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Health risks associated with seaweed strandings: sulfur gases and antimicrobial resistant (AMR) bacteria from decaying *Ulva intestinalis* and *Sargassum muticum*

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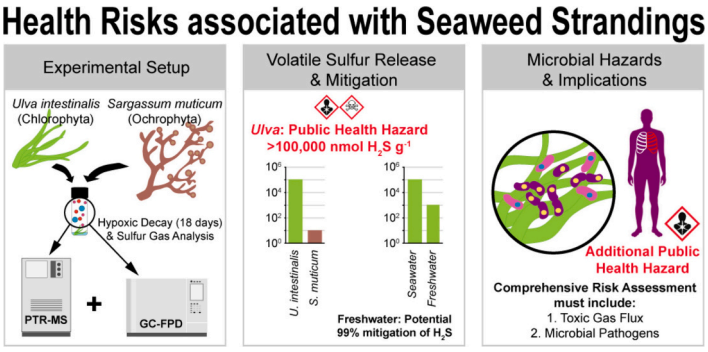
HIGHLIGHTS

- Decomposing seaweed emits toxic sulfur volatiles causing respiratory illness and death.
- Sulfur emissions were significantly higher for *Ulva* than for *Sargassum* in seawater.
- Freshwater addition can substantially reduce the release of harmful volatiles.
- Decaying *U. intestinalis* promoted anaerobic pathogens, posing additional health risks.

GRAPHICAL ABSTRACT



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ABSTRACT

Seaweed strandings can cover several km^2 with many 1000s of tonnes of biomass and are of international concern. They have a substantial environmental impact locally, including through the release of malodorous corrosive and toxic volatiles causing respiratory illness and death. The toxic gases hydrogen sulfide and ammonia have been suggested as the main hazardous gases but limited information on the diversity and quantity of volatiles released from decomposing seaweeds is available. Here we use proton-transfer reaction mass spectrometry (PTR-MS) and gas chromatography with flame-photometric detection (GC-FPD) to quantify sulfur gases released from decaying *Ulva intestinalis* (Chlorophyta) and *Sargassum muticum* (Ochrophyta) in seawater and freshwater under hypoxic conditions for up to 18 d. The amounts of sulfur gases in seawater incubations were 131,653 and 64 nmol g^{-1} seaweed freshweight in *U. intestinalis* and *S. muticum*, respectively. Production rates in freshwater were often significantly lower (range 68–99% decrease) than in seawater, suggesting that freshwater addition to seaweed strandings may mitigate against the release of harmful volatiles. Analysis of the bacterial composition of decaying *U. intestinalis* revealed that seaweed strandings can promote the growth of facultative

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anaerobic pathogens including antimicrobial resistant (AMR) bacteria and these may pose additional health hazards to the public. It is timely to monitor the microbial composition and flux of toxic gases when assessing and mitigating the substantial health risks associated with seaweed strandings.

1. Introduction

Seaweed nuisance blooms are causing international environmental concern since they are increasingly frequent and severe (Li et al., 2023; Smetacek and Zingone, 2013). Species of the green seaweed genus *Ulva* and the brown seaweed genus *Sargassum* are recurrently documented in the scientific literature and the wider media for causing 'green tide' and 'golden tide' nuisance blooms, respectively, that are increasing in their spatial coverage by >10% per year since 2003 (Qi et al., 2025). Primarily, their nuisance stems from 'strandings' of large amounts of biomass over short periods (days to weeks) that can harm coastal environments, deter tourism, affect well-being and use of natural spaces (recreation and fisheries) (Resiere et al., 2023).

Although seaweeds are typically not harmful to humans, microbial activity results in the decay of seaweed biomass into an unpleasant mass that releases bad-smelling, corrosive and toxic gases which can affect people and infrastructure near the sea. It is likely that the increased microbial degradation leads to oxygen drawdown (hypoxia or anoxia) in the centre of the strandings and this stimulates the release of gases including methane (CH_4), ammonia (NH_3), hydrogen sulfide (H_2S) and volatilised arsenic (Abdool-Ghany et al., 2026; Resiere et al., 2023). Some of these gases are corrosive, can damage electronic equipment including phone and power-supply networks, or be suffocating or toxic to various organisms including humans (Resiere et al., 2023). Tragically, two persons and several animals died in separate incidents after inhaling toxic gases from decaying seaweed along beaches of the French coast. Often, individuals suffer eye irritation and respiratory illness and are at higher risk of pregnancy problems during periods of seaweed strandings (Boggild and Wilson, 2019; de Lanlay et al., 2022). In the case of *Sargassum*, adverse health effects and toxicity relating to H_2S exposure is documented in 1000s of patients. Mild health effects (e.g. headache, nausea, eye irritation) are expected at 1–5 ppm, the exposure limit evacuation level in some countries is at 20 ppm, lung irritation starts at 100 ppm and sudden unconsciousness and death within 4–8 h occurs at 500 ppm (Guidotti, 2010). H_2S concentrations often exceed 5 ppm below and mostly <2 ppm above piles of seaweed with much lower concentrations (<0.1 ppm) recorded 10 m from the shoreline but *Sargassum* cleanup workers experience higher concentrations exceeding national exposure levels (Rodríguez-Martínez et al., 2024; Rodríguez-Martínez et al., 2026). Court-case information suggests that one of the fatalities during an *Ulva* stranding in France was exposed to H_2S levels exceeding 1000 ppm. Hence, medical practitioners are now warning of the increasing cases of gas poisoning from nuisance blooms and advocate limiting the long-term exposure for vulnerable populations and the closure of affected areas followed by costly removal of seaweed within two days of mass strandings (Boggild and Wilson, 2019). This can be logistically and financially challenging: For example, one of the largest seaweed strandings of *Ulva prolifera* occurred during the Chinese Olympic games in Qingdao in 2008 that covered 15 km^2 with 700,000 t of biomass that had to be removed from coastal environments involving >10,000 workers at a cost exceeding US$100 million (Hu et al., 2010).

Knowledge gaps exist around the succession and diversity of microbial communities associated with seaweed strandings (Hyndes et al., 2022). The anaerobic environment created during seaweed decomposition could support proliferation of pathogens typically present in coastal waters near urban sites. For example, the 'flesh-eating' pathogen *Vibrio vulnificus* was previously found to be enriched in biofilms on decomposing seaweed (Saha et al., 2020) and various enteric bacteria have been found on surfaces of ready-to-eat seaweed products (Lovdal et al., 2021). The proliferation of antimicrobial resistance (AMR) is also highly likely in biofilms on the surfaces of seaweeds in polluted environments (Liu et al., 2024), making their investigation in this context critically important.

The first objective of our study was to assess the diversity of sulfur gases in two species of seaweed (*Ulva intestinalis* and *Sargassum muticum*) that are abundant in the hypernutrified River Colne, United Kingdom. These species were selected due to their documented potential to cause seaweed blooms and nuisance strandings in the United Kingdom and neighbouring countries (Davison, 2009; Lamb et al., 2025). Chlorophytes including *Ulva* spp. accumulate relatively high intracellular concentrations of the compatible solute dimethylsulfoniopropionate (DMSP), a direct precursor of volatile dimethyl sulfide (DMS), that range from 7 to 128 μmol g^{-1} freshweight, whereas Ochrophytes such as *Sargassum polycystum* contain less than 1 μmol DMSP g^{-1} freshweight (Van Alstyne and Puglisi, 2007). Taken together, this suggests that *U. intestinalis* and *S. muticum* investigated in this study may show different potentials for the release of DMS and other sulfur volatiles.

