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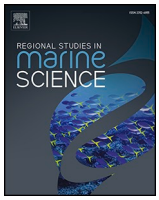

A tropical scleractinian coral reaches the Mediterranean: *Tubastraea* sp. in the Levantine Sea

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ABSTRACT

The spread of non-indigenous species (NIS) in the Mediterranean Sea is a serious concern to its marine biodiversity and ecosystem stability. In the eastern Mediterranean, the Levantine Sea's waters are warmer than in other regions and its native populations decline. In this study, we documented the first occurrence of the scleractinian coral *Tubastraea* sp. in the Mediterranean, based on genetic and morphological characterization. We recorded *Tubastraea* sp. (three adults and two recruits) on artificial structures of the shipwreck MS Zenobia off Cyprus in February 2025, in a shaded area at 25 m depth surrounded by sciaphilic epibenthic communities, despite a chronic oil pollution. From 2011 to 2025, a monitoring of seawater in the shipwreck revealed a warming trend, with the longest warming period from July 2023 to May 2025. This warm scenario may have been conducive to the recruitment of *Tubastraea* sp. Further research is required to identify the potential spread of *Tubastraea* sp. and its ecological implications. This finding has strengthened the importance of long-term studies of benthic community composition on different substrata and habitats off Cyprus for biodiversity monitoring.

1. Introduction

Biological invasion of non-indigenous species (NIS) beyond their native distribution range is a major threat to marine biodiversity worldwide (Bax et al., 2003; Molnar et al., 2008; Rilov and Crooks, 2009) and poses serious challenges to ecosystem stability and conservation efforts (Bax et al., 2001; Mačić et al., 2018). This process is mostly driven by human activities and climate-related changes (Stachowicz et al., 2002; Leprieur et al., 2008), resulting in unprecedented modern rates of species introduction (Ricciardi, 2007). In this context, the Mediterranean Sea represents a well-studied marine hotspot of bioinvasions (Galil, 2000; Rilov and Galil, 2009). The impacts of NIS into this temperate basin are exacerbated by the fact that the Mediterranean Sea is a small, semi-enclosed water body that hosts an outstanding biodiversity, with almost half of the species being endemic (Myers et al., 2000; Bianchi and Morri, 2000; Coll et al., 2010; Costello et al., 2017).

The main vectors and drivers of NIS include the opening and subsequent enlargements of the Suez Canal, intense maritime traffic, aquaculture, and aquarium trade (Galil, 2009; Katsanevakis et al., 2014; Mannino et al., 2017; Zenetos et al., 2012). Most Mediterranean NIS are either tropical Indo-Pacific or Indian Ocean invaders, which have

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propagated through the Suez Canal, or (sub)tropical Atlantic taxa introduced through human activities or naturally via the Gibraltar Portal (Galil, 2008; Galil et al., 2015). The spread of thermophilic species has been also facilitated by the remarkable sea surface temperature warming that the Mediterranean Sea has experienced since the last decades (Vargas-Yáñez et al., 2008; Nykjaer, 2009; Lejeusne et al., 2010; Pastor et al., 2020). This is especially true in the Levantine Sea, the easternmost sector of the Mediterranean Sea delimited by Turkey, Syria, Lebanon, Palestine, Israel, Egypt, and Dodecanese islands, which is the warmest portion of the entire basin and has warmed by about 3 °C in the last three decades (Ozer et al., 2017). As such, the Mediterranean Sea is characterized by the so-called processes of 'tropicalization', *i.e.*, the simultaneous increase in temperature and abundance of tropical species within the basin (Bianchi and Morri, 2003; Bianchi, 2007), and 'meridionalization', *i.e.*, the northward range expansion of warm-water species from the southern areas of the Mediterranean Sea (Boero et al., 2008; Bianchi et al., 2018). At a regional scale, the Levantine Sea harboured the highest number of NIS, with a number approximately four times higher than the western Mediterranean Sea (Galil, 2008; Zenetos and Galanidi, 2020; Galanidi et al., 2023). Multiple concurrent factors have contributed to this geographical disparity (Galil and Zenetos, 2002; Rilov and Galil, 2009). These include the role of the eastern Mediterranean Sea as the gateway for Lessepsian newcomers through the Suez Canal (Galil et al., 2017), its relatively warm waters, which have experienced a greater increase in temperature compared to the western Mediterranean Sea (Nykjaer, 2009; Shaltout and Omstedt, 2014), and the impoverishment and decline of native species that could potentially leave vacant niches for the NIS (Oliverio and Taviani, 2003; Albano et al., 2021). In this context, Cyprus represents a hotspot of marine bioinvasions in the Mediterranean Sea due to major shipping routes and the proximity to the Suez Canal. Indeed, recent inventories documented that marine NIS doubled in the last 20 years, highlighting the role of Cyprus as an early-warning sentinel for the arrival and spread of thermophilic species in the Levantine Sea (Michail et al., 2026).

To date, although nearly 1000 NIS have been recorded in the Mediterranean Sea, with molluscs, arthropods, fishes, and macrophytes being the most represented taxa, whereas only eight anthozoan NIS have been reported in the basin (Galil, 2008, 2009; Zenetos and Galanidi, 2020; Galanidi et al., 2023). Specifically, two NIS of sea anemones (Hexacorallia, Actiniaria), namely *Diadumene cincta* and *Diadumene lineata*, have been identified from Italian and Slovenian waters and the Adriatic Sea (Pax, 1925; Verlaque, 1981; Bikemeyer, 1996; Tiralongo et al., 2022). Çinar et al. (2014) reported the tube-dwelling anemone *Pachycerianthus multiplicatus* (Hexacorallia, Ceriantharia) on muddy bottoms in Turkey, a cold-water species probably arrived in the Mediterranean Sea through ballast water. Three NIS of octocorals (Octocorallia, Malacalcyonacea) have been recorded from the Levantine Sea (Fine et al., 2005; Grossowicz et al., 2020; Nativ et al., 2023; Badreddine et al., 2023; Shlesinger et al., 2024; Kletou et al., 2025). In particular, the Lessepsian migrant *Melithaea erythraea* may have a limited invasive potential as it has been reported only in small aggregations at two sites in Israel to date (Fine et al., 2005; Grossowicz et al., 2020). Conversely, in the last few years the Indo-Pacific species *Dendronephthya hemprichii* has been found both in Israel and Lebanon (Nativ et al., 2023; Badreddine et al., 2023; Shlesinger et al., 2024) and, in particular, Shlesinger et al. (2024) described a dense and healthy population of this octocoral species on an artificial structure in Israel. Recently, Kletou et al. (2025) reported the occurrence and rapid proliferation of the fast-growing tropical octocoral *Carijoa* on artificial substrata and boulders at multiple locations in Limassol, Cyprus. Finally, two non-Lessepsian NIS of hard corals (Hexacorallia, Scleractinia) have been reported in the Mediterranean Sea, namely *Oculina patagonica* (*e.g.*, Zibrowius, 1974; Zibrowius and Ramos, 1983) and *Oulastrea crispata* (Hoeksema and Ocaña Vicente, 2014; Mariani et al., 2018). Since its first observation in the Ligurian Sea (Zibrowius, 1974), the former species has been recorded from multiple countries in both the western and eastern Mediterranean Sea, probably introduced by shipping from the Straits of Gibraltar and subsequent maritime traffic with the basin (*e.g.*, Bitar and Zibrowius, 1997; Fine et al., 2001; Sartoretto et al., 2008; Salomidi et al., 2013; Rubio-Portillo et al., 2014). Nevertheless, genetic analyses indicated that *O. patagonica* has not been recently introduced from the western Atlantic Ocean, questioning its non-indigenous status (Leydet and Hellberg, 2015). The Indo-Pacific reef coral *O. crispata* is an opportunistic colonizer capable of living also in non-reefal cold waters (Yajima et al., 1986; Yamano et al., 2024). It has been noticed firstly on rocky substrate in Corsica (Hoeksema and Ocaña Vicente, 2014) and, later, in a port and in a granitic reef in Spain (Mariani et al., 2018) and, given its morphological similarity with *O. patagonica* and *Cladocora caespitosa*, the species may have been overlooked.

