

## Research Article

## Invading grass-like alga transforms rippled sand bars into bumpy muddy flats: arrival of a game changer in the Wadden Sea?

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### Abstract

In the wake of biological globalization, translocated species of high bio-engineering capacity increasingly change bottom topography of sedimentary coasts. A *Vaucheria*-taxon (Xanthophyceae) of unknown origin is spreading at the transition between intertidal and subtidal zones, while resident *Vaucheria*-species are confined to the upper shore in the Wadden Sea (European Atlantic). Near the island of Sylt, dense turfs of green filaments rapidly expanded over an area of 180 ha within 3 years. The unicellular filaments reach about 5 cm out of and 5 cm into the sediment. Felted rhizoids provide firm anchorage. Dry phytomass (up to 208 g m<sup>-2</sup>) was similar to that of intertidal seagrass beds. Residual filaments overwinter in the sediment and give rise to renewed growth in late spring. In addition, oospores germinate. Fine particles are trapped by the turf during summer, generating laminated cohesive mud. Muddy hummocks arise up to 20 cm above ambient sand flats, alternating with troughs but gradually merge into coherent and pertinacious plateaus of mud. This shift in bottom topography and sediment composition may potentially change the mud balance of tidal basins, and the capacity of tidal flats in catching up with accelerating sea-level rise.

**Key words:** invasion, algal turf, bioengineering, mud, tidal flats, *Vaucheria*

### Introduction

Coastal ecosystems are particularly susceptible recipients for species shipped across oceans beyond natural dispersal (Cohen and Carlton 1995; Ruiz et al. 2000; Wolff 2005; Ruesink et al. 2006; Buschbaum et al. 2012). Effects on residents are hard to predict and precaution is advised (Anton et al. 2019; Pyšek et al. 2020). Marine algal invasions are a prominent component (Inderjit et al. 2006). Particularly strong ecological effects are known from translocated foundation species or ecosystem engineers (i.e., Crooks 2002; Ruesink et al. 2006; Wallentinus and Nyberg 2007; Sousa et al. 2009; Walles et al. 2015; Guy-Haim et al. 2017). Most notorious are mats of green algae of the genus *Caulerpa*, spreading rapidly and blanketing resident benthos including seagrass beds, thus nicknamed “killer algae” (Meinesz 1999). However, their ecological effects proved more complex than initially

anticipated. Introduced species of this genus behaved differently, benthic assemblages and habitats differed in responses, and long-term invasion dynamics varied (i.e., Gribben and Wright 2006; Klein and Verlaque 2008; Gribben et al. 2009; Bulleri et al. 2010; Pérez-Ruzafa et al. 2012; Glasby 2013; Montefalcone et al. 2015). Nevertheless, *Caulerpa*-invasions became major drivers of ecological change at many coasts.

Although smaller and not closely related to *Caulerpa* (Chlorophyceae), the genus *Vaucheria* (Xanthophyceae) shows some striking similarities. Species identity within both genera needs clarification, both have siphonous green thalli, form extensive mats, which may accumulate sediment. In coastal areas, species of *Vaucheria* tend to grow in dense turfs, and may give rise to conspicuous hummocks (Krieg et al. 1988; van de Vijssel et al. 2020), superficially resembling cushions of filamentous green algae or mosses. In the North Sea, *Vaucheria*-species are common but usually inconspicuous, occur at upper shores in muddy estuaries or in salt marshes, and generally have received little attention (but see Simons 1975; Polderman 1979a, b; Christensen 1987; Krieg et al. 1988; van de Vijssel et al. 2020).

In 2020, we discovered two taxa of *Vaucheria* thriving at and below low tide level where none were found before in the well-studied Wadden Sea (eastern North Sea, European Atlantic). Rybalka et al. (*in press*) identified one as *V. cf. velutina*, genetically distinct from *V. velutina* C. Agardh, 1824 (syn. *V. thuretii* Woronin, 1869) growing in nearby salt marshes at the upper shore. No niche extension from the upper shore had taken place. Instead, we assume an introduction from distant coasts where populations of *V. velutina* also have been reported from lower shores, i.e., Florida (Gallagher and Humm 1981) or the southern Pacific (Womersley 1987; Wilcox 2012). Presumably, the cosmopolitan morphotaxon *V. velutina* comprises a complex of hidden species awaiting revision by employing chloroplast DNA-sequencing (Andersen and Bailey 2002). The same applies to *V. longicaulis* Hoppaugh, 1930, also discovered in the Wadden Sea for the first time, spreading at the lower shore next to *V. cf. velutina*. In NW-Europe it has been found since the 1990s at the British Channel (Christensen 1996) and in the Rhine delta (Stegenga et al. 2006). The latter authors regard *V. longicaulis* as introduced to The Netherlands. At Sylt in the northern Wadden Sea, *V. cf. velutina* is growing in summer and *V. longicaulis* in autumn and early winter (Rybalka et al. *in press*). The latter species remained confined to rather small patches in 2020, and we focus on *V. cf. velutina* in this study because it spread over vast areas, displaced lugworms and provided habitat to small fauna (Reise et al. 2022), and generated conspicuous muddy hummocks, which is the focus of this study.

In the Wadden Sea, a large proportion of tidal flats consists of rippled sand, maintained by the permanent reworking of lugworms, *Arenicola marina* (Reise et al. 2010). Lugworms dwell in U-shaped burrows and recycle the upper layer of sediment 10–20 times per year through their guts

(Cadée 1976), prevent clogging of the interstices of sand with fine particles and organic material, and increase sediment permeability (Volkenborn et al. 2007). Around low tide level, large individuals of relatively low abundance prevail (Reise et al. 2001). At this “senior home” of lugworms, we encountered the invading *V. cf. velutina*, generating muddy hummocks.

