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DO ALTERNATE STABLE STATES OCCUR IN NATURAL ECOSYSTEMS? EVIDENCE FROM A TIDAL FLAT

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Abstract. Studies from a wide variety of ecosystems indicate that primary producers may protect their environment against degrading processes such as erosion by water current or wind. Theoretical analyses showed that the dynamics of these systems are governed by positive feedback. We investigated the implications of a positive feedback between growth of benthic diatoms and erosion of silt in tidal flat systems. A simple mathematical model shows that alternate stable states may occur in systems with positive feedback between diatom growth and silt accumulation, particularly in sediments with intermediate bottom shear stress. High diatom cover, high silt content, and low levels of erosion characterize one state. The other state is dominated by erosion, and hence both diatom cover and silt content are low. In an experimental study, we tested the critical model assumption that the growth rate of diatoms increases with the silt content of the sediment. Net growth of diatoms was significantly higher on silt than on sandy sediment after nine days of incubation, supporting the premise that diatom–silt interactions are governed by positive feedback. Furthermore, we compared model predictions to data on the physical and biological properties of sediments of a tidal flat. In accordance with our model, the silt content of sediments with intermediate to high bottom shear stress showed a clear and significant bimodal distribution, which may reflect the existence of alternate stable states. At low bottom shear stress, silt content was better explained by a unimodal distribution, as was predicted by our model. Patterns in chlorophyll *a* content were less clear. Nevertheless, chlorophyll *a* content was best explained by a bimodal distribution at high bottom shear stress, and in two of the three periods at low bottom shear stress. Our study indicates that the positive feedback between enhanced production of diatoms and decreased erosion of sediment significantly affects the dynamics of intertidal flat systems.

Key words: benthos; bottom shear stress; diatoms; diatom–sediment interaction; erosion; multiple stable states; phytobenthos; positive feedback; sediment; silt.

INTRODUCTION

Positive feedback between primary producers and environmental conditions has been identified for a wide variety of systems (Wilson and Agnew 1992). Plants promote the infiltration of water into the soil (Elwell and Stocking 1976, Walker et al. 1981), decrease erosion-induced losses of valuable nutrients (Elwell and Stocking 1976), and prevent accumulation of salt in the topsoil (Srivastava and Jefferies 1996), hence promoting plant growth. Mathematical studies have shown that positive feedback between plants and their environment may induce two alternative stable vegetation states (Walker et al. 1981, Rietkerk and Van de Koppel 1997, Van de Koppel et al. 1997). The concept of multiple stable states has proved valuable in explaining vegetation changes in coral reefs (Knowlton 1992), in semi-arid grasslands and arctic tundra (Noy-Meir 1975, May 1977, Rietkerk and Van de Koppel 1997, Van de Koppel et al. 1997), and in shallow lakes (Scheffer et al. 1993).

Although the concept of multiple stable states offers an attractive framework for the explanation of irreversible changes in ecosystems, direct empirical evidence for their existence in natural systems is scarce. This is likely to be caused by a variety of conceptual and experimental problems (Petraitis and Latham 1999). Several authors have debated the appropriate criteria for testing the existence of multiple stable states (Sutherland 1974, 1990, Connell and Sousa 1983, Peterson 1984, Petraitis and Latham 1999). Narrow definitions of community boundaries may have invoked very strict criteria for testing of multiple stable states, thereby dismissing systems in which alternate stable states are caused by feedback through environmental change (Sutherland 1990).

Positive feedback between primary producers and their environment is not necessarily limited to terrestrial systems. Benthic diatoms decrease erosion of sediment due to water current on marine tidal flats by secreting extracellular polymeric substances (EPS) (Neumann et al. 1970, Holland et al. 1974, De Boer

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1981, Paterson 1988, 1994, Paterson and Daborn 1991, Underwood and Paterson 1993*a, b*, Sutherland et al. 1998*a, b*). EPS form connective strands between diatoms, sediment grains, and associated particles (Grant et al. 1986, Paterson 1994). Extensive EPS networks, also called biofilms, increase sediment cohesion, and decrease bottom roughness and surface frictional drag (Vos et al. 1988, Paterson 1989), thereby reducing the susceptibility of the sediment to erosion (Sutherland et al. 1998*b*). As a result, high densities of diatoms significantly alter the frequency and magnitude of resuspension events (Neumann et al. 1970, Holland et al. 1974, Grant et al. 1986, Sutherland et al. 1998*b*). Reduction of resuspension rates will, in turn, have a great impact on diatom population dynamics (De Jonge and Van Beusekom 1995). Apart from the direct effects of erosion on diatom densities, there are a number of important indirect effects. Frequent and severe erosion will selectively remove clay and silt particles from the sediment, since the shear velocity needed to erode particles increases with particle size (Allen 1985, Vos et al. 1988, Daborn et al. 1993). Sediment with a low silt or clay content provides a less favorable substrate for diatom growth than silt- or clay-rich sediment. Diatoms were eroded easily in experiments with a low silt fraction, in part due to the occurrence of migrating ripples (Grant et al. 1986). Furthermore, sand movement may impose severe losses in diatom cell numbers resulting from cells being broken by collisions with sand grains (Delgado et al. 1991). Finally, an organic layer often covers the surface of sediment particles (Mayer 1994). This layer may provide a source of nutrients when the organic material is mineralized (Keil et al. 1994). Since sediments dominated by silt or clay particles have a much higher specific surface area, they are likely to be a much better source of nutrients for diatom growth. These nutrients may be important to diatom production, especially if nutrient levels in the overlying water are insufficient. Hence a positive feedback may exist, in which diatoms decrease erosion of silt, which in turn leads to high diatom growth and survival.

Despite the vast body of literature on diatom–sediment interactions, little is known of the dynamic implications of positive feedback between diatom growth and sediment composition. In the first part of this paper, we investigate a simple model of diatom growth and silt accretion, based on the general characteristics of diatom–sediment relationships. An important focus of our analysis is the effect of changes in the shear velocity of the overlying water, which is a dominant forcing factor in tidal flat ecosystems. Secondly, we test the critical model assumption that diatoms can obtain higher net growth rate on sediments with high silt or clay content compared to sediments consisting of sand only. Finally, we compare the predictions of the mathematical analysis to patterns in silt fraction and diatom density on a tidal flat in the Westerschelde, The Netherlands (3°45′ E, 51°25′ N).

A POSITIVE FEEDBACK MODEL

In this section we develop and analyze a general model describing the dynamics of silt particles and diatom cells within a relatively homogeneous patch of sediment on a tidal flat. The silt content of the sediment is determined by deposition from the overlying water column, and resuspension of silt from the flat to the water column. A dominant factor affecting both deposition and resuspension of sediment in tidal flat ecosystems is the shear stress imposed by water current upon the bottom (Allen 1985). The relationships between bottom shear stress, deposition and erosion of silt, and population dynamics of diatoms are highly nonlinear, and the processes involved interact strongly (Montague 1986, Paterson 1988, Dade et al. 1990, Amos et al. 1992*a, b*). To maximize the generality and robustness of the predictions, we do not explicitly specify the functions in our analysis, but rather use their general properties to derive our results. This will allow us to study the general behavior of the system without having to resort to cumbersome mathematical treatment of the complex functions used to describe sediment behavior (see Allen 1985 for a review).

