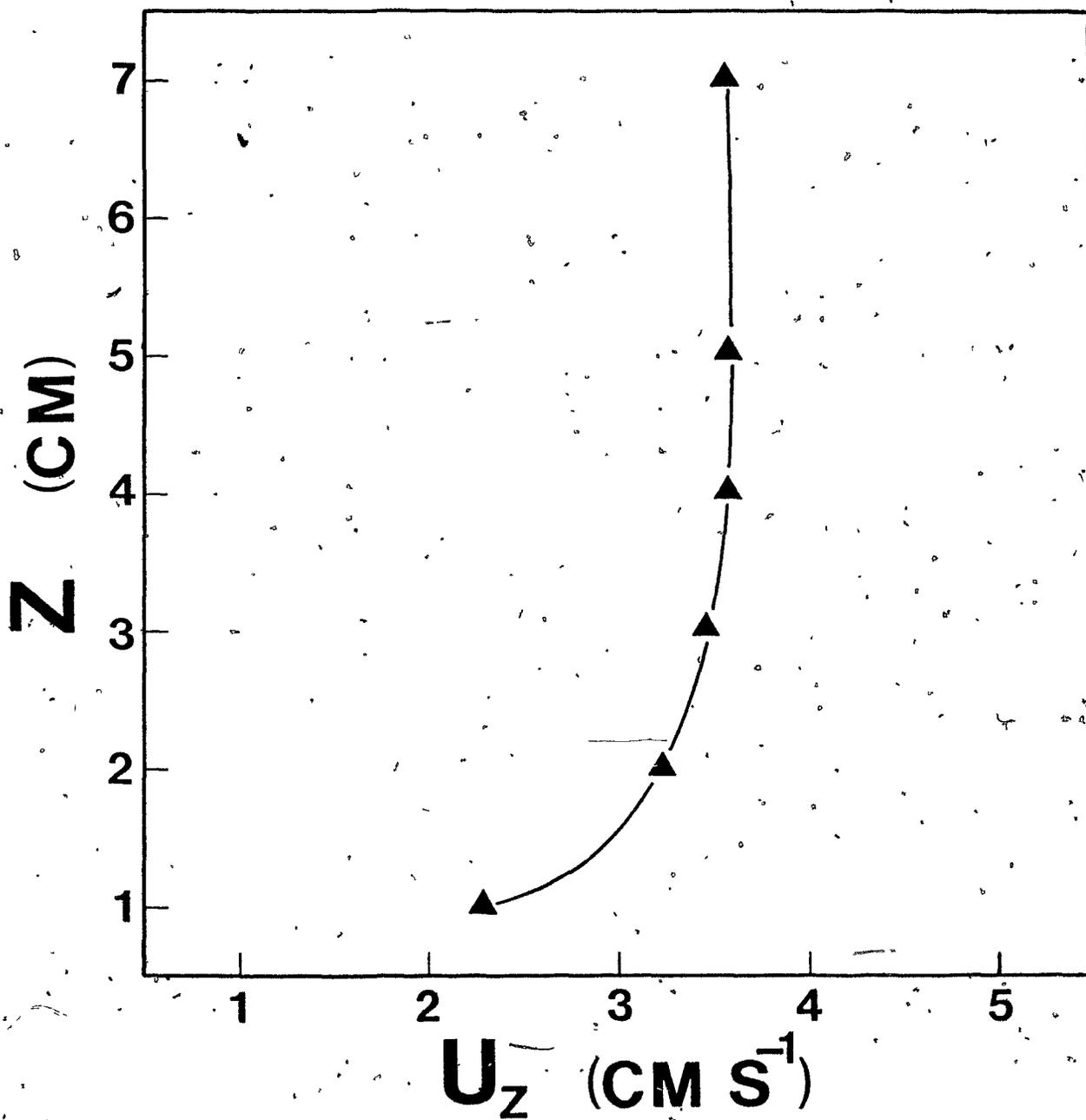
A simple arrangement for visually measuring velocity profiles involves mounting identical transparent grids on opposite sides of the flume and suspending a pipette full of dye above the center of the channel. Velocity at a particular height is measured by releasing a drop of dye just upstream of the starting mark on the grid, then timing it as it travels the length (10 or 20 cm) of the grid, ensuring that it remains at the same height. Runs are repeated until enough replicates have been obtained to give a reliable mean value. The method is tedious but accurate for mildly turbulent flows up to  $10 \text{ cm s}^{-1}$ . Care should be taken to ensure that there is no cross-channel transport. Vertical resolution depends on channel width, but it is usually accurate to within 2 mm. A typical velocity profile

taken by this method is presented in Fig. 2. The log-linear regression coefficient is 0.999 for the points in the logarithmic layer and calculations with Eq. 4 (Chapter 1) indicate that  $u_*^* < 0.05u$ , typical of fully developed natural boundary layers (Tritton, 1977).

Thermistor anemometry provides a means of quantifying flow patterns at small spatial scales (Comte-Bellot, 1976). Thermistors have a coefficient of resistance with temperature of about  $-4\% (\text{°C})^{-1}$  (Horowitz & Hill, 1980), thus their incorporation into the appropriate circuitry can be used to measure temperature and convective cooling of the thermistor element as a function of flow. Steinhart and Hart (1978) and Bennet (1981) have tested various higher-order fitting schemes for the relationship of resistance vs temperature for oceanic applications.

In the most common applications the thermistor is used as a variable element in a voltage divider or a resistance bridge. The power dissipated in the thermistor maintains its temperature at 20-40°C above that of the fluid. The thermistor's resistance is known through calculation from the circuit output. Due to variation in the thermal boundary layer around an individual sensor, each must be calibrated, paying attention to the thermistor's angular response. Glass-tipped thermistor "beads" are available in a variety of shapes, with tip diameters as small as .02 cm (Chriss & Caldwell, 1984a). Detailed reviews of thermistor anemometry can be found in Comte-Bellot (1976) and Gust (1982). Vogel

Figure 2: Profile of velocity ( $u_z$ ) vs height above bottom ( $z$ ), taken in the flume by flow visualization with dye streams. The linear regression of velocity on log (height above bottom) yields a regression coefficient of 0.999. Boundary-layer thickness in this case was 3.6 cm and  $u_* = 0.20$  cm/s. The procedure is described in the text.



(1981) provides a design for a temperature-compensated resistor bridge circuit, as well as names and addresses of suppliers. An analogous method, using a flush-mounted thermistor film, gives a more direct measure of the shear stress at the bed and has been used for measurements of localized shear stress (Paola, 1983). This must be done with care, because sedimentation quickly alters the thermal conductivity of the sensor and affects its calibration.

Although the components needed for thermistor anemometry are inexpensive, calibration can require substantial time and effort. Numerous schemes exist, from optically monitored rotating tables to variable speed lathes, to move the thermistor through still, unstratified water at a known speed. We have found that the most suitable alternative is to mount the thermistor in a pipe through which water is run at a known velocity.

This can be done either in a turbulent flow, where the pipe flow is measured by timing dye pulses (as described above) or, as Vogel (1981) has suggested, in laminar pipe flow. Vogel's method allows use of the Hagen-Poiseuille equation to calculate the velocity at the centerline from the discharge rate. The trick is to establish laminar flow in a pipe of large enough diameter that the thermistor will not impede the flow. Since the onset of turbulence is predicted classically to occur at  $Re > 2000$ , a 1" (2.54 cm) diameter pipe limits laminar flow to velocities under  $8 \text{ cm} \cdot \text{s}^{-1}$ .

Fortunately, methods for extending the range of laminar

flow are well known. It is commonly possible to maintain laminar flow up to  $Re$ 's of 12,000 using a modified version of Osborne Reynolds' pipe flow apparatus (Fig. 3), which has been incorporated into the flume laboratory. This is done by baffling the supply input to reduce turbulence, flaring the inlet of the calibration pipe and using a long enough smooth-walled acrylic pipe to develop a fully laminar profile. The flow centerline is located from the thermistor output signal, at which point the signal and discharge rate are recorded. Discharge is measured with a stopwatch and graduated glass cylinder. The procedure is repeated through a range of velocities at the same temperature as the flow in the flume.

#### Data Logging and Control

Although thermistor measurements of velocity profiles can be read from a voltmeter or strip chart recorder, it is much more convenient (and accurate) to use an electronic data logger attached to a microcomputer. A number of very inexpensive data-logging and micro-controller boards are available, most with resident versions of high-level computer languages (Basic, Pascal, etc.). The flume laboratory at Dalhousie uses an Octagon Systems (Westminster, Colo.) SYS-2A board through the serial port on an Osborne 1-B microcomputer to integrate, digitize, store and process thermistor data (Fig. 4).

Confidence in one's estimate of  $u^*$  increases with an increasing number of measurements made within the log layer

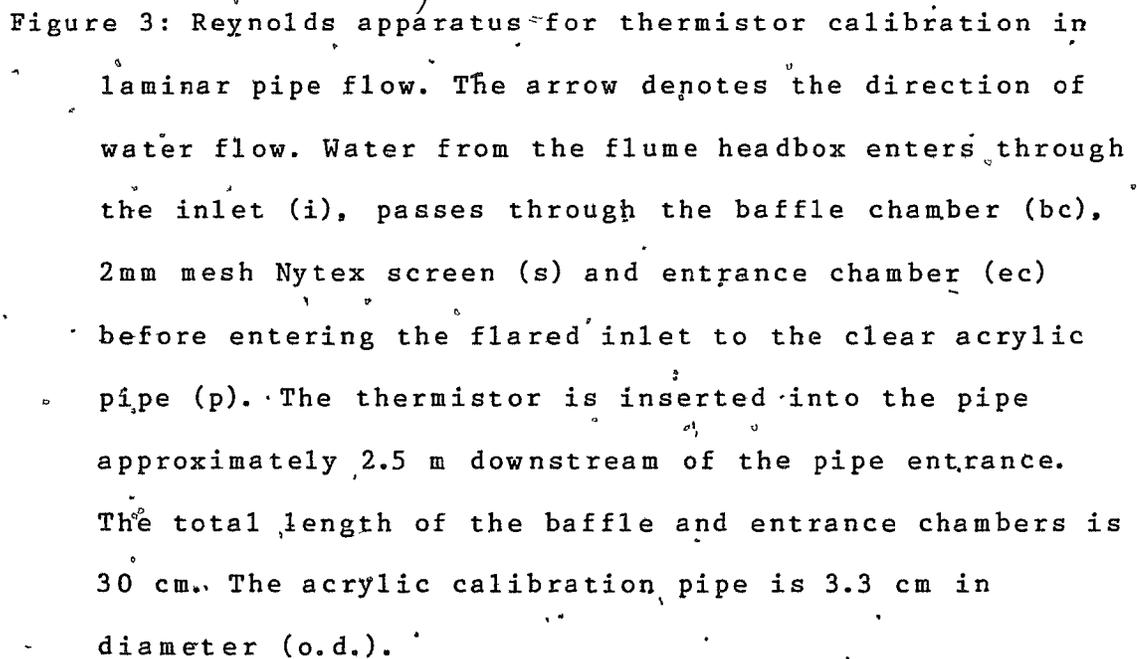


Figure 3: Reynolds apparatus for thermistor calibration in laminar pipe flow. The arrow depicts the direction of water flow. Water from the flume headbox enters through the inlet (i), passes through the baffle chamber (bc), 2mm mesh Nytex screen (s) and entrance chamber (ec) before entering the flared inlet to the clear acrylic pipe (p). The thermistor is inserted into the pipe approximately 2.5 m downstream of the pipe entrance. The total length of the baffle and entrance chambers is 30 cm. The acrylic calibration pipe is 3.3 cm in diameter (o.d.).

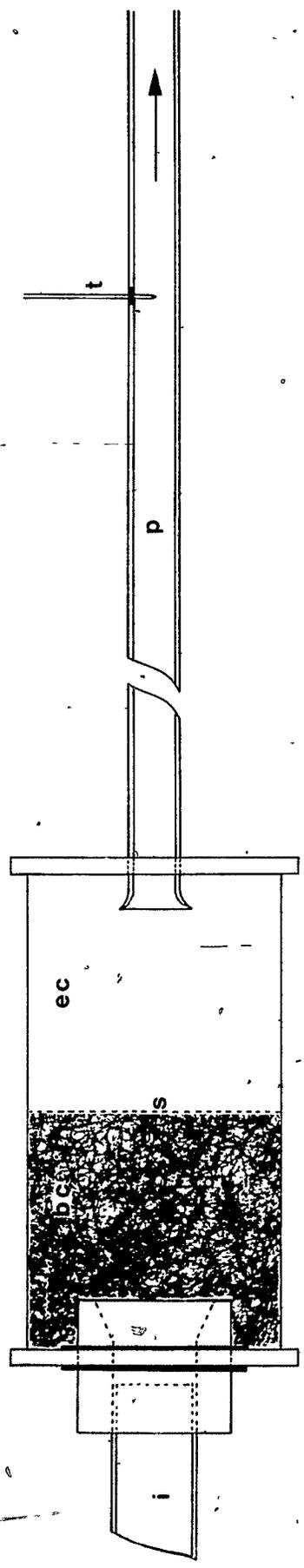
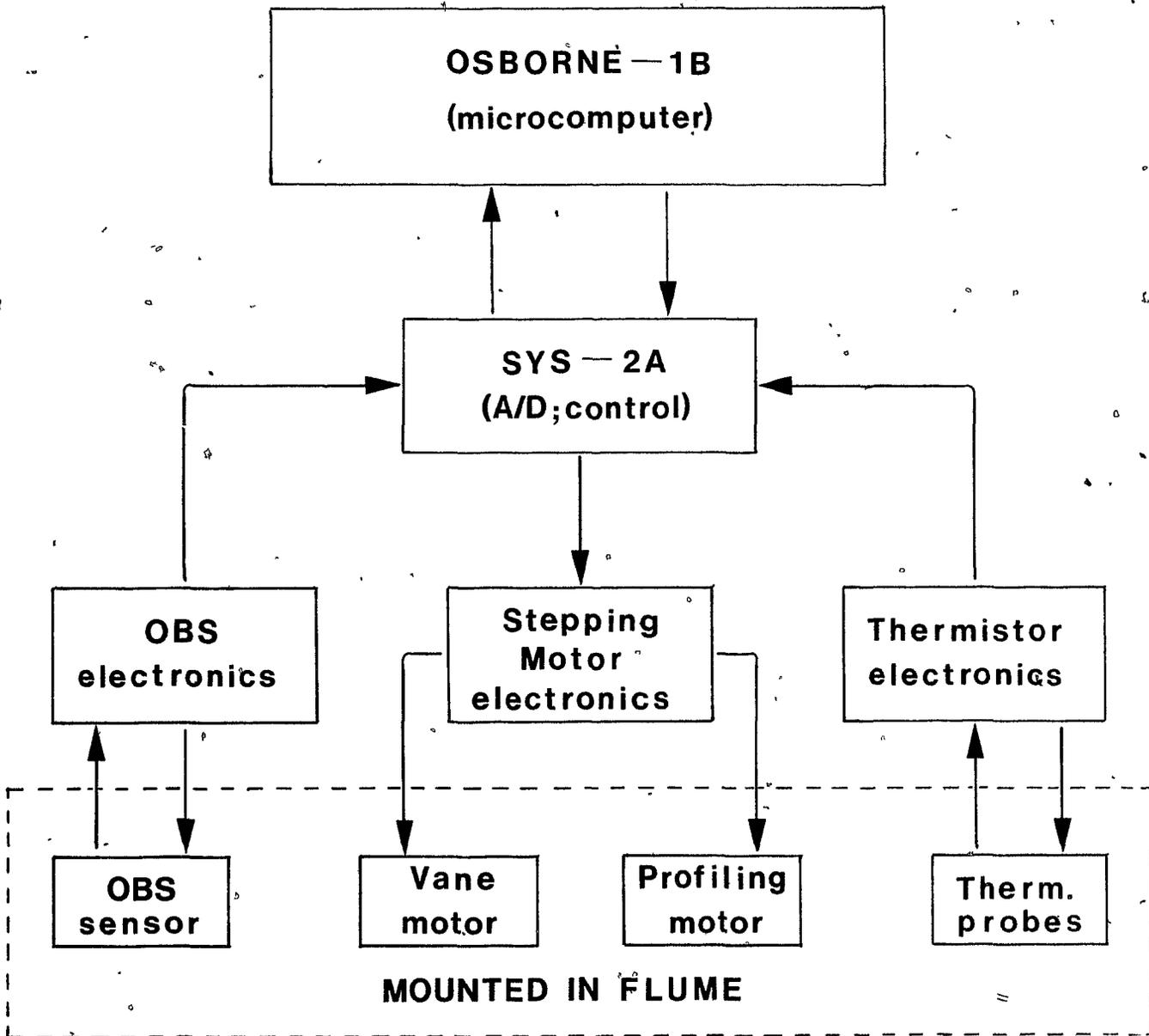


Figure 4: Schematic of data-logging and control systems used with the Dalhousie flume. See text for details of operation. A/D denotes analog-to-digital converter. OBS denotes the optical back-scatterance instrument. Arrows indicate the direction of flow of information.



(see Appendix I). In the compressed boundary layer in a flume this means making measurements at fine spatial scales. This can be done with a micromanipulator or vernier gauge. A more accurate profiling system consists of a movable carriage regulated by a lead screw and stepping motor (Fig. 4). This system allows vertical steps of 0.1mm which can be pre-programmed on the computer to produce automated velocity profiles. Some companies provide ready-to-run controller boards, although the cost is high, often twice that of the separate components.

#### Other velocity methods,

Various electrochemical techniques are available for measuring velocity, but most involve using fluids toxic to organisms (see Vogel, 1981). The most benign and widely used is the hydrogen bubble generator. The application of a 5 Volt potential to a very fine cathode wire in seawater will produce bubbles small enough to be nearly neutrally buoyant yet still be visible. Wildish and Kristmanson (1984) used this technique by timing how long it took the bubbles to fill the gap between the anode and the cathode. Other visualization techniques used with biological systems include milk and denatured egg albumin (Carey, 1983).

Mechanical methods such as miniature cup anemometers and deflection of buoyant objects have been used occasionally (Young & Southard, 1978). Neither provides good spatial resolution. A Pitot tube and manometer provide a

simple, compact system for directly measuring the dynamic pressure (stagnation pressure-static pressure) at a point in the flow. As long as the flow is uniform (parallel streamlines), steady, and there is no substantial change in surface slope between the two pressure ports, the method is direct and accurate at high flow rates. The velocity is obtained by applying the Bernoulli equation; its precision will depend on how sensitive a manometer is used.

Although fine-tipped thermistors disturb the flow relatively little, some devices are totally non-invasive. The most elegant is the Laser Doppler Velocimeter (LDV, Penner & Jerskey, 1973). Another non-invasive technique is high-speed cinematography, provided fine tracer particles (e.g. hydrogen bubbles) are already present in the flow. Using this technique in stereo photogrammetric configuration allows 3-dimensional determination of particle paths and flow but data analysis is time consuming. For a non-biological example of its application see Kent and Eaton (1982).

### **Suspended sediments**

Some problems require knowledge of the concentration of suspended particles in the flow, either as a bulk concentration or as a gradient. The equilibrium concentration profile of particles of a given fall velocity,  $w_s$ , is given by the Rouse equation (Vanoni, 1946; Raudkivi, 1976; Middleton and Southard, 1978; Nowell et al, 1981). The specific form of the equation and its relationship to the

horizontal flux of seston are presented in Chapter 3.

