Wind stress limitation of benthic secondary production in shallow, soft-sediment communities

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ABSTRACT: Local wind fields can determine the magnitude of coastal benthic secondary production (BSP) via regulation of metabolically-important environmental factors (e.g. water temperature, mixing depth, food supply, sediment transport) by wind-forced hydrodynamics. This hypothesis was tested using 201 published estimates of BSP and local wind field 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 analysis demonstrated that wind stress, tidal height, shelter indices and water temperature explained ~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 (E Canada), 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 m (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), can potentially 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 energetic 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 energetic 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 speed, 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 determine 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 measurement was less than variation due to spatial wind effects. Published Macro-BSP estimates were calculated by using either the summation of growth increments or by using production:biomass ratios (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):

$$\log_{10}R_a = 0.367 + 0.993 \log_{10}P_a \qquad (1)$$

Chemical oxygen demand of the sediment was subtracted from estimates of total sediment oxygen uptake to calculate benthic respiration. BPP and PPP had been determined using either the ^{14}C or O_2 exchange techniques. All units of production were standardized (kJ m^{-2} yr^{-1}) using the following conversions (Holme & McIntyre 1971): 1 cal = 4.185 J; 1 g ash-free dry weight = 4.23 kcal; 1 g carbon = 12 kcal; 1 ml O_2 (mg O_2) respired = 4.83 cal (3.38 cal).

Physical variables. Wind velocities (V) were obtained from climatological records (e.g. British Meteorology Office 1952, U.S. Navy Marine Climatic Atlas 1974, Ruffner 1978). Surface wind stress ($\hat{\tau}_o$) was estimated by:

$$\hat{\tau}_o = \rho_a \quad C_d \cdot V^2 \qquad (2)$$

where ρ_a = air density (1.3 kg m^{-3}); C_d = a V-dependent drag coefficient (1.14 × 10^{-3} for $V \leq 10$ m s^{-1} and [0.49+0.065(V)] × 10^{-3} when V is greater than 10 m 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 −1.0 in the Phi grain size scale.

Water temperature and salinity were available from the literature. The data set and sources of all variables are available from the author.

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 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, 2 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

A total of 201 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 1).

The maximum production of an entire benthic community in these data (~ 8000 kJ m^{-2} yr^{-1}) was relatively similar to that of the Meio-BSP (~ 6500 kJ m^{-2} yr^{-1}; Table 1). Mean annual production of macrofauna and meiofauna were not significantly different ($\overline{x} = 703$ and 800 kJ m^{-2} yr^{-1} respectively; $p > 0.05$). Mean annual pelagic and benthic primary production (~ 7000 and 5000 kJ m^{-2} yr^{-1}, respectively) were greater than Total-BSP by a factor of 2 to 3.

The contribution of the microbenthos to Total-BSP ($\sim 60\%$; Fig. 1) is consistent with recent suggestions that the bacterial contribution to Total-BSP should be lower than the 90% level traditionally assumed

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

| Variable	Mean	CV (%)	Min	Max	N
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					
Temp. (C)	11.8	(44.9)	3	29	145
Salinity (‰)	25.3	(28.1)	6	37	143
Depth (m)	13.7	(200.7)	0.5	200	145
Tidal height (m)	2.6	(126.9)	0	14	145
Sediment (0–5)	3.0	–	2	5	145
Headwind (deg.)	86.1	(59.8)	1	180	62
Fetch (km)	42.8	(161.0)	0.05	323	145
Wind stress (Pa)	0.05	(38.0)	0.01	0.08	144
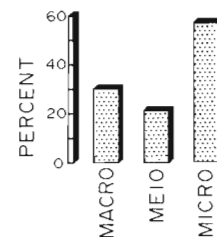
Fig. 1. Relative contributions of macro-, meio- and microbenthic secondary production to total benthic secondary production (obtained from the literature). Calculations were performed only from study sites where Total-BSP and one of the remaining size fractionated production estimates were known. Microbenthic production was calculated by difference

(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 to 30% of Total-BSP.