Let S be the silt content of the sediment, and D be diatom density, both expressed in g/m². The rate of change of silt and diatoms within this patch can be modeled by the following set of differential equations:

$$\frac{dS}{dt} = I(\tau) - e(\tau, S, D)S \qquad (1A)$$

$$\frac{dD}{dt} = g(S, D)D - l(\tau, S, D)D \qquad (1B)$$

where $I(\tau)$ is the deposition rate of silt particles, which is a function of the bottom shear stress τ, $e(\tau, S, D)$ is the per particle rate of erosion of silt, which is a function of τ, S, and D; $g(S, D)$ is the per capita growth rate of the diatom population as a function of S and D; and $l(\tau, S, D)\ D$ is the per capita loss rate of diatoms due to erosion or damaging, as a function of τ, S, and D.

The general properties of the functions can easily be obtained from the literature. The deposition of sediment $I(\tau)$ is either independent, or a decreasing function of the bottom shear stress (Allen 1985). Erosion of sediment $e(\tau, S, D)$ remains low at low bottom shear stress, but increases dramatically near a threshold shear stress value (often referred to as the critical shear stress; Paterson and Daborn 1991, Sutherland et al. 1998*b*, Willows et al. 1998). Beyond this threshold, it increases with the shear stress imposed upon the sediment surface. Extracellular polymeric substance (EPS) excretion by diatoms increases the cohesiveness of the sediment, which results in an increase in the threshold shear stress at which sediment erosion initiates (Underwood and Paterson 1993*b*). With constant water velocity, the rate of erosion $e(\tau, S, D)$ decreased linearly with increasing diatom density under experimental con-

TABLE 1. The general model.

Populations:

$S(t)$ = silt content of the sediment at time t (g/m^2)

$D(t)$ = diatom density in the sediment at time t (g/m^2)

Function used in model:

$I(\tau)$ = deposition of silt on the sediment (g·m^{-2}·time^{-1})

$e(\tau, S, D)$ = specific erosion of silt from the sediment (time^{-1})

$g(S, D)$ = per capita growth rate of diatoms (time^{-1})

$l(\tau, S, D)$ = per capita loss rate of diatoms due to erosion (time^{-1})

Properties of functions:

Deposition of silt:

$$\frac{\partial I(\tau)}{\partial \tau} \leq 0$$

Erosion of silt:

$$\frac{\partial e(\tau, S, D)}{\partial \tau} \geq 0; \quad \frac{\partial e(\tau, S, D)}{\partial S} < 0; \quad \frac{\partial e(\tau, S, D)}{\partial D} < 0;$$

$$e(0, S, D) = 0; \quad e(\infty, S, D) = \infty; \quad e(\tau, S, \infty) = 0;$$

$$e(\tau, \infty, D) = 0$$

Growth of diatoms:

$$\frac{\partial g(S, D)}{\partial S} \geq 0; \quad \frac{\partial g(S, D)}{\partial D} < 0; \quad g(S, K) \leq 0$$

Erosion-induced loss of diatoms:

$$\frac{\partial l(\tau, S, D)}{\partial \tau} \geq 0; \quad \frac{\partial l(\tau, S, D)}{\partial S} < 0; \quad \frac{\partial l(\tau, S, D)}{\partial D} < 0;$$

$$l(0, S, D) = 0; \quad l(\infty, S, D) \to \infty$$

ditions (Sutherland et al. 1998*a, b*). Cohesive forces between silt particles may protect silt against erosion, and hence result in decreased erosion with increasing silt content of the sediment. Little is known, however, of the importance of physical cohesion relative to biological binding.

Silt-rich sediments may be a source of nutrients to diatoms, as they usually have a high rate of mineralization of organic matter and high porewater concentrations of dissolved nutrients (Underwood and Kromkamp 1999). Sand flats, on the other hand, are more oligotrophic (Heip et al. 1995). Therefore, we consider diatom growth to be an increasing function of the silt content of the sediment. If, however, nutrient concentrations in the water column are high, this effect is probably rather small. In dense biofilms, net diatom production is likely to be low due to selfshading or low CO$_2$ availability (Kromkamp et al. 1995, Underwood and Kromkamp 1999), irrespective of nutrient availability. This will impose an upper limit to diatom density. Hence we assume that per capita diatom growth $g(S, D)$ decreases with increasing diatom density, and that diatom growth is negative beyond maximum diatom density K, independent of the silt content of the sediment. Nutrient limitation in sediments with low silt content, however, may result in negative net diatom growth at diatom densities below K. Losses of diatoms due to resuspension and damaging $l(\tau, S, D)$ increase with bottom shear stress. Erosive losses decrease with increasing diatom densities because of biofilm formation (Sutherland et al. 1998*b*). Erosive losses further decrease with increasing sediment silt content, because sediment with a high silt content provides a better substrate for the formation of biofilms. In the empirical part of this paper, we will further address this assumption. We have listed the general mathematical properties of the functions in Table 1.

Graphical analysis

The dynamics of this system can be analyzed using graphical methods (e.g., Yodzis 1989). In Fig. 1, we have depicted the silt isocline (at which there is no change in silt content) and the diatom isocline (at which there is no change in diatom density) in the silt–diatom plane. Silt content increases to the left of the silt isocline, whereas it decreases to the right. Diatom density increases underneath the diatom isocline, whereas it decreases above. The diatom isocline levels off to maximum at high S due to density-dependent limitation.

At the intersections of the isoclines, both silt and diatoms are in equilibrium. The equilibrium is stable if both isoclines have a positive slope, and the slope of the silt isocline exceeds the slope of the diatom isocline. This implies that the system will return to this equilibrium after a small perturbation. The equilibrium is unstable if any of the isoclines has a negative slope, or if the slope of the silt isocline is smaller than the

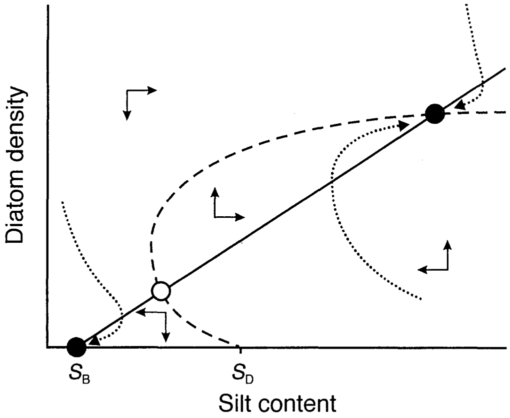

FIG. 1. The zero-change isoclines of silt (solid line) and diatoms (dashed line) in the silt–diatom plane. Solid circles represent stable equilibria; open circles represent unstable equilibria. The dotted lines depict trajectories with different initial conditions. The horizontal vectors depict the direction of change of silt content, and the vertical vectors depict the direction of change of the diatom density. See *Graphical analysis* in the text for further explanation. The graph is made using a specific example of system 1: $dS/dt = I - e_{\max}[a/(a + D)]\tau S$; and $dD/dt = r(1 - D/K)D - l_{\max}[b/(b + S)]\,[c/(c + D)]\tau D$.

