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First record of the non-native seagrass *Halophila stipulacea* (Forsskål) Ascherson in Mallorca (Balearic Islands, Spain): Expanding its Western Mediterranean distribution

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Abstract

Halophila stipulacea is one of the first Lessepsian migrants to colonize the Mediterranean Sea (in 1894) after the opening of the Suez Canal. Since then, it has progressively expanded its distribution westward across the basin. Here, we report for the first time the presence of *H. stipulacea* in Palma Bay (Mallorca, Balearic Islands, Spain), representing the westernmost known occurrence of the species in the Mediterranean Sea. Initial surveys revealed that *H. stipulacea* patches (growing on sandy bottoms at ca. 16 m depth) were not stable in the colonized area, disappearing in the first reported location (November 2023) and being found in nearby areas a few months later (January 2024). Additionally, we collected samples at both sites to assess biomass and morphological traits of *H. stipulacea* in its early stages of colonization. Morphological data indicate that *H. stipulacea* in November 2023 exhibited larger leaf areas and longer rhizome internode length, producing smaller shoots in winter, when minimum registered temperatures were 14.5° C. We highlight the need for continued monitoring to assess the spread and possible ecological impacts of *H. stipulacea* on native species in the recently invaded areas.

Keywords: Introduced species; Biological invasion; Lessepsian migration; Herbivory.

Introduction

Halophila stipulacea (Forsskål) Ascherson, 1867 is a dioecious tropical seagrass native to the Red Sea, the Persian Gulf, and the Indian Ocean (Den Hartog, 1970). It is one of the first Lessepsian migrants to enter the Mediterranean Sea following the opening of the Suez Canal in 1869 (Por, 1978), with the first record reported in 1894 in Rhodes Island (Fritsch, 1895). Over the following decades, it steadily colonized the eastern Mediterranean basin (Lipkin, 1975; Winters *et al*., 2020), whereas its expansion into the western Mediterranean has been slower and more gradual, being first recorded on Vulcano Island (Italy) in 1995 (Acunto *et al*., 1995), and more than a decade later in Sicily (2006; Gambi *et al*., 2009), followed by Tunisia (2010; Sghaier *et al*., 2011), Cannes, France (2021; Thibaut *et al*., 2022) and Corsica (2022; Cnudde *et al*., 2023).

In addition to the Mediterranean Sea, *H. stipulacea* has also invaded the Caribbean, being first reported in Grenada in 2002, likely introduced via recreational yachts arriving from the Mediterranean (Ruiz & Ballantine, 2004). Since then, it has rapidly spread to other eastern Caribbean islands, Venezuela, and Florida (USA) (Vera *et al*., 2014; Ruiz *et al*., 2017; Scheibling *et al*., 2018; Campbell *et al*., 2025), leading to the displacement of native seagrasses (Willette & Ambrose, 2012; Steiner & Willette, 2015). Here, we report for the first time the presence of *H. stipulacea* in Mallorca, Balearic Islands (Spain), which now represents the westernmost record of the species in the Mediterranean. We also present data on its morphological characteristics, shoot density, and evidence of herbivory in the colonized areas.

Materials and Methods

On 11 October 2023, the crew of the boat from Fishing Tourism Activities N'ALEGRIA sighted *H. stipulacea* for the first time on Palma Bay (39.5473° N, 2.6726° E). The affected area was explored with a remotely operated vehicle (ROV) on 7 November 2023, revealing patches of *H. stipulacea* at a depth of 15-16 meters on a sandy bottom (Fig. 1B and 1C).

Following this initial observation, an area of approximately 200 m^2 was explored near the location of first observation (Fig. 1A) via SCUBA. *Halophila stipulacea* patches were sampled on November 2023 and January 2024 at two locations (Location A: 39.5473° N, 2.6726° E; Location B: 39.5464° N, 2.6721° E). Each sampling consisted of exploring the sea bottom to find an area covered by *H. stipulacea* and collecting quantitative samples (n=11 in November, n=13 in January) using 20 x 20cm quadrats randomly placed within *H. stipulacea* patches, maintaining a minimum distance of 2 meters between quadrats. Samples were then transported to the laboratory, where they were stored at -20° C for further processing.

