Marine Turf of an Invasive Alga Ousts Lugworms From Lower Shore

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Abstract

Bare sandy flats at and below low tide level were observed in 2020 to have been invaded by an introduced grass-like alga, *Vaucheria* cf. *velutina* (Xanthophyceae). A dense algal turf accumulated and stabilized mud where resident seniors of the lugworm *Arenicola marina* had reworked rippled sand. Algae and worms were incompatible. Initially, rising patches with algal turf alternated with bare pits where lugworms crowded. Their bioturbation inhibited young algae, while the felt of established algal rhizoids clogged feeding funnels of worm burrows. Eventually, the mosaic pattern of competitors gave way to a coherent algal turf without lugworms. Concomitantly, a rich small-sized benthic fauna took advantage of the novel algal turf. This exotic *Vaucheria* has the potential for taking over at the lower shore of the Wadden Sea (eastern North Sea, European Atlantic).

Introduction

In an increasingly interconnected human world, invasive alien species transform ecological webs, particularly on island and coastal ecosystems (Anton et al. 2019; Pyšek et al. 2020). In marine and estuarine sediments, effects may escalate when alien sediment stabilizers rival with resident destabilizers for bio-engineering dominance (Crooks 2002; Sousa et al. 2009; Guy-Haim et al. 2017). We here present the story of a regime shift from marine sandy bottom reworked by resident lugworms *Arenicola marina* towards a muddy turf of an invading alga with an extensive rhizoid felt in the sediment. This is a striking example for ecological change in the wake of biological globalization. In the Wadden Sea, resident lugworms recycle the upper layer of sediment 10–20 times per year through their guts (Cadée 1976) and keep the sand permeable with their reworking and irrigating activities (Volkenborn et al. 2007). The seniors of lugworms dwell at modest density on sand bars of the lower shore (Beukema and de Vlas 1979; Lackschewitz and Reise 1998; Reise et al. 2001). There, loose sand and strong hydrodynamics keep this habitat free from macroalgal growth. A nascent invasion of an exotic member of the genus *Vaucheria* (Xanthophyceae) is about to change this.

Based on plastid encoding *rbcL*-gene sequences and *psbA/rbcL* spacer region, the *Vaucheria* at the lower shore is distinct from that at upper shore salt marshes, although morphology suggests it belongs to the cosmopolitan *V. velutina* C. Agardh 1824 (Rybalka et al., submitted). We suspect a complex of hidden species, and refer to the population of the lower shore as *V. cf. velutina* until taxonomic revision. Green unicellular filaments, up to 8 cm long and with a mean density of 1.5 mm^{-2} , are anchored with felted rhizoids down to 5 cm in the sediment. In only three years, this *Vaucheria* spread over an area of 180 ha at the lee side of the island of Sylt in the northern Wadden Sea, generating bumpy mud with hummocks up to 20 cm higher than ambient sand flats (Reise et al., submitted).

Lugworms are sedentary but keep the upper sediment layer in motion by feeding funnels with downward sliding surface sediment and by mounds of fecal strings with ejections about every half hour (Riisgård and Banta 1998; Wendelboe et al. 2013). This sediment reworking activity seems incompatible with sediment stabilizing *Vaucheria*. Interference competition is to be expected between such antagonistic

benthic bioengineers. What are the mechanisms at work and how does the competitive contest proceed? How is this cascading into associated benthos? We here present observations on the initial phase of an invasion by an alien species which may have far-reaching and lasting effects on benthic processes in the Wadden Sea and beyond.

Area And Methods

In the northern Wadden Sea, the List tidal basin at the Danish-German boundary comprises 400 km² with vast intertidal and shallow subtidal sandy flats, intersected by deep channels (Gätje and Reise 1998). Tides are semi-diurnal with a range of almost 2 m. Salinity ranges from 26 to 32, and mean water temperatures from 0 to 20°C with a recent warming of 1°C since the 1980s (Rick et al. 2021). Muddy beds of *Vaucheria* cf. *velutina* were first discovered in June 2020 from +0.2 m to – 0.5 m relative to mean low tide level at shoals in Blidsel Bay, east of northern Sylt (54°97' N, 08°38' E; Rybalka et al., submitted; Reise et al., submitted). All investigations reported here were carried out at that site.