#### Methods

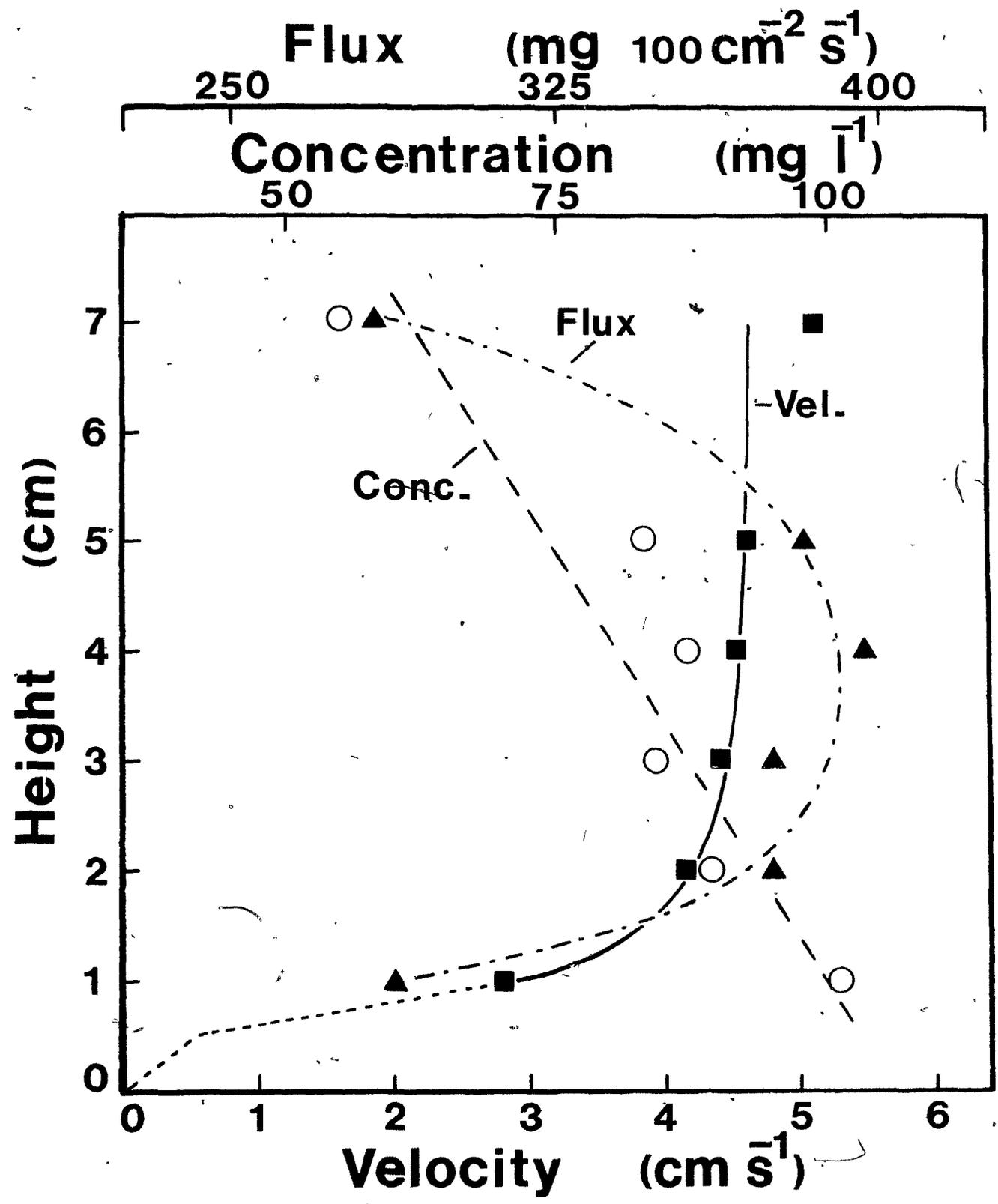
A major advantage of a flow-through flume is that particles can be introduced into the flow. Particles supplied from a carboy of concentrate (e.g. phytoplankton) are mixed into the flume manifold using a peristaltic pump. This allows upstream-downstream comparisons of particle load, studies of deposition to the bed, or determination of uptake by organisms. The most straightforward approach to sampling suspended sediment concentrations is to aim a tube into the flow and remove sediment-laden water (Downing et al, 1981; Nielsen et al, 1981; Nielsen, 1983). Although few studies (Vanoni, 1946; Wildish & Kristmanson, 1984) have attempted to match the velocity at the sampling tube ( $U_s$ ) to the velocity at that height in the flow ( $U_a$ ), large deviations from isokinetic sampling will cause serious artifacts in estimating concentration. Vanoni (1946) suggests that  $U_a > U_s$  will overbias the estimate while  $U_a < U_s$  will underbias it. However, W.D. Grant (pers. com) suggests that matching velocity at the sampling tube opening to within 50% of the ambient flow velocity will avoid serious artifacts.

A siphon sampling array has been used in the flume during this study to sample concentration gradients of natural sediments in suspension. Isokinetic sampling is maintained to within 25% of the ambient velocity, and a

constriction in the tube and conduit (teflon tubing) compresses streamlines to accelerate the flow and minimize settling in the lines. A concentration profile of natural organic-mineral aggregates obtained with this method is presented in Fig. 5, showing a substantial gradient increasing toward the bottom, as would be predicted by the Rouse equation.

Various optical devices can be used to measure suspended sediment concentration. Mounting a transmissometer on the outside walls provides a non-intrusive approach, but it suffers from sensitivity to forward light scattering by bubbles and the integration of effects across the width of the channel, including both walls. An Optical Back-Scatterance Sensor (OBS) described in Downing et al. (1981) is now a part of the flume instrumentation at Dalhousie. The back-scatterance of a small volume (1.3 ml) of water is measured at rapid rates. Due to the poorly defined back-scatter angle, Mie scattering theory cannot be applied, so the instrument must be calibrated with suspensions of the sediment being measured. The instrument is sensitive to both organic and inorganic suspensions down to concentrations of a few  $\text{mg l}^{-1}$ . It can be used to detect resuspension from cores or particle removal in upstream-downstream comparisons. Test calibrations of the OBS with glacial clays as well as beach sands yield highly linear calibration curves, but the slope and y-intercept are both sensitive to flocculation effects.

Figure 5: Vertical profiles of velocity (■), suspended particulate matter (SPM) concentration (○), and horizontal flux of SPM (▲) for a single flume experiment. The velocity and flux curves were fitted by eye. The concentration curve is a least squares regression ( $r=0.9096$ ). Water depth was 9.0 cm. Boundary layer thickness was 4.5 cm. Deviation of the 7 cm velocity point is due to surface acceleration from air conditioning currents in the laboratory. The dashed portion of the velocity curve represents the log-linear profile ( $r=0.9976$ ) extrapolated downward to the height of the calculated viscous sublayer ( $\delta_{vs1}=12\nu/u_* = 0.5\text{cm}$ ) and a linear profile extrapolated from there to the boundary.



### **Alternative methods**

More complex and expensive equipment such as the LDV which be used to measure concentrations of suspended material. Another technique used successfully to measure suspended particles is acoustic backscatter. Orr and Grant (1982) have demonstrated that this technique can detect single sand grains in suspension over ripple beds and Orr and Rhoads (1982) demonstrated its utility for profiling the top 2 cm of surficial sediments. However it requires sophisticated, expensive equipment and skilled technical help.

### **Alternative Flume Designs**

In contrast to flow-through systems, a wide variety of recirculating flumes, from small, annular channels (Taghon et al., 1984) to large "racetrack"-shaped flumes of 10 m length, have been used in biological studies. Recirculation saves water, a practical concern where large volume supplies are not available.

Driving the flow in recirculating flumes is complex. Taghon et al. (1984) used an annular channel of 1 meter radius and 10 cm width to study fecal pellet transport and breakdown. The flume was kept level and the flow was driven by the motion of a surface friction plate, in turn rotated by a hydraulic drive in a separate, inner channel. This method allows essentially infinite length for boundary layer development while not forcing the water through a pump,

which could destroy particles or organisms. Its disadvantages include the development of a surface boundary layer, complicating the flow pattern, in addition to other flow artifacts common to curved channels. Vogel (1981) presented a design for an impeller-driven recirculating flow tank which has also been used by Carey (1983). Another way of recirculating water is to use a large paddlewheel. This moves large volumes of water but does little damage to particles and organisms traveling in suspension. To minimize turbulence the paddle vanes can be articulated so the pushing surface remains normal to the boundary. Because even the simplest form of paddlewheel requires skilled construction techniques this method is usually reserved for large expensive flumes.

The main drawback common to all flumes with curved channels is the development of secondary circulation patterns. These are characteristically helical flows which violate the assumption that the log layer profile develops two-dimensionally. This makes the calculation of bed shear stresses from velocity profiles impossible. The usual remedy in racetrack-type flumes is to place baffles, by trial and error adjustment in the curved sections of channel, before the rectification step.

#### **Further Design Considerations**

In experiments at high flows (e.g. ripple migration) a flow-through flume of limited length may not have a fully developed boundary layer over the working section. Even with

fine vertical positioning of a thermistor, it may be difficult to measure enough points in the boundary layer to determine  $u_*$ . Under these circumstances, free-stream measurements may still provide a valuable indication of flow strength, even though shear stress cannot be calculated. There are many conditions under which any flume design will be limited; as long as these limitations are considered, valuable experimental results can still be obtained. Even simple observations on the behaviour of organisms and organic particles under normal flow conditions are sorely lacking in marine benthic ecology.

There are also several ways that one can augment the thickness of a flume boundary layer. A common means for doing this is by "tripping" the boundary layer. This is a technique that has long been used in studies with wind tunnels (Cermak & Arya, 1971) and it can be applied to flumes. The strategy is to use a row of roughness elements, (small stones, etc.) that span the channel and create an internal boundary layer, much like that behind an isolated roughness element (Arya, 1975; Paola, 1983). If the elements are of appropriate size and spacing and are placed near the entrance, the boundary layer will intersect the free surface at some point downstream and the flow will be fully developed from there on. The "appropriate" size and spacing will depend on flow speed and depth and must be determined by trying different configurations and measuring velocity profiles downstream. A more complex device that shows

promise is the "elliptic wedge generator" of Ligrani et al. (1979, 1983, 1985). It consists of a set of spires and a small barrier placed in the flow. Adjustment of spacing and height will affect the flow properties. The device has been successfully used to create thickened wind tunnel boundary layers with the same momentum and heat flux characteristics as in natural boundary layers.

Flow rectification has already been discussed but an additional point should be made. Depending on the configuration of diffuser material, the flow coming out the entrance may not exhibit a smooth surface. If visible surface ripples or waves are present, they should be damped out to minimize their interaction with the walls. This is most easily done with a short length of thin plastic or rubber sheet attached to the entrance which is allowed to trail several centimeters downstream on the surface.

#### **Flume Application**

Although simple in design, the flume designed and constructed for the present study has been used for studies involving both bedload and suspended load transport of organic detrital particles, as well as the stabilizing effects of microbial films in binding surface sediments.

Grant et al. (in press) used the flume to control flow over cores taken from Eastern Passage, Halifax Harbour. The experiments showed several characteristic stages of

erosional transport, explaining how bedform migration could account for the small-scale patchiness of algal films observed in the field. SEM micrographs of natural and flume samples showed the binding effect of microbial extracellular exudates (from diatoms) and changes in sediment microtopography after erosion. Comparison of biogenic binding effects on calm and stormy days indicated that the films have a significant effect on the exchange of organic matter between the sediment and the water column. These studies are continuing with bacterial films.

Experiments presented in Chapter 3 assess the role of the horizontal flux of organic particles in the ecology of benthic suspension feeders. Modelling the vertical profile of particle flux indicates that, depending on the relation of particle settling velocity, shear stress and roughness, the height at which maximum horizontal flux occurs may be the bed surface or several centimeters above it. Flume experiments with natural sediments show the same pattern, when flux is calculated from the product of measured profiles of velocity and sediment concentration (Fig. 5). At high flow rates, suspension feeders must extend farther into the water column to maximise their food intake. Work presented in Chapter 4 assesses the diet of a suspension-feeding spionid polychaete (Spio setosa) subjected to changing regimes of flow and particle concentration.

### Summary and Conclusions

Flumes are essential tools for the quantitative study

of biologically important boundary-layer processes. Binding by biofilms and erosion by tube-wake turbulence are only two important biological effects on sediment transport that have been elucidated in flume studies. Small-scale feeding studies as well as horizontal organic flux and the growth of organisms are easily controlled and measured in flow channels. These problems, along with many other studies of primary importance in quantitative marine benthic ecology, are amenable to imaginative new applications using flumes.

The simplest design, that of a straight, flow-through channel, is ideal for studies of erosion and deposition of organic particles. Losses from or additions to natural core samples can be followed easily by changes in concentration in the sediment and water column. When long particle residence times or "infinite" bottom length are required, recirculating designs may be useful, but caution must be taken to account for secondary circulation patterns.

Simple devices are available to measure velocity and suspended sediment profiles. Although time-consuming, they are direct and require no calibration. Inexpensive technological means for velocity measurement and sensor positioning are available, but they require more time to set up and calibrate. Their advantages are greater precision and ease of use.

Because the boundary-layer must develop, a channel of sufficient length is required if bed shear stresses are to be calculated from velocity profiles. Often, the design of

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the flume channel will be a compromise between length, available space, and cost. Even relative measures of flow may be appropriate for certain experiments, especially when they are combined with behavioural observations. One may also employ various tricks to create thick boundary layers in relatively short lengths of channel.

As long as the appropriate dimensional scaling holds between the laboratory and natural environment, and the operator remembers that he or she is creating a model of the natural system, flumes allow unique opportunities to study benthic processes. Their potential utility in the study of physical processes in benthic ecology is undeniable, largely because natural flows are complex and difficult to study in the field, even with a battery of expensive and sophisticated equipment. Flumes offer the opportunity to make detailed observations and measurements while controlling the speed with which water moves through the system, the turbulent stress exerted by the fluid on the bottom, as well as the particle load. Important questions of large-scale detritus transport and small-scale (organism sized) food availability are best addressed with this experimental tool. The measurements may be as simple or complex as required, but they are repeatable and well characterized, unlike the situation in the field. Increasing use of this technique will continue as benthic ecologists become more aware of the importance of horizontal advection in marine ecosystems.

CHAPTER 3

The Dynamics of Near-Bed Seston Flux  
and Suspension-Feeding Benthos

## INTRODUCTION

Few subtidal benthic marine environments attain rates of in situ primary production sufficient to fuel the observed community metabolism. Benthic detritivores are generally forced to rely on advective sources for their food supply (Miller et al., 1984; LaBarbera, 1984) and thus are dependent on the fluid medium for transport of this material. Benthic suspension-feeders are especially adapted to the forces of drag and shear encountered in the benthic boundary layer. Although these fluid forces disperse particles and create local gradients in velocity and concentration, prior considerations (summarized in LaBarbera, 1984) of suspension-feeding have made the tacit assumption that the organisms take their ration from an essentially homogeneous medium. This idea may stem from the extensive study of pelagic filter-feeders which feed in an environment where, at local scales, the concentration of food particles is considered to be uniform. Another legacy of the attitudes developed from plankton research is the assumption that there is little or no differential transport of the predator and prey items - that they are both suspended in, and subject to, the same fluid forces. The last point illustrates a fundamental difference in the physical nature of the benthic and pelagic environments. Suspension-feeding organisms anchored in the bottom may take advantage of vertically settling material but primarily feed on seston flowing horizontally past them. Warner (1977) has

shown how the shapes of their feeding structures are often adapted to local current conditions.

Recent attention to the ecological significance of the benthic boundary layer (McCave, 1974; Vogel, 1981; Nowell & Jumars, 1984) has pointed out that the near-bed region is one of strong vertical gradients of flow velocity and particle concentration. The significance of this physical regime has been examined in light of the reciprocal effects of organisms, sediments and fluid acting to determine the grain characteristics of the bed (Nowell et al., 1981; Eckman et al., 1981; Eckman & Nowell, 1984; Grant, 1985; Grant et al., in press). The consequences for deposit feeding benthos have been examined in terms of substrate stability (Eckman et al., 1981; Jumars et al., 1981), but also in terms of the lateral transport of food particles to an essentially sedentary fauna (Jumars & Nowell, 1984; Miller et al., 1984). This represents a shift from an earlier orientation that assumed an exclusively vertical supply of organic materials (Rowe & Smith, 1977; Honjo et al., 1982) to the benthos. The processes that laterally distribute and sort the material falling out of the water column are now seen to be as important as vertical settling in determining the availability of this material as food.

In this chapter I describe and analyze the horizontal flux of organic and inorganic particles in the near-bed (0-10 cm) region, and its significance to suspension-feeding benthos. I use an analytical approach to the hydrodynamics

of particle flux and apply it to flume experiments using natural sediments. Finally, the feeding ecology of a tube-dwelling polychaete, Spio setosa, is examined in light of the predicted flux profiles.

#### Suspension-Feeding Benthos:

I will consider here only those organisms classed as "passive suspension feeders" (sensu Warner, 1977; LaBarbera, 1984), but the general approach will have relevance to all benthic suspension-feeding organisms. Many organisms, previously considered as uniquely deposit-feeding, are now known to take at least some portion of their ration from suspension. The common tellinid bivalve, Macoma balthica, takes over 50% of its food by suspension feeding (Hummel, 1985) while spionid polychaetes (Taghon et al., 1980; Dauer et al., 1981; Dauer, 1984), dendrochirote holothurians and ophiuroids (LaBarbera, 1984) have been observed using their appendages to intercept suspended particles traveling past them, although the behavioural demarcation between suspension- and deposit-feeding may be problematic, as in some Amphipoda (Mills, 1967). Nevertheless, there is mounting evidence that many macrobenthic species may at some time take part of their ration from suspension.

As I mentioned in Chapter 1, Rubenstein and Koehl (1977) concluded that direct interception and inertial impaction were the two most important mechanisms for particle capture used by marine seston feeders. LaBarbera

(1984) supports this contention. Taghon (1984) used scaled models to look at palp orientation in spionid polychaetes as a function of the Reynolds number of the flow. He concluded that the feeding responses of spionids are adaptive and are the most efficient possible under given flow conditions. Again, this analysis assumes a uniform suspension of particles. Inertial impaction relies on there being a difference in the densities of the particle and the fluid medium. The density difference between seawater and most organic particles in suspension is so small that the particles essentially follow streamlines and tend to be diverted with the flow around a single filter element. The greater mass and inertia of the inorganic fraction means that they are less likely to be diverted, serving to increase their effective capture. Thus the hydrodynamics of filtering may work against optimal capture of organic particles in a complex suspension. Any behavioural adaptation that may minimize this effect should confer an advantage.

Experimental studies of the food supply to suspension-feeding benthos have looked both at the mass transport of seston (Wildish & Kristmanson, 1979, 1984) and at changes in particle trajectory (Carey, 1983) caused by turbulence near the seabed. Wildish and Kristmanson (1979) considered the vertical flux of material, augmented by near-bottom turbulence. Their concern was with large-scale effects acting on populations. They did not consider the vertical

structure of the velocity or particle concentration fields, or their effects on differential horizontal transport of seston.

Vertical structure is important because it is the product of the velocity and particle concentration fields together that determine the flux of material past an organism suspension-feeding at the sediment-water interface. The shape of the flux profile determines whether the greatest flux of edible particles occurs close to the bed or somewhere above it. Consideration of concentration alone can be misleading; it must be recognized that the interaction with the near-bed current regime determines the availability of these particles to benthic organisms. Particles that settle at different rates will also behave differently in a given flow. It is possible that hydrodynamic sorting will result in the horizontal flux of suspended sand grains being greater slightly closer to the bed than the flux of suspended large diatoms. A suspension-feeder able to reach the extra centimeter or two into the water column would thus increase the quality of its ration.

To investigate the specific form of the flux profile over a range of flow conditions, I developed a model based on the theoretical equations for two-dimensional velocity and particle concentration profiles.