In the laboratory, for each replicate quadrat, total shoot density (shoots m^{-2}) was quantified by counting the number of shoots of *H. stipulacea* present in the quadrat. To determine dry weight biomass (DW; g DW m^{-2}), aboveground (leaves and sheaths) and belowground (rhizomes and roots) biomass, as well as epiphyte load (g DW epiphytes / g DW leaves), epiphytes were scraped from the leaves using a microscope slide, all parts of the shoots were dried separately (60°C for 48 hours) and weighed following the methodology described in Hernán *et al*. (2017) (Fig. 2).

At the shoot level, morphological traits were measured for each shoot, including number of leaves, leaf length and width, and rhizome internode length. Additionally, each leaf was categorized based on its tip condition as Intact (no signs of damage), Broken (mechanically damaged) (Fig. 3C), and/or exhibiting consumption marks by herbivores (Herbivory) (Fig. 3D). When herbivore marks were present, they were identified and assigned to crustaceans (isopods/amphipods), the fish *Sarpa salpa*, or/and gastropods, based on characteristic damage patterns pre-

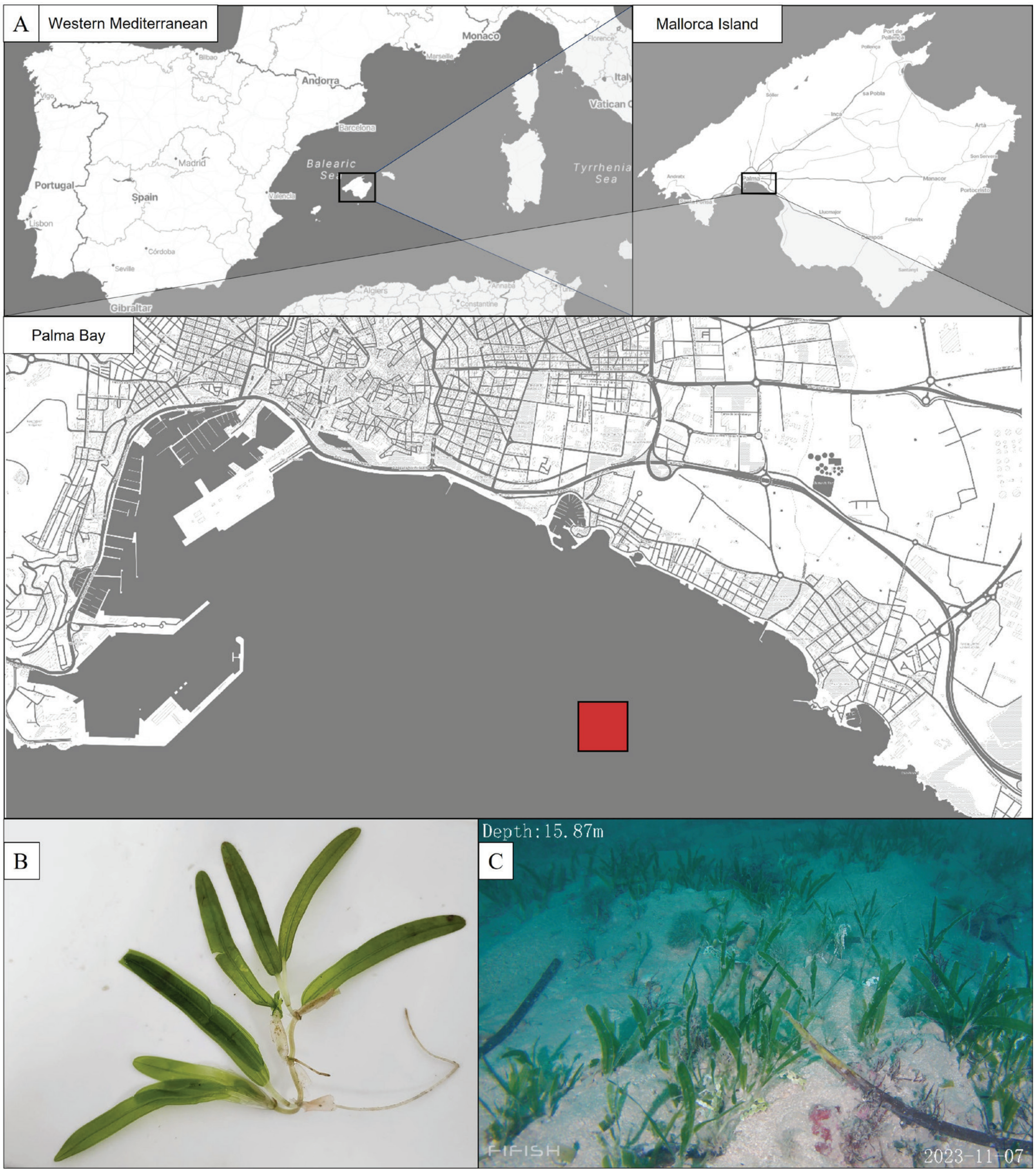

Fig. 1: (A) Map of Palma Bay (Mallorca, Spain) with the location where we sampled *H. stipulacea* indicated with a red square. (B) Fragment of *H. stipulacea* obtained on 11 October 2023. (C) First ROV images of *H. stipulacea* growing on sandy bottoms at Palma Bay on 7 November 2023.

viously described in seagrasses (e.g., Tomas *et al*., 2005; Rueda & Salas, 2007; Tomas *et al*., 2015) (Fig. 3D).

The data was processed and visualized using R version 4.3.2. Shoot density, aboveground and belowground dry weight biomass, mean leaf area, mean rhizome internode length, epiphyte load, and mean leaf number (dependent variables) were compared between sampling months (November 2023 and January 2024; independent