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Use of photosynthetic pigments in sediments as a tracer for sources and fates of macrophyte organic matter

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ABSTRACT: Seaweed beds often cover significant parts of intertidal and shallow subtidal soft bottoms. Field and laboratory experiments have previously demonstrated that seaweed detritus can cause rapid population and somatic growth of deposit-feeding invertebrates. We assayed the photosynthetic pigments in sediments of False Bay, Washington, USA, to identify means of detecting lateral transport of particulate organic matter (POM) from beds of green algae (*Ulva* and *Enteromorpha*). Using a transect from open waters towards the head of the bay, we tested the following hypotheses: (1) net transport moves POM throughout the whole bay, towards sand flats in the inner part of the bay; (2) seaweed beds have only local spatial effects on the input of POM. Only the second hypothesis proved consistent with the data. Calculations based on recovery of the pigment lutein indicate that the deposition of seaweed detritus is sufficient to stimulate deposit-feeder population growth. In all sediments, both principal components analysis and simple correlation analysis consistently identified 2 negatively correlated sets of photosynthetic pigments, which could be associated with diatoms and macrophytes, respectively. The multivariate inverse relationship further strengthens a combination of lutein and chlorophyll *b* as a marker for the source of macrophyte organic matter.

INTRODUCTION

Particulate organic matter (POM) derived from decomposing phytoplankton and seaweeds is of major trophic importance in marine ecosystems. Even in shallow shelf waters, benthic secondary production depends mainly on the deposition of phytoplankton debris from the surface waters (Peinert et al. 1982, Christensen & Kanneworf 1986, Rudnick & Oviatt 1986, Pfannkuche & Thiel 1987, Grebmeier & McRoy 1988). Benthos of the deep sea obviously depend upon POM derived from shallower waters, and benthic activity often increases soon after seasonal increases of deposition (Carney 1989).

In most benthic environments, bacteria are the numerically dominant microbes, but they are insufficient as a food source for deposit-feeding benthos (Wetzel 1977, Cammen 1980, Kemp 1987, Tunnicliffe & Risk 1977). Intertidal and very shallow subtidal habitats have abundant diatoms and these may be a sufficient food source for some deposit-feeding populations (Lopez & Levinton 1987, Morrisey 1987). Because many sources of shallow water POM are relatively indigestible, it was thought that microbes such as bacteria and diatoms were the dominant proximate source of deposit feeder nutrition (e.g. Newell 1965, Fenchel 1970, Hargrave 1970, Kofoed 1975, Yingst 1976, Bianchi & Levinton 1984). Even poorly digestible detritus, however, may be so abundant in some muddy sediments that a low assimilation efficiency may still yield a significant trophic return (Cammen 1980, Levinton 1980, Levinton & Stewart 1988). Seaweed detritus and diatom detritus may be far more digestible, and experimental studies show that some seaweeds can promote population growth in the benthos by direct ingestion (e.g. Tenore 1975, 1977) or by indirect subsidy of microbial production (Tenore & Hanson 1980, Levinton 1985).

Seaweed beds often cover intertidal mud and sand flats where deposit feeders are common. The green seaweed genera *Ulva* and *Enteromorpha* are the typical dominants of such beds. Both have filmy fronds, which are easily eroded by tide and wave action. In False Bay, Washington, USA, large amounts of green seaweeds accumulate in the upper intertidal and supratidal, where they decompose mainly by fermentation (Hylleberg & Henriksen 1980, Hylleberg & Riis-

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Vestergaard 1984). Eventually, in late fall and winter, the beds break up. It is not clear how these beds contribute POM to the sediments and to the benthos. The deposition of large amounts of material on the strand suggests extensive transport throughout the Bay. However macrofaunal studies suggest otherwise. Benthic abundance in False Bay is greatest in 2 areas that coincide with extensive coverage of seaweeds (pers. obs.; see also Pamatmat 1966). This would suggest a more local source-sink cycle for seaweed detrital transport.

In this report, we use photosynthetic pigments as tracers of POM, with the specific intention of asking whether the movement of seaweed detritus produces only local, or bay-wide spatial patterns of deposition in sediment of seaweed detritus. Pigments have been used successfully to identify the source plants in aquatic systems (e.g. Gorham 1960, Wright & Jeffrey 1987, Bianchi & Findlay 1990). To do this, we first identify pigments that are useful markers, and then analyze spatial data running along a transect from the bay mouth, landward to its head, with subsampling of transects from within, to outside of, 3 seaweed beds. Our evidence suggests that transport is mainly local. There is evidence for deposition near the seaweed beds, but none for accumulation in the intertidal sediments in the landward portion of the bay, except when seaweed beds occur there.

METHODS

We collected samples of sediment and algae from False Bay, located on San Juan Island, Washington, USA (Fig. 1). False Bay covers an area of ca 10^6 m^2, is an intertidal sandy flat subject to extensive sediment resuspension and transport (Miller & Sternberg 1988) and is dominated by deposit-feeding macroinvertebrates (Pamatmat 1966). Green seaweed beds are common throughout the bay, especially near the mouth and at the bay head. Hylleberg & Henriksen (1980) estimated the 1974 standing crop of *Ulva* to be 34 tons dry weight. Our sampling design includes 11 stations arrayed from the mouth to the inner portion of the bay. The sampling was stratified to include 3 short transects from within to outside of 3 algal beds. Stns 1 to 4 ('*Enteromorpha-Ulva* bed transect') range from extensive cover of *Enteromorpha* sp., some *Ulva fenestrata*, and scattered brown seaweeds (Stns 1 & 2) to bare sand with scattered pieces of *Ulva*. Stns 5 to 7 ('*Ulva* bed transect') range from bare sand, with slight coverage of *Ulva*, to a dense *Ulva* bed. Stns 10 & 11 ('*Ulva-Zostera* bed transect') include a bare sand station (Stn 10) near a sparse *Zostera marina* bed (Stn 11), which is covered extensively by *Ulva*. All stations were located on a map

