

The consequences of changes in abundance of *Callianassa subterranea* and *Amphiura filiformis* on sediment erosion at the Frisian Front (south-eastern North Sea)

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Abstract In the early 1990's a conspicuous shift took place in the density of two key macrofauna species at the Frisian Front (SE North Sea). The density of the formerly dominant brittlestar *Amphiura filiformis* showed tenfold reduction and remained low throughout the observation period (1986–2000). In the same period, the burrowing mud shrimp *Callianassa subterranea* showed a fourfold increase in density. Since the Frisian Front is a transition area where tidal currents fall just below the erosion threshold of silt and bioturbating mud shrimps can potentially affect the sediment erosion threshold, we examined the effects of the species on sediment erodibility. Two experiments were conducted in laboratory annular flumes. In the first experiment we compared the effects of pre-shift and

post-shift combinations of the two species on the erodibility of Frisian Front sediment. The results indicated that the erosion was facilitated by a combination of high densities of *C. subterranea* and low densities of *A. filiformis*, representing the situation in the late 1990s. The difference in erodibility was already apparent at velocities equal to the critical near-bed current speed measured at the Frisian Front. In the second experiment the effects of pre- and post-shift densities of *A. filiformis* on sediment erodibility were compared. This showed that low *A. filiformis* densities as found in the late 1990's facilitate erosion, but the effect is only significant at velocities above the critical near-bed velocity in the field. At the latter velocity, no significant difference in erodibility was found between the two *A. filiformis* densities. This implies that the difference in turbidity in the first experiment was mainly due to the activity of *C. subterranea*. The experimental results indicate that resuspension at the Frisian Front may occur more frequently as a result of the shift towards a *Callianassa* dominated community. More frequent resuspension of bottom sediment, most likely amplified by the climate induced increase of wind strength in the North Sea, may hamper the recovery of the *A. filiformis* adult population.

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Introduction

The interaction between physical and biological stability of North Sea sediments has been a focus of many studies most of which have been directed at intertidal communities. Reasons for the emphasis on shallow habitats is that they are more energetic and thus susceptible to physical disturbance than sediments underlying deeper water, they are highly productive, have high natural values and, importantly, are accessible and allow manipulation. Many studies on intertidal sediments have demonstrated the importance of biofilms in concert with activities of organisms for substrate and community stability (e.g., Meadows et al., 1990; Flach, 1992; Widdows & Brinsly, 2002; Widdows et al., 2004; de Brouwer et al., 2005).

The significance of sediment stability for subtidal benthic communities in the North Sea has been primarily acknowledged in the context of disturbance by bottom trawling (Kaiser et al., 2000). Natural disturbance of sediment stability and its effect on benthic community structure have been sparsely explored in the North Sea (Rowden et al., 1998a; Kröncke et al., 2004) or elsewhere (Rhoads & Young, 1970; Aller, 1997). The available data show that also in deeper water biologically reworked sediments can be resuspended with negative consequences for the fauna when subject to storm or peak currents. A special role in this context is played by engineering species whose activities structure the habitat (Jones & Lawton, 1994). Changes in the density of such engineers can have a profound impact on other species and the ecosystem as a whole (Coleman & Williams, 2002).

With climate models predicting increasing storminess in the North Sea (Woth, 2005), sediment stability may become an important factor for the North Sea subtidal fauna similarly as in the peripheral intertidal areas (Wolters et al., 2005). Despite a tendency for an increase in stormy days in the North Sea (Schroeder, 2003), annual monitoring of macrobenthos in Dutch sector of the North Sea since 1991 has revealed no large-scale changes thus far (Daan & Mulder, 2005). Locally, however, marked changes were found in the dominance of species particularly in the Frisian Front (Fig. 1) which is a transitional

area between the sandy Southern Bight and the silty Oyster Ground (Creutzberg et al., 1984; Cramer, 1990). Here two keystone species i.e., the filter-feeding brittlestar *Amphiura filiformis* (Müller, 1776) and the deep burrowing thalassinid shrimp *Callianassa subterranea* (Montagu, 1808), showed a conspicuous shift in abundance (Amaro, 2005 for details). Between 1992 and 1997 the density of *A. filiformis* steeply declined to a level one order of magnitude lower (1,400 vs. 100 ind. m⁻²). The collapse of *A. filiformis* coincided with an increase of *C. subterranea* from 60 to more than 300 ind. m⁻². Causes for the species shift are unresolved (Amaro et al., 2003). Equally puzzling is the lack of recovery of the *A. filiformis* population since this species has annual reproduction (Duineveld & Van Noort, 1986) and recovered 5 years after a comparable crash in the German Bight (Schroeder, 2003).

