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THE EFFECTS OF BEDLOAD SEDIMENT TRANSPORT
ON BENTHIC RECRUITMENT AND PRODUCTION
WITH EMPHASIS ON THE SOFT-SHELL CLAM *MYA ARENARIA* L.

by

Craig William Emerson

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

at

Dalhousie University
Halifax, Nova Scotia
July, 1990

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DALHOUSIE UNIVERSITY

FACULTY OF GRADUATE STUDIES

The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled "The Effects of Bedload Sediment Transport on Benthic Recruitment and Production with Emphasis on the Soft-Shell Clam *Mya Arenaria* L"

by Craig William Emerson

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

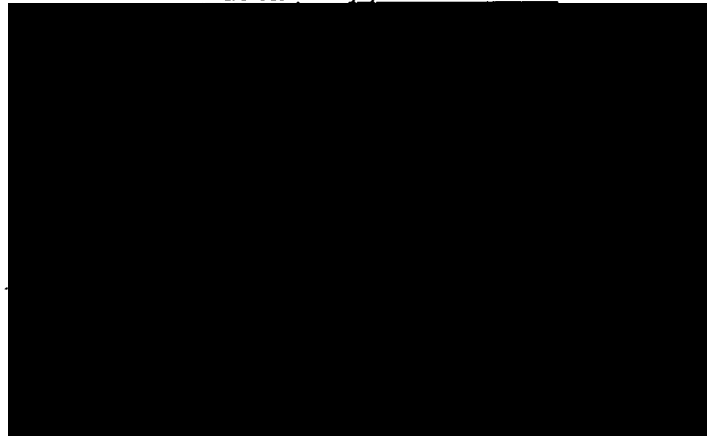
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ABSTRACT

A series of field and laboratory studies was conducted to determine whether changes in recruitment and production of coastal benthic populations could be attributed to local variations in bedload sediment transport. An empirical model provided the first evidence of bedload-benthos interaction; it was hypothesized that sediment transport was responsible for the negative correlation between sea-surface wind stress and benthic secondary production (BSP) in a multivariate model explaining ~90 % of the annual variation in BSP.

This hypothesis was tested after developing and calibrating a cylindrical sub-surface bedload trap for use in shallow water. From trap deployments on intertidal sandflats at Eastern Passage, N.S., it was determined that recruitment to a population of soft-shell clams (*Mya arenaria*), was controlled largely by the passive transport of juveniles (1+ cohort) during bedload transport (max. >2600 clams·m⁻¹·d⁻¹). A relatively short period between spat settlement and the onset of fall storms likely contributed to the complete removal of the 0+ cohort from the high-energy sandflat.

Additional evidence linking bedload transport to benthic production was revealed in laboratory experiments which tested the effects of sediment disturbance and water flow on *Mya arenaria* tissue growth. After 10 months, maximum growth (60 % increase in dry wt.) was observed in clams exposed to daily disturbance of the top centimeter of sediment; no level of disturbance resulted in growth rates lower than those of undisturbed clams in minimal flow ($U=0.4$ cm·s⁻¹; 10 % wt. increase). An increased sestonic food supply was responsible for the positive influence of flow but the benefits of sediment disturbance could not be identified.

In related experiments, most clams (1-7 cm shell length) could survive a 50-cm sand burial, but died under 25 cm of mud. The inability to re-establish normal living depths after exposure during sediment erosion may increase the susceptibility of clams living in mud to further erosion and epibenthic predation. Thus, results from theoretical, field and laboratory investigations supported the concept of a physical regulation of coastal benthic energy flow.

ABBREVIATIONS AND SYMBOLS

ACI	allometric condition index
BPP & PPP	benthic and pelagic primary production
BSP	benthic secondary production
C_d	drag coefficient
C_o or R_a	annual benthic respiration
C_s	annual primary production
D	sediment grain diameter
d_o	orbital diameter
E	wave energy
EF	effective fetch
F	fetch
f_m	peak wave frequency
f_w	sediment friction factor
g	acceleration due to gravity
H	headwind index
H_{max}	maximum wave height
H_s	significant wave height
h_{sed}	crest to trough sediment ripple length
k	growth rate to L_∞
K_g	kurtosis of sediment grain size distribution
L	sediment ripple wavelength
LD ₅₀	burial depth under which 50 % of the clam population survived
L_t	maximum shell length
L_∞	length at which growth rate is zero
M	mobility number of sediment (~Shield's entrainment function)
MSD	minimum significant difference
NLD	normal living depth of <i>Mya arenaria</i>

P_a	annual benthic secondary production
POM	particulate organic matter
q_{max}	maximum bedload transport
Q_{10}	metabolic ratio over 10°C
R	rate of oxygen consumption
R_a or C_o	annual benthic respiration
SC	shell cavity
SFDT	shell-free dry tissue
Sk_I	skewness of sediment grain size distribution
T	wave period
TCOD	total community oxygen demand
T_e	average annual water temperature
TH	tidal height
t_o	age of clam when length is zero
U & V	vector components of velocity
$U_{m.crit}$	critical threshold orbital velocity
U_*	shear velocity
U_{*crit}	critical shear velocity
Z	water depth
Z_m	water column mixing depth
ϕ	= $-\log_2(\text{grain size, mm})$
θ_{crit}	critical dimensionless bed shear stress
ρ_s	sediment density
τ	surface shear stress

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CHAPTER ONE
GENERAL INTRODUCTION

Bedload Sediment Transport and the Benthos

Prior to the 1980's, the interaction between sediment and the benthos had been assessed primarily within a static framework. The effects of grain size on recruitment, feeding and distribution (see review by Gray 1974) and the biological control of sedimentological variables, including grain size (Mills 1967, Rhoads 1967) and compaction (Levinton 1977), were revealed by numerous investigations. The "trophic group amensalism" hypothesis (Rhoads & Young 1970) unified many of these results: when deposit feeders disturb the sediment, they exclude suspension feeders by preventing larval settlement and clogging filtering appendages. The importance of sediment transport was implicit in these studies, but its role in benthic energy flow was rarely examined.

Following the lead of Donald Rhoads (*Yale University*) and Arthur Nowell (*University of Washington*), many researchers studying the interaction between sediment transport and the benthos have concentrated on the biological control of sediment stability and water flow in the benthic boundary layer. Benthic macro-organisms were shown to regulate sediment movement by changing the bed shear stress around animal tubes (Eckman et al. 1981, Eckman 1983), altering sediment stability through bioturbation and mucous secretions (Holland et al. 1974, Rhoads 1974, Rhoads et al. 1978, Yingst & Rhoads 1978, De Boer 1981, Grant et al. 1982, Grant 1988), changing the exposure of grains to flow (Rhoads & Stanley 1964, Fenton & Abbott 1977), and affecting particle momentum (Nowell et al. 1981, Jumars & Nowell 1984). Comparatively little has been learned about the biological responses to sediment transport.

Wildish's (1977) hypothesis that benthic macrofaunal production may be linked to the transport of suspended sediment has received much support (Bricelj et al. 1984, Rhoads et al. 1984, Muschenheim 1987*a,b*, Miller & Sternberg 1988, Grant et al. 1990), however the role of bedload sediment transport, which is intuitively of equal or greater importance to the benthos, has received little attention. The few existing studies of bedload-benthos interaction have identified several possible mechanisms by which bedload transport may regulate benthic community structure, mortality rate, and nutrition in both coastal and deep-sea areas (Grant 1981,1983,1985, Miller 1989, Aller 1989). Unfortunately, the lack of a suitable bedload sampler for use in marine nearshore regions has precluded the direct measurement of bedload transport in conjunction with the measurement of biological variables. If such data can be obtained, it may be possible to increase our ability to predict changes in the benthos resulting from increasing coastal development and an expanding commercial shellfishery.

The purpose of my thesis research was to determine the effects of bedload sediment transport on benthic energy flow in shallow soft-sediment communities. The distinction between bedload sediment transport and suspended sediment transport is often vague and is a continuing subject of controversy (Murphy & Aguirre 1985). Following Dyer (1986), I have defined bedload as those grains that are rolling, sliding, or saltating within a few grain diameters of the bed and are travelling more slowly than the fluid. The suspended load comprises grains travelling with the water at the same velocity and which are supported by turbulence. In the most general sense, 'energy flow' refers to biological processes such as respiration, individual and population growth (i.e. production), and mortality. 'Recruitment' is the addition of individuals to a population. By

identifying mechanisms linking bedload transport to benthic production in the field and laboratory, I hope to improve the modelling of benthic communities and contribute, thereby, to the rational exploitation of marine biological resources.

Organization of Thesis

The thesis is a collection of individual studies which share, for the most part, the hypothesis that sediment transport causes variations in benthic energy flow. First, empirical models were constructed from published data to illustrate the link between sediment transport and annual benthic heterotrophic production (Chapter 2). Results from the statistical models were then used to direct subsequent field and laboratory research. After the development and rudimentary calibration of a bedload sampler (Chapter 3), the influence of bedload transport on macrofaunal demography was determined on a low- and a high-energy intertidal sandflat (Chapter 4). After it was shown that bedload transport can control the density of a soft-shell clam population (*Mya arenaria*), indirect evidence that bedload transport may also influence the metabolism of benthic communities was obtained by estimating the contribution of *M. arenaria* to total community oxygen demand (Chapter 5). In addition, laboratory experiments were conducted to determine the direct and indirect effects of sediment disturbance on clam growth (Chapter 6) and mortality (Chapter 7). A brief summary of results and conclusions is presented in Chapter 8.

Chapters 2-7 are independent reports consisting of an *Abstract, Introduction, Methods & Materials, Results*, and a *Discussion* section; for convenience, appendices and a combined reference list were placed at the end of the thesis. Tables and

figures immediately follow the page on which they were first cited. Occasional repetition in sections which describe study sites, methods or rationale was necessary to maintain the integrity of each chapter.

CHAPTER TWO
WIND STRESS LIMITATION OF BENTHIC SECONDARY PRODUCTION
IN SOFT-SEDIMENT COMMUNITIES

ABSTRACT

Local wind fields will determine the magnitude of benthic secondary production (BSP) by regulating metabolically-important environmental factors (e.g. water temperature, mixing depth, food supply, sediment transport) via wind-forced hydrodynamics. This hypothesis was tested using 201 published estimates of BSP and wind data. Wind stress was significantly correlated with total-, macro-, and meio-benthic secondary production in a negative manner ($r^2 = 0.32, 0.12, 0.52$ respectively; $P < 0.001$). Multiple regression analyses demonstrated that wind stress, tidal height, shelter indices and water temperature explained $\sim 90\%$ of the variance in total-BSP. Neither benthic nor pelagic primary production contributed to a significant reduction in BSP variance. Data support the concept of a physical regulation of coastal benthic energy flow and suggest that the effect of wind stress on BSP is mediated largely by sediment transport.

INTRODUCTION

Tight vertical coupling has been incorporated consistently into models describing pelagic-benthic energetics because the sedimentation of phytoplankton, fecal pellets and detritus represents a major source of particulate organic matter (POM) for the benthos (Rowe 1971, Hinga et al. 1979, Hopkinson 1985). An empirical model developed by Hargrave (1973) successfully utilized annual primary production (C_s) and depth of mixing (Z_m) to predict the magnitude of benthic respiration (C_o) in predominantly deep-water communities: $C_o = 55(C_s/Z_m)^{0.39}$. It was recognized, however, that this model is unlikely to apply in near-shore areas with high advective flow, where allochthonous POM could contribute substantially to the carbon budget.

The vertical flux of POM is frequently insufficient to account for the observed benthic metabolism in numerous coastal communities, and lateral advective input is invariably incorporated to balance the energy budget (Graf et al. 1984, Hargrave & Phillips 1986, Gordon et al. 1987). Conversely, an apparent excess of POM sedimentation has been recognized at a site in the lower Bay of Fundy (Emerson et al. 1986). It was suggested that this excess was laterally transported to an extensive horse mussel bed in an adjacent area of the Bay. Other studies have shown that horizontal POM flux resulting from riverine, wind and tidal forcing may equal or exceed autochthonous benthic and pelagic primary production (Wolff 1977, Hartwig 1978, Lesht & Hawley 1987). It is apparent that hydrodynamically-active ecosystems must be modelled in a framework which combines these horizontal fluxes with the traditional concept of a vertical energy link.

In the Bay of Fundy, tidal currents may be a major determinant of benthic distribution and production by controlling settlement, growth and feeding of benthic animals (Wildish & Peer 1983). In addition, the influence of wind-forced

hydrodynamics on the plankton and the sediment has been widely recognized even in strongly tidal environments (Levasseur et al. 1983, Soniat et al. 1984, Pejrup 1986). Although the effects of wind forcing are most apparent in shallow depths, storms can generate significant sediment disturbance at depths greater than 100 meters (Drake & Cacchione 1985). It is likely therefore, that wind-field analysis will improve models of benthic energetics because the effects of many physical processes on biological production can be integrated in the local wind stress.

The development of a surface mixed layer by wind forcing may limit the amount of photosynthetically-derived POM available to the benthos by determining the availability of nutrients and light necessary for primary production (Pingree 1980, Lewis et al. 1984, Demers et al. 1987), and by regulating the residence time (and therefore the utilization) of POM in the water column (Hargrave 1973). Oxygenation of anoxic bottom water (Soniat et al. 1984), and an increase in the depth of oxygen penetration into the sediment by wind-forced wave action (Rutgers van der Loeff 1981), have the potential to increase aerobic benthic metabolism.

Wind may also influence the benthos by increasing bottom currents beyond the critical erosion velocity of the sediment. Subsequent sediment transport (i.e. bedload and suspended load) may result in an energy subsidy, whereby previously buried POM is made available to a food-limited community. In addition, sediment disturbance has been shown to enhance metabolic activity in both micro- and macrofauna (Findlay et al. 1985, Jumars & Self 1986, Miller & Jumars 1986). Alternatively, sediment transport may exert an energy stress via resource depletion, direct inhibition of suspension feeding and burial of non-motile organisms and

removal of epi- and infauna during storms. It follows that a balance between stress and subsidy from sediment movement will be reflected in the production and community structure of the benthos.

The utility of wind analysis in investigations of benthic energy flow was assessed by 1) determining if wind and coastal benthic production are correlated using published estimates of benthic secondary production and wind speeds and 2) by including wind in a data base of biologically-important environmental variables which could be used to develop a general empirical model of benthic production. In addition to providing estimates of benthic production on a wide spatial scale, it is hoped that this model will stimulate and facilitate further research by identifying those variables most likely responsible for variations in benthic metabolism.

MATERIALS AND METHODS

Biotic Variables

Estimates of benthic secondary production (BSP) and benthic/pelagic primary production (BPP/PPP) were obtained from the literature. BSP was partitioned into total benthic secondary production (Total-BSP), total macrobenthic secondary production (Macro-BSP) and total meiobenthic secondary production (Meio-BSP), where possible. The lack of direct measurements of microbenthic secondary production prevented the addition of this dependent variable to the production models. It was possible, however, to estimate the relative proportion of Total-BSP accounted for by the microbenthos by calculating the difference between Total-BSP and [Meio-BSP + Macro-BSP] at some study sites.

Species-specific production estimates were excluded unless their contribution to total production was measured. Every effort was made to obtain BSP, BPP and PPP

estimates from the same location and year, however pairing of PPP with BSP on tidal flats was frequently restricted to the use of PPP estimates at adjacent subtidal sites.

Selection of production data was not restricted to those studies which employed identical methods of estimation; i.e., it was assumed *a priori* that methodological variation in BSP was less than variation due to spatial wind effects. Although this will not be true in all cases, the method used to estimate BSP of a particular size class was relatively consistent. For example, published Macro-BSP estimates were usually calculated using production:biomass ratios (see Crisp 1971). Determination of annual production of the total- and meio-fauna (P_a , kcal·m⁻²·yr⁻¹) from respiration estimates (R_a) followed Schwinghamer et al. (1986):

$$\log_{10}R_a = 0.367 + 0.993 \log_{10}P_a \quad (2.1)$$

Chemical oxygen demand (COD) of the sediment was subtracted from estimates of total sediment oxygen uptake to calculate benthic aerobic respiration. If an estimate of COD was not provided, it was assumed that CODs of fine and coarse grain sediments were 50 % and 25 %, respectively. BPP and PPP were determined using either the ¹⁴C or O₂ exchange techniques. All units of production were standardized (kJ·m⁻²·yr⁻¹) using the following conversions (Holme & McIntyre 1984): 1 cal = 4.185 J; 1 g ash-free dry weight = 4.23 kcal; 1 g carbon = 12 kcal; 1 ml O₂ (mg O₂) respired = 4.83 cal (3.38 cal).

Physical Variables

Wind velocities (V) were obtained from climatological records (e.g. British Meteorology Office, Environment Canada, U.S. Navy Marine Climatic Atlas, Ruffner 1978). Surface wind stress (τ) was estimated by:

$$\tau = \rho_a \cdot C_d \cdot V^2 \quad (2.2)$$

where ρ_a = air density ($1.3 \text{ kg}\cdot\text{m}^{-3}$) and C_d = a V -dependent drag coefficient (1.14×10^{-3} for $V < 10 \text{ m}\cdot\text{s}^{-1}$ and $[0.49 + 0.065(V)] \times 10^{-3}$ when V is greater than $10 \text{ m}\cdot\text{s}^{-1}$; Thompson et al. 1983).

Two shelter indices indicated the relative protection of a study site from the wind: 1) Effective fetch (EF) was defined as the maximum distance along the sea surface on which the annual mean wind exerts stress, and 2) headwind index (HW) was the difference between the annual mean wind direction and the direction of maximum exposure of the study site (0° = min. shelter, 180° = max. shelter). Tidal height was included as a rudimentary index of tidal current and degree of air exposure at intertidal sites.

Sediment grain size is important to many processes that affect benthic community structure and function, however such data were seldom included in published studies of benthic production. Accordingly, a qualitative sediment size index was assigned to each study site: 0 to 5 = 4.0 to -1.0ϕ . Water temperature and salinity were available from the literature.

Statistical Analyses

The data distribution of each variable was normalized where necessary by log, inverse or square-root transformations. Analysis of residuals indicated which transformation best removed the dependence of variance on the given regressor variable, rather than that which maximized r^2 . Initial identification of the environmental variables significantly related to the production variables was accomplished by constructing a Pearson correlation matrix (SPSS-X). A model-1 least squares regression (Sokal & Rohlf 1981) was performed to examine the

relationship between each dependent variable (Total-BSP, Macro-BSP, Meio-BSP) and correlated variables. Analysis of covariance was employed to assess differences among slopes of all wind stress and production regressions.

The relationship of wind stress and the remaining environmental variables to benthic secondary production was examined through stepwise multiple linear regressions (SPSS-X) that selected the best predictors at $\alpha=0.05$. Because the number of study sites where the headwind index could be calculated was limited, two multiple regressions were performed for each dependent BSP variable. First, a regression was calculated using the entire data set (but excluding HW), and second, the regression was re-calculated using data only from those study sites where HW could be calculated.

RESULTS

Data Set

Two-hundred and one published estimates of benthic secondary production were obtained without restrictions based on location of study site. Many diverse geographical areas were represented in the data set (e.g. New Zealand, Bermuda, southern India, Venezuela), however the prevalence of north temperate data sources (Canada and western Europe) should be noted (Appendix I).

The maximum production of an entire benthic community in these data ($\sim 8000 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) was relatively similar to that of the Meio-BSP ($\sim 6500 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$; Table 2.1). Macrofaunal and meiofaunal production were not significantly different (mean = 703 & 800 $\text{kJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ respectively; $P>0.05$). The mean annual pelagic and benthic primary production (~ 7000 & $5000 \text{ kJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, respectively) were greater than Total-BSP by a factor of two to three.

Table 2.1

Descriptive statistics of biological and environmental variables in the total data set; BSP = benthic secondary production, B/PPP = Benthic/Pelagic primary production ($\text{kJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), CV = coefficient of variation.

Variable	Mean	CV (%)	Min	Max	<i>n</i>
Biotic					
Total-BSP	2833	(81)	197	7969	70
Macro-BSP	703	(101)	16	3895	93
Meio-BSP	800	(157)	2	6430	38
BPP	4492	(97)	0	27187	89
PPP	7248	(119)	200	43921	105
Abiotic					
Temperature (C)	11.8	(44.9)	3	29	145
Salinity (‰)	25.3	(28.1)	6	37	143
Water Depth (m)	13.7	(200.7)	0.5	200	145
Tidal Height (m)	2.6	(126.9)	0	14	145
Sed. Type (0-5)	3.0	-	2	5	145
Headwind (deg.)	86.1	(59.8)	1	180	62
Fetch (km)	42.8	(161.0)	.05	323	145
Wind Stress (Pa)	0.05	(38.0)	.01	.08	144

The contribution of the microbenthos to Total-BSP (~60 %, Fig. 2.1) is consistent with recent suggestions that the bacterial contribution to Total-BSP should be lower than the 90 % level traditionally assumed (Schwinghamer et al. 1986). Meiofaunal metabolism has been considered to be a small fraction of macrofaunal metabolism (e.g. Gerlach 1971), but it is not apparent in this data set; Macro- and Meio-BSP both represented ~20-30 % of Total-BSP.

Low mean annual water temperature illustrates the prevalence of temperate study sites (Table 2.1). A number of estuarine sites resulted in a relatively low mean salinity (25.3 ‰). Mean depth, tidal height and effective fetch had high coefficients of variation. Most benthic study sites were less than 20 m in depth, and the range in mean annual wind stress was relatively narrow (0.01-0.08 Pa).

Wind Stress and Benthic Production

The correlation matrix (Table 2.2) shows that every component of primary and secondary production was significantly correlated with at least one of the wind variables (wind stress, effective fetch, headwind index). In particular, wind stress and effective fetch were significantly correlated with all size components of benthic secondary production. These relationships indicate that, as wind stress increases and shelter from the wind decreases, mean annual benthic production decreases.

Although there was considerable variance in the relationship between Macro-BSP and wind stress (Fig. 2.2b), wind stress accounted for 32 and 52 % of the variance in Total-BSP and Meio-BSP, respectively (Fig. 2.2a,c). The intercepts of the regression equations were very similar ($y \sim 3$), and analysis of covariance indicated that the slopes of the regression lines were significantly different ($P = 0.028$).

Table 2.2

Pearson correlation matrix of biological production ($\text{kJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) and environmental variables: Tot, Mac, and Mei, are total-, macro-, and meio-benthic secondary production. BPP and PPP represent benthic and pelagic primary production.

	Tot	Mac	Mei	BPP	PPP	Te	Z	Sal	TH	Sed	EF	HW	τ
Total	1	.54 ***	.77 ***	.65 ***	.51 ***	.39 ***	.	-.22 *	-.23 *	.	-.33 **	.45 **	-.56 ***
Macro		1	.68 ***	-.18 *	.	-.35 **
Meio			135 *	.	.28 *	.	-.51 ***	.	-.72 ***
BPP				1	.	.33 **	-.31 **	.	.	.	-.37 ***	.34 *	.
PPP					1	.27 **54 ***	.
Temperature (C)						1	-.40 ***	.21 **	-.18 *19 *
Depth (m)							1	.27 **
Salinity (‰)								1	.	.	.32 ***	.	.
Tidal Height (m)									1	.	.	-.40 ***	-.31 ***
Sediment Type (0-5)										1	.	.	.
Effective Fetch (km)											1	-.27 *	.
Headwind Index (degrees)												1	.
Wind Stress (Pa)													1

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, . = not significant

Figure 2.1

Relative contributions of macro-, meio- and micro-benthic secondary production to total benthic secondary production obtained from published estimates. Standard deviations are indicated; $n = 39, 20$ and 20 for macro, meio, and micro size fractions, respectively. Calculations were performed only from study sites where total-BSP and one of the remaining size-fractionated production estimates were known. Microbenthic production was calculated by difference.

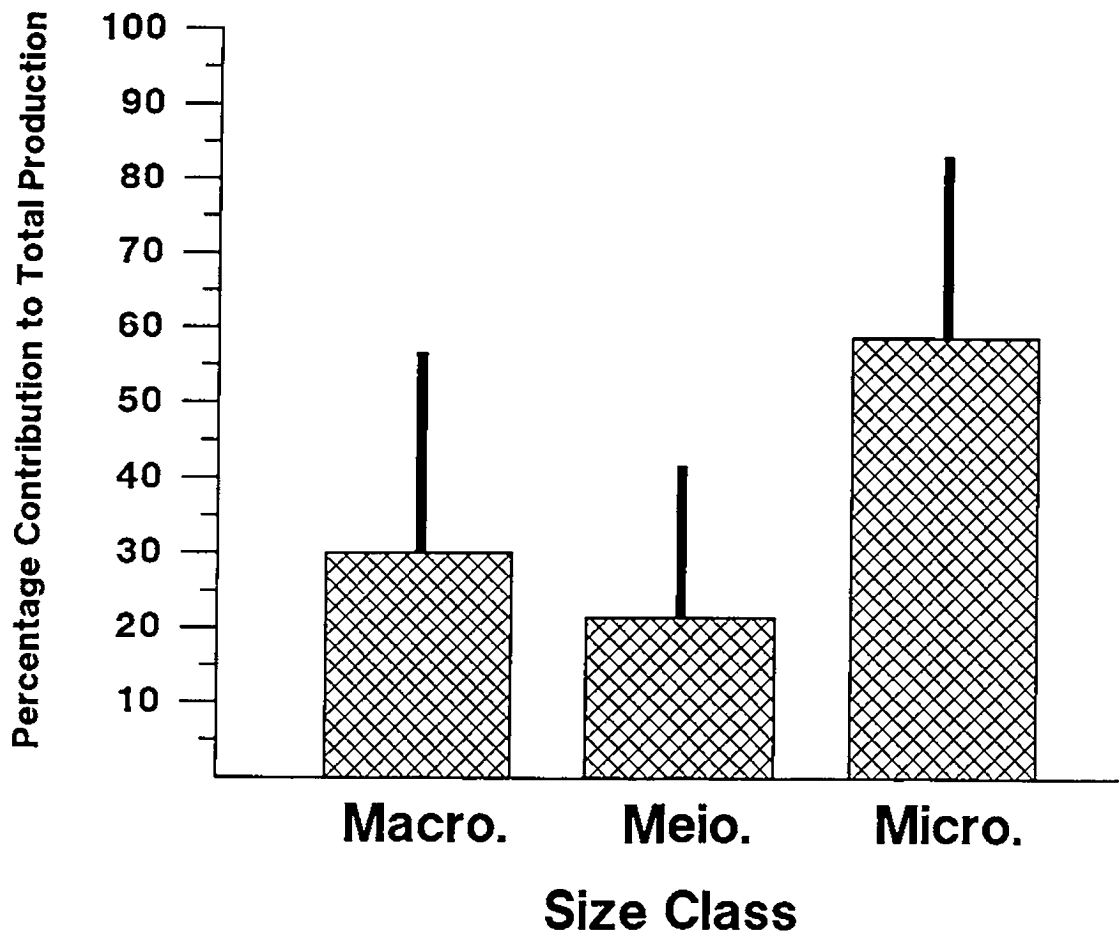


Figure 2.1

Figure 2.2

Simple linear regressions of wind stress and total- (A), macro- (B), and meio-benthic production (C). Coefficient of determination, number of data points and regression equation are listed.

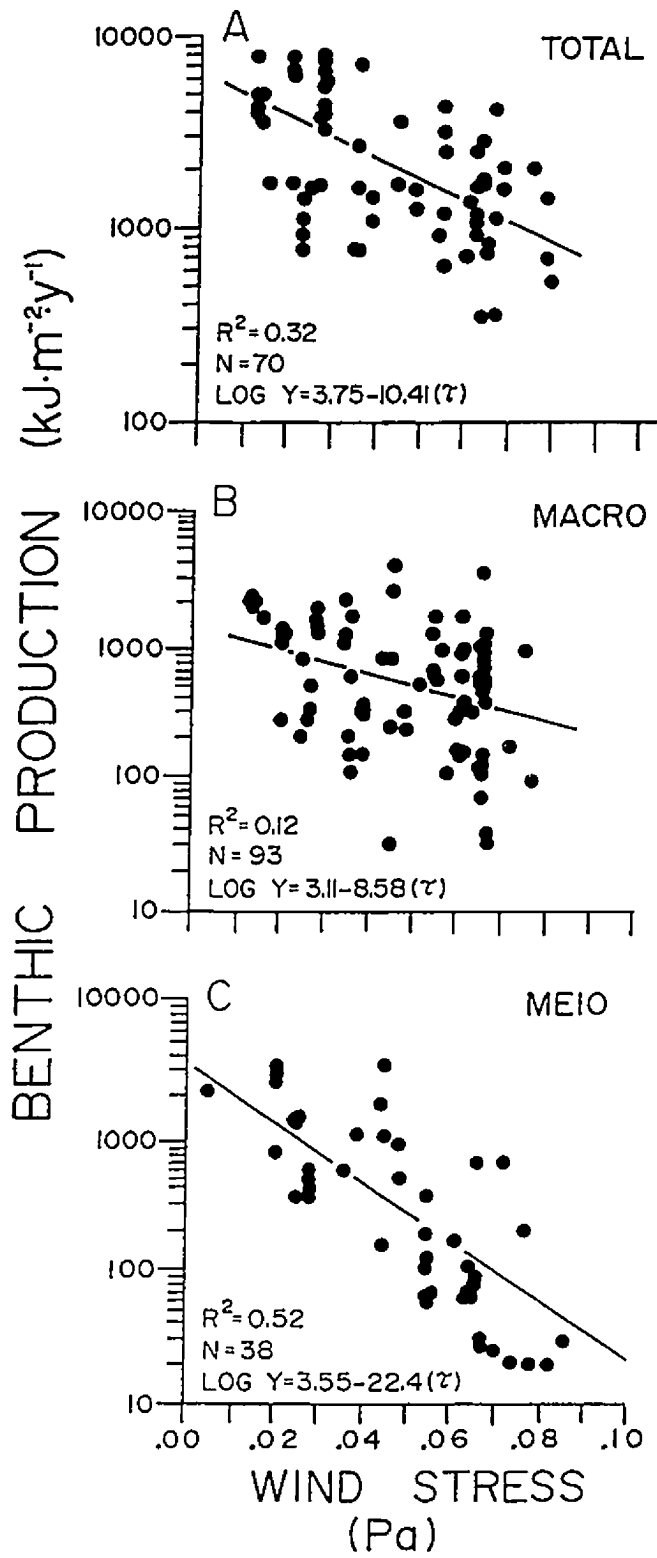


Figure 2.2

The correlation matrix also revealed significant relationships between water temperature, water depth, salinity, tidal height and various biological variables (Table 2.2). Sediment type was not correlated with any other variable.

Multiple Regression Models

Four of the five regression models incorporated wind stress as the most significant variable accounting for the observed variation in benthic secondary production (Table 2.3). Only in the *Total-BSP model was wind stress subordinate; tidal height was the primary predictor variable. In the full Total- and Macro-BSP models, all predictor variables were directly wind-related (τ ,EF,HW) except for mean annual water temperature in the Total-BSP model, and water depth in the Macro-BSP model.

The addition of the headwind index to the Total-BSP model increased the amount of variance which could be explained from 64 to ~90 %. In addition, the high degree of scatter in the observed vs. modelled plot of Macro-BSP was significantly reduced ($r^2 = 0.60$ from 0.23) with the inclusion of the headwind index (Fig. 2.3; Table 2.3). The equation intercepts in all size group production models were equal to ~4.

All models included physical variables exclusively, although the correlation matrix (Table 2.2) indicated a significant relationship existed between both benthic and pelagic primary production and total benthic secondary production. Meio-BSP and Macro-BSP were not significantly correlated with either BPP or PPP. Mean annual water temperature was included in the Total-BSP models, however, its contribution was relatively low. Established relationships between bacterial concentration, POM and sediment surface area (e.g. Yamamoto & Lopez 1985)

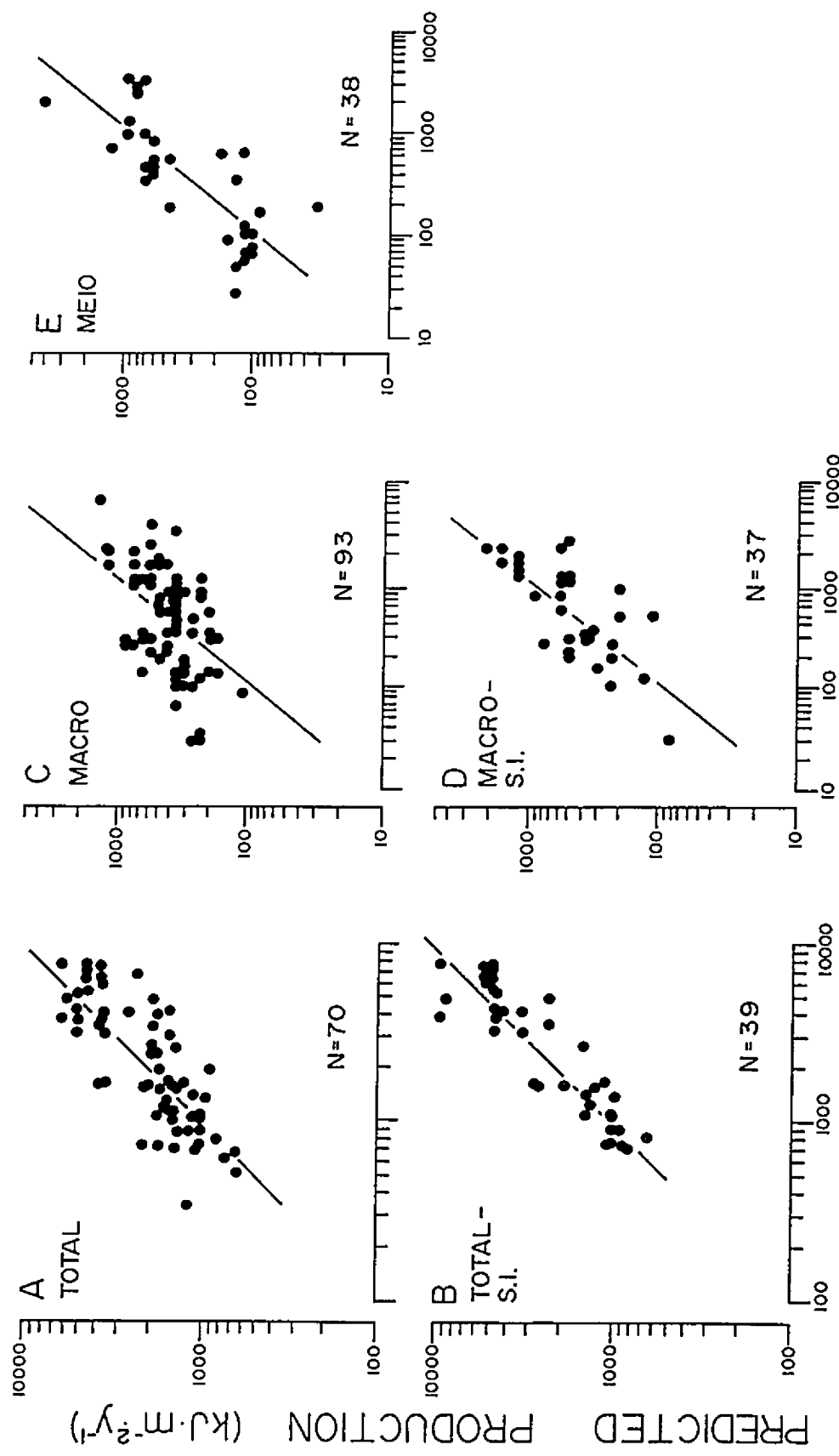
Table 2.3

Stepwise multiple regression models describing log-transformed Total-, Macro- and Meio-benthic secondary production ($\text{kJ}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$). '*' indicates models for those sites where the Headwind index (HW) could be calculated. τ = mean wind stress (Pa), TH = tidal height (m), Te = mean water temperature (C), EF = effective fetch (km), Z = depth (m).