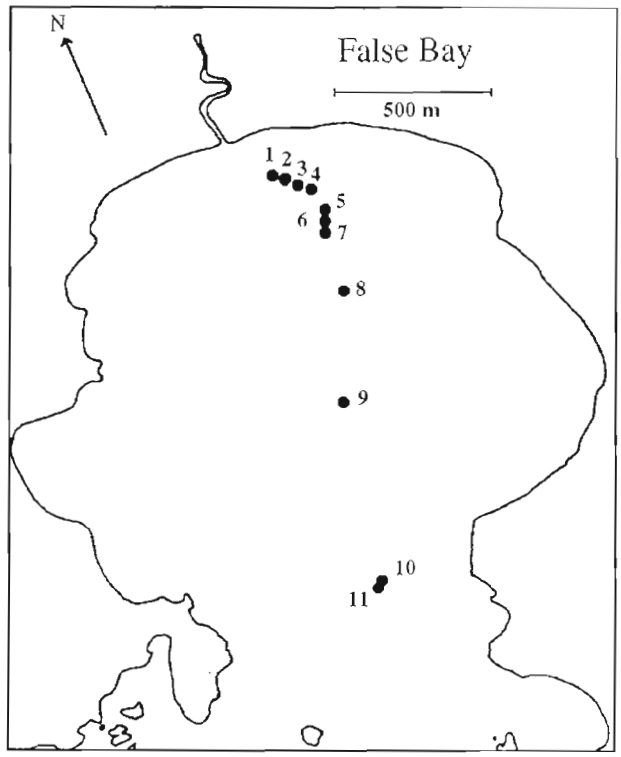

Fig. 1. False Bay, Washington, USA, showing locations of the 11 stations

by compass siting and triangulation to shore locations and to boulders located by Pamatmat (1966).

All stations were sampled for sediment particle analysis at the time of LLW on August 6, 1990. Approximately 500 ml of sediment less than ca 1 cm deep was collected for particle analysis. The sediment was washed in fresh water to dissolve salts, dried overnight at 50 °C, weighed and then sieved through 4000, 2000, 1000, 500, 250, 125, and 62.5 µm metal sieves. Fractions were separated, dried at 50 °C and weighed. The silt-clay fraction (sediment less than 62 µm) was calculated by difference.

To sample photosynthetic pigments from sediments, all stations were sampled on the same day at the time of LLW. Sampling dates were June 9, August 13, and October 18, 1989. At each station, 3 syringe mini-cores of sediment were obtained (core dimensions: 1.5 cm diameter × 1.1 cm deep = 2 cm^3 sediment volume). Cores were immediately placed on ice and transported to the Friday Harbor Laboratories, where 100% acetone was added to each sample, which then were sonicated for 5 min and placed overnight in the dark at 4 °C. Each sample was then centrifuged at 14 000 rpm in a microcentrifuge, and the supernatant fractions were removed and stored at −80 °C, for never more than 4 d. The 100% acetone extraction was determined by Bianchi et al. (1988) to be optimal in preventing

allomerization. We found the extraction efficiency to be as follows: chlorophyll *a*, 78.5% ± 0.014 SD; lutein, 73.1% ± 0.023 SD (relative to 3 successive extractions).

To analyze pigments of macrophytes, 3 individuals each of *Ulva fenestrata* (from Stn 7), *Enteromorpha* sp. (Stn 1), and *Zostera marina* (Stn 11) were obtained at random locations within each plant bed. Portions of healthy tissue of each were bagged individually, returned to the laboratory, and frozen at −80°C. Samples were then blotted dry, and wet-weighed. Plant tissue was extracted in 5 ml 100% acetone using a Polytron (Kinematica, Switzerland) homogenizer at moderate speed for 15 s. Extracts were centrifuged at 14 000 rpm in a microcentrifuge; the supernatant fractions were stored at −80°C until analysis. To roughly estimate diatom pigment content, 2 laboratory cultures of *Cylindrotheca closterium* were obtained in log-phase growth in f/2 medium and under constant light. Three 5 ml aliquots from each culture were removed and sedimented at 12 500 × *g* for 10 min at 0°C. The pellet was washed once with 10 ml 0.2 µm filtered sea water, repelleted, and resuspended in 1 ml acetone. The suspension was sonicated for 1 min, and then centrifuged to remove cell debris.

Reversed-phase ion-paired HPLC of pigments was performed on an Alltech Absorbosphere C 18 column (4.5 mm ID × 250 mm L; 5 µm packing). The mobile phase was programmed at a flow rate of 1 ml min^{-1}, using a Spectra-Physics SP8700 solvent delivery system, to obtain a linear gradient of 100% solvent A to 100% solvent B over 30 min, with a final hold for 20 min (solvent A = 80% methanol / 10% ion pairing reagent / 10% water; solvent B = 70% methanol / 30% acetone. The ion pairing reagent contained 1.5 g tetrabutyl ammonium acetate (FLUKA) and 7.5 g ammonium acetate per 100 ml distilled water).

Peaks were detected on a Spectra-Physics SP8440 variable wavelength detector set to read absorbance at 440 nm and processed using a Spectra-Physics SP4270 integrator. Peak identification was accomplished by comigration with a purified standard (U.S. Environmental Protection Agency) of all assayed pigments (obtained courtesy of T. S. Bianchi). Calibration was achieved by injection of purified chlorophyll *a* (SIGMA), and near simultaneous determination of purity using a spectrophotometer. We used Sigma chlorophyll *a* from *Anacystis nidulans* and dissolved ca 1 mg in 2 ml 100% acetone under reduced light. We injected 5 µl into the HPLC to determine retention time and detector response, and ran a scan of spectrum from 350 to 750 nm. The absorbance reading at lambda max of 662 nm was recorded. The concentration is $(A_{662} - A_{750})/E_{662}$, where A represents absorbance and E_{662} is the specific extinction coefficient (in units of A.U. (absorbance units) g^{-1} l cm^{-1}. The detector response was then determined, using the calculated concentration of chlorophyll *a*. Quantities of all other pigments were calculated using their published specific extinction coefficients (Mantoura & Llewellyn 1983), standardized to the value for chlorophyll *a*. Where necessary extinction coefficients were revised according to more recent calibration data (T Bianchi pers. comm.) and corrections were made for the wavelength differences between lambda max and the monitored wavelength (440 nm). When appropriate, total pigment composition of a sample was expressed as weight-percent of each component, calculated using integrated peak areas divided by their respective absorbance standardization factor. We were particularly concerned about the identification of the peak for lutein, because it was found to migrate close to other pigments in absorbance chromatograms. To verify this pigment we collected in August 1990 samples of macrophytes and 3 samples of sediment from 3 areas of False Bay and used a Shimadzu HPLC system (2 LC-6A pumps, an SCL-6B pump controller, SPD-6AV uv-vis detector, and a CR501 integrator) coupled with an LDC fluoroMonitor III fluorescence detector, to prepare and run samples as described above. The material corresponding to the lutein peak could not be detected with fluorescence, further confirming its identification as lutein.