According to Creutzberg et al. (1984) the distribution of macrofauna across the Frisian

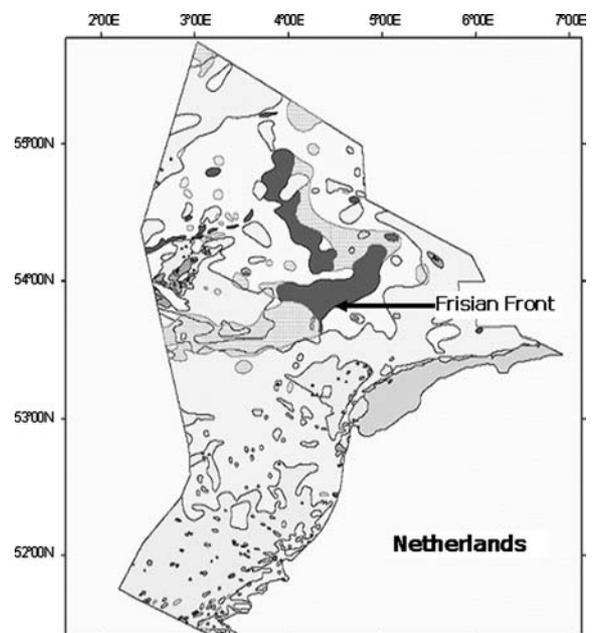


Fig. 1 Sediment distribution in the Dutch Continental Sector of the North Sea. Dark colours denote fine sediment. The arrow marks the Frisian Front visible as an east to west elongated mud patch between 53° 30' and 54° 00' N (source map: Netherlands Institute of Applied Geoscience TNO 1986)

Front is the result of interaction between autecology and hydrography determining near bed particle behaviour. Inspired by Creutzberg et al. (1984) we hypothesize that the non-recovery of *A. filiformis* is due to a change in resuspension of sediment from the seabed probably related to the concurrent increase of *C. subterranea*. This assumption is founded on three arguments. Firstly, the Frisian Front marks the point in the southern North Sea where maximum tidal currents drop below the critical velocity allowing fine particles to settle (Creutzberg & Postma, 1979). Subtle changes in the flow or sediment stability therefore rapidly evoke resuspension. Secondly, the increase of *C. subterranea* is likely to have a negative impact on the substrate stability. Burying *C. subterranea* deposit large quantities of sediment as mounds around their tunnel opening ($11\text{--}15 \text{ kg DW m}^{-2} \text{ y}^{-1}$, Stamhuis et al., 1997). These mounds increase the boundary roughness and shear stress making the sediment more susceptible to erosion (Rowden et al., 1998b). Thirdly, evidence from a variety of habitats, including the North Sea and the Frisian Front, shows that many organisms collecting food at sediment-water interface, such as bivalves but also tubicolous polychaetes and echinoids, are negatively affected by suspended sediment (Nicholls et al., 2002; Witbaard et al., 2001, 2005).

To verify if the species shift has a potential impact on sediment stability at the Frisian Front, we measured sediment erodibility in annular laboratory flumes stocked with pre- and post-shift densities of the two species and of *A. filiformis* alone. We further made in situ observations on sediment resuspension at the Frisian Front during several months in order to determine the natural circumstances when resuspension occurs. We discuss the findings with emphasis on their effects on filter-feeder organisms such as *A. filiformis*.

Materials and methods

Study area

The Frisian Front in the SE North Sea forms the transition zone between the Southern Bight and the Oyster Grounds (Fig. 1). The former area is

covered with coarse to medium sandy sediment, and the water column is permanently mixed with relatively high tidal current velocities. The Oyster Grounds have silty sediment, a stratified water column in summer, and weak tidal currents (Creutzberg & Postma, 1979). The Frisian Front sediment contains locally elevated concentrations of silt (15–20%), organic carbon and phytopigments indicative for (temporary) deposition of suspended particulate material. The fresh organic material is locally produced in the frontal zone (Creutzberg, 1985) while the silt is advected from the UK coast (De Haas & van Weering, 1997). The Frisian front has elevated levels of macrobenthic biomass and metabolic activity (Cramer 1985). Because biodiversity is also higher the Frisian front has been designated as a future protected area under the OSPAR convention and EU Habitat Directive (Lindeboom et al., 2005). Measurements for this study were conducted at a characteristic location in the Frisian Front ($53^{\circ} 42' \text{ N}$, $4^{\circ} 30' \text{ E}$, depth 36 m) which has been an annual monitoring station since 1991. The species shift at this monitoring station has been described in detail by Amaro (2005).

Experimental set up

Two experiments were performed in this study. In experiment 1 we tested whether the shift in abundances of the two species has an effect on sediment erodibility. For this purpose four containers were stocked with high densities of *A. filiformis* ($1,500 \text{ ind. m}^{-2}$) and low densities of *C. subterranea* (36 ind. m^{-2}), representing the abundances at the monitoring station in the early eighties. These containers were tested against four containers with low densities of *A. filiformis* (107 ind. m^{-2}) and high densities of *C. subterranea* (229 ind. m^{-2}), representing the situation in the late nineties. In experiment 2 we investigated the effect of different densities of *A. filiformis* on erodibility. Three containers with high densities of *A. filiformis* were tested against three containers with low densities representing the densities in the eighties ($1,500 \text{ ind. m}^{-2}$) and late nineties (107 ind. m^{-2}), respectively.

