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Temperate marine macrophytes are highly variable sources of Biogenic Volatile Organic Compounds - a comparative study from the Baltic Sea and NE Atlantic

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Abstract

Biogenic Volatile Organic Compounds (BVOC), emitted by Earth's ecosystems, affect several chemical processes in the atmosphere that have profound climate impacts. Despite their climate relevance, global BVOC budget estimations are still highly uncertain, with ocean-derived emissions being particularly poorly constrained. Marine macrophytes (i.e. macroalgae and seagrass) are a large and widespread organismal group whose BVOC emission rates are particularly poorly quantified. In this study, we set out to address this knowledge gap by quantifying *ex situ* the BVOC emission rates of three temperate macrophytes (*Zostera marina*, *Fucus vesiculosus* and *Ulva intestinalis*) with a Vocus proton-transfer-reaction time-of-flight mass spectrometer (Vocus PTR-TOF). To capture and improve our understanding of the variability of macrophyte BVOC emissions, our quantifications were repeated across two contrasting coastal regions: the northeastern Atlantic (Ireland) and northern Baltic Sea (Finland). The three macrophytes emitted a wide range of BVOCs, with a total of 166 different compounds detected. Although many BVOCs were emitted by all macrophytes, significant differences were observed in the total emission profiles, both between and within species. Interestingly, the seagrass *Zostera* exhibited significantly higher overall BVOC emission rates per unit biomass than the two macroalgae and showed clearly differing intraspecific emission profiles across the two regions. Regarding individual compounds, dimethyl sulfide (DMS) was emitted at the highest rates, but many other compounds (e.g., sesquiterpenes and $C_{10}H_{21}O^+$) also displayed notable emission rates. Although many of the observed BVOCs are commonly investigated compounds (e.g., DMS and terpenoids), our results show that macrophyte BVOC emissions comprise a large number of different compounds, suggesting that future studies would benefit from targeting a wider range of BVOCs than currently considered. Our results highlight macrophytes as highly variable sources of BVOCs, whose better inclusion into marine BVOC budgets should be strived for. However, more robust data are needed, and future research should also focus on investigating the dynamics driving macrophyte BVOC emissions, their variability, and their eventual fate in the environment.

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1 Introduction

Volatile Organic Compounds (VOCs) comprise thousands of molecules with low boiling points and high saturation vapor pressures. VOCs are emitted by many natural and anthropogenic sources into the atmosphere and drive the formation of ozone and secondary organic aerosol as well as prolong the lifetime of methane by reducing atmospheric oxidation capacity (Guenther et al. 2012; Boy et al. 2022). Aerosols provide a net cooling effect on the climate, as they increase solar scattering and can form cloud condensation nuclei (CCN) driving the formation of new clouds and altering cloud properties (e.g., reflectivity, lifetime, and extent; Gantt et al., 2012*).* Beyond their role in climate forcing, VOCs and aerosols also influence air quality and human health by contributing to the formation of secondary pollutants (Arfin et al., 2023). Through these chemical processes, VOCs have a substantial effect on atmospheric chemistry and the climate, which makes it important to understand the various sources contributing to the global atmospheric VOC-budget. Biogenic volatile organic compounds (BVOCs), originating from the natural world in contrast to anthropogenic sources, make up the majority (>80%) of the total global VOC budget (Guenther et al., 1995; Carpenter et al., 2012). It is well known that terrestrial ecosystems (forests at the forefront) emit BVOCs in massive quantities, but major knowledge gaps exist concerning BVOC emissions originating from the oceans and coasts (Pozzer et al., 2022; Exton et al., 2015; Zhao et al., 2023; Wang et al., 2025); as a result, the contributions of marine life to the global budget of VOCs are still poorly defined (Yu & Li, 2021) and require further attention.

In the marine realm, most research on BVOC emissions has focused on the open oceans, phytoplankton, and the most emitted marine BVOC, dimethyl sulfide (DMS) (e.g., Carpenter et al., 2012; Zhao et al., 2023; Yu & Li, 2021; Wang et al., 2025). Generally, high primary productivity drives higher marine BVOC emissions and nutrient-rich productive coastal areas exhibit higher BVOC concentrations and higher loadings of organics in the marine aerosols than open oceans (Wang et al., 2025; Fu et al., 2011; Kang et al., 2018). Phytoplankton, especially during and after blooms, emit large quantities of BVOCs into the water, that due to the close proximity to the sea-air interface can enter the atmosphere in large quantities. Through their BVOC emissions, phytoplankton directly affect climatic processes (e.g., marine secondary organic aerosol production). For instance, DMS emissions have a strong impact on the marine sulfur cycle and the global sulfur budget (Stefels et al. 2007; Asher et al. 2017). When DMS is released into the atmosphere, it can be oxidized to sulphuric acid, which in turn is an important driver of new atmospheric aerosol particles and subsequently CCN (Hoffman et al., 2016). Although DMS has been the major focal point for marine BVOC research, emissions of many other BVOCs have been recorded, including other sulfur containing compounds, terpenoids, nitrogen-containing compounds, and volatile halocarbons (Zhao et al., 2023; Wang et al., 2025). However, oceans are vast and biologically diverse making measuring BVOCs emissions from marine areas both challenging and expensive, which has made synthesising marine BVOC emissions difficult. Therefore, current atmospheric models still underestimate marine BVOC emissions (Wang et al., 2025) and to fill these gaps, more data and a broader understanding of marine BVOC dynamics are needed. Overall, there is an increasing need to better understand the biology underlying marine BVOC emissions. Although phytoplankton are the largest biological sources of BVOCs in the oceans, the strong focus on this particular organismal group might have concealed the importance of other marine primary producers, especially in productive coastal areas.

Benthic macrophytes (seagrasses and macroalgae) are primary producers that grow on shallow bottoms along coastal seas and often form the foundation of marine ecosystems. The organisms and the ecosystems they create sustain many vital ecosystem services such as coastal protection, carbon sequestration and fisheries production (Nordlund et al., 2017; Eger et al., 2023). Although the organisms are known to produce a large variety of BVOCs, the rates at which macrophytes (and especially seagrasses) release BVOCs are poorly quantified (Saunier et al., 2025a) and therefore their contribution to the global atmospheric BVOC-budget remains largely undefined. The potential quantities of BVOC-emissions are substantial, as these organisms cover significant areas globally (macroalgae >6 million km^2 and seagrass meadows >250 000 km^2; Duarte et al., 2022; McKenzie et al., 2020), support high biomass year-round (unlike phytoplankton with a more ephemeral occurrence through blooms) and grow at shallow depths close to the sea-air interface. However, to elucidate this potential, more high-quality quantitative emission rate data are needed. Many previous macrophyte BVOC studies have been done destructively, e.g., by measuring BVOC contents of ground plant material (Rubino et al., 2022; Hornicar et al., 2014; Jerkovic et al., 2018; Coquin et al., 2024). While such studies can provide valuable information about the BVOCs produced by macrophytes, they do not provide information about which BVOCs are emitted into the water nor at what rates. BVOC measurements have also often been done with methods that allow accurate qualitative identification of volatile compounds (e.g., gas chromatography–mass spectrometry, GC-MS) but lack

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the ability to quantify emission rates (Maruti et al., 2018; Wada & Hama, 2012). Several studies have also focused on measuring emission rates of only certain compound groups (e.g., halocarbons; Abrahamsson et al., 2003; Leedham Elvidge et al., 2013) or specific compounds (e.g., isoprene; Hrebien et al., 2021), which makes the data-incorporation to total BVOC-budgets challenging. Finally, many experiments that have quantified macrophyte emission rates, have been performed during low tide conditions (i.e. organisms exposed to the atmosphere, e.g., Sartin et al., 2001 & 2002), and although valuable, these data do not necessarily correspond to emissions that occur while the organisms are submerged underwater. Hence, only a few studies have measured emission rates of submerged marine macrophytes (e.g., Saunier et al., 2025b; Bravo Linares et al., 2010), and more data and insights are needed to establish impact and variability of macrophyte BVOC emissions.

