AN ECOLOGICAL 'CASCADE' EFFECT : MIGRATORY BIRDS AFFECT STABILITY OF INTERTIDAL SEDIMENTS

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ABSTRACT

A comprehensive study of factors controlling the erodibility of fine-grained intertidal sediments found that sediment strength increased with the arrival of large numbers of migratory shorebirds. Before the birds came, sediment cohesion resulted in part from secretion of polysaccharides by benthic diatoms whose production was controlled mainly by a grazing amphipod, *Corophium volutator*. When the birds arrived, *Corophium* behavior and abundance changed, bioturbation and grazing pressure on the diatoms decreased, and the production of cohesion-inducing carbohydrates rose. The results emphasise the importance of biological processes in affecting sediment stability, and the limitations of laboratory-based measurements of sediment properties used in models of cohesive sediment behavior.

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It is a commonplace of ecology that in simple ecosystems the effects of the activities of organisms in the topmost trophic level(s) may be traced through much or all of the food chain, so that the structure of the ecosystem may be said to be largely derived from this 'top-down' influence. Organisms at the bottom of the chain are assumed to be closely tied to features of their physical environment. Sometimes this relationship is reciprocal in that the organisms themselves exert a detectable influence on the abiotic world. We present evidence here suggesting that the foraging activities of a top predator 'cascade' down through lower trophic levels to affect the dynamic properties of estuarine sediments, and thus change the relationships between those sediments and the physical (oceanographic and atmospheric) factors that normally control their distribution.

Predicting the behavior of intertidal sediments is important wherever human activities (e.g., dredging, harbour or causeway construction) effect changes in coastal and estuarine environments. While the behavior of coarse, non-cohesive sediments is reasonably well known, accurate prediction is extremely difficult in the case of fine-grained, cohesive sediments because of variations in sediment composition, atmospheric effects, and biological processes. In addition, most work on sediment behavior and properties has been conducted in laboratory environments, often with non-living, reformed sediments whose properties are substantially different from those *in situ* (Amos and Mosher 1985; Luckenbach 1986; Amos et al. 1988; Gust and Morris 1989). During 1989 a comprehensive, interdisciplinary study of sediment properties was carried out on a tidal flat in the Bay of Fundy to determine the relative importance of atmospheric, oceanographic and biological factors to sediment erodibility. A principal objective was to obtain accurate data for use in numerical models constructed to explore the possible effects of a tidal power barrage on sediment distribution in the estuary. The essential parameter for numerical models is the critical shear velocity or critical erosion friction velocity (U_{*crit}), the water velocity at which the sediment begins to erode. This is a variable related to the shear strength (τ) at the sediment surface (Otsubo and Muraoka 1988). In cohesive sediments, the natural cohesion of clay particles may be greatly augmented by organic compounds produced by plants and animals inhabiting the sediment (Grant et al. 1986; Meadows and Tufail 1986; Decho 1990; Paterson and Daborn 1991).

The study (**LISP** - for Littoral Investigation of Sediment Properties - **89**) involved more than 30 scientists from a wide array of disciplines. It was carried out on the Starrs Point tidal flat in the Southern Bight of Minas Basin, where mixed, semi-diurnal tides average 11.5 m in range, producing a vertically homogeneous water column and leaving an intertidal zone up to 4 km in width (Daborn and Pennachetti 1979; Amos et al. 1988). The water is turbid, with sediment concentrations varying from 20-800 mg.L^{-1} over the flat. In spite of its superficial muddy appearance, the flat is principally a silty-sand with <20 %

clay; consequently it is essentially a non-cohesive sediment. Amos et al. (1988) showed that the sediment surface became significantly stronger (i.e., less erodible) during late summer, a change that was attributed to atmospheric drying at low tide. We noted, however, that several biological changes were occurring at the same time, and consequently it was not possible to assign the cause of the sediment "armouring" unequivocally.

The approach taken during LISP 89 was to monitor as continuously as possible all properties and processes affecting the sediments over a three-week period in late July when changes in sediment strength had been noted previously. This period encompassed days (25 - 26 July) when low water coincided with solar noon, at which time atmospheric effects on the intertidal zone would be maximal. Every effort was made to obtain measurements *in situ* : critical erosion velocity was measured during immersion by 'Sea Carousel', an annular flume designed for field use (Amos et al. in press); surface shear strength was measured over the low tide period using 'INSIST' (Faas et al. 1992), and Paterson's Cohesive Strength Meter (CSM) (Paterson 1989). Atmospheric and oceanographic parameters were recorded continuously.

