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Invasive *Vaucheria* aff. compacta (Xanthophyceae) and its distribution over a high Arctic tidal flat in Svalbard

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ABSTRACT

The high Arctic Svalbard tidal flat ecosystem is impacted by global warming, which could allow invasion by additional species with changes in the environment supporting their growth. The transport of additional species to Svalbard could be aided by an increase in the numbers of people traveling there. Anthropogenic activities related with global warming create opportunities for organisms to move across previously isolated regions, thus advancing biotic homogenization and extinctions. Our study focused on essential quantitative and qualitative information about the occurrence of widespread mats of the invasive siphonaceous yellow-green alga *Vaucheria* aff. *compacta* in the Adventfjorden tidal flat. We outline the present ecological state of *V.* aff. *compacta* mats (land cover estimation) and discuss the origin and future development of this microphytobenthic community. Phylogenetic analyses based on *rbc*L genes confirmed that the studied alga is closely related to *V. compacta*, inside the section Piloboloideae. With the help of a drone mapping survey, we estimated that *V.* aff. *compacta* area cover was about ca 231.1 m^2 (± 10.55%, n = 11) across the drone mapped tidal flat area of 2475 m^2. We confirmed that invasive *V.* aff. *compacta* is a coastal cosmopolitan species widely disseminated on shores in both hemispheres. Invasive *V.* aff. *compacta* is an important component of the Adventforden sea-land ecotone, which affects large-scale changes within the intertidal system, stabilizes the sediment coming in with the regular tides and protect the seashore ecosystem against erosion. As a result of global warming in the Arctic, invasive *V.* aff. *compacta* facilitates the greening of the Arctic.

1. Introduction

Coastal ecosystems are one of the most productive, and also highly dynamically complex, bio-geosystems in the Arctic (ACIA, 2005; Ardyna et al., 2020; Leu et al., 2015; Smoła et al., 2017), and which are subjected to the periodic cycles of tidal variations. Temporal habitat structures and biodiversity (Dunton et al., 2012; McGovern et al., 2020) are potentially impacted by global warming including **the growth of travel activity** (e.g. Hanssen-Bauer et al., 2019; Søreide et al., 2020). Here, in coastscapes, there is very strong coupling between the sea and the land, and the shallow depths create a tight pelagic-benthic interaction (McGovern et al., 2020).

In Svalbard, estuaries at the mouths of rivers, lagoons, and tidal flats are a very common type of coastscape where sediments are deposited. There is an extensive gradient network of wetlands, streams and brackish ponds with broad mudflats, which are occupied by a highly productive microphytobenthos community (Søreide et al., 2020). Biological communities in these habitats need to cope with a high degree of variability in salinity, temperature, sedimentation, light and nutrient availability (e.g. Weslawski et al., 1999).

The microphytobenthos is a typical community of microscopic organisms from the surficial sediment of an intertidal flat. It consists of various assemblages of substrate-dwelling photosynthetic diatoms, cyanobacteria, flagellates and microalgae (Cartaxana et al., 2016). Microphytobenthic communities are crucial elements of these coastal ecosystems. These communities form sticky coatings on sediment particles and detrital surfaces and act as a stabilizing anchor to buffer cells and their extracellular processes during the frequent physical stresses

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(Decho, 2000). Stabilization of sediments against re-suspension is one of the most important ecological roles of this community. In the Arctic, especially during spring, increased light radiation and coastal nutrient availability from earlier snowmelt and ice breakup produce favourable conditions for the growth and productivity of these estuaries and coastal flat communities.

Several factors determine the distribution, abundance, and biomass of these microphytobenthic organisms. According to the continuum theory, coastal benthic communities vary and disperse across the seabed in relation to the continuous variation of environmental factors and produce a mosaic of discontinuous units (Oksanen and Minchin, 2002; Ysebaert et al., 1998).

Therefore, repeated spatial vegetation mapping is required for identifying drivers of microphytobenthos distribution. Due to the unstable and very soft sediment in such areas, and hence reduced accessibility, unmanned aerial vehicles (UAV, drones) may provide an extended and detailed view of the studied area. The number of environmental biology studies based on drone surveys continually increases (Nowak et al., 2018). Applications of drones in plant ecology range from individual plant imaging to ecosystem monitoring, adding thus detailed information to data obtained from space and aerial remote sensing and field studies (Cruzan et al., 2016; Sun et al., 2021; Tay et al., 2018). This may be especially valuable in rapidly changing and remote landscapes, as can be found in the Arctic and Antarctica. In the Polar Regions, UAVs have been used, for instance, for monitoring Antarctic moss vegetation (Lucieer et al., 2014), vegetation mapping (Eischeid et al., 2021) and for monitoring of invasive plant species in Svalbard (Bartlett et al., 2021). So far, no drone mapping was performed on polar microphytobenthos, although this method was used in the tropics (Aristizabal-Botero et al., 2021).

The Adventfjorden estuary and tidal flat, which is located near Longyearbyen (Svalbard), is one of the most intensively studied Arctic coastal habitats (Dobrzyn et al., 2005; Weslawski et al., 1993, Weslawski et Szymelfenig 1999; Weslawski et al., 1999; Zajaczkowski, 2008). The tidal flat produces networks of wetlands which are inhabited by conical structures that are 1–2 cm high dominated by *Gyrosigma eximium* together with other diatoms, filamentous green algae and cyanobacteria (Oscillatoriales). These green, conical structures cover large parts of this area (Wiktor et al., 2016). However, our microscopic survey of microbial mats at this site revealed that the main biomass of these colonies was produced by the xanthophycean alga *Vaucheria* sp., while *Gyrosigma eximium* colonized its empty dead (Kvíderová et Elster 2017; Kvíderová et al., 2019). Therefore, we consider *Vaucheria* sp. mats as the main primary producer in the Adventdalen tidal flat area.

