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Relationships among bottom sediment, benthic fauna, and suspended sediment concentration at a sandy shoreline, Hamana-ko (Honshu, Japan): Implications for sediment entrainment

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Abstract: The relationships among sedimentary texture, suspended sediment concentration, and benthic community were analyzed from shallow subtidal environments at Hamana Bay, Japan. Meiofaunal communities of the upper centimeter of the bottom sediment are dominated by nematodes and harpacticoid copepods; juvenile gastropods and bivalves, ostracodes, and tardigrads are locally abundant. Sessile and slow-moving mobile macrofauna of the top few centimeters of bottom sediment are dominated by polychaetes and the gastropod *Umbonium moniliferum*, all of which are quite variable in distribution. Both macrofaunal and meiofaunal community composition are moderately correlated with sedimentary texture and depth. Sediment in all locations analyzed was fine to medium sand, with mud concentrations less than 3% of the sample by weight.

Suspended sediment concentrations (SSC) varied over two orders of magnitude, from 3.7 to 152.5 mg/ℓ. SSC does not correlate statistically significantly with any individual variable, but is best related to biotic components such as nematode abundance and mobile macrofaunal abundance. There is a relatively strong relationship between SSC and the first axes of principal components analyses of the biotic assemblages and the sedimentary textural properties, even independent of current conditions at the time of collection. That is, a linear combination of the biotic and sedimentary variables representing a high percentage of variability in the data provides the best predictor of SSC. Generally, samples with few mobile epifauna, large numbers of polychaete tubes, and large numbers of nematodes (which may produce large quantities of organic exudates) are associated with lower SSC, while the highest SSC values are found in areas with relatively large numbers of mobile macrobenthos.

Key Words: suspended sediment concentration, sediment entrainment, sediment erosion, Hamana-ko, animal-sediment relationships, benthos

INTRODUCTION

It is well-known that benthic organisms affect the sedimentary properties of the substrate in which and upon which they live, and that in turn sediment properties affect the sort of organisms that can successfully colonize it (e.g., SANDERS 1958, MCCALL & TEVESZ 1982, NOWELL *et al.* 1981, JUMARS & NOWELL 1984, AMOS *et al.* 1992). Biota may stabilize sediment by excretions that bind sedimentary particles, or destabilize sediments by increasing water content, increasing bottom roughness, or breaking physical or organic bonds between sedimentary grains (FEATHERSTONE & RISK 1977, RHOADS *et al.* 1978, LEE & SCHWARTZ 1980,

ECKMAN *et al.* 1981, GRANT *et al.* 1982). One of the most fundamental properties of sediment is its stability in the face of current flow, i.e., its entrainability or erodibility, and a considerable literature exists concerning its measurement with respect to physical factors such as grain size, current strength, water content, mineralogy of the sediment, and water content (e.g., HJULSTRÖM 1935, MILLER *et al.* 1977, YALIN 1977, MEHTA 1986, 1989, MAA 1992). However, the feedback relationships between organisms and entrainability are poorly understood. Understanding these relationships will have implications both for understanding natural ecological processes and for the influence of human disturbance in coastal areas (RHOADS &

BOYER 1982).

A number of authors have attempted to quantify the relationships between erosion and benthos by creating experiments in which the bottom velocity is controlled. Several studies have observed organism-erosion relationships using laboratory flumes, using either a block of natural sediment with the sediment-water interface preserved (GRANT *et al.* 1982) or by defaunating the sediment and then observing the effects of adding individual taxa to the sediment (MCCALL *et al.* in prep; DAVIS 1993). However, it is difficult to recreate the conditions of the field in the laboratory (YOUNG & SOUTHARD 1978, MAA *et al.* 1991), i.e., to recreate the sediment surface structure on the scale of sedimentary grains, the natural biotic communities, the benthic boundary layer flow structure, and the nature and distribution of organic molecules. Some studies been done using a flume in site in the field (e.g., AMOS *et al.* 1992, MAA *et al.* 1993, ROSS & IMADA in prep). Flumes, however, require a great deal of equipment, making frequent deployment and thus obtaining data from numerous ecological contexts difficult; further, one still risks artificially affecting entrainment rates (e.g., during deployment of the flume or creation of unnatural bottom flow structure).

In this study we have measured the SSC at random points in time and space, and contrasted the measured SSC with local environmental variables. We are unaware of any previous studies that have searched for relationships among entrainment and environmental variables using natural SSC values and information on local bottom sediment and biota. The lack of previous studies on naturally occurring levels of SSC with respect to biota may be due largely to the perception that it is difficult to distinguish the effects of individual processes that work together to create the observed SSC. We believe it is worthwhile to explore the statistical relationships among variables using natural data, and to seek potentially causal relationships that could then be tested under controlled conditions.

For this study we chose 20 points essentially randomly in space and time to measure SSC and measured some of the variables that may explain variations in SSC. The number of data points is not large with respect to the number of variables investigated, and the number of variables investigated is only a subset of those that may be important, but the study illustrates the sort of work that may enable an expansion of basic knowledge about sediment transport and aquatic benthos. The purpose of this report is: to present integrated sedimentologic and faunal data from the shoreline of Hamana-ko; to discuss strategies and problems in measuring animal-sediment relationships and entrainability in natural environments; and, using the data of this study, to speculate briefly about some possible biotic factors influencing suspended

sediment concentration.

Reasoning and assumptions behind this study

We have concentrated upon data that can be relatively quickly taken, to determine the feasibility of identifying relationships among erodibility and environment in natural environments, without need of extensive equipment, personnel, and time. In particular, we did not collect much data regarding the velocity of the flow impinging on the bottom, or the recent history of this flow prior to sampling. While the absence of flow data may make relationships among other environmental variables less clear, we propose that it will not make their contributions to SSC undecipherable.

Our presumption is based upon the idea that a faster current may erode little more than a slower current if both currents are below the critical velocity for most of the sediment. Moreover, the bottom sediment grain size is roughly the same among the studied sites, thus there is little difference in critical velocity among the sites, (e.g., HJULSTRÖM (1939) and later studies), therefore differences in SSC generally cannot be ascribed to either variations in mean grain size or to mean water energy (attainment of critical stress for the particular grain size). Hence other factors, such as subtle variations in sediment cohesion, may affect the amount of fines removed from sands, or biota may control the likelihood that high entrainment occurs.

There are 2 critical assumptions in the structure of this study. One is that SSC can be used as an estimator of local sediment erodibility; the second is that it is statistically plausible to use about 20 points chosen randomly in time and space to infer potential relationships among variables. Erodibility is generally defined by either the erosion threshold, i.e., critical current velocity, at which erosion begins, or the erosion rate (AMOS *et al.* 1992). Though related, the erosion threshold and erosion rate are not the same, and one can imagine circumstances under which any one type of sediment may have initially a higher erosion threshold, while a second type of sediment, over time under a certain critical stress, yields a greater rate of erosion. However, both of these are very difficult to measure under natural conditions. In our case, assuming that settling velocity of the eroded sediment is high and/or that currents quickly carry away locally entrained sediment (without bringing in large quantities of suspended material from elsewhere), the suspended sediment concentration (SSC), which is relatively easily measured, should mirror the erosion rate to a sufficient degree that SSC may be used as a proxy for erosion rate.

Of course, some caution must be used concerning the extrapolation of suspended sediment concentration to local entrainability. The velocity needed

to keep a grain in suspension is smaller than that for its initial erosion. Since the settling velocity of the clay-sized suspended sediment recovered from our filters may be hours or even days, nearly all the suspended material may have floated in from outside the field locations, perhaps even directly from rivers entering the bay. Arguing against that is the very large small-scale temporo-spatial variability in the SSC; sediment being transported over more than a few meters would be quickly mixed to a temporo-spatially homogeneous concentration. However, the lowest concentrations measured may represent such a background level from allochthonous sources.

Temporally isolated values of SSC: The logic behind comparing the SSC at randomly chosen points in time to learn about organism-sediment relationships rests on the assumptions that the median SSC at different sites may vary and be measurable and that temporally most SSC values at one site hover relatively close to the median value — closely enough that if points are selected at random from the 2 sites, the sample with the higher SSC will have more likely come from the site with the higher median SSC.

The suspended sediment (SS) observed in this study may not be from the well-sorted fine to medium sand, but instead from finer particles from the interstices of the sand. One can see this from the median particle size of the SS collected on filters, and also from the observation that current velocities are generally under the critical velocity for the sandy grain sizes, but erosive for some part of the muddy and finest sand fractions. We make the assumption from observations of both direct measurements and turbidometer recordings that background SSC is very low and does not differ greatly between sites, and cannot explain large variations in SSC. Thus, the major difference among sites will be the susceptibility of mud-sized particles to enter into suspension at very small current speeds or biotic sedimentary disturbance, with occasional variations due to entrainment of sand-sized particles. Mud particles will not act with the high cohesion that they do in mud-dominated sediments, and thus presumably have a much lower critical stress than indicated by typical Hjulström-type figures. The amount of erosion of such fines may vary according to several conditions: the amount of fines; the nature of fines — their tendency to be bound as pellets or to be attached to other grains by organic matter; the exposure of fines to currents through bioturbation; the surface roughness; active biological transport; or the degree of activity of macrofauna. Mud suspension will also be affected by its settling rate, its tendency to stick to other grains or to aggregate, or to stick to the bottom again if direct contact is made through turbulent flow (e.g., SELF *et al.*

1989, STOLZENBACH *et al.* 1992).

If we choose a point at random from the temporal SSC curve at some site 'a' (equivalent to taking a sample at one site at Hamana-ko) and a point at random at another site 'b', we hope that the probability is high that the point from the curve at 'a' will in fact be higher than at 'b'. The likelihood of this will increase if the larger erosional events responsible for most of the SSC (1) are transitory and (2) are not frequent with respect to sampling time, i.e., that most sites are well into the settling phase (past the inflection point of an exponentially declining temporal SSC curve) after an erosion event. If the number of events is fairly frequent with respect to the sampling interval, then we must also consider that the probability of finding $SSC(a) > SSC(b)$ is decreased if the number of erosional events (rises in shear velocity, u_* , to above the threshold stress) at 'b' is much higher than at 'a'. It has been shown using a turbidometer (Fig. 1) that the high SSC is a very transitory event; from video-camera observations some of the so-called "suspended" sediment during these transitory events may actually be undergoing saltation. SSC is normally at a fairly uniform level, presumably the sum of a low level of allochthonous suspended sediment transported into the local area and material remaining in suspension after a local erosion "event" (generally a wave). Based on observations from a continuously monitoring turbidometer, the number of events is small.

Thus, conditions seem to be satisfied that if entrainability at some site 'a' is sufficiently larger than that at 'b,' we will see it if we have a sufficiently large number of data points. We expect the data to have a great deal of scatter, and thus low correlations among variables, even if in nature the relationships are tight, because of the temporally random nature with respect to u_* with which the data were collected.

Observations at Hamana-ko

For this study we made preliminary observations of the relationships between sediment entrainment and benthic communities *in situ*, in shallow water sandy environments of a shallow brackish lagoonal bay known as Hamana-ko. In this paper we report simple empirical relationships between the benthic community, sedimentary texture, and suspended sediment concentration above the bottom. This paper also provides a brief review of some of the factors relevant to organism-sediment relationships in sandy sediments. In a later report (ROSS & IMADA, in prep), we will describe the construction of a straight flume for use in the field for controlling current velocity for performing experiments upon sediment entrainability.