Low mean annual water temperature illustrates the prevalence of temperate study sites (Table 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. The majority of benthic study sites were less than 20 m in depth. The range in mean annual wind stress was relatively narrow (0.01 to 0.08 Pa).

Wind stress and benthic production

The correlation matrix (Table 2) shows that every component of primary and secondary production was significantly correlated with at least one of the wind

Table 2. Pearson correlation matrix of biological production (kJ m^{-2} 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	WS
Total	1	0.54 •••	0.77 •••	0.65 •••	0.51 •••	0.39 •••	—	−0.22 •	−0.23 •	—	−0.33 ••	0.45 ••	−0.56 •••
Macro		1	0.68 •••	—	—	—	—	—	—	—	−0.18 •	—	−0.35 ••
Meio			1	—	—	—	0.35 •	—	0.28 •	—	−0.51 •••	—	−0.72 •••
BPP				1	—	0.33 ••	−0.31 ••	—	—	—	−0.37 •••	0.34 •	—
PPP					1	0.27 ••	—	—	—	—	—	0.54 •••	—
Temperature (°C)						1	−0.40 •••	0.21 ••	−0.18 •	—	—	—	0.19 •
Depth (m)							1	0.27 ••	—	—	—	—	—
Salinity (‰)								1	—	—	0.32 •••	—	—
Tidal height (m)									1	—	—	−0.40 •••	−0.31 •••
Sediment type (0–5)										1	—	—	—
Effective fetch (km)											1	−0.27 •	—
Headwind index (deg.)												1	—
Wind stress (Pa)													1

• $p < 0.05$, •• $p < 0.01$, ••• $p < 0.001$, −: not significant

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. 2b), wind stress accounted for 32 and 52 % of the variance in Total-BSP and Meio-BSP respectively (Fig. 2a, c). The intercepts of each regression equation were very similar (b ≈ 3), and analysis of covariance indicated that slopes for each regression were significantly different ($p = 0.028$).

The correlation matrix also revealed significant relations among water temperature, water depth, salinity, tidal height and various biological variables (Table 2). Sediment type was not correlated with any other variable.

Multiple regression models

Four of the 5 regression models incorporated wind stress as the most significant variable accounting for the observed variation in benthic secondary production

(Table 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 versus modelled plot of Macro-BSP was significantly reduced ($R^2 = 0.60$ from 0.23) with the inclusion of the headwind index (Fig. 3; Table 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) indicated a significant relation 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. The established relation between bacterial concentration, POM and sediment surface area (Yamamoto & Lopez 1985), was not apparent in the data, however the ab-
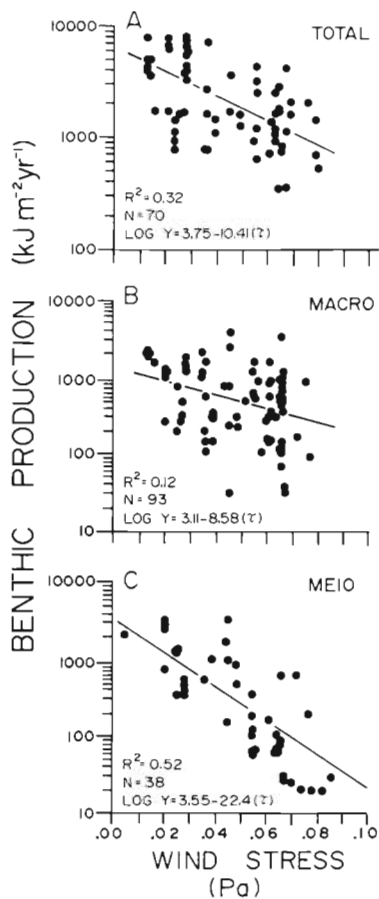
Fig. 2. Simple linear regressions of wind stress and (A) total-, (B) macro-, and (C) meio-benthic production. Coefficient of determination, number of data points and regression equation are listed

sence of significant correlations of BSP (or BPP) with sediment type must be interpreted with regard to the very qualitative index and narrow range by which sediment type was described.

