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Rapid invasion of the non-indigenous brown alga *Stypopodium schimperi* in the Adriatic Sea

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Abstract

In this study, we report the first record of the brown alga *Stypopodium schimperi* in the Adriatic Sea, which also represents the northernmost occurrence of this Lessepsian species within the Mediterranean. Species identification was confirmed through morphological examination and molecular analyses based on genotyping of the chloroplast genes *rbcL*, *psbA*, and *psaA*. During a 3-year observation period, *S. schimperi* demonstrated a vigorous increase in both coverage and spatial distribution. Starting from a few observed thalli in autumn 2020, coverage reached 100% over a large area. Consequently, this resulted in a drastic reduction of native macroalgae on rocky bottoms, mostly at depths of 5–20 m, which we quantified via photo-quadrat analyses along a gradient of its coverage. In conclusion, this non-indigenous species has the potential to become one of the most invasive in the Adriatic Sea, with a high likelihood of spreading further into the northwestern Mediterranean.

Keywords: invasive algae; Adriatic Sea; *Stypopodium schimperi*.

Introduction

The Mediterranean Sea is considered a hotspot for biological invasions, with hundreds of naturalized marine non-indigenous species (hereinafter referred to as NIS) (Tsiamis *et al.*, 2019; Zenetos *et al.*, 2022; Galanidi *et al.*, 2023). Among these, nearly 150 non-indigenous macrophytes have been identified, including species with cryptogenic or data-deficient status, some of which exhibit invasive characteristics and have significant impacts on biodiversity and the marine ecosystem (Verlaque *et al.*, 2015; Galanidi *et al.*, 2023; van der Loos *et al.*, 2024).

Stypopodium schimperi (Kützinger) Verlaque & Boudouresque (Phaeophyceae, Dictyotales) is a brown macroalga native to the Western Indian Ocean, originally described from the Red Sea in Egypt as *Zonaria schimperi* Kützinger (Guiry & Guiry, 2025). It is most likely a Lessepsian migrant that entered the Mediterranean Sea through the Suez Canal, where it was first recorded in 1973 as *Spatoglossum asperum* J. Agardh on the coast of Israel (Verlaque *et al.*, 2015).

Today, *S. schimperi* is widely distributed in the southeastern part of the Mediterranean Sea, on the coasts of Libya, Egypt, Israel, Lebanon, Syria, Cyprus, Turkey and Greece (Verlaque & Boudouresque, 1991; Hoffman & Dubinsky, 2010; Tsiamis *et al.*, 2010, 2019; Verlaque *et al.*, 2015; Bitar *et al.*, 2017; Katsanevakis *et al.*, 2020;

Çinar *et al.*, 2021). In some of these countries, it has become abundant and is considered an invasive species that can reduce or even displace native organisms (Mayhoub & Billard, 1991, as *Stypopodium zonale* (J. V. Lamouroux) Papenfuss; Bitar *et al.*, 2000, 2017; Boudouresque & Verlaque, 2002; Katsanevakis *et al.*, 2020). Moreover, it has been listed as one of the 100 most dangerous invasive marine species in the Mediterranean Sea (Stefartaris & Zenetos, 2006). However, while its status as an invasive species is based on expert judgment, detailed impact studies on local species and habitats remain lacking (Mayhoub & Billard, 1991; Bitar *et al.*, 2000, 2017; Hoffman, 2014; Katsanevakis *et al.*, 2020; Çinar *et al.*, 2021), as is the common case for most introduced macroalgae (Davidson *et al.*, 2015).

In the Adriatic Sea, *S. schimperi* was first recorded in autumn 2020 (Fig. 1) (Lučić *et al.*, 2022). Expanding on this preliminary report, we provide a more detailed account of this first observation and the subsequent spread of this species over a 3-year period. We used morphological features and molecular markers for the taxonomic identification of the species. Based on photo-quadrat analyses and 3 years of field observations, we document its severe invasive features and rapid spread. The observed settlement represents a significant northward expansion of *S. schimperi*, a species that according to our observations, has the potential to become the most inva-

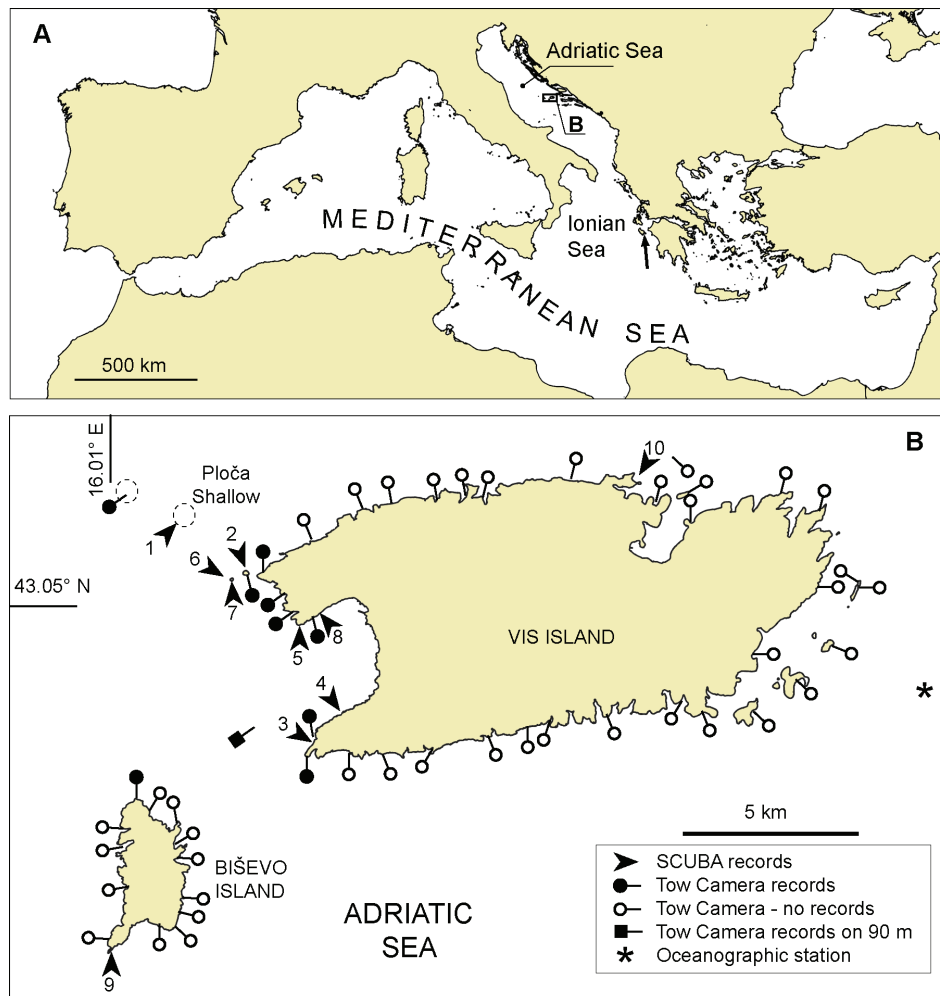


Fig. 1: Records of *Stypopodium schimperi* in the Vis Archipelago. A: Geographic location of the Vis Archipelago within the Mediterranean and the Adriatic Sea. Arrows indicate a previous record of *S. schimperi* from the Ionian Sea (Dimitriadis *et al.*, 2021). B: Detection and monitoring sites for *S. schimperi* within the Vis Archipelago: Site 1, first record in the Adriatic Sea (September 2020); Sites 2–4, additional records in 2020; Sites 5–6, records in 2021; Site 7, photo-quadrat analyses site in 2022; Sites 8–10, additional records in 2022.