An additional objective was to assess whether freshwater – for example from rainfall or when sprayed onto stranded biomass from a reservoir, lake or groundwater – would significantly affect the production of sulfur gases. Whereas seawater contains 28 mM sulfate, lakes, rivers, and groundwater have up to 100 times less sulfate (Zak et al., 2021). This difference affects the microbial production of H_2S by sulfate-reducing microbes (bacteria and archaea), hence, freshwater addition may mitigate against microbial H_2S in seaweed strandings. Since microbial activity is likely the main driver of the production of sulfur gases in seaweed strandings (Domínguez-Maldonado et al., 2024), we also explored the presence of AMR bacteria and quantified microbial community composition in one experiment with *U. intestinalis*. Our findings provide first insight into the diversity of sulfur gases and bacteria in decaying seaweed and suggest that freshwater addition may mitigate the release of harmful volatiles including the acutely toxic H_2S.

2. Materials and methods

A series of three independent experiments was conducted with decaying biomass of *Ulva intestinalis* and *Sargassum muticum* to simultaneously investigate the effects of seawater and freshwater conditions: Experiment 1 (7 July 2023) was an exploratory study using proton-transfer reaction mass spectrometry (PTR-MS) to qualitatively examine the diversity of sulfur-containing and other volatiles. Experiment 2 (*U. intestinalis*: 2–20 October 2023; *S. muticum*: 19 February–8 March 2024) used gas chromatography with flame-photometric detection (GC-FPD) to quantify a selection of predominant sulfur gases. Experiment 3 quantified AMR bacteria and the community composition of bacteria in seawater, freshwater and *U. intestinalis* after a 5-d incubation (3–8 October 2024).

2.1. Sample collection

Using haphazard sampling, seaweeds were collected from the foreshore (*U. intestinalis*; ~500 g) or submerged structures of a floating pontoon (*S. muticum*; ~750 g) in Brightlingsea, Essex (geographical coordinates: 51° 48′ 17.8236″ N, 1° 1′ 24.9132″ E). Seawater was collected from the incoming tide. Instead of using distilled water in our freshwater additions, we investigated the effect of natural lake water including its diverse associated biota on the release of gases in seaweed incubations since this is more relevant for future applications that aim to mitigate release of harmful volatiles in seaweed-stranding scenarios. Hence, freshwater was collected from Upper Campus Lake, University of

Essex (51° 52′ 42.6642″ N, 0° 56′ 56.3454″ E; salinity of 0.3 (Hanna salinity tester HI-98319)). Samples were transported in a cooler box to the laboratory at the University of Essex within 1 h after collection and kept in a cold room (4 °C) for <24 h until sample preparation.

2.2. Sample preparation (Experiments 1 and 2)

A staggered approach was used to prepare triplicate samples from a single sampling point for the analysis of volatiles. PTR-MS samples were prepared 1, 2, 4, and 8 days before analysis whereas GC-FPD samples were set-up approximately every 30 min on the day of first measurements to account for the time taken for gas-chromatographic quantification that followed on days 1, 2, 4, 7, 10, 14 and 18. Seaweeds were centrifuged with 10 'push-spins' using a salad spinner to remove excessive liquid (step 1). Obvious epibionts (e.g. amphipods) were removed before an aliquot of seaweed was washed for approximately 5 s in freshly collected seawater (seawater treatment) or lake water (freshwater treatment). This was followed by removal of excess water via a second salad-spinner centrifugation (step 2). The spinner was washed with tap water between steps to suppress cross-contamination of microbial components between samples. Using haphazard sampling, seaweed biomass was weighed in triplicates to approximately 100 mg (qualitative Experiment 1) or 250 mg (quantitative Experiment 2; *U. intestinalis* 250 ± 13.6 mg; *S. muticum* 255 ± 35.8 mg using a mixture of biomass from stipe, blades and air vesicles) and transferred into a crimp-seal vial of 20 mL volume that was closed gas-tightly with a Teflon-coated butyl rubber septum (Pharma-Fix, Merck Life Science UK Ltd). Addition of 200 μL seawater or lake water ensured sufficient humidity and the desired salinity environments. Triplicate vials without seaweed addition were used as negative controls.

2.3. Incubations

It is likely that large decaying seaweed strandings have a dark, hypoxic core at a temperature above ambient. Using hypodermic needles connected to incoming and outgoing flow lines, a low-oxygen environment was created by flushing each vial with nitrogen gas shortly after sample preparation (PTR-MS: 200 mL min^{-1} for 2 min) or immediately after GC measurements of headspace gases (GC-FPD: 80 mL min^{-1} for 2 min). Samples were incubated in the dark (Plant-Growth Chamber MLR-351, Sanyo Gallenkamp, Loughborough, UK) at a temperature of ~26 °C (25.9 ± 0.04 °C) that was monitored using a temperature data logger (HOBO MX2202, Onset, Bourne, MA, USA) and represents a typical high air temperature in the UK summer. These conditions initiated the anaerobic partial decay of seaweeds from the start of our incubations.

2.4. Quantification of intracellular dimethylsulfoniopropionate (DMSP)

Following the method described elsewhere (Kerrison et al., 2012), algal thalli free from obvious epibionts were haphazardously selected on the day of sample collection (*U. intestinalis*: 106 ± 14.5 mg, $n = 4$; *S. muticum*: 102 ± 5.8 mg, $n = 5$), transferred into a sample vial (volume 4.92 mL) that contained 3 mL 0.5 M NaOH before immediate gas-tight closure with a Teflon-coated silicone septum. After alkaline hydrolysis of DMSP to DMS at 26 °C for 5 d, headspace was injected directly into the gas chromatograph for quantification. Peak areas were calibrated with a series of known DMSP concentrations (Kerrison et al., 2012).

2.5. Proton-transfer reaction mass spectrometry

Sample vials were transported and stored in a cool box until analysis at the PTR-MS laboratory (<10 h). The temperature range during transport and storage was 24.9 to 25.6 °C with a mean temperature of 25.3 ± 0.21 °C (temperature data logger). The instrument used for the PTR-MS analyses was a prototype from which a commercial model (PTR3c, Kore Technology Ltd., Ely, UK) was developed. It uses a time-of-flight (ToF) mass spectrometer with a mass resolution of 5500 M/δM (Full Width at Half Maximum). The reagent ion used was hydronium (H_3O^+). Depending on analyte concentration, 100 or 25 μL headspace was injected with a gas-tight syringe (SGE Trajan, Milton Keynes, UK) through a septum into a 100 sccm flow of nitrogen gas going to the reactor. The reactor was operated at a room temperature of 25 °C and held at a constant pressure of 1.2 mbar throughout. Data from control treatments (excluding seaweed) with either seawater or freshwater were acquired before collecting data for treatments including seaweed.

