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Volatilome differences between native and invasive seagrass species in the Caribbean area

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Biological invasions are one of the major threats to ecosystem services and biodiversity. Thus, it is crucial to understand the mechanisms involved in the invasion success of alien species. In addition to generalist traits and high tolerance that enable persistence in novel environments, invasive species can use volatile chemical compounds from specialized metabolism [biogenic volatile organic compounds (BVOCs)] to compete with native species, a process known as allelopathy. These compounds could contribute to invasions in marine environments, and the associated mechanisms need to be deciphered. The aim of this study was to characterize the volatilome (i.e., all BVOCs produced by a species) of two Caribbean native seagrass species (*Syringodium filiforme* and *Thalassia testudinum*) and one invasive (*Halophila stipulacea*). For that purpose, leaf samples were collected, and BVOCs were trapped through headspace solid-phase microextraction followed by analyses in GC-MS. *H. stipulacea*'s volatilome was significantly different from the two native species, with the presence of compounds showing, in literature, allelochemical properties (e.g., geranyl acetone, 6-methyl, 5-hepten-2-one, and cyclohexane isothiocyanate). We hypothesized that these compounds could be "novel weapons" to enhance the invasion success of *H. stipulacea*, but it needs further investigations in the laboratory (e.g., mesocosms) as well as *in situ*.

KEYWORDS

BVOCs, seagrass, biological invasions, allelopathy, chemical weapon

Introduction

Biological invasions are considered as one of the major threats to native ecosystems' integrity (Ehrenfeld, 2010). Invasive species, once settled, can affect ecological processes (Gandhi and Herms, 2010), engineer ecosystem structure (Crooks, 2002), or affect community dynamics (Yurkonis et al., 2005). Therefore, they can significantly alter ecosystem functioning that may result in a significant modification of ecosystem services provided. Moreover, this threat will increase with climate change (Hulme, 2017). Thus, it is crucial to understand underlying mechanisms to biological invasions to better counteract

their consequences. However, most of the studies on biological invasions are performed on terrestrial environments, whereas marine environments are still poorly studied (Lowry et al., 2013; Mačić et al., 2018) despite the highlighting of numerous biological invasions (Chan and Briski, 2017; Rilov and Crooks, 2009).

Halophila stipulacea, a native seagrass from the Indian Ocean and the Red Sea (Mejia et al., 2016; Spalding et al., 2003), is considered a highly invasive species (Lowe et al., 2000; Winters et al., 2020). In the Mediterranean Sea, the first occurrences of *H. stipulacea* were recorded in 1894 near Greek coasts following the opening of the Suez Canal in 1869 (Winters et al., 2020). Even though this species is now found in many places, especially in eastern parts of the Mediterranean Sea (e.g., Greece, Tunisia, Libya, Syria, and Lebanon; Sghaier et al., 2011), observations point toward a relatively limited “invasion success” in this region (Nguyen et al., 2020). However, in the Caribbean Sea, where it was observed for the first time in 2002 near Grenada (Ruiz and Ballantine, 2004), *H. stipulacea* quickly colonized a large part of the Eastern Caribbean (e.g., Dominica, Martinique, and Virgin Islands) as well as the coasts of South America (e.g., Venezuela) in a decade (Winters et al., 2020). Moreover, it has been shown that *H. stipulacea* even displaces native seagrass species (e.g., *Syringodium filiforme*) by monopolizing their spaces (Willette and Ambrose, 2012), whereas in the Mediterranean Sea, *H. stipulacea* forms multispecies beds, especially with *Cymodocea nodosa* (Chiquillo et al., 2023). These differences in *H. stipulacea* invasion success between both areas is probably due to warmer conditions in the Caribbean Sea compared to the Mediterranean Sea. The actual tropicalization of the Mediterranean Sea could increase the invasiveness potential of *H. stipulacea* (Nguyen et al., 2020). For example, in Cap Monastir, a small patch of *H. stipulacea* (0.2 ha) covered more than 2 ha after only 4 years and displaced *C. nodosa* (Sghaier et al., 2014). Thus, this species starts to colonize northern and western parts of the Mediterranean Sea and could be an important problem in the future (Thibaut et al., 2022).