Chlorophyll and carbohydrate concentrations of surficial sediments were measured on cores taken with a syringe. The top 2 mm of three adjacent sediment cores were combined into a single composite sample to reduce the effect of natural patchiness. Three replicate composite samples were taken at each sample time. Samples were frozen and stored before analysis. Chlorophyll *a* analysis was based on the spectrophotometric technique described by Jensen (1978) and carbohydrate analysis on the method of Kochert (1978). Surface scrapes (i.e., top 1-3 mm) of sediment were collected with a spatula, wet-weighed, and dried in a vacuum oven at 55°C to constant weight to determine water content. Dried samples were then ashed in a muffle furnace at 450°C for eight hours to determine organic content (Davies 1974). The roles played by biological processes in sediment stability were also examined experimentally by measuring sediment properties in areas treated with formalin (to remove all biota) and DCMU (to inhibit photosynthesis by benthic diatoms).

Results of this complex study show that the strength of surface sediments changes considerably on two different time scales. Upon first exposure to the air as the tide falls, shear (= cohesive) strength of the sediment as measured by 'INSIST' was low, usually $\tau<30$ Pa; with continued exposure, however, cohesion increased to 50 - 140 Pa before return of the tide. The change is represented by the vertical bars in Figure 1. Similar results were obtained with the CSM. Determinations of soluble carbohydrates (probably mucopolysaccharides) showed that these also increased during exposure (Fig. 2), presumably being secreted by epipelic diatoms congregated at the mud surface during low tide. Interestingly, although our data are limited (3-4 composite samples on each hour following initial exposure), it seems that the sedimentary soluble carbohydrate does not increase noticeably during the first hour; this corresponds to the time when *Corophium volutator*, the dominant grazer on the flat, is to be seen actively crawling at the surface (Boates and Smith 1989). After the first hour these amphipods generally remain in their burrows, presumably to avoid high temperatures, and/or desiccation.

Treatment with DCMU to inhibit photosynthesis decreased the cohesion 'build-up' during the next exposure period, but this inhibition was not evident following the next flood, presumably because the DCMU was washed out of the sediment by the tidal waters. Dehydration of the sediment may be a contributory factor in increasing cohesion; however, cohesive strength still increased during rainy periods (e.g., 17, 20, 28 July - cf. Fig. 1). When the cohesion data are normalised to the amount of radiation received during the exposure periods, the enhancement of cohesion per unit of radiation was greater on cloudy days than on sunny ones (Daborn 1991). This would be expected if the cohesion was due largely to benthic diatom production, which might exhibit photoinhibition at high light intensities. Upon immersion by the rising tide, the enhanced cohesion mostly disappeared, although it was evident that the <u>initial</u> values of cohesive strength were somewhat higher in the last week of July compared with earlier dates (Table 1).

Sediments poisoned with formalin showed that biological processes contributed significantly to the surface properties of the sediment. Initially, there was a decrease in cohesion, associated with lower carbohydrate production (Table 2) and because clays began to winnow out of the surface (Daborn 1991). After two days (four tidal cycles), treated areas developed rippled bedforms characteristic of non-cohesive deposits. After two more days, however, exposure during the low tide was accompanied by a much greater enhancement of cohesion, reaching values of more than 170 Pa one week after formalin treatment and correlated with higher chlorophyll values (Table 2). Soluble carbohydrate concentrations were also higher at the end of the experiment than at the beginning, but the intermediate values were anomalously low. The critical shear stress for erosion determined by Sea Carousel four days after treatment was notably higher on the treated site than on Control sites (Table 1). Subsequently, the rippled surface disappeared, to be replaced by a more normal bioturbated surface generated by the foraging habits of the amphipod *Corophium volutator*.

We interpret these measurements as follows : the 'mudflat' is actually a non-cohesive sandy silt, which exhibits a low (but measurable) cohesion when first exposed by the receding tide. This initial cohesion is probably related to the low clay content (<20%) of these sediments. During low tide exposure, however, there develops a transient but significant increase in shear strength. This is caused partly by atmospheric effects (i.e., drying), but measurements of the internal friction angle suggest this is a minor factor : in fact, the internal friction angle almost always <u>decreased</u>, indicating that the surficial sediments were less compacted at the end than at the beginning of the exposure period (Faas et al. 1992). We conclude that much of the enhanced cohesion is caused by extracellular polymeric substances (principally mucopolysaccharides) excreted by benthic diatoms.