#### **MODEL DEVELOPMENT**

##### **Analytical:**

Dimensionally, the horizontal flux of suspended

particulate matter is defined as the Mass per unit Time per unit Area, with area in coordinates normal to the axis of flow. Thus flux is equivalent to the product of velocity and concentration. As we are concerned only with advective, and not diffusive processes, time-averaged measures of the velocity and concentration profiles can be used to calculate the average flux profile. Theoretical formulations exist to predict both of these quantities as a function of the flow, bed roughness and particle fall velocity. This allows us to derive an analytical model of how the horizontal flux profile should vary under changing conditions.

#### Velocity:

The Karman-Prandtl formulation of a logarithmic velocity profile was presented in Chapter (1) as Equation (4). The slope of the velocity profile, and the shear-generated turbulence in the boundary layer, is expressed by the shear velocity,  $u_*$ . For a more thorough explanation of these terms the Appendix, as well as Middleton and Southard (1978), Nowell and Jumars (1984), or Tritton (1977). For the sake of analytical tractability, the existence of a viscous sublayer very close to the bed will be ignored. If present, it is generally less than 1 cm thick, so that its effect on this analysis is minimal.

#### Concentration:

Rouse (1937) first formulated a theory for the vertical distribution of sediment in suspension. Detailed explanations may be found in Vanoni (1946), Raudkivi (1976) and Middleton

and Southard (1984). It expresses the sediment concentration,  $C_z$ , at a height  $z$  above the bed in terms of the ratio of the fall velocity of the sediment,  $w_s$ , to the friction velocity,  $u_*$ :

$$C_z = C_a \left(\frac{a}{z}\right)^p \quad (5)$$

where  $C_a$  is a reference concentration at height  $a$  above the bed and the exponent  $p$ , referred to as the 'Rouse Number', is the ratio of  $w_s$  to  $u_*$ :

$$p = w_s / ku_*$$

The flux profile may then be expressed as a function of height above the bed:

$$F_z = u_z \cdot c_z \quad (6)$$

Substituting equations (1) and (3) for  $U(z)$  and  $C(z)$  we obtain:

$$F_z = C_a \left[ \left(\frac{a}{z}\right)^p \cdot \left(\frac{u_*}{K} \ln \frac{z}{z_0}\right) \right] \quad (7)$$

Taking the derivative and setting it to zero yields an expression for the height of the flux maximum for a given sediment in a steady, uniform flow:

$$\frac{\partial F}{\partial z} = \frac{1}{z} \left(\frac{a}{z}\right)^p - \frac{p a}{z^2} \ln \frac{z}{z_0} \left(\frac{a}{z}\right)^{p-1} = 0$$

$$z_{\max} = z_0 \exp\left[\frac{1}{p}\right] \quad (8)$$

Numerical:

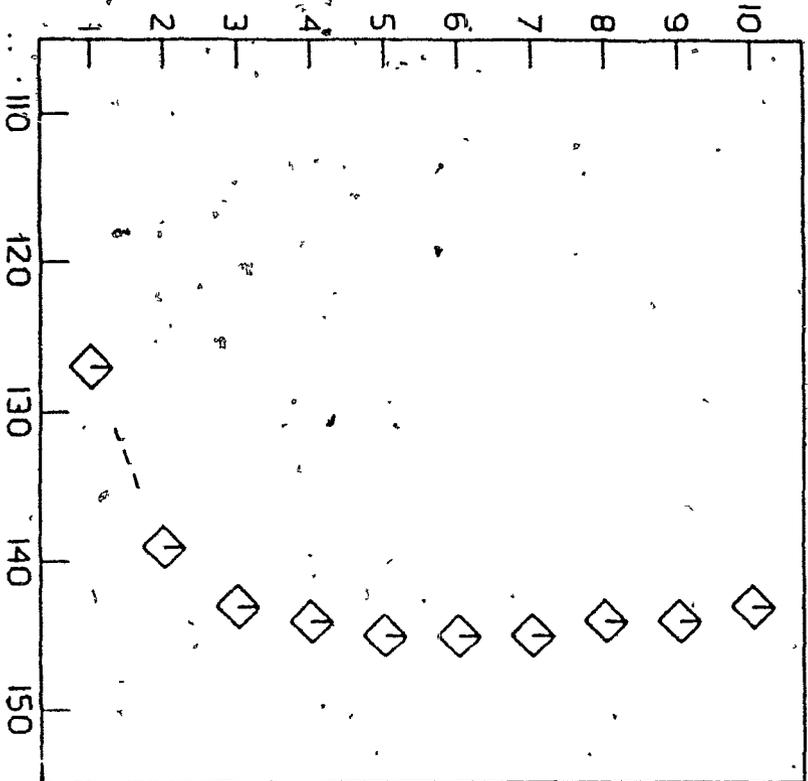
A different approach involves taking the derived expression for the flux profile (Equation 7) and examining it for a large range of  $u_*$ ,  $w_s$  and  $z_0$ . Fig (6) shows a typical plot of the flux profile.

The specific shape of the flux profile is dependent on the vertical range modelled. Indeed, the flux will always ultimately decrease with height as seston concentration decreases outside of the boundary layer and the velocity profile becomes uniform. I am concerned here only with the near-bed region, somewhat arbitrarily defined as the ten centimeters immediately overlying the bed. This is the region of greatest relevance to the feeding of estuarine suspension feeders.

To determine the conditions under which the flux profile a) increases toward the bed, b) increases away from the bed, or c) is relatively uniform within the near-bed region, the skewness ( $\gamma_1$ ) was calculated for each profile modelled. Profiles where the flux decreases with distance from the bed ("bottom heavy") exhibit a  $\gamma_1 > 0$ , those with the flux increasing with distance from the bed ("top heavy") are characterized by a  $\gamma_1 < 0$ . Fig. (7) shows the results of this analysis plotted in parameter space. The curve describes the combinations of  $u_*$ ,  $w_s$  and  $z_0$  for which  $\gamma_1 = 0$ , i.e. where the

Figure 6: Model profile of the vertical gradient of horizontal seston flux. The parameter values used are:  $z_0=0.1$  cm,  $u_*=0.20$  cm s<sup>-1</sup>,  $w_s=0.02$  cm s<sup>-1</sup> and  $p=0.25$ .

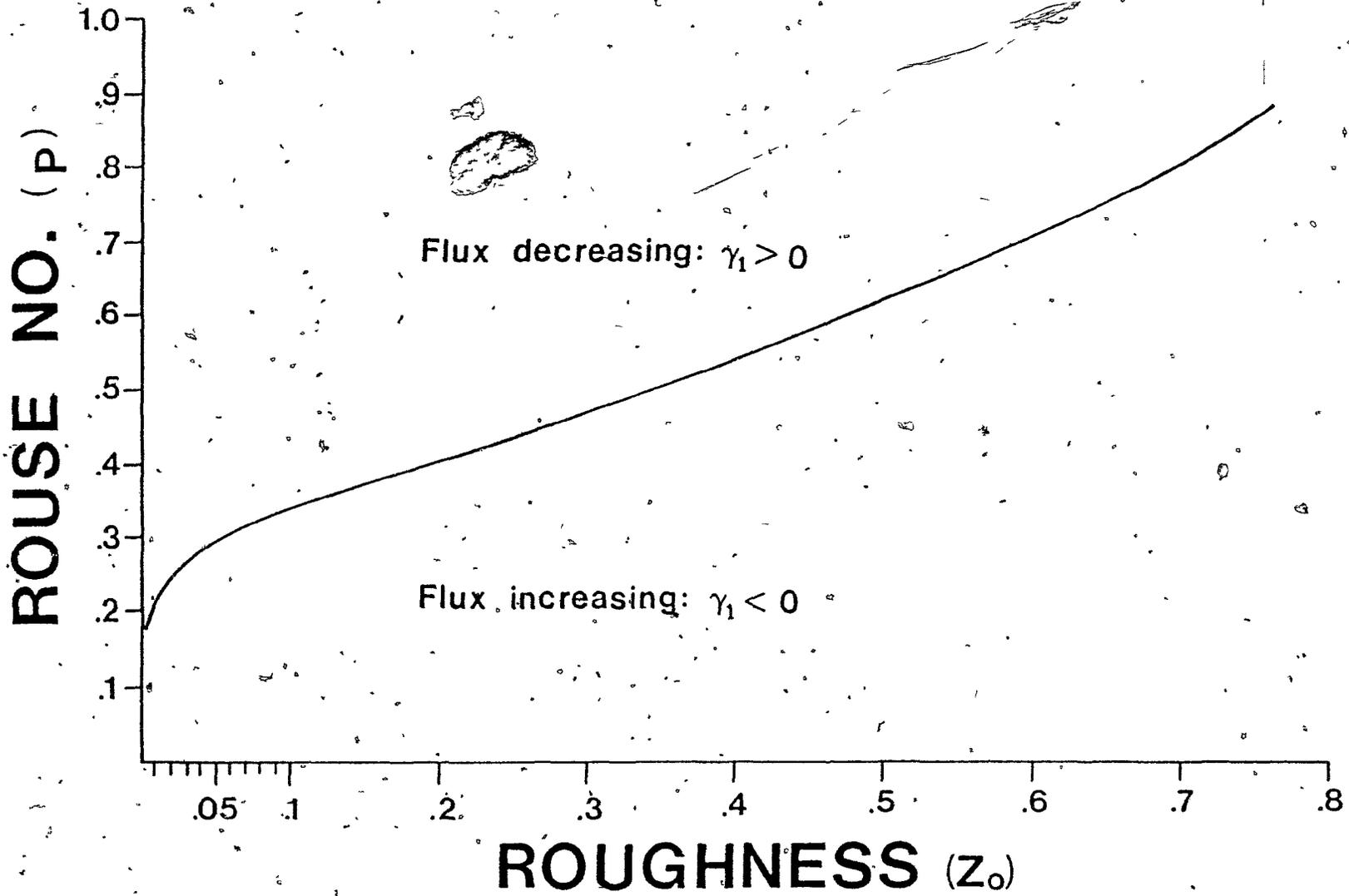
HEIGHT (CM)



FLUX

Figure 7: Parameter space plot of zero skewness isopleth.

Skewness describes flux profiles calculated from Equation (5) and indicates whether the flux increases ( $\gamma_1 < 0$ ) or decreases ( $\gamma_1 > 0$ ) with proximity to the bed.



flux profile is uniform. The range of the Rouse No. examined here is well below the critical value of 2.5, which defines the theoretical change from suspended to bedload transport (Middleton & Southard, 1978). Thus we are considering only sediment in suspension. The result shows that, over the range of  $p=0.2$  to  $0.9$  and  $z_0=0.01$  to  $0.75$  cm there is a transition from "bottom-heavy" to "top-heavy" flux profiles. At lower values of  $p$  the flux maximum is above the bottom; this is in fact generally true for cases where  $w_s < 10u_*$  i.e. for particles of relatively low specific density. The effect of increasing the roughness of the bottom is to increase the value of  $p$  at which the flux maximum will be found above the bed. Thus, as the bed gets rougher, heavier fractions of the sediment will have flux maxima above the bed.

Particles of different settling velocities, when exposed to the same flow, will be subject to hydrodynamic sorting. Equation (8) predicts that, in a seston mixture composed of mineral grains, organic-mineral aggregates (OMA's), plankton and resuspended benthic microalgae, denser particles will exhibit flux maxima closer to the bottom than the less dense fractions. This also represents a sorting of potential food particles of differing quality. Under these conditions, a benthic suspension-feeder will gain an energy advantage by increasing the height above bottom at which it feeds. If a suspension-feeder increases the organic portion of its ration by reaching another centimeter or two into the water column, the energetic cost of building and maintaining

a tube may well be repaid.

## METHODS

### Laboratory Experiments:

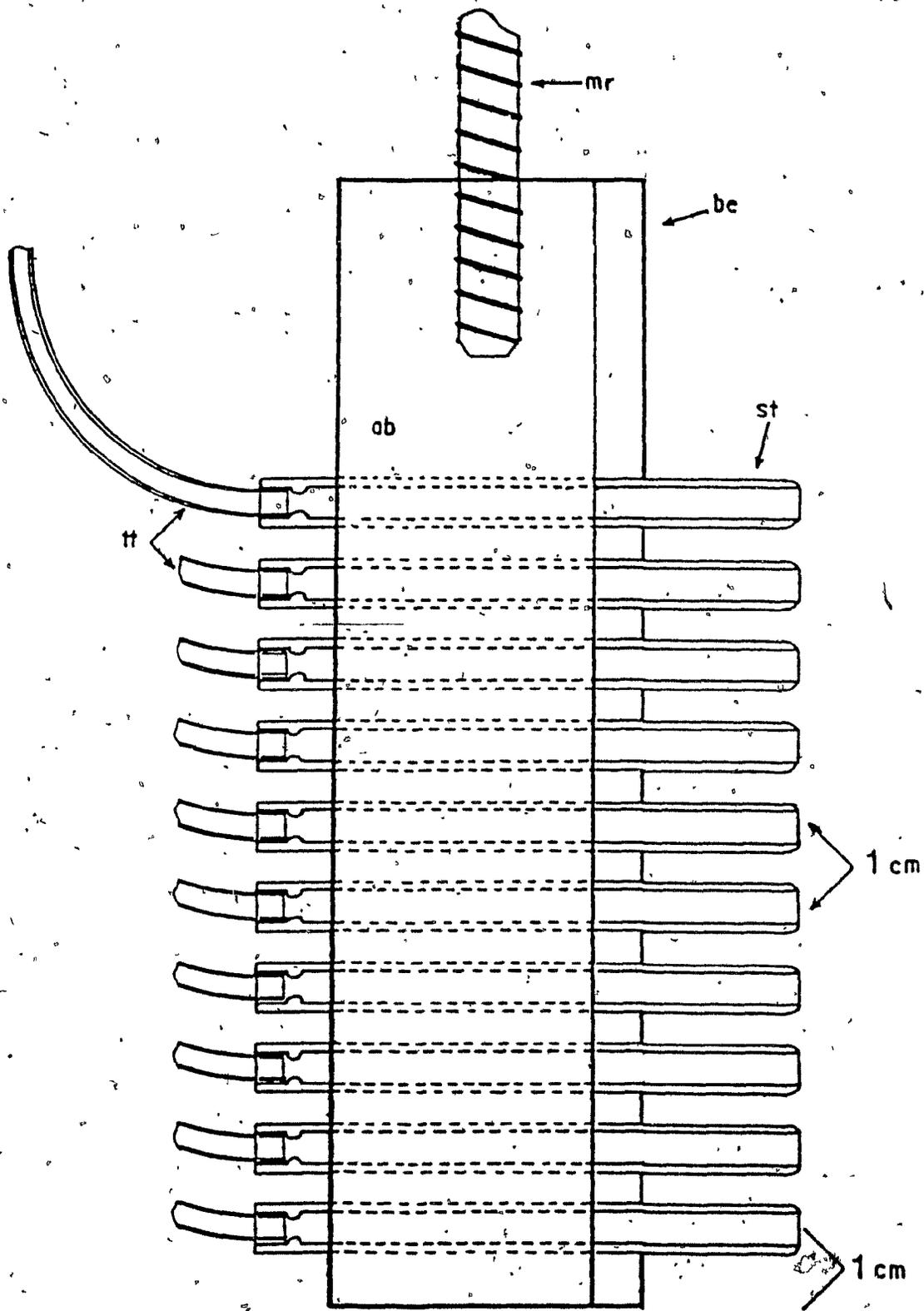
The experiments were run in the Dalhousie seawater flume, described in Chapter (2). Filtered seawater from the Dalhousie Aquatron was mixed with concentrated suspensions of seston (described below) pumped into the flume manifold. Flow velocities were determined in two ways. At low velocities ( $<10 \text{ cm s}^{-1}$ ) dye pulses at discrete heights above the bottom were timed along a 10 cm path (see Chapter 2). A Thermometrics FP-14 thermistor in a bi-polar voltage divider provided fine-scale velocity resolution while a separate thermistor circuit measured the water temperature.

Thermistors were temperature calibrated using the fitting scheme of Steinhart and Hart (1968). Velocity calibrations used a pipe flow method, suggested by Vogel (1981), in the apparatus described in Chapter (2). An Octagon Systems SYS-2A microcontroller in series with an Osborne-1B microcomputer provided data logging and A/D conversion. Only experiments where the boundary-layer was fully developed were used for analysis. The criterion for full development was taken as a value of  $u_*$  (calculated from the measured velocity profile) less than or equal to 0.05 times the free-stream velocity. This is typical of observed natural boundary layers (Tritton, 1977).

Seston concentrations were sampled at six heights (1-5, 7 cm) using the apparatus shown in Fig. (8). The design

Figure 8: Seston sampling apparatus used in flume

experiments. The tube array is suspended by a machined rod (mr) attached to an instrument platform (see Figure 1, Chapter 2) spanning the flume. The acrylic block (ab) with a leading beveled edge (be) supports glass sampling tubes (st), centered 1 cm apart. Clear Tygon tubing (tt) runs from the sampling tubes to the collection jars (not shown).



agrees with suggestions put forward by the Inter-Agency Committee on Water Resources (1941). Glass sampling tubes of 0.55 cm diameter were mounted in an acrylic block. The leading edge of the block was beveled and the block was suspended in the flume by a machined rod attached to one of the instrument platforms that span the flume. To ensure isokinetic sampling, velocities at the inlet of each sampling tube were adjusted, by a Hoffman clamp on the Tygon tubing, to match the flow at that height above the bed. In practice the sampling velocity was set to 25% above ambient to minimize settling in the Tygon tubing that carried the sampled water to the six collection jars. A constriction at the rear of each glass tube further accelerated the flow into the smaller diameter Tygon tubing. These measures worked well to minimize settling in the lines, although the lines were always rinsed into separate jars at the end of a flume run, and treated as all other samples (see below). Only the slowest flume flow rates (free-stream velocity  $< 1.0 \text{ cm s}^{-1}$ ) resulted in settling that required correction, and then only for the 1 and 2 cm samples.

Samples were filtered through pre-combusted Gelman AE glass fibre filters ( $1 \mu\text{m}$  nominal pore diameter), rinsed with filtered seawater and dried at  $60^\circ\text{C}$  for 48 hours before weighing. Filtered seawater blanks were used to correct for salt retention. Samples were also ashed at  $500^\circ\text{C}$  for 12 hours for bulk organic matter determinations.

### Natural Sediments:

To determine the concentration and flux profiles of a natural seston, sediment was scraped from the top 3mm of a fine sand flat at Eastern Passage, N.S., and returned to the laboratory. The flat receives high organic loading from Halifax Harbour and is also characterized by a dense infauna, the most conspicuous members being Mya arenaria and S. setosa. Gentle resuspension in filtered seawater and decanting through a 250  $\mu\text{m}$  sieve provided a concentrated suspension. During an experiment stirring kept the suspension even and prevented time-dependent changes in concentration in the flume flow. This was tested by placing an Optical Backscatterance Sensor (OBS, see Downing et al., 1981) at a fixed height in the flow. OBS output remained constant over an hour-long experiment, indicating a concentration of  $61.3 \text{ mg l}^{-1}$ . (calibration  $r^2 = 0.98$ ).

Due to length limitations of the flume, flow rates had to be kept low. This was done both to ensure a fully-developed boundary layer and to allow enough residence time, for the seston distribution to reflect the hydrodynamic conditions. With an estimated effective settling velocity of  $0.14 \text{ cm s}^{-1}$ , 50 s residence time would be required for the sediment to "clear" from a 7 cm water depth. With 250 cm of channel length available, the maximum flow rate that allows this much residence time is  $5 \text{ cm s}^{-1}$ . Thus four experiments were run at  $u_*'$ s ranging from 0.1 to  $0.24 \text{ cm s}^{-1}$  (approximately  $4.9 \text{ cm s}^{-1}$  maximum free-stream velocity). To

fully adhere to the "equilibrium" seston distribution of the Rouse equation, a channel length of 15 to 20 meters would be required. These experiments approximate the short-term response of the sediment-water system to upstream resuspension. Given the dynamic environment characteristic of shallow estuarine environments (distributed roughness, bioturbation), the experimental conditions may be more representative than an idealized "equilibrium".

