

Fish facilitate wave resuspension of sediment

Marten Scheffer¹

Department of Aquatic Ecology and Water Quality Management, Agricultural University Wageningen, P.O. Box 8080, NL-6700 DD Wageningen, The Netherlands

Rob Portielje

RIZA, P.O. Box 17, 8200 AA Lelystad, The Netherlands

Luis Zambrano

Departamento de Zoología Instituto de Biología, UNAM, Apartado Postal 70-185, México D.F. 04510, México

Abstract

The resuspension of sediment by waves or currents is a major cause of turbidity in many shallow waters. Here we show that bottom-feeding fish greatly facilitate this process by reducing the erosion resistance of the sediment. We use a fish-removal experiment from a large Dutch lake to show that the absence of fish makes sediment resistant to wind effects, and we use controlled lab experiments to demonstrate that the effect of fish can be explained by the characteristic hole-punching behavior used in the search for food. Undisturbed sediment in the laboratory consolidated rapidly. The critical water velocity needed for resuspension roughly doubled in 2 weeks. However, the acquired erosion resistance could be virtually eliminated by holes corresponding to only 2% of the sediment area. An analysis of a model based on our experimental results suggested that benthivorous fish may prevent sediment consolidation that, in the absence of fish, would sufficiently stabilize the sediment during a quiet period to resist wave resuspension during subsequent windy periods. Our results imply that, even in exposed shallow lakes that are turbid because of wind resuspension, a temporary reduction of fish stock may work as “shock therapy” to restore an alternative stable clear-water state.

Resuspension of sediment by water movement is an important phenomenon in shallow waters (Kristensen et al. 1992; Evans 1994; Scheffer 1998) and has been modeled extensively (Carper and Bachmann 1984; Aalderink et al. 1985; Bengtsson and Hellstrom 1992). A review of field studies in a range of aquatic systems suggested that ~85% of the suspended matter flux to sediment may be due to resuspended material (Evans 1994). Wave resuspension may be an especially dominant cause of turbidity in large shallow lakes (Scheffer 1998), where the average flux of wave induced resuspension may be as high as $300 \text{ g m}^{-2} \text{ d}^{-1}$ (Kristensen et al. 1992). Most simulation models have computed the shear stress caused by moving water and assumed that resuspension occurs rather suddenly once a critical shear stress level is exceeded (Carper and Bachmann 1984; Bengtsson and Hellstrom 1992; Blom and Aalderink 1998). However, the critical shear stress level for resuspension may vary widely. It depends on the type of sediment and also increases over time if the sediment is left undisturbed. Such consolidation is due to physical processes and to the often

rapid development of a community of benthic algae, bacteria, and other microorganisms at the sediment surface that form a protective crust (Delgado et al. 1991).

Although sediment resuspension is mostly associated with wave action, the bottom-feeding activity of fish may also cause a resuspension of sediment (Meijer et al. 1990; Yahel et al. 2002). Benthivorous fishes such as common carp (*Cyprinus carpio*) and bream (*Abramis brama*) ingest sediment, from which food particles are retained by filtering through gill rakers (Lammens and Hoogenboezem 1991). The fine-sediment particles that are not retained by the fish become suspended in the water. Given that these fish may process up to five times their body weight of sediment per day, the effect on turbidity can be considerable in waters with high fish densities (Breukelaar et al. 1994).

The interaction between wave and fish effects on sediment resuspension has never been addressed. Nonetheless, the link seems obvious. Foraging benthivores leave small pits (2–4 cm across) in the sediment surface (Lammens and Hoogenboezem 1991). Observations of sediment in lakes where benthivorous fish are abundant have often shown the sediment surface to be almost entirely covered by such foraging craters (Scheffer 1998). It seems likely that this disturbance of the microbially consolidated top layer of sediment would affect resistance to shear stress. Also, changes in bottom microtopography increase its roughness and, hence, should increase the shear stress experienced at the same water velocity. To explore the possible consequences of the interplay between fish behavior and wind effects on sediment stability, we analyzed the effect of fish removal on wind resuspension in the large, shallow Lake Wolderwijd (The Netherlands),

¹ Corresponding author (Marten.Scheffer@Aqec.wkao.wau.nl).