As a proxy of lugworm abundance on ambient sand flats, fecal mounds of *Arenicola marina* were counted per unit area (10 m² at very low to 0.25 m² at high density) during low tide exposure. As a proxy of body size, diameters of fecal strings were estimated to the nearest millimeter. Sixteen individuals were dug out, cleaned and put on blotting paper, and then into calibrated cylinders with seawater for measuring individual volume to the nearest 0.1 cm³. Length of relaxed worms was estimated to nearest centimeter.

To measure *Vaucheria*, tubes of 10 cm² cross section and sharpened lower edge, were gently screwed through the algal turf to a depth of 5 cm. Obtained sediment cores were washed through a 125-µm mesh and algal tufts were picked up with forceps. These were further washed to remove adhering sand grains. Entangled tubes of spionid worms were individually pulled out and other algae (mainly *Rhizoclonium* and *Ectocarpus*) were removed when present. *Vaucheria* was then put on blotting paper for 6 h in sunlight to dry. Weight to nearest mg was used as a proxy for the phytomass of *Vaucheria*. This was done with 3 replicate samples taken along a 150-m transect with intervals every 25 m, reaching from bare ambient sand flat through a belt of young growth and into the interior of an established bed of *Vaucheria* on June 23 in 2020. Concomitantly, algal cover was categorized from 0 with no green filaments above sediment surface, 1 with few filaments, 2 with modest density and 3 with complete cover at 10-cm² areas, replicated 20 times at each interval. Along the same transect the abundance of lugworm fecal mounds was counted per 0.25 m², also replicated 20 times at each interval.

Abundance of live associated benthic fauna was estimated from sieved sediment cores for three size categories: (1) obligatory and temporary meiofauna retained by a 63-µm mesh by decanting of seawater from a beaker with 1 cm³ (1 cm² core to 1 cm depth) of surface sediment. Decanting was repeated until no more animals were retained, and residual sand in the beaker was also inspected. Individuals were pipetted from petri dishes under a stereo microscope, identified to major taxon and counted. Four replicates were taken from ambient bare sand 50 m outside the *Vaucheria*-bed and from muddy

hummocks inside the bed on June 17 in 2020. (2) Mesofauna (small-sized macrofauna) retained by a 250-µm mesh, washing 10-cm² sediment cores (depth from surface to 5 cm) in seawater. Individuals were picked up with forceps, identified under stereo microscope and counted. Six replicates were taken from ambient bare sand and from the *Vaucheria*-bed (see above) on June 12 in 2020. Additional replicates were taken July 03 at the young *Vaucheria*-belt with a mosaic of patches with dense growth alternating with pits of bare sand. To assess small benthic fauna specifically associated with above-ground green siphons of *Vaucheria*, these were clipped at the sediment-water interface on 6 areas of 50 cm² and then washed over a 125-µm mesh. (3) To retain also larger macrofauna, cores of 50 cm² (depth from surface to 20 cm) were sieved through a 1-mm mesh. Ten replicates were taken from bare sand 50 to 100 m outside the *Vaucheria*-bed, and from inside the bed at muddy hummocks and at sandy troughs from July 13 to 22 in 2020. Differences in abundance were tested with the non-parametric U-test from Wilcoxon, Mann and Whitney.

Results

Lugworm population

Arenicola marina constitutes a major component of the benthic fauna in terms of bioturbation and biomass. Mean worm size increases and abundance decreases from upper to lower shore. In Blidsel Bay, worms at an upper site (400 m from shoreline at about mid-tide level) were smaller but more abundant than worms at the lower site (2 km from shoreline at spring low tide level) where *Vaucheria* was spreading. Young lugworms occurred at the upper shore and were notably absent from lower shore. There, individuals dug up from their deep (> 20 cm) burrows were on average 3-times bigger and 2-times longer than lugworms at the upper shore site in June 2020 (Table 1). This difference in size was also apparent from diameters of defecated strings of sand. On the other hand, abundance of fecal mounds was 4-times lower at the lower shore compared to upper shore. Total biovolume of lugworms per unit area was 27 % higher at the upper compared to lower site (156 and 114 cm³ m⁻²).