In this study, we set out to quantify the underwater BVOC emission rates of three benthic macrophytes (the seagrass *Zostera marina L.*, brown algae *Fucus vesiculosus L.* and green algae *Ulva intestinalis L.*) that are commonly found in temperate waters around the Northern Hemisphere. Common eelgrass (*Z. marina*) is the most widespread and well-studied seagrass species in the Northern Hemisphere, but only limited knowledge exists about the BVOCs these plants emit naturally (qualitative but destructive sampling presented in Coquin et al., 2024) and no BVOC emissions rates have previously been quantified. Gut weed (*U. intestinalis*) and bladderwrack (*F. vesiculosus*) are macroalgae, and while some information exists about their BVOC emissions into air (e.g., Bravo-Linares et al., 2010; Broadgate et a., 2004; Hornicar et al., 2014), BVOC emissions during submersion are poorly understood and quantified. Here, we used a Vocus proton-transfer-reaction time-of-flight mass spectrometer (Vocus PTR-TOF) to quantify BVOC emission rates in controlled incubation experiments. The selected macrophytes were collected from two marine regions that differ substantially from each other, the oceanic eastern Atlantic (Ireland) and brackish Baltic Sea (Finland). The markedly different environmental conditions (e.g., salinity, annual temperature range, submersion regimes) impact the physiology of the macrophytes (e.g. Bäck et al., 1992), but all three species still commonly occur in both marine regions. Using this comparative approach, our main aims were to establish 1. the type and rate of BVOCs emitted by these three common macrophytes, 2. how similar/dissimilar BVOC emissions are between the different macrophyte species and 3. how variable the emissions are within-species when comparing two marine regions with very differing environmental conditions. Hence, the overarching goal was to advance our understanding of BVOC emission rates originating from temperate marine macrophytes and provide an important step towards clarifying how these primary producers contribute to coastal and global BVOC budgets.

2 Methods

2.1 Study regions

The fieldwork and BVOC-measurements were performed in May and August 2025, in Ireland and Finland, respectively. In Ireland, BVOC measurements were performed at Mace Head Atmospheric Research Station (MHD), that is situated on the west coast of Ireland on the shore of the North Atlantic Ocean (Fig 1a). In Finland, measurements were conducted at Tvärminne Zoological Station (TZS) that is located on the southern tip of Finland next to the Baltic Sea (Fig 1a). Due to the stations' excellent placement, all macrophytes were collected from the near vicinity of the respective stations.

The environment and local biology differ considerably between the studied marine regions. At Mace Head, salinity fluctuates around 30 psu, while in the brackish waters outside TZS salinity is quite stable around 5-6 psu. The Finnish coastal waters experience large annual temperature fluctuations, reaching >20° C in the summer and freezing conditions during the winter months, while on the Irish coast the seawater fluctuates less (6.5-18.5° C at COMPASS Mace Head Buoy 2 km of the coast; data accessed through https://erddap.marine.ie/). Coincidentally, during both campaigns, the relevant sea areas were experiencing marine heatwaves, with seawater reaching over 20° C in the shallows outside Mace Head in May (personal observation, 16° C measured at Mace Head Buoy) and over 22° C on the Finnish coast in August (Monitoring data from TZS, MONICOAST: www.helsinki.fi/monicoast). The Baltic Sea is well known to be highly eutrophic, which has considerable effects on local biology e.g., high pelagic and filamentous algae production that affects benthic light availability. On the west coast of Ireland seawater is less nutrient-rich, translating to better visibility and lower biological activity in the water column. Tidal regime also differs significantly between regions. At Mace Head, low tide occurs twice a day (tidal difference during campaign ~3m), while the coastal areas of Finland are tideless, though some water-level fluctuations occur irregularly due to weather-related drivers (e.g. atmospheric pressure, wind).

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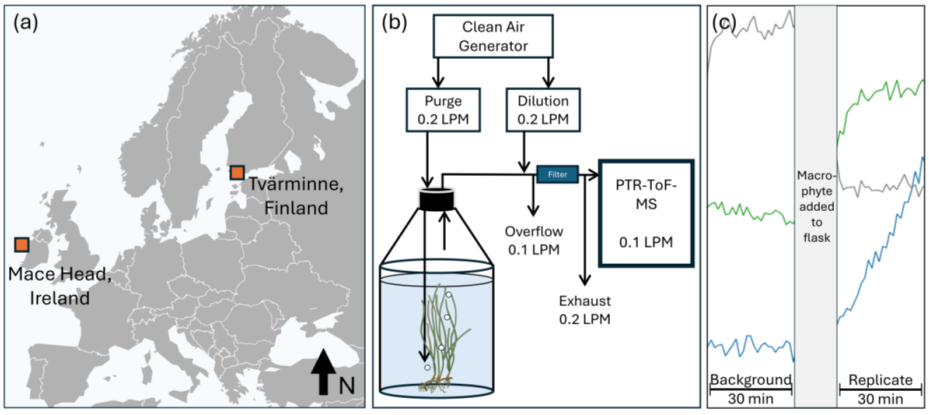

Figure 1: (a) Locations of the two study sites in Europe. (b) Schematic of the incubation setup. (c) Example data of three compounds with differing responses (see Section 2.6 for details on interpretation) after macrophyte addition: green line = Emission that quickly stabilizes, blue line = Emission that keeps increasing, and grey line = Consumption. Macrophyte image from Integration and Application Network (IAN), University of Maryland Center for Environmental Science (https://ian.umces.edu/).

2.2 Seawater collection and treatment

At both study sites, the seawater used in experiments was pumped from a depth of approximately 5 m from the nearby sea (Ireland: Carna Research Station which is about 5 km from MHD; Finland: TZS). Prior to the experiments in Ireland, we evaluated whether background signal quality could be improved by filtering the seawater (5 µm pore filter) and autoclaving (121ºC for 20 min) the filtered seawater. Filtering the water improved the background signal, while autoclaving worsened the measurement quality by increasing certain BVOC emissions. Although the exact source of these increased emissions could not be identified, we assume that they originated either from the plastic canister in which the water was autoclaved or from microorganisms that burst due to the sterilisation process. Based on these findings, filtered but not autoclaved seawater was used at both study sites (5 µm filter in Ireland and 0.2 µm filter in Finland). In Finland, the finer filter was necessary to reach satisfactory background measurements due to high amounts of organic particles/microorganisms being present in the water. Additionally, before measurements, the filtered seawater was bubbled in 20L containers for at least 12 h to further reduce BVOC concentrations in background measurements. This practice was added to the measurement protocol after test incubations revealed high DMS concentrations in the background measurements that did not stabilize during the incubation, thereby negatively affecting the quality of the results.

2.3 Macrophyte collection

The three selected macrophyte species belong to distinct organismal groups. Bladderwrack (*Fucus vesiculosus,* hereafter *Fucus*) is a perennial brown macroalgae (Orchrophyta, Phaeophyceae) that usually grows attached to rocky substrates. Gut weed (*Ulva intestinalis,* hereafter *Ulva*) is a green macroalgae (Chlorophyta, Ulvophyceae), that unlike the two other species investigated has an annual lifecycle. Common eelgrass (*Zostera marina,* hereafter *Zostera*) is a perennial marine flowering plant (Zosteraceae, Angiospermae). It has roots that anchor it to soft-sedimentary seafloors where it can create dense underwater meadows.

Macrophytes were collected in the morning of emission measurements and kept submerged in mesh bags prior to incubations. During both campaigns, we collected and measured all replicates (n=5) per species during the same day and all three species during the same week. The different macrophyte species were measured on separate days, because it was not feasible to collect *Zostera* every day and we wanted to measure BVOC emissions from fresh specimens. *Zostera* was collected by snorkeling in Ireland (1 m depth during low tide) and by SCUBA in Finland (4-meter depth). Instead of individual plants, *Zostera* replicates consisted on average, of 22 and 15 shoots in Ireland and Finland, respectively. The shoot counts differed between countries, because plants were larger in Finland, and >20 shoots would not have fit in the incubation flask. Each *Ulva* replicate consisted of algae thalli

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(fronds) collected from a specific rockpool. Hence, *Ulva* from 5 separate rockpools were measured at both study sites ensuring independent material. Replicates of *Fucus* consisted of individual intact thalli that were gently removed from the rocky substrate. The collection of *Fucus* replicates was semi-random, because the algae had to be small enough to fit the 5-liter incubation-flask. At Mace Head, *Fucus* grows in the intertidal zone and falls dry twice a day, while *Fucus* in the northern Baltic Sea always remain submerged.