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measured the effect of foraging craters on sediment erosion resistance under controlled conditions in the laboratory, and analyzed a dynamic model of the interaction of fish and wind effects.

Methods

Fish removal experiment in Lake Wolderwijd—Lake Wolderwijd is a large (26 km²), wind-exposed lake in the central Netherlands. Water depth varies 0.5–2.5 m, with a mean depth of 1.6 m. The lake is part of a chain of similar lakes that separate reclaimed lands from the former shore of the large Lake IJsselmeer. Lake Wolderwijd was created in 1968 and has been turbid because of eutrophication since the early 1970s. Because a reduction of nutrient loading during the 1980s had little effect, the fish stock was reduced drastically during the winter of 1990/1991 in an attempt to promote a shift to a clear-water state (Meijer and Hoser 1997). Using seine nets of up to 1,200 m and various other fishing gears, the total fish biomass was reduced from ~20 to 4.6 g m⁻² (Meijer and Hoser 1997). Although recruitment occurred, the biomass of benthivorous fish was maintained at roughly the same low level during the subsequent 2 yr through additional fishing pressure (Meijer and Hoser 1997).

To evaluate the effect of fish removal on wind resuspension, we analyzed 4 yr of monthly routine measurements of suspended solids concentration in the lake in relation to wind speed measured at a nearby weather station. We used regression and nonparametric tests to relate the average wind speed on the day of sampling measured at the nearby Lelystad airport weather station to suspended solid concentrations in water samples that were routinely taken, on a monthly basis, from an open-water area in the center of the lake. Suspended solid concentrations were measured according to methods defined by the Netherlands Normalization Institute (<http://www.nen.nl>) that comply with international standards.

Laboratory experiments—To explore the effect of fish foraging-related damage of the sediment surface on erosion resistance, we performed experiments in two types of tanks: (1) seven transparent plastic (Perspex) cylinders with 60-cm diameter and (2) 12 cubic tanks of 1 m². In both types of tanks, the bottom was covered with a 7-cm layer of mineral clay (obtained from riverine clay deposits used for making bricks). We inoculated the sediment of each tank with 5 liters of mixed mud obtained from the bottom of a eutrophic lake. We added 40 cm of water and introduced *Daphnia magna*, to keep the phytoplankton biomass low. The water temperature was maintained between 20°C and 23°C, and the tanks were exposed to a daily dark:light regimen of 10:14 h (125 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$). In preliminary experiments, erosion resistance roughly doubled in 2 weeks. We standardized the sediment incubation period used for all subsequent experiments to 16 d.

In the Perspex cylinders, we made artificial holes in the sediment with a tube (1.2 cm diameter), extracting the sediment captured within the tube. Making different numbers of such holes resulted in a disturbed area of 0.3%–2.5% of the total sediment surface. In the 1-m² tanks, we evaluated

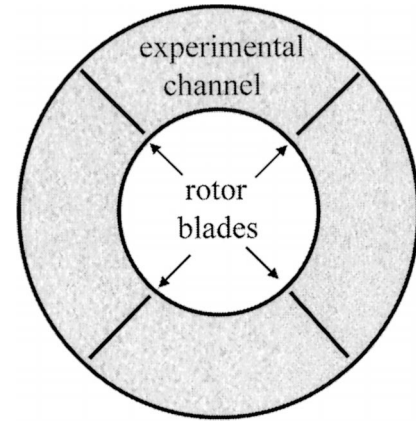


Fig. 1. Schematic top view of the experimental setup used to measure the erosion resistance of the sediment. The device contains of two concentric cylinders (60 and 45 cm diameter \times 40 cm high) that enclose a circular experimental channel in which water (40 cm deep) over the sediment layer is put in controlled motion by a rotor with four blades (see text for details on measurements).

the effect of benthivorous fish on the sediment and compared the results with effects of our mechanical perturbation. Two treatments (four replicate tanks for each) with different abundances of well-fed fish (30 and 60 g of *Carassius auratus*) were left for 5 d. Fish size was 9–13.5 cm. In tanks with 30 g of fish, we used one larger (13 cm) or two smaller (10.5 cm) fish, whereas, in tanks with 60 g of fish, we used three of them. On the fifth day, we did the mechanical perturbation (2.2% of the total area) in four control tanks for comparison, carefully removed fish from the other tanks, and measured the sediment resistance to shear stress in all tanks.