Sediment for the experiments was collected with a boxcorer in the vicinity of the monitoring

station in June 2003 (Fig. 1). Eight large circular PVC containers (diameter 0.74 m; height 1.30 m; Fig. 2) were filled with a 0.5 m deep layer of sediment to provide enough space for *C. subterranea* to construct burrows of realistic size (Witbaard & Duineveld, 1989). In the laboratory, the sediment was defaunated by exposing the containers to fresh water for 2 weeks. Sieving the samples was not an option due to the risk of losing the silt fraction. The defaunated containers were placed in a climate room set at 11°C and supplied with aerated running sea water of ambient salinity (S) of $\sim 34 \text{ g l}^{-1}$. A smaller PVC cylinder (0.45 m diameter, 1.0 m height) was inserted in the centre of each container thereby creating an outer circular flow channel (0.28 m^2), in which the erosion experiments were performed (see below). The water depth in the channels was about 0.6 m.

Experimental organisms were collected on two occasions (December 2003 and February 2004) a few miles north of the monitoring station. A total number of 3,600 *A. filiformis* and 600 *C. subterranea* were picked from boxcore samples ($n = 250$) while washing these over a sieve. We selected relatively large specimens of the two species to ensure sufficient burrowing activity in the experiments. Specimens of *C. subterranea* had an average carapace length of $5.5 \pm 1.0 \text{ mm}$, and *A. filiformis* an average disc diameter of $5.1 \pm 0.8 \text{ mm}$. Animals were transported to the laboratory climate room where they were kept for 2 weeks in running seawater ($T = 11^\circ\text{C}$, $S = 34$) as adjustment to experimental conditions. After stocking the flow channels with the appropriate

densities, containers were left undisturbed for another 3 weeks to allow animals to construct burrows and mix the sediment. Mixing was essential because a thin veneer of fine particles had settled on the surface after filling the containers with sediment and water. During this period the containers were flushed with oxygenated seawater ($T = 11^\circ\text{C}$, $S = 34$) to prevent nutrient accumulation and oxygen depletion. Cultured *Isochrysis* (circa $50 \times 10^8 \text{ cells day}^{-1}$) was daily added as food. After termination of experiment 1, the containers were defaunated again with fresh water and dead or moribund animals were removed until no more appeared at the surface. The sediment was subsequently homogenised by hand in order to remove burrows. After restocking the containers with *A. filiformis* for experiment 2, they were flushed and left undisturbed for another period of 3 weeks.

Measurement of sediment erodibility

To measure the impact of species composition on the erosion of the sediment in the circular channels of the containers, a series of gradually increasing flow velocities was generated by means of the Hydrocopter of Scheffer et al. (2003). This instrument has been designed to generate a water current of adjustable velocity below its four horizontally rotating paddles that are suspended from a rotor placed on top of a container (Fig. 2). The upper edges of the paddles orbited just below the water surface and the distance between their lower edges and the sediment was 0.3 m. During the experiments the speed was stepwise increased

Fig. 2 Experimental containers being filled on board (left) and installed in thermo-controlled room (right). In the foreground the Hydrocopter mounted on top of a container



from 2 till 19 rounds per minute (rpm) with steps of 1 rpm. Before starting the experiment the relationship between the rotor speed (rpm) and the actual water velocity below the paddles was calibrated using a velocity meter (RC2, Aqua Data, UK, accuracy 0.5 cm s^{-1} , see Scheffer et al., 2003). Measured water velocities over the experimental range were virtually equal to the speed of the rotor blades. Tests at the lowest, not-erosive rotor speeds revealed that speed had to be kept constant during 5 min to obtain a constant reading of the turbidity in the channel. This interval was used along the stepwise increasing speed gradient.

During the experiments the relative amount of resuspended particles in the water was continuously measured with an optical backscatter sensor (OBS) (Seapoint™) situated below the paddles at 0.2 m above the sediment. The sensing volume of the OBS is within 5 cm of the sensor, enabling measurements close to the sediment. The instrument detects light (880 nm) scattered by suspended particles and generates an output voltage proportional to the turbidity or the suspended solids. A data logger (Signatrol SL707) was used to record the rotor speed and associated turbidity every 8 s. To avoid that selective settlement of once resuspended particles in previous experiments could change the surface sediment characteristics, and so bias the erodibility in later experiments, each container was used only once during an experiment. Replicate observations for each species combination were gathered from 4 (experiment 1) or 3 (experiment 2) separate containers.

Using the current velocity (cm s^{-1}) calculated from the rotor speed and the associated average relative turbidity derived from the OBS recordings, turbidity curves were constructed. To compare the sediment erosion between the containers with contrasting species combinations we used the half saturation velocity V_{T50} following Scheffer et al. (2003). This value represents the water velocity when turbidity surpasses the 50% level in the steepest section of the curve. Since the OBS recordings were cut off at the saturation level of the sensor, V_{T50} is a relative measure for comparison of erodibility. For each of the replicates in the experiments the V_{T50} was estimated graphi-

cally. The replicate V_{T50} values found for the two contrasting species compositions within one experiment were tested for statistically significant differences (Mann–Whitney U -test). In order to compare the experimental species combinations at in situ current levels that are relevant for resuspension in the field, we made field measurements of near-bed current velocity and turbidity in summer 2001.