The siphonaceous yellow-green alga *Vaucheria* de Candolle (family Vaucheriaceae, class Xanthophyceae, Stramenopiles), frequently occurs in freshwater, marine, and terrestrial habitats forming greenish mats, often appearing as velvety, felt-like coatings on various substrata. The algae can be found in almost any wetland habitat, including mudflats, salt marshes, estuaries, wet farmlands, and pond fringes (Schagerl and Kerschbaumer, 2009). *Vaucheria* taxonomy is based on the morphospecies concept. The genus is subdivided into several sections according to their antheridia morphology (Entwisle, 1988; Rieth, 1980), however, species identification may be difficult due to overlapping characteristics among closely related species (Rieth, 1980). The bio-geography and ecology of *Vaucheria* species have been largely disregarded, mainly because the taxonomy of this genus is based on sexual organs, which can be found only sporadically in nature (Foerster et al., 2004). However, from several observations it seems that *Vaucheria* prefer a low temperature growing optima (Schagerl and Kerschbaumer, 2009). In previous Svalbard ecophysiological studies (Kvíderová et Elster 2017; Kvíderová et al., 2019), *Vaucheria* sp. occurrence was recorded in the estuary and tidal flat of the Adventelva near Longyearbyen. Although the occurrence of *Vaucheria borealis* in Svalbard was mentioned by (Skulberg, 1996), very rich carpets of *Vaucheria* sp. in the extremely unstable environment of the estuary and tidal flat in the Adventelva probably represent a very unique and probably invasive alga species, which is presently moving into the high Arctic ecosystem (Kvíderová et Elster 2017).

This study aims to provide essential quantitative and qualitative information about the present distribution of the Adventfjorden estuary and tidal flat microphytobenthic community. Our objective was to outline the present ecological state of *Vaucheria* sp. mats (land cover estimation) and discuss the origin and future development of this microphytobenthic community. This information should help us to understand how the Adventfjorden estuary and tidal flat, and its microphytobenthic community react to the effects of climate change and increasing anthropogenic pressures, as well as the profound on-going transformations of coastal areas in the Arctic.

2. Material & methods

2.1. Study area description

Adventfjorden is a small sub-inlet on the southern side of Isfjorden, central Svalbard (Fig. 1).

Part of this inlet is constituted of a relatively large tidal flat, South-West (78°7′N) – North-East (78°27′N) oriented, in the vicinity of Longyearbyen (Nilsen et al., 2008). The Adventfjorden tidal flat stretches out over 3 km SW-NE and over 1 km NW-SE. Two large lateral pools filled with watery silty sediment surround the mudflat: Moskuslaguna on the northern side and an unnamed pool in the south (Weslawski et al., 1999). The Adventfjorden tidal flat forms an open system receiving enriched Adventelva's riverine inputs from the land, which provide considerable nutrients for microphytobenthos growth (Weslawski et al., 1999). From the seaside, the tidal flat is open to transformed Atlantic waters carried along by the West Spitsbergen Current. This conveyed mixed water mass was reported to profoundly affect local abiotic parameters throughout Isfjorden even up to its innermost branches including the Adventfjorden mud flat (Berge et al., 2005; Nilsen et al., 2008). The Adventfjorden tidal flat is shallow with regular, M2, semi-diurnal tides with a maximum amplitude of 190 cm (Byun and Hart, 2020). Geographical location of the studied tidal flat is shown in Fig. 1.

The tidal flat represents a system of periodically changed muddy pools - flats and gravel terraces. In the west, it is delimited by Longyearbyen and on the south by a road with nests of barnacle goose (*Branta leucopsis*) and dog kennels behind the road (Supplementary material 1).

2.2. Setting of field studies

The Czech Research station in Longyearbyen started to monitor the Adventfjorden tidal flat area and close surroundings in August 2015. The first description of the habitat types and microphytobenthic community composition evaluation were conducted at this time. A drone mapping survey and description of the spatial distribution of *Vaucheria* sp. mats across the tidal flat were conducted in August 2017. In addition, in August 2017, *Vaucheria* sp. samples were collected for subsequent phylogenetic analyses. The locality was also regularly visited out of the summer period (in April 2017 and October 2017) and the state of the *Vaucheria* sp. community was documented. Three transects (Transect I, II and III) were established with three or four sampling sites in each transect to cover the diversity of the environments in the tidal flat (Fig. 1). Also phylogenetic analyses were performed on freshwater samples of *Vaucheria*, collected on the bank of a muddy little stream in Bjørndalen Valley, Svalbard (N 78°13‘7.1“, E 15°20’21.8“; Jimel et al., 2021).

