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Seasonal and Spatial Shifts in the Volatile Chemical Profile of *Cymodocea nodosa* Across Marine and Lagoon Ecosystems

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Abstract: Biogenic volatile organic compounds (BVOCs) are produced by marine organisms but remain largely understudied in seagrasses. To address this gap, this study investigates BVOC profiles from *Cymodocea nodosa* across seasons and between two ecosystem types: open-sea sites (Antibes, Saint Tropez, Porto Vecchio) and coastal lagoons (Thau, Urbino, Carteau). BVOCs were collected using headspace solid-phase microextraction (HS-SPME) and analyzed by gas chromatography–mass spectrometry (GC-MS). A total of 171 compounds were identified (145 in summer, 117 in spring, 115 in winter, and 103 in autumn). Volatilome composition varied significantly with season, explaining 26.1% of the explained variance, followed by site differences (14.1%), while ecosystem type had minor effects (<5%). Functional diversity indices supported these patterns, indicating higher richness and abundance in summer, including 31 volatile compounds solely detected in summer. *C. nodosa* exhibited stress-related profiles, with geranyl acetone, β-cyclocitral, β-ionone, dimethylsulfide (DMS), and dihydroactinidiolide positively correlating with light, temperature, and salinity. Molecular networking showed the highest metabolite diversity and abundance in Urbino, including additional terpenoids and chlorinated and nitrogen-containing compounds. These findings highlight a haline- and heat-responsive phenotype and demonstrate strong seasonal and spatial variability in *C. nodosa* BVOC profiles,

suggesting the presence of distinct Mediterranean site-specific chemical signature requiring further integrative metabolomic and genetic investigation.

Keywords: Seagrasses, Mediterranean Sea, BVOC, seasonality, environmental parameters

1. Introduction

Volatile organic compounds (VOCs) are low-molecular compounds (< 300 Da) characterized by low boiling points and high vapor pressures (higher than 0, 01 kPa at 20 °C) [1]. Biogenic VOCs (BVOCs) that belong to the specialized metabolism of terrestrial plants, bacteria, algae, fungi and animals. Their emissions from terrestrial plants represent over 90% of global VOC emissions [2,3]. They belong to different biochemical families such as terpenoids (*e.g.,* isoprene, monoterpenes, and sesquiterpenes), phenolic compounds including benzenoids (*e.g.,* benzaldehyde) and phenylpropanoids (*e.g.,* cinnamyl alcohol), nitrogen and sulfur compounds (*e.g.,* isothiocyanates), and fatty acid derivatives such as green leaf volatiles (GLVs) [4]. BVOC emissions are highly dependent on seasonal variations since phenology, temperature and light are key drivers of their synthesis and release [5,6]. For instance, in a Mediterranean forest dominated by *Quercus sp,* short-chain oxygenated VOCs and isoprene for *Q. pubescens* and mainly monoterpenes for *Q. ilex*, presented higher mixing ratios in summer, enhanced by the high temperature and solar radiation in this season compared to winter [6,7]. More specifically [7] observed an increase in limonene emissions from this species in August and in α-pinene emissions in May. By contrast, *Olea europaea* L. shows a decrease in α-pinene emissions in May, August and February [7]. However, during summer, monoterpene emissions from *Quercus ilex* decline markedly under drought conditions, while irrigated individuals emit up to 82% more monoterpenes over the same period [8]. Such a seasonal cycle of BVOC emissions allows plants to counterbalance the oxidative pressure they experience during abiotic stresses, thanks to the antioxidant properties of BVOCs [5,9,10]. Indeed, it has been suggested that BVOCs, particularly terpenoids, play a protective role against cellular oxidation occurring during abiotic stresses, including heat, light,

drought, and ozone (O_3) exposure. BVOCs act through three main mechanisms in response to these stresses. BVOCs are integrated into the lipidic thylakoid membranes of chloroplasts, thereby contributing to maintain their organization and function (carbon assimilation) even under abiotic stress conditions. They also have the capacity to act as a direct antioxidant through scavenging reactions [11]. Moreover, BVOCs can also function as a hormone-like molecules acting at the gene level and regulate transcripts and proteins of the antioxidant system and may act as a defence priming signal [12]. Therefore, these compounds can strongly affect resistance and resilience mechanisms and eventually, ecosystem functioning.

In the context of global change, investigating BVOCs could reveal new insights into ecosystem adaptation and resilience to environmental changes expected in the future [13]. Once released into the atmosphere, BVOCs influence atmospheric chemistry by forming ozone (O_3) and secondary organic aerosols (SOA) through reactions with oxidants like OH• and NO_3• [14]. These processes influence air pollution, climate, ecosystems, and human health, emphasizing the importance of characterizing BVOC sources, quantifying their emissions and identifying the environmental factors that drive them [14,15].

While BVOCs emitted from terrestrial ecosystems have been extensively studied since the 1980s, with over 2500 articles published since 1990 and global emissions estimates exceeding 1 PgC yr^{-1} (10^{15} gC yr^{-1}) [16], marine environments remain still comparatively underexplored [10,17,18]. Current knowledge showed that oceans emit a large diversity of BVOCs, mainly highlighted in pelagic zones. These emissions are linked to sea surface processes [19], phytoplankton [20], and bacteria [18,21]. However, recent reviews have highlighted a significant research gap regarding benthic organisms, with only 112 studies on macroalgae, 4 on seagrasses, and 2 on corals [10,18]. Expanding our knowledge of marine BVOCs could provide valuable insights into ecosystem trajectories under current and projected environmental conditions. As observed in terrestrial environments, it is plausible that, marine BVOCs play a protective role under stress.

Among benthic ecosystems, BVOCs emissions from seagrasses meadows, comprising approximately 70 species [22,23], remain largely unexplored. These ecosystems form vast meadows covering more than 300, 000 km^2 according to the most conservative estimates [24], and more than 1, 500, 000 km^2 worldwide [25]. Seagrass meadows provide numerous essential ecosystem services including

nursery habitats, food sources, coastal protection, sediment stabilization and carbon sequestration [26,27]. Despite they contribute less than 1% of total marine primary production, seagrasses are responsible for sequestering 10% of carbon stored in ocean sediments over millennia and thereby playing a key role climate change mitigation [28,29]. Nevertheless, these ecosystem services are in decline, as seagrass meadows are being lost at an alarming rate of 110 km^2 each year worldwide [30]. The combination of natural and anthropogenic stressors in coastal environments induce responses in marine plants, modifying their morphological and physiological traits [31–33]. In some case, this can lead to abrupt changes that causes the disappearance of the key species and a modification of the associated ecological functions [34]. Investigate volatile specialized metabolites emitted by seagrasses, could allow to better describe the mechanisms of acclimation, adaptation, and defence used by plants to cope with environmental pressures, before irreversible losses occur.

The semi-enclosed nature of the Mediterranean Sea means that it tends to warm up more quickly than other regions of the globe [35,36], making it a hotspot for climate change [37,38]. A temperature increase between +0.81 and +3.71 °C is projected by 2075–2100 in the upper layer of sea surface (0–150 m) [13,39]. Beyond the expected rapid increase in average surface temperature [39–42], the Mediterranean Sea is also significantly impacted by marine heatwaves (MHWs). Recent studies show that these have become more frequent, intense, spatially extensive, and severe in recent decades [43–48]. Among Mediterranean coastal ecosystems, the effects of climate change are amplified in coastal lagoons. In these environments, the effects of climate change are mainly reflected in a marked rise in temperatures (+1.6 °C between 2000 and 2019 for the Thau lagoon [49]), a decrease in precipitation and a trend toward gradual salinization linked to declining inflows from the watershed [50]. Marine heatwaves, already frequent in the Mediterranean, are particularly amplified in lagoons [51,52], creating extreme thermal anomalies and intensifying existing pressures [53,54]. In the Mediterranean coastal zone, seagrass meadows covered about 468.54 km^2 in 2016 [55] but have already suffered significant declines due to extreme climatic events, diseases, anthropogenic activities -including coastal development, trawling, fish farming or dredging and filling-, as well as climate change and invasive species. Overall, Mediterranean seagrass meadows have declined by 50% since 1842 with up to 75% of suitable habitats projected to be loss by 2050, and a risk of functional

extinction by 2100 [56,57]. In the Western Mediterranean Sea, common seagrass species include *Posidonia oceanica* (L.) Delile, *Cymodocea nodosa* (Ucria) Asch., *Zostera marina* L., and *Zostera noltei* Hornem [58]. While *P. oceanica* is found exclusively in the open coastal water, *Z. marina* and *Z. noltei* are mainly distributed in Mediterranean coastal lagoons where hydrogeochemical and meteorological forcing factors are highly variable (salinity fluctuations, nutrient dynamics and water level fluctuations) [59,60]. *C. nodosa* is described in both open marine and lagoonal environments.[58,61]. It ranks second, after *P. oceanica*, in terms of surface areas coverage in the Mediterranean Sea [62]. This warm-affinity species is distributed across the Mediterranean, including coastal lagoons, and extends into the Sea of Marmara and part of Atlantic Ocean [62]. While local regressions have been observed in areas under intense anthropogenic pressure, *C. nodosa* appears to be more influenced by long-term natural fluctuations, such as variations in salinity, herbivory and climate change. This species may benefit from global warming [58] by enhancing net foliar growth in spring and stable growth in summer [63]. The BVOCs profile of *C. nodosa* remained undescribed until recently, with the first characterization published in 2024 [64]. This autumn sampling highlights the emission of 59 compounds, reflecting a hight level of chemical diversity (alcohols, aldehydes, alkanes, alkenes, esters, ethers, ketones and sulfur compounds) from different biosynthetic pathways (benzenoids, fatty acid derivatives, polyketides, sulfur-containing compound, terpenoids). To date, no other studies have investigated the volatilome of this species. However, previous studies have shown that marine BVOCs emitted by benthic organisms can respond to abiotic variations, particularly through seasonality but limited to autumn and spring [65], or between late spring and late summer [66,67].

This study aims to fill the current gap in understanding seagrass BVOC production, particularly in relation to environmental factors and seasonal variability, through a characterization, for the first time, of *C. nodosa* volatilome across a full annual cycle coupled with a comparison between open-sea and lagoon ecosystems. For this purpose, a screening of BVOCs from *C. nodosa* was carried out over a seasonal cycle across multiple sites. The objectives are (1) to characterize the effect of season and ecosystem types (marine vs lagoon) on the volatilome of *C. nodosa* and (2) to highlight potential temperature and salinity stress biomarkers on the volatilome of *C. nodosa*. We hypothesize that *C. nodosa* exhibits i/ higher BVOC relative abundance and higher compound diversity in

summer coinciding to heat stress and ii/ larger variations of volatilome in coastal lagoon environments due to their more pronounced environmental fluctuations.