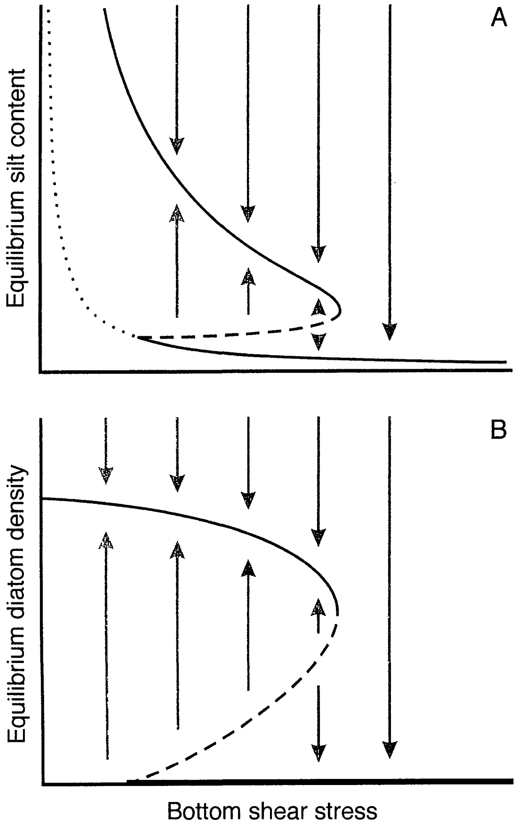

FIG. 2. (A) Equilibrium silt content, and (B) diatom density as a function of bottom shear stress (τ). The dashed line depicts unstable equilibria. Two stable states are found at intermediate bottom shear stress. The dotted line represents the relationship between silt content and bottom shear stress in a system without diatoms. For further details on model specifics see Fig. 1.

slope of the diatom isocline. The system will move away from an unstable equilibrium if disturbed. A boundary equilibrium is found at the intercept of the silt isocline and the silt axis, at $S = S_B$ and $D = 0$. If diatoms are absent, the silt content will equilibrate at a value of S_B. In the specific configuration used in Fig. 1, diatoms need a minimal silt content in order to establish on the sediment. This silt level is depicted in Fig. 1 as S_D. If $S_B < S_D$, there is insufficient silt on a bare flat for diatoms to grow and compensate for erosion-induced losses. Hence the boundary equilibrium is stable. If $S_B > S_D$, diatoms will be able to colonize a bare flat, and the boundary equilibrium is unstable. In the Appendix we give a formal derivation of the stability criteria. In Fig. 1, both the internal equilibrium and the boundary equilibrium are stable. This implies that two stable states may occur in diatom–silt models. Depending on initial conditions, our system may either develop to bare sediment with a low silt content, or to silt-rich sediment with high diatom cover.

Fig. 2 depicts the consequences of changes in bottom shear stress on equilibrium silt content and diatom density. At low bottom shear stress (low water velocity), there is little effect of erosion, and hence only one stable state is found, characterized by high silt (Fig. 2A) and diatom levels (Fig. 2B). At intermediate shear stress, alternate stable states may occur. In one state, bare sediment with low silt content prevails. A high silt content and a dense cover of diatoms characterize the other state. At high bottom shear stress, losses due to erosion dominate sediment and diatom dynamics, and only one stable state is found with no diatoms and little silt.

The patterns depicted in Fig. 2 are based on a simple form of system 1 where erosion decreases gradually with increasing diatom densities, and direct effects of silt on diatom growth are ignored. These are realistic assumptions for diatom–silt interactions in eutrophic estuaries (Kromkamp et al. 1995, Sutherland et al. 1998*a*, Underwood and Kromkamp 1999), since estuaries often provide a nutrient-rich environment. In the Appendix we show that the potential for multiple stable states is a general property of system 1, independent of the specific functions. It is well possible, however, that models with more complex relationships between components may have more than one internal stable equilibrium. A thorough analysis of the potential for two or more internal stable states will require further specification of the functions used in system 1, and extensive mathematical treatment beyond the scope of this paper.

EMPIRICAL SUPPORT

The positive feedback interaction consists of two components. First, diatoms are assumed to decrease the rate of erosion of sediment, and hence promote a high sediment silt content. Second, a high sediment silt content should lead to high net diatom growth. Although many papers report on reduction of erosion of sediment by diatom films (Neumann et al. 1970, Holland et al. 1974, De Boer 1981, Paterson 1988, 1994, Paterson and Daborn 1991, Underwood and Paterson 1993*a, b*, Sutherland et al. 1998*a, b*), there is only limited evidence supporting the premise that diatom growth is limited in sediments with low silt content. Below, we present experimental evidence for this critical model assumption. We performed two experiments in which net growth of diatoms on sand and on silt were compared. In both experiments, we tested the hypothesis that diatoms grow better on silt than on sand. In the first experiment, diatoms were grown either under intertidal or subtidal conditions, using nutrient-enriched seawater as a medium. The second experiment used only seawater without enrichment, to induce nutrient limiting conditions.

In the second section (see *Materials and methods; Observational data*), we relate the predictions of the model to observations on silt fraction and diatom content of the sediment on a tidal flat. The model predicts that, on the scale of a patch of sediment, alternate stable states may exist, particularly at intermediate bottom shear stress levels. Alternate stable states occurring on a small scale may be reflected by a bimodal distribution in this variable when sampling is repeated in space to cover larger scales such as an entire tidal flat (Scheffer 1998). Hence silt content and diatom densities are expected to follow a unimodal distribution at very low or very high bottom shear stress, whereas a bimodal distribution may be found at intermediate bottom shear stress. In this section, we investigate distributions of silt and diatoms on an estuarine tidal flat. The patterns occurring in these variables are related to bottom shear stress estimates. Furthermore, we test the alternative hypothesis that macrofaunal abundance may explain the observed patterns.

MATERIAL AND METHODS

Experiments

The experiments on the effects of substrate type on diatom growth used small recirculating flume systems to culture diatoms. The flumes were constructed from stainless steel, following the specifications of Kamermans and Huitema (1994). Sediment was placed in a container in the center of the flume (50 × 10 cm by 12 cm high.) The remaining part of the flume was covered with aluminum foil to prevent growth of diatoms outside of the test sections. The test section was filled with either silt-dominated (median grain size 27 μm) or sand-dominated (median grain size 182 μm) sediment obtained from a tidal flat in the Westerschelde. Sediment was frozen prior to the experiment for at least 24 h to kill all living macrobenthic animals. The flumes were filled with 20 L of 0.2-μm filtered seawater. Since we were primarily interested in the response of diatoms as a functional group, rather than the response of specific species, we inoculated the flumes with a mixture of diatoms obtained from both sand-dominated and silt-dominated sediment. Flow speed of the water at 3 cm above the top of the sediment was ~10 cm/s. The flumes were placed in a 15°C room and illuminated for 16 h/d with Osram L40W/20S TL-tubes (Osram Sylvania, Danvers, Massachusetts, USA). We compensated for evaporation of water from the flumes by adding demineralized water every second day.