2.3. Tidal flat microphytobenthos

2.3.1. Community sampling

The algal community was analysed from all habitats (periodically changed system of muddy pools and channels) across the tidal flat

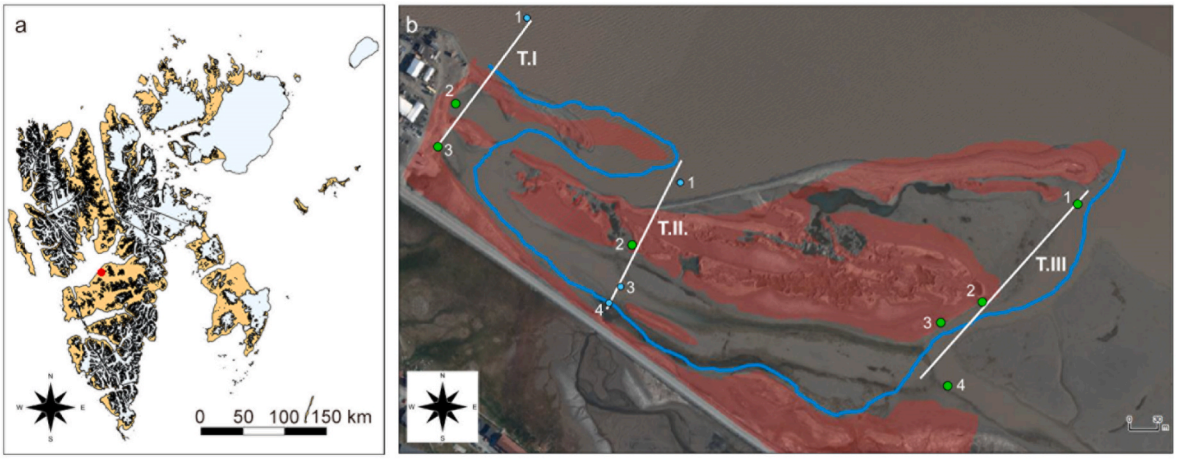

Fig. 1. Map of Svalbard with marked area of the Adventfjorden (a). In the south-west part of the inlet there is a system of periodically changed flats of muddy streams/pools with gravel terraces (b). Detailed map of the sampling area with transects I, II and III. Transects are numbered from west to east and sampling sites from north to south. *Vaucheria* sp. samples for phylogenetic identification were collected in transect I – the most south sampling site 3 (T.I.3), transect II – sampling site in the centre (T.II.2), transect III - two most south sampling sites (T.III.3, 4). The red zone delimits the high tide front and the blue line the low tide channel (August 2017), only raw estimation. Sampling sites in green refer to the presence of *Vaucheria* sp. (b). Map source: Norwegian Polar Institute (2014). Map processing QGIS 3.0. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

transects (Fig. 1 b) to determine their dominant morphospecies. Photographic documentation was provided. Morphospecies composition identification was determined according to Blum (1972) and Rieth (1980). Photomicrographs were taken using an Olympus BX53 light microscope equipped with 20 × and 40 × magnification lenses using an Olympus DP72 digital camera (Olympus, Japan). The microphotographs

Fig. 2. Epipelic and/or tychoplanktonic extensive mats of *Vaucheria* sp. occur at or slightly below the low tide area (a). The mats are produced by gelatinous clusters of densely agglomerated filaments (like a little shrub) (b) which produce mats with mosaic-like structures. *Vaucheria* sp. produce sparsely branched or unbranched filaments of coenocytic cells (c), and sexual spherical antheridia borne terminally on separate long siphons (d).

were processed together with species identification using ProMicra 2.3 (ProMicra, Czech Republic).

2.3.2. Vaucheria sp. laboratory phylogeny analyses

Selected *Vaucheria* sp. samples collected in transects I, II and III (Fig. 1 b – T.I.3, T. II.2, T. III.3, 4) and from Bjørndalen Valley (see above) were used for the molecular characterization. In the laboratory of the Czech research station in Longyearbyen, the gelatinous clusters of densely agglomerated filaments (Fig. 2 b) were washed from fine sediments, frozen and later transported to the Czech Republic (Phycology Centre, Institute of Botany, Czech Academy of Science in Třeboň). In the laboratory, we separated apical segments of single *Vaucheria* sp. filaments and used them for molecular characterization. Twenty μl of InstaGene matrix (Bio-Rad laboratories) were added to the frozen samples (several filaments from each sample) of *Vaucheria* sp. before being vigorously vortexed for several seconds, incubated at 56 °C for 30 min and heated to 99 °C for 8 min. Then 1 μL of supernatant was directly used as a template for PCR and added to 19 μL of MasterMix consisting of 14.2 μL H_2O, 4 μL buffer, 0.3 μL of each forward and reverse primers, and 0.2 μL MyTaq polymerase. The chloroplast *rbc*L region was obtained using newly designed primers Vaucheria_F2 (5′- TAA GTC TGT ACA AGA GCG TAC -3′) and Vaucheria_R (5′- GTG TAA YTC TCA TTC AAA -3′). PCR amplification was carried out under the following conditions: initial denaturation at 95 °C for 4 min followed by 35 cycles of denaturation at 95 °C for 1 min, annealing at 50 °C for 1 min and elongation at 72 °C for 1.5 min, with a final extension at 72 °C for 10 min. The PCR products were checked using 0.8% agarose gel electrophoresis stained with ethidium bromide and purified by Agencourt AMPure XP (Beckman Coulter) according to the manufacturer's protocol. The purified PCR products were sequenced in Macrogen Europe (Amsterdam, Netherlands). The PCR products were ca 1500 bp long. After sequencing by both forward and reverse primers, we got the sequences ca 1430 bp in length.