Measurement of sediment erosion resistance—We measured the resistance of sediment to erosion by exposing it to a water flow of gradually increasing velocity. The experimental setup (Fig. 1) consisted of two concentric cylinders (60 and 45 cm diameter \times 40 cm high) enclosing a circular channel of water that could be brought into motion by a rotor with four blades. The cylinders were carefully placed on the experimental sediment (in experiments in the Perspex cylinders, only the inner cylinder needed to be placed), avoiding perturbing the sediment as much as possible. We placed an electrical rotor with adjustable speed on top of the cylinders. Four blades (12 cm width \times 20 cm height) suspended from the rotor caused a water current of adjustable velocity in the circular channel between the two cylinders. We continuously followed the suspended sediment concentration using an infrared light sensor situated between the blades and the sediment.

At the start of the erosion experiments, we turned on the rotor with an initial speed of 1.89 rpm and subsequently increased the speed by 0.3 rpm every 15 s until a final speed of 19.3 rpm was reached. We checked the relationship between rotor revolutions per minute and the actual water velocity produced by the blades at the sediment surface using an electromagnetic velocity meter (accuracy 0.5 cm s⁻¹, RC2; Aqua Data) situated at the bottom of the cylinder. Measured water velocities over the experimental range were vir-

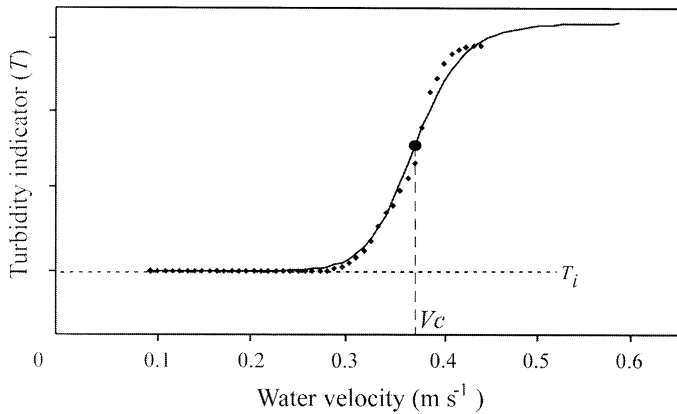


Fig. 2. Example of a turbidity curve obtained by gradually increasing water speed in the experimental setup (Fig. 1). The curve (Eq. 1) was fitted to the experimental data (dots), minimizing the sum of squares, and used to obtain an objective indicator (R) of erosion resistance of the sediment. The relative indicator (T) of turbidity was measured with an infrared sensor.

tually equal to the speed of the rotor blades. The water speed stabilized within <10 s after the rotor settled at a particular speed.

During the erosion experiments, we recorded the values of the rotor speed and water turbidity each second. We used the light attenuation measured by our infrared sensor as a relative indicator (T) of turbidity. Turbidity indicator values plotted against the rotor (or water) velocity (V , m s^{-1}) showed a sigmoidal relationship (e.g., Fig. 2) to which we fitted a Hill function by means of minimization of the sum of squares:

$$T = T_i + T_r \frac{V^p}{V^p + R^p} \quad (1)$$

where T_i is the turbidity indicator value before erosion and T_r is the maximum turbidity indicator increment due to re-suspension. The half-saturation constant, R , approximates the critical water velocity at which erosion increases most steeply. We used this parameter as an indicator of the resistance of the sediment to erosion.

Results and discussion

The field experiment—Before fish had been removed from Lake Wolderwijd, suspended solid concentrations in our time series rose steeply with wind speed (Fig. 3, upper panel; Spearman's correlation coefficient 0.50; $P = 0.01$). By contrast, in the years with reduced fish biomass (1991–1992), no significant effect of wind on suspended solids existed, although the highest wind speeds were recorded during this period (Fig. 3, lower panel; Spearman's correlation coefficient = -0.01 ; $P = 0.97$).