2. Results

2.1 Main factors influencing the volatilome

Regardless of season and sampling site, *C. nodosa* emitted a total of 171 compounds: 145 are detected in summer, 117 in spring, 115 in winter and 103 in autumn (Supplementary Table S1). Dimethyl sulfide (DMS) is the most emitted compound in relative abundance in summer (21.8%) and autumn (15.2%). In winter and spring, the most emitted compounds are alkanes (22% of heptadecane and 21.7% of octadecane in spring and 28% of octadecane and 22.6% of heptadecane in winter). A substantial number of compounds (71, Figure 1) are common to all four seasons. Among them, 33 belonged to FAD (including decanal, pentadecanal, and isopropyl myristate), 17 are terpenoids (including β-cyclocitral, β-ionone, citral, geraniol and geranyl acetone), shikimates (3 compounds, benzaldehyde, benzenacetaldehyde and dibutyl phthalate), 7 benzenoid-compounds (1-butylheptyl-benzene, 1-butyloctyl-benzene, 1-ethylnonyl-benzene, 1-pentylheptyl-benzene, 1-pentylhexyl-benzene, 1-propyloctyl-benzene and 1-propylnonyl-benzene), 2 alkaloids (isothiocyanate cyclohexane and methoxy-phenyl oxime), 1 polyketide (2-pentylfuran), 1 sulfur compound (dimethylsulfide, DMS) and 7 unknown compounds. Moreover, each season exhibited specific BVOCs, especially in summer with 31 solely detected in summer compared to other seasons (3 in spring and autumn and 2 in winter, Figure 1). For example, 3-hexen-1-ol, amorphene, cubenene, humulene, menthol, undecanal and zonarene are only detected in summer. The other compounds specific to a given season are 1, 7-diisopropylnaphthalene, nerol and palmitic acid in autumn, bornyl acetate and 2 unknown compounds in spring and in winter (Supplementary Table S1).

According to the RDA model, chemical profiles explained 24% of the total variance (12.7% for axis 1 and 11.3% for axis 2) according to all considered factors (Figure 2). All factors as well as their interactions have a significant impact on the chemical profile of BVOCs (RDA model, $p < 0.001$, Supplementary Figure S2). Among the factors, season emerged as the primary driver, with temperature explaining 26.1% of the variance explained by the RDA model. Next in order of importance were the interaction between seasons and sites (18.6%), the site

effect alone (14.1%), the ecosystem factor in interaction with the season (4.1%) and finally the ecosystem factor alone (2.8%) (Figure S1). While the interaction between season and site and the type of ecosystem are significant factors (RDA model, $p < 0.001$), their explanatory power was considerably lower compared to season and site effects.

2.2. Volatilome composition per season and sites

The total functional diversity index also revealed significant seasonal variation in chemodiversity, confirming that the summer volatilome is more abundant and more diverse than in other seasons (functional Hill diversity, $p < 0.001$, Figure 3), consistent with the RDA results.

At site level, the total functional diversity index also shows significant higher values in summer except for Saint-Tropez site (Figure 3). Spring appears to be the least diverse season in terms of compounds compared to the other seasons at both Thau and Urbino sites. In summer, Urbino and Carteau present the highest chemodiversity sites, followed by Porto-Vecchio and Antibes while Thau and Saint-Tropez exhibit the lowest diversity. In winter and spring, differences between sites can also be observed, whereas in autumn, functional diversity is the same across all sites (Figure 3).

2.3 correlation between compounds and three abiotic parameters in two lagoons

To deeper explore the impact of abiotic parameters on BVOC profiles, the analyses focused on the two significantly different yet comparable sites: Urbino and Thau lagoons. These sites were selected due to the contrasting environmental conditions and the availability of continuous temperature, light and salinity data monitored year-round.

During 2024, the mean monthly water temperature ranged from 10.4 °C to 23.3 °C in Thau and from 12 °C to 27 °C in Urbino. Salinity varied from 38.3 to 40.4 PSU in Thau and from 40.3 to 42.5 PSU in Urbino (Supplementary Table S2). The mean monthly light ranged from 115.5 10^6 to 1 756.5 10^6 lumens m^{-2} d^{-1} in Thau and from 5.1 10^6 to 1 752.8 10^6 lumens m^{-2} d^{-1} in Urbino. Spearman's correlations

revealed several compounds significantly correlated with these three parameters, with correlation coefficients exceeding 0.75 (p<0.01) (Table 1, 2 and 3).

In the Thau lagoon, 19 compounds are significantly correlated with temperature (11 positively and 8 negatively), compared to 30 compounds in the Urbino lagoon, (24 positively and 6 negatively). At both sites, β-ionone, DMS and dihydroactinidiolide are positively correlated, while octadecane and 2, 2, 4-trimethyl-1, 3-pentanediol diisobutyrate is negatively correlated. However, 1-ethylnonyl benzene increases with temperature in Thau (ρ=0.82), whereas in Urbino it decreases (ρ=-0.94) (Table 1).

Light is positively correlated with 3 compounds in the Thau lagoon: one unknown (ρ=0.8) and two benzenoids (1-butylheptyl-benzene and 1-ethylnonyl-benzene, ρ=0.76) whereas 7 fatty acid derivatives decrease significantly with light increasing (*e.g.,* nonadecane, tridecanal, 1-heptadecene) (Table 2). In the Urbino lagoon, only one unknown compound is negatively correlated with light (ρ=-0.76). Terpenes (e.g., menthol, trans-calamenene), including apocarotenoids such as geranyl acetone or β-cyclocitral increase significantly with light (ρ=0.96 and ρ=0.79, respectively) as one phenylpropanoid (phenylethyl alcohol).

In the Thau lagoon, three terpenes are positively correlated with salinity: cis-geraniol (ρ=0.96), citral (ρ=0.95) and neral (ρ=0.8). In the Urbino lagoon, 11 compounds are correlated with salinity: 5 fatty acid derivatives decrease significantly (*e.g.,* hexadecane, heptadecane, 2, 2, 4-Trimethyl-1, 3-pentanediol diisobutyrate octadecane and nonadecane, ρ from -0.95 to -0.76) and one terpene β-ionone epoxide (ρ=0.89) (Table 3). Two terpenes are positively correlated with salinity: β-farnesene (ρ=0.76) and dihydroactinidiolide (ρ=0.76) and a chlorinated compound, (1-chlorododecane, ρ=0.76).

In both sites, *C. nodosa* increases the relative abundance of geranyl acetone and β-cyclocitral in response to light and temperature stress, β-ionone and DMS under temperature stress, and dihydroactinidiolide under combined temperature and salinity stress. Conversely, relative abundance of FAD was generally reduced under these conditions. Notably, all stress-related compounds were produced in higher amount in the Urbino than in Thau lagoon. Over the year, *C. nodosa* from the Urbino lagoon released 4.7 times more geranyl acetone, 17.7 times more

β-cyclocitral, 8.8 times more β-ionone, 2.1 times more DMS and 10.3 times more dihydroactinidiolide compared to the Thau lagoon.

3.3 comparison of compound composition between two lagoons

Furthermore*, C. nodosa* produces a total of 138 compounds in Urbino, while 117 compounds were identified in Thau. Several compounds were exclusively detected in Urbino including 11 additional terpenoids, chlorinated (1-chlorododecane) and nitrogen compounds (N, N-dimethyltetradecylamine). Considering all identified compounds, their mean abundance in Urbino is 2.7 times higher than in Thau. At both sites, DMS is the dominant compound, with production levels 1.6 times higher in Urbino compared to Thau.

Molecular network analysis revealed four main clusters of structurally similar compounds associated mainly with the fatty acids derivates pathways (Figure 4). In general, our samples in the Thau lagoon have fewer compounds and a less complex network of molecules compared to *C. nodosa* in the Urbino lagoon. The main cluster found in the two networks is the alkane compounds (*e.g.,* tetradecane, hexadecane, octadecane). The second cluster composed of aldehyde showed site-specific differences. For example, dodecanal and pentadecanal are present in individual of the Urbino lagoon but not in the Thau lagoon. The third cluster highlighted similar compounds present in the two sites with geranyl acetone and citral but also two compounds found in Urbino but not in Thau (2, 4-heptadienal and E-2-octadienal). The fourth last main cluster shows additional site-specific differences: Urbino lacks of 2, 6-dimethylcyclohexanol and Thau lacks 6-methyloctan-1-ol and dicaprylyl ether. Finally, Urbino also contains 1-hydroxy-2, 4, 4-trimethylpentan-3-yl, 2-methylpropanoate, 3-Z-heptadecene, amorphene, benzaldehyde and cyclohexyl isothiocyanate in comparison to Thau where these compounds were absent.

3. Discussion

3.1 Volatilome composition

Our results on volatilome composition highlight that *Cymodocea nodosa* produces a wide variety of volatile compounds over the seasonal cycle, belonging to multiple chemical families and bearing diverse chemical functions. This observation is consistent with findings in other marine organisms [10,18,21]. In our previous studies on Mediterranean seagrass species, the number of compounds

detected in *C. nodosa* during autumn was lower (59) compared to the number identified in this study (103) despite using the same SPME fiber collection method. This increase in chemical richness likely reflects the broader ecological and genetic diversity of the sites surveyed in this study, which may contribute to a wider metabolomic expression. However, the types of compounds identified are largely consistent with those reported by Coquin *et al.*, (2024) with similar proportions. Fatty acids represent the majority, followed by terpenes which are the main biomarkers of *C. nodosa* (citral, humulene, camphor and neral). These are followed by sulfur compounds including DMS, as well as compounds from shikimates and phenylpropanoid pathway (benzaldehyde, benzeneacetaldehyde and dibutyl phthalate), and one polyketide (2-pentylfuran). Other marine organisms such as macroalgae or corals also produce these compounds [18,68–70].

3.2 Season variation of the volatilome

Seasonality was found to be the most influential factor shaping the volatilome of *C. nodosa* with significantly different composition across seasons. Winter and spring were the least distinct from one other, displaying both the lowest number of season-specific compounds and the fewest number of BVOCs overall. In winter, the reduced diversity of the volatilome likely reflects plant dormancy as already observed in terrestrial environments [71,72]. In spring, metabolic activity is allocated to growth and thus on central metabolism [73,74]. Thus, during both seasons, specialized metabolism is not triggered according to the growth-differentiation balance hypothesis (GDBH, [75,76]. Autumn presented an intermediate volatilome, between summer and winter, likely due to senescence. Finally, summer exhibited the most diverse volatilome with 31 season-specific compounds detected. Among these compounds half are fatty acids and the others are terpenoids, most of them are sesquiterpenes, one is a monoterpenoid (menthol) and one is an oxygenated terpenoid belonging to the apocarotenoid class (methyl-ß-cyclogeranate). Particular BVOC emissions during summer have already been reported in terrestrial environments [6] but remain poorly documented in marine environments. Indeed, existing studies in marine environments have mostly focused on seasonal comparisons limited to autumn and spring [65], or between late spring and late summer [66,67], providing data over a complete annual cycle.