Before measuring their BVOC-emissions, the macrophytes were carefully cleaned and rinsed with filtered seawater to remove sediment and potential epibiota. It was especially important to rinse *Ulva*-replicates, because during test incubations we noticed that unrinsed replicates released certain BVOCs at very high concentrations immediately when the algae were submerged in the flask, which was likely due to *a priori* accumulation of BVOCs on the surface of the algal matrix. This was unwanted as it obscured the measurement of real-time emission rates.

2.4 Vocus PTR-TOF

BVOCs were measured using a Vocus proton-transfer-reaction time-of-flight mass spectrometer (Vocus PTR-TOF, Tofwerk AG/Aerodyne Research, Inc.), a high-sensitivity instrument described by Krechmer et al. (2018). The instrument is designed to quantify BVOC concentrations in the air but has rarely been used to measure BVOC concentrations in water. The system employs a low-pressure discharge reagent ion source to generate H_3O^+ ions, which are then coupled to a Focusing Ion-Molecule Reactor (FIMR). The FIMR consists of a resistive glass tube with a radio frequency (RF) quadrupole field that collimates the ion beam, minimizing wall losses. For this study, the FIMR was operated at a reactor pressure of 2.5 mbar and an axial voltage gradient of 450 V, resulting in an E/N ratio (electric field to gas number density) of approximately 120 Td. The reactor temperature was maintained at 100°C. Ions were detected by a time-of-flight mass spectrometer operating with a mass resolving power of 4500 m/Δm at m/z 100 Th. Data were acquired at a time resolution of 6 seconds.

The ionization mechanism in the Vocus PTR-TOF is proton transfer reaction, which is a relatively "soft" ionization technique that predominantly yields the protonated molecular ion (MH^+) for most compounds of interest, though fragmentation becomes more common with larger and more functionalized molecules (Zhang et al., 2025; Li et al., 2022). The selectivity of the Vocus PTR-TOF is primarily governed by the proton affinity (PA) of the target analytes relative to the reagent ions. Using H_3O^+ as the reagent ion, the instrument selectively ionizes VOCs with a PA greater than that of water (691 kJ/mol), efficiently suppressing the detection of major atmospheric constituents such as N_2, CO, and others. The sensitivity of the Vocus PTR-TOF is influenced by the proton affinity, fragmentation patterns, and transmission efficiencies of the analytes. Fragmentation can occur depending on the functional groups present and the energetic conditions within the reactor. In the Vocus FIMR, the collision energy is modulated by the E/N ratio. For this study, the reactor conditions were optimized to balance the suppression of water clusters and minimize collision-induced dissociation.

For any analyte molecule, knowledge of its proton transfer rate constant (kPTR) and the instrument's response to VOC standards under the applied operating conditions allows straightforward determination of the Vocus PTR-TOF sensitivity for that molecule. During the campaign, the Vocus PTR-TOF was calibrated weekly using a gas-phase standard (Apel-Riemer Environmental, Inc.), which contained 19 compounds. The sensitivity of these compounds can be found in Table S1. Based on the calibration results of known compounds in the gas mixture, the transmission efficiency and the relationship between kPTR and sensitivity factors were determined, as shown in Figures S1 and S2. For detected species with known PA, the sensitivity factors can be calculated based on the established relationship between kPTR and sensitivity. For compounds with unknown PA, we used an averaged kPTR value of 2.5×10^{-9} cm^3 $molecules^{-1}$ s^{-1}. The error introduced by this assumption is less than 50%, assuming no significant fragmentation occurs during ionization.

2.5 Experimental and analytical setup

Incubations were performed in a 5-liter filtration flask, made airtight during incubations with custom-made Teflon corks. Before the start of each incubation, the airtightness of the flask and incubation setup was checked with a flowmeter. During the whole measurement period (30 min), the seawater was purged with clean air (produced by Vocus ZeroAir) through a Teflon tube with a flow rate of 0.2 LPM (Fig. 1b). The purging flow was pushed through a metallic bubbling stone that created small bubbles, increasing the area of the purged air and enhancing the effectiveness of capturing and transporting BVOCs into the headspace. From the headspace, the 0.2 LPM flow containing purged BVOCs continued out from the flask through another Teflon-tube. Before entering the Vocus PTR-TOF, the flow was mixed with a clean air dilution flow (0.2 LPM) to decrease the humidity and thereby risks

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for water condensation in the lines or in the filter (PTFE membrane filter, pore size 1.0 µm, Advantec MFS. Inc.) in front of the Vocus. Of the total 0.4 LPM flow, 0.1 LPM entered the PTR, while the rest was pumped out from the system or exhausted (Fig. 1b). The flows were controlled by mass flow controllers (Alicat Scientific, Inc. USA).

For the background measurements, the flask was filled with 4.5L of filtered seawater. Immediately after finishing a background measurement, a macrophyte-replicate was added to the flask (without replacing the seawater) and its BVOC emissions were measured. The macrophytes were tied to Teflon sticks to keep them submerged. During all incubations, the flask was illuminated by two LED-lamps with light spectrums suitable for submerged plants (Fluval Plant LED). The light environment inside the flask corresponded to ~200 PAR (Photosynthetically Active Radiation). The seawater temperature in all incubations was ~20° C. The BVOC emissions from both background and actual replicates were purged and measured for 30 minutes. Between replicates, the flask was rinsed twice with MilliQ-water. After measurements, the macrophyte-replicates were dried (60° C, 48 h) to acquire their individual dry weight (hereafter DW).

2.6 Identification of BVOC emissions and data extraction

Post-processing of Vocus PTR-TOF data was performed using the data analysis package "Tofware" (version 4.0.2, www.tofwerk.com/tofware) running in the Igor Pro (Wavemetrics, v.9.0, OR, USA) environment. High-resolution peak fitting was conducted to deconvolve overlapping isobaric ions, sharing the same nominal mass. The peak shape was determined empirically from isolated high-intensity ions and applied to fit the entire mass spectrum. Molecular formulas were assigned to fit peaks based on mass defects and isotopic pattern matching. BVOC emissions were identified by evaluating time-series data for all identified peaks (m/z 19–400 Th). A peak was classified as a macrophyte-derived BVOC and included in subsequent analyses, if a distinct change relative to the seawater background was observed in at least three out of the five replicates within a treatment.

Despite filtering and pre-bubbling of seawater background measurements did not always properly stabilize during the incubation period, which also affected the quality of the subsequent measurement of macrophyte BVOC emissions. For instance, if the seawater contained high concentrations of a BVOC that continued to decrease during the entire background measurement, it could mask emissions from the macrophytes (BG1 and Sample1 in Fig. S3). Due to failed background measurements, two replicates (a Finnish *Zostera*- and *Ulva*-replicate) were removed from further analysis. Problems with background measurements also occurred in other replicates (mainly in Finland) for individual data points (e.g., first data point in Fig. S3) and if the results were deemed unreliable in the data preprocessing stage, the data points were classified as NA in the final data set.

For emission rate calculations (see Section 2.7), we only used data collected during the last 15 minutes of both background and macrophyte incubations. The emissions of most compounds reached a stable plateau in the first 15 minutes of the measurements (Fig. 1c, Fig. S3), but the concentration of some compounds kept increasing during the whole measurement period. The compounds that stabilized are assumed to be limited by the emission rate of the macrophyte, and their transfer from the water into the sampled air is rapid. This is the case for poorly soluble compounds, such as hydrocarbons. The compounds that kept increasing throughout the measurement are most likely the more water-soluble compounds (e.g., Br_2CH^+ and DMS; Table S2) for which the concentrations in the sample air are more limited by the water-to-air transfer. All data points (1 measurement/minute for each compound) from the last 15 minutes were averaged, after which the background averages were subtracted from the macrophyte averages to acquire cps-values (counts per second) for how much macrophytes were emitting each compound. The raw signal intensities (counts per second) were converted to mixing ratios (ppb) using reaction rate constants and the instrument-specific transmission curve as described in Section 2.4. Emission rates could then be accurately deduced for compounds whose concentrations stabilized during the incubations (see Section 2.7). For compounds that failed to reach a stable concentration, the emission rates could still be estimated, though these estimates are not considered accurate because they systematically underestimate the true emissions (all instances marked in Table S2). Despite underestimations, the comparisons between experimental treatments for these compounds are valid due to the same sampling period across all replicates. Some BVOCs also clearly decreased following the addition of a macrophyte (Fig. 1c). We attribute this behaviour to BVOC consumption, but did not attempt to determine any consumption rates, as the observed decrease will depend on the initial concentrations available in the background water and possible balances between emission and consumption. All instances where BVOCs were consumed during macrophyte incubations are listed in the supplementary materials (Table S2).