The identity of lutein was further confirmed with the following method, adapted from Wright & Shearer (1984). This involved the use of the Shimadzu HPLC described above, using a linear gradient from initial conditions of 90% acetonitrile : 10% water to final conditions of 100% ethyl acetate, over 20 min with a flow rate of 2 ml min^{-1}. Initial conditions were then restored over 5 min, and the system was allowed to equilibrate for 5 min prior to the injection of the next sample. The identify of lutein was further confirmed by collecting the peak found to migrate at ca 7.4 min retention time and the absorbance spectrum was obtained. Absorbance maxima were found at 422, 447, and 472 nm, with a shoulder at 422 nm. These maxima agree closely with the values reported by Wright & Shearer for the pigment lutein. In no case did any of our extracts show evidence of more than 5% area of a component migrating very close to lutein, as does the carotenoid pigment zeaxanthin in certain phytoplankton extracts (Wright & Shearer 1984). These results apply to samples run of *Ulva*, *Zostera*, *Enteromorpha* and 3 sediment samples.

We attempted to estimate the amount of algae present as inventory in the sediment by calculating wet weight biomass using laboratory-established relationships between lutein (or chlorophyll *b*) and algae from which the pigments were extracted. Since this estimate incorporates both sampling error in the recovery of

pigment from the sediment and error in the calculated yield of pigment from plant tissue, we computed its standard deviation as follows:

$$S_{X/Y} = \frac{\overline{X}}{\overline{Y}} \sqrt{\frac{S_X^2}{\overline{X}^2} + \frac{S_Y^2}{\overline{Y}^2}}$$

where $S_{X/Y}$ = standard deviation of estimate of inventory (g algae m^{-2}); $\overline{X}$ = mean pigment recovery from sediment (µg m^{-2}); S_X = variance in sediment pigment recovery; $\overline{Y}$ = mean pigment yield from algae (µg g^{-1} tissue); S_Y = variance in pigment recovery from plants.

For comparison to previous studies, we determined ratios of dry weight to wet weight, for 5 samples each of the 3 macrophytes. The ratio of dry weight to wet weight was (± SE): *Ulva fenestrata*, 0.232 ± 0.009; *Enteromorpha* sp., 0.284 ± 0.005; *Zostera marina*, 0.172 ± 0.016. Benthic diatoms were counted for a limited number of stations. Methods were modified after Levinton & Bianchi (1981). We used 10 replicates for each station, and counted 20 grids per replicate.

The relative abundance of macroalgae in the 3 beds was crudely estimated by a combination of video transects and field measurement of the size of the beds. Video transects were conducted and a random number table was used to establish a matrix of 25 sampling points, from which algal coverage was estimated. The size of the 3 beds was estimated by staking corners and measuring compass directions and distances using a measuring tape.

Statistical analyses were performed using SYSTAT (SYSTAT Corporation, Evanston, Illinois, USA).

RESULTS

Fig. 2 shows pigment profiles for *Ulva fenestrata*, *Enteromorpha* sp., *Zostera marina*, and the diatom *Cylindrotheca closterium*. Several qualitative patterns are obvious. A few pigments are diatom-specific (in our study, but not universally) relative to the macroalgae and *Zostera*, including chlorophyll *c*, fucoxanthin, and violaxanthin. The macroalgae and *Zostera* all contain chlorophyll *b* and lutein, which are absent in diatoms. Simple patterns in lutein or chlorophyll *b* might therefore test for spatial patterns in macrophyte-derived