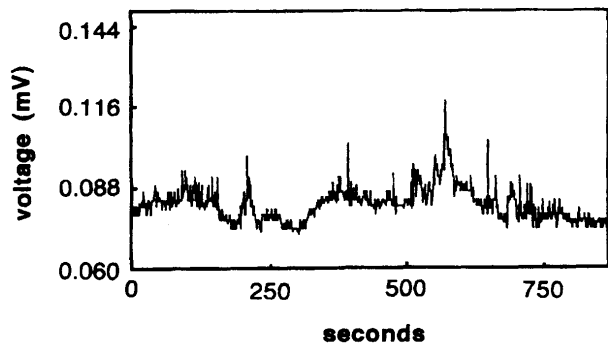


Fig. 1 Turbidometer data, showing voltage every second for about 15 minutes, reflecting suspended sediment concentration (SSC) in ambient water. The data was taken at about 15:20 to 15:35 on 28 July 1994. Note that suspended sediment concentration peaks only during brief events, and quickly returns to a lower level. The voltage was not properly calibrated to SSC, thus the actual magnitude of the SSC is not shown.

Field sites

We observed sediment entrainment and biotic assemblages at Hamana-ko, literally translated from Japanese, Lake Hamana. Hamana is actually a brackish-water bay with a very narrow opening to the Pacific Ocean on the central eastern coast of Honshu, Japan (Fig. 2). The depth of the mouth is only about 1 m deep, with a deeper canal for boat traffic, creating a lagoon with water circulation dependent largely on tidal flow. The waves at Hamana-ko are gentler than those along the open sea coast, making working conditions feasible.

The bay varies spatially in its salinity and water energy, and thus in its sedimentary and biotic characteristics. The bay has a sandy bottom near the shores along the half of Hamana-ko closest to the inlet; the central areas of the bay, and upper reaches of the bay, have a mud bottom (IKEYA & HANDA 1972, SANUKIDA & MATSUSHITA 1986). The studies we performed were in the shallow subtidal and intertidal parts of sandy beaches facing the largest parts of the bay. The Hamana-ko bottom environment is significantly modified by aquaculture, fishing and shell-fish collecting, swimming, and boating. We made our observations at three locations that are accessible by road vehicle, and which vary slightly in salinity, sediment texture, biota, and frequency of human disturbance. The locations will be referred to here as locations A, B, C, and D.

Locations A and B, at Marakushi Gate, are just east of a bridge connecting the "back" (north) of the bay with the land spit that mostly closes the mouth of the bay. The concrete stilts of the bridge form a wave block from the center of the bay so that sediments shoreward of the block (B) are slightly finer than several tens of meters downshore from the bridge (A). This area has

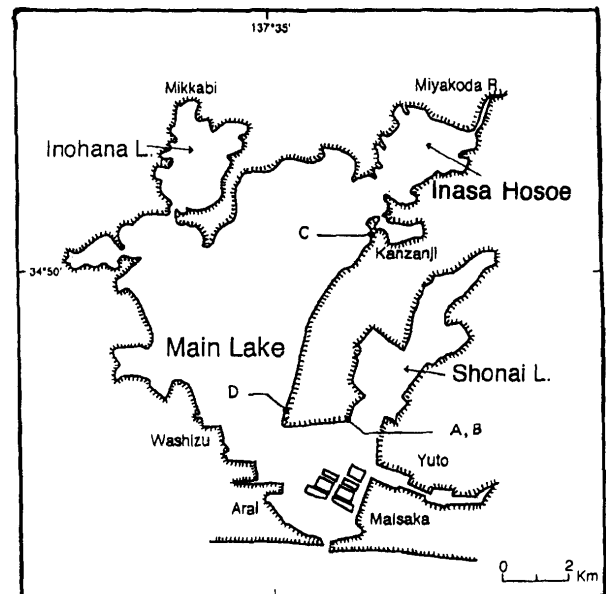


Fig. 2 Map of Hamana-ko. The bay opens at the southern end, between Arai and Malsaka, into the Pacific Ocean.

abundant edible bivalves that are collected with a rake-like tool at low tide, thus there is severe human disturbance that occurs nearly daily, at low tide, along the intertidal part of the shoreline. There had been, however, little or no human disturbance since the previous low tide at the times and sites sampled. In addition, motorboats pass within about 50 m of the shore, increasing wave energy and throwing up entrained sediment.

Location D, at Marakushi Beach, is a sand beach several hundred meters further into the bay from site A. It is likely frequently disturbed in summer by swimmers, but was disturbed only patchily by wind surfers at the time of our study. Location C, at Kanzanji Beach, is a sand beach toward the inside of the bay, in front of a hotel. This beach is frequently disturbed in summer, but was probably little disturbed at the time of our study. Locations C and D may be strongly affected by waves induced by westerly winds in winter.

With one exception, all samples were taken within a one-week period from 25 October to 2 November 1994; the exception is one sample from Murakushi Gate from July 28. Most samples were taken on 25 and 26 October. The others were taken in association with an *in situ* flume study, indicated by the suffix "f" attached to sample numbers in the tables. At Hamana-ko there is seasonality in water temperature and salinity, wave conditions, stratification of the lake, and fresh water and particulate input, and consequent effects upon the biota and likelihood of human activities. Thus these results are particularly time dependent

(cf. MAA 1993). OGURI (1995 MS) reviewed the seasonality in sediment properties and sedimentary flux toward the center of the basin.

METHODS — FIELD STUDIES

At each site suspended sediment concentration and suspended sediment grain size distribution were measured. In addition, five possible forcing factors were estimated: depth, water velocity, macrofauna, meiofauna, and bottom sediment grain size distribution. Water temperature was measured using a standard mercury thermometer; salinity was determined indirectly by measuring water density using an Akanuma gravitometer and then factoring out the effect of temperature.

Suspended sediment concentration was measured by drawing 50 ml of water into a plastic syringe with a mouth opening of 3 mm. Time for extraction of one sample was about 20 seconds. The samples were taken about 5 cm above the sediment surface. The samples were brought back to the laboratory in 50 ml bottles and filtered, and the filters were weighed.

Suspended sediment concentration was also measured using an optical (infrared) backscatter turbidometer (model OBS-1, manufactured by the D & A Instrument Co., Washington State, U.S.A. [DOWNING *et al.* 1981, MAA *et al.* 1992], integrated with software as the "Microlite" instrument system by Coastal Leasing, Inc., Massachusetts, U.S.A.), which measured sediment concentration continuously (once per second) by an infrared light ray sensor. However, mechanical and calibration problems made some of this data unreliable.

Suspended sediment grain size distribution was estimated by cutting 1 cm squares from the interior of the filters (avoiding both the center and the edge, which tend to have higher concentrations) and observing them by scanning electron microscopy. A part of the filter was chosen at random under the SEM, and grains at selected points along a transect across the monitor were chosen for measurement. Only grains with a major axis length greater than $0.5 \mu\text{m}$ were measured, because others should have passed through the filter.

Water velocity was measured by observing the movement of a black plastic ball 5 mm in diameter hung from a nylon string under a clear acrylic stand, such that the ball hung 5 cm above the bottom (Fig. 3). The ball density was slightly greater than sea water, so that it sunk in still water but was highly sensitive to moving water. The movement of the ball was recorded by placing an underwater video camera upon the top of the acrylic stand, and video recording for about one minute, covering the time that the suspended sediment sample was taken. The relationship between current velocity and movement of the ball in a horizontal field was determined empirically by timing

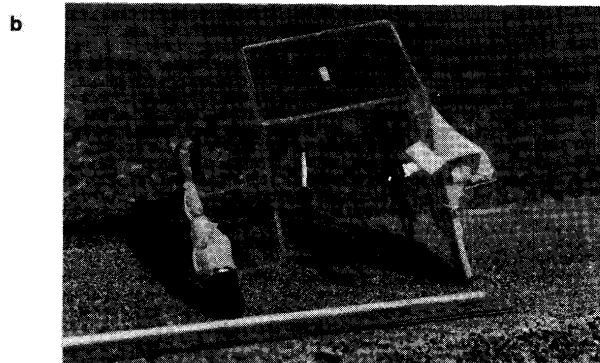


Fig. 3 Video-camera support. (a) Turbidometer (upright metal cannister) attached to camera support. (b) The turbidometer sensor is attached to a flap so that it sits about 5 cm above the bottom. The black bead hanging from fishing line from the camera support was used to observe current flow and wave motion. The pinwheel was also intended for observing current flow. The longer right limb of the support is placed into the sediment for stability. The video camera housing is placed directly above the support, and an underwater light is shone through the right side.

the speed of particles traveling across the field of view. The "velocity" of the tidal flow was weak during the experiment, but flow was also caused by the circular orbit of waves; while this motion is different than that of a true current, it apparently has similar erosional characteristics (NOWELL & JUMARS 1987), and it was considered that the similarity in water movement between wave orbits and currents is sufficiently high to obtain at least a qualitative estimation of the relationship between water movement and sediment entrainment. Technical difficulties with the video camera resulted in only 8 measurements of water movement. It is actually u_* that is important for sedimentary processes at the sediment surface (e.g., YALIN 1977). u_* , however, is nearly linearly related to u .

Table 1 Salinity and water temperature of the 3 locations.

Location	Date	Salinity ‰	Water temperature °C
Murakushi gate	10/25/1994	30.50	22.0
	11/2/1994	29.38	23.0
Kanzanji beach	10/26/1994	31.70	23.2
	10/31/1994	28.73	22.6
Murakushi beach	10/26/1994	31.76	21.8
	11/1/1994	30.54	21.1

Table 2 Water depth of the samples at each site. Depth with respect to mean sea level is a rough estimate. LT=low tide, HT=high tide; plateau refers period within 1 hour, before and after, tidal extreme.

Location	Date	Sample number	time of measurement	measured depth (cm)	depth with respect to MSL (cm)	tidal state
Marakushi Gate	94-07-28	A1f	14:30	32	36	LT, plateau
		A2	14:21	2	0	LT, plateau
	94-10-25	A3	15:39	35	30	rising
		A4	14:50	44	40	rising
		A5	15:07	47	43	rising
		A6	15:26	30	25	rising
		A7	15:53	15	9	rising
	94-11-02	A8f	12:50	29	22	rising
Under bridge	94-10-25	B1	16:14	15	8	rising
		B2	16:22	22	15	rising
		B3	16:33	38	31	rising
Kanzanji Beach	94-10-25	C1	11:47	40	36	falling
		C2	12:14	56	53	falling
		C3	12:36	61	59	falling
		C4	12:56	65	63	falling
	94-10-31	C5f	13:39	37	26	HT, plateau
Marakushi Beach	94-10-25	D1	15:40	30	26	rising
		D2	16:02	37	33	rising
		D3	16:19	34	29	rising
		D4	16:32	15	10	rising
	94-11-01	D5f	15:36	54	47	rising

at a point x in the benthic boundary layer; since this study is concerned merely with identifying (potentially causative) correlations among variables, we simply use u_x instead of u_x^* in our analyses.

Depth was measured using a meter stick at the time of sampling (Table 2). Depth with respect to local mean sea level was estimated by linearly interpolating between tidal extremes. Tides at Kanzanji are delayed about 2 hours from those of the open ocean around Maisaka, and tides at Murakushi are delayed about 90 minutes (NONAKA *et al.* 1973). Also, the magnitude of the tidal range within Hamana-ko is considerably damped, to roughly 25 to 30% of the open-ocean range. Because of uncertainties in the exact timing and magnitude of tidal ranges at our sites, estimates of depth with respect to mean sea level are only approximate, but are probably within ± 10 cm. All sites were subtidal, less than 1 m deep.

Sediment at each site was cored using a plastic (PVC) corer 4.4 cm in diameter. The core was divided into half cm sections in the top centimeter, and divided into one centimeter sections down to five centimeters. This sediment was fixed in formalin at the site, and changed to alcohol and

stained with rose bengal in the laboratory.

The first half centimeter was used for the meiofaunal and grain size analyses. This sediment was first wet sieved over a 0.063 mm sieve. The water residue, containing particles 63 μ m, was saved; its volume was measured, it was well mixed, and approximately one half liter was removed and filtered over a 0.45 μ m filter. The mud remaining on the filter was weighed, and the weight was divided by the fraction of the water residue volume that had been filtered, in order to find the total weight of mud in the sample.