The most appropriate partition-specific substitution models were selected by ModelTest 2.1.4. The BIC-based model selection procedure selected GTR + I + Γ model for the 1st *rbc*L and 3rd *rbc*L codon partitions, and the K80 + I model for the 2nd *rbc*L codon partition. The phylogenetic tree was inferred with Bayesian inference (BI) by using MrBayes version 3.2.6 (Ronquist et al., 2012), carried out on a partitioned dataset to differentiate among *rbc*L codon positions. All parameters were unlinked among the partitions. Two parallel Markov Chain Monte Carlo (MCMC) runs were carried out for 8 million generations each with one cold and three heated chains. Trees and parameters were sampled for every 100 generations. Convergence of the two cold chains was checked and "burnin" was determined by use of the "sump" command. Bootstrap analyses were performed by maximum likelihood (ML) and weighted parsimony (wMP) criteria using RAxML 8.1.20 (Stamatakis, 2014) and PAUP v.4.0b10, respectively. The ML bootstrapping (100 pseudoreplicates) was run on the dataset partitioned to individual genes with the rapid bootstrapping procedure. The evolutionary model used was the default GTR+Γ. The wMP bootstrapping (1000 replicates) was performed using heuristic searches with 1000 random sequence addition replicates, TBR swapping, and random addition of sequences (the number was limited to 10,000 for each replicate). A weight was assigned to the characters using the rescaled consistency index on a scale of 0–1000. New weights were based on the mean of the fit values for each character over all of the trees in memory.

2.4. Drone survey to estimate Vaucheria sp. area coverage

Vaucheria sp. occurred at specific sites across the tidal flat. *Vaucheria* sp. felt-like coatings were collected near the gravel terraces and not across the whole tidal flat since the mud was too soft making it impossible to walk there. In August 2017, we therefore estimated the spatial distribution of *Vaucheria* sp. occurrence by use of an unmanned aerial vehicle (drone) mapping survey (Fig. 1). Of the 11 sites constituting our field sampling design, we failed to map three (T.I.1, T. II.1 and T. III.1), because no *Vaucheria* sp. occurred at points T.I.1 and T. II.1. At site T. III.1, *Vaucheria* sp. was present, however due to strong wind we could not finish the drone mapping of this study site. Here, we estimated the *Vaucheria* sp. area cover with help of an ADA Cosmo 30 Mini laser distance meter. The DJI F-306 Phantom 2 RC drone (DJI, China) equipped with a H3-3D gimbal and GoPro 4 Black RGB camera (GoPro, USA) was used. Image processing was performed using QGIS 3.0. Pre-processing of the drone images was applied to correct for exposure and gain. Furthermore, to help visualize the distribution of *Vaucheria* sp. across the tidal flat floor, the properties of the raster images were modified. Based on the combined study of the drone images and *in situ* observations, we determined that *Vaucheria* sp. mats cover area occurs in pixels in the Green Band (GB) ranging between 130 and 145 pixel value. To highlight *Vaucheria* sp. presence on the drone images, the rendering of the raster layer was modified to a single pseudocolor band in the GB. Then a red colour ramp was chosen for linear interpolation of which the selected range of pixel values was coloured in bright red. The remaining pixel values were set as black pixels. The raster layer was then superimposed to the original raster.

To estimate *Vaucheria* sp. cover area, polygonal masks of 225 m^2 were delimited and extracted from the original raster images, encompassing each study point respectively. Consecutively, the resulting raster was stripped of their constitutive RGB spectral bands using the SCP plugin (version 6.3.0) in QGIS. The isolated raster containing the green band of each site was kept for post-processing. Last, the spectral class signatures of the later raster were exported as txt files. The abundance of *Vaucheria* sp. expressed as a percentage of the covered area of the 225 m^2 squares was calculated as

$$Abundance\ (\%) = 100 \times \frac{pixels^{GB}}{pixels^{total}} \quad \text{(Eq. 1)}$$

where the $pixels^{GB}$ is the pixel count in the GB (pixel values from 130 to 145) corresponding to *Vaucheria* sp. occurrence and $pixels^{total}$ is the total pixel count included in the analysis.

The mean *Vaucheria* sp. covered area ($A_{Vaucheria}$) of the tidal flat was estimated as

$$A_{Vaucheria}\ (m^2) = \frac{Abundance}{100} \times A_{flat} \quad \text{(Eq. 2)}$$

where the Abundance value is obtained from Eq. (1) and A_{flat} is the area of the flat in m^2 calculated from QGIS.

2.5. Statistical analysis

All statistical analyses were carried out using Statistica 13.0 (Dell, 2015). Differences among transects were analysed using the non-parametric Kruskal-Wallis and Unequal N HSD tests. The results were considered statistically significant for $P < 0.05$.

3. Results

3.1. Spatial and temporal microphytobenthos distribution

Extensive mats of *Vaucheria* sp. were recorded in the south-west part of the Adventjorden tidal flat close to the vicinity of Longyearbyen (Fig. 1). The tidal flat habitat and its community is delimited by the high tide line (blue line in Fig. 1 b) where periodically flooded muddy pools - flats (Supplementary material 1) cover the largest area and are dominated by extensive mats of *Vaucheria* sp. The alga occurs preferably at or slightly above the low tide line (Fig. 2 a). The height of the green layer of gelatinous clusters produced by *Vaucheria* sp. can reach several centimetres (in maximum up to 6–7 cm) and alter their macroscopic appearance depending on tidal flooding (Fig. 2 a, b). If the felt-like coatings are out of water (Supplementary material 2), they produce

gelatinous clusters of densely agglomerated filaments like mosaic structures (like a little shrub). If *Vaucheria* sp. clusters are immersed in sea water (Supplementary material 2), they produce grass-like communities. However, when water movement and waves exceed a particular limit, the water can mechanically disturb the mats of agglomerated filaments (Supplementary material 2). During the tidal flood, the surface of *Vaucheria* sp. clusters are covered or enwrapped in soft sediments (Supplementary material 2), which are brought by the high tide. However, for a short time after the tidal flood, the clusters are exposed to air and again produce agglomerated filaments like little shrub mosaic structures (Supplementary material 2). There is soft black sediment under the layer of *Vaucheria* sp. clusters where anaerobic conditions probably occur (Supplementary material 2).