DISCUSSION

Of 10 biological and physical variables considered, mean annual wind stress accounted for the most variation in 4 out of 5 models of benthic secondary production. This is consistent with the trophic group mutual exclusion hypothesis (Wildish 1977) which states that benthic productivity is food limited and that current acts as the exclusion mechanism; i.e. hydrodynamics control benthic energy flow.

It is apparent, from the significant negative correlations between wind stress and benthic secondary productivity, that the positive influence of wind forcing on production (e.g. increased organic seston flux: Frechette & Bourget 1985, 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 ($U \cdot_{crit}$) of the sediment, and (2) the effects of wind-forced currents which exceed $U \cdot_{crit}$.

Below $U \cdot_{crit}$, 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

Table 3. Stepwise multiple regression models describing log-transformed Total-, Macro- and Meio-benthic secondary production (kJ m^{-2} yr^{-1}). • 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), lg: log-transformed

| Step	Dependent variable	Model	R^2	F Signif.
1.	Total	$=3.8-10.4(\tau)$	0.34	0.0000
2.	(N=70)	$=3.9-13.2(\tau)-0.3(\lg TH)$	0.47	0.0000
3.		$=3.6-11.7(\tau)-0.3(\lg TH)+0.02(Te)$	0.52	0.0000
4.		$=3.7-11.4(\tau)-0.3(\lg TH)+0.02(Te)-0.1(EF)$	0.64	0.0000
1.	•Total	$=3.4-0.4(\lg TH)$	0.36	0.0014
2.	(N=39)	$=3.9-0.4(\lg TH)-13.0(\tau)$	0.64	0.0000
3.		$=3.9-0.2(\lg TH)-18.4(\tau)-0.1(\lg EF/HW)$	0.83	0.0000
4.		$=3.7-0.2(\lg TH)-16.9(\tau)-0.1(\lg EF/HW)+0.02(Te)$	0.87	0.0000
1.	Macro	$=3.1-8.6(\tau)$	0.12	0.0006
2.	(N=93)	$=3.2-9.7(\tau)-0.1(\lg Z)$	0.23	0.0000
1.	•Macro	$=3.4-18.2(\tau)$	0.28	0.0007
2.	(N=37)	$=4.2-16.8(\tau)-0.4(\lg EF/HW)$	0.41	0.0001
		$=4.5-16.8(\tau)-0.5(\lg EF/HW)-0.2(\lg Z)$	0.60	0.0000
1.	Meio	$=3.5-22.4(\tau)$	0.52	0.0000
2.	(N=38)	$=3.5-19.7(\tau)-0.2(\lg Z)$	0.63	0.0000