In the first experiment, we used seawater obtained from the Oosterschelde (28 g/kg), and diluted to 25 g/kg with demineralized water, which is approximately the salinity of the Westerschelde (Fig. 3). Nutrients, trace elements, and vitamins were added according to Kester et al. 1967. Four flumes were filled with silt-dominated sediment, and four were filled with sand-dominated sediment. Two of each type were submerged continuously, with ~4 cm of overlying water. The others were submerged during the dark period, but were pulled out of the water for 5 h/d during the illuminated period, to simulate a tidal regime. Light intensity on the sediment was 23 μmol photons·m^{-2}·s^{-1} during the periods in which both tidal treatments were submerged. During the time in which the containers involved in the tidal treatment were pulled out of the water, light intensity changed to 61 μmol photons·m^{-2}·s^{-1} for the emerged treatment and 35 μmol photons·m^{-2}·s^{-1} for the submerged treatment, due to repositioning of the TL-tubes. The second experiment differed from the first in that only seawater was used as medium for diatom growth, all treatments were submerged for the entire experimental period, five replicates were used per treatment, and a light intensity of 23 μmol photons·m^{-2}·s^{-1} was maintained throughout the experiment. In both experiments, the sediment was incubated for nine days.

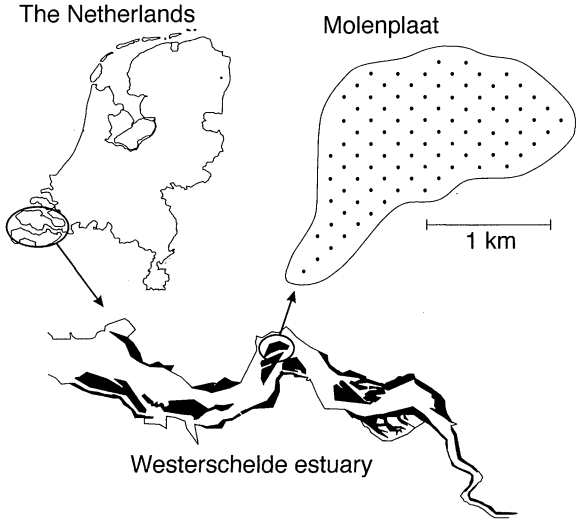

FIG. 3. The Molenplaat study area in the Westerschelde. Dots in the Molenplaat map represent the sample grid.

At the end of the experiments, three sediment samples were obtained from the upper 5 mm of the sediment in each container. Samples were freeze dried, and analyzed for chlorophyll *a* content spectrophotometrically, following the method of Lorenzen (1967) after a 24-h extraction in 90% methanol, and using an absorption coefficient of chlorophyll *a* of 13.9 μg·ml^{-1}·cm^{-1} (Iwamura et al. 1970). Average chlorophyll *a* content per sediment core was used in the analysis to avoid pseudoreplication. One sample of water was taken per flume and analyzed for nutrient content using colorimetric techniques. We calculated the amount of nutrients stored in diatom biomass in the sediment cores using the mean chlorophyll *a* figures per treatment, a carbon to chlorophyll *a* ratio of 30 (g:g) (Wetsteyn and Kromkamp 1994), and Redfield carbon to nutrient ratios (e.g., Valiela 1995). Results of both experiments were analyzed with a two-factor fixed effects analysis of variance (ANOVA). Data were log-transformed prior to the analysis if this improved the homogeneity of variances. Data did not violate the assumptions of ANOVA unless specified.

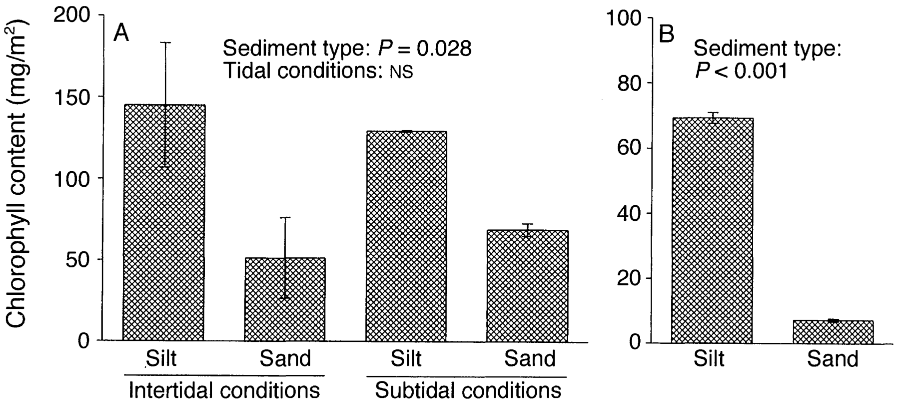

FIG. 4. Effects of sediment type on chlorophyll *a* content of the upper 5 mm of the sediment after nine days of incubation. In (A) diatoms were grown in a nutrient-enriched medium; in (B) nutrients were in limited supply. Error bars represent ± 1 SE.

Observational data

Data on sediment characteristics and chlorophyll *a* content, which is an estimate of total algal abundance (Underwood and Paterson 1993*b*), were obtained from the Molenplaat, a tidal flat in the Westerschelde in the southwest of the Netherlands (Fig. 3). In 1995, a spatial grid of 92 sample points was established, with a minimal distance of 130 m between adjacent points (Fig. 3). At each point, two samples were taken of the upper 1 cm of the sediment (12.3 mm diameter cores), in which silt fraction (<63 μm) and chlorophyll *a* content were determined. One sample was taken of the upper 30 cm (110-mm diameter core), in which densities and biomass (ash-free dry mass) of macrobenthic species were determined. Samples were obtained on 22 March, 30 June, 28 September, and 12 December of 1995. In March, only a subset of the total grid was sampled, containing 89% of the grid points sampled in the other months, and the chlorophyll *a* content of the sediment was not determined.

The bottom shear stress on the sediment was estimated using the two-dimensional hydrodynamic model of the Molenplaat, developed by Delft Hydraulics (Delft Hydraulics 1997). This model predicts the depth-averaged flow velocity of the water during a tidal cycle, using a variably spaced rectangular grid with grid size between 20 and 40 m. The model domain was centered around the Molenplaat tidal flat and extended ~10 km upstream and downstream of the flat. Open boundary conditions were derived from a two-dimensional hydrodynamic model for the whole Westerschelde, using a 100-m grid size. The model uses a detailed description of the bathymetry and bottom roughness of the sediment as its input parameters. The depth-averaged flow velocity in turn is used to estimate the maximal bottom shear stress within a tidal cycle. Bottom shear stress estimates at sediment sample points were obtained with the nearest-neighbors method, using a neighborhood of 80 × 80 m around each sample point.