Based on repetitive observations from 2015 to 2019, consistent patterns in the development of the Adventfjorden tidal flat *Vaucheria* sp. extensive mats were seen. The initial stadia of the gelatinous clusters appeared already at the beginning of July 2015 (Supplementary material 2), and the mats of *Vaucheria* sp. were normally well developed by

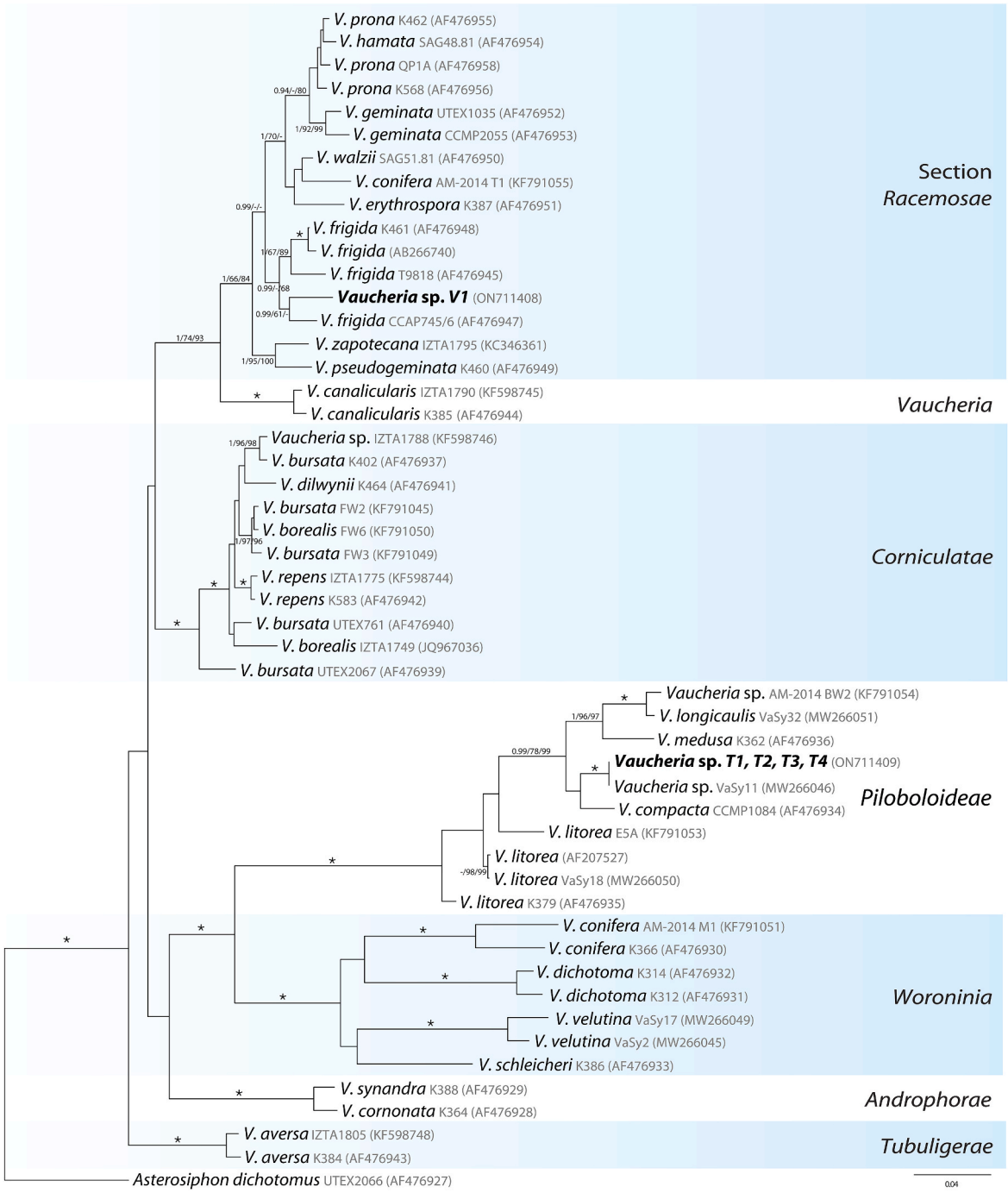

Fig. 3. Phylogeny of the genus *Vaucheria* (Xanthophyceae) obtained by Bayesian inference of the *rbc*L alignment with *Asterosiphon dichotomus* selected as the outgroup. Values at the tree nodes indicate statistical support; MrBayes posterior probability (left), maximum likelihood bootstrap (middle) and maximum parsimony bootstrap (right). Only statistical supports higher than 0.95/60/60 are shown. Asterisks mark the branches with the highest statistical support (1.00/100/100). New sequences of *Vaucheria* samples from the Svalbard transect are given in bold. The alignment was 1462 bp long. In the case of including shorter sequences, the missing nucleotides were supplemented by "N".

the beginning of August (regular observations 2015–2019).

3.2. Vaucheria sp. phylogenetic identification

The siphonaceous yellow-green algae *Vaucheria* sp. was selected for detailed morphological (Fig. 2 b, c, d) and phylogenetic analyses since it was identified as the dominant component of the tidal flat extensive mats by the drone survey. In addition, a freshwater *Vaucheria* sp. from a stream in Bjørndalen valley was investigated. A light microscope view showed that *Vaucheria* sp. coenocytic siphonaceous branches of filaments, diameter ranging between 25 and 40 μm (Fig. 2 c), were attached to the substrate by numerous thin colourless rhizoids (Fig. 2 b). The often macroscopic cells contain a large number of discoid plastids (Fig. 2 c), with or without pyrenoids. In our samples, we did not record asexual reproduction (zoospores, aplanospores, and akinetes). However, very sporadically we recorded sexual spherical antheridia, size 125–145 μm, borne terminally on separate long siphons (Fig. 2 d). The Bjørndalen valley *Vaucheria* sp., from a bank of a muddy little stream, differed in morphology, did not create such a morphologically robust thallus, but even here we did not record either asexual (zoospores, aplanospores, and akinetes) or sexual (oogonia and antheridia) reproduction.