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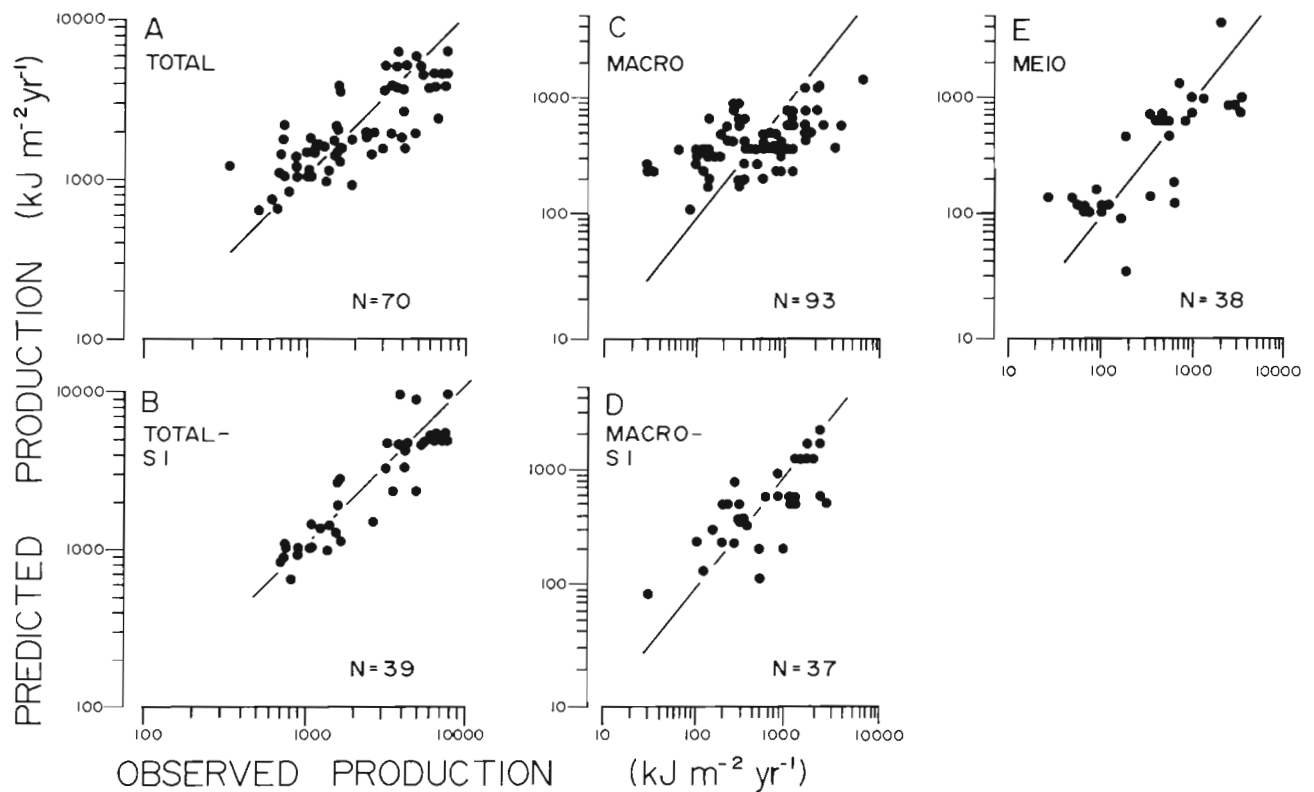
Fig. 3. Observed (A) total-, (C) macro-, and (E) meio-benthic production plotted against predicted production derived from regression analyses. Plotted line represents a 1:1 relationship. (B) Total- and (D) macro-production plots include only those data from sites for which headwind index could be calculated. SI: shelter index

Sverdrup's critical depth model of phytoplankton photosynthesis (Parsons et al. 1984). Simply stated, if the critical depth (the depth at which 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 would 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 would contribute to lower community productivity at high wind stress (vis-à-vis increased water turbulence) include direct inhibi-

tion 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 $U \cdot _{crit}$ is exceeded.

The cumulative effect of the many biologically-important processes associated with sediment transport are manifest in the productivity of the benthos. When $U \cdot _{crit}$ 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 shear velocity ($U \cdot$), 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 to 20 cm 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 $\tau = 0.07$ Pa (in the higher range of the wind-stress data set), $U\cdot = 23.2$ cm s^{-1}, which is well above (20$\times$) the $U\cdot_{crit}$ of natural sediment ($U\cdot_{crit} = 0.66$ to 1.38 cm s^{-1}; Grant & Bathmann 1987). The probable overestimate of $U\cdot$ resulting from the above assumptions is balanced by underestimates inherent in the wind stress formula (Eq. 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 $U\cdot$ is consistent with observations of significant POM resuspension at depths greater than 6 m caused by winds less than 4 m s^{-1} ($\tau = 0.02$ Pa; Demers et al. 1987). Even at depths greater than 100 m, winter storms can generate a $U\cdot$ 10 times larger than $U\cdot_{crit}$, and can transport ~ 1000 kg m^{-2} d^{-1} of resuspended sediment across the continental shelf (Drake & Cacchione 1985).