Statistical analysis of the observations

The data on silt and chlorophyll *a* levels were analyzed as follows. The overall trend in silt or chlorophyll *a* content of the sediment with respect to bottom shear stress in each month was determined using least-squares regression and the model: $Y = aX^b + c$, where X is silt content. Data were log-transformed prior to the analysis if this improved the homogeneity of variances. We tested for bimodal distributions by fitting on the residuals of the least-squares regression to both the normal distribution function and a bimodal function given by $P = q\ N(x, \mu_1, \sigma_1) + (1 - q)\ N(x, \mu_2, \sigma_2)$, where q is a constant between 0 and 1, N is the normal distribution with mean μ_1 and standard deviation σ_1, and x is either silt fraction or chlorophyll *a* content. Distributions were fitted using the maximum likelihood method (Sokal and Rohlf 1995). The distribution of a variable was considered bimodal if the bimodal model gave a significantly better fit than the unimodal model, as determined by the log-likelihood ratio (which explicitly takes into account the increase in the number of parameters). Seasonal differences in silt and chlorophyll *a* content were analyzed using the Kruskal-Wallis nonparametric analysis of variance (Sokal and Rohlf 1995). Differences in macrobenthic densities were analyzed using ANOVA. The Mann-Whitney *U* test was used when the assumptions of ANOVA were violated.

RESULTS

Experiments

The first flume experiment revealed a significant effect of silt content on net diatom biomass accumulation, as measured by the chlorophyll *a* content of the sediment after nine days of incubation (Fig. 4A; ANOVA, sediment type, $F_{1,4} = 11.4$, $P = 0.028$). No effect was found of the imposed tidal regime or of the interaction between tidal regime and sediment type on diatom growth (ANOVA, tidal regime, $F_{1,4} = 0.002$, $P =$

TABLE 2. Nutrient concentration in μmol per liter in the start-up medium and the final concentrations per treatment.

Treatment	n	NH_4^+	NO_x^-	H_4SiO_4	PO_4^{3-}
Experiment I					
Start-up medium		3.91×10^{-3}	5906	158.6	51.6
Silt/emerged	2	130.0 (84.1)	2065 (3)	69.4 (46.0)	8.5 (3.5)
Sand/emerged	2	3.6 (0.1)	1961 (40)	35.7 (33.0)	4.6 (0.3)
Silt/submerged	2	106.7 (13.4)	1043 (110)	14.5 (0.6)	4.2 (0.8)
Sand/submerged	2	5.5 (2.1)	1527 (298)	4.3 (0.9)	6.3 (0.5)
Stored in diatom biomass; calculated using Redfield ratios					
Silt/emerged	2	164.2 (43.2)		136.8 (36.0)	10.3 (2.7)
Sand/emerged	2	58.0 (28.1)		48.4 (23.4)	3.6 (1.8)
Silt/submerged	2	146.5 (0.4)		122.1 (0.4)	9.2 (0.0)
Sand/submerged	2	78.0 (4.4)		65.0 (3.7)	4.9 (0.3)
Experiment II					
Start-up medium		0.0	28.8	11.1	2.1
Silt	5	18.72 (6.85)	29.63 (4.62)	2.89 (0.80)	0.23 (0.07)
Sand	5	0.15 (0.00)	1.55 (0.37)	2.04 (0.22)	0.52 (0.09)
Stored in diatom biomass; calculated using Redfield ratios					
Silt	5	78.5 (1.9)		65.4 (1.6)	4.9 (0.1)
Sand	5	8.0 (0.5)		6.7 (0.4)	0.5 (0.0)

Note: Standard error is reported in parentheses.

0.967; interaction, $F_{1,4} = 0.532$, $P = 0.506$). Concentrations of ammonium (NH_4^+), NO_x^- ($NO_2^- + NO_3^-$), silicate (H_4SiO_4), and phosphate (PO_4^{3-}) in the medium after the experiment were on average higher than concentrations that are considered limiting to diatom growth (Table 2; limiting concentrations dissolved inorganic nitrogen, <2 μmol/L; phosphate, <0.5 μmol/L; silicate, <5 μmol/L; Fisher et al. 1988). This suggests that the availability of these nutrients did not limit diatom growth in the first experiment. Ammonium concentrations were significantly higher in the silt treatment than in the sand treatment (Table 2; ANOVA, $F_{1,6} = 10.3$, $P = 0.018$).

The second experiment revealed an order of magnitude difference in net diatom growth between sediment types (Fig. 4B; ANOVA, $F_{1,8} = 289$, $P < 0.001$), indicating that diatoms can realize a much higher growth rate on silt than on sand if nutrient supply from the overlying water is low. The concentrations of ammonium and NO_x^- were found to be significantly higher in the silt treatment than in the sand treatment, whereas phosphate was found to be significantly higher in the sand treatment (ANOVA, ammonium, $F_{1,8} = 7.35$, $P = 0.027$; NO_x^-, $F_{1,8} = 53.7$, $P < 0.001$; phosphate, $F_{1,8} = 6.87$, $P = 0.031$). Silicate concentration did not differ significantly between the treatments (ANOVA, $F_{1,8} = 1.76$, $P = 0.355$). In the silt treatment, the sum of nutrient uptake by diatoms and the nutrients recovered from the water after the experiment exceeded the nutrients supplied via the medium for dissolved inorganic nitrogen, phosphate, and silicate. In the sand treatment, this did not occur. This suggests that silt, as opposed to sand, can be an important source of nutrients to benthic diatoms in nutrient limited conditions.

Observational data

A negative relationship was found between the silt content of the sediment and the maximum shear stress estimate (τ_{max}) for the data obtained in March (Fig. 5A; $r = 0.88$, $F_{2,81} = 142$, $P < 0.001$), June (Fig. 5B; $r = 0.84$, $F_{2,88} = 115$, $P < 0.001$), September (Fig. 5C; $r = 0.83$, $F_{2,89} = 101$, $P < 0.001$), and December (Fig. 5D; $r = 0.71$, $F_{2,89} = 44.45$, $P < 0.001$). Silt content differed significantly between the seasons (Kruskal-Wallis test; $\chi_3^2 = 45.0$, $P < 0.001$). No significant effect of season was found when March was omitted (Kruskal-Wallis test; $\chi_2^2 = 0.43$, $P = 0.81$), which indicates that the main effect of season was caused by the difference between March and the other seasons. The data obtained in June, September, and December seemed to have a bimodal distribution at high τ_{max} levels (Fig. 5B–D). We tested this observation by dividing the data set into two sections, using an arbitrary threshold value of $\log_{10}(\tau_{max}) = 0$ (τ_{max} in units of newtons per square meter). As an example, we depicted the frequency distribution of silt fractions in June, after the removal of the negative trend, for both $\log(\tau_{max}) \leq 0$ and $\log(\tau_{max}) > 0$ (Fig. 6A,B). Note the bimodal pattern at $\log(\tau_{max}) > 0$ in Fig. 6B. Silt distribution was found to be significantly better explained by a bimodal distribution to the right of $\log(\tau_{max}) = 0$ for all seasons (Log-likelihood ratio test: March, $\chi_3^2 = 7.88$, $P = 0.049$; June, $\chi_3^2 = 44.4$, $P < 0.001$; September, $\chi_3^2 = 16.6$, $P = 0.001$; December, $\chi_3^2 = 50.0$, $P < 0.001$). To the left of $\log(\tau_{max}) = 0$, the bimodal distribution gave no significant improvement (Log-likelihood ratio test: March, χ_3^2 1.23, $P = 0.747$; June, $\chi_3^2 = 2.11$, $P < 0.551$; September, $\chi_3^2 = 1.38$, $P = 0.711$), except for December ($\chi_3^2 = 13.2$, $P = 0.004$). The bimodal distribution at