On a global perspective, few species of hard corals have been documented as introduced. Hoeksema et al. (2012) documented the presence of dead encrusting colonies of the Atlantic reef coral *Favia fragum* on a gas cylinder beached on the North Sea shore of the Netherlands. After an accidental introduction, individuals of the Indo-Pacific tropical species *Fungia scutaria* have been found in the Caribbean Sea (Bush et al., 2004; LaJeunesse et al., 2005), posing limited concerns in terms of invasiveness (Sammarco et al., 2010). Recently, a potential invasive species of Indo-Pacific *Acropora* has been observed in Venezuela, arrived probably through the aquaria trade (Villamizar et al., 2026). Conversely, the azooxanthellate *Tubastraea* is a well-studied case of a highly invasive tropical coral that has spread rapidly from the Indo-Pacific into multiple regions worldwide starting from the 1940s (*e.g.*, Riul et al., 2013; Creed et al., 2017; Dutra et al., 2023). Recent integrative studies have expanded the known diversity of the genus, validating four new species in the Southwestern Atlantic (*T. grandidentata*, *T. megalostoma*, *T. columnata*, and *T. ramosa*) and bringing the total number of accepted species to 16 (Serra et al., 2026). Currently, nine species are considered invasive or non-indigenous outside their native ranges, including the historically recognized invaders *T. coccinea*, *T. tagusensis*, and *T. micranthus*, together with *T. aurea, T. faulkneri*, and the four newly validated species (Sammarco et al., 2010, 2014; Silva et al., 2011; Precht et al., 2014; Serra et al., 2026). For example, the Indo-Pacific *T. coccinea* has invaded the Caribbean, the Gulf of Mexico, and the southwestern Atlantic (Fenner, 2001; Fenner and Banks, 2004; Mantelatto et al., 2011; Derouen et al., 2020; Crivellaro et al., 2021; Bastos et al., 2022), recently reaching also the Canary Islands, in the eastern Atlantic (Brito et al., 2017; López et al., 2019).

Currently, the known Mediterranean scleractinian fauna belonging to the family Dendrophylliidae includes representatives of the genera *Dendrophyllia*, *Cladopsammia*, *Balanophyllia*, *Leptopsammia* and *Astroides* (Zibrowius, 1980; Altuna and Poliseno, 2019). In this study, we documented the first record of a non-indigenous coral, *Tubastraea* sp., in the Levantine Sea, eastern Mediterranean, on artificial structures of a shipwreck off Cyprus in 2025. We provided genetic and morphological characterizations of this coral and we described the habitat where it was recorded.

2. Materials and methods

2.1. Study site

The MS Zenobia was a RORO-type ferry and passenger ship that sank in 1980 in Larnaka Bay, Cyprus, eastern Mediterranean Sea (34° 55.128' N, 33° 39.354' E). The large metal structure (length 172 m) rests on the bottom (43 m depth) on its port side (Fig. 1). In consequence, the transverse steel ribs of the starboard side form the functional upper surface, which is referred to as "up", "top" or "ceiling" in the text. The ship capsized with lorries, vehicles and cargo that contribute to increase the multiple irregular surfaces and heterogeneity of habitats provided by railings, frames, staircases, cargo hatches, cut-outs, side openings, ramps, car decks, etc. The area of study in the shipwreck is at 25–27 m

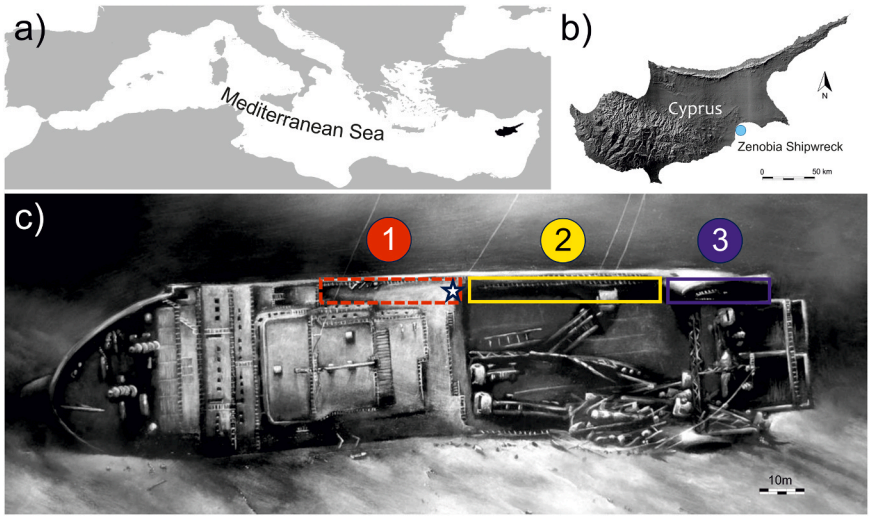

Fig. 1. Location of the MS Zenobia shipwreck in Cyprus, eastern Mediterranean Sea, where *Tubastraea* colonies were observed (a-b). Surveyed areas along the starboard-side of the MS Zenobia shipwreck (c): (1) upper car-deck (internal); (2) car/cargo deck (external); (3) funnel (smokestack). Position of the temperature dataloggers is indicated by the star.