In situ measurement of current velocity and turbidity at the Frisian Front

For the measurement of near-bed current velocity and turbidity, a benthic lander (Fig. 3) was deployed at the monitoring station for a 7 weeks period between 24 July and 12 September 2001 (Fig. 4). The lander was equipped with an acoustic current meter (FSI™) set at an averaging interval of 2 min, and an Optical Backscatter Sensor (Seapoint™). Both instruments were mounted 0.5 m above the seabed. Wind gener-

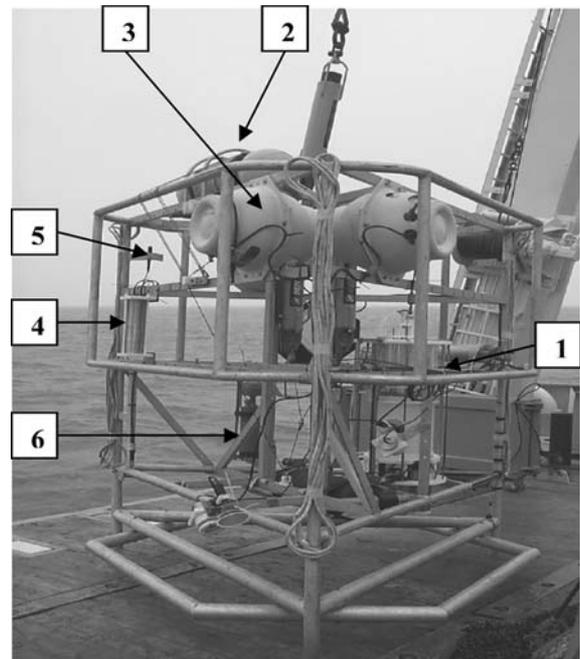


Fig. 3 Benthic lander with particle trap to collect pelagic larvae (1), pop-up system (2), floats containing batteries (3), OBS logger (4) and sensor (5) and current meter (6). Note in 2001 a FSI-acoustic current meter was used instead of the Anderaa RCM11 shown

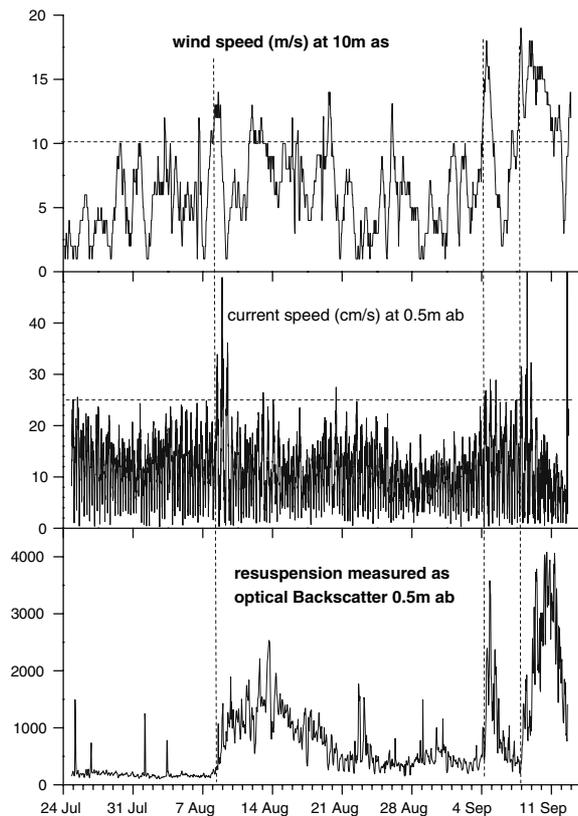


Fig. 4 Wind data (m s^{-1} at 10 m above sea), current speed (cm s^{-1} at 0.5 m above seabed), and resuspension (measured as optical backscatter at 0.5 m above seabed) recorded between 24th July and 12th September 2001 at the Frisian Front. Vertical dotted lines indicate the start of periods with enhanced resuspension showing associated wind speed and current velocity as horizontal lines

ated wave currents can make a significant contribution to the near-bed current speed and resuspension in the North Sea (Williams et al., 1998). We did not measure wave heights at our study site during the period of observation. Nearest wave data for the period are available for platform K13, 100 km WSW of our lander position (www.knmi.nl). Because the K13 site is shallower and this has an affect on wave height, we refrained from using them. Instead we used hourly wind speed data from the platform K13 (www.knmi.nl/hydra). Since wind speeds are constant over larger areas independent of depth we combined near-bed current and turbidity with K13 wind data to determine the empirical relation between critical current velocity for resuspension of sediment and the wind strength.