Step	Dependent Variable	Model	r^2	F Significance
1.	TOTAL	= 3.8 - 10.4(τ)	0.34	0.0000
2.	(n=70)	= 3.9 - 13.2(τ) - 0.3(log TH)	0.47	0.0000
3.		= 3.6 - 11.7(τ) - 0.3(log TH) + 0.02(Te)	0.52	0.0000
4.		= 3.7 - 11.4(τ) - 0.3(log TH) + 0.02(Te) - 0.1(EF)	0.64	0.0000
1.	*TOTAL	= 3.4 - 0.4(log TH)	0.36	0.0014
2.	(n=39)	= 3.9 - 0.4(log TH) - 13.0(τ)	0.64	0.0000
3.		= 3.9 - 0.2(log TH) - 18.4(τ) - 0.1(log EF/HW)	0.83	0.0000
4.		= 3.7 - 0.2(log TH) - 16.9(τ) - 0.1(log EF/HW) + 0.02(Te)	0.87	0.0000
1.	MACRO	= 3.1 - 8.6(τ)	0.12	0.0006
2.	(n=93)	= 3.2 - 9.7(τ) - 0.1(log Z)	0.23	0.0000
1.	*MACRO	= 3.4 - 18.2(τ)	0.28	0.0007
2.	(n=37)	= 4.2 - 16.8(τ) - 0.4(log EF/HW)	0.41	0.0001
3.		= 4.5 - 16.8(τ) - 0.5(log EF/HW) - 0.2(log Z)	0.60	0.0000
1.	MEIO	= 3.5 - 22.4(τ)	0.52	0.0000
2.	(n=38)	= 3.5 - 19.7(τ) - 0.2(log Z)	0.63	0.0000

Figure 2.3

Observed total- (A), macro- (C) and meio-benthic production (E) plotted against predicted production derived from regression analyses. Plotted line represents a 1:1 relationship. Total- (B) and macro- (D) production plots include only those data from sites for which headwind index could be calculated. SI = Shelter index.



OBSERVED PRODUCTION ($\text{kJ}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$)

Figure 2.3

were not apparent in the data; the absence of significant correlations of BSP (or BPP) with sediment type was probably a result of the inability to accurately quantify sediment grain size.

DISCUSSION

Of ten biological and physical variables considered, mean annual wind stress accounted for the most variation in four out of five models of benthic secondary production. This is consistent with the trophic group mutual exclusion hypothesis (Wildish 1977), which states that benthic production is food limited and that current acts as the exclusion mechanism; i.e., hydrodynamic forces control benthic energy flow.

It is apparent from the significant negative correlations between wind stress and benthic secondary production, that the positive influence of wind forcing on production (e.g. increased seston flux; Fréchette & Bourget 1985*b*, and a lowered redox potential discontinuity; Boynton et al. 1981, Rutgers van der Loeff 1981) is often subordinate to wind-related biological stress. Detrimental effects of wind-forced hydrodynamics on the benthic community can be partitioned into (1) those resulting from water movement below the critical shear velocity (U_{*crit}) of the sediment, and (2) the effects of wind-forced currents which exceed U_{*crit} .

Below U_{*crit} , wind mixing can decrease the availability of primary production to the benthos by directly inhibiting photosynthesis and by increasing the residence time of particulate organic matter within the water column. The first effect has been summarized in Sverdrup's critical depth model of phytoplankton photosynthesis (see Parsons et al. 1984). Simply stated, if the critical depth (the depth at which total water column photosynthesis equals respiration) is less than the

depth of mixing, no net primary production can take place. It is reasonable to assume, therefore, that annual primary production should be lower in areas where high winds frequently mix the phytoplankton below the critical depth. Secondly, the increase in retention time of photosynthetically-derived POM within the water column will favour the consumption of POM by planktonic heterotrophs.

The former effect is not likely to be significant because the shallow mean depth represented in the data set (14 m) minimizes possible light limitation resulting from plankton downwelling. The significance of the latter effect will be minimal because the food supply to shallow benthic communities is not solely dependent on the passive sinking of POM. Intertidal suspension feeders have been shown to rapidly filter a large proportion of the water column, thus effectively competing with the plankton for available seston (Nichols 1985, Smaal et al. 1986, Emerson et al. 1988). Alternative mechanisms which should contribute to lower community productivity at high wind stress (*vis à vis* increased water turbulence) include direct inhibition of suspension feeding (Wildish & Kristmanson 1979, Wildish & Peer 1983) and a decreased likelihood of larval settlement (Rhoads & Young 1970). It is likely, however, that the dominant negative effects of wind forcing on shallow, coastal communities occur when U_{*crit} is exceeded.

The cumulative effect of the many biologically-important processes associated with sediment transport are manifest in the production of the benthos. When U_{*crit} is exceeded, the erosion and transport of fine, organic-rich particles initially will subsidize a food-limited community (De Jonge & Van den Bergs 1987, Grant et al. 1987). However, prolonged erosion, or an increased U_* , will raise the proportion of non-nutritive inorganic particles in the seston, lower primary production via shading from an increased suspended particulate load, and deplete POM in the sediment.

This scenario is analogous to the 'reverse ramp function' described for scallop growth (Wildish et al. 1987); after initial increases in growth with current speed, growth inhibition was observed with flows of $>10\text{-}20\text{ cm}\cdot\text{s}^{-1}$. The postulated mechanism of scallop growth inhibition involved a reduction in food ration due to a reduction in filtration rate.

The importance of sediment movement to benthic energetics has been highlighted in the scaling arguments of Miller et al. (1984). They contend that food availability to epibenthic deposit feeders can be determined primarily from the examination of sediment transport rate and particle residence time, along with several biological factors. Organism removal (Thistle 1988) and direct mortality resulting from abrasion and burial (Yeo & Risk 1979, Maurer et al. 1986) are some of the more catastrophic phenomena associated with increased bedload at higher current speeds.

The requisite conditions for bulk sediment transport at the study sites subject to high wind stress are present if it is assumed that as the water depth approaches zero (e.g. on intertidal flats) the bottom shear stress can be approximated by the estimated surface wind stress. If $\tau = 0.07\text{ Pa}$ (in the higher range of the wind-stress data set), $U_* = 23.2\text{ cm}\cdot\text{s}^{-1}$, which is well above (20x) the U_{*crit} of most fine sediments (e.g. $U_{*crit} = 0.66\text{-}1.38\text{ cm}\cdot\text{s}^{-1}$; Grant & Bathmann 1987). The probable overestimate of U_* resulting from my simple assumptions is balanced by underestimates inherent in the wind stress formula (Eqn. 2.2; see Thompson et al. 1983) and by additional interactive tidal and residual shear stresses imposed on the sea bed (Pattiaratchi & Collins 1985). Furthermore, my approximation of U_* is consistent with observations of significant POM resuspension at depths greater than 6 meters caused by winds less than $4\text{ m}\cdot\text{s}^{-1}$ ($\tau = 0.02\text{ Pa}$; Demers et al. 1987). Even

at depths greater than 100 m, winter storms can generate U_* ten times larger than U_{*crit} , and can transport $\sim 100 \text{ kg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ of resuspended sediment across the continental shelf (Drake & Cacchione 1985).

The relationships between wind stress and the three size classes of BSP in the data set are consistent with the effects of burial, abrasion, and organism removal associated with wind-forced bedload transport. In regressions of wind stress and BSP, the highest correlation and steepest slope was observed for meiobenthic secondary production. Total-BSP, 80 % of which is accounted for by micro- and meiofaunal production (Fig. 2.1), was also highly correlated with wind stress. Because these smaller organisms ($< 1 \text{ mm}$) inhabit the sediment interstices or live directly on grain surfaces, they are particularly vulnerable to the effects of sediment transport (Palmer & Molloy 1986, Fegley 1987). Macrofauna are less susceptible because of their relative size, mobility or ability to burrow (Grant 1981). Removal of food supply, inhibition of feeding, injury from abrasion, and direct mortality will translate a high susceptibility to sediment transport into a lower annual secondary production. If the wind stress-production correlations were a consequence of bedload transport, the coefficient of determination should increase as the size of organism responsible for production decreases. Results from both multiple and simple regression analyses have clearly reflected these patterns.

Although these regression results cannot be attributed uniquely to the effects of sediment transport, the differential expression of other wind-forced effects is more likely to be observed with mode of feeding (deposit vs. suspension feeders) than with size of organism. For example, a wind-related decrease in primary production would induce acute restrictions in food supply to suspension feeders, yet only affect deposit feeders (regardless of size) over a longer term.

Benthic Production Models

My empirical approach to describing benthic energetics has identified the dominant role of physical variables; approximately 90 % of the variation in total benthic secondary production can be explained by wind stress, tidal height, effective fetch, headwind index and mean annual water temperature. Benthic and pelagic primary production were not selected as predictor variables in any benthic production model. The results are particularly intriguing in view of previous studies which have emphasized the dominant role of primary production in benthic energy flow. It should be re-emphasized however, that the absence of primary production from the multiple regression models may be due to the collection of BSP and primary production data at different times. Although the results of the regression analyses do not exclude the possibility that low benthic production at high wind stress was a consequence of a decrease in photosynthetically-derived food (from light limitation due to increased turbidity; Hargrave et al. 1983), the absence of B/PPP in the models substantiates the hypothesis of Wildish & Kristmanson (1979) that an impoverished community is limited by effects of hydrodynamic forcing (e.g. sediment instability or a direct feeding inhibition) and not by a limited food supply.

The relatively high Q_{10} of bacteria and other microfauna should imply that water temperature contributes significantly to the variance in Total-BSP. Indeed, this is reflected in the results (Table 2.3), however the inclusion of annual mean water temperature resulted in only a small improvement to the model (~5 %). Previous studies have indicated that changes in water temperature alone accounted for >50 % of the short-term variation in benthic metabolism (Hargrave 1969a, Grant 1986). These discrepancies may be resolved through the refinement of data collection;

better spatial and temporal matches between BSP estimates and environmental variables, and an emphasis on variance rather than on mean values (e.g. frequency of storms) will improve the models.

In summary, the empirical models presented in this study have suggested that wind, tidal and temperature data (all easily and routinely measured) can be employed to predict the annual secondary production of the benthos in coastal, soft-bottom communities. At present, the exact mechanisms linking these environmental variables to benthic production are uncertain, however I hope that with the identification of these dominant variables, elucidation of the mechanisms regulating benthic production will be facilitated. In addition, the results show that investigations of vertical energy exchange must consider horizontal fluxes of particulate matter to clearly describe processes leading to pelagic-benthic energy coupling.

CHAPTER THREE
**THE SIMULTANEOUS MEASUREMENT OF BEDLOAD SEDIMENT
TRANSPORT AND PASSIVE FAUNAL TRANSPORT ON INTERTIDAL
SANDFLATS**

ABSTRACT

A simple and inexpensive sampler to measure bedload sediment transport in shallow subtidal or intertidal areas is described. The cylindrical sub-sediment trap with an aspect ratio of 20 (height:diameter) is an improvement over conventional bedload samplers which are difficult to use in shallow areas or fail to collect biological material associated with bedload. Traps deployed on a low-energy intertidal sandflat for six months provided daily estimates of bedload transport (quartz grains: $0.001\text{-}40\text{ kg}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$), passive infaunal transport (e.g. the bivalve *Mya arenaria*, max: $800\text{ ind}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$), and organic detrital flux (e.g. macrophyte fragments, max: $400\text{ g}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$). Bedload rates estimated by the traps were compared to predictions from a numerical bedload model to evaluate the trap's collection and retention efficiency. A high correlation between observed (trap) and predicted (model) rates showed that the traps measured high- and low-frequency variability in bedload transport. Potential applications of the traps in benthic oceanography include recruitment and recolonization studies.

INTRODUCTION

It is believed that movement of the substrate during wind or tidal forcing is an important mechanism controlling community structure and function of shallow, soft-sediment benthos. Although indirect evidence of a tight coupling between bedload sediment transport and the benthos is accumulating (Emerson 1989, Miller 1989), technical limitations have inhibited the direct measurement of bedload transport at time and space scales most relevant to biological processes. To elucidate bedload-benthos interaction, a standard method for directly measuring the transport of bedload and organic material must be developed.

Bedload transport, the movement of particles in continuous or near-continuous contact with the bed, may affect the benthos by controlling food supply, through mortality rate, and by redistributing individuals. Scaling arguments (Miller et al. 1984), laboratory experiments (Jumars & Self 1986), and field studies (Luckenbach et al. 1988, Miller & Sternberg 1988) have indicated that food available to deposit feeders may be primarily a function of the organic particle flux associated with sediment transport. Mortality from abrasion (Miller 1989) and increased predation pressure when infauna become eroded from the sediment (Grant 1981) have also been attributed to sediment transport. If infauna survive erosion, subsequent dispersal by bottom currents may alter recruitment to nearby populations (Palmer 1988*b*). Unfortunately, due to the difficulty of measuring both bedload and biotic transport, the importance of these factors to benthic communities has not been fully evaluated.

Unlike fluxes of particles in suspension, bedload transport cannot be calculated by combining measures of flow velocity and particle concentration. Fluorescent tracers (Sauzay 1973), buried plates (Gordon & Desplanque 1983), and

high-precision tidal flat surveys (Anderson et al. 1981) have been used to estimate *net* bedload transport. Methods for measuring *gross* transport, which may be the more relevant variable for biological studies, have had varying degrees of success. Time-lapse photography of bedform migration (Kachel & Sternberg 1971, Amos et al. 1988) or acoustic sampling (Lowe 1989) may be more accurate than theoretical models (e.g. Vincent et al. 1982) but the equipment is expensive and difficult to deploy in intertidal areas. Direct measurements from a bedload trap would be best because traps allow a representative sample of the moving particles to be collected and retained for analysis. Although there are several types of near-bed traps (e.g. Helley-Smith sampler: see Ludwick 1989), sub-sediment traps have not been used in the marine nearshore environment.

The ideal bedload trap for benthic oceanographers would measure the transport of organic material, such as detritus, benthic algae and infauna, which is associated with grain movement, in addition to the rate of sediment transport. This paper describes a bedload trap which satisfies these criteria, and which is currently being used to quantify the effects of bedload transport on mortality, recruitment and metabolism in a coastal benthic community. Before these effects can be gauged, an assessment of the trap's collection and retention efficiency is required. The challenge of evaluating an instrument for which there are no established standards was met by comparing bedload estimates from trap deployments with predictions generated by a theoretical bedload model. The results of this evaluation, a description of trap design and deployment, and preliminary biogenic flux data are presented.

METHODS AND MATERIALS

Bedload Trap Design and Deployment

Collectors which rest on the sediment surface have the disadvantages of retarding the flow and collecting the horizontal suspended load. With no structure above the sediment, a cylindrical 'pit' sampler is ideal for intertidal flats and is the only trap which is "consistently accurate without extensive calibration" (Hubbell et al. 1985, Rosati & Kraus 1989). The aspect ratio (trap height:trap diameter) of the traditional pit sampler ($AR < 1$) must be increased to at least 5 to limit resuspension and removal of relatively light organic particles (cf. Bloesch & Burns 1980, Gardner 1980, Blomqvist & Håkanson 1981, Butman 1986, Baker et al. 1988). The choice of trap diameter must be a balance between pragmatism and collection efficiency; a large diameter trap may collect bedload efficiently but would necessitate an unwieldy length and permit the entry of unwanted large mobile macrofauna. A small-diameter trap may be easy to deploy but will probably underestimate the transport of saltating material with long jump lengths.

Consideration of these constraints resulted in a bedload trap with a 3-cm diameter and an aspect ratio of 20 (Fig. 3.1). With this diameter, the trap should collect the majority of saltating grains 100-1000 μm in diameter (Murphy & Amin 1979) and prevent large macrofauna such as crabs and demersal fish from disturbing the collections. It was assumed that with a length of 60 cm an effective aspect ratio of at least 5 will be maintained even during periods of high sediment accumulation in the trap.

A simple deployment procedure minimized the disturbance of sediment surrounding the trap: after an open-ended shoring pipe was pushed into the

Figure 3.1

Longitudinal cross-section of the bedload sampler showing trap components and linear dimensions. The sediment trap and shoring pipe are constructed of clear plexiglass and PVC, respectively. Tops of the pipe and trap are flush with the sediment surface. A dark band (lamination) in the collected sediment is composed of organic material that accumulates at the end of each tidal cycle (see text for details). Collected sediment rarely reached the level indicated; on average, sediment filled only the bottom 5-10 cm of the trap.

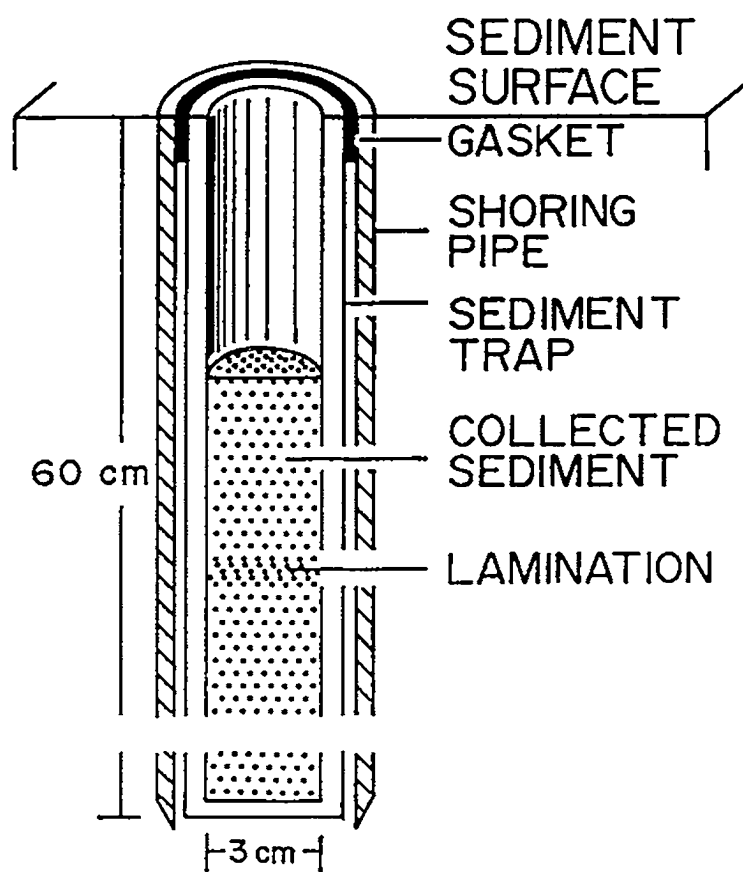


Figure 3.1

sediment as far as possible, a corer was used to excavate the sediment within the pipe. This procedure was repeated until the top of the pipe was flush with the sediment surface and enough sediment was removed to permit the insertion of a cylindrical trap containing filtered seawater (1.2 μm filter pore size). A rubber gasket secured the trap opening at the same level as the pipe and prevented sediment from lodging between the pipe and trap.

From a preliminary trial on an intertidal sandflat, it was found that a trap of clear plexiglass allowed the amount of sediment collected during one tidal cycle to be discerned as distinct laminations in the trapped material. During a tidal cycle, the less dense silt and macrodetrital material accumulated above the heavier sand. The sand which collected during the subsequent flood tide, (usually of light colour), compressed the previously-collected organic material into a distinct dark band (Fig. 3.1). Because the accumulated sediment became consolidated progressively, each tidal accumulation could be quantitatively removed from the trap. As a result, bedload transport could be resolved on a tidal-cycle time scale even if traps were sampled after two days.

Study Site

Bedload traps were deployed between July and December 1988 on a 3 ha intertidal sandflat at Eastern Passage, Halifax Harbour, Nova Scotia (Fig. 3.2). Median grain size and slope of the intertidal flat were 250 μm (<1 % silt-clay content) and $\sim 1^\circ$, respectively. The gastropod *Hydrobia* sp., the polychaete *Spio setosa*, and the bivalves *Gemma gemma*, *Mya arenaria* and *Macoma balthica* dominated the macrofauna. Further ecological details of this sandflat are available from Hargrave & Phillips (1981), Grant (1986) and Emerson et al. (1988).

Figure 3.2

Location and size of the study area on the Eastern Passage sandflat in outer Halifax Harbour, Nova Scotia. The enlarged diagram shows the approximate location of the bedload traps and the buried plates within the 300 m² sampling area. The sizes of the plates and the traps are not to scale. The two traps indicated by dark circles (•) were in continuous use for 6 months. Depth contours and the direction of the *U* component of wind velocity (and true North) are indicated. Intertidal flats are shaded using vertical lines.

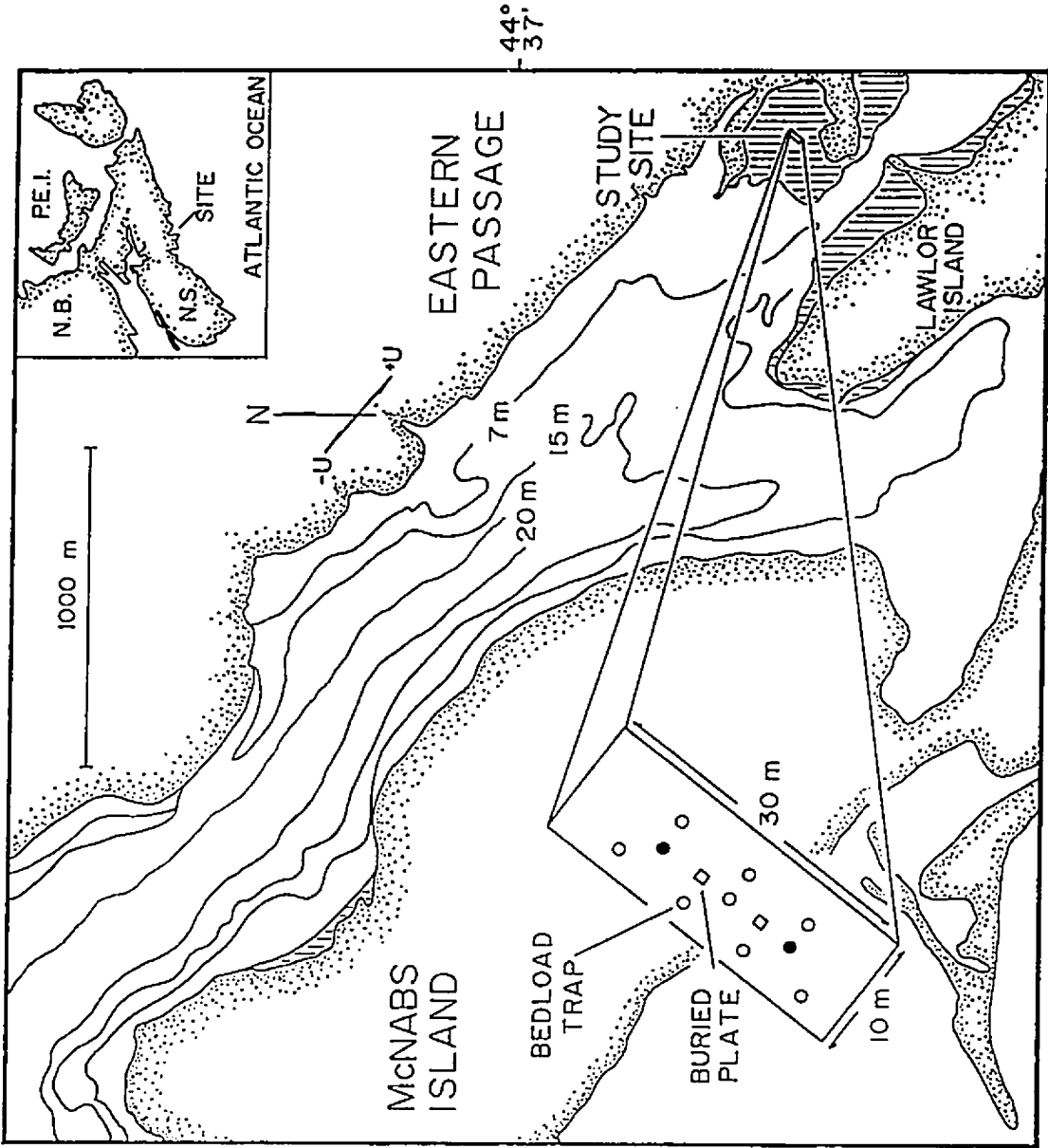


Figure 3.2

In addition to its proximity to the laboratory, the Eastern Passage sandflat was chosen because the physiographic features of this area facilitated the comparison of observed bedload rates with predictions from a theoretical model. Because many bedload models are based on wave-tank experiments, their predictions would be most suitable for sites which resemble wave tanks. This study site, at the southeast end of the long narrow channel (max. fetch = 10 km) with a relatively uniform decrease in water depth, met this criterion.

Trap Deployment

Initially, 10 bedload traps were deployed throughout a 300 m² sampling area (Fig. 3.2) but because between-trap variation in bedload estimates did not decrease significantly with more than 2 traps (CV=20-30 %, analysis of variance, $P > 0.05$), only 2 replicate traps were used after August. Periodic deployment of 10 traps after August (twice per month) indicated that sampling variation remained relatively low (CV < 33 %) under higher levels of bedload transport.

On at least 22 days each month, traps containing bedload were replaced at low tide with new traps containing filtered seawater; no more than 2 successive days separated trap retrievals. Macrofauna were picked out of the bedload samples and preserved in 10 % formalin. After the remaining material was dried to constant weight (70°C), macrodetrital material, such as fragments of kelp and seagrass, was separated from the sediment (sand grains) by sieving the sample through a 500 μm mesh. Although some biogenic material could not be separated from the sediment in this manner, greater than 96 % of the sample dry weight was sand; the detrital fraction was underestimated by approximately 10 %. Bedload transport was expressed as sediment dry weight per meter (extrapolated from the trap diameter)

per day (~25 hr = 2 tidal cycles). The passive transport of bivalves was expressed as number of individuals per meter per day. Fauna which are more mobile than clams (e.g. amphipods and isopods) could be quantified only as the number of individuals found in a trap on each sampling day.

In addition to the measure of gross sediment transport from the bedload traps, net sediment transport was determined from the daily change in sediment height above two 900 cm² plexiglass plates, initially buried at 20 cm depth (Fig. 3.2). Sediment height was measured by inserting a thin graduated rod vertically into it until the rod reached plate depth. If sediment ripples were present, the rod was inserted into the trough. Sampling precision was approximately ± 3 mm. Results were expressed as deviations from the average height of sediment above the two plates.

The density of macrofauna was determined from 5 sediment cores (17.5 cm diameter x 10 cm depth) collected daily within the sampling area. Cores were not taken within 2 m of either a bedload trap or a buried plate and the same area was not re-sampled at a later date. After the core samples were sieved (1.5 mm mesh), amphipods, isopods and two of the dominant bivalves (*Mya arenaria* and *Macoma balthica*) were enumerated. *M. arenaria* longer than 3 cm in shell length were not included in density estimates because a 10 cm sampling depth was not adequate to estimate their density (Emerson et al. 1988, Zwarts & Wanink 1989).

Evaluation of Bedload Trap Efficiency

A rigorous calibration of the traps was not possible because there are no instruments which measure intertidal bedload transport with a known accuracy. However, the utility of the traps could be assessed by comparing the size of trap

samples with predictions from a theoretical bedload model. Although numerical models cannot predict bedload rates with 100 % accuracy, they are able to reproduce accurately the temporal variation of bedload transport (Williams et al. 1989). For many benthic studies, a measure of temporal variation, rather than an absolute rate, may be the variable of primary interest. Therefore, a good correlation between trap samples and model bedload estimates would demonstrate that the bedload traps may be useful in biological applications.

By combining a common wind-wave model with a published bedload formula, a predictive bedload model for the Eastern Passage sandflat was constructed (Appendix II). Several bedload formulae are available (see Ludwick 1989, King & Seymour 1989), but most are based on mean, time-averaged steady flow in open channels and do not account for oscillatory flow. The formula derived by Sleath (1982b) was chosen because it is based on oscillatory transport and incorporates a coefficient of friction for rippled beds and a threshold of sediment motion. The major difference between this and other formulae is the exponent of the Shield's parameter, the dimensionless bed shear stress (θ , Appendix II, Eqn. AII-12). Empirical evidence has suggested that Sleath's choice of θ may be most appropriate for estimating bedload transport (King & Seymour 1989).

Hourly wind speed and direction for wave modelling were obtained from the Atmospheric Environment Service, Bedford N.S., which operates a meteorological station within 4 km of the study site. Wind was partitioned into U and V vector components after adjusting the wind direction so that the N-S axis was parallel to the NW-SE channel (310° - 130° , Fig. 3.2). Therefore, NW winds became the maximal $+U$ component and were directed onto the study site, whereas SE winds

(maximal $-U$ component) did not directly have impact on the study site. The V component was not analyzed because the short fetch along this axis (<300 m) prohibited significant wind-wave generation by along-shore winds.

Hourly sealevel data measured with tide gauges in Halifax Harbour were obtained from the Marine Environmental Data Service, Ottawa. Hourly sealevel data were included in the model because wave height and period, orbital velocity, and bed shear stress are all influenced by water depth (Appendix II, Eqns. AII-6-9). Changes in water depth also regulate the duration of tidal flat exposure to air; during a spring tide, the study site was exposed for ~ 7 hours longer per day than during a neap tide. As a result, there was a greater potential for wave-forced bedload transport to occur during a neap tide. Maximum water depth over the study site was 1.6 m and the average duration of air exposure during low tide was 11 hours per day. Because the semidiurnal tidal currents across the study site were relatively low (max. <10 $\text{cm}\cdot\text{s}^{-1}$), I assumed *a priori* that tidal forcing alone was insufficient to generate bedload transport (cf. Grant et al. 1986a, Peterson 1986).

RESULTS AND DISCUSSION

Predicted vs. Observed Bedload Rates

Trap and model estimates showed that the timing of discrete bedload events and seasonal trends corresponded well (Fig. 3.3 C&D). The maximum observed rate of bedload transport (Nov. 21; 35 $\text{kg}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$) coincided with that predicted by the model. Seasonally, both the observed and predicted bedload time series could be partitioned into three periods: (1) a summer period of minimal transport (<1 $\text{kg}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$) coinciding with predominantly low $+U$ winds ($<<5$ $\text{m}\cdot\text{s}^{-1}$, Fig. 3.3A), (2) a fall plateau with increased winds ($5-7$ $\text{m}\cdot\text{s}^{-1}$) of longer duration and higher bedload

Figure 3.3

Time series of (A) the U component of wind velocity (6-hour means), (B) daily height of sediment above the buried plates (average from 2 plates) expressed as the deviation from mean sediment height, (C) daily gross sediment transport measured by bedload traps, and (D) daily gross sediment transport predicted from the theoretical model (see Appendix II). Note the change in scale from (C) to (D).

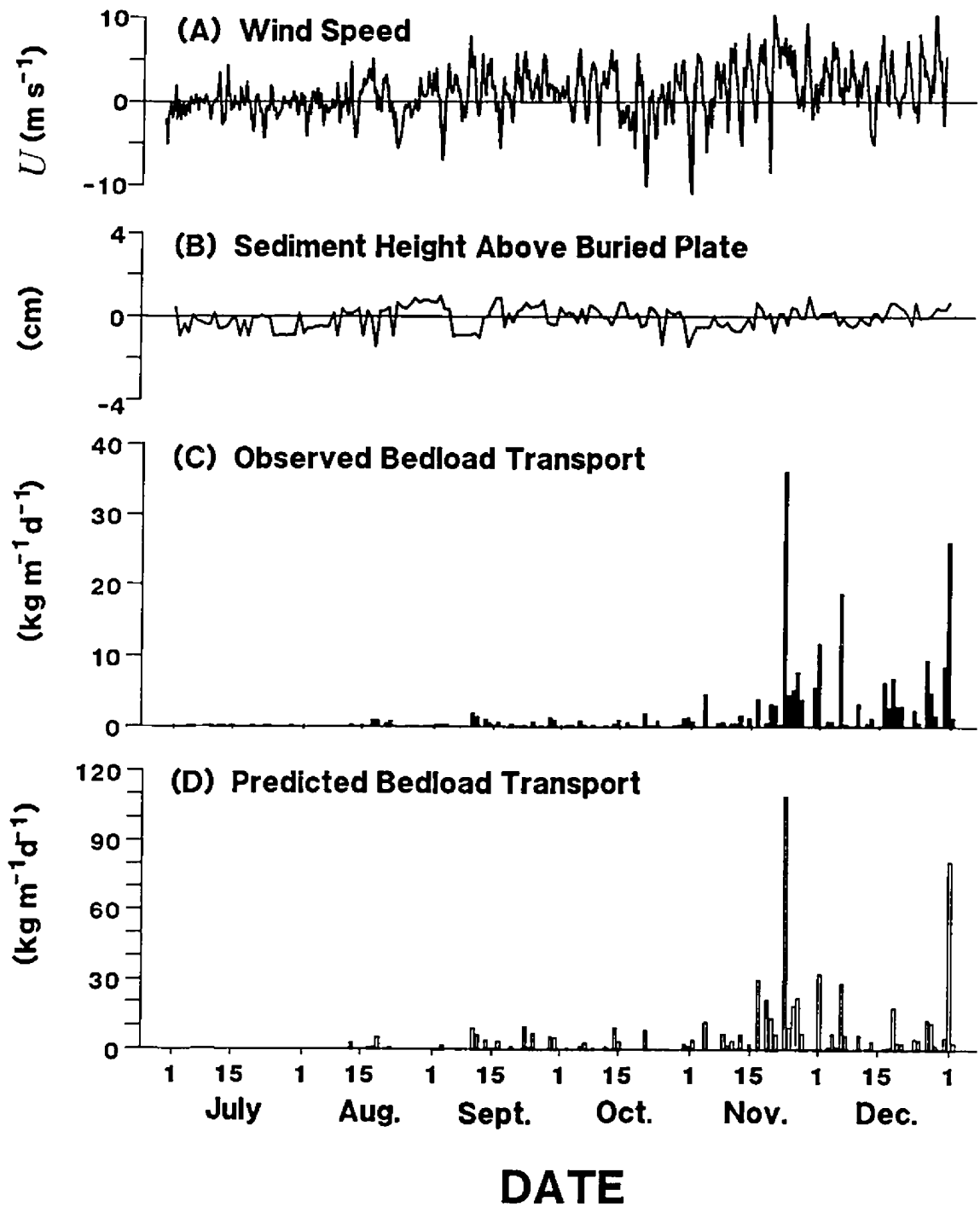


Figure 3.3

rates (0.02-10 kg·m⁻¹·d⁻¹), and (3) a late fall/early winter period of highest winds (~10 m·s⁻¹) and maximum bedload transport (35 and 110 kg·m⁻¹·d⁻¹; trap and model, respectively). Although bedload transport was usually high during the last period, high-frequency variation in both wind speed and direction was often reflected in the bedload transport; it was not uncommon to observe rates of 20 kg·m⁻¹·d⁻¹ immediately following a low of 0.02 kg·m⁻¹·d⁻¹ (e.g. on December 5).