Numerous studies have highlighted what are the characteristics that make a non-native species a successful invader (Van Kleunen et al., 2010). In principle, they should present high reproductive capacity (sexual and/or asexual), wide phenotypic plasticity, high dispersal ability, and strong competitive ability. *H. stipulacea* presents those characteristics, namely a high tolerance to irradiance (35 to 450 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), to salinity levels (24 to 70 g.L⁻¹), as well as to water temperatures (17°C–42°C, Winters et al., 2020). Moreover, this species also shows a very efficient asexual reproduction by fragmentation or vegetative rhizome growth (Smulders et al., 2017) and is more fecund than larger seagrass species (Malm, 2006). Furthermore, the receiving environment should, in theory, exhibit “invadable” characteristics such as an elevated level of disturbance for the native species, availability of empty niches, a low level of biotic resistance, and a high availability of resources (Olyarnik et al., 2009). It has been thought that *H. stipulacea* only colonized disturbed native ecosystems. However, new evidence in the field showed that *H. stipulacea* displaces native species in the Caribbean Sea and, to a lesser extent, in the Mediterranean sea (Sghaier et al., 2014; Willette and Ambrose,

2012). Chiquillo et al. (2023) have demonstrated that *H. stipulacea* had a negative impact on *S. filiforme* and *C. nodosa* growth, whereas the presence of native species facilitates *H. stipulacea* settlement in a laboratory experiment. These results strongly indicate that this species is a driver of its own invasion success, implying that *H. stipulacea* can invade intact native ecosystems.

Allelochemicals mostly belong to specialized metabolism and act as defense compounds to suppress other plant competitors (Kong et al., 2019). Among those compounds, it has been shown that biogenic volatile organic compounds (BVOCs) are allelochemicals in terrestrial environments (Effah et al., 2019; Santonja et al., 2019; Xie et al., 2021). For instance, BVOCs emitted by *Solanum lycopersicum* foliage inhibited seed germination of the tropical species *Amaranthus mangostanus* (Kim and Kil, 2001). It has been hypothesized that BVOCs from invasive species could enhance their competitiveness since they could inhibit native species germination and/or growth, with the magnitude of the effect being regulated by co-evolution (Clavijo McCormick et al., 2023; Mollo et al., 2015). Thus, according to this hypothesis, species A would be more prepared for the biochemicals of species B if they evolved together compared to species C, which came from another biome (Callaway and Ridenour, 2004). Similar allelopathic processes, involving BVOCs, were also highlighted in marine environments (Allen et al., 2016; Sudatti et al., 2020), such as octanol showing an inhibitory effect on spore germination of *Ulva prolifera* (Zhang et al., 2014). Since BVOCs are lipophilic molecules, they are insoluble in water. When mediating marine species interactions, we consider that they are mainly involved in short-range or contact communication in marine environments (Mollo et al., 2014). However, they could also act on higher ranges since BVOCs can move in water through filaments over long distances (Webster and Weissburg, 2009) or their solubility can be punctually increased by water physico-chemical properties (Sander, 2023). To really decipher the action range of marine BVOCs, further investigations are required.

The aims of this study were to highlight the volatilome (i.e., all volatile compounds from a species) of the three main seagrass species from Martinique. In this area, *H. stipulacea* was detected in 2006 for the first time. Its presence was confirmed in 2010, and since then, the species has shown a wide distribution along the Martinique coasts at the expense of native species, mainly *S. filiforme* (Maréchal et al., 2013). Our hypothesis is that *H. stipulacea* could have a different volatilome compared to both native species, which might explain a part of its invasion success in the Caribbean area. Moreover, we expected to detect compounds from *H. stipulacea* having allelopathic properties, in comparison to literature, highlighted in terrestrial and marine species.

Materials and methods

Plant material

Three seagrass species were studied: two endemic species, namely, *Thalassia testudinum* and *Syringodium filiforme*, and the

invasive species *Halophila stipulacea*. *T. testudinum* and *H. stipulacea* belongs to Hydrocharitaceae, whereas *S. filiforme* belongs to the Cymodoceaceae family. The three species were located on the same site, Grande Anse d'Arlet (N14°29'34"O61°5'10"). Sampling was done on the 27th of November 2024 and kept in seawater during the transportation to the laboratory.

