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ARTICLE

Tracing the westward front: molecular and morphological evidence of the expansion of the non-native oyster *Dendostrea* cf. *crenulifera* (Ostreidae) in the Mediterranean Sea

Explorando el frente de avance hacia el oeste: evidencia molecular y morfológica de la expansión de la ostra alóctona *Dendostrea* cf. *crenulifera* (Ostreidae) en el mar Mediterráneo

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Abstract: The Mediterranean Sea is a major hotspot of non-indigenous species, many of which arrive through the Suez Canal and spread via vessel-mediated transport. Among them, the tropical oyster *Dendostrea* cf. *crenulifera* has long been affected by taxonomic uncertainty. By integrating morphological characters with mitochondrial *cox1* sequences from 38 specimens collected in nine localities of Greece, Croatia and Italy, we provide the first molecularly validated evidence of its occurrence outside the Levantine basin. New records from the Aegean Sea, Libyan Sea, Ionian Sea, Adriatic Sea and southern Tyrrhenian Sea extend the known range by more than 1000 km westwards. Specimens from Crete were found on natural rocky substrates, whereas those from all western localities occurred exclusively on artificial structures in harbours and marinas, supporting hull fouling as the primary vector of spread. The ability of this tropical oyster to establish in environmentally diverse basins, including areas where native oysters occur, suggests the potential for spatial overlap and competitive interactions. The early detection of this range expansion offers opportunities for monitoring and for the assessment of its ecological implications.

Keywords: Mediterranean Sea; biological invasions; Ostreidae; *Dendostrea* cf. *crenulifera*; molecular identification; range expansion; vessel-mediated transport; *cox1*

Resumen: El mar Mediterráneo constituye un importante centro de concentración de especies no indígenas, muchas de las cuales llegan a través del canal de Suez y se dispersan mediante el transporte asociado a embarcaciones. Entre ellas, la ostra tropical *Dendostrea* cf. *crenulifera* ha estado durante largo tiempo afectada por incertidumbre taxonómica. Mediante la integración de caracteres morfológicos con secuencias mitocondriales de *cox1* procedentes de 38 ejemplares recolectados en nueve localidades de Grecia, Croacia e Italia, aportamos la primera evidencia validada molecularmente de su presencia fuera de la cuenca levantina. Nuevos registros en el mar Egeo, el mar de Libia, el mar Jónico, el mar Adriático y el sur del mar Tirreno amplían su distribución conocida en más de 1.000 km hacia el oeste. Los ejemplares de Creta se encontraron sobre sustratos rocosos naturales, mientras que los de todas las localidades occidentales aparecieron exclusivamente sobre estructuras artificiales en puertos y marinas, lo que respalda la incrustación en cascos como principal vector de dispersión. La capacidad de esta ostra tropical para establecerse en cuencas ambientalmente diversas, incluidas áreas donde habitan ostras nativas, sugiere un potencial solapamiento espacial y posibles interacciones competitivas. La detección temprana de esta expansión de rango ofrece oportunidades para su seguimiento y para la evaluación de sus implicaciones ecológicas.

Palabras clave: mar Mediterráneo; invasiones biológicas; Ostreidae; *Dendostrea* cf. *crenulifera*; identificación molecular; expansión del área de distribución; transporte mediado por buques; *cox1*

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Supplementary information ↓

1. INTRODUCTION

The Mediterranean Sea is a global hotspot for the introduction of non-indigenous species (Galil 2007, Zenetos *et al*. 2022). Such introductions are mainly driven by maritime traffic and the opening of the Suez Canal. To date, nearly 1000 non-indigenous taxa have been reported, and the number of established species increased by about 40% just between 2010 and 2021 (Zenetos *et al*. 2022, Toso *et al*. 2025). This

massive colonization of the basin has profoundly impacted the composition of native communities (Daly-Yahia *et al*. 2013, Winters *et al*. 2020, Bottacini *et al*. 2024) and the functioning of coastal ecosystems (Peleg *et al*. 2020, Steger *et al*. 2024). Additionally, global warming is making large sectors of the basin increasingly suitable for non-indigenous species which are often of tropical origin and thus benefit from warmer conditions (Albano *et al*. 2021a). Warming is also weakening thermal and oceanographic barriers, facilitating the spread of species within the basin (Azzurro and D'Amen 2022) and allowing new pathways of invasion to be established (Albano *et al*. 2024a). In this context, documenting colonization routes and tracking the expansion fronts of non-indigenous species is essential both to understand invasion dynamics and to guide effective management and conservation measures.

The key question whether initial colonization events are followed by secondary spread into other sectors of the basin is, however, often hindered by taxonomic challenges. The identity of non-indigenous species is often not well known, and names are attributed without solid taxonomic foundations due to the combination of uninformative morphological characters, poor knowledge on the biodiversity in the often tropical native ranges and declining taxonomic expertise (Albano *et al*. 2021b, 2024b, Garzia *et al*. 2024). A case-in-point is the molluscan family Ostreidae (oysters), which is regarded as one of the most taxonomically intractable among bivalves due to their high intra-specific morphological variability (Salvi and Mariottini 2017, 2021).

Specifically, *Dendostrea* Swainson, 1835 is a genus of Indo-Pacific oysters first recorded in the Levantine basin (the easternmost sector of the Mediterranean Sea) back in the late 1990s (Çeviker 1999, 2001), but the specific identity of Mediterranean populations has been subject to long-standing nomenclatural confusion (Crocetta *et al*. 2015), reflecting the high morphological plasticity of the group and the poor reliability of shell characters alone for species identification (Lam and Morton 2003, Liu *et al*. 2011, Salvi *et al*. 2014, 2022, Salvi and Mariottini 2021). Recent integrative studies, combining morphology and molecular data, have shown that Mediterranean populations represent a single lineage that is currently referred to as *D.* cf. *crenulifera*, whose native range spans from the Red Sea to the western Indian Ocean (Delcour *et al*. 2025, Oliver *et al*. 2025). Phylogeographic analyses further revealed high genetic diversity and a lack of population structure across Mediterranean populations, a pattern consistent with multiple vessel-mediated introductions followed by demographic expansion after establishment (Delcour *et al*. 2025).

