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Bio-dependent bed parameters as a proxy tool for sediment stability in mixed habitat intertidal areas

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Abstract

The stability of cohesive and non-cohesive sediments in a mixed intertidal habitat within the Ria Formosa tidal lagoon, Portugal, was examined during two field campaigns as part of the EU F-ECTS project. The cohesive strength meter Mk III was used to determine critical erosion shear stress (τ_c) within a variety of different intertidal habitats and substrata, including *Spartina maritima* fields and *Zostera noltii* beds. The best predictor(s) for τ_c were derived from a range of properties measured for the surface sediments (chlorophyll *a*, colloidal carbohydrate, water, organic content, % fraction < 63 μm , and seabed elevation). Pigment biomarkers were used to identify the dominant algal groups within the surface phytobenthic assemblage.

Strong, seasonally dependent relationships were found between τ_c and habitat type, chl *a*, colloidal carbohydrate and bed elevation. Typically, critical erosion thresholds decreased seawards, reflecting a change from biostabilisation by cyanobacteria in the upper intertidal areas, to biostabilisation by diatoms on the bare substrata of the channel edges. In the late summer/early autumn, cyanobacteria were the main sediment stabilisers, and colloidal carbohydrate was the best bio-dependent predictor of τ_c across the entire field area. In the late winter/early spring, cyanobacterial activity was lower, and sediment stabilisation by *Enteromorpha clathrata* was important; the best predictor of τ_c was bed elevation. The implications and use of proxies for sediment stability are discussed in terms of feedback and sedimentation processes operating across the intertidal area.

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1. Introduction

Intertidal sediment stability depends upon the physical and biological properties of the surface

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sediments (Mehta, 1993; Black, 1997; Paterson, 1997; Paterson et al., 2000; Whitehouse et al., 2000; Andersen, 2001; de Deckere et al., 2001), the effects of waves and tidal currents during immersion (Grant et al., 1997; Allen and Duffy, 1998) and climatic conditions during exposure (Amos et al., 1988; Paterson et al., 1990). On intertidal sand and mudflats, modelling and field observations point to the existence of feedback mechanisms

which operate between the microalgae that colonise the substrata, and the sediments that are transported in suspension in the water column. For example, it is suggested that bio-mediated accumulation of mud on the intertidal flat helps to ‘protect’ benthic microalgae from erosion by waves and tidal currents (Van de Koppel et al., 2001; Herman et al., 2001). On sandflats it has been proposed that an increase in the surface mud content associated with benthic microalgal populations is a precursor for saltmarsh development (Coles, 1979).

When waves and tidal currents propagate over a vegetated intertidal flat, dissipation of wave motion (Möller et al., 1999) and a reduction in unidirectional current velocity occurs (Fonseca, 1982), resulting in a decrease in applied bed shear stress values. The velocity structure within the saltmarsh canopy, as well as the role of halophytic plants in promoting the deposition of sediment is the subject of ongoing research (Fonseca, 1996; Shi et al., 1996, 2000; Brown et al., 1998; Christiansen et al., 2000; Neumeier and Ciavola, submitted). Recent numerical modelling to predict the short-term evolution of an intertidal mudflat in Venice lagoon highlights the role of seagrasses in the reduction of bed shear stress and protection of sediment from erosion by storms (Cappucci et al., 2001). These areas of investigation have practical implications for the artificial restoration of mudflats using dredged material (e.g. Hosokawa, 1996; Imamura, 1996), and for the evaluation of habitat loss following accidental pollution events.

The critical erosion threshold of intertidal sediments is a measure of sediment stability, and an important parameter to model the morphodynamic evolution of estuaries (Whitehouse and Mitchener, 1998). However, the derivation of τ_c is time-consuming, and there is a lack of suitable in situ instrumentation particularly where a large spatial coverage is required in as short a time as possible in order to gain a ‘synoptic’ overview of intertidal sediment stability. Such an overview is important because physical and biological parameters that affect sediment stability (e.g. de-watering, EPS production and macrofaunal grazing) can change significantly on time-scales of a few hours to a few days (Amos et al., 1988;

Austen et al., 1999; Paterson and Black, 2000). In addition, the onset of rain can cause dramatic changes in sediment stability within a few seconds (Paterson et al., 1990). This imposes an effective limit on the duration and area of any field campaign in which the aim is to determine intertidal sediment stability from the properties of the surface sediments.

Further limitations arise depending on the substrate characteristics and interval between measurements of the field instruments. Some of the smaller in situ erosion devices, e.g. SedErode (Mitchener et al., 1996) and Mini Flume (Amos et al., 2000), are fairly portable, but are capable only of a few measurements per emergence period. Furthermore, due to their relatively large ‘footprint’ area, they are not able to operate on substrata densely colonised by plants. An exception is the cohesive strength meter (CSM) (Tolhurst et al., 1999), a highly portable instrument capable of a large number of measurements during a single intertidal exposure period. The small footprint of the CSM enables assessment of τ_c on the bare substrata within saltmarsh, seagrass or seaweed stands, making it ideal for use in mixed habitats.

Despite its versatility, the use of single or multiple CSMs is restricted to providing a quasi-synoptic overview of sediment stability during any particular point in space and time. The use of chl *a* or colloidal carbohydrate as proxies for τ_c is possible provided that a strong functional relationship exists between chl *a* and microalgal-derived extra-cellular polymeric substances (EPS) in intertidal surface sediments (Paterson et al., 1994; Underwood et al., 1995; Black, 1997). This has led to suggestions that (for certain substrata and algal assemblages) remote sensing of colour changes and chl *a* content in surficial sediments may be useful as a synoptic method for the derivation of intertidal flat stability (Grant and Gust, 1987; Hakvoort et al., 1998; Paterson et al., 1998; Riethmüller et al., 1998). However, this technique is only suitable for bare intertidal areas, as substrata lying beneath plant canopies are not available for assessment by remote sensing.

This paper aims to determine intertidal sediment stability at a mixed habitat site within the Ria

Formosa lagoon, Portugal. Habitats assessed were the saltmarsh stands of *Spartina maritima* and *Sarcocornia perennis*, the seagrass stands of *Zostera noltii*, and the bare sediments. As far as we are aware, this is the first work to assess the stability of sediments within *Zostera noltii* beds using an in situ erosion device. We examined the use of bio-dependent bed parameters as proxy tools for sediment stability across the entire intertidal area and for specific habitats. Reasons for the temporal and spatial variation in observations between seasons and habitats are discussed, together with feedback processes operating between biological and physical components of the intertidal system.

2. Materials and methods

2.1. Study area

The Ria Formosa is a highly productive tidal lagoon that extends along the southern coast of Portugal, separated from the sea by a 55 km long barrier island chain. It comprises a range of vegetation communities including saltmarshes, seagrasses and benthic macro- and microalgal mats. The study site, Ramalhete, is located some 5 km from the city of Faro, and is close to one of the channels that connects directly with the Atlantic Ocean (Fig. 1).

The intertidal zone corresponds to an area of about 30 km², and has a mean elevation of 0.4–0.5 m above MLWS. At spring tides, the water surface area varies between 17 and 84 km². Intertidal sediments consist of sandy mud and muddy sands, with the mud fraction dominated by silts, and the sand fraction consisting of medium to coarse grains. The organic matter content is generally low, in the order of 10% of the total mass (Andrade, 1990). The dynamics of the lagoon are dominated by the tidal exchange of water through the six inlets linking the lagoon communities to the coastal ocean ecosystems; average water depth is approximately 2 m and the tidal range varies from a maximum of 3.7 m (springs) to a minimum of 0.4 m (neaps). Watershed discharge is sporadic, and dependent on rainfall

occurring mainly between October and April. Salinity values range between 35.5 and 36.9 for all the year, except during short periods following heavy rainfall when surface water salinity may be as low as 15. Water temperature varies between 12°C in winter and 27°C in the summer (Falcão et al., 1991).