Headspace solid-phase microextraction

BVOCs collection was performed according to methods used in Coquin et al. (2024). It was done within 24h after seagrass harvesting. Before collection, each sample was taken out of the tanks, and each leaf was gently scraped with a scalpel to remove epiphytes while taking care to prevent leaf damage. One gram of cut fresh leaves was placed into small pieces in 20-ml glass vials and hermetically sealed with PTFE/silicone septa. Vials were maintained in a water bath at 50°C for 10 min for equilibrium, and the headspace solid-phase microextraction collection took place for 1h. Collection of BVOCs from the headspace was carried out manually using an SPME fiber (DVB/CAR/PDMS, Supelco Co., Bellefonte, USA). Blanks were performed using the same vials without plant material. After sampling, the SPME fibers were stored at −20°C before injection in GC-MS. BVOCs collection was carried out in six replicates for each species.

Gas chromatography–mass spectrometry analyses

Analyses were performed according to methods used in Coquin et al. (2024) on a GC instrument (7890B GC, Agilent Technologies, Santa Clara, USA) equipped with an HP5-MS column (30 m × 0.25 mm × 0.25 µm, Agilent Technologies, Santa Clara, USA) coupled to an MS instrument (MSD5977A, Agilent Technologies, Santa Clara, USA). Thermal desorption of the fibers was directly carried out to the GC column through the injector for 15 min at 250°C in splitless mode. The gradient temperature was initially set at 70°C (2 min), then reached 200°C at 3°C/min^{−1} and finally reached 315°C at 15°C/min^{−1}. This temperature was, then, held for 5 min. Helium was used as a carrier gas with a constant flow of 1 ml/min^{−1}. The EI mode was operated at 70 eV, and the mass range was 40–450 amu. The identification of VOCs was based on the comparison of their retention indices (RIs), determined using the retention times of a series of alkanes (C₈ to C₄₀), and on a spectral match with the NIST20 mass spectral libraries. In parallel, blank samples, which consisted of sampling without plant material, were performed. Then, compounds detected in blanks were subtracted from samples.

Chemical profile

To highlight chemical profiles of each species, compounds were classed according to their chemical family/biosynthesis pathway (alcohol, alkane, alkene, aldehyde, benzenoid, terpene, sulfur/

nitrogen compound, halogenated compound, and other). Then, relative abundances of groups, in percentage, were calculated. Moreover, a Venn diagram was built according to detected specific compounds per species through Venny 2.0.2 (<https://bioinfogp.cnb.csic.es/tools/venny/index2.0.2.html>).

Statistical analyses

All statistical analyses were performed on absolute abundances with R software (4.3.3) and metaboanalyst (<https://www.metaboanalyst.ca/>). Partial Least Squares–Discriminant Analysis (PLS-DA) was performed with the RVAideMemoire and pls packages on non-transformed and auto-scaled (mean 0, standard deviation 1) data, giving all compounds equal weight. To highlight volatilome differences according to species, PERMANOVA and pairwise tests were performed to test differences between groups (1,000 permutations for each). VIP scores (Variable Importance in Projection), obtained through PLS-DA, were used to highlight the ten most discriminant compounds. A VIP score summarizes the variable contribution to the model. A variable is considered relevant for the model when its VIP score is above 1. Then, Kruskal–Wallis tests followed by a Dunn post-hoc test were performed on these compounds between species after checking the normality and the homoscedasticity of the dataset.

Results

A total of 104 compounds were detected (Supplementary Files S1), with 90, 89, and 85 compounds present in *H. stipulacea*, *S. filiforme*, and *T. testudinum*, respectively (Figure 1A). The three species shared numerous compounds but also presented specific compounds (6 for *H. stipulacea*, 8 for *S. filiforme*, and 3 for *T. testudinum*). Volatilome profiles between species were quite different, with alcohol (e.g., 3-hexen-1-ol) being the major component of *S. filiforme* and *T. testudinum* (24.6 and 74.5%, respectively, Figure 1B). Then, *S. filiforme* volatilome included alkene (16.9%, e.g., 1-pentadecene) and aldehyde (9.6%, e.g., decanal). Concerning *T. testudinum*, the second major components were aldehyde (5.8%) followed by alkane (5.6%). By contrast, for *H. stipulacea*, major compounds of its volatilome were alkanes, representing 35% (e.g., tridecane), followed by aldehyde (15.8%) and alcohol (9.6%).