The elimination of wind resuspension cannot be explained by an increase in aquatic vegetation, because the percentage of lake area covered by submerged plants has remained practically constant over the 4 yr of the study (5.7%, 6.9%, 7.0%, and 6.2% of lake area) (Meijer and Houser 1997). In a small corner of the lake, charophyte beds developed ($<1\%$ and

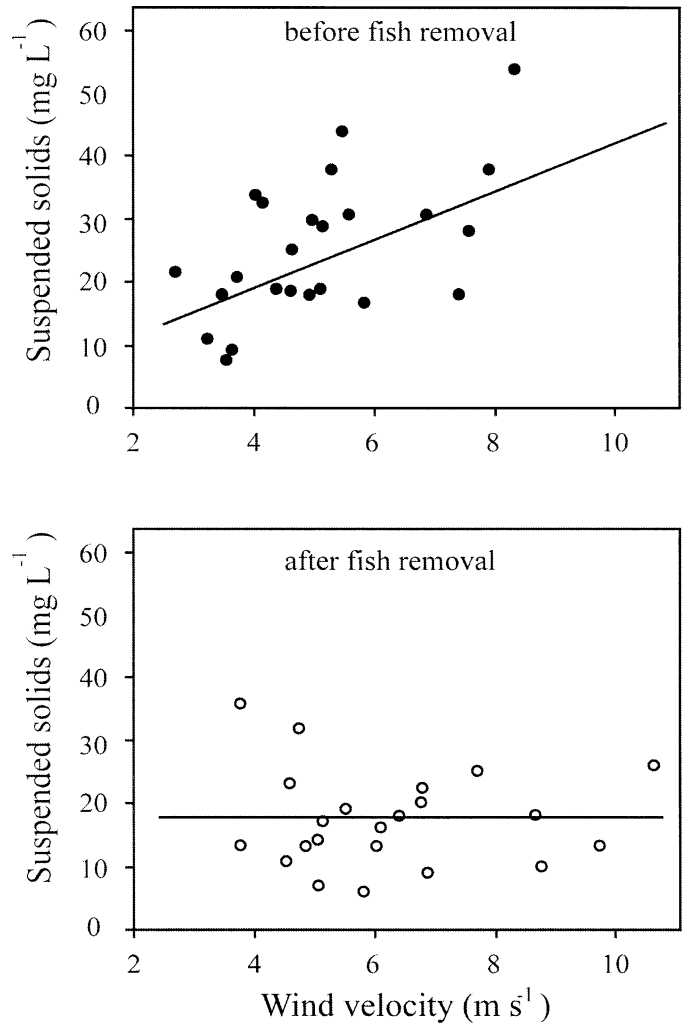


Fig. 3. Relationship between wind velocity (W) and suspended solids concentrations (Y) in Lake Wolderwijd before and after fish removal. Each panel represents 2 yr of monthly data. The slope of the regression line in the upper panel ($Y = 4.2 + 4.2W$, $R^2 = 33\%$) is significantly different from 0 ($P < 0.01$), but there is no significant relationship between wind and suspended solids after fish removal (lower panel).

3% of moderate-to-dense fields in 1991 and 1992, respectively). Although local clarity was observed above the beds in 1993, the local charophyte beds seem unlikely to have affected turbidity during our study years (Meijer and Houser 1997). Also, an increased growth of benthic algae in response to enhanced light conditions seems rather unlikely, given that the lake remained turbid (Secchi depth, 0.6 m in 1991 and 0.4 m in 1992). A decrease in benthivorous fish foraging activity seems to be the most obvious possible cause of the apparent increase in sediment resistance to wind resuspension. In fact, the area of sediment surface disturbed daily by foraging activity is likely to have decreased more than the 75%–80% drop in fish biomass itself. This is because food density (Chironomids and snails) increased sharply in response to the fish depletion (Meijer and Houser 1997). Because fish have to search through less sediment if