depth, between the upper car deck (behind the accommodation complex and bridge block) and the external funnel base (smokestack), aft on the superstructure (Fig. 1). The starboard-side upper car-deck is a semidark zone where oil accumulates in puddles on the ceiling, in the shallow recesses between ribs (*i.e.*, confined dark areas). Positive buoyant debris of diverse nature (*e.g.*, insulating materials, plastics, polystyrene foam) are also found in large quantities piling up in the oil puddles. This "anthropogenic flotsam" is highly movable and constantly changes position because of the impact on the ceiling by exhalation bubbles from scuba divers swimming through the large bays of the car-deck. This is a popular dive route to reach the wide door apertures, hatchways and companion passageways in the starboard hull. The external area included in the study corresponds to the shaded top of the originally exposed car/cargo deck until the external funnel base and adjacent structures (ca. 25 m depth) (Fig. 1). The funnel itself forms a long horizontal surface protected from direct solar irradiation. Scleractinian corals, sponges and other taxa found in the seemingly extreme environment of the MS Zenobia's upper car-deck have been studied by Jimenez et al. (2017) and Nardi et al. (2024), who compared it to other areas of the superstructure, such as the funnel.

2.2. Survey and collection of samples

The first *Tubastraea* sp. colony was found in February 2025 during a routine visit to the entrance of the car deck to replace temperature data loggers. To confirm the presence of other colonies in the wreck, the entire ceiling area of the upper car-deck (675 m^2) was surveyed by two to three divers along repetitive parallel transects along the ceiling extending from the end of the car deck to the entrance and vice versa. Each survey involved approximately 30 – 35 min of dedicated search effort, with dive duration planned to remain within the no-decompression limits for the operating depth (ca. 25 – 27 m) and breathing gas (EAN30). Overall, the survey effort comprised five dives (three with two divers and two with three divers), corresponding to approximately 360 – 420 diver-minutes (ca. 6 – 7 diver-hours) of targeted visual searches. Headlamps, hand-held torches and video lights were used to inspect the dark areas. Given the large quantities of floating debris constantly shifting position on the ceiling and the stirring up of droplets of oil, divers had to keep at least 1 m distance between each other. The inspection of the shipwreck sections from the entrance of the car-deck until the external funnel base (327 m^2) and the funnel base and its vertical structure (253 m^2), was along parallel transects as well. Light was needed by divers to inspect open hatches and confined spaces behind metal structures. Three adult colonies of *Tubastraea* sp. found in the car-deck were sampled by scraping-off the coral from the attachment surface using a metal spatula. Two colonies were bleached in sodium hypochlorite, rinsed with fresh water, and air-dried for morphological analyses. The two specimens have been deposited at the Enalia Physis coral collection, Cyprus and University of Milano-Bicocca, Milan, Italy (specimen MED1456). A tissue sample (specimen MED1455) was collected from the third colony and preserved in 96% ethanol for subsequent molecular analysis. The remaining portion of this latter colony was kept in aquarium for observations. The two recruits could not be found again due to the constant drift of the buoyant debris.

2.3. Morphological analyses

Skeleton observations from one of the bleached colonies (specimen MED1456) were undertaken using an OM System Tough TG-7 camera (Tokyo, Japan) or ZEISS SteREO Discovery V12 microscope (Oberkochen, Germany) equipped with a ZEISS Axiocam 712 color (Oberkochen, Germany). Following multiple studies addressing the skeletal features of the family Dendrophylliidae (Cairns, 2001; Cairns and Kitahara, 2012; Figueroa et al., 2019; Yiu et al., 2021; Bastos et al., 2022; Yiu and Qiu, 2022; Serra et al., 2024), we investigated the following six macromorphological characters of the corallum: growth pattern and development, intercorallite distance, coenosteum structure, calice shape, septa arrangement, and columella structure. Special attention was given to micromorphological details, such as septal and theca ornamentation, which are considered robust autapomorphic characters for the genus (Serra et al., 2026). Additionally, the following six morphological characters were measured for six corallites from a single colony: greater and lesser calicular diameter, greater and lesser columella diameter, maximal fossa depth, and maximal corallite projection (Table S1). The morphometric measurements were taken by analyzing the digital images obtained at the microscope with ImageJ 1.54 g (Schneider et al., 2012). Finally, *in-vivo* photos of *in-situ* colonies were used to annotate the color of coenosarc, polyps, and tentacles.

2.4. Molecular analyses

Total genomic DNA was extracted from a single specimen of *Tubastraea* sp. (specimen MED1455) using DNeasy® Blood & Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer protocol. A

mitochondrial region encompassing the ATP8 gene, an intergenic spacer, and a portion of the cytochrome *c* oxidase I (COI) was selected following Figueroa et al. (2019) as this molecular locus (hereafter ATP8-COI) distinguished three *Tubastraea* species from the Gulf of Mexico. The mitochondrial marker was amplified using the primers CS-F16 and CS-R16 (Lin et al., 2011) and polymerase chain reaction (PCR) conditions by Figueroa et al. (2019) with the following thermic cycle: 95 °C for 3 min, 30 cycles of 94 °C for 30 s, 48 °C for 45 s, 72 °C for 90 s, and a final extension of 72 °C for 10 min. PCR product was checked through 1.5% agarose electrophoretic run, purified, and directly sequenced in both directions by Macrogen Europe (Milan, Italy) using an ABI 3730xl DNA Analyser (Applied Biosystems, Waltham, CA, USA). The obtained sequence has been submitted to NCBI Nucleotide GenBank under the accession number PZ303848.