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The use of a Vocus PTR-TOF allowed us to detect the emissions of a large range of compounds (C_1-C_{15}; Excel). However, when a Vocus PTR-TOF is used as the sole analytical method the exact identity of the measured molecules cannot usually be identified, because the method is mass-selective, which means that isomers cannot be separately distinguished. Therefore, we used the GLOVOCS-database (Yáñez-Serrano et al., 2021) to assign potential identities to our measured compounds (Table S3). Most compounds have several potential identities and although the GLOVOCS database is extensive, many especially larger compounds were not found in the database. Certain well studied compounds could with good confidence be appointed their identity (e.g., $C_2H_7S^+$ = DMS).

2.7 Emission rate calculation

Emission rates standardized to mass ($\boldsymbol{ER_{mass}}$; ng BVOC/g macrophyte DW/ h) for the emission-data collected with the Vocus PTR-TOF were calculated using the following equations:

$$\boldsymbol{ER_{mol/min}} = \frac{\boldsymbol{C_{ppb} * N_{ppb} * D * F_{flow}}}{\boldsymbol{N_A}}$$

$$\boldsymbol{ER_{mass}} = \frac{\boldsymbol{ER_{mol/min} * M_m}}{\boldsymbol{DW}} * \boldsymbol{t_h}$$

Where $\boldsymbol{ER_{mol/min}}$ is the emission rate in moles/min, $\boldsymbol{C_{ppb}}$ is the measured ppb-concentration of each emitted compound, $\boldsymbol{N_{ppb}}$ is the number of molecules corresponding to 1 ppb ($2.5x10^{10}$ molecules/cm^3), $\boldsymbol{D}$ stands for the dilution (=2 in this study), $\boldsymbol{F_{flow}}$ is the purging flow (0.2 LPM=200 cm^3/min), $\boldsymbol{N_A}$ is the Avogadro constant, $\boldsymbol{M_m}$ is the molar mass of emitted compounds, $\boldsymbol{DW}$ is the dry weight of incubated macrophyte, $\boldsymbol{t_h}$ is for 60 min/h.

2.8 Data analysis

All statistical analyses were performed in RStudio (R version 4.3.0). AI models were used to assist with writing parts of the R code, but AI was never allowed to work directly with the data. We used a standardized principal component analysis (PCA) to compare BVOC profiles (compound identities and emission rates) between experimental treatments (6 treatments: 3 Macrophytes × 2 Regions) and to evaluate variability within each treatment. As PCAs cannot handle NA-values, we removed compounds that included NA-values from the ordination analysis. This resulted in the PCA being ran with 117 compounds of the total 170 compounds (166 compounds showing emissions and 4 compounds that were only consumed in the dataset). To explore if BVOC emissions differed significantly between treatments, a permutational multivariate ANOVA (PERMANOVA; Bray-Curtis distance, 999 permutations; vegan package by Oksanen et al., 2022) was performed on the reduced data. As the analysis cannot handle negative values, a constant was added to the data to ensure positive values. Beforehand, a permutation test for homogeneity of multivariate dispersions (betadisper, vegan package; Oksanen et al., 2022) was used to confirm that the group dispersions were similar between treatments. Afterwards, pairwise comparisons were performed to investigate which treatments emitted significantly different BVOC profiles from each other.

To explore if the treatments differed in their total BVOC emission rates and the rates of highly emitted individual compounds, we used one-way ANOVAs followed by Tukey's post-hoc tests. If data failed to adhere to the assumptions of ANOVA (normality and homogeneity of variance), data were analysed with a non-parametric Kruskal Wallis test, followed by Dunn's test (Holm correction).

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3 Results

Across the two marine regions and three macrophyte species, we were able to detect emissions of 166 different compounds. Most unique compounds were identified from Finnish seagrass (108 + 1 unidentified, where "unidentified" means that we could not assign an elemental formula to the observed peak), while the lowest number of compounds was emitted by Finnish Ulva (73 + 1 unidentified, Fig. 2c). Only 32 compounds were measured in every treatment (Macrophyte*Region), but 72 of the total compounds were emitted by each macrophyte species in at least one region. Most identified compounds were hydrocarbons (CH) or oxygenated hydrocarbons (CHO), but each macrophyte species also emitted several S- and N-containing compounds (Fig. 2c). We were also able to quantify the emission rates of two halogenated compounds (Br_2CH^+ and CH_3I^+) from the two macroalgae. In addition to emissions, we identified the consumption of 11 compounds, of which 4 were only consumed and not emitted by any macrophyte (Table S2). All the compounds detected in this study and their average emission rates are listed in Table S2.

The PCA organized the different treatments as mostly separate groups (Fig. 2a; 52.8 % of the variation explained by PCs 1 and 2), with only little overlap between treatments. The PERMANOVA result supported this observation as BVOC emissions differed significantly between most treatments (pseudo-F=13.07, R^2=0.748, p=0.001). *Ulva* emissions in each region clumped closest together in the PCA space and this pair was also one out of two pairs that did not significantly differ from each other (PERMANOVA, p=0.2). Moreover, the BVOC emission profiles of Irish *Ulva* and *Fucus* did not differ significantly (p=0.4). The rest of the treatment pairs differed significantly from each other. This indicates that the three macrophyte species mostly produced significantly different BVOC profiles, but also, that the within-species emissions for *Fucus* and *Zostera* differed significantly between regions. These differences were not only driven by differing emissions rates, but the compounds emitted within-species also showed clear differences between regions, with only 70, 67 and 46 compounds being shared within-species for *Zostera*, *Fucus* and *Ulva*, respectively (Table S2). This means that only 55 % (*Zostera*, total compounds 126), 58% (*Fucus*, total 115), 46 % (*Ulva*, total 98) of the total compounds emitted by the species were found in both regions. Overall, the ordination plot suggests that BVOC emissions were affected by the marine region (Northern Baltic Sea vs Eastern Atlantic) with Finnish and Irish replicates being drawn to opposite sides of the PCA space.