A scatterplot of predicted (model) versus observed (trap) bedload estimates revealed two discrepancies: (1) theoretical transport rates were usually higher than trap estimates by a factor of two to three, and (2) the linear relationship between observed and predicted estimates was absent at low bedload rates (Fig. 3.4). Rather than a trapping bias, the first discrepancy was most likely a result of model limitations. Because most bedload formulae have been derived using clean quartz grains, numerical models often overestimate bedload transport in sediments containing high microbial densities. Stabilization of the sediment by microbial binding is common at Eastern Passage and many other coastal areas (Grant et al. 1986b, Grant 1988). Overestimates also may have resulted from an inappropriate choice of the maximum wave height constraint ($H_{max} = 0.73 \times$ water depth: Appendix II). Guza and Thornton (1985) have suggested that wave heights in shallow water are only 20-40 % of offshore incident waves. Regardless of the cause, a relatively constant difference between predicted and observed bedload rates did not imply that the bedload traps were ineffective. The change in the predicted vs. observed relationship at low levels of bedload, however, may indicate an important deficiency of the bedload traps.

Figure 3.4

Predicted (model) versus observed (trap) bedload transport on the Eastern Passage sandflat. Two separate regression functions were fitted to the data using a 'piecewise' regression model (see text). The solid line is the least-squares 'best fit', and indicates the point at which the observed vs. predicted relationship becomes linear ($0.1 \text{ kg}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$; predicted). The coefficient of determination between 0.1 and $1000 \text{ kg}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$ (predicted) was 0.65 , ($P < 0.001$); below $0.1 \text{ kg}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$, the slope was not significantly different from zero ($P > 0.05$). A 1:1 relationship is indicated by the dashed line.

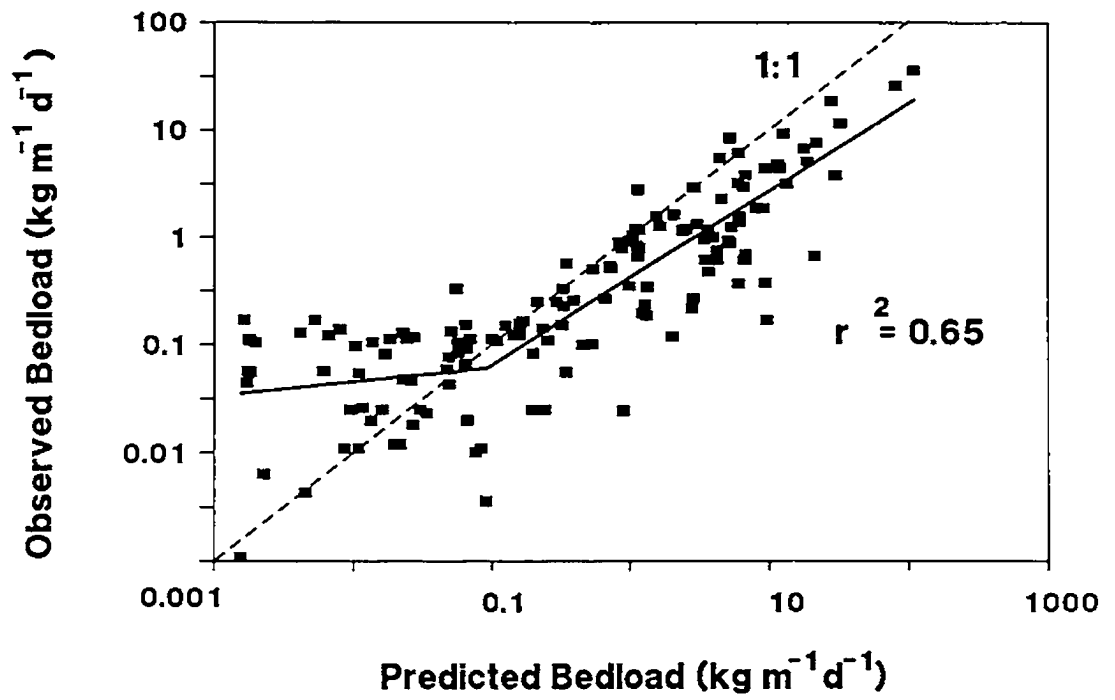


Figure 3.4

The second discrepancy was examined by determining the point at which the observed bedload rates exceeded predicted rates using a piecewise linear regression procedure which objectively separated the data into two linear regressions (Wilkinson 1988, Fig. 3.4). There was a significant linear relationship between the observed and predicted bedload estimates from 0.1 to 100 $\text{kg}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$ on the x -axis ($r^2=0.65$, $P<0.001$). When traps accumulated more material than predicted (e.g. below $0.1 \text{ kg}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$), the slope of the regression line was not significantly different from zero ($P>0.05$). In addition, on eight days throughout the sampling period bedload was collected in the traps although none was predicted. It is likely that this discrepancy also resulted from simplifications in the model rather than a problem with the traps.

Although I recognized that the absence of wave refraction, multiple critical thresholds, and wave-tide interaction would decrease predictive accuracy, I was not able to incorporate these factors into the model. Each of the simplifications could lead to underestimates of bedload, particularly at low levels of transport. First, I assumed that only $+U$ winds would induce bedload transport. While adequate for most days, this assumption was invalid when $-U$ winds were highest (i.e. minimum $+U$ winds). At these times, waves 0.5-1.5 m in height were observed travelling northwest through the channel between Lawlor Island and Eastern Passage, refracting, and then impinging on the study site. Secondly, because the mean sediment grain size ($250 \mu\text{m}$) was used in the critical threshold equations (Eqns. AII-10-13, Appendix II) rather than a range of grain sizes, the transport of particles less than $250 \mu\text{m}$ under relatively small waves could not be predicted (see Nickling 1988). This problem was likely to be insignificant because the sediment was well sorted. Lastly, although spring tidal currents alone did not generate bedload

transport, the combination of tidal and wave forcing may have exceeded the critical shear stress of the sediment even though the component forces were small (Vincent et al. 1982, Pattiaratchi & Collins 1984,1985). Therefore, for several reasons it is probable that discrepancies in the relationship between trap and model estimates result from limitations of the model rather than from a trapping bias of the bedload sampler.

One important limitation of the trap was its inability to maintain an effective aspect ratio of 5 during the storm on November 21. When the level of trapped sediment rose to within 15 cm of the trap, resuspension and removal of material may have resulted in an underestimation of bedload and biotic transport during this peak of bedload transport. Therefore, a trap length of 60 cm (aspect ratio = 20) appears to be inadequate to monitor bedload transport greater than $35 \text{ kg}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$. When bedload transport was less, typical of the other days, trap and model estimates were closely correlated, showing that the trap worked well. Moreover, the traps did not exhibit many of the problems, such as scouring around the trap mouth, that have been documented in other studies (Savidge & Taghon 1988).

Transport of Biological Material

Mya arenaria, the soft-shell clam, was a frequent component of the material collected in the bedload traps (Fig. 3.5A). Although it is able to burrow, *M. arenaria* is relatively sedentary (Medcof 1950), only emerging from the sediment during prolonged exposure to anoxia (*pers. obs.*: laboratory experiments). Its presence in the traps, therefore, indicates that clams were passively transported across the sediment surface after being eroded from the sediment. A significant positive correlation between bedload transport and clam transport (Table 3.1) is consistent

Table 3.1

Correlation coefficients (r) determined from simple linear regressions between log-transformed biological and physical variables. Flux estimates were obtained from bedload traps and density estimates were obtained from core samples. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, · Not tested.

	Bedload Transport ($\text{kg}\cdot\text{m}^{-1}\text{d}^{-1}$)	<i>Mya arenaria</i> Transport ($\text{ind}\cdot\text{m}^{-1}\text{d}^{-1}$)	Detrital Transport ($\text{kg}\cdot\text{m}^{-1}\text{d}^{-1}$)
<i>Mya arenaria</i> Transport ($\text{ind}\cdot\text{m}^{-1}\text{d}^{-1}$)	0.69 ***	·	·
<i>Mya arenaria</i> Density ($\text{ind}\cdot\text{m}^{-2}$)	-0.39 ***	-0.57 ***	·
Amphipod Density in Traps	·	·	0.25 *
Isopod Density in Traps	·	·	0.38 **

Figure 3.5

Bar graphs representing the (A) daily passive transport of the soft-shell clam *Mya arenaria*, (C) daily organic detrital flux, and the daily presence of (E) amphipods and (G) isopods in the bedload traps. The transport of *Macoma balthica* is not included because it was only found in the traps on November 21 ($\sim 60 \text{ ind}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$). Densities of (B) *M. arenaria*, (D) *M. balthica*, (F) amphipods, and (H) isopods in the sediment surrounding the bedload traps are indicated. Vertical lines in the graphs of density represent standard deviations.

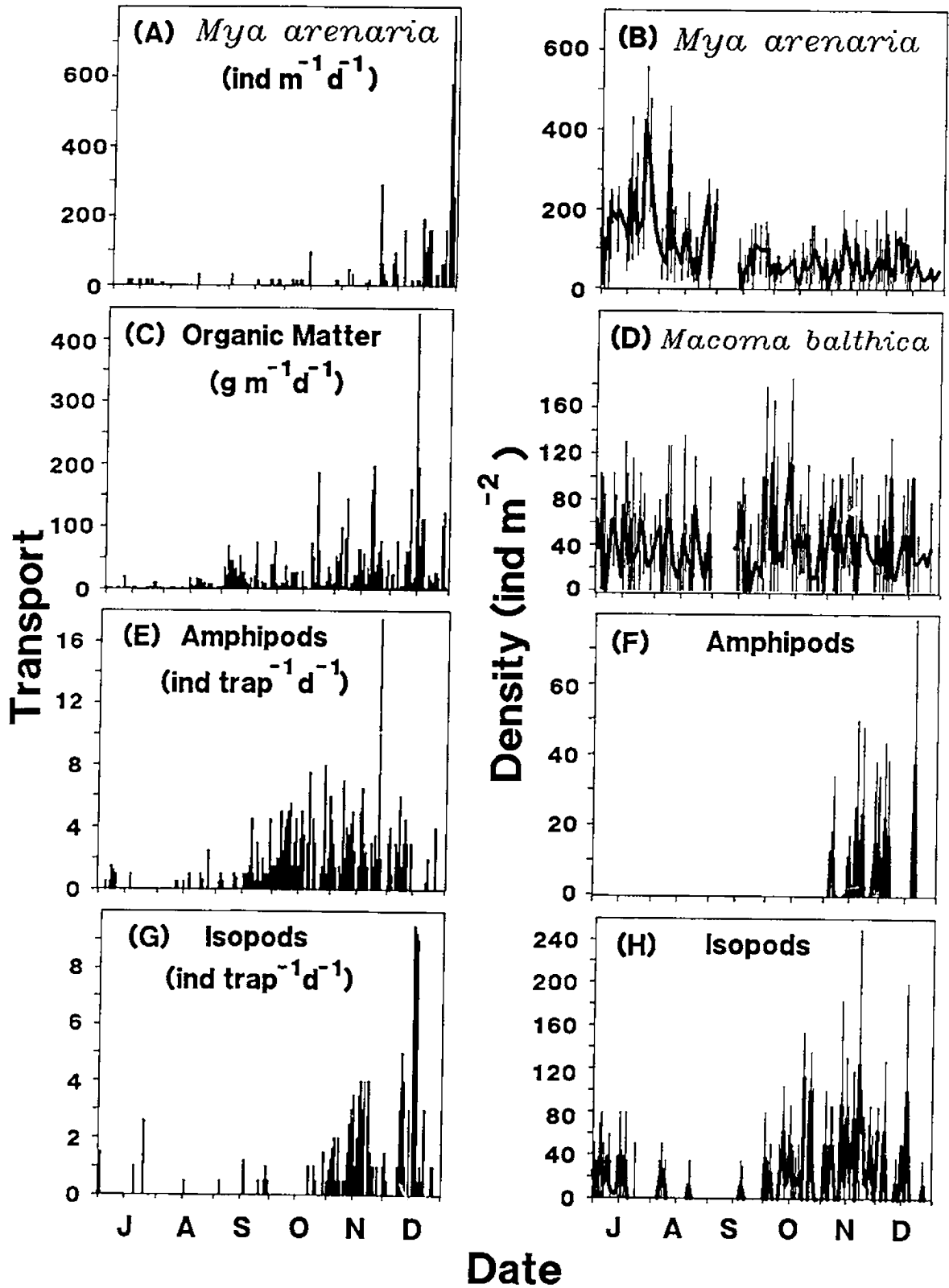


Figure 3.5

with this hypothesis. The bivalve *Macoma balthica*, which also resides in the upper 10 cm (Fig. 3.5D), was only observed in the traps on November 21, the time of maximum bedload transport. These preliminary observations indicate that the traps may be useful in recruitment and recolonization studies for some species.

For many benthic invertebrates with a planktonic life stage, it is not known whether the observed population density is more a function of the magnitude of spat settlement (metamorphosed larvae) or of post-settlement mortality (Peterson 1986, Fairweather 1988). By deploying bedload traps, it has been shown that passive transport of infauna during periods of high bedload transport should be considered an additional source of recruits or as a mechanism for the removal of individuals living in soft-sediment communities. Although the average transport of *Mya arenaria* was low ($<10 \text{ ind}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$), transport often exceeded $100 \text{ ind}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$, reaching a maximum of $800 \text{ ind}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$. Bedload transport may have been responsible for a net removal of clams at Eastern Passage because clam density was negatively correlated with both bedload transport and passive clam transport (Table 3.1). Bedload appeared to be less important to *Macoma balthica*, probably because *M. balthica* is able to burrow more deeply than *M. arenaria* of the same size (Commito 1982).

The traps also provided data on mobile organisms that would otherwise be difficult to obtain. Because amphipods and isopods can either swim or burrow, they were not always detected in my study because technical limitations restricted sampling to the collection of cores at low tide. On several days, core samples did not reveal the presence of amphipods and isopods even though they were found in the traps (Fig. 3.5 E-H). In a process analogous to the addition of "swimmers" to pelagic sediment traps (Lee et al. 1988), these mobile detritivores were probably

attracted by the accumulation of organic matter within the traps (Fig. 3.5C; max. accumulation = 20 g dry wt). The significant positive correlations between macrodetrital flux and the density of both amphipods and isopods in the traps support this contention (Table 3.1).

The ability to measure organic detrital flux may help determine the amount of food available to both deposit- and suspension-feeding organisms because a significant percentage of their diet may consist of the organic matter imported during bedload transport (Miller & Sternberg 1988). If the rate of gross organic transport is combined with a measure of the net incorporation of carbon into the surface sediment (see Grant 1985), both the response time of the benthos to food additions and the efficiency with which this food is utilized may be determined. In addition, bedload transport data may demonstrate the relative importance of physical and biological processes to the incorporation of organic matter into the sediment.

Net Sediment Transport

Previous attempts to explain biological phenomena in terms of sediment transport have used the change of sediment surface level as the primary index of sediment movement (Landahl 1988, Grant et al. 1990). As a measure of erosion and deposition (i.e. net transport) this variable is useful, but it does not provide a good measure of total sediment movement. The time series of sediment height above the buried plates (Fig. 3.3B) did not record the high sediment transport that was observed in early winter (Fig. 3.3C). Apparently, erosion and deposition were in balance during periods of high bedload transport. A change of population density occurring during this period would not be attributed to passive transport using only

buried plate data. Because bedload traps measure the magnitude of transport without indicating whether erosion or deposition has occurred, I suggest that the combined use of bedload traps and buried plates would be the most efficient and practical way to elucidate the effects of bedload transport on shallow, soft-sediment benthos.

At present, cylindrical bedload traps are being used to examine the relationship between bedload transport and faunal recruitment, phytobenthic production, and total sediment oxygen demand on high and low-energy intertidal sandflats. Much of the previous literature documenting benthos-sediment interaction has concentrated on the effects of the benthos on sediment transport (e.g. Rhoads & Young 1970, Jumars & Nowell 1984, Grant 1988). Simple but efficient bedload traps of the kind I have described should facilitate the study of sediment transport effects on the benthos.

CHAPTER FOUR

THE INFLUENCE OF BEDLOAD TRANSPORT ON RECRUITMENT TO
POPULATIONS OF THE SOFT-SHELL CLAM (*MYA ARENARIA*) ON LOW-
AND HIGH-ENERGY INTERTIDAL SANDFLATS

ABSTRACT

Cylindrical sub-sediment bedload traps were deployed in a low- and a high-energy intertidal sandflat to elucidate the relationship between bedload sediment transport, passive clam transport, and recruitment to populations of *Mya arenaria*. Daily measurements for 10 months indicated that clam transport occurred with high frequency (max. rate >2600 clams \cdot m $^{-1}$ \cdot d $^{-1}$) and only during periods of bedload transport. At the sheltered sandflat, clam transport was positively correlated with bedload transport ($r^2=0.26$, $P<0.001$) and negatively correlated with the density of clams in the top 10 cm of sediment ($r^2=0.22$, $P<0.001$). At the high-energy study site, clam transport accounted for an order of magnitude increase in clam density in the fall and a precipitous density decrease during the maximum bedload transport event (36 kg \cdot m $^{-1}$ \cdot d $^{-1}$, Nov. 3). Spat settlement was responsible for less variation of clam density than passive clam transport. I suggested that clam transport associated with bedload transport may control population demography in temperate areas and may balance the effects of overfishing on commercial clam flats.

INTRODUCTION

Persistent indications that the demography of coastal benthos is regulated by sediment transport have failed to incite an evaluation of bedload transport as a regulator of recruitment in soft sediments. Movement of the bed has been frequently linked to settlement success (Kraeuter & Castagna 1989), mortality (Kranz 1973), food supply (Rhoads & Young 1970), growth (Emerson *in press,a*), and population distribution (Matthiessen 1960, Rees et al. 1977). However, attempts to explain the observed density and distribution of a population continue to examine the variation in larval settlement and post-settlement survivorship without a knowledge of local sediment dynamics. If simultaneous measurements of bedload transport, population density and spat settlement can be obtained, it may be possible to account for unexplained variation in the distribution and growth of macroinfaunal populations.

Although predation and competition can limit the abundance of free-swimming and settled recruits (Woodin 1976, Peterson 1986, Crowe et al. 1987, Hunt et al. 1987, Zajac et al. 1989), hydrodynamic forcing during the planktonic larval period is often a more important factor controlling adult densities (Eckman 1979, Hannan 1984, Johnson & Hester 1989). Settling larvae, may actively select substrates (Muus 1973, Woodin 1986), but it is likely that settlement ultimately depends on the magnitude of near-bottom turbulence (Butman 1989) and passive entrainment around bottom structures (Eckman 1983,1987). It has become apparent, however, that the extent to which hydrodynamics control benthic recruitment may not be limited to the regulation of planktonic larval distributions or settlement success.

When bottom currents exceed the critical shear stress of the sediment, the movement of the bed may affect recruitment rates by importing or exporting individuals that become trapped within migrating bedforms or become exposed to dispersive currents when sediment is eroded (Palmer 1988b). The influence of bedload transport will not be limited to catastrophic sediment disturbance (e.g. Paul et al. 1975, Yeo & Risk 1979, Desrosiers et al. 1984) because tidally-forced bedform migration may be sufficient to redistribute infauna (Grant 1981,1983). It is possible, therefore, that the magnitude and frequency of bedload transport caused by wind or tidal forcing may control the population density and distribution of relatively sedentary infauna.

Mya arenaria, the soft-shell clam, is an ideal species with which to test the hypotheses that (1) passive transport of infaunal bivalves can occur during bedload transport, (2) passive transport is correlated with population density, and (3) passive transport via bedload is more important to population recruitment than spat settlement. High numbers of young clams live in the upper few centimeters of sediment where the effects of bedload transport would be greatest (Emerson et al. 1988, Zwarts and Wanink 1989). In addition, *M. arenaria* is highly resistant to abrasion (Driscoll 1967) and burial (Emerson et al. *in press,b*), and can rapidly reburrow after inadvertent exposure (Baptist 1955). Lastly, because *M. arenaria* does not have a well-developed foot, rapid changes in the density or distribution of a clam population will probably be a result of passive transport rather than active migration. If passive transport does occur, and if it can be linked to density changes, the traditional assumption that clam populations rely almost exclusively on spat settlement for recruits must be re-examined (e.g. Brousseau 1978b).

MATERIALS AND METHODS

Study Sites

The effect of bedload transport on recruitment to populations of *Mya arenaria* was determined on two intertidal sandflats separated by a small sand/grass peninsula at Eastern Passage N.S. (Fig. 4.1). The study areas were confined to a 300 m² area in the mid-intertidal of each sandflat. Semi-diurnal tidal currents in the channel between the peninsula and Lawlor Island have been shown to exceed 100 cm·s⁻¹ (Muschenheim 1987a) but were less than 10 cm·s⁻¹ over the intertidal study area and were insufficient for the generation of bedload transport (cf. Grant et al. 1986a). Maximum water depth over both sandflats was 1.6 m, and the average daily duration of air exposure was 8 hours.

The proximity of the two sandflats ensured that each study area was exposed to the same precipitation, solar radiation, air temperature and water mass, while providing a temporal contrast in wind-wave forcing. The 'exposed' sandflat, which faced the Atlantic Ocean, was subject to large waves throughout the year, whereas several islands and a restricted harbour fetch (~10 km) usually protected the 'sheltered' sandflat. Only during high northwest winds were large waves (~1 m height) observed approaching the sheltered site. Despite the difference in exposure to hydrodynamic forcing, each sandflat had a similar grain size distribution (median grain size = 250 µm, silt-clay content = <1 % by weight) and a surface slope of approximately 1°. Sediment ripples of 1 cm height and 2-3 cm wavelength were often observed at the exposed sandflat, but rare in the sheltered site study area.

Mya arenaria is one of the dominant macrofaunal species on the sheltered sandflat; average clam density in spring was 250 ind·m⁻² (max.=800 ind·m⁻²;

Figure 4.1

Location of the exposed and sheltered sandflats (1.5 and 3 ha, respectively) at Eastern Passage, outer Halifax Harbour, Nova Scotia. Intertidal areas are shaded with diagonal lines. Bathymetry, location of the meteorological station, and direction of the wind vector components are indicated ($+U \sim 310^\circ$).

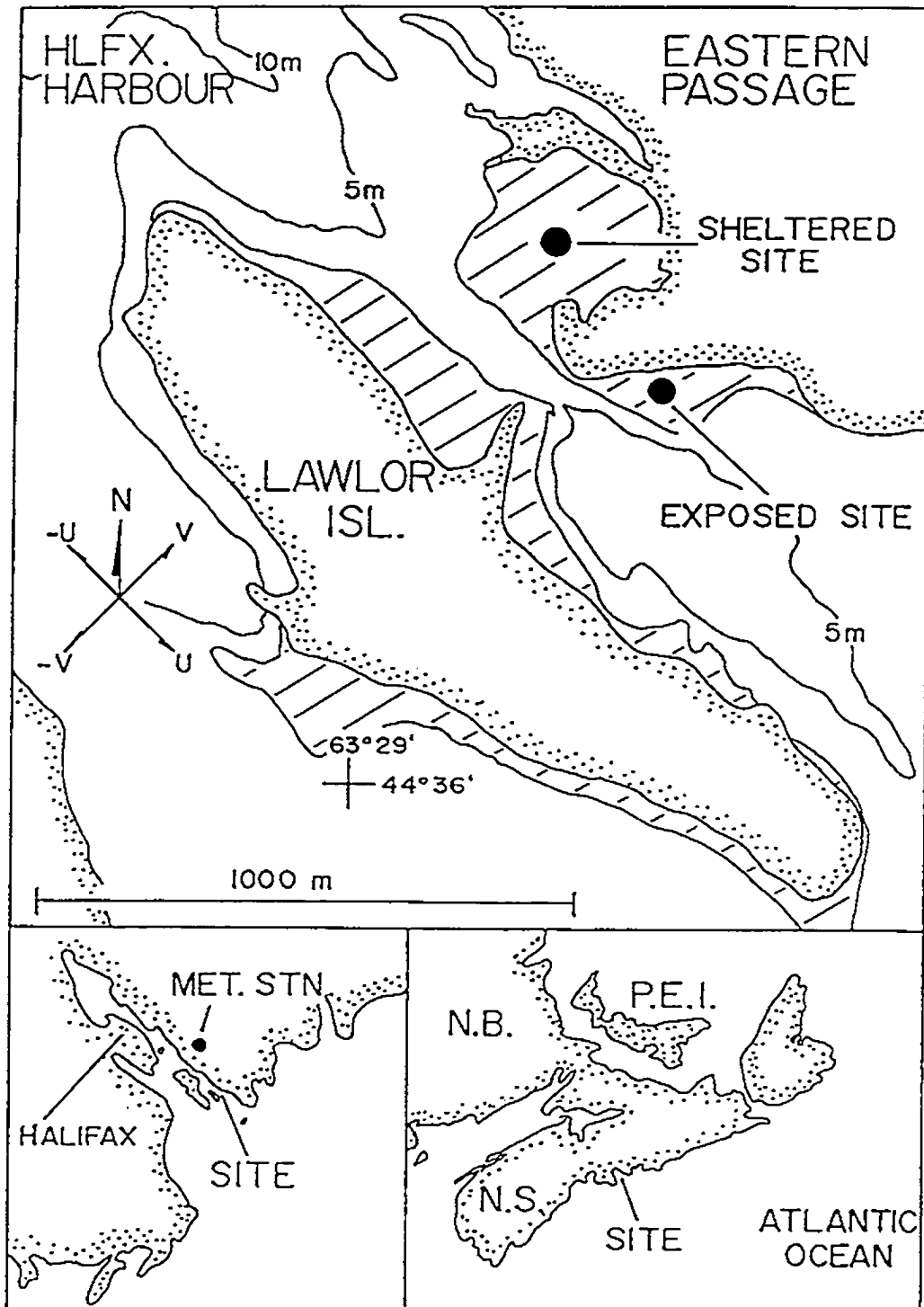


Figure 4.1

Emerson et al. 1988). Although a comprehensive survey of the *M. arenaria* population on the exposed site has not been conducted, a cursory observation of numerous siphon holes throughout the study area ($>100 \text{ m}^{-2}$) suggested that *M. arenaria* was also a dominant component of the exposed-site community. Other macrofauna common to both sandflats included the bivalve *Macoma balthica*, and the polychaetes *Nereis diversicolor* and *Spio setosa*. The bivalve *Gemma gemma*, the gastropod *Hydrobia minuta*, and the polychaete *Arenicola marina* were unique to the sheltered site, whereas the surf clam *Spisula* sp. was found only on the exposed sandflat. Both sandflats were subject to moderate levels of fish-bait digging (*M. arenaria*, *A. marina*) from April to October.

Sampling Protocol

Sampling was conducted from July 1, 1988 to April 30, 1989 to ensure that a wide range of bedload transport would be encountered and to adequately monitor the period of *Mya arenaria* spat settlement (late summer to early fall; Brousseau 1987). All samples were collected daily despite the contention that samples should be highly concentrated at low frequencies for long-term benthic studies (Shaffer & Cahoon 1987). Although low-frequency collection may be optimal for variables such as annual primary production, such sampling would have been inadequate to measure episodes of bedload transport. Because wind is responsible for most of the bedload transport on the sandflats (Emerson, *submitted*), and because most of the energy in the local wind field is contained between the 2- and 10-day periods (Petrie & Smith 1977), a sampling period of one day was mandatory. Accordingly, all samples were collected at alternate low tides; each 'day' lasted approximately 25 hours (1 tidal cycle = 12.5 hr).

On average, the study areas were sampled 22 days each month (min.=20 days, max.=30 days) with no more than two consecutive days separating sample collection. The only exceptions to this schedule were in early September and early November, when 7 and 4 consecutive days could not be sampled, respectively. During these periods, bedload transport was estimated indirectly from a numerical bedload model described in Chapter 3.

Sediment temperature (5 cm depth) and water temperature (20 cm depth) were monitored with a mercury thermometer ($\pm 0.2^{\circ}\text{C}$). Hourly wind speed and direction, air temperature, and precipitation were obtained from the Atmospheric Environment Service, Bedford N.S., which operates a meteorological station within 4 km of the study sites. Wind was partitioned into U and V vector components after adjusting the reference axis so that true north was rotated to 310° (Fig. 4.1). As a result, true northwest winds ($+U$ component) impinged directly upon the sheltered sandflat, whereas the exposed sandflat was subjected to southwest winds ($-U$ component). Hourly sealevel data measured by tide gauges in Halifax Harbour were obtained from the Marine Environmental Data Service, Ottawa.

Sediment and Faunal Transport

Direct measurements of bedload transport (i.e. gross sediment transport) were obtained with sub-sediment bedload traps consisting of acrylic cylinders (60 cm length, 3 cm internal diameter), each surrounded by a PVC shoring pipe (Fig. 3.1). By remaining in the sediment, the pipes permitted the frequent replacement of the bedload trap without disturbing the surrounding sediment. The tops of both the trap and pipe were flush with the sediment surface, and a rubber gasket prevented particles from collecting between the pipe and trap. From an assessment of the

trap's collection and retention efficiency (Chapter 3), it was concluded that the traps were useful for the measurement of the daily and seasonal variation in bedload transport but possibly not for the measurement of absolute bedload transport. In addition, traps with an aspect ratio of 20 and a length of 60 cm may underestimate bedload transport when rates exceed $35 \text{ kg}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$.

Initially, 10 replicate traps were deployed at each study site with a minimum distance of 5 m between traps. Because the variation between trap collections on one day ($\sim 20\%$) did not decrease with more than two traps, two replicate traps were used after August. Macrofauna were picked out of the bedload samples and preserved with 10% formalin. After the remaining material was dried to constant weight (70°C), kelp and seagrass detritus were separated from the sand grains by sieving with a $500\ \mu\text{m}$ mesh. Although some small fragments of biogenic material could not be separated from the sand in this manner, ashing (500°C) and weighing indicated that at least 96% of the sediment dry weight was composed of sand grains; the detrital fraction was underestimated by approximately 10%. Subsamples of the trapped sediment and the surface sediment (0-2 cm depth) within 5 m of the traps were retained for grain-size analysis.

Bedload transport was expressed as sediment dry weight per meter (extrapolated from the trap diameter) per day ($\sim 25 \text{ hr} = 2 \text{ tidal cycles}$). The transport of clams was expressed as number of individuals per meter per day. Because the amphipods and isopods that were found in the traps were highly mobile, they were quantified as the number of individuals found in a trap on each sampling day. Material collected by traps which had become partially clogged with *Laminaria* fronds or small crabs, *Carcinus maenas*, was discarded.

Net sediment transport, the balance between erosion and deposition, was determined from the daily change in sediment height above two 900 cm² plexiglass plates, initially buried at 20 cm depth. Sediment disturbed during the initial deployment was allowed to equilibrate for 2 weeks prior to the first height measurement. Sediment height was measured by inserting a thin graduated rod vertically into the sediment until reaching plate depth. If sediment ripples were present, the rod was inserted into the trough. Sampling precision was approximately ± 3 mm. Results were expressed as deviations from the average height of sediment above the two plates.

Clam Density

The population density of *Mya arenaria* was determined from 5 sediment cores (300 cm² x 10 cm depth) collected daily within each study area. Cores were not taken within 2 m of either a bedload trap or a buried plate and the same area was not re-sampled at a later date. After the core samples were sieved (1.5 mm mesh), clams were measured, enumerated, and preserved in 10 % formalin. Clams longer than 3 cm in shell length were not included in density estimates because a 10-cm sampling depth is not adequate to estimate their numerical density (Emerson et al. 1988, Zwarts and Wanink 1989). Bimonthly collections of box-core samples (0.1 m² x 25 cm depth) indicated that clams within the top 10 cm of sediment constituted 34-76 % of the total population density.

The density of clam spat (metamorphosed larvae <1000 μ m in length) was estimated from 10 sediment cores (3 cm² x 1 cm depth) collected daily within each study area. Spat were not observed below 3 mm sediment depth. The entire sediment core was stained with Rose Bengal and preserved in 10 % formalin. Spat

were separated from the sediment by wet-sieving (250 μm mesh) to facilitate the enumeration of spat under a binocular microscope. No attempt was made to distinguish newly-settled clam spat from established spat. All variables were log-transformed before statistical analysis to normalize their distributions.

RESULTS

Bedload Transport

Seasonal bedload variation at both study sites was consistent with the prediction that the most intense oceanic response to wind stress occurs in the fall due to a sharp transition from minimal summer winds to strong winter storms (Smith et al. 1978, Fig. 4.2A). During the summer calm ($|U| \leq 4 \text{ m}\cdot\text{s}^{-1}$), bedload transport was negligible at the sheltered site (mean $< 1 \text{ kg}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$) and usually less than $5 \text{ kg}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$ on the exposed site (Fig. 4.2 C&D). At the exposed site, the mid-October transition to a period of predominantly high bedload ($10\text{-}20 \text{ kg}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$) was preceded by two bedload peaks which were followed by at least two weeks of negligible transport. The transition to higher bedload at the sheltered site was delayed until mid-November by a slow seasonal shift to the high NW winds required for the generation of large waves at this site. Exposed-site bedload transport remained relatively high until April, whereas rates rarely exceeded $5 \text{ kg}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$ from February through April at the sheltered site.

Although the average bedload transport on the exposed sandflat was six times greater than that observed on the sheltered site, the maximum transport rate at both study sites was $\sim 36 \text{ kg}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$ (Nov. 3 & 21, exposed & sheltered site, respectively). During these maxima, the level of trapped sediment rose to within 10 cm of the trap

Figure 4.2

Time series of the (A) daily average of the U -component of wind velocity, (B) daily maximum range in sealevel, (C) daily bedload transport and net sediment transport on the sheltered study site, and (D) daily bedload transport measured with traps and sediment height above the buried plates. Sediment height is expressed as the deviation from the mean sediment height during the 10-month sampling period.