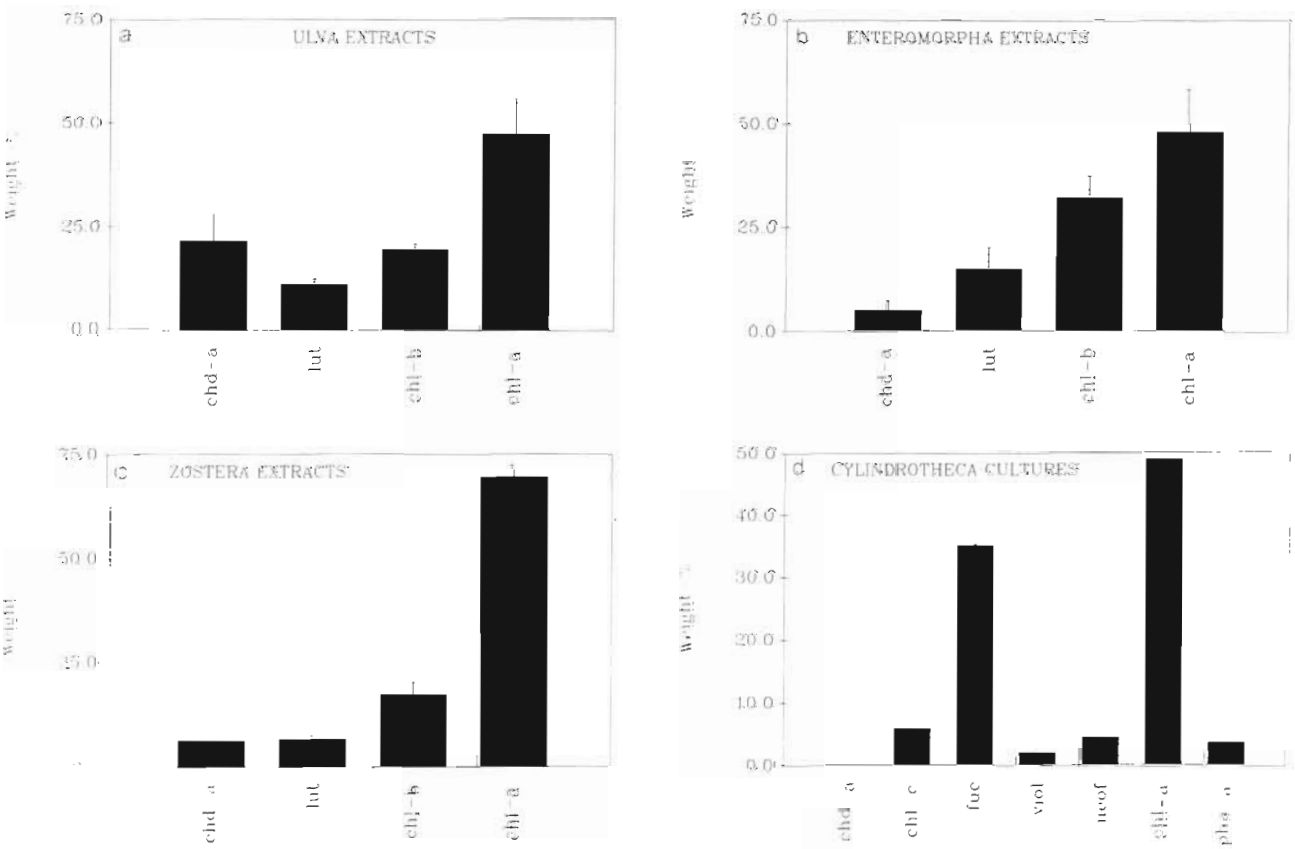

Fig. 2. Pigment profiles of fresh (a) *Ulva fenestrata*, (b) *Enteromorpha* sp., (c) *Zostera marina*, and (d) *Cylindrotheca closterium*. chd-a: chlorophyllide *a*; lut: lutein; chl-a: chlorophyll *a*; chl-b: chlorophyll *b*; chl-c: chlorophyll *c*; fuc: fucoxanthin; viol: violaxanthin; neof: neofucoxanthin; pha-a: phaeophytin *a*

POM deposition relative to the seaweed beds and the overall transect.

Table 1 gives the particle size distribution for the sediments. Most are fine to medium sands with modal particle sizes in the 125 and 250 μm classes. The only strikingly different stations are 1 and 7, which are the centers of the *Enteromorpha* and *Ulva* beds, respectively. These sites are rich in gravel, which may be good attachment sites for the algae. Stn 11 is rich in *Ulva*, which is not related to sediment particle size, but rather to attachment sites on eel grass.

There were distinct differences in the areal coverage of the 3 beds and in the relative algal coverage. The areas were as follows: *Enteromorpha-Ulva* bed, 3250 m^2; *Ulva* bed, 890 m^2; *Ulva-Zostera* bed, 4440 m^2. The relative densities were: *Enteromorpha-Ulva*, 12.65 ± 3.84 (SD, n = 20); *Ulva*, 8.15 ± 2.28; *Ulva-Zostera*, 11.40 ± 5.83. A 1-way ANOVA shows significant differences in algal coverage among beds ($F = 6.008$, $p = 0.004$). An a posteriori test shows that this is explained by a significantly lower coverage in the *Ulva* bed, while the *Enteromorpha-Ulva* and *Ulva-Zostera* beds are indistinguishable in their higher coverage.

Fig. 3 shows the distribution of lutein for the 3 dates, in 3 transects from seaweed beds to bare sands, with a bare sand station (no. 8) used for comparison as a background sample. This background station was hundreds of meters from any of the seaweed beds. There is a striking similarity in all 3 transects. Lutein concentration diminishes with distance from the bed. The drop is gradual in the *Enteromorpha* bed, but precipitous (reaches close to background levels 25 m away) in the *Ulva* and *Enteromorpha* beds. The more gradual decrease from the *Ulva-Enteromorpha* bed may relate to the bed's large size and to the relatively quiet waters at the head of the bay. There is a slight complication in the *Enteromorpha* bed transect, since *Ulva* colonized and spread near to the 77 m station by August, which may have reduced the gradient in lutein concentration. Although the *Ulva-Zostera* bed was the largest of the 3 examined, it is at the mouth of the bay, where water movement is stronger, perhaps making deposition adjacent to the bed very local, or absent.

Average lutein concentrations for each of the 11 stations are illustrated in Fig. 4. A 2-way ANOVA shows significant heterogeneity for both station differences ($F = 9.118$, $p < 0.001$) and sampling time ($F = 15.735$, $p < 0.001$). There is no monotonic trend from the mouth to the head of the bay. Lutein does seem to accumulate in the sediments from August to October in the inner bay Stns 1 to 4. These comprise the *Enteromorpha* bed transect, and more lutein seems to accumulate in the sediments within the bed. In the *Ulva* and in the *Ulva-Zostera* transects, lutein accumulates from June to August, but then there is a modest drop between August and October. Stns 5, 8 & 9 are most distant from seaweed beds and show no temporal or spatial evidence for large scale lutein accumulation.

Table 2 shows a Pearson product-moment correlation matrix for sediment pigment concentrations assayed in June, August, and October, over all 11 stations (the original data set, consisting of 3 replicates for 7 pigments over 11 stations, is available on request by mail). Inspection for correlations is tricky statistically, since one inevitably discovers significant correlations when many coefficients are examined. However a Bartlett's analysis of all 3 matrices shows an extremely low probability ($<<0.001$) that the correlation matrices are random. In all 3 months there is a striking negative correlation between lutein and chlorophyll *b*, and the other pigments. The negative correlations for lutein are the most striking; there are 11 (of 15 possible) negative correlations, all of which are associated with pigments probably derived from diatoms (see Fig. 2). Even though not all of the correlation coefficients are significant at the $p < 0.05$ level, the overall pattern is probably nonrandom (e.g. probability of getting 5 negative cor-

Table 1. Percent (by weight) in the sediment of particle size classes

Station	> 4000 μm	> 2000 μm	> 1000 μm	> 500 μm	> 250 μm	> 125 μm	> 62 μm	< 62 μm
1	14.66	11.48	5.68	12.95	22.71	8.30	13.68	10.55
2	0.80	1.68	2.72	6.25	23.16	29.00	21.80	14.60
3	0.00	0.00	0.00	3.58	54.24	13.70	23.66	4.82
4	0.00	0.00	0.00	0.07	16.92	43.06	26.42	13.53
5	0.00	0.00	0.08	0.56	36.34	36.86	19.76	6.40
6	0.00	0.00	0.10	0.96	13.10	64.84	15.18	5.82
7	16.96	6.82	3.52	11.52	20.77	17.48	17.28	5.65
8	0.00	0.02	0.00	1.48	36.50	37.32	21.14	3.54
9	0.00	0.00	0.00	3.42	21.46	56.48	16.68	1.96
10	0.00	0.00	0.02	2.88	58.40	29.81	1.76	7.13
11	0.00	0.00	0.02	0.76	71.74	23.47	0.58	3.43