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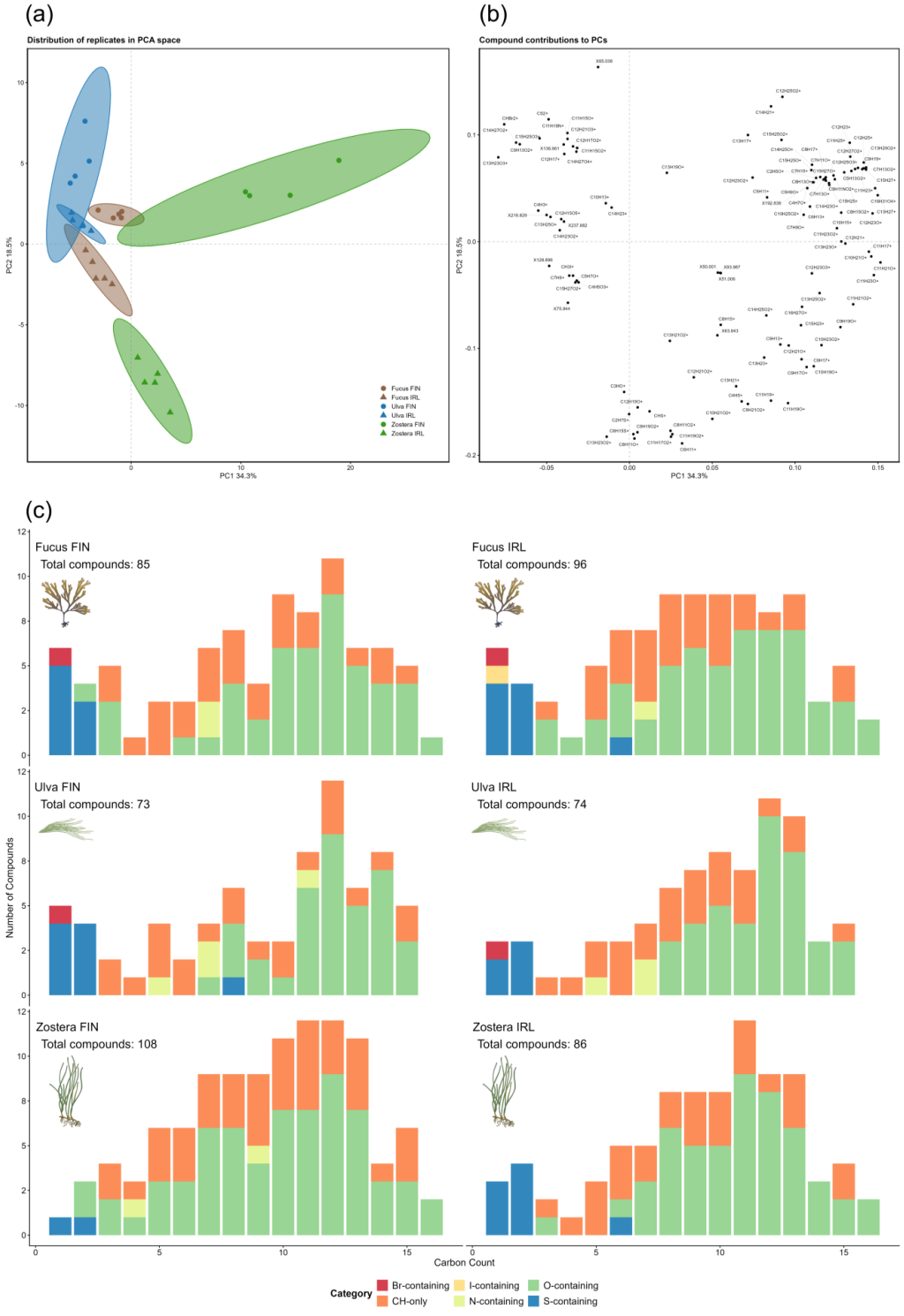

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Figure 2: (a) PCA showing the distribution of replicates and treatments in the PCA space. Ellipses highlight confidence levels of 95% (b) Loadings of the different compounds and how they contribute to Principal components 1 and 2. (c) Overview of the compounds found in each treatment, organised by carbon count and characteristics of the compounds. The chemical formula and potential identity of all compounds can be found in Table S2. In addition to the depicted total compounds, each treatment emitted at least 1 unknown compound (unknown carbon count and category); 1 unknown compound for all Finnish treatments, 2 unknown compounds for *Zostera* and *Fucus* IRL, and 4 unknown compounds for *Ulva* IRL. Macrophyte images from Integration and Application Network (IAN), University of Maryland Center for Environmental Science (https://ian.umces.edu/).

Total BVOC emission rates differed significantly between treatments (ANOVA, $F(5, 22) = 14.18$, $p < 0.001$), with *Zostera* emitting BVOCs at significantly higher rates than the two macroalgae in both regions (Fig. 3a). The *Zostera* replicates emitted on average 52.9 and 54.4 ng/g DW/h in Finland and Ireland respectively, while for the rest of the treatments total emission rates stayed below 20 ng/g DW/h (Fig. 3a). The high total emission rates of seagrass (especially in Finland) were largely due to many compounds being emitted at medium rates (1-2 ng/g DW/h) (Fig. 3d & Fig. 4). DMS ($C_2H_7S^+$) was clearly the most emitted single compound, and its emissions contributed 30% of the total emission rates. DMS emission rates differed significantly between treatments (Kruskal Wallis, $\chi^2(5) = 17.48$, $p = 0.004$), with Irish *Zostera* emitting it at higher rates than Finnish *Zostera* and *Fucus* (Fig. 3b). DMS was the most emitted BVOC by each treatment except for Finnish *Zostera*, which in turn, emitted sesquiterpenes ($C_{15}H_{25}^+$) at higher rates (9.6 ng/g DW/h). Sesquiterpene emission rates differed significantly between treatments (Fig. 3c; Kruskal Wallis, $\chi^2(5) = 25.46$, $p < 0.001$).

Besides DMS and sesquiterpenes, the BVOCs with highest emission rates were hydrocarbons and oxygenated hydrocarbons occupying a large size distribution (C_5-C_{15}, Fig. 4). The most emitted oxygenated hydrocarbons (Fig. 4) were ($C_{10}H_{21}O^+$ (potentially Decanal/Decanone/Menthol), $C_{10}H_{23}O_2^+$ (potentially 1,2-Decanediol), $C_{13}H_{23}O^+$, $C_{12}H_{25}O_3^+$ and $C_{12}H_{23}O_3^+$). In addition to sesquiterpenes, hydrocarbon emissions were dominated by ($C_5H_9^+$ (many possible identities but likely a mix of isoprene and fragments of larger terpenoids and aldehydes), $C_5H_{11}^+$ (several possible identities and fragments), $C_8H_{13}^+$ (potential terpene fragment), and $C_6H_9^+$ (several possible identities and fragments). A nitrogen-containing compound ($C_7H_{12}NO^+$ (potentially 1-Azabicyclo[2.2.2]octan-3-one) and a volatile halocarbon ($CHBr_2^+$ (potentially Dibromomethane)) was also present in the highest quartile of emissions (Fig. 4). Many compounds with the highest emission rates were emitted by all treatments (Fig. 4), but some of these compounds were also found to be species- (e.g., $C_3H_7O^+$ (Acetone)), treatment- (e.g., $C_{11}H_{25}^+$ & $C_{14}H_{21}O_2^+$) or region-specific (e.g., $C_3H_5^+$).

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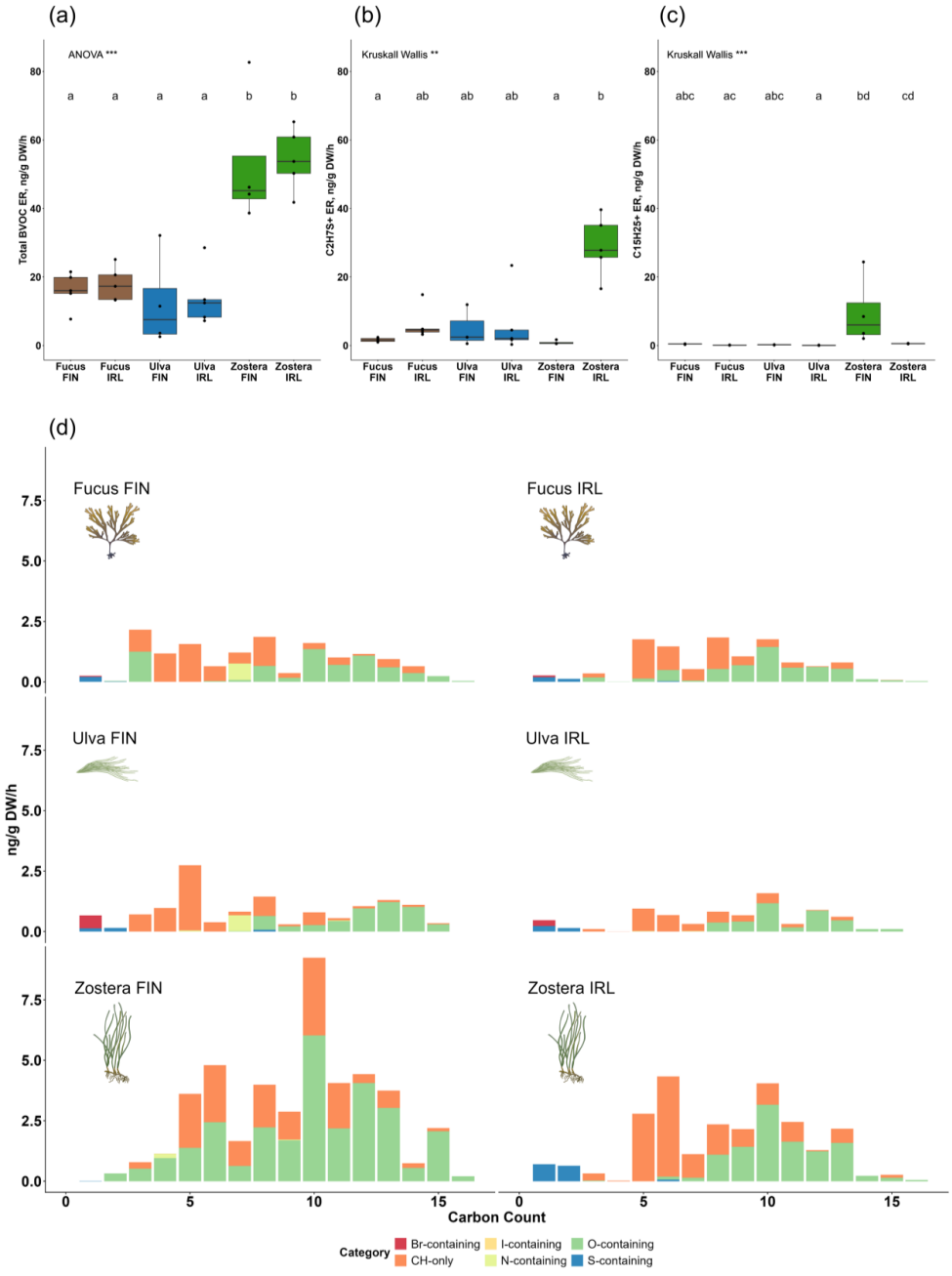