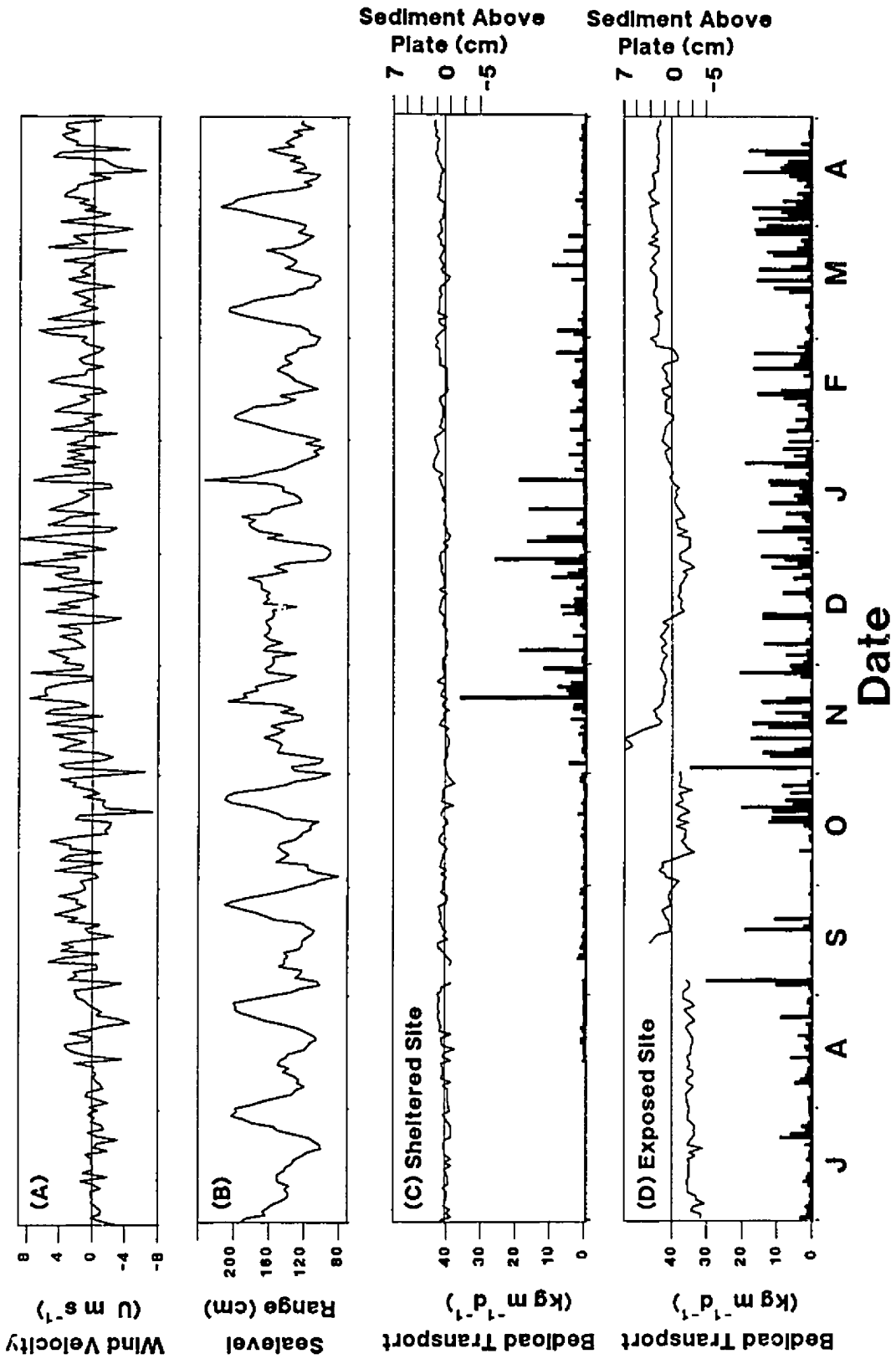


Figure 4.2

opening. Although the effective trap aspect ratio decreased below 5 at these times, the grain size distribution of the trapped sediment was not significantly different from that of the surrounding sediment ($P > 0.05$).

Without high winds, spring tidal currents were insufficient to produce high rates of bedload transport (e.g. late-July, Fig. 4.2B). Even with high winds, minimal bedload transport was occasionally observed when 100 % of the sandflat was covered by 40 cm of snow and ice (Fig. 4.3C); direct observation of the sediment surface near the traps revealed little ice scouring at these times. 'Ice-armouring' occurred at both sites when the air temperature was very low (Fig. 4.3C), but the freezing of interstitial water in the top 1.5 cm of sediment had little potential to stabilize the sediment since the sediment remained frozen for only 15 minutes after submergence by the rising tide. At warmer temperatures, surface runoff from rain or melting ice created channels in the sediment surface but not within either study area (cf. Rope et al. 1988).

Net Sediment Transport

The high sediment transport indicated from the bedload traps deployed at the sheltered site in November and January was not apparent in the time series of sediment height (Fig. 4.2C). The low-amplitude, high-frequency variation that was observed in the sediment height (± 1 cm) could be attributed to sampling error and/or the presence of sediment ripples (average height = 0.8 cm). A significant correlation between sediment height and time ($r^2 = 0.20$, $P < 0.001$, $n = 250$) suggested that there was a net sediment deposition of 2 cm by the end of the 10-month sampling period. There was no evidence of significant episodes of deposition or erosion at the sheltered study site.

Figure 4.3

(A) Daily ranges in air temperature and mean water temperature, (B) daily precipitation (rain and snow), and (C) the daily percentage of ice/snow cover on the sheltered sandflat. Ice/snow cover did not occur at the exposed study site. Days on which ice-armouring was observed are indicated.

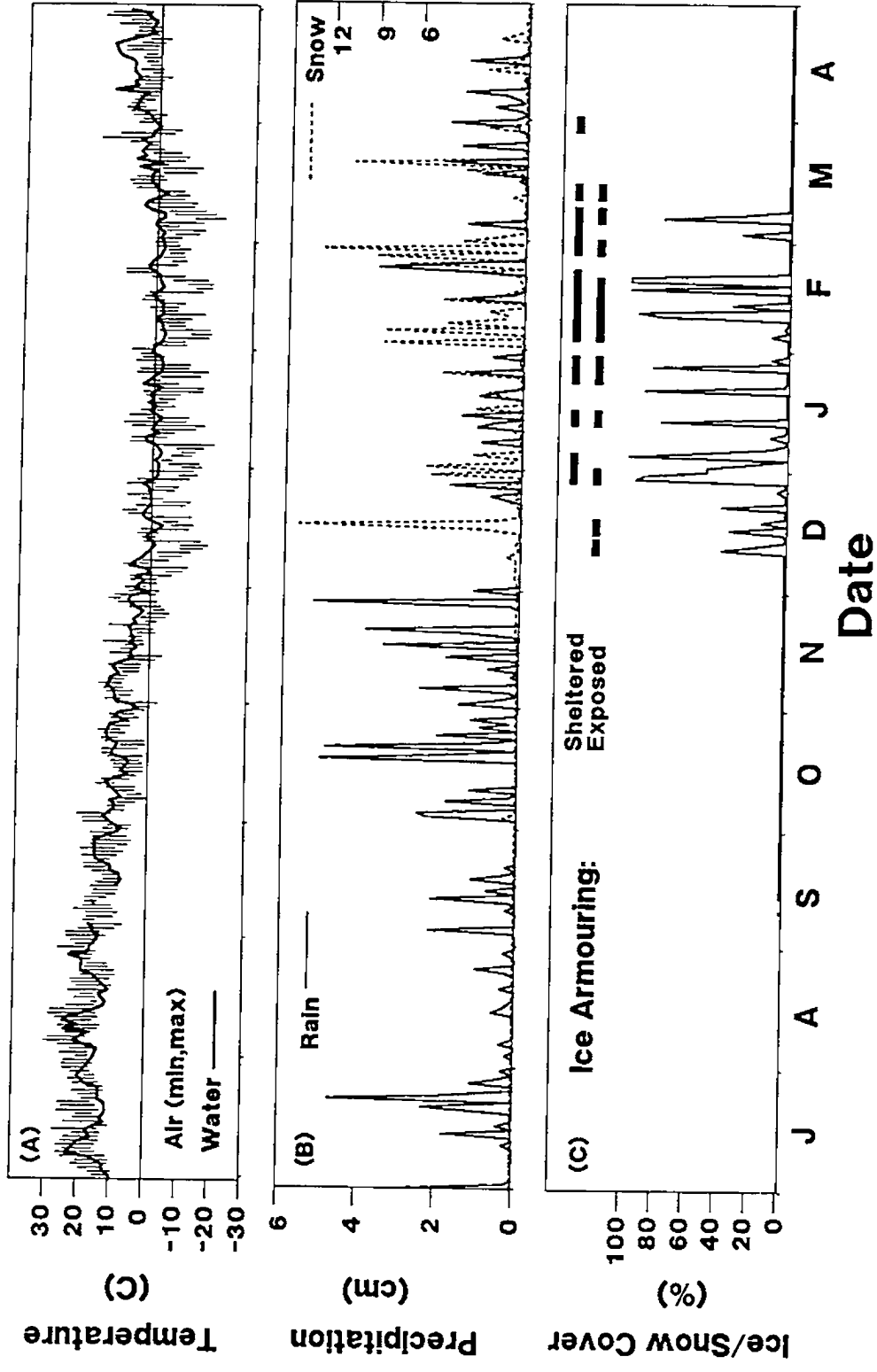


Figure 4.3

Two periods of rapid deposition followed by gradual erosion were the only perturbations in the otherwise gradual rise of the exposed-site sediment surface during the sampling period (Fig. 4.2D). After storms on September 5 and November 3 deposited at least 5-8 cm of sediment onto the exposed site, the sediment surface was eroded to pre-deposition levels within two months. A positive correlation between sediment height above the buried plate and time ($r^2=0.51$, $P<0.001$, $n=250$) indicated a net deposition of ~6 cm during the 10-month study period. Again, several periods of high sediment transport that had been detected with the bedload traps were not revealed by daily measurements of sediment height (e.g. mid-April).

Clam Transport and Population Density: Sheltered Site

Transport of *Mya arenaria* across the sediment surface was observed throughout the sampling period (Fig. 4.4B). Although average clam transport was low (~1 ind·m⁻¹·d⁻¹), maximum rates exceeded 750 ind·m⁻¹·d⁻¹. Between-trap variation in estimates of clam transport was less than 20 % whereas day-to-day variation was greater than 100 %. Clams of 4 cm shell length were occasionally found in the traps, but 80-95 % of the clams collected during the early winter period of high clam transport were only 8-15 mm long. Mean shell length of the clams within the top 10 cm of sediment was 22 mm (min.=4 mm, max.=28 mm). All clams that had been trapped could reburrow if placed on the sediment surface.

A visual comparison indicated that the seasonal variation of passive clam transport was similar to variation of the bedload transport time series (Fig. 4.4 A&B). In mid-November there was an abrupt transition from a summer period of

Figure 4.4

(A) Daily bedload transport, (B) daily passive clam transport, and (C) daily clam density (\pm SD) in the upper 10 cm of the sediment on the sheltered study site. At no time were spat observed in the top 1 cm of sediment.

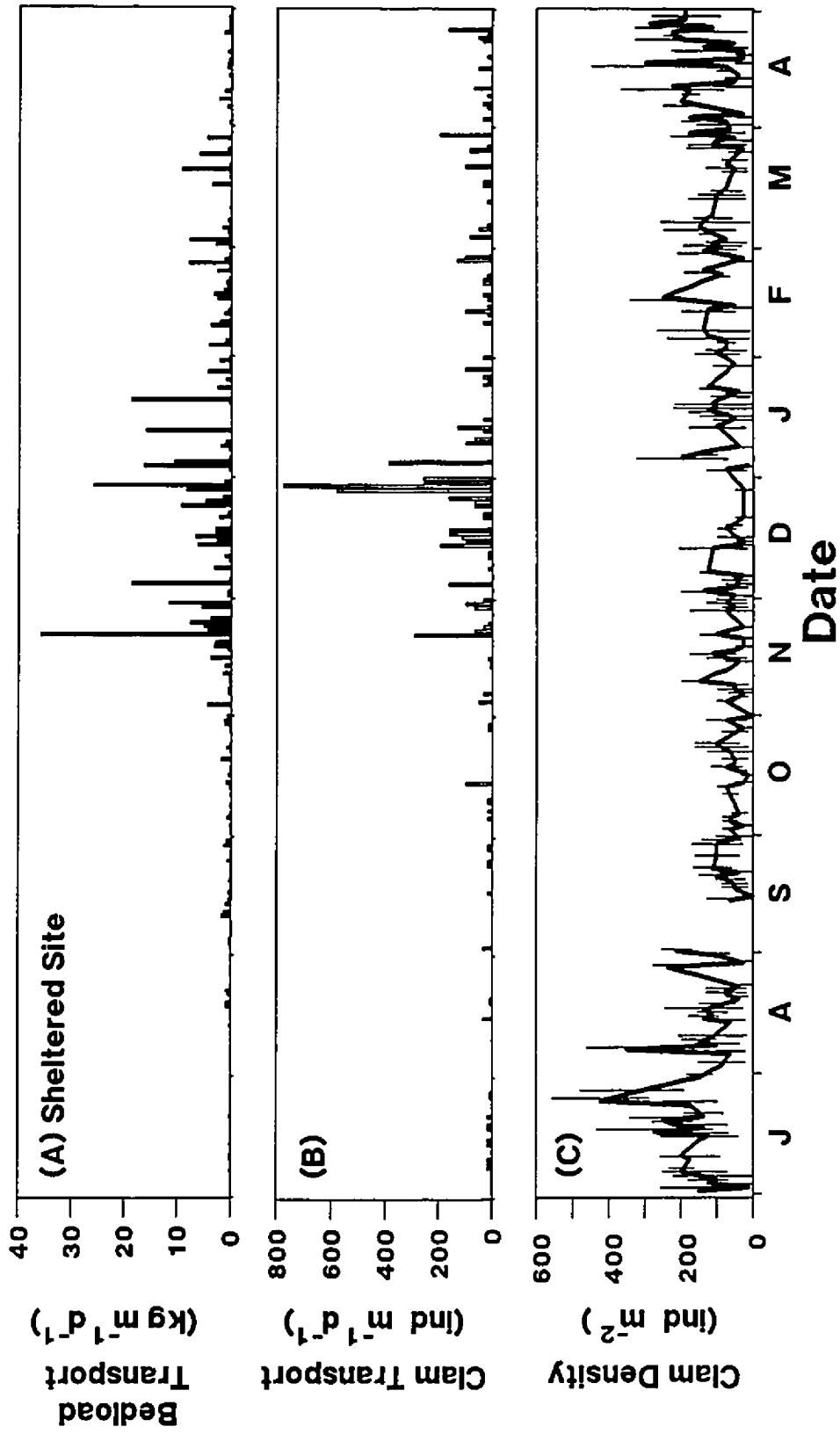


Figure 4.4

low clam transport to high transport in winter followed by moderate transport throughout the remaining sampling period. Clam transport maxima coincided with the bedload peaks on November 20 and December 28.

From a simple linear regression, it was determined that bedload transport was responsible for ~26 % of the variation in passive clam transport ($r=-0.51$, $P<0.001$, $n=250$). Additional evidence of a link between bedload and *Mya arenaria* was that clams were found in the traps only if bedload transport had occurred, although bedload transport was sometimes observed without clam transport. Neither sediment height above the buried plates, nor the daily change in sediment height was significantly correlated with passive clam transport ($P>0.05$).

Initially, the link between bedload and clam transport did not appear to be extended to changes in local population density. With the exception of an obvious density peak in late-July (423 ind·m⁻²), high sampling variation (CV=67 %) prevented the detection of smaller peaks and seasonal trends (Fig. 4.4C). It was clear, however, that during the period of maximum clam transport, clam density in the top 10 cm of sediment remained relatively constant (~80 ind·m⁻²). Nonetheless, a significant negative correlation existed between clam transport and clam density ($r^2=0.22$, $P<0.001$, $n=236$) for the entire sampling period. Bedload transport, sediment height, and the daily change in sediment height were not correlated with clam density ($P>0.05$).

No clam spat were observed in the top 1.0 cm of sediment even though *Mya arenaria* usually spawn in early fall on the eastern shore of Nova Scotia (Burke & Mann 1974). Clam larvae in the water column were not sampled during the study period.

Clam Transport and Population Density: Exposed Site

Despite a separation of less than 300 m, the population dynamics of *Mya arenaria* at the exposed site were markedly different from those at the sheltered sandflat. In addition to higher peaks in both clam transport and density, high numbers of clam spat were observed in the surface sediment (23000 ind·m⁻²; Fig. 4.5D). Although average clam transport was still relatively low (5 ind·m⁻¹·d⁻¹), transport was greater than 2000 ind·m⁻¹·d⁻¹ on three days in September. These three peaks and a prolonged period of high clam transport in mid-October (400-1000 ind·m⁻¹·d⁻¹) corresponded to periods of high bedload transport; bedload transport was significantly correlated with clam transport ($r=0.33$, $P<0.001$, $n=250$).

The density of clams in the top 10 cm of sediment rapidly increased from 200 to 2000 ind·m⁻² immediately following the high levels of bedload and clam transport in early September (Fig. 4.5C). A subsequent rise to >5000 ind·m⁻² also corresponded to a period of high bedload and clam transport. The size distribution of clams within the prolonged fall density peak (mean = 9 mm, range = 6-28 mm) was similar to that of clams which had been transported during the three peaks in September (mean = 9 mm, range = 6-15 mm), however clam transport and population density were poorly correlated ($r^2=0.044$, $P=0.004$, $n=236$). Bedload sediment transport was not significantly correlated with clam density ($P>0.05$).

Removal of clams on November 3, 5, and 15 reduced the clam population to 4 % of the peak density levels. Surprisingly, relatively few clams were collected in the bedload traps when bedload transport was highest (Nov. 3). Excavation of ambient sediment below 10 cm depth indicated that the reduction of clam density was not a sampling artifact, because there were no clams smaller than 3 cm shell length below the depth of sampling. The clam population density remained relatively low until

Figure 4.5

(A) Daily bedload transport, (B) daily passive clam transport, (C) daily clam density (\pm SD) in the upper 10 cm of sediment, and (D) daily clam spat density in the upper 1 cm of sediment at the exposed study site. The dashed line in (B) refers to the cumulative clam transport from Sept. 5 to Oct. 20. '**' in (C) refers to the density of clams in an area adjacent to the study site (see *Discussion*). The dashed line in (D) shows the hypothetical cumulative density of the 0-age-group if the clam spat had grown to 6 mm.

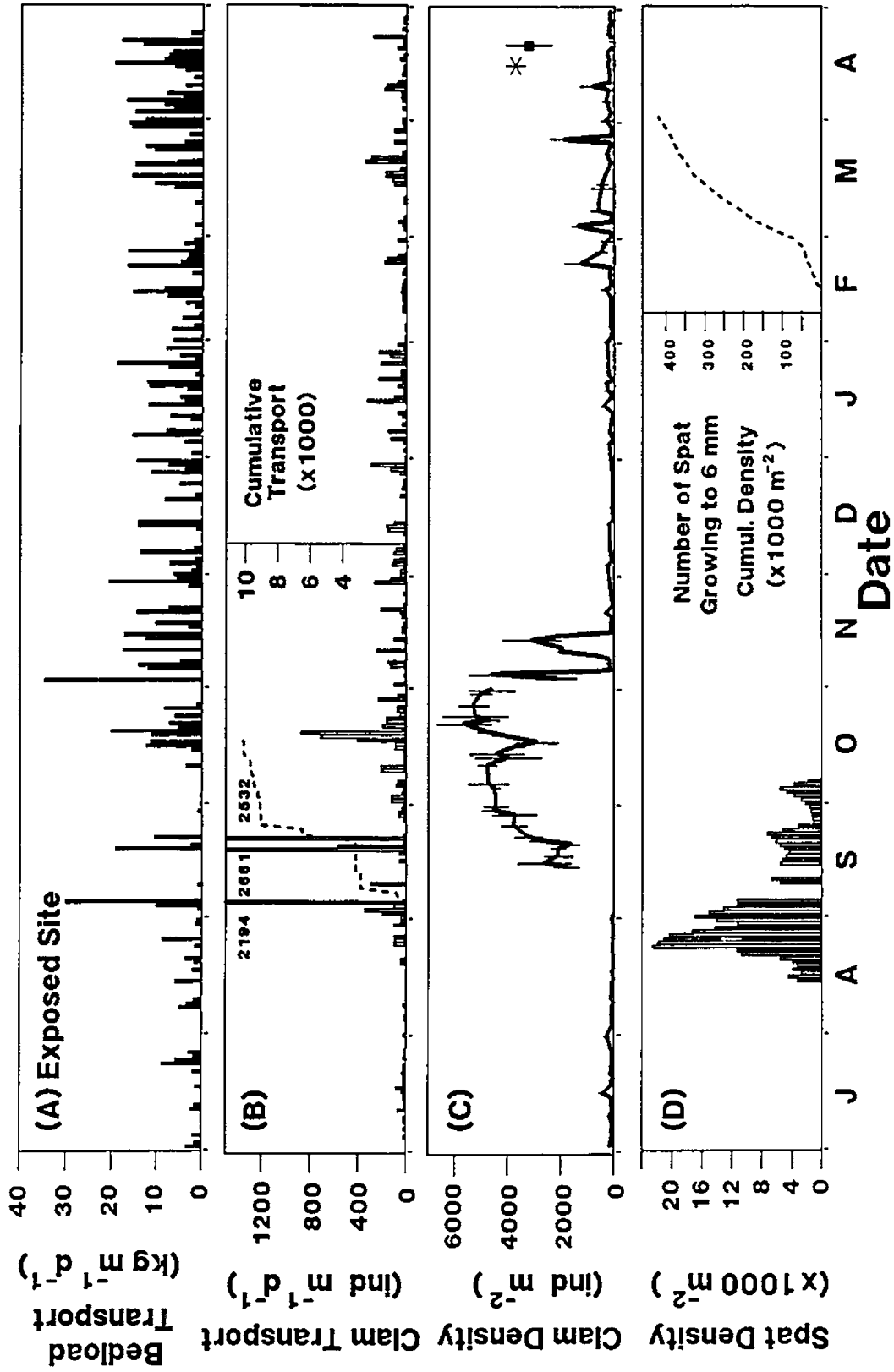


Figure 4.5

the end of April, with the exception of a few minor peaks in February and March consisting of clams 10-15 mm in length ($\sim 1500 \text{ ind}\cdot\text{m}^{-2}$). The population density from December to April was approximately twice that of the preceding summer.

Net Sediment Transport and Clam Density

Although gross sediment transport (i.e bedload) was not a good predictor of clam density, net sediment transport measured by changes in sediment depth explained up to 52 % of the variation in clam density on the exposed site. When the entire data set was used, no significant correlation was found between clam density and sediment height above the buried plates ($P > 0.05$), however the scatterplot of these two variables revealed two distinct data clusters (Fig. 4.6). As a result, it was hypothesized that a correlation using only data within the period of peak density (Sept. 10 - Nov. 3) would be significant. When tested, a significant negative relationship was found between the log of clam density during the fall peak and the sediment height above the buried plates ($r^2 = 0.52$, $P < 0.001$, $n = 46$). A second correlation, using data outside the peak period, revealed a significant positive relationship ($r^2 = 0.21$, $P < 0.001$, $n = 191$) between population density and the height of sediment above the buried plates.

The correlation between the daily change in sediment height and clam density on the exposed site was not significant. Clam density on the sheltered sandflat was not correlated with either sediment height or the change in sediment height.

Figure 4.6

Relationships between clam density and the height of sediment above the buried plates. Two density-dependent simple linear regressions were calculated; the upper regression used data from within the fall peak of clam density (Sept. 10 - Nov. 3), and the lower regression was calculated using the remaining data. Coefficients of determination are indicated; $P < 0.001$ for both regressions. A regression using the entire data set was not significant ($P > 0.05$).

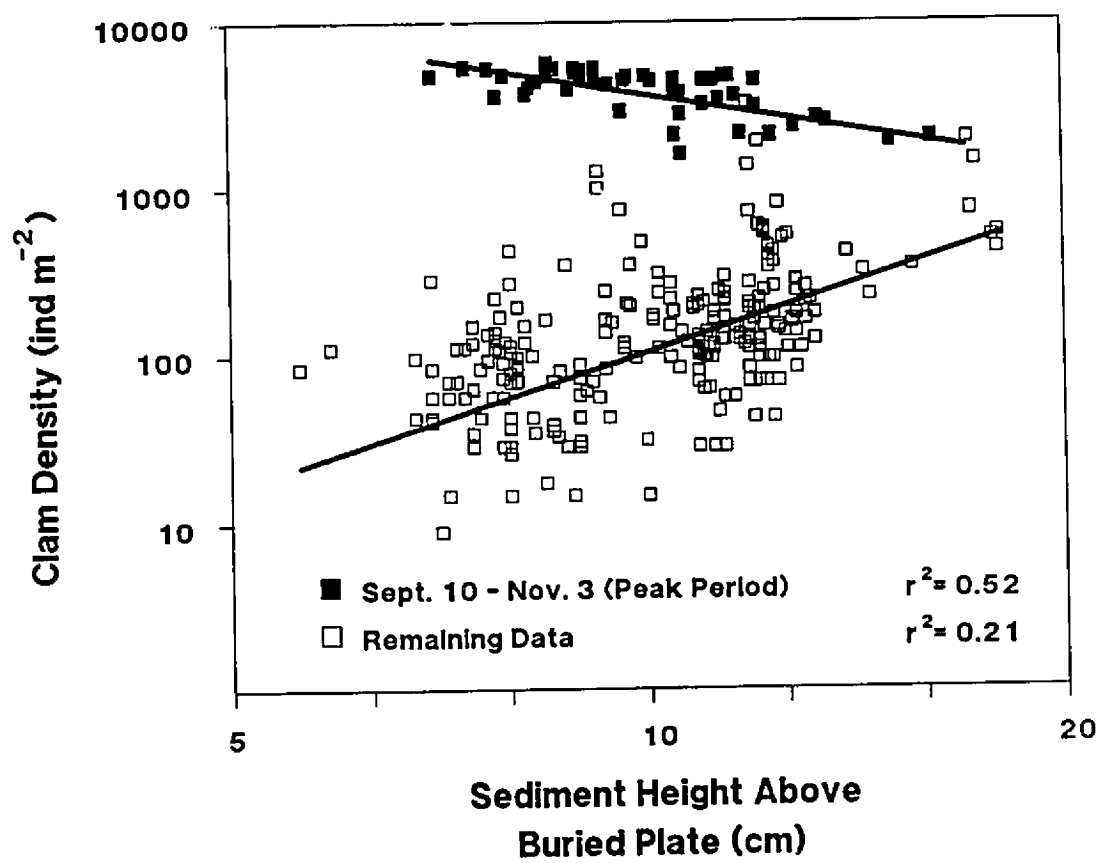


Figure 4.6

DISCUSSION

Bedload and Passive Clam Transport

On both low- and high-energy intertidal sandflats, the transport of juvenile *Mya arenaria* across the sediment surface was observed throughout a 10-month sampling period. Until now, this phenomenon had been mentioned primarily as an anecdotal reference in a variety of studies (Kellogg 1901, Baptist 1955, Savidge & Taghon 1988). Because juvenile immigration has often been assumed to be negligible (see Brousseau 1978a), the frequency with which clam transport was observed and the occasional transport rates in excess of $2600 \text{ ind}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$ suggest that recruitment processes of *M. arenaria* and other infauna living in the sediment surface must be re-examined.

The positive correlation between bedload and clam transport at both study sites and the observation that clam transport was only observed during periods of bedload transport indicate that clams were transported passively. Active emergence and subsequent dispersion of small clams ($\sim 2 \text{ mm}$) has been reported (Baptist 1955), however clams of the sizes found in the traps (6-40 mm) usually remain in their burrows (Medcof 1950, Brousseau 1978a). Further, it is unlikely that clams would actively expose themselves to high predation risk on the sediment surface unless they had been subjected to some hidden stress within the sediment or if dispersal was advantageous. The large resident clam population, the rarity of infaunal predators, and the greater benefit of dispersal at the planktonic larval stage suggest that clams were passively removed from the sediment. In any event, active immigration could not fully account for the transport of more than $2000 \text{ ind}\cdot\text{m}^{-1}\cdot\text{d}^{-1}$ into the study area when there were fewer than $200 \text{ ind}\cdot\text{m}^{-2}$ in the sandflat (Sept. 5, Fig. 4.5 B&C).

If passive transport is characteristic of most intertidal soft-sediment communities, previous reports of active migration by *Mya arenaria* may actually reflect the passive transport associated with bedload transport. To verify the existence of a "wandering stage", Smith (1955) monitored the recolonization of azoic intertidal sediment in Massachusetts for 19 months. From the appearance of clams in this sediment, Smith concluded that they had actively migrated across the sediment surface. I suggest that 'active' recolonization may be explained equally well by the passive importation of clams during sediment transport. Indeed, Smith observed the highest recolonization rates during the fall, when high bedload transport would be expected.

The low correlation between bedload and clam transport may have resulted from the high spatial patchiness common in populations of *Mya arenaria* (e.g. Witherspoon 1982, Emerson et al. 1988), but it is more likely that clams were not tightly coupled to bedform migration; rather, clams were probably eroded from the sediment and subsequently transported by bottom currents. For example, clams on intertidal flats which were relatively more exposed, such as those at the south end of Lawlor Island (Fig. 4.1), may have been transported to the study site, where comparatively low bedload rates were measured. This hypothesis is consistent with the observation of high numbers of clams in the traps without a corresponding high clam density in the surrounding area. Only by measuring bedload transport on an expanded spatial scale would the correlation between bedload and clam transport be expected to increase.

Recruitment at the Sheltered Site

The high potential for passive juvenile recruitment to the sheltered sandflat clam population was not realized. Whether the sediment was unsuitable (Newell & Hidu 1982) or bottom currents inhibited reburrowing (Butman 1987), the numerous small clams which passed across the sediment surface from November to January did not become established. Even if these clams had been able to temporarily reburrow, the regression analysis indicated that the net effect of bedload transport was to remove clams from the population. From July to April, this export was not balanced by recruitment from spat settlement.

In view of several reports of *Mya arenaria* spawning without subsequent spat settlement (Pfitzenmeyer 1962, Brousseau 1978a), the absence of spat on the sheltered flat was unusual only in comparison to the high numbers of spat on the nearby exposed sandflat. High turbulence, which would have limited settlement, was more likely to exist on the exposed site than on the sheltered site, and dense algal mats which would have inhibited settlement (Ólafsson 1988) were not observed within the study area, although they were present elsewhere on the sheltered sandflat.

The differential settlement of *Mya arenaria* may have been caused by the high density of the bivalve *Gemma gemma* on the sheltered flat (>30000 ind·m⁻²) and their absence on the exposed site. It has been hypothesized that an inverse relationship exists between *G. gemma* and *M. arenaria* because recently-settled *M. arenaria* larvae are not able to survive in a dense assemblage of *G. gemma* due to resource competition or predation (Bradley & Cook 1959, Sanders et al. 1962, cf. Woodin 1976). Thus, a biological rather than a physical limitation may account for the absence of the 1988 (0+) cohort on the sheltered study site.

Recruitment on the Exposed Sandflat

Despite the contention that spat settlement is the only significant source of recruitment for *Mya arenaria* (Brousseau 1978b), spat settlement was of relatively minor importance to the clam population at the exposed study site. In early September, the step-wise increase in cumulative clam transport (Fig. 4.5B) closely resembled the increase in clam density at that time (Fig. 4.5C). The similarity between the size structure of the trapped clams and that of the clam population during the fall density peak was additional evidence that clam transport was linked to local population density. It is possible that the two-week period of negligible bedload transport following the peaks in clam transport allowed the temporary establishment of the imported clams. A similar establishment period was not observed after high rates of clam transport at the sheltered site.

The relatively slow growth rate of *Mya arenaria* in temperate latitudes negates the possibility that the growth of spat was responsible for the large peak in population density. Using published parameters of the von Bertalanffy growth equation derived for nearby clam populations (Table 4.1), and assuming a two-week planktonic period (Needlar & Ingalls 1944, Ayers 1956), the mean time required for a 500 μ m spat to grow to 6 mm (i.e. the smallest clam within the density peak) would be ~170 days (Fig. 4.5D). The implicit assumption that spawning occurred during a spring tide (late July) was supported by a previous study of temperate clam populations (Battle 1933). Only if it is assumed that every clam grew at the maximum rate could the growth of spat account for the presence of 6 mm clams in the density peak. Even with this invalid assumption, the presence of the majority of clams (mean length = 9 mm) would not be explained. I suggest, therefore, that the

Table 4.1

Parameters of the von Bertalanffy growth equation ($L_t = L_\infty(1 - \exp(-k(t - t_0)))$) where L_t = shell length (mm) at time t , L_∞ = length at zero growth, k = growth rate to L_∞ , and t is the age (yr) at given length, and t_0 is the age at which length is zero. The average of each variable was used to calculate the time required for a newly-settled clam ($\sim 500 \mu\text{m}$ length) to grow to 6 mm. Clam populations were located in Nova Scotia unless otherwise indicated.

L_∞	k	t_0	Location	Source
127.9	0.063	-0.668	W Chezzetcook	Witherspoon 1982
84.8	0.110	-0.407	NE Chezzetcook	Witherspoon 1982
94.2	0.097	-0.352	SE Chezzetcook	Witherspoon 1982
81.6	0.099	-0.171	Potato Island	Appeldoorn 1983
117.9	0.080	0.460	Annapolis Basin	Angus et al. 1985
98.1	0.110	0.081	Three Fathom Harbour	Mullen & Woo 1985
123.5	0.088	0.221	Clam Harbour	Mullen & Woo 1985
67.4	0.170	1.330	Buckmans Creek, New Brunswick	Angus & Woo 1985
127.9	0.088	-0.164	Eel River Cove, New Brunswick	Robert 1979

passive transport of juvenile clams during bedload transport was responsible for the September increase in clam density. The mechanism for the rapid removal of these clams in early November was less apparent.

Although there is little doubt that predation can decimate clam populations (e.g. 99.8 % density decrease during 5 months: Möller & Rosenberg 1983), biological factors were unlikely to be responsible for the removal of 2000-4000 clams-m⁻² in 24 hours in early November. Major clam predators such as gulls (*Larus argentatus*, *L. marinus*, *L. delawarensis*), green crabs (*Carcinus maenas*), nemertean (*Cerebratulus lacteus*), and gastropods (*Lunatia heros*) were rare on the exposed sandflat, and feeding pits associated with flatfish predation were not observed within the study area. The absence of damaged shells in both the sediment and the bedload traps was also indicative of a low predation rate. Lastly, in an area of low sediment transport adjacent to the exposed study site, clam density remained high (~2000 ind-m⁻²) until April. Although this estimate was derived from a collection of 10 cores on only one day (April 22; ** Fig. 4.5C), the observation of numerous siphon holes in this area from September to April indicated that clam predation on the exposed sandflat was relatively low. Export of clams after sediment erosion was the most likely explanation of the rapid removal of thousands of clams from the study area.

Sediment transport may also have been responsible for the complete removal of the 0+ cohort from the exposed site after October. It is unlikely that the absence of these clams (1-4 mm) resulted from a sampling artifact. Clams less than 2.5 mm in length could potentially pass through the 1.5 mm mesh used to sieve the samples ($\log \text{ clam width} = 0.984(\log \text{ length}) - 0.204$, $r^2 = 0.997$, $n = 198$), however, when these very small clams grew larger than 2.5 mm, they should have appeared in the

samples. An increase in the population was not evident in the clam density time series (Fig. 4.5C); the minor peaks in February and March consisted of clams too large (> 15 mm) to belong to the 1988 cohort. This cohort's absence in the samples sieved with a 63 μ m screen was additional evidence that clams had been removed from the surface sediment; other studies have shown a similar removal (Brousseau 1978b, Möller & Rosenberg 1983).