Normally, surface features result from bioturbation by foraging amphipods, which graze on the diatoms (and bacteria), and thus limit their growth and the production of cohesion-developing carbohydrates. When the biota are removed, fine sediments winnow away, and bedforms characteristic of non-cohesive sediments appear. Evidence from poisoning experiments suggests that epipelic diatoms recolonise treated areas much more rapidly than the invertebrates (Amos et al. 1988, Coles 1979, Daborn 1991 and unpublished information), and in the absence of grazers the diatoms grow unrestrained, resulting in even greater sediment strength developed during exposure. When the amphipod population is reestablished, the diatoms come under greater control, and enhancement of cohesion during low tide is less.

The second temporal effect seen during LISP 89 occurred over a longer time scale. Toward the end of July critical erosion friction velocity measured under water increased from 0.71 cm.sec^{-1} to 1.68 cm.sec^{-1}, indicating that the sediment had become more resistant to erosion. Initial values of shear strength (measured with INSIST) were also higher during the last week of July (Table 1), but since this was not correlated with changes in the internal friction angle, the increased cohesion cannot be attributed to sediment compaction. Measurements reflecting biological activity showed coincident changes : soluble carbohydrate concentration was significantly higher ($t = -3.414$, $p = 0.002$) and chlorophyll content nearly so ($t = -1.901$, $p = 0.07$) in measurements made after 22 July than before. Organic content was also sharply higher during the latter period (Fig. 3); this cannot be explained solely in terms of the increase in soluble carbohydrates because the change is orders of magnitude greater. *Corophium* abundance declined by more than 50% during this time (Fig. 4). More importantly, however, *Corophium* were not seen crawling at the surface of the sediment after the 23rd-24th July, although they were extremely abundant prior to this date. The disappearance of *Corophium volutator* coincided with the arrival of large numbers of migratory shorebirds, particularly the Semipalmated sandpiper (*Calidris pusilla* L.). This species feeds selectively upon

Corophium at rates estimated at >10,000 *Corophium* per bird per day (Boates 1980; Hicklin and Smith 1984). The Minas Basin is the principal fall feeding ground for all the small shorebirds that breed in the eastern and central arctic and winter in the Caribbean and South America (Morrison 1977). Arrival of these predators is a dramatic and sudden event in mid-summer. In 1989 large flocks (5-10,000 birds) were first noted on 21st-23rd of July, and bird numbers reached a peak of >100,000 during the next week (K. Mawhinney, personal communication). Consistent monitoring of bird numbers was not carried out at Starrs Point in 1989, but the other major bird feeding site at Mary's Point, New Brunswick was monitored regularly by the Canadian Wildlife Service. Data are included in Table 1. With the appearance of the birds, the behavior of the *Corophium* changed : they no longer crawled about the sediment surface during the ebbing tide, but apparently remained within their burrows where they are less susceptible to predation (Goss-Custard 1970; Boates and Smith 1988).

Thus the arrival of the birds resulted both in continued decline in the number of *Corophium* present, and in a change in their behavior. We believe that the decline in *Corophium* activity produces secondary consequences (increased chlorophyll, carbohydrates and organic matter in the sediments) that reflect greater production by benthic diatoms. The increased production, as a tertiary effect, results in increases in the cohesive strength (i.e., decreased erodibility) of the sediments themselves.

CONCLUSION

In spite of our attempts at a fully comprehensive study, methodological and analytical uncertainties limit the conclusiveness with which these events can be interpreted. For example, mass balance calculations indicate that changes in soluble carbohydrate over the study period represent only a small fraction of the total changes in organic matter estimated by loss-on-ignition measurements. This leads to the further hypothesis that in the absence of bioturbation, increased cohesiveness of surficial sediments might result in trapping of some of the fibrous organic matter that is abundant in the leading edge of flooding water (i.e., the "microbore"), leading to a progressive enrichment of the sediment surface with non-soluble organic matter (Anderson 1983; Daborn and Pennachetti 1979). These changes in organic matter, and the interactions occurring between sediments and water during reflooding require further investigation.