Our sequence was phylogenetically investigated together with the ATP8-COI sequences generated by Figueroa et al. (2019) and by extracting this molecular region from the mitochondrial genomes of *Tubastraea* species available in NCBI Nucleotide GenBank (Table S2). The ATP8-COI region identified from the mitochondrial genome of *Dendrophyllia cribrosa* (JQ290080) was used as outgroup for the phylogeny reconstruction hypothesis following Figueroa et al. (2019). Multiple sequence alignment was performed using MAFFT 7.450 (Katoh et al., 2002; Katoh and Standley, 2016) with the iterative refinement method E-INS-I. The best-fitting substitution model was selected using jModelTest 2.1.9 (Darriba et al., 2012) and, according to the Akaike Information Criterion (AIC), the HKY + G was identified. Phylogeny reconstruction inference was carried out under both maximum likelihood (ML) and Bayesian inference (BI) criteria. ML tree was obtained using RAxML 8.2.12 (Stamatakis, 2014) and the graphical front-end raxmlGUI 2.0.14 (Edler et al., 2021), with 1000 rapid bootstrap replicates. BI analysis was conducted using MrBayes 3.2.6 (Huelsenbeck and Ronquist, 2001; Ronquist et al., 2012), with four Markov chains of 3 million generations implemented in two runs, saving one tree every 300 iterations. The recovery of analysis convergence was estimated using Tracer 1.7 (Rambaut et al., 2018), setting the first 25% trees to be discarded as burn-in. Additionally, to increase the phylogenetic dataset, all the already published COI sequences of *Tubastraea* spp. were downloaded from GenBank (Table S2) and were aligned to the above-mentioned sequences. The obtained alignment was trimmed to the length of the shortest sequences and then used for phylogeny reconstructions under both ML and BI criteria, as previously detailed. Finally, a median-joining haplotype network was built using PopART 1.7 (Leigh and Bryant, 2015) under default parameters.

2.5. Seawater temperature monitoring

The epibenthic communities of the MS Zenobia have been significantly impacted by changes in the thermal regime of the seawater in Cyprus and in the Levantine Sea in general (*e.g.*, Garrabou et al., 2022; Nardi et al., 2024). In consequence, a long temporal data series (2011–2025) of seawater temperature (SWT) from data loggers set to record temperature every 30 min at the entrance of the car-deck (25 m depth), was used to provide a characterization of the thermal conditions in the study area (monthly averages). The last three years are of particular interest due to the changes reported by Nardi et al. (2024) during that same time period. Monthly averages, min and max temperature were calculated for the entire data set and anomalies were produced by subtracting from each month the long-term average

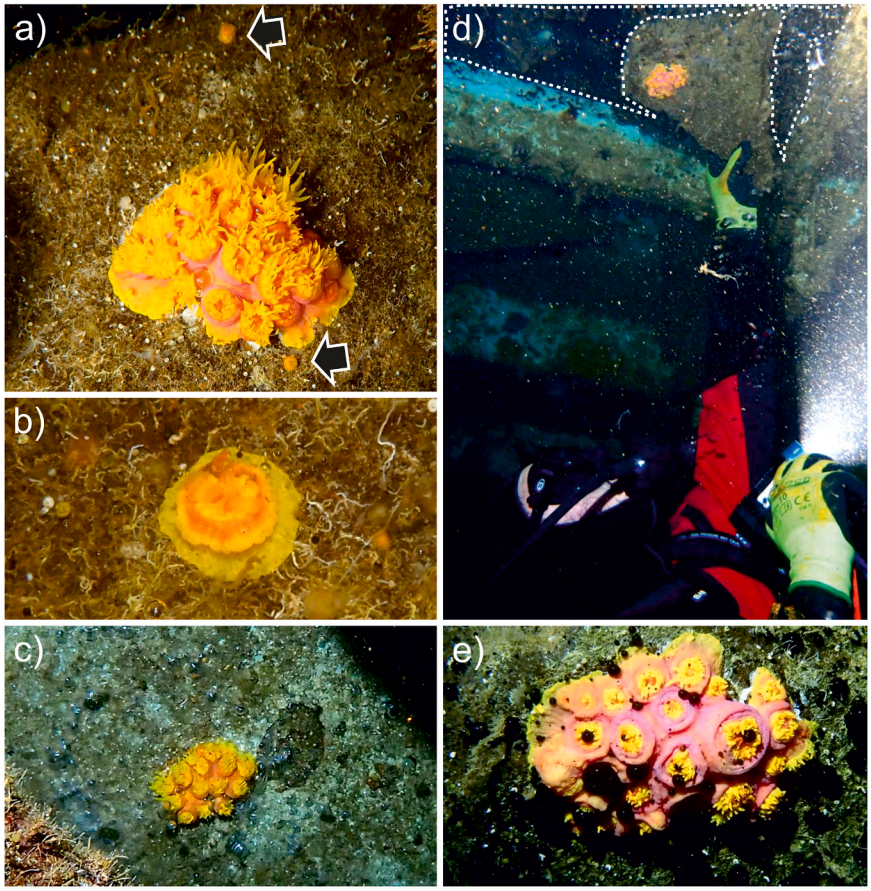

Fig. 2. Colonies of *Tubastraea* sp. on the MS Zenobia shipwreck. (a) Specimen MED1456 and two recruits (arrows). (b) Detail of one recruit. (c) Specimen MED1455, used for the molecular analyses. (d) Specimen on styrofoam "floating" in a pond of oil (dashed line); the diver is retrieving the styrofoam from the oil. (e) Screengrab showing droplets of oil between polyps, tentacles and oral cavities of one colony (d).

(2011–2024) for that month.

3. Results

3.1. In-situ observations

A total of three *Tubastraea* sp. colonies and two recruits were found in the car-deck area (Fig. 2a-c). Two of the colonies and the recruits were attached to the heavily encrusted metal surface of the ceiling in dark conditions and were surrounded and partially hidden by floating debris and close to the edge of oil ponds. The small recruits were partially hidden by a large floating plank of unknown original purpose as well as plastic containers. The third colony was settled on a piece of polyurethane foam (styrofoam) that shifted position constantly along the ceiling of the car-deck in a semi-dark area (Fig. 2d). All colonies were observed with oil droplets on their surfaces, between tentacles and inside oral cavities (Fig. 2e). These droplets were caused by the impact of exhalation bubbles by divers from the surveying team as well as from recreational divers visiting this section of the shipwreck. No other *Tubastraea* colonies were found in the external areas of the wreck's structure.