Andrade (1990) distinguishes three types of intertidal flat, according to distinctive characteristics, e.g. elevation, sediment type and position within the lagoonal system: (1) back-barrier flats are located behind the spits which delimit the lagoon at its eastern and western boundaries; they have a weak hydrodynamical regime, consist of fine sediment, and are located at a higher elevation than the other types; (2) flood-delta flats, correspond to the innermost part of tidal inlets and are essentially sand deposits, often covered by bedforms generated during the flood-tide and (3) creek-edge flats, the most common type across the lagoon, located along main channels and secondary creeks furthest away from the inlets. Here a distinctive sediment zonation is found moving across the profile from the lower to the upper intertidal, with a fining upward trend. Saltmarshes are found at ever increasing density as one moves away from the inlets. In the Ria Formosa, vegetation colonises a substrate which often has a significant sand component, although there is some evidence that the presence of the vegetation seems to increase the content of mud.

The spatial distribution of aquatic vegetation in the Ria Formosa depends closely upon the seabed position in relation to the low tide elevation. The upper intertidal area, only flooded during high tides, is dominated by the saltmarsh species *Spartina maritima* and *Sarcocornia perennis*. The lower intertidal flats are the habitat of *Zostera noltii* seagrass beds, and green (*Enteromorpha* spp, *Ulva* spp) and brown (*Fucus vesiculosus*) macroalgal mats. *Enteromorpha* spp and *Ulva* spp are very abundant in winter, when production peaks are observed and large amounts of biomass can be produced in a very short time after rainy periods. In the summer the abundance of green algae is low, probably controlled by desiccation; at this time, much of the intertidal area is covered by algal mats of cyanobacteria.

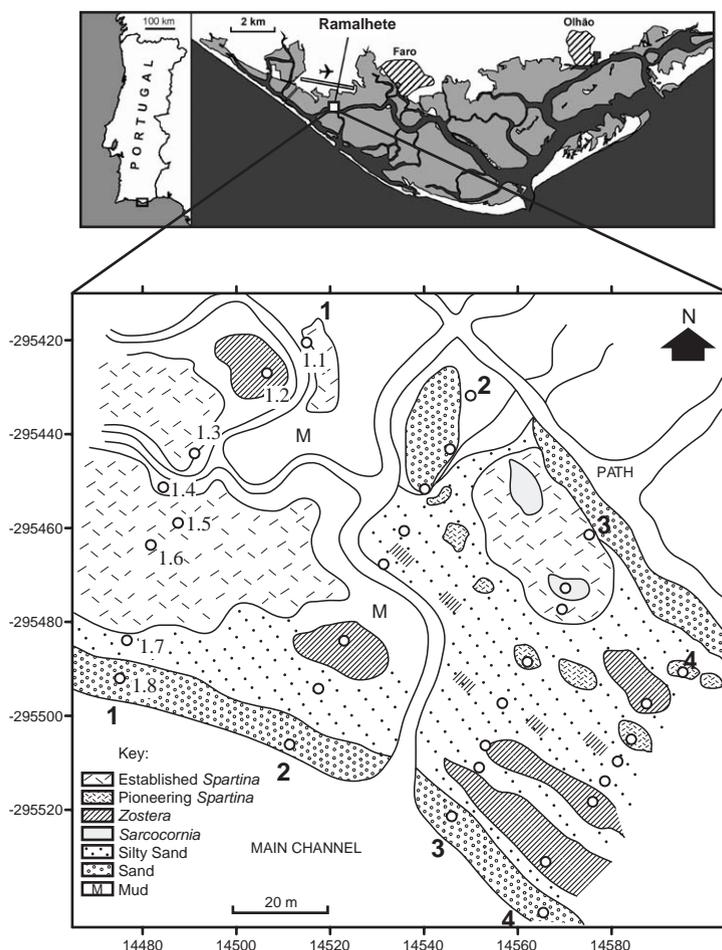


Fig. 1. Location of the Ria Formosa lagoon and the Ramalhete study area, on the south coast of Portugal. Habitats and cross-shore transects (nos. 1–4) are shown. Stations were numbered $n.1$ to $n.8$ (upper to lower intertidal), where n = transect number. Co-ordinates are referred to the Portuguese linear grid system centred at Melriça.

For the present study, two field campaigns were conducted at Ramalhete: campaign no. 1, from 28th to 30th September 2000 (considered typical of late summer/early autumn intertidal flat conditions); and campaign no. 2, from 6th to 8th April 2001 (typical late winter/early spring conditions). On both occasions, 32 stations were sampled in four cross-shore transects (nos. 1–4) of 60–90 m in length. Transects covered the entire intertidal area, and encompassed a range of different habitat and substrata types (Fig. 1). The study area was chosen because of its wide habitat variety and proximity to the Ramalhete field station of the University of Algarve. Critical erosion thresholds were derived

in the field; analysis of the surface sediments (biochemical, water, and organic content, and % fraction $<63\ \mu\text{m}$) was undertaken at the University of Southampton. Throughout campaign 1, the weather remained warm and dry, with a light NE to NW wind (mean velocity $3.6\ \text{m s}^{-1}$), and an overcast sky, with occasional sunny spells; mean seawater temperature was 19°C . A period of increased wind velocities ($10\text{--}12\ \text{m s}^{-1}$) from the SW occurred at the end of the main sampling period, during tidal immersion on the evening of 29th September. Throughout campaign 2, the weather was dry and sunny, with light on- and offshore breezes, and a mean sea level air pressure

of ~ 1035 mb; mean seawater temperature was 18°C .

Sampling station positions and elevations, including habitat boundaries and channel locations, were obtained using a Nikon DTM-310 electronic Total Station.

2.2. Sediment stability measurements

The CSM Mk III was used to derive τ_c . The CSM is an in situ erosion device, which employs the stress induced by a perpendicular water jet to erode the surface of exposed intertidal sediments. An empirical calibration (Tolhurst et al., 1999) based on the equations of Bagnold (1966), modified by McCave (1971), allows the eroding pressure to be expressed in terms of an equivalent horizontal bed shear stress (τ_0); a maximum τ_0 of 9.1 N m^{-2} is achievable. The CSM test chamber has a footprint of $7 \times 10^{-4}\text{ m}^2$, and houses an infrared transmitter and receiver diode. The small size of the chamber allows deployment on substrata between plants where larger erosion devices are unable to operate (Fig. 2). Jet pressure is increased incrementally, whilst light transmission is logged by an onboard computer. A real time display allows the operator to monitor the light transmission within the erosion chamber as each test proceeds. τ_c was defined as occurring at

the first incremental pressure-step with a mean transmission value of less than 90%, based on the characteristics of the erosion profiles (T. Tolhurst, pers. comm.). For a full description of the CSM, see Tolhurst et al. (1999).

At each station, replicate tests ($n = 4$) were conducted on the exposed substrate. If there was no decrease in the percent light transmission at the end of each of 3 consecutive tests, no erosion was deemed to have occurred and a minimum τ_c value of 9.1 N m^{-2} was assigned to that particular station. Similarly, for a station which displayed both erosion and no erosion, it was possible to assign a minimum τ_c value. Independent verification of no erosion was provided by visual comparison of the CSM footprint with a footprint where erosion was known to have occurred (Fig. 3). It was not possible to obtain τ_c values during either field campaign at station 2.3 due to the high permeability of the sand, and the resultant lack of water retention in the CSM chamber.

2.3. Surface sediment properties

Replicate surface scrape samples ($n = 3$) for biochemical, grain-size, water and organic content analyses were collected immediately adjacent to CSM test sites, then chilled (light-excluded) in resealable plastic bags. Samples for biochemical



Fig. 2. The CSM chamber deployed between pioneering plants of *Spartina maritima* (station 3.4) during campaign 2. Note the filamentous chlorophyte, *Enteromorpha clathrata*, draped over the *Spartina* plants and, in places, incorporated into the sediment surface between the plants.