Table 1 *Arenicola marina* at Blidsel Bay upper and lower shore in June 2020

	Upper shore	Lower shore
Volume of lugworms (cm ³)	4.1 ± 1.4 [2-6] (n=8)	12.9 ± 3.4 [8-19] (n=8) *
Length of lugworms (cm)	12.7 ± 2.3 [9-16] (n=8)	20.5 ± 3.4 [17-26] (n=8) *
Fecal string diameter (mm)	2.8 ± 0.5 [2-4] (n=20)	4.8 ± 0.9 [3-6] (n=20) *
Fecal mounds 0.25 m ⁻²	9.5 ± 2.1 [0-5] (n=15) *	2.2 ± 1.3 [0-4] (n=20)

Means $\pm$ standard deviation and range [] of replicates (n); * significantly ($p < 0.05$) higher values (U-test)

This spatial lugworm pattern was still apparent in August but differences between upper and lower shore were less striking. Fecal string diameter had decreased at the lower shore and increased at upper shore: 3.2 ± 1.0 (n=30) and 4.0 ± 0.3 mm (n=30) (compare with Table 1). Also, abundance of fecal mounds per 0.25 m^2 had increased at lower and decreased at upper shore: 4.6 ± 1.5 (n=60) and 8.8 ± 2.2 (n=30). These tendencies suggest that some lugworms may have migrated from upper to lower shore during summer.

Mosaic pattern of lugworms and *Vaucheria*-turf

Vaucheria cf. *velutina* had invaded sand flats occupied by very large lugworms dwelling at relatively low abundance in a patchy manner. Variance of fecal mound abundance (SD/mean) at 0.25-m^2 scale was 59 % at lower shore compared to 22 % at upper shore (see Table 1). Hardly recognizable, parallel sand waves at m-scale were less frequented by lugworms than the shallow pits between at the exposed lower shore. Since early June in 2020, new growth of *Vaucheria* had advanced from an existing bed in northern and western direction in a wide belt, preferentially colonizing the slightly elevated sand waves (Reise et al., submitted). A mosaic pattern emerged (Fig. 1). The overall abundance of lugworm fecal mounds in the young mosaic-belt remained similar to that at bare ambient sand further north. However, fecal mounds concentrated at bare pits with 3.9 ± 0.9 [3-5] (n=10) 0.25 m^2 , while at 1 to 4 cm higher plateaus with a dense algal turf these were almost absent (0.1 ± 0.3 [0-1] (n=10) 0.25 m^2) ($p < 0.01$, U-test). This was counted June 17 and suggests that lugworms moved their burrows away from establishing turfs and aggregated in pits (Fig. 1). In the innermost part of the established *Vaucheria*-bed, lugworms were almost gone (fecal mound abundance of 5.8 ± 3.4 per 10 m^2 [n=6], corresponding to 0.15 per 0.25 m^2).

The mechanism of competition between *Arenicola* and *Vaucheria* could be observed directly (Fig. 1 and 2). While fecal mounds produced by lugworms bury green algal filaments, their feeding funnels are clogged by tufts of algae with their felt of rhizoids. These resisted the downward sliding of loose sand. An inverse relation between lugworms and algal turf was apparent along a transect, running from bare sand flat across patches of young *Vaucheria*-growth alternating with lugworms, and from there further into old *Vaucheria*-growth with hummocks and troughs, established since 2019 and partly already 2018 (Fig. 3). Note that in Fig. 3, data are scaled up to m^2 from counting areas of 0.25 m^2 for lugworm fecal mounds and 10 cm^2 for measuring cover and dry weight of *Vaucheria*. This exaggerates variance because patchiness decreased from small to larger scale. This is caused by subtle sand waves at the bare sand flat, by a mosaic of plateaus with dense turf and pits with lugworms where *Vaucheria* commenced growing since June, and in the old bed by alternating hummocks and troughs. Some lugworms persisted in troughs but none on hummocks.

In August 2020, the mosaic pattern in the young growth became blurred and overall abundance of fecal mounds had decreased by 59 % from 8.0 ± 8.4 (n=20) in June to 3.3 ± 1.9 (n=60) fecal mounds per m^2 in

August ($p < 0.05$, U-test). This shows the gradual displacement of lugworms by *Vaucheria*.

Associated benthos

While large burrowing lugworms became displaced by a turf of *Vaucheria*, this does not hold true for meiofauna (Table 2). Abundance was entirely dominated by nematodes (83 and 76 % in bare sand and in algal turf, respectively). At the level of major meiofaunal taxa differences between habitats were minor. Only juvenile macrofauna of meiofaunal size showed a clear preference for algal turf ($p < 0.05$, U-test). Most of them were juvenile mud snails crawling on green filaments.