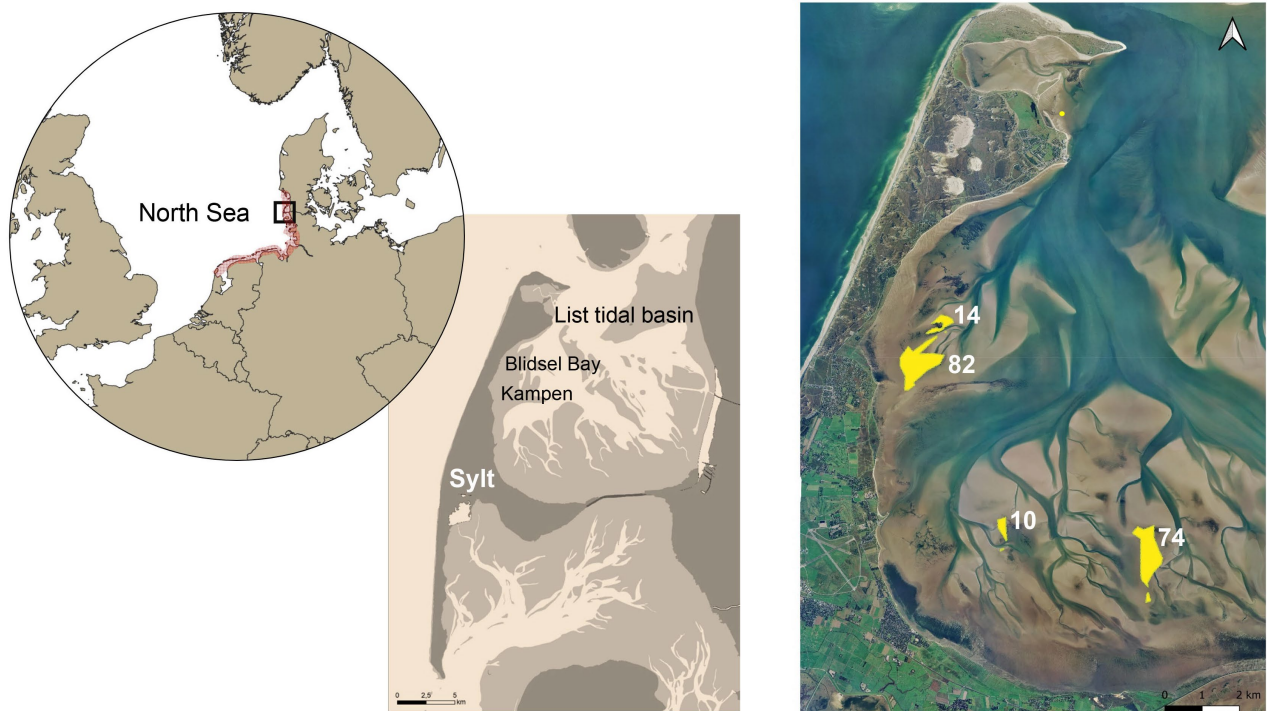
With its arrival, a completely new mode of life is spreading in a habitat where other macroalgae tend to be rare because solid substrate for attachment is scarce. *V. cf. velutina* overcomes this obstacle by rhizoids penetrating deep into the sediment, providing firm anchorage. The alga monopolizes space, traps and fixes suspended matter, which may initiate a cascade of ecological change. We hypothesize permanent changes in bottom topography and sediment composition where *V. cf. velutina* took over. We specifically ask, (1) How did the initial spread proceed? (2) What algal properties could modify sedimentation processes? (3) Which sediment properties changed where *V. cf. velutina* had established? (4) How are arising bedforms changing over time? Finally, we speculate what may be the overall effect of this invading alga on the ability of the sedimentary bottom to catch up with accelerating sea-level rise in the wake of global warming. In a companion paper (Reise et al. 2022) we deal with cascading effects on resident benthos.

## Materials and methods

### *Study site*

The Wadden Sea comprises the largest coherent belt of sedimentary tidal flats globally, ranging from meso- to macrotidal and from estuarine to fully marine conditions (Reise et al. 2010). Tidal basins are sheltered by a chain of barrier islands. In the northern Wadden Sea, the List tidal basin at the Danish-German boundary comprises an area of 400 km<sup>2</sup> (Figure 1). Of these, 33% are tidal flats, 57% are shallow subtidal flats down to 5 m, intersected by deep channels and an inlet with 10% of the area (Gätje and Reise 1998). Mean tidal range of semi-diurnal tides is almost 2 m, and salinity is between 26 and 32 PSU. Water temperatures fluctuate between 0 and 20 °C with an increase of 1 °C since the 1980s (Johannes J. Rick *pers. comm.*). Parameters of eutrophication (N, P) increased until the late 1990s and since then have declined again.

Sediments are primarily sandy with a few mud flats at southern and northern fringes of the basin where causeways connect the two barrier islands with the mainland (Pejrup et al. 1997). Intertidal seagrass beds declined since the 1930s (Dolch and Reise 2010) while former mussel beds became invaded by introduced Pacific oysters (Reise et al. 2017), followed by several exotic macroalgae of which *Sargassum muticum* has formed extensive kelp beds in the shallow subtidal zone (Schories et al. 1997; Lang and Buschbaum 2010). The mainland is under intensive agricultural use and islands are crowded with tourism. The tidal basin is part of National Parks



**Figure 1.** The Wadden Sea (reddish) at the eastern fringe of the North Sea. List tidal basin (enlarged rectangle) with shaded tidal flats between the island of Sylt and the Danish-German mainland. Composited aerial image (AWI, August 31, 2008) taken during an extreme low tide with exposed intertidal and shallow subtidal flats. Areas (yellow, in hectares) covered by *Vaucheria cf. velutina* in September 2020 were recorded at spring low tides by GPS.

(Germany: Nationalpark Schleswig-Holsteinisches Wattenmeer; Denmark: Nationalpark Vadehavet) and is included in the UNESCO Wadden Sea World Heritage Site.