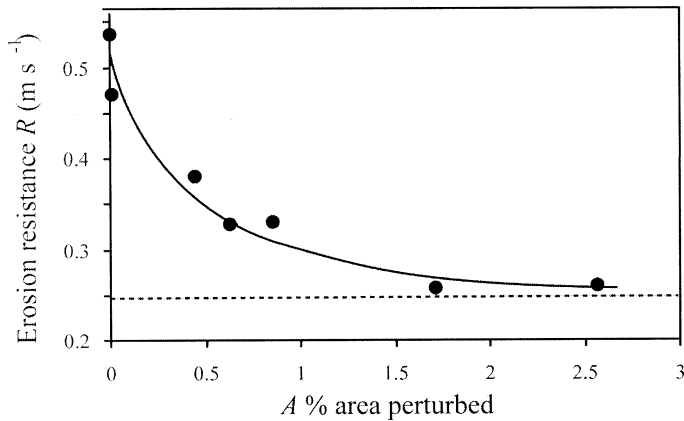


Fig. 4. Effect of manually punched holes (1.2 cm individual diameters) corresponding to different fractions of the total sediment area on erosion resistance (R , see Fig. 2) of the sediment.

food density is high, this implies a drop in sediment disturbed per fish (Zambrano et al. 2001).

Laboratory experiments—To assess whether the foraging activity of benthivorous fish might explain the sensitivity of lake sediment to wave resuspension, we analyzed the erosion resistance needed to suspend lake sediment under controlled conditions in the laboratory. In an unconsolidated state, our experimental sediment could be resuspended by a water velocity $\sim 0.25 \text{ m s}^{-1}$. Left undisturbed, the resistance to erosion roughly doubled in 2 weeks and continued to increase slowly afterward (data not shown). However, mechanical perturbation, done by punching holes with a tube, resulted in a sharp decline (Fig. 4) of the sediment resistance to erosion (Spearman's correlation coefficient = 0.92; $P = 0.003$). A number of holes corresponding to $\sim 2\%$ of the sediment surface was sufficient to reduce erosion resistance to a value

similar to that of the unconsolidated state. The effect roughly followed an inverse saturating pattern. More than 50% of the erosion resistance built up during the 2 weeks of consolidation was eliminated by punched holes corresponding to only 0.5% of the total area.

In the 1 m^2 tanks that we used to study the effects of fish on sediment stability, the unperturbed consolidated sediment reached a higher erosion resistance than sediment in the Perspex cylinder set of experiments discussed above. In fact, the sediment in some tanks consolidated so well that the water velocity in our experimental setup was insufficient to cause erosion. We omitted these tanks from consideration, which implies that our estimate of erosion resistance of undisturbed sediment ($R > 0.6 \text{ m s}^{-1}$, first column in Fig. 5, based only on the tanks in which we could resuspend the sediment) represents an underestimate. Fish that were allowed to forage for 5 d in the tanks reduced the erosion resistance of sediment (Fig. 5). Sediment in tanks with 60 g of fish m^{-2} had a significantly lower erosion resistance (post hoc Tukey test, $P = 0.03$) than that in mechanically perturbed tanks. Although the comparison to unperturbed sediment is difficult to determine because of the limited capacity of our equipment, the results from the tanks with manually punched holes (second column) allowed a comparison with the previous set of experiments. Average erosion resistance was comparable in tanks with 30 g of fish m^{-2} and in the mechanically perturbed sediment (post hoc Tukey test, $P = 0.97$). These experiments thus indicate that the fish reduced erosion resistance as least as much as mechanically punched holes that were sufficient to virtually eliminate acquired erosion resistance in the other experiment.

A model of interactive effects of fish and waves—The field and laboratory experiments suggest a particular interplay of the effects of benthivorous fish- and wave-induced shear stress on sediment stability. To explore the potential conse-