2.6. Gas chromatography

Repeated gas measurements in the headspace of the vial were conducted for 18 d following the methods described elsewhere (Franchini and Steinke, 2017). Depending on the concentration of measured gases, 5, 10 or 200 μL (*U. intestinalis*) or 200 μL (*S. muticum*) of vial headspace was directly injected into a gas chromatograph (Shimadzu GC 2010, Milton Keynes, UK) using gas-tight syringes (SGE Trajan, Milton Keynes, UK). The GC was equipped with a flame-photometric detector and a 60 m × 0.53 mm × 5 μm analytical column with a nonpolar phase of cross-bond dimethyl polysiloxane (RTX-1; Thames Restek UK Ltd., Saunderton, UK). Injector and detector temperatures were set to 200 and 250 °C, respectively. This instrument configuration can quantify sulfur gases including, amongst others, hydrogen sulfide (H_2S), carbonyl sulfide (COS), methane thiol (MeSH), dimethyl sulfide (DMS) and dimethyl disulfide (DMDS; Supplementary Table S1, Fig. S1). Depending on the concentration of sulfur gases, two injections using different oven-temperature programmes were used. The initial injection (Method 1: 200 μL splitless injection) enabled the separation of H_2S and COS, and quantification of low-concentrated volatiles. However, H_2S and/or DMS were sometimes highly concentrated, and this resulted in saturation of the detector when using Method 1. Hence, we used a second injection (Method 2: 5 or 10 μL injections with a split of 1:10 which resulted in co-elution of H_2S and COS) to quantify H_2S and DMS in such samples. The concentration of COS quantified with Method 1 was subtracted from the concentration calculated from the area of the co-eluting COS and H_2S peak when using Method 2. The oven-temperature programme for Method 1 was 40 °C for 5 min, then increased to 120 °C at 15 °C min^{-1} and held for further 20 min (total programme time was ~36 min). The oven-temperature for Method 2 and for the quantification of DMSP was isothermal at 120 °C.

2.7. Instrument calibrations, data and statistical analyses

The high-resolution PTR-MS technique was used for qualitative purposes and has a sensitivity of ~1000 counts s^{-1} ppb^{-1} of analyte. It is particularly versatile for real-time analysis, and so for each sample, the data acquisition was begun and the evolution of volatiles of interest was plotted in real time during the gas injections. Afterwards, a mass spectrum was extracted from each data set, usually between 10 and 20 s in duration, according to the appearance of the volatile profiles. Data plots comprise total integrated ion signals of the analytes of interest for any given sample injection. The mean abundance of sulfur volatiles in the controls without seaweed addition ($n = 3$) were subtracted from treatments with seaweed.

Gas chromatographic data were collected and peak areas integrated using instrument-specific software (GCsolution version 2.10.00 SU1; Shimadzu, Milton Keynes, UK). Peak areas were square-rooted to linearise the detector response. Limits of detection and quantification (LOD and LOQ) were approximately 0.5 and 1.5 pmol sulfur, respectively (Franchini and Steinke, 2017) with an uncertainty of <5% (mean = 1.3%, range 0.07 to 4.22%; $n = 22$). The mean of the square-rooted peak areas of sulfur volatiles in the controls without seaweed addition ($n = 3$) were subtracted from treatments with seaweed before sulfur concentrations were calculated and normalised to seaweed freshweight (SFW)

biomass.

The GC-FPD was calibrated with H_2S, COS, DMS and DMDS standard solutions (200 μL) in 20 mL vials. H_2S standard solution was freshly prepared by dissolving sodium sulfite (752 μM Na_2S in milliQ water; Arcos Organics/Thermo Scientific Chemicals, Loughborough, UK) and adding 0, 1, 2, 5, 8 and 11 μL of this to 200 μL of N_2-purged HCl (32%) followed by immediate gas-tight closure. Reaction of Na_2S with HCl inside the vial resulted in the release of equimolar quantities of H_2S. COS standard solution was freshly prepared by dissolving sodium-thiocyanate (740 μM NaSCN in milliQ water; Arcos Organics/Thermo Scientific Chemicals, Loughborough, UK) and adding 0, 2, 5, 8, and 11 μL of this to 200 μL of N_2-purged H_2SO_4 (50%) followed by immediate gas-tight closure and heating to 40 °C for 30 min. Reaction of NaSCN with H_2SO_4 inside the vial resulted in the release of equimolar quantities of COS. DMSP standard solution (75 mM; synthesised from DMS and acrylate as described in Chambers et al. (1987)) was prepared in acidified milliQ water and serially diluted to 75 and 750 μM before using volumes of 0, 5 and 10 μL to add 0, 1.8, 3.6, 5.2, 18.3, 35.7 and 52.5 μM DMSP to 200 μL of NaOH (0.5 M) followed by immediate gas-tight closure. Alkaline hydrolysis of DMSP with NaOH inside the vial resulted in the release of equimolar quantities of DMS (Franchini and Steinke, 2017). DMDS standard solution (750 μM) was prepared by adding 6.6 μL DMDS (Sigma-Aldrich/Merck, Gillingham, UK) to 100 mL milliQ water using a gas-tight syringe. Volumes of 0, 2, 5, 8 and 11 μL of this were added to 200 μL artificial seawater followed by immediate gas-tight closure. Vials with standard solutions were vortexed for 20 s, incubated for >1 h at 26 °C and vortexed again (20 s) before injection of 200 μL headspace gas for gas chromatographic analysis.

Identification of gas-chromatographic peaks was by retention time (Supplementary Fig. S1) and instrument calibrations provided linear regression data presented in Supplementary Table S2. The retention time of MeSH was verified by injecting headspace of DMDS (Sigma-Aldrich/Merck, Gillingham, UK) that contained traces of COS, MeSH and DMS as contaminants. Pooled data from all calibrations were used to quantify methanethiol and an unidentified sulfur compound that eluted at approximately 22.9 min (referred to as RT22.9).

Gas chromatographic data were processed and visualised in Microsoft Excel version 2407. Statistical analyses using Linear Mixed-Effects Models (family = Poisson) with volatile concentration as the dependent variable and treatment and time as the independent variables were conducted in R-Studio using the R-package '*lme4*' (R version 4.3.3; RStudio 2024.04.2).

2.8. Composition of bacterial community (Experiment 3)

Samples were prepared as described for Experiments 1 and 2, and incubated in darkness at 26 °C for 5 d. To account for the larger biomass used in this experiment (*U. intestinalis*: 1033 ± 56.5 mg; *S. muticum*: 604 ± 63.9 mg), the volume of seawater and lake water added to the samples was adjusted to 800 μL. To characterise the *Ulva intestinalis* holobiont, 250 mg of seaweed was added to a 1.5 mL microcentrifuge tube with 500 μL of ultrapure sterile water. To remove the bacteria from the surface of the seaweed, the samples were sonicated for 30 min and then vortexed at maximum speed using a Vortex-Genie 2 adapter (Qiagen, UK) for 20 min. Then 250 μL of the liquid was transferred to a PowerBead Pro Tube and bacterial DNA was isolated and purified using a DNeasy PowerSoil Pro Kit (Qiagen, UK) according to the manufacturer's instructions, with the following modification: As there was high level of PCR inhibition in the samples, the wash steps were repeated twice, and the samples were further processed with a DNeasy PowerClean Pro Cleanup Kit (Qiagen, UK) according to the manufacturer's instructions. Amplicon sequencing of the full bacterial 16S rRNA genes present in each sample was then completed on MinION (Mk1B, Oxford Nanopore, UK) using the 16S Barcoding Kit 1–24 (SQK-16S024) and a MinION Flow Cell (R10.4.1) according to the manufacturer's instructions. The run time parameters were 72 h run time, with 1.5 h pore-scan frequency, minimum read length of 200, fast model basecalling, using MinKNOW version 24.02.8, Bream 7.9.8, Dorado 7.3.11, MinKNOW Core 5.9.12, yielding a median read length of 1547 and mean Q-score of 8.5. The basecalled data were then processed with the wf-16s Nextflow (https://github.com/epi2me-labs/wf-16s) workflow on EPI2ME (https://github.com/epi2me-labs) to identify the bacterial amplicons present in each sample with the following parameters: min Q-score of 10, a minimum and maximum read length of 800 and 2000 respectively using the Kraken2 classifier to species level on the NCBI 16/18s database (Cole et al., 2014; Wood et al., 2019). All statistical analyses were carried out in R 4.2.2 'Innocent and Trusting' (R Core Team, 2022). Data were normalised to an even read-depth according published recommendations (McKnight et al., 2019; Weiss et al., 2017). To test for taxa that were differentially abundant between fresh and seawater incubations, we used multivariate generalised linear models (with a negative binomial error term to account for overdispersion) to explore changes in community composition (Wang et al., 2012). Multivariate and univariate *p* values were obtained by log-likelihood ratio tests and model-free bootstrapping with 10,000 permutations of probability integral transform residuals. The figures were prepared with the R package 'ggplot2' (Wickham, 2016), the sequence data were processed with the R package 'Phyloseq' (McMurdie and Holmes, 2013), and multivariate generalised linear models were fitted with the R package 'Mvabund' (Wang et al., 2012).