Indeed, as with many other Lessepsian species, *D.* cf. *crenulifera* appears to have first settled and spread in the Levantine basin (Çeviker 1999, 2001, Crocetta *et al*. 2015, Delcour *et al*. 2025) due to its proximity to the Suez Canal and the warm, oligotrophic and saline waters similar to those of the Red Sea (Por 1978, Golani 2010, Furfaro *et al*. 2025). This study provides new records from the Aegean Sea, the Libyan Sea, the Adriatic Sea and the southern Tyrrhenian Sea, significantly extending the known range. Due to the taxonomic challenges outlined above, we adopted an integrative approach pooling morphological and molecular evidence. We provide the first data on the marked westward range expansion of this species and present an updated overview of its Mediterranean distribution, along with a discussion of the ecological and conservation implications.

2. MATERIALS AND METHODS

2.1. Sampling

A total of 38 oysters, morphologically attributed to *Dendostrea* sp., were collected from nine localities of Greece, Croatia and Italy. Photographic documentation of living specimens in the field and of the sampling sites is provided in Figure 1. Dry shells from these samples were deposited as reference vouchers in the Malacological Collection of the University of L'Aquila, the Stazione Zoologica Anton Dohrn in Naples and the Museo Civico di Storia Naturale di Torino. Detailed specimen information and geographic coordinates are provided in Table 1.

Table 1. List of oyster specimens examined in this study, with voucher numbers (*: specimens illustrated in Figure 3) and inventory numbers, collection localities and coordinates, GenBank accession numbers for *cox1* sequences, and collection data (date, collector [legit], depth and habitat).

Voucher	Inv. Numb.	Locality ID	Locality	Lat	Lon	*cox-1* Genbank accession number	Collection date	Legit	Depth (m)	Habitat
OS1857	OS1857	1	Greece: Crete, Porto di Fermon	35° 0’ 53.28’’ N	25° 51’ 3.59’’ E	PX498339	21/09/2024	M. Garzia, N. Delcour	0.2-0.5	natural rocky substrates such as vertical walls and exposed rocks
OS1860	OS1860	2	Greece: Crete, Voulisma beach	35° 7’ 39.36’’ N	25° 44' 31.56’’	PX498340	21/09/2024	M. Garzia, N. Delcour	0.2-2.4	exposed rocks lying on sandy bottoms near the shore
OS1862	OS1862					PX498344				
OS1863	OS1863					PX498355				
OS1864	OS1864					PX498350				
OS1865	OS1865					PX498341				
OS1866	OS1866					PX498342				
OS1888	OS1888	3	Greece: Crete, Lygaria beach	35° 24’ 2.88’’ N	25° 1’ 34.67’’ E	PX498356	23/09/2024	M. Garzia, N. Delcour	0.2-0.5	natural rocky substrates such as vertical walls and exposed rocks
OS1889	OS1889					PX498351				
OS1890*	OS1890					PX498319				
OS1891	OS1891					PX498343				
OS1892	OS1892					PX498352				
OS1903	OS1903	4	Greece: Crete, artificial gulf of Lavris next to the Geropotamos beach	35° 24’ 54.72’’ N	24° 38’ 45.24’’ E	PX498353	23/09/2024	M. Garzia, N. Delcour	0.2-0.5	natural rocky substrates such as vertical walls and exposed rocks
OS1905	OS1905					PX498349				
OS1906	OS1906					PX498347				
OS1907	OS1907					PX498354				
OS1902*	OS1902					PX498320				

OS1880	OS1880	5	Greece: Crete, Agios Onoufrios beach	35° 32’ 54.96’’ N	24° 3’ 46.07’’ E	PX498345	22/09/2024	M. Garzia, N. Delcour	0.2-0.5	natural rocky substrates such as vertical walls and exposed rocks
OS1881	OS1881					PX498348				
OS1882	OS1882					PX498346				
OS2075*	OS2075	6	Italy: Tricase Porto	39° 55’ 54.48’’ N	18° 23’ 45.24’’ E	PX498325	11/10/2024	P. Mariottini, G. Furfaro	0.2-0.5	attached to the walls of the harbour
OS2030*	SZN-MOL0056	7	Croatia, Dubrovnik-Neretva, Mjlet Isl., Luka Saplunara	42° 41’ 52.8’’ N	17° 44’ 25.8’’ E	PX498321	16/08/2024	P.G. Albano	0.5	attached to mooring ropes of small boats
OS2031*	SZN-MOL0057					PX498322				
OS2032	SZN-MOL0058					PX498323				
OS2076	SZN-MOL0059					PX498324				
OS2207	MRSN M5008	8	Italy: Reggio Calabria, Melito di Porto Salvo	37° 55’ 18.12’’ N	15° 45’ 6.11’’ E	PX498327	12/08/2024	S. Giacobbe	0.2-5	attached to mooring buoys or mooring ropes of small boats
OS2208	MRSN M5009					PX498328				
OS2209*	MRSN M5010					PX498332				
OS2211*	MRSN M5011					PX498329				
OS2212	MRSN M5012					PX498330				
OS2213	MRSN M5013					PX498331				
OS2210	MRSN M5014					PX498333				
OS2230	MRSN M5015					PX498335				
OS2231	MRSN M5016					PX498334				
OS2232	MRSN M5017					PX498336				
OS2233	MRSN M5018					PX498337	12/07/2025			
OS2234	MRSN M5019					PX498338				
OS2229*	OS2229	9	Italy: Stromboli, harbour	38° 47’ 7.44’’ N	15° 11’ 25.44’’ E	PX498326	24/06/2025	D. Salvi	0.8	attached to the pilings of the harbour for ships and hydrofoils