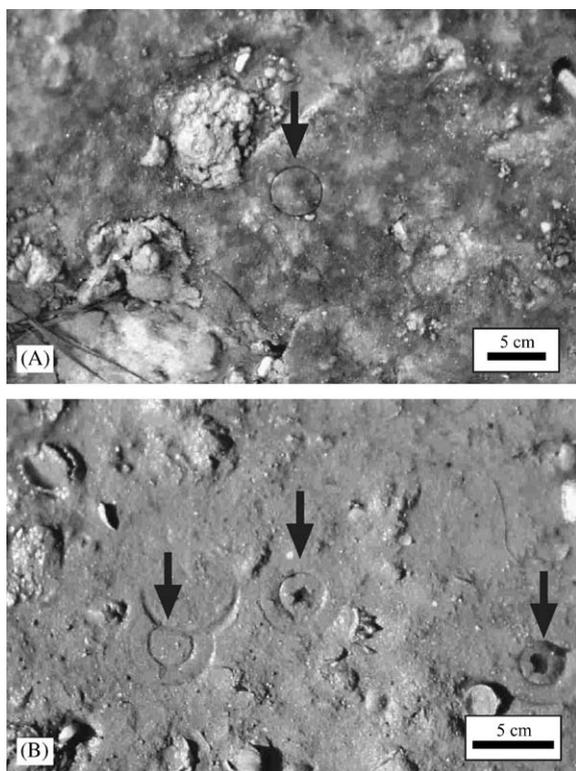


Fig. 3. (A) Footprint of the CSM chamber on a filamentous algal mat (station 2.1), providing visual evidence for no erosion. (B) Footprints of the CSM chamber on silty sand (station 3.5); erosion of the sediment surface has occurred at two of the replicate test sites.

analysis were freeze-dried in the dark, then stored at -80°C . Samples for water, organic content and grain-size analysis were kept at -80°C . All the samples were maintained in a frozen state until laboratory analysis in the UK (one week later).

2.4. Algal pigment analysis

Sediment chl *a* content was measured fluorometrically, and quantified using the modified equations of Parsons et al. (1984). Along transect no. 3 (Fig. 1), chlorophylls and carotenoids were quantified using reversed-phase high performance liquid chromatography (HPLC) in order to examine the surface sediment phyto-benthic assemblage.

For both procedures, samples were extracted in 90% acetone, ultrasonicated for 30 s, then centri-

fuged at 3000 rpm for 15 min. For the fluorometric method, the supernatant was measured in an Aminco Fluoro-Colorimeter before and after acidification with 2 drops of 10% HCl. Relative fluorescence was calibrated spectrophotometrically (CECIL CE292) against the absorbance of a chl *a* standard, measured at 665 nm, with a turbidity correction at 750 nm (Jeffery and Humphrey, 1975). In the HPLC analysis, the supernatant was filtered through a $0.2\ \mu\text{m}$ Nyaflor membrane filter. Pigments were determined using a $5\ \mu\text{m}$ C-18 column, and a modification of the Mantoura and Llewellyn (1983) method, described by Barlow et al. (1993). A limitation of this method is that the zeaxanthin and lutein peaks co-elute. Pigments were identified by a comparison of peaks and retention times with commercially available standards, or with monocultures having well-documented pigment markers. Good peak separation was achieved for chlorophylls and carotenoids, with the exception of fucoxanthin in campaign 2. At this time, the fuco peak was complicated by the close elution of another pigment, believed to be 19'-*cis*-neoxanthin (F. Mantoura, pers. comm.), particularly in mid to upper intertidal samples. Peridinin was present at all stations (except 3.8) in campaign 1, but was not detected during campaign 2. The main pigments and their retention times (min) used in this paper are fucoxanthin (4.7), 19'-hexanoyloxyfucoxanthin (5.4), zeaxanthin/lutein (7.3), chl *b* (9.6) and chl *a* (10.5). Sediment chlorophyll and carotenoid contents were expressed as mass per dry weight (DW) of sediment.

Marker pigments chosen as representative of particular phylogenetic groups were: fuco (diatoms), hex-fuco (prymnesiophytes), zeaxanthin (cyanophytes), and chl *b* + lut (chlorophytes). Fuco may also occur in groups other than diatoms (e.g. prymnesiophytes, dinophytes), and macrophytes can contribute to the zeaxanthin/lutein and chl *b* content. However, the marker pigments used in this study have been used routinely in intertidal sediment studies (e.g. Barranguet et al., 1997; Dransfeld, 1999; Lucas and Holligan, 1999; Lucas et al., 2000, 2001).

Optical microscopy was conducted on sediments from silty-sand and *Spartina* habitats to provide

a control for the HPLC data. During campaign 2, the filamentous chlorophyte *Enteromorpha clathrata* was identified in sediments from these habitats. Pure samples of *E. clathrata* from station 3.4 (pioneering *Spartina*) were freeze dried, then analysed by HPLC (as described above) to characterise the species' pigment biomarkers.

2.5. Colloidal carbohydrate

Sediment colloidal carbohydrate content was quantified using a double saline extraction (Underwood et al., 1995) and a phenol-sulphuric acid assay (Dubois et al., 1956). Colloidal carbohydrate was defined as the carbohydrate content extracted in saline (25) at 20°C. Samples were agitated for 20 s, incubated for 15 min, then centrifuged at 3000 rpm (2000g) for 15 min. The supernatant absorbance values were measured spectrophotometrically (CECIL CE292) at 485 nm, and calibrated against a standard curve of absorption versus glucose concentration. Colloidal carbohydrate content was expressed as glucose equivalent (GE) content per dry sediment weight.

2.6. Water, organic content and grain-size analysis

Sediment water and organic content were determined gravimetrically after drying to constant mass at 50°C, then heating to 500°C for 6 h, respectively. A Coulter LS130 particle sizer was used for grain-size analysis on the thawed samples after removal of organic material using H₂O₂.

2.7. Statistical analyses

Between campaign variability was assessed using paired *t*-tests on the biochemical and physical sediment properties for each transect and habitat type. Tukey comparison of means and ANOVA were used to compare between transects and habitats. Covariability between parameters was analysed using Pearson product moment correlation; PCA was used to examine whole data set variability. Covariance analysis (comparison of regression lines) was used to examine whether functional relationships between

parameters within each campaign were constant over the two campaigns. Multiple and bivariate regression models for τ_c were derived using best-subset and stepwise multiple regression to reduce predictor variables.

For statistical comparisons between habitats, stations were classified according to 4 major habitat types: *Spartina*, *Zostera*, silty sand and sand. Stations that were not assigned to one of the habitat types (1.4, 2.1—filamentous algal mats; 1.5—muddy pool; 3.2—*Sarcocornia perennis*) were omitted from subsequent statistical analyses. Where a minimum τ_c value was derived for a particular station (see above), this was the value used in statistical tests. Standard transformations were applied to the data where necessary to comply with the statistical requirements of homogeneity of variance and normality of distribution. Significant differences were considered at $p < 0.05$.

3. Results

3.1. Sediment stability

The distribution of τ_c across the Ramalhete study site varied both temporally and spatially, reflecting a strong habitat-dependent signal (Fig. 4). In general, τ_c decreased in a seawards direction, with the lowest values (0.5–0.9 N m⁻²) occurring on the sandy substrata of the main channel sides. In campaign 1, it was not possible to erode the surface sediments at 6 stations ($\tau_c > 9.1$ N m⁻²); of these, 4 were in *Spartina* habitats, and 2 (Stations 1.4 and 2.1) were filamentous algal mats. In campaign 2, erosion occurred at all stations with τ_c distributed more homogeneously across the field area. Between campaigns 1 and 2, mean τ_c in *Spartina* habitats decreased by at least 20%; within the *Zostera* stands, there was little change in mean τ_c between campaigns. In sand and silty sand habitats, mean τ_c increased by ~75% and at least 50%, respectively.