To extract meiofauna from the sediment, sandy sediment was poured into a 1 liter graduated cylinder filled with tap water. The mixture was tipped upside down several times, and less dense material was immediately decanted into the 63 μ m sieve and then poured into an acrylic tray for observation. This process was repeated several times. The meiofauna, foraminifera, diatoms, and biologic shell debris were counted and identified to the class or phylum level. After observation, the decanted residue was stored in alcohol.

The sand-sized sediment was dried and passed through sieves of 1, 0.5, 0.25, 0.125, and 0.063 mm and each size fraction weighed.

The macrofauna data is only semi-quantitative, in that the depth and weight of the samples were not measured, but were estimated by eye. Macrofaunal density was estimated by submerging a garden trowel (semi-horizontally) to a sediment depth of about 3 cm and washing this heaping trowelful of sediment over a 1.44 mm sieve. At most sites three trowel samples were taken; the data represents the average number of macrofauna and tubes contained in the samples. At the 4 "f" sites, 10 samples were taken, from the site to 3 m oceanward of the site. The summarized data for this site represents a weighted average, the weights inversely proportional to the distance from the site (for example, the 10th sample, farthest from the site, counts 1/10th that of the sample directly at the site). The number of empty shells and amount of shell debris and other gravel were also recorded. All material recovered in the sieve was identified in the field and immediately returned to the water.

Rapidly moving macrofauna such as decapod crustaceans were frequently observed near the strandline, but were not seen within the sampling sites and not recorded. A moderate number of small holothurians were present at Kanzanji Beach, but were not within our area of sampling.

Results: Physical measurements

Suspended sediment concentrations vary over nearly two orders of magnitude, from 3.7 to 1525 mg/ ℓ and vary greatly even at sites from the same location (Table 9). The variation in concentration is as much a function of timing as of

Table 3 Grain size distribution and descriptive statistics of the top 0.5 cm bottom sediment at each site.

Location	Date	Sample number	Grain size						Average size		Median size		Sorting	Skewness	Kurtosis
			<0 φ (%)	0-1 φ (%)	1-2 φ (%)	2-3 φ (%)	3-4 φ (%)	>4 φ (%)	φ	mm	φ	mm			
Marakushi Gate	94-07-28	A1f	0.00	1.47	39.34	55.88	3.03	0.28	2.11	0.23	2.2	0.22	0.84	-0.16	0.94
		A2	0.00	2.98	60.99	35.21	0.33	0.50	1.84	0.28	1.7	0.31	0.82	0.10	0.82
	94-10-25	A3	0.00	2.29	46.86	48.00	1.14	1.71	2.03	0.24	2.0	0.25	0.82	0.00	0.82
		A4	0.35	2.45	47.90	45.80	1.75	1.75	2.01	0.25	2.0	0.25	0.86	0.03	1.16
		A5	0.00	2.10	44.76	48.95	2.10	2.10	2.07	0.24	2.1	0.23	0.86	-0.11	1.09
		A6	0.00	1.49	47.76	46.27	2.99	1.49	2.05	0.24	2.0	0.25	0.86	-0.06	1.09
		A7	0.00	2.94	62.30	34.49	0.27	0.00	1.82	0.28	1.8	0.29	0.83	0.03	0.88
	94-11-02	A8f	0.00	3.23	51.87	41.33	0.85	2.72	1.98	0.25	1.9	0.27	0.88	0.12	1.31
Under bridge	94-10-25	B1	0.00	0.52	5.15	82.47	10.82	1.03	2.57	0.17	2.8	0.14	0.93	-0.38	1.54
		B2	0.00	2.00	34.67	57.00	4.33	2.00	2.20	0.22	2.2	0.22	0.83	0.00	0.92
		B3	0.00	0.92	26.73	65.44	4.61	2.30	2.31	0.20	2.3	0.20	0.84	0.03	0.87
Kanzanji Beach	94-10-25	C1	0.00	0.00	3.35	53.70	42.78	0.18	2.90	0.13	1.9	0.27	0.81	0.34	0.87
		C2	0.49	1.48	4.93	81.28	11.82	0.00	2.52	0.17	2.8	0.14	0.93	-0.42	1.43
		C3	0.00	0.51	10.71	81.12	7.65	0.00	2.46	0.18	2.6	0.16	0.91	-0.27	1.15
		C4	0.00	0.60	6.27	77.31	15.22	0.60	2.59	0.17	2.8	0.14	0.91	-0.42	1.23
		C5f	0.76	2.42	38.67	55.74	2.42	0.00	2.07	0.24	2.1	0.23	0.91	-0.04	1.33
	94-10-31	C5f	0.76	2.42	38.67	55.74	2.42	0.00	2.07	0.24	2.1	0.23	0.91	-0.04	1.33
Marakushi Beach	94-10-26	D1	0.00	3.25	50.35	45.71	0.46	0.23	1.94	0.26	1.9	0.27	0.90	0.11	1.33
		D2	0.00	2.13	51.91	45.53	0.43	0.00	1.94	0.26	1.9	0.27	0.83	0.03	0.88
		D3	0.00	1.83	47.71	49.54	0.92	0.00	2.00	0.25	2.0	0.25	0.90	-0.04	1.33
		D4	0.47	1.89	50.00	46.70	0.47	0.47	1.96	0.26	1.9	0.27	0.88	0.32	1.15
		D5f	0.00	2.52	55.61	41.19	0.69	0.00	1.90	0.27	1.9	0.27	0.88	0.00	1.31

Table 4 Maximum observed water velocity during sampling at 8 of the sites.

Location	Date	Sample number	Water velocity (max) (cm/s)
Murakushi gate	7/28/1994 10/25/1994	A1f	
		A2	
		A3	
		A4	
		A5	
		A6	
		A7	
Under bridge	11/2/1994 10/25/1994	A8f	
		B1	
		B2 B3	
Kanzanji beach	10/26/1994 10/31/1994	C1f	24
		C2	45
		C3	39
		C4	12
		C5f	
Murakushi beach	10/26/1994 11/1/1994	D1	60
		D2	42
		D3	21
		D4	36
		D5f	

location, since the concentration is expected to oscillate over periods as short as the frequency of waves approaching the shore, though larger scale variation is undoubtedly a function of larger waves (caused either by wind or passing boats).

The median suspended sediment grain size was between 1 and 3.2 μm , i.e., clay-sized, thus at least in abundance of individual grains the entrained sediment is primarily clay, in spite of the dominantly sandy bottom sediment (Table 3).

The median size of the bottom sediment grains at all sites varies between 1.8 ϕ (0.29 mm) and 2.8 ϕ (0.14 mm), with generally finer sand at Kanzanji Beach and under the bridge at Marakushi Gate (Table 4). None of the samples are strongly skewed in their grain size distribution. Sediment larger than coarse sand (1 mm) is insignificant in all samples. Mud content ranges from near 0 to about 3%, and is present in quantities over 1%

only at Marakushi Gate. Core profiles generally show finer sand in the upper half centimeter of the bottom sediment than below.

Maximal water velocity varied between 12 and 60 cm s^{-1} (Table 4). The autumn temperature and salinity at all three sites was nearly identical, from about 21 to 23 $^{\circ}\text{C}$ and approximately 30 p.p.t., respectively (Table 1).

RESULTS: BIOTIC MEASUREMENTS

Macrofaunal molluscan communities are strongly zoned by water depth (A. Kitamura, pers. comm., 1994), but differences in faunas also exist by locality (Tables 5, 8). Marakushi Gate is known for its abundance of the intertidal venerid bivalve *Ruditapes philippinarum* (Adams & Reeve) (listed in the tables under its former generic position, *Tapes*); the shallow subtidal trochid gastropod *Umbonium moniliferum* (Lamarck) dominated the macrofauna in most samples at Marakushi Gate, but was not found at either of the other localities. The nassariid gastropod *Reticunassa festiva* (Powys) (listed in the tables by its former generic position *Hinia*) and the potamidid gastropod *Batillaria multiformis* Adams were found in very small quantities at Marakushi Gate and Kanzanji Beach.

There are two size classes of organically-bound tubes presumably belonging to polychaetes: very thin flexible tubes about 2 mm in diameter and up to several cm long, and thicker, more rigid, tubes about 5 mm in diameter and about 1 cm long. The larger polychaete tubes are present at Marakushi Gate and Kanzanji Beach. The small tubes are extremely abundant along some parts of Kanzanji Beach, and are variably abundant at Marakushi Gate and at Marakushi Beach, where they were the only obvious sign of macrofauna.

In summary, Marakushi Gate seems to have abundant mobile macrofauna, Kanzanji Beach showed evidence primarily of tube-building macro-

Table 5 Average number of macrofauna per trowel (approx. 1 kg wet weight) of sediment at each site.

Location	Date	Sample number	number of samples averaged	fat worm tubes	thin worm tubes	bivalve Tapes philippinarum	snails			Total macrofauna
							Batillaria multiformis	Umbonium monoliferum	Hinia festiva	
Marakushi Gate	94-07-28	A1f	10 wt'd	0.0	0.3	0.0	0.0	4.6	0.0	4.9
	94-10-25	A2	3	0.0	1.0	0.0	0.0	0.0	0.0	1.0
		A3	3	0.0	2.0	0.0	0.0	5.0	0.0	7.0
		A4	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		A5	3	5.0	4.0	0.0	0.0	0.0	0.0	9.0
		A6	3	0.0	4.0	0.0	0.0	10.0	0.0	14.0
		A7	3	0.0	0.0	0.0	0.0	2.0	0.0	2.0
	94-11-02	A8f	10 wt'd	0.0	1.5	0.1	0.5	8.8	0.5	11.5
Under bridge	94-10-25	B1	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		B2	3	0.0	0.0	0.0	0.0	4.0	0.0	4.0
		B3	3	0.0	9.0	0.0	0.0	0.0	0.0	9.0
Kanzanji Beach	94-10-25	C1	3	0.0	3.3	0.0	0.0	0.0	0.0	3.3
		C2	3	0.0	5.3	0.3	0.0	0.0	0.0	5.6
		C3	3	0.3	4.3	0.0	0.0	0.0	0.0	4.6
		C4	3	0.7	22.3	0.7	0.0	0.0	0.0	23.6
	94-10-31	C5f	10 wt'd	1.4	0.4	2.0	0.1	0.0	0.0	3.9
Marakushi Beach	94-10-26	D1	3	0.0	0.7	0.0	0.0	0.0	0.0	0.7
		D2	3	0.0	0.3	0.0	0.0	0.0	0.0	0.3
		D3	3	0.0	0.3	0.0	0.0	0.0	0.0	0.3
		D4	3	0.0	1.0	0.0	0.0	0.0	0.0	1.0
	94-11-01	D5f	10	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 6 Average number of meiofauna per 10 grams (dry weight) of sediment in the top 0.5 cm bottom sediment at each site.