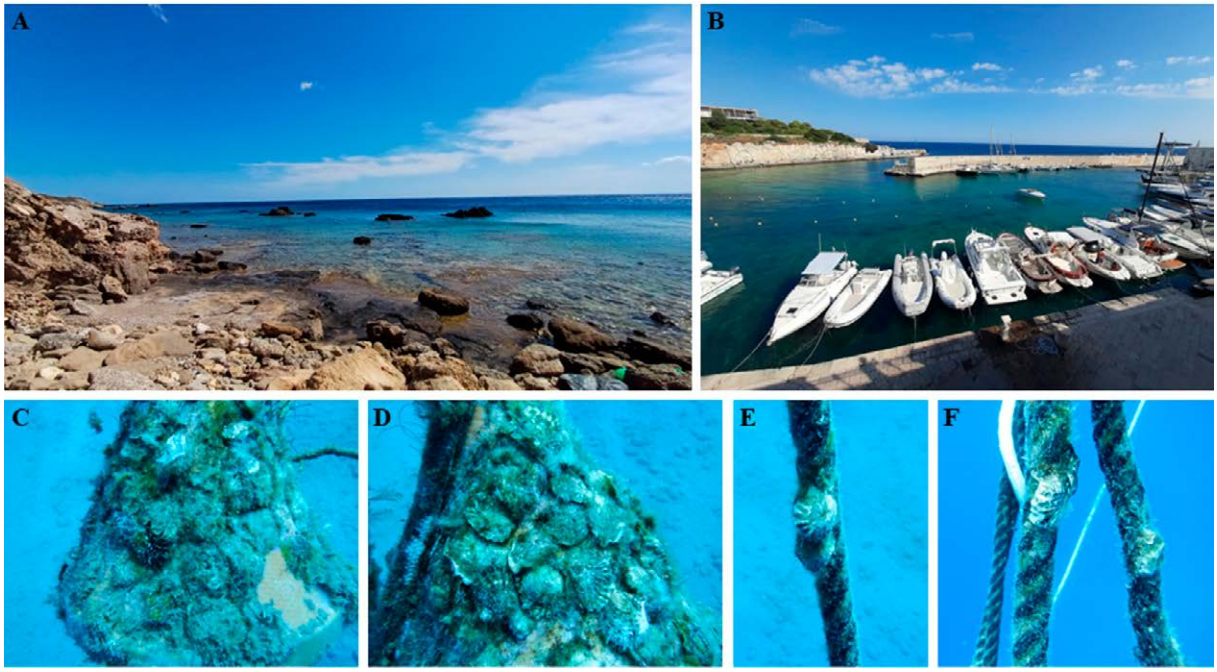

Figure 1. Examples of sampling sites and substrate types: natural rocky shore habitat in Crete (A); Tricase Porto marina (B). Living specimens observed in situ at Melito di Porto Salvo (Italy) on mooring buoy (C-D) and ropes (E-F).

2.2. DNA extraction, amplification and sequence analysis

For molecular analyses, the adductor muscle of each specimen was dissected and preserved in 95% ethanol. Genomic DNA was extracted following the high-salt protocol (Sambrook *et al*. 1989) or a modified CTAB method (Doyle and Doyle 1987, Miladi 2018). The mitochondrial *cox1* fragment was amplified via PCR with primers LCO1490 and HCO2198 (Folmer *et al*. 1994), using conditions previously applied in related works (Salvi *et al*. 2010; Crocetta *et al*. 2015). PCR success was verified on 2% agarose gel. Sequencing of PCR products was performed by Genewiz (www.genewiz.com) or by Macrogen Europe (https://www.macrogen-europe.com). All newly obtained *cox1* sequences were queried against the NCBI nucleotide database using BLASTn (Johnson *et al*. 2008) to assess sequence identity. For each sequence, the five highest-scoring matches were retained.

Phylogenetic relationships among haplotypes recovered in this study and those reported by Delcour *et al*. (2025) were reconstructed using the median-joining network method (Bandelt *et al*. 1999) implemented in PopART v.1.7 (Leigh and Bryant 2015), with ε set to 0. Eleven sequences with more than 5% ambiguous bases were excluded from the analysis.

2.3. Shell morphology assessment

Shells of all specimens collected from the nine Mediterranean localities were examined under a stereomicroscope. Images of representative individuals were captured using an OLYMPUS TOUGH TG-6 settled on a photographic support.

Guided by the molecular results, shell characters were compared with reference specimens of *D.* cf. *crenulifera*, as illustrated by Oliver *et al.* (2025). Morphological assessment focused primarily on features such as the hinge attachment area, the overall shape of both valves, margin configuration, chomata morphology and internal valve colouration.

2.4. Geographic distribution

We used QGIS software v3.30.2-'s-Hertogenbosch (QGIS Development Team 2022) to map sampling localities and previous records of *D.* cf. *crenulifera* supported by molecular identifications.