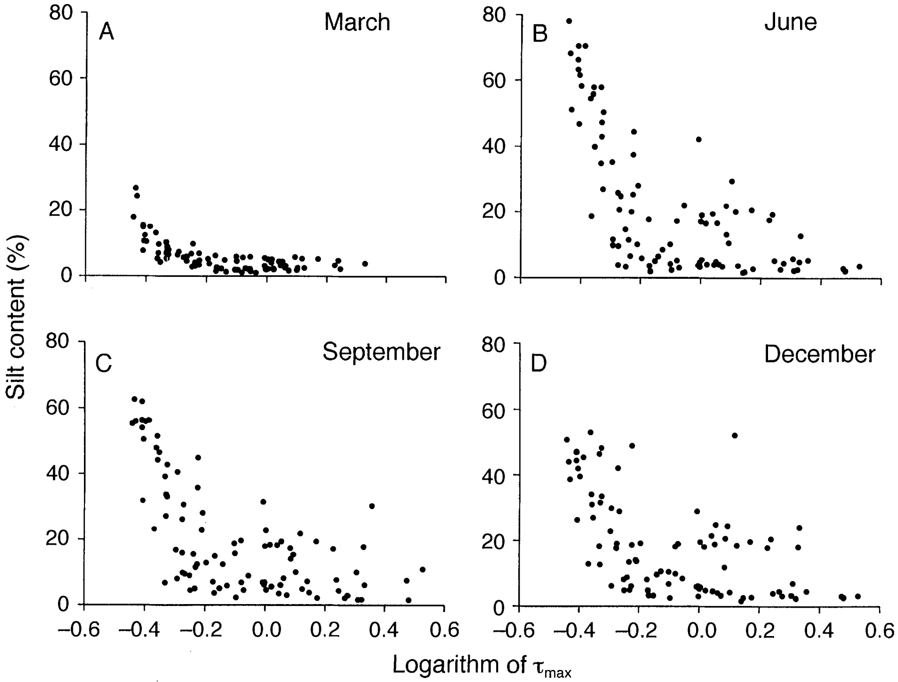

FIG. 5. Silt fraction in the upper 1 cm of the sediment vs. the maximal bottom shear stress (τ_{max}) estimate ($\log_{10}$ values; τ_{max} in units of newtons per square meter) on the Molenplaat tidal flat in (A) March, (B) June, (C) September, and (D) December. Each point represents a single sample. The measure τ_{max} is a model estimate of the maximal bottom shear stress during a tidal cycle. Note the bimodal distribution in silt content at $\log(\tau_{max}) > 0$.

$\log(\tau_{max}) < 0$ in December was caused by five points protruding to the right in Fig. 5D. We do not think that the position of these points is related to positive feedback. The analysis was insensitive to the exact position of the threshold in June, September, and December; small changes in threshold value had no effect on significance. In the March data set, the significance of a bimodal distribution at high $\log(\tau_{max})$ was highly sensitive for changes in the position of the threshold. Therefore, we conclude that there is only very weak evidence for bimodal distribution at high bottom shear stress in March.

The chlorophyll *a* content showed a slight but significant negative relationship with bottom shear stress in all seasons (Fig. 7A–C; June, $r = 0.37$, $F_{2,85} = 6.72$, $P = 0.002$; September, $r = 0.36$, $F_{2,89} = 6.64$, $P = 0.002$; December, $r = 0.28$, $F_{2,89} = 3.84$, $P = 0.025$). Clustering around states was much less apparent in the chlorophyll *a* data than in the silt data (See Fig. 6C, D for the June data set). Still, chlorophyll *a* content was found to be significantly better explained by a bimodal distribution at $\log(\tau_{max}) > 0$ for all measured seasons (Log-likelihood ratio test; June, $\chi^2_3 = 8.55$, $P = 0.036$; September, $\chi^2_3 = 10.3$, $P = 0.016$; December, $\chi^2_3 = 9.94$, $P = 0.019$). A significant bimodal distribution was also found for $\log(\tau_{max}) \leq 0$ in both September and December (Log-likelihood ratio test: September, $\chi^2_3 = 8.97$, $P = 0.030$; December, $\chi^2_3 = 8.23$, $P = 0.042$), whereas in June a bimodal distribution gave no significant improvement (Log-likelihood ratio test; June, $\chi^2_3 = 1.23$, $P = 0.747$). No significant effect of season was found on chlorophyll *a* content (Kruskal-Wallis test; $\chi^2_2 = 6.23$, $P = 0.101$). A positive correlation between silt content and chlorophyll *a* concentration was found (Not shown; $r = 0.54$, $t = 6.42$, $P < 0.001$) at $\log(\tau_{max}) > 0$, using the combined data of June, September, and December. This implies that clusters with high silt values correspond to clusters with high chlorophyll *a* values.

We tested the alternative hypothesis that the bimodal distribution of silt and chlorophyll *a* at high bottom shear stress was caused by increased macrobenthic activity in the low silt cluster, such as bioturbation of the sediment or grazing of diatoms. Sample points at $\log(\tau_{max}) > 0$ were divided in two groups on basis of silt content. Sample points with a silt content <12% were assigned to the low-silt group, whereas sample points with silt content >12% were assigned to the high-silt group. No significant differences were found in the biomass of deposit feeders, surface deposit feeders, omnivores, or suspension feeders between the low-silt and the high-silt group (Table 3). Individual species did not show significant differences, except for *Bathyporeia pilosa,* which was significantly higher in the low-silt group, but had a low biomass at all sites, and *Heteromastus filiformis,* which was significantly higher in the high-silt group (Table 3). Mean biomass of the macrobenthic functional groups and most individual