Nonetheless, the temporal trends are consistent. As in our earlier study (Amos et al. 1988) sediment strength increased during the latter part of July coincident both with greater subaerial exposure, and with the seasonal arrival of an abundant predator of the principal invertebrate grazer. When the shorebirds arrive, changes in both abundance and behaviour of *Corophium* result in a release of the diatoms, as evidenced by chlorophyll values, and at the same time consequently the properties of the surface sediment change. Biological activities clearly play significant roles in determining the geotechnical and sedimentological properties of the intertidal sediments on Starrs Point flat. These results emphasise the limitations of standard laboratory studies of sediment properties, especially when dealing with cohesive sediments, and cast serious doubts on their predictive value (Paterson and Daborn 1991). There seems little prospect of fully understanding the *in situ* behaviour of intertidal sediments except through comprehensive, interdisciplinary field studies.

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REFERENCES

AMOS, C.L. and D.A. MOSHER. 1985. Erosion and deposition of fine-grained sediments from the Bay of Fundy. Sedimentology 32 : 815-832.

AMOS, C.L., N. VAN WAGONER and G.R. DABORN. 1988. The influence of subaerial exposure on the bulk properties of fine-grained intertidal sediment from Minas Basin, Bay of Fundy. Est. Coast. & Shelf Sci. 27 : 1-13.

AMOS, C.L., J. GRANT, G.R. DABORN and K. BLACK. Sea carousel - a benthic, annular flume. Est. Coast. & Shelf Sci. In press.

BOATES, J.S. 1980. Foraging Semipalmated sandpipers, *Calidris pusilla* (L.) and their major prey *Corophium volutator* (Pallas) on the Starrs Point mudflat, Minas Basin. Unpub. M.Sc. thesis, Acadia University.

BOATES, J.S. and P.C. SMITH. 1988. Crawling behaviour of the amphipod *Corophium volutator* and foraging by semipalmated sandpipers, *Calidris pusilla*. Can. J. Zool. 67 : 457-462.

COLES, S.M. 1979. Benthic microalgal populations on intertidal sediments and their role as precursors to salt marsh development. *In* R.C. Jefferies and A.J. Davies (Eds.) Ecological Processes in Coastal Environments. 1st Eur. Symp. Brit. Ecol. Soc., Blackwell Sci., Oxford, pp. 25-42.

DABORN, G.R. 1991. LISP-89 : Littoral Investigation of Sediment Properties. Final Report. Acadia Centre for Estuarine Research, Publication No. 17, Wolfville, N.S. 239 p.

DABORN, G.R. and C. PENNACHETTI. 1979. Physical oceanographic and sedimentological studies in the Southern Bight of Minas Basin. Proc. Nova Scotian Inst. Sci. 29 : 315-333.

DAVIES, B.E. 1974. Loss-on-ignition as an estimate of soil organic matter. Soil Sci. Soc. Amer. Proc. 38 : 150.

DECHO, A.W. 1990. Microbial exopolymer secretions in ocean environments : their role(s) in food webs and marine processes. Oceanogr. Mar. Biol. Ann. Rev. 28 : 73-153.

FAAS, R.W., H.A. CHRISTIAN and G.R. DABORN. 1992. Biological control of mass properties of surficial sediments : an example from Starr's Point Tidal Flat, Minas Basin, Bay of Fundy. Proc. Nearshore and Estuarine Cohesive Sed. Workshop, St. Petersburg, Florida. In press.

GOSS-CUSTARD, J.D. 1970. Feeding dispersion in some over-wintering wading birds. *In* J.H. Crook (Ed.) Social Behaviour in Birds and Mammals. Academic Press, N.Y. Pp. 3-35.

GRANT, J., V.V. BATHMAN and E.L. MILLS. 1986. The interaction between benthic diatom films and sediment transport. Est. Coast. and Shelf Sci. 23 : 225-238.

GUST, G. and M.J. MORRIS. 1989. Erosion thresholds and entrainment rates of undisturbed *in situ* sediments. J. Coast. Res. Special Issue No. 5 : 87-99.

HICKLIN, P.W. and P.C. SMITH. 1984. Selection of foraging sites and invertebrate prey by migrant Semipalmated sandpipers *Calidris pusilla* (L.) in Minas Basin, Bay of Fundy. Can. J. Zool. 62 : 2201-2210.