3. RESULTS

3.1. Molecular identification

We successfully generated *cox1* sequences for all 38 collected specimens, which have been deposited in GenBank (accession numbers PX498319 - PX498356). BLASTn analyses performed on *cox1* sequences consistently recovered *D.* cf. *crenulifera* as the closest match, with sequence identities ranging from 97.4% to 100%. See Table 2 for details on the top five matches of the eight sequences selected as references, each representing one locality where multiple similar sequences were available. The BLAST matches reported in Table 2 primarily support the assignment of the newly collected oysters to *D.* cf. *crenulifera*; by contrast, their usefulness for identifying precise source populations is limited because the same or very similar *cox1* haplotypes occur across multiple previously sampled regions, as shown in the phylogenetic network (Fig. 2). Consistent with this pattern, the median-joining network revealed no evident phylogeographic structure among eastern, central and western Mediterranean samples. Furthermore, several haplotypes recovered in the newly sampled localities were not found in the eastern Mediterranean dataset of Delcour *et al.* (2025), pointing to additional haplotypic variation within the Mediterranean basin.

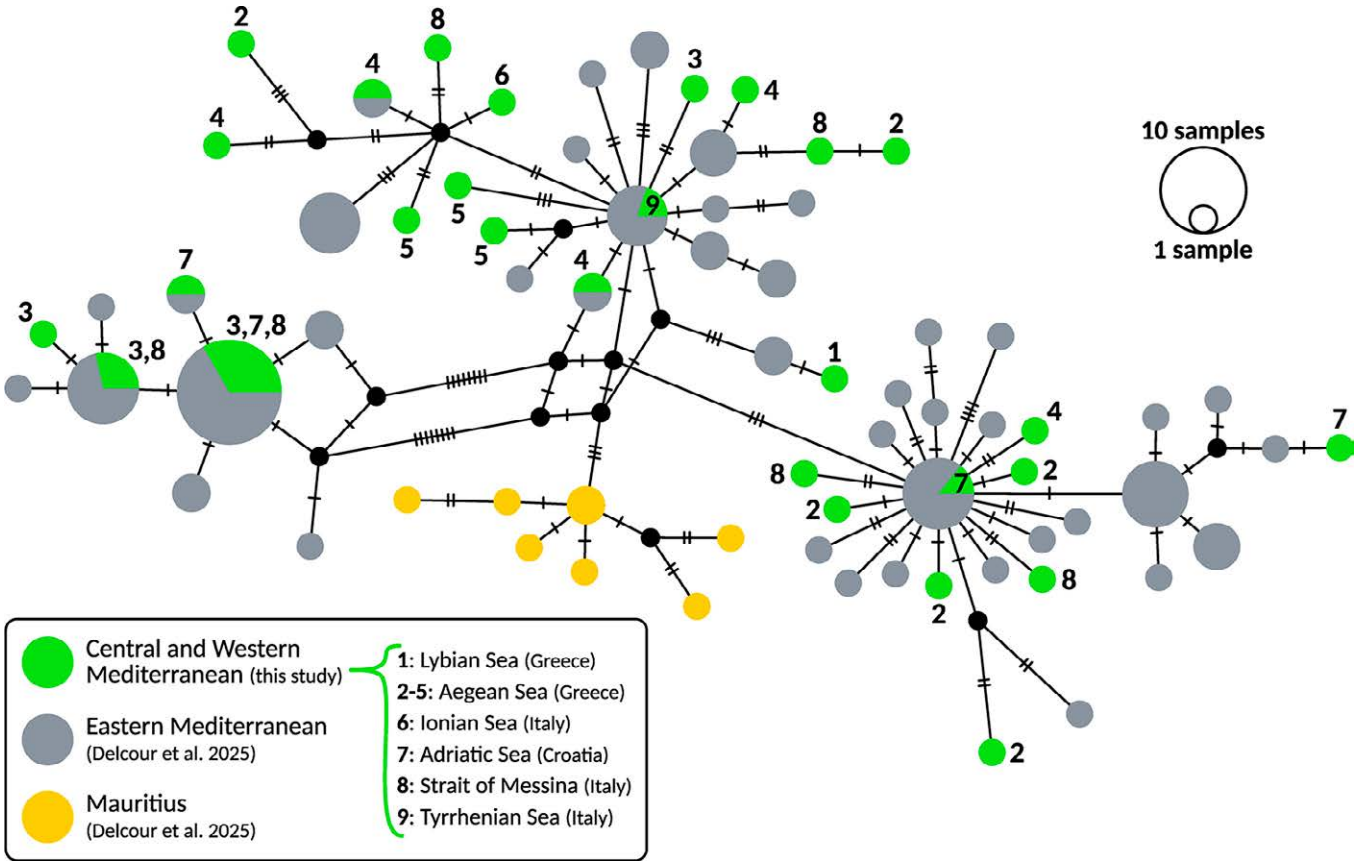

Figure 2. Median-Joining haplotype network illustrating relationships among haplotypes of *Dendostrea* cf. *crenulifera* recovered in this study from central and western Mediterranean localities (green) and those reported by Delcour *et al.* (2025) from the eastern Mediterranean Sea (grey) and Mauritius (yellow). The network shows no evident phylogeographic structure across Mediterranean samples, while several haplotypes from the newly sampled localities were not previously detected. Numbers correspond to locality identifiers given in Table 1.