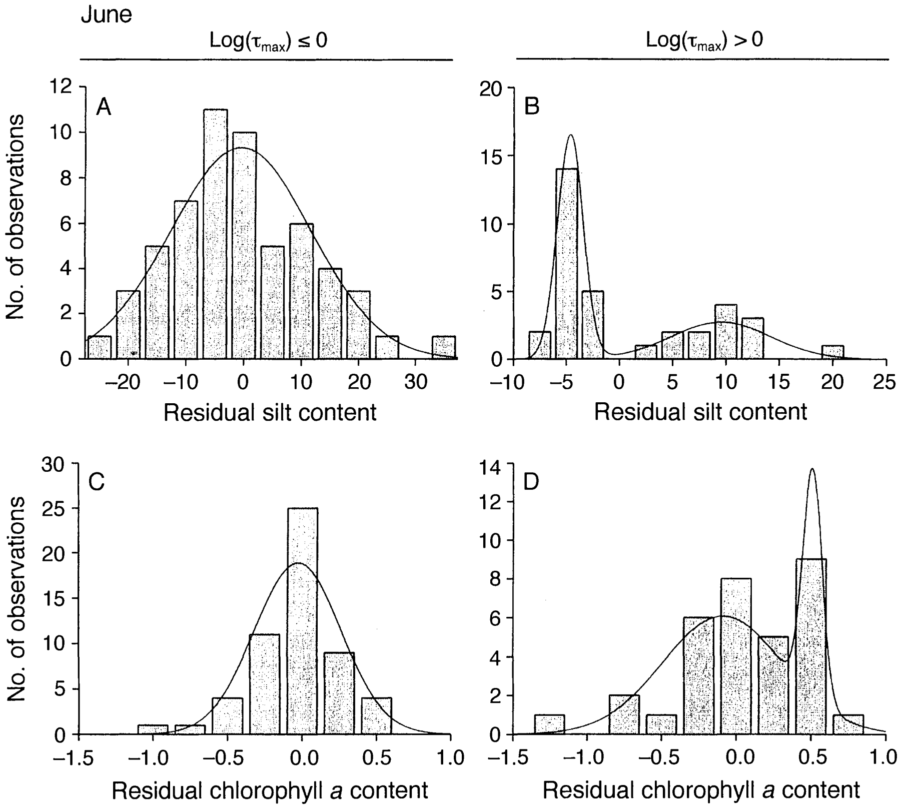

FIG. 6. Distribution of the residual silt fraction and chlorophyll *a* content after removal of the negative trend in the data. Left and right graphs represent the data at $\log(\tau_{max}) \leq 0$ (A, C) and $\log(\tau_{max}) \geq 0$ (B, D), respectively. Curves represent the fitted probability distribution; a bimodal distribution is shown when it explained the data significantly better than the normal distribution.

species tended to be highest in the high-silt group, opposite to the expectations of the alternative hypothesis. Difference in chlorophyll *a* content was highly significant between the two groups (Table 3).

DISCUSSION

The mathematical analysis presented in this paper indicates that the generally observed functional relationships between erosion, silt content, and diatom growth may lead to the existence of alternate stable states in tidal flat systems. Interactions between diatoms and silt in the sediment induce positive feedback between net silt accumulation and diatom growth. Increase in silt content in a sandy substrate improves conditions for diatom growth. This may lead to a runaway response in which increased diatom density leads to increased silt content and vice versa, until an upper equilibrium is reached. If the initial increase is too small, however, conditions remain adverse for diatom growth, and the system returns to the sandy state. Beyond a threshold bottom shear stress, two alternate stable states may appear in tidal flat systems, as is demonstrated in our analysis.

In order to function as a positive feedback system, the interaction between diatoms and silt should be shaped in such a way that an initial change of the system is amplified by the interaction (DeAngelis et al. 1986). An overwhelming body of evidence exists on the first part of this interaction; i.e., a reduction of erosion of sediment by diatom films or microbial mats, leading to high sediment silt content (Neumann et al. 1970, Holland et al. 1974, De Boer 1981, Paterson 1988, 1994, Paterson and Daborn 1991, Underwood and Paterson 1993*a*, *b*, Sutherland et al. 1998*a*, *b*). Much less evidence exists in the literature on the second part; i.e., the positive effects of high silt content of the sediment on the growth rate and survival of diatoms. The experiments we present confirm that this component of the positive feedback is evident in tidal flat ecosystems. Independent of the tidal regime and the degree of nutrient limitation, diatoms obtained a higher rate of growth on silt-dominated sediment than on sand-dominated sediment. The experiment indicated that silt-rich sediments can be an important source of nutrients such as nitrogen, phosphorous, and silicate, which may result in an order of magnitude difference in growth rate of diatoms cultured on silt, as compared to sand, under low nutrient conditions. Oxygen bubbles, likely resulting from photosynthesis, were observed in diatom films in the sand treatment of the first

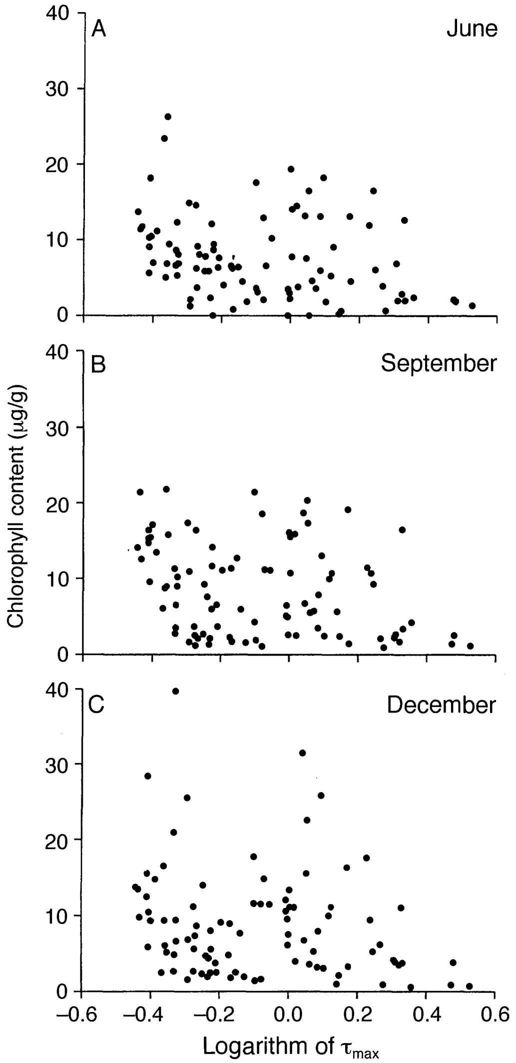

FIG. 7. Chlorophyll *a* content (μg/g) in the upper cm of the sediment vs. the maximal bottom shear stress estimate ($\log_{10}$-transformed; τ_{max} in units of newtons per square meter) on the Molenplaat tidal flat in (A) June, (B) September, and (C) December. See Fig. 5 for further explanation.

experiment with nutrient-enriched medium. These bubbles caused the diatom film to rupture. Blistering of biofilms due to the production of oxygen has been reported in other experimental studies (Yallop et al. 1994, Sutherland et al. 1998*b*) and has been observed in the field (Sutherland et al. 1998*a*). The entrapment of oxygen bubbles within the biofilm would decrease sediment bulk density and produce lift forces, which would make the sediment more susceptible to erosion (Sutherland et al. 1998*a*). Furthermore, submerging of sediment in the tidal treatment caused biofilms on sand to detach from the sediment. This leads to losses of diatoms from the sediment, even at a current speed insufficient to invoke erosion. In the silt-rich treatment, blistering of biofilms, both in the tidal and subtidal treatments, was absent. High rates of oxygen consumption, as a consequence of the high organic matter content of silt-dominated sediments, may account for the observed differences in bubble formation.

In mathematical literature, stable states are also called "attractors" (e.g., Lewontin 1969, Yodzis 1989). When disturbed, a system will develop towards this attractor, although it may never reach it due to continuous perturbation by, for instance, the weather. If two attractors are predicted on the scale of a patch, sampling on a larger scale (with intervals between sample points exceeding average patch size) will result in a bimodal distribution of the involved variables (Scheffer 1998). The maxima in this distribution would reflect the equilibrium values as predicted by the model. In agreement with our model predictions, we found bimodal distributions in both silt and diatom content of sediment on the tidal flat sampled in this study. The silt content of the sediment clustered around 5% and 20% in sediment with high bottom shear stress in the June, September, and December samples (Fig. 5). Although clustering was much less evident in diatom densities, as measured by chlorophyll *a* content, than in silt content, a bimodal distribution still provided a significant increase in fit over a normal distribution, especially at high bottom shear stress. A high rate of disturbance may obscure the appearance of attractors in the data. Diatom populations are known to be very sensitive to factors such as grazing and weather conditions (Paterson and Daborn 1991, Underwood and Paterson 1993*a, b*, Underwood and Kromkamp 1999), which may explain the low degree of clustering in the chlorophyll *a* data relative to the silt data.