#### *How did the initial spread proceed?*

Observations on *Vaucheria* at the lower shore commenced early in June 2020 when it was first discovered. We measured areal spread of *Vaucheria*-beds using a GPS 72H (Garmin) while walking along the circumference of individual beds. This was only possible when spring low tides and offshore winds coincided. Otherwise, lower boundaries of beds remained submerged. The local tide gauge at List harbor provided tidal elevations, and we used daily water level forecasts given by the Federal Maritime and Hydrographic Agency (BSH). At the site Blidsel Bay, we circumnavigated the bed on June 17, June 26 and September 19, 2020. Other beds were located and circumnavigated during exceptional low tides in September 2020.

To reconstruct when these *Vaucheria*-beds commenced developing we used two approaches. The occasionally taken aerial shots of the site at Blidsel Bay were inspected for absence or presence of dark shading of the exposed sand bar. This served as a hint for the first appearance of the formation of a *Vaucheria*-bed. As a second approach, we took 24 sediment cores with a cross-section of 10 cm<sup>2</sup> to a depth of 20 to 25 cm at the central part of the bed at Blidsel Bay, and visually inspected those for the occurrence and depth of layers composed of dead *Vaucheria*-filaments. Additional

cores taken outside this established *Vaucheria*-bed never revealed any such dead filaments.

*What algal properties could modify sedimentation processes?*

We quantified growth of *V. cf. velutina* by counting density of green filaments, by measuring green filament lengths, and by estimating dry weight in August 2020 at Blidsel Bay. We distinguished between growth at the higher edge and lower central part of the bed already present at June 17, and in the area that became vegetated until June 26, named pioneer belt. For counting density, we gently drilled a corer with sharpened lower edge and a cross section of 2 cm<sup>2</sup> down to 5 cm depth. Obtained sediment cores were washed through a 500- $\mu$ m mesh, retaining the intertwined filaments. Of these, green siphons of > 10 mm length were counted under 10x magnification. Six cores were from vegetated patches in the pioneer belt (August 12, 2020), six from vegetated hummocks at the edge of the old bed and four from the continuously vegetated central part of the bed (August 15, 2020).

In addition to filament density, length of filaments above sediment surface may have effects on sedimentation processes. On September 02, 2020, we clipped siphons at sediment-water interface, and determined lengths to nearest mm for 30 filaments at the pioneer belt, vegetated hummocks and the continuously vegetated central part of the bed (same as for density of filaments).

In an attempt to estimate phytomass at Blidsel Bay on August 08, 2020, we took 4 sediment cores of 50 cm<sup>2</sup> to a depth of 5 cm from the pioneer belt, vegetated hummocks and the continuously vegetated central part of the bed, then washed with tap water through a 500- $\mu$ m mesh. We separated the retained algal tufts of *Vaucheria* from other algae (mainly *Rhizoclonium riparium*) and removed entangled worm tubes manually. Four samples from each of the three habitats were dried for 3 d at 80 °C, and then were weighed.

*Which sediment properties changed where V. cf. velutina had established?*

At Blidsel Bay in June 2020, we took cores with a cross section of 10 cm<sup>2</sup> from high hummocks and from an ambient lugworm sand flat 50 m north of the *Vaucheria*-bed. Water and organic content for the upper 6 cm of sediment was measured by weight loss after drying at 80 °C and ignition at 500 °C, respectively. Relative penetration depth was estimated by dropping a weight of 500 g (40 mm in diameter) from 1 m height. Salinity was measured with an ATC refractometer.

For sediment analyses, cores with a cross section of 10 cm<sup>2</sup> were taken to a depth of 36 cm from a *Vaucheria*-hummock and from ambient lugworm sand flat 50 m north from the *Vaucheria*-bed at Blidsel Bay in June 2020. Cores were sliced into an upper 1 cm layer and from thereon into intervals



of 5 cm each. Subsamples were chemically treated following the procedure used in Hass et al. (2010) in order to remove carbonate and organic matter prior the grain-size analyses, performed using a CILAS 1180L (3P Instruments GmbH & Co. KG, Odelzhausen, Germany) laser-diffraction particle sizer (range: 0.04–2500  $\mu\text{m}$ ). Statistics of grain-size results (based on volume percentage data) were calculated using the program GRADISTAT (version 8.0) (Blott and Pye 2001) and are based on Folk and Ward (1957).

### *How are arising bedforms changing over time?*

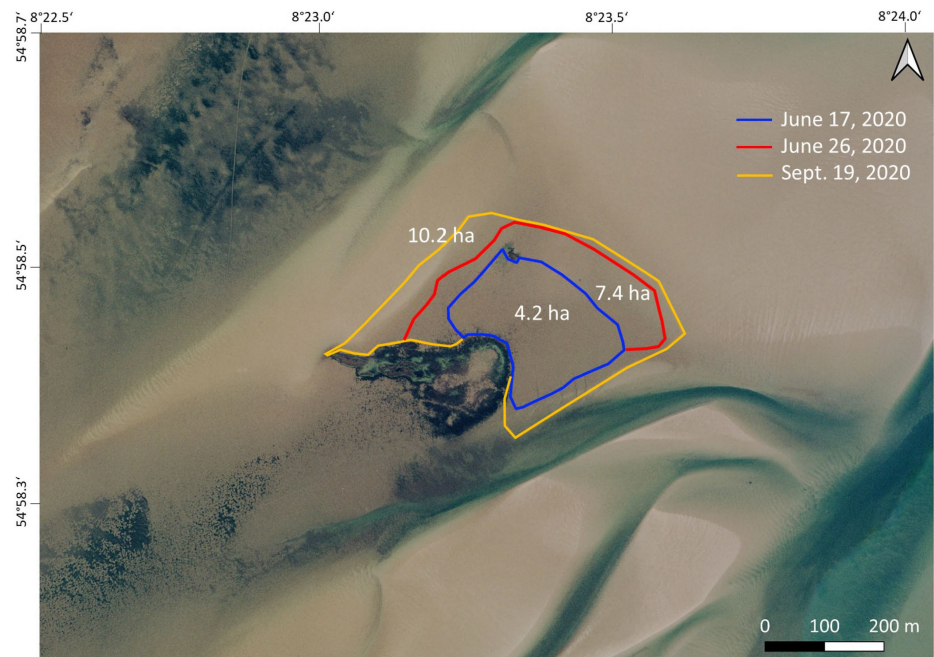
Height of muddy hummocks and plateaus vegetated by *Vaucheria* was estimated relative to ambient sediment surface using a folding rule bent at right angle. We measured in the pioneer belt, and at the high edge and lower central part of the bed already established when first encountered in early June. At Blidsel Bay and Kampen, most measurements are from August/September 2020. The latter was the only site accessible for further measurements in winter (February/March) and early spring (May 2021). We base most of our interpretation of bedform succession on qualitative notes and on photographs taken when walking around and across all beds we encountered. Concomitantly, we took qualitative notes on the state of above ground algal filaments. In parallel, we kept samples of *V. cf. velutina* in covered petri dishes at a windowsill under room temperature (usually 16 to 18 °C), exchanging seawater weekly. The same we did with vegetated sediment cores kept under seawater. This was an attempt to learn about seasonal growth, reproduction, overwintering and regrowth in spring. This is essential for understanding the persistence of the new bedforms.