Table 2. BLASTn results for eight reference *cox1* sequences, each representing one locality with multiple similar sequences; top five database matches are shown with accession numbers, reported and current scientific names (*: according to Oliver *et al*. 2025), voucher/isolate, pairwise identity, sequence length and query coverage

Query sequence ID (Locality)	Top five best BLAST matches						
	Accession	**Reported scientific name**	**Current scientific name***	**Voucher / Isolate**	**Pairwise Identity**	**Accession length**	**Query Coverage**
OS2030 Croatia: Mjlet Island	KJ946451.1	*Dendostrea* sp. MO-2014	*Dendostrea* cf. *crenulifera*	BAU1419	99.07 %	649	100%
	KJ946446.1	*Dendostrea* sp. MO-2014	*Dendostrea* cf. *crenulifera*	BAU1414	98.3 %	649	100%
	PV543794.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS512	98.3 %	648	100%
	PV543797.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS535	98.15 %	648	100%
	PV543798.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS537	97.99 %	648	100%
OS2031 Croatia: Mjlet Island	KJ946452.1	*Dendostrea* sp. MO-2014	*Dendostrea* cf. *crenulifera*	BAU1417	99.69 %	649	100%
	KJ946450.1	*Dendostrea* sp. MO-2014	*Dendostrea* cf. *crenulifera*	BAU1418	99.69 %	649	100%
	PV543794.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS512	97.69 %	648	100%
	PV543797.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS535	97.53 %	648	100%
	KJ946446.1	*Dendostrea* sp. MO-2014	*Dendostrea* cf. *crenulifera*	BAU1414	97.38 %	649	100%
OS2229 Italy: Stromboli island	KJ946446.1	*Dendostrea* sp. MO-2014	*Dendostrea* cf. *crenulifera*	BAU1414	99.23 %	649	100%
	PV543794.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS512	99.23 %	648	100%
	KJ946451.1	*Dendostrea* sp. MO-2014	*Dendostrea* cf. *crenulifera*	BAU1419	99.07 %	649	100%
	PV543797.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS535	99.07 %	648	100%
	PV543798.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS537	98.92 %	648	100%
OS2075 Italy: Tricase Porto	KJ946446.1	*Dendostrea* sp. MO-2014	*Dendostrea* cf. *crenulifera*	BAU1414	99.38 %	649	100%
	PV543794.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS512	98.77 %	648	100%
	KJ946451.1	*Dendostrea* sp. MO-2014	*Dendostrea* cf. *crenulifera*	BAU1419	98.61 %	649	100%
	PV543797.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS535	98.61 %	648	100%
	PV543798.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS537	98.46 %	648	100%
OS2211 Italy: Reggio Calabria	KJ946451.1	*Dendostrea* sp. MO-2014	*Dendostrea* cf. *crenulifera*	BAU1419	99.38 %	649	100%
	PV543794.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS512	98.92 %	648	100%
	PV543797.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS535	98.77 %	648	100%
	PV543798.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS537	98.61 %	648	100%
	KJ946446.1	*Dendostrea* sp. MO-2014	*Dendostrea* cf. *crenulifera*	BAU1414	98.3 %	649	100%

OS2209 Italy: Reggio Calabria	KJ946451.1	*Dendostrea* sp. MO-2014	*Dendostrea* cf. *crenulifera*	BAU1419	99.8 %	649	78%
	PV543794.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS512	99.01 %	648	78%
	PV543797.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS535	98.81 %	648	78%
	KJ946446.1	*Dendostrea* sp. MO-2014	*Dendostrea* cf. *crenulifera*	BAU1414	98.61 %	649	78%
	PV543798.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS537	98.61 %	648	78%
OS1890 Greece: Crete, Lygaria	KJ946452.1	*Dendostrea* sp. MO-2014	*Dendostrea* cf. *crenulifera*	BAU1417	100 %	649	100%
	KJ946450.1	*Dendostrea* sp. MO-2014	*Dendostrea* cf. *crenulifera*	BAU1418	99.69 %	649	100%
	PV543794.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS512	97.69 %	648	100%
	PV543797.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS535	97.53 %	648	100%
	KJ946446.1	*Dendostrea* sp. MO-2014	*Dendostrea* cf. *crenulifera*	BAU1414	97.38 %	649	100%
OS1902 Greece: Crete, Geropotamos	KJ946446.1	*Dendostrea* sp. MO-2014	*Dendostrea* cf. *crenulifera*	BAU1414	99.07 %	649	100%
	PV543794.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS512	99.07 %	648	100%
	KJ946451.1	*Dendostrea* sp. MO-2014	*Dendostrea* cf. *crenulifera*	BAU1419	98.92 %	649	100%
	PV543797.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS535	98.92 %	648	100%
	PV543798.1	*Dendostrea* cf. *crenulifera*	*Dendostrea* cf. *crenulifera*	OS537	98.77 %	648	100%

3.2. Morphological assessment

The analysed shells showed irregularly oval to ligulate or curved shapes (Fig. 3). Shells were generally thick and robust, with flat and fragile specimens occurring only rarely. Very occasionally, frondose morphs were observed (Fig. 3C). The irregular margins on both valves showed the typical crenulations of genus *Dendostrea.* The lower valve showed a large attachment area, frequently cupped, and externally sculptured with rounded radial ribs. Digital extensions were frequently observed externally close to the interface with the substratum (Fig. 3G'). The upper valve was weakly convex, often flat, and the external sculpture mostly consisted of poorly preserved remnants of radial folds at the margins. Internally, both valves were mostly lustrous white and variously tinged in green or brown, often with a purple or reddish-brown margin. Simple chomata occurred sparsely on the dorsal margin close to the hinge area, and pustular (lophine) chomata occurred between crenulations and on the posterior margin. The hinge area was frequently wide with a thick ligament.

3.3. Ecological notes

On Crete, specimens were found on natural rocky substrates such as vertical walls and exposed rocks, or on exposed rocks lying on sandy bottoms near the shore, at depths of 0.2–2.4 m (Tab. 2; Fig. 1A). In contrast, all specimens from Croatia and Italy were collected on artificial substrates in harbours or marinas (Fig. 1B), colonizing pylons, buoys and ropes at depths down to 8 m (Fig. 1C–F). Shell morphology varied markedly with substrate, ranging from flattened and fragile forms on buoys to small and robust forms on ropes (Fig. 3E-F). Specimens were frequently associated with *Pinctada radiata* (Leach, 1814) and with other fouling bivalves, including *Anomia ephippium* Linnaeus, 1758 and *Brachidontes pharaonis* (P. Fischer, 1870) (Fig. 1C–D).