2.9. Assessment of AMR bacterial pathogens in the seaweed holobiont

To determine the presence of extended-spectrum beta-lactamase (ESBL)-producing bacteria (beta-lactam resistance) and vancomycin-resistant *Enterococcus* (VRE) in the seaweed holobiont, two selective media were used: VRE ChromoSelect Agar (Merck UK) to select for VRE, and ESBL ChromoSelect Agar Base (Merck UK) for ESBL-producing enteric bacteria. Supernatant (50 μL) from the previous step before DNA extraction was spread on VRE ChromoSelect Agar (Merck UK) and incubated at 37 °C for 48 h, with blue or blue-green colonies indicating *Enterococcus faecalis*; and a second 50 μL was spread on ESBL ChromoSelect Agar Base (Merck UK) and incubated at 37 °C for 48 h, with purple or pink colonies indicating *E. coli*, green colonies members of the *Klebsiella*, *Enterobacter*, *Serratia* and *Citrobacter* spp. (KESC group), and colourless to brown colonies *Proteus*, *Morganella* and *Providencia* spp. Any negative plates were incubated for a further 24 h to confirm lack of growth.

3. Results

3.1. DMSP concentrations

DMSP concentration was approximately 1000-fold higher in *U. intestinalis* (mean ± standard deviation = 15.5 ± 2.65 μmol g^{-1} SFW, range = 12–18 μmol g^{-1} SFW, n = 4) than in *S. muticum* where the standard deviation around the mean was substantially larger (17.9 ± 15.44 nmol g^{-1} SFW, range = 3–35 nmol g^{-1} SFW, n = 5; Supplementary Table S3). In comparison to *U. intestinalis* (tubular frond), *S. muticum* has a more heterogenous morphology that includes stipe, blade and vesicles. Sampling small masses of its biomass using single sampling points likely increased the variance in DMSP concentrations.

3.2. PTR-MS qualitative assessment (Experiment 1)

PTR-MS analysis revealed four dominant volatiles (H_2S, COS, Methiol and DMS) produced at various rates over an 8 d incubation (Supplementary Fig. S2). The analysis indicated the presence of thioformic acid (O═CH—SH) but DMDS or ammonia (NH_3) were not detected.

3.3. Gas chromatographic quantification of sulfur volatiles (Experiment 2)

A total of 13 different sulfur volatiles produced peak areas above the LOD at different maximum concentrations and depending on the incubation conditions. Of these, six produced peak areas above the LOQ, hence, were dominating the total release of sulfur with five identified by their retention times as: H_2S, COS, MeSH, DMS, and DMDS. Additionally, one unidentified sulfur compound (RT22.9) eluted 22.9 min into the chromatography run in the incubations with *U. intestinalis* (Supplementary Fig. S3).

In *U. intestinalis*, the order of maximum mean sulfur concentrations (highest to lowest = 39,827 to 15 nmol g^{-1} SFW) were H_2S > DMS > MeSH > COS > RT22.9 > DMDS and samples from freshwater treatments sometimes showed less H_2S, COS and MeSH in comparison to the samples from seawater treatments (Supplementary Fig. S3). It is important to note that DMDS contains two sulfur atoms per molecule and the number of sulfur atoms for RT22.9 are unknown, hence, the concentration of DMDS can be calculated as half of the DMDS sulfur concentration but cannot be estimated for RT22.9. Maximum mean sulfur concentrations in samples with *S. muticum* were substantially lower than samples from *U. intestinalis* and showed an order of DMS > MeSH > COS > H_2S > DMDS (range = 38 to 1.3 nmol g^{-1} SFW). There was no clear difference between the seawater and freshwater treatments with *S. muticum*.

3.3.1. Cumulative amounts of volatiles

Since each concentration measurement was followed by the removal of the sample headspace and exchange with nitrogen gas to promote hypoxic conditions, we also calculated the cumulative amount of sulfur volatiles released over the incubation period to facilitate comparison with PTR-MS data (Fig. 1 and Supplementary Fig. S1). This confirmed that the release of sulfur volatiles was species specific and often quasi-linear for a few days after starting the incubation with the total cumulative amount of sulfur volatiles in seawater and freshwater treatments of 131,653 and 27,724 nmol g^{-1} SFW in *U. intestinalis* and 64 and 60 nmol g^{-1} SFW in *S. muticum*, respectively. Furthermore, the calculated cumulative amounts demonstrated that treatment with FW significantly decreased the release of H_2S, COS and MeSH in *U. intestinalis* (General Linear-Effect Model; $p = 0.001$) and DMS in *S. muticum* ($p < 0.01$). In contrast to this, the FW treatment increased the release of MeSH in *S. muticum* (not significant) and DMDS in both species (significant difference for *S. muticum*; $p < 0.001$).

3.3.2. Production rates of sulfur volatiles

Data for the cumulative amounts of sulfur volatiles were used to calculate the daily net-production rates of sulfur volatiles (Fig. 2). Highest production rates in *U. intestinalis* occurred on days 4 (MeSH, DMS and DMDS at 659, 6586 and 29 nmol g^{-1} SFW d^{-1}, respectively) and 7 (H_2S and COS at 13,274 and 59 nmol g^{-1} SFW d^{-1}, respectively). In *S. muticum*, highest rates of production for H_2S and DMS were on Day 2 (1.8 and 19.4 nmol g^{-1} SFW d^{-1}) and for MeSH and DMDS on Day 14 (1.7 and 0.3 nmol g^{-1} SFW d^{-1}). The general patterns for *U. intestinalis* suggest that the production of MeSH, DMS and DMDS is at maximum rates in the first five days with rates decreasing quickly after this period. In contrast, production rates for H_2S and COS were at maximum on day 7 of the incubation and remained relatively high until at least day 10. Overall, the production rates were much lower in *S. muticum* and either showed maximum rates before day 5 (H_2S, COS, DMS) or only started increasing after day 10 (MeSH, DMDS).