Then, to go further, PLS-DA were performed to take into account the volatilome profile as well as the compounds abundance (Figure 2). The Classification Error Rate (CER) equals to 0.14, indicated that this analyse was quite robust. PLS-DA showed that volatilomes were graphically separated from each other, suggesting that the three species had different volatilomes (in terms of compounds and abundance). This result was confirmed by PERMANOVA, indicating a significant effect of species (p -value<0.01). Then, pairwise test was performed to highlight differences between species and clearly showed that *H. stipulacea* volatilome was different from the two other species (p -value<0.01) whereas native species did not show any difference in their volatilome. According to VIP scores extracted from PLS-DA

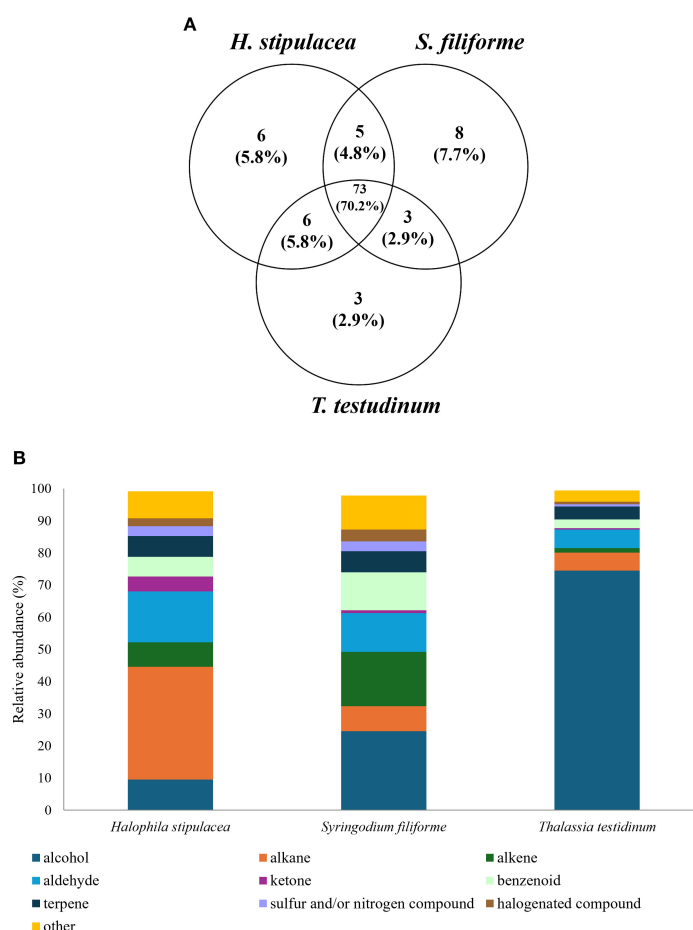


FIGURE 1

(A) Venn diagram based on detected compounds for each species and (B) Volatilome profiles according to chemical families (alcohol, alkane, alkene, aldehyde, ketone, benzenoid, terpene, sulfur and/or nitrogen compound, halogenated compound, and other) in relative abundance (%) according to the species with $n=6$.

(1.5<VIP scores, [Supplementary Files S2](#)), 10 compounds were highlighted as the most discriminant between the three species ([Table 1](#)).