Results

Field measurements of current velocity, turbidity, and wind

In Fig. 4 we have combined the horizontal current and OBS records both at 0.5 meter above the seafloor with the wind speed at platform K13 for the period 24 July–12 September 2001. Spring tides in this period fell on July 22, August 6 and 21, and September 4th. The start of the three major turbidity peaks in the 7-weeks period is marked by dotted lines in Fig. 4. Apparently spring tides alone do not always cause a major resuspension event as can be seen around 21 August. This is in agreement with observations by Williams et al. (1998) in the adjacent Oyster Ground. The first peak on August 8th is preceded by 2 weeks without any major increase of turbidity in which the horizontal current speed did not exceed 25 cm s^{-1} and the wind speed was lower than 10 m s^{-1} . At the time the first turbidity peak occurred, the near-bottom current speed reached values between 28 and 34 cm s^{-1} . At the K13 platform the westerly wind at that time exceeded 10 m s^{-1} and reached a speed of 13 m s^{-1} giving rise to a wave height (H_{m0}) of approximately 2 meter. The second peak on September 4th coincided with a maximum near-bed current speed of $26\text{--}29 \text{ cm s}^{-1}$, while the wind exceeded 10 m s^{-1} accelerating up to 15 m s^{-1} . The first two turbidity events occurred at times when spring tidal currents were boosted by waves associated with wind speed higher 10 m s^{-1} (more than windforce Bft 5). The third event occurred between spring and neap tide when wind accelerated from 10 to 18 m s^{-1} . Resulting near-bed currents ranged from 28 to 30 cm s^{-1} and kept bottom material resuspended for more than 5 days. As a conservative estimate for the critical horizontal current speed (tides and waves) required for resuspension of Frisian Front sediment we took a near-bed current speed of 25 cm s^{-1} measured at 0.5 m above seabed.

The above value of 25 cm s^{-1} served as a benchmark to evaluate the differences in erodibility in the laboratory experiments at current velocities representing natural conditions. For a proper comparison between field and experimen-

tal situation we recalculated this in situ value measured at 0.5 m above seabed to a recording height of 0.3 m in the flume tank using a logarithmic velocity profile in the Karman-Prandtl equation (Rowden et al., 1998b). For this conversion we used estimates for bottom roughness length (z_0) viz. 0.0007–0.79, calculated by Rowden et al. (1998b). The first value belongs to a smooth bed and second to a fully developed *C. subterranea* mound structure that is not subject to resuspension. The resulting values for the critical horizontal current speed at 0.3 m fall in a narrow range of 22–23.9 cm s⁻¹. We took 22 cm s⁻¹ as the speed at which to compare turbidity in the different experiments as we expected that mounds were fully developed.

Experiment 1

Sediment erodibility was measured in three containers with pre-shift densities of *C. subterranea* and *A. filiformis* and in four containers with post-shift densities of the species. A failure of the OBS led to loss of data from one container with pre-shift densities. Curves describing the increase in turbidity with increasing current speed were averaged per treatment and are depicted in Fig. 5. The differences between the half saturation velocities V_{T50} (see Scheffer et al., 2003) belonging to the pre- and post-shift treatments were statistically significant (Mann–Whitney *U* test, $P = 0.034$). This indicates that sediment erosion is facilitated by relatively high densities of *C. subterranea* and low densities of *A. filiformis* representing the situation in the late 1990s. At a current velocity of 22 cm s⁻¹ in the experimental setting which is equivalent to the critical erosion speed in the field, a statistically significant difference in the level of turbidity was found between the containers with pre- and post-shift densities of the two species (Mann–Whitney *U* test, $P = 0.034$).

Experiment 2

In experiment 2 the effect of *A. filiformis* on erodibility was measured in three containers with pre-shift and three containers with post-shift densities. The average turbidity curves derived

from measurements in the three replicate containers are depicted in Fig. 6. The differences between the half saturation velocities V_{T50} belonging to the pre- and post-shift treatments were statistically significant albeit marginally (Mann–Whitney *U* test, $P = 0.049$). The difference between the curves in Fig. 6 implies that at the lowest V_{T50} (28 cm s⁻¹) resuspension is impeded by high (pre-shift) densities of *A. filiformis* or, conversely, resuspension is facilitated by low (post-shift) densities. More significant in the context of our field observations is that at a critical current velocity of 22 cm s⁻¹, there was no significant differences in turbidity between containers with pre- and post-shift densities of *A. filiformis* (Mann–Whitney *U* test, $P = 0.275$).

Discussion

Experimental results and applicability to the field

The aim of this study was to find experimental evidence for a change in the erosion characteristics of the Frisian Front sediment due to the concurrent increase of *C. subterranea* and decrease of *A. filiformis* populations. Technical specifications of this study set limitations to our observations and interpretation. The experimental containers had to have sufficient surface area and filled with a sediment layer of at least 0.5 m to enable *C. subterranea* build its natural burrow system. The required dimensions and robustness meant we had to use large PVC containers (Fig. 2) instead of transparent cylinders (cf. Scheffer et al., 2003) or existing flow-calibrated flume tanks. The opaque containers excluded making observations on behaviour or distribution during the resuspension runs with the Hydrocopter. Differences in patchiness between replicates, for instance, may have been a cause for the variance in our data. Patches of organisms alternating with bare sediment most likely yield a different erodibility than more regularly dispersed individuals. However, we could not obtain information about the distribution of the animals after they were released in the containers.