variable) using a non-parametric Wilcoxon rank-sum test (Wilcoxon, 1945). Sea surface temperature (SST) was obtained for the sampling area between 1 November 2023 and 31 January 2024 from the High Resolution L4 Sea Surface Temperature Reprocessed (This study has been conducted using E.U. Copernicus Marine Service Information), which provides long-term SST time series over the Mediterranean Sea at a resolution of 0.05°. The R package 'ncdf4' (Pierce, 2025) was used for reading the downloaded NetCDF file and mean, maximum and minimum SST values were calculated from the extracted data.

Results

In November 2023 and January 2024, we observed *H. stipulacea* patches in Palma Bay (Mallorca Island, Spain), located less than 3 km from the Port of Palma (Fig. 1A). Initial surveys revealed a spatially heterogeneous and temporally variable distribution of *H. stipulacea* in the study area. In November 2023, we observed *H. stipulacea* patches (1 - 2 m²) separated by 1–2 meters at Location A (Fig. 1B), reflecting a patchy spatial distribution; however, by January 2024, the previously observed patches were no longer detectable at this location. Additional visual surveys in adjacent areas identified established small patches (<1 m²) with a sparse distribution, separated by approximately 5 meters (pers. obs. A. Arona), as well as loose uprooted fragments, approximately 100 meters away from the initial location (Location B). In all these areas *H. stipulacea* was growing over sandy bottoms along a depth range between 15 and 18 meters. During the sampling events, sea surface temperatures ranged from 19.4 °C ± 0.2 (SE, November 2023) to 15.1 °C ± 0.1 (SE, January 2024) in Palma Bay (EU Copernicus marine service information). However, these values are provided as a general environmental context and do not represent *in situ* temperatures at the sampling depth (c.a. 15 m).