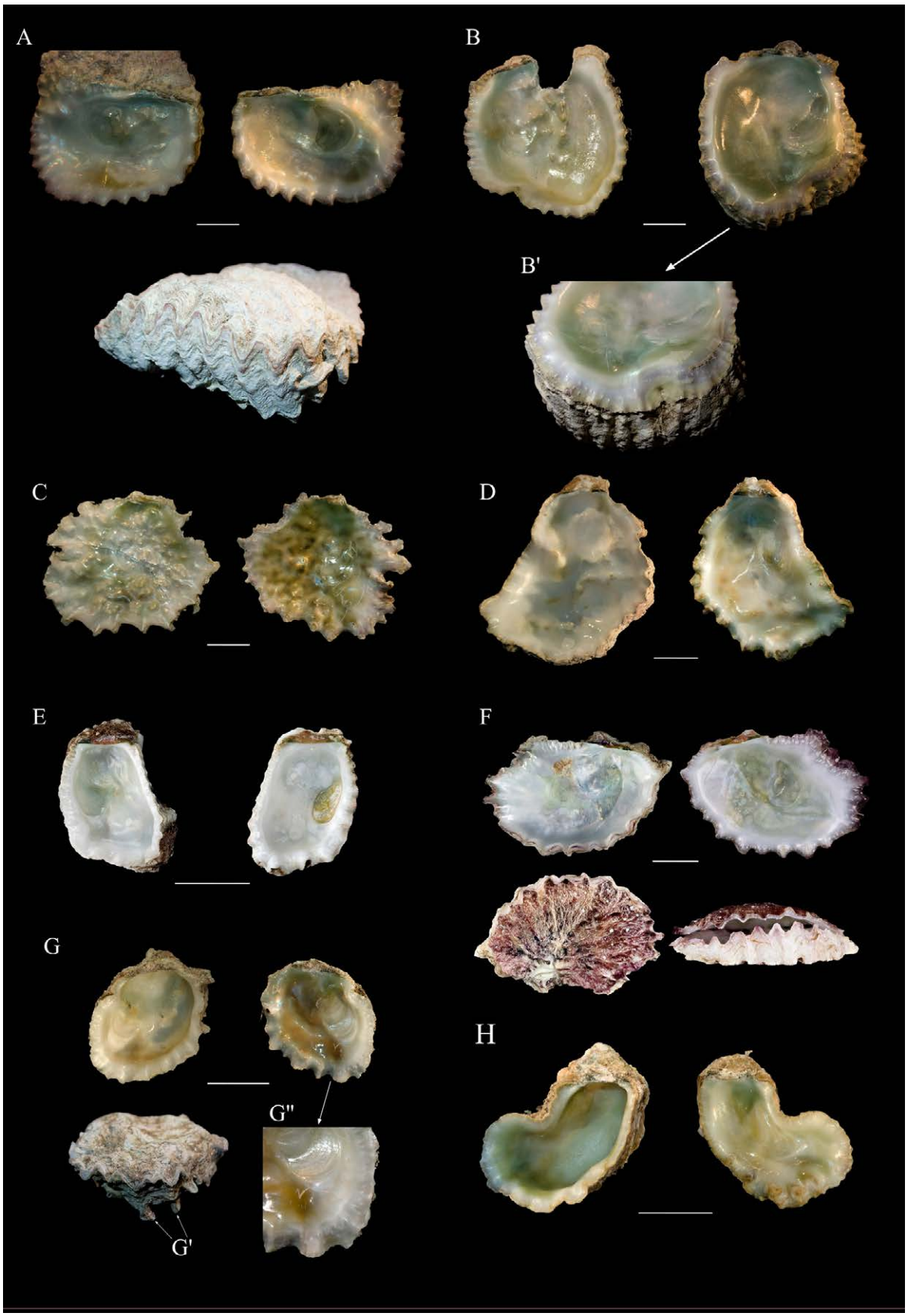

Figure 3. *Dendostrea* cf. *crenulifera* shells from six Mediterranean localities. A. OS2030 Croatia, Mjlet Isl. B. OS2031 Croatia, Mjlet Isl. B. Details of pustular (lophine) chomata. C. OS2075 Italy, Apulia, Tricase Porto. D. OS2229 Italy, Stromboli harbour. E. OS2211 Italy, Reggio Calabria, Melito di Porto Salvo. F. OS2209 Italy, Reggio Calabria, Melito di Porto Salvo. G. OS1890 Greece, Crete, Lygaria beach. G' Arrows indicate digital extensions. G'' Details of pustular (lophine) chomata. H. OS1902 Greece, Crete, Geropotamos beach. Scale bars =1 cm.

3.4. Distribution of *D.* cf. *crenulifera*

Molecularly validated specimens indicate a westward range extension of *Dendostrea* cf. *crenulifera*. The species, previously recorded from the eastern Mediterranean, was detected in the Libyan Sea (southern Crete; locality 1), southern Aegean Sea (northern Crete; localities 2-5), Adriatic Sea (Mijet, Croatia; locality 7), Ionian Sea (Tricase Porto, Italy; locality 6), Strait of Messina (Reggio Calabria, Italy; locality 8), and southern Tyrrhenian Sea (Stromboli Island, Aeolian Archipelago, Italy; locality 9). The updated Mediterranean distribution of this non-native oyster is presented in Figure 4.