JENSEN, A. 1978. Chlorophylls and carotenoids. *In* J.A. Hellebust and J.S. Craigie (Eds.) Handbook of Phycological Methods. Cambridge University Press, pp. 59-74.

KOCHERT, G. 1978. Carbohydrate determination by the phenol-sulphuric acid method. *In* J.A. Hellebust and J.S. Craigie (Eds.) Handbook of Phycological Methods. Cambridge University Press, pp. 95-98.

LUCKENBACH, M.W. 1986. Sediment stability around animal tubes: the roles of hydrodynamic processes and biotic activity. Limnol. Oceanogr. 31 : 779-787.

MEADOWS, P.S. and A. TUFAIL. 1986. Bioturbation, microbial activity and sediment properties in an estuarine ecosystem. Proc. Roy. Soc. Edinb. 90B : 129-142.

MORRISON, R.I.G. 1977. The use of the Bay of Fundy by shorebirds. *In* G.R. Daborn (Ed.) Fundy Tidal Power and the Environment. Acadia Univ. Inst. Publ. No. 28, Wolfville, N.S., pp. 187-199.

OTSUBO, K. and K. MURAOKA. 1988. Critical shear stress of cohesive bottom sediments. J. Hydraul. Eng. 114 : 1241-1256.

PATERSON, D.M. 1989. Short-term changes in the erodibility of intertidal cohesive sediments related to the migratory behaviour of epipelic diatoms. Limnol. Oceanogr. 34 : 223-234.

PATERSON, D.M. and G.R. DABORN. 1991. Sediment stabilisation by biological action : significance for coastal engineering. *In* D.H. Peregrine and J.H. Loveless (Eds.) Developments in Coastal Engineering. Univ. Bristol, U.K., pp. 111-119.

Figure Captions

Figure 1. Enhancement in shear strength of surface sediments during low tide.

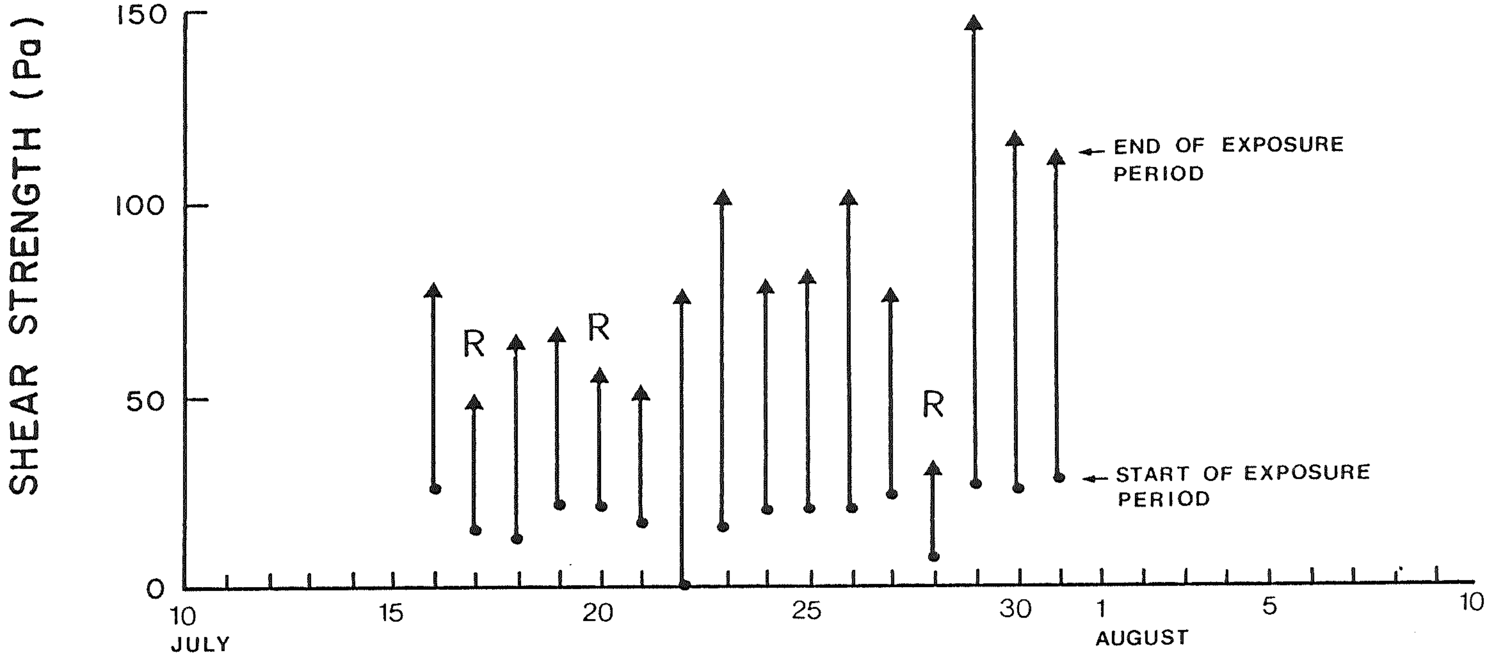
Key : ● - Initial value on falling tide; ▲ - maximum value before reimmersion on rising tide. R = rainy days.