Net Sediment Transport

Sediment height above the buried plates, the index of deposition and erosion, accounted for more of the variation in clam density on the exposed site than either bedload or clam transport (Fig. 4.6). The density-dependence of the relationship between sediment height and clam density resulted from the net erosion during the fall density peak and the net deposition observed at all other times. Before and after the density peak, it was more likely that net deposition was associated with importation rather than clam removal. An apparent removal during deposition resulting from a sampling artifact was unlikely because clams can burrow upwards when buried (Emerson et al. *in press,b*), and sediment beneath the sample cores contained no clams <3 cm in shell length. Removal during occasional periods of erosion was unlikely because the clams live below the most mobile layer of sediment (0-2 cm) and can burrow even deeper when waves or currents increase (Baptist 1955, Breum 1970, cf. Palmer 1984, Fegley 1987). As a result, sediment height would be positively correlated with clam density on either side of the fall peak, as shown in Fig. 4.6.

Sediment height was negatively correlated with clam density during the fall peak of clam density. At the beginning of the peak, sediment height was greatest

and clam density was relatively low ($\sim 2000 \text{ ind}\cdot\text{m}^{-2}$). The gradual erosion of sediment during the following 7 weeks reduced the sediment height, but it did not prevent the establishment of clams which had been transported into the area because bedload transport was minimal during this period. As a result, the relationship between clam density and sediment height during the fall density peak was opposite to that observed at other times. I expected that a correlation with sediment height expressed as a rate (i.e. net sediment transport) would have removed such ambiguities; in fact, the daily change in sediment height was not correlated with clam density at either study site ($P > 0.05$).

A second anomaly in the observed relationship between density and sediment height resulted from the problem of calculating net sediment transport using daily measurements. On November 3, a storm caused the deposition of at least 8 cm of sediment onto the exposed study site, but instead of clam importation, a precipitous decrease in clam density was observed. The possibility that clams were removed during a period of erosion within the storm could not be substantiated from the measurement of sediment height on the following day; only the net effect of the storm could be determined.

If clams were removed during the peak bedload event, why were there so few clams in the traps? In contrast to the clams present before the fall peak, clams making up the density peak were small (6-15 mm), lived closer to the sediment surface, and were very susceptible to removal during the maximum bedload event on November 3. Unfortunately, the 20-cm-deep traps were inadequate to accurately monitor the clam transport associated with sediment removal because sediment had almost completely filled the traps. As a result, the traps' ability to collect and retain small clams and other light particles was probably reduced.

Implications of Passive Clam Transport

Because of occasional reports of clam washout during storms (Baptist 1955), a link between bedload transport, clam transport, and clam density was not unexpected. However, intense long-term sampling on low- and high-energy sandflats showed that clam transport is not limited to large storms, and that its significance is not restricted to *Mya arenaria* recruitment because all soft-sediment infauna living near the sediment-water interface will be susceptible to the movement of their substrate. The results also provided clear evidence of the risk in estimating annual secondary production from biomass samples which are obtained at a low temporal frequency (e.g. for *Mya arenaria*, Loo & Rosenberg 1989). This problem would be particularly acute on temperate sandflats, where bedload transport may control the age structure of a population.

If average annual water temperature is low, clam maturation will be delayed (Pfitzenmeyer 1965) and spawning and settlement will occur immediately before the fall transition to high bedload transport. If the period between settlement and high bedload transport is short, the ability of becoming established will be limited. As a result, the age structure of clam populations in moderate- or high-energy areas may comprise a few cohorts which recruited to the population in a year of anomalously-low bedload transport (or high water temperature). The complete removal of the 1988 cohort on the exposed study site demonstrated that the absence of a cohort from a population may result from factors other than the biological processes such as predation and competition.

Another consequence of the passive transport of *Mya arenaria* across the sediment surface is its potential to compensate for overfishing on commercial clam flats. Depressions in the bed, as areas of reduced shear stress, are sites where

organic matter accumulates (Nowell & Jumars 1984) and mobile fauna collect (Savidge & Taghon 1988). It is possible, therefore, that the numerous pits created by intense clam digging could entrain any clams which pass across the sediment surface and thereby enhance the recovery of the clam population. By actively creating sediment depressions, it may be possible to increase the recruitment to depopulated clam flats; indeed, a good crop of clams has been linked to the digging of furrows by clam "farmers" (Needler & Ingalls 1944).

CHAPTER FIVE
POPULATION STRUCTURE, BIOMASS, AND RESPIRATION OF *MYA*
ARENARIA ON A TEMPERATE SANDFLAT

ABSTRACT

A population survey of the soft-shell clam *Mya arenaria* was conducted to indirectly determine the clam's contribution to total community respiration on a temperate sandflat (Eastern Passage, Nova Scotia). High spatial patchiness was indicated by a 94 % coefficient of variation associated with an average clam density of 251 ind·m⁻²; density ranged from 30 to 810 ind·m⁻². The average clam length was 27 mm (~3-yr-old). Oxygen consumption of *M. arenaria* measured in the laboratory was described by the weight-dependent regression: $\log R = 0.558 \log W + 0.461$, where R is oxygen uptake ($\mu\text{l O}_2\cdot\text{h}^{-1}$) and W is dry tissue weight (mg). By applying respiration measurements to estimates of clam biomass in the field, it was shown that the clam population consumes $\sim 9.2 \text{ mg O}_2\cdot\text{m}^{-2}\cdot\text{h}^{-1}$. Although macrofauna often represent a minor fraction of benthic metabolism, comparisons with published estimates of total community oxygen demand at this sandflat suggest that *M. arenaria* can account for 90 % of benthic community respiration in the spring.

INTRODUCTION

The modelling of energy flow in marine food webs is essential to estimations of ecosystem production (Pamatmat 1984), and to the optimal management of commercially important resources such as the soft-shell clam *Mya arenaria*. Metabolic measurements (e.g. oxygen uptake) are useful indicators of energy flow and have been of great value in the examination of energy cycling in a wide variety of benthic environments (Dye 1980, Asmus 1982*a*, Hargrave et al. 1983, Grant & Hargrave 1987, Smith 1987).

Benthic metabolism may be particularly important to coastal ecosystems via benthic-pelagic energy coupling (Kelly et al. 1985, Pollehner 1986). It has been shown that benthic nutrient regeneration may account for 40-100 % of pelagic nutrient demand (Fisher et al. 1982, Pomroy et al. 1983, Flint & Kamykowski 1984, Wassmann 1986). In addition, benthic macrofauna, such as suspension feeders, may affect pelagic and benthic biomass through the removal of food from the water column and subsequent biodeposition (Bayne et al. 1976, Cloern 1982, Officer et al. 1982, Peterson 1982, Dame et al. 1984, Fréchette & Bourget 1985*a*, Doering et al. 1986, Peterson & Black 1987).

An important controversy in the study of benthic energy cycling involves the proportion of total community metabolism accounted for by the macrofauna; several studies suggest that macrofauna are a relatively minor component of benthic metabolism (Kannevorff & Christensen 1986, Schwinghamer et al. 1986), while others indicate the macrofaunal contribution to be high (Pamatmat 1968, Asmus 1982*a*, Murphy & Kremer 1985). Such discrepancies are particularly evident in studies of intertidal habitats, which are major sites of production, recruitment, and feeding for a wide variety of species (Reise 1985).

Despite the widespread occurrence of *M. arenaria* in temperate intertidal areas, there exist no data which characterize its contribution to benthic metabolism and energy flow in intertidal communities. The objectives of this study were: (1) to determine population structure, biomass, and distribution of *M. arenaria* as requisites for benthic energy flow studies, and (2) to ascertain the importance of the clam population to total benthic metabolism via respiration measurements. Because total and size-partitioned (e.g. micro-, meio- and macro-benthos) estimates of benthic respiration exist for a local sandflat (Eastern Passage, Nova Scotia), a unique opportunity was presented to compare the oxygen consumption of a commercially-important clam population to that of the remaining benthic community. As a result, the current debate about the metabolic contribution of macrofauna could be investigated on a site-specific scale. Van Raalte (1978) indicated that macrobenthic biomass at Eastern Passage is dominated by *M. arenaria*, but its importance relative to smaller macro, meio-, and microfaunal metabolism was unknown at the beginning of my work.

MATERIALS AND METHODS

Study Site

Sampling was conducted on a sheltered 3-ha sandflat in Eastern Passage, Halifax Harbour, Nova Scotia (Fig. 5.1). The slope and maximum tidal range of the flat are 0.9° and ~2 m, respectively. Intertidal exposure due to a semidiurnal tide is complicated by a seiche of 2-h period. The annual range of water temperature (-1-16°C) is much less than that of the air (approximately -20 to 30°C).

Macrofauna include *Arenicola marina*, *Macoma balthica*, *Mya arenaria*, *Nephtys* sp., *Nereis* sp., and *Spio setosa*. *Zostera marina* and *Fucus* sp., which inhabit the

Figure 5.1

Location of study site near Eastern Passage, Nova Scotia. H, M, and L refer to high-, mid-, and low-intertidal zones, respectively (numbers identify stations.) Shaded area represents LLW-intertidal zone.

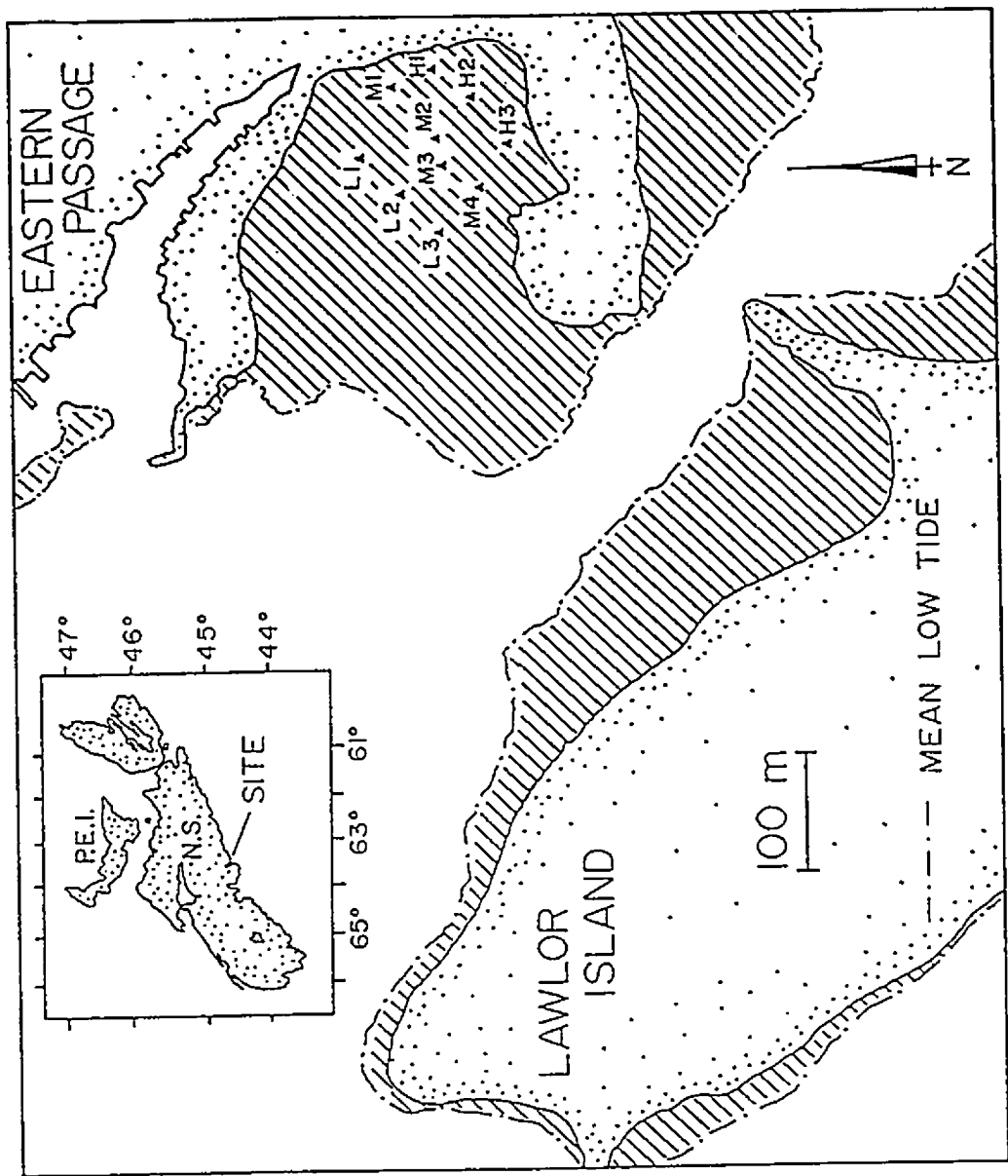


Figure 5.1

lower intertidal up to 20 cm above chart datum, delimit the lower range of the clam. The tidal flat is subject to chronic sewage and low-level oil contamination, recreational use, and clam digging.

Field Collection

Collections of *M. arenaria* were made on March 13 & 28, 1987 at low tide. A total of 24 quadrats were sampled using a 0.1-m² 20-cm deep metal frame. Ten stations were examined (Fig. 5.1): three at the upper tidal limit of the clam (1.2 m above chart datum), four at mid-tide (60 cm above chart datum), and three at the clam's lower tidal limit (20 cm above chart datum), with two to six replicate (i.e. samples < 2 m apart) quadrats at each station. Clams were separated from the sediment by sieving (5-mm mesh) in the field. Initial sieving through a 0.5-mm screen indicated a minimum clam length of 9 mm. Two quadrats were randomly chosen for partitioning into 0-4, 4-8, 8-12, 12-16, and 16-20-cm sediment depth sections. All clams to be used in respiration experiments were transported to the laboratory in 4°C seawater.

A sediment-temperature profile was constructed from 0 to 16 cm depth. Location of the redox potential discontinuity was indicated by the division between the aerobic (brown) and anaerobic (black, sulfide-rich) sediment layers. Six sediment cores were obtained for grain-size analysis; moment measures (e.g. skewness, kurtosis, etc.) followed Folk (1974).

Laboratory Analysis

Fifty-eight live clams were weighed (wet weight), dried at 70°C for 30 h (dry weight), and combusted at 480°C for 4 h (ash-free weight). For use in both length-age and length-tissue weight regressions, the shell length of all clams was

measured to the nearest 0.1 mm with a sliding hand micrometer. This facilitated the estimation of both age and dry tissue weight of each of the several hundred clams that were collected. Dry tissue weight was determined by weighing dried (70°C for 30 h) tissue removed from the shells of an additional 29 clams. Clam age was calculated using the following allometric growth equation derived from Witherspoon (1982):

$$\log \text{ age (yr)} = 1.339 \log \text{ length (mm)} - 1.392. \quad (5.1)$$

Age groups were identified using probability analysis (Harding 1949).

Respiration

Thirty-three clams (11-1540 mg dry tissue weight) were acclimated in 4.5°C, 31‰ (ambient) flowing sea water for 4 days prior to transfer to individual incubation chambers (an average of 2.2 mg dry tissue ml⁻¹ of chamber). Incubation water was stirred throughout the experiment by a magnetic stir-bar. Oxygen consumption of clams and sea water was determined over 1 hr from endpoint measurements using a calibrated Diamond Electro-Tech chemical microsensor (model 1201). Oxygen reduction did not exceed 30 % of initial oxygen concentration. Respiration in control chambers (sea water only) accounted for <10 % of clam oxygen uptake.

Clam population respiration was calculated by determining individual biomass (from the length-tissue weight regression), applying a weight-dependent respiration equation, and summing for all clams in a quadrat. Benthic respiration, excluding that of *M. arenaria* and other large macrofauna, was calculated from Grant (1986):

$$\ln R = 1.76 \ln T - 2.42, \quad (5.2)$$

where R is benthic respiration ($\text{mg O}_2\text{-m}^{-2}\text{-h}^{-1}$) and T is temperature ($^{\circ}\text{C}$). Chemical oxygen demand of the sediment was assumed to be 30.3 % of R (Grant 1986). No attempt was made to correct for antagonistic or synergistic effects on clam respiration which might have resulted from fractionation techniques of community respiration analysis (see Pamatmat & Findlay 1983).

RESULTS

Sediment

Sediment temperature decreased from 8.6°C at the surface to 2.7°C at 20 cm depth (Fig. 5.2). Mean grain size of surface sediment ($260\ \mu\text{m}$) was similar at all three intertidal levels. On average, sediment was moderately well sorted ($\sigma = 0.4\text{-}0.7$), and normally distributed ($\text{Sk}_1 = -0.05\text{-}0.232$, $\text{K}_G = -0.8\text{-}1.2$); the highest silt fractions (3-4 %) were observed in the low-intertidal, and decreased to 0.5 and 0.01 % in the mid- and high-intertidal zones, respectively. Depth of the redox potential discontinuity ranged from 3 cm in the high-intertidal to <5 mm in the low-intertidal.

Population Structure

A total of 602 clams was collected; these had a mean length of 27.0 mm (min.=9.8, max.=64.8) corresponding to a mean age of ~ 3 yr. Average density of *M. arenaria* was $251\ \text{m}^{-2}$ (± 237 SD), with the minimum ($30\ \text{m}^{-2}$) in the high-intertidal zone, and the maximum $810\ \text{m}^{-2}$ in the low intertidal zone. Patchiness in *M. arenaria* is common; Witherspoon (1982, 1984) has shown two orders of magnitude variation in clam density within Nova Scotian tidal flats.

Although Witherspoon (1982) found that the largest clams were located in the low-intertidal zone, Fig. 5.3b suggests the reverse. The highest proportion of small

Figure 5.2

Mean grain size distribution of sediment (0-12 cm in depth) for high-, mid-, and low-intertidal zones. Sediment temperature is for mid-intertidal zone.

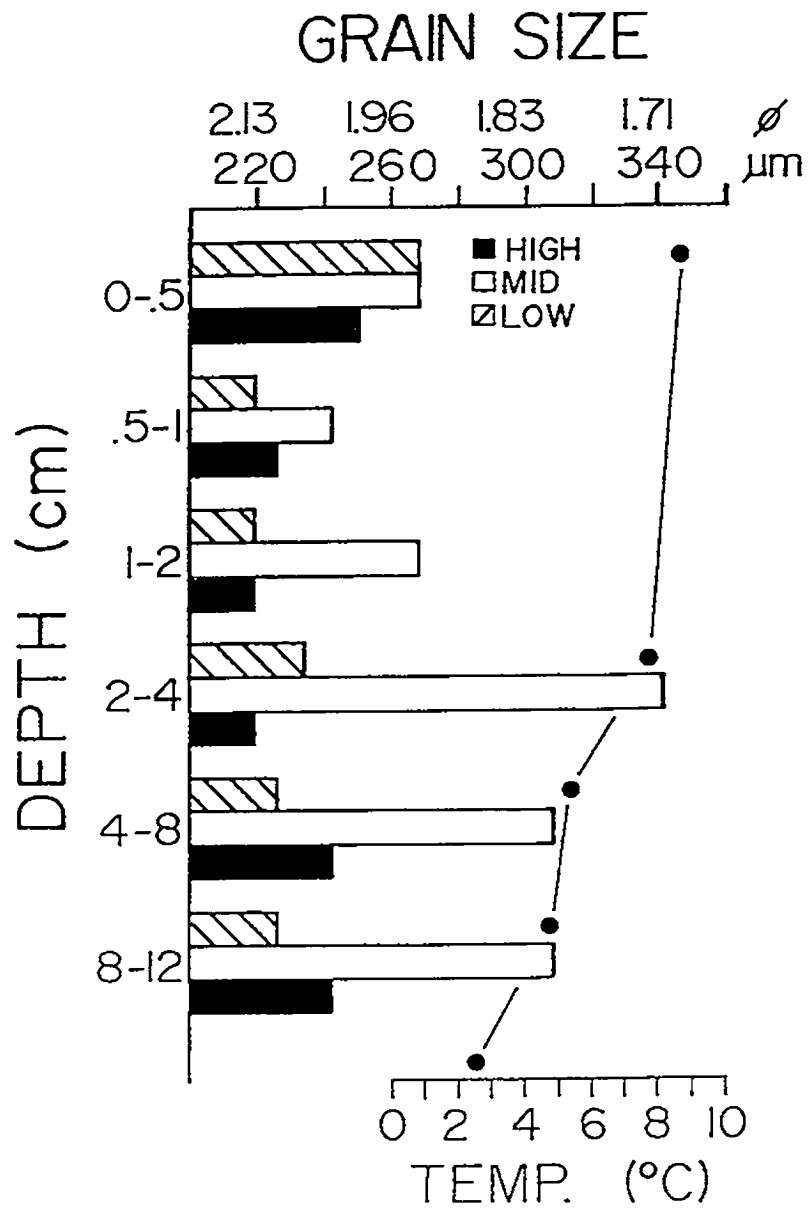


Figure 5.2

Figure 5.3

(A) Length-frequency histogram of all *Mya arenaria*. Normal curves represent age groups determined by probability analysis (Harding 1949). (B) Length-specific proportion of clams at high-, mid-, and low-intertidal zones.

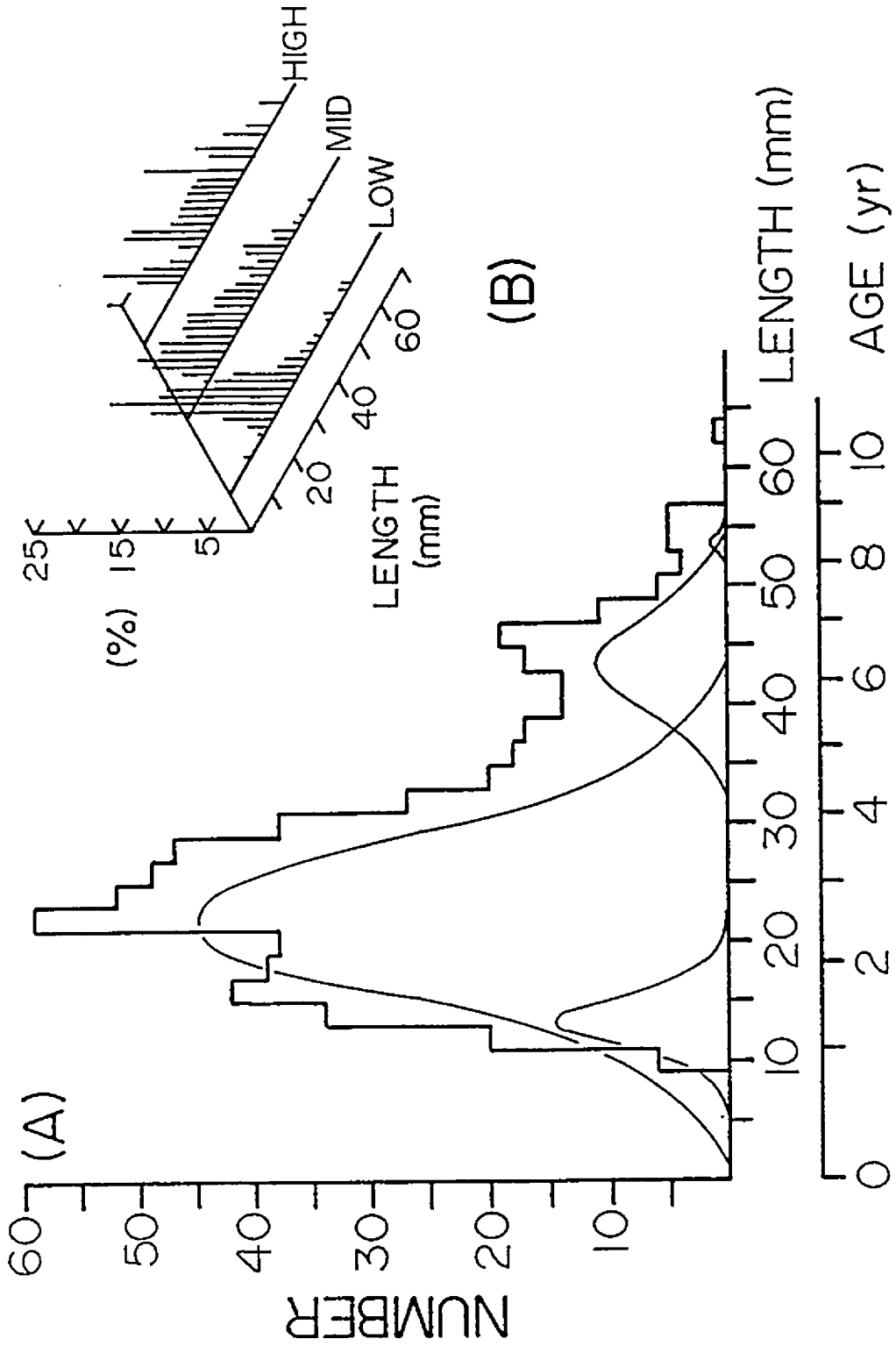


Figure 5.3

clams was found in the low-tide zone, and the largest clam was collected from the high-intertidal. Mean clam lengths for high-, mid- and low-intertidal zones were 35.3 (± 13.0 SD), (± 11.2 SD), and 26.3 (± 7.0 SD), respectively. Such data may support Matthiessen's (1960) hydrodynamic concentration hypothesis; larger clams are deposited on the foreshore and smaller individuals are returned seaward in the backwash. Alternatively, commercial exploitation may have significantly altered the size structure of the benthic community as has been demonstrated in a rocky intertidal area by Ortega (1987). In the low-intertidal where clam-digging is concentrated, clams > 50 mm were not abundant (Fig. 5.3b), a probable result of a catch minimum limit of 49 mm in Nova Scotia (Witherspoon 1982).

The majority of clams were observed between 0 and 8 cm sediment depth. The smallest individuals were found between 0 and 4 cm, while the largest were concentrated at 8-12 cm (Fig. 5.4). Although quadrats were sampled to 20 cm depth, no clams were found below 16 cm. Because small clams are thought to be restricted to shallow sediment depths by their relatively short siphons, it is surprising that some clams < 20 mm in length were observed at 12-16 cm depth.

Probability analysis of length-frequency data revealed four discernible age groups (Fig. 5.3a). The modes represent separate year classes and their location indicates the approximate mean length of that year class (Holme & McIntyre 1984). The 2+ cohort (62 % of the population) was characterized by the mode at 23 mm length. Smaller peaks were evident at 13, 44 and 54 mm, corresponding to 1+, 6+, and 8+ cohorts. It should be stressed, however, that the accuracy of cohort identification in clams > 2 yr of age is usually low using the Harding (1949) method; accordingly, discussion will focus on the 1+ and 2+ cohorts. The age at length of

Figure 5.4

Depth-specific size-frequency data for *Mya arenaria* collected at station M3.

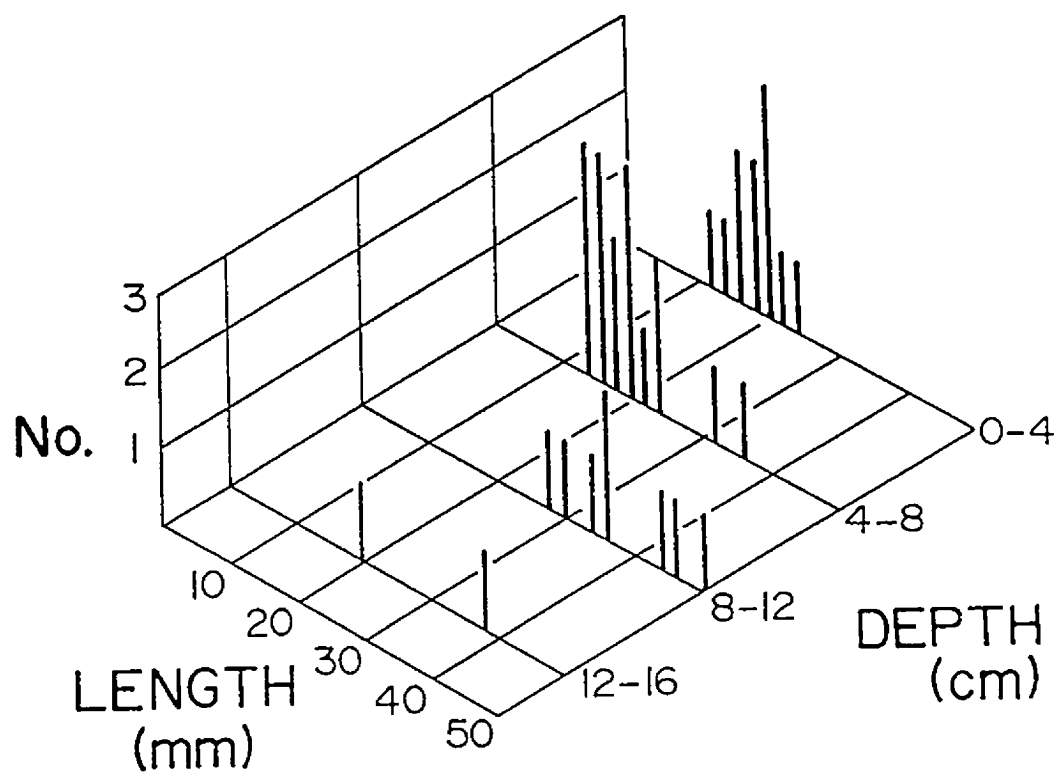


Figure 5.4

these two cohorts is consistent with growth and length data of a nearby population of *M. arenaria* (Burke & Mann 1974, Witherspoon 1982). Relatively high mortality or removal of the 1+ cohort is likely.

Clam Biomass

M. arenaria (with shell) had a water content of 61.58 % (± 2.63 SD, $n=58$) and organic matter content of 14.44 % (± 2.5 SD, $n = 58$); neither percentage was correlated with age ($P > 0.10$). Shell-free dry tissue weight of all clams was determined from the following calculated relationship:

$$\begin{aligned} \log \text{ tissue weight (g)} &= 3.16 \log \text{ length (mm)} - 5.36 & (5.3) \\ (n = 29, r^2 = 0.977, P < 0.001) \end{aligned}$$

Average biomass for all quadrats was 57.8 g dry tissue weight·m⁻² (± 28.4 SD). Mid-intertidal zone clam biomass was highest (72.7 g·m⁻², ± 54.3 SD), followed by that at low and high zones (Table 5.1).

Oxygen Consumption

Although substantial variation in oxygen consumption of the smallest clams was evident, the weight vs. oxygen uptake regression was highly significant (Fig. 5.5):

$$R = 2.89 W^{0.558}, \quad (5.4)$$

where R is oxygen consumption ($\mu\text{l O}_2\cdot\text{h}^{-1}$) and W is dry tissue weight (mg) of *M. arenaria*. The intercept a of the regression line (0.461) lies close to the suggested mean of 0.496 for suspension and deposit-feeding molluscs. The allometric exponent b , however, appears relatively low compared with most other molluscs (mean = 0.727, SD=0.13, range = 0.438-1.090; Bayne & Newell 1983).

Table 5.1.

Mean concentration, biomass (dry-tissue weight), and oxygen consumption of *M. arenaria* in high-, mid-, and low-intertidal zones at Eastern Passage, Nova Scotia. Parentheses enclose SD.

Tidal Height	<i>n</i>	Density (m ⁻²)	Biomass (g·m ⁻²)	Oxygen Uptake (mg O ₂ ·m ⁻² ·h ⁻¹)
High	6	73 (±61)	36.8 (±42.0)	4.27 (±4.24)
Mid	12	322 (±229)	72.7 (±54.3)	11.48 (±8.36)
Low	6	287 (±295)	49.3 (±28.4)	9.50 (±7.74)

Figure 5.5

Regression of log oxygen consumption of *Mya arenaria* as a function of log dry tissue weight. Dotted boundaries represent 95 % confidence limits.

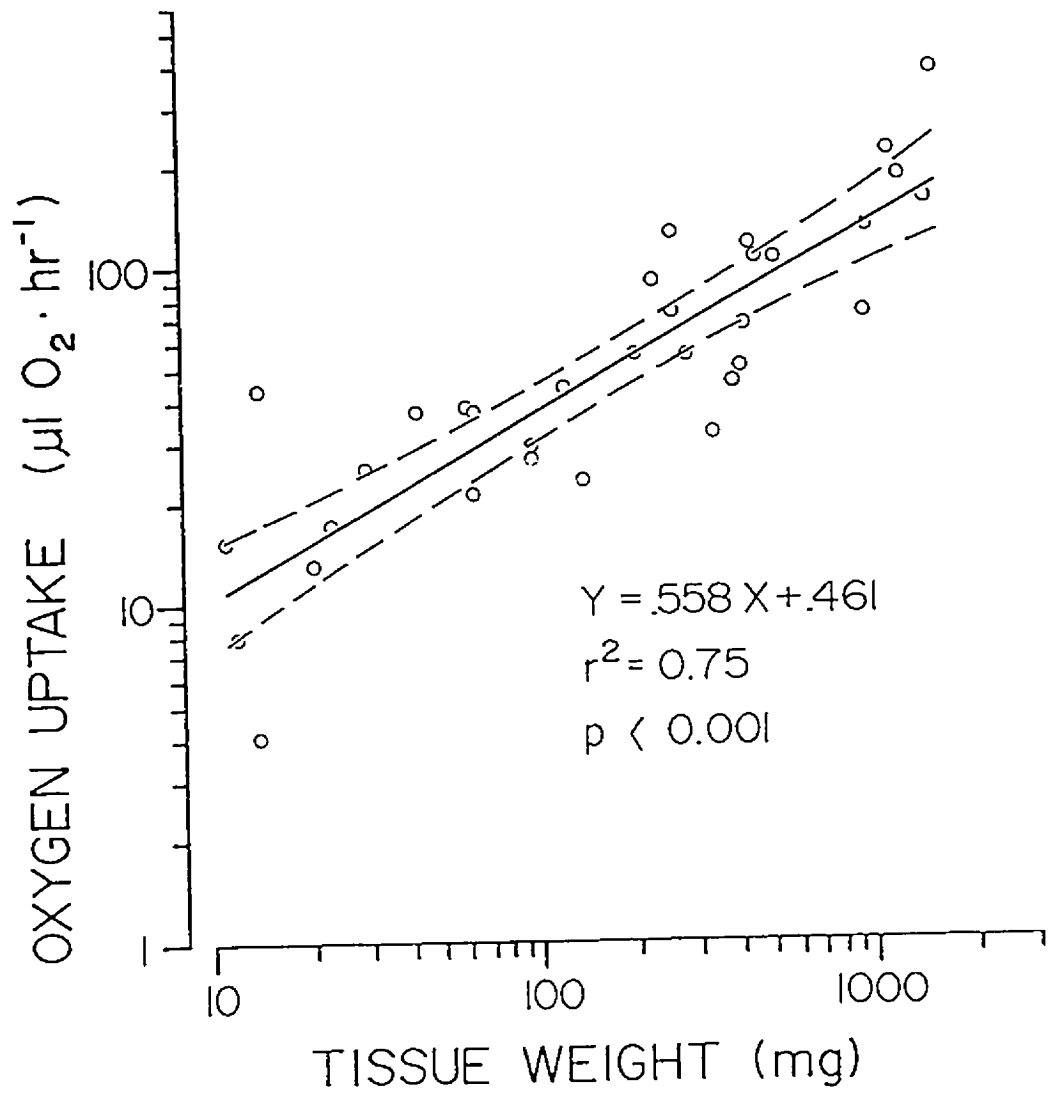


Figure 5.5

Respiration of the Benthos

In contrast to their different clam densities, quadrats in mid- and low-intertidal zones exhibited similar magnitudes of clam population oxygen consumption (11.5 and 9.5 mg O₂·m⁻²·h⁻¹ respectively, Table 5.1). The higher proportion of small clams in the low-tide zone, and their concomitant higher weight-specific respiration, is likely to account for this similarity. A low level of population respiration in the high intertidal zone reflects the lower density of clams (by a factor of two) at this site. High variation in population respiration estimates results from the patchy distribution of clams.