An additional experiment was run at  $u_* = 0.22 \text{ cm s}^{-1}$  to collect samples for SEM analysis. Sampling tubes were run directly into a filter manifold and filtered onto Nuclepore 1 micron polycarbonate filters, fixed and carbon coated and viewed on a Cambridge Autoscan Scanning Electron Microscope at the Bedford Institute of Oceanography.

#### Field Studies:

S. setosa, obtained from Eastern Passage, were dissected to obtain gut samples of recently ingested material. The animals were removed from their tubes as the tide went out, narcotized in 6%  $\text{MgCl}_2$  and returned to the lab within one hour. The foregut region (approximately 60 setigers after the pharynx) was dissected and the contents perfused with filtered seawater. Samples were stored in 1% formaldehyde at 4°C until analysis.

Samples were filtered onto Nuclepore polyester filters (1  $\mu\text{m}$  pore diameter), cleared with glycerol and examined at 200X under a Zeiss light microscope. 30 fields were counted for the particles in the categories listed in Table (1).

Only samples that yielded >100 particles in 30 fields were used for analysis. Some samples were treated with Hetzberg's Iodine stain after a brief acid hydrolysis. The polychromatic stain is specific for chitin, cellulose and carbohydrate, allowing differential recognition of OMA's and gut lining sloughed off during the perfusion.

In addition to S. setosa gut contents, samples of the ambient surficial sediment were taken from Eastern Passage. A modified 1 cc syringe was used to core the top 3mm of sediment. Samples were placed in plastic scintillation vials and preserved with 1% formaldehyde at 4°C. Prior to filtration the samples were briefly shaken, allowed 10 seconds to settle and decanted. Due to the amount of material present, only 15 1/4-fields were counted from each sample. Other details of analysis were the same as for the S. setosa gut samples.

Although it may be misleading to try to characterize a poorly sorted sediment by a single fall velocity, the concept of "effective fall velocity" has been applied to estuarine sediments by Krone (cited in McCave, 1979). An effective fall velocity of 0.14 cm/s was established for the Eastern Passage surficial sediment after settling trials in a 20cm column in a cold room at 6°C (to match flume conditions) and agreed well with the value of 0.15 cm s<sup>-1</sup> determined by Krone's method (see Chapter 4).

An in situ record of suspended particle concentration and S. setosa's feeding response was obtained during a

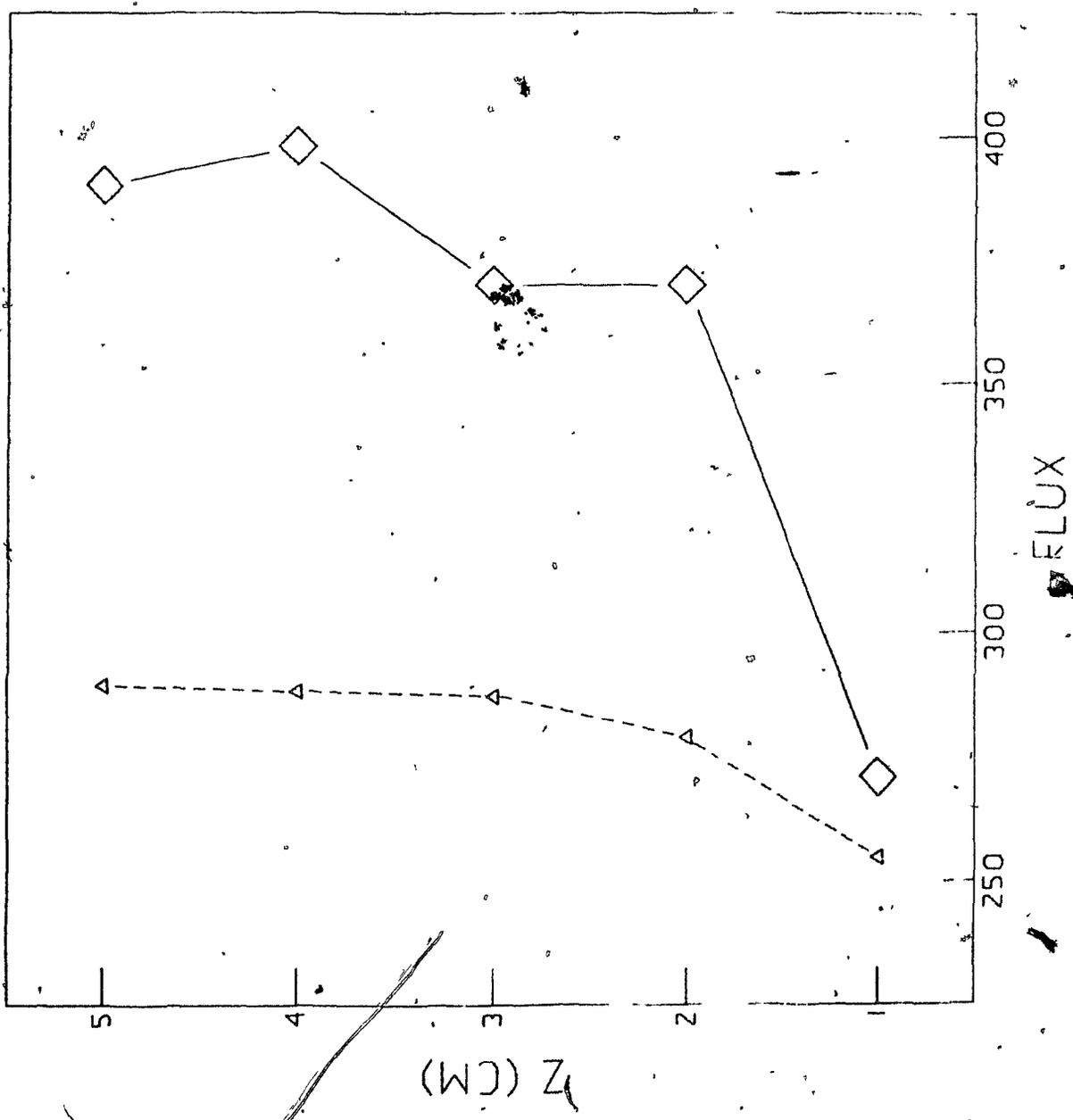
single tidal cycle, using a Benthos Instruments plankton silhouette camera. The instrument consists of a 35mm camera and data chamber in line with a collimated strobe, separated by a 4cm-wide aperture. The aperture is flooded with ambient water and particles. The camera is usually suspended in the water column and triggered on a pre-programmed schedule. For this work, the camera was equipped with a remote triggering control allowing a variety of sampling schedules as well as single shot control. The camera was placed in the sediment, with several S. setosa tubes centered in the aperture and aligned with the predominant longshore current flow to minimize interference. The camera was left in place from slightly before tidal coverage of the S. setosa patch, until all wave action had ceased after tidal ebb. The shooting sequence was set at 3 shots, 8 seconds apart, cycling every two minutes for an eight minute period. This pattern was repeated every 16 minutes. In addition, manually triggered series of three shots were taken at approximately 15-minute intervals, resulting in an 8 1/2-hour tidal record of over 500 shots.

## RESULTS

### Flume Flux Experiments:

Figure (9) compares the model and flume results with Eastern Passage sediment exposed to a flow at  $u_* = 0.24 \text{ cm s}^{-1}$ . The model and flume results agree in general trend. Exact numerical agreement is not expected for two reasons: 1) for

Figure 9: Model (dashed line) and experimental (solid line).  
flux profiles for Eastern Passage sediment ( $w_s = 0.14 \text{ cm s}^{-1}$ )  
in a flow with  $u_* = 0.24 \text{ cm s}^{-1}$  and  $z_0 = 0.01 \text{ cm}$ .



analytical tractability, only the ideal, non-depth-limited forms of the velocity and concentration equations were used, and 2) the physical assumptions behind the Rouse equation (viscous forces unimportant; no inter-particle collisions) fail to hold very close to the bed. How close "very close" may be is not specified by sedimentologists, but presumably it is the region where suspended merges with bedload transport, within the first centimeter above the bed. The form of the experimental curve at 7 cm is due to the limitation of boundary-layer development in the flume. The experimental boundary layer was 4.9 cm thick. This means that above that height there is no further increase in flow velocity, so that as the concentration continues to decrease so does the local sediment flux. The model curve is not limited in this way (through the 10 cm height modelled), although the same decrease in the flux would be expected beyond the top of the Boundary layer. In the development of his suspended sediment equation Rouse (1937) made the stated assumption that the boundary layer extends for the full depth of the water column. As the flux model is based in part on this equation, it cannot be expected to yield reasonable results beyond the boundary layer. Nevertheless, the qualitative agreement between theory and observation supports our basic understanding of the physics controlling particle availability to benthic suspension-feeders. Through the range of experimental  $u_*$  values (0.11 to 0.24 cm s<sup>-1</sup>) with Eastern Passage sediment, the flux profile went

progressively from "bottom heavy" to "top heavy", supporting the contention that sediment of a given fall velocity ( $w_s$ ) exhibits flux maxima higher off the bed as flow rate increases.

A measure of the "relative flux" was taken as the flux at 1cm relative to that at 7 cm. The experimental results in four experiments ranging from  $u_* = 0.11$  to  $0.24 \text{ cm s}^{-1}$  are compared with modelling results in Fig. (10). Again the general shapes of the curves agree showing that, for sediment of a given effective settling velocity, increasing the flow rate results in a shift from "bottom-heavy" to "top-heavy" flux profile. Conversely, in a given flow the heavier (inorganic) sediment fraction will tend toward "bottom heavy" flux profiles while the lighter fraction (organic and OMA) will show a more uniform or even "top heavy" profile.

Figure (11) shows the SEM photographs of the types of material predominating at different heights in the flow at  $u_* = 0.22 \text{ cm s}^{-1}$ . It is superimposed on the flux profile for a similar flow ( $u_* = 0.24 \text{ cm s}^{-1}$ ) and shows a predominance of sand grains and large diatoms at 1cm above the bottom. At 2 cm large diatoms are still predominant, with some smaller mineral grains, sometimes bound into aggregates. The 3cm sample shows a predominance of large OMA's with some smaller enmeshed diatoms. At 4cm and near the flux maximum OMA's are still predominant, although smaller. Some terrestrially-derived plant material is also evident. Although the latter

Figure 10: Model (dashed line) and experimental (solid line) determinations of relative flux, covering a  $u^*$  range of 0.11 to 0.24  $\text{cm s}^{-1}$ . Relative flux is taken as the flux at 1 cm divided by the flux at 7 cm.

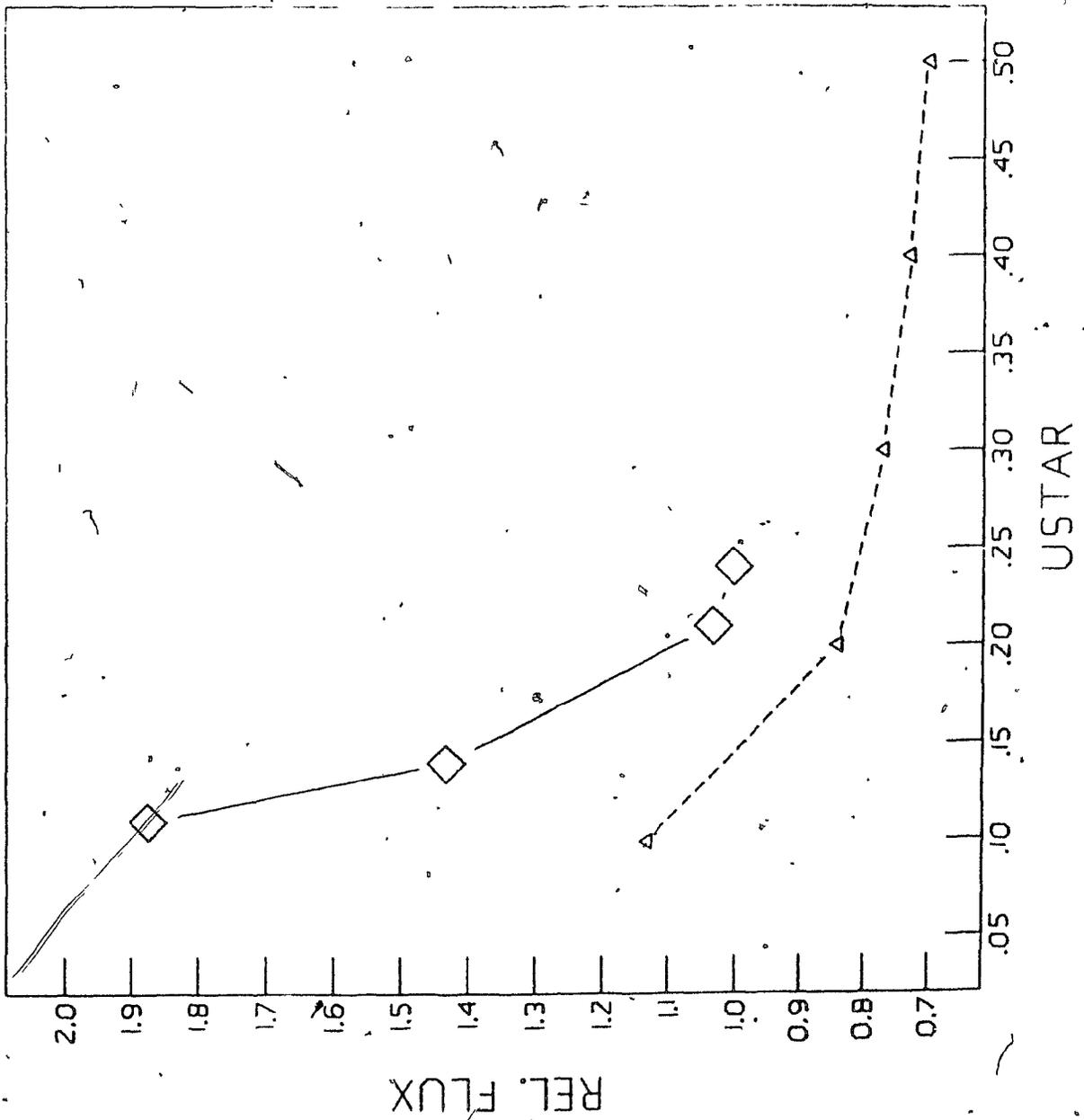
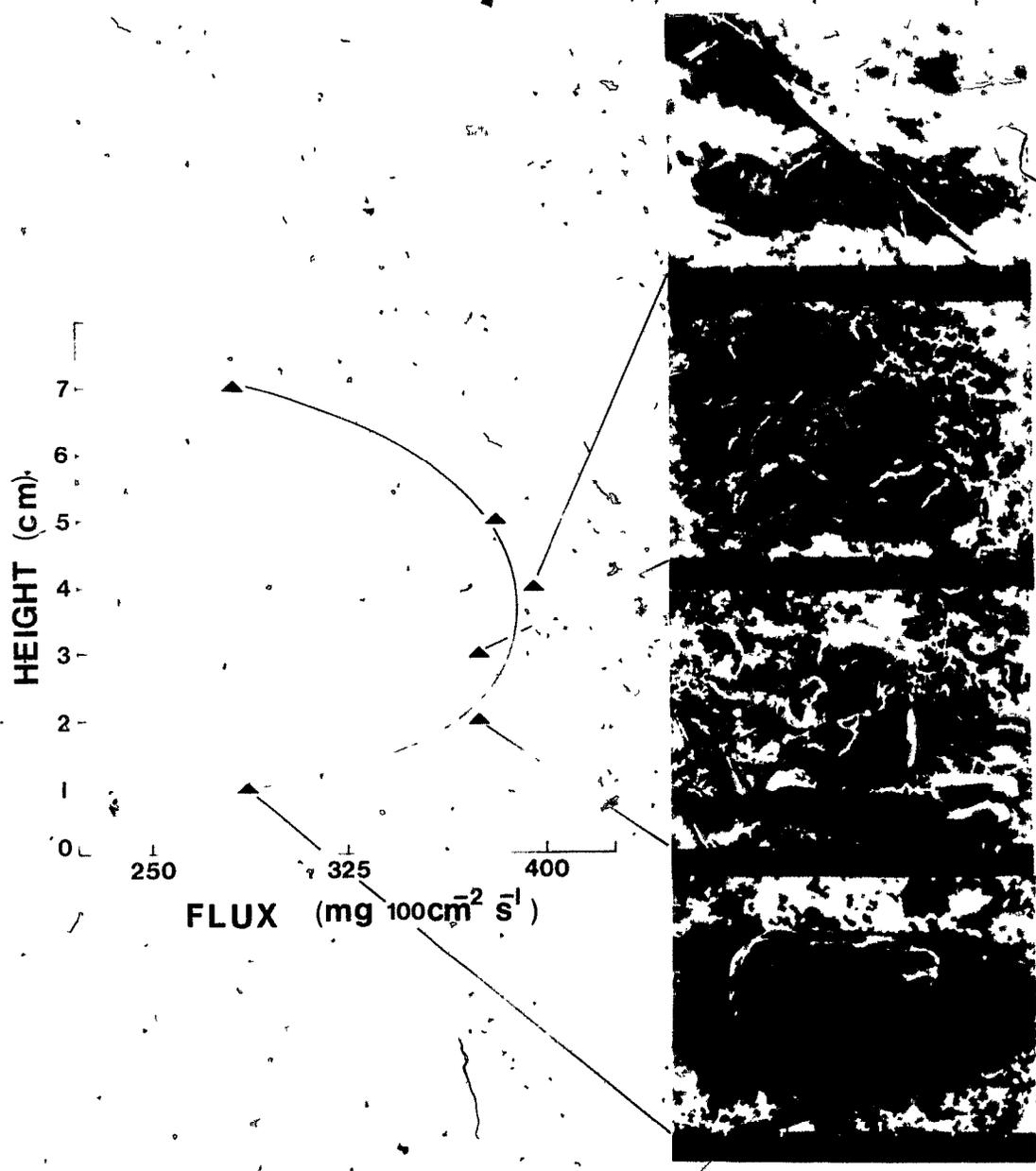


Figure 11: Scanning electron micrographs of seston samples taken in a flow with  $u_* = 0.22 \text{ cm s}^{-1}$ . Micrographs are related to their positions in an experimental flux profile taken in a flow with similar shear velocity ( $u_* = 0.24$ ).



material would seemingly be refractory and of little nutritional value to benthic organisms, field results with S. setosa indicate otherwise. Thus the flux maximum also seems to be coincident with a maximum in the organic content or quality of the seston in flux.

#### Field Experiments:

##### Spio setosa

The Spio setosa population at Eastern Passage is conspicuous, but patchy, with densities of up to 750 individuals per square meter. Tubes often coalesce into small mounds in the densest patches. The animals have two generations per year, as reported by Simon (1967) for populations in New Hampshire. Tube destruction is common and greatest during storms, primarily due to beach scouring by storm-tossed macroalgae. If broken at the surface, the tube is generally rebuilt to its original height in 24-48 hours. S. setosa starts feeding immediately after the tube is covered by the incoming tide, often holding its palps coiled in the wave swash. The same behaviour is observed on the falling tide.

Gut analyses showed a surprising number of large plant fragments. Locally abundant tufts of Enteromorpha supplied suspended strands to the nearby S. setosa patches and they showed up in the guts of the worms. Initial analysis indicated that they were absorbed very quickly in the S. setosa gut, usually within 2-3 hours. In contrast, small

twigs or Spartina root fragments were often found projecting from the hindgut when the animal was broken during sampling. Occasionally tri-radiate calcareous spicules (Porifera: Calcareo) would be found, probably after a storm had dislodged sponges and other epifauna from the deeper channels.