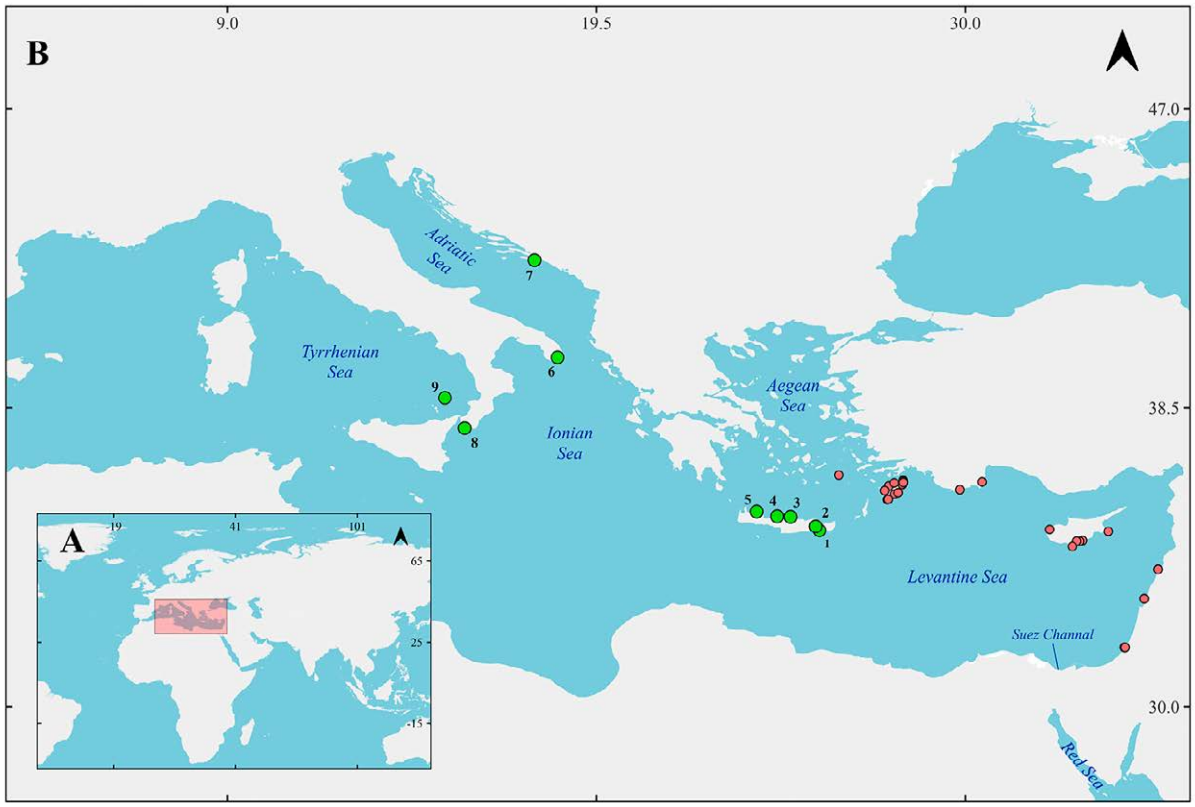

Figure 4. Mediterranean distribution of *Dendostrea* cf. *crenulifera* based on molecularly validated specimens. Red circles indicate records from previous studies (Crocetta *et al*. 2015, Delcour *et al*. 2025, Oliver *et al*. 2025), and green circles represent specimens from the present study. New records confirm the species in the Libyan Sea, Aegean Sea, Adriatic Sea, Ionian Sea and Tyrrhenian Sea, extending its known range across most of the Mediterranean, except the northwestern sectors.

4. DISCUSSION

4.1. Range expansion of *Dendostrea* cf. *crenulifera* and vectors of dispersal

Based on newly collected and molecularly validated specimens, we showed a substantial westward extension of the known range of *Dendostrea* cf. *crenulifera*, which until recently was thought to be confined to the Levantine Basin (Crocetta *et al.* 2015; Delcour *et al.* 2025). Indeed, our new records confirmed its presence in several additional basins: the Libyan Sea (southern Crete), the southern Aegean Sea (northern Crete), the Adriatic Sea (Mijet, Croatia), the Ionian Sea (Tricase Porto and Melito di Porto Salvo, Italy), and the southern Tyrrhenian Sea (Stromboli Island, Aeolian Archipelago, Italy). Taken together with previously published molecularly assessed records (Crocetta *et al*. 2015, Delcour *et al*. 2025, Oliver *et al*. 2025), these findings provide the most up-to-date overview of the distribution of this non-indigenous oyster in the Mediterranean, highlighting that the species now occurs over most of the basin, with the only exception of the northwesternmost sectors (Fig. 4). We note, however, that several records from the central Mediterranean historically attributed to *Dendostrea* cf. *folium* or *D.*

frons (Linnaeus, 1758) (e.g., Ulman *et al.* 2017; Gerovasileiou *et al.* 2017) were based on shell morphology alone and predate the recent taxonomic clarification of the Mediterranean lineage. These records are therefore plausible candidates for *D.* cf. *crenulifera*, but they still require molecular confirmation before being confidently incorporated into the reconstructed invasion history of this species in the basin.