Small fauna retained by 125- μ m mesh from green algal siphons clipped at sediment surface were primarily juvenile macrofauna. Means ($\pm$ standard deviation) for all individuals above sample areas of 50 cm² were 381 ± 165 ($n = 6$), of which 79 % were mud snails *Peringia ulvae* (301 ± 154), 8 % young bivalves (31 ± 14), 5 % small and young Annelida (17 ± 12), 4 % young Malacostraca (14 ± 8) and 17 ± 8 were small sea slugs of the species *Alderia modesta* and one *Limapontia depressa*. All slugs were small (< 5 mm) but already produced egg masses attached to filaments of *Vaucheria*.

Small macrofauna retained by a 250- μ m mesh was 4-times more numerous and 3-times more diverse in species within algal turf than on bare sand flat (Table 3). This difference is mainly caused by young mollusks and small annelid worms, although most of the young *P. ulvae* were too small to be retained. Only amphipods were more numerous at the sand flat habitat but not significantly because of strong patchiness (U-test). When in early July a similar set of samples was taken at the young belt of *Vaucheria* which had emerged since the beginning of June 2020, no significant differences had yet developed between pits with lugworms and plateaus with algal turf. All individuals found below 10 cm² were 2.67 ± 2.80 at pits and 3.17 ± 1.94 at algal turf. However, the species composition at the young algal turf already resembled that of the old turf shown in Table 3 with a dominance of spionid polychaetes.

Table 2 Meiofauna cm⁻³ retained by 63- μ m mesh of surface sediment at bare sand flat and algal turf on muddy hummocks ($n = 4 + 4$) in Blidsel Bay, June 17-18, 2020

	Sand flat	Algal turf
All individuals	269 $\pm$ 98	320 $\pm$ 117
Nematoda	223 $\pm$ 94	242 $\pm$ 96
Copepoda	19 $\pm$ 13	34 $\pm$ 16
Ostracoda	18 $\pm$ 8	10 $\pm$ 3

Other taxa	10 ± 2	19 ± 5
Juvenile macrofauna: Polychaeta and Mollusca,	< 1	17 ± 7
including young <i>Peringia ulvae</i>	< 1	10 ± 5

Given are means ± standard deviation

Table 3 Mesofauna (small macrofauna) 10 cm⁻² (0 to 5 cm depth) retained by 250-µm mesh at bare sand flat and at algal turf on muddy hummocks (n = 6 + 6). Blidsel Bay, June 12 in 2020

	sand flat	algal turf
All individuals	2.33 ± 2.34	10.33 ± 2.80 *
Number of species	1.83 ± 1.17	6.00 ± 1.67 *
Juvenile Mollusca (4 spp.)	0.17 ± 0.41	3.00 ± 2.00 *
Amphipoda (3 spp.)	1.17 ± 2.40	0
<i>Pygospio elegans</i>	0.67 ± 0.52	2.17 ± 1.17
<i>Streblospio benedicti</i>	0	2.00 ± 1.26 *
<i>Tubificoides benedeni</i>	0	1.83 ± 0.98 *
Others (7 spp.)	0.33 ± 0.52	1.33 ± 1.51

Given are means ± standard deviation; * significantly (p < 0.05) higher (U-test)

Table 4 Macrofauna 50 cm⁻² (0 to 20 cm depth) retained by a 1-mm mesh (n=10) at bare sand flat, at algal turf on muddy hummocks and at troughs in between, Blidsel Bay in July 2020

	Bare sand flat	Algal turf	
		Troughs	Hummocks
All individuals	5.1 ± 5 [0-15]	19.1 ± 22.6 [1-48]	104.6 ± 21.5 [83-138] *
Number of species	2.3 ± 1.2 [0-4]	4.6 ± 2.9 [1-10]	8.4 ± 2.4 [6-12]
Sum of species	9	16	23
<i>Urothoe poseidonis</i>	2.9 ± 4.3 [0-14]	0	0
<i>Pygospio elegans</i>	0.5 ± 0.7 [0-2]	3.9 ± 5.0 [0-14]	54.8 ± 21.5 [24-85] *
<i>Streblospio benedicti</i>	0	9.8 ± 15.2 [0-39]	40.1 ± 12.1 [19-56] *
Others (25 spp.)	1.7 ± 1.5 [0-4]	5.4 ± 3.4 [1-11]	17.1 ± 9.07 [6-40]