For transect 2, a significant difference in mean τ_c existed between the two campaigns ($p = 0.03$, $n = 7$). For silty sand habitats, a weak difference in mean τ_c was detected ($p = 0.06$, $n = 5$). There was no significant difference between campaigns for the mean (pooled data set) τ_c values (Table 1).

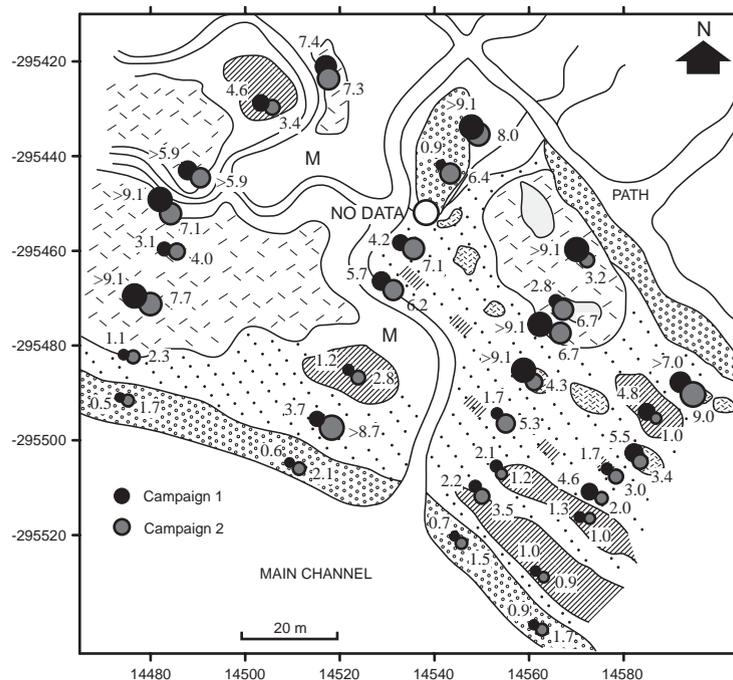


Fig. 4. Spatial distribution of τ_c (N m^{-2}) at Ramalhete during campaigns 1 and 2.

Table 1

Mean (\pm SD) sediment property values for campaigns 1 and 2 at Ramalhete (ns = not significant)

Sediment property	Campaign 1	Campaign 2	<i>p</i>
τ_c (N m^{-2})	> 4.2 (3.1)	> 4.4 (2.6)	ns
Chl <i>a</i> ($\mu\text{g gDW}^{-1}$)	52.3 (50.7)	27.4 (26.8)	< 0.0005
Colloidal carbohydrate ($\mu\text{g GE gDW}^{-1}$)	1210 (1520)	483 (459)	< 0.0005
Water (%)	30 (16)	32 (18)	ns
Organic (%)	3 (7)	3 (3)	ns
Bed elevation (m)	0.02 (0.55)	0.03 (0.53)	ns
Fraction < 63 μm (%)	12 (17)	17 (16)	ns

3.2. Sediment properties

Chl *a* displayed a large temporal and spatial variation across the study area, with a strong, seasonally dependent signal. During campaign 1, chl *a* contents ranged between 2 and 202 $\mu\text{g gDW}^{-1}$; the highest values occurred within *Spartina* habitats and at station 1.4 (filamentous algal mat). In campaign 2, chl *a* was distributed more evenly (range 1–89 $\mu\text{g gDW}^{-1}$). Patchiness

(coefficient of variation, \pm standard deviation) at the centimetre scale was greater in campaign 1 (24% \pm 22%) than in campaign 2 (18% \pm 12%). Between campaigns, significant differences in mean chl *a* content existed for transects 3 ($p = 0.046$, $n = 7$) and 4 ($p = 0.001$, $n = 8$); also for *Spartina* ($p = 0.034$, $n = 7$) and *Zostera* ($p < 0.0005$, $n = 9$) habitats. The mean *Spartina* habitat chl *a* content was 102.0 $\mu\text{g gDW}^{-1}$ in campaign 1 and 48.9 $\mu\text{g gDW}^{-1}$ in campaign 2; mean *Zostera* chl *a* was 45.1 and 18.1 $\mu\text{g gDW}^{-1}$, respectively (Fig. 5A). A highly significant difference in overall chl *a* content existed between the two campaigns (Table 1).

The distribution of sediment colloidal carbohydrate content varied in much the same way as chl *a*, with values ranging between 65 and 7839 $\mu\text{g GE gDW}^{-1}$ in campaign 1, and between 14 and 2012 $\mu\text{g GE gDW}^{-1}$ in campaign 2. Similarly, the highest values occurred within the *Spartina* and on filamentous algal mats. Significant differences in mean colloidal carbohydrate content between campaigns existed for transects 2 ($p = 0.001$), and 4 ($p = 0.001$), and for *Spartina* ($p = 0.01$)

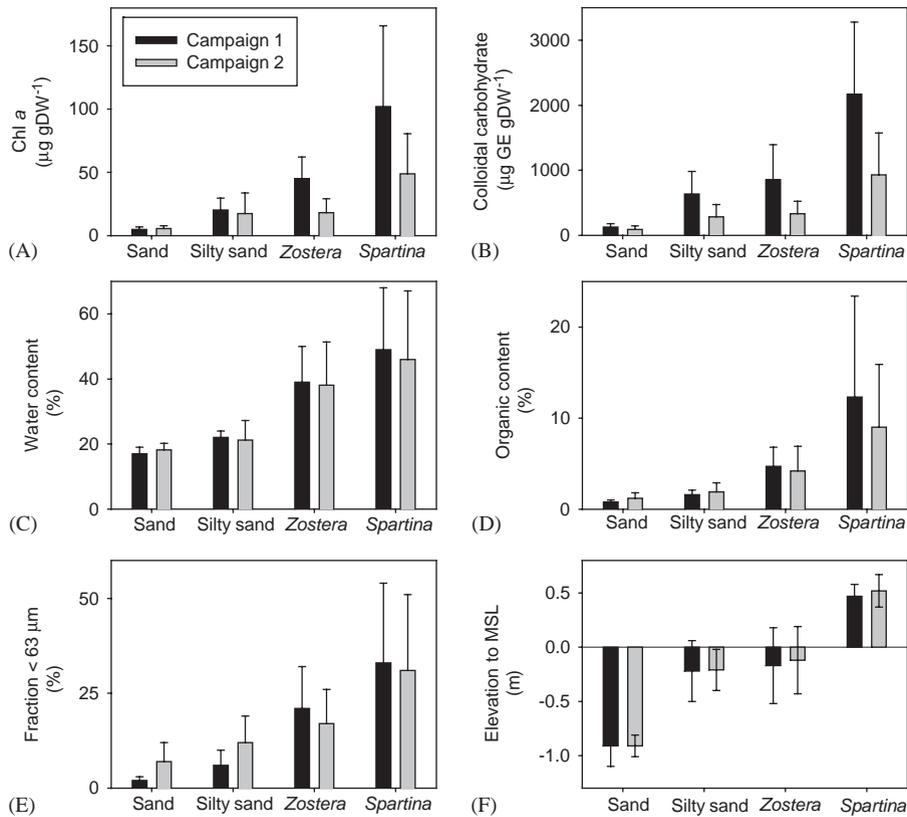


Fig. 5. Mean sediment property values (\pm SD) for sand, silty sand, *Zostera* and *Spartina* habitats during campaigns 1 and 2: (A) chl *a*, (B) colloidal carbohydrate, (C) water content, (D) organic content, (E) % fraction $<63\ \mu\text{m}$ and (F) elevation. Significant trends ($p < 0.05$) were found for: chl *a* (campaign 1), water content (campaigns 1 and 2), % fraction $<63\ \mu\text{m}$ (campaigns 1 and 2), elevation (campaigns 1 and 2).

and *Zostera* ($p = 0.006$) habitats. Mean *Spartina* colloidal carbohydrate content was $2170\ \mu\text{g GE gDW}^{-1}$ in campaign 1, and $930\ \mu\text{g GE gDW}^{-1}$ in campaign 2; mean *Zostera* colloidal carbohydrate was 854 and $332\ \mu\text{g GE gDW}^{-1}$, respectively (Fig. 5B). There was a highly significant difference in the overall colloidal carbohydrate content between campaigns (Table 1).

