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Research Article

High genetic diversity and lack of structure underlie the invasion history of the non-indigenous oyster *Dendostrea* cf. *crenulifera* (Mollusca, Ostreida, Ostreidae) spreading in the eastern Mediterranean Sea

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Abstract

Since the opening of the Suez Canal in 1869, hundreds of Indo-Pacific species have rapidly colonised the Mediterranean. Understanding the spatial and temporal patterns of this biological invasion is crucial for assessing its ecological impact. A notable example is the non-indigenous oyster *Dendostrea* sp., first discovered in Türkiye in 1998 and later found throughout the easternmost Mediterranean, though its identity remained uncertain. This study clarifies the taxonomic identity and the introduction pathways of *Dendostrea* sp. using molecular analyses. Over 100 specimens from 25 sites in the eastern Mediterranean, as well as Île d'Ambre and Rodrigues in the Mauritius Archipelago (the native range), were sequenced for mitochondrial DNA (COI) and compared to 422 sequences from GenBank. Phylogenetic and species delimitation analyses identified the Mediterranean oysters as *D.* cf. *crenulifera*, conspecific with oysters from Rodrigues. The Mediterranean populations exhibited high genetic diversity, lack of phylogeographic structure and showed no evidence of a founder effect. These findings suggest that *D.* cf. *crenulifera* entered the Mediterranean over two decades ago through multiple shipping-mediated introductions from its native range and successfully established, likely aided by the decline of native biodiversity. The observed genetic diversity pattern across the Mediterranean indicates high propagule pressure driving the species' invasion history, which likely underpins its establishment success by reducing the deleterious consequences of population bottlenecks and overcoming the so-called genetic paradox. This study underscores the value of molecular surveys in identifying taxonomically challenging non-indigenous species and uncovering their invasion histories.

Key words: Alien, bivalve, cox1, phylogenetics, phylogeography, systematics, true oyster

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Introduction

Increased international trade and transportation, combined with ongoing global warming, have accelerated global biotic homogenisation (Occhipinti-Ambrogi and Galil 2010). The shifts in environmental conditions and the weakening of ecological and geographical barriers have facilitated the introduction and establishment of numerous marine non-indigenous species (NIS) outside their native ranges, reaching even the most remote places on the Planet (Occhipinti-Ambrogi and Galil 2010; Ardura et al. 2021). Some NIS are fast expanding species that quickly establish in local communities leading to sudden changes and increasing pressures on native species (i.e. by predation, changes in habitats through ecosystem engineering and the introduction of pathogens and parasites). NIS introductions also affect various socio-economic services, including fisheries and aquaculture, human health and infrastructure (Streftaris and Zenetos 2006; Tsirintanis et al. 2022).

The Mediterranean Sea, particularly its eastern sector, is currently experiencing a collapse of native biodiversity and is home to a massive invasion of tropical species entering from the Suez Canal or transported by shipping (Albano et al. 2021a, b; Toso et al. 2024). In 2021, almost 1000 NIS were reported in the Mediterranean Sea, with established species increasing by 40% since 2010 (Zenetos et al. 2022). Indeed, establishment rates also increased in the last decade, from ~ 3% yearly during 2011–2021 to ~ 6% between January 2020 and December 2021 (Zenetos et al. 2022). Mollusca are amongst the most diverse marine NIS, with 230 taxa representing more than 20% of the NIS established in the Mediterranean Sea (Zenetos et al. 2022).

The vast introduction of molluscan NIS into the Mediterranean Sea is primarily attributed to international maritime traffic (specifically through ballast water and hull fouling) and the opening of the Suez Canal that broke a long-standing biogeographic barrier (Galil 2008; Crocetta et al. 2013; Nunes et al. 2014; Tempesti et al. 2020). One of the main dispersal pathways into the Mediterranean is thus from the Red Sea and the broader Indo-West Pacific realm, with the eastern Mediterranean being particularly impacted due to its proximity to the Canal (Galil 2008; Zenetos et al. 2009; Nunes et al. 2014; Galil et al. 2015a, b; Tempesti et al. 2020). This process, known as Lessepsian invasion (Por 1978), has been enhanced by the widening of the Suez Canal in 2015 (Galil et al. 2015a, b) that allowed greater hydraulic, hence biological, connectivity and ship traffic. Additionally, the global increase in sea surface temperatures (SST) and salinity in the eastern Mediterranean Sea and the subsequent local extinctions of native species that make resources available (Albano et al. 2021a) are facilitating new introductions and the intra-basin spread of those that have occurred already (Raitsos et al. 2010; Albano et al. 2021a).