Given are means ± standard deviation and range []; * significantly ($p < 0.05$) higher values at hummocks than at sand flat (U-test)

Macrofauna retained by a 1-mm mesh from bare sand was rather poor in abundance and species richness, compared to troughs and hummocks in the old *Vaucheria*-bed (Table 4). At hummocks with a dense turf and absence of lugworms, abundance was 20 times higher than in bare sand. Troughs with a moderate or very patchy turf were intermediate. Differences in species richness were modest. As shown in Table 4 by standard deviations and wide ranges of data, macrofauna was highly patchy at the 50-cm² scale, most conspicuous at troughs in the *Vaucheria*-bed. Only amphipods, mainly *Urothoe poseidonis* associated with lugworm burrows, were more abundant in bare sand and there comprised 76 % of all individuals. Troughs and hummocks in the *Vaucheria*-bed were entirely dominated by annelids (94 %). Among the tube-dwelling spionid worms, *Pygospio elegans* occurred at all three habitats but was most abundant in dense algal turf, together with *Streblospio benedicti* and *Polydora cornuta*, while the more agile *Spio martinensis* was most abundant at troughs. Of these tube-dwellers, relatively small individuals were retained by the 1-mm mesh because tubes were entangled in tufts of *Vaucheria*. Although crabs (*Carcinus maenas*, *Hemigrapsus takanoi* and *Pagurus bernhardus*) and periwinkles (*Littorina littorea*) were abundant on adjacent beds of oysters and mussels, *Magallana (Crassostrea) gigas* and *Mytilus edulis*, these remained rare in *Vaucheria*-beds.

Exposed sand flats at and below low tide level were usually devoid of macroalgae, while *Vaucheria*-beds intermittently accumulated drift algae between July and September. Of these, *Rhizoclonium riparium* and *Ectocarpus* spp. were the most persistent (Fig. 4). The latter grew massively as epiphytes in adjacent kelp beds on *Sargassum muticum*, and probably drifted from there to the *Vaucheria*-bed. Other species were

more ephemeral but frequent at times: *Cladophora albida*, *Ulva* spp., *Gracilaria vermiculophylla*, *Dasya bailouviana*, *Heterosiphonia* (*Dasysiphonia*) *japonica*, *Porphyra* sp., *Ceramium virgatum* (*rubrum*), *Polysiphonia* sp., *Fucus vesiculosus*, *Elachista fucicola*, *Sargassum muticum* and *Dictyota dichotoma*. In July and August, these drifting macroalgae could cover the *Vaucheria*-bed but were removed again by rough weather. No smothering of *Vaucheria* was detected.

Discussion

This study refers the beginning displacement of the most characteristic benthic species in the European Wadden Sea, the lugworm *Arenicola marina*, from the lower shore by an invasive alga forming dense turfs and accumulating mud where loose sand prevailed before. This benthic regime shift raises several questions. What may cause the spatial gap between *Vaucheria*-algae at the upper shore and the recent spread at the lower shore? How could feeble algae establish between sediment reworking lugworms, and then even displace such vigorous worms? Could the invading *Vaucheria* endanger the lugworm population? While the impact of *V. cf. velutina* on *A. marina* and its associated fauna is clearly negative, dense algal turfs also offer a novel type of habitat for other benthos. Who benefits from the algal turf?

Contest between invading *Vaucheria* and resident *Arenicola*

In the Wadden Sea, species of the genus *Vaucheria* are common at upper shores, particularly on estuarine mud flats and in salt marshes (i.e., Simons 1975; Polderman 1979 a,b; Krieg et al. 1988). At the lower shore, *Vaucheria* was unknown until we discovered *V. cf. velutina* at and below low tide level near the island of Sylt in summer 2020 (Rybalka et al., submitted; Reise et al., submitted). In addition, we found *V. longicaulis* at the lower shore for the first time in the Wadden Sea (Rybalka et al., submitted). However, this second taxon was only found since September 2020, occurred in small patches only, and effects on other benthos were not investigated. We regard both as recent invaders, possibly introduced from coasts where they also occur at lower shores. If correct, the recent spread at and below low tide level cannot be explained by niche expansions from the upper shore. What could explain the gap in the vertical distribution of *Vaucheria* at mid shore between high and low tide level?