The detection of specific compounds in summer may be linked to the particularly severe abiotic stressors affecting seagrasses during this period [77]. Terpenoids are well known for their defensive role against abiotic stresses in terrestrial

ecosystems [11] and may play similar function in marine ecosystems [10,78]. In phytoplankton, terpenoid emissions have been shown to increase in response to elevated light and temperature [79,80] potentially reflecting their antioxidant activity — either through direct interaction with reactive oxygen species (ROS) or indirectly by helping to stabilize cellular membranes. Our findings support this hypothesis, as we observed positive correlations between terpenoids – mainly apocarotenoids (e.g., geranyl acetone, β-cyclocitral) and dihydroactinidiolide - and temperature followed by salinity and light in two sites. Apocarotenoids result from the oxidative cleavage of carotenoids, which can occur via enzyme-catalyzed reactions or ROS-induced degradation [81]. These compounds may also act as precursors for phytohormones like abscisic acid and serve as signalling molecules involved in oxidative stress responses and growth regulation [81,82]. These multiple functions could explain the pattern observed although further mechanistic research is required to confirm the BVOC role in seagrasses.

In agreement with our study, specific compounds have already been detected in high amounts in summer in other marine organisms. For example, the brown alga *Cystoseira compressa* (Esper) Gerloff & Nizam produces more geranyl acetone in August compared to other months [83]. Similarly, the coral *Acropora intermedia* Brook, emits geranyl acetone at 27 °C, not at 32 °C [84]. Comparable results have been observed on the brown algae *Halopteris scoparia* L., which produce geranyl acetone between May to June but not during the hottest months [85]. The anti-radical activity of geranyl acetone could potentially aid against environmental stresses although this effect remains quite weak [86]. Geranyl acetone could favour energy dissipation during transient and moderate stresses, rather than extreme environmental stresses as suggested for monoterpenes in temperate terrestrial species [87]. Nevertheless, further mechanistic research is required to decipher the role of geranyl acetone and more globally of apocarotenoids as well as their dependence to the main environmental parameters.

DMS, resulting from the enzymatic degradation of dimethylsulfoniopropionate (DMSP), was another summer compound detected in our study, showing positive correlations with temperature. Similar findings were highlighted in corals, although responses vary depending on the severity of the stress and the species involved [88]. In addition to temperature, DMS emissions are also influenced by other environmental parameters such as light [89], air exposure

and tides [90] or H_2O_2 exposure [91]. These variations are likely linked to the antioxidant properties of DMS, which has been shown to scavenge hydroxyl radicals (•OH), one of the most reactive forms of reactive oxygen species (ROS) [92].

FADs (such as hexadecane, nonadecane, tridecanal) have shown strong negative correlations with all three environmental parameters (temperature, salinity and light). As a whole, FADs are associated to the membrane degradation [11], and their reduced abundance under high stress may suggest less oxidative damage and degradation to cellular membranes. Conversely, within this group, we also detected the green leaf volatile (GLV) 3-hexen-1-ol, but only during the summer months when all parameters increase. GLVs are short-chain FADs formed by six carbon atoms, issued from the degradation of long-chain fatty acids present in leaf membranes through the LOX pathway [93]. Thus, the occurrence of this volatile during summer alone could be a marker of stress conditions for *C. nodosa*. One possible explanation is that the increase of 3-hexen-1-ol and other antioxidant compounds such as apocarotenoids may help to maintain membrane stability [11]. However, this interpretation remains hypothetical and requires further validation through targeted biochemical and physiological studies.

Finally, two compounds in our study were positively correlated with temperature (benzaldehyde) and temperature and light (phenylethyl alcohol). These compounds are issued from the interlinked shikimic acid and phenylpropanoid pathways [100]. In terrestrial plants, phenylpropanoids respond to biotic and abiotic *stimuli* such as drought, salinity [101], ultraviolet [102] or variation of the full light spectrum [95]. *C. nodosa* acclimates rapidly to different environmental conditions and, in particular, light, seasonal temperature fluctuations and nutrient load [96,97]. These capabilities are tightly explained by the annual production of phenylpropanoids such as benzaldehyde, a key component against some stresses such as light intensity and high temperature [98,99]. Benzaldehyde and benzenacetaldehyde have already been found in *P. oceanica* and seaweeds [65,94].

3.3 Specific site volatilome

Finally, sites have a greater impact on volatilome variability than the broader distinction between open sea and coastal lagoon environments. Coastal lagoons are semi-enclosed systems characterized by limited genetic exchange and

high environmental heterogeneity, which can vary considerably from one site to another in terms of surface, depth, turbidity, temperature and salinity for example. A similar pattern has been observed in a terrestrial plant with distinct volatilomes within the same island in Sardinia. In the Orchid *Himantoglossum robertianum* (Loisel.) P. Delforge, differences in VOC profiles were positively linked to the distance between populations and reflected the climatological features of each sampling site. A similar pattern is observed here: the coastal lagoon of Urbino (Corsica) and the open-sea site of Porto-Vecchio (Corsica) exhibit greater similarity to each other than the two lagoon sites of Urbino and Thau. This suggests that regional climatic conditions and spatial proximity may exert a stronger influence on volatilome composition than ecosystem type alone. A long and peculiar paleogeographic history, prolonged geographical isolation, and high geomorphological diversity have significantly contributed to this richness, since isolation is one of the main causes of speciation [103].

Whatever the season, Urbino appears to be the saltiest and warmest site while Thau, presents intermediate conditions compared to the other sites. *C. nodosa* is known for its great morphological and functional plasticity and is considered a more eurybiontic species, better adapted than *P. oceanica* to harsh environmental conditions [104,105]. As shown in our results, temperature and salinity seem to be important drivers of the volatilome composition (see above) with Urbino displaying a distinct chemical profile compared to Thau. Notably, *C. nodosa* from Urbino produces 9.5 times more apocarotenoids in total than those collected in Thau. Seagrasses maintain turgescence by sustaining low water potential (Ψw) and osmotic potentials (Ψp) relative to seawater [106,107]. However, increased salinity reduces the Ψw gradient, limiting water uptake and turgor maintenance. To restore water balance, marine macrophytes, including seagrasses, rely on osmotic adjustment *via* solute accumulation [108,109]. In the short term (minutes to hours and days), this involves rapid ion uptake (Na^+, Cl^-) [106,110]. This mechanism could explain the presence of a chlorinated compound (1-chlorododecane) in Urbino but not in Thau.

Seagrasses also accumulate osmolytes such as soluble carbohydrates, organic acids, soluble nitrogen-containing compounds [106,111,112]. Once again, only Urbino's *Cymodocea* produces nitrogen-containing compounds (methoxy-phenyl-oxime) and isothiocyanate cyclohexane, a sulfur and nitrogen containing compound. Methoxy-phenyl oxime is also emitted by a coral-symbiont (*Cladocopium goreavi*

LaJeunesse & H.J.Jeon, [69]) and a brown algae (*Lessonia searlesiana* Asensi & de Reviers, [113]). Isothiocyanate cyclohexane has a similar biosynthesis pathway than DMS and can act as a defence compounds to cope with abiotic and biotic stresses as well as signal molecules [114]. It has been measured in other marine organisms, such as coral (*Acropora intermedia*, [84]) and red algae (*Bangia fuscopurpurea* (Dillwyn) Lyngbye, [115,116]). In addition, *C. nodosa* from Urbino produced higher amounts of DMS than in Thau, likely reflecting elevated levels of DMSP. This compound has been described as a well-established osmolyte for marine life, especially in phytoplankton and bacteria [117,118]. Intracellular concentration of DMSP is maintained at high basal concentrations, providing a buffering capacity that helps organisms cope with transient salinity stress or osmotic shock [118]. A study conducted on two phytoplankton species revealed a positive correlation between DMS concentration and salinity, which could result from an upward regulation of intracellular DMSP due to osmotic stress [119]. Further investigations would be necessary to determine whether this pattern also occurs in seagrasses.

High proline and sugar levels in Mediterranean *C. nodosa* populations may explain their broad salinity tolerance in a wide variety of environments [105,120,121]. Therefore, BVOC studies could offer deeper insights into the biochemical strategies employed by *C. nodosa* under saline and thermal stress and better understand its resistance in front of current and future environmental conditions. To go further, controlled mesocosm experiments simulating gradients of environmental parameters are essential to understand seagrass stress responses by monitoring direct volatile emissions through a dynamic system and a PTR-MS [122]. These measurements will have to be coupled with plant physiology evaluation. Such an approach would allow us to unravel the mechanisms of metabolic plasticity and acclimation of *C. nodosa* to a range of environmental constraints, ultimately shedding light on how this seagrass responds to fluctuating salinity and temperature in its environment.

The high salinity and temperature conditions in the Urbino lagoon likely induced a distinct volatilome, significantly different from that observed in the Thau lagoon. This pattern suggests the presence of a haline and heat stress-responsive phenotype of *C. nodosa* in Urbino. This finding strongly supports the existence of local ecotypes adapted to different environments through phenotypic plasticity. Another explanation could be the presence of different chemotypes in

the two lagoons, driven by genotype differentiation. Chemotypes in marine plants have already been identified based on flavonoids. For example, three geographically distinct flavonoid chemotypes were identified in *Zostera noltei* on the basis of their respective major compounds [123]. A similar phenomenon may also apply to BVOC especially since previous studies have demonstrated genetic differentiation of *C. nodosa* across the Mediterranean–Atlantic transition region [124] and within the Aegean Sea [125]. To validate the existence of BVOC-based chemotypes in *C. nodosa*, broader geographic sampling combined with DNA-based genotyping and metabolomic profiling will be essential. Furthermore, to fully characterize the Urbino phenotype plasticity, future studies should also investigate phenolic compounds and key metabolites from central metabolic pathways, which may contribute to local adaptive responses.

The aim of this study was to characterize the influence of seasonality, ecosystem types (open sea vs coastal lagoon) and abiotic parameters on the volatilome of *Cymodocea nodosa*. An hight chemical diversity was found with a total of 171 volatile compounds. Variance in the chemical profiles was primarily explained by the season (26.1%), followed by the different sites (14.1%) and to a lesser extent the ecosystem factor (2.8%). The total functional diversity index revealed significantly higher VOC abundance and diversity in summer with 31 compounds unique to this season. *C. nodosa* volatilomes exhibited distinct stress-responsive profiles notably rich in terpenes, including apocarotenoids (e.g., geranyl acetone, β-cyclocitral, β-ionone) and DMS. Volatilome composition was strongly correlated with light, temperature and salinity, revealing greater diversity, abundance and unique metabolites in the coastal lagoon Urbino, including additional terpenoids, chlorinated and nitrogenous compounds. These results underline seasonal and spatial variability in *C. nodosa* BVOC profile and suggest the potential occurrence of distinct site-specific chemical signature across the Mediterranean Sea. Further investigations combining DNA sequencing and metabolomic profiling of this species at multiple sites in the Mediterranean Sea are warranted to better understand the ecological and evolutionary drivers of this chemical diversity.