sive non-indigenous benthic organism in the Adriatic Sea. To date, its settlement in the Adriatic Sea also represents the northernmost known location in the Mediterranean where a Lessepsian organism, across all marine taxonomic groups, has radically outcompeted native organisms.

Materials and Methods

Field observations, sample collection, and spatial distribution

The first observation of *S. schimperi* occurred during a SCUBA survey of the Vis Archipelago in September 2020, which was conducted as part of NIS inventory assessment (Site 1 in Fig. 1B). Following this first record, several randomly chosen sites in the south part of Vis Island were surveyed to estimate *S. schimperi* spatial distribution (Fig. 1B, Table 1).

In September 2021, October 2022, and October 2023, SCUBA surveys were conducted at previously investigated locations, with additional sites included to collect data on *S. schimperi* distribution, ecological preferences, and

impacts (Fig. 1B, Table 1). Each site inspection involved two divers surveying at depths of 0–30 m during a 40 min SCUBA dive. These field surveys, along with additional sampling in June and August 2022, were used to collect samples for molecular and morphological analyses. Only thalli collected in August 2022 were analyzed for the presence of reproductive organs. Samples for herbarium preservation and morphological research were preserved in a 4% formaldehyde solution, while fresh fragments were silica-dried for DNA extraction. Herbarium vouchers were deposited at the Institute of Oceanography and Fisheries in Split, Croatia.

To detect the presence of *S. schimperi* on the spatial scale of the entire Croatian coastline, we examined 3700 benthic video transects obtained by towed cameras, which were collected in 2022 and 2023 through the scope of the project “Mapping of coastal and benthic marine habitats within the Croatian national territory of the Adriatic Sea.” Most video transects covered the bottom at depths of 2–40 m, which represents the optimal depth range for *S. schimperi* development.

Through public awareness efforts across various media platforms, we initiated a citizen science program to

Table 1. Approximations of *Stypopodium schimperi* density presented as the number of thalli or bottom coverage at inspected sites in the Vis Archipelago during the 2020–2023 period (see Fig. 1B). Estimates were made on the rocky bottom at depths of 5–20 m, based on 40-minute SCUBA dives performed by two divers.

Site no.	Sept. 2020	Sept. 2021	Oct. 2022	Oct. 2023
1	5 thalli	>>1000 thalli	100%	100%
2	5 – 10 thalli	>>1000 thalli	100%	100%
3	5 – 10 thalli	>>1000 thalli	100%	100%
4	5 – 10 thalli	>>1000 thalli	100%	100%
5	-	100%	100%	100%
6	-	>>1000 thalli	100%	100%
7	-	-	100%	100%
8	-	-	>100 thalli	>>1000 thalli
9	-	-	5 – 10 thalli	-
10	-	-	>100 thalli	>>1000 thalli

determine the distribution of *S. schimperi* along the entire Croatian coastline.

Impact assessment

The impact of *S. schimperi* on the benthic community was assessed based on algal coverage using the photo-quadrat method at Site 7 in June 2022 (Figs. 1B, 2D). We selected an area with a gradient of *S. schimperi* cov-

erage parallel to the coastline. A measuring tape (100 m) was used as a reference line and deployed at a depth of 10 m, starting from an area with high *S. schimperi* coverage and extending to an area with sporadic presence of the species. A depth of 10 m is considered the average depth with maximum *S. schimperi* density (Fig. 2C). Along this reference line, every 10 m (including 0 and 100 m) was designated as a “photo-quadrat site”, where we captured images of three quadrats (50 cm x 50 cm) (Fig. 2D). The photo-quadrats were randomly positioned at depths of