Phylogenetic analyses based on *rbc*L genes confirmed that all examined *Vaucheria* samples from Svalbard (Adventdalen tidal flat and Bjørndalen Vally freshwater stream) as two lineages within the genus *Vaucheria* (Xanthophyceae) (Fig. 3). Both lineages were genetically distinct from all other *Vaucheria* species sequenced so far. The samples from the Adventdalen transects (Fig. 3, T.I.3-T1, T. II.2-T2, T. III.3-T3 and T. III.4-T4) are a sister lineage to a clade within Piloboloideae comprising *V. compacta*. In addition, the ecological characteristics of our specimens from the Adventdalen tidal flat best resembled *V. compacta* and we therefore named it as *Vaucheria* aff. *compacta*. The freshwater *Vaucheria* sp. from Bjørndalen Valley (Fig. 3, V1) we used for comparison was genetically distinct from *Vaucheria* aff. *compacta* and formed a new lineage in a sister position to *Vaucheria frigida*, section Racemosae. The newly obtained sequences have been deposited in GenBank under accession numbers ON711408-9. Supplementary material 3 has been updated accordingly.

4. Discussion

Marine algae constitute a major component of invasive alien species along coasts when it is defined as rapid proliferation after anthropogenic aided translocation (Anton et al., 2019). The effect of invasive species is escalating when combined with climate change (Pyšek et al., 2020). However, the genus *Vaucheria* de Candolle (Xanthophyceae) was not consider as an invasive group of species.

Here, we have described the spatial and temporal distribution of *Vaucheria* aff. *compacta* in the Adventfjorden tidal flat including phylogenetic identification and its drone area cover estimation. The study of *Vaucheria* aff. *compacta* spatial and temporal distribution and phylogenetic identification is followed by characterization of the local Adventfjorden tidal flat chemical and physical habitat together with estimation of its ecological impact on the functions, distribution and structure of the local *Vaucheria* aff. *compacta* benthic microflora (Souquieres et al. Polar Biology, under rewiev).

Furthermore, because of the occurrence of extensive mats of invasive *Vaucheria* aff. *compacta* in the Adventfjorden tidal flat, the study of the distribution, phylogenetic identification and drone area cover estimation was preceded by a detailed ecophysiological study of its photosynthetic performance. Photosynthesis was evaluated in a series of *in situ* and *ex situ* measurements based on the variable chlorophyll fluorescence and gasometric approaches (Kvíderová et al., 2019). *In situ* measurements demonstrated an enormous environmental plasticity in temperature, PAR, UVR, and emersion period duration with respect to photosynthetic activity. *Vaucheria* aff. *compacta* was acclimated to the prevailing low-light conditions, but was able to tolerate high-light conditions on sunny days of the late Artic summer.

4.1. Invasive Vaucheria aff. compacta – adventfjorden tidal flat dominant microphytobenthos species

It was discovered that, inside of the tidal flat, the populations of microbenthos were dominated by extensive mats of *Vaucheria* sp. (Supplementary material 2; Supplementary material 4) (Kvíderová et Elster 2017; Kvíderová et al., 2019). A community of *Vaucheria* sp. was already found in the Adventfjorden tidal flat in summer 2010 and described by Wiktor et al. (2016), see Figs. 2 and 3, page 338 of the aticle. However, these authors suggested that the diatom *Gyrosigma eximium* produced the highest biomass.

Vaucheria, de Candolle 1801 are siphonaceous yellow-green algae with oogamous reproduction, which typically occur in wetland habitats such as mudflats, salt marshes, estuaries, mangroves, streams, channels, lakes and ponds (Baker et al., 2012; Guiry et Guiry, 2020). About 70% of *Vaucheria* species are terrestrial to limnetic and the remainder are coastal with brackish, amphibious or fully marine habitats (Christensen, 1996, Wilcox, 2012). Some of the coastal species, including *Vaucheria compacta*, are cosmopolitan and were recorded from the Indo-Pacific and Atlantic shores of both hemispheres, including the North Sea (Schneider et al., 1993; Andersen et Bailey, 2002; Muralidhar et al., 2014; Rybalka et al., 2022). Phylogenetic analyses based on *rbc*L genes showed that the studied samples (Fig. 3, samples T1, T2, T3, T4) are a sister lineage to a clade within Piloboloideae, comprising *V. compacta*. In this study of a high Arctic phytobenthos community of the Adventfjorden tidal flat, the *Vaucheria* sp. most resemble *V. compacta* thus we named it as *Vaucheria* aff. *compacta*. We checked newly available sequences, and found there are indeed several sequences relevant to our study. Accordingly, we inferred a phylogenetic tree, including five new sequences generated by Rybalka et al. (2022), specifically, new sequences of the section Piloboloideae, and the newly genetically characterized species *V. velutina*. Interestingly, we found one isolate (VaSy11) studied by Rybalka et al. (2022) to be genetically identical to our *Vaucheria* samples T1, T2, T3 and T4. In addition, the studied *Vaucheria aff. compacta* morphologically resembles the description of a group in Piloboloideae (*V. compacta*, *V. medusa*, *V. litorea*) mentioned by Andersen and Bailey (2002). Also, with respect to the ecological characteristics of *Vaucheria compacta* and on the basis of our previous experiences, we have visited and analysed the possible occurrence of *Vaucheria* sp. In many tidal flat localities across Svalbard (Fig. 5). *Vaucheria compacta* was absent in many tidal flats across Svalbard (Fig. 5). We propose with very high probability that *Vaucheria* aff. *compacta* is an invasive species which has started to occupy the Adventforden tidal flat presently. The Longyearbyen marine port can be a possible source of *Vaucheria* aff. *compacta* inoculum. This port has one of the highest rates of shipping traffic in the high Arctic and is near the Adventfjorden tidal flat area. Here, many ships from the whole world come frequently, and transport of *Vaucheria* aff. *compacta* inoculum attached on a ship's hull is certainly possible. Because of the extraordinariness and rarity of *Vaucheria* aff. *compacta* occurrence in Adventfjorden, the specimen is starting the greening of the High Arctic tidal flats.