## **Results**

### *Initial spread of Vaucheria at the lower shore of Sylt*

Abundant filaments of *V. cf. velutina* at the lower shore were first encountered in the List tidal basin east of the island of Sylt early in June 2020, at the site Blidsel Bay (Figures 1, 2). The population was spreading until autumn 2020. In September the total area with dense growth in coherent beds was estimated to at least 180 ha, primarily occurring at four sites, 1 to 4 km seaward from shorelines (Figure 1). These beds of *Vaucheria* were positioned + 0.2 m to –0.5 m relative to mean low tide level. This corresponds to water depths of 2 to 3 m at high tides. At tidal channels, some growth was even observed down to 1 m below mean low tide level. Spring tide exposure lasted for up to 2 h, while during neap tides and onshore winds these *Vaucheria*-beds remained submerged.

A major new spread of young growth into ambient sand flats appeared in June, then continued more slowly until September 2020 and more than doubled the entire area of the *Vaucheria*-bed at Blidsel Bay (Figure 2). Beds of *Vaucheria* at the lower shore were visible from the air as dark shading on



**Figure 2.** Spread of *Vaucheria* cf. *velutina* from overwintered bed (blue) into adjacent sand flats in June (red) and until September 2020 (yellow), measured by walking along boundaries between bed and ambient bare sand flat with GPS. Underlying aerial image is from August 31, 2008. Black patches near the *Vaucheria*-bed are from beds with mixed mussels and oysters, while other dark patches further away mostly stem from *Sargassum*-kelp anchored by clumps of oysters. Photo by AWI.

exposed sand flats. However, shading was too similar to that of other algae or seagrass for detection or mapping purposes. Nevertheless, comparisons between images from 2020 and the years before suggest that at Blidsel Bay the bed of *Vaucheria* was already present in 2019 and that initial growth commenced in 2018, while images from 2017 and earlier showed bright, bare sand at the same site.

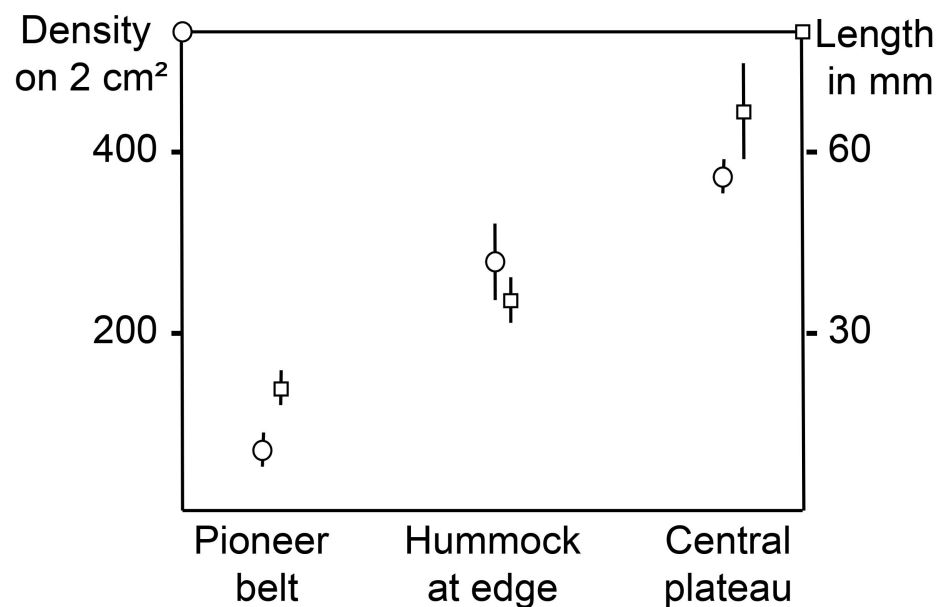
At this bed, one or two layers of dead, horizontally deposited *Vaucheria*-filaments occurred in sediment cores (see Figure 5, right core). Mean sediment depth of such layers was 83 mm (22 out of 24 cores) and 125 mm depth (16 cores). On average, thickness of the upper layer was 26 mm and of the lower layer 13 mm. The filament fragments were rather short ( $32 \pm 10$  mm,  $n = 10$ ), and included occasionally rhizoids and oospores. At Blidsel Bay, buried layers of dead siphons occurred not in bare ambient sand and not in the pioneer belt (see Figure 2). At Kampen, one such layer occurred but none at the two beds in the southern part of the tidal basin (see Figure 1).