As shown, lugworm abundance at mid shore is higher than at lower shore. A general pattern with a belt of young worms at upper shore, high adult density at mid shore and low densities further offshore is generally known for the Wadden Sea (i.e., Farke et al. 1979; Flach and Beukema 1994; Reise et al. 2001). Lugworm exclusion experiments (Volkenborn et al. 2009) and observations at patchy freshwater seeps avoided by lugworms (Zipperle and Reise 2005) have shown that in the absence of bioturbating lugworms, tube-builders and species requiring a more stable sediment surface took advantage. This implies that a small alga dependent on a firm rooting in sediment could be suppressed where lugworm bioturbation is high. We suggest that this may be responsible for the disjunct occurrence of turf-building *Vaucheria* in the Wadden Sea, and why the introduced taxa could only establish at the lower shore where lugworm abundance is low. However, this hypothesis still needs to be tested by transplant experiments.

Initial growth of *Vaucheria* was observed on slightly elevated sand waves of the lower shore (Reise et al., submitted). These may offer a window of opportunity for the invader where deposition prevails over erosion. Once *Vaucheria* succeeded in getting anchored, its growth habit may constitute a preadaptation to displace lugworms. We suggest the key mechanism is clogging feeding funnels with felted rhizoids and long filaments as could be observed directly (Fig. 1). Clogging curtails the nutrition of lugworms. Instead of fueling microalgae at funnels with upwelling burrow water (Chennu et al. 2015), lugworms now supply *Vaucheria* with nutrients while this alga is inhibiting the downward slide of surface sediment. This will be aggravated by shading of the sediment surface once *Vaucheria* attained high coverage, which inhibits diatom growth at sediment surface, a major food of lugworms (Rijken 1979; Retraubun et al. 1996; Engel et al. 2012).

Such antagonistic mechanisms have also been proposed for interactions between intertidal seagrass *Zostera* and *Arenicola*. Seagrass is much larger but otherwise similar to *V. cf. velutina* with a mesh of roots and narrow blades. At high lugworm density and sheltered conditions, bioturbation may suppress seed germination and young *Zostera*, while dense growth of seagrass may inhibit lugworm feeding by roots and by shading of benthic microalgae (Philippart 1994; Valdemarsen et al. 2011; Suykerbuyk et al. 2012; Goerlitz et al. 2015). Similar as with *V. cf. velutina* on lugworm flats, also sharp boundaries and mosaic patterns are common (Eklöf et al. 2011). Juvenile lugworms may aggregate in patches of seagrass when avoiding to intermingle with adults (own observations). For this ephemeral phenomenon, no correspondence occurred at sites with *V. cf. velutina* because juvenile lugworms rarely occur at the lower shore. Another antagonistic relation occurs between lugworms and clusters of *Spartina*-grass at the upper shore (van Wesenbeeck et al. 2007).

Lugworm bioengineering intensity may reach a tipping point, probably conditional on ambient hydrodynamics, above which sediment stabilizing *Vaucheria* have to give way to sediment destabilizing lugworms. This could explain the emergent mosaic pattern of plateaus with a dense algal turf and few lugworms alternating with bare sand bioturbated by lugworms which aggregated at patches not yet occupied by the turf. Apparently, instead of swimming away, lugworms simply move their feeding funnels away from spreading algal turfs and thereby aggregate with their neighbors doing the same. Such aggregates with concerted sediment reworking activity may in turn retard a further spread of young algae. The consequence are arising depositional plateaus generated by sediment stabilizing algae, alternating with eroding pits still intensively reworked by lugworms.

Such a mosaic pattern is even more conspicuous in *Vaucheria*-beds of the previous year, here in the form of muddy hummocks covered by dense turf, alternating with troughs where lugworms persevere and the algal turf remains patchy. There, height differences have become more pronounced. Nevertheless, at the oldest part of the bed, a coherent turf of elongated algae has taken over. There hummocks and troughs have leveled out. Most likely, this is an effect of preceding winter storms (Reise et al., submitted). In addition, at the central part of the bed, hydrodynamics is lower than at elevated edges. This may result in a more even deposition of fine organic particles and in turn raise sulfide concentrations in the sediment. This could cause the last lugworms to leave the place. Such a complete displacement of lugworms may

take three years because the mosaic pattern of the antagonists is slowing down the takeover of *Vaucheria*. Where hydrodynamic conditions are stronger, the mosaic pattern may perpetuate.