#### Ingested Particles:

A comparison of gut material taken from Spio setosa with material in the top 3 mm of Eastern Passage sediment is presented in table (1). Significant differences ( $p < .001$ , Wilcoxon Rank Sum test) between the gut and ambient samples occur in four categories of organic/inorganic ratios. In these instances the S. setosa's foregut samples were always enriched in organic particles relative to the ambient sediments. Although it is problematic to try to analyze OMA's found in a polychaete gut, the aggregates were more abundant but similar in general structure, to those found in the surficial sediment samples. This result would certainly be predicted from the modelling and flume work. Either they were representative of natural aggregates or of the similar handling conditions of the gut and ambient samples. Of special note, diatoms, which were abundant in the sediments, were almost absent from the S. setosa gut samples. In light of Spio's observed non-selectivity, this may be due to Spio's feeding higher off the bottom than where the maximum flux of diatoms occurs, or to substantial binding (as reported by Grant et al., 1986) of these sediments. In either case the

Table 1. Ratios of organic to inorganic particles from ambient surficial sediment and gut contents of Spio setosa sampled at Eastern Passage, Nova Scotia. The particle types considered are Organic-Mineral Aggregates (OMA), Benthic Diatoms, Quartz grains and Macro-Algal Fragments (Algae). Differences in median tested by Wilcoxon rank-sum test.

| <u>Particle Types</u> | <u>Ratios</u>       |                 |                   |
|-----------------------|---------------------|-----------------|-------------------|
|                       | <u>Ambient Sed.</u> | <u>Spio Gut</u> | <u>N</u> <u>P</u> |
| OMA/Quartz grains     | 0.73                | 1.69.           | 18    .001        |
| Algae/Quartz grains   | 0.04                | 0.58            | 18    .001        |
| Diatoms/Quartz grains | 0.50                | 0.04            | 18    .001        |
| Diatoms/OMA           | 0.66                | 0.02            | 18    .001        |

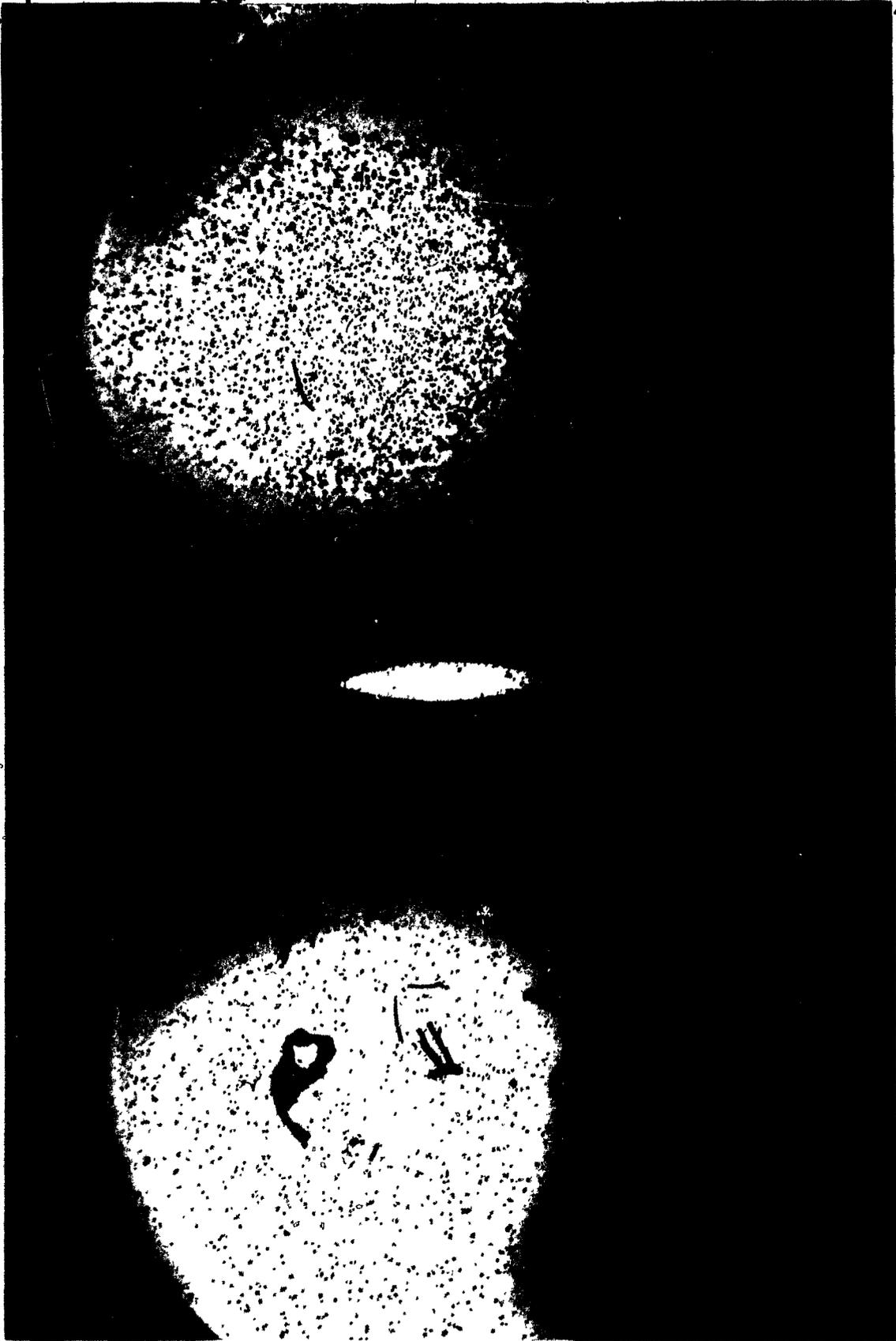
observations show that S. setosa takes its ration primarily from suspension and not by deposit-feeding. The conclusion is supported by the greater occurrence of macroalgal and terrestrial plant fragments in S. setosa's guts than in the sediments. The results of the in situ plankton camera experiment demonstrates the relevance of this finding.

#### Plankton Camera:

The plankton silhouette camera, illustrated in Eisma et al. (1983), has been used previously to photograph large, non-living particles in suspension (Eisma et al., 1983; Kranck, 1984). Typical silhouette photos from the Eastern Passage series are presented in Fig. (12). Due to the size of the camera it was expected that there may be distortion of flow streamlines through the aperture. Whether there was acceleration or deceleration of the flow is not known. Occasional resuspension was observed and there was sedimentation within the aperture during the time series. The sedimentation was due mostly to bedload transport at the beginning of the flood cycle and was eroded away late in the ebb cycle. Even if the in situ concentration profiles are distorted, the long-period effects discussed below are unaffected, as was S. setosa's feeding response to the material in suspension.

Analysis of the 8-hr tidal series of plankton camera photographs revealed the first pictorial evidence of S. setosa engaged in suspension-feeding in situ (Fig. 12). Secondly, there is a periodic influx of large particles of

Figure 12: Plankton silhouette camera photographs, taken 15 min. apart during tidal series. At left, S. setosa is visible in suspension-feeding mode, while seston concentration is low. At right, suspension feeding in high seston concentrations.



macrophyte detritus in suspension (Fig. 12, left), material that is not found in surficial sediment samples. S. setosa can be seen actively feeding on this and other suspended materials, as is borne out by the gut analyses. Visual counts of suspended particles at three heights (0-1, 2-3, and 4-5 cm) in the photographs showed that particles larger than 90  $\mu$ m are almost uniformly distributed above the bottom if averaged over the tidal cycle, although the instantaneous profile is variable. Assuming a local  $u_x$  of 0.25-0.50 cm/s (estimated from timed dye marker measurement of the free-stream velocity) in the longshore direction, the flux of this uniformly distributed material would "track" the velocity profile and exhibit a maximum flux several centimeters above the bottom. The influx of macrophyte detritus has a period of around two hours.

The results of the depth-integrated particle concentrations are presented in Fig. (13) for all particles larger than 90  $\mu$ m, and in Fig. (14) for particles larger than 300  $\mu$ m. They are presented as three-point running means to smooth the data. The distinct periodicity in both the greater than 300  $\mu$ m fraction and the greater than 90  $\mu$ m fraction comes close to matching the approximately 2-hour dominant seiche period characteristic of outer Halifax Harbour (McGonigal et al., 1974). The relationship between seiches and seston variability has been discussed by Kranck (1980), who noticed a similar phenomenon in Petpeswick Inlet, Nova Scotia. Her investigation of short-period (45

Figure 13: Tidal cycle time series of seston concentration, measured from plankton camera photographs. All particles greater than 90  $\mu\text{m}$  are represented. Three-point running means were used to smooth the data.

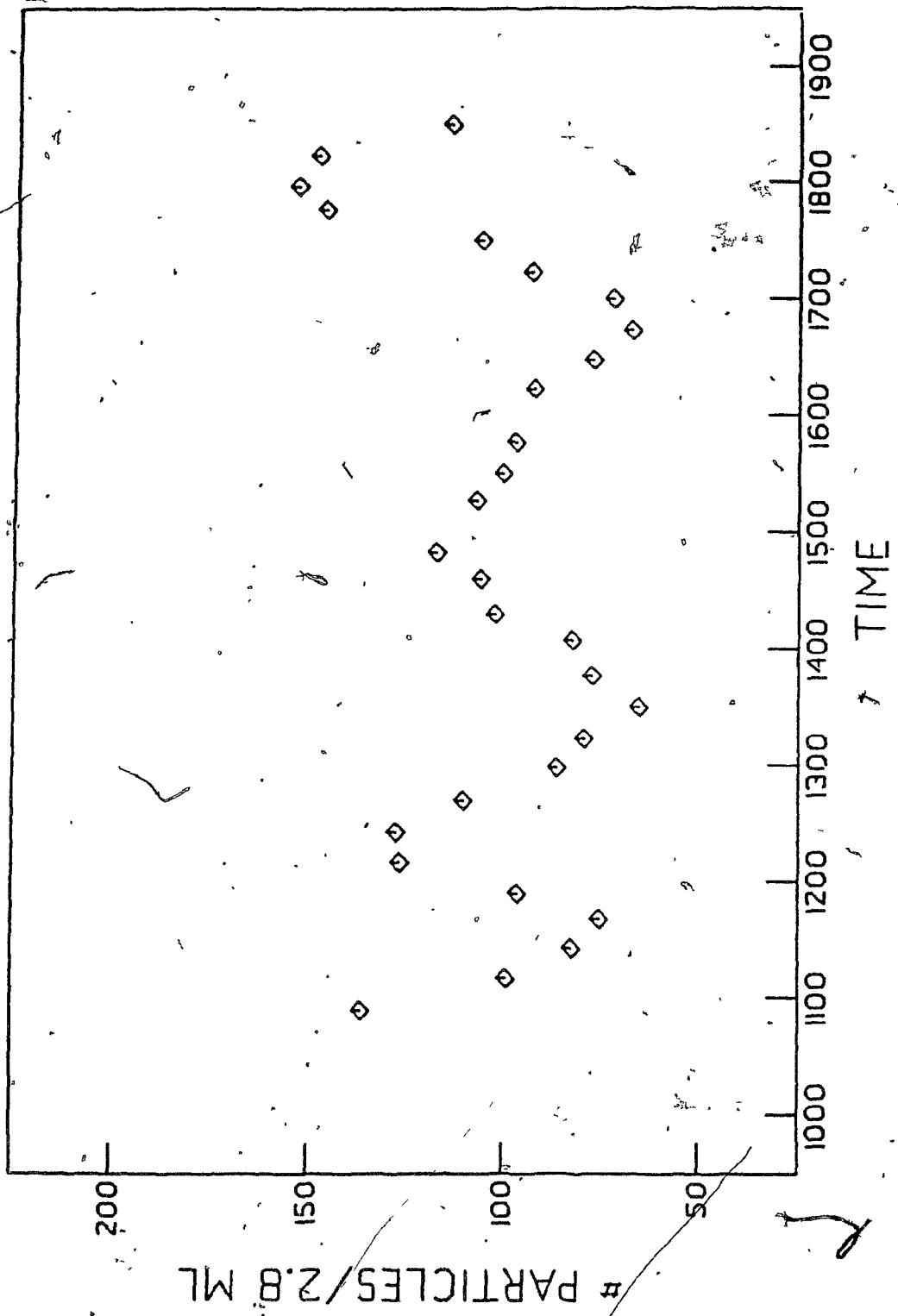
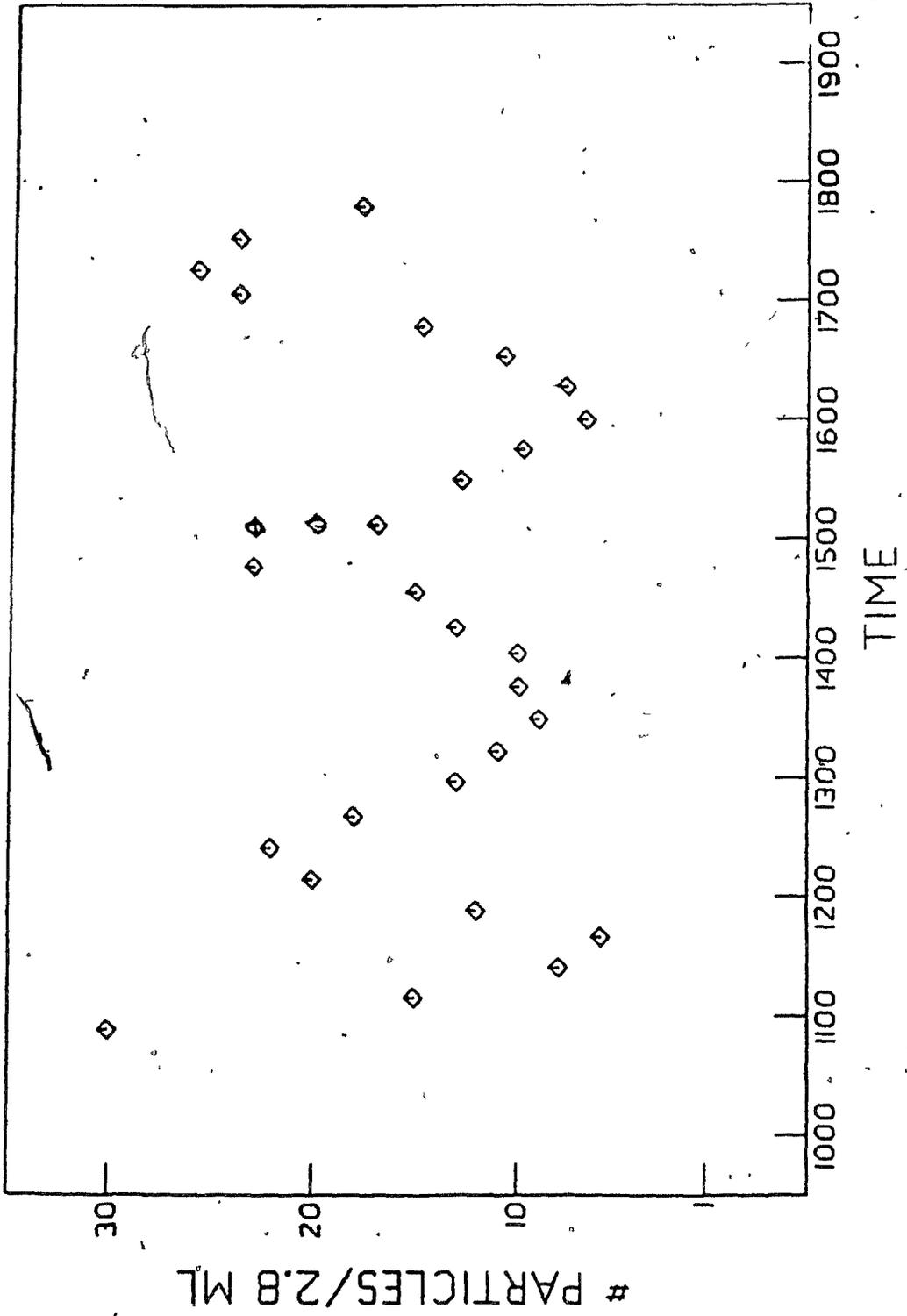


Figure 14: Tidal time series of seston concentration, measured from plankton camera photographs. All particles greater than 300  $\mu\text{m}$  are represented. Three-point running means were used to smooth the data.



minute) seston variations concluded that they were seiche-related, through associated changes in turbulence levels and continual floc formation and breakup due to these changes. She also cited evidence of seston response to seiche periods of 15-20 minutes in St. Margaret's Bay, Nova Scotia. The analysis of the photographic record has been limited to 15-minute intervals and is too coarse to resolve such short-period variation, although it may well occur. It is appropriate to the longer-period oscillation shown, which was also observed while in the field. This record shows that larger aggregates as well as suspended macrophyte detritus show a variation related to the dominant seiche period.

#### DISCUSSION

Two fundamental consequences of the analytical and numerical models are 1) the flux profile is variable and may increase or decrease with distance from the bed (Fig. 7) and 2) in a given flow, the maximum flux of denser (inorganic) particles will occur closer to the bed than that of lighter (organic and OMA) material (Equation 8). The flume experiments testing (1) have shown that the flux profile changes from "bottom heavy" to "top heavy" with increasing values of  $u_*$  (Fig. 10).

The application of dynamic similarity in comparing the lab and field situations demands that one recognize the boundary-layer developed in the flume as a scaled model of

the naturally-occurring one in the field. In natural boundary-layers the logarithmic portion is generally limited to the lower 15% (Grant & Madsen, 1986). The laboratory boundary-layer was fully logarithmic to 5cm in 10cm of water. The S. setosa population at Eastern Passage probably never receives more than 1 to 1 1/2 meters of water coverage and is exposed to a longshore current of between 2 and 10 cm s<sup>-1</sup> (estimated by dye stream) when fully covered. Allowing for a 1 meter thick depth-limited boundary-layer means that the bulk flux maxima would occur somewhat higher in the field than in the laboratory.

The  $u_* = 0.24 \text{ cm s}^{-1}$  experiment incorporating SEM particle analysis (Fig. 11) indicated that the effects of hydrodynamic sorting proposed by Equation (8) do indeed occur. Although not quantifiable on the SEM stubs, visual inspection of the sample series (1-5,7 cm) showed a progression from large, inorganic particles to smaller and more organic material with increasing distance from the bed. The 1 cm sample contained large quartz grains, some clean, some coated, as well as larger diatoms. Very few aggregates were observed, although that may be due to their mechanical disruption by flow shear or abrasion by contact with the bottom and bedload material. Indeed, this sample probably combines material truly in suspension with bedload material travelling in saltation. The 2 cm sample consisted of some quartz grains and diatoms, often bound together in an organic matrix (OMA). At 3 cm larger OMA's start to appear.

These seemed to contain relatively few embedded diatoms or large quartz grains and, in spite of their size, were probably of low specific density. They appeared much the same (after SEM preparation) as do the large flocculated aggregates reported by Eisma et al. (1983) from the Ems estuary. An important question arises concerning the physical strength of these macro-aggregates. Large flocs are fragile and notoriously hard to sample without breaking (Kranck & Milligan, 1980; Eisma et al., 1983; Honjo et al., 1984). They may also break up while settling out of the water column into the shear field of the benthic boundary-layer. Kranck (1984) has shown that these large flocs disaggregate into smaller, more stable units. Although larger flocs tend to settle rapidly (Chase, 1979; Kranck, 1984), their disaggregation may then more easily resuspended (Kranck & Milligan, 1985) so that, except at periods of slack water, this material never really reaches the bottom.

The 4 cm sample is less concentrated and contains smaller aggregates, very small diatoms and some plant debris. The 5 and 7 cm samples (not shown) are quite similar to the 4 cm sample, although less concentrated. The aggregates seem especially free of large embedded inorganic particles and probably consist of silt to clay-sized grains held in an organic matrix. Kranck (1984) reported an optimum organic/inorganic ratio of 2:1 to 3:1 for floc formation, so this seston is probably quite organic-rich. Bulk organic content (by ashing, 500°C) of the surficial (3mm) sediment

at Eastern Passage was 30%. The thin surface layer (300  $\mu\text{m}$ ) is probably very close to the proportions indicated for flocculated aggregates.