#### *Properties of V. cf. velutina, which could modify sedimentation processes*

A characteristic feature of beds of *V. cf. velutina* are pointed tufts formed by adjacent filaments bending with their tips towards each other during low tide exposure (Figure 3). Upright filaments enveloped by a film of water join each other like poles of a tipi tent. This easily distinguishes *V. cf. velutina* from filamentous green algae in the field. In August 2020, density of these green filaments increased from the pioneer belt towards the central



**Figure 3.** Muddy hummocks during low tide exposure in June 2020, tufted with *Vaucheria* cf. *velutina*. In the foreground, a faint touch of green appears on elevated ridges by young growth on otherwise bare sand. Note seeping ground water at base of hummocks staining sediment black. Right: Filaments with rhizoids washed free from sediment. Scale indicates length of filaments above and below sediment surface. Photos by K. Reise.



**Figure 4.** Density of green filaments (> 10 mm long) on 2 cm<sup>2</sup> (left scale, o) and length of green filaments in mm (right scale, □) at Blidsel Bay in August 2020, increasing from pioneer belt to high hummocks and central plateau of *Vaucheria*-bed. Vertical bars indicate 1 standard deviation.

bed at Blidsel Bay (Figure 4). Density reached up to two siphons per mm<sup>2</sup> or more than 1 million per m<sup>2</sup>.

While rhizoid penetration depth in the sediment was generally between 30 to 50 mm in established beds (Figure 3), length of green portions was more variable with season and site. In early September 2020, mean length of green siphons clipped at sediment-water interface was  $20 \pm 3$  mm [range 13–25] at the pioneer belt and increased towards the central bed at Blidsel Bay (Figure 4). There mean length of green siphons was  $67 \pm 8$  [range 47–80] mm. Adding below ground portions, maximum length may reach up to





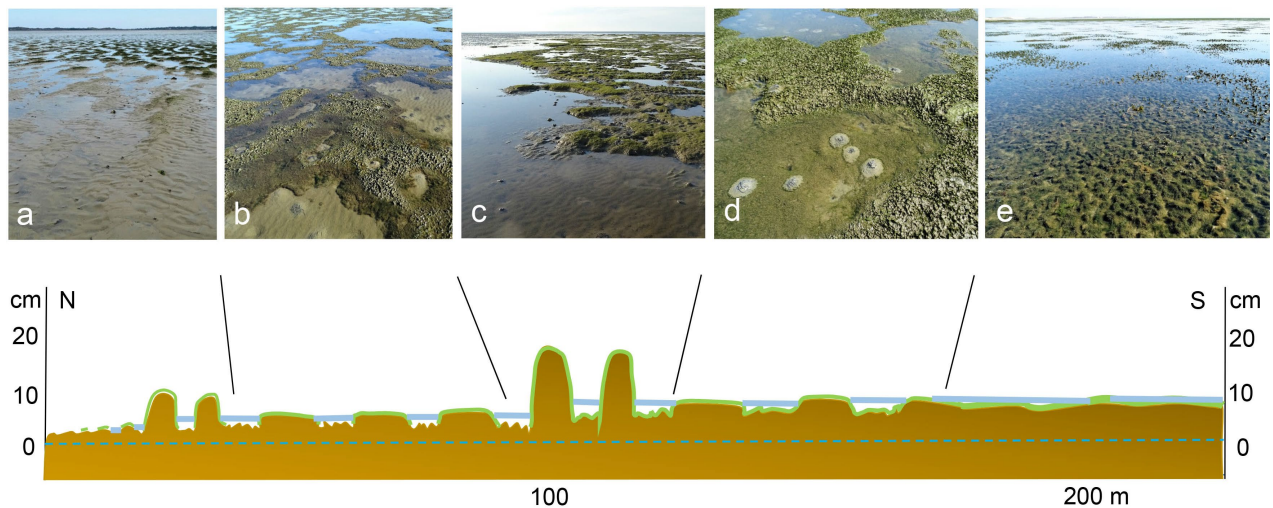
**Figure 5.** Sediment cores from left to right: Bare sand flat, young and old bed of *Vaucheria* cf. *velutina*, the latter with a layer of dead, black filaments at 10 cm depth. Photo by K. Reise.

130 mm. Diameter of green siphons was  $123 \pm 14 \mu\text{m}$  [range 100–140] ( $n = 18$ ) and tapered at colorless to slightly pink rhizoids to  $40 \mu\text{m}$  or less. Single branching occurred in 28% of green siphons (usually about 40% of total length), while multiple branching into thin rhizoids was the rule.

Dry phytomass of *Vaucheria* at Blidsel Bay, calculated per  $\text{m}^2$  for August 2020 was  $74 \pm 16 \text{ g}$  in the pioneer belt,  $116 \pm 26 \text{ g}$  on high hummocks, and  $208 \pm 34 \text{ g}$  on plateaus of the central bed.

#### *Sediment characteristics*

Sediment underneath dense turfs of *Vaucheria* was soft and muddy, while it consisted of rippled sand, reworked by lugworms *Arenicola marina* in ambient areas (Figure 5). Underneath hummocks with *Vaucheria*, sediment was laminated, visible by layers of varying blackness below a thin brownish surface layer of a few millimeter. This contrasted with ambient sand flats where the brownish surface layer extended between 10 to 30 mm depth, followed by a rather homogenous light to dark grey sediment (Figure 5 left core). Digging within *Vaucheria*-beds elicited a strong smell of sulfide, while there was only a faint smell in the bioturbated bare sand. In the upper 60 mm of sediment cores, water content at low tide exposure was higher at hummocks covered by *Vaucheria* (29%) than at adjacent lugworm sand flat (21%). Organic content was 4-fold higher (1.6% weight loss after ignition) at hummocks compared to ambient lugworm flat (0.4%). Penetration depth of a dropped weight was 4-times deeper at *Vaucheria*-hummocks ( $38 \pm 3 \text{ mm}$ ,  $n = 12$ ) than at ambient lugworm sand flat ( $10 \pm 1 \text{ mm}$ ,  $n = 6$ ).