Location	Date	Sample number	(total)		adult	juvenile	n/c ratio	snails	bivalves	ostracodes	tardigrades	others	total meiofauna	diatom strings	plant tissues
			nematodes	copepods	copepods	copepods									
Marakushi Gate	94-07-28	A1f	576.9	76.2	66.1	10.2	7.6	0.0	2.5	8.3	15.2	101.7	780.8	0.0	0.0
	94-10-25	A2	324.0	176.9	125.6	51.2	1.8	5.0	0.0	54.5	6.6	3.3	570.2	1.7	0.0
		A3	1737.1	331.4	285.7	45.7	5.2	80.0	0.0	160.0	0.0	262.9	2571.4	0.0	0.0
		A4	2258.7	566.4	412.6	153.8	4.0	293.7	7.0	244.8	111.9	21.0	3503.5	0.0	35.0
		A5	951.0	251.7	125.9	125.9	3.8	55.9	28.0	83.9	97.9	167.8	1636.4	0.0	28.0
		A6	3373.1	626.9	298.5	328.4	5.4	89.6	0.0	328.4	298.5	119.4	4835.8	0.0	0.0
		A7	433.2	219.3	133.7	85.6	2.0	26.7	0.0	85.6	10.7	0.0	775.4	0.0	21.4
	94-11-02	A8f	42.5	8.5	8.5	0.0	5.0	10.2	3.4	47.6	1.7	0.0	113.9	0.0	0.0
Under bridge	94-10-25	B1	412.4	185.6	144.3	41.2	2.2	10.3	0.0	82.5	0.0	61.9	752.6	30.9	0.0
		B2	633.3	180.0	126.7	53.3	3.5	6.7	6.7	66.7	13.3	13.3	920.0	0.0	6.7
		B3	1391.7	258.1	147.5	110.6	5.4	18.4	27.6	92.2	46.1	119.8	1953.9	0.0	73.7
Kanzanji Beach	94-10-25	C1	151.4	44.0	21.1	22.9	3.4	1.8	10.6	7.0	0.0	21.1	235.9	3.5	0.0
		C2	571.4	295.6	88.7	206.9	1.9	0.0	39.4	29.6	0.0	9.9	945.8	236.5	9.9
		C3	387.8	571.4	102.0	469.4	0.7	5.1	61.2	112.2	0.0	112.2	1250.0	61.2	163.3
		C4	1277.6	1086.6	632.8	453.7	1.2	11.9	495.5	65.7	0.0	41.8	2979.1	65.7	6.0
	94-10-31	C5f	60.4	528.7	114.8	413.9	0.1	0.0	55.9	9.1	0.0	24.2	678.2	120.8	100.0
Marakushi Beach	94-10-26	D1	524.4	208.8	146.2	62.6	2.5	4.6	2.3	11.6	13.9	0.0	765.7	0.0	2.3
		D2	502.1	238.3	153.2	85.1	2.1	8.5	0.0	17.0	0.0	17.0	783.0	0.0	8.5
		D3	64.2	275.2	137.6	137.6	0.2	0.0	0.0	0.0	0.0	0.0	339.4	18.3	18.3
		D4	801.9	575.5	339.6	235.8	1.4	0.0	0.0	47.2	0.0	18.9	1443.4	18.9	9.4
	94-11-01	D5f	96.1	82.4	51.5	30.9	1.2	0.0	0.0	12.6	0.0	6.8	197.9	0.0	0.0

fauna, and Marakushi Gate had very little living macrofauna.

The density of meiofauna, in number of organisms per gram, varies by an order of magnitude (113.9 to 4835.8 (10g)⁻¹ of surface sediment [10g is the standard unit in the measurement of meiofaunal density]), and is as variable within locations and between (Tables 6, 8). The meiofauna at most sites is dominated numerically by nematodes, followed by copepods at many sites; juvenile bivalves, juvenile mollusks, ostracodes, and

tardigrads are locally abundant. Tardigrads and juvenile gastropods were common at some sites at Marakushi Gate, juvenile bivalves were common at Kanzanji Beach, and ostracodes were locally abundant at some sites at both Marakushi Gate and Kanzanji Beach. Confirming the findings for macrofaunal mollusks, the abundance of juvenile gastropods and bivalves at Marakushi Beach was very low.

Table 7 Ratios of abundances among mobile and sessile macrofauna and meiofauna.

Location	Date	Sample number	sessile	mobile	% mobile	1000 x macro/meio	
			macrofauna	macrofauna			
Marakushi Gate	94-07-28	A1f	0.3	4.6	93.4%	5.3	
	94-10-25	A2	1.0	0.0	0.0%	2.2	
		A3	2.0	5.0	71.4%	13.8	
		A4	0.0	0.0		0.0	
		A5	4.0	0.0	0.0%	14.8	
		A6	4.0	10.0	71.4%	38.3	
		A7	0.0	2.0	100.0%	5.4	
		A8f	1.6	10.0	87.0%	159.1	
Under bridge	94-10-25	B1	0.0	0.0		0.0	
		B2	0.0	4.0	100.0%	12.1	
		B3	9.0	0.0	0.0%	18.8	
Kanzanji Beach	94-10-25	C1	3.3	0.0	0.0%	20.8	
		C2	5.6	0.3	5.4%	22.2	
		C3	4.3	0.0	0.0%	12.0	
		C4	23.0	0.7	2.9%	16.9	
		C5f	2.4	2.1	82.4%	3.1	
Marakushi Beach	94-10-26	D1	0.7	0.0	0.0%	1.6	
		D2	0.3	0.0	0.0%	1.3	
		D3	0.3	0.0	0.0%	2.2	
		D4	1.0	0.0	0.0%	2.3	
		94-11-01	D5f	0.0	0.0		0.0

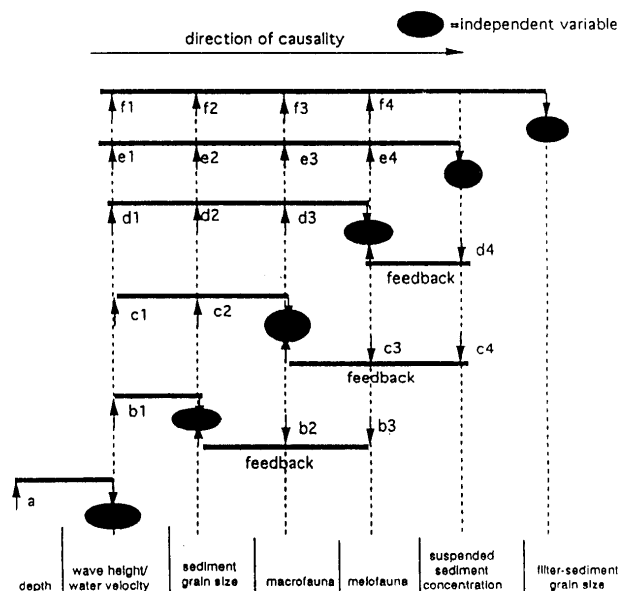
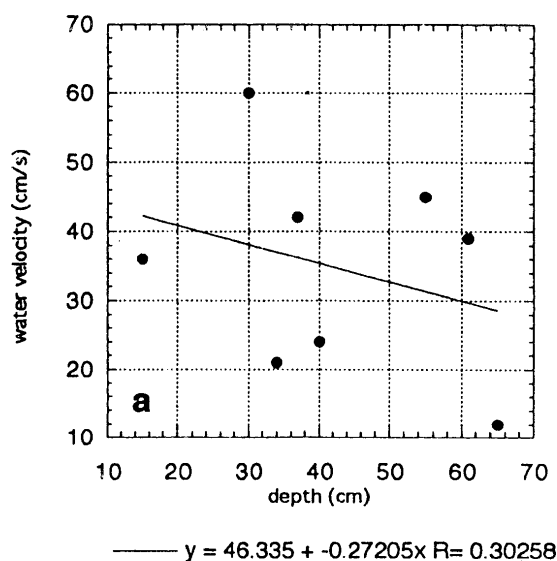


Fig. 4 Possible network of causal relationships among biological and physical variables. The coefficients identify particular relationships.

DATA ANALYSIS

In order to better understand the relationships among these variables, the data was subjected to a variety of ordination and regression techniques. We were particularly interested in determining the variables that have some impact upon suspended sediment concentrations. A flowchart of hypothesized possible relationships among the variables is shown in Fig. 4. The variables were regressed against one another, using the hypothesized causative variables as the regressors. Both linear and nonlinear models were tested, using the "MGLH" and "Nonlin" routines of the commercial statistics package SYSTAT (WILKINSON 1989), and the linear

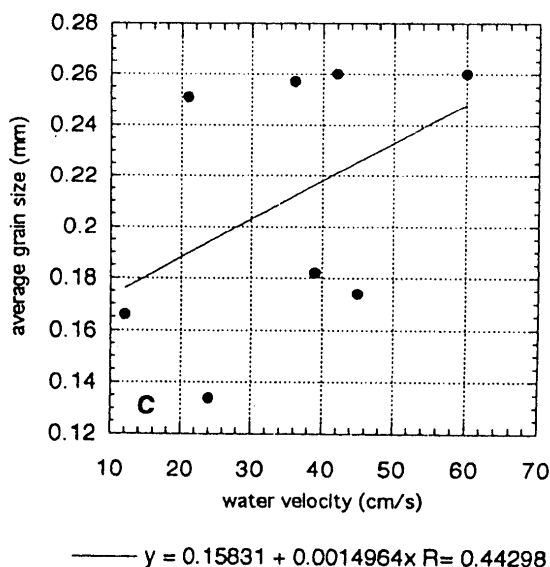
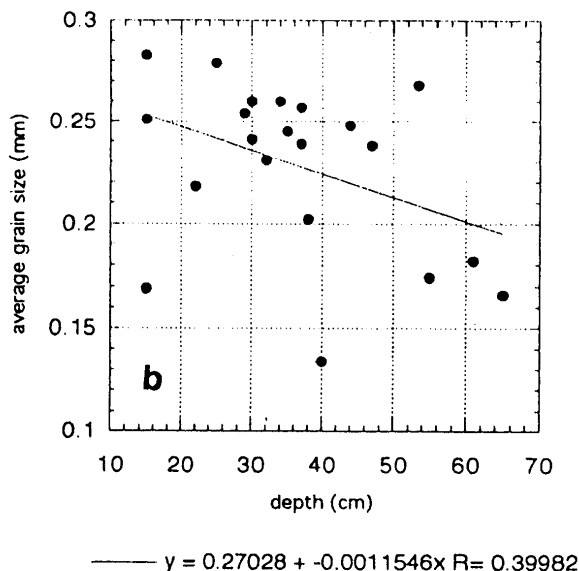


Fig. 5 Relationships among water velocity, measured depth, and mean sediment grain size.

Table 8 Thanatocoenosis (shelly material from biota) at each site. Meiofaunal shells units are number of empty shells per gram of dry sediment from the top 0.5 cm of the sediment surface. "Shelly gravel" refers to broken macrofaunal shells; the number refers to a subjective categorization of the amount of shelly gravel per trowel of sediment, from 0 (no shelly gravel) to 3. Macrofaunal shell units are the average number of empty shells per trowel of sediment.

Location	Date	Sample number	meiofauna			shell gravel	macrofauna			
			snails	bivalves	ostracodes		<i>Tapes philippinarum</i>	<i>Batillaria multiformis</i>	<i>Umbonium monoliferum</i>	<i>Hinia festiva</i>
Marakushi Gate	94-07-28	A1f	0.0	0.0	2.5	0.1	0.0	0.0	0.0	0.0
	94-10-25	A2	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
		A3	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
		A4	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0
		A5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		A6	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0
		A7	0.0	0.0	0.0	0.0	1.0	0.0	1.0	0.0
		A8f	0.0	0.0	32.3	0.0	0.0	0.0	1.3	0.0
Under bridge	94-10-25	B1	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
		B2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		B3	0.0	0.0	0.0	1.0	2.0	0.0	1.0	0.0
Kanzanji Beach	94-10-25	C1	0.0	0.0	0.0	0.3	2.0	0.0	0.0	0.0
		C2	0.0	0.0	0.0	0.3	3.3	0.0	0.0	0.0
		C3	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0
		C4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	94-10-31	C5f	0.0	9.1	0.0	0.2	0.0	0.0	0.0	0.0
Marakushi Beach	94-10-26	D1	0.0	0.0	0.0	1.0	2.3	0.0	0.7	0.0
		D2	0.0	0.0	0.0	1.0	1.3	0.0	0.7	0.0
		D3	0.0	0.0	0.0	0.7	1.7	0.0	0.7	0.0
		D4	0.0	0.0	0.0	1.0	0.3	0.0	0.3	0.0
	94-11-01	D5f	0.0	0.0	0.0	0.0	1.5	0.0	0.0	0.0

Table 9 Suspended sediment concentration (SSC) and median grain size of the suspended sediment at each site.