3.2. Morphology

Live colonies of *Tubastraea* sp. from Cyprus exhibit coenosarc and polyps ranging from pink to orange, with an orange oral disc and yellow tentacles (Fig. 2). The living tissue often extends beyond the limits of the corallum or the founder polyp, suggesting the possibility of new polyps developing from preexisting skeletal structures beneath this tissue, although further observations are needed to confirm this process. The colonies are massive to encrusting, with a plocoid to sub-phaceloid polyp arrangement (Fig. 3a). The specimen illustrated in Fig. 3 measures 5.3 × 6.0 cm along its greatest axes, covering an area of approximately 21.8 cm^2 and reaching a maximum height of 2.0 cm. The corallum consists of 23 corallites (Fig. 3a, b), with an average projection of 3.8 ± 0.6 mm, ranging from 3.3 mm to 5.0 mm (Fig. 3c, d). The coenosteum is highly porous, with a synapticulotheca forming moderately thick intercostal grooves (Fig. 3e); in some polyps, these grooves subdivide the corallite wall, producing deep cuts. As a result, the corallite margin becomes irregular and acquires a lance-like appearance (Fig. 3c, d). Central corallites are moderately spaced, whereas peripheral ones are more closely arranged (Fig. 3a). Calyces range from circular to elliptical, with larger diameters between 9.9 mm and 11.2 mm and smaller diameters from 8.2 mm to 10.1 mm (Fig. 3a–c). The septal arrangement follows a hexameral pattern rather than the Pourtalès Plan, with 28–34 septa, organized in four cycles, described by the formula S1 ≥ S2 ≥ S3 > S4; S1 – S3 complete; S4 incomplete and/or rudimentary (Fig. 3b). Septal faces are densely ornamented with rounded, slightly pointed, and spaced granules (Fig. 3f, g). Primary septa are regular and smooth, while S2 to S4 display irregular margins with laciniate projections; in larger polyps, these septa may extend straight toward and reach the columella (Fig. 3b). Fusions between S3 and S4 were observed (Fig. 3b). The columella is bulky, spongy, and well developed (Fig. 3b, c, h), measuring 4.7 – 8.3 mm in its greater diameter and 3.5 – 6.2 mm in its smaller diameter. The fossa depth ranges from 3.0 mm to 5.3 mm, with an average of 4.0 ± 0.8 mm (Fig. 3c, f). On the coenosteum at the basal margin of the corallum, we observed some tube-like skeletal microstructures, with an approximate diameter of 0.2 – 0.6 mm, likely induced by the presence of associated worm-like invertebrates (Fig. S1).

3.3. Molecular analyses

The total ATP8-COI alignment used for the phylogenetic reconstruction analyses consisted of 859 base positions of which no indels and only 14 variable sites were identified. The phylogenetic reconstruction using both ML and BI criteria showed similar topologies, therefore only the ML tree is shown with bootstrap values and Bayesian posterior probabilities mapped on each node (Fig. 4a). A first clade with moderately high support (ML bootstrap value: 88; Bayesian posterior probability: 0.96) included *T. tagusensis* from Brazil and Gulf of Mexico, *T. diaphana* from Brazil, Taiwan and an unspecified locality in the USA, and *T. micranthus* from Japan. A second, divergent clade with lower support (ML bootstrap value: 70; Bayesian posterior probability: 0.92) included *T. coccinea* from Brazil and Gulf of Mexico and three sequences of *Tubastraea* spp. from Gulf of Mexico and Cyprus. The total COI alignment consisted of 446 base positions, with no indels and 24 variable sites. Also, in this case ML and BI criteria revealed similar topologies and therefore only the ML tree is shown with bootstrap values and Bayesian posterior probabilities mapped on each node (Fig. S2). In this case, the only moderately well-supported clade was the one including the specimen from Cyprus, the other sequences found in the same clade in the ATP8-COI reconstructions, and some additional sequences from multiple Atlantic and Indo-Pacific localities. However, the other phylogenetic relationships were overall poorly resolved.

For the haplotype network analysis based on the ATP8-COI dataset, we removed *Dendrophyllia cribrosa* from the multiple alignment, resulting in eight variable sites. The results of the network were consistent with the phylogenetic reconstructions (Fig. 4b), with two haplogroups

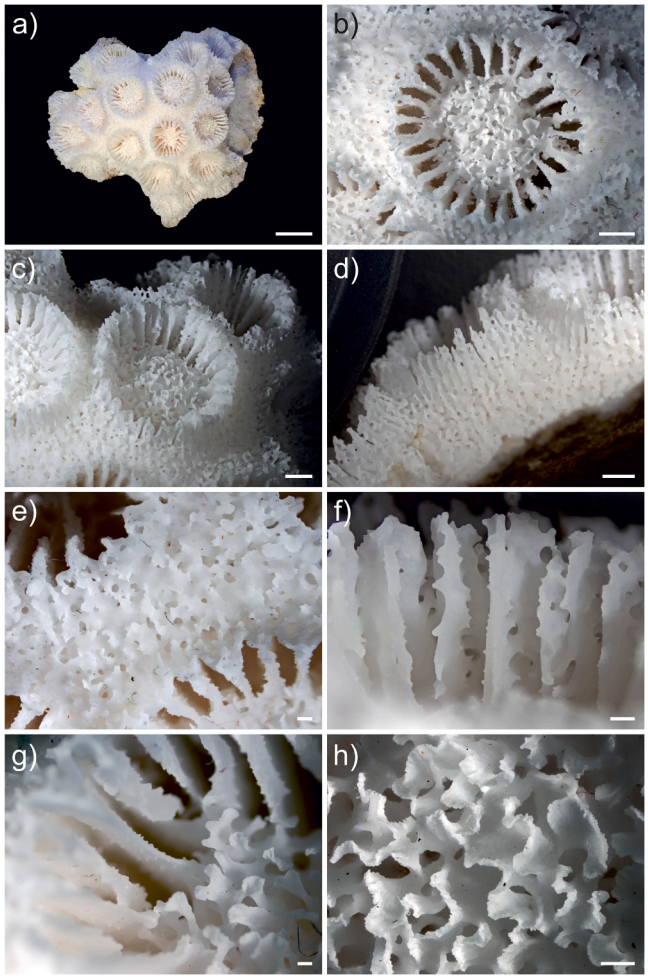

Fig. 3. Skeletal morphology of *Tubastraea* sp. (specimen MED1456). (a) Massive to encrusting corallum highlighting the plocoid to sub-phaceloid corallite arrangement, (b, c) calicular view of corallites showing the hexameral septal distribution in four cycles, (d) lateral view of a corallite showing the porous synapticulotheca, (e) detail of the highly porous coenosteum, (f, g) close-ups of septa (S1 – S4) showing septal face ornamentation, (h) detail of the columella. Scale bars: (a) 10 mm, (b, c, e) 2 mm, (d, f, g, h) 0.5 mm.