Mosaic patterns are a recurrent phenomenon caused by aggregate settlement of space occupants or by clonal growth of plants or colonial animals. This spatial organization may be dynamic due to life time limitations or disturbances or remain in a quasi-permanent state (Remmert 1991; Rietkerk and van de Koppel 2008; van de Vijssel et al. 2020). The mosaic of an introduced *Vaucheria* alternating with resident *Arenicola* demonstrates that such patterns emerge spontaneously and do not require joint evolutionary history. The scale of patches is probably predetermined by hardly discernable, parallel sand waves separated by slight depressions. Both, *Vaucheria* and *Arenicola* respond to these in opposite ways and then modify and reinforce the pattern by antagonistic bioengineering and positive feedbacks.

Threat to the lugworm population?

Could the displacement of senior lugworms at the lower shore by *Vaucheria* destabilize the entire population? Numerically, the share of lugworms dwelling at the lower shore in the Wadden Sea may be small (Beukema and de Vlas 1979). Although sedentary during most of its life, lugworms migrate occasionally, not only as juveniles but also as adults (Reise 1985; De Cubber et al. 2019). The latter may migrate downslope to avoid crowding, escape cold spills or predation (Farke et al. 1979; Reise et al. 2001). At the lower shore, abundances were 4-times lower than around mean tide level and young worms were notably absent. On the other hand, the lower sandy shore accommodates the largest and presumably oldest worms. Even if these worms contribute disproportionately to gamete production, their effect on population size would remain marginal because of density dependence at the mid shore population center (Flach and Beukema 1994; Reise et al. 2001). The role of senior lugworms at lower shore for the entire population could be a reinsurance in the case of rare, exceptionally harsh winters causing high mortality in the intertidal zone as observed in winter 1998/99 (Reise et al. 2001).

Provision of novel habitat

Meiofauna seems indifferent to algal turf colonizing bare sand. For this size group, however, better taxonomic resolution would have been required than shown in Table 2. On the other hand, juveniles of the intertidal macrofauna when still of meiofaunal size, show a clear preference for the algal turf. The novel habitat functions as nursery. Altogether, ten species of young bivalves were encountered in the algal turf. Of particular abundance were juveniles of the small mud snail *Peringia ulvae* with up to 10 individuals per cm² in June, crawling at the green filaments and feeding on epiphytes such as sessile diatoms but not on *V. cf. velutina* itself. This constitutes a spontaneous mutual benefit for *Vaucheria* getting cleaned and for *P. ulvae* finding additional food. More generally, juvenile macrofauna likely found shelter in the algal turf against epibenthic predators such as shrimp (*Crangon crangon*).

For tube-dwelling spionid polychaetes which occurred with more than two individuals per cm² in dense algal turf not only shelter against epibenthic predators may have been important but also the sediment stabilizing effect of *V. cf. velutina*. Young growth of *Vaucheria* did not suffice. Perhaps the canopy of

algal filaments was too thin or since June no significant larval settlement had taken place. On tidal flats in the Firth of Forth (Scotland) with a low density of lugworms a similar preference of spionid polychaetes for patches of *Vaucheria* was observed, comprising even the same species (*Pygospio elegans*, *Polydora cornuta* and *Streblospio benedicti*) (Bolam and Fernandes (2002; pers. communication).

Of special interest is the obligatory feeding of the tiny sea slug *Alderia modesta* on cushions or turfs of *Vaucheria* (Hartog 1959; Seelemann 1967; Rasmussen 1973; Ligthart 2009). Similar to *Elysia*, also *A. modesta* saves chloroplasts from their diet for photosynthesis on their own (kleptoplasty: Clark et al. 1990; Rumpho et al. 2011). With the appearance of *V. cf. velutina* at the lower shore of the Wadden Sea, *A. modesta* could widen its narrow niche at salt marshes of the upper shore down to the subtidal zone. This was already observed in the Oosterschelde (Rhine delta) where *V. longicaulis* is spreading since 1993 (Ligthart 2009). Whether *A. modesta* would be capable of stopping the *Vaucheria* invasion at the lower shore, remains to be seen. In summer 2020 its abundances were too low for thinning out algal turfs. However, under confined lab conditions few individuals could completely wipe out *Vaucheria* (own observations). The role of other mesoherbivores such as gammarid amphipods also needs further investigation. Large herbivores, such as brent geese or widgeon were not yet observed grazing at low shore *Vaucheria*.