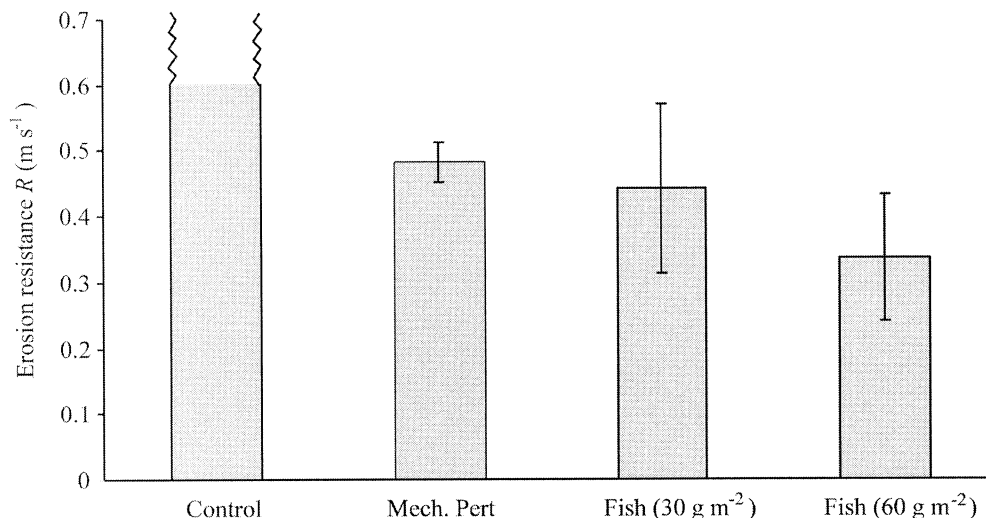


Fig. 5. Erosion resistance of sediment in experimental tanks perturbed manually by punching holes (2.2% of surface), compared with undisturbed sediment and those exposed to 30 and 60 g m^{-2} of fish left to forage in the sediment for 5 d. Error bars denote standard deviations. Note that sediment in some undisturbed tanks became so firm that they could not be resuspended by our device.

Table 1. Interpretation and dimensions of variables and parameters for the model (Eqs. 2, 3) and the default values used for the simulations shown. Note that dimensions of h_f and F are arbitrary—the model is sensitive only to the value of h_f relative to that of F .

		Notation	
R	—	m s^{-1}	Critical water velocity at which erosion occurs
R_0	0.25	m s^{-1}	Erosion resistance of unconsolidated sediment
R_{\max}	1	m s^{-1}	Maximum R in the absence of fish
$R_{\max f}$	—	m s^{-1}	Maximum R in the presence of fish
F	—	—	Dimensionless indicator of fish foraging intensity
h_f	0.5	—	Value of F leading to a 50% reduction in erosion resistance
S	—	m s^{-1}	Wave-induced shear stress at the sediment surface
c	0.06	d^{-1}	Maximum rate of increase of R due to consolidation
e	0.4	d^{-1}	Maximum rate of decrease of R due to wave induced erosion
p	10	—	Determines the steepness of increase of erosion with S around R
α	15	—	Ratio between daily averaged wind speed and shear stress S at sediment surface

quences of such an interaction further, we formulated a simple model of the effect of fish foraging intensity (F) and wave-induced shear stress (S) on the dynamics of acquired sediment erosion resistance (R):

$$\frac{dR}{dt} = c \left(1 - \frac{R}{R_{\max f}} \right) - e(R - R_0) \frac{S^p}{S^p + (R + R_0)^p} \quad (2)$$

The first term represents the consolidation process, whereas the second term represents loss of resistance due to wave-induced erosion. With respect to consolidation, we assumed that acquired sediment resistance increases over time, approaching a saturation level ($R_{\max f}$) that is a declining function of the foraging intensity of benthivorous fish (F) in the lake:

$$R_{\max f} = \frac{R_{\max} h_f}{h_f + F} \quad (3)$$

where R_{\max} is the maximum erosion resistance in the absence of any fish and h_f is a half-saturation fish biomass at which the maximum erosion resistance is reduced by 50%. The wave erosion rate approaches its maximum value (e) asymptotically with increasing shear stress through a sigmoidal function that increases rather sharply around $R + R_0 = S$. The parameter R_0 represents the erosion resistance of unconsolidated sediment (which will vary from very high for gravel to practically nil for “fluid” organic sediment). The interpretation and dimensions of variables and parameters as well as the default values used are summarized in Table 1. The values for R_0 , R_{\max} , and c were based on the laboratory experiments. h_f and e were chosen rather arbitrarily within realistic ranges.