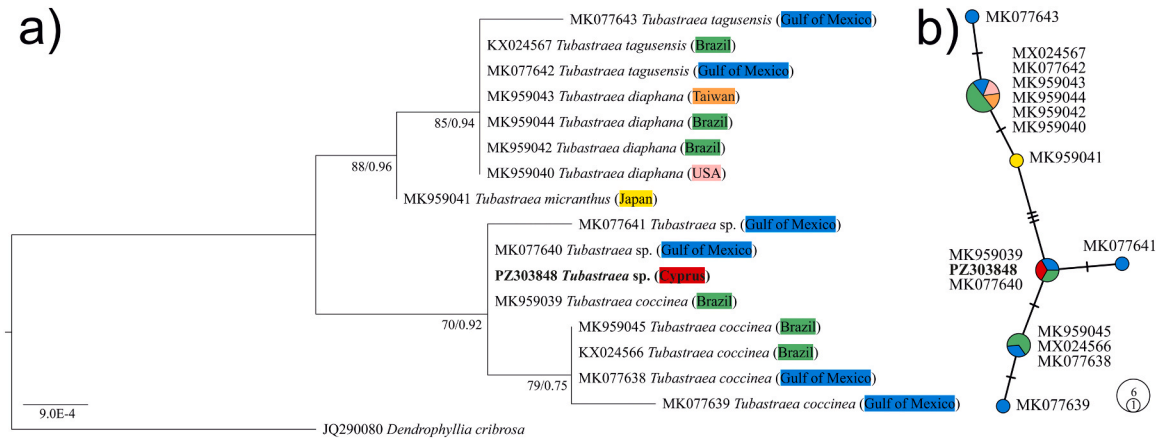

Fig. 4. Evolutionary relationships of *Tubastraea* sp. found in Cyprus (eastern Mediterranean Sea) with other *Tubastraea* species (multiple localities in Atlantic and Pacific Ocean) based on a mitochondrial region encompassing the ATP8 gene, an intergenic spacer, and a portion of the cytochrome *c* oxidase I gene (859 bp). Colors refer to collection localities. The specimen from Cyprus is in bold and colored in red. (a) Maximum likelihood (ML) reconstruction, with numbers at nodes representing bootstrap values (≥ 50) and Bayesian posterior probabilities (≥ 0.7), respectively. Alpha-numeric codes before species names are the GenBank accession numbers. (b) Median-joining haplotype network of *Tubastraea* sequences.

separated by three substitutions and corresponding to the two main clades found in the phylogenetic analyses. Overall, seven haplotypes were recovered, three of which were represented by more than one sequence. Specifically, *Tubastraea* sp. from Cyprus shared the same identical sequence with a *T. coccinea* from Brazil (GenBank accession number: MK959039) and with a *Tubastraea* sp. from Gulf of Mexico (GenBank accession number: MK077640). Another haplotype was shared by three sequences of *T. coccinea* from Brazil and Gulf of Mexico and a haplotype was shared by two sequences of *T. tagusensis* from Brazil and Gulf of Mexico and by four sequences of *T. diaphana* from Brazil, Taiwan, and USA. The remaining four haplotypes occurred only in one sample each.

3.4. Seawater temperature monitoring

The seawater temperature record from the car-deck showed noticeable warm and warmer than-normal periods that have occurred during the last 14 years (Fig. 5a). The first of the most prominent periods with the highest warm anomalies lasted 11 months, from November 2017 to December 2018 (> 2.5 °C), and the second lasted eight months, from August 2022 to March 2023 (> 2 °C) (Fig. 5b). However, the longest warming period on record lasted 23 consecutive months, from July 2023 to May 2025, although the anomalies were less pronounced (0.5 – 1.7 °C).

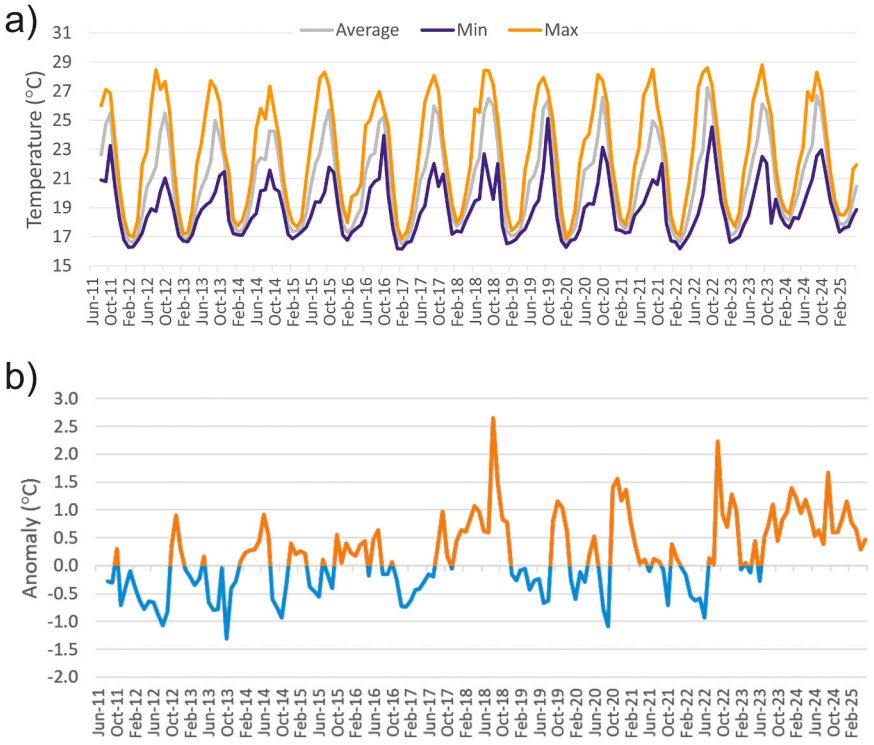

Fig. 5. Seawater temperature (August 2011-May 2025) monthly average (a) and anomalies (b). Warmer and colder-than-average anomalies are shown in orange and light blue, respectively. Date format MMM-YY.

4. Discussion

In this study, we reported the first occurrence of the tropical scleractinian coral *Tubastraea* sp. in the Mediterranean Sea and provided a morphological and genetic characterization of the organism. The non-indigenous coral has been observed on consolidated and unstable surfaces of the MS Zenobia shipwreck in Cyprus at around 25 m depth. The coral colonies occurred in a semi-dark sector of the wreck that, although under the influence of a chronic leakage of oil, hosts diversified sciaphilic epibenthic communities of sponges, corals, bryozoans, polychaetes, and other organisms (Jimenez et al., 2017). The find of *Tubastraea* sp. brings the total number of scleractinian corals in Cyprus to 17 (Jimenez and Zibrowius unpublished data).