Shoot density of *H. stipulacea* was significantly lower at the site sampled in November 2023 (mean ± SE = 135 ± 39.7 shoots m^{-2}) compared to the site in January 2024 (237 ± 35.5 shoots m^{-2}) (Fig. 2A), whereas total aboveground biomass (g DW m^{-2}) did not significantly differ between sampling times (Fig. 2B). In contrast, belowground biomass was significantly higher (*p-value* < 0.01) at the site sampled in November 2023 (5.77 ± 1.36 g DW m^{-2}) than in January 2024 (1.43 ± 0.27 g DW m^{-2}) (Fig. 2C). Similarly, mean leaf area (2.1 ± 0.56 cm^2 shoot^{-1} vs. 0.86 ± 0.21 cm^2 shoot^{-1}) tended to be (not statistically significant) larger in November 2023 than in January 2024, and rhizome internode mean length (1.91 ± 0.17 cm vs. 1.25 ± 0.14 cm), was significantly longer in November 2023 than in January 2024 (Figs. 2D, 2E). There was no significant difference in epiphyte load between sampling dates (0.12 ± 0.51 g epiphyte DW g^{-1} leaf DW in November 2023 and 0.22 ± 0.08 g epiphyte DW g^{-1} leaf DW in January 2024) (Fig. 2F).

In November 2023, *H. stipulacea* shoots exhibited lower number of leaves (1.36 ± 0.1 shoot $^{-1}$) compared to January 2024 (1.78 ± 0.06 shoot $^{-1}$) (Fig. 3A). Across both