We propose that *Vaucheria* aff. *compacta* is an invasive species also on the basis of previous studies where *Vaucheria compacta* (Collins) Collins ex W.R. Taylor 1937 is one of the most common and widespread species (e.g. in Baltic Sea - Nielsen (1995), Kontula and Fürhapter (2012) , in Norway - Rueness (2001), in Scandinavia - Karlson et al. (2020) etc.) However, *Vaucheria compacta* was never recorded before in the high Arctic Svalbard tidal flats. Phylogenetic analyses based on the *rbc*L genes of *Vaucheria* aff. *compacta* also showed that *Vaucheria medus*a are closely related (Fig. 3, samples T1, T2, T3, T4). *Vaucheria medusa* T.A. Christensen, section Piloboloideae is a marine-brackish northern European species. The known distribution of the species includes Sweden, Denmark, Germany, Norway, Great Britain and the Netherlands. Recently, it was discovered on the southern shore of Neva Bay, in the

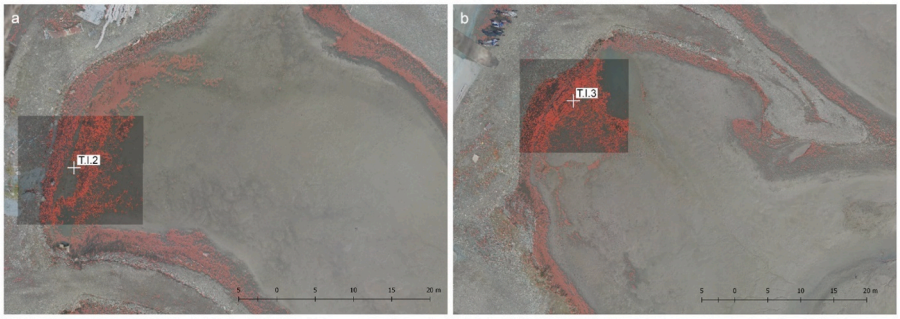

Fig. 4. Distribution and area cover of *Vaucheria* aff. *compacta* extensive mats documented in drone pictures, in T.I.2 and T.I.3 of the studied tidal flat. The square area represents 225 m^2. The *Vaucheria* aff. *compacta* colonized areas are marked red. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

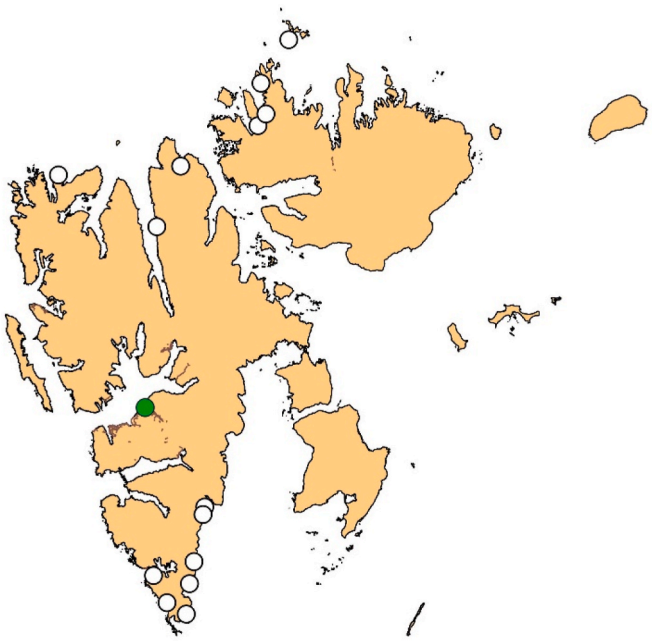

Fig. 5. The occurrence of *Vaucheria* aff. *compacta* in Svalbard. Green circle – observed, empty circle – not found. Map source: Norwegian Polar Institute (2014), map processing QGIS 3.0. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Gulf of Finland (Vishnyakov, 2019). As a control sample, the freshwater Bjørndalen valley samples of *Vaucheria* sp. (Fig. 3, sample V1), part of a project focussed on the winter survival of *Tribonema* cf. *minus* (Jimel et al., 2021), was selected and phylogenetic analyses based on *rbc*L genes were performed. The *rbc*L analyses showed that these *Vaucheria* sp. samples are genetically distinct from the Adventfjorden tidal flat transect samples, forming a lineage in a sister position to *Vaucheria frigida*, section Racemosae. *Vaucheria frigida* (Vaucher) De Candolle is a common cosmopolitan species, widely distributed and frequently collected from both terrestrial and aquatic habitats (Hoppaugh, 1930, Schagerl et Kerschbaumer, 2009). This marks its first recording in high Arctic Svalbard.