**Figure 6.** Schematic profile across advancing *Vaucheria* cf. *velutina*-bed from left (N) to right (S) in Blidsel Bay. Low tide water levels (blue line) are banked-up by hummocks. “0” on the cm-scale corresponds to spring low tide level (broken line). a: pioneer growth on sand waves, with emerging hummocks in the back in August 2020; b: mosaic of plateaus with *Vaucheria* and bare pits with lugworm burrows in the young belt in July 2020; c: high *Vaucheria*-hummocks from 2019 in June 2020; d: mosaic from 2019 with plateaus and troughs, both with *Vaucheria* in July 2020; e: smoothed plateaus where *Vaucheria* occurred since 2018 in August 2020. Photos by K. Reise.

Salinity above sediment and at depth of > 20 cm was the same, both, within the *Vaucheria*-bed and ambient sand flat, indicating absence of freshwater seepage from below.

*Vaucheria*-hummocks were composed of cohesive mud while bare ambient areas consisted of loose sand. Mean grain size was homogeneously distributed over depth intervals at the lugworm sand flat ( $146 \pm 5 \mu\text{m}$ ), while at *Vaucheria*-hummocks means were smaller and more heterogeneous ( $114 \pm 30 \mu\text{m}$ ). Accordingly, sediment was well sorted at the lugworm flat and poorly sorted at hummocks. Mean grain size variation between layers was most pronounced in the upper 16 cm of cores, with  $149 \pm 4 \mu\text{m}$  and  $104 \pm 36 \mu\text{m}$  at lugworm sand flat and *Vaucheria*-hummock, respectively. Mud (silt) content was twice as high and highly variable for vertical intervals at hummocks ( $16 \pm 11\%$ ,  $n = 8$ ) compared to lugworm sand flat ( $8 \pm 1\%$ ,  $n = 8$ ).

#### *Bedforms changing over time*

Bedforms of *V. cf. velutina* undergo succession (Figure 6). We infer this from observations at the bed in Blidsel Bay. Here new growth commenced in June 2020 beyond edges that had formed in 2019, and where sediment cores with two layers of dead filaments suggest that the innermost part of this bed became established already in 2018. This amounts to a 3-year time span.

Faint growth on bare sand flat started synchronously over a wide belt in June 2020. At the outer edge growth of small filaments preferentially occurred on sand waves with parallel longitudinal axes all across the sand flat (0.5 to 1.5 m wide and several m in length). By growing on these barely discernible ridges, *V. cf. velutina* enhanced deposition and stabilized the sand. As side effect, these developing shallow ridges deflected water flow,





**Figure 7.** Sandy lugworm flat partly covered by bumpy bed of *Vaucheria* cf. *velutina* in June, and after a mosaic of young growth and bare patches had spread until September 2020. Below: Sandy lugworm flat and *Vaucheria*-bed with sharp boundaries facing north and east before and after winter 2020/21. Although raised mud had turned bare in winter, boundaries with ambient sand remained distinct. Photos by K. Reise.

causing enhanced scouring at interspaces between ridges. This pattern developed into dome-shaped ridges covered by a dense turf, alternating with bare troughs. In the shelter of such elongated hummocks modest plateaus with turfs alternated with bare patches (Figures 6, 7). These were of irregular size and shape. Gradually and with delay, bare patches became vegetated too. Differences in elevation had increased to  $93 \pm 25$  mm [range 50–130] ( $n = 42$ ). Such bumpy bottom topography was still apparent in the old bed, particularly at the former edge (Figures 6, 7). There, mean height of hummocks above water level during low tide was  $81 \pm 13$  mm [range 60–110] ( $n = 30$ ). Troughs in between were of variable depth:  $118 \pm 46$  mm [range 50–260] ( $n = 60$ ) below low tide water level. These heights and depths added up to a mean difference of about 20 cm with a range of 11 to 37 cm.

Edges of *Vaucheria*-beds often formed a distinct boundary to bare ambient sand flat, particularly where facing north or east (Figure 7), often accompanied by scouring along edges. From the high hummocks along edges, surface topography smoothed towards the interior bed. Dome-shaped hummocks flattened into plateaus. The mosaic of plateaus and troughs also became more spacious. Differences in height decreased to about 5 cm. There, *V. cf. velutina* colonized troughs until coverage by filaments became even.

In winter 2020/21, elevations and depressions in the *Vaucheria*-bed were almost bare of filaments but persisted (Figure 7). Two storms with wind speeds up to 11 Bft, and a long fetch from southeast, hit the muddy

elevations. This caused erosion at edges of hummocks and the plateaus became rippled. At erosion scarps, buried filaments resurfaced, usually mixed with other algae, which deposited in the *Vaucheria*-bed during summer. In February 2021, 12 d with drifting ice shoals of up to 1.5 m in thickness also hit the mud deposits generated by *V. cf. velutina*. Ice scouring left traces as if off-road vehicles had crisscrossed *Vaucheria*-beds. Storm and ice events decreased differences in elevation between hummocks/plateaus and troughs to  $97 \pm 15$  mm [range 70–120] ( $n = 42$ ) by the end of February 2021 where in summer 2020 hummocks were twice as high. Nevertheless, the basic bumpy pattern persisted.

In August 2020, plenty of spherical oogonia (280 to 320  $\mu\text{m}$  in diameter), sessile on old siphons, were observed. Antheridia did not develop. In October 2020, green siphons above sediment surface turned brownish, mainly due to attached diatoms. Siphons above sediment surface broke off and mud remained bare during winter. However, when bare sediment from beds was brought to the lab, covered with seawater, positioned on window sill, and under room temperatures, new green thalli emerged within days. These grew out of pale or brownish, buried old siphons with small green portions. From bare mud collected in early December 2020, siphons were  $71 \pm 21$  mm [range 36–102] ( $n = 10$ ) in length with a green portion of 48% after 48 d under lab conditions. Assuming linear growth over this interval, daily length increments of green siphons were 0.7 mm. Under similar conditions, green growth from hibernating siphons collected March 31 in 2021 amounted to  $0.5 \text{ mm d}^{-1}$  after 14 d ( $6.9 \pm 1.5$  mm [range 4–11] ( $n = 60$ ) in length).