Location	Date	Sample number	Concentration (g/l)	Median grain size (μm)
Murakushi gate	7/28/1994	A1f	0.0621	2.3
	10/25/1994	A2	0.0333	2.2
		A3	0.0164	2.8
		A4	0.0295	1.0
		A5	0.0105	2.3
		A6	0.0056	2.8
		A7	0.0208	3.0
		A8f	0.0777	2.3
Under bridge	10/25/1994	B1	0.0396	2.3
		B2	0.0130	3.5
		B3	0.0102	2.0
Kanzanji beach	10/26/1994	C1	0.0512	2.6
		C2	0.0116	3.2
		C3	0.0097	1.0
		C4	0.0062	2.6
	10/31/1994	C5f	0.1525	2.3
Murakushi beach	10/26/1994	D1	0.0110	2.0
		D2	0.0051	1.7
		D3	0.0081	2.1
		D4	0.0037	3.0
	11/1/1994	D5f	0.0380	2.8

regression routine in the program Kaleidoscope. For the iterative nonlinear estimation procedure, a quasi-newton loss function was used. High correlations between pairs of variables are shown in Table 10; regression equations are illustrated on the plots, and other selected results are shown in Table 11.

Fig. 5 shows that there is little relationship among the water velocity, measured depth, and average grain size of the bottom sediment within the temporo-spatial range observed.

At the high taxonomic level used for this study,

Table 10 Correlations greater than 0.7 among faunal and sedimentological variables.

meiofauna	— meiofauna	Pearson correlation
nematodes	— ostracodes	0.909
nematodes	— tardigrades	0.836
nematodes	— snails	0.734
copepods	— bivalves	0.724
snails	— ostracodes	0.731
ostracodes	— tardigrades	0.825
macrofauna	— macrofauna	
<i>Batillaria multiformis</i>	— <i>Hinia festiva</i>	0.784
macrofauna	— meiofauna	
small worm tubes	— bivalves	0.914
bivalves	— bivalves	0.937
<i>Batillaria multiformis</i>	— ostracodes	0.982
<i>Hinia festiva</i>	— ostracodes	0.997
sessile macrofauna	— bivalves	0.928
benthos	— bottom sediment	
diatoms	— grain size skewness	-0.797
bivalves	— coarse sand	0.726
benthos	— SSC	
bivalves	— SSC	0.809
bivalves	— SSC	0.746

most faunal elements do not correlate well with depth. Selected plots of some of the better relationships are shown in Fig. 6. In each case, it is actually the range, or variance, in specimen densities that increases with measured depth, so that the

Table 11 Selected results of regression of environmental variables against suspended sediment concentration (SSC) and SSC grain size. Units for nematodes: number per 10 grams of dry sediment; small worm tubes and *U. moniliferum*: number per trowel (approx. 1 kg wet sediment); sediment grain size: mm, suspended sediment (SS) grain size: μ m; suspended sediment concentration (SSC): grams per liter; velmax = maximum velocity during 1 minute observation period: cm per second. For regressions using MGLH, *refers to regressed variables statistically significant at $p < 0.1$, **at $p < 0.01$.

estimated equation	multiple R	R ²	adjusted R ²	P	points	SYSTAT routine
SSC = 0.0275 - 0.00322 PCA4F1 - 0.0175 PCA4F1*PCA6F1	0.694	0.481	0.161	01<p<05	18	nonlin
SSC = 0.00734 + 0.0315 PCA4F1 * PCA6F1	0.643	0.414	0.052	01<p<05	18	nonlin
log(SSC) = -1.79 - 0.227 PCA4F1* - 0.133 PCA6F1	0.481	0.231	0.129	0.139	18	MGLH
SSC = 0.0297** - 0.0187 PCA4F1* - .00966 PCA6F1	0.470	0.221	0.117	0.154	18	MGLH
log(SSC) = -1.79* - 0.174 PCA4F1	0.384	0.147	0.094	0.116	18	MGLH
SSC = 0.0333* - 0.000027 nematodes* + 0.000052 copepods - 0.0021 small worm tubes + 0.00439 <i>U. moniliferum</i>	0.535	0.286	0.067	0.319	18	MGLH
SSC = 0.42817** - 0.000020 nematodes - 0.000813 small worm tubes + 0.00323 <i>U. moniliferum</i>	0.479	0.230	0.065	0.286	18	MGLH
SSC = 0.0468 - 0.000022 nematodes* - 0.043553 mean grain size	0.473	0.224	0.120	0.150	18	MGLH
SSC = 0.0669* - 0.000021 nematodes + 0.000507 velmax - 0.205 mean grain size	0.815	0.664	0.413	0.186	8	MGLH
SSC = 0.0346 - 0.000021 nematodes - 0.00873 velmax	0.541	0.293	0.010	0.420	8	MGLH
SSC = 0.0416** - 0.000015 nematodes	0.369	0.136	0.091	0.099	21	MGLH
log(SSC) = -0.517 - 0.465 log(nematodes)**	0.562	0.316	0.280	0.008	21	MGLH
mean SSC grain size = 3.72 - 0.662 PCA4F1 - 0.688 PCA4F1*PCA6F1	0.916	0.838	0.093	p<0.01	18	nonlin
mean SSC grain size = 3.83 - 0.293 PCA4F1*PCA6F1	0.909	0.827	0.034	p<0.01	18	nonlin
mean SSC grain size = 0.694 + 2.95 * velmax	0.612	0.374	0.270	0.107	8	MGLH

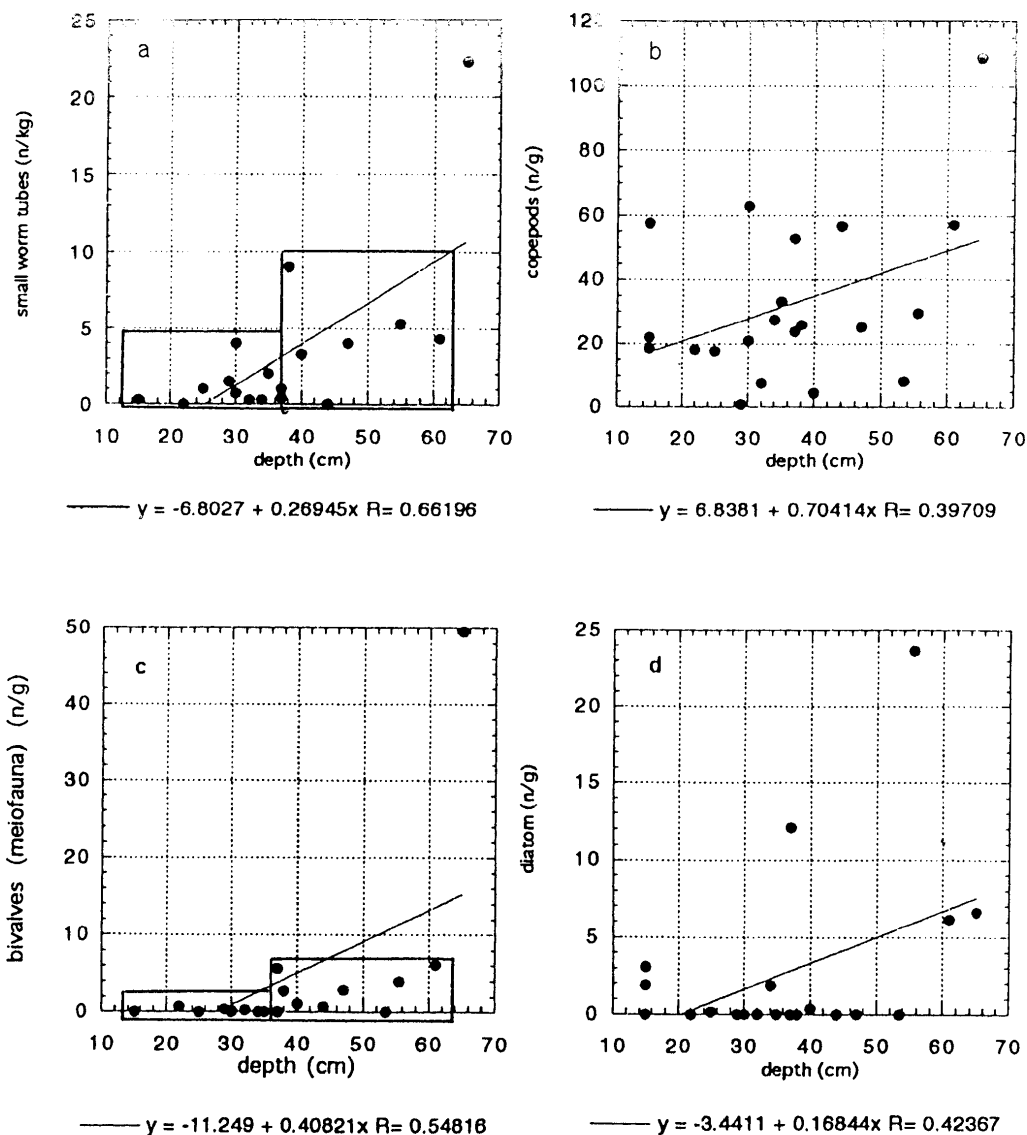


Fig. 6 Relationships of selected taxa to measured depth. Boxes highlight the fact that trends in taxon abundance with depth reflect a change in variance rather than a tightly correlated monotonic relationship.

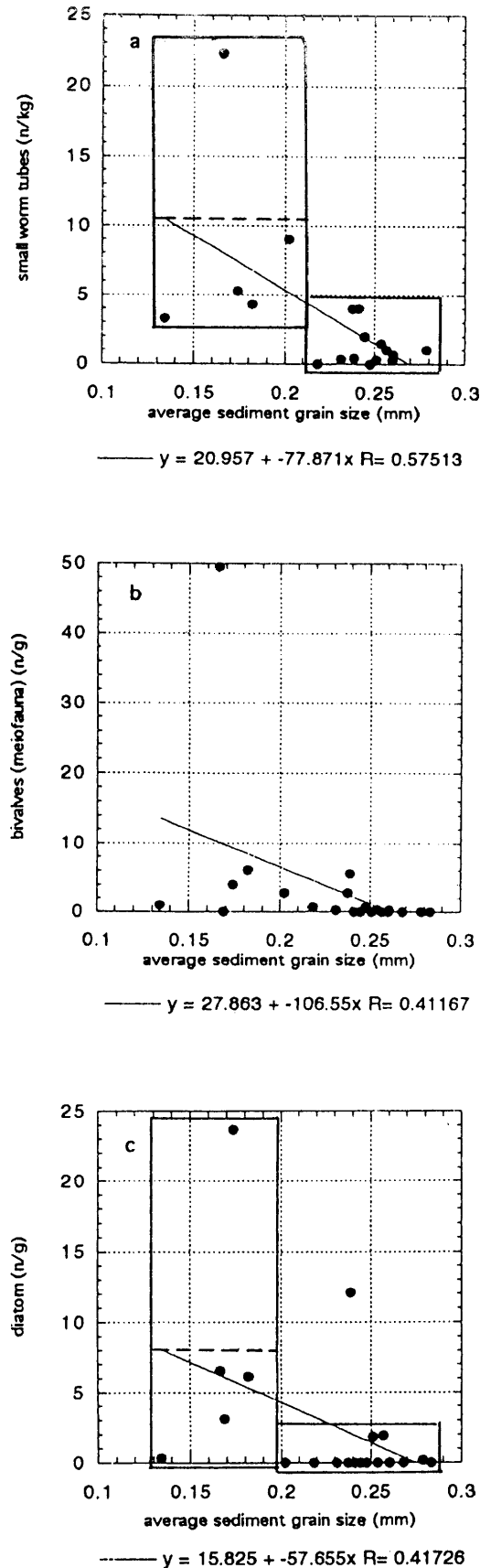


Fig. 7 Relationships of selected taxa to mean grain size. Boxes highlight the fact that trends in taxon abundance with grain size reflect a change in variance rather than a tightly correlated monotonic relationship.

average density increases with depth (i.e., the maximum densities occur deeper, but minimum densities (near zero) can occur anywhere, shallow or deep). For both meiofauna and macrofauna the samples with the highest densities also are deeper samples. Small worm tubes increase in average abundance with depth; a similar, but less convincing pattern, is present for juvenile bivalves and diatoms. Copepods shows no depth relationship, except that the deepest sample in the study also happened to have the highest copepod densities.