3.4. Bacterial diversity

The bacterial assemblage present during the decomposition of *U. intestinalis* was dominated by anaerobes such as Firmicutes in both treatments. In particular, in the freshwater incubations Firmicutes (specifically *Clostridium*) made up 80 ± 32% of the community, but also in seawater incubations where Firmicutes contributed 46 ± 22%. The seawater incubations also had high relative abundance of Bacteroidota (25 ± 11%) and Spirochaetes (19 ± 17%). The high variation in the latter was driven by one replicate where Spirochaetes contributed 39% of the bacterial assemblage, with Spirochaetes making up 9.8 and 8% of the bacterial community in the other two replicates. Freshwater incubations also had a high relative abundance of Proteobacteria (12 ± 3%). However, while both treatments were dominated by Firmicutes, there were significant differences in the specific taxa present in each treatment. Seventy-eight taxa showed significantly different abundances between the treatments (Fig. 3) with almost all the taxa significantly associated with freshwater being Clostridia (32 of the 49), notably *Terrisporobacter petrolearius*, *Proteiniclasticum aestuarii*, and *C. thiosulfatireducens*. In contrast the taxa with the largest increase in the seawater treatment were species from the phylum Spirochaetota: *Pleomorphochaeta caudata* and *P. naphthae* along with *Fusobacterium perfoetens*. There was also a significant increase in the abundance of the Bacteroidota taxa *Dysgonomonas termitidis*, *Draconibacterium mangrove*, *D. halophilum*, *Paludibacter propionicigenes*, and *Ancylomarina longa*. Although no pathogens were present at high relative abundances (>50 16S rRNA reads), pathogens detected at low levels included *Clostridium tetani*, *Clostridioides difficile*, *Clostridium botulinum*, *Clostridium haemolyticum*, *Peptostreptococcus anaerobius*, *Staphylococcus aureus*, *S. haemolyticus* and *E. faecalis*.

3.5. Antimicrobial resistant bacteria

No resistant bacteria were cultured from the control (day 0) samples (Table 1). The most-abundant resistant bacteria species isolated from the decomposing seaweed was vancomycin-resistant *E. faecalis* (VRE), which showed high abundance in seawater (2000 ± 3455 colony-forming units (CFU) g^{-1} SFW) and freshwater (1297 ± 1028 CFU g^{-1} SFW) incubations with *U. intestinalis*, contrasting with *S. muticum* where VRE was only found in the freshwater incubations (264 ± 285 CFU g^{-1} SFW). There were also vancomycin-resistant colonies that could not be identified based on colony morphology in the seawater treatments for both seaweeds (19.4 ± 34 and 10 ± CFU g^{-1} SFW for *S. muticum* and *U. intestinalis*, respectively). ESBL-producing bacteria were only detected in freshwater *U. intestinalis* incubations, including *E. coli* (8 ± 14 CFU g^{-1} SFW) and the KESC group (2 ± 3 CFU g^{-1} SFW). Unidentified biofilm-type colonies were observed on *U. intestinalis* decomposing in fresh and seawater conditions (10 ± 17 and 15 ± 26 CFU g^{-1} SFW for fresh and seawater respectively; Table 1).

4. Discussion

The ocean and coastal wetlands are recognised as substantial sources of volatile sulfur compounds that are produced by diverse abiotic and biotic processes (Kelly et al., 1994; Reed et al., 2024). However, we know little about the environmental impact of seaweed strandings in general and lack detailed information about their associated microbial communities and release of harmful volatiles which makes the assessment of their health risks challenging (Rodríguez-Martínez et al., 2024).

GC-FPD analysis revealed the production of five and six abundant sulfur volatiles in *S. muticum* and *U. intestinalis*, respectively. Another seven sulfur volatiles with minor abundance were detected in *U. intestinalis* but not further considered here since their concentrations were often below the LOQ of the GC-FPD method. The GC-FPD data broadly matched results from the exploratory PTR-MS experiment with H_2S and DMS being dominant volatiles in *U. intestinalis* followed by COS and MeSH.

A recent mesocosm study by Kwak et al. (2026), highlights the need to quantify volatile emissions from strandings. They find that a 14-d incubation of *Sargassum* sp. at 27 °C shows a maximum emission factor of 2550 μg H_2S kg^{-1} d^{-1} (equivalent to 74.8 nmol g^{-1} SFW d^{-1}) on day 2.

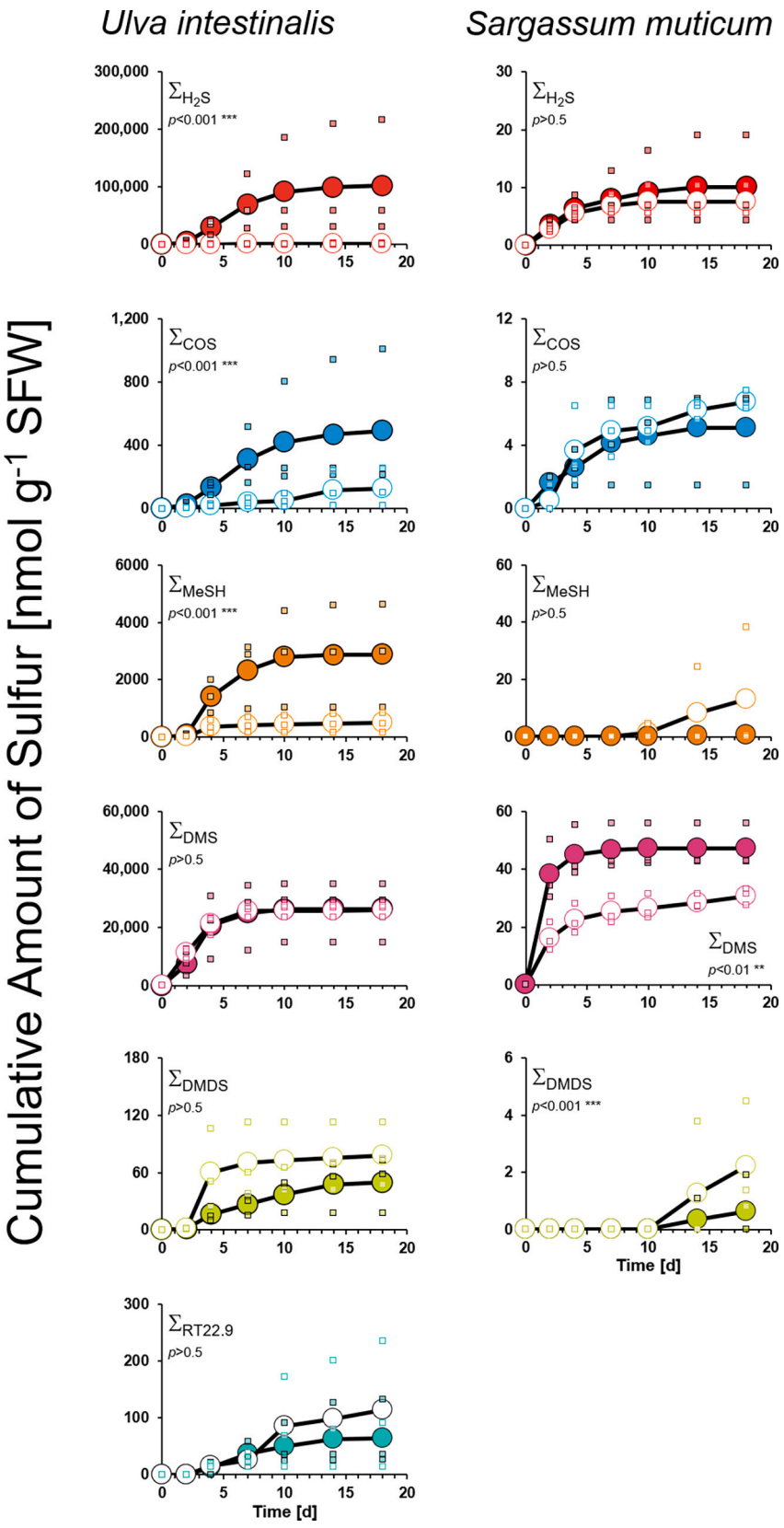

Fig. 1. Cumulative amount of volatile sulfur released from decaying seaweed. Hypoxic incubations with *Ulva intestinalis* (left) and *Sargassum muticum* (right) at 26 °C for 18 d. Shown are mean values after incubation in seawater (SW; closed circles) or freshwater (FW; open circles). Data were normalised to seaweed freshweight (SFW) biomass with biological triplicates presented using squared symbols (RT22.9 = unidentified sulfur volatile). Please note variable scaling along the y-axes. Asterisks and associated *p*-values indicate the level of statistical difference between SW and FW treatments.