Spring 2021 was unusually cold. We encountered first green filaments on muddy hummocks not before May 11. At May 24, mean length of green filaments was  $14 \pm 3$  mm [range 7–17] ( $n = 25$ ) with a mean filament density of  $11 \pm 5 \text{ cm}^2$  [range 5–17] ( $n = 4$ ) on hummocks at Kampen. This is about ten times less than in August 2020 at Blidsel Bay. Water temperature was 10 to 11 °C. In June, brownish oospores found in the sediment at both sites, germinated.

## Discussion

For the first time, growth of introduced *Vaucheria cf. velutina* at the lower shore of the Wadden Sea is described. This *Vaucheria* persists in large muddy beds, and a rapid spread occurred in 2020 on sandy flats. Turfs of *Vaucheria* trap silt upon sand and raise the bottom by up to 20 cm in 3 years. This may change balance and distribution of mud in tidal basins, and may have implications for adaptations to accelerating global sea level rise.

Layers of dead *Vaucheria*-filaments in the sediment as well as aerial images indicate that spread in the form of coherent beds commenced in 2018. Although at rather inaccessible sites, their conspicuousness as raised



beds precludes that these went unnoticed for many years if being present. We assume that *V. cf. velutina* constitutes a recent invader to the lower shores at the island of Sylt and to the entire Wadden Sea (Rybalka et al. in press). Why and how could this alga establish and spread at the lower shore where none have been before? What is the effect on the sedimentary environment and bottom topography?

### *Establishment*

For macroalgae, rippled sand reworked by lugworms constitutes an unfavorable and unreliable substrate to live upon. Occasionally green algae occur. This may happen when drifting algal strings became stranded in feeding pits of lugworm burrows (Reise 1983). In summer 2020, we also observed green algae of the genus *Ulva* growing attached to abundant cockles *Cerastoderma edule* or their empty shells. Also tube caps of *Lanice conchilega* on low intertidal sand flats offered suitable substrate. The phenomenon of filamentous green algae covering otherwise unsuitable sandy flats in the Wadden Sea was common when the level of eutrophication was high but then declined again since the late 1990s (van Beusekom et al. 2009).

In contrast to these green algae, *V. cf. velutina* does not require help of other species for anchorage in loose sand and is thus more likely to persist once established. Biomass of *Vaucheria* at maximum growth in August was in the same magnitude as that of ephemeral green algal mats (i.e., Fletcher 1996; Pihl et al. 1999; Reise et al. 2008) or seasonal maxima for intertidal seagrass beds (i.e., Philippart 1995; Auby and Labourg 1996; Nacken and Reise 2000). Young pioneering growth of *V. cf. velutina* occurred primarily on slightly elevated, elongated sand ridges and was rare at vales in between. This indicates that weather dependent, temporary sediment stability or net deposition facilitate establishment while erosional conditions are inhibitory. Erosion may also explain that often in front of high bed boundaries new growth remained absent. These elevated edges of *Vaucheria*-beds may channel tidal flow in parallel to their front, and this entails scouring which results in unfavorable conditions for the establishment of new growth in *Vaucheria* (see Figure 7 for erosion pits along edges).

At ridges where deposition dominates over erosion, young growth appeared first and this also might have been the window of chance for the very first propagules of *V. cf. velutina* that had arrived in List tidal basin. Such conditions at the lower shore could have been provided in the shelter of beds with mixed mussels and oysters. These occur in the vicinity of the *Vaucheria*-bed with traces of a dense turf already in 2018 (see Figure 2). Before the formation of a first coherent bed, there may have been several years of marginal existence at the brim of extinction, until particularly benign consecutive conditions facilitated development of a large population. Only after that, the probability of getting extinct again decreased towards zero. Although winter conditions were harsh, spring 2021 unusually cold, and re-growth on the existing *Vaucheria*-beds retarded, all beds persisted.

### *Vaucheria cf. velutina* as ecosystem engineer

The stabilization of loose sand is an obvious property of densely growing filaments of *V. cf. velutina*. With 1 to 2 green siphons per mm<sup>2</sup>, reaching down to 5 cm into the sand with branching and felted rhizoids, and with green filaments up to 8 cm above sediment surface, sand grains cannot be moved freely anymore by waves or currents, and hydrodynamics are diverted away from the sediment surface. Fonseca et al. (1982), Koch et al. (2006) and Marin-Diaz et al. (2020) described this for seagrass. This vascular plant is larger than *Vaucheria* but otherwise of similar growth with roots and slender leaves. Also similar to rhizomes of seagrasses such as *Zostera noltei* in the Wadden Sea, filaments of *V. cf. velutina* overwinter in the raised mud beds and give rise to re-growth in spring. Although no antheridia occurred, oospores germinate next summer, suggesting parthenogenesis. The relative importance of re-growth from overwintering thalli and germination from oospores needs further research.

As a corollary of dense turfs reducing and deflecting tidal flow, *V. cf. velutina* changed the entire sediment characteristics from loose sand to cohesive mud. Flocks of fine particles with organic material are trapped from turbid tidal waters by a dense canopy of filaments which also prevents resuspension and thus accumulates otherwise transient suspended matter as known from seagrass beds (Chen et al. 2007; Wilkie et al. 2012). The algal turf enriches sand flats with fine and organic particles which on bare sand flats with bioturbating lugworms would not be retained. Besides changing grain size distribution and sediment biogeochemistry, the increased net deposition raises the sediment surface. This is particularly evident at the edge, and may be reinforced by lugworm bioturbation on the adjacent sand flat (Reise et al. 2022). Wendelboe et al. (2013) measured high export rates of fine particles when sediment reworking of lugworms combined with high current velocities. For *Vaucheria*, mud deposition is not detrimental. As observed on windowsill, green filaments increase their length by almost one mm per day. This would be sufficient to overcome suffocation by accumulating sediment. The gradual change from loose sand to cohesive mud may reinforce the durability of the rooted turf at the lower shore where currents and waves can be strong.