The relationships between wind stress and the 3 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. 1), was also highly correlated with wind stress. Because these smaller organisms (< 1 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 uniquely attributed to the effects of sediment transport, the differential expression of other wind-forced effects are more likely to be observed between mode of feeding (deposit vs. suspension feeders) than between size of organism. 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; ca 90 % of the variation in total benthic secondary production can be explained by wind stress, effective fetch, headwind index, tidal height, 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 lack of spatial and temporal correlations between sites of published primary production data and those of benthic secondary production may be responsible for the absence of primary production from the multiple regression models. 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 food supply limitation.

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 3), however the inclusion of annual mean water temperature resulted in only a minimal 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 1969, 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.

Appendix 1. 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. * Intertidal tidal height (m)

Location		Z	No. stns	Mei	Mac	Tot	BPP	PPP	Source
Australia	34° 04′ S, 151° 09′ E	5	1	–	X	–	–	X	Rainer (1982)
Belgium	51° 15′ N, 03° 00′ E	55	6	X	–	–	–	–	Heip et al. (1984)
Bermuda	32° 30′ N, 64° 40′ W	2	2	X	X	X	–	X	Smith et al. (1972)
Britain	57° 20′ N, 02° 00′ W	3*	1	X	X	–	X	X	Baird & Milne (1981)
	57° 20′ N, 02° 00′ W	3*	1	–	X	–	X	–	Leach (1970), Chambers & Milne (1975)
	57° 48′ N, 02° 00′ W	25	1	–	–	X	–	X	Steel & Baird 1968, Davies (1975)
	57° 48′ N, 05° 36′ W	5*	1	–	X	X	X	X	Mc Intyre & Eleftherion (1968), Van Es (1982)
	55° 10′ N, 01° 25′ W	58	1	–	X	–	–	–	Buchanan & Warwick (1974)
	55° 00′ N, 03° 00′ E	50	1	X	X	–	X	X	Jones (1984)
	50° 50′ N, 01° 10′ W	3*	1	–	X	–	–	–	Hibbert (1976)
	35° 15′ N, 04° 03′ W	8	1	–	X	–	–	–	Hughes (1970)
	50° 14′ N, 04° 16′ W	2*	1	–	X	–	X	X	Joint (1978)
	50° 24′ N, 04° 16′ W	2*	1	X	X	X	X	–	Warwick & Price (1975), Warwick et al. (1979), Colijn & de Jonge (1984)
	51° 30′ N, 00° 45′ E	2*	1	–	X	–	–	–	Mossmann (1978)
	51° 40′ N, 04° 28′ W	14	1	–	X	–	–	–	Warwick et al. (1978)
	50° 27′ N, 04° 13′ W	3*	1	X	X	X	X	–	Ellison (1984)
Canada	44° 37′ N, 63° 30′ W	60	1	–	–	X	–	X	Hargrave (1980)