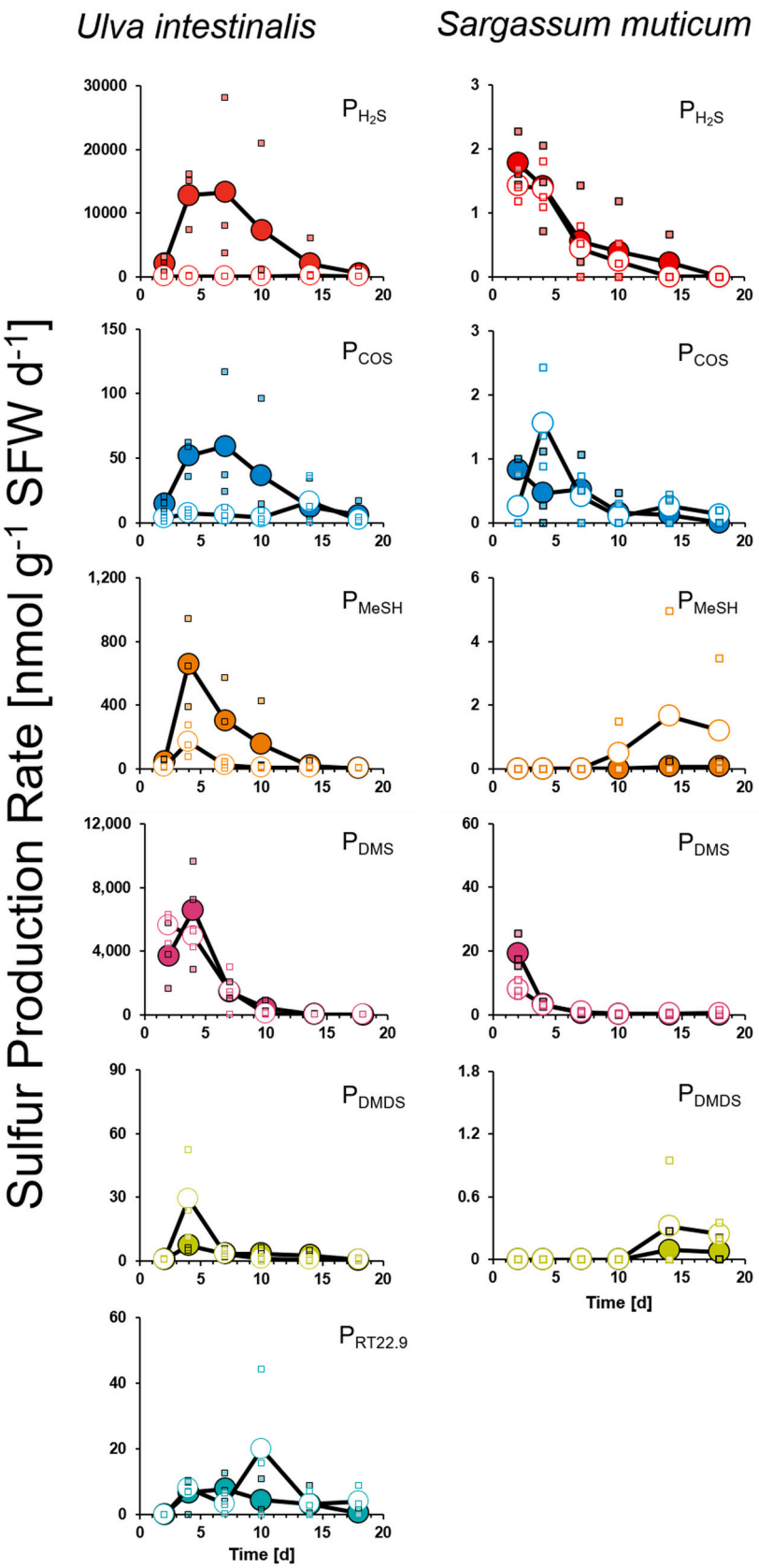

Fig. 2. Net-production rate of volatile sulfur released from decaying seaweed. Hypoxic incubations with *Ulva intestinalis* (left) and *Sargassum muticum* (right) at 26 °C for 18 d. Shown are mean values after incubation in seawater (SW; closed circles) or freshwater (FW; open circles). Data were normalised to seaweed freshweight (SFW) biomass with biological triplicates presented using squared symbols (RT22.9 = unidentified sulfur volatile).

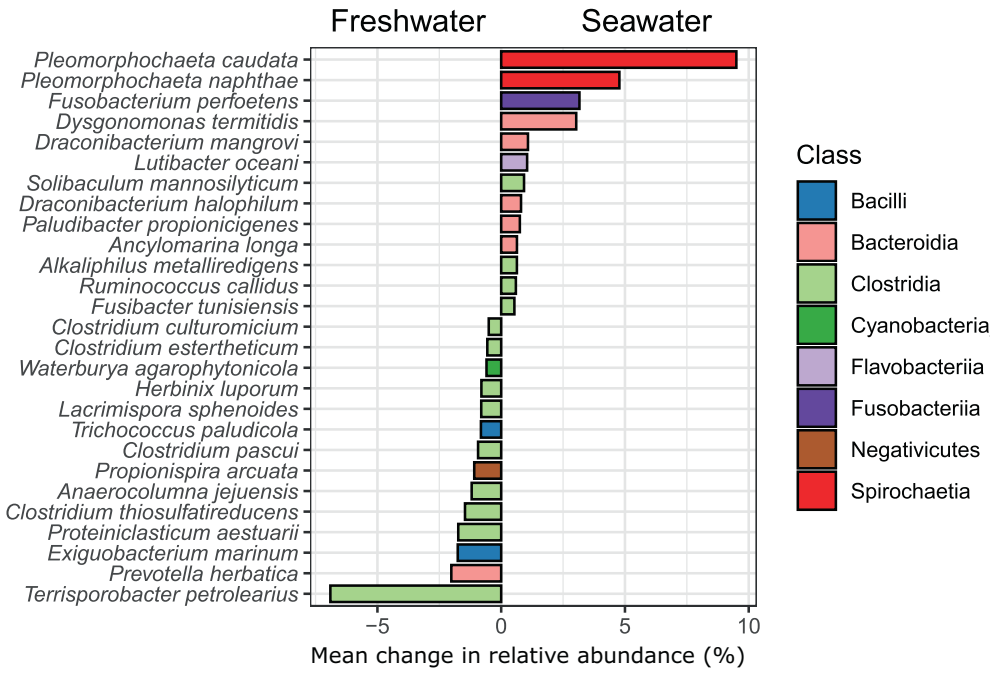

Fig. 3. Change in relative abundance of bacteria identified on decomposing *Ulva intestinalis*. A positive value indicates an increase in taxa associated with seawater, a negative value an increase in taxa associated with freshwater. Only the top 25 most-abundant species with a significant association are shown (adjusted *p*-value < 0.05, multivariate GLM with negative binomial error distribution).

Table 1
Assessment of antimicrobial resistant bacterial pathogens in the seaweed holobionts. Number of colony-forming units (CFU) per g of seaweed freshweight (SFW) for vancomycin-resistant *Enterococcus* (VRE) and extended-spectrum beta-lactamase (ESBL)-producing bacteria. Seaweed was incubated for 5 d. Data show mean ± standard deviation rounded to nearest CFU ($n = 3$). 'Unknown' = putative identification impossible.