We cautiously did not assign a species name to the *Tubastraea* colonies observed in Cyprus because of multiple factors, including the fact that both the morphological and molecular assessments were based on very limited material. (i) The identification of *Tubastraea* corals based on macromorphology is hampered by a complex taxonomy history of the genus and by the high intraspecific morphological variation of skeletal characters (Boschma, 1953; Cairns, 2001; Bastos et al., 2022, 2026). In addition, morphological plasticity in modular growth has been documented in *Tubastraea* colonies under different hydrodynamic conditions (Tanasovici et al., 2022). Furthermore, several new species of *Tubastraea* have been described during the last years (Yiu et al., 2021; Yiu and Qiu, 2022; Serra et al., 2024, 2026) and also various unidentified morphotypes have been reported (Arrigoni et al., 2014; Figueroa et al., 2019; Bastos et al., 2022), suggesting that our understanding of the current species richness within this coral genus may be incomplete. The skeletal morphology of the Cyprus specimen exhibits a regular hexameral distribution of septa, a critical diagnostic character that distinguishes it from congeners defined by the complex septal fusions of the Pourtalès plan, such as *T. dendroida*, *T. megacorallita*, *T. violacea*, and *T. stimpsonii* (Yiu et al., 2021; Yiu and Qiu, 2022; Mehrotra et al., 2023). Beyond the exclusion of these clades, the specimen displays distinct features from other hexameral congeners described by Serra et al. (2024). Its massive plocoid growth differs from the arborescent branching of *T. ramosa* and the slender dendroid columns of *T. columnata*. Additionally, the bulky columella and closer arrangement of corallites distinguish it from *T. faulkneri*, while the presence of only four septal cycles and cylindrical corallites further separate it from *T. aurea*, which typically possesses five cycles and conical corallites. Furthermore, the irregular lance-like corallite margins differ from the smooth thecal margins of *T. coccinea* and *T. diaphana*, while the absence of a fifth septal cycle separates it from *T. megalostoma* (Serra et al., 2024). (ii) Our molecular analyses based on the mitochondrial ATP8-COI region showed that the studied sample clustered together with *T. coccinea* from Brazil and an unidentified *Tubastraea* morphotype from USA (Gulf of Mexico). This is not surprising since molecular studies of scleractinian corals based on single mitochondrial and nuclear markers often generated unresolved phylogenies and failed to detect species boundaries (Kitahara et al., 2016) as the result of, for example, the slow evolution rate of mitochondrial genome in Anthozoa (Huang et al., 2008), incomplete lineage sorting (van Oppen et al., 2001; Bastos et al., 2026), and the presence of pseudogenes (Márquez et al., 2003). Conversely, the use of reduced-genome representation approaches, such as targeted capture of ultraconserved elements and exonic loci (Quattrini et al., 2018; Cowman et al., 2020), have been demonstrated to resolve both deep and shallow evolutionary relationships in corals (*e.g.*, Quek et al., 2023; Bridge et al., 2024; Vaga et al., 2025). Therefore, the application of such genomic techniques and additional sampling would help to elucidate both the species assignment and the geographic origin of the *Tubastraea* colonies observed in Cyprus. (iii) In accordance with recent findings suggesting high level of local retention and rare long-distance dispersal (Figueiredo et al., 2013; Wood et al., 2014), genomic studies indicated that geographic distribution ranges of several scleractinian species are smaller than traditionally predicted (*e.g.*, Bongaerts et al., 2021; Bridge et al., 2024; Terraneo et al., 2025). As such, the unknown geographical origin of the *Tubastraea* colonies found in Cyprus represents an additional limitation that led us to conservatively not assign a species name to the studied coral material.

A total of five colonies (three adults and two recruits) of *Tubastraea* sp. were observed in the MS Zenobia shipwreck during our systematic intense surveys, although we cannot rule out the potential presence of additional *Tubastraea* corals in other areas of the artificial reef. Given the limited number of colonies encountered, no ecological effects and specific interactions with the local epibenthic communities can be determined in relation to the arrival of this non-indigenous coral in Cyprus, to date. However, its affinity for dim to dark habitats may increase the competition with other epibenthic species for resources (*e.g.*, space, food) in the already limiting environment. Furthermore, the presence of tube-like skeletal microstructures (Fig. S1) suggests the possible establishment of close associations with other invertebrates. Tubular skeletal modifications are known to be induced by a variety of coral-associated organisms, including, among the others, hydrozoans, amphipods, and polychaetes (*e.g.*, Bergsma, 2009; Molodtsova et al., 2016; Manca et al., 2019). Nevertheless, the nature of these structures in the *Tubastraea* colonies observed in Cyprus remains unclear, as they were detected only on bleached skeletons and no direct evidence of associated invertebrates was observed in *in vivo* photographs. Moreover, documented associations between *Tubastraea* species and other invertebrates are scarce and mainly involve motile epibiotic organisms (Stella et al., 2011), although invasive *Tubastraea* colonies have been reported to host a native Christmas tree worm species in the Caribbean (Hoeksema and ten Hove, 2017). Considering that other scleractinian corals NIS can host diverse native fauna (Villamizar et al., 2026), and that coral-associated organisms can also benefit their hosts (Gates and Ainsworth, 2011), the characterization of these associations is crucial to better assess both the potential invasiveness and ecological impacts of scleractinian NIS.

Tubastraea corals outside their native distribution ranges have been demonstrated to be highly invasive (Creed et al., 2017; Dutra et al., 2023). For example, the invasive *T. coccinea* and *T. tagusensis* were capable to alter the coverage, composition, and structure of benthic communities in the tropical Atlantic Ocean and the Caribbean (Miranda et al., 2016, 2018), including the competitive removal of native species (Creed, 2006; dos Santos et al., 2013; Mantellato and Creed, 2014) and the indirect facilitation of the establishment of other invasive species (Vinagre et al., 2018; Tanasovici et al., 2020), with potential negative modifications of ecosystem functioning. The biological invasion of these species has been enhanced by peculiar life history traits such as the ability to settle on both natural and artificial substrates (Creed and De Paula, 2007; Tanasovici et al., 2020), high asexual reproduction rates (Capel et al., 2017, 2019), various reproductive strategies (Capel et al., 2014; de Paula et al., 2014; Luz et al., 2020), flexible life history strategies characterized by high annual reproductive activity and dynamic recruitment (Glynn et al., 2008; Bastos et al., 2024), and fast growth rates (Vermeij, 2005, 2006). Some of these opportunistic biological features apply also to *Tubastraea* sp. found in Cyprus. For example, it has been observed on artificial structures of the shipwreck, where also other epibenthic organisms occur (Jimenez et al., 2017). The fact that one colony was on polyurethane foam confirms the high dispersal potential *Tubastraea* has, as it was reported in the southwestern Atlantic where *Tubastraea* utilizes this “anthropogenic flotsam” (Faria and Kitahara, 2020). Furthermore, the presence of recruits alongside adults highlights the colonization potential of this newly recorded non-indigenous coral in the studied area.