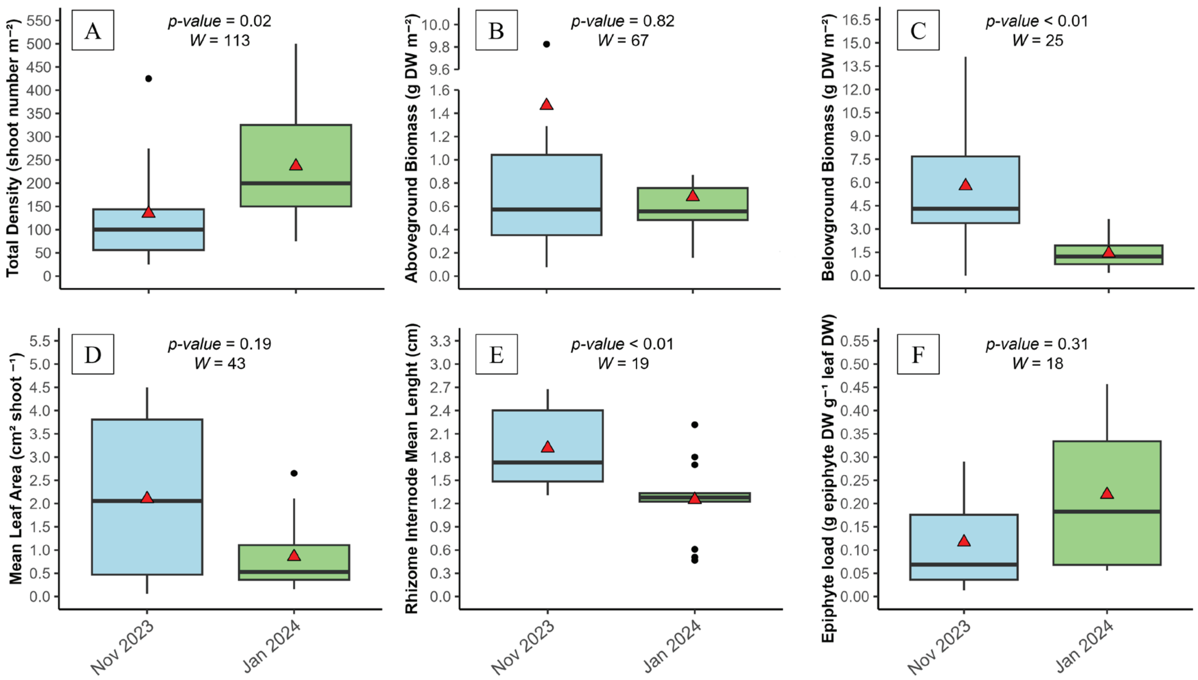

Fig. 2: Boxplot distribution and mean value (red triangle) of *H. stipulacea*: (A) total shoot density (shoots m^{-2}), (B) total aboveground (g DW m^{-2}), (C) belowground biomass (g DW m^{-2}), (D) mean leaf area (cm^2 shoot^{-1}), (E) rhizome internode mean length (cm), and (F) epiphyte load (g epiphyte DW g^{-1} leaf DW) on 29 November 2023 (n=11) and 30 January 2024 (n=13).

sites and dates, leaves exhibited signs of mechanical and biological damage. There was no significant difference (*p-value* = 0.68, *W* = 58) in the percentage of intact leaves between November 2023 (75.7%) and January 2024 (71.9%). Overall, about 13% of leaves had broken tips (*p-value* = 0.47, *W* = 76.5) and ca. 12% exhibited signs of herbivory (*p-value* = 0.23, *W* = 83.5) (there were no significant differences among times; Fig. 3A). Herbivory marks were evident in both sampling periods, though the identity and prevalence of herbivores varied through time. In November 2023, 38.5% of the feeding marks were attributed to the fish *S. salpa*, 23.1% to gastropods, 30.8% exhibited combined marks of both *S. salpa* and gastropods, and **7.7%** to amphipods/isopods. However, in January 2024, the 54.8% of marks were associated with *S. salpa*, the 3.4% with gastropods and the 41.9 % with amphipods/isopods (Fig. 3B).

Discussion

Our study documents, for the first time, the presence of *Halophila stipulacea* in Palma Bay (Mallorca Island, Spain), marking the westernmost record of this invasive species in the Mediterranean to date. We observed temporal variation in shoot density and morphology, with lower shoot density and mean number of leaves per shoot but larger leaf area and internode length in fall (November) compared to winter (January). These changes suggest active clonal growth (Georgiou *et. al.*, 2016; Wesselmann *et al.*, 2020) and highlight the ability of *H. stipulacea* to cope with different environmental conditions (e.g., lower light availability and lower temperatures in winter). Herbivory pressure was consistent across both sampling periods, and we found no evidence of sexual reproduction. Taken together, our findings suggest that *H. stipulacea* is capable of establishing persistent populations in Palma