	54° 31′ N, 05° 33′ W	1*	1	X	X	X	X	–	Boaden & Elhag (1984)
	45° 44′ N, 64° 29′ W	12*	1	X	X	X	X	X	Prouse et al. (1984), Schwinghamer et al. (1986)
	45° 44′ N, 64° 29′ W	12*	1	–	–	X	X	X	Hargrave et al. (1983)
	45° 44′ N, 64° 29′ W	12*	1	–	X	–	X	X	Colijn & de Jonge (1984), Cranford et al. (1985)
	45° 44′ N, 64° 29′ W	12*	2	–	X	–	X	X	Hawkins (1985)
	45° 44′ N, 64° 29′ W	12*	1	–	X	–	–	–	Peer (1984)
	45° 49′ N, 64° 20′ W	14*	1	–	X	–	X	–	Cranford et al. (1985)
	45° 46′ N, 64° 40′ W	14*	1	–	X	–	X	–	Cranford et al. (1985)
	45° 47′ N, 64° 32′ W	14*	1	–	X	–	X	–	Cranford et al. (1985)
	45° 45′ N, 64° 37′ W	14*	1	–	X	–	X	–	Cranford et al. (1985)
	45° 20′ N, 64° 37′ W	12*	7	–	–	X	X	X	Hargrave et al. (1983)
	45° 50′ N, 64° 20′ W	12*	1	–	X	–	X	X	Peer (1984), Prouse et al. (1984)
	45° 45′ N, 64° 37′ W	11*	1	–	X	–	X	X	Peer (1984), Prouse et al. (1984)
	45° 20′ N, 64° 10′ W	10*	3	–	X	–	X	X	Peer (1984), Prouse et al. (1984)
	45° 10′ N, 64° 15′ W	12*	2	–	X	–	X	X	Peer (1984), Prouse et al. (1984)
	45° 00′ N, 66° 00′ W	100	1	–	X	–	–	X	Wildish & Peer (1983), Emerson et al. (1986)
	44° 45′ N, 56° 10′ W	2*	1	–	X	–	–	X	Burke & Mann (1974)
	44° 37′ N, 63° 30′ W	2*	1	–	X	X	X	–	Hargrave & Phillips (1981), Grant (1986)
	44° 37′ N, 66° 30′ W	2*	1	–	–	X	X	–	Van Raalte (1978)
	49° 09′ N, 123° 54′ W	6*	1	X	–	X	X	–	Naimann & Silbert (1979)
	44° 15′ N, 63° 00′ W	60	1	–	X	–	–	X	Mills & Fournier (1979)
	42° 15′ N, 68° 00′ W	50	1	X	X	–	X	X	Sissenwine et al. (1984)
	44° 25′ N, 64° 00′ W	60	1	–	X	–	–	X	Platt (1971), MacKinnon (1973)
	44° 35′ N, 64° 00′ W	60	1	–	X	–	–	X	Hargrave & Phillips (1986)
	44° 25′ N, 64° 00′ W	60	1	–	–	X	–	X	Hargrave (1973)
	45° 43′ N, 61° 32′ W	30	1	–	X	–	–	X	Hargrave & Phillips (1986)
Denmark	55° 03′ N, 08° 25′ E	1*	3	–	X	X	X	X	Asmus (1982a, b), Reise (1985)
	55° 43′ N, 11° 43′ E	0.5	3	–	X	–	X	X	Birklund (1977), Colijn & de Jonge (1984)
	55° 58′ N, 12° 41′ E	28	1	–	X	X	X	X	Gargas (1970), Kanneworff & Christensen (1986)
	56° 55′ N, 09° 10′ E	8	1	–	–	X	X	–	Van Es (1982)
	55° 03′ N, 08° 25′ E	2*	2	–	X	X	X	X	Asmus & Asmus (1985)
	56° 20′ N, 12° 50′ E	20	5	–	–	X	X	–	Graneli & Sundback (1986)
Finland	59° 50′ N, 23° 12′ E	46	1	–	X	–	–	X	Kuparinen et al. (1984)
F.R. Germany	54° 40′ N, 10° 00′ E	22	1	X	X	–	–	X	Nichols (1977a)
	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 (1975), Von Brockel (1975)
	54° 40′ N, 10° 00′ E	20	1	X	–	X	–	X	Arntz & Brunswig (1976), Von Brockel (1975)
	54° 01′ N, 07° 49′ E	34	1	X	X	X	–	–	Gerlach et al. (1985)