		Antimicrobial resistant taxa identified (CFU g^{-1} SFW)				
Resistance		Vancomycin		ESBL-producing bacteria		
Putative identification		*E. faecalis*	Unknown	*E. coli*	KESC group	Biofilm
	Control	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
	Freshwater	264 ± 285	0 ± 0	0 ± 0	0 ± 0	0 ± 0
S. muticum	Seawater	0 ± 0	19 ± 34	0 ± 0	0 ± 0	0 ± 0
	Control	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
	Freshwater	1297 ± 1028	0 ± 0	8 ± 14	2 ± 3	10 ± 17
U. intestinalis	Seawater	2000 ± 3455	10 ± 17	0 ± 0	0 ± 0	15 ± 26

This is higher than our maximum production rate on day 2 of the seawater microcosm incubation with *S. muticum* at 26 °C (1.78 nmol g^{-1} SFW d^{-1}) but lower than the peak release of H_2S from *U. intestinalis* on day 7 (13,274 nmol g^{-1} SFW d^{-1}), illustrating the potentially high differences in H_2S release depending on the seaweed species and incubation conditions. Taken together, our results suggest that the anaerobic incubation of seaweeds can be a substantial source of malodorous and toxic sulfur volatiles but that their diversity and quantity are species-specific.

Measurements in seaweed strandings or the surrounding air could assist with extrapolating from defined enclosed laboratory experiments to the natural environment. A time-series of atmospheric H_2S concentrations at a Caribbean site regularly affected by *Sargassum* strandings, demonstrates ambient concentrations >5 ppm for more than 50 d a year in some locations (Resiere et al., 2021) and concentrations in decaying *Sargassum* strandings can reach 50–100 ppm (Rodríguez-Martínez et al., 2024; Rodríguez-Martínez et al., 2026). These values exceed the long-term exposure limit of 5 ppm (Supplementary Table S1) and underline the requirement for mitigation strategies that aim to protect from acute and chronic H_2S exposure after future seaweed strandings (see Section 4.4).

The nitrogen-containing gas ammonia has been suggested to be of concern to human health near seaweed strandings (Resiere et al., 2023) but scientific data on this are scarce and the PTR-MS data suggested that ammonia was not produced by either species in our experiment. An investigation of the microbial communities associated with *Sargassum* spp. leachates suggests that ammonia production may commence >30 d after start of the incubation (Domínguez-Maldonado et al., 2024), suggesting that ammonia could become a health concern in older seaweed strandings.

Factors including species diversity, ambient temperature, humidity and salinity will likely affect the release of volatiles and our measurements are impacted by random errors introduced when using single sampling points. It is also premature to infer whether certain taxonomic groups produce more of the sulfur volatiles investigated than others. A recent review identifies 15 genera that caused nuisance blooms between 1976 and 2018 (Joniver et al., 2021) and future studies could address volatile diversity and quantity by screening more seaweed genera. This may include, for example, species from the most-frequently recorded blooming genus *Ulva*, such as *U. prolifera*, *U. compressa* and *U. rigida* (Hu et al., 2010), *Sargassum* seaweeds *S. natans* and *S. fluitans* (Smetacek and Zingone, 2013), and selected red seaweeds, for example, *Gracilaria* spp. (phylum Rhodophyta) (Joniver et al., 2021).

4.1. Contribution of microbial processes to volatile profiles

Abiotic production of organosulfur compounds via photochemistry (Reed et al., 2024) is possible at the illuminated surface of seaweed strandings but was inhibited in our dark incubations. Hence, it is most likely that the biological production from the development and succession of microbial consortia during the seaweed-decay process substantially added to the observed patterns in sulfur-volatile production. This may also explain the sometimes-large variance in our results since the differential biological succession of specific microbial taxa could have resulted in various outcomes in volatile production even when temperature and light conditions were relatively stable. Microbial growth resembling bacterial colonies or fungal hyphae was evident in some replicates but not in others by day 7 (Supplementary Fig. S4) suggesting that the profiles of volatile release at the end of the incubation may differ greatly between replicates despite the relatively homogenous starting and incubation conditions. Temperature will likely affect the diversity and succession of microbial consortia. Whereas we provided a constant 26 °C in our incubations, natural seaweed strandings will receive variable external heating from climate-zone dependent solar radiation (e.g. tropical, subtropical or temperate zones) and variable internal heating from the microbial degradation processes with the temperature in the core of deeper seaweed strandings often >10 °C above ambient levels. It is likely that samples incubated at a range of temperatures will present different outcomes.

Uncovering the details on the microbial processes resulting in the transformation of sulfur compounds were beyond the scope of this research but are reviewed elsewhere (Zhou et al., 2025). Here, we focus on selected examples to illustrate the diversity in their production and related processes contributing to the overall release of sulfur volatiles from various environments (e.g. ocean, coastal wetlands, soil) (Kelly et al., 1994). Anaerobic sulfur/sulfate-reduction by microorganisms (bacteria and archaea) or sulfate-independent processes including the bacterial degradation of sulfur-containing amino acids substantially contribute to H_2S production in marine sediments (Jørgensen et al., 2019). Similar biotic processes in seaweed strandings will likely drive the release of H_2S, the most-abundant sulfur volatile in our experiments. For example, anaerobic digestion of seaweed typically produces 50–70% methane, 30–45% carbon dioxide, <2% hydrogen and <3.5% H_2S (Milledge and Harvey, 2018). The seawater incubations contained at least ten-times more sulfate (28 mM in seawater) than our freshwater incubations (maximum in lakes = 2.6 mM) (Zak et al., 2021). Hence, growth of sulfate-reducing microbes was likely limited in the incubations with freshwater and promoted with seawater. The seawater incubations showed a significant increase of bacteria in Spirochaetota and Bacteroidota – two phyla typically not associated with sulfate-reduction. However, novel lineages of these phyla that encode the dissimilatory sulfate-reduction pathway (DsrAB enzyme complex, converting SO_4^{2-} into sulfide (H_2S/HS^-) commonly observed in Desulfobacterota) were recently identified in an anoxic hypersaline Arctic spring (Magnuson et al., 2023). Furthermore, *Fusobacterium* spp. are recognised for their production of H_2S from the enzymatic desulfhydration of cysteine (Barton et al., 2017), suggesting that diverse microbial processes will have contributed to the significant production of H_2S in the seawater incubations with *U. intestinalis*. Fermentative and hydrolytic bacteria such as Clostridia were abundant in the freshwater incubations and have been demonstrated as versatile producers of H_2S using various metabolic routes (Barton et al., 2017). For example, *C. thiosulfatireducens* (Fig. 3), a species that reduces thiosulfate and elemental sulfur to sulfide in the presence of casamino acids (Hernandez-Eugenio, 2002), was significantly associated with the freshwater incubation of *U. intestinalis*.