### Comparison with other intertidal *Vaucheria*-beds

The ridge-and-runnel pattern which emerged along outer fringes resembles bedforms described for mats of *V. compacta* on upper mud flats in the Westerschelde estuary in the Netherlands (van de Vijssel et al. 2020; van de Vijssel 2021). Further inside, an irregular mosaic of plane plateaus covered by algal turf alternate with bare pits of bumpy topography due to feeding funnels and fecal mounds of lugworms (*Arenicola marina*) (for further details see Reise et al. 2022). The elevational differences between plateaus and pits increased over the course of summer. However, lugworms did not

manage to keep pits bare but merely slowed down the succession. Nevertheless, the contest between sediment stabilizing *Vaucheria* and sediment destabilizing *Arenicola* seems to be the underlying process of the mosaic pattern inside the new belt. Such a biogenic pattern was not observed by van de Vijssel et al. (2020) at upper muddy shore. While the outer fringe with elongated hummocks and runnels was initiated by hydrodynamics and then evolved further by scale-dependent positive feedbacks as described by van de Vijssel et al. (2020), the mosaic of turfs and bare pits at the inner belt was caused by a contest between bioengineering species (Reise et al. 2022).

The interior part of the bed remained completely submerged even during spring low tides because the outer edges were higher (Figure 6). However, in autumn 2020 a runnel became incised, dewatering towards a deep channel at the eastern boundary of this *Vaucheria*-bed at Blidsel Bay. At extreme low tides, the ebbing water in that runnel even formed small cascades where breaching the elevated edge. One may expect that with increasing areal size and age of *Vaucheria*-beds, such runnels develop further and become more. Similar self-organized patterns were observed and modelled by van de Vijssel (2021) for *Vaucheria*-beds on upper shore mud flats.

*Vaucheria compacta*-mats as described from mud flats in the Elbe estuary (Schulz-Steinert and Kies 1996) and in the Westerschelde estuary by van de Vijssel et al. (2020) lack a deep anchorage by long rhizoids. These mats may even be rolled off like a carpet by an occasional rough sea (Hartog 1959; Frank Perk *pers. comm.*). Spread on loose sand at the lower shore with stronger hydrodynamics than at upper shore mud flats would thus be impossible for this species. We conclude that the extensive beds of *V. cf. velutina* at the lower shore of Sylt could only establish and expand there because of its deep anchorage. Another precondition is a sufficient supply of mud particles which can be trapped and accumulated by the dense turf to form elevated beds.

### *Balance of mud*

In the Wadden Sea, the main supply of mud originates from the North Sea and accumulates on high intertidal flats and supra-tidal salt marshes (Oost et al. 2021). Rectangular systems of brushwood groins combined with ditching have enhanced mud deposition, gradually creating marshland. This has been consecutively embanked in the course of centuries. Thus, progressive land claim has detached mud deposits from the sediment dynamics in the Wadden Sea. Land claim combined with estuarine channel deepening for navigation, has led to an amplification and asymmetry of tides, increasing turbidity and further promoting the landward transport of silt. Mud supply, transport and deposition have turned problematic for ecosystem function and adaptation to sea level rise.

The appearance of mud accumulating *Vaucheria*-beds at the lower shore intercepts landward deposition of mud. This new sink for mud may be similar to that of seagrass, mussel and oyster beds. Compared to other tidal basins in the Wadden Sea, trapping efficiency of the List tidal basin for mud is extremely low due to physiographic and hydrodynamic properties (Pejrurp et al. 1997; Pedersen and Bartholdy 2006). Adding to the recent spread of American razor clams and Pacific oysters (Reise and van Beusekom 2008), *Vaucheria* may reduce turbidity to the advantage of pelagic primary production and unhampered food uptake by filter feeders. Permanent stabilization of mud at the lower shore by *Vaucheria* could expand tidal flats and confine channels, adding to the effects of estuarine biofilms (Brückner et al. 2021).

Another aspect is the distribution of mud deposition in tidal basins which occurs predominantly at the upper landward fringe and sometimes along tidal divides (Friedrichs 2011; Oost et al. 2021) and this may be crucial for keeping pace with sea level rise (Madsen et al. 2010; Braat et al. 2017; Becherer et al. 2018; Benninghoff and Winter 2019). *Vaucheria* cf. *velutina* spreading at the lower shore has the potential to alter this pattern. Depending on the net mud supply to tidal basins, *Vaucheria* may either increase the net accumulation rate of mud or initiate an internal redistribution of mud from upper to lower shores. Which one of these processes would prevail has implications on the capacity of the tidal zone to keep up with an accelerating sea level rise in the wake of global warming.

## Conclusions

A novel habitat of bumpy mud deposits emerged at the intertidal-subtidal transition zone, when an introduced *Vaucheria*-alga established near the island of Sylt in the Wadden Sea in 2018. Green filaments are thin but dense, trapping fine sediments in summer, and the felted mesh of pink rhizoids consolidates the trapped deposits. This raises the sediment surface up to 20 cm above ambient flats. Although smoothed somewhat by rough winter conditions, the mud deposits persist where once sandy flats prevailed. Colorless to brownish filaments hibernate below the mud surface and give rise to new growth in spring, while germinating oospores may accomplish extensions of algal beds. This new mode of biogenic mud accumulation at the lower shore may contribute to water clarity, and facilitate depositional processes in response to sea-level rise. If algal spread continues, this may become a game changer for the Wadden Sea ecosystem.

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## Authors' contribution

Research conceptualization: all. Sample design and methodology: KR 80%, RM 20%. Investigation and data collection: KR 80%, RM 20%. Data analysis and interpretation: KR 50%, RM 25%, NR 25%. Writing roles: KR 70%, RM 20%, NR 10%.

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