It is possible that factors other than diatom–silt interactions explain the observed patterns. Cohesion between particles is much higher in silt relative to sand. Hence an increase in silt content of the sediment will improve sediment cohesion and decrease the vulnerability of sediment to erosion. This would on its own result in a positive feedback, without the need for biological factors. In empirical studies of the relationship between microbial binding of sediment and erosion, however, sediment lacking biofilm cover was found to erode at shear stress levels below 1 N/m^2 (Underwood and Paterson 1993*b*, Yallop et al. 1994). The formation of extracellular polymeric substance (EPS) networks, excreted by diatoms, is reported to increase the resistance of sediment to erosion by a factor ranging from 1.25 to 20 (Vos et al. 1988, Paterson and Daborn 1991, Paterson 1994, Yallop et al. 1994). Hence it is unlikely that cohesional forces, without the influence of EPS networks formed by microorganisms, can explain the bimodal patterning in Fig. 5, which mainly occurs at shear stress values in excess of 1 N/m^2. This corresponds to the general notion that physical parameters are insufficient to explain the erosive behavior of silt-rich sediments in situ (e.g., Paterson 1994).

Alternatively, bioturbation by benthic macrofauna may decrease sediment silt and chlorophyll *a* levels by

TABLE 3. Differences in the biomass of chlorophyll *a* (μg/g) and of deposit feeders, surface deposit feeders, omnivores, and suspension feeders (g/m^2) between the high- and low-silt cluster at log (τ_{max}) > 0.

Biomass	Low-silt group	High-silt group	*F* or *U*	*P*
Chlorophyll *a*	0.50	1.30	$F = 50.206$	0.000***
Deposit feeders	3.89	6.44	$F = 2.452$	0.120
Omnivores	0.22	0.25	$F = 0.048$	0.826
Surface deposit feeders	1.76	2.36	$F = 0.981$	0.324
Suspension feeders	1.14	2.08	$F = 1.146$	0.286
Arenicola marina	2.71	3.09	$F = 0.065$	0.799
Bathyporeia pilosa	0.18	0.03	$U = 4.066$	0.000***
Cerastoderma edule	0.94	1.98	$F = 1.595$	0.209
Heteromastus filiformis	0.87	2.77	$U = -3.473$	0.001***
Hydrobia ulvae	0.15	0.15	$F = 0.000$	0.993
Macoma balthica	1.31	1.87	$F = 1.305$	0.256
Mya arenaria	0.20	0.10	$F = 0.098$	0.755
Nereis diversicolor	0.18	0.24	$F = 0.162$	0.688
Scoloplos armiger	0.27	0.48	$F = 2.362$	0.127
Scrobicularia plana	0.07	0.17	$F = 0.449$	0.504

Notes: Arenicola marina and *Heteromastus filiformis* dominate the deposit feeder functional group; surface deposit feeders are mainly *Macoma balthica, Bathyporeia pilosa,* and *Hydrobia ulvae*; omnivores are mainly *Nereis diversicolor*; and suspension feeders consist mainly of *Cerastoderma edule* and *Mya arenaria.* Individual species that comprised >1% of the total biomass within a group are included. *F* values are from ANOVA; U values are from Mann-Whitney *U* tests.

*** $P < 0.001$.

mixing the silt-rich top layer with the deeper sand-rich sediment layers. Grazing of diatoms could further decrease chlorophyll *a* levels. Hence it is conceivable that differences in macrofaunal densities explain the chlorophyll *a* and silt patterns. Data on macrofaunal abundance in the Molenplaat did not support this hypothesis. The biomass of (deep) deposit feeders, surface deposit feeders, omnivores, suspension feeders, and most of the individual species were not significantly different between the two clusters. Significant differences between the clusters were found in *Heteromastus filiformis* and *Bathyporeia pilosa.* The biomass of *H. filiformis,* a deep deposit feeder, was lowest in the low-silt cluster. Therefore, bioturbation by *H. filiformis* cannot explain low silt content. The densities of *Bathyporeia pilosa* were too low to affect the silt content of the sediment. Hence we believe that macrobenthic activity does not offer a clear explanation for the bimodal patterns at high bottom shear stress. Chlorophyll *a* content differed greatly between the two states, and a relatively high degree of correlation was found between chlorophyll *a* and silt content. This suggests that diatom–silt feedbacks are a more likely cause.

Still, the possibility that the patterns we observed result from factors other than diatom–silt interactions cannot be ruled out. Conclusive evidence of the existence of alternate stable states can only be provided by experimental tests of predictions, either in the field or in mesocosm studies (Peterson 1984, Petraitis and Latham 1999). Long-term experiments, which are needed to reach equilibrium conditions, are difficult to accomplish in non-axenic mesocosm conditions. Field experiments could potentially demonstrate multiple stable states if they were performed on a sufficiently broad spatial and temporal scale. A suitable experiment would be removal of the silt-rich top layer on a tidal flat on a scale that is sufficiently large to minimize the effects of the depression created. If water shear velocity were sufficiently high, the sediment would remain sandy for a relatively long period.

Recent studies on microbial mediation of sediment structure and behavior argue that including microbiological processes is vital in predicting the erosive behavior of sediments in situ (Paterson and Daborn 1991, Daborn et al. 1993, Paterson 1994). They stress that predictions should be based on a "suite" of both physical and biological variables in order to give reliable estimates of sediment structure and dynamics (Paterson 1994). Our study indicates, however, that this strategy will only improve predictions in sediments with a low bottom shear stress. In sediments with intermediate shear stress levels (±1–3 N/m^2; i.e., maximal shear stress in our study), a potential for alternate stable states may induce variation in sediment structure that is not related to variation in physical or environmental conditions. Rather, it is caused by a runaway response of the system to small disturbances (Fig. 5). Hence for a particular range of shear stress, sediment structure may prove to be intrinsically unpredictable, since small disturbances may result in structurally different sediment.

The interaction between diatoms and silt on tidal flats may provide an interesting example of the functioning of positive feedback in ecosystems. Recognition of positive feedback mechanisms is vital in our effort to understand and predict the behavior of natural systems (e.g., Connell and Slatyer 1977). Positive feedback may lead to threshold behavior (Noy-Meir 1975, May 1977, Van de Koppel et al. 1996), and hence to dramatic and unexpected reactions of ecosystems to small disturbances, as was found in arctic and semi-arid regions (Van de Koppel et al. 1997). Furthermore, positive feedback significantly decreases the power of models made to predict ecosystem properties on the basis of physical or environmental parameters, as found in studies on the behavior of intertidal sediments. Therefore, further understanding of the functioning and triggering of positive feedback may be relevant not only to fundamental ecology, but also to our ability to predict the behavior of specific ecosystems.

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APPENDIX

Derivation for stability of the equilibria and effect of changes in bottom shear stress on equilibria is available in ESA's Electronic Data Archive: *Ecological Archives* E082-040.