My observations in the flume indicate that large OMA's are a preferred food item for S. setosa. A unique feeding behaviour has been observed in S. setosa which intercept a large floc. If such a particle is trapped while the palps are in coiled position, the palp which trapped the particle is lowered to the bed and the other palp ceases feeding to lower and cross over the first one. This allows both food grooves to contact the floc and rapidly transport it to the mouth. At lower flow speeds, both palps come together in the water column to guide the particle to the mouth. Such behaviour suggests the importance of suspended OMA's as a food source for S. setosa. With an adult palp length of 2-3 centimeters and tubes up to .4 centimeters high, S. setosa seems well adapted to maximize its chances of intercepting OMA's while avoiding bedload and suspended particles with low organic/inorganic ratios.

Strong evidence that S. setosa is primarily a suspension-feeder is given by the feeding ratios in Table (1). The abundance of diatoms in the sediment samples and their virtual absence from the S. setosa gut samples show that S. setosa must be feeding above the sediment-water interface. Post-capture particle selection by S. setosa can be ruled out because they are decidedly non-selective when observed feeding under the microscope. Also, when diatoms

are provided in suspension in the flume they soon appear in Spio guts. Grant et al. (1986) showed significant sediment binding due to diatom films. This keeps the diatoms themselves out of suspension. Even if the diatoms are bound to the sediment, it is likely that they would be dislodged by a deposit-feeding S. setosa's surprisingly strong palps. These data, combined with Dauer's (1981) finding that S. setosa built tubes tall enough to prevent its palps from reaching the sediment surface, indicate that the Eastern Passage population ~~was~~ feeding solely from suspension or on material adhering to the tops and sides of the tubes. As further evidence that S. setosa feeds above the sediment surface, two species of nematodes common in sediment samples were never seen in S. setosa guts, although it is possible that these were absorbed very quickly if ingested.

As was expected from preliminary observations, plant fragments were more common in the S. setosa gut than in ambient sediment samples. As the suspended sediment supply in the flume experiments was taken from these surficial sediments, there was little macrophyte detritus in the seston. The role of this component of the seston in S. setosa's feeding ecology was further elucidated by the plankton camera experiments.

The response of S. setosa can be seen in Fig. (12). They were seen suspension-feeding throughout the 8 1/2 hours of tidal coverage. No obvious periodicity related to long-period seston concentration was observed; they seemed to

feed more or less continuously. This is the first observation of spionids suspension-feeding throughout a tidal cycle. It illustrates the importance of this mode of feeding to the group. Although spionids were formerly thought of as primarily deposit-feeders with facultative ability to feed from suspension, their ability to suspension-feed makes it possible for them to occur in the densities observed at Eastern Passage. A 10 cm worm, with about 8 cm of gut following the mouth, pharynx and esophagus and a gut internal diameter of 0.3 mm, has a gut volume of 2.26 ml. Laboratory feeding experiments with organic-coated glass beads (300  $\mu$ m median grain size) indicate that S. setosa can fill its gut in 45 to 75 minutes. If it feeds continuously, it would replace its gut volume a minimum of 6.8 times in the 8 1/2 hours of tidal coverage. If we assume that by deposit-feeding S. setosa would have access to the top 3 mm of the sediment column it would require a radial palp length of just over 4 cm to cover enough sediment surface (assuming no replenishment) to meet its needs. In dense assemblages, this amount of surface area is not available to individual S. setosa and their ration must come directly from suspension. Miller and Jumars (1984) reported that spionids deposit-feeding in dense assemblages decrease their feeding rates as fecal material accumulates.

Quite apart from the areal requirements, the quantity of material ingested by deposit- versus suspension-feeding will be drastically different. Gut contents of S. setosa forced

to suspension-feed in flow in the lab appear different from those that are allowed to deposit feed in quiescent conditions. The gut contents of suspension-feeders have a much more "fluffy" texture, probably representing more labile material than the deposit-feeders are able to take in. The energetic costs of constantly scanning the sediment surface versus holding the palps erect or coiled in a flow are not known but are worth investigating. Any rigorous optimization argument would have to account for this metabolic cost.

Of special note is the active feeding response of S. setosa in high concentrations of macro-algal detritus; they often intercept large suspended fragments. The direct nutritional value of this material is probably low (Tenore, 1983), but it may be the bacterial epiflora found on suspended detritus that is most important. During the summer months there are also numerous fragments of labile chlorophyte species in suspension.

Most importantly, these organic detrital particles of low specific density (but high concentration) are in almost uniform suspension. If their uniform concentration profile is combined with a fully logarithmic velocity profile (typical of well-mixed estuaries, Anwar, 1983), the resulting flux profile will "track" the velocity profile and increase continually with height above the bed. Thus the higher a suspension-feeder such as S. setosa can reach into the water column the greater is the flux past its

appendages. The benefit is twofold, for in reaching into the region of greater organic flux S. setosa places itself above the region of maximum flux of inorganic components.

It appears that the conspicuous sand tubes of Spio setosa are adaptive in at least two ways. They protect the worm in a dynamic sedimentary environment, where mechanical abrasion from bedload transport would make it difficult to feed during periods of strong current flow and maximum material flux. The tubes also elevate S. setosa out of the region in which inorganic components of the sediment predominate, both as bedload and suspended load, into a region where the flux of material more useful as food is increasing with height above the bed.

CHAPTER 4

The Role of Hydrodynamic Sorting of Seston  
in the Nutrition of a Benthic Suspension Feeder:  
Spio setosa (Polychaeta: Spionidae)

## INTRODUCTION

Benthic suspension feeders are inherently dependent on allochthonous food sources. Since these materials are transported by the fluid environment, they are subject to forces which sort and distribute them. This has been tacitly recognized in the few studies addressing food supply to suspension-feeding benthos, which have followed one of two paths: mechanistic studies focusing on small-scale physical interactions which affect particle capture (Rubenstein & Koehl, 1977, Carey, 1983, LaBarbera, 1984) and ecosystem or regional studies of large-scale physical factors and their role in transporting food materials to suspension feeders (Wildish & Kristmanson, 1979, 1984, Wildish & Peer, 1983, Rhoads et al., 1984). There is a need to reconcile these two approaches. I have attempted to do so in the study of the hydrodynamic constraints on food supply to passive suspension feeders; presented in Chapter (3). This study is a continuation of that work, focusing on the effect of the flow regime on the ration actually ingested by a suspension-feeding spionid polychaete, S. setosa.

In Chapter 1 I reviewed Rubenstein and Koehl's (1977) approach to the mechanics of suspension feeding and in Chapter 3 I pointed out that inherent in their approach was the tacit assumption that organisms feed in a homogeneous suspension. This assumption may well apply in the water column, but it is not valid near the benthic boundary. Jumars and Nowell (1984) point out that near-bed suspensions

will be homogeneous only when the shear velocity ( $u_*$ ) of the flow is two orders of magnitude greater than the particle fall velocity ( $w_s$ ). This means that for almost any natural situation there will be a gradient in particle concentration near the benthic boundary. The effects of strong boundary layer gradients in velocity and particle concentration on the flux profile were presented in Chapter 3, where I derived an expression for the height of maximal horizontal flux (equation 8).

Equation (8) predicts that particles of different fall velocities will exhibit horizontal flux maxima at different heights above the bed. There is not only a gradient in particle concentration but also in particle type, and hydrodynamic sorting affects the types of particles available for capture. The particles are invariably a poorly sorted mixture of organic and inorganic materials and their relative efficiency of capture will certainly be due in part to inertial impaction.

Both Rubenstein and Koehl (1977) and LaBarbera (1984) have emphasized direct interception as the main mechanism used by marine filter feeders. The arguments presented above suggest that inertial impaction may also play an important role at the benthic boundary. The role of inertial impaction increases with increasing flow velocity and density difference. The product of these is dimensionally equivalent to the flux. Since the flux of dense (inorganic) particles increases while that of lighter (organic) particles

decreases closer to the bed (Chapter 3), the role of inertial impaction should be greatest close to the bed.

The combined effects of hydrodynamic sorting and inertial impaction during particle capture suggest that any organism capable of reaching above the bed to obtain its ration will benefit by reaching into a layer where more particles are moving past its feeding appendages (higher flux) and higher proportions of the particles are organic. Closer to the bed, the higher flux of inorganic particles means that inertial impaction will play a greater role. Farther from the bed, the quality of the ration increases and the effects of inertial impaction are lessened. Rhoads et al. (1984) recognized the importance of the near-bed region, which they called the 'Benthic Turbidity Zone' (BTZ), to suspension feeding organisms. They did not discuss the significance of particle stratification within the BTZ due to hydrodynamic sorting. Sorting of this kind was shown experimentally in Chapter 3; it is the purpose of this chapter to determine whether or not it is relevant to the feeding ecology of benthic suspension feeders in general, and of S. setosa in particular. Feeding experiments in controlled flow were used to show the proportions of different particle types ingested by S. setosa feeding at different heights above the bed. These results are compared with the material ingested by S. setosa in the field to determine the effect of hydrodynamic sorting on estuarine suspension feeders.

## METHODS

## Field Site:

All field samples in this study were taken from the intertidal area of a fine sand beach at Eastern Passage, N.S., at the mouth of Halifax Harbour. The area has a SE exposure and is next to a narrow channel where currents exceed two knots ( $102 \text{ cm s}^{-1}$ ). The harbour side of the channel receives large amounts of organic matter from a fish plant and other sources of refuse. During both flood and ebb stages of the tide the longshore flow is from NE to SW, i.e. towards the channel, at speeds of 2 to  $10 \text{ cm s}^{-1}$ . The area also is subject to the approximately two-hour seiche which is typical of the harbour as a whole (McGonigal et al., 1972; see Chapter 3).

Spio setosa:

Field study of the distribution of Spio setosa at Eastern Passage started in May and ended in November, 1985, resulting in a total of 580 quadrats sampled during 15 days within the study period. The quadrats were  $(20 \text{ cm})^2$  and were deployed in a three-zoned, stratified random sampling program. This program resulted from preliminary observations, but the study showed that only two distinct regions were statistically justified.

My observations of S. setosa at Eastern Passage revealed that they are large (10-15 cm), form conspicuous sand tubes up to 5 cm in height and have two generations per

year. The S. setosa population at Eastern Passage is confined to a narrow region of the intertidal area near the channel. Sampling revealed a patchy distribution with maximum densities of 720 adult individuals  $m^{-2}$ . At these densities the distinctive sand tubes formed by S. setosa coalesce into raised mats, although solitary tubes are also present.)

#### Field Samples:

Samples of S. setosa for analysis of gut contents were taken as soon as the tide uncovered their tubes. Narcotization with 6%  $MgCl_2$  for approximately one hour preceded dissection and perfusion of the gut contents with filtered seawater. Only the first 60 setigers after the pharynx were perfused to obtain the material most recently eaten and minimize the effect of differential transport of materials within the gut. Narcotized worms were perfused within 2 hours because preliminary studies showed that some of the less refractory material could be digested after that time. Although narcotization was necessary to permit dissection and perfusion it did allow a certain period of time (about one hour) for the digestive process to work before sampling of the gut contents. Samples were preserved in 1% buffered formalin and refrigerated. This method of storage gave excellent preservation of all types of particles examined. For example, diatoms and algal mats still had full pigment colours more than 6 months after sampling.

Sample counting involved filtration through Nuclepore polyester filters (1  $\mu\text{m}$  pore diameter), backed by Gelman AE glass fibre filters for support and to show any evidence of leakage. The filters were cleared with glycerol and viewed at 200x under a Zeiss light microscope with phase contrast. Some samples were stained with Hertzberg's iodine solution after a brief hydrolysis. This was not done commonly since the hydrolysis disrupted diatoms and delicate organic-mineral aggregates (OMA's). Counting 30 full fields per filter ensured adequate coverage of the filter surface. Samples yielding less than 100 particles in 30 fields were excluded from the analysis. Descriptions of the particle types identified are presented in Table (2).

Surficial sediment from among the S. setosa tubes was sampled with a syringe-core to a depth of about 3 mm., taking a sediment volume of 0.3  $\text{cm}^3$ . Preservation was identical to that of the S. setosa gut samples. Before filtration samples were gently shaken by hand to suspend the organic fraction, allowed to settle for 10 seconds and decanted into the filter manifold. Due to the density of particles on the filters, 15 quarter-fields per filter were counted.

In both the S. setosa and ambient sediment samples ten standard particle types (Table 2) were recognized. Particles not fitting into any of these categories were relegated to the 'other' category, which represented less than 2% (ambient sediment: mean = 0.76%  $\pm$  0.58%, n=10, S.

Table 2. Particle categories used for analysis of *Spio setosa* gut contents and Eastern Passage surficial sediment. Abbreviations are those used in tables 2 through 4. In all following tables these conventions hold: 'TORG' = 'ALGL' + 'TOMA', 'TOMA' = 'SOMA' + 'LOMA' + 'AOMA', and 'TQTZ' = 'SQTZ' + 'LQTZ' + Spicules.

| Particle Category | Abbreviation | Description   |
|-------------------|--------------|---|
| Organic           | 'TORG'       | Particles of mostly organic composition   |
| Algal Fragments   | 'ALGL'       | Algal and other plant fragments, 100-1000µm   |
| Sheet             |              | single-cell thickness, sheetlike  |
| Filament          |              | single-cell thickness, filamentous  |
| Other             |              | various, some of terrestrial origin   |
| Diatoms           | 'DIAT'       | Mostly pennate, but some centric, diatoms.<br>Sizes from 5µm to 80µm  |
| Organic-Mineral   | 'TOMA'       | Aggregates of mineral grains and precipitated organic material  |
| Aggregates        |              |   |
| Small             | 'SOMA'       | aggregates <50µm in diameter  |
| Large             | 'LOMA'       | aggregates 50µm to 500µm in diameter  |
| Amorphous         | 'AOMA'       | aggregates >50µm in diameter, made of colloidal-sized particles   |
| Quartz            | 'TQTZ'       | Mineral grains not bound into aggregates  |
| Small             | 'SQTZ'       | grains <50µm in diameter  |
| Large             | 'LQTZ'       | grains >50µm in diameter  |
| Other             |              | Particles not described above, comprising less than 2% of all particles counted.<br>Cuticle fragments<br>Crustacean parts (cirriped, amphipod)<br>Cyanophyte (mats, single-cell thick)<br>Egg cases (gastropod)<br>Foraminifera (empty and living tests)<br>Nematodes, 2 spp. (sediments only)<br>Spicules, triradiate (Porifera: Calcareo) |

setosa gut: mean  $\pm 0.90\% \pm 0.59\%$ ,  $n=15$ ) of all particles counted.

Samples of the tubes of S. setosa were taken for analysis of carbohydrate, by the method of Dubois et al. (1956), and for determination of bulk organic matter (dried at  $50^{\circ} \text{C}$  for 48 hours and ashed at  $500^{\circ} \text{C}$  for 12 hours). Samples of the ambient sediment within S. setosa patches were treated similarly.

#### Flume Experiments:

Feeding experiments with S. setosa were carried out in the Dalhousie seawater flume described in Chapter 2. S. setosa and their tubes were excavated at Eastern Passage and placed in the flume's removeable corebox (Chapter 2). The corebox was returned to the lab, placed in the flume and allowed to acclimate in slow flow for approximately one week. A veneer (2-3 mm) of Eastern Passage sediment was spread on the flume floor and extended approximately two meters upstream of the corewell. Shortly before an experiment about half of the S. setosa tubes were removed to bed level. A typical experimental configuration is shown in Fig. (15). The worms living in the shortened tubes (referred to as the 'low group') almost invariably resumed feeding immediately after the disturbance, except that they were forced to feed within 2 cm (extended palp length) of bed level. Worms in the undisturbed tubes (referred to as the 'high group') were similarly unaffected and fed at 4-6 cm above bed level (tube height = 4 cm).

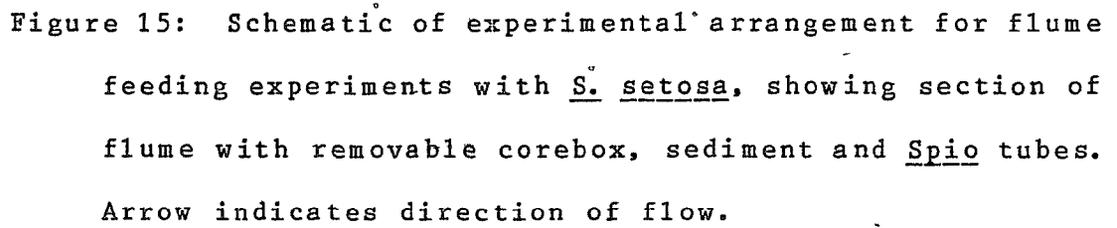
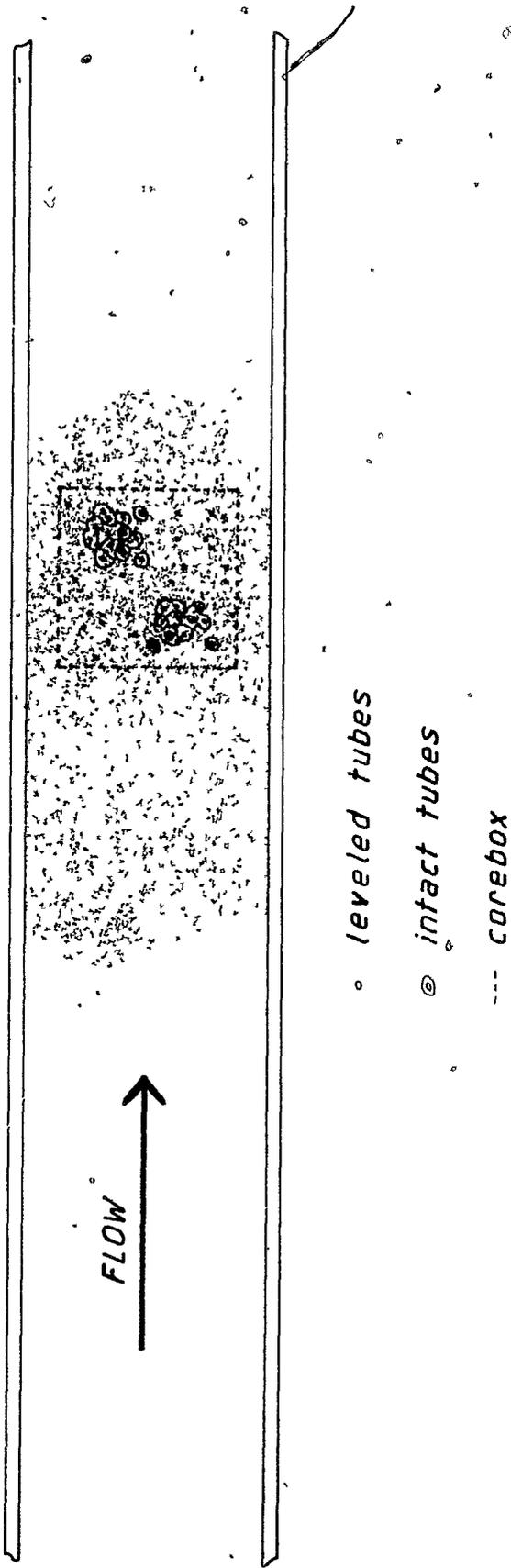


Figure 15: Schematic of experimental arrangement for flume feeding experiments with S. setosa, showing section of flume with removable corebox, sediment and Spio tubes. Arrow indicates direction of flow.