No significant differences in the water or organic content of sediments, for either transects or habitats, were detected between the two campaigns. For both campaigns, the highest mean water and organic contents (48% and 10%, respectively) occurred within *Spartina* habitats; the lowest mean contents (18% and 1%, respectively) were in sandy substrata (Figs. 5C and D).

The mean size-class of the surface sediments varied from clay/very fine silt (*Spartina* habitat) to medium sand (sand habitat). Between campaigns, there was little change in the mean grain-size of *Spartina* habitats: sediment remained very poorly sorted and platykurtic with near symmetrical skewness (Table 2). For *Zostera* habitats, there was a small increase in mean grain-size between campaigns. In silty sand habitats, there was a decrease in mean grain-size in campaign 2, however sediments remained very poorly sorted and fine/strongly fine skewed in both campaigns. For sandy habitats, mean grain-size increased slightly, whilst sediments remained moderately well sorted, fine to strongly fine skewed and leptokurtic/mesokurtic. The mean % fraction $<63\ \mu\text{m}$ was greatest in *Spartina* (32%) and

Table 2

Statistical parameters of grain-size (Folk, 1974) for the different habitats during campaigns 1 and 2 at Ramalhete

Parameter	Campaign	<i>Spartina</i>	<i>Zostera</i>	Silty sand	Sand
Mean (μm)	September 2000	3	7	67	279
	April 2001	4	13	27	335
Sorting (ϕ)	September 2000	2.6	3.3	3.0	0.6
	April 2001	3.1	3.6	3.5	0.5
Skewness	September 2000	-0.1	-0.1	0.7	0.3
	April 2001	-0.1	0.0	0.2	0.2
Kurtosis	September 2000	0.8	0.8	1.9	1.4
	April 2001	0.8	0.8	0.6	1.0

Zostera habitats (19%), and lowest in silty sand (7%) and sand (5%) substrata, as expected (Fig. 5E). For both *Spartina* and *Zostera* habitats, the mean % fraction $<63\mu\text{m}$ was greater during campaign 1 than during campaign 2. For transect 2, a significant difference ($p = 0.001$) in the mean % fraction $<63\mu\text{m}$ existed between campaigns 1 (8%) and 2 (16%).

Mean habitat elevations (referred to MSL) were 0.50 m (*Spartina*), -0.15 m (*Zostera*), -0.22 m (silty sand), and -0.91 m (sand: stations 1.8, 2.8, 3.8, 4.8). Analysis of partial regression coefficients suggested that the elevation trend was significant on its own, and not through the relationship with habitat ($p = 0.066$) (Fig. 5F). Between campaigns, no significant differences in mean elevation were detected for either transects or habitats.

Between transects, no significant differences were detected for τ_c , or any of the biochemical and physical sediment properties during either campaign. Between habitats, τ_c and all the sediment properties except elevation ($p = 0.001$) were highly significantly different from each other in campaign 1. During campaign 2, a highly significant difference was detected for elevation and colloidal carbohydrate, and a significant difference for τ_c and the remaining sediment properties.

3.3. Phytobenthic assemblage

Fuco to chl *a* ratios by weight along transect 3 varied between 0.11 and 0.36 during the two campaigns, with the highest values occurring on muddy substrata below dense *Sarcocornia* cover;

ratios tended to increase towards the main channel, reflecting a greater diatom influence at the more seaward stations (Fig. 6). Zea to chl *a* ratios decreased towards the main channel during both campaigns, indicating a reduced influence by cyanobacteria in the lower intertidal sediments; the highest ratios (0.09 and 0.11) occurred at the upper shore *Spartina* stations. Lut + chl *b* to chl *a* ratios were higher in the mid to upper shore stations in campaign 2 than in campaign 1, with a maximum ratio of 0.27 occurring in the upper shore *Spartina* stand. Hex-fuco to chl *a* ratios tended to increase towards the main channel during campaign 1, but decrease in the same direction during campaign 2, reflecting a seasonal change in phytoplankton (prymnesiophyte) deposition from the water-column. The HPLC analysis of pure *E. clathrata* revealed a lut + chl *b* to chl *a* ratio of 0.52 (SD 0.03).

Mean fuco to chl *a* ratios were significantly higher ($p = 0.012$) in campaign 2 (0.28) than in campaign 1 (0.21). No other significant differences in means were detected between campaigns for the remaining pigment biomarkers. During campaign 1, fuco ($r^2 = 0.959$, $p < 0.0005$), zeo ($r^2 = 0.813$, $p = 0.005$) and hex-fuco ($r^2 = 0.808$, $p = 0.015$) ratios were significantly correlated with seabed elevation; in campaign 2, only zeo ($r^2 = 0.832$, $p = 0.004$) and lut + chl *b* ($r^2 = 0.797$, $p = 0.007$) ratios were significantly correlated.

Microscopic analysis of sediments from *Spartina* and silty sand habitats confirmed large numbers of cyanobacteria (*Microcoleus* spp, *Oscillatoria* spp, *Anabaina* spp, and *Chroococcus* spp) present in the surface assemblage during both campaigns.

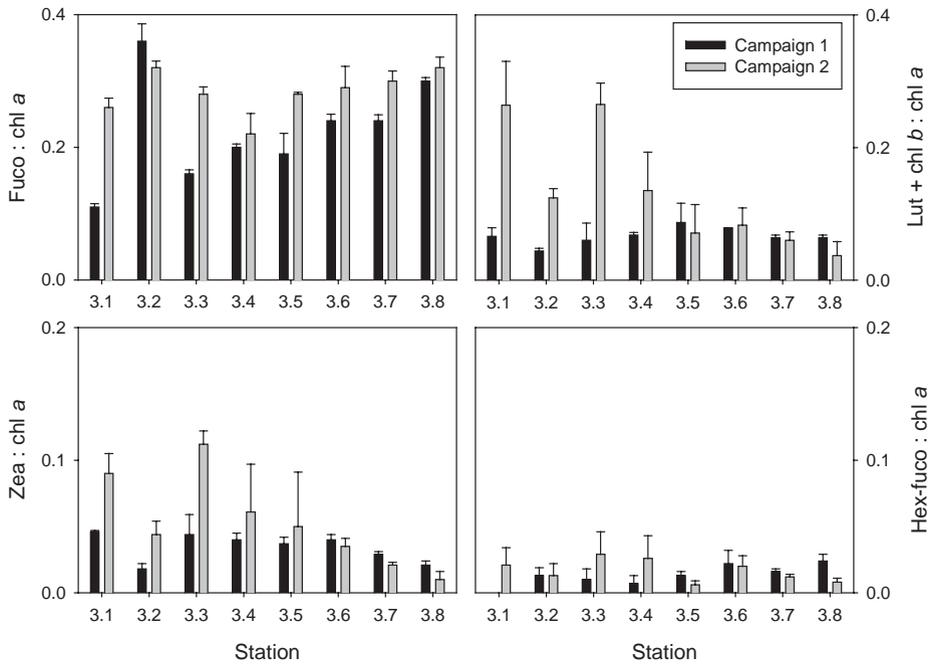


Fig. 6. Accessory chlorophyll and carotenoid to chl *a* ratios during campaigns 1 and 2. Note: different ordinate scales for zeaxanthin and hex-fuco to chl *a* [Fuco: fucoxanthin; Lut: lutein; Zea: zeaxanthin; Hex-fuco: 19' Hexanoyloxyfucoxanthin].