Figure 3: (a) Total BVOC, (b) DMS ($C_2H_7S^+$) and (c) sesquiterpene ($C_{15}H_{25}^+$) emission rates (ng/g DW/h) of all treatments. Boxplots show median (line in box), upper and lower quartiles (box), 1.5 × interquartile range (vertical line) and outliers (dots). Different letters above boxplots denote significant differences ($p < 0.05$). (d) Overview of average BVOC emission rates for each treatment organised by the carbon count and chemical characteristics of the compounds. DMS ($C_2H_7S^+$) and sesquiterpene ($C_{15}H_{25}^+$) emission rates are not included in panel (d). The identity of all compounds and their average emission rates can be found in Table S2. Macrophyte images from Integration and Application Network (IAN), University of Maryland Center for Environmental Science (https://ian.umces.edu/).

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Figure 4: The top quartile of emitted compounds (excluding DMS and sesquiterpenes) with the highest emission rates measured in this study. Each measured datapoint is included in the figure and shown as an individual circle (several replicates per treatment overlapping). Unavailable datapoints (NA), datapoints that showed consumption and measurements where no emissions were detected are marked in the figure with their corresponding symbols (see legend). The rest of the compounds observed in this study (not part of the highest quartile) are presented in the supplementary material (Fig. S4-6). Macrophyte images from Integration and Application Network (IAN), University of Maryland Center for Environmental Science (https://ian.umces.edu/).

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4 Discussion

Our study demonstrates that temperate marine macrophytes emit highly diverse and variable BVOC profiles. The three studied macrophytes (*Fucus vesiculosus*, *Ulva intestinalis* and *Zostera marina*) emitted hundreds of compounds, with dozens of compounds contributing with rates over 1 ng/g DW/h to the total BVOC emissions. BVOC emissions differed significantly between the three species, but notably, also stark differences were found within-species between regions, both in the magnitude of emission rates and the identity of emitted compounds. Our results provide novel insights to the chemical profiles of the studied macrophytes and highlight potential pathways these emissions can impact the environment both above and below the surface. Here, we discuss the key reasons that enabled high quality BVOC quantifications in seawater, possible factors explaining the high intra- and interspecific variability and critical questions that need to be answered so that the atmospheric impact of macrophytes can eventually be estimated.

4.1 Macrophyte BVOC emission rates and compound diversity

4.1.1 DMS and terpenoids, commonly investigated compounds emitted at highest rates

Dimethyl sulfide (DMS) was the highest emitted compound by all studied macrophytes except Finnish *Zostera*. DMS accounted for 30% of total BVOC emissions in our study, which is consistent with the well-established role of DMS as the most abundant BVOC in the global ocean and highlights the potential contribution of macrophytes to coastal DMS budgets. In this study, Irish *Zostera* showed the highest DMS emission rates, which was surprising because Coquin et al. (2024) did not detect any DMS emissions from the species in the Mediterranean Sea. DMS is produced during dimethylsulfoniopropionate (DMSP) breakdown, which among other things plays a role in antioxidation and osmoregulation of marine primary producers (Zhang et al., 2019 and references within). The role of DMSP as an osmolyte offers a potential explanation to why DMS emissions were lower in the brackish Baltic Sea compared to the fully saline Atlantic. Besides DMS, terpenoids represent some of the most important marine BVOCs and are frequently discussed in marine atmospheric chemistry (Yu & Li, 2021; Zhao et al., 2023) and several clear terpenoid signals also appear in our data. Notably, Finnish *Zostera* emitted sesquiterpenes at high rates, which is an interesting result given that sesquiterpenes are rarely measured in high quantities in marine systems. Seagrasses are more closely related to terrestrial plants than macroalgae, which may help explain the comparatively strong sesquiterpene emissions. It is also possible that the seagrasses were suffering from some unknown stressor (e.g., the prevailing marine heatwave), as sesquiterpene emissions are known to increase with stress levels in terrestrial plants (Bourtsoukidis et al., 2025). In contrast to the larger sesquiterpenes, isoprene was not released at particularly high concentrations by any treatment, and this is especially evident when considering that the isoprene signal ($C_5H_9^+$, Fig. 4) likely also contains signal from fragments of larger molecules (Coggon et al., 2024). Additionally, the last group of commonly investigated terpenoids, monoterpenes ($C_{10}H_{17}^+$), were emitted by all treatments except Finnish *Fucus*, but at even lower rates than isoprene (Fig. 4). In summary, neither DMS nor terpenoids completely dominate the macrophyte emission profiles, and total emissions were instead composed of numerous smaller contributors (see section 4.1.2 for more discussion). This suggests that coastal macrophytes may influence local, climate-relevant atmospheric chemistry through a more chemically diverse set of emissions compared to both pelagic phytoplankton and terrestrial plants. Still, the link between macrophyte emissions into the water and the air-sea exchange remains poorly resolved and needs to be assessed in more detail in future studies.

4.1.2 High diversity of macrophyte BVOC emissions

Beyond DMS and terpenoids, we detected a high diversity of BVOCs originating from the macrophytes (total detected compounds: 126 for *Zostera*, 115 for *Fucus*, 98 for *Ulva*), with the number of compounds clearly exceeding previous reports for these specific species (Coquin et al., 2024; Bravo Linares et al., 2010; Hornicar et al., 2014; Broadgate et al., 2004). For instance, we quantified the emissions of over a 100 BVOCs from *Zostera* that have not been reported previously, and similar numbers are true for the two macroalgae. We can attribute this increase in observed compounds to several factors: 1) Improvements in sensitivity of instruments have decreased VOC detection limits, 2) we performed a completely non-targeted analysis, analysing the entire mass spectrum to identify signals that systematically increased during incubations, and 3) we report elemental formulas which can only be tentatively linked to molecules, unlike e.g. GC-MS approaches that can provide unambiguous molecular assignments. The bulk of the emissions (both in terms of unique compounds and emission rates) were comprised by hydrocarbons and oxygenated hydrocarbons that exhibited great diversity, with emissions occupying a wide size range (majority spread evenly in C_6-C_{13} range). The wide and quite even range of emissions is interesting,

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because it is in stark contrast to terrestrial emissions, often dominated by isoprene and monoterpenes (Guenther et al., 2012). The detected emission profiles highlight a diversity of BVOCs that has previously remained largely unexplored in macrophyte- and even marine context. Importantly, several of these unexplored compounds had high molecular weights, with 10 or more C-atoms, meaning that they have the potential to impact atmospheric aerosol formation if transported into the air, since aerosol yields typical scale with molecular size (Lim & Ziemann, 2009). Thus, especially the larger (oxygenated) hydrocarbons detected should be investigated further, in particular with reference to what fraction of them ultimately can enter the atmosphere. Ambient coastal BVOC observations, such as those from the continuous measurements at the newly established coastal SMEAR-station at Tvärminne Zoological Station (Thakur et al., 2025), can help shed insights into this question. Conversely, ambient datasets are complex and information about potential sources (as presented here) can greatly aid their exploration and analysis. The wide range of compounds detected in our work will hopefully also spur efforts to investigate these new compounds using targeted techniques that can identify their molecular structures.