The presence of ecotypes, species complexes and cryptic diversity amongst molluscs complicates the taxonomic identification of NIS and consequently the understanding of invasion patterns, geographic distribution and the number of taxa involved. Oysters (Bivalvia: Ostreidae, Rafinesque, 1815) are a particularly difficult case where misleading morphology and controversial or confused taxonomy hinder accurate species identification. This group of bivalves is understudied and morphological identification is challenging due to phenotypic plasticity and a lack of reliable morphological diagnostic characters (Lam and Morton 2006; Xia et al. 2009; Salvi et al. 2014; Guo et al. 2018; Salvi and Mariottini 2021). Molecular approaches have proven extremely useful in resolving taxonomic uncertainties and ensuring accurate species identifications (Wang et al. 2004; Raith et al. 2015; Pejovic et al. 2016; Cavaleiro et al. 2019; Al-Kandari et al. 2021; Salvi et al. 2021, 2022; McDougall et al. 2024). When combined with comprehensive population sampling, molecular approaches can provide insights into the genetic structure of NIS populations, crucial for understanding the invasion process and its success (Lee 2002; Wellband et al. 2017; Geburzi et al. 2020; Oyarzún et al. 2024).

The difficulty in morphologically identifying oysters is well illustrated by the NIS of the genus *Dendostrea* Swainson, 1835, which is currently spreading throughout the eastern Mediterranean Sea. First detected in southern Türkiye in 1998 (Çeviker 2001), this species was subsequently recorded in Cyprus in 2008 (Zenetos et al. 2009), Greece in 2010 (Zenetos et al. 2011), Albania and Malta in 2016 (Ulman et al. 2017; Gerovasileiou et al. 2017) and Syria in 2019 (Ragkousis et al. 2023), with additional records reported in Cyprus, Greece, Türkiye and Syria between 2015 and 2021 (Karachle et al. 2016; Ulman et al. 2017; Ragkousis et al. 2023). Most authors attributed these records to the species *Dendostrea frons* (Linnaeus, 1758) (Çeviker 2001; Zenetos et al. 2009, 2011) based on shell features. The first molecular assessment of Mediterranean specimens of this non-indigenous oyster, using a DNA-barcoding approach, concluded that populations from the Aegean Sea (Greece) were conspecific with populations from the Levantine Sea (Türkiye), despite showing high phenotypic plasticity (Crocetta et al. 2015). However, the taxonomic identification was inconclusive because the closest match with GenBank sequences of *Dendostrea folium* (Linnaeus, 1758) had a genetic distance typically observed between distinct oyster species (Crocetta et al. 2015).

In this study, we generate DNA sequence data from *Dendostrea* non-indigenous oysters collected through extensive sampling in the eastern Mediterranean Sea, as well as from its putative native range (western Indian Ocean) and compared with available DNA sequences and reference *Dendostrea* specimens in museum collections.

The first aim of this study was to provide a molecular and taxonomic assessment of the *Dendostrea* oyster, with an improved sequence dataset including oysters from the Indian Ocean. The second aim was to perform population genetics analyses using an improved Mediterranean coverage of the species to identify potential pathways, vectors and processes driving this introduction and spread.

Material and methods

Sampling, DNA purification, amplification and sequencing

Eighty oyster specimens, morphologically identified as putative *Dendostrea* sp., were collected from 25 sampling sites across the eastern Mediterranean. Sixteen specimens, whose dry shells are housed in the National Museum of Wales (NMW; Suppl. material 1), were collected from three sites in the Mauritius Archipelago, specifically two sites at Rodrigues Island and one at Île d'Ambre to fill the lack of GenBank sequences regarding the Indo-Pacific Ocean as stated by Crocetta et al. (2015). The dry shells of the Mediterranean specimens are stored in the Malacological Collection at the University of L'Aquila, the Stazione Zoologica Anton Dohrn and the Natural History Museum in Vienna as reference vouchers (Suppl. material 1). Specimens and coordinates of the sampling sites are reported in Table 1 and Suppl. material 1. The adductor muscle of each specimen was excised and fixed in 95% ethanol for molecular analysis.

DNA extraction was performed using the high-saline method (Sambrook 1989). The mitochondrial marker COI was amplified through PCR using primers LCO1490 and HCO2198 (Folmer et al. 1994), following protocols described in previous studies (Salvi et al. 2010; Crocetta et al. 2015). DNA presence was tested on 2% agarose gel electrophoresis. Sanger sequencing of PCR products was carried out by the company Genewiz® (www.genewiz.com), using the same primers employed for amplifications. Raw sequences were trimmed on Geneious Prime® v.2024.0.4 (Biomatters Ltd), using as a reference the complete mitochondrial genome of *Crassostrea virginica* (GenBank accession number AY905542; Milbury and Gaffney (2005)). Our dataset includes 96 specimens spanning eleven localities in Rhodes (Greece), six in Cyprus, six in Israel, one in Lebanon, two in Rodrigues and one in Île d'Ambre (Table 1, Fig. 1).