Fig. 5 Turbidity at different current velocities in experiment 1 comparing effects of pre-shift species combinations (high densities of *A. filiformis*, low densities of *C. subterranea*) with post-shift ones (low densities of *A. filiformis*, high densities of *C. subterranea*). Mean V_{T50} values are depicted

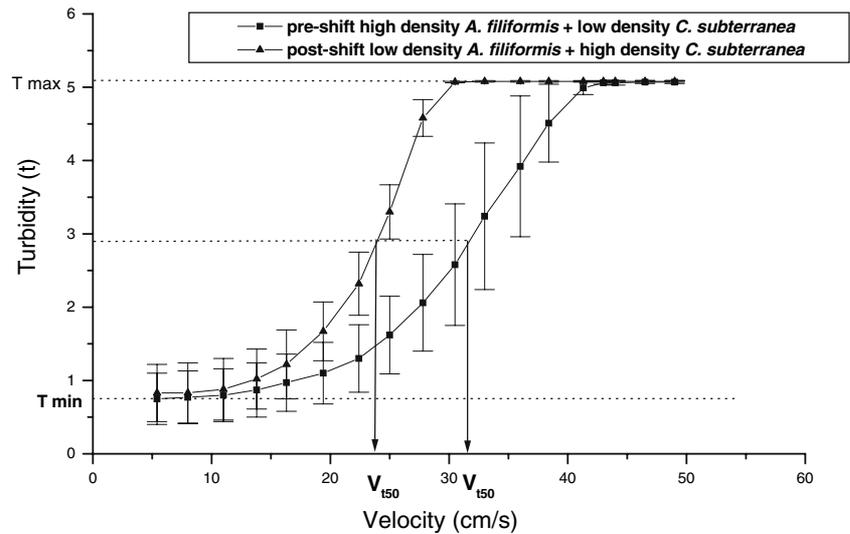
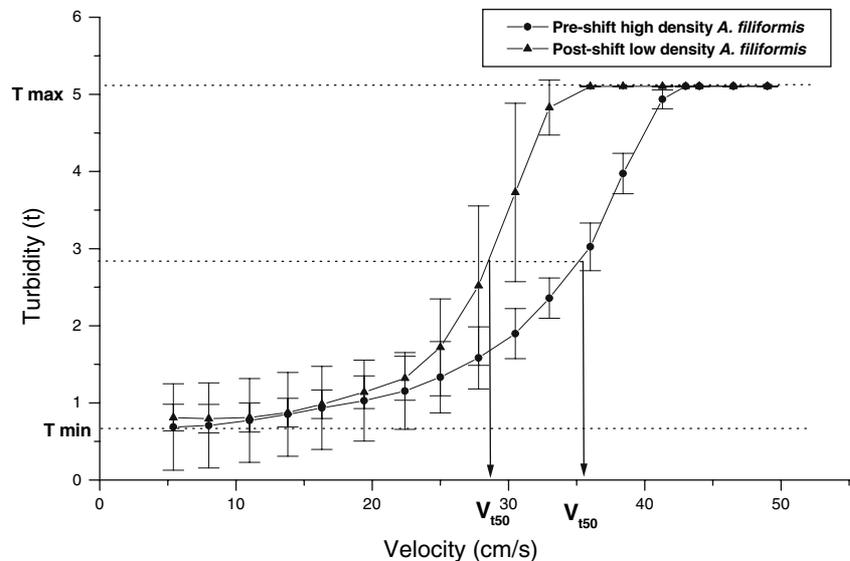


Fig. 6 Turbidity at different current velocities in experiment 2 comparing effects of pre-shift high densities of *A. filiformis* with post-shift low densities. Mean V_{T50} values are depicted



The results of the experiments showed that the two density combinations produced statistically significant V_{T50} values (Figs. 5, 6). In experiment 1, mean V_{T50} is significantly lower (24 cm s^{-1}) with post-shift *C. subterranea* and *A. filiformis* densities than with the pre-shift densities of both species ($V_{T50} = 32 \text{ cm s}^{-1}$). In experiment 2 we found a lower mean V_{T50} with post-shift low densities of *A. filiformis* than with pre-shift densities i.e., 28 versus 36 cm s^{-1} . Converting the V_{T50} values to velocities 0.5 m above the seabed yields a range between 27 and 36 cm s^{-1} for experiment 1 and between 32 and 41 cm s^{-1}

for experiment 2, respectively. Both ranges are outside the normal range of tidal currents measured at the Frisian Front (Fig. 4), and also above the critical near-bed erosion velocity of 25 cm s^{-1} at the Frisian Front. We therefore also tested the turbidity levels due to the different density combinations in experiments 1 and 2 at a speed of 22 cm s^{-1} which corresponds with the critical erosion velocity observed in the field. Only in experiment 1 we found a significant difference in turbidity. This implies that the difference in erosion threshold in experiment 1 is mainly due to activity of *C. subterranea*.