Many of the BVOCs emitted at the highest rates were shared amongst all six treatments (i.e. DMS, sesquiterpenes and 34 % of the top quartile presented in Fig. 4). The three studied species are taxonomically and physiologically very distinct from each other, which makes the shared compounds and their potential functions noteworthy. The results suggest that despite their evolutionary divergence, macrophytes may share a core BVOC profile linked to the organisms' core functions/processes. For instance, BVOCs emitted by phytoplankton function as intermediate and end products of crucial internal processes (e.g., photosynthetic metabolism, antioxidant activities, and carbon fixation; Halsey & Giovannoni, 2023 and references within). However, compared to phytoplankton, little is known about the full spectrum of physiological and ecological roles that BVOCs serve in macrophytes, and the newly identified compounds can provide clues about the functioning and ecology of these common macrophytes. For instance, BVOCs are known to serve as important info-chemicals within and between species, having a profound effect on the ecology of marine ecosystems (Fink, 2007). However, detailed information about which individual compounds affect which processes is very poorly understood. The production and release of certain BVOCs can also aid the organism to deal with stressors (e.g., high temperature, salinity fluctuations). In relation to this, volatilomics has frequently been discussed in marine BVOC literature during the last decade (e.g., Steinke et al., 2018; Lawson et al., 2019), with the core idea that by monitoring stress related BVOCs the status/health of whole ecosystems can potentially be determined. Thus, better information on BVOCs emitted by macrophytes can potentially help explain ecological processes within and across trophic levels.

4.2 Intraspecific variation of macrophyte BVOC emissions

Although BVOC emissions of the three macrophytes were more similar within-species than between species, substantial intraspecific variation was also observed. Within the treatments (Macrophyte * Region), emission profiles were consistent across replicates (Fig. 2a), but significant differences were evident among marine regions for *Fucus* and *Zostera*. Emission rates of specific compounds showed intraspecific differences (see e.g., Fig. 3 b&c; DMS and sesquiterpenes for *Zostera*), but many compounds were also emitted in only one of the studied regions (see Fig. 4 & Fig. S4-6). Some differences in emission rates were expected (e.g., driven by differing seasons & temperatures), but the large differences in the identities of emitted compounds were more surprising (only ~50 % of compounds shared within species for all three species between regions). Here, we cannot pinpoint the exact factors driving these differences within-species, but below we discuss the most likely contributing factors.

Macrophyte BVOC emissions respond to several abiotic factors such as temperature, light, seasonality and organic pollution (Saunier et al., 2025a and references within). Light and temperature are important triggers of BVOC emissions, and changes in these drivers can rapidly affect emissions (Broadgate et al., 2004; Zhao et al., 2023; Wang et al., 2025). In this study, light and temperature were kept comparable throughout the incubations and likely had a negligible effect on the differences exhibited here. However, season and overall natural environment differed between regions, and differences in growth environment prior to collection likely affected the measured BVOC emissions. Additionally, season-specific developmental processes likely also affect macrophyte BVOC emissions. For instance, in terrestrial plants, factors like flowering, leaf senescence, and dormancy affect BVOC emissions (Kesselmeier & Staudt,1999). However, how these processes affect BVOC emissions from seagrasses and macroalgae remains unknown; in ecological context it would for instance be interesting to investigate whether seagrass flowers release certain compounds that attract pollinators similarly to terrestrial plants (van Tussenbroek et al., 2016; Dötterl & Gershenzon, 2023). In addition, the growth environment likely also drives BVOC emissions by affecting macrophyte metabolism, physiology or stress (Bäck et al., 1992). For instance, the stark differences

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in salinity and nutrient availability between regions likely affected the emissions (as has been observed with phytoplankton; Zhao et al., 2023 and references within).

The macrophyte populations of Finland and Ireland have been separated for millennia, leaving populations ample time to adapt to their local environmental conditions (e.g., salinity, temperatures, tides, etc.). Therefore, within-species genetic diversity will differ significantly between regions, which in turn could affect the organisms BVOC emissions, e.g., through metabolic responses to local conditions. For example, permanent exposure to low salinity/high nutrients in the Baltic Sea has likely modified biochemical profiles, with direct influence on both emission profiles and rates. However, the effect of genetic diversity on BVOC emissions is completely unexplored for macrophytes, leaving the influence of population-specific genetics an important question to answer. The quantified BVOC emissions were likely also affected or directly released by the microbial communities associated with the macrophytes, as microbes are known to produce and consume many BVOCs (Lemfack et al., 2018). For instance, seagrass meadows host diverse microbial communities active in the many phases of DMS production (e.g., DMSP-demethylation, DMSP-cleaving and DMS-oxidization; Jonkers et al., 2000), and regional differences in these communities could potentially explain why BVOC emissions differed so greatly within the studied species. Additionally, the fact that we found region-specific compounds emitted by all three macrophytes, suggests that these were formed by site-specific circumstance such as local microbial communities.

The Baltic Sea is an outlier when compared to most marine regions globally, that despite very low salinities and high nutrient loads, harbours marine macrophytes. It is possible that if this study was performed at different locations along the eastern Atlantic coast, macrophyte BVOC emissions (especially compound identities) would have been more similar between sites than shown here, due to more similar environmental conditions. Regardless, when comparing our results with *Zostera marina* BVOC-data collected from the Mediterranean Sea (Coquin et al., 2024), it becomes apparent that large differences even occur between fully saline regions. Of the 51 BVOCs detected by Coquin et al., (2024) only 12 fit compounds emitted by the seagrass in this study (out of 126 in total). Differing methodologies between studies (GC-MS and destructive sampling in Coquin et al., 2024) partly explain this large difference, but overall, these findings demonstrate that relying on data from a single site or population is insufficient to accurately estimate macrophyte BVOC emission rates or characterize their emission profiles. Hence, future emission estimates need to be compiled from several locations with differing environmental conditions. Our understanding of the dynamics governing macrophyte BVOC emissions lags knowledge of emissions from terrestrial plants by decades (e.g., Peñuelas & Llusià, 2001, Kesselmeier & Staudt, 1999) and investigating these dynamics will be crucial so that large scale emission estimations can eventually be established.

4.3 Methodological and experimental considerations

4.3.1 Methodological insights and issues

Detecting BVOC emissions accurately in seawater is challenging. Several methodological decisions contributed to the unusually high number of BVOCs detected in this study, but two factors were deemed especially crucial and are worth highlighting: 1. High quality background measurements & 2. Online measurements. Combined, these two allowed us to detect and quantify reliably even minuscule emission peaks (0.01 ng/g DW/h), that might have remained classified as undefined noise with many other approaches. With high quality background measurements, we are referring to the (mostly) stable emissions from seawater that were achieved by filtration and pre-bubbling of the seawater, but also to the fact that every background measurement was highly comparable with its paired macrophyte measurement. Background measurements (seawater only) showed highly variable emissions between replicates (Fig. S3) and if all macrophyte emissions would have been compared to the same background measurement, data quality would have suffered. Therefore, the simple decision of adding a macrophyte into a previously quantified water-background, clearly improved the precision and sensitivity of our measurements, and we recommend that future studies adopt this practice when feasible. With online measurements, data is collected continuously over the whole measurement period in contrast to offline measurements that would have resulted in one total emission datapoint for the whole incubation period. Continuous data allowed us to observe how emissions evolved over time and to pinpoint even small increases in emissions that might have fallen within the error margins of an offline method. Additionally, only due to online measurements were we able to identify that certain background measurements failed and that some compounds kept increasing during the whole incubation period (Fig. 1c), which improved the correctness and quality of data. The online methodology used here also has some drawbacks. Especially the fact that the Vocus PTR-TOF does not allow for the exact identification of compounds is a clear disadvantage. In future studies, we suggest combined

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methodological approaches (e.g., as nicely done by Saunier et al., 2025b) that allow both accurate quantification and identification of emitted BVOCs.