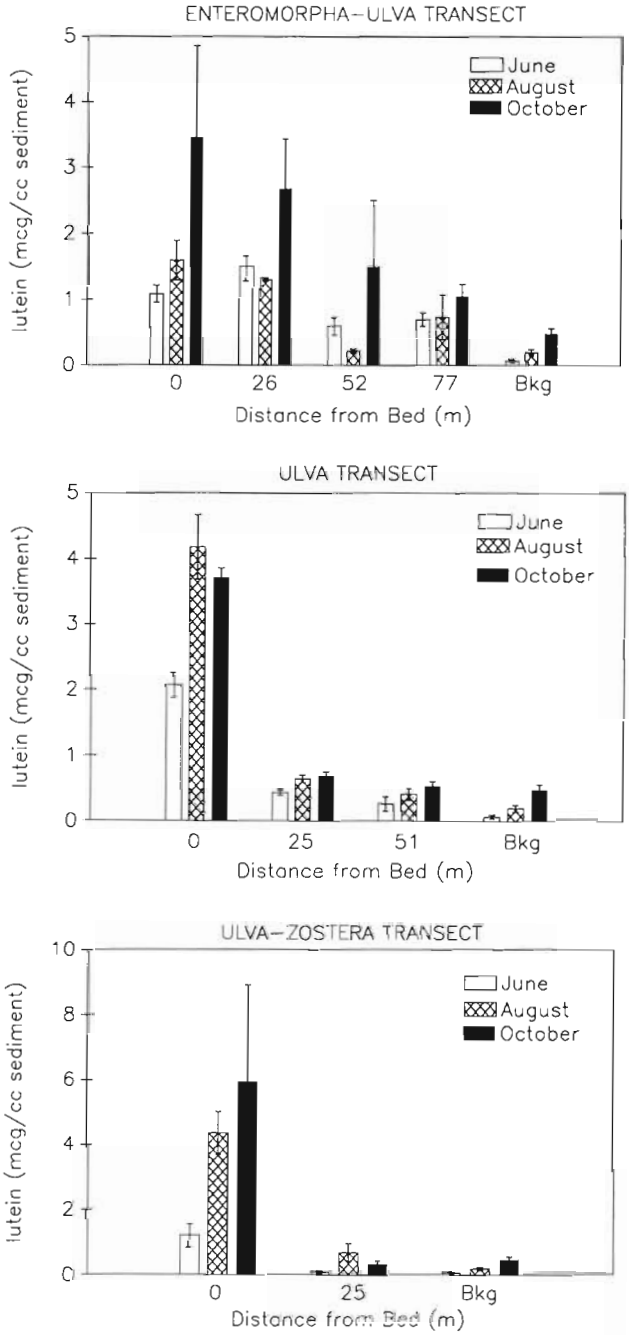

Fig. 3. Average lutein concentrations in the sediment in the 3 seaweed bed transects, for the 3 sampling dates

relations in one monthly sampling is 0.5^4 or 0.06). The negative relationship is also conspicuous for chlorophyll *b*.

Pigment concentration data were also subjected to principal component analysis. In the June, August, and October samplings, 2 components explained, respectively, 87.7, 83,8, and 71.0 % of the total variance. In all 3 cases, the loadings on the 2 components (Table 3) show evidence for one diatom-related axis and another

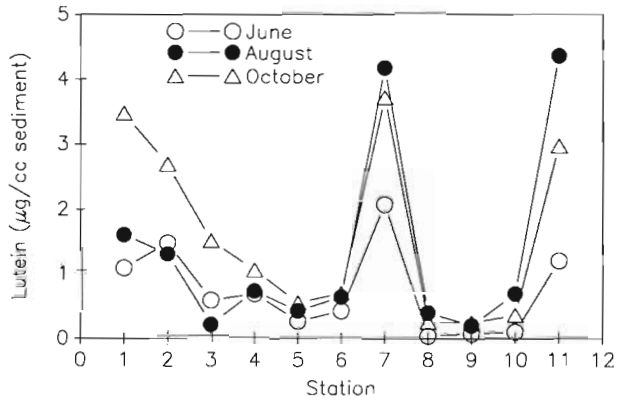

Fig. 4. Average lutein concentrations in sediments from the 11 stations, arranged from bay mouth (Stn 11) to bay head (Stn 1).

seaweed-eelgrass-related principal component axis. Principal component plots generally show stations scattered or arrayed along a line with the greatest variation along the seaweed-eelgrass-related axis.

Given pigment concentrations, it is possible to make a crude estimate of algal deposition (Table 4). Knowing the relationship of pigments to algal biomass, we present the wet weight algal biomass corresponding to the pigment concentrations found in the sediment. This can only be converted to deposition if we assume that all pigment degraded from the previous season, and none degraded during our sampling. The latter clearly is not true, so we are probably giving a minimum estimate of deposition in the 1989 season, corresponding directly to the inventory of pigment in the sediment. Unfortunately, the standard deviations are quite high, since they are calculated both from variation among the sediment samples and among the macrophyte samples assayed for pigment content. In stations remote from seaweed beds (8 & 9), loadings based upon lutein are relatively low. Within seaweed beds (Stns 1, 7 & 11), however, the values are far higher, ranging from 37 to 643 g m^{-2}. Overall, calculations based upon chlorophyll *b* yield much lower estimates of biomass.

Diatom abundances for the *Ulva* bed and *Ulva-Zostera* bed transects are illustrated in Fig. 5. In both cases, diatom standing stock is greater outside the bed on bare sands.