On close investigation, a cocktail of negative, neutral and positive effects on residents may always be the case with invaders (Thieltges et al. 2006). Superficially, there is some similarity of the *Vaucheria*-turf with episodic mats of green algae on tidal flats in response to eutrophication. These suffocated endobenthic fauna underneath but provided habitat to opportunists and epibenthic snails such as *Peringia ulvae* (i.e., Nicholls et al. 1981; Reise 1983; Raffaelli et al. 1999; Bolam et al. 2000). However, *Vaucheria* is not ephemeral and attract a rich small fauna (Bolam and Fernandes 2002; this study). This follows the generalization of Crooks (2002) that invaders increasing habitat complexity entail higher abundances and species richness in residents. Although leaves of seagrass are taller and broader and roots go deeper than in *V. cf. velutina*, effects of *Zostera* on associated fauna are strikingly similar, i.e., high abundances of tube-building spionid polychaetes and epibenthic mud snails (i.e., Reise 1978; Orth et al. 1984; Reise et al. 1994; Philippart 1995) and inhibition of lugworms (see above). Mixing of seagrass beds and *Vaucheria* was not observed. As beds of *Zostera* are declining on tidal flats of northern Sylt (Dolch and Reise 2010), the novel habitat of *Vaucheria* at the lower shore may offer a partial compensation for certain species.

Conclusions And Outlook

An alien alga is displacing a resident keystone bioengineer at the lower shore of the Wadden Sea. Conversely, where lugworm density is high, spread of *Vaucheria* may be inhibited. *Vaucheria* and *Arenicola* cannot coexist and arrange in a mosaic fashion until the latter is expelled completely. A habitat of bare loose sand and reworked by lugworms is transformed into bumpy mud, hold together by a felt of rhizoids and covered by a dense turf of thin filaments. Lugworms and their benthic associates are

eventually driven out while other benthos finds shelter under a filamentous canopy, benefits from stabilized sediment or algal food. Presumably, the invasion will proceed as there is ample bare sandy sediment at the lower shore equivalent to what has already been vegetated near the island of Sylt. Similar occurrences of *Vaucheria velutina* are known from lower shores of Florida (Gallagher and Humm 1981) and the southern Pacific (Wilcox 2012; Womersley 1987) but species identity still has to be confirmed by molecular genetics

Declarations

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Conflict of interest Both authors declare that they have no conflicts of interest.

Ethical approval This study does not comprise animals that are regulated under national or EU ethical guidelines.

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Figures

Figure 1

Vaucheria cf. *velutina* advancing in a mosaic fashion on a sand flat of the lower shore in Blidsel Bay, June 2020. Plateaus with dense algal turf alternated with lighter pits occupied by *Arenicola marina*. In the course of summer, algae also spread at pits (image upper right). Feeding funnels of lugworms became clogged by algae, while lugworms deposited fecal castings upon algal turf (lower right)

Figure 2

Turf of *Vaucheria* cf. *velutina* in Blidsel Bay, July 2020 with lugworm fecal mound. Right: Algal tuft cleaned from sediment with green filaments above and a felt of pink rhizoids below. Thicker than rhizoids are entangled tubes of spionid worms

Figure 3

Abundance of *Arenicola marina* fecal mounds (columns) and proxies for the presence (green lines for relative cover and dry weight, respectively) of *Vaucheria* cf. *velutina* (vertical bars refer to standard deviation), along a transect from bare sand flat (left) across a belt of young algal growth and into hummocks and troughs within old growth (right). Blidsel Bay at Sylt, June 23 in 2020

Figure 4

Brownish braids of *Ectocarpus* at *Vaucheria*-hummocks (left) and wads of green *Rhizoclonium* (right) with floating mud snails *Peringia ulvae* (light dots) between tufts of *Vaucheria*, Blidse Bay in July 2020