In experiment 2, a 10-fold difference in *A. filiformis* density did not significantly affect sediment erosion at current velocities close to the normal tidal range. The difference in turbidity between *A. filiformis* densities at V_{T50} (Fig. 6), when erosion already has set in, possibly reflects the effect of large numbers of entangled arms holding the sediment matrix together. Earlier Rowden et al. (1998a) reported a decrease of seabed rigidity with increasing densities of *A. filiformis* in cores from the Oyster Grounds and argued that critical erosion shear stress and erodibility is lowered accordingly. We have no clear-cut explanation for the discrepancy between the results of experiment 2 and those of Rowden et al. (1998a). One possibility is that brittlestar activity is also important for altering bed rigidity. Observations by Loo et al. (1996) and Solan & Kennedy (2002) show that *A. filiformis* is mainly active during periods of strong flow. Since we applied no directional flow in the acclimation periods preceding the experiments, *A. filiformis* induced alteration of the bed rigidity was perhaps too small to produce an effect in our experiments.

There appears to be more agreement concerning the effect of *C. subterranea*. In the Oyster Grounds north of our site, Rowden et al. (1998b) found that mound formation by 45 *C. subterranea* per m^2 in summer caused a significant increase of bottom boundary roughness length (z_0) with a maximum of 0.79. By combining this value with the mean near-bed currents in the field using the Karman-Prandtl equation, they estimated a maximum shear velocity (u_*) of 0.52 cm s^{-1} . As no erosion of bed sediment was recorded with their moored instruments, above shear velocity was apparently below the critical value (u_{*CT}). The latter was estimated by Williams et al. (1998) to be 1.36 cm s^{-1} for the seabed at this site. We have no estimate for the z_0 at our site to calculate shear velocity as in Rowden et al. (1998b). However, the u_{*CT} belonging to a horizontal near-bed velocity of 25 cm s^{-1} at 0.5 m can be approximated using the modified version of the Karman-Prandtl equation (Jähmlich et al., 2002). This assumes a logarithmic profile and yields a u_{*CT} of 0.96 cm s^{-1} . A similar value, i.e., 0.98 cm s^{-1} , is found when the approximation in Ziervogel & Bohling (2003) is used. A theoretical estimate of

u_* for cohesionless sediment of the same grain size as on our site yields a value of 0.8 cm s^{-1} (van der Wegen, 2005). Hence, u_{*CT} estimates for our site taken from other sources vary from 0.8 to 1.36 cm s^{-1} corresponding to unconsolidated sediment and sediment with a population of 45 *C. subterranea* per m^2 , respectively. Our estimates of $0.96\text{--}0.98 \text{ cm s}^{-1}$ fall within this range but are substantially lower than the 1.36 cm s^{-1} of Williams et al. (1998). Values of u_{*CT} reported for other subtidal fine sand habitats also fall in the above range but are generally higher than 0.96 cm s^{-1} (e.g., Maa et al., 1993; Jago et al., 2002; Ziervogel & Bohling, 2003). The difference with Williams et al. (1998) is explained by the fact that *C. subterranea* density at our site was 2–5-fold higher leading to increased sediment expulsion rates. Using estimates from Rowden et al. (1998b), our *C. subterranea* population potentially deposits a layer of 0.3–0.8 mm per m^2 of unconsolidated wet sediment each month. A concomitant drop in u_{*CT} toward values belonging to unconsolidated sediment is therefore plausible.

Although neither Rowden et al. (1998b) nor Williams et al. (1998) observed summer erosion they point at the likelihood of resuspension when near bed currents are boosted by storm waves especially in summer when z_0 due to activity of *C. subterranea* is maximal. Our observations and estimates of u_{*CT} appear to be in agreement with their inferences about effects of *C. subterranea* on erodibility.

Frequency of resuspension at the Frisian Front

Our experimental results imply that, presuming nothing else changed, resuspension occurs presently more frequently than in the early 1980s solely due to the increased density of *C. subterranea*. In his analysis of changes in the macrofauna in the German Bight, Schroeder (2003) pointed to the increase of strong and stormy winds in the last decades near Helgoland. On a broader scale Siegismund & Schrum (2001) showed that in the period 1988–1997 strong wind conditions in the North Sea extended over a longer period than in the previous period. Our field data from the Frisian Front indicate that wave (wind) generated currents are important to