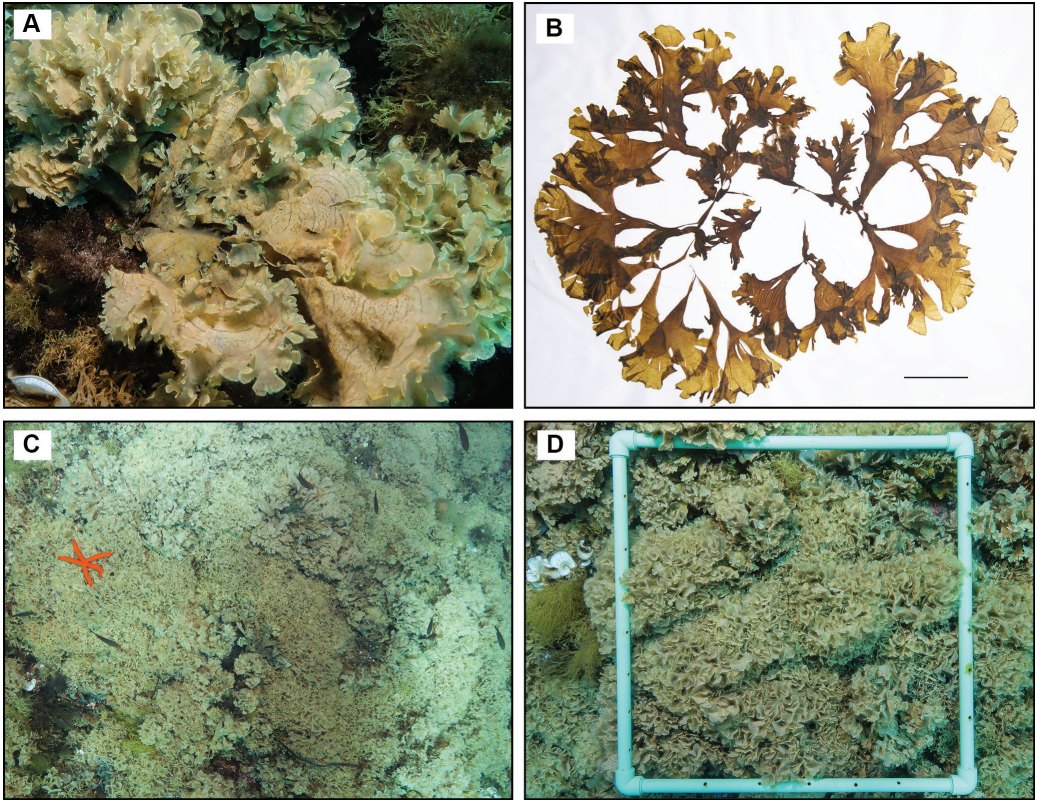


Fig. 2: *Stypopodium schimperi* from the Vis Archipelago. A: Thalli *in situ* at Site 7. B: Mature herbarium specimen (scale bar = 10 cm) collected in September 2022 from Site 1 at 15 m depth. C: Dense coverage of the rocky bottom at Site 7, where the impact assessment study was performed, with starfish *Ophidiaster ophidianus* (Lamarck, 1816). D: The quadrat used in the impact assessment study (50 cm x 50 cm), with *Padina pavonica* (up left) and *Dictyota* sp. (middle left) visible outside the quadrat. Photographs A, C, and D were taken at 10 m depth in early June 2022 at Site 7 (see Fig. 1B).

between 8 and 12 m. Images were taken with a Canon EOS 90D digital camera using an Ikelite DS-161 strobe. For the analyses of algal coverage, each image was digitally divided into six sub-quadrats using Adobe Lightroom software. Each sub-quadrat was used to estimate the percentage cover of dominant algal taxa, with robust estimates for 25, 50, 75, and 100% cover (Bianchi *et al.*, 2003). Algal taxa with coverages of less than 25% were noted but not quantified. In total, this photo-sampling design resulted in 11 analyzed photo-quadrat sites along the reference line, with each containing 27 sub-quadrats (3 photo-quadrats x 9 sub-quadrats). Since algae of the genera *Taonia* J. Agardh and *Dictyota* J. V. Lamouroux were often mixed and difficult to identify at the species level from the photographs, they were treated as a single entity (the *Taonia-Dictyota* complex) in the photo-quadrat analysis. Species coverage was calculated cumulatively for each photo-quadrat site, aggregating all sub-samples obtained from the three photo quadrats.

Abiotic parameters

Data on sea surface temperature (SST), collected using a CTD instrument and seawater transparency (measured with a Secchi disk) were obtained from an oceanographic database (Baza pokazatelja, 2025) for the oceanographic station “Stončica”, where data have been collected monthly. The dataset was analyzed for the 2015-2022 period.

DNA sequencing and phylogenetic analysis

Genomic DNA was extracted from 5-10 mg of silica gel-dried tissue using a standard CTAB extraction method (Shan *et al.*, 2011). After a DNA quality and quantity check using an Implen NanoPhotometer™ N50 UV/Vis

spectrophotometer, three plastid-encoded genes *psbA*, *psaA*, and *rbcL* were amplified using the primers listed in Table 2. The amplification of selected genetic markers was performed under the conditions described by Bittner *et al.* (2008), after which PCR product purification and single-end forward sequencing were performed by Macrogen Inc. (Amsterdam, The Netherlands).

Phylogenetic relationships among individuals were analyzed separately for each gene using the Maximum Likelihood method (ML) using IQ-TREE 2 (version 2.2.0.3. pre-release) (Minh *et al.*, 2020). Obtained sequences were aligned using the MUSCLE algorithm implemented in a substitution model search, which was performed using ModelFinder (-MFP) implemented in the IQ-TREE 2 pipeline (Kalyanamoorthy *et al.*, 2017). Thereafter, the best-fit model according to the Bayesian Information Criterion (BIC) was chosen for phylogenetic tree reconstruction. A ML tree for the *psaA* marker was generated using a Transition model (AC=AT and CG=GT) with empirical base frequencies (+F) and discrete Gamma model (+G4) via -m TIM2+F+G4. Furthermore, the ML tree for the *psbA* marker was built using the General Time Reversible model (GTR) via -m GTR+F+I, while that for the *rbcL* marker using the GTR+F+G4 model. All phylogenetic analyses were computed with 1000 ultra-fast bootstrapping replicates (Hoang *et al.*, 2018) and random seed numbers generating 100 starting Maximum Parsimony trees. Consensus phylogenetic trees for each gene were visualized and edited with FigTree v. 1.4.4 (Rambaut, 2018) and Inkscape v1.3.2 (Inkscape, 2020).

Results

Filed observations

The first observation of *S. schimperi* in the Adriatic Sea occurred on September 6th, 2020 at Ploča Shallow

Table 2. List of primers used in the present study and PCR annealing temperatures.

Primer name	Direction	Gene	Sequence (5'→3')	Annealing T(°C)	Reference
<i>psaA_130F</i>	F	<i>psaA</i>	AACWACWACTTGGATTGGAA	48	(Yoon <i>et al.</i> , 2002)
<i>psaA_940R</i>	R	<i>psaA</i>	TATGDCCAATWCCCCAATT	48	(Bittner <i>et al.</i> , 2008)
<i>psaA_870F</i>	F	<i>psaA</i>	GGNGGWYTATGGTTAAGTGA	48	(Yoon <i>et al.</i> , 2002)
<i>psaA_1760R</i>	R	<i>psaA</i>	CCTCTWCCWGGWCCATCRCAWGG	48	(Yoon <i>et al.</i> , 2002)
<i>psbA_F</i>	F	<i>psbA</i>	ATGACTGCTACTTTAGAAAGACG	46	(Yoon <i>et al.</i> , 2002)
<i>psbA_R1</i>	R	<i>psbA</i>	GCTAAATCTARWGGGAAGTTGTG	46	(Yoon <i>et al.</i> , 2002)
<i>rbcL-68F</i>	F	<i>rbcL</i>	GCNAAAATGGGNWAYTGGGATGC	52	(Draisma <i>et al.</i> , 2001)
<i>rbcL-708R</i>	R	<i>rbcL</i>	TTAAGNTAWGAACCYTTAACTTC	52	(Bittner <i>et al.</i> , 2008)
<i>rbcL-543F</i>	F	<i>rbcL</i>	CCWAAATTAGGTCTTTCWGGWAAAAA	52	(Bittner <i>et al.</i> , 2008)
<i>rbcL-1381R</i>	R	<i>rbcL</i>	ATATCTTTCCATARRTCTAAWGC	52	(Burrowes <i>et al.</i> , 2003)

(43.06322° N, 16.02986° E) located in the Vis Archipelago in Croatia (Site 1 in Fig. 1B, Table 1). Five thalli were found on the rocky bottom at depths of 10–20 m. The minimum depth of the Ploča Shallow is 10 m. Although the bottom remains rocky down to 30 m, it is predominantly overgrown by a seagrass *Posidonia oceanica* (Linnaeus) Delile meadow. Subsequent surveys at three additional sites revealed approximately 5–10 thalli per site, developing at depths of 5–20 m (Sites 2–4 in Fig. 1B). The abundance of *S. schimperi* at the sites inspected in 2020 had greatly increased by September 2021. The bottom was colonized by thousands of thalli at depths of 5–20 m, extensively covering the rocky substrate. In 2022, *S. schimperi* covered 100% of the rocky bottom at the sites and depths where it had been sporadically observed in 2020 (Sites 1–4 in Fig. 1B, Table 1).