It is important to note that the BVOC profiles measured for the different macrophytes are not complete. With any single analytical method, it impossible to capture the complete range of BVOCs. For instance, with a PTR-TOF, volatile halocarbons cannot be measured because their proton affinities are lower than that of water, which makes the ionization reaction thermodynamically unfavourable. Conversely, while GC-MS systems easily resolve these non-polar halocarbons, they often have trouble measuring highly polar or thermally labile oxygenated VOCs due to adsorption losses on the chromatographic column. Additionally, in our dataset some detected compounds are likely fragments of larger molecules, whereas others that we report as single compounds may in fact represent multiple distinct species (e.g., structural isomers). Moreover, it is important to note that macrophyte BVOC emissions exhibit pronounced diel- and seasonal variability (e.g., Saunier et al., 2025b; Broadgate et al., 2004, Coquin et al., 2026). The above-mentioned factors are not captured in our dataset and should be kept in mind when comparing results across studies. Currently, publicly available macrophyte emission rate data is very scarce, and the scant data that is available is not easily comparable. Developing standardized approaches for reporting, harmonizing, and integrating data generated by different analytical methods should become a priority for marine/macrophyte BVOC emission rate datasets, so that once more data is collected, they can more easily be combined to scale up emission/budget estimations.

4.3.2 *Ex situ* vs *in situ*

In this study, we removed the macrophytes from their natural habitat, which likely altered the BVOC-emissions of the organisms to some degree, e.g., due to increased stress and wounding. While not providing the absolute truth of emissions, controlled *ex situ* studies are still very useful for investigating species specific emissions in high detail and can aid in acquiring accurate *in situ* data in the future. High quality *in situ* measurements will be needed to accurately quantify BVOC emissions of undisturbed macrophyte ecosystems, including all relevant biotic interactions and components (e.g., macrophytes, fauna, sediment and microbes). However, in the Baltic Sea and other marine areas with inherently high BVOC concentrations in the water column, acquiring high quality background measurements for *in situ* experiments will be challenging, especially if offline measurements are deployed. Based on our results, if background concentrations are very high, macrophyte emissions might not be high enough to allow detection from the water-background signal. If not accounted for, we predict that this can easily lead to incorrect emission rate calculations and lower the number of detected compounds. Thus, *in situ* data sets will likely not achieve the accuracy and clarity of our *ex situ* measurements, and therefore the datasets presented here can help predict and untangle more complex *in situ* data.

4.3.3 The unknown fate of macrophyte BVOCs

The majority of BVOCs emitted by macrophytes into seawater will likely not reach the surface or enter the atmosphere. In the open ocean only a small fraction of total concentrations in the water column enters the atmosphere e.g., ~10 % of total DMS (Yang et al., 2013; Hopkins et al., 2023). Several processes in the water column (including microbial degradation, photooxidation, below surface chemical reactions) affect the fate and end-destination of BVOCs (Hopkins et al., 2023; Wang et al., 2025). These processes will also be important for determining the fate of BVOCs emitted by macrophytes, but when comparing macrophyte-dominated shallow areas to the open ocean, there are several differences that might affect the ratios reaching the surface. Firstly, macrophytes generally occupy shallow coastal environments and most often grow above 30 m depth, whereas pelagic phytoplankton can occur throughout the upper water column to much greater depths. This shorter distance to the surface might increase the odds of compounds reaching the atmosphere. In the intertidal zone macrophytes are exposed daily to the atmosphere during low tide, and this likely further enhances atmospheric emissions. For instance, corals can emit very large quantities of DMS into the atmosphere when above the low tide level (Hopkins et al., 2016). Additionally, wave build up, crashing waves and overall increased coastal hydrodynamics can potentially also affect atmospheric emissions, due to increased water movement, sea spray and water surface breakage. However, how these processes affect atmospheric BVOC emissions at the coasts are poorly quantified, leaving scarce knowledge of where macrophyte BVOCs end up. Therefore, establishing the fractions of BVOC reaching the atmosphere and the overall fate of compounds are crucial objectives in the future, so that measurements like ours and eventual *in situ* measurements can more precisely be put into atmospheric context.

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4.4 Outlook

Terrestrial deforestation has been shown to reduce BVOC emissions, with direct effects on atmospheric processes and local climate (Tripathi et al., 2025), and the large losses of forested areas during the last centuries have led to significant reductions in atmospheric BVOCs and SOAs (Vella et al., 2025). During the last century global macrophyte cover has also reduced greatly (e.g., 40-60 % decline of kelp forests and ~19 % of seagrass; Wernberg et al., 2019, Dunic et al., 2021) and the negative trend is expected to continue (Manca et al., 2024). Such losses have already impacted rates of marine BVOC emissions to some degree and will continuously do so in the future, with unknown climate impacts as a result. However, this particular ecosystem service has largely remained unexplored for macrophytes. Similarly to the Blue Carbon boom of the last decade (Macreadie et al., 2021), if macrophyte BVOC emissions and their climate impact can be estimated, the information would bring much needed attention and value to these threatened ecosystems, which in turn could be used to aid their conservation.

In this study the seagrass *Zostera* showed the highest standardized total emission rates in both marine regions and very similar rates between regions. Globally, algae (both micro- and macro-) will still be larger BVOC-sources than seagrasses due to their substantially larger spatial coverage and biomass. Yet, our results (together with Saunier et al., 2025b) show that seagrasses emit many atmospherically relevant BVOCs at notable rates. For the seagrass genus *Zostera*, a global mean biomass dry weight per area has recently been estimated (226 g DW/m^2; Foster et al., 2025), and by using this value, the total BVOC emission rates calculated in this study (Fig. 3a) translate to 12.0 and 12.3 µg BVOCs/m^2/h in Finland and Ireland, respectively. At present, the low amount of data and high unexplained variability in emissions make it unreliable to upscale these estimations even further (e.g., to global emissions with seagrass coverage data). Large-scale emission estimates are not only lacking for seagrasses, but all macrophytes and, in the future, more research efforts should be made to acquire quantitative and qualitative macrophyte emission data so that macrophytes emissions can eventually be added to marine BVOC budgets.

5 Conclusions

Our measurements reveal temperate marine macrophytes as highly diverse BVOC sources, exhibiting substantial variability of emissions across multiple biological levels. At the species-level, we found that the individual macrophytes emit hundreds of different compounds, showcasing a chemical diversity that has rarely been reported in the marine realm. Between species, we found clear differences in the BVOC profiles (both in emitted compounds and emission rates) of the three macrophytes, but interestingly, all species still share a core suite of emitted compounds. Within species, across the two marine regions, *Fucus* and *Zostera* emitted surprisingly different BVOC profiles and unravelling the drivers behind these pronounced differences represents an important task for the future. Overall, our results show that macrophytes emit many atmospherically relevant BVOCs, underscoring the need to better incorporate these emissions into global budgets. Linked to this, an important conclusion of this study is that acquiring reliable estimates of species-specific BVOC emission profiles and rates, requires observations from multiple populations growing in contrasting environmental conditions. Consequently, collection of more high quality data, alongside a better understanding of what drives the high measured variability, will be needed so that global macrophyte BVOC emissions can eventually be calculated. This study offers some of the most complete data on macrophyte BVOC emission rates to date, pinpoints crucial methodological advancements and open questions, and can serve as a foundational puzzle piece for advancing our understanding of global macrophyte BVOC emissions.

Data availability

All BVOC emission rates measured during the study will be available after acceptance at: https://bolin.su.se/data/coastclim (10.17043/coastclim-1).

Supplement

The supplement related to this article is available online:

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Author contributions

Max Gräfnings: Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing (original draft preparation), Writing (review and editing); Yuanyuan Luo: Investigation, Methodology, Writing (review and editing); Jian Zhao: Investigation, Methodology, Writing (review and editing); Claudia L. Cara-Ortega: Resources, Writing (review and editing); Kirsten N. Fossum: Resources, Writing (review and editing); Frans Graeffe: Methodology, Writing (review and editing); Lu Lei: Resources, Writing (review and editing); Dagmar B. Stengel: Resources, Writing (review and editing); Roseline C. Thakur: Methodology, Writing (review and editing); Jurgita Ovadnevaite: Funding acquisition, Writing (review and editing); Mikael Ehn: Conceptualization, Funding acquisition, Methodology, Supervision, Writing (review and editing); Camilla Gustafsson: Conceptualization, Funding acquisition, Supervision, Writing (review and editing).

Competing interests

The contact author has declared that none of the authors has nay competing interests.

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