On average, oxygen uptake by *M. arenaria* represented 90 % of published values of total community oxygen demand (TCOD, ~10 mg of O₂·m⁻²·h⁻¹; Table 5.2). The sum of clam respiration estimates from this study and that of the remaining fauna (Grant 1986) is exactly equal to TCOD estimates from two independent investigations (Table 5.2). Although experimental error and natural annual variation in community biomass (Beukema & Essink 1986) would usually preclude the comparison of respiration rates calculated in separate studies, it is encouraging to note the similarity of TCOD estimates from studies in different years.

DISCUSSION

Bayne and Newell (1983) suggest 0.70 as an average value of the allometric exponent *b* in the relationship between respiration and body weight for molluscs, and cite few estimates less than 0.6. My study indicates that *M. arenaria* is one of the few suspension feeders whose *b* value is less than 0.6 (Eqn. 5.4). This supports the results of Kennedy & Mihursky (1972) who found an even lower value of 0.489

Table 5.2.

Partitioning of total community oxygen demand (TCOD) into contributions by *M. arenaria* and micro- and meiofauna.

Component	Oxygen Uptake (mg O ₂ ·m ⁻² ·h ⁻¹)	Source
<i>M. arenaria</i>	9.2	Present Study
Micro-, meio- & macrofauna*	0.9	Grant (1986)
	Σ = 10.1	
TCOD	10.1	Hargrave & Phillips (1981)
TCOD	10.0	Van Raalte (1978)

* exclusive of *Mya arenaria*

when examining juvenile *M. arenaria* acclimated to 3°C. The biological meaning of b is still obscure, but in general, it signifies a decrease in metabolic rate with increasing body size when b is less than unity (Raymont 1983). Because Rodhouse (1979) demonstrated that b decreases with decreasing temperature in *Ostrea* sp., it is likely that the value of 0.558 found in the present study reflects the capacity adaptations (*sensu* Precht 1958) necessary in the relatively cold waters of Atlantic Canada.

M. arenaria accounts for the majority of oxygen consumed by the Eastern Passage intertidal benthos in the spring. As temperature increases, the high temperature coefficient of the non-*Mya* community respiration ($Q_{10}=6.5$, 6-16°C; Grant 1986) means that this component of total benthic oxygen demand will increase faster than respiration due to *M. arenaria* ($Q_{10} = 2-3$, 10-20°C, Kennedy & Mihursky 1972). Thus, the contribution of the clams to total community metabolism will be at a maximum in colder periods of the year.

Many studies of subtidal TCOD have shown that the contribution of benthic macrofauna is often surpassed by micro- and meiofaunal respiration (e.g. Hargrave 1969*b*, Smith 1973, Kemp & Boynton 1981). Investigations on intertidal sandflats, however, have demonstrated that macrofaunal respiration is a larger and possibly the largest component of total community respiration (68-84 % of TCOD; Pamatmat 1968, Asmus 1982*a*, Boaden & Elhag 1984). The partitioning of TCOD in these habitats is probably mediated by many complex factors, such as community composition and environmental conditions (e.g. periodic exposure to air).

Observations from both the literature and the present study suggest an additional factor may have contributed to low microfaunal metabolism; the relatively low microfaunal respiration measured in the sandy intertidal may be due

partially to the minor fine-grained component of the sediment. Because bacterial abundance in sediment is inversely correlated with grain size (Hargrave 1972, Dale 1974, Rublee & Dornseif 1978, Yamamoto & Lopez 1985), communities on coarse-grained sediments (lower surface area, lower organic matter) may exhibit a reduced microbial contribution to TCOD compared with those of fine-grained sediments. Consequently, a larger portion of TCOD in sandy sediments results from macrofaunal respiration. In contrast, Schwinghamer et al. (1986) have shown that macrofaunal respiration accounts for only a small (7 %) fraction of annually-averaged TCOD in a muddy intertidal community.

Sediment quality can also directly influence the dominance of *M. arenaria* via effects on bivalve growth. Sediment characteristics will affect the establishment, growth rate, and shell allometry of *M. arenaria* (Newell & Hidu 1982, Witherspoon 1984). The fine sand at the Eastern Passage tidal flat is an optimal substrate for the clam because it allows a biophysical compromise between the high growth observed in fine-grained substrata (Newcombe 1935, Newell & Hidu 1982) and siphon-clogging problems due to resuspension of mud and silt (Kühl 1972, Schafer 1972). Swan (1952) has found that *M. arenaria* grows fastest in sand.

It is probable that the clam dominance on the sandflat was not unique to 1987. Analysis of climatic and growth data suggest that the average densities in other years may actually be higher than those observed during this study. Size-frequency results show a substantially smaller 1+ cohort compared with that of the 2+ cohort (Fig. 5.3a). Unlike more southerly flats, where *M. arenaria* spawns twice annually (Brousseau 1978b), only one recruitment period, early fall, is observed on the Canadian Atlantic coast (Burke & Mann 1974, Witherspoon 1982). The delay in spawning is probably a result of the water not reaching the critical spawning

temperature (10-12°C; Nelson 1928) until relatively late in the season. As a result of the delay, young clams produced from a fall spawning period are particularly susceptible to high mortality caused by abnormally severe winters (Beukema et al. 1978). Such a winter was experienced in 1986-87, as manifested by the presence of Gulf of St. Lawrence ice in Halifax harbour (a 1-in-25 yr phenomenon). Increased mortality and decreased recruitment of the 1+ cohort may have occurred due to the persistence of cold water temperatures. Alternatively, this cohort may have been removed during episodes of high bedload transport (Chapter Four).

Climatic and other environmental anomalies are also likely to affect growth rates. Menesguen and Dreves (1987) have shown that variation in mean annual growth is correlated with temperature anomalies. Other factors, such as chronic oil pollution at Eastern Passage, are not likely to influence the clam population to a large extent. MacDonald and Thomas (1982) and Gilfillan et al. (1976) have demonstrated reduced growth of *M. arenaria* resulting from heavy crude oil spills, however growth reduction of clams exposed to low level residual oil has not been demonstrated.

The dominance of *M. arenaria* in community respiration has important implications for benthic energy flow at the Eastern Passage sandflat. Filter feeding by benthic bivalves enhances the transport of particulate matter from the water column to the benthos (Haven & Morales-Alamo 1966, Doering et al. 1986). By applying an empirical equation relating filtering rate to clam biomass and density (Coughlan & Ansell 1964), I estimated that the water covering the tidal flat (~30 x 10⁶ l) can be filtered by the *M. arenaria* population in ~5 h. Although this is only a preliminary estimate, similar magnitudes of filtration are well-established (see

Nichols 1985, Smaal et al. 1986). The transfer of seston to the sediment via clam filtration may be an important mechanism by which the food supply to deposit feeders is maintained at Eastern Passage.

CHAPTER SIX

THE INFLUENCE OF SEDIMENT DISTURBANCE AND WATER FLOW ON
THE GROWTH OF THE SOFT-SHELL CLAM *MYA ARENARIA*

ABSTRACT

The importance of sediment disturbance and water flow to the production of the soft-shell clam *Mya arenaria* was assessed in laboratory flumes by measuring growth rates of clams exposed to a gradation of bed shear stress, free-stream velocity, and frequency and depth of sediment disturbance for 10 months. In the absence of sediment disturbance, tissue growth was directly proportional to both free-stream (U) and shear (U_*) velocity ($r^2 = 0.64$ & 0.72 , respectively, $P < 0.001$). I suggested that increased organic seston flux linked higher water flow to higher growth. In all treatments, maximum growth rates (60 % increase in dry wt.) were observed with daily disturbance of the top centimeter of sediment. No level of disturbance resulted in growth rates lower than those of undisturbed clams in low flow ($U = 0.4 \text{ cm}\cdot\text{s}^{-1}$, $U_* = 0.1 \text{ cm}\cdot\text{s}^{-1}$). The stimulation of growth under maximum sediment disturbance was removed when U exceeded $\sim 3 \text{ cm}\cdot\text{s}^{-1}$ ($U_* = 0.7 \text{ cm}\cdot\text{s}^{-1}$). An energy budget for *M. arenaria* indicated that the amount of organic material suspended during sediment disturbance was insufficient to account for the increased growth of clams subjected to high levels of disturbance. I hypothesized that sediment disturbance associated with intense clam harvesting, and changes in local hydrography resulting from coastal development, may be responsible for the unexplained growth variation in commercial clam stocks.

INTRODUCTION

Current speed, through its control of food supply or oxygen exchange, is a dominant physical mechanism limiting sublittoral macrofaunal production (Wildish 1977). For suspension-feeding epifaunal bivalves such as *Ostrea edulis* (Walne 1972), *Mytilus edulis* (Wildish & Kristmanson 1984, Fréchette & Bourget 1985a,b), *Modiolus modiolus* (Wildish & Kristmanson 1985), and *Argopecten irradians* (Cahalan et al. 1989), the linkage mechanism has been confirmed as maintenance of food ration. Only when flows exceed a threshold velocity will decreased growth be observed, due to direct feeding inhibition (Wildish et al. 1987), inorganic dilution of suspended particulate organic matter (Gerrodette & Flechsig 1979), or clogging of filtering appendages (Rhoads & Young 1970).

Water flow may regulate the production of infauna by an additional physical mechanism. Recent evidence has suggested that the balance between increased mortality and a nutritional subsidy resulting from sediment disturbance may regulate the production of the micro- and meio-benthos (Findlay et al. 1985, Palmer 1988a, Emerson 1989), but the combined effects of water velocity and sediment disturbance on the growth of macroinfauna are unknown. With increasing coastal development, the response of nearshore species, such as the soft-shell clam *Mya arenaria*, to changes in flow and disturbance must be evaluated if benthic energetics are to be effectively modelled.

The experimental control necessary to establish the response of clams to sediment disturbance and flow requires laboratory studies. Because the contact of *Mya arenaria* with the water column is limited to the sediment-water interface, two problems must be overcome if laboratory results are to be relevant to natural

populations: (1) For infauna, it is not adequate to describe the flow solely in terms of U , the free-stream velocity, and (2) clams, unlike epifauna, cannot be easily positioned on the bottom of a flow chamber (e.g. Walne 1972).

The velocity gradient within the boundary layer produces a stress on the bed (τ) which can be expressed by U_* , the shear velocity: $U_* = \sqrt{\tau/\rho}$, where ρ is the density of seawater. Thus, for *M. arenaria*, U_* is an appropriate descriptor of the boundary flow. By measuring both U_* and U , the effects of water flow on clam growth can be replicated and generalized.

Paradoxically, to determine the effects of flow on clam growth, clams must be removed from the flow; i.e., the second problem can be eliminated by simulating the clam's natural environment within the flume. By using a skin-friction probe which measures both U and U_* , and by constructing a series of flumes, each with a natural substrate base, I have tested the null hypothesis that sediment disturbance and water flow do not account for growth variation in *M. arenaria*.

MATERIALS AND METHODS

Experimental Protocol

An experimental population of 82 clams was obtained from an intertidal sandflat at Eastern Passage, Nova Scotia (described in Emerson et al. 1988). All clams were from the same cohort (4-yr-old, avg. shell length = 33.9 mm, CV=6.8%) to remove growth variation due to age differences. Although clams from lower latitudes can reach sexual maturity at 25 mm shell length (Pfitzenmeyer 1965, Commito 1982, Brousseau 1987b), clams on a nearby tidal flat reach maturity only after reaching 40 mm in length (Witherspoon 1982). In addition, the higher growth rate of these relatively small clams maximized the possibility of detecting significant

changes in growth. This is particularly important in laboratory experiments in which the quality of diet is often sub-optimal, and because of the relatively slow growth rate of *Mya arenaria* in temperate latitudes (Witherspoon 1982).

To determine the effects of flow and sediment disturbance on the production of clams, net growth of individual *Mya arenaria* held in a series of flumes was measured from the end of June 1988 to April 1989. Two clams were 'planted' in each of 41 flumes containing a sediment base. The experiment consisted of 7 levels of sediment disturbance (treatments). For the first, the sediment in 5 flumes remained undisturbed. In the remaining 6 treatments, increasing levels of sediment disturbance (see below) were allocated equally to the remaining 36 flumes; i.e., the first treatment was replicated 5 times, whereas the remaining treatments were replicated 6 times. A similar range of flow was allocated to each treatment; in general, each treatment was applied in 2 flumes in which the flow was low ($U = 0.1-2 \text{ cm}\cdot\text{s}^{-1}$, $U_* = 0.1-0.2 \text{ cm}\cdot\text{s}^{-1}$), 2 flumes in which the flow was high ($U = 4-6 \text{ cm}\cdot\text{s}^{-1}$, $U_* = 0.5-0.7 \text{ cm}\cdot\text{s}^{-1}$), and 2 flumes in which the flow was in the mid-range ($U = 2-4 \text{ cm}\cdot\text{s}^{-1}$, $U_* = 0.2-0.5 \text{ cm}\cdot\text{s}^{-1}$). In the undisturbed treatment, however, 2, 1 and 2 flumes were allocated low, mid and high flow rates, respectively. Ambient water temperature ($1.5-16.0^\circ\text{C}$) and salinity ($31 \pm 1 \text{ ‰}$) were maintained throughout the experiment. The depth of the redox potential discontinuity was 3-10 mm in each flume; it was not related to flow, but was positively related to degree of disturbance (linear regression, $r^2=0.39$, $P<0.01$).

Several allometric growth indices were calculated: percent increase in shell length, shell height and shell width (length of axis joining each valve apex). These linear indices were combined to produce a fourth index, percent increase in shell-cavity volume (SC-volume), approximated by the volume of an ellipsoid.

Because the direct measurement of soft-tissue growth was not possible, a final and most relevant growth index, percent increase in shell-free dry tissue weight (SFDT-weight), was measured indirectly using the relationship between shell morphometry and soft-tissue biomass. Simple linear regressions calculated between SFDT-weight and each morphometric variable indicated that SC-volume (which incorporated all linear dimensions) was the best predictor of SFDT-weight ($\log \text{SFDT-weight (mg)} = 1.03[\log \text{SC-volume (ml)}] + 1.83, r^2=0.994, n=202$). Although shell growth and soft-tissue growth are not always tightly coupled (Hilbish 1986, Borrero & Hilbish 1988), shell growth has been used as a practical measure of bivalve production (Nielsen 1985, Peterson & Fegley 1986). My approach has the added advantage that bias common with direct weight measurement of *Mya arenaria* (Hawkins & Rowell 1987) is eliminated by indirect estimation.

Flume Design

The dimensions of each flow-through flume were restricted to minimize the demand on water supply (Fig. 6.1). The objective in flume design was to provide a range of flows ($\sim 0.1\text{-}6 \text{ cm}\cdot\text{s}^{-1}$) in a smooth-turbulent boundary layer. Critical shear velocities of Eastern Passage sediment were not exceeded in the flumes ($U_{*crit} < 0.95 \text{ cm}\cdot\text{s}^{-1}$: Grant et al. 1986b), and minimum flows were sufficient to maintain both an aerobic sediment-water interface and water and sediment temperatures equivalent to those in flumes of higher flow. Free-stream velocity was defined as the 10-second average of water velocity 1.5 cm above the sediment. Shear velocity was measured at the sediment-water interface adjacent to each siphon. Both U_* and U were measured using a skin friction probe with an accuracy of $\pm 10 \%$ and a minimum threshold of $U_* = 0.1 \text{ cm}\cdot\text{s}^{-1}$ (Gust 1987).

Figure 6.1

Schematic representation of experimental flumes. Position of clam (size not to scale) is shown in the cut-away section. Total number of flumes was 41.

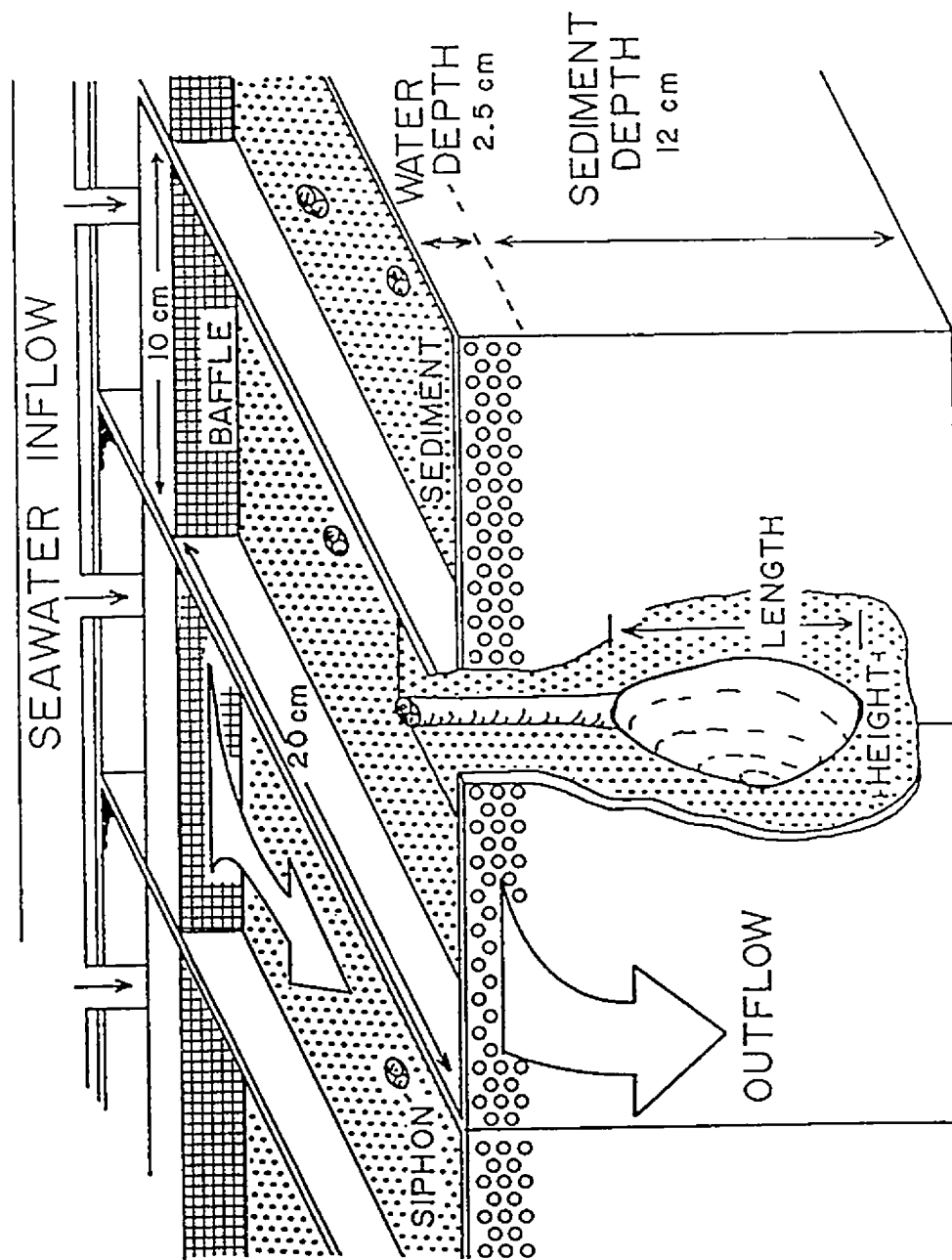


Figure 6.1

Filtered seawater, provided by the Dalhousie Aquatron, was pumped into each flume through a T-shaped, perforated diffuser facing the bottom of the intake reservoir. Turbulence was homogenized further by directing flow through a screen (baffle thickness = 1 cm, mesh size ~3 mm). At the exit was a perforated plate, a compromise between a solid weir which can produce upstream non-conformities in the boundary layer, and a free fall, which requires a larger water supply and restricts water depth in low flows. Water depth in all flumes was 2.5 cm (± 3 mm). Uniformity of flow in the test section was created by the 4:1 ratio of flume width to water depth. With this ratio, and a side-wall boundary roughness lower than that of the sediment, secondary circulation and side-wall boundary-layer effects were minimized (see Nowell & Jumars 1987).

The bottom of each flume was covered with a 12 cm deep layer of sieved (1 mm mesh) sediment from the Eastern Passage intertidal flat. Median grain size after sieving ($220\mu\text{m}$) was similar to that of Eastern Passage sediment ($200\text{-}250\mu\text{m}$). Sediment depth in each flume was greater than that required by clams to attain their natural living depth within the sediment (Emerson et al. 1988). Clam densities in the flumes were 50 % lower than those at Eastern Passage (Emerson et al. 1988). During planting, clams were oriented so that the inhalent-exhalent siphon axis was perpendicular to the direction of current; this prevented pumping of exhaled water (Vincent et al. 1988). Clams were progressively offset from the flume's midline to limit downstream effects by the upstream clam. The distance between the inlet and the upstream clam and between the two clams in a flume were both ~6 cm. All clams were acclimated to the seawater system for one week prior to planting, and to the flumes for an additional week prior to sediment disturbance.

Every three days, clams were fed a diet of ground (to 300 μm) dry cereal in suspension (15 $\text{J}\cdot\text{g}^{-1}$ cereal: 17 % protein, 2 % lipid, 81 % carbohydrate); their ration was approximately 30 % of clam SFDT-weight. Diet was supplemented by phytoplankton (*Chaetoceros gracilis*; ~2 % of tissue weight) once per month. Food addition lasted approximately 10 minutes, during which time flume inflow was reduced to 10 % of the normal flow rate.


Application of Sediment Disturbance

To isolate the effect of sediment disturbance from that of water flow, it was necessary to maintain subcritical shear velocities in the flumes. Sediment was artificially disturbed by injecting water into the sediment surface through a T-shaped sprinkler head of width equivalent to each flume. The entire sediment surface was raked by manually directing the water jets into the sediment surface for 10 seconds, during which time flume outflow was reduced to 50 % of normal flow rates. By adjusting sprinkler pressure, the top 1 or 10 mm of sediment could be disturbed. Depth of disturbance was determined by visually detecting the maximum depth of disturbance when the sprinkler was directed into a sediment core consisting of alternating 2-mm-deep layers of white and dark sand.

Depths and frequencies of sediment disturbance were chosen to reflect natural time and spatial (vertical) scales of sediment transport at Eastern Passage (Emerson, unpubl. data). A sediment disturbance hierarchy comprising combinations of frequency (absent, monthly, weekly, daily) and depth of sediment disturbance (0 mm, 1 mm, 10 mm; Table 6.1), was used in all statistical analyses. In the mid-range (Degrees 3-5), I assumed that frequency rather than depth was the dominant component of disturbance. Thus, the level of sediment disturbance from

Table 6.1

Frequency, approximate depth and degree of sediment disturbance in flumes containing *Mya arenaria*. The hierarchy of sediment disturbance (Levels 1-7) was used in all statistical analyses.

Frequency of Disturbance	Depth of Disturbance	Degree of Disturbance	Level	
Absent	0 mm	Lowest	1	
Monthly	1 mm		2	
Monthly	10 mm		3	
Weekly	1 mm		4	
Weekly	10 mm		5	
Daily	1 mm		6	
Daily	10 mm		Highest	7

monthly, deep raking was less than that of shallow, weekly raking.

RESULTS

The mean initial shell length (33.9 mm, CV=6.8 %), height (20.7 mm, CV=7.1 %), and width (12.5 mm, CV=7.1 %) of the entire experimental population increased by 3.7 % (CV=96.8 %), 5.6 % (CV=67.0 %), and 3.2 % (CV=19.1 %), respectively, after 10 months. Mean percentage increase of both initial shell cavity volume (4.6 ml, CV=19.1 %) and SFDT-weight (330.9 mg, CV=19.6 %) was 13 % (CV=88 %). Mortality (<7 % during 10 months) was not related to flow rate or level of sediment disturbance. Analyses of results were partitioned into the determination of (1) the effects of flow (U and U_*) on growth in the absence of sediment disturbance, and (2) the interacting effects of sediment disturbance and flow on growth.

The first objective could be met by relatively simple linear regression analyses but the second required analysis of covariance (ANCOVA) and a multiple comparison technique. In the ANCOVA, clam growth was the dependent variable, level of sediment disturbance (1-7) was the factor, and water flow (either U or U_*) was the covariate. To isolate any significant effects identified by ANCOVA, the GT2 multiple comparison method was used.

Sokal and Rohlf (1981) have recommended the GT2 method to test for significant differences between means adjusted for the covariate. In this technique, a minimum significant difference (MSD) was calculated for each adjusted mean: $MSD = (\text{critical value}) \times (\text{standard error of the adjusted mean})$, where critical value refers to the statistical distribution appropriate to a given test, in this case, the studentized maximum modulus. If comparison intervals ($\text{mean}_{adj} \pm MSD$) did not

overlap, means were considered to be significantly different. For a detailed explanation of this technique, refer to Sokal and Rohlf (1981: pp. 242-252). Effects of flow and sediment disturbance on growth were illustrated further using a kriging procedure (see below). To normalize the distributions and homogenize the variance, all growth indices were arcsine-transformed, and the flow variables were log-transformed.

Water Flow and Clam Growth

The experimental design allowed the measurement of flow effects on clam growth in the absence of sediment disturbance. Simple linear regressions were calculated between the percentage growth in SFDT-weight and both flow variables (Fig. 6.2). In separate regressions, log-transformed free-stream velocity and shear velocity explained 64 % and 72 % of the variation in arcsine-transformed clam growth. Throughout the range of flows tested ($U = 0.1-5.8 \text{ cm}\cdot\text{s}^{-1}$, $U_* = 0.1-0.5 \text{ cm}\cdot\text{s}^{-1}$), there was no evidence of growth inhibition; growth was directly proportional to flow. Because shear velocity was highly correlated with, indeed dependent upon, free-stream velocity ($r^2=0.80$), it was impossible to determine the independent effects of U and U_* on clam growth. Nonetheless, it appeared that shear velocity was a better predictor of clam growth than free-stream velocity.

An effect of clam position (upstream or downstream) on clam growth could not be discerned by analysis of covariance, using position as the factor and U or U_* as the covariate ($P>0.05$). As a result, the preceding regressions were calculated independently of clam position. Regressions using the other growth indices all showed the same trend with U and U_* as the SFDT-weight growth index. For conciseness, these additional flow-growth relationships were not illustrated.

Figure 6.2

Simple linear regressions calculated between (A) the percentage increase in shell-free dry tissue weight of *Mya arenaria* and free-stream velocity, and (B) weight increase and shear velocity. Data included only those clams which grew in the absence of sediment disturbance (during a 10-month period). Coefficients of determination and 95 % confidence limits are indicated. Sample size was 10 for both regressions. SFDT-weight has been arcsine-transformed and flow variables were plotted on a logarithmic scale.

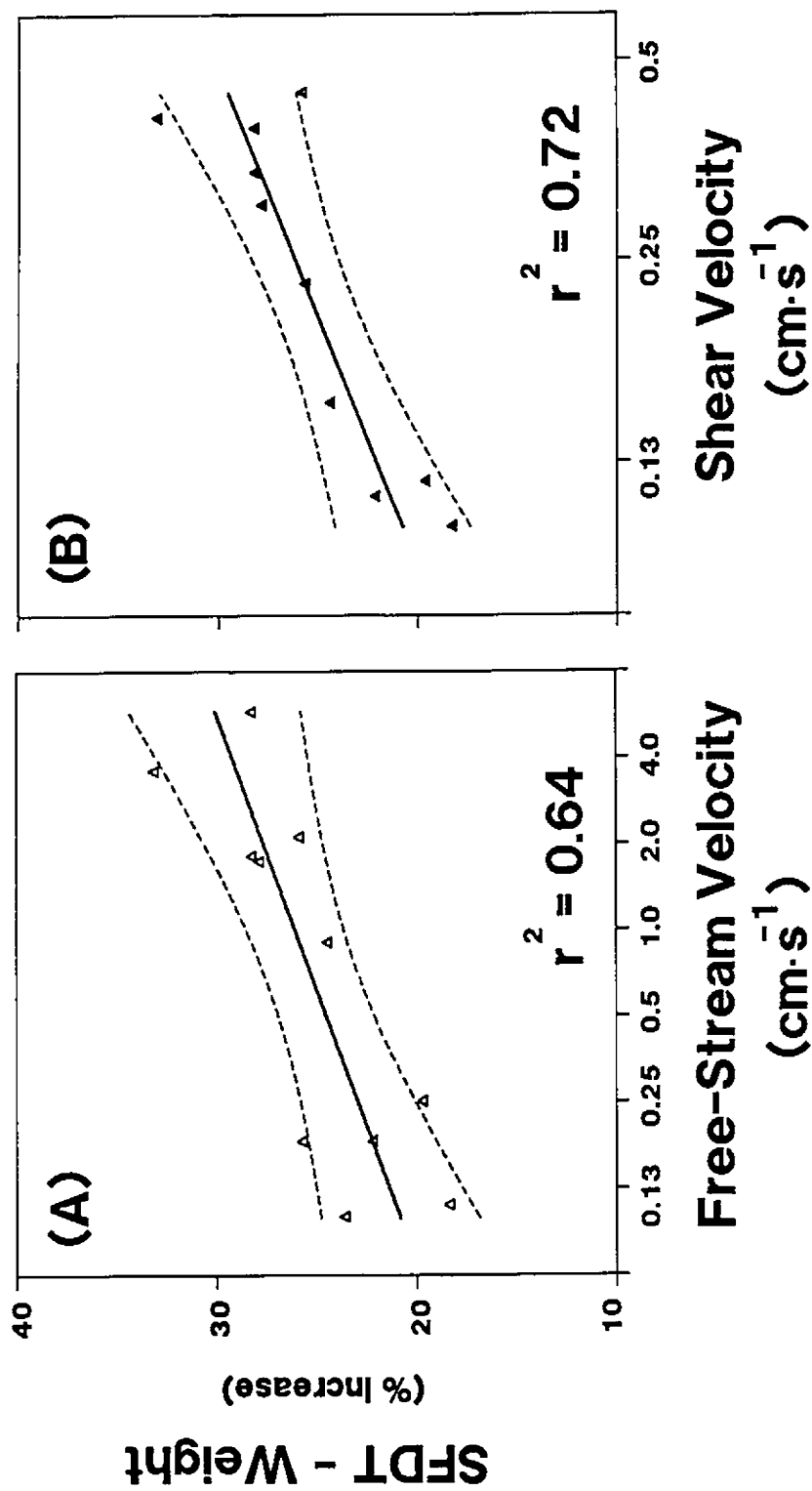


Figure 6.2

Coefficients of determination for the additional regressions with free-stream velocity were 0.42, 0.38, 0.64, and 0.62 for shell length, height, width, and cavity volume growth indices, respectively.

Effects of Sediment Disturbance on Clam Growth

With free-stream velocity as the covariate, significant differences resulting from sediment disturbance were found in all growth indices with the exception of shell height (Table 6.2). Because of a non-significant relationship between growth in shell height and sediment disturbance, it could not be assumed that the growth of SC-volume would be significantly linked to degree of disturbance. It appeared, however, that increases in length and width compensated for shell height, because a significant relationship was calculated between SC-volume and sediment disturbance. With shear velocity as the covariate, all growth indices were significantly related to the degree of sediment disturbance with the exception of the percentage increase in shell height. In most cases, however, the levels of significance calculated using the shear-velocity covariate were lower than those using free-stream velocity.

GT2 multiple comparisons revealed that the effect of increasing sediment disturbance on clam growth was not uniform (Fig. 6.3). (Because multiple comparison results for U and U_* covariates were identical, only treatment effects adjusted for U_* are shown.) A bimodal distribution of comparison intervals of all growth indices was observed. Although there was a large amount of overlap, four distinct components appeared within each distribution. First, undisturbed clams grew approximately 8 % less than those which experienced the minimum degree of sediment disturbance. Second, an increase in disturbance from Degree 2 to 3

Table 6.2

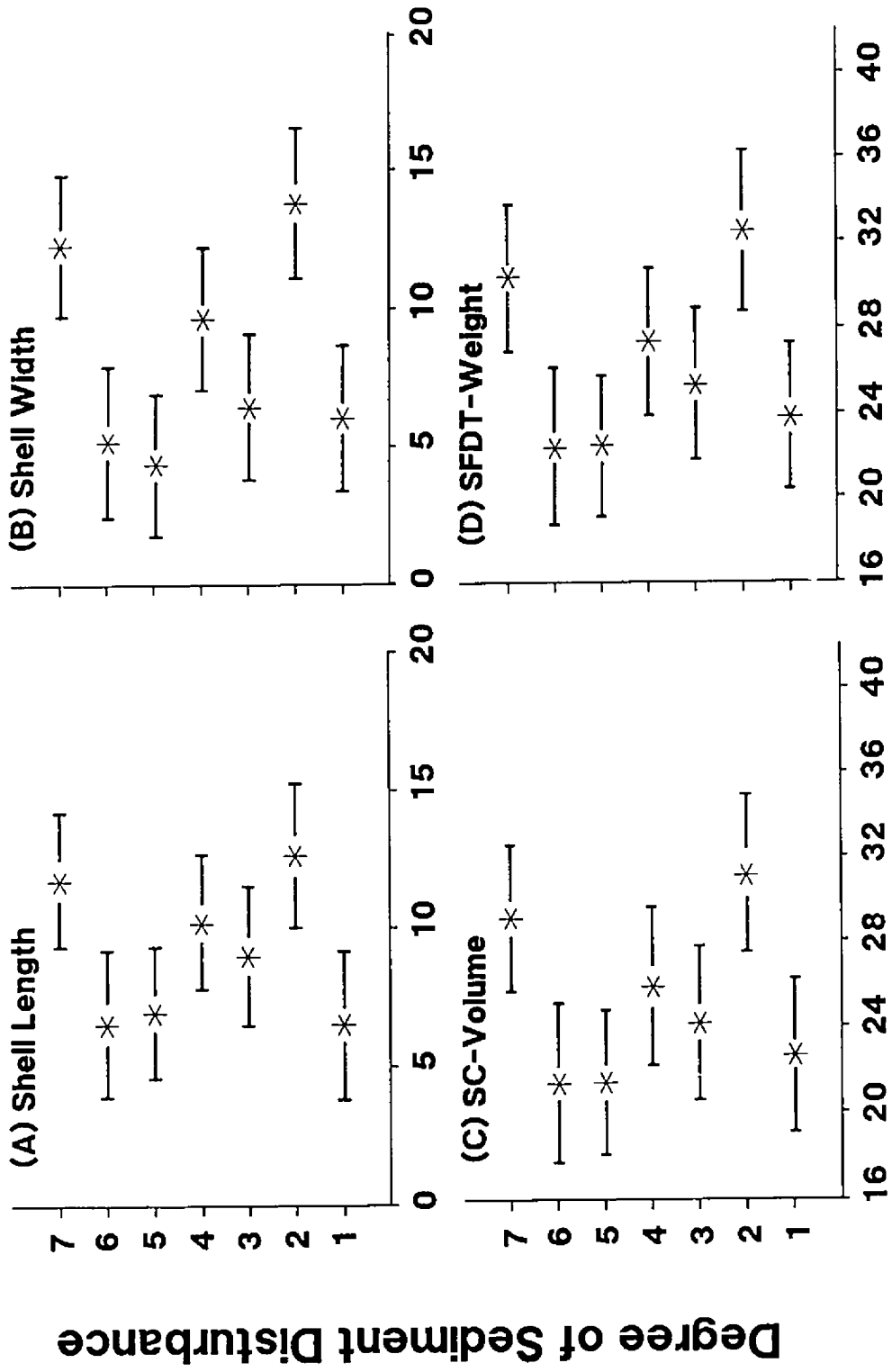
F statistics from ANCOVA tables indicating the response of clam growth to sediment disturbance, with either free-stream or shear velocity as the covariate. As a prerequisite to ANCOVA, results of tests for homogeneity of slopes are indicated.