In general, at all sites where *S. schimperi* was detected at the early stages of its spread (with a maximum of tens of thalli), its density increased to thousands of thalli within the second year, eventually reaching 100% coverage by the third year of invasion. In that stage of expansion, it completely covers rocky bottoms over hundreds of square meters at depths of 5–20 m, with almost no other erect macroalgae present within the dense *S. schimperi* colonies.

Stypopodium schimperi prefers a well-lit rocky substrate at a depth of 5–25 m and does not colonize *P. oceanica* seagrass meadows.

In 2023, *S. schimperi* fragments were observed on the seafloor at a depth of 90 m using a towed camera, suggesting long-distance drift (Fig. 1B). In October 2023, at the newly discovered sites (Site 10 in Fig. 1B), where *S. schimperi* was absent in 2019 (as confirmed by the authors under national Water Framework Directive monitoring), it formed settlements with over 30% coverage, including thousands of scattered thalli (Table 1).

Large-scale surveys along the entire Croatian coastline, involving citizen science and more than 3700 bottom transects conducted using towed cameras in 2022 and 2023, did not detect *S. schimperi* outside the Vis Archipelago (Fig. 1B).

Photo-quadrat analyses

Of the 297 photo sub-quadrats analyzed, only *Taonia-Dictyota* complex, *Padina pavonica* (Linnaeus) Thivy, *Halopteris scoparia* (Linnaeus) Sauvageau, and *S. schimperi* demonstrated coverages of 25% or higher within a single sub-quadrat. Algal taxa with less than 25% coverage included *Caulerpa cylindracea* Sonder (another NIS), *Acetabularia acetabulum* (Linnaeus) P. C. Silva, *Laurencia* complex and *Amphiroa rigida* J. V. Lamouroux.

Considering the cumulative coverage for each photo-quadrat site, *S. schimperi* exceeded 90% along the first 40 m of the reference line. This coincides with the almost complete disappearance of native algal species in the vegetation layer visible in the photographs (Figs. 2D, 3). Although the presence and coverage of native macroalgae increased between the 40th and 100th meters of the reference line, *S. schimperi* coverage remained mostly dominant, ranging from 20 to 60% (Fig. 3).

Abiotic parameters

During the 2015–2022 period, the minimum and maximum SST measured at the oceanographic station (Fig. 1B) were 13–14°C in winter (February and March) and 22.5–26.5°C in summer (August), respectively. During the 2019–2022 period, transparency measurements taken using a Secchi disk ranged from an average of 20 m in winter to 24 m in summer.

Morphology of *Stypopodium schimperi*

The morphological features of specimens collected from the Vis Archipelago are generally consistent with the description of *S. schimperi* provided by Verlaque & Boudouresque (1991). The thallus is fan-shaped with deep longitudinal tears, reaching up to 40 cm in size. The

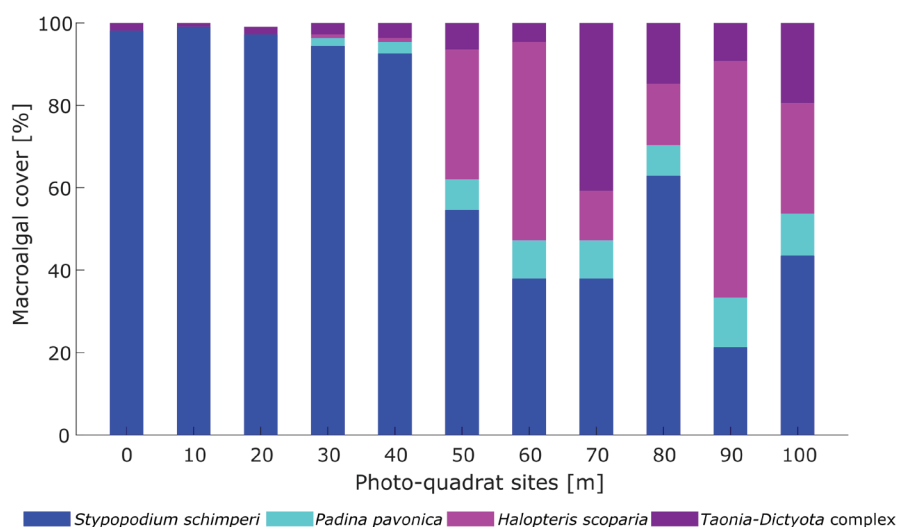


Fig. 3: Average macroalgal species cover (%) based on photo-quadrat analyses (Site 7 in Fig. 1B). Photographs were captured in June 2022 at 8–13 m depth every 10 m over a reference line (100 m).

blade is light brown when young and dark brown when mature, sometimes exhibiting a blue iridescence. It is not calcified, fixed to the substrate by a rhizoidal holdfast, and easily detachable. Hairs are grouped and form regular concentric bands or lines on both sides of the thallus, parallel to the blade margin. In surface view, cortical cells are rectangular (10-22 μm x 33-72 μm) or square (15-24.5 x 17.5-32 μm), elongated toward apical cells (Fig. 4A).

In the transverse section, cortical pigmented cells are arranged in a single layer throughout the thallus (9-16 μm long and 10-16 μm high), with colorless medulla cells (22.5-26 μm long and 22.5-36.8 μm high) in 2-4 cell-layers in the apical and middle portions and 4-6 cell-layers in the basal part (Fig. 4B-D). The thickness of the thalli is 350-400 μm in the basal part, 300-400 μm in the middle portion, and 200-300 μm in the upper part of the blade (Fig. 4B-D).

While sporophytes, male gametophytes, and sterile thalli were found, female specimens were not observed. Sporangia are numerous, borne on a stalk cell, 110-125 μm in diameter when mature, and scattered or grouped on both sides of the thallus, mostly in the middle portion of the blade and between concentric bands of hairs (Fig. 4E). Within the sporangia, tetraspore development was rarely observed. The examination of thalli, collected in

mid-August (n = 46), indicated that approximately half were sporophytic, while the remainder were mostly sterile.

Only a few thalli of the male gametophyte were found in mid-August. Antheridial sori are extensively developed in the form of irregular zig-zag patches (Fig. 4F), mostly on the middle and upper portions of both sides of the blade.