4. Materials and Methods

4.1. Study Sites

During 2024, *C. nodosa* samples were collected in winter (January), spring (April) summer (July) and autumn (October) in three open sea sites located in gulfs. These areas are less affected by currents, which facilitates the presence of *C. nodosa*. These sites include the Gulf of Saint-Tropez, the Gulf of Juan in Antibes, and the Gulf of Porto-Vecchio. The other three sites are coastal lagoons: Thau, Carteau and Urbino) (Figure 5). All sites have sandy bottoms.

Among lagoon sites, Thau lagoon is the second largest coastal lagoon on the French coastline, covering area of 75 km^2. It is roughly 21 km long, 8 km wide and has a mean depth of 4.5 m [126]. Carteau cove is also considered a coastal lagoon, with similar variability in hydrogeochemical parameters. It spans a surface area of 10 km^2 and has a mean depth of 5 m [127,128]. Urbino lagoon, located on the eastern coast of Corsica, covers 7.6 km^2 with a mean depth of 5 m and a maximum depth of 10 m [61]. All samples were collected between 0 and 1 m deep, except in Porto-Vecchio, where *C. nodosa* were sampled at 2-3 m deep. Environmental conditions (salinity, temperature and light) were measured at each site during every sampling campaign and data are available in the Supplementary Table S3. In Thau and Urbino lagoons, water temperature (Starmon mini, °C), and light (HOBO UA-002-64, lumens m^{-2} d^{-1}) were continuously monitored every 10 minutes using autonomous sensors. Salinity (NKE Instrument) was also monitored every 15 or 10 minutes in Thau and Urbino lagoons, respectively.

4.2. Plant sampling

Cymodocea nodosa, classified as Least Concern on the IUCN Red List of Threatened Species, was the focus of this study. The permissions to request exemptions for protected species have been requested and granted by the competent authorities for these samples, in accordance with the French legislation. Species were collected in shallow water, immediately placed in plastic bags containing seawater and transported in a cooler. Plant material was formally identified *in situ* by Salomé Coquin at all sites, Vincent Ouisse in Sète, Vanina Pasqualini in Corsica, and Catherine Fernandez in Carteau, Antibes, and Saint Tropez using established and unambiguous morphological characters of *C. nodosa*. No voucher specimen was deposited because sampling permits for this regulated species strictly limited biomass collection, and all collected material was allocated to analyses, leaving no intact specimen suitable for herbarium

preservation. In the laboratory, *C. nodosa* from each site was placed to separate 30 L tanks filled with synthetic seawater, prepared using a commercial sea salt mixture (Instant Ocean, Aquarium Systems, France) dissolved in deionised water. The salinity and temperature were adjusted to match *in situ* conditions. A bubbling system was also installed to ensure water oxygenation.

4.3. Headspace Solid-Phase Microextraction (HS-SPME)

BVOC collection was performed as described by Coquin *et al.* (2024) [64]. Leaf samples were cut into small pieces and 1 g of fresh material was placed (separately for each individual) into 20 mL glass vials, hermetically sealed with PTFE/silicone septa. The vials were maintained in a water bath at 50 °C for 10 min to allow equilibrium., HS-SPME collection was carried out for 1 h using a SPME holder equiped with a pre-conditioned 50/30 µm DVB/CAR/PDMS fiber (Supelco Co., Bellefonte, PA, USA). Blanks were performed using the same vials without plant material. After sampling, the SPME fibers were stored at −20 °C until analysis by GC-MS. BVOC collection was conducted in 5 replicates per each site and per season.

4.4. Gas Chromatography–Mass Spectrometry (GC-MS) analyses

Analyses were performed using the same method as described in Coquin *et al.* (2024), with a gaz chromatography instrument (7890B GC, Agilent Technologies®, Santa Clara, USA) equipped with an HP5-MS column (30 m × 0.25 mm × 0.25 µm; J&W Agilent Technologies®, Santa Clara, USA) coupled to a mass spectrometer (MSD5977A, Agilent Technologies®). Identification of VOCs was based on the comparison of their retention indices (RIs), determined using the retention times of a series of n-alkanes (C_8 toC_{20}), and on a spectral match with the NIST20 mass spectral libraries. To confirm the identity of certain terpenes, several standards were injected (β-cyclocitral, α-citral, β-citral, geranylacetate, α-ionone, β-ionone and geraniol). The relative abundance, that is, the relative percentage of each compound per sample, was calculated. The final table of all detected BVOCs for each species, included the relative abundance per compound classified according to the metabolomic pathways (fatty acid derivative, polyketide, shikimate, terpenoid, and unknown), is available in Supplementary Information (Supplementary Table S1). Unknown compounds are noted with their retention time “RT” and their major ion “i.” Compounds only found in one sample (singleton compound) and all compounds detected in blanks were removed from the final table.

4.5. Diversity index

Chemical diversity was calculated with the total functional diversity index, FD (Q). This index quantifies the effective total dissimilarity between compounds in the sample, combining richness, evenness, and disparity into a single metric and can mask independent variations in each component [129,130]. It was calculated using the Functional Hill Diversity index and the CHEMODIV R package [130]. The functions of the CHEMODIV package allow for a comprehensive analysis of the diversity and dissimilarity of a set of phytochemical samples [130]. The NPCTable function classifies compounds into three hierarchical levels corresponding to biosynthetic pathways superclass and class by accessing the tool at https://npclassifier.gnps2.org/ and downloading the classifications [131]. Next, the compDis function generates a dissimilarity matrix between compounds, calculated on the basis of the biosynthetic classification by NPClassifier and the structural properties of the compounds (PubChem fingerprints).

Then, the total functional diversity index, FD(Q) is calculated according to the formula:

$$ {}^{q}FD(Q) = \left[\sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij} \left(\frac{p_i p_j}{Q} \right)^{q} \right]^{1/(1-q)} $$

where *S* is the total number of compounds in the sample and *pi* and *pj* are the relative abundances of compounds *i* and *j*, and *dij* is the dissimilarity between compounds *i* and *j*. The parameter *q* is the diversity order and controls the sensitivity of the measure to the relative abundances of the compounds. Q is Rao's Q [132].

4.6. Statistical analysis

Statistical analyses were performed using R (version 4.5.1). Graphical representations were generated with vegan, VennDiagram, ggplot2 and CHEMODIV R packages. RDA was performed to explore the influence of the different factors studied: the four seasons, six sampling-site and two types of ecosystems (coastal lagoon and open sea) after a log10-transformation. These statistics revealed differences in the chemical profiles and both qualitative and semi-quantitative composition of BVOCs across seasons and sites. An ANOVA test was applied to assess statistical differences between sites at each season in terms

of chemical diversity. In addition, correlations between all emitted compounds and environmental parameters (temperature (°C), salinity (PSU) and light (lumens m^{-2} d^{-1})) in the Thau and Urbino lagoons were assessed using Spearman's non-parametric correlation with the *cor.test* function. Only water temperatures and salinity at 4 a.m. were retained in order to exclude daily temperature variations linked to weather conditions. Daily Light was calculated as the total amount of light received per square meter per day (lumens m^{-2} d^{-1}), by summing 10 minutes-interval light intensity measurements over daylight hours.

Mean water temperature, salinity and light were then calculated for each month of sampling (Supplementary Table S2). The correlations selected are those that are significant and exceed 75%. To further distinguish the volatilome between Thau and Urbino sites in summer, a second RDA was performed. The 50 most discriminant compounds based on the length of the vectors on RDA1 were extracted to calculate a matrix dissimilarity on PubChem fingerprints. This matrix was used to generate and plot a molecular network with molNet and molNetPlot functions. These networks represent compound dissimilarities, calculated by compDis, and visualize their abundance simultaneously.

References

1. Goldstein, A. H. & Galbally, I. E. Known and unexplored organic constituents in the earth's atmosphere. *Environ. Sci. Technol.* **41**, 1514–1521 (2007).
2. Guenther, A. *et al.* A global model of natural volatile organic compound emissions. *J. Geophys. Res. Atmospheres* **100**, 8873–8892 (1995).
3. *Volatile Organic Compounds in the Atmosphere*. (Blackwell Pub, Oxford ; Ames, Iowa, 2007).
4. Dudareva, N., Klempien, A., Muhlemann, J. K. & Kaplan, I. Biosynthesis, function and metabolic engineering of plant volatile organic compounds. *New Phytol.* **198**, 16–32 (2013).

5. Ormeño, E. *et al.* Exogenous Isoprene Confers Physiological Benefits in a Negligible Isoprene Emitter (Acer monspessulanum L.) under Water Deficit. *Plants* **9**, 159 (2020).
6. Saunier, A. *et al.* Effect of mid-term drought on *Quercus pubescens* BVOCs' emission seasonality and their dependency on light and/or temperature. *Atmospheric Chem. Phys.* **17**, 7555–7566 (2017).
7. Llusia, J., Penuelas, J. & Gimeno, B. Seasonal and species-specific response of VOC emissions by Mediterranean woody plant to elevated ozone concentrations. *Atmos. Environ.* **36**, 3931–3938 (2002).
8. Lavoir, A.-V. *et al.* Drought reduced monoterpene emissions from the evergreen Mediterranean oak *Quercus ilex*: results from a throughfall displacement experiment. *Biogeosciences* **6**, 1167–1180 (2009).
9. Niinemets, Ü. Mild versus severe stress and BVOCs: thresholds, priming and consequences. *Trends Plant Sci.* **15**, 145–153 (2010).
10. Saunier, A. *et al.* Biogenic volatile organic compounds from marine benthic organisms: a review. *Mar. Environ. Res.* **209**, 107162 (2025).
11. Vickers, C. E., Gershenzon, J., Lerdau, M. T. & Loreto, F. A unified mechanism of action for volatile isoprenoids in plant abiotic stress. *Nat. Chem. Biol.* **5**, 283–291 (2009).
12. Pollastri, S., Baccelli, I. & Loreto, F. Isoprene: An Antioxidant Itself or a Molecule with Multiple Regulatory Functions in Plants? *Antioxidants* **10**, 684 (2021).
13. IPCC, I. P. O. C. C. *Climate Change 2022 – Impacts, Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. (Cambridge University Press, 2023). doi:10.1017/9781009325844.