Due to the high genetic diversity, lack of phylogeographic structure and the absence of evidence of a founder effect, this species was likely introduced into the Mediterranean Sea through multiple vessel-mediated invasion events (Delcour *et al.* 2025). Not only ships, but also smaller recreational boats may act as effective vectors. Indeed, living specimens of *Dendostrea* (identified as *D. folium* sensu lato but most likely referring to this species) were recorded on boat hulls moored in several marinas in the eastern Mediterranean in 2015–2016 (Ulman *et al.* 2017, 2019). Consistently, most of our specimens were collected from artificial structures within harbours and marinas, such as pilings, ferry docks or mooring ropes of small recreational boats (Fig. 1). These environments are well known hotspots for the establishment and secondary spread of non-indigenous marine organisms (Coutts and Taylor 2004, Davidson *et al.* 2010, Toso *et al.* 2025). Therefore, the expansion of *D.* cf. *crenulifera* across several thousand kilometres of coastline was more likely driven by anthropogenic transport than by natural spread, particularly given its limited larval dispersal potential (Delcour *et al.* 2025). The occurrence of previously unrecorded haplotypes in central and western localities further suggests that the Mediterranean haplotype diversity of this species remains incompletely sampled and, together with the lack of geographic structure in the network (Fig. 2), does not support a simple east-to-west stepping-stone spread. Instead, this pattern is consistent with either short-range secondary spread among unsampled populations or multiple introduction events.

4.2. Ecological implications of a broad-scale expansion

The westward and northward spread of *D.* cf. *crenulifera* over more than 1000 km is not only biogeographically noteworthy but also ecologically meaningful. This tropical oyster, primarily distributed in the Red Sea and the western Indian Ocean (Oliver *et al.* 2025), has successfully colonized environmental conditions that are substantially different from its presumed native range. While the Levantine basin is environmentally similar to the Red Sea, being characterized by high temperatures, elevated salinity and oligotrophy (Por 1978, Golani 2010), the central and western Mediterranean are characterized by more variable thermal, salinity and nutrient regimes. Notably, its occurrence on both sides of the Strait of Messina (e.g., Melito Porto Salvo and Stromboli) is particularly relevant, as the passage into the Tyrrhenian Sea may be facilitated by shipping rather than by adaptation to the cold-water conditions of the Strait, which usually limit the northward spread of tropical species. Yet, the ability of *D.* cf. *crenulifera* to persist in the cooler Tyrrhenian environment compared with the Ionian–Levantine basin (Coll *et al.* 2010) demonstrates ecological plasticity, a trait often associated with invasive success (Lockwood *et al.* 2013). Similar patterns have been observed among various Lessepsian organisms, including other molluscs (e.g. the pearl oyster *Pinctada radiata*, the oval bubble snail *Lamprohaminoea ovalis* and the Red Sea mussel *Brachidontes pharaonis*), fishes (e.g. *Sphyraena chrysotaenia* and *Fistularia commersonii*) and macroalgae (e.g. *Caulerpa cylindracea* and *Womersleyella setacea*), which initially became established in the Levantine Basin but subsequently expanded into cooler central and western Mediterranean waters (Azzola *et al.* 2022, Azzurro *et al.* 2013, Battiata *et al.* 2024, Garzia *et al.* 2024, Piazzi and Cinelli 2003, Png-Gonzalez *et al.* 2021, Zenetos *et al.* 2010). The capacity of *D.* cf. *crenulifera* to tolerate such diverse ecological conditions suggests that this species is following a similar trajectory and becoming a widespread invader.

4.3. Potential interactions with native oysters

In the Levantine Basin, *D.* cf. *crenulifera* has colonized shallow natural and artificial hard substrates that lack native oysters. Many tropical non-indigenous species in the Levantine Sea have expanded into niches that were poorly occupied by native Mediterranean species at the habitat scale, although this effect should be interpreted in light of the collapse of native diversity that has been going on for at least two decades (Albano *et al.* 2021a, Rilov 2016, Steger *et al.* 2024). However, the scenario is

dramatically different in the Aegean, Ionian, Adriatic and Tyrrhenian seas. These regions are inhabited by two native oysters, *Ostrea edulis* Linnaeus, 1758 and *Ostrea stentina* Payraudeau, 1826, which occur in similar habitats. Therefore, the expansion of *D.* cf. *crenulifera* into these areas raises the possibility of competitive interactions, underscoring the importance of early detection as provided in this study. Although direct ecological and socio-economic impacts remain to be quantified, the frequent occurrence of *D.* cf. *crenulifera* on artificial substrates and in fouling assemblages suggests that this species should be monitored as a potential space-occupying competitor in shallow hard-bottom communities and as a possible contributor to fouling pressure in port and marina environments (Tsirintanis *et al.* 2022). Early detection of the westward expansion of this species offers the opportunity to evaluate its ecological impacts and assess its invasive potential before widespread establishment occurs.

5. CONCLUSION

The integration of morphological and molecular data revealed that *Dendostrea* cf. *crenulifera* is no longer confined to the Levantine basin but is now established in several central Mediterranean sectors. This range expansion, most likely facilitated by fouling on boat and ship hulls, demonstrates both the high dispersal potential and the ecological adaptability of this non-indigenous oyster. The early detection of its presence in areas inhabited also by native oysters underscores the urgent need for monitoring and targeted assessments to evaluate its ecological impact and potential invasiveness in the entire Mediterranean Sea.

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Daniele Salvi: Conceptualization, Sample collection, Genetic data collection, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. Matteo Garzia: Conceptualization, Sample collection, Genetic data collection, Formal analysis, Methodology, Writing – review & editing. Salvatore Giacobbe: Sample collection, Writing – review & editing. Marina Morabito: Genetic data collection, Formal analysis, Methodology, Writing – review & editing. Nathan Delcour: Sample collection, Genetic data collection, Formal analysis, Methodology, Writing – review & editing. Giulia Furfaro: Sample collection, Writing – review & editing. Paolo Mariottini: Sample collection, Writing – review & editing. Paolo G. Albano: Conceptualization, Sample collection, Writing – original draft, Writing – review & editing.

Competing interests

The authors have declared that no competing interests exist.

Statement on the use of Artificial Intelligence

Not applicable.

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