Thalli are epilithic. However, seedlings and young specimens are also observed developing epiphytically on *Codium bursa* (Oliv.) C. Agardh and especially on *H. scoparia* (Fig. 5A). Old thalli usually bear numerous proliferations that develop from the blade surface and margins (Fig. 5B).

Molecular results

According to an initial BLAST search, obtained sequences from vouchers collected at the Vis Archipelago showed the highest similarity to specimens identified as *S. schimperi* that were collected in Turkey, Greece, and Lebanon (Table 3). Datasets for separated-gene phylogenies were obtained from sequences of Dictyotales available in GenBank: *rbcL* alignment consisted of 28 sequences and 1752 sites, of which 294 were parsimony

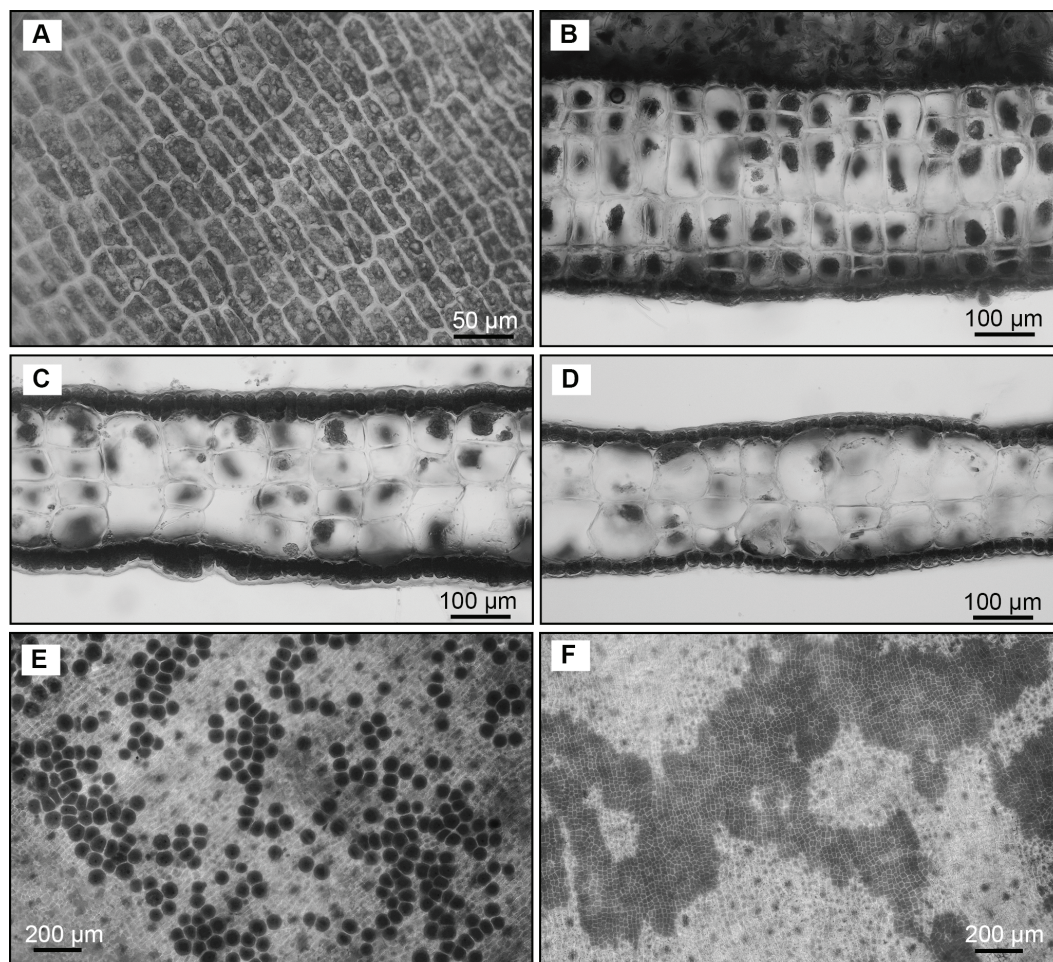


Fig. 4: *Stypopodium schimperi* from the Vis Archipelago. A: Surface view of the cortical cells in the middle portion of the thallus. Transverse section of basal (B), middle (C), and upper (D) parts of the blade. E: Surface view of the spores. F: Surface view of the antheridial sori.

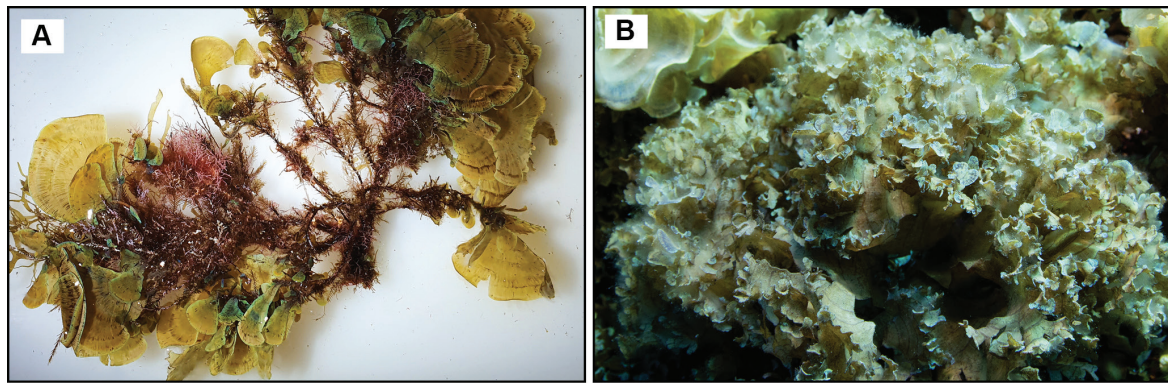


Fig. 5: *Stypopodium schimperi*. A: Juvenile specimens densely covering branches of the native Mediterranean species *Halopteris scoparia*. B: Mature specimens *in situ* with numerous blade proliferations. Both photographs were taken in October.

informative; *psbA* alignment consisted of 20 sequences and 976 sites, of which 113 were parsimony-informative sites; and *psaA* alignment consisted of 18 sequences and 1579 sites, of which 381 were parsimony-informative sites, with total of five new specimens of *S. schimperi* from the Adriatic Sea (Table 3). Genus *Padina* Adanson was used as an outgroup in all three datasets (Fig. 6). All three genes resolved Adriatic *S. schimperi* within monophyletic clades with other *S. schimperi* available in GenBank, with bootstrap values (BS) of 89, 99, and 99 for *rbcL*, *psbA*, and *psaA*, respectively, (Fig. 6). In the *rbcL* phylogeny, Adriatic *S. schimperi* was resolved as sister to the *S. schimperi* identified in Lebanon (BS = 89, Fig. 6A), while remainder of the *Stypopodium* genus was resolved as monophyletic (BS = 100) and sister to the genus *Dictyota* (BS = 97, Fig. 6A). Within the *psbA* phylogeny, more specimens of *S. schimperi* were available and thus resolved in a monophyletic clade (BS = 99) with Adriatic vouchers (Fig. 6B). The monophyly of the entire genus according to *psbA* (BS = 86, Fig. 6B) is less supported in respect to *rbcL* but similar to *psaA* (BS = 81, Fig. 6C).