14. Scott, C. E. *et al.* The direct and indirect radiative effects of biogenic secondary organic aerosol. *Atmospheric Chem. Phys.* **14**, 447–470 (2014).
15. Hallquist, M. *et al.* The formation, properties and impact of secondary organic aerosol: current and emerging issues. *Atmospheric Chem. Phys.* **9**, 5155–5236 (2009).
16. Cai, M., An, C. & Guy, C. A scientometric analysis and review of biogenic volatile organic compound emissions: Research hotspots, new frontiers, and environmental implications. *Renew. Sustain. Energy Rev.* **149**, 111317 (2021).
17. Rinnan, R., Steinke, M., Mcgenity, T. & Loreto, F. Plant volatiles in extreme terrestrial and marine environments. *Plant Cell Environ.* **37**, 1776–1789 (2014).
18. Saha, M. & Fink, P. Algal volatiles – the overlooked chemical language of aquatic primary producers. *Biol. Rev.* **97**, 2162–2173 (2022).
19. Kilgour, B. *et al.* Variation in toxicity and ecological risks associated with some oil sands groundwaters. *Sci. TOTAL Environ.* **659**, 1224–1233 (2019).
20. Zhao, M., Xiao, H., Sun, D. & Duan, S. Investigation of the Inhibitory Effects of Mangrove Leaves and Analysis of Their Active Components on Phaeocystis globosa during Different Stages of Leaf Age. *Int. J. Environ. Res. Public. Health* **15**, (2018).
21. Yu, Z. & Li, Y. Marine volatile organic compounds and their impacts on marine aerosol—A review. *Sci. Total Environ.* **768**, 145054 (2021).
22. Larkum, A. W. D. *et al.* Seagrass conservation biology: an interdisciplinary science for protection of the seagrass biome. *Seagrasses Biol. Ecol. Conserv.* 595–623 (2006).
23. Short, F. T. *et al.* Extinction risk assessment of the world's seagrass species. *Biol. Conserv.* **144**, 1961–1971 (2011).

24. Duarte, C. M., Middelburg, J. J. & Caraco, N. Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* **2**, 1–8 (2005).
25. Jayathilake, D. R. M. & Costello, M. J. A modelled global distribution of the seagrass biome. *Biol. Conserv.* **226**, 120–126 (2018).
26. Jiang, Z. *et al.* Home for Marine Species: Seagrass Leaves as Vital Spawning Grounds and Food Source. *Front. Mar. Sci.* **7**, (2020).
27. Monnier, B., Pergent, G., Mateo, M. Á., Clabaut, P. & Pergent-Martini, C. Quantification of blue carbon stocks associated with *Posidonia oceanica* seagrass meadows in Corsica (NW Mediterranean). *Sci. Total Environ.* **838**, 155864 (2022).
28. Fourqurean, J. W. *et al.* Seagrass ecosystems as a globally significant carbon stock. *Nat. Geosci.* **5**, 505–509 (2012).
29. Mateo, M. A., Romero, J., Pérez, M., Littler, M. M. & Littler, D. S. Dynamics of Millenary Organic Deposits Resulting from the Growth of the Mediterranean SeagrassPosidonia oceanica. *Estuar. Coast. Shelf Sci.* **44**, 103–110 (1997).
30. Waycott, M. *et al.* Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc. Natl. Acad. Sci. U. S. A.* **106**, 12377–12381 (2009).
31. Cabaço, S., Machás, R. & Santos, R. Individual and population plasticity of the seagrass *Zostera noltii* along a vertical intertidal gradient. *Estuar. Coast. Shelf Sci.* **82**, 301–308 (2009).
32. Peralta, G., Brun, F. G., Hernández, I., Vergara, J. J. & Pérez-Lloréns, J. L. Morphometric variations as acclimation mechanisms in *Zostera noltii* beds. *Estuar. Coast. Shelf Sci.* **64**, 347–356 (2005).

33. Soissons, L. M. *et al.* Seasonal and latitudinal variation in seagrass mechanical traits across Europe: The influence of local nutrient status and morphometric plasticity. *Limnol. Oceanogr.* **63**, 37–46 (2018).
34. Connell, S. D. *et al.* Testing for thresholds of ecosystem collapse in seagrass meadows. *Conserv. Biol.* **31**, 1196–1201 (2017).
35. Diffenbaugh, N. S., Pal, J. S., Giorgi, F. & Gao, X. Heat stress intensification in the Mediterranean climate change hotspot. *Geophys. Res. Lett.* **34**, (2007).
36. Zittis, G., Hadjinicolaou, P., Klangidou, M., Proestos, Y. & Lelieveld, J. A multi-model, multi-scenario, and multi-domain analysis of regional climate projections for the Mediterranean. *Reg. Environ. Change* **19**, 2621–2635 (2019).
37. Giorgi, F. Climate change hot-spots. *Geophys. Res. Lett.* **33**, (2006).
38. Tuel, A. & Eltahir, E. a. B. Why Is the Mediterranean a Climate Change Hot Spot? *J. Clim.* **33**, 5829–5843 (2020).
39. Soto-Navarro, J. *et al.* Evolution of Mediterranean Sea water properties under climate change scenarios in the Med-CORDEX ensemble. *Clim. Dyn.* **54**, 2135–2165 (2020).
40. Galli, G., Solidoro, C. & Lovato, T. Marine Heat Waves Hazard 3D Maps and the Risk for Low Motility Organisms in a Warming Mediterranean Sea. *Front. Mar. Sci.* **4**, (2017).
41. Giorgi, F. & Lionello, P. Climate change projections for the Mediterranean region. *Glob. Planet. Change* **63**, 90–104 (2008).
42. Pisano, A. *et al.* New Evidence of Mediterranean Climate Change and Variability from Sea Surface Temperature Observations. *Remote Sens.* **12**, (2020).

43. Darmaraki, S. *et al.* Future evolution of Marine Heatwaves in the Mediterranean Sea. *Clim. Dyn.* **53**, 1371–1392 (2019).
44. Holbrook, N. J. *et al.* A global assessment of marine heatwaves and their drivers. *Nat. Commun.* **10**, 2624 (2019).
45. von Schuckmann, K. *et al.* Copernicus Marine Service Ocean State Report, Issue 3. *J. Oper. Oceanogr.* **12**, S1–S123 (2019).
46. Garrabou, J., Ledoux, J.-B., Bensoussan, N., Gómez-Gras, D. & Linares, C. Sliding Toward the CollapseCollapse of Mediterranean Coastal Marine Rocky Ecosystems. in *Ecosystem Collapse and Climate Change* (eds Canadell, J. G. & Jackson, R. B.) 291–324 (Springer International Publishing, Cham, 2021). doi:10.1007/978-3-030-71330-0_11.
47. Ibrahim, O., Mohamed, B. & Nagy, H. Spatial Variability and Trends of Marine Heat Waves in the Eastern Mediterranean Sea over 39 Years. *J. Mar. Sci. Eng.* **9**, (2021).
48. Oliver, E. C. J. *et al.* Longer and more frequent marine heatwaves over the past century. *Nat. Commun.* **9**, 1324 (2018).
49. Lagarde, F. *et al.* Phénomène d'Eaux Vertes à Picochlorum en lagune de Thau pendant les années 2018 et 2019. Observations environnementales. https://doi.org/10.13155/80087 (2021) doi:10.13155/80087.
50. Derolez, V. *et al.* Hydrologie et phytoplancton des lagunes méditerranéennes sous pression du changement climatique (2001-2022) (Projet HYPHEAT'Lag). https://doi.org/10.13155/104925 (2025) doi:10.13155/104925.
51. Marin, M., Feng, M., Phillips, H. E. & Bindoff, N. L. A Global, Multiproduct Analysis of Coastal Marine Heatwaves: Distribution, Characteristics, and Long-Term Trends. *J. Geophys. Res. Oceans* **126**, e2020JC016708 (2021).

52. Cook, F. *et al.* Marine heatwaves in shallow coastal ecosystems are coupled with the atmosphere: Insights from half a century of daily in situ temperature records. *Front. Clim.* **4**, (2022).
53. Lloret, J., Marín, A. & Marín-Guirao, L. Is coastal lagoon eutrophication likely to be aggravated by global climate change? *Estuar. Coast. Shelf Sci.* **78**, 403–412 (2008).
54. De Wit, R. Biodiversity of coastal lagoon ecosystems and their vulnerability to global change. *Ecosyst. Biodivers.* **14**, (2011).
55. De los Santos, C. B. *et al.* Recent trend reversal for declining European seagrass meadows. *Nat. Commun.* **10**, 3356 (2019).
56. Chefaoui, R. M., Duarte, C. M. & Serrão, E. A. Dramatic loss of seagrass habitat under projected climate change in the Mediterranean Sea. *Glob. Change Biol.* **24**, 4919–4928 (2018).
57. Marbà, N., Díaz-Almela, E. & Duarte, C. M. Mediterranean seagrass (*Posidonia oceanica*) loss between 1842 and 2009. *Biol. Conserv.* **176**, 183–190 (2014).
58. Boudouresque, C. F., Bernard, G., Pergent, G., Shili, A. & Verlaque, M. Regression of Mediterranean seagrasses caused by natural processes and anthropogenic disturbances and stress: a critical review. **52**, 395–418 (2009).
59. Obrador, B., Moreno-Ostos, E. & Pretus, J. L. A dynamic model to simulate water level and salinity in a Mediterranean coastal lagoon. *Estuaries Coasts* **31**, 1117–1129 (2008).
60. Stumpp, C., Ekdal, A., Gönenc, I. & Maloszewski, P. Hydrological dynamics of water sources in a Mediterranean lagoon. *Hydrol. Earth Syst. Sci.* **18**, 4825–4837 (2014).

61. Garrido, M., Lafabrie, C., Torre, F., Fernandez, C. & Pasqualini, V. Resilience and stability of *Cymodocea nodosa* seagrass meadows over the last four decades in a Mediterranean lagoon. *Estuar. Coast. Shelf Sci.* **130**, 89–98 (2013).

62. Pergent, G. *et al. Mediterranean Seagrass Meadows : Resilience and Contribution to Climate Change Mitigation. A Short Summary.* (IUCN, 2012).

63. Bourdier-Lombardot, C., De Wit, R., Soissons, L., De Ronne, E. & Ouisse, V. Experimental Assessment of the Impact of Marine Heatwave Intensity on Three Marine Angiosperm Species in a Mediterranean Lagoon Environment. *Estuaries Coasts* **49**, 52 (2026).

64. Coquin, S. *et al.* Chemical Diversity of Mediterranean Seagrasses Volatilome. *Metabolites* **14**, 705 (2024).

65. Mirzayeva, A., Castro, R., G. Barroso, C. & Durán-Guerrero, E. Characterization and differentiation of seaweeds on the basis of their volatile composition. *Food Chem.* **336**, 127725 (2021).

66. Radman, S., Čagalj, M., Šimat, V. & Jerković, I. Seasonal Variability of Volatilome from Dictyota dichotoma. *Molecules* **27**, 3012 (2022).