(Units : Pascals).

Figure 2. Change in sediment carbohydrate concentrations during a single low tide exposure.

Figure 3. Mid-summer changes in mean concentrations of chlorophyll *a* (●), soluble carbohydrate (◇), and organic matter (■ - as % dry weight) of surface sediments on Starrs Point tidal flat, Minas Basin, July 1989. (Vertical bars show 1 S.D.).

Figure 4. Mean abundance of *Corophium volutator* on Starrs Point tidal flat, Minas Basin, July 1989. (Vertical bars show 1 S.D.)



Daborn et al.

Figure 1

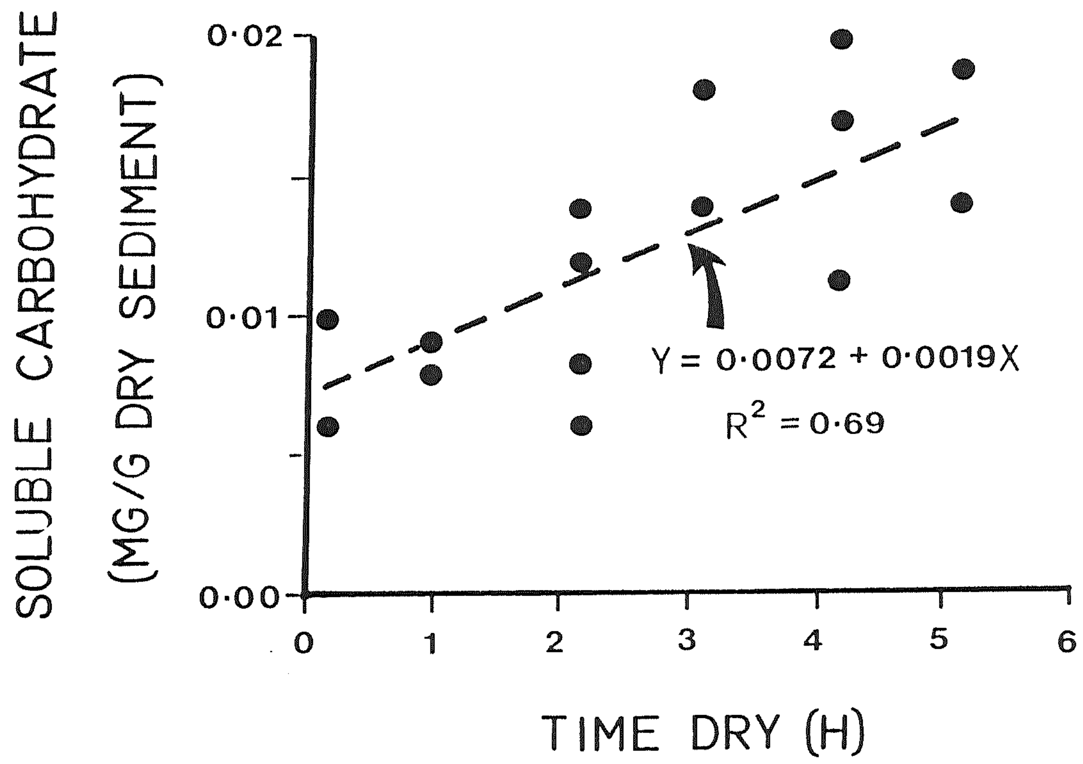


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Figure 2

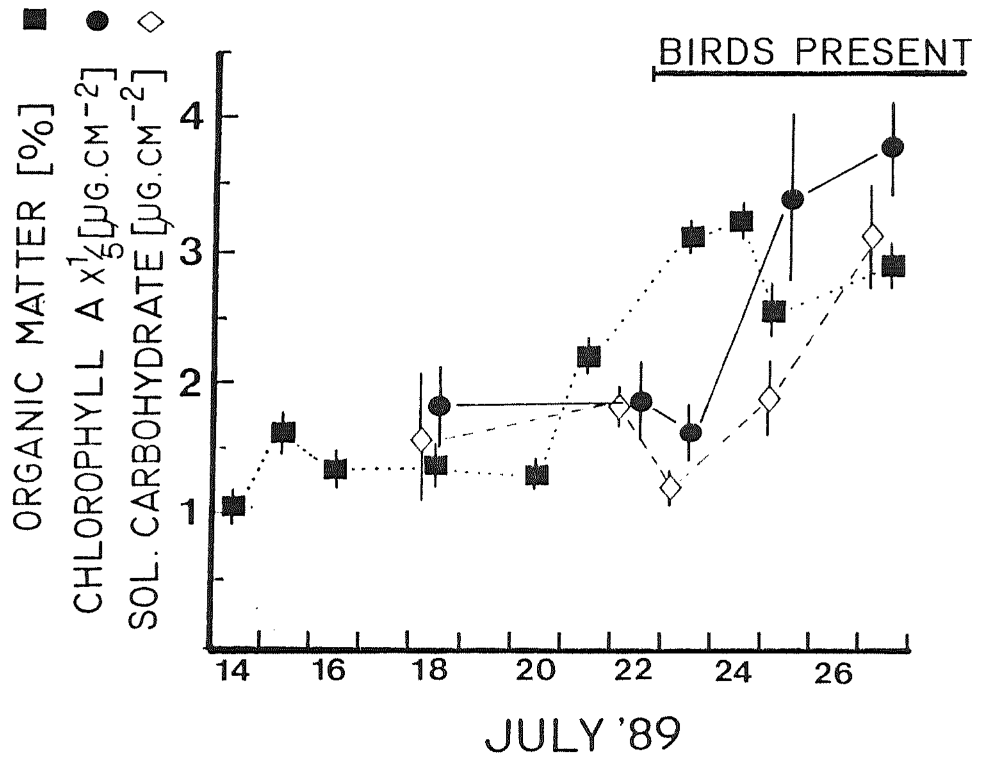

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Figure 3

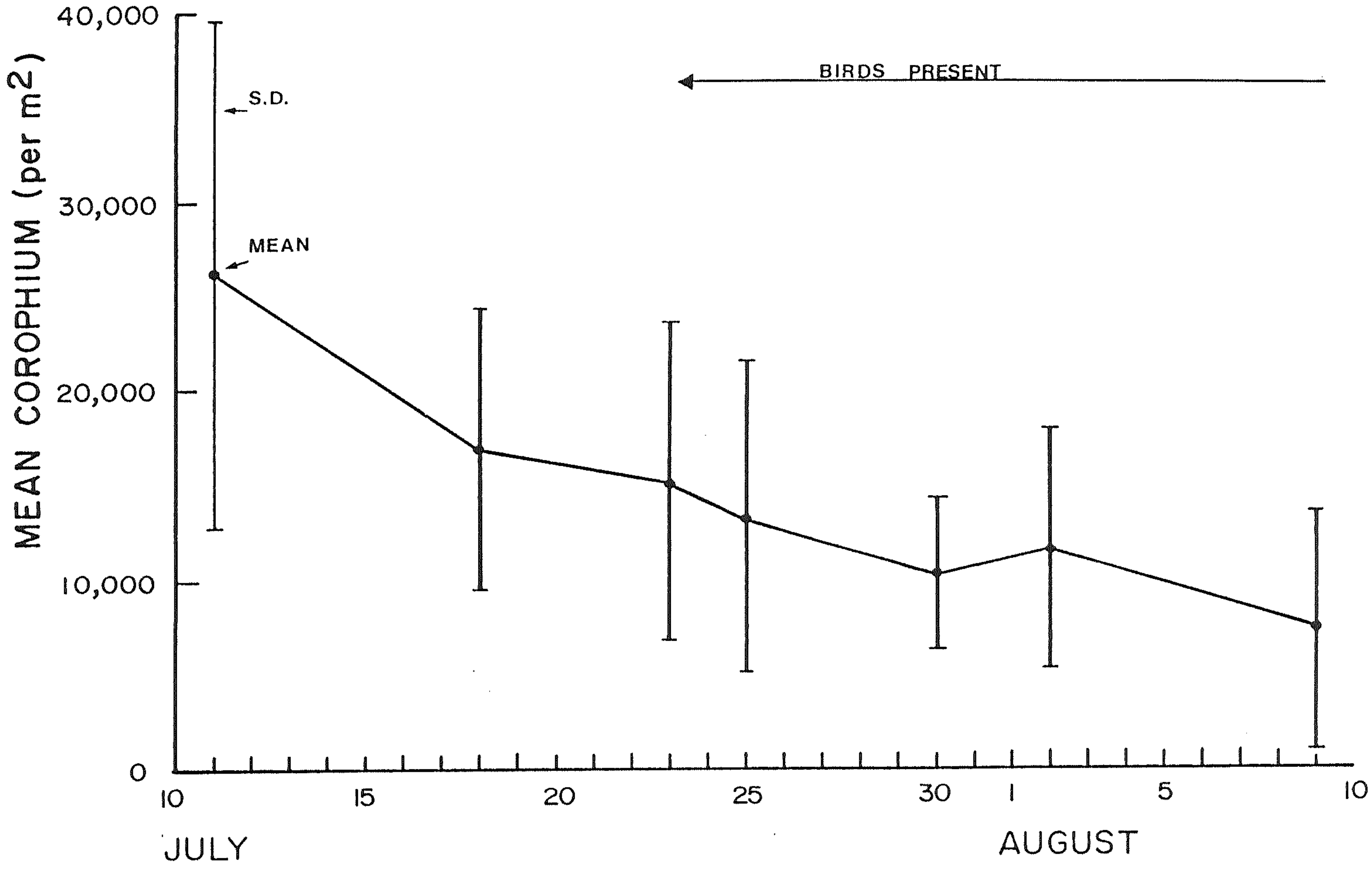

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Figure 4