Recent branching within the *S. schimperi* clade in the *psaA* gene (BS = 99, Fig. 6C) is similar to branching-off in the *rbcL* phylogeny, but with higher support (BS for *rbcL* branching = 89, Fig. 6A).

Discussion

The Adriatic Sea is highly susceptible to biological invasions, as evidenced by the number of recorded NIS (Tsiamis *et al.*, 2019). It is an important area for their primary introduction, mainly due to shipping and oyster farming in its northern parts (Occhipinti Ambrogi, 2000; Marchini *et al.*, 2015; Galanidi *et al.*, 2023; Sfriso *et al.*, 2023). It is also a region where NIS, previously introduced elsewhere in the Mediterranean Sea, spread through secondary dispersal facilitated by human-mediated transport or natural processes, as in the case of *Caulerpa taxifolia* (M. Vahl) C. Agardh and *C. cylindracea* (Žuljević *et al.*, 2004, 2019). A significant portion of these NIS consists of Lessepsian migrants, which are species of Red Sea or-

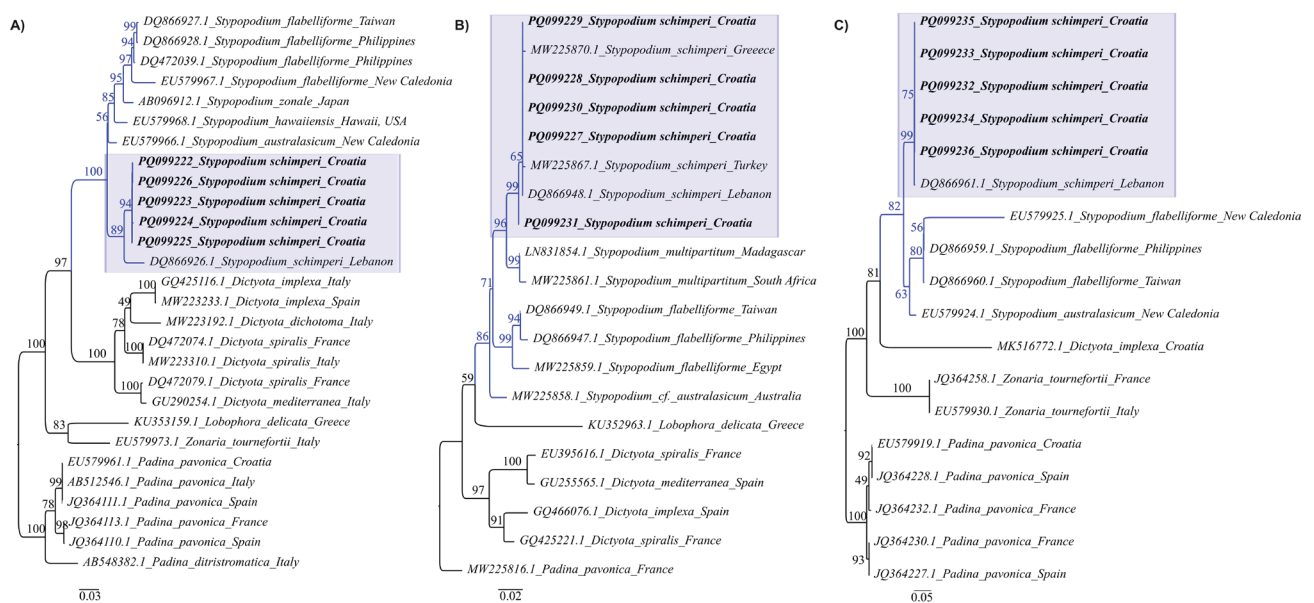


Fig. 6: Maximum likelihood trees based on *rbcL* (A), *psbA* (B), and *psaA* gene (C) sequences. Each sequence is represented with a GenBank accession number and taxon name. The blue highlighted node represents monophyletic *Stypopodium schimperi*. Numbers at each node indicate bootstrap values in % (referred to as BS in the text) based on 1000 replicates, while substitutions per site give the length of branches. *Padina pavonica* is drawn as the root.

Table 3. Specimens used in the present study, along with their GenBank accession numbers and sampling locations (new sequences provided in this study are written in bold letters).