DISCUSSION

Overall, sediment surveys suggest a pigment profile that reflects a diatom fingerprint. This is not surprising, since benthic diatoms are very abundant at all sites. However, the distribution of seaweed- and seagrass-derived pigments are superimposed clearly upon the diatom background. Green seaweeds form discrete beds in False Bay. If pigments mark particulate trans-

Table 2. Pearson product-moment correlations (lower left), and probabilities of significance (upper right) for pigment concentration data for the 3 sampling periods (ns: not significant; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

June data	Chlpd *a*	Chl *c*	Fucox.	Viola.	Lutein	Chl *b*	Chl *a*
Chlorophyllide *a*	–	***	***	***	ns	ns	***
Chlorophyll *c*	0.932	–	***	***	*	ns	***
Fucoxanthin	0.943	0.993	–	***	*	ns	***
Violaxanthin	0.924	0.965	0.964	–	ns	ns	***
Lutein	−0.296	−0.426	−0.396	−0.276	–	**	*
Chlorophyll *b*	−0.012	−0.098	−0.076	−0.108	0.475	–	ns
Chlorophyll *a*	0.727	0.859	0.851	0.78	−0.394	0.133	–
August data	Chlpd *a*	Chl *c*	Fucox.	Viola.	Lutein	Chl *b*	Chl *a*
Chlorophyllide *a*	–	***	***	***	ns	ns	**
Chlorophyll *c*	0.798	–	***	***	ns	ns	***
Fucoxanthin	0.861	0.97	–	***	ns	ns	***
Violaxanthin	0.785	0.0836	0.886	–	ns	ns	***
Lutein	−0.127	−0.281	−0.234	0.038	–	***	ns
Chlorophyll *b*	−0.056	−0.198	−0.236	−0.167	0.686	–	ns
Chlorophyll *a*	0.47	0.827	0.758	0.613	−0.317	−0.099	–
October data	Chlpd *a*	Chl *c*	Fucox.	Viola.	Lutein	Chl *b*	Chl *a*
Chlorophyllide *a*	–	***	***	***	ns	ns	ns
Chlorophyll *c*	0.96	–	***	***	*	ns	ns
Fucoxanthin	0.971	0.986	–	***	ns	ns	ns
Violaxanthin	0.871	0.861	0.868	–	ns	ns	ns
Lutein	−0.19	−0.352	−0.283	−0.091	–	***	ns
Chlorophyll *b*	−0.083	−0.193	−0.135	0.052	0.652	–	ns
Chlorophyll *a*	0.192	0.319	0.336	0.294	−0.073	0.319	–

Table 3. Principal component statistical loadings by the various pigment concentrations on principal component axes I and II, for the 3 sampling periods

	Sampling time					
	June		August		October	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Chlorophyllide *a*	0.936	0.131	0.847	0.218	0.959	0.064
Chlorophyll *c*	0.995	0.022	0.977	0.048	0.991	−0.039
Fucoxanthin	0.992	0.053	0.986	0.071	0.988	0.029
Violaxanthin	0.958	0.083	0.886	0.256	0.902	0.221
Lutein	−0.466	0.711	−0.315	0.878	−0.345	0.771
Chlorophyll *b*	−0.104	0.904	−0.282	0.850	−0.157	0.927
Chlorophyll *a*	0.876	0.169	0.806	−0.015	0.362	0.444

port, our data suggest that deposition of seaweed detritus is localized to within and near the edges of the beds. The remainder is either dispersed evenly throughout the bay, leaves the bay, or accumulates and decomposes on the shoreline. In summer, large amounts of material rot on the shoreline on all quiet margins of False Bay. Our overall transect, however, suggests that there is no net shoreward deposition in sediments towards the head of the bay, as opposed to the mouth. The overall pattern is localized deposition, combined with washup of material in the supratidal zone.

Photosynthetic pigments would not be expected to be persistent or conservative markers, since they degrade upon herbivore grazing (Shuman & Lorenzen 1975, Hawkins et al. 1986, Bianchi et al. 1988), microbial degradation (Bianchi et al. 1988), and probably through abiotic chemical processes as well. Lutein seems to be relatively stable (Bianchi & Findlay 1991, Bianchi et al. 1991, Repeta & Gagosian 1987), and may be a good marker for movement of macroalgae and seagrasses. Like lutein, chlorophyll *b* is associated with the green macrophytes. Our data do not show chlorophyll *b* to have as strong a negative correlation with

Table 4. Estimate of dry plant biomass in sediment (g m^{-2}), corresponding to estimates derived from lutein and chlorophyll *b* concentrations. For *Enteromorpha-Ulva* transect (Stns 1 to 4): calculations use pigment-biomass relationships for *Enteromorpha*; for *Ulva* transect (Stns 5 to 7): data derived from *Ulva*; for *Ulva-Zostera* transect (Stns 10 & 11): calculations based upon Ulva; for Stns 8 & 9: calculations based on relationships for *Ulva*. Standard deviation in parentheses

Stn	Pigment					
	Lutein			Chlorophyll *b*		
	June	August	October	June	August	October
1	68.3 (31.8)	100.7 (56.0)	218.0 (175.7)	25.6 (24.1)	21.4 (22.6)	36.7 (42.0)
2	92.8 (43.4)	82.2 (34.2)	169.0 (107.7)	31.0 (29.4)	17.6 (14.1)	13.9 (11.7)
3	37.3 (22.0)	14.1 (6.6)	94.93 (115.4)	0	6.3 (5.1)	46.2 (66.5)
4	43.8 (21.0)	46.2 (41.2)	66.5 (33.7)	0	4.7 (3.8)	9.1 (7.7)
5	40.1 (28.5)	63.4 (22.4)	81.5 (16.7)	0	14.6 (2.8)	12.7 (9.1)
6	63.4 (10.3)	95.2 (17.4)	103.8 (16 8)	6.2 (4.6)	20.9 (7.7)	15.4 (11.6)
7	306.0 (51.5)	616.0 (130.4)	548.4 (49.4)	42.0 (7.0)	46.6 (21.4)	52.9 (15.5)
8	6.1 (6.1)	59.1 (13.9)	37.6 (10.9)	60.7 (39.4)	6.8 (0.9)	10.5 (3.2)
9	11.0 (6.5)	29.8 (13.6)	36.2 (10.5)	0	0	0
10	15.1 (11.6)	102.7 (68.7)	53.6 (19.9)	0	0	0
11	177.3 (89.7)	643.0 (173.6)	438.49 (116.0)	0	157.0 (127.7)	10.3 (5.7)

diatom-related pigments as does lutein, and this may reflect degradation. Relative to fresh seaweeds, the recovery of chlorophyll *b* from the sediment is less than that for lutein.