Datasets and molecular analyses

To perform a comprehensive phylogenetic assignment of the Mediterranean *Dendostrea*, a total of 422 COI sequences of Ostreinae species were mined from GenBank. These GenBank sequences and the 96 newly-generated sequences were combined in Dataset 1 (DS1), totalling 518 sequences. The DS1 was aligned using G-INS-i algorithm in MAFFT v.7.490 (Katoh 2002; Katoh and Standley 2013) under default parameters.

A Neighbour-Joining (NJ) phylogenetic tree was built, based on genetic distances computed under the Kimura-2-parameter (K2P) evolutionary model (Kimura 1980) using MEGA11 (Tamura et al. 2021), with pairwise deletion of ambiguous sites. Node support was assessed by the bootstrap method with 1000 replicates. The tree topology was visualised using FigTree v.1.4.4 (Rambaut 2009). In order to assign our specimens to molecular operational taxonomic units (MOTU), a species delimitation analysis was performed using the Assemble Species by Automatic Partitioning (ASAP) method (Puillandre et al. 2021). ASAP was run under the K2P model and the first partition was chosen according to the best ASAP score.

Based on species delimitation results, the sequences assigned to the MOTU including the Mediterranean *Dendostrea* sp. specimens constitute Dataset 2 (DS2). Six sequences with > 5% of ambiguous bases were filtered out from DS2 (Suppl. material 1), which reduced its final size to 84 sequences.

Phylogenetic relationships amongst haplotypes of DS2 were inferred using the Median-Joining (MJ) network method (Bandelt et al. 1999), as implemented in PopART v.1.7 (Leigh and Bryant 2015), with the parameter ε set to zero. Main haplogroups (i.e. clusters of closely-related haplotypes) within the MJ network were mapped across sampling localities in QGIS v.3.30.2 to disclose potential phylogeographic patterns. Sampling sites closer than 8 km were shown as a single sample in the map, but a single site haplotype map is available in Suppl. material 2.

For each region and for the whole Mediterranean Sea, the number of haplotype (N), Nei's haplotype diversity (h) and nucleotide diversity (π) were assessed using the package *pegas* v.1.3 on R v.4.3.1. To account for uneven sampling size between regions, standardised estimates of h, π and haplotype richness (H) were obtained following the re-sampling procedure described in Salvi et al. (2013) on Python v.3.10.11 using 1000 iterations and a re-sampling size of eight for the comparison between Mediterranean regions and between

Table 1. Geographical information on the sequences of *Dendostrea* cf. *crenulifera* and *D. sandvichensis*. Details are given on the 96 sequences of *Dendostrea* cf. *crenulifera* assigned to the MOTU "Ost21" (dataset DS2) and the sequences of *Dendostrea sandvichensis* from Île d'Ambre. The locality codes refer to the sample codes used in Fig. 2B.

Country	Region	Localities (code)	n
Greece	Astypalaia	Astypalaia (AST)†	2
Greece	Rhodes West	Ákra Mérmigka (RHO0)†	2
Türkiye	Türkiye	Olympos (TUR1)†	2
Türkiye	Türkiye	Kekova (TUR2)†	2
Greece	Rhodes East	Paralia Antoni Kouin (RHO12)	6
Greece	Rhodes East	West of Touristiko Limani (RHO12)	1
Greece	Rhodes East	Agia Marina Beach (RHO12)	3
Greece	Rhodes East	Jordan Beach (RHO12)	2
Greece	Rhodes West	Kopria Beach (RHO5)	5
Greece	Rhodes West	Port of Fanes (RHO6)	4
Greece	Rhodes West	Kerameni Beach (RHO7)	2
Greece	Rhodes East	St Paul's Bay (RHO8)	7
Greece	Rhodes East	West of Prasonisi Beach (RHO13)	2
Greece	Rhodes East	South of Mavros Kavos Beach (RHO13)	5
Cyprus	Cyprus	Zygi Marina (CYP17)	2
Cyprus	Cyprus	West of Cape Dolos (CYP17)	3
Cyprus	Cyprus	St Raphael Marina (CYP17)	4
Cyprus	Cyprus	Polis Municipal Beach (CYP14)	6
Cyprus	Cyprus	Akrotiri Peninsula (CYP15)	1
Cyprus	Cyprus	Turtle Beach (CYP16)	1
Israel	Israel/Lebanon	West of Rosh HaNikra Islands (ISR1)	14
Israel	Israel/Lebanon	Ashqelon (ISR2)	9
Lebanon	Israel/Lebanon	Tyre (LEB)	3
Mauritius	Rodrigues	Passage Grand Bassin (ROD1)	5
Mauritius	Rodrigues	Baie Nord (ROD2)	3
Mauritius	Île d'Ambre	Bassin Trou Polite	8

n: number of sequences; †: GenBank sequences (KJ946446–KJ946453).