Pennate and centric diatoms (species not identified) were present in increasing numbers towards the main channel. In campaign 2, *E. clathrata* was present in the surface phytobenthic assemblage at both habitats. In *Spartina* and pioneering *Spartina* habitats at the saltmarsh front, *E. clathrata* was draped over the stands, and filaments were incorporated into the sediments between plants, and into the silty sand substrata further seawards (see Fig. 2).

3.4. Correlation of sediment properties

During campaign 1, τ_c was significantly correlated ($p < 0.05$) with water and organic content, and highly significantly correlated ($p < 0.0005$) with chl *a* and colloidal carbohydrate content, elevation and % fraction $< 63 \mu\text{m}$ (Table 3). In campaign 2, τ_c was significantly correlated with chl *a* and colloidal carbohydrate content, as well as % fraction $< 63 \mu\text{m}$, and highly significantly correlated with elevation. Chl *a* and colloidal carbohydrate were highly significantly correlated during both campaigns. For the combined data set from

both campaigns, all sediment properties were highly significantly correlated except τ_c with water content, and bed elevation with both water content and chl *a*. Comparison of regression lines to investigate whether the functional relationships established between parameters within each of the seasons were continued over the two seasons showed that for most sediment properties, and despite some significant differences in intercepts, such relationships were maintained (Table 4). Exceptions were between water content and τ_c , and water content and organic content.

In the PCA for campaign 1, 83% of the total variability in the data was described by PCs 1 and 2. The PC loadings showed chl *a*, colloidal carbohydrate, organic and water content, and % fraction $< 63 \mu\text{m}$ to be closely correlated (Fig. 7A); the position of τ_c suggests a positive, but weaker correlation with this group. Elevation and τ_c were clearly correlated with each other. The *Spartina* habitat *n*-scores discriminated from other *n*-scores by displaying a close affiliation to elevation and τ_c , as well as chl *a*, colloidal carbohydrate, organic and water content, and % fraction $< 63 \mu\text{m}$. Sand

Table 3

Significant Pearson product moment correlations ($p < 0.05$) between τ_c and sediment properties for campaigns 1 (first value) and 2 (second value), and the combined data set (third value)

Campaign 1, Campaign 2, Campaigns 1 + 2	τ_c	Chl <i>a</i>	Coll carbo	Bed elevation	Water content	Organic content
Chl <i>a</i>	0.75 0.45 0.57					
Coll carbo	0.83 0.57 0.64	0.88 0.95 0.91				
Bed elevation	0.71 0.59 0.65	0.45 0.41 0.41	0.50 0.52 0.48			
Water content	0.58 ns 0.39	0.90 0.92 0.85	0.79 0.86 0.75	0.35 0.39 0.37		
Organic content	0.58 ns 0.57	0.87 0.90 0.80	0.77 0.88 0.69	ns 0.53 0.45	0.94 0.96 0.93	
% fraction <63 μm	0.66 0.43 0.57	0.88 0.87 0.81	0.82 0.85 0.74	ns 0.57 0.44	0.91 0.90 0.90	0.96 0.96 0.94

Bold figures indicate highly significant correlation ($p < 0.0005$) (ns = not significant).

Table 4

p values from the analysis of covariance (comparison of regression lines) for the intercept and slope

Intercept slope	τ_c	Chl <i>a</i>	Coll carbo	Bed elevation	Water content	Organic content
Chl <i>a</i>	0.010 0.070					
Coll carbo	0.022 0.096	0.782 0.638				
Bed elevation	0.290 0.186	0.024 0.756	0.002 0.950			
Water content	0.015 0.019	0.942 0.066	0.360 0.471	0.959 0.939		
Organic content	0.178 0.095	< 0.0005 0.253	< 0.0005 0.125	0.206 0.325	< 0.0005 < 0.0005	
% fraction <63 μm	0.148 0.161	0.012 0.995	0.002 0.663	0.202 0.206	0.038 0.054	0.007 0.106

Bold figures indicate significant differences at $p < 0.05$. The first value in each column is the intercept, the second one is the slope.

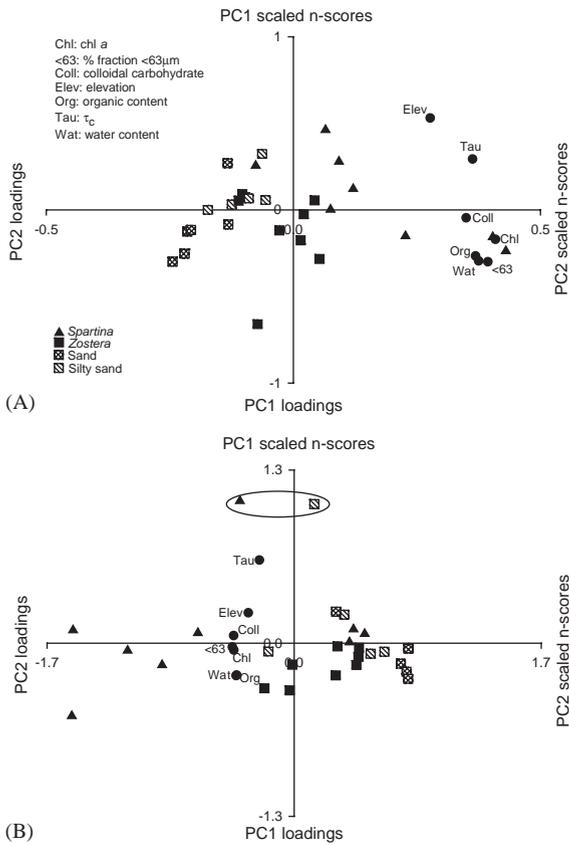


Fig. 7. PCA biplot of loadings and scaled n -scores for: (A) campaign 1 and (B) campaign 2 (see text for explanation of the two data points within the ellipse).

n -scores discriminated with less elevation and τ_c than silty sand n -scores. Both sand and silty sand were characterised by low chl a , colloidal carbohydrate, organic and water content, as well as low % fraction <63 μm . *Zostera* displayed less elevation and τ_c than *Spartina*, with more chl a , colloidal carbohydrate, organic and water content, as well as higher % fraction <63 μm , than sand or silty sand; it was not, however, strongly related to any of the loading terms.

For campaign 2, 79% of the total variability was described by PCs 1 and 2. Elevation was more closely correlated with chl a , colloidal carbohydrate, organic and water content, and % fraction <63 μm , than during campaign 1, whilst maintaining a positive correlation with τ_c (Fig. 7B). As in campaign 1, *Spartina* discriminated from sand,

whilst the remaining groupings were approximately similar. However, in contrast to campaign 1, there was less discrimination between habitats, seen in the positive PC1 n -score cluster containing the four habitat types. Two data points (Station 2.7, silty sand and station 4.1, *Spartina*) that correlate with the PC2 axis (see ellipse, Fig. 7B) appear to show high sediment stability whilst remaining intermediate with other parameters. Factors influencing the positions of these points are unclear, but may be related to the presence of: (1) *E. clathrata* observed in the sediment at station 2.7 and (2) a cyanobacterial mat at station 4.1.