67. Radman, S., Čagalj, M., Šimat, V. & Jerković, I. Seasonal Monitoring of Volatiles and Antioxidant Activity of Brown Alga Cladostephus spongiosus. *Mar. Drugs* **21**, 415 (2023).

68. Kajiwara, T. *et al.* Distribution of an enzyme system producing seaweed flavor: conversion of fatty acids to long-chain aldehydes in seaweeds. *J. Appl. Phycol.* **5**, 225–230 (1993).

69. Lawson, C. A., Possell, M., Seymour, J. R., Raina, J.-B. & Suggett, D. J. Coral endosymbionts (Symbiodiniaceae) emit species-specific volatilomes that shift when exposed to thermal stress. *Sci. Rep.* **9**, 17395 (2019).

70. Li, S. *et al.* A review of volatile compounds in edible macroalgae. *Food Res. Int.* **165**, 112559 (2023).
71. Peñuelas, J., Rutishauser, T. & Filella, I. Phenology Feedbacks on Climate Change. *Science* **324**, 887–888 (2009).
72. Satake, A. *et al.* Plant Molecular Phenology and Climate Feedbacks Mediated by BVOCs. *Annu. Rev. Plant Biol.* **75**, 605–627 (2024).
73. Brahim, M. B. *et al.* Bathymetric variation of epiphytic assemblages on Posidonia oceanica (L.) Delile leaves in relation to anthropogenic disturbance in the southeastern Mediterranean. *Environ. Sci. Pollut. Res.* **21**, 13588–13601 (2014).
74. Mabrouk, L., Ben Brahim, M., Hamza, A., Mahfoudhi, M. & Bradai, M. N. A Comparison of Abundance and Diversity of Epiphytic Microalgal Assemblages on the Leaves of the Seagrasses Posidonia oceanica (L.) and Cymodocea nodosa (Ucria) Asch in Eastern Tunisia. *J. Mar. Sci.* **2014**, 275305 (2014).
75. Lerdau, M., Litvak, M. & Monson, R. Plant chemical defense: monoterpenes and the growth-differentiation balance hypothesis. *Trends Ecol. Evol.* **9**, 58–61 (1994).
76. Loomis, W. Growth-differentiation balance vs. carbohydrate-nitrogen ratio. in vol. 29 240–245 (1932).
77. Shields, E. C., Parrish, D. & Moore, K. Short-Term Temperature Stress Results in Seagrass Community Shift in a Temperate Estuary. *Estuaries Coasts* **42**, 755–764 (2019).
78. Saunier, A. *et al.* Volatilome differences between native and invasive seagrass species in the Caribbean area. *Front. Mar. Sci.* **12**, (2025).

79. Meskhidze, N., Sabolis, A., Reed, R. & Kamykowski, D. Quantifying environmental stress-induced emissions of algal isoprene and monoterpenes using laboratory measurements. *Biogeosciences* **12**, 637–651 (2015).
80. Shaw, E. C., Gabric, A. J. & McTainsh, G. H. Response to comment on 'Impacts of aeolian dust deposition on phytoplankton dynamics in Queensland coastal waters'. *Mar. Freshw. Res.* **61**, 504–506 (2010).
81. Felemban, A., Braguy, J., Zurbriggen, M. D. & Al-Babili, S. Apocarotenoids involved in plant development and stress response. *Front. Plant Sci.* **10**, 1168 (2019).
82. Imtiaz, H., Arif, Y., Alam, P. & Hayat, S. Apocarotenoids biosynthesis, signaling regulation, crosstalk with phytohormone, and its role in stress tolerance. *Environ. Exp. Bot.* **210**, 105337 (2023).
83. Generalić Mekinić, I. *et al.* Seasonal Changes in Essential Oil Constituents of Cystoseira compressa: First Report. *Molecules* **26**, 6649 (2021).
84. Lawson, C. A. *et al.* Heat stress decreases the diversity, abundance and functional potential of coral gas emissions. *Glob. Change Biol.* **27**, 879–891 (2021).
85. Čagalj, M., Radman, S., Šimat, V. & Jerković, I. Detailed Chemical Prospecting of Volatile Organic Compounds Variations from Adriatic Macroalga *Halopteris scoparia*. *Mol. Basel Switz.* **27**, 4997 (2022).
86. Stobiecka, A. Comparative study on the free radical scavenging mechanism exerted by geraniol and geranylacetone using the combined experimental and theoretical approach. *Flavour Fragr. J.* **30**, 399–409 (2015).
87. Loreto, F. & Fineschi, S. Reconciling functions and evolution of isoprene emission in higher plants. *New Phytol.* **206**, 578–582 (2015).

88. Deschaseaux, E. S. M. *et al.* Effects of environmental factors on dimethylated sulfur compounds and their potential role in the antioxidant system of the coral holobiont. *Limnol. Oceanogr.* **59**, 758–768 (2014).
89. Fischer, E. & Jones, G. Atmospheric dimethysulphide production from corals in the Great Barrier Reef and links to solar radiation, climate and coral bleaching. *Biogeochemistry* **110**, 31–46 (2012).
90. Hopkins, F. E., Bell, T. G., Yang, M., Suggett, D. J. & Steinke, M. Air exposure of coral is a significant source of dimethylsulfide (DMS) to the atmosphere. *Sci. Rep.* **6**, 36031 (2016).
91. Ross, C. & Alstyne, K. L. V. Intraspecific variation in stress-induced hydrogen peroxide scavenging by the ulvoid macroalga ulva lactuca 1. *J. Phycol.* **43**, 466–474 (2007).
92. Sunda, W., Kieber, D. J., Kiene, R. P. & Huntsman, S. An antioxidant function for DMSP and DMS in marine algae. *Nature* **418**, 317–320 (2002).
93. Matsui, K. Green leaf volatiles: hydroperoxide lyase pathway of oxylipin metabolism. *Curr. Opin. Plant Biol.* **9**, 274–280 (2006).
94. Jerković, I. *et al.* Phytochemical study of the headspace volatile organic compounds of fresh algae and seagrass from the Adriatic Sea (single point collection). *PLOS ONE* **13**, e0196462 (2018).
95. La Camera, S. *et al.* Metabolic reprogramming in plant innate immunity: the contributions of phenylpropanoid and oxylipin pathways. *Immunol. Rev.* **198**, 267–284 (2004).
96. Marbà, N. *et al.* Growth and population dynamics of Posidonia oceanica on the Spanish Mediterranean coast: elucidating seagrass decline. *Mar. Ecol. Prog. Ser.* **137**, 203–213 (1996).

97. Pérez, M. & Romero, J. Photosynthetic response to light and temperature of the seagrass *Cymodocea nodosa* and the prediction of its seasonality. *Aquat. Bot.* **43**, 51–62 (1992).

98. Barman, M. & Mitra, A. Floral maturation and changing air temperatures influence scent volatiles biosynthesis and emission in *Jasminum auriculatum* Vahl. *Environ. Exp. Bot.* **181**, 104296 (2021).

99. Fu, X. *et al.* Benzene oxidation by Fe(III)-activated percarbonate: matrix-constituent effects and degradation pathways. *Chem. Eng. J.* **309**, 22–29 (2017).

100. Santos-Sánchez, N., Francenia, Salas-Coronado, R., Hernández-Carlos, B. & Villanueva-Cañongo, C. Shikimic Acid Pathway in Biosynthesis of Phenolic Compounds. in *Plant Physiological Aspects of Phenolic Compounds* (eds Soto-Hernández, M., García-Mateos, R. & Palma-Tenango, M.) (IntechOpen, 2019). doi:10.5772/intechopen.83815.

101. Sharma, A. *et al.* Response of Phenylpropanoid Pathway and the Role of Polyphenols in Plants under Abiotic Stress. *Molecules* **24**, 2452 (2019).

102. Jaganath, I. B. & Crozier, A. Dietary Flavonoids and Phenolic Compounds. in *Plant Phenolics and Human Health* 1–49 (John Wiley & Sons, Ltd, 2009). doi:10.1002/9780470531792.ch1.

103. De Agostini, A. *et al.* Volatile Organic Compounds (VOCs) Diversity in the Orchid Himantoglossum robertianum (Loisel.) P. Delforge from Sardinia (Italy). *Diversity* **14**, 1125 (2022).

104. Cebrián, J., Pedersen, M. F., Kroeger, K. D. & Valiela, I. Fate of production of the seagrass Cymodocea nodosa in different stages of meadow formation. *Mar. Ecol. Prog. Ser.* **204**, 119–130 (2000).

105. Drew, E. A. Factors affecting photosynthesis and its seasonal variation in the seagrasses Cymodocea nodosa (Ucria) Aschers, and Posidonia oceanica (L.) Delile in the Mediterranean. *J. Exp. Mar. Biol. Ecol.* **31**, 173–194 (1978).

106. Touchette, B. W. Seagrass-salinity interactions: physiological mechanisms used by submersed marine angiosperms for a life at sea. *J. Exp. Mar. Biol. Ecol.* **350**, 194–215 (2007).

107. Tyerman, S., Oats, P., Gibbs, J., Dracup, M. & Greenway, H. Turgor-volume regulation and cellular water relations of Nicotiana tabacum roots grown in high salinities. *Funct. Plant Biol.* **16**, 517–531 (1989).

108. Sandoval-Gil, J. M., Marín-Guirao, L. & Ruiz, J. M. Tolerance of Mediterranean seagrasses (Posidonia oceanica and Cymodocea nodosa) to hypersaline stress: water relations and osmolyte concentrations. *Mar. Biol.* **159**, 1129–1141 (2012).

109. Sandoval-Gil, J. M. *et al.* Plant–water relations of intertidal and subtidal seagrasses. *Mar. Ecol.* **36**, 1294–1310 (2015).

110. Flowers, T. J. & Colmer, T. D. Salinity tolerance in halophytes. *New Phytol.* 945–963 (2008).

111. Murphy, L. R., Kinsey, S. T. & Durako, M. J. Physiological effects of short-term salinity changes on Ruppia maritima. *Aquat. Bot.* **75**, 293–309 (2003).

112. Pulich Jr, W. M. Variations in leaf soluble amino acids and ammonium content in subtropical seagrasses related to salinity stress. *Plant Physiol.* **80**, 283–286 (1986).

113. Berneira, L. M. *et al.* Evaluation of volatile organic compounds in brown and red sub-Antarctic macroalgae. *Braz. J. Bot.* **44**, 79–84 (2021).

114. Jahangir, M., Abdel-Farid, I. B., Kim, H. K., Choi, Y. H. & Verpoorte, R. Healthy and unhealthy plants: The effect of stress on the metabolism of Brassicaceae. *Environ. Exp. Bot.* **67**, 23–33 (2009).

115. Kajiwara, T., Matsui, K., Akakabe, Y., Murakawa, T. & Arai, C. Antimicrobial Browning-Inhibitory Effect of Flavor Compounds in Seaweeds. *J. Appl. Phycol.* **18**, 413–422 (2006).