boost maximum tidal currents at spring tide above the critical erosion velocity (Fig. 4). Taking the wind data from platform K13 being nearest to the Frisian Front we plotted the sum of hours wind above 10 m s^{-1} for the whole year and for two separate seasons in the period 1980–2000 (Fig. 7). The lines show consistently higher values in the 1990s compared to the 1980s in both seasons. The windiest period is evidently winter. However, wind also increased in the period May–September when the seabed is most sensitive to erosion due to faunal activity. This increasing trend of strong winds has most likely given rise to increased incidence of resuspension at the Frisian Front in the nineties. In addition, the simultaneous increase in abundance of *C. subterranea* possibly amplified this effect. During the period of this study we did not find a clear-cut change in the sediment composition at our site indicative for more resuspension. More recently, Daan & Mulder (2005) reported that from 2001 onwards the silt fraction along the southern border of the Frisian Front had significantly dropped. In this border zone sediment changes from sand to silty sand in concert with a decrease of maximum tidal currents (Creutzberg & Postma, 1979). Being the transition between erosive and depositional

circumstances, this zone is particularly vulnerable to changes in the hydrodynamic regime caused by wind climate.

The failing recovery of the *Amphiura filiformis* population

Although the reason for the collapse of *A. filiformis* is beyond the scope of this paper it is striking that this break down of numbers is not a local phenomenon. Schroeder (2003) described a parallel collapse of the *A. filiformis* population living in fine sediment in the White Bank (German Bight) in the early 1990s. The White Bank population regained its original abundance 5 years after the collapse while at the Frisian Front no recovery was observed up to now. Although more hypotheses can be forwarded to explain failing recovery (e.g., predator control, parasitism, reduction of eutrophication) we have focused in this study on increased sediment resuspension.

Resuspension has several important negative effects on organisms living near the sediment-water interface by causing a decrease in the quality of near-bottom seston, physical disturbance, chemical alterations and removal of settlers. Seston quality is an important cue for particle uptake by suspension feeding organisms such as tentaculate polychaetes and bivalves. Resuspended fine sediment lowers seston quality and hence negatively affects energy intake and growth (Bock & Miller, 1997; Urrutia et al., 1996; Nicholls et al., 2003; Archambault et al., 2004). In a study on growth in 3 interface feeding species (bivalves, heart urchin) in the North Sea, Witbaard et al. (2001) found higher growth rates in coarser sandy sediment than in the fine-grained Frisian Front. The authors attribute this to poor quality of the seston in the silty station when it becomes mixed with resuspended silt (Duineveld & Boon, 2002). Also growth in *A. filiformis* depends for a large degree on the presence of fresh high quality organic matter (Skold & Gunnarsson, 1996; Loo et al., 1996). Since *A. filiformis* is an interface suspension feeder active at high flow rates, more frequent and longer periods with higher loads of suspended particles caused by an enhanced erodibility may interfere with its energy

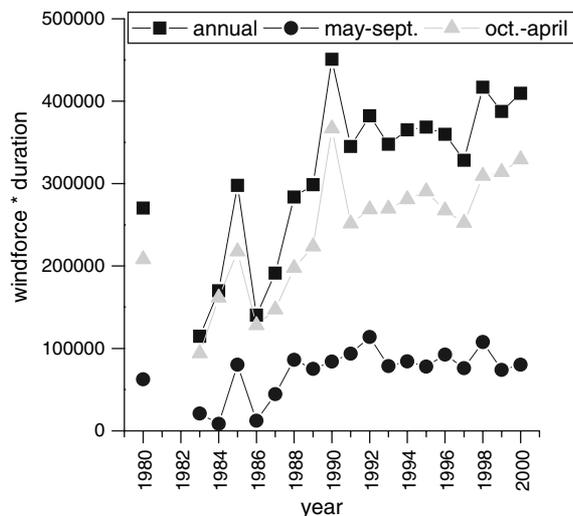


Fig. 7 Trend in wind sum i.e., speed (in m s^{-1} if $>10 \text{ m s}^{-1}$) * duration (in hours) at platform K13 in the period 1980–2000 (source: www.knmi.nl/hydra). Separate curves are drawn for the total wind sum, and wind sum for two periods viz. May to September and October–April

uptake. This may keep its population from optimizing its growth and reproduction. Resuspension of the thin oxygenated top layer in the Frisian Front can furthermore make the sediment less attractive to settling larvae due to biogeochemical changes though the effect is not long-lasting (Marinelli & Woodin, 2002). Resuspension of recently settled larvae in an unstable silty seabed may also cause mass mortality (Rhoads & Young, 1970) especially if larvae run the risk of being advected outside the suitable habitat. Such a risk would be high in the Frisian front since the mud patch has a limited length (Fig. 1).

More studies especially on the larval stages of the two species are needed to clearly separate cause and effect in the persistent shift in abundance of *C. subterranea* and *A. filiformis*. Our present experiments indicate that resuspension at the Frisian Front may occur more frequently as a consequence of the shift in dominance pattern that took place in the 1990s. The potential effect of the shift will be amplified by the changed wind pattern in the North Sea. Apart from consequences for ecologically important species as *A. filiformis* other rare species will be also affected by intensified resuspension. Among them the large suspension feeding bivalves (*Arctica islandica*, *Mya truncata*) which form an important argument to consider the Frisian Front as a future Marine Protected Area.

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