A concentrated sediment slurry pumped into the flume provided a facsimile of natural seston in the feeding experiments. It was prepared by resuspending surficial sediment (top 3mm) from Eastern Passage in filtered seawater in the lab, and was decanted after allowing 10 seconds for the larger sand grains to settle. This procedure gave a final concentration of about  $1050 \text{ mg l}^{-1}$ . This translated to a bulk seston concentration of around 60 to  $70 \text{ mg l}^{-1}$  in the experimental flow in the flume, representative of turbulent estuarine conditions. The bulk organic content of the slurry was variable, but ranged from 17-33% (by weight, ashed at  $500^{\circ}\text{C}$ ).

Feeding experiments ran for 45 to 75 minutes. Gut clearance experiments indicated that 45 minutes was the minimum time required for the foregut to clear. During an experiment I periodically observed the feeding activity of both groups (high- vs low-level), monitored the seston concentration in the flume and took velocity profiles with anemometry equipment (Chapter 2). Seston monitoring with an Optical Backscatterance Sensor (OBS, Downing et al., 1981) showed very consistent bulk concentrations. Thermistor anemometer velocity profiles were log-transformed and used to calculate the shear velocity,  $u_*$ , and roughness length,  $z_0$ , of the experimental flow, as discussed in Chapter (2).

At the end of an experiment I rapidly inserted ABS plastic coretubes into the corebox, isolating both groups of worms. I then drained the flume, removed the corebox,

separated the two groups of worms and sieved (300  $\mu\text{m}$  mesh) them from the sediments. Worms were fixed immediately in 2% buffered formalin to rapidly stabilize the gut contents. Total time taken from the end of the experiment until the worms were in the fixative was 15-20 minutes. 18 to 24 hours after fixation the gut contents were removed and processed similarly to the field samples.

Although estuarine sediments are complex mixtures of organic and inorganic particles which settle at vastly different rates, the characterization of such a sediment by a single 'effective fall velocity' is often useful (McCave, 1979). Two methods were used to determine the effective fall velocity of Eastern Passage sediment. A 20cm settling tube containing a suspension of Eastern Passage seston was placed in a cold room at 6° C. The suspension was thoroughly mixed and sampled periodically. The samples were filtered through pre-combusted Gelman AE glass fibre filters, dried and weighed. The 90 minute time course is plotted in Fig. (16). Effective fall velocity was determined as the settling distance divided by the time taken to reach the median concentration.

The second method used was Krone's concentration gradient method (McCave, 1979). A measured concentration gradient from a flume flow at  $u_* = 0.24 \text{ cm s}^{-1}$  (Chapter 3) was plotted as  $C/C_a$  vs  $(d-z)/z$  on logarithmic axes (Fig. 16).  $C$  is the measured concentration at a height,  $z$ , above the boundary in a flow of depth,  $d$ .  $C_a$  is the 'reference

Figure 16: Settling tube experiment for Eastern Passage  
surficial sediment, settling over 20 cm path at 60 C.

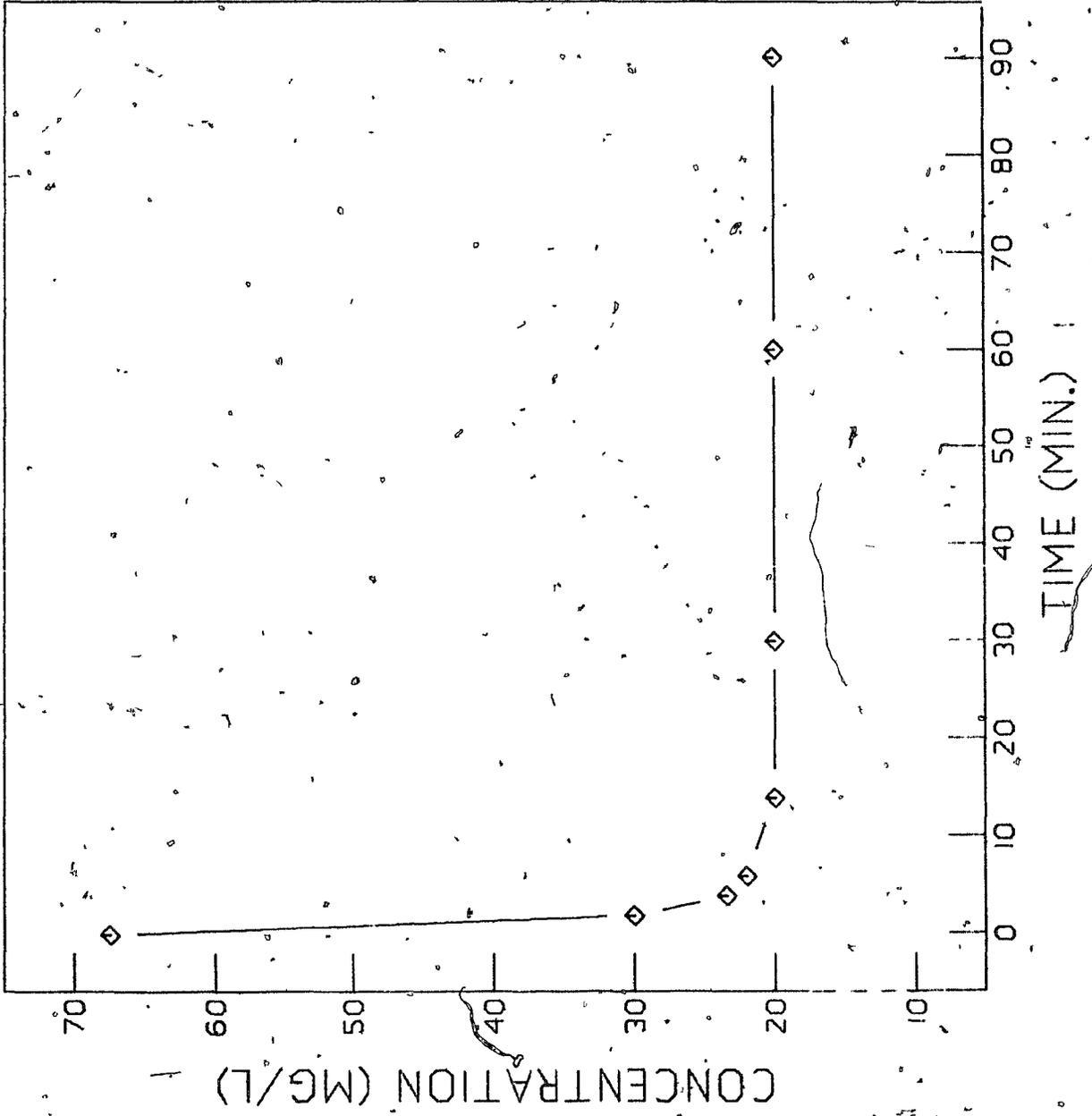
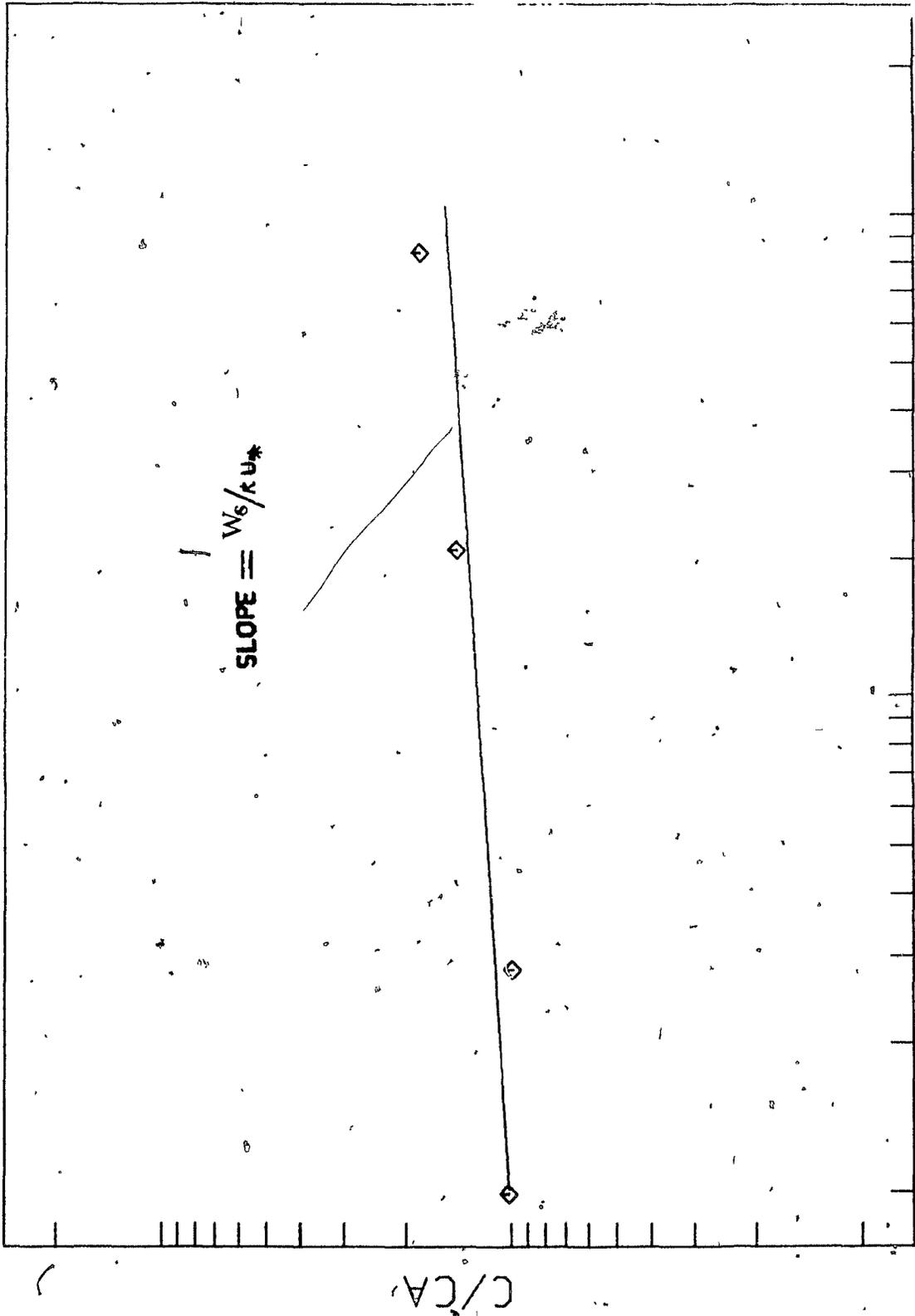


Figure 17: Log-log plot of seston concentration profile from  
a flume experiment at  $u_* = 0.24 \text{ cm s}^{-1}$ . Terms are defined  
in the text.



concentration' at the reference height,  $a$ , close to the bed. The effective settling velocity,  $w_{se}$ , is calculated from the slope of the curve which, by Krone's method, was equal to  $w_{se}/Ku_*$ .

## RESULTS

### Feeding Experiments:

The results of the feeding experiments, comparing S. setosa feeding at different heights above the bed, at high and low flow rates, are presented in Tables (3) and (4) respectively, where the data are in the form of ratios of selected organic to inorganic components. The particle types are as outlined in Table (2) and match roughly equivalent particle sizes (e.g. SQTZ and SOMA are roughly the same size). A one-tailed test of the difference between groups was made using the Wilcoxon Rank Sum test (Bradley, 1968).

At the higher flow rate ( $u_* = 0.52 \text{ cm s}^{-1}$ ) only three of the seven chosen categories showed significant differences between feeding groups (Tables 3 and 4). Mean values were higher for the high-feeding group in all categories but one (SOMA/SQTZ). This may be due in part to small sample sizes, but the generally higher organic/inorganic ratios at the lower flow rate ( $u_* = 0.27 \text{ cm s}^{-1}$ ) suggest a hydrodynamic factor may also be responsible. Equation (8, Chapter 3) predicts that there will be a hydrodynamic sorting of the particles in suspension. As shear-generated turbulence increases (increasing  $u_*$ ) sorting will be less evident, due

Table 3. Results of flume feeding experiment with Spio setosa at high flow rate ( $u_* = 0.52 \text{ cm s}^{-1}$ ). 'High' and 'Low' groups represent worms suspension feeding from their tubes at 4 to 6 and 0 to 2 cm above the bed, respectively. Between-group differences were tested by the Wilcoxon Rank Sum test and  $\alpha$  denotes the level of significance. Categories are as defined in Table 2 and in the text.

|              | CATEGORY            |                     |                     |                     |                     |                     |                     |
|--------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
|              | <u>SOMA</u><br>SQTZ | <u>LOMA</u><br>LQTZ | <u>AOMA</u><br>TQTZ | <u>ALGL</u><br>DIAT | <u>DIAT</u><br>SQTZ | <u>TOMA</u><br>TQTZ | <u>TORG</u><br>TQTZ |
| <u>GROUP</u> |                     |                     |                     |                     |                     |                     |                     |
| High         | 1.09                | 1.81                | 1.62                | 0.54                | 0.58                | 1.14                | 2.76                |
| Low          | 1.20                | 0.42                | 0.57                | 0.41                | 0.35                | 1.10                | 1.66                |
| $\alpha$     | n.s.                | 0.01                | 0.05                | n.s.                | n.s.                | n.s.                | 0.01                |
| n            | 11                  | 9                   | 11                  | 10                  | 11                  | 11                  | 11                  |

Table 4. Results of flume feeding experiment with *Spio setosa* at low flow rate ( $u_* = 0.27 \text{ cm s}^{-1}$ ). 'High' and 'Low' groups represent worms suspension feeding at 4 to 6 and 0 to 2 cm above the bed, respectively. Between-group differences were tested by the Wilcoxon Rank Sum test and  $\alpha$  denotes the level of significance. Categories are as defined in Table 2 and in the text.

|              | CATEGORY            |                     |                     |                     |                     |                     |                     |
|--------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
|              | <u>SOMA</u><br>SQTZ | <u>LOMA</u><br>LQTZ | <u>AOMA</u><br>TQTZ | <u>ALGL</u><br>DIAT | <u>DIAT</u><br>SQTZ | <u>TOMA</u><br>TQTZ | <u>TORG</u><br>TQTZ |
| <u>GROUP</u> |                     |                     |                     |                     |                     |                     |                     |
| High         | 1.10                | 2.22                | 4.57                | 0.16                | 0.23                | 1.26                | 5.26                |
| Low          | 0.87                | 0.62                | 0.14                | 0.14                | 0.22                | 0.79                | 0.81                |
| $\alpha$     | .025                | .001                | .001                | n. s.               | n. s.               | .001                | .001                |
| n            | 19                  | 19                  | 19                  | 16                  | 17                  | 19                  | 19                  |

to greater mixing in the near-bed region. The increased  $u_*$  value in the first experiment resulted in more thorough mixing of seston and greater similarity in the organic/inorganic ratios between the low- and high-feeding groups. Not only were the ratios higher in the second experiment (lower  $u_*$ ), but the difference between the low- and high-feeding groups was more pronounced.

The fact that there were no significant between-group differences in the category DIAT/SQZ, implies a basic similarity in their hydrodynamic behaviour in suspension (Tables 3 and 4). The majority of diatoms were pennate and in the same general size range as the small quartz grains (<50  $\mu\text{m}$ ) although their modal size was probably slightly larger than that of the small quartz grains. Even their ratios in the surficial sediments were quite similar (Table 5). The consistently low ratios of algal fragments to diatoms, however, were a function of there being very few algal fragments in the seston slurry. This reflects their virtual absence in the sediments from which the slurry was made, although photographic evidence (Chapter 3) shows that they occur periodically in dense suspension at Eastern Passage.

The greatest difference between the high and low groups occurred in the ratios of amorphous and total organic particles to total quartz particles (Tables 2 and 3). The role of amorphous OMA's is evident in both the high and low flow rate experiments. The ratios reflect a fact that was

evident during perfusion of the S. setosa guts: the gut contents from the high-feeding group always appeared 'fluffier' in texture.

The role of seston, and OMA's in particular, in the nutrition of spionid polychaetes has become more obvious from recent observations of their feeding behaviour. In Chapter (3) I reported a specialised behaviour aimed at capturing and retaining large aggregates when they are encountered in the flow. Observations made in the flume during S. setosa's acclimation period reaffirm previously reported feeding behaviours and palp orientations of spionids (Taghon, et al., 1980, Dauer, 1981). With increasing current speed, S. setosa changes its palp position from sweeping and flailing over the bed (deposit feeding) to holding the palps vertically in the flow (suspension feeding) to an arched orientation of the palps and then to progressively tighter coiled orientations.

Table (5) presents comparisons of the gut contents of S. setosa from Eastern Passage with the surficial sediment on two separate dates. The particle categories are the same as in Table (2). Differences between the two groups are tested by the Wilcoxon Rank Sum test. The ratios of amorphous OMA's (AOMA) to total quartz (TQTZ) were very high in the S. setosa gut samples in both summer and fall, but due to the virtual absence of OMA's from the sediments in the summer the ratios and statistics were not calculable. The converse situation holds for the ratio of diatoms (DIAT)

Table 5. Organic/inorganic particle ratios for Spio gut contents and surficial sediment from Eastern Passage, Nova Scotia. Between-group differences were tested by the Wilcoxon Rank Sum test and  $\alpha$  denotes the level of significance. Categories are as defined in Table 2 and in the text. '--' denotes insufficient sample size for the Wilcoxon test.

|                 | CATEGORY            |                     |                     |                     |                     |                     |                     |
|-----------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
|                 | <u>SOMA</u><br>SQTZ | <u>LOMA</u><br>LQTZ | <u>AOMA</u><br>TQTZ | <u>ALGL</u><br>DIAT | <u>DIAT</u><br>SQTZ | <u>TOMA</u><br>TQTZ | <u>TORG</u><br>TQTZ |
| <u>SUMMER</u>   |                     |                     |                     |                     |                     |                     |                     |
| <u>7/8/85</u>   |                     |                     |                     |                     |                     |                     |                     |
| Spio gut        | 1.11                | 2.21                | 6.17                | --                  | --                  | 1.30                | 7.34                |
| Sediment        | 0.70                | 0.72                | --                  | 0.10                | 0.32                | 0.70                | 0.67                |
| $\alpha$        | .025                | n.s.                | --                  | --                  | --                  | .025                | .025                |
| n               | 8                   | 8                   | --                  | --                  | --                  | 8                   | 8                   |
| <u>FALL</u>     |                     |                     |                     |                     |                     |                     |                     |
| <u>10/11/85</u> |                     |                     |                     |                     |                     |                     |                     |
| Spio gut        | 0.80                | 2.20                | 9.46                | --                  | --                  | 1.03                | 10.20               |
| Sediment        | 0.96                | 0.53                | 0.05                | 0.18                | 0.18                | 0.86                | 0.77                |
| $\alpha$        | n.s.                | .005                | .005                | 0.10                | n.s.                | n.s.                | .025                |
| n               | 10                  | 10                  | 10                  | 6                   | 7                   | 10                  | 10                  |

to small quartz grains. Although diatoms are readily observed in gut from S. setosa feeding on resuspended sediment in the flume, they are almost never seen in guts of S. setosa taken from the field. In Chapter (3) I interpreted this as evidence that most of the S. setosa population at Eastern Passage feeds several centimeters above a stabilized bed in which the diatoms are an important binding element. This is supported by observations in Grant et al. (1986).

Ratios of algal fragments (ALGL) to diatoms were marginally greater in S. setosa guts in the fall and not so in the summer. In spite of S. setosa's observed feeding on these large macro-algal fragments, they are not often found in the foregut. They are, however, often seen in the hindgut and may be subject to differential transport through the gut. Ratios of OMA's to quartz grains were variable, showing no seasonal pattern. Ratios of total organic (TORG) to total quartz (TQTZ) show significant differences in both summer and fall and, while there was no between-group difference in the ratio of total OMA's (TOMA) to total quartz grains in the fall, there is no discernable seasonal trend. This probably reflects a greater daily than seasonal variation in conditions of particle availability. Pooled samples for the period during March through November, 1985, show significantly greater values in the S. setosa guts in the following categories: SOMA/SQTZ, LQMA/LQTZ, AOMA/TQTZ, and TORG/TQTZ (Table 5).