The optimum (multiple regression) model for the entire intertidal area in campaign 1 was: $\log_{10} \tau_c = 0.53 \log_{10} \text{colloidal carbohydrate} + 0.26 \text{elevation} - 1.03$ ($r^2 = 0.774$, $p < 0.0005$). The best bio-dependent linear regression model for τ_c was obtained using colloidal carbohydrate as the predictor (Fig. 8A). During campaign 2, the optimum model was obtained using the single predictor variable, elevation (Fig. 8B). For

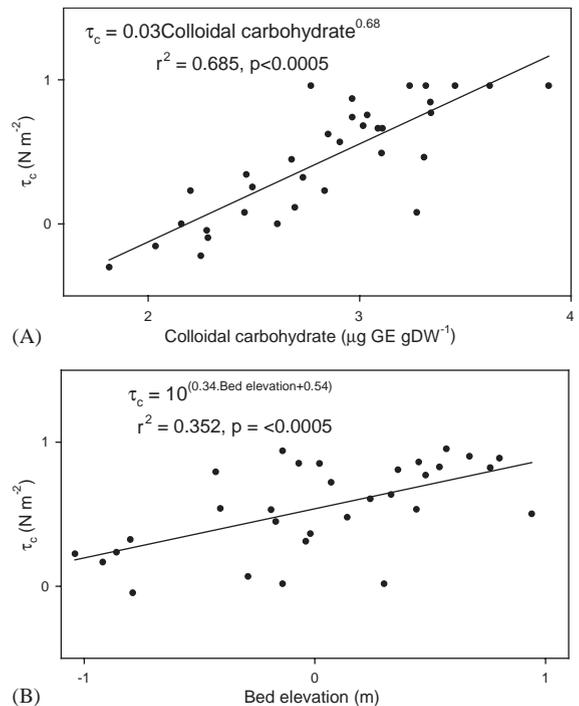


Fig. 8. Pooled data linear regression models for τ_c : (A) campaign 1 and (B) campaign 2.

Table 5
Significant ($p < 0.05$) habitat linear regression models for τ_c during campaigns 1 and 2

Campaign	Habitat	Regression equation ($\tau_c =$)	r^2	p
1	Silty sand	0.27Chl $a^{0.84}$	0.884	0.017
		0.01Coll carbo $^{0.93}$	0.865	0.022
2	<i>Spartina</i>	2.32Chl $a^{0.27}$	0.673	0.024
		0.87Coll carbo $^{0.30}$	0.802	0.006
		2.46Fraction < 63 $\mu\text{m}^{0.29}$	0.720	0.016
2	Sand	10 $^{0.45}$ Elevation $+0.65$	0.969	0.002
		0.36Organic content $^{2.44}$	0.992	<0.0005
		0.27Fraction < 63 $\mu\text{m}^{1.12}$	0.939	0.007

individual habitats, significant linear regression models for τ_c were restricted to silty sand habitats in campaign 1, and *Spartina* and sand habitats in campaign 2 (Table 5).

4. Discussion

4.1. Algal assemblage

At Ramalhete, the maximum ratios of pigment markers to chl a were 0.36 (fuco), 0.26 (lut + chl b), 0.09 (zea) and 0.02 (hex-fuco). These ratios were lower generally than those found in similar algal assemblage studies on more diatom-dominated cohesive and non-cohesive intertidal flat sediments. For example, on the Molenplaat, Westerschelde estuary, Netherlands, mean fuco to chl a and zea to chl a ratios of 0.86 and up to 0.32, respectively, were reported; for sandy sites, fuco to chl a ratios were 0.58 (Lucas et al., 2000). On an intertidal mudflat in Southampton Water, UK, an annual maximum fuco to chl a ratio of ~ 0.40 was reported (Dransfeld, 1999).

The interpretation of algal assemblages from pigment ratios requires care as environmental and physiological factors (e.g. light regime, temperature, nutrient supply, growth status and position of the oxic/anoxic boundary) can have a significant influence on them. For example, chlorophylls and carotenoids degrade generally at a faster rate in oxic compared with anoxic sediments. Reasons for

the low pigment marker to chl a ratios at Ramalhete reflect low dominance in the algal assemblage by any particular phylogenetic group, and probably indicate either the general state of oxic/anoxic conditions in the surface sediments, or high surface grazing activity, or a combination (Lucas and Holligan, 1999). The higher fuco to chl a ratios (0.36 and 0.32) at station 3.2 are due probably to exceptional pigment preservation in anoxic surface sediments below the dense covering of *Sarcocornia* spp, which was moved aside for sample collection and CSM tests. It is likely that the presence of the chlorophyte marker pigment 19' c -neo, which at times co-eluted with fuco, was responsible for the generally higher fuco to chl a ratios in campaign 2.

4.2. Sediment stability within the different habitats

Our results show that mean τ_c in the *Spartina* habitats decreased from $> 7.6 \text{ N m}^{-2}$ (campaign 1) to $> 6.3 \text{ N m}^{-2}$ (campaign 2). In the same habitats, mean colloidal carbohydrate content and % fraction < 63 μm were greater during campaign 1 than campaign 2 (Figs. 5B and E). These data suggest that both cohesion caused by a high mud content ($> 30\%$) (e.g. Mehta, 1993; Panagiotopoulos et al., 1997), and adhesion caused by high EPS content (e.g. de Winder et al., 1999), were responsible for the higher sediment stability in campaign 1. Microscopic and HPLC analysis, as well as field observations made during sample collection, point to unicellular and filamentous cyanobacteria as the source of the sediment EPS. Paterson and Black (2000), for sediments recently deposited within the saltmarsh system in the Humber estuary, UK, reported an increase in τ_c (using a CSM Mk III) from $\approx 0.4 \text{ N m}^{-2}$, 1 h after emersion, to $\approx 6.6 \text{ N m}^{-2}$, 6 h after emersion, invoking de-watering and biostabilisation by EPS as likely mechanisms. At Ramalhete, no temporal trend in sediment stability was detected, and sediments within the saltmarsh stands remained moist, but not waterlogged, throughout emergence.

In contrast to *Spartina* habitats, mean τ_c values for silty sand increased from 2.8 N m^{-2} (campaign 1)

to $> 5.4 \text{ N m}^{-2}$ (campaign2), and for sand from 0.7 to 2.7 N m^{-2} , respectively. Over the same period, mean colloidal carbohydrate contents fell, whilst mean % fraction $< 63 \mu\text{m}$ increased (Figs. 5B and E). Similarly, mean τ_c values for transect 2 increased from > 3.6 to $> 5.9 \text{ N m}^{-2}$, with mean colloidal carbohydrate contents falling from 829 to $303 \mu\text{g GE gDW}^{-1}$, and mean % fraction $< 63 \mu\text{m}$ increasing from 8% to 16% . Whilst it seems likely that addition of $< 63 \mu\text{m}$ sediment was at least partly responsible for enhanced sediment stability in these habitats and along transect 2, the mud contents during both campaigns were less than those found by Panagiotopoulos et al. (1997) to increase significantly the erosion threshold for sandy sediments. We suggest, therefore, that surface sediment binding by filaments of *E. clathrata* was responsible for the increased sediment stability in these habitats and along transect 2 during campaign 2. Although *E. clathrata* was also present in *Spartina* and *Zostera* habitats in campaign 2, its presence was insufficient to produce the level of stabilisation caused by the cyanobacteria in these habitats in late summer/early autumn.

Despite the fact that sediments in the *Zostera* habitats were generally unconsolidated with a high water content, intermediate τ_c values (0.9 – 4.6 N m^{-2}) and a mean fuco to chl *a* ratio of 0.27 for both campaigns suggest that sediment stabilisation in these areas was enhanced by microalgal biostabilisation.