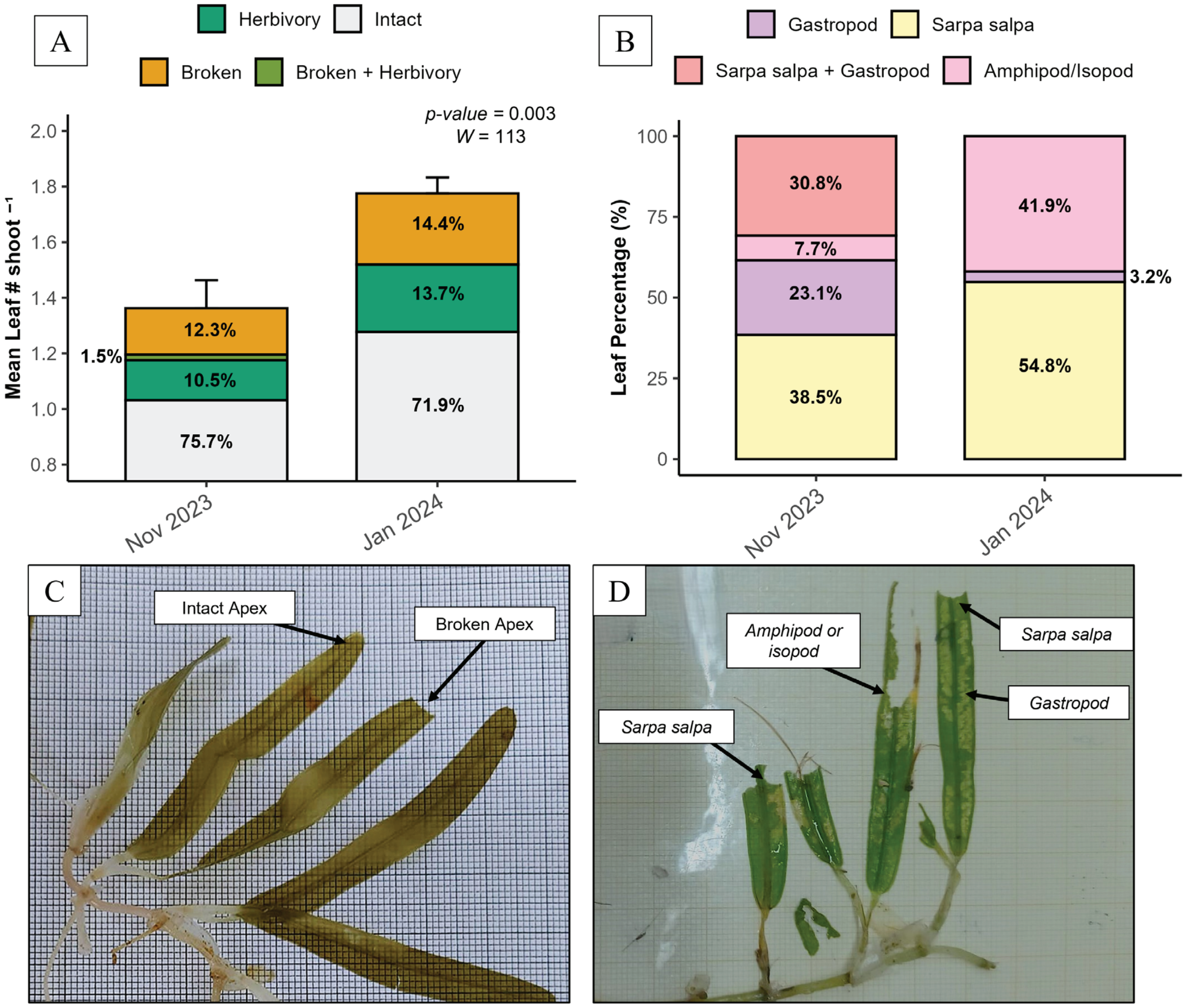

Fig. 3: (A) *H. stipulacea* mean leaf number shoot $^{-1}$ (± standard error) in November 2023 and January 2024, with a stacked representation of apex condition percentages. (B) Leaf percentage with marks and bites based on herbivore origin. (C) Examples of intact and broken leaves and (D) herbivore bite marks caused by the fish *S. salpa*, gastropod, and amphipod/isopod.

Bay and may continue to spread, highlighting the need for ongoing monitoring.

Harbours are recognized as key entry points for exotic marine species due to the frequent arrival of vessels and the large number of organisms they can unintentionally transport (Mannino & Balistreri, 2017; Carreño & Lloret, 2021). In the western Mediterranean, reported observations of *H. stipulacea* have been associated with harbour-adjacent locations (Gambi *et al*., 2009; Thibaut *et al*., 2022; Cnudde *et al*., 2023). Following this pattern, Palma Bay, which hosts several harbours, including the Port of Palma, the largest on the Island, has experienced invasions by other non-native macrophytes in recent years, including *Halimeda incrassata* (J. Ellis) J. V. Lamouroux (Alós *et al*., 2016) and *Caulerpa cylindracea* Sonder (Ballesteros *et al*., 1999). This context underscores the likelihood of *H. stipulacea* having arrived via anthropogenic vectors (most plausibly shipping or recreational boating) rather than secondary natural dispersal from a previously invaded area.