Several organisms, namely small polychaetes and diatoms, show rather strong increases in the range of specimen density with decreasing average grain size (Fig. 7). *Umbonium moniliferum*, nematodes, juvenile gastropods, tardigrades, and ostracodes all demonstrate increasing range of abundance with increases of mud content (over a mud content range of only a few percent) (Fig. 8).

In order to reduce the extensive faunal and sedimentological data to a few variables representing a high percent of the variance in the data, principal component analyses (PCA) were performed upon the data. The result of the PCA upon the faunal data, using both macro- and meiofauna, is shown in Fig. 9. The first two axes account for 53.5% of the variance in the data. It is apparent that Murakushi Gate samples cluster together, near zero on each of the first 2 axes, because of the barrenness of their faunas. The samples from Murakushi Gate and Kanzanji Beach form two non-overlapping groups, overlapping with those of Murakushi Beach in samples that were relatively barren of life.

The second PCA faunal axis is correlated with grain size, but it is not immediately apparent what controls the first PCA faunal axis.

A PCA of the sedimentary data was performed, in which the grain size average, median, standard deviation, skewness, and kurtosis, and also the amount of shell debris were taken into account. In spite of the similarity in sedimentary conditions, the three localities form primarily non-overlapping groups along the first 2 PCA axes (Fig. 10). The first two axes account for 56.7% of the variance in the data. The sites vary primarily in the grain size, sorting, and mud content.

SSC is not closely related to velocity, sediment grain size, or depth (Fig. 11 and Table 11). SSC is apparently related to particular faunal elements (Fig. 12), particularly if the data are log-transformed. For example, at sites at which nematodes or worm tubes were especially abundant, SSC was always low (for nematodes, $R^2 = 0.369$, $p = 0.10$; if both of the variables are log-transformed, $R^2 = 0.562$, $p = 0.008$); the converse was not necessarily true, that is, at low abundance SSC may be either high or low. In contrast, when the fauna has a high representation by mobile forms (Table 7), SSC could be high or low; at low abundance of

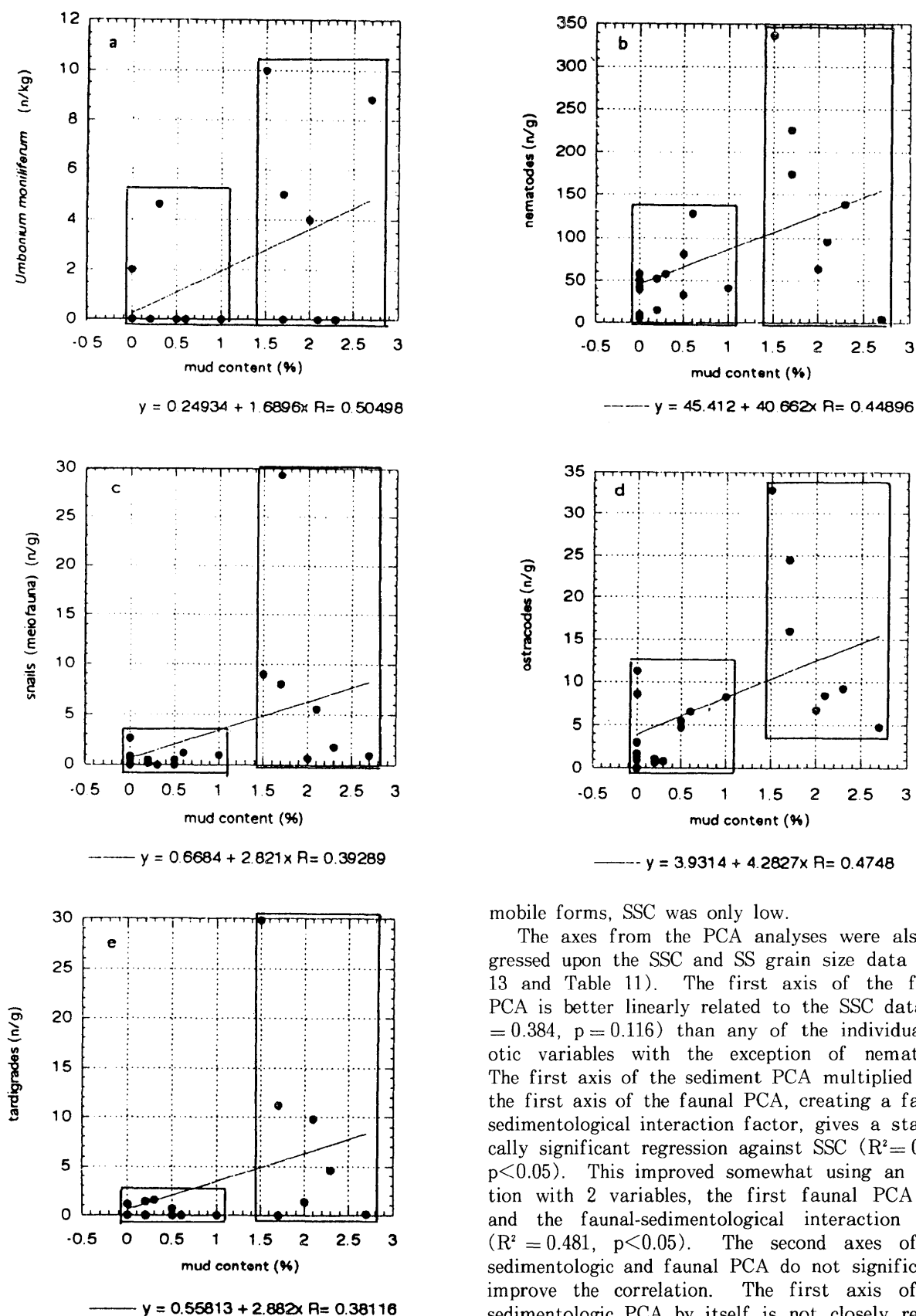


Fig. 8 Relationships of selected taxa to mud content. Boxes highlight the fact that trends in taxon abundance with mud content reflect a change in variance rather than a tightly correlated monotonic relationship.

mobile forms, SSC was only low.

The axes from the PCA analyses were also regressed upon the SSC and SS grain size data (Fig. 13 and Table 11). The first axis of the faunal PCA is better linearly related to the SSC data ($R^2 = 0.384$, $p = 0.116$) than any of the individual biotic variables with the exception of nematodes. The first axis of the sediment PCA multiplied with the first axis of the faunal PCA, creating a faunal-sedimentological interaction factor, gives a statistically significant regression against SSC ($R^2 = 0.414$, $p < 0.05$). This improved somewhat using an equation with 2 variables, the first faunal PCA axis and the faunal-sedimentological interaction term ($R^2 = 0.481$, $p < 0.05$). The second axes of the sedimentologic and faunal PCA do not significantly improve the correlation. The first axis of the sedimentologic PCA by itself is not closely related to SSC like the first axis of the faunal PCA, but does substantially improve the R^2 of a regression also containing the first axis of the faunal PCA ($R^2 = 0.481$, $p = 0.154$).

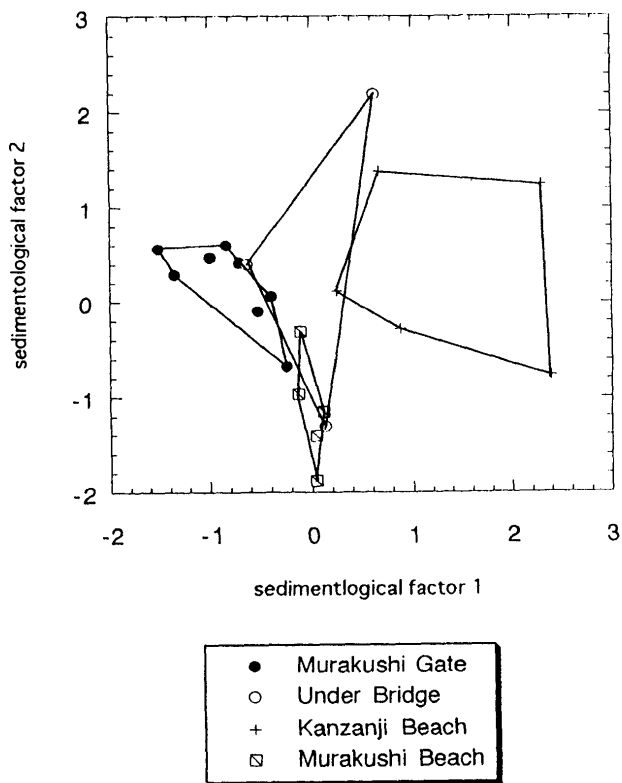


Fig. 9 Principal components analysis on faunal data, axis 1 vs. 2.

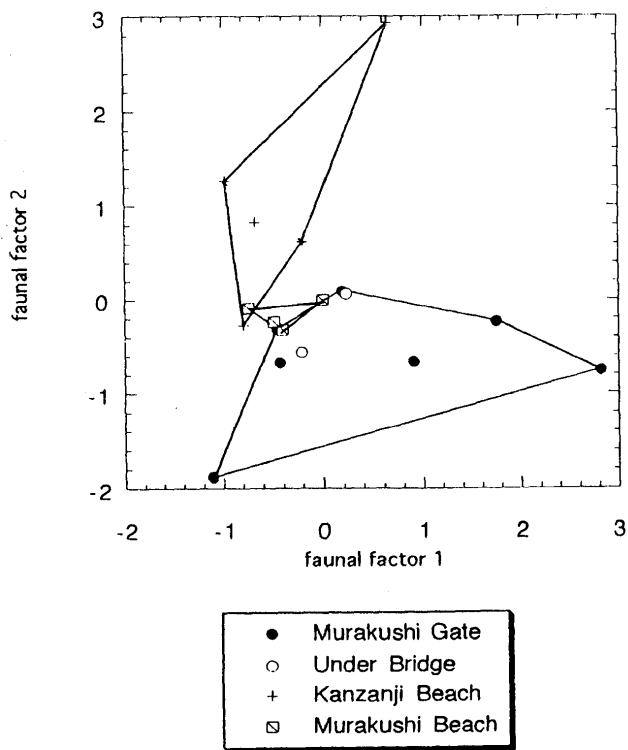


Fig. 10 Principal components analysis on sedimentary data, axis 1 vs. 2.