116. Kamenarska, Z. *et al.* Volatile compounds from some Black Sea red algae and their chemotaxonomic application. (2006).

117. Bullock, H. A., Luo, H. & Whitman, W. B. Evolution of Dimethylsulfoniopropionate Metabolism in Marine Phytoplankton and Bacteria. *Front. Microbiol.* **8**, (2017).

118. Kirst, G. O. Osmotic Adjustment in Phytoplankton and MacroAlgae. in *Biological and Environmental Chemistry of DMSP and Related Sulfonium Compounds* (eds Kiene, R. P., Visscher, P. T., Keller, M. D. & Kirst, G. O.) 121–129 (Springer US, Boston, MA, 1996). doi:10.1007/978-1-4613-0377-0_11.

119. Zhuang, G., Yang, G., Yu, J. & Gao, Y. Production of DMS and DMSP in different physiological stages and salinity conditions in two marine algae. *Chin. J. Oceanol. Limnol.* **29**, 369–377 (2011).

120. Pirc, H. Seasonal changes in soluble carbohydrates, starch, and energy content in Mediterranean seagrasses. *Mar. Ecol.* **10**, 97–105 (1989).

121. Pirc, H. & Wollenweber, B. Seasonal changes in nitrogen, free amino acids, and C/N ratio in Mediterranean seagrasses. *Mar. Ecol.* **9**, 167–179 (1988).

122. Saunier, A. *et al.* BVOC emissions from Posidonia oceanica, the most abundant Mediterranean seagrass species. *Chemosphere* **378**, 144392 (2025).

123. Grignon-Dubois, M. & Rezzonico, B. Phenolic chemistry of the seagrass *Zostera noltei* Hornem. Part 1: First evidence of three infraspecific flavonoid chemotypes in three distinctive geographical regions. *Phytochemistry* **146**, 91–101 (2018).

124. Alberto, F. *et al.* Genetic differentiation and secondary contact zone in the seagrass Cymodocea nodosa across the Mediterranean–Atlantic transition region. *J. Biogeogr.* **35**, 1279–1294 (2008).

125. Gkafas, G. *et al.* Genetic diversity and structure of Cymodocea nodosa meadows in the Aegean Sea, eastern Mediterranean. *Appl. Ecol. Environ. Res.* **14**, 145–160 (2016).

126. Cataudella, S., Crosetti, D. & Massa, F. Mediterranean coastal lagoons: sustainable management and interactions among aquaculture, capture fisheries and the environment. *Gen. Fish. Comm. Mediterr. Stud. Rev.* I (2015).

127. Ruitton, S., Mayot, N. & Astruch, P. *Etude et Cartographie Des Biocénoses Marines Remarquables Du Golfe de Fos (Bouches-Du-Rhône, France). Synthèse Bibliographique.* 1–66 (2008).

128. Letourneur, Y., Darnaude, A., Salen-picard, C. & Harmelin-vivien, M. Spatial and temporal variations of fish assemblages in a shallow Mediterranean soft-bottom area (Gulf of Fos, France). *Oceanol. Acta* **24**, 273–285 (2001).

129. Chao, A., Chiu, C.-H. & Jost, L. Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annu. Rev. Ecol. Evol. Syst.* **45**, 297–324 (2014).

130. Petrén, H., Köllner, T. G. & Junker, R. R. Quantifying chemodiversity considering biochemical and structural properties of compounds with the R package chemodiv. *New Phytol.* **237**, 2478–2492 (2023).

131. Kim, H. W. *et al.* NPClassifier: a deep neural network-based structural classification tool for natural products. *J. Nat. Prod.* **84**, 2795–2807 (2021).

132. Chiu, C.-H. & Chao, A. Distance-based functional diversity measures and their decomposition: a framework based on Hill numbers. *PloS One* **9**, e100014 (2014).

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Figures

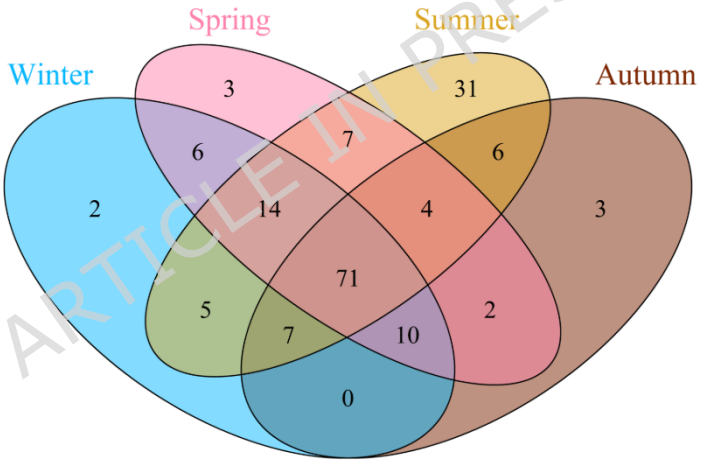

Figure 1 - Venn diagram analysis of the number of shared and season-specific volatile compounds in *Cymodocea nodosa* between seasons.

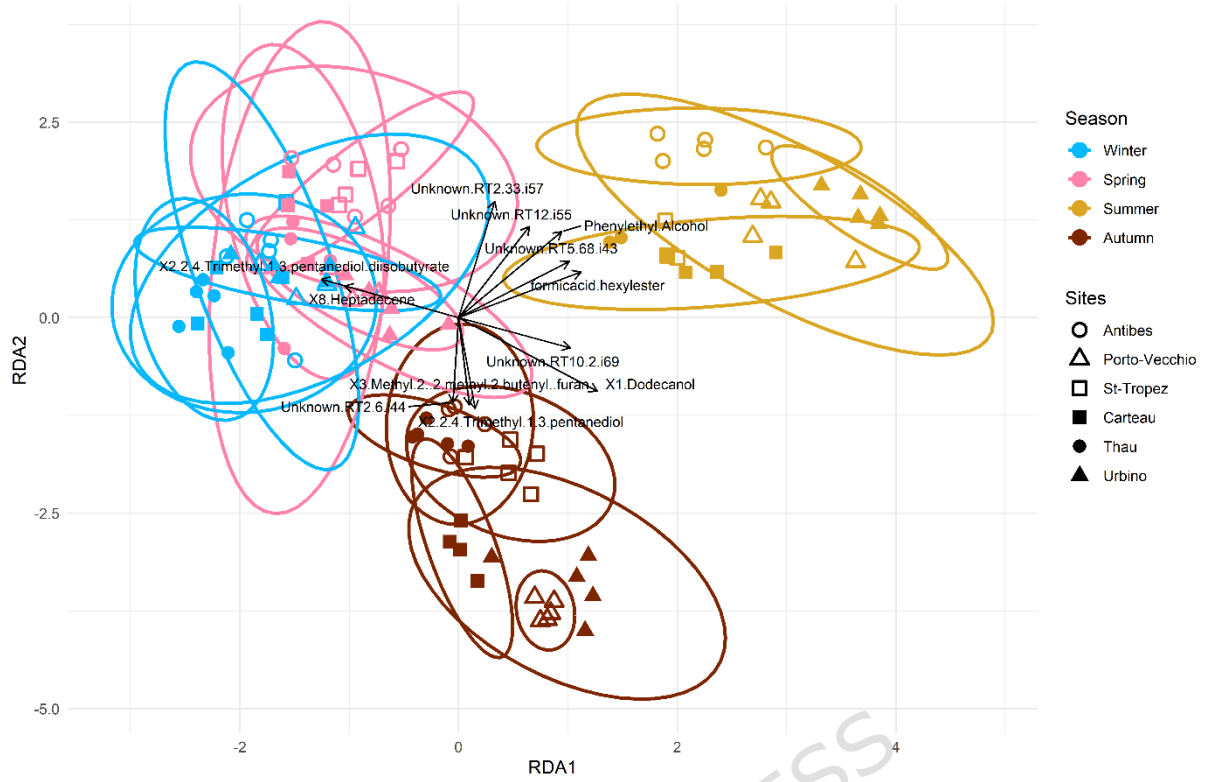

Figure 2 - Graphical representation of the RDA model differentiating the volatilome of *Cymodocea nodosa* according to season (colors) and sampling sites (shape).

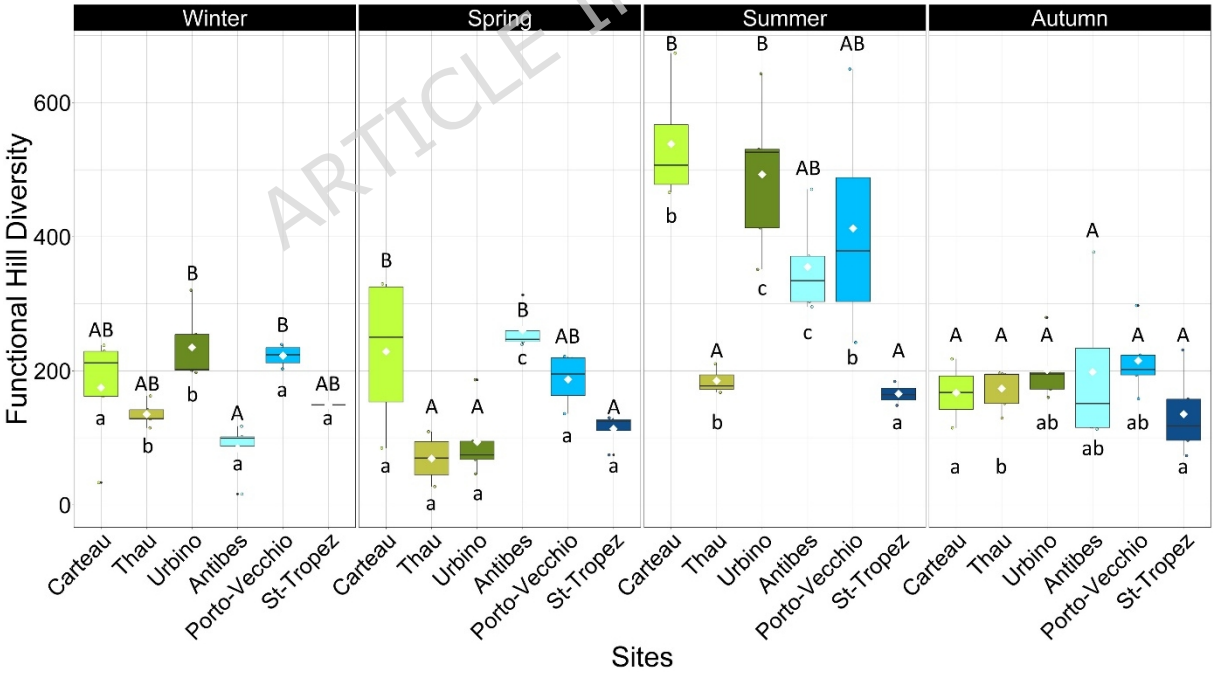

Figure 3 - Chemoecological indexes of volatile compounds produced by *Cymodocea nodosa* per site and per season. In green the coastal lagoon sites and in blue the open sea sites. Bars represent mean ± SE with n = 5. The white squares with the value indicate the mean index. Two ways ANOVA was performed

to highlight differences between sites and season and significant variations were detected (*p-value* < 0.05). Capital letters indicate significant differences between sites per season with A < B and lowercase letters indicate significant differences between sites through seasons with a < b < c.