Species name	Sampling location	GenBank accession number		
		<i>rbcL</i>	<i>psbA</i>	<i>psaA</i>
<i>Dictyota dichotoma</i>	Italy: Naples, Posilipo	MW223192		
<i>Dictyota spiralis</i>	France: Languedoc-Roussillon, Banyuls	DQ472079	EU395616	
<i>Dictyota implexa</i>	Italy: Naples, Posilipo	GQ425116		
<i>Dictyota implexa</i>	Spain: Catalunya, Gerona, Palamas	MW223233	GQ466076	
<i>Dictyota implexa</i>	Croatia: Split			MK516772
<i>Dictyota mediterranea</i>	Spain: Balears, Mallorca	GU290254	GU255565	
<i>Dictyota spiralis</i>	France: Ile de Frioul	DQ472074	GQ425221	
<i>Dictyota spiralis</i>	Italy: Sicily, Giardini Naxos	MW223310		
<i>Lobophora delicata</i>	Greece: Ladiko Bay, Ladiko, Rhodes		KU352963	
<i>Lobophora delicata</i>	Greece: Saronicos	KU353159		
<i>Padina ditristomatica</i>	Italy: Augusta Syracuse, Brucoli	AB548382		
<i>Padina pavonica</i>	Croatia: Split	EU579961		EU579919
<i>Padina pavonica</i>	Spain: Catalunya, Llanca	JQ364111		JQ364228
<i>Padina pavonica</i>	France: Ile de Frioul		MW225816	JQ364232
<i>Padina pavonica</i>	Italy: South East Sicily	AB512546		
<i>Padina pavonicoides</i>	France: Provence, Port-Cros	JQ364113		JQ364230
<i>Padina pavonicoides</i>	Spain: Asturias, Oviedo	JQ364110		JQ364227
<i>Styopodium australasicum</i>	New Caledonia: South Province, Ile des Pins	EU579966		EU579924
<i>Styopodium australasicum</i>	Australia: New South Wales, Newcastle		MW225858	
<i>Styopodium flabelliforme</i>	Egypt: Marsa Alam		MW225859	
<i>Styopodium flabelliforme</i>	New Caledonia: Loyalty Islands, Lifou	EU579967		EU579925
<i>Styopodium flabelliforme</i>	Taiwan: Kaisung, Pratas Island	DQ866927		DQ866960
<i>Styopodium flabelliforme</i>	Taiwan: Kaisung, Pratas Island		DQ866949	
<i>Styopodium flabelliforme</i>	Philippines: Bohol, Pangloa Island, Alona Beach	DQ866928	DQ866947	DQ866959
<i>Styopodium flabelliforme</i>	Philippines: Bohol, Cabilao Island	DQ472039		
<i>Styopodium hawaiiensis</i>	USA: Hawaii, Oahu, Lanikai	EU579968		
<i>Styopodium multipartitum</i>	Madagascar: Anosy, Pointe d'Ambero		LN831854	
<i>Styopodium multipartitum</i>	South Africa: Sodwana Bay, Jesser Point		MW225861	
<i>Styopodium zonale</i>	Japan: Kagoshima, Okiakime Is	AB096912		
<i>Styopodium schimperi</i>	Lebanon	DQ866926		DQ866961
<i>Styopodium schimperi</i>	Lebanon		DQ866948	
<i>Styopodium schimperi</i>	Greece: Rhodes, Ladiko Bay		MW225870	
<i>Styopodium schimperi</i>	Turkey: Muradiye, Manisa		MW225867	
<i>Styopodium schimperi 1</i>	Croatia: Vis, Komiža	PQ099222	PQ099227	PQ099232
<i>Styopodium schimperi 2</i>	Croatia: Vis, Komiža	PQ099223	PQ099228	PQ099233
<i>Styopodium schimperi 3</i>	Croatia: Vis, Komiža	PQ099224	PQ099229	PQ099234
<i>Styopodium schimperi 4</i>	Croatia: Vis, Komiža	PQ099225	PQ099230	PQ099235
<i>Styopodium schimperi 5</i>	Croatia: Vis, Komiža	PQ099226	PQ099231	PQ099236
<i>Zonaria tournefortii</i>	France: Provence, Port-Cros			JQ364258
<i>Zonaria tournefortii</i>	Italy: Sicily, Palermo	EU579973		EU579930

igin that entered the Mediterranean following the opening of the Suez Canal (Spanier & Galil, 1991). Notably, 14 Lessepsian fish species have already been recorded in the Adriatic (Lipej *et al.*, 2022). The establishment and further spread of Lessepsian migrants within the Mediterranean are facilitated by the successive warming of seawater (Lejeune *et al.*, 2010). Despite sea warming, the SST in the Adriatic Sea, particularly during winter, remains approximately 10°C lower than in the Red Sea (Pastor *et al.*, 2018; Shaltout, 2019). Such a temperature difference may be an important factor preventing the proliferation of Lessepsian species and their vigorous expansion within the Adriatic, unlike in the southeastern part of the Mediterranean, where winter SST poses no obstacle for species that evolved in tropical seawater (Hoffman *et al.*, 2011; Hoffman, 2014).

Here, the presented morphological and molecular studies of *Stypopodium* specimens from the Vis Archipelago undeniably indicate that they belong to the species *S. schimperi*, previously identified in the southeastern Mediterranean, an area densely populated with numerous Lessepsian seaweeds (Verlaque & Boudouresque, 1991; Verlaque *et al.*, 2015). Among all Lessepsian seaweeds with high taxonomic confidence, *S. schimperi* has the northernmost known distribution in the Mediterranean Sea (Verlaque *et al.*, 2015; van der Loos *et al.*, 2024), and it is the only Lessepsian macroalga detected in the Adriatic to date.

Moreover, *S. schimperi* in the Vis Archipelago represents the northernmost record of a Lessepsian organism, across all marine taxonomic groups, which has drastically outcompeted native organisms and significantly altered indigenous communities within the Mediterranean. It is also the northernmost locality for this species in the world (Guiry & Guiry, 2025).

Notably, SST in the Vis Archipelago is colder during the winter period (13–14°C) when compared to the Mediterranean's Levantine area, where the mean February temperature in Haifa Bay was measured at approximately 20°C (Hoffman *et al.*, 2011, and references therein for details). The expansion and vigorous proliferation of *S. schimperi* into the colder Middle Adriatic, where no other Lessepsian seaweeds are yet spreading and where no other Lessepsian organisms, across all marine taxonomic groups, demonstrate invasive characteristics, raises an important question: Does the Vis Archipelago population of *S. schimperi* have a Red Sea origin or warm temperate roots with a genotype more resistant to colder water? This might be similar to the case of the green alga *C. taxifolia*, which was initially classified as a tropical species but was later found to originate from a warm temperate region of Australia (Meusnier *et al.*, 2004). Outside of the Mediterranean Sea, *S. schimperi* has been rarely recorded as a native species, with occurrences reported in the Red Sea (Egypt), Somalia, Sudan, and South Africa near the border with Mozambique (Vieira *et al.*, 2021; Guiry & Guiry, 2025). As a NIS species, it has also been reported in the Azores, where it was detected in 1997 at a depth of 62 m, with no remarks on its invasiveness (Sansón *et al.*, 2002).

The Vis Archipelago is most likely the first area where *S. schimperi* established its settlements along the Croatian coast of the Adriatic Sea. Despite extensive public awareness efforts and large-scale surveys involving citizen science, combined with over 3700 bottom transects using drop-down cameras, no invaded areas outside of the Vis Archipelago have been detected. If the *S. schimperi* population from the Vis Archipelago originated from another site along the Croatian coast, that initial location should have been detected by now given the rapid spread and invasive behavior of *S. schimperi* observed in the study region, and the extensive, multi-approach surveys conducted to date.

This context raises the following question: where might *S. schimperi* have arrived in the Vis Archipelago from, and what could have been the vector of its introduction? To the best of our knowledge, the closest observation of *S. schimperi* was made in 2009 along the shores of Zakynthos Island (Greece, Ionian Sea), approximately 700 km south-southeast of the Vis Archipelago (Fig. 1A).

Several benthic NIS, such as the seaweeds *C. cylindracea*, *Asparagopsis taxiformis* (Delile) Trevisan, and *Lophocladia trichoclados* (C. Agardh) F. Schmitz, the mollusk *Aplysia dactylomeda* (Rang, 1828), and the decapod *Percnon gibbesi* (H. Milne Edwards, 1853), arrived in the Ionian Sea before spreading to the eastern Adriatic, mainly in the waters of Montenegro and Croatia (Tsiamis *et al.*, 2019). Given this dispersal pattern, currents are assumed to be the predominant vector for the secondary spread of NIS species northward, with the Ionian Sea serving as a stepping stone for their entry into the Adriatic (Žuljević *et al.*, 2004; Katsanevakis *et al.*, 2011). The spread of NIS from the Ionian Sea may be linked to the Ionian bi-modal oscillating system (Civitarese *et al.*, 2010; Gačić *et al.*, 2010), which could explain the presence of some non-native planktonic species in the Adriatic during changes in Ionian Sea circulation (Pećarević *et al.*, 2013).