Table 1. Temporal changes in sediment properties and environmental variables on a macrotidal flat.

July 1989	Initial Shear[a] Strength (Pa)	Friction[a] Angle (°)	Critical Shear[b] Stress for Erosion (Pa)	Water Content (Wt : Wt) (%)	Birds[c]	Weather
17	12	40.1	1.0	37.4		Heavy rain in night
18	9	38.7		41.8	300	
19	26	35.6		37.0	>1,000	Sunny
20[d]					>5,000	Rain
21	9	40.8	0.50	38.0	10,000	Cloudy
22	0	41.9	1.30	36.6		Cloudy
23	20	37.4	1.50	32.6		Sunny
24[d]					15,000	Sunny
25	12	41.8	2.50[e]	32.6	15,000	Sunny
26	15	42.0		36.2	15,000	Sunny
27	27	38.3		32.7		Occasional showers
28[d]					35,000	Light rain
29	32	39.5		37.6		Sunny
30	36	35.3	2.00	39.3		Sunny
31	34	34.9	1.90	39.0	60,000	Sunny

(a) 'INSIST' measurements determined shortly after exposure of the test site on the falling daytime tide. Friction angle is a measure of particle interlocking in the sediments: higher values indicate more dense packing, and lower values a more open structure.

(b) "SEA CAROUSEL" measurements conducted during inundation.

(c) Estimated numbers of migratory shorebirds at Mary's Point, New Brunswick.

(d) 'INSIST' and 'SEA CAROUSEL' measurements made at a more seaward site where grain size was more coarse (60% sand) than at inner sites (35-40% sand). Data for the seaward site are omitted from the table, but are incorporated in Figure 1.

(e) Measurement made on a site treated with formalin on 21 July 1989.

Table 2. Enhancement of sediment cohesion during recovery from treatment with formalin. (Data obtained from INSIST)

Date	Days Following Treatment	Initial Shear Strength (Pa)	Final Shear Strength (Pa)	Chlorophyll *a* (μg.cm^{-2}) [S.D.]	Carbohydrate (μg.cm^{-2}) [S.D.]
23 July	2	12	91	2.26 [0.54]	1.01 [0.14]
25 July	4	19	111	3.01 [0.21]	0.46 [0.07]
27 July	6	19	170	4.27 [0.34]	2.60 [0.35]