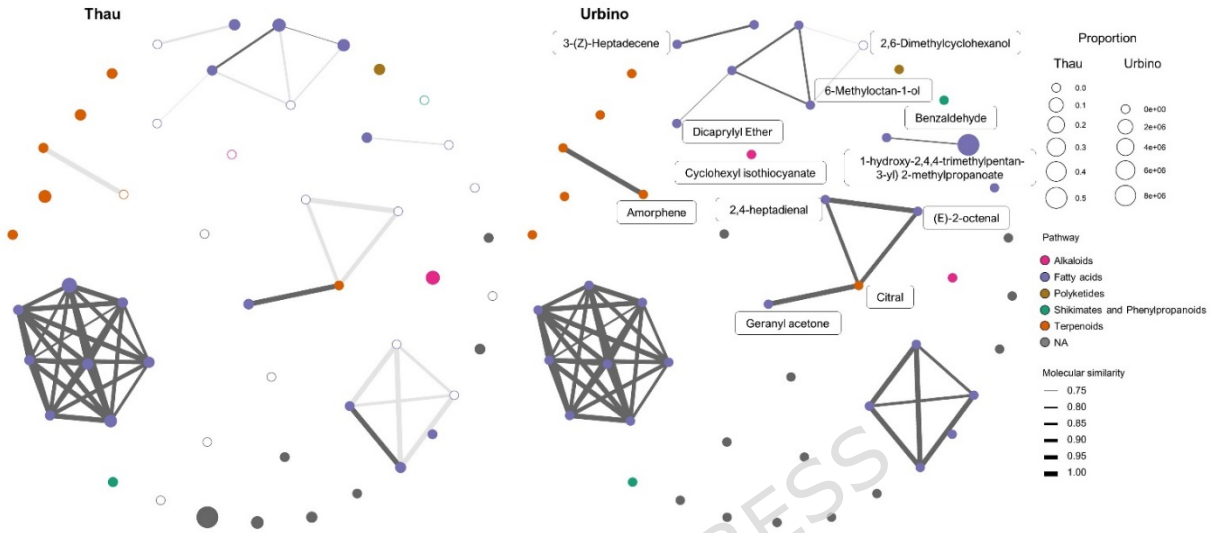

Figure 4 - Molecular networks of the 50 first discriminated compounds in RDA model found in *Cymodocea nodosa* during summer in Thau lagoon (at the left) and in Urbino lagoon (at the right), visualized by the molNetPlot function in the CHEMODIV package. Edge width represents similarities ≥ 0.75 between compounds. 'NA' indicates that the compound could not be classified. Node colour represents the pathway classification from NPClassifier (white fill represents zero values), and the node size represents proportional abundance. The labeled compounds highlight the main compounds in clusters and differences between the two networks.

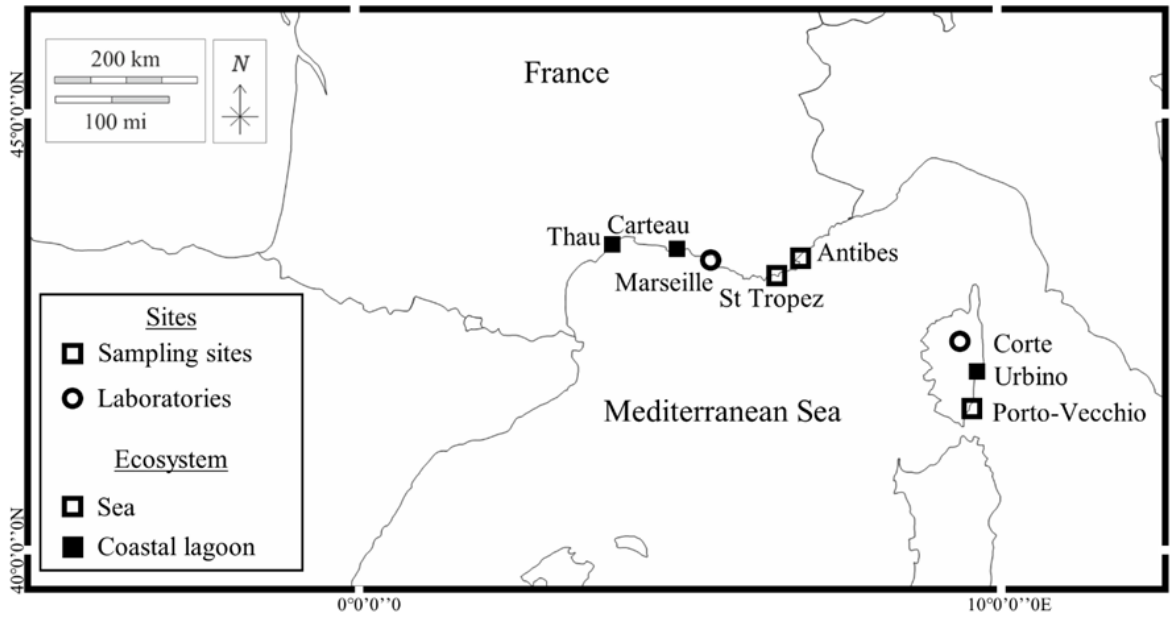

Figure 5- Sampling sites of *Cymodocea nodosa* in western Mediterranean Sea (square shapes) in three coastal lagoons (filled squares) and three open sea-sites (unfilled shapes) and laboratory analysis sites (circle shapes).

Table 1 - Spearman's correlation coefficient (ρ) highlighting the compounds emitted by Cymodocea nodosa in the Thau and Urbino lagoons, that significantly correlated at over 75% with temperature; p< 0.01 (**), p< 0.001 (***).

Sites	Compounds	**ρ**	p
Thau	B-Ionone	0.96	***
	B-Cyclocitral	0.93	***
	Dihydro-B-Ionone	0.86	***
	1-Propyloctyl Benzene	0.86	***
	1-Butylheptyl Benzene	0.82	***
	1-Ethylnonyl Benzene	0.82	***
	Unknown.Rt7.6.I41	0.81	***
	2, 6-Dimethylcyclohexanol	0.76	***
	Dimethylsulfide	0.76	***
	Decanal	0.75	***
	Dihydroactinidiolide	0.72	**
	Hexadecane	-0.92	***
	Octadecane	-0.92	***
	8-Heptadecene	-0.9	***
	Heptadecane	-0.85	***

	2, 2, 4-Trimethyl-1, 3-Pentanediol Diisobutyrate	-0.85	***
	Nonadecane	-0.82	***
	3-Z-Heptadecene	-0.8	***
	Butyl Octyl Phthalate	-0.8	***
Urbino	B-Cyclocitral	0.95	***
	Unknown.Rt10.2.I69	0.89	***
	B-Ionone	0.87	***
	2-Pentylfuran	0.87	***
	Cis-Geraniol	0.85	***
	Dms	0.84	***
	Unknown.Rt10.45.I69	0.83	***
	(Z)-3-Heptadecene	0.82	***
	Unknown.Rt37.8.I100	0.8	***
	1-Pentadecene	0.8	***
	Dihydroactinidiolide	0.78	***
	Geranyl Acetone	0.78	***
	Benzaldehyde	0.77	***
	2, 4-Heptadienal	0.76	***
	Farnesane	0.76	***
	Pentanoic Acid, 2, 2, 4-Trimethyl-3-Carboxyisopropyl, Isobutyl Ester	0.76	***
	Hexyl Formate	0.76	***
	Menthol	0.76	***
	Unknown.Rt41.I105	0.76	***
	Unknown.Rt8.5.I57	0.76	***
	Phenylethyl Alcohol	0.76	***
	Trans-Calamenene	0.76	***
	1-Dodecanol	0.76	***
	Methoxy-Phenyl-Oxime	0.75	***
	1-Ethylnonyl Benzene	-0.94	***
	2, 2, 4-Trimethyl-1, 3-Pentanediol Diisobutyrate	-0.85	***
	1-Propylnonyl Benzene	-0.79	***
	Octadecane	-0.78	***
	B-Ionone Epoxide	-0.77	***
	Unknown.Rt 32.9.I105	-0.76	***

Table 2 - - Spearman's correlation coefficient (ρ) highlighting the compounds emitted by Cymodocea nodosa in the Thau and Urbino lagoons, that significantly correlated at over 75% with light (p< 0.001).

Sites	Compounds	**P**
Thau	Unknown.Rt12.I55	0.84
	1-Butylheptyl Benzene	0.76
	1-Ethylnonyl Benzene	0.76
	Unknown.Rt33.8.I227	-0.95
	Nonadecane	-0.85
	Eicosane	-0.85
	9-Nonadecene	-0.83
	Tridecanal	-0.82
	Heneicosane	-0.81
	(Z)-3-Heptadecene	-0.8
	1-Heptadecene	-0.76
Urbino	Geranyl Acetone	0.96
	Unknown.Rt10.45.I69	0.83
	Unknown.Rt5.68.I43	0.82
	Unknown.Rt12.I55	0.79
	B-Cyclocitral	0.79
	2, 4-Heptadienal	0.76
	Farnesane	0.76
	Pentanoic Acid, 2, 2, 4-Trimethyl-3-Carboxyisopropyl, Isobutyl Ester	0.76
	Hexyl Formate	0.76
	Menthol	0.76
	Unknown.Rt41.I105	0.76
	Unknown.Rt8.5.I57	0.76
	Phenylethyl Alcohol	0.76
	Trans-Calamenene	0.76
	Unknown.Rt32.9.I105	-0.76

Table 3 - Spearman's correlation coefficient (ρ) highlighting the compounds emitted by Cymodocea nodosa in the Thau and Urbino lagoons, that significantly correlated at over 75% with salinity (p< 0.001).

Sites	Compounds	**ρ**
Thau	Cis-Geraniol	0.96
	Citral	0.95
	Neral	0.8
Urbino	N-Decanoic-Acid	0.76

1-Chlorododecane	0.76
B-Farnesene	0.76
1-Dodecanol	0.76
Dihydroactinidiolide	0.76
Hexadecane	-0.95
Heptadecane	-0.92
B-Ionone Epoxide	-0.89
2, 2, 4-Trimethyl-1, 3-Pentanediol Diisobutyrate	-0.81
Octadecane	-0.78
Nonadecane	-0.76