Growth Index	Homogeneity of Slopes	Treatment	Covariate	
		Sediment Disturbance	Free-stream Velocity	Shear Velocity
Shell Length	1.39 NS	3.03 *	10.89 **	
	0.48 NS	2.58 *		4.82 *
Shell Height	1.24 NS	1.26 NS	8.30 **	
	0.22 NS	1.12 NS		2.32 NS
Shell Width	1.88 NS	7.58 ***	32.79 ***	
	1.09 NS	5.38 ***		13.08 ***
SC-Volume	1.72 NS	4.15 ***	18.16 ***	
	0.45 NS	3.19 **		6.73 *
Soft-tissue Weight	1.70 NS	4.15 ***	18.09 ***	
	0.45 NS	3.19 **		6.72 *
Condition Index	1.21 NS	1.45 NS	1.15 NS	
	1.01 NS	1.48 NS		1.04 NS

* $0.05 \geq P > 0.01$ ** $0.01 \geq P > 0.001$ *** $0.001 \geq P$ NS Not significant

Figure 6.3

Mean clam growth adjusted for shear velocity (covariate) at all levels of sediment disturbance. Levels of sediment disturbance are defined in Table 6.1. The horizontal bars represent 95 % comparison intervals (GT2 method). Means whose intervals overlap were not significantly different. The shell-height growth index was not included because ANCOVA results indicated a non-significant relationship with sediment disturbance. SC = shell cavity, SFDT = shell-free dry tissue.



Percentage Increase

Figure 6.3

generally resulted in a slower growth rate, although a statistically significant decrease was found only for the shell width growth index (Fig. 6.3B). Third, although there appeared to be a general trend of decreasing growth with increasing degrees of sediment disturbance (Deg. 3 to 6), there were no significant differences between the growth of clams subjected to monthly disturbances of 10 mm depth (Deg. 3) and that of clams disturbed daily to 1 mm depth (Deg. 6). Lastly, clams exposed to the maximum degree of sediment disturbance (Deg. 7) grew approximately 8 % larger than clams under daily, shallow disturbance (Deg. 6). The effect of maximum sediment disturbance was not significantly different from that of least disturbance (Deg. 2).

The combined effects of water flow and sediment disturbance on soft-tissue growth of *Mya arenaria* were illustrated using a distance-weighted, least-squares kriging program (Wilkinson 1988: Fig. 6.4). By providing an objective method of data interpolation, such programs are useful for identifying general trends (Gilbert & Simpson 1985), especially when the results of ANCOVA and GT2 analyses can be used as interpretive guides. Kriging was particularly useful in the present study since the interacting effects of flow and sediment disturbance on clam growth were difficult to visualize using only ANCOVA and GT2 analyses. Interpretation of surface topography in the model generated for the SFDT-weight growth index was restricted to the area covering the higher flows ($U_* \geq 0.1 \text{ cm}\cdot\text{s}^{-1}$) because of the low accuracy of the skin-friction probe in minimal flows (Gust 1987).

Clams subjected to maximum sediment disturbance under low flows ($U_* = 0.1 \text{ cm}\cdot\text{s}^{-1}$) showed maximum growth rates (60 % increase). As degree of disturbance decreased at this level of flow, the bimodal pattern first indicated by the GT2 analysis was observed. Undisturbed clams in low flow had lowest growth rates (10

Figure 6.4

The relationship between percentage growth in shell-free dry tissue weight, degree of sediment disturbance, and shear velocity (U_*), predicted from a distance-weighted, least-squares kriging model. The levels of sediment disturbance are defined in Table 6.1.

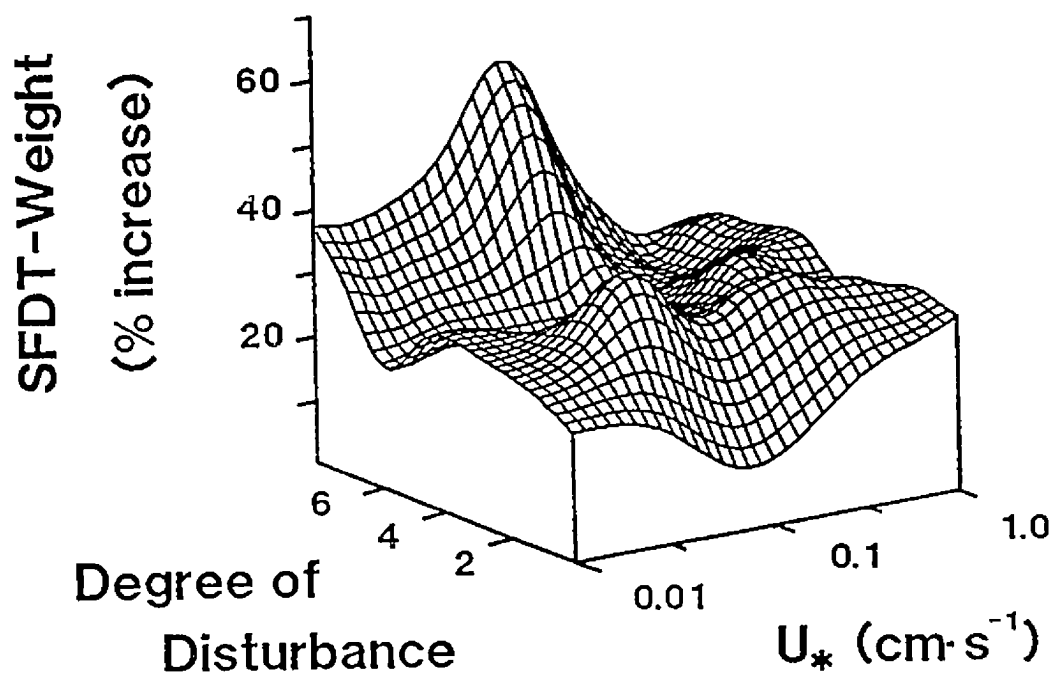


Figure 6.4

% increase). The growth rate of clams subjected to disturbance was frequently greater, and never less, than that of undisturbed clams. As indicated by the simple linear regressions (Fig. 6.2), clam growth was directly proportional to shear velocity ($U_* = 0.1-0.7 \text{ cm}\cdot\text{s}^{-1}$) in the absence of disturbance. Over the same range of U_* , but at maximum levels of disturbance, clam growth was inversely proportional to shear velocity. Allocation of significance to the remaining surface features was not warranted.

Non-treatment Effects on Clam Growth

Difficulties of simulating natural conditions in the laboratory can lead to abnormally high levels of non-treatment stress which may restrict the extrapolation of laboratory results to natural populations. Low levels of laboratory stress in my experiments were indicated by the comparable growth rates of experimental clams and those in a nearby field population, and the low mortality in the experimental population. The increase in shell length of the experimental clams if they had remained in the field was calculated using published parameters of the Von Bertalanffy growth equation (Eqn. 6.1).

$$L_t = L_\infty (1 - e^{-k(t-t_0)}) \quad (6.1)$$

where L_t = a given shell length, L_∞ = length at which growth rate is zero, k = growth rate to L_∞ , t = age (yr) at given length (from *annual* shell growth rings), and t_0 = age at which length is zero. On a nearby clam flat, Chezzetcook Harbour N.S., $L_\infty = 127.880$ (SE=3.73), $k = 0.063$ (SE=0.0025) and $t_0 = -0.688$ (SE=0.0259) (Witherspoon 1982). The predicted shell growth *in situ* is 12.0 % in 10 months, however this rate does not reflect the seasonal growth variation observed in bivalves (Hilbish 1986, Peterson & Fegley 1986). For *Mya arenaria*, growth during the

seasons during which the experiment was conducted (late summer, fall, winter) is only 30 % of annual growth (Newcombe 1935). As a result, a more reasonable estimate of growth under natural conditions would be 3.6 %, an increase which corresponds to that observed in the experimental population (average = 3.7 %).

Condition index analysis also indicated low laboratory stress. The allometric condition index (ACI) is useful as a rapid assessment of the ecophysiological status of bivalves: $ACI = SFDT\text{-weight}/SC\text{-volume}$ (Brown & Hartwick 1988; Bonsdorff & Wenne 1989). A decrease in the ACI often reflects slow growth resulting from environmental stress. On average there was only a 10 % decrease in the ACI of the experimental population after 10 months (from an initial mean ACI of 71.4, $CV=6\%$). ANCOVA results indicated that this reduction was common to all experimental clams (Table 6.2); animals in each treatment were affected equally by non-treatment stress.

DISCUSSION

Effects of Flow on Growth Rate

If they are food limited, suspension feeders will benefit from the increased organic seston flux of high flows until a critical velocity (U_{crit}) is reached, beyond which growth is inhibited. Wildish et al. (1987) have demonstrated that for *Placopecten magellanicus* $U_{crit} = 10 \text{ cm}\cdot\text{s}^{-1}$, and Eckman et al. (1989) have shown that the growth of *Argopecten irradians concentricus* at $U = 17.2 \text{ cm}\cdot\text{s}^{-1}$ was significantly less than at $U = 1.4\text{-}8.6 \text{ cm}\cdot\text{s}^{-1}$. Under the low flows of the present study ($U_{max} < 6 \text{ cm}\cdot\text{s}^{-1}$) it would appear that the positive correlation between growth of *Mya arenaria* and water velocity (in the absence of sediment disturbance) was a simple consequence of more food. However, the experiment was designed to

specifically exclude this mechanism linking growth to water flow.

By ensuring that the clams were not food limited, it was intended that factors other than increases in food might be identified as responsible for higher growth in higher flows. Unfortunately, the difficulty of maintaining an optimum food ration in flow-through systems during prolonged periods may have produced food-limited conditions. The situation was confounded by the continuous addition of organic seston (e.g. algal cells, bacteria, detritus) via the 'filtered' seawater system. Although these particles were small ($\leq 30\mu\text{m}$), bivalves have been shown to utilize particles smaller than $10\mu\text{m}$ efficiently (Riisgård 1988).

The concentration of total seston in the flume water column was found to be $1.5\text{ mg dry wt}\cdot\text{l}^{-1}$ (CV = 82 %), yielding a minimum flux (flumes with lowest flows) of at least $13\text{ mg}\cdot\text{hr}^{-1}$. Even if one assumes an abnormally low organic content of the seston (~40 % by weight), it appears likely that natural seston in the seawater system provided the bulk of the food ration. Therefore, clams in higher flows experienced a greater seston flux and, consequently, a greater growth potential than clams in low flows. This situation is consistent with a recent field study in which horizontal seston flux appeared to be a major factor affecting growth of another infaunal suspension-feeding bivalve, *Mercenaria mercenaria* (Grizzle & Morin 1989).

A seston depletion effect (Wildish & Kristmanson 1985), in which downstream clams received significantly less seston than upstream ones, was unlikely. First, an effect of clam position on the growth of clams (in the absence of sediment disturbance) could not be detected by analysis of covariance. Second, calculations of water flow and clam pumping rate suggested that upstream clams did not affect the food supply of downstream clams. The slowest flow in the flume array was $9\text{ l}\cdot\text{hr}^{-1}$ ($U \sim 0.1\text{ cm}\cdot\text{s}^{-1}$), and the pumping rate of *Mya arenaria* was approximately 3.9

l·hr⁻¹·g⁻¹ SFDT-weight (see Jørgensen & Riisgård 1988). Because the heaviest clam in the experimental population was 487.7 mg, the maximum combined pumping rate of two clams in one flume was only 3.8 l·hr⁻¹, well below the slowest flow rate. I suggest, therefore, that upstream clams had little or no effect on the growth of downstream clams by causing depletion of seston.

Additional insight into the mechanisms governing flow and growth could not be deduced from measures of shear velocity in this experiment; the independent effects of U_* and U on clam growth could not be differentiated because of the high dependence of U_* on U . The primary value of U_* measurement was to simulate natural flow conditions and to provide a standard of comparison for future studies. As the independent variable, U_* is preferable to U since the clams experience shear stress rather than the bulk layer flow. It was not surprising, therefore, that U_* was a better predictor of clam growth than U in the absence of sediment disturbance.

Effects of Sediment Disturbance on Growth Rate

Empirical models have suggested that the generally negative correlation between hydrodynamic forcing and the production of many benthic communities is partly a response to sediment movement (Emerson 1989). This is in direct contrast to the observation that *Mya arenaria* grew fastest under the highest degree of sediment disturbance and did not grow more slowly under any degree of disturbance. Because the models incorporated flows beyond U_{*crit} for long periods, this discrepancy may be a simple result of scale differences between the models and the present study. Moreover, Emerson's (1989) size-specific models indicated that the general negative relationship between growth and sediment disturbance was much less significant for macrofauna than for smaller organisms, probably because

macrofauna are more resistant than micro- and meio-fauna to mortality caused by abrasion and erosion due to sediment movement (cf. Munro et al. 1978, Palmer 1988a, Miller 1989). Nonetheless, high clam growth at a relatively high level of sediment disturbance was unexpected.

Mya arenaria is very sensitive to mechanical and other stimulation (Jørgensen & Riisgård 1988). When disturbed, the valve gape is reduced and the siphon and mantle edges are retracted, thereby reducing pumping and ingestion rates. However, slower growth due to interruption of feeding was subordinate to the growth benefits of sediment disturbance. The few examples describing a positive relationship between sediment disturbance and the benthos have usually involved entire communities (via recruitment: Fegley 1988) or the microfauna (via nutrient supplements: Findlay et al. 1985), but not, until now, individual macrofauna.

The most likely mechanism for increased growth of *Mya arenaria* experiencing sediment disturbance was increased food from resuspended particulate organic matter (POM). It is probable that high concentrations of benthic algae, microfauna and detritus in the top centimeter of sediment were made available as a result of sediment disturbance (see Wildish 1977). This is consistent with the evidence of flow-disturbance interaction (Fig. 6.4); additions of POM during disturbance were of greatest benefit during slow flow. The benefit was removed when the residence time of POM decreased (e.g. under higher flows), probably because clams could not utilize the POM before it was flushed from the flume.

A nutritional link between disturbance and growth appeared reasonable, but the construction of a simple energy budget made the rejection of this hypothesis necessary. Sediment disturbance added a maximum of 15 mg dry wt of organic matter to the water column, but during the 7 minutes required for clams to resume

normal pumping activity, the food supplement was reduced to a maximum of 1 mg POM. Even if the clams were able to utilize ~50 % of the supplement (an overestimate given the relatively high flume flow rates and low clam pumping rates), clams subjected to the maximum degree of sediment disturbance would receive a maximum food supplement of only ~150 mg dry wt organic matter during 10 months. If I assume a maximum gross production efficiency of 6 % (for infaunal suspension feeders; Bayne and Newell 1983), such a supplement could not account for the entire growth increase (~26 mg soft tissue) in clams subjected to daily, deep sediment disturbance compared with clams experiencing daily shallow disturbance. Furthermore, it is obvious that increased food from disturbance could not account for the higher growth of clams subjected to monthly, shallow disturbance compared with growth of undisturbed clams. It is possible that sediment disturbance indirectly provided an energy subsidy by influencing the growth of other, smaller organisms within the sediment (Findlay et al. 1985), however it is not clear how this production would become available to the clams.

In summary, high-frequency, low magnitude sediment disturbance may provide a positive, (rarely a negative), growth potential for natural populations of *Mya arenaria*. Experimental limitations and the complexity of the problem have precluded identification of the link between disturbance and growth, however it is possible that a mechanism other than increased food may exist.

Implications to Natural Clam Populations

The results of my flume experiments have allowed the identification of two factors by which coastal development and fishing pressure may indirectly influence the growth of clam populations. If a tidal-power barrage in the upper Bay of Fundy

is constructed, Wildish et al. (1986) have predicted a 50 % decrease in shear stress on a major clam tidal flat (see Witherspoon 1984). In addition to changing sedimentation patterns, their results suggest that lower shear stress may reduce the amount of suspended food available to clams and favour a shift to a deposit-feeding community (Wildish & Peer 1983). Changes of this kind may not be entirely negative; although hydrographic changes may reduce the food supply to one clam flat, another may be favoured.

Increases in fishing effort may be responsible indirectly for variation in clam population growth, but again, an entirely negative effect on the population is not necessarily the only outcome. Removal of market-size (sexually mature) clams may increase the potential for growth because of the high level of sediment disturbance on commercial clam flats. This phenomenon may partially account for the unexpected observation that clams survive to the pre-recruit and recruit stages much better in areas which are heavily fished than in areas closed to fishing (Angus et al. 1985). It is likely that modelling of clam population growth will improve with the inclusion of sediment disturbance and water flow as predictor variables.

CHAPTER SEVEN
INDIRECT EFFECTS OF CLAM DIGGING ON THE VIABILITY OF
SOFT-SHELL CLAMS, *MYA ARENARIA*

ABSTRACT

A series of laboratory experiments was conducted to determine whether non-lethal burial or exposure could alter the normal living depth of *Mya arenaria* in sand and mud. After two weeks, clams which were buried under 1-15 cm of medium-fine sand were found deeper than the controls, whereas clams which were exposed on sand (and had subsequently reburrowed) were able to re-establish their normal living depth. In contrast, clams buried under 1-15 cm of mud were able to attain their normal living depth within two weeks, but exposed clams had reburrowed to abnormally shallow depths. An increased likelihood of predation at shallow sediment depths was compounded by the 60 % slower reburrowing speed of exposed clams in mud than in sand. An additional experiment determined the depth of burial under which at least 50 % of a laboratory clam population could survive (LD_{50}). For small (<5 cm in shell length), mid-size (3-5 cm) and large (>5 cm) clams in sand, LD_{50} s were >75 cm, >75 cm and between 50-75 cm, respectively. In mud, the LD_{50} of clams less than 5 cm in length was <25 cm, and between 25 and 50 cm for clams greater than 5 cm in length. It was concluded that the indirect mortality level associated with commercial and recreational harvesting will be much greater on intertidal mudflats than on sandflats.

INTRODUCTION

The impact of clam harvesting on the density of both pre-recruits and unharvested recruits must be measured if the management of commercial stocks is to be successful. Typically, population growth models incorporate estimates of fishing pressure on recruits because these market-size clams are often the sexually mature component of the population (e.g. for *Mya arenaria*, Brousseau 1978a,b). The effects of harvesting on the remaining clams, however, often are not accounted for, despite studies which have demonstrated that indirect effects such as the destruction of prey refuges are important to the viability of clam populations (Peterson et al. 1987). For *M. arenaria*, measurement of these effects is particularly relevant since the soft-shell clam is widely exploited in North America (Bourne 1989).

Where tidal range is small, hydraulic clam dredges are often used (Pfitzenmeyer & Drobeck 1967), but digging with a tined fork (clam hack) is still the predominant method of clam fishing in North America. Digging is relatively efficient, but up to 50 % of the pre-recruits and 20 % of the unharvested recruits may be killed by shell breakage or smothering from burial within the tailings (Medcof & MacPhail 1967). Exposure on the sediment surface is also a factor leading to increased mortality due to predation. Clam digging may impose an additional stress which is not immediately evident; if harvesting causes a vertical displacement of the living depth of unharvested clams, future population densities may be affected because the survival and growth of infaunal suspension feeders are inherently linked to their distance from the sediment-water interface (Quammen 1984, Esselink & Zwarts 1989, Zwarts & Wanink 1989).

The well-documented burrowing ability of *Mya arenaria* (Medcof 1950, Glude 1954, Pfitzenmeyer & Drobeck 1967, Kühl 1972) implies that clams should be able to re-establish their normal living depth in response to non-lethal burial or exposure. However, if clams cannot return to their original depth, their susceptibility to predation, freezing, desiccation, and erosion may change. Admittedly a vertical displacement may result from long-term changes in rates of sedimentation or erosion, but burial or inadvertent exposure during clam digging are likely to be the dominant regulators of clam depth in areas of high fishing effort.

In this study, the influence of non-lethal burial and exposure on the living depth of *Mya arenaria* was measured to determine the potential of clam digging to indirectly modify the demography of a clam population. Because sediment type can alter burrowing ability (Trueman et al. 1966b), laboratory experiments were conducted in both sand and mud. Reburrowing speed and burial mortality of *M. arenaria* were also measured after a survey of the literature indicated that these variables were either poorly quantified or contradictory. By combining the results from these three experiments with existing models of fishing pressure, the estimation of clam population growth on heavily-fished intertidal flats should be improved.

MATERIALS AND METHODS

For each experiment, clams and sediment from 0-20 cm depth were obtained between September 1988 and April 1989 from a sandflat (<5 % silt-clay content, 250 μ m [2 ϕ] median grain size) at Eastern Passage, Nova Scotia, and from a mudflat (>95 % silt/clay content, i.e. median grain size <63 μ m [>4 ϕ]) at Chezzetcook Harbour, N.S. These clam populations have been described by Witherspoon (1982),

and Emerson et al. (1988). In the laboratory, sediment was placed in plastic tanks of 100 l capacity (i-w-h: 80-30-40 cm) creating a sediment depth of 20 cm. Filtered (30 μ m mesh) natural seawater of ambient temperature (2-12°C) and salinity (~31 ‰) filled the remaining 20 cm of each tank. Flow-through seawater residence time was approximately 10 minutes.

Before being added to the tanks, sand was sieved (1 mm mesh) to remove potential clam predators. Because the natural compaction of the sediment was altered, sand was allowed to set under flowing seawater for two weeks prior to experimentation. Trueman et al. (1966a) found that 24 hours was sufficient for disturbed sediment to regain a natural level of compaction. Depth of the redox potential discontinuity (RPD) after two weeks (and at the end of the experiment) was identical to that observed on the Eastern Passage sandflat at time of collection (~1.5 cm). To maintain its natural cohesive structure, mud was sieved only after completion of the experiment; predators were not observed in either sand or mud. The RPD of mud was located between 0.5 and 2 cm depth throughout the experiment.

Within one hour of collection, clams were sorted according to shell length, placed into the experimental tanks, and manipulated according to each experimental design (see below). During acclimation and experimentation, clams were provided with dried, ground cereal in suspension (15 J·g⁻¹ cereal; 10 % body wt·d⁻¹). Any cereal which accumulated on the sediment surface was removed with a pasteur pipette. Combined with detrital and algal seston within the seawater system (~1 mg·l⁻¹, 60 % organic matter), a diet of cereal has been shown to allow growth of *Mya arenaria* for at least ten months (Emerson, *in press,a*).

Vertical Displacement

Two-hundred and ninety clams (0.2-6.4 cm length) were partitioned into six treatments to determine if non-lethal burial or temporary air exposure could modify a clam's normal living depth in both sand and mud: (1) Control-Mud, (2) Control-Sand, (3) Buried-Mud, (4) Buried-Sand, (5) Exposed-Mud, and (6) Exposed-Sand. Two tanks were used for each control and four tanks for each of the remaining treatments. In each control tank, 50 clams (mean length = 3.1 cm) were 'planted' in an upright position so that the shell was completely covered by sediment (density = 25 clams \cdot 0.15m⁻²).

In the burial treatments, clams were planted within eighteen 18 cm diameter clusters, each comprising 5 clams (1-6 cm length) at a density equivalent to that of the control population. A small wooden stick marked the general location of each clam, but the exact location was identified from the appearance of the siphon. After an acclimation period of one month, three clusters were randomly assigned to one of three burial subtreatments: 1, 7 and 15 cm burial depths, chosen to reflect natural scales of burial by tailings from clam digging (Glude 1954, *pers. obs.*). (Burial depth refers to the depth of sediment placed over the original substrate surface and not to the actual depth of the clam, the latter varying in accordance with clam size.) Burial piles were created by placing a plastic collar (18 cm diameter) over each cluster and filling it with sand or mud. The time to first appearance of each clam's siphon at the new sediment surface was then measured.

In each exposed treatment, after the tanks were drained, 50 clams (1-6 cm in length) were placed horizontally on the sediment surface (density = 25

clams-0.15m²). In synchrony with the natural tide at Eastern Passage, seawater was slowly pumped back into the tanks. With one exception (when a tank seal failed), this was the only time an artificial tide was created in the experimental tanks.

Six weeks after the clams were introduced into each tank, the depths of control, buried and 'exposed' clams were measured. Here, depth was defined as the distance between the sediment-water interface and the uppermost part of the clam shell. Normal living depth referred to the depth of a clam in the control populations, whereas equilibrium depth was the depth of a clam which had been buried or exposed.

Burrowing Speed

To determine how rapidly clams could reburrow beneath the sediment surface after exposure, the procedure for the exposure treatments in the preceding experiment was duplicated. In this experiment, the dependent variable was the time required for a clam to burrow completely beneath the sediment surface after being covered by seawater. Other measurements included the initial distance between the anterior edge of the valve of the horizontal clam and the sediment surface. It was hypothesized that this measurement indicated the clam's ability to reburrow successfully.

Burial Mortality

The size-dependent survival of clams buried under 25, 50 and 75 cm of mud and sand was assessed after the results from the first experiment (see below) indicated that burial by up to 15 cm did not result in significant clam mortality. For the burial bioassay, clams (1-7 cm length) were planted in sand and mud in the same manner as in the first experiment and allowed to acclimate to laboratory conditions

for one month prior to burial. Five replicate clams in each of 3 size classes (<3, 3-5, and >5 cm length) were buried under each of the 3 burial depths in both sediment types (total = 90 clams). Acrylic cylinders (9 cm diameter) were used to contain the burial pile. Because the cylinders exceeded the height of the tanks, seawater had to be pumped into them and allowed either to drain through the sediment within the cylinder or to overflow the side of the cylinders. After two weeks, the equilibrium depth and the vitality of each clam were determined. Clams were considered to be dead if the siphon did not retract when touched or if the tissue had started to decompose. Cylinders empty of sediment were placed on 20 additional clams (1-6 cm shell length) to create a control population for this experiment.

RESULTS

Vertical Displacement

Analyses of covariance (ANCOVAs) were performed on each combination of treatments to determine if the exposure or burial treatments significantly altered the normal (i.e. control) linear relationship between living depth and log-transformed clam length (Table 7.1). First, the hypothesis of homogeneity of slopes was tested. If slopes were heterogeneous, further ANCOVA was not warranted, otherwise, the homogeneity of the y-intercepts was tested. Any significant differences were illustrated by calculating and plotting the simple linear regressions of depth versus size in each treatment. Surprisingly, equilibrium depth was not dependent on the burial depths used in the experiment (ANCOVA $P > 0.05$). As a result, the statistical procedure described above incorporated data pooled from all burial depths.

TABLE 7.1

The linear relationships between clam (*Mya arenaria*) length and living depth in each treatment were compared using analysis of covariance. Data in table include ANCOVA *F* statistics calculated to test (i) homogeneity of slopes (above double line) and (ii) homogeneity of intercepts (below double line) of each treatment combination. If slopes were heterogeneous, the test for homogeneity of intercepts was not warranted.

TREATMENT	Sand		Mud		
	Buried	Exposed	Control	Buried	Exposed
Control: Sand	8.0 **	0.3 NS	0.1 NS	1.5 NS	0.02 NS
	-	1.5 NS	127.1 ***	10.6 **	0.4 NS
Buried: Sand		5.2 *	18.7 ***	1.5 NS	7.8 **
		-	-	0.7 NS	-
Exposed: Sand			16.7 ***	0.5 NS	0.2 NS
			-	4.5 *	0.6 NS
Control: Mud				3.5 NS	0.3 NS
				0.6 NS	5.5 *
Buried: Mud					1.3 NS
					9.0 **

* $0.05 > P \geq 0.01$ ** $0.01 \geq P \geq 0.001$ *** $P \leq 0.001$

NS Not significant - Test not warranted

Results indicated several significant differences in the relationship between living depth and clam size from treatment to treatment. The equilibrium depths of clams (3-6 cm shell length) which had been buried in sand were significantly deeper than those of both the control and exposed clams (Fig. 7.1 A&B), although for smaller clams, this difference was not significant (t -tests, $P > 0.05$). The control population and the clams which had been exposed were found at equivalent depths (Table 7.1).

When the experiment was duplicated using mud, the significant treatment effects were reversed. Clams which had been exposed were found at shallower depths than either control or buried clams (Fig. 7.1 C&D), and buried clams were found at depths equivalent to the control clams (Table 7.1). Because there were no exposed clams less than 1 cm in length, the ANCOVA which had initially established the relationship between the control and exposed clam depths may have been biased. Accordingly, the ANCOVA was recalculated using only control clams greater than 1 cm in length. The result of the re-analysis confirmed that the regression intercepts were significantly different ($P = 0.03$). A similar re-analysis of the mud and sand control data (Fig. 7.1E) also verified the original ANCOVA results (Table 7.1); clams in sand were found at shallower depths than those living in mud.

Although mortality in the controls was 3 % and 5 % in sand and mud, clams which had been exposed on either sediment type or buried under sand did not die. Seven percent of all clams buried under mud were found dead, but this level of mortality was not significantly greater than that of the mud control population

Figure 7.1

Linear regressions between shell length of *Mya arenaria* and depth of sediment above clam for control, buried and exposed treatment populations in sand and mud. Regression slopes which intersect are significantly different; those which do not intersect have significantly different y -intercepts (see Table 7.1). Equations and coefficients of determination of all regressions are indicated. Regression slopes which are not significantly different are not illustrated.

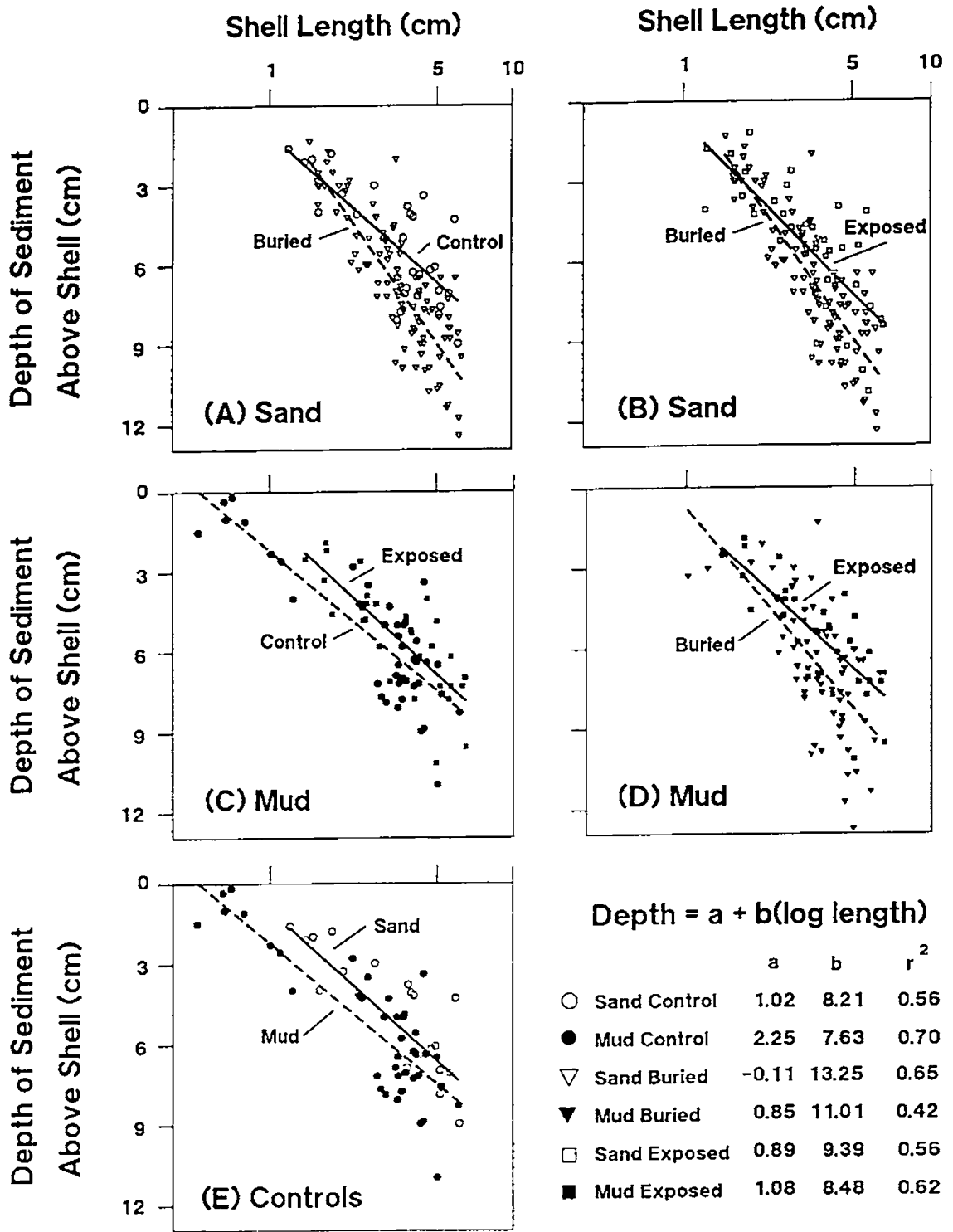


Figure 7.1

($P > 0.05$). No relationship was detected between burial depth, or size of clam, and mortality. The time to first appearance of the siphon, which ranged from 3 to 233 minutes, was not correlated with either clam size or burial depth ($P > 0.05$).

Burrowing Speed

Within 1 to 3 minutes after submergence, all clams which had been placed horizontally on the sediment surface began to burrow by extending the foot toward the sediment. Less than 2 minutes later, small clams (0.2-0.5 cm length) had completely reburrowed into the sediment, although larger clams (6-8 cm) required 10 to 22 hours (Fig. 7.2). Approximately 80 % of the variation in time taken to burrow completely below the sediment surface was accounted for by clam size. Sediment type also significantly influenced the burrowing speed (ANCOVA, $P = 0.001$); exposed clams on mud took approximately 1.6 times longer to burrow under the sediment surface than those on sand.

Although all clams were observed to extend their foot, 6 % of clams longer than 5 cm had not reburrowed into either sand or mud after 24 hours. The distance between the sediment surface and the anterior edge of the valve of these clams was 5-8 mm. When they were repositioned so that the anterior edge of the valve was touching the sediment, every clam was able to reburrow within 6 hours. Reburrowing difficulties were not restricted to large clams; 60 % of the clams less than 2 cm in length were supported by the surface tension of the rising seawater and remained floating until manually pushed through the air-water interface after 2 hours.

Figure 7.2

Sediment-specific linear regressions relating shell length of *Mya arenaria* exposed on the sediment surface to time of reburial (shell completely hidden). Regression equations, number of clams and coefficients of determination are indicated.