Halophila stipulacea displayed a dynamic distribution in Palma Bay, with patch disappearance and new patch formation between fall and winter. Similar dynamics have been reported in other Mediterranean *H. stipulacea* populations, for which typically their range is contracted during winter months and expands during summer (Nguyen *et al*., 2020). Once it has arrived to an area, *H. stipulacea* fragments may be redispersed by anchoring of vessels (Gambi *et al*., 2009) or by fragment dispersion through water column after storms (Smulders *et al*., 2017), likely facilitating this transient patch structure. For instance, Gambi *et al*. (2018) documented *H. stipulacea* recolonizing an area in Palinuro (Italy) seven years after its presumed local extinction in 2011. Notably, floating fragments of *H. stipulacea* were observed off the coast of Palinuro in 2012 (Gambi & Barbieri, 2013), suggesting that the species may have persisted in the area.

The observed morphological changes, particularly the higher number of leaves with smaller leaf area in winter could suggest a seasonal leaf turnover. This pattern may reflect the replacement of larger, degraded leaves observed in fall, by smaller, undamaged ones in winter. In fact, a reduction in leaf size has previously been suggested as a morphological adaptation that enhances resistance to low temperatures in this species (Nguyen *et al*., 2020). In the western Mediterranean, winter temperatures do not appear to limit the survival of *H. stipulacea*, as its lower thermal tolerance threshold is ca. 8 °C (Wesselmann *et al*., 2020). Thibaut *et al*. (2022) observed a meadow of *H. stipulacea* covering 16.5 ha of dead matte of *Posidonia oceanica* in Cannes (France), where minimum temperatures reached 13 °C. Additionally, they reported shoot densities ranging from 143 to 437 shoots m^{-2}, which align closely to the densities observed in Palma Bay (from 135 ± 39.7 shoots m^{-2} in November 2023 to 237 ± 35.5 shoots m^{-2} in January 2024; Fig. 2A), reinforcing the notion that this species can thrive in temperate conditions in the Western Mediterranean.

Our data also suggest that there is active clonal growth of *H. stipulacea* (which can occur between 13 ºC to 30 ºC, Georgiou *et al*., 2016) in Palma Bay, as indicated by the higher shoot density combined with lower rhizome internode length in winter compared to fall (Fig. 2A, Fig. 2E). No evidence of sexual structures was observed, implying that the species relies on vegetative propagation (fragmentation and rhizome elongation) for initial colonization or at least during fall and winter seasons, a strategy commonly observed in Mediterranean populations (Procaccini *et al*., 1999; Nguyen *et al*., 2018). This reproductive strategy has led to low genetic diversity in the Mediterranean populations of *H. stipulacea,* especially in the most recently invaded areas, compared to native populations (García-Escudero *et al*., 2024). However, warming of the Mediterranean may change these reproductive strategies. For example, in 2012 on Chios Island (Greece), fruiting in *H. stipulacea* was observed, possibly as a response to elevated temperatures (Gerakaris *et al*., 2015), suggesting environmental triggers may influence reproductive mode.

In its native range, *H. stipulacea* is consumed by a variety of herbivores, including dugongs, sea urchins, and herbivorous fish (Preen, 1989; Hulings & Kirkman, 1982; Mariani & Alcoverro, 1999). In the Mediterranean Sea, consumption by fish (*S. salpa*) has only been detected in October 2017 in Italy (Gambi *et al*. 2018). Interestingly, meadows studied in the same area a decade earlier (June 2007) did not exhibit herbivory marks on the leaves (Gambi *et al*., 2009). Aligned with this temporal pattern, our observations indicate that fish grazing pressure during the early invasion stages of *H. stipulacea* in Palma Bay is relatively low when compared to other Mediterranean sites (ca. 13% in Palma vs. 40-50% in Italy) during the same season (fall – winter) (Gambi *et al*., 2018, Di Genio *et al*., 2021). This could be a result of *S. salpa* requiring a learning period (of potentially several years) to recognize the new invader as a valuable food resource, as it has been observed for *C. cylindracea* (Santamaría *et al*., 2022).