the Mediterranean Sea and Rodrigues. The 95% confidence intervals of diversity estimates were computed by bootstrap re-sampling using the Python module SciPy v.1.15.2 with 1,000 replicates under the 'basic' method. Haplotype accumulation curves of the entire Mediterranean Sea, Rhodes and Cyprus were calculated using the function *haploAccum*() from the R package ape v.5.7-1 with 1000 iterations under the "random" method. For the whole Mediterranean Sea, the Chao1 asymptotic estimator for haplotype richness (Chao 1984) was assessed using the R package iNEXT (Hsieh et al. 2016). Finally, to assess population genetic structure between regions within the Mediterranean Sea (Table 1), Rodrigues was filtered out of DS2 and the 82 sequences left were used for the analysis of molecular variance (AMOVA; Excoffier et al. (1992)) with the R package *poppr* v.2.9.6. The components of covariance were tested with the function *randtest*() from the package *ade4* v.1.7-22 with 1,000 permutations (Excoffier et al. 1992).

Morphological assessment

Shell morphology of specimens from the Mediterranean, Île d'Ambre and Rodrigues was assessed under a microscope. Photos of selected specimens were recorded using a Nikon D750 camera either connected to a Leica Z6 stereomicroscope or mounting a 60 mm 1:1 macro lens. All photographs were stacked using Helicon Remote and rendered using Helicon Focus. Based on molecular results, the shells were compared with the type materials of *D. crenulifera* and *D. sandvichensis*, as well as with the specimens illustrated in Oliver et al. (2004). The main morphological characteristics considered in the assessment included the attachment area (hinge), the shape of upper and lower valves, the shape of margins, the types of chomata and the inner colouration of valves.

Results

Phylogenetic relationships

The dataset DS1 included 518 sequences and 649 aligned positions (base pairs, bp), amongst which 306 were variable (47.1%) and 253 were phylogenetically informative (39%).

Twenty-nine MOTUs were identified amongst the 518 sequences of Ostreinae analysed (Fig. 1A), based on the lowest-score ASAP partition (score = 7.0) chosen according to the procedure described in Puillandre et al. (2021). Nine MOTUs were represented by a single sequence. Amongst the remaining 20 MOTUs, 16 received very high bootstrap support on the Neighbour-Joining tree (bootstrap, BS ≥ 95), three received good support (95 > BS ≥ 80) and one received low support (BS = 66).

All the 89 Mediterranean *Dendostrea* sp. specimens clustered in a single well-supported MOTU named "Ost21" (BS = 99; ASAP *p*-value = 8.76e-01; Fig. 1). This MOTU also includes eight sequences of *Dendostrea* sp. from Türkiye and Greece from Crocetta et al. (2015), as well as sequences from Rodrigues. The MOTU "Ost21" is highly divergent (K2P-distance > 8%) from its closest sister clade "Ost18-Ost19-Ost20" (Fig. 1). This sister clade "Ost18-Ost19-Ost20" refers to sequences of specimens from south China and Malaysia (i.e. southern Chinese Sea) with unresolved nomenclature (Suppl. material 3). Within MOTU "Ost21", there is no geographic structure with sequences from different Mediterranean regions admixed in multiple sub-clades and with Rodrigues sequences nested within them (Fig. 1). Intra-clade genetic distances (K2P-distances) within the MOTU "Ost21" range from 0% to 3.35% (*p*-distance = 3.25%), with an average of 1.53% (*p*-distance = 1.50%). Mean genetic distance (K2P-distance) between Mediterranean and Rodrigues specimens is 1.74% (*p*-distance = 1.70%).

The eight sequences of *Dendostrea* specimens from Île d'Ambre clustered in a distinct MOTU named "Ost14" together with topotypic specimens of *Dendostrea sandvichensis* from Hawaii plus other sequences from the Pacific Ocean and the Caribbean Sea (BS = 99; ASAP *p*-value = 4.00e-01; Fig. 1). Within this clade, genetic distances (K2P-distances) range from 0 to 4.68% (*p*-distance = 4.47%), with an average of 1.58% (*p*-distance = 1.55%). Mean genetic distance (K2P-distance) between Île d'Ambre and Rodrigues specimens is 19.4% (*p*-distance = 16.8%).