Multivariate analysis of pigment concentrations among the sampling sites demonstrates that the macrophyte markers lutein and chlorophyll *b* load heavily on one principal component, whereas all other pigments but chlorophyll *a* load heavily on the other. This further strengthens the value of the 2 markers, since they do not covary with the diatom-related pigments, which might be predicted from the diatom count data.

These data provide the first evidence for intermediate scale localization of transport of POM on sand flats. Because of this localization, and because of the relatively simple means we have developed to track it, the possibility arises of testing the hypothesis that degraded seaweed detritus is of trophic importance to somatic growth and population size of deposit feeders. Laboratory evidence strongly suggests that detritus

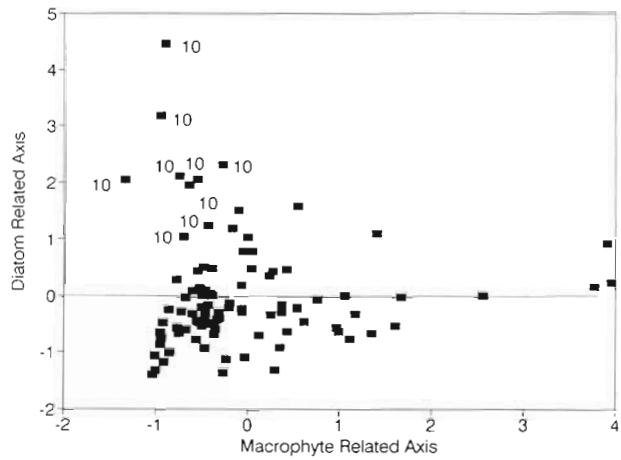

Fig. 5. Diatom standing stocks for stations of the *Ulva* transect and the *Ulva-Zostera* transect, taken on August 26 & 27, 1989

derived from labile seaweeds provide a strong subsidy for deposit-feeder growth, especially for annelids (Tenore 1975, 1977, Levinton 1985). Field and laboratory studies both show a subsidy of diatom production, which also is consumed by deposit feeders (Levinton 1985). But there is no evidence for such a subsidy in False Bay. Diatoms and diatom-related pigments are in fact less abundant in the seaweed beds, which probably relates to shading by seaweeds or seagrasses. Our data do not prove, however, that diatoms are unimportant, nor do we wish to imply that sedimenting planktonic diatoms are unimportant in False Bay.

While crude and laden with statistical variation, the estimates of pigment inventory-derived detritus in sediment near seaweed beds are very high, typically above 50 to 100 g m^{-2} (Table 4). These estimates, however, are based upon the standing inventory of lutein and chlorophyll *b* in the sediment. We have no data to demonstrate that all lutein from the previous season was degraded, so it is not clear that these estimates refer to accumulations only in the spring of 1989. Furthermore, degradation of lutein obviously makes this an underestimate of deposition. Previous field and laboratory experiments (Levinton 1985, Levinton & Stewart 1988, Levinton unpubl.) demonstrated that 25 to 50 g m^{-2} of *Ulva* dry weight deposition is sufficient to stimulate rapid population growth of the deposit-feeding oligochaete *Paranais litoralis*. The estimated inventory therefore may be of great nutritional importance to (at least) population growth of smaller deposit feeders (e.g. spionid polychaetes) and perhaps somatic growth of larger deposit feeders in False Bay. The methods used in these studies can now be used to design experiments in spatial gradients of seaweed detrital transport.

Overall patterns in False Bay suggest at least a tantalizing correlation between benthic biomass and sea-

weed abundance. Benthic surveys in False Bay (Pamatmat 1969, pers. obs.) show a peak of abundance at the *Ulva-Zostera* bed and at the head of the bay, in the vicinity of the *Enteromorpha-Ulva* bed and other green seaweed beds. It is possible that POM contributes to this abundance. *Ulva* accumulations can degrade conditions for benthos when decomposition consumes oxygen and renders the sediment anoxic (Thom & Albright 1990), but this does not seem to be the case in False Bay. Hylleberg & Riss-Vestergaard (1984) estimated that 1 to 10% of False Bay's green seaweed October biomass is consumed by the polychaete *Nereis brandti* alone. While several macroinvertebrates seem to be poor at digesting *Ulva* detritus, amphipods feed actively on *Ulva* particles and may consume up to half of the annual net production. It is possible, however, that other factors independently cause increases of both green seaweeds and benthos, so only field experiments can verify the hypothesis of seaweed detrital subsidy of benthic production.

Our method provides a useful framework within which field experiments on detritus deposition can be designed. Since the marker lutein can be used approximately as a spatial indicator of the deposition of macroalgal detritus, it is possible to design field experiments of detrital addition in sediments that are strongly influenced and beyond the reach of macroalgal deposition.

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LITERATURE CITED

Bianchi, T. S., Dawson, R., Sawangwong, P. (1988). The effects of macrobenthic deposit-feeding on the degradation of chloropigments in sandy sediments. J. exp. mar. Biol. Ecol. 122: 243–255

Bianchi, T S., Findlay, S. (1990). Plant pigments as tracers of emergent and submergent macrophytes from the Hudson River. Can. J. Fish. Aquat. Sci. 47: 492–494

Bianchi, T S., Findlay, S. (1991). Decomposition of Hudson River macrophytes: photosynthetic pigment transformations and decay constants. Estuaries 14: 65–73

Bianchi, T S., Findlay, S., Dibb, J. E. (1991). Early diagenesis of plant pigments in Hudson River sediments. Geochim. Cosmochim. Acta (in press)

Bianchi, T S., Levinton, J. S. (1984). The importance of microalgae, bacteria and particulate organic matter in the somatic growth of *Hydrobia totteni* J. mar. Res. 42: 431–443

Cammen, L. M. (1980). The significance of microbial carbon in the nutrition of the deposit feeding polychaete *Nereis succinea*. Mar Biol. 61. 9–20

Carney, R. S. (1989). Examining relationships between organic carbon flux and deep-sea deposit feeding. In: Lopez, G. R., Taghon, G. L., Levinton, J. S. (eds.) The ecology of marine deposit feeders. Springer-Verlag, Berlin, p. 24–58