It is well-documented that multiple independent introductions as hull fouling of vessels and oil and gas platforms have been the most probable vectors for the colonisation and propagation of *Tubastraea* species in the Atlantic Ocean and the Caribbean, with subsequent range expansion via passive larval transport through oceanic currents (de Paula and Creed, 2004; Sammarco et al., 2004; Silva et al., 2014; Capel et al., 2019; Coelho et al., 2022; Crivellaro et al., 2022; Ohanna et al.,

2025; Batista et al., 2026). Conversely, dispersal of larvae mediated by ballast water seems to be an unlikely hypothesis for *Tubastraea* spread (Creed et al., 2017). As such, although the potential source of introduction for the *Tubastraea* sp. corals found in Cyprus remains unknown, shipping traffic (through vessels, oil rigs and platforms, or docks) may represent a probable pathway of dispersal of the observed non-indigenous tropical coral. This is supported by the capacity of *Tubastraea* colonies (*T. coccinea*) to resist seawater drag and turbulence produced by relatively high-speed moving vessels during prolonged periods of time (Batista et al., 2026). The shipping pathway of introduction and dispersion has been proposed also for other scleractinian corals in the Mediterranean Sea, such as *Oulastrea crispata* (Hoeksema and Ocaña Vicente, 2014; Mariani et al., 2018), and, more in general, represents a major introduction mean for many benthic newcomers in this temperate basin (Galil and Zenetos, 2002; Galil, 2008).

Noteworthy is the fact that we recorded *Tubastraea* sp. on the MS Zenobia during a warm period in which the epibenthic communities of the wreck significantly deteriorated. Widespread mortality of species of corals, sponges and bryozoans, for example, were documented in the monitored areas at the MS Zenobia (Nardi et al., 2024). In Cyprus, positive thermal anomalies during prolonged Marine Heat Waves (MHVs) are usually associated with prevalence of disease and mortality of Mediterranean epibenthic organisms (Jimenez et al., 2016; Garrabou et al., 2022). However, non-native species originating from warmer areas seem to fare better during the rise in seawater temperature and they are recorded in higher abundance (Jimenez and Resaikos unpublished data). While the *Tubastraea* sp. colonies and recruits exhibited no signs of external damage (*i.e.*, partial tissue mortality), four scleractinian coral species in the same area (*Madracis pharensis*, *Polycyathus muellerae*, *Caryophyllia inornata*, and *Phyllangia mouchezii*) showed partial mortality and tissue lesions exposing areas of the corallite. Interestingly, experimental studies have shown that both temperature and competition with native species can influence the physiological performance of the invasive *Tubastraea coccinea* in Brazil (Almeida Saá et al., 2020). Nevertheless, although the current data showed a temporal coincidence between the first observation of *Tubastraea* sp. and the recent seawater temperature rising in Cyprus, further research is needed to understand whether the warming period was necessary for the establishment itself or whether it could enhance future expansion of this organism.

The fact that this community of corals in the MS Zenobia is exposed to oil and frequently in contact with it, may add to the effect of the MHWs. Polycyclic aromatic hydrocarbons (PAHs) found in crude oil and gasoline, for example, are known to have lethal and sub-lethal effects on corals in diverse levels of biological organization, from the genetic and cellular to the physiological and morphological (Turner and Renegar, 2017; Menezes et al., 2023). Corals (*M. pharensis*) in the oil contaminated section of the MS Zenobia seem to have cellular and physiological adaptations to the exposure to PAHs in contrast to conspecifics in oil-free sections of the shipwreck (Nardi et al., 2024). There are few assessments of the resistance of *Tubastraea* to contaminants including sodium hypochlorite, acetic acid, antifouling chemicals and PAHs (*e.g.*, Altvater et al., 2017; Fukushima et al., 2022; Martins et al., 2024; Barbosa et al., 2025; Kassuga et al., 2025). The limited evidence suggests that *Tubastraea* is less resistant to certain types of oil but less sensitive than other coral species to antifouling agents. Further ecotoxicological testing of *Tubastraea* corals is deemed necessary.

To conclude, this study documented the arrival of a non-indigenous tropical scleractinian coral in the Mediterranean Sea. The genetic similarity observed between the Cyprus specimen and lineages from the Southwestern Atlantic and the Gulf of Mexico suggests a genetic affinity between these geographically distant populations, possibly facilitated by global maritime traffic. Nevertheless, being this similarity based on limited molecular data and sampling, it should not be interpreted as a direct evidence of demographic connectivity or a specific geographic origin. Therefore, although molecular similarities exist, we conservatively maintain the designation *Tubastraea* sp. due to the known limitations of single mitochondrial markers in resolving species boundaries within this genus. Although *Tubastraea* species are known to be highly invasive outside their native geographical distribution ranges (*e.g.*, Creed et al., 2017), only a few colonies of *Tubastraea* sp. were observed on the MS Zenobia shipwreck in Cyprus. Given that the global diversity of *Tubastraea* has been historically underestimated and that record-breaking marine heatwaves in the Levantine Sea may be providing a foothold for thermophilic invaders, the presence of these recruits is a significant alert. As such, we strongly encourage long-term monitoring surveys of the benthic communities associated with the wreck and the surrounding area, *e.g.*, ports, shipwrecks, artificial structures, and natural habitats, to detect the possible spread of this non-indigenous coral. Given the well documented invasiveness nature of the genus and the early stages of colonization (one site, MS Zenobia shipwreck), we suggest performing early removals of this coral. This is highly relevant due to the extremely challenging environment of the study site for the detection of recruits (i.e., shifting floating debris in oil ponds), as experienced during our surveys when we unsuccessfully tried to find again the two recruits observed in the first dives. The find of *Tubastraea* sp. in Cyprus is another challenge to Mediterranean biodiversity conservation and management that undoubtedly will generate controversy and discussion due to public perceptions.

CRediT authorship contribution statement

Carlos Jimenez: Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Formal analysis, Conceptualization. **Vasilis Resaikos:** Writing – review & editing, Methodology, Investigation. **Nathália Bastos:** Writing – review & editing, Formal analysis. **Francesca Benzoni:** Writing – review & editing, Formal analysis. **Davide Maggioni:** Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Formal analysis. **Roberto Arrigoni:** Writing – review & editing, Writing – original draft, Resources, Methodology, Formal analysis, Conceptualization.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2026.105497.

Data availability

The sequences generated were submitted to genbank and will be made available after publication. Any other information is available from authors upon request.

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