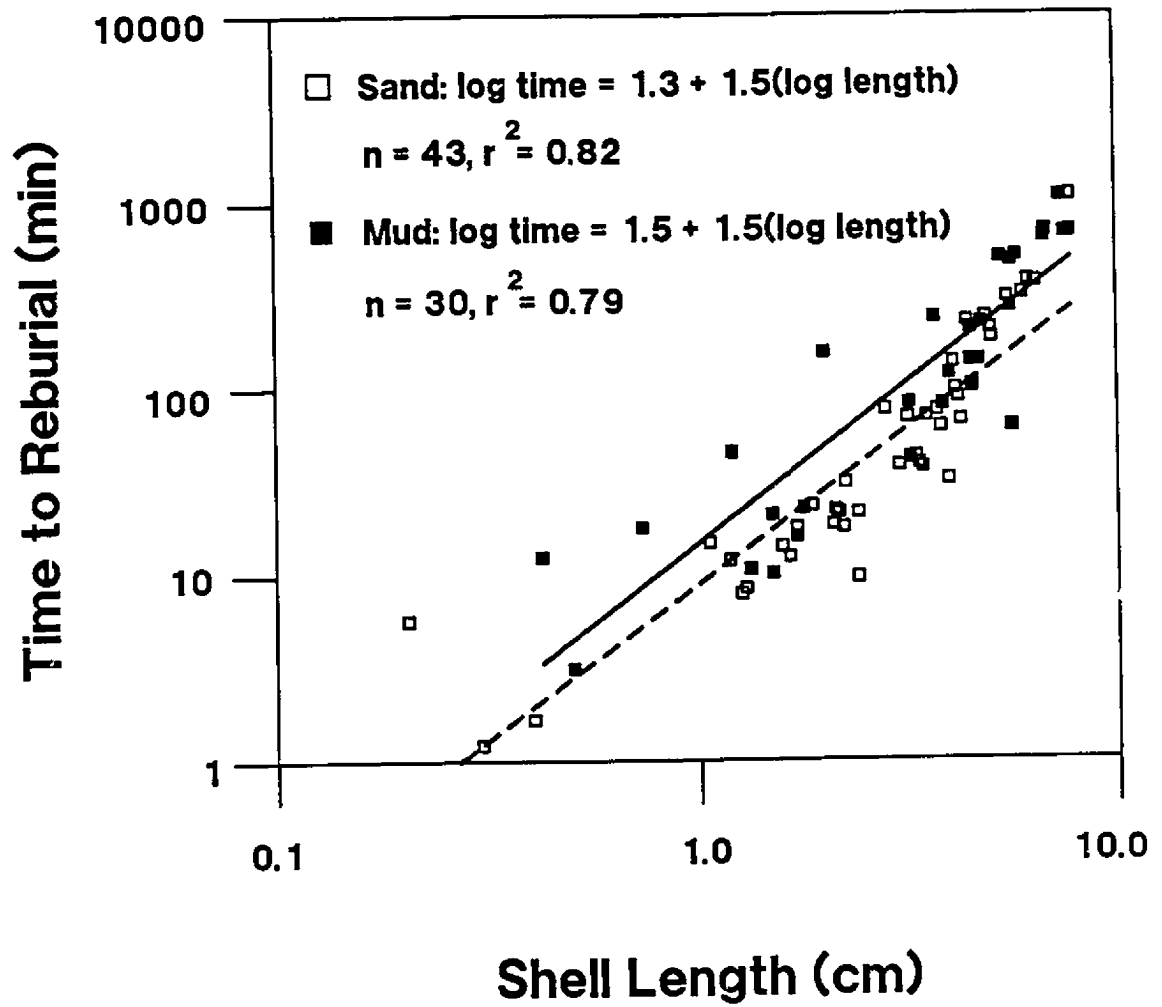


Figure 7.2

Burial Mortality

All size-classes of clams were able to burrow upwards and re-establish connection with the water column when buried under 25 cm of sand (Fig. 7.3A). The small clams (<3 cm) burrowed to normal living depths but the larger clams were found at depths 3-4 cm below those of control clams of similar size. When the burial depth was increased to 50 cm, mortality (20 %) was observed only in clams ≥ 5 cm in length. The maximum burial depth (75 cm) caused 0-40 % mortality in clams of less than 5 cm shell length, and 60 % mortality of the largest clams. Burial LD₅₀, the depth under which at least 50 % of the clams died, was greater than 75 cm for clams less than 5 cm in length and between 50 and 75 cm for the largest clams. No mortality was observed in either the sand or mud control populations.

Burial under mud resulted in high mortality in all size classes of clams and under all burial depths (Fig. 7.3B). The only exception was for large clams (>5 cm) buried under 25 cm of mud. For clams less than 5 cm, burial LD₅₀ was between 15 and 25 cm, while that of larger clams was between 25 and 50 cm. Before they died, most clams had burrowed upward to the original sediment-water interface.

DISCUSSION

Vertical Displacement

The negative impacts of clam digging on a population of *Mya arenaria* are not limited to the removal of market-size clams and shell breakage of the remaining clams. Exposure of pre-recruits and the deposition of tailings on clams adjacent to harvest sites may increase the susceptibility of unharvested clams to predation, desiccation, or freezing. My results have shown that the normal living depth of *M. arenaria*, which is directly coupled to these sources of mortality, can be altered by

Figure 7.3

Mortality and vertical position of *Mya arenaria* after burial under 25, 50 and 75 cm of sand or mud. The equilibrium depth (clam position) two weeks after burial is the mean of 5 replicates (SD is indicated by thin vertical line). Normal living depths were obtained from the control populations (SD is indicated by thick vertical line).

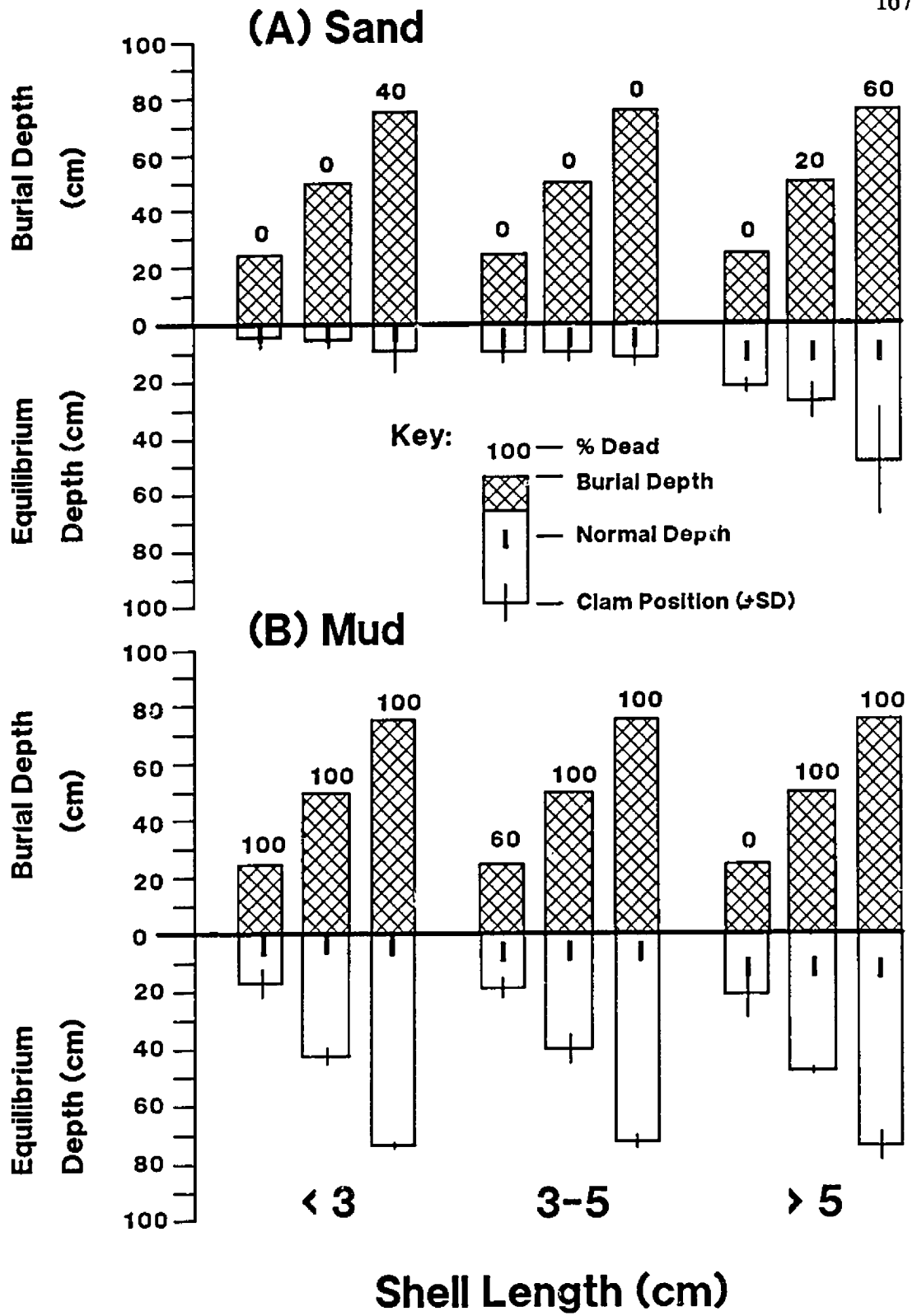


Figure 7.3

inadvertent exposure and burial. An increase in mortality with a change in living depth may account for some of the unexplained density variation in several commercial clam stocks (e.g. Brousseau 1978b, Lindsay & Savage 1978).

In mud, clams which were exposed on the sediment surface reburrowed to shallower depths than those occupied by an undisturbed population. Although this depth discrepancy was only a few centimeters (Fig. 7.1C), the risk of being eaten by shorebirds (e.g. *Numenius arquata*) is approximately twice as high for *Mya arenaria* living at 11 cm depth than for those at 14 cm (Zwarts & Wanink 1984). Blue crab (*Callinectes sapidus*) and green crab (*Carcinus maenas*) predation on *M. arenaria* living in the top 14 cm of sediment, already high in many areas (Blundon & Kennedy 1982, Jensen & Jensen 1985), may increase because of the smaller effort required to reach the shallower clams. Infaunal predators, however, such as gastropods (*Lunatia heros*; Commito 1982) or nemertean (*Cerebratulus lacteus*; Kalin 1984), would be unlikely to benefit from a relatively small vertical displacement of their prey.

Other depth-related factors would be of minor importance to clam survival and growth if the living depth were to decrease. *Mya arenaria* is very resistant to temperature extremes (Medcof & MacPhail 1967) and is not likely to be killed by freezing or desiccation due to an upward displacement of living depth. Living at a shallower depth may increase susceptibility to "washout" during bed erosion, but this would be more likely to cause a redistribution than mortality (Rees et al. 1977). However, on the extensive clams flats in the Bay of Fundy, erosion from ice scouring has resulted in extensive mortality of benthic organisms (Gordon & Desplanque 1983).

It is possible that an increased risk of predation and erosion may be partially offset by nutritional benefits in being closer to the sediment surface. Roberts et al. (1989) have hypothesized that the bivalve *Mercenaria mercenaria* vertically migrates to avoid avian predators at low tide and to maximize its feeding at high tide. Because it is possible that its siphon can be extended higher into the water column when living at shallower depths, *Mya arenaria* may also benefit from increased access to high-quality seston away from the sea bed (see Muschenheim 1987b). Presumably, such a benefit would be eliminated where 'siphon nipping' is prevalent (e.g. De Vlas 1979).

It is clear that the potential negative effects of non-lethal burial or exposure were more pronounced in mud than in medium-fine sand. Clams exposed on sand had little difficulty re-establishing their normal living depths, and the shift to deeper living depths of clams buried under ≤ 15 cm of sand may reduce the risk of predation and erosion. If clams can survive and likely benefit from a deeper living depth, why are natural sandflat populations found at shallower depths? First, the clams may be limited by the physical compaction of the sediment (Trueman et al. 1966a); beyond some threshold depth, the frictional resistance of the shell during burrowing may not be overcome. Second, the unnatural siphon extension required to live deeper than normal may result in an energy cost to the clam. Because the bivalve ciliary gill pump can generate only low hydrostatic pressure (Jørgensen & Riisgård 1988), the capacity to efficiently process water depends upon a low siphonal resistance to water flow. Resistance should vary linearly with siphon length, hence a longer siphon may be energetically sub-optimal for *Mya arenaria*.

Surprisingly, Jørgensen and Riisgård (1988) indicated that siphon length had no effect on pumping rate. Thus, a physical rather than a physiological mechanism probably regulates the living depth of clams.

Burrowing Speed

Predictive equations relating size and burrowing speed exist for several bivalves (e.g. *Donax denticulatus*: Stanley 1970), but until now (Fig. 7.2) only a qualitative relationship had been demonstrated for *Mya arenaria* (Baptist 1955, Pfitzenmeyer & Drobeck 1967). The time between exposure and complete reburial is critical to the survival of *M. arenaria*. Exposure to air *per se* during low tide is not usually lethal (*pers. obs.*), but the risk from avian predators, especially from gulls, is greatly increased. Continued exposure during high tide also increases the probability of being eaten by demersal fish or crabs. My results suggest that, as a clam ages, burrowing speed becomes increasingly important to clam survival compared with the duration of low-tide exposure. Because clams cannot burrow unless they are submerged (Trueman 1968), the risk of visually-cued predation can be considered to be the sum of reburial time and the duration of low tide exposure. Clearly, the risk of predation for small clams is more a function of the duration of air exposure (~ 3 hr-tidal cycle⁻¹) than reburial speed (~ 5 min). For older clams with slow reburial speeds (> 10 hr), duration of low tide becomes relatively less important to survival.

Exposed clams on mud required 1.6 times as long to completely reburrow as those on sand, despite the higher resistance to burrowing imposed by the coarser grain size of sand (Newell & Hidu 1982). The higher viscosity of sand should also decrease burrowing speed by increasing the resistance to the opening of valves

(Trueman 1954, Trueman et al. 1966*a*). These factors, however, are most relevant when a clam is burrowing within the sediment. My anomalous results were most likely caused by the difficulty of obtaining the anchorage necessary to retract the shell downward in mud (Trueman et al. 1966*b*).

Pedal anchorage depends upon the weight of sediment above the foot, the effect of suction beneath the foot, and the frictional effect caused by adhesion of sediment to the foot (Trueman 1967). Mud is generally cohesive, but in the non-cohesive top layer these three factors are small compared to values in the more compact sand. However, once the clam becomes partially buried in the sediment, the easier penetration of the shell in mud will compensate for weaker retraction (see Trueman 1967). Thus, the primary factor limiting reburial speed in mud was probably the time required for initial anchorage, rather than an intrinsically slower burrowing rate.

Two additional reburrowing difficulties were experienced by the largest and the smallest clams on both mud and sand. When the anterior edge of the shell (i.e. closest to the foot) was not in contact with the sediment, large clams (>5 cm length) could not reburrow, probably because the foot is too short to bring the relatively heavy body into a vertical position (Kühl 1972). Second, many of the smallest clams were held at the water surface, either by surface tension and/or air trapped within the mantle cavity. Neither of these phenomena is likely to be responsible for significant mortality. Invariably, in the first case, exposed large clams (i.e. market size) will be harvested, and in the latter case, surface tension suspension would occur only in the calmest conditions and even then would likely cause redistribution rather than direct mortality.

Burial Mortality

The ability of small clams to survive burial depths of greater than 70 body lengths (Fig. 7.3A) is vivid evidence that "clams are tough" (Medcof & MacPhail 1967), but apparently only in medium-fine sand. The previous experiment indicated that clams were able to survive a 15 cm mud burial, but it appeared that any further increase in burial depth (25-75 cm) resulted in almost total mortality of all size classes (Fig. 7.3B). The only exception, that of large clams under 25 cm mud burial, was probably a result of *Mya*'s ability to extend the siphon to the sediment-water interface without having to burrow upwards. In general, however, larger clams are particularly vulnerable to burial in both sand and mud because the foot does not develop as fast as the rest of the body (Kranz 1973).

The dependency of survival on sediment type results from faster depletion of oxygen and accumulation of toxic compounds in finer sediments (Maurer et al. 1986) and greater inhibition to upward burrowing in a mud burial pile than in sand. If a clam is not immediately crushed by burial, survival becomes dependent on the time required to get its siphon to the surface, the rate of oxygen depletion within the burial pile, and the rate of accumulation of toxic compounds in the pore water. *Mya arenaria* is very resistant to low oxygen concentrations and high levels of ammonia and hydrogen sulfide, but only for short periods (Theede et al. 1969, Malouf & Bricelj 1989). In fine-grained sediments, where upward burrowing was inhibited (see below), short-term resistance was likely insufficient to permit escape. Presumably, small clams were able to survive a 75 cm sand burial because the high porosity of sand allowed oxygenated water to percolate through the burial pile and delayed the accumulation of toxic compounds.

The difficulty of burrowing upwards in mud also contributed to high mortality. In contrast to the results of Nichols et al. (1978), all clams were able to burrow upwards to some extent, but the majority of clams in mud could not reach normal living depths. A sand burial pile compacts rapidly to create a relatively uniform substrate through which to burrow (Kranz 1973). In mud, the burial pile is often a heterogeneous mix of both fluidized and highly cohesive sediment. Although it may be easier to penetrate the relatively fluid sections of mud, these zones do not provide adequate pedal support for extension. Conversely, cohesive sections provide good support for upward extension but inhibit shell penetration. This hypothesis is consistent with the observation that most clams in mud were unable to burrow upwards beyond the original sediment-water interface.

A comparison of my data with previous work proved to be of limited value because the few existing data on the ability of *Mya arenaria* to survive burial are often contradictory. Kranz (1973) cited previous work demonstrating that *M. arenaria* could survive a 10-cm burial with little difficulty, yet his own results showed only a 15 % probability of survival. Turk and Risk (1981) supported Kranz's results by documenting 20 % survival under 9 cm burial. They determined that the LD₅₀ was 6 cm in fine sand and 24 cm in coarse sand. In contrast, the results of my study indicated that 80-100 % of clams of all lengths could survive a 50 cm medium-fine sand burial, and several a 75 cm burial (Fig. 7.3A). Differences in sediment grain size may account for much of the variation of survivorship, but some of the variation may have resulted from differences in experimental technique and in the hypotheses being tested.

Long-term acclimation to laboratory conditions is essential when testing the hypothesis that undisturbed clams can be killed by tailing burial. When clams are brought from the tidal flat into the laboratory, they are stressed; if the clams are immediately subjected to an additional stress (e.g. burial), they are more susceptible to mortality (cf. Peterson & Black 1988). In most burial studies, however, clams are buried only a few hours after collection. It is not surprising, therefore, that the laboratory experiments of Kranz (1973: acclimation time $\ll 24$ hr) showed significant mortality under relatively shallow burial.

Additional variation in published mortality data may be caused by the difference between burial resulting from sedimentation and that from tailings or dredge spoils. The direct effects of increased sedimentation during a long period are compounded by associated factors such as high suspended sediment loads or low water circulation, both of which exert a chronic stress on *Mya arenaria* (Appeldoorn 1983, Malouf & Bricelj 1989). Burial by tailings, however, is an acute stress causing direct physical damage or suffocation. Therefore, clams which are buried by deposition of unconsolidated sediment are likely to have different rates of mortality to those buried by tailings (see Turk & Risk 1981).

Summary and Conclusions

Tailing burial of *Mya arenaria* adjacent to sandflat harvest sites (≤ 15 cm) can create a temporary non-lethal increase in the living depth of clams until the tailing piles become eroded. Only when burial depths are ≥ 50 cm does significant (20-60 %) mortality of large (> 5 cm) and small (< 3 cm) clams result. Burial of this magnitude is unlikely to result from clam digging, but it may occur during dredging operations and large storms. Exposed, undamaged clams can rapidly reburrow into

medium-fine sands to re-establish their normal living depths. In mud, clams require relatively more time to reburrow, and they reburrow to abnormally shallow depths where the risk of predation can be high. In addition, undisturbed clams which become buried under more than 25 cm of mud are almost certain to die.

The results clearly indicate that the variation in population impact likely to result from current clam harvesting practices depends on substrate type. The mortality level associated with any given level of harvesting effort will be much greater on clam flats having a mud substrate (most commercial flats) than on those consisting of medium-fine sand. In consequence, management practice should reflect these differences; on sandflats, there is little to be gained from breaking up the clumps of soil turned over with the clam hack since tailing burial will probably not result in mortality. On muddy bottoms, however, any effort on the part of the fishermen to reduce the size of tailing piles is likely to enhance the survival of both buried and exposed clams.

CHAPTER EIGHT
SUMMARY AND CONCLUSIONS

The Effects of Bedload Transport on Benthic Organisms

The production of shallow, soft-sediment benthos can be predicted accurately with incredibly few, commonly measured variables, despite the intricacies of energy flow between organisms with diverse feeding strategies and life histories, and which are exposed to the complex hydrodynamics of coastal regions. Wind stress, tidal height, shelter indices and water temperature explained ~90 % of the variation of total benthic heterotrophic production. The identification of these variables as dominant regulators of production lead to the formation and testing of hypotheses that will be relevant to the successful management and exploitation of marine benthic invertebrates.

The empirical models in Chapter 2 provided the first evidence that bedload transport is responsible for variation in benthic production and that the significance of this relationship varies with faunal size class. Sea-surface wind stress, a surrogate for sediment transport, was highly correlated with meiofaunal production ($r=-0.73$) yet explained only 12 % of the variation in macrobenthic production. This contrast suggests that bedload transport is primarily a detriment to organisms living within sediment interstices and of little consequence to macrofauna. Alternatively, the poor correlation with macrofaunal production may imply that bedload is both a liability and a benefit to larger organisms since it is probable that any movement of the sea bed will be important to benthic fauna.

A deepening of the aerobic sediment layer and food supplementation during bedload transport will confer a growth advantage on macroinfauna which are resistant to abrasion. When bedload rates are excessive, however, food may be removed, suspension feeding will be interrupted, and organisms may become buried or displaced. Because it is hardly likely that stress and subsidy will exist in perfect

balance, direct measurements of bedload transport should improve predictions of macrobenthic production, but unlike meiofauna, generality cannot be assured. Feeding strategy, life stage, and proximity to the sediment-water interface must be known before there is a reasonable chance of estimating the net effect of bedload transport on the macrobenthos.

Many infaunal suspension feeders are restricted to the upper layers of sediment where the effects of bedload transport are greatest. Siphonate bivalves, such as the clam *Mya arenaria*, are partially protected from this mobile layer when they are old and live relatively deep, but younger clams are susceptible to erosion and all clams will restrict their feeding during sediment transport. An intertidal field study showed that small clams were frequently eroded from the bed and redistributed by bottom currents. Spat settlement is *not* the only source of recruits for *M. arenaria*; indeed, significant correlations between transport of juvenile clams and population density suggested that recruitment to any population living in the upper layers of sediment will be controlled in part by the frequency and magnitude of bedload transport.

Although a rapid increase and a precipitous decline in clam density could be attributed to clam transport during bedload peaks, the demography of a clam population is not solely a function of physical processes. When water temperatures are low, gonadal maturation may be delayed and subsequent spawning and settlement will occur close to the onset of fall storms. Because clam spat will have difficulty becoming established in the short interval between settlement and increased bedload transport under these circumstances, the 0+ cohort is very

susceptible to removal. As a result, the age structure of a clam population may be dominated by the cohorts which recruited when major bedload events did not occur or when water temperatures were unusually high.

The movement of clams across the sediment surface may be particularly important to populations subject to intense harvesting, because surface depressions caused by clam digging may entrain clams that would otherwise be unable to reburrow. The deliberate creation of pits on heavily-fished clam flats, or in areas where natural predation is high, may be a useful management tool to enhance the recovery of depleted stocks, but the potential advantage must be weighed against the inadvertent burial or exposure of resident clams.

When clams are buried or exposed as a result of harvesting or sediment transport, the grain size distribution of the substrate will determine the likelihood of survival. My laboratory experiments indicated that a majority of clams of all sizes can survive burial under 50 cm of sand, whereas most clams will die under 25 cm of mud. In addition, clams exposed on mud reburrow more slowly than on sand and cannot re-establish their normal living depths. Because most commercial clam flats consist of mud, my proposal to enhance the importation of clams by bedload transport may have limited merit; tailings from digging may kill undisturbed clams and imported clams will be highly susceptible to epibenthic predation because they would live abnormally close to the surface. Nonetheless, clam "farmers" have claimed that digging furrows can ensure a good crop.

Even if bedload transport fails to directly or indirectly kill, or to redistribute infauna, suspension feeders will still be stressed whenever bedload transport occurs. *Mya arenaria* is very sensitive to mechanical stimulation and will quickly retract its siphon if disturbed. It is probable, therefore, that clam growth will be reduced if the

frequency of bedload transport is high, because feeding and gill ventilation will be inhibited. It is difficult to reconcile this logic with my laboratory observation that clams subjected to daily disturbance of the top 10 mm of sediment grew faster than undisturbed clams. Since a food subsidy from sediment resuspension could not account for the differential growth, physiological studies may be required to identify the mechanism.

It is an axiom of science that "further study" is always required, but to conduct additional research without an appreciation of the goals already achieved is counterproductive. My theoretical, field and laboratory investigations have shown that the growth of fauna in benthic communities can be predicted from a few, commonly measured variables, and that factors which cause variations in individual or population growth are often linked to bedload transport. Future studies of commercial species (i.e. macrofauna) must consider not only the frequency and magnitude of sediment transport and sediment type, but size class, feeding strategy, life stage, and mobility if the net effect of bedload transport on macrobenthic production is to be determined accurately.

Appendix I

Sources of data used in regression analysis (X) of benthic production and environmental variables. Depth (Z,m), number of stations, secondary production (meio-, macro- and total-benthic), and primary production (benthic and pelagic) are listed. * refers to intertidal tidal height (m).

Appendix I continued

Location	Z	#	Mei	Mac	Tot	BPP	PPP	Source	
Canada	44 23 N	60	1	-	X	-	-	X	MacKinnon 1973, Platt 1971
	64 00 W								
	44 35 N	60	1	-	X	-	-	X	Hargrave & Phillips 1986
	64 00 W								
	44 25 N	60	1	-	-	X	-	X	Hargrave 1973
64 00 W									
Denmark	45 43 N	30	1	-	X	-	-	X	Hargrave & Phillips 1986
	61 32 W								
	55 03 N	1*	3	-	X	X	X	X	Asmus 1982 <i>a,b</i> Reise 1985
	08 25 E								
	55 43 N	0.5	3	-	X	-	X	X	Birklund 1977 Colijn & de Jonge 1984
	11 43 E								
	55 58 N	28	1	-	X	X	X	X	Karlneworff & Christensen 1986, Gargas 1970 Van Es 1982
	12 41 E								
	56 55 N	8	1	-	-	X	X	-	
	09 10 E								
55 03 N	2*	2	-	X	X	X	X	Asmus & Asmus 1985	
08 25 E									
56 20 N	20	5	-	-	X	X	-	Graneli & Sundback 1986	
12 50 E									
Finland	59 50 N	46	1	-	X	-	-	X	Kuparinen et al. 1984
	23 12 E								
India	09 42 N	1*	2	-	X	X	-	X	Ansell et al. 1978
	76 18 E								
Malaysia	05 00 N	3*	1	-	X	X	-	X	Berry & Othman 1983
	100 00 E								
The Nether- lands	53 15 N	1*	1	-	X	-	X	X	Beukema 1982, Cadée 1980, Postma & Rommets 1970
	05 00 E								
	53 45 N	50	1	X	X	X	X	X	De Wilde & Beukema 1984, Colijn & de Jonge 1984
	02 55 E								
	53 10 N	2*	1	-	X	-	X	X	Kuipers et al. 1981, Postma & Rommets 1970
05 00 E									
53 20 N	1*	3	-	-	X	X	X	Van Es 1977, 1982, Colijn & Venekamp 1977	
06 55 E									
52 56 N	2*	1	X	X	-	X	X	Witte & Zijlstra 1984, Cadée & Hegeman 1977	
04 53 E									

Appendix I continued

Location	Z	#	Mei	Mac	Tot	BPP	PPP	Source		
USA	41 35 N 71 20 W	7	1	X	X	-	-	X	Rudnick et al. 1985, Durbin & Durbin 1981	
	38 25 N 76 25 W	9	2	-	-	X	-	X	Kemp & Boynton 1980, Postma & Rommets 1970	
	38 25 N 76 25 W	4	2	-	-	X	-	X	Kemp & Boynton 1980, Postma & Rommets 1970	
	44 33 N 124 04 W	3	1	-	X	-	X	-	Kemp 1987, Riznyk & Phinney 1972	
	47 35 N 122 30 W	22	1	-	-	X	-	X	Hargrave 1973	
	38 25 N 76 25 W	1*	5	-	-	X	X	-	Kizzo & Wetzel 1985	
	31 27 N 81 12 W	5	1	X	X	-	X	X	Hopkinson 1985	
	31 23 N 81 13 W	7	1	X	X	X	X	X	Smith 1973	
	31 23 N 81 17 W	9	1	X	X	X	X	X	Fallon et al. 1983, Colijn & de Jonge 1984	
	31 23 N 81 17 W	1	1	X	X	X	X	X	Van Es 1982	
	47 44 N 122 30 W	140	1	-	X	-	-	X	Nichols 1975, Pamatmat & Banse 1969	
	48 30 N 123 05 W	4*	1	-	X	X	X	X	Pamatmat 1968	
	37 45 N 122 15 W	3*	3	-	X	-	-	-	Nichols 1977a	
	33 45 N 118 15 W	2*	1	-	X	X	-	-	Murphy & Kremer 1985	
	32 45 N 117 20 W	50	2	-	-	X	X	-	Hartwig 1976	
	34 06 N 119 05 W	2*	3	-	-	X	X	-	Shaffer & Onuf 1983	
	10 30 N 64 15 W	4	2	-	X	X	X	X	Edwards 1973	
	West Germany	54 40 N 10 00 E	22	1	X	X	-	-	X	Nichols 1977b

Appendix I continued

Location	Z	#	Mei	Mac	Tot	BPP	PPP	Source	
West Germany	54 40 N 10 00 E	1	1	-	-	X	-	X	Van Es 1982
	54 40 N 10 00 E	11	1	X	X	X	-	X	Van Es 1982
	54 40 N 10 00 E	15	1	X	X	X	-	X	Arntz & Brunswig 1975a, Von Bröckel 1975
	54 40 N 10 00 E	20	1	X	-	X	-	X	Arntz & Brunswig 1975b, Von Bröckel 1975
	54 01 N 07 49 E	34	1	X	X	X	-	-	Gerlach et al. 1985

Appendix II

Development of the Bedload Model

The theoretical bedload model is composed of three parts: (1) estimation of significant wave height and period from wind, sea level, and fetch data, (2) calculation of orbital velocities and bed shear stress, and (3) prediction of bedload rates.

Wave Hindcasting

Predictions of significant wave height and period followed the *HINDWAVE* model developed for coastal engineering (Hawkes 1987). Integration of the wave energy spectrum (E), given as a function of frequency (f), was used to calculate hourly wave height and period data (the *JONSWAP* equation; Hasselmann et al. 1973):

$$E(f) = \alpha g^2 (2\pi)^{-4} f^{-5} \exp\left(-1.25\left(\frac{f}{f_m}\right)^{-4}\right) 3.3^\eta \quad (\text{AII-1})$$

where $\alpha = 0.032(f_m U/g)^{2/3}$, f_m (the peak frequency, Hz) = $2.84g^{0.7}F^{-0.3}U^{-0.4}$, U = wind speed ($\text{m}\cdot\text{s}^{-1}$), F = fetch (m), g = acceleration due to gravity ($\text{m}\cdot\text{s}^{-2}$), and $\eta = \exp(-(f-f_m)^2)/(0.14f_m^2)$. To check whether wave height was controlled by fetch length or duration of wind, the duration (t , seconds) was converted to an equivalent fetch length:

$$F = 0.008515(t)^{1.298} (g)^{0.29} U^{0.702} \quad (\text{AII-2})$$

The smaller of the two fetches (real, or from Eqn. AII-2) was assumed to control wave generation and used in all calculations.

The significant wave height (H_s) was the average height of the largest one third of the waves, and wave period (T) was the average time between successive "upcrossings" of the mean sea level (Hawkes 1987):

$$H_s = 4\sqrt{m_0} \quad (\text{AII-3})$$

$$T = \sqrt{\frac{m_0}{m_2}} \quad (\text{AII-4})$$

where

$$m_n = \int E(f) f^n df. \quad (\text{AII-5})$$

Because the *JONSWAP* model excluded interaction with the sea bottom, a shoaling function was added which constrained the wave height in shallow water (St. Denis 1969). Predicted wave height (Eqn. AII-3) was reduced by a reduction factor (r) when waves felt the bottom (i.e. water depth/wave period² < 0.8 m·s⁻²) along the distance Δx :

$$r = \left(1 + \frac{\phi f H}{K T^4} \Delta x \right)^{-1} \quad (\text{AII-6})$$

where

$$K = \left(\tanh(\beta) \left(1 + \frac{2\beta}{\sinh(2\beta)} \right) \right)^{-\frac{1}{2}}, \quad (\text{AII-7})$$

$$\phi = \frac{64\pi^3}{3g^2} \left(\frac{K}{\sinh(2\beta)} \right)^3, \quad (\text{AII-8})$$

$\beta = 2\pi h/\lambda$, and $\lambda = T\sqrt{gh}$. The limiting condition imposed on the solution was $H_{max} = 0.73h$, where h was water depth.

Estimation of Orbital Velocity

Assuming generation of primarily shallow water waves over the tidal flat (i.e. $h < \lambda/20$), the orbital velocity (U_m) could be expressed by:

$$U_m = \frac{H}{2} \sqrt{\frac{g}{h}} \quad (\text{AII-9})$$

The threshold of sediment movement under waves has been related to the mobility number (M) of sediment (\approx Shield's Entrainment function; Dyer 1986). Komar and Miller (1975), have shown that for grain sizes $< 500 \mu\text{m}$, the threshold of motion may be represented by the critical mobility number (M_{crit}):

$$M_{crit} = 0.21 \sqrt{\frac{d_o}{D}} \quad (\text{AII-10})$$

where D is the grain diameter and d_o is the orbital diameter ($= 2 A_b$, where $A_b = a / \sinh(2\pi h / \lambda)$ and $a = H/2$). The threshold orbital velocity ($U_{m, crit}$) could then be calculated:

$$U_{m, crit} = \sqrt{\gamma g D M_{crit}} \quad (\text{AII-11})$$

where $\gamma = (\rho_s - \rho_w) / \rho_w$ and $\rho_{sed} = 2.6 \text{ g}\cdot\text{cm}^{-3}$.

Estimation of Bedload Transport

The threshold conditions for sediment transport were expressed in terms of the dimensionless bed shear stress, Θ (Dyer 1986):

$$\Theta = \frac{\frac{1}{2} f_w \rho_w U_m^2}{(\rho_s - \rho_w) g D} \quad (\text{AII-12})$$

where f_w (a friction factor) $= (h_{sed}/L)/(a/L)$, h_{sed} = crest to trough ripple height, and L = ripple wavelength (Sleath 1982a). The maximum bedload transport rate (q_{max}) was predicted by (Sleath 1982b):

$$\frac{q_{max} \sqrt{\rho_w}}{\sqrt{(\rho_s - \rho_w) g D^3}} = 5.2 (\Theta - \Theta_{crit})^{\frac{3}{2}} \quad (\text{AII-13})$$

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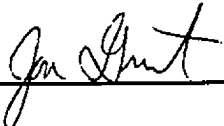

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