Christensen, H., Kanneworf, E. (1985). Sedimenting phytoplankton as a major food source for suspension and deposit feeders in the Oresund. Ophelia 24: 223–244

Christensen, H., Kanneworf, E. (1986). Sedimentation of phytoplankton during a spring bloom in the Oresund. Ophelia 26: 109–122

Fenchel, T (1970). Studies on the decomposition of organic detritus from the turtle grass *Thalassia testudinum*. Limnol. Oceanogr. 15: 14–20

Gorham, E. (1960). Chlorophyll deriviatives in surface muds from the English lakes. Limnol. Oceanogr. 5: 29–33

Grebmeier, J. M., McRoy, C. P. (1988). Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Sea. I. Food supply and benthic biomass. Mar Ecol. Prog. Ser 48: 57–67

Hargrave, B. T (1970). The utilization of benthic microflora by *Hyalella azteca*. J. Anim. Ecol. 39: 427–437

Hylleberg, J., Riis-Vestergaard, H. (1984). Marine environments; the fate of detritus. Akademisk Forlag, Copenhagen

Hylleberg, J., Henriksen, K. (1980). The central role of bioturbation in sediment mineralization and element re-cycling. Ophelia 1 (Suppl.): 1–16

Kemp, P. F. (1987). Potential impact on bacteria of grazing by a macrofaunal deposit-feeder, and the fate of bacterial production. Mar. Ecol. Prog. Ser 36: 151–161

Kofoed, L. H. (1975). The feeding biology of *Hydrobia ventrosa* Montagu. I. The assimilation of different components of the food. J. exp. mar. Biol. Ecol. 19: 233–241

Levinton, J. S. (1985). Complex interactions of a deposit feeder with its resources: roles of density, a competitor, and detrital addition in the growth and survival of the mudsnail *Hydrobia totteni*. Mar. Ecol. Prog. Ser. 22: 31–40

Levinton, J. S. (1980). Particle feeding by deposit feeders: models, data, and a prospectus. In: Tenore, K. R., Coull, B. C. (eds.) Marine benthic dynamics. University of South Carolina, Columbia, p. 423–429

Levinton, J. S., Bianchi, T S. (1981). Nutrition and food limitation of deposit feeders. I. The role of microbes in the growth of mud snails (Hydrobiidae). J. mar. Res. 39: 531–545

Levinton, J. S., Stewart, S. M. (1988). The effects of sediment organics, detrital input, and temperature on demography, production, and body size of a deposit feeder. Mar. Ecol. Prog. Ser. 49: 259–266

Lopez, G. R., Levinton, J. S. (1987). Ecology of deposit-feeding animals in marine sediments. Q. Rev. Biol. 62: 235–260

Mantoura, R. F. C., Llewellyn, C. A. (1983). The rapid determination of algal chlorophyll and carotenoid pigments and their breakdown products in natural waters by reverse-phase high-performance liquid chromatography. Anal. Chim. Acta 151: 297–314

Miller, D. C., Sternberg, R. W. (1988). Field measurements of the fluid and sediment-dynamic environment of a benthic deposit feeder. J. mar. Res. 46: 771–796

Morrisey, D. J. (1987). Effect of population density and presence of a potential competitor on the growth rate of the

mud snail *Hydrobia ulvae* (Pennant). J. exp. mar. Biol. Ecol. 108: 275–295

Newell, R. C. (1965). The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. Proc. zool. Soc. Lond. 144: 25–46

Pamatmat, M. M. (1966). The ecology and metabolism of a benthic community on an intertidal sandflat (False Bay, San Juan Island, Washington). Ph. D. thesis, University of Washington

Peinert, R., Savre, A., Stegman, P., Stienen, C., Haardt, H., Smetacek, V (1982). Dynamics of primary production and sedimentation in a coastal ecosystem . Neth. J. Sea Res. 16: 276–289

Pfankuche, O., Thiel, H. (1987). Meiobenthic stocks and benthic activity on the NE-Svalbard Shelf and in the Nansen Basin. Polar Biol. 7: 253–266

Repeta, D., Gagosian, R. B. (1987). Carotenoid transformations in coastal marine waters. Nature, Lond. 295: 51–54

Rudnick, D. T., Oviatt, C. A. (1986). Seasonal lags between organic carbon deposition and mineralization in marine sediments. J. mar. Res. 44: 815–837

Shuman, F. R., Lorenzen, C. J (1975). Quantitative degradation of chlorophyll by a marine herbivore. Limnol. Oceanogr 20: 580–586

Tenore, K. R. (1975). Detrital utilization by the polychaete *Capitella capitata*. J. mar Res. 33: 261–274

Tenore, K. R. (1977). Growth of *Capitella capitata* cultured on various levels of detritus derived from different sources. Limnol. Oceanogr 22: 936–941

Tenore, K. R., Hanson, R. B. (1980). Availability of different detritus with aging to a polychaete macroconsumer, *Capitata capitata*. Limnol. Oceanogr 25: 553–558

Thom, R. M., Albright, R. G. (1990). Dynamics of benthic vegetation standing-stock, irradiance, and water properties in central Puget Sound. Mar. Biol. 104: 129–141

Tunnicliffe, V., Risk, M. J. (1977). Relationships between the bivalve *Macoma balthica* and bacteria in intertidal sediments: Minas Basin, Bay of Fundy. J. mar. Res. 35: 499–507

Wetzel, R. L. (1977). Carbon resources of a benthic salt marsh invertebrate *Nassarius obsoletus* (Mollusca: Nassariidae). In: Wiley, M. (ed.) Estuarine processes, Vol. 2. Academic Press, New York, p. 293–308

Wright, S. W., Jeffrey, S. W (1987). Fucoxanthic pigment markers of marine phytoplankton analyzed by HPLC and HPTLC. Mar Ecol. Prog. Ser 38: 259–66

Wright, S. W., Shearer, J. D. (1984). Rapid extraction and high-performance liquid chromatography of chlorophylls and carotenoids from marine phytoplankton. J. Chromat. 294: 281–295

Yingst, J. Y (1976). The utilization of organic matter in shallow marine sediments by an epibenthic deposit-feeding holothurian. J. exp. mar Biol. Ecol. 23: 55–69

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