4.2. *Vaucheria aff.cCompacta area cover estimation*

For the first time, to our knowledge, the area cover estimation of a polar tidal flat microphytobenthos was performed using a drone mapping survey. The mean *Vaucheria* aff. *compacta* area cover was about 231.1 m^2 (±10.55%, n = 11) of the drone surveyed part (2475 m^2) of the tidal flat area, which could be considered as an important primary producer in this ecosystem. The photosynthesis measurements performed by Kvíderová et al. (2019) provided basic data on primary productivity, but spatial and temporal variability in *Vaucheria* cover area and its physiological state must be considered for detailed calculations of ecosystem productivity. The regular drone surveys during the vegetation season, using multispectral and hyperspectral cameras, could provide vegetation indices as proxies of the physiological performance, as has been already done for higher plants Glenn et al. (2008) and van der Meij et al. (2017). Multispectral and hyperspectral images with a robust reference spectra library may be also used for determination of community or individual plants (Chi et al., 2021) The mapping of tidal flat microphytobenthos could provide additional data on *Vaucheria* aff. *compacta* distribution as a probable invasive species on Svalbard.

However, there are several limitations for regular monitoring in the Adventfjorden tidal flat area. In addition to considerations for drone use summarized in Duffy et al. (2018), this tidal flat area is subject to a specific regime of flying, as it is included in the 5 km drone prohibition zone of the Svalbard Airport. Therefore, permission from the Longyearbyen AFIS is necessary before the flight and possible restrictions due to air traffic must be considered during research planning (Avinor, 2022).

3.3. *Vaucheria aff. compacta drone spatial distribution mapping and area cover estimation*

Vaucheria aff. *compacta* appeared to grow at or slightly below the low tide mark (Fig. 1 b) and was found principally along the path of the main low tide channel. We estimated the spatial distribution of *Vaucheria* aff. *compacta* by its extensive occurrence of turfs (Fig. 4 a - T.I.2 and b - T.I.3, Supplementary material 4: T. II.2, TIII.2, T. II.3, T. III.3 and T. III.4, in T. II.3 no *V.* aff. *compacta* was present, in T. II.4 – mosses and vascular plants were recorded).

Vaucheria aff. *compacta* covered 231.1 m^2 (±10.55%, n = 11) of the surface of the studied 2475 m^2 **across the drone mapped tidal flat** area (Table 1). *Vaucheria* aff. *compacta* was the most abundant microphytobenthos (area covered) across Transect III with a mean area cover

Table 1
Vaucheria cf. *compacta* extensive mats area cover across the studied Adventdalen tidal flatbed expressed as percentage of *Vaucheria* cf. *compacta* covered area in 225 m^2 squares at each sampling site. Abbreviation: s.d. – standard deviation. Superscript letters indicate groups determined by Unequal N HSD test for P = 0.05.

		Transect I	Transect II	Transect III
Site	1	0	0	17
	2	17	8	16
	3	20	0	20
	4	n/a	0	18
Mean ± s.d.		12.33 ± 10.78^{ab}	2.00 ± 4.00^{a}	17.75 ± 1.71^{b}

of 17.75%, directly next to the mouth of the river (Supplementary material 4 T. III.2, 3, and 4 and Table 1). In TI, *Vaucheria* aff. *compacta* covered a little bit less area, about 12.33% (Table 1) in comparison with T. III. The microphytobenthos presence of *Vaucheria* aff. *compacta* was rare across T. II, reaching only 2.0% of the total area cover (Table 1, Supplementary material 4). However, these differences among the transects were not statistically significant (Kruskal-Wallis test $H_{(2,11)} = 5.327$, $P = 0.0697$), probably due to the large variability in Transect I. Nevertheless, a statistically significant difference in cover was found between Transects II and III. (Table 1).

For estimation of area covered by *Vaucheria* aff. *compacta* in August 2017, the total flat area (A_{flat}) was defined by QGIS as 2475 m^2. If the mean abundance of 10.55% is considered (Table 1), *Vaucheria* aff. *compacta* covered ca 231.1 m^2 of the studied tidal flat area.

The studied tidal flat area was visited also outside the peak summer season in April 2017 and October 2017. No visible *Vaucheria* aff. *compacta* mats were recorded at those times. The tidal flatbed was covered by dry and/or frozen sediment in October 2017 and by snow and ice in April 2017.

5. Conclusion

Microorganisms, including the studied invasive *Vaucheria* aff. *compacta*, as primary producers, are important components of the tidal flat ecotone in Svalbard **Adventfjorden tidal flat**. Here affect large-scale changes within intertidal systems and protect sea shore ecosystem against erosion. This research report documents spatial distribution of *Vaucheria* aff. *compacta* (2015–2017) and suggest its origin. Invasive algae *Vaucheria* aff. *compacta* is important ecosystem engineers which drive many other processes through the interaction between minerals, cellular filaments and organic polymers forming 3-dimensional mat-like structures and facilitates colonization by higher plants, by providing nutrients and carbon to the tidal flat sediment. This is quite important, given that global warming in the Arctic is amplified and facilitates the greening of the Arctic, a phenomenon which is associated with increased biomass coverage and the subsequent succession of life, including invasive species, into the Arctic.

CRediT authorship contribution statement

Josef Elster: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Claude-Eric Souquieres:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Iva Jadrná:** Writing – review & editing, Visualization, Validation, Resources, Methodology, Investigation, Formal analysis, Data curation. **Pavel Škaloud:** Writing – review & editing, Visualization, Validation, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Janne E. Søreide:** Writing – review & editing. **Jana Kvíderová:** Writing – review & editing, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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