In addition to fish grazing, our observations suggest that invertebrates, including gastropods and crustaceans (probably amphipods and / or isopods), are also grazing on *H. stipulacea*. In Greece, consumption of *H. stipulacea* by the exotic gastropod *Syphonota geographica* was suggested in 2003, based on the presence of identical compounds in the mollusk's viscera and in the seagrass (Mollo *et al.*, 2008). However, the identity of these invertebrate grazers in Palma Bay remains unknown. Given that herbivory may act as a natural control mechanism, potentially limiting the species' invasive capacity, identifying consumers of *H. stipulacea* is important. For example, the native herbivorous fish *S. salpa* and the sea urchin *Paracentrotus lividus* are strong consumers of *C. cylindracea* and contribute to limiting its invasion in the Mediterranean Sea (Cebrian *et al*., 2011; Tomas *et al*., 2011a, b; Santamaría *et al*. 2021, 2022). Similarly, in the invaded Caribbean regions, grazing by the turtle *Chelonia mydas (*Christianen *et al*., 2019) and fish diversity and abundance (Smulders *et al*., 2022) can also play a crucial role in limiting the expansion of *H. stipulacea.*

The ecological implications of *H. stipulacea* colonization are significant. The establishment of *H. stipulacea* in some areas of the Mediterranean has led to the displacement of native seagrass species. For instance, along the Tunisian coast, *Cymodocea nodosa* disappeared within four years in areas invaded by *H. stipulacea* (Sghaier *et al*., 2014). Similarly, in Limassol (Cyprus), native seagrasses (*P. oceanica* and *C. nodosa*) disappeared, whereas *H. stipulacea* doubled its coverage over a six-year period (Winters *et al*., 2025). On the other hand, the invasion of this species may enhance carbon sequestration in the invaded areas (Wesselmann *et al*., 2021), as well as increase the abundance and diversity of the associated invertebrate communities when compared to native seagrass species and unvegetated areas (Willette & Ambrose, 2012; Valdez *et al*., 2021). Additionally, *H. stipulacea* has been associated with pharmacological benefits, including antimicrobial, antioxidant, anticancer, anti-inflammatory, anti-metabolic disorder, and anti-osteoclastogenic activities (Chebaro *et al.*, 2024).

The potential for successful spread and similar impacts of *H. stipulacea* in Palma Bay should not be underestimated, particularly under continued tropicalization of the basin (Bianchi & Morri 2003; Borghini *et al*., 2014) and increased connectivity with the Red Sea as a result of the expansion of the Suez Canal (Galil *et al*., 2015), which may increment *H. stipulacea* propagule pressure. Therefore, continued monitoring of *H. stipulacea* colonization is essential to evaluate its expansion patterns and potential ecological impacts on native species in Palma Bay.

This study is limited to a short temporal window and restricted spatial extent. While our findings provide critical baseline information at the beginning of the invasion process, longer-term monitoring is necessary to determine seasonal cycles, potential establishment, and long-distance dispersal. Additionally, genetic analyses could reveal the origin of this population and clarify whether it represents a single introduction or multiple events. Further research should assess competitive interactions with native seagrasses and examine functional impacts on benthic biodiversity and ecosystem functioning.

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Authors contribution: Andrés Arona: Field sampling, Data curation, Data analysis, Visualization, Writing – original draft. Lucia Loubet: Conceptualization, Field sampling, Sample processing, Writing – review & editing. Gema Hernan: Writing – original draft, Writing – review & editing, Data analyses, Visualization, Supervision, Methodology. Balma Albalat: Field sampling, Writing – review. Emmanuela Orero-Rubio: Field sampling, Writing – review. Xesca Reynés: Field sampling, Writing – review. Benjamí Reviriego: Investigation, Writing – review & editing. Enric Ballesteros: Conceptualization, Investigation, Methodology. Fiona Tomas: Conceptualization, Writing – original draft, Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition.

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