Appendix 1 (continued)

Location		Z	No. stns	Mei	Mac	Tot	BPP	PPP	Source
India	09° 42′ N, 76° 18′ E	1*	2	–	X	X	–	X	Ansell et al. (1978)
Malaysia	05° 00′ N, 100° 00′ E	3*	1	–	X	X	–	X	Berry & Othmann (1983)
The Netherlands	53° 15′ N, 05° 00′ E	1*	1	–	X	–	X	X	Postma & Rommets (1970), Cadée (1980), Beukema (1982)
	53° 45′ N, 02° 55′ E	50	1	X	X	X	X	X	Colijn & de Jonge (1984), De Wilde et al. (1984)
	53° 10′ N, 05° 00′ E	2*	1	–	X	–	X	X	Postma & Rommets (1970), Kuipers et al. (1981)
	53° 20′ N, 06° 55′ E	1*	3	–	–	X	X	X	Colijn & Venekamp (1977), Van Es (1977, 1982)
	52° 56′ N, 04° 53′ E	2*	1	X	–	–	X	X	Cadée & Hegeman (1977), Witte & Zijlstra (1984)
	52° 56′ N, 04° 53′ E	2*	15	X	X	–	X	X	Beukema & Cadée (1986)
	51° 45′ N, 04° 00′ E	0.3*	1	–	X	–	X	X	Wolff (1977), Wolff & DeWolff (1977)
New Zealand	42° 00′ S, 171° 00′ W	200	1	X	X	X	X	X	Juniper (1982), Probert (1986)
	41° 12′ S, 173° 55′ W	11	2	–	–	X	X	–	Kaspar et al. (1985)
Norway	60° 16′ N, 05° 06′ E	0.2	1	–	X	–	–	X	Johannessen (1973)
South Africa	34° 10′ S, 18° 20′ E	3*	1	X	X	X	–	–	Koop & Griffiths (1982)
	33° 58′ S, 25° 39′ E	2*	1	–	X	X	–	–	Dye (1981)
	33° 58′ S, 25° 39′ E	2*	1	–	X	X	–	–	McLachlan et al. (1981)
Sweden	58° 47′ N, 17° 41′ E	46	1	–	X	–	X	X	Cederwall (1977)
	58° 15′ N, 11° 28′ E	1	2	X	X	–	X	X	Rosenberg et al. (1977), Evans (1983)
	58° 23′ N, 11° 30′ E	0.2*	7	–	X	–	X	X	Rosenberg et al. (1977), Moller & Rosenberg (1982)
	58° 45′ N, 17° 52′ E	10	1	X	X	X	–	X	Jansson et al. (1984)
	58° 45′ N, 17° 52′ E	3	1	X	X	X	X	X	Schwinghamer et al. (1986)
USA	41° 06′ N, 73° 00′ W	10	1	X	X	X	X	X	Riley, (1956), Carey (1967)
	41° 00′ N, 73° 00′ W	10	1	–	X	–	–	X	Hargrave & Phillips (1986)
	41° 20′ N, 72° 10′ W	2	1	X	–	–	X	X	Marshall (1970)
	41° 25′ N, 71° 27′ W	2	1	X	–	–	X	X	Marshall (1970)
	41° 15′ N, 72° 47′ W	1*	1	–	X	–	X	X	Marshall et al. (1971), Platt (1971), Edwards & Welsh (1982)
	41° 30′ N, 70° 40′ W	15	1	–	–	X	–	X	Kanwisher (1962)
	40° 30′ N, 74° 00′ W	40	1	–	–	X	–	X	Smith (1978)
	41° 35′ N, 71° 20′ W	7	1	X	X	–	–	X	Durbin & Durbin (1981), Rudnik et al. (1985)
	38° 25′ N, 76° 25′ W	9	2	–	–	X	–	X	Postma & Rommets (1970), Kemp & Boynton (1980)
	38° 25′ N, 76° 25′ W	4	2	–	–	X	–	X	Postma & Rommets (1970), Kemp & Boynton (1980)
	44° 33′ N, 124° 04′ W	3	1	–	X	–	X	–	Riznyk & Phinney (1972), Kemp (1987)
	47° 35′ N, 122° 30′ W	22	1	–	–	X	–	X	Hargrave (1973)
	38° 25′ N, 76° 25′ W	1*	5	–	–	X	X	–	Rizzo & 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	Pamatmat & Banse (1969), Nichols (1975)
	48° 30′ N, 123° 05′ W	4*	1	–	X	X	X	X	Pamatmat (1968)
	37° 45′ N, 122° 15′ W	3*	3	–	X	–	–	–	Nichols (1977b)
	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)
Venezuela	10° 30′ N, 64° 15′ W	4*	2	–	X	X	X	X	Edwards (1973)

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 mechanism linking these environmental variables to benthic production is uncertain, however it is hoped 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 in order to clearly define pelagic-benthic energy coupling.

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