Some of the earliest records of alga *C. cylindracea*, the decapod crab *P. gibbesi*, and the fish *Pterois miles* (Bennett, 1828) in the eastern Adriatic Sea were reported from the Vis Archipelago (Žuljević *et al.*, 2004; Dragičević *et al.*, 2021; Nejašmić *et al.*, 2021). Those species likely arrived in the area via currents from the Ionian Sea (Poulain, 2001). Vegetative fragments of *S. schimperi* do not float but can be effectively dispersed by wind-generated waves and currents, as observed by divers in the Vis Archipelago (pers. obs.) and recorded by a towed camera at a depth of 90 m. However, the dispersal of large thalli over hundreds of kilometers is likely limited. Proliferations of the blade, which may serve for vegetative reproduction, can be dispersed more efficiently. The production of numerous spores and possibly zygotes (although we observed mature male gametophytes) likely enables the effective long-distance dispersal of microscopic reproductive propagules by currents and waves. Therefore, hydrodynamic processes are most likely the vectors responsible for the introduction of *S. schimperi* to the Vis Archipelago, as they were for the aforementioned newcomers. As a NIS, *S. schimperi* is widely distributed

throughout the southeastern Mediterranean basin, where it has demonstrated invasive characteristics in some areas (Mayhoub & Billard, 1991; Bitar *et al.*, 2000, 2017; Hoffman, 2014; Katsanevakis *et al.*, 2020; Çinar *et al.*, 2021). In Lebanon, it was reported as a single non-indigenous macroalga exhibiting the characteristics of an invasive species among many NIS seaweeds in the 1990s, featuring large fronds and a substantial quantity of algal tissue, that completely replaced native algal assemblages (Bitar *et al.*, 2000).

After the 2000s, it became abundant along the entire Lebanese coast down to a depth of 45 m, impacting native benthic species (Bitar *et al.*, 2017). In Syria, it was first reported (as *S. zonale*) in 1979 and became largely dominant by the end of the 1980s, with large amounts of algal wrack washing up on shorelines (Mayhoub & Billard, 1991). It also became invasive in Rhodes Island (Greece) before 2009 (Tsiamis *et al.*, 2010) and along the Aegean and Levantine coasts of Turkey, where it demonstrated remarkable range expansion with the development of dense populations in the 2010s (Çinar *et al.*, 2021). Regarding the Ionian Sea, no reports indicated its invasive characteristics (Bardamaskos *et al.*, 2009). On Zakynthos Island, it was not detected during surveys conducted in the same region 10 years after the record in 2009 (Dimitriadis *et al.*, 2021). Its spread and impact on the Vis Archipelago resemble reports from Lebanon and Syria (Mayhoub & Billard, 1991; Bitar *et al.*, 2000). However, a quantitative study of its impact in the southeastern Mediterranean, where it has demonstrated invasive characteristics, is missing, as is information on its current status.

The final concern to be addressed is the factors that may have promoted the rapid development and invasive nature of *S. schimperi* in the southeastern Mediterranean and the Vis Archipelago in the Adriatic, despite it not expanding in the Ionian Sea. Similar to the location in the Ionian Sea (Dimitriadis *et al.*, 2021), the Vis Archipelago represents an area of high biodiversity, featuring pristine seagrass *P. oceanica* meadows and rocky habitats overgrown by seaweeds, with minimal anthropogenic disturbance (Žuljević *et al.*, 2009), which might enhance resilience to biological invasions according to the now-challenged diversity-invasibility hypothesis (Elton, 1958). Today, an increasing number of authors dispute the presumed link between disturbances and invasive species (Boudouresque & Verlaque, 2012 and references therein), instead supporting the biotic acceptance theory, which predicts an increase in the spread and abundance of invasive species in areas of high biodiversity (Fridley *et al.*, 2007 and references therein), as is the case in the Vis Archipelago. The development of *S. schimperi* colony is facilitated by its toxicity, which serves as a repellent against Mediterranean herbivorous organisms, similar to other *Stypopodium* species (Gerwick *et al.*, 1979; Gerwick & Fenical, 1981). As previously reported for *S. zonale* (which is known to be toxic to herbivorous fish (Gerwick & Fenical, 1981), we observed a similar rusty coloration leaking from the collected specimens of

S. schimperi. Additionally, we noted an almost complete absence of bite marks on algal thalli. As potential consumers of *S. schimperi*, Lessepsian herbivorous fishes such as *Siganus* spp. are still sporadically recorded in the southern portion of the Adriatic Sea (Lipej *et al.*, 2022). However, as demonstrated by the example of the Red Sea, *Siganus* spp. do not prefer consuming *Stypopodium* algae (Lundberg *et al.*, 2013).

Further spread of *S. schimperi* in the Adriatic Sea might follow a “boom-and-bust” population dynamic, as observed with many invasive NIS, with *C. taxifolia* being considered a textbook example. Within a few years, this green alga became dominant in many Mediterranean areas but then rapidly declined and even completely vanished, as in the Adriatic (Žuljević *et al.*, 2019; Kleitou *et al.*, 2025). On the other hand, *S. schimperi* might continue to spread rapidly. Its vigorous increase in coverage on infralittoral rocks, from sporadic specimens to dense populations over just 3 years in the study area, along with drastic replacement of native algae, suggests its potential to become one of the most invasive benthic NIS in the eastern Adriatic Sea, where the infralittoral zone is predominantly rocky.

Stypopodium schimperi might also expand its distribution to the western part of the Mediterranean, where it seems that no Lessepsian seaweeds (at least those with clear origin and taxonomic status) have been detected to date (van der Loos *et al.*, 2024). The western Mediterranean shares similar characteristics, e.g. SST, salinity (Baza pokazatelja, 2025; SOMLIT, 2025) and benthic communities (Žuljević *et al.*, 2009; La Rivière *et al.*, 2021), with the Vis Archipelago. In this scenario, and alongside the dramatic spread of *Rugulopteryx okamurae* (E.Y. Dawson) I.K. Hwang, W. J. Lee & H.S. Kim in the western Mediterranean (García-Gómez *et al.*, 2020; Ruitton *et al.*, 2021; Borriglione *et al.* 2024) and its recent expansion into the Adriatic Sea (Bottalico *et al.*, 2024), the northern areas of the Mediterranean Sea are facing a shift from the “green algae invasion” characterized by *C. taxifolia* and *C. cylindracea* to a “brown algae invasion” due to *R. okamurae* and highly conquering *S. schimperi*.

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