An analysis of the model shows that equilibrium resis-

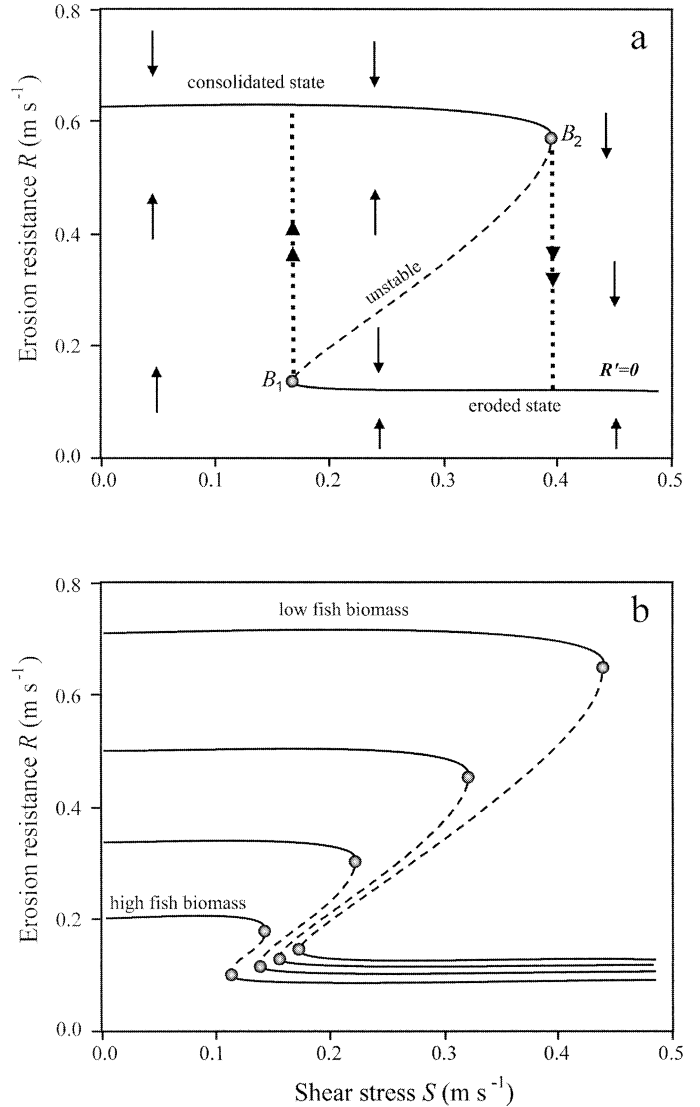


Fig. 6. Effect of shear stress (S) on the equilibrium erosion resistance (R solved for $R' = 0$) in the model (Eqs. 2–3). (a) Arrows indicate the direction of change if the system is out of equilibrium. They show that the dashed equilibrium (the saddle) is unstable. The vertical transitions with double arrows correspond to “catastrophic shifts” between the consolidated and eroded stable states at critical erosion resistance rates corresponding to saddle-node bifurcation points (B_1 and B_2). (b) Higher fish biomass causes the bifurcation points to occur at lower shear stresses. (Panel a is computed for $F = 0.3$; the curves in panel b are for $F = 2, 1, 0.5$, and 0.2 , respectively.)

tance as a function of shear stress takes the form of a “catastrophe fold” (Fig. 6). Over a certain range of shear stresses, both the consolidated and eroded state were stable. With slowly increasing shear stress, the resistance of consolidated sediment collapsed at a critical value (B_2) to a stable low level (the eroded state). Recovery of the consolidated state only happened when shear stress was reduced below another lower level (B_1). Note that erosion resistance for both bifurcation points was higher for sediment that was less easily resuspended (had a higher R_0) (data not shown). Benthivo-