Distribution patterns throughout the study were patchy,

with variance-to-mean ratios  $>1$  (range: 1.45 to 27.09). The most densely populated area lay on a raised sand spit, close to the channel. It was seldom characterised by sand ripples. The more sparsely occupied area lay a few tens of meters down the beach, was frequently rippled, and was bordered at its upper zone by a dense cover of pebbles and cobble. Within this region S. setosa densities were often greatest in the cobbled zone. This situation continued until mid summer, by which time dense patches of chlorophytes (Enteromorpha sp.) had displaced the S. setosa population. The abundance pattern reversed in early October, when a new set of juvenile S. setosa appeared and persisted at greatest density in the previously sparse area. Pre-settlement densities ranged from 8 to 723  $m^{-2}$ . The post-settlement range was 25 to 2002  $m^{-2}$  and the overall mean density was 408  $m^{-2}$  during the study period.

Due to the frequency with which storms scour the beach at Eastern Passage, a separate study was conducted to determine the time required by S. setosa to reconstruct its tube. Eight meter square quadrats were marked off with soda straws in the middle of the region occupied by S. setosa. Two of these were left untouched as controls, while the other six were leveled and allowed to recover, after noting the number and heights of all S. setosa tubes in each quadrat. The same data were taken at daily intervals for a week. On the fifth day of the study, a storm washed large amounts of macrophyte detritus over the beach, effectively

ending the study. An index of tube recovery was devised as:

$$I_r = \frac{\sum Q_i / \sum Q_0}{\sum C_i / \sum C_0} \quad (9)$$

where  $Q_i$  and  $C_i$  are the mean daily values of the product of tube number and tube height in the experimental and control quadrats, and  $Q_0$  and  $C_0$  are the mean values of the product of tube number and tube height before the start of the experiment.

The regression of hours on  $I_r$  ( $R^2=0.93$ ) yielded an estimated time of 64 hrs. for recovery to the initial condition ( $I_r=1.0$ ). Recovery thus takes an average of two and a half days. This agrees with Dauer's (1981) observations that S. setosa in laboratory aquaria build substantial tubes within 48 hours.

Results of the carbohydrate assay on a sample of S. setosa tubes showed no significant differences from the ambient sediment (S. setosa tubes: 0.14 mg g<sup>-1</sup> sediment, ambient: 0.12 mg g<sup>-1</sup> sediment as glucose equivalents). This does not rule out the possibility that S. setosa reprocesses the sedimentary carbohydrate and replaces it in different form while building the tube. Given the frequency with which S. setosa is forced to reconstruct its tube, its energetic outlay for this activity must be considerable.

Both methods of determining the effective fall velocity of Eastern Passage surficial sediment agreed closely. Settling tube analysis (Fig. 16) yielded a median settling time of 143 seconds through a 20 cm settling path, resulting

in a median settling velocity of  $0.14 \text{ cm s}^{-1}$ . The concentration gradient method used in the flume allows one to characterize the 'effective settling velocity' (McCave, 1979) from the slope of the plot of  $C/C_a$  against  $(d-z)/z$ , shown in Fig. (17). From these data the effective settling velocity of the surficial sediment at Eastern Passage is  $0.15 \text{ cm s}^{-1}$ . This represents the material most likely to be transported either as bedload or suspended load. The Rouse number,  $p$ , is often used as an index to predict whether a given sediment will travel as bedload or in suspension (Nowell et al., 1981; Middleton & Southard, 1984). Values of  $p > 2.5$  indicate bedload transport, while  $p$ -values  $< 2.5$  indicate transport in suspension. Estimating  $u_*$  as 0.05 times the free-stream velocity (Tritton, 1977) yields values ranging from 0.22 to  $0.64 \text{ cm s}^{-1}$  for the longshore flow at Eastern Passage. This means that  $p$  ranges from 1.70 to 0.58 and that the sediment travels as suspended load. This material forms the bulk source of S. setosa's ration, but the flume experiments show that it doesn't behave homogeneously in flow and that the height at which S. setosa feeds above the sediment has a great effect on the quality of the ration it receives.

#### DISCUSSION

The quality of material ingested is important to detritivores and is often reflected in behavioural responses, such as adjustment of their ingestion rate (Cammen, 1980). The feeding experiments in the flume show

that S. setosa gains an energetic advantage from feeding above the sediment-water interface. Although it is impossible to quantify the amount of material ingested and assimilated, the food quality of the material, expressed as ratios of organic to inorganic particles, is clearly better at some distance from the sediment-water interface.

Bowen (1984) contrasted the roles of food chains based on 'morphous' and 'amorphous' detritus, equivalent to the 'Total OMA' and 'amorphous OMA' categories, respectively, of my study. Morphous detritus consists of larger (100 $\mu$ m or larger) aggregates, composed of recognizable cells, mineral grains and a large microbial binding component. Amorphous detritus is derived from dissolved organic matter, forms smaller aggregates (50 $\mu$ m or less) and is much more efficiently assimilated (60-85%, Bowen, 1984) than other detrital components. Results of the flume experiments and observations of feeding behaviour of S. setosa revealed the central role of amorphous OMA in the nutrition of this organism. The worm exhibits specialized behaviour to capture and hold large aggregates and expends energy to build a tube that allows it to feed in a region where the proportion of these particles is much greater than at the bed.

The implications of this finding extend farther than just the feeding ecology of this species. Many industrial and agricultural pollutants are associated with the very fine fraction of suspended sediments in coastal areas and are concentrated into larger aggregates by flocculation

(Kranck, 1974). These flocs exhibit faster fall rates than would be predicted by theory solely on the basis of their size and shape (Chase, 1979), and 'filter' the estuarine water column (Kranck, 1984). They are quite fragile, tend to break up near the bottom and remain in suspension in the near-bottom region (Kranck, 1984). Rhoads et al. (1984) reported elevated levels of PON, POC and chlorophyll a in this region, which they called the Benthic Turbidity Zone (BTZ), and emphasized the potential of this region for controlled bottom rack mariculture. The accumulation of estuarine pollutants by benthic organisms specializing on amorphous OMA is one path of entry of this material into estuarine food chains (Bowen, 1984). Concentration of toxic materials in primary consumers, such as S. setosa, could result in further accumulation in demersal fishes and organisms at higher trophic levels. The substantial intertidal and subtidal populations of S. setosa at Eastern Passage may be a significant pathway for bio-accumulation of the pollutants in the demersal fishes of Halifax harbour.

The field results of S. setosa gut analysis show substantial increases in morphous and amorphous OMA's in the gut contents compared to the surficial sediments. This is not due to post-capture selection since microscopic observation of S. setosa's feeding behaviour revealed post-capture rejection only of particles physically too large to be ingested. The similarity of the ratio DIAT/SQTZ in both flume experiments (where diatoms were provided in

suspension) and in the sediments at Eastern Passage shows that, once suspended, diatoms are hydrodynamically similar to small quartz grains. The interaction between small and large OMA's and their equivalent quartz grain sizes is more variable. Generally, the value of LOMA/LQZT for S. setosa on both dates at Eastern Passage is similar to that for S. setosa feeding above bed level in the lower flow rate experiment. This suggests that prevailing conditions at Eastern Passage are better represented by that experiment.

This last conclusion must be taken with caution, as the flume conditions are simplified from those in nature. One limitation of most flume work is the lack of wave effects, which can be considerable at Eastern Passage. Grant and Madsen (1986) have pointed out the role of the wave boundary layer in sediment resuspension. Waves increase bottom shear stress and resuspend sediments that the ambient flow cannot. Modelling the transport of surficial sediments solely on the basis of steady, non-oscillatory flow over uniform topography is a great simplification. Nevertheless, both the flume and field studies indicate that the role of both morphous and amorphous OMA's is crucial in the ration of S. setosa, which takes advantage of the hydrodynamic sorting of seston in the near-bed region.

Sand tubes constructed by S. setosa allow individuals to colonize a dynamic sedimentary environment. They provide protection from abrasion by constantly shifting sand grains. They also allow the worm to reach above the region of

bedload and maximum inorganic suspended load flux. S. setosa pays a price for living in this environment, by having to frequently rebuild the tube. If it takes two to two and a half days to reconstruct a tube, the worm is prevented from feeding at its optimal height for that time. Any frequency of disturbance greater than this would presumably exclude S. setosa. The main cause of tube destruction at Eastern Passage is scour by storm-tossed wrack. Often this material remains on the beach and sand flat for weeks after the storm and continues to scour. During this time there are no apparent S. setosa tubes and the worms' feeding must be drastically curtailed. In summer months, disturbances of this order are infrequent, occurring perhaps once a month, but beach scour by wintertime storms is almost constant. The S. setosa population at Eastern Passage during winter is usually limited to the harbourside section of beach and is drastically reduced on the oceanside. At these times it may be the populations living in relatively quiescent waters that provide the base for seasonal recolonization of more dynamic environments. It is in these more dynamic areas, however, that the population realizes its greatest production.

The question of S. setosa production is intimately tied up with the question of food supply, food preference and hydrodynamics. Jumars et al. (1982) proposed a mechanism of passive particle selection by tentaculate deposit feeders, including spionids, which would favour retention of lighter,

smaller particles. Denser, larger particles are more easily dislodged during transport to the mouth from their point of contact on the tentacle or palp. If this applies to tentaculate suspension feeders, it would counteract the effect of inertial impaction in trapping denser particles. This effect would be even greater if the palp were held farther from the bed, in a region of higher flow and increased drag force on captured particles (Jumars et al., 1982; Taghon, 1982). S. setosa's specialised behaviour to retain large aggregates (Muschenheim, ms.) involves covering the particle with both palps (greater contact surface) and immediately pulling it down to bed level and into a region of lower flow.

An adult S. setosa of 15 cm length weighs about 0.5 grams, wet weight. Based on field measurements, this represents a mean standing stock of 204 g m<sup>-2</sup> of wet biomass and a maximum value of 362 g m<sup>-2</sup>. Such biomass may be quite localised but, if renewed annually, can equal the highest annual production rates of benthic suspension feeders seen in the lower Bay of Fundy by Wildish and Peer (1983). Their data were dominated by the lamellibranch, Modiolus modiolus, which, although not a 'passive' suspension feeder (sensu LaBarbera, 1984), as is S. setosa, is a suspension feeding organism in the benthic boundary layer and is subject to the same hydrodynamic conditions.

S. setosa's preference for morphous and amorphous OMA's raises the question of transport of pollutants through the

estuarine-trophic system, since flocculation and enhanced settling of colloidal sized particles rapidly deliver pollutants to the boundary layer (Kranck, 1974; Bowen, 1984; Melack, 1985). Once near the bottom, these aggregates may settle out or be transported as near-bed suspended load and become available to benthic suspension feeders.

Resuspension of bottom sediments may also make pollutants available to benthic suspension feeders. Once suspended by current or wave action or bioturbation, the surficial sediment at Eastern Passage travels mostly in suspension, and so does any flocculated material accumulated in the sediment. Since there is a sub-layering of seston within the BTZ, the height to which a suspension feeder can reach determines the quality of the material it receives.

CHAPTER 5  
Summary and Conclusions

The goal of this thesis has been to isolate and examine the hydrodynamics of particle flux gradients under simple conditions (reduced bed roughness, unidirectional flow, no wave effects) and relate the findings to the feeding ecology of one species of benthic suspension feeder (Spio setosa: Polychaeta). The experimental approaches used, flume techniques (Chapter 2), analytical and experimental study of seston flux (Chapter 3) and its effect on the ingested ration of S. setosa (Chapter 4) were combined with field studies of the distribution, abundance and feeding ecology of S. setosa at Eastern Passage, N.S. (Chapters 3 and 4) to yield the following conclusions:

i.) Analytical modelling of the simplest forms of the equations predicting flow and seston concentration revealed the conditions under which specific patterns of flux arise (Chapter 3). As is the case with most modelling in ecology (Wangersky, 1978), the aim was not to produce predictive formulae but to gain an appreciation of the interaction of the physical variables. The two principle findings of the modelling efforts are that the profile of seston flux varies with the fall velocity of the sediment ( $w_s$ ), the shear velocity of the flow ( $u_*$ ) and the bed roughness ( $z_0$ ). Flux may increase or decrease with distance from the bed. Equation (8) predicts that the flux of denser particles will occur closer to the bed than that of lighter particles or, conversely, that the flux maximum of a given sediment occurs higher off the bed as the flow rate increases.

ii.) The flume seston experiments (Chapter 3) showed that both consequences of the analytical model were substantiated with natural sediments. The flux maximum of sediment of a given settling velocity occurs farther from the bed as  $u_*$  (hence flow rate) increases. Hydrodynamic seston sorting is supported qualitatively by microscopic evidence of samples from different heights above the bed. Large sand grains, large diatoms and dense OMA's are prevalent closest to the bed while flocs of various sizes, small diatoms and macrophyte fragments dominate farther up. As the flux increases away from the bed, so does the food value of the material.

iii.) Benthic suspension feeders may take advantage of hydrodynamic sorting to maximize the organic fraction of their ingested ration. Particles with very low fall velocities ( $<.01u_*$ ) have uniform concentration profiles and flux profiles that track the velocity profile. The flux of these particles thus increases with distance from the bed and, in the lowest 15% of the boundary layer, in approximately logarithmic fashion.

iv.) The relevance of these effects to benthic suspension feeders (under the conditions outlined above) is borne out by the feeding experiments in the flume (Chapter 4). S. setosa feeding 4-6 cm above the sediment ingest a significantly higher proportion of organic particles than those feeding at 0-2 cm above bed level. The proportion of morphous and amorphous OMA's in S. setosa's gut, both in the

flume and in the field is greater than found in the surficial sediment at the field site. This and the lack of diatoms found in S. setosa from the field indicate that the worm obtains its ration primarily from suspension and at a height several centimeters above the bed. If fed diatoms in suspension, S. setosa readily ingests them. The ratio of diatoms to small sand grains in S. setosa and in bed sediments indicates that these two particle types behave similarly in flow. It is most likely that active binding of diatoms to the bed keeps them out of suspension and out of S. setosa's gut in the field.

v.) Field investigations of seston concentration and S. setosa's feeding behaviour (Chapter 3) support the notion of its dependence on suspended material. Temporal variation in the flux of large particles (macrophyte detritus, large OMA's) coincides with the natural seiche period of the site. The vertical distribution of these particles is nearly uniform when averaged over the tidal cycle, meaning that the flux increases with distance from the bed. S. setosa feeds on this material throughout the tidal cycle at a height about 3-5 cm above the bed.

vi.) S. setosa's reliance on suspended morphous and amorphous organic-mineral aggregates (OMA's) is supported by observation in the laboratory (Chapter 3) and field sampling (Chapter 4). The overall ratio of organic to inorganic components is consistently greater in S. setosa's gut than in the surficial sediments at Eastern Passage. Individual

seston components show various patterns, but no seasonal effect was detectable between summer and fall of 1985.

vii.) S. setosa densities reach a maximum of over 2000 individuals  $m^{-2}$  in early fall. At such densities they must obtain their ration from suspension, as not enough space is available for deposit feeding. Physical factors, especially beach scour during storms, limit the amount of time that S. setosa can spend feeding above the bed. Field tests indicate that it takes S. setosa an average of 64 hours to reconstruct its tube. During this time it must feed close to the bed and obtains a less than optimal ration. Although S. setosa attains its greatest biomass in dynamic sedimentary environments, winter storm scour results in exclusion from these sites. The sparser populations inhabiting relatively quiescent, protected waters, are probably responsible for maintaining the population as a whole.

viii.) The agreement between the modelling, flume and field results indicates that hydrodynamic control of seston flux is relevant to the ecology of at least one species (S. setosa) of passive suspension feeder, and probably to others. The simplified environment of the experimental flume (Chapter 2) allowed isolation of the factors controlling the flux profile, yet was not so simplified as to produce trivial results. In spite of focussing on an estuarine environment, the results are relevant to shelf and deep-sea environments, especially where passive suspension feeders are abundant.

APPENDICES

APPENDIX I

## Derivation of the Logarithmic Velocity Profile:

The form of the velocity profile above a flat boundary is semi-logarithmic. Details of its derivation can be found in any fluid dynamics text (e.g. Tritton, 1977). Most simplistically, the stress,  $\tau$ , in a fluid is related to the velocity gradient through the molecular dynamic viscosity,  $\mu$ .

Expressing this in terms of the kinematic viscosity,  $\nu$ , yields:

$$\tau = \rho \nu \frac{\partial u}{\partial z} \quad (10)$$

Where  $\rho$  is the fluid density,  $z$  is height above the boundary, and  $u$  is the mean streamwise velocity. For larger-scale phenomena,  $\nu$  is replaced by an analogous "eddy viscosity",  $K_v$ , with units of velocity times length or, in this case,  $u_*$  times  $z$ :

$$K_v = K z u_* \quad (11)$$

where  $K$  is a constant (von Karman's constant), characteristic of turbulent wall flows and experimentally determined to be 0.41 under most conditions.  $u_*$  is the shear velocity defined in Chapter (1). The relationship then becomes:

$$\frac{\partial u}{\partial z} = \frac{u_*}{K} \frac{1}{z} \quad (12)$$

Since  $u_*$  and  $K$  are constant for any given steady, uniform flow, this integrates to:

$$u_z = \frac{u_*}{K} \ln(z) + C \quad (13)$$

With further dimensional considerations (see Landau and

Lifshitz, 1959) the constant of integration is taken to be equal to

$$-\frac{u_*}{K} \ln(z_0) \quad (14)$$

where  $z_0$  is a parameter related to bed roughness, so,

$$u_z = \frac{u_*}{K} \ln \frac{z}{z_0} \quad (15)$$

which is the same as Equation (4, Chapter 1).

Analytically,  $z_0$  is the  $z$ -intercept, but the logarithmic relationship does not hold very close to the wall, where viscous forces dominate. This region, the viscous sub-layer (VSL) is on the order of  $12 \nu/u_*$  thick, with a linear velocity profile given by:

$$u_z = z(u_*)^2/\nu \quad (16)$$

The flow is then called "hydraulically smooth". In the ocean, VSL's from a few millimeters to a couple of centimeters thick have been reported from measurements made on the continental shelf off the coast of Oregon (Caldwell & Chriss, 1979; Chriss & Caldwell, 1984). If the flow is strong enough, or the bottom rough enough, the condition of "hydraulically rough" flow exists and the VSL is present only in the interstices of the bed.

From arguments presented in Tritton (1977, p. 275) there is no discontinuity between the two layers and the stress is assumed to be constant with height this close to the boundary. This means that a stress calculated from

logarithmic layer measurements is the same as the stress acting at the bed. Taking a series of velocity measurements and regressing  $u_z$  on  $\log(z)$  will permit calculation of  $z_0$  and  $u_*$  and, subsequently, the bed shear stress from Equation (4, Chapter 1). One should note that, for the regression to be statistically significant, there must be enough data points to resolve the profile. In the compressed boundary layers created in flumes, this requires instruments and methods with suitable spatial resolution. More on the calculation of bed shear stress can be found in Middleton and Southard (1977).

APPENDIX II

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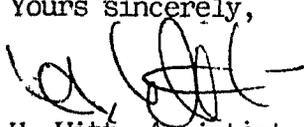
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CANADA

July 22, 1986.

Dear Dr. Muschenheim,

Further to our telephone conversation of yesterday, we herewith confirm that permission is given to use the material <sup>\*</sup> /or parts thereof published in the article by yourself and co-authors entitled 'Flumes for benthic ecologists: theory, construction and practice' in 'MARINE ECOLOGY PROGRESS SERIES', Volume 28, p. 185-196 providing proper acknowledgement is made to the original source of publication.

Yours sincerely,

  
H. Witt, Assistant

\* for your Ph. D. thesis

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