The second most-abundant sulfur volatile in our experiments was DMS which showed particularly high concentrations in the incubations with *U. intestinalis*. In marine environments, DMS is produced enzymatically from its biological precursor DMSP, a secondary metabolite accumulated to relatively high concentrations in chlorophyte seaweeds including *U. intestinalis* (Van Alstyne and Puglisi, 2007). It is likely that bacterial degradation of DMSP provided major pathways for the release of DMS and MeSH (Curson et al., 2011). The microbial biomethylation of highly abundant H_2S was a possible additional source of DMS and MeSH (Sela-Adler et al., 2016). Hence, the high abundance of specific sulfur compounds may result in the production of others. For example, MeSH may have been converted to COS and/or DMDS (Bentley and Chasteen, 2004) which could explain the sequential maxima in MeSH and COS production rates on days 4 and 7, respectively. Further processes resulting in COS include the microbial consumption of cystine, cysteine and thiocyanate (Meredith et al., 2018) whereas methanethiol can react to DMDS and dimethyl trisulfide (DMTS) in the presence of ascorbate, Fe(III) ions and H_2S (Chin and Lindsay, 1994). It is possible that DMTS was the source of the peak observed at a retention time of 22.9 min (RT22.9), but initial checks of its retention time were inconclusive so that the identity of RT22.9 remains unresolved. Furthermore, the PTR-MS analysis suggested the presence of thioformic acid (O=CH-SH), another candidate for the identity of RT22.9 in the GC-FPD measurements. DMS has been suggested to decompose to COS but a recent theoretical study suggests that the production of hydroperoxymethylthioformate from DMS can limit COS release and result in thioperhemiacetals that lead to formic and thioformic acids (Vereecken et al., 2025).

4.2. Health risks from sulfur volatiles

Due to its high concentration, reactivity and acute toxicity (Supplementary Table S1), H_2S is likely a major contributor to the reported adverse effects including corrosion of metallic objects and ill health or death. The acute health effects of this gas are well researched (Guidotti, 2010) since it presents a lethal occupational and environmental hazard, and is the second most-often reported fatal gas inhalation in the workplace (7.7% – after carbon monoxide at 36%). Chronic effects of H_2S materialise at exposure of less than 10 ppm when inhalation triggers a transition from aerobic to anaerobic cellular metabolism. Less is known about the toxicology of the other sulfur volatiles but the mode of action of DMS in humans is similar to that of H_2S (Demchuk et al., 2018) and the 8-hour time-weighted average and short-term exposure limits for MeSH and DMDS are substantially lower than that for H_2S (Supplementary Table S1). This suggest that even low concentrations of MeSH and DMDS produced in seaweed strandings may contribute to the overall ill health effects experienced in their vicinity. Since COS and DMDS also carry the risk of acute toxicity, monitoring their concentrations during episodes of ill health is advisable. It is premature to speculate about local concentrations surrounding seaweed strandings since these will be highly dependent on environmental conditions, for example, the wind speed and resulting mixing of toxic gases in the overlying atmosphere. Repeated field measurements conducted at stranding sites could quantify gas-flux rates in the undisturbed seaweed and during removal efforts – important information that can feed into atmospheric dispersal models to predict the effects of seaweed strandings on public health.

4.3. Health risks from environmental bacterial contamination

Many of the bacterial taxa identified on decomposing seaweed were associated with the gut microbiome/faeces of humans and animals (including *Clostridium* spp., *Enterococcus* spp. *Fusobacterium perfoetens*, *Dysgonomonas termitidis*, and various *Ruminococcus* spp.). Furthermore, faecal microorganisms (not isolated at the start of incubations) were able to proliferate on *U. intestinalis* to >1000 CFU g^{-1} *E. faecalis* over 5 d. This supports that decomposing seaweed provides a microenvironment suitable for regrowth of faecal anaerobic bacteria (anaerobic/low oxygen and elevated nutrients and temperature). Preventing regrowth of anaerobic bacteria in the environment is a core challenge in managing

wastewater treatment and supporting a healthy environment (O'Mullan et al., 2017; Prest et al., 2016). By providing an environment capable of supporting microbial growth, decomposing seaweeds pose a potential public health risk by subsequently generating a source (for example, to water, air, or directly to humans and animals) of faecal microorganisms, including pathogens (Abdool-Ghany et al., 2025). Furthermore, we were able to isolate bacteria resistant to beta-lactam antibiotics and the aminoglycoside vancomycin (which is reserved for the treatment of complicated and otherwise-resistant infections) from the surface of decomposing seaweed. The most abundant resistant bacterium detected was VRE (Vancomycin-resistant *E. faecalis*). Although detected on both genera, *U. intestinalis* supported a higher load, likely due to genus-specific traits of the host. For example, *S. muticum* produces secondary metabolites, such as phlorotannins, which may inhibit bacterial colonisation and growth. VRE are an emerging and significant challenge in healthcare (World Health Organisation, 2024). They can cause a variety of infections (e.g. urinary tract infection) with AMR *E. faecalis* responsible for >100,000 deaths in 2019, the 12th highest of any bacteria (Murray et al., 2022). The presence of VRE in decomposing seaweed is therefore clearly a health concern, either as a risk of direct infection, a source for onwards dispersal of AMR bacteria or genes via horizontal gene transfer across the One-Health (human-animal-environment) Continuum (Kim and Cha, 2021). The risks are varied, ranging from environmental dissemination into water systems, contamination of aquatic organisms, and potential transmission to humans, highlighting the complex pathways through which resistant bacteria can spread (Cheung et al., 2025).

4.4. Effect of freshwater addition

Washing of *S. muticum* in freshwater before anaerobic digestion delays the production of methane (Milledge et al., 2018). This suggest that at locations where freshwater is readily available, its addition to seaweed strandings may alter the production of volatiles, knowledge that could be used to mitigate the release of toxic and malodorous gases and lessen deleterious health effects where the logistical requirements for freshwater additions could be managed successfully. Our data suggest significant decreases in the production of H_2S, COS and MeSH with freshwater addition in *U. intestinalis*. Where spraying of seaweed strandings with freshwater, for example with a firehose or other application, is feasible, mitigation of the release of toxic gases could minimise the risks to removal workers or beach users. However, potential decrease in toxic gases must be balanced with possible stimulation of growth of pathogens in freshwater that may impact public health.

To summarise, seaweed strandings release diverse sulfur gases at quantities that may produce health risks to coastal users. Acutely toxic volatiles (e.g. H_2S, COS and DMDS) are of particular concern but the sometimes highly concentrated DMS and MeSH may add to the prevalence of respiratory illnesses experienced in the vicinity of recent strandings. Additionally, decaying seaweed promotes the growth of bacterial pathogens that may result in infection when people encounter stranded material or after transmission of bioaerosolised particles. Where readily available, freshwater addition may offer a cost-effective strategy to mitigate the release of volatiles in certain species. Spraying seaweed strandings with freshwater can decrease the release of toxic volatiles. This may provide local stakeholders with extra time to organise the removal of seaweed biomass and could create benefits through the sustainable use as a fertiliser additive in agriculture or as raw material for anaerobic digestion to produce renewable biogas.

CRediT authorship contribution statement

Michael Steinke: Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Leslie Galstaun:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Struan Tait:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Georgia Longhurst:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Millie M. Corbould:** Investigation. **Fraser Reich:** Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation. **Robert M.W. Ferguson:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Methodology, Investigation, Conceptualization.

Declaration of competing interest

The authors declare no competing interests.

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Appendix A. Supplementary data

Supplementary tables listing the characteristics of sulfur gases quantified in this study (Table S1), linear regression data for calibrations with various sulfur gases (Table S2), and DMSP concentrations in *Ulva intestinalis* and *Sargassum muticum* (Table S3). Supplementary Figures showing an example chromatogram for day 14 of the seawater incubations with *Ulva intestinalis* (Fig. S1), PTR-MS qualitative assessment of sulfur gases produced by decaying *Ulva intestinalis* and *Sargassum muticum* (Fig. S2), gas-chromatographic quantification of volatile sulfur released from *Ulva intestinalis* and *Sargassum muticum* (Fig. S3), and photographs of incubation vials in the experiment with *Ulva intestinalis* (Fig. S4) (PDF). Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2026.182057.

Data availability

Data will be made available on request.

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