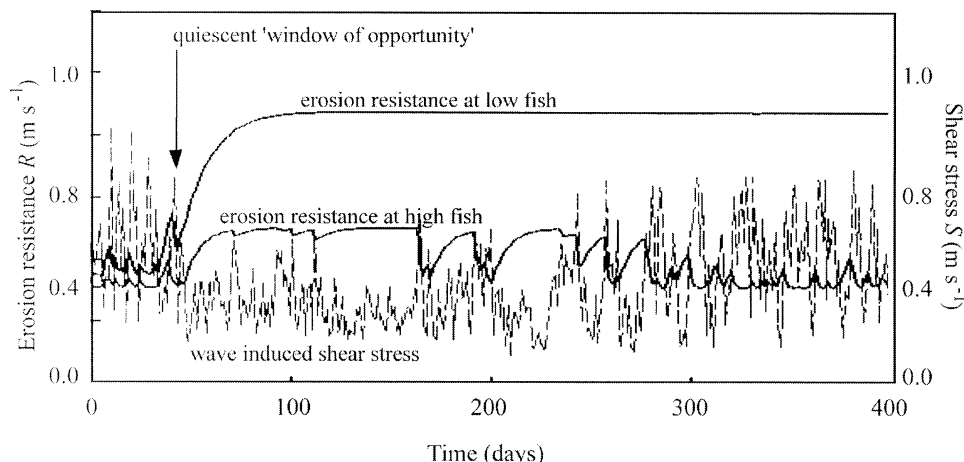


Fig. 7. Time graph generated by the model (Eqs. 2–3) showing how randomly varying shear stress due to waves (fluctuating line) may affect the erosion resistance of sediment (heavy lines) at low ($F = 0.2$ h) vs. high densities of bottom-feeding fish ($F = 2$ h). During a period of calm weather resulting in low shear stresses (the window of opportunity), the sediment may shift to a stable consolidated state at low, but not at high, fish densities. Ratio of wind: shear stress = 15, $R_{\max} = 1.0$, $R_0 = 0.25$.

rous fish foraging is predicted to reduce the erosion resistance levels at which collapse and recovery take place (Fig. 6b).

The effects of relatively rapid fluctuations in the environment (S) cannot be directly derived from such equilibrium graphs (Rinaldi and Scheffer 2000). Therefore, we simulated the behavior of the system in a realistic situation in which the shear stress was fluctuating in proportion to daily averaged wind velocity obtained from the Lelystad airport weather station (Fig. 7). In the simulation, wave action may have prevented consolidation until a period of low wind speed occurred (around day 50). This quiescent “window of opportunity” (Holmgren and Scheffer 2001) allowed erosion resistance to increase. In the presence of a dense fish population, this consolidation effect is not sufficient to prevent wave resuspension during a subsequent windy period. By contrast, if the fish density is low (e.g., because of recent biomanipulation), the window of opportunity allows a consolidation to an alternative stable state that is resistant even to relatively strong wave action.

A complete bifurcation analysis to show how model behavior depends on the parameter values is beyond the scope of the present article. However, the occurrence of alternative stable states (see Fig. 6) depends largely on the slope of the increase of resuspension around an erosion resistance, as has been argued elsewhere for a similar generic model (Scheffer et al. 2001). Such a steep increase around a critical value is widely accepted (Bengtsson and Hellstrom 1992) and corresponds well to our own experimental findings (Fig. 2). Another indication that our alternative stable-state result is probably realistic is the fact that this phenomenon has been found independently in a study of microbial crusts preventing erosion on tidal mud flats (Van de Koppel et al. 2001).

Although the qualitative results seem rather robust, our data do not allow the development of a quantitative model for predicting the critical level of fish reduction needed to allow sediment consolidation in any particular lake. Clearly,

the effect of fish on sediment stability will not be of significance in cases where wind resuspension is very rare—for instance, in small, sheltered, or relatively deep lakes. Nor will it be important if the size:depth ratio of a lake is such that wind resuspension itself is very frequent, preventing consolidation altogether. However, further work would be needed to allow an estimation of the threshold fish biomass to effectively prevent wind resuspension in lakes in the intermediate range.

The emerging picture is that, in the absence of benthivorous fish, lake sediment may consolidate rapidly during periods with little wave action. Even in large shallow lakes such as Lake Wolderwijd, consolidation during such quiet periods may apparently allow the sediment to become firm enough to resist the shear stress caused by waves during windy periods. On a longer timescale, this may allow colonization by submerged macrophytes that further protects sediment against wave resuspension and promotes water clarity, potentially leading to a clear, vegetated state that is stable in the long run (Scheffer et al. 1993; Scheffer 1998). Although there have been doubts as to whether fish-stock reduction may be effective to clear lakes in which wave resuspension is an important cause of turbidity (Hosper and Meijer 1993), our results imply that a temporary reduction of fish stock may still work as shock therapy to restore such turbid lakes to an alternative, stable, clear-water state.

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