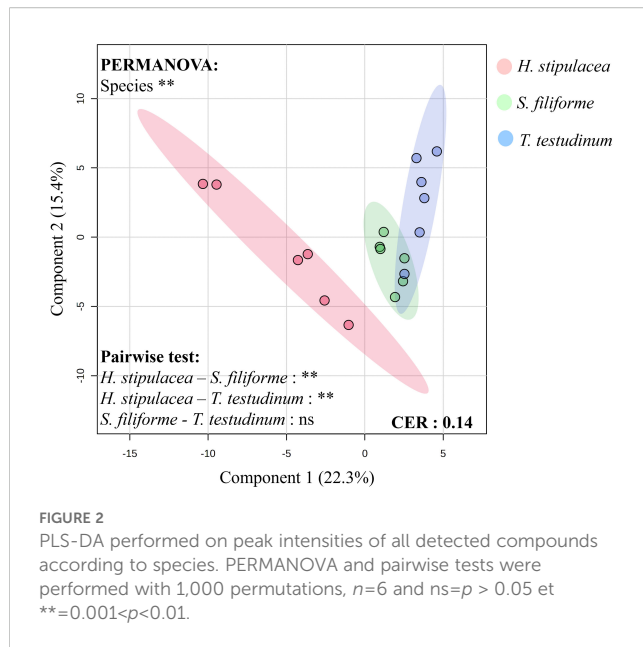
Nine of the 10 most discriminant compounds were present in higher quantities in *H. stipulacea* by 2 to 63-fold more. Only 3-hexen-1-ol abundance were higher in *T. testudinum* compared to both other species.

Discussion

Our results showed, for the first time in the Caribbean area, that the invasive seagrass *H. stipulacea* had a volatilome significantly different from both native species, *S. filiforme* and *T. testudinum* (both showing similar volatilomes). This suggests that volatilomes do not seem to be driven by phylogeny since both species belonging to the same family showed different volatilomes (*T. testudinum* and *H. stipulacea* from the Hydrocharitaceae family). Similar findings have been highlighted on bryophytes ([Yáñez-Serrano et al., 2024](#)). Moreover, our results revealed the presence of several compounds in *H. stipulacea* volatilome, highlighted as allelochemicals in literature. For instance, within the

most discriminant compounds, apocarotenoids (geranyl acetone and 6-methyl, 5-hepten-2-one also known as sulcatone) and isothiocyanates (cyclohexane, isothiocyanate) have shown strong allelopathic effects in terrestrial and marine species, as discussed below ([Moreno et al., 2021](#); [Motmainna et al., 2021](#)).

Regarding the apocarotenoids, [Jüttner \(1979\)](#) showed an inhibition of cyanobacterial growth when exposed to 6-methyl, 5-hepten-2-one and even a lethal effect for geranyl acetone. Similar inhibitory effects on growth were highlighted on a green microalga, *Auxenochlorella pyrenoidosa*, until a concentration threshold ($10\text{mg}\cdot\text{ml}^{-1}$) where no growth was observed ([Ikawa et al., 2001](#)). That could result in disturbances of both glucose uptake and respiration and/or on pigment production as shown on freshwater isolates of *Chromobacterium lividum* and *Arthrobacter* sp ([Reichardt, 1981](#)). Another type of allelochemical has been highlighted in our study, namely cyclohexane isothiocyanate. This compound belongs to isothiocyanates, well known to be produced through the degradation of glucosinolates by the enzyme myrosinase ([Kliebenstein et al., 2005](#)). It has been shown that Brassicaceae extracts, the main terrestrial plant family producing isothiocyanates ([Ramirez et al., 2020](#)), reduced germination and



growth in several legume species such as *Phaseolus vulgaris*, *Medicago sativa*, and *Cuscuta campestris* (Almhemed and Ustuner, 2023; Choesin and Boerner, 1991; Smith, 2000). It has to be noted that other compounds detected in *H. stipulacea* present also allelopathic impacts (e.g., DMS, dihydroactinidiolide, and terpenoids), although they are less abundant than the previously discussed compounds. All together, these compounds could help *H. stipulacea* in its invasion success and to settle into a new habitat and replace native species, but this needs further investigation.

Study limitations

Observations from previous works showed that *H. stipulacea* affected native species growth under control and field conditions in