4.3. Proxies for sediment stability

Strong correlations ($r = 0.88$ and 0.95) existed between chl *a* and colloidal carbohydrate across the entire intertidal area during both campaigns at Ramalhete (Table 3). Underwood et al. (1995) reported a similar strength relationship ($r = 0.89$) for the diatom-rich, cohesive sediments in the Severn Estuary, UK. The strong chl *a*-EPS relationships at Ramalhete suggest that remote sensing of chl *a* is a viable tool for detecting sediment stability in this area. However, despite the strength of the chl *a*-EPS relationship, statistical analysis did not select chl *a* as a best predictor of τ_c for the pooled data (hence the

entire intertidal area) either in late summer/early autumn or in late winter/early spring. Andersen (2001) found a comparable result in the study of seasonal variability on mudflats in the Danish Wadden Sea.

For habitats, chl *a* was selected as the best predictor of τ_c for silty sand in campaign 1, and a significant predictor in *Spartina* habitats in campaign 2 (Table 5). However, as remote sensing of chl *a* in areas covered by *Spartina* meadow would measure primarily plant, not sediment chl *a*, the use of remotely sensed chl *a* to detect sediment stability at Ramalhete is restricted to silty sand habitats in the late summer/early autumn. Our findings agree with those of a comprehensive study of intertidal flats in the Danish and German Wadden Sea (Riethmuller et al., 2000), in which the relationship between chl *a* and τ_c was found to be highly site specific; variability between sites was explained by changes in the intensity of surface reworking (e.g. herbivorous grazing), and in the composition of the benthic microalgal assemblage. Other significant predictors of sediment stability for individual habitats were colloidal carbohydrate (silty sand and *Spartina*), fraction $< 63 \mu\text{m}$ (*Spartina* and sand), elevation (sand), and organic content (sand) (see Table 5).

For the entire intertidal area, colloidal carbohydrate was selected as the only wholly bio-dependent predictor of τ_c . Whilst remote sensing of colloidal carbohydrate is not presently possible, collection and analysis of sediment samples for colloidal carbohydrate content is relatively rapid and simple, and could permit a quasi-synoptic survey of a reasonably large area within a few emergence periods, assuming constant conditions.

Elevation was selected as a predictor of τ_c during both late summer/early autumn and late winter/early spring. Elevation measurements over intertidal areas by sightings using a Total Station are reasonably rapid, giving either absolute or relative values depending on the existence of a nearby benchmark. However, to obtain spatial coverage of a large intertidal area, the use of more than one Total Station with multiple operators is required. This is likely to introduce operator errors, and restricts effectively the area for which

elevation measured by this method is useful as a predictor of τ_c to the area capable of being surveyed by a single survey team over a few emergence periods. The use of remote sensing (altimetry) to measure surface elevation is possible using a variety of different platforms and sensors (Bufton et al., 1991; Benveniste et al., 2001), although resolution is limited presently to 0.1–0.15 m. Altimetry, coupled with suitable ground-truthing to account for differences in habitat, may provide the most useful method currently available of remotely sensing sediment stability in mixed habitat intertidal areas.

4.4. Sedimentation processes

In the present study, the sediment mud content increased in vegetated areas, in agreement with the results of Andrade (1990). In a concurrent study at Ramalhete (Neumeier and Ciavola, in press), suspended sediment concentrations (SSCs) measured within the saltmarsh vegetation and above the adjacent (unvegetated) sandy and silty sandy substrata during fair weather were between 3 and 15 mg l⁻¹. Short-term sedimentation rates were highest on the sandy channel bank (5–21 g m⁻² tide⁻¹), and lowest on the saltmarsh (1–5 g m⁻² tide⁻¹), with intermediate values on the unvegetated muddy substrata and within the *Zostera* beds (Ciavola et al., 2001). These values can be compared with inorganic SSCs of $>1 \times 10^3$ mg l⁻¹ for muddy intertidal flats and $<1 \times 10^3$ mg l⁻¹ for sandy intertidal flats (Amos, 1995). Given a paucity in sediment supply and lower deposition rates amongst the *Spartina* than on the bare substrata, what are the mechanisms for sedimentation within the saltmarsh and the pioneering *Spartina* at the marsh front?

Whilst laboratory studies show that a reduction in the critical shear velocity within the saltmarsh canopy will favour the deposition of cohesive sediment (Shi et al., 1996), in situ and flume studies elsewhere, in agreement with Neumeier and Ciavola (in press), indicate that the shear stresses which develop as the flow encounters vegetation result in lower deposition rates amongst *Spartina* plants than on bare substrata (Pethick et al., 1990;

Shi et al., 2000). Furthermore, results from the Biological Influences On interTidal Areas (BIO-TA) project suggest that the saltmarsh canopy has little effect on sediment deposition, but acts as a sediment stabiliser during periods of erosion (Brown et al., 1998).

During campaigns 1 and 2, the apparent source of cohesive sediment was the mud adjacent to the tributary channels (see Fig. 1), implying a local origin for any minerogenic sedimentation occurring on the saltmarsh at these times. During periods of heavy rainfall in winter, the siliclastic supply to the Ria Formosa lagoon may increase through riverine input of sediments from the nearby hills (Andrade, 1990). The high wind event during campaign 1 caused physical disturbance to the sediment surface, and a higher SSC than during fair weather (U. Neumeier, pers. comm.), however there was no visual evidence for enhanced deposition, as seen after storm conditions in other saltmarshes (e.g. Stumpf, 1983; Reed, 1989).

Whilst saltmarsh development at Ramalhete is primarily minerogenic, evidenced by the low organic sediment content, the high surface cyanobacterial content and the incorporation of filamentous organic material into the substrata appear to play a role in saltmarsh accretion. When suspended siliclastic material is available in the water column, retention of sediment on the established saltmarsh is enhanced by the high EPS content and the filamentous nature of the algal mat (e.g. Paterson and Daborn, 1991). In winter, especially after heavy rainfall, *E. clathrata* is incorporated into the sediment surface on silty sand and within the *Spartina* meadow. On bare substrata, this may stabilise the surface sediment sufficiently to allow the development of pioneering *Spartina* stands, and thus the advance of the saltmarsh front. The filaments of the *E. clathrata* matrix trap and retain the higher levels of suspended fines in the water column over the unvegetated flats in winter. The new sediment provides a nutrient source for the establishment of pioneering *Spartina* on the otherwise low organic content sand. In common with the benthic microalgae, *E. clathrata* may also act as a precursor to saltmarsh development.

5. Conclusions

- Colloidal carbohydrate and elevation are the best predictors of mixed habitat intertidal sediment stability (τ_c) in the Ria Formosa lagoon system during late summer/early autumn and late winter/early spring, respectively. Further investigations are required to ascertain the site-specific nature of these predictors by comparisons with similar lagoon systems, e.g. Venice. Whilst the remote sensing of sediment colloidal carbohydrate is not achievable at present, satellite and aerial altimetry may be useful methods for the measurement of bed elevation, particularly if the present resolution of 0.1–0.15 m is improved.
- For specific habitats, a limited number of proxies for τ_c are available. For example, the use of sediment chl *a* content as a proxy for τ_c is possible for silty sand in the late summer/early autumn, and for *Spartina* habitats in the late winter/early spring. However, remote sensing for chl *a* in *Spartina* stands will detect the canopy, not the sediment, chlorophyll signature. Other significant predictors for specific habitats are: colloidal carbohydrate (silty sand and *Spartina*); % fraction <63 μm (*Spartina* and sand); elevation (sand) and organic content (sand).
- Saltmarsh development in the Ramalhete intertidal area is seasonally dependent on both sediment supply and biological activity within the surface sediments. In the summer months, cyanobacteria dominate the phyto-benthic assemblage, particularly within the *Spartina* sediments. Trapping and retention of fines is assisted by the action of sediment EPS and the filamentous nature of the algal mat. In winter, *Enteromorpha clathrata* is advected onto the bare substrata of the mid intertidal, forming a drape over the *Spartina* canopy, particularly at the saltmarsh front. Here, it is incorporated into the sediment surface, trapping and binding material from the water column, and forming a suitable substrate for the establishment of halophytic plants.

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