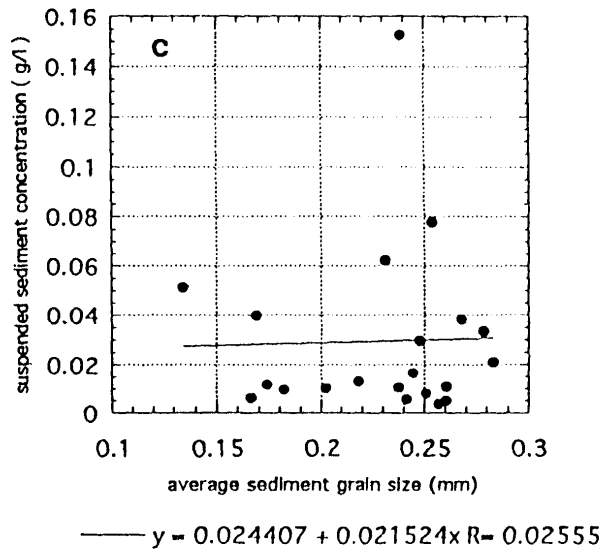
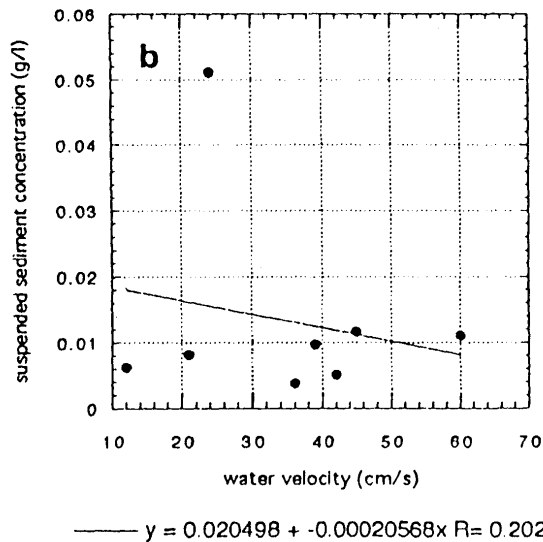
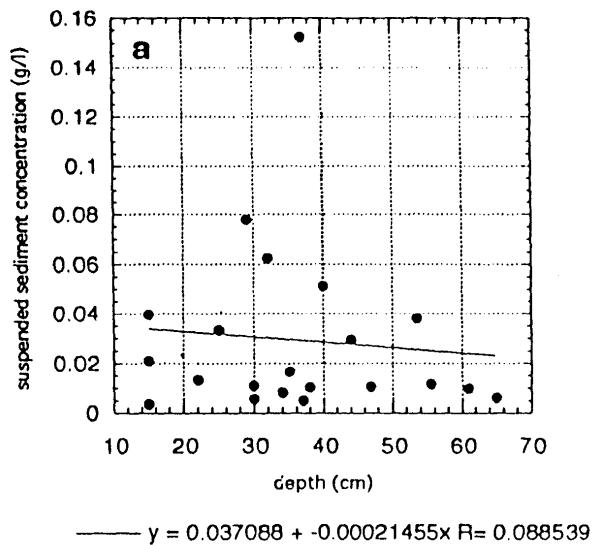


Fig. 11 SSC vs grain size, current velocity, and measured depth.

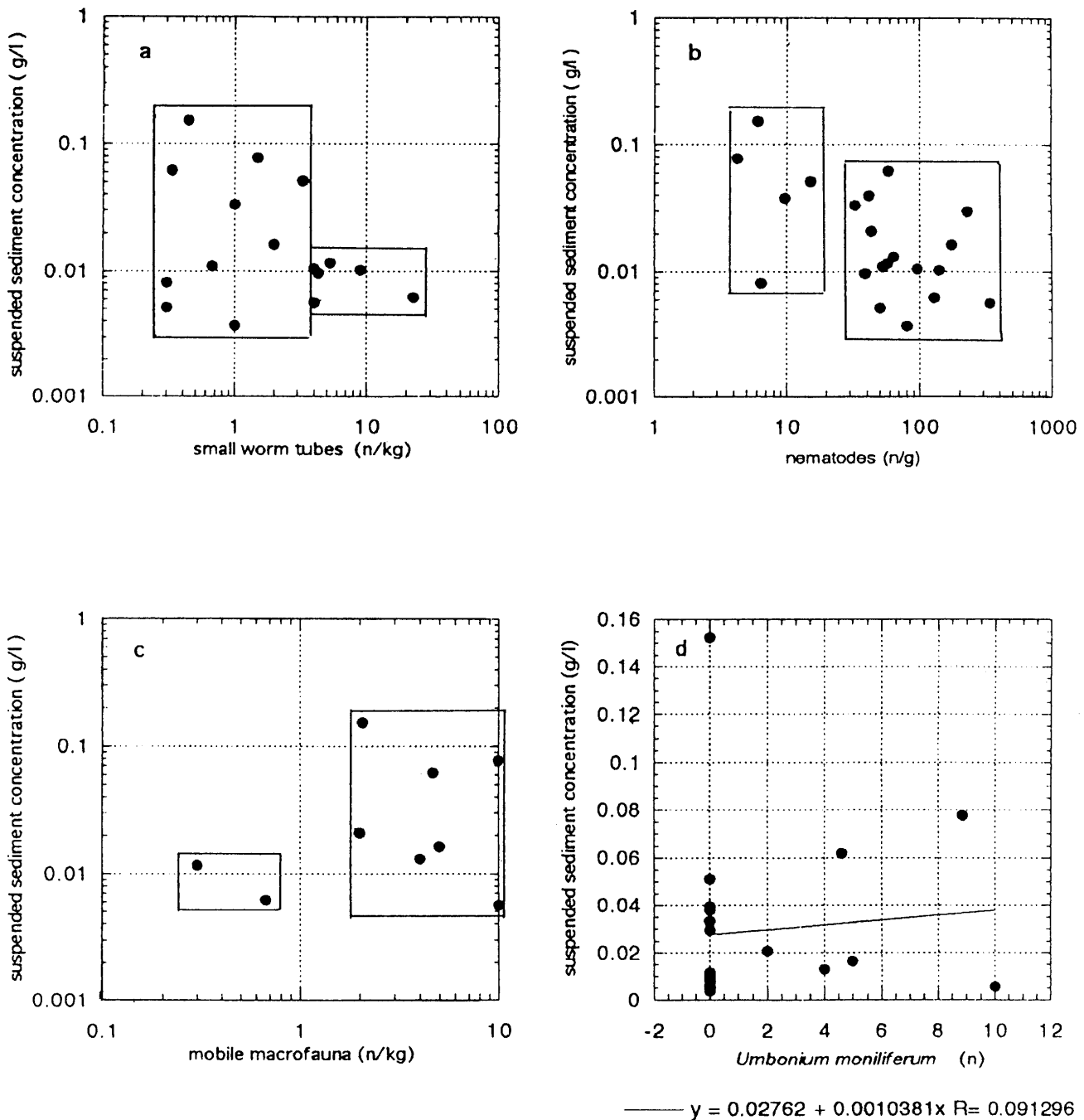


Fig. 12 SSC vs. selected taxa. Note that because of the log transform, sites with no worm tubes or no mobile fauna are not plotted. Boxes indicate possible trends in the data.

The SS grain size does not vary according to any of the measured physical variables except for water velocity ($R^2=0.612$, $p=0.107$), for which only 8 data points are available (Fig. 14 and Table 11). It should be noted, however, that our grain measurement sample size may have been too low to encounter some of the larger sediment grains, i.e., perhaps suspended sediment is always dominantly clay-sized in terms of particle abundance, but that small percentages (<5%) of sand-sized grains are

responsible for much of the SS mass. Like SSC, SS grain size too seems to be best related to the interaction of the first axes of the faunal and sedimentologic PCA analyses.

LABORATORY AQUARIUM STUDIES

The tracks and trails and other positive surface relief caused by biota undoubtedly change the critical shear velocity (BOYER 1980) and may result in

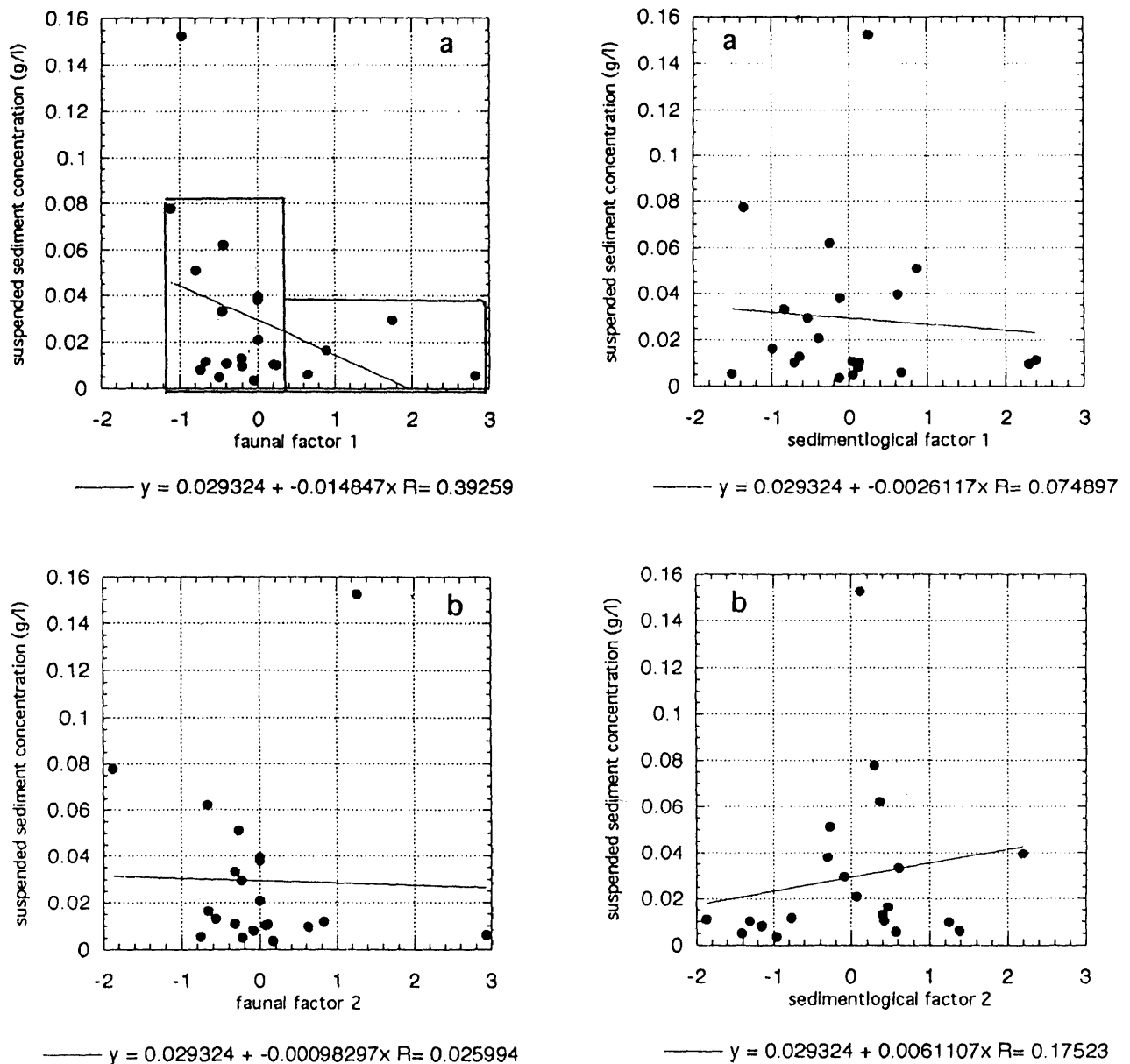


Fig. 13 SSC vs. faunal and sedimentologic PCA axes 1 and 2. Boxes in (a) indicate change in variance of SSC with magnitude of PCA axis 1.

a complicated patchwork of entrainability. Effects of biota upon Hamana-ko sediments were observed in the laboratory in order to predict more specifically the effects of macrofaunal organisms on bottom sediment. Although in the aquarium experiments we observed changes in the surface topography, known as "roughness elements" in the context of fluid dynamics, we did not record such observations in the field. To our knowledge, the surface roughness of biotic structures remains essentially unquantified (RHOADS & BOYER 1982, GRANT 1983). Determining biotically constructed roughness elements may be possible using high resolution three dimensional image analysis; temporal trends

of the biotic effects may be calculated by recording images at specific intervals and subtracting out the topography from the starting state of each corresponding interval.

Surface sediment (approximately upper 2 cm) and overlying water was recovered from Murakushi Gate at Hamana-ko and returned to the laboratory in 5-liter plastic buckets. Immediately after returning to the university this sediment was placed in aquaria and the water aerated. Most tanks were about 16×31 cm in lateral dimensions, and about 0.5 liters of sediment was required per centimeter of sediment on the bottom of the tank. The tanks were about half-filled with sediment, 7 cm of

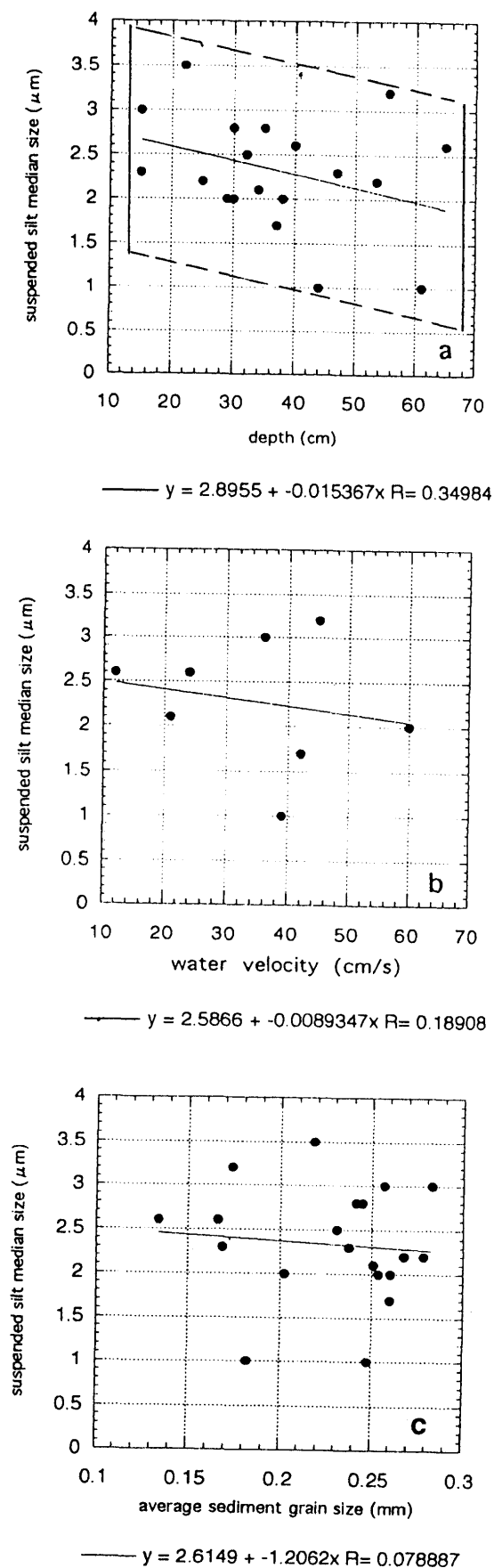


Fig. 14 SSC grain size vs. bottom sediment grain size, current velocity, and measured depth.

sediment under 7 cm of water. The tank was observed on a daily basis for biotic structures forming in the tank. The temperature of the aquarium was allowed to track that of room temperature, which was not far different from the natural water temperature of Hamana-ko in the fall. Salinity was maintained by covering the tank to prevent significant evaporation and adding distilled water to replace evaporated water. The upper surface of the sediment was more muddy than in natural conditions, because mud was the last to settle after inserting sediment into the tank and was not sorted by natural currents.

The most obvious sediment disturbance was caused by the gastropod *Umbonium moniliferum*, about 1 cm in shell height, which plow along the sediment surface, leaving a small 1-2 mm high ridge on either side of an 8 mm wide trail. The snail may rest partially buried, with the top or side of the upper whorls exposed. There are frequently tubes, partially or entirely of polychaetes, about 0.5 to 2 mm thick, either from the surface downward, or U-shaped (open at the surface at either end). The vertically-oriented tubes may be longer than 2 cm; the largest U-shaped burrow observed was about 8 mm from the surface to the "minimum" point. There were small piles of thin elongated (approximately 2 mm long, 0.4 mm wide) fecal pellets in a circle or semi-circle around some of the vertical tubes. A number of other minute trails (about 1 mm wide and less than 1 mm deep) by unidentified organisms crossed the tanks.

Crabs and shrimp were observed to disturb the sediment considerably, and in some cases to throw sediment directly into the water column. However, the population density of these taxa within the field area seems to be small compared to that of some of the less mobile fauna, and are not considered in the following discussions.

DISCUSSION

The concordant spatial variations in the faunal and sedimentologic data is hardly surprising, as sediment texture is perhaps the most frequently identified variable behind benthic community composition (e.g., NOWELL & JUMARS 1987). While this relationship may be caused by interactions between fauna and sediment, the two may also be correlated because of their mutual relationships to other spatially-varying environmental variables not measured here (e.g., wave energy).

Relationships of variables to SSC

Based on the regressions of available factors against the measured SSC, we receive the encouraging result that the best predictor of SSC is best correlated to some function of the greatest variability in the data. Though difficult to quantify,

intuitively it seems unlikely that the PCA variables would provide a much better match to SSC than individual variables unless this combination were indeed relevant to SSC.

We also find, however, that several of the faunal variables seem to constrain the level of SSC. The sites with the lowest SSC are invariably associated with high concentrations of nematodes and/or polychaete tubes, both of which have been reported in other studies to have a stabilizing effect on sediment erosion (nematodes: REIMANN & SCHRAGE 1978; polychaetes: RHOADS *et al.* 1978, but see also discussion in RHOADS & BOYER 1982). In fact, the good relationship between faunal PCA axis 1 and SSC may stem in part from the abundance of nematodes, which are both related to SSC and an important component of the first PCA faunal axis. It seems at first counterintuitive that nematodes should be stabilizers, since they might be imagined to break bonds between grains during their movement. However, intertidal nematodes frequently attach themselves to grains, using mucus secreted by the caudal and pharyngeal glands in order to adhere to sand grains (REIMANN & SCHRAGE 1978). This secretion may bind grains together if the nematode density is sufficiently high. CULLEN (1973) has published observations of nematodes changing the sedimentary fabric of muds by creating lacunae, possibly mucus-strengthened, through burrowing activities.

The mechanism for binding of sediment by polychaete tubes operates through the organic matrix of the tube walls. These walls are strong enough to come out in one piece when surface sand is mixed, as occurred during our macrofaunal sampling. Kitazato (pers. comm.) has speculated that such tubes may be especially important for stabilization where anoxia prevents rapid disintegration of the tube organics by bacteria; this may be more clearly the case for fully anoxic bottoms, e.g., during the summer in the deeper part of Hamana-ko, (OGURI 1993MS), but may play some role just below the sediment surface even at our nearshore sites where oxygen levels decrease just below the surface.

Mobile macrofauna in general, and *U. monoliferum* and meiofaunal bivalves in particular, are abundant at sites at which the most extreme SSC are found. The converse is not true: there are low SSC values at some sites with *U. monoliferum*, which is what would be expected if there were little flow, independent of any organisms' affect on critical velocity. One can explain the association of *U. monoliferum* with high SSC by their tendency to increase surface roughness of the bottom during their crawling and burrowing. It is not clear whether small bivalves, through frequent burrowing or siphoning, might lead to sediment entrainment, or whether adult bivalves, not collected because of the depth in the sediment of their life-position,

may be responsible for this.

Review of some variables not accounted for

We list several kinds of data not collected that would likely be relevant to SSC. The list is intended not merely to show alternative explanations for patterns compiled in this study, but is presented also in the context of considering the potential of future compilations of natural data in the analysis of sediment entrainment.

Agglomeration of grains: Grain agglomerations were destroyed during wet sieving. An example of agglomeration would be clay present in the samples as sand-sized pelloids that behave more like sand grains than individual clay particles. In this case, predictions based on the assumption of mud entrainment at very low flow velocities may be incorrect, and may explain why the percent mud is not better correlated with SSC. Floc formation also influences the settling velocity of entrained particles, which influences significantly the temporal trend of SSC after initial entrainment (KINEKE & STERNBERG 1989).

Organic content of the fraction of organically-coated grains, of fecal pellets, or of organic globules: Fecal pellets and organic globules may increase cohesiveness through bonding, but may themselves be more easily transported than sand because of their low densities. The organic content and coating of grains may increase cohesiveness, but just as importantly may affect the abundance of deposit feeders that further affect the surface properties.

Organic encrustation of sand grains: JOHNSON (1974) observed samples in a variety of samples off Woods Hole; several of his samples (#3 to 6) were similar in textural characteristics to those investigated from Hamana-ko; within these samples, 10 - 30% of the grains were encrusted. Such encrustations likely change erosional properties.

Quantitative estimates of sedimentary structures: Roughness elements created by animal activities presumably increase sediment entrainment, though their effects may be dwarfed by those of physically created ripples. It may be informative to test their effect by calculating, for a given area around the site, how many mounds, ripples, and other sedimentary disturbances exist.

Water content: The effect of water content is more apparent for sediments that are compactable, that is, finer cohesive sediments. The effect of subtle variations in water content, through positioning of sand grains or through position of small amounts of clays and silts with respect to sand pore spaces, is not well known.

Cyanobacterial and benthic diatom mats: Numerous authors have suggested that cyanobacterial and benthic diatom mats increase sediment

consolidation (e.g., bacteria: CORPE 1974; diatoms: HOLLAND *et al.* 1974), though only within the past two decades have there been quantitative data to back up this claim. The sort of organic substances that form on cohesive and non-cohesive sediments is generally different; those describing bacterial organic secretions (known as extracellular polymeric substances, or EPS) and stabilizers in sandy sediments include DADE *et al.* 1990 and YALLOP *et al.* 1994. Epipsammitic diatoms have also been frequently implicated in stabilizing sands (HOLLAND *et al.* 1974).

While we did count diatoms during our observation of meiofaunal content, we counted only larger diatoms that were caught in a 63 μm sieve. In addition, it is possible that the actual density of diatoms would have been found to be higher if we had used special techniques for isolating diatom assemblages (e.g., TAKAHASHI & KOIZUMI 1987).

Along with diatoms, bacteria are the most common organisms implicated with adhesive organic substances. Though bacteria are most often associated with sediments in environments with relatively little circulation and perhaps with decreased benthos that might have disturbed bacterial mats, bacterial adhesion has been found in sandy ripples in intertidal environments (BOER 1981).

Nature of the bottom flow: Bottom erosion would seem to be likely affected by the nature of the bottom flow, e.g., the degree to which the flow can be considered smooth or turbulent, or if it is subcritical (flow information and boundary layer effects transmitted downstream) or supercritical (see review by NOWELL & JUMARS 1987).

Temporo-spatially integrated erosion rates: SSC at one point in space and time may be the product of erosion over a wide area and over some period of time. In studies of SSC from a lake, it can be only grossly estimated over what area the grains have eroded and how sediment has been concentrated or diluted at the point at which the SSC sample has been taken. It is thus impossible to calculate the rate of erosion, i.e., erosion per area and per time, with any precision.

SUMMARY AND CONCLUSIONS

The sedimentary texture, benthic fauna, and suspended sediment concentrations were measured at 21 sites at 4 locations in Hamana-ko, Japan. Though demonstrating intralocality variation in all factors, nevertheless each location seems to have a subtly different sedimentary regime and faunal assemblage.

In spite of the myriad complications that may influence sediment entrainment, extremely variable suspended sediment concentrations, absence of data for such central variables as shear velocity and polysaccharide concentration, and temporo-spatially limited data sets, a pattern consistent with that of

previous studies emerges: the density of nematodes, which are believed to excrete large amounts of mucus, is inversely correlated to SSC; the density of polychaete tubes, which are also believed to stabilize sediment, is inversely correlated to SSC; the abundance of mobile epifauna, which are commonly believed to break apart mucilage-bound sediment and increase surface roughness, is positively correlated with SSC; and the density of juvenile bivalves, which through borrowing may also break apart cohesive sediment, also is positively related to SSC. The first factor of a PCA of the entire fauna provides the best correlate of all to SSC, and an interaction variable faunal PCA axis 1 x sedimentological PCA axis 1, provides the best correlate to SSC of any tried. It thus appears that a faunal signal is present in the SSC data collected. Though control of some of the individual variables, e.g., in laboratory studies, is useful for understanding their effects individually, it may be that interactive factors can be best studied using statistical techniques applied very large data sets of *in situ* data.

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