both Caribbean and Mediterranean seas and even, replaced them in some specific locations (Chiquillo et al., 2023; Sghaier et al., 2014; Willette and Ambrose, 2012). This invasion success can be explained by its high tolerance to wide ranges of environmental conditions implying a better capacity to compete with native species (Winters et al., 2020). In addition, allelopathic effects from *H. stipulacea* could potentially enhance its invasion success but this is not investigated yet. Our work brings evidence on the presence of several compounds with such properties present in higher abundances in the invasive species (e.g., isothiocyanates and apocarotenoids). Even though allelopathic effects of these compounds were not tested in this study, these compounds have shown allelopathic effects in literature. Moreover, the *H. stipulacea* exotic volatilome, compared to native species, could be an advantage for its invasion success in this region (Winters et al., 2020). According to the theory, the strength of allelopathic effects is conditioned by evolutionary history shared by community species (Callaway and Aschehoug, 2000; Hierro and Callaway, 2021). Therefore, the introduction of an alien species in a native environment can alter habitats by releasing specialized metabolites (volatile and non-volatile) and can be considered as a « novel weapon » for the successful invasion of an alien species (Callaway and Ridenour, 2004). It has been already demonstrated, in terrestrial environments, with greater allelopathic effects of the invasive weed *Chromolaena odorata*, originating from South America, on Chinese native species compared to another South American species (Hu and Zhang, 2013). For *H. stipulacea*, all these hypotheses still need to be tested, especially because in some cases, neutral or even positive allelopathic effects can also be observed (Orr et al., 2005). To answer these questions, it would be necessary to perform growth experiment on native species exposed to BVOCs from both invasive and native species under laboratory and field conditions (Gross, 2023; Lv et al., 2021). It would be also necessary to determine the range of action of these compounds (short vs. long distances) with diffusion tests and concentration assessments directly into water. Moreover, it is well known that phenolic

TABLE 1 Peak intensities of the ten most discriminant compounds (based on VIP scores from PLS-DA) according to the species.

Compounds	<i>H. stipulacea</i>	<i>S. filiforme</i>	<i>T. testudinum</i>
pentadecane	291139734 ± 32968046 a	12518137 ± 2639858 b	19473312 ± 3890254 b
geranyl acetone	11892425 ± 1297379 a	5339537 ± 1226886 b	3367621 ± 544173 b
tetradecane	10529653 ± 930601 a	1168082 ± 337676 b	2437330 ± 370721 b
3-hexen-1-ol	n.d. c	4930033 ± 3690997 bc	1587266248 ± 322438591 a
dodecanal	13125210 ± 1726599 a	2074243 ± 675814 b	3133752 ± 390225 b
6-methyl, 5-hepten-2-one	34805172 ± 8800795 a	546438 ± 546438 b	n.d. b
benzaldehyde	27021028 ± 8618983 a	7818287 ± 3554188 ab	n.d. b
undecanal	3188719 ± 930280 a	596118 ± 390743 b	188084 ± 188084 b
cyclohexane, isothiocyanate	25580448 ± 6938908 a	1960997 ± 899917 b	3386687 ± 1319280 b
1-dodecanol	12630120 ± 2095409 a	3120520 ± 1107447 b	4112568 ± 1332406 b

n.d. means not detected.

Kruskal-Wallis tests followed by a Dunn *post hoc* test were performed to highlight significant differences between species with a > b > c. Mean ± SE and $n=6$.

compounds, another type of specialized metabolites that are non-volatile, have allelopathic effects (Li et al., 2010). Since it has been shown that *H. stipulacea* produce this type of compounds (Chebaro et al., 2024, highlighted only for their bioactive properties and not their ecological roles), it is possible that *H. stipulacea* allelopathic effects on native species could also result from those non-volatile compounds. Thus, it would be interesting to evaluate allelopathic potential of combined volatile and non-volatile metabolites to have the full picture of *H. stipulacea* allelopathic potential.

Perspectives

Detection of potential allelochemical is just the first step to highlight allelopathic interactions in marine invasive species such *H. stipulacea*. Further investigations are required to understand if and how these compounds impact competition between marine native and invasive species. That would help to better understand *H. stipulacea* dynamics and evaluate its invasion success under current and future environmental conditions.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

AS: Formal Analysis, Writing – review & editing, Conceptualization, Investigation, Writing – original draft. SC: Formal Analysis, Writing – review & editing, Conceptualization, Investigation, Writing – original draft. LH: Investigation, Writing – review & editing, Writing – original draft. CO: Writing – original draft, Investigation, Writing – review & editing. BdM: Writing – original draft, Writing – review & editing, Investigation. CL: Investigation, Writing – review & editing, Writing – original draft. EO: Writing – review & editing, Writing – original draft. CF: Conceptualization, Investigation, Writing – review & editing, Writing – original draft.

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Conflict of interest

Authors CO and BdM were employed by AQUASEARCH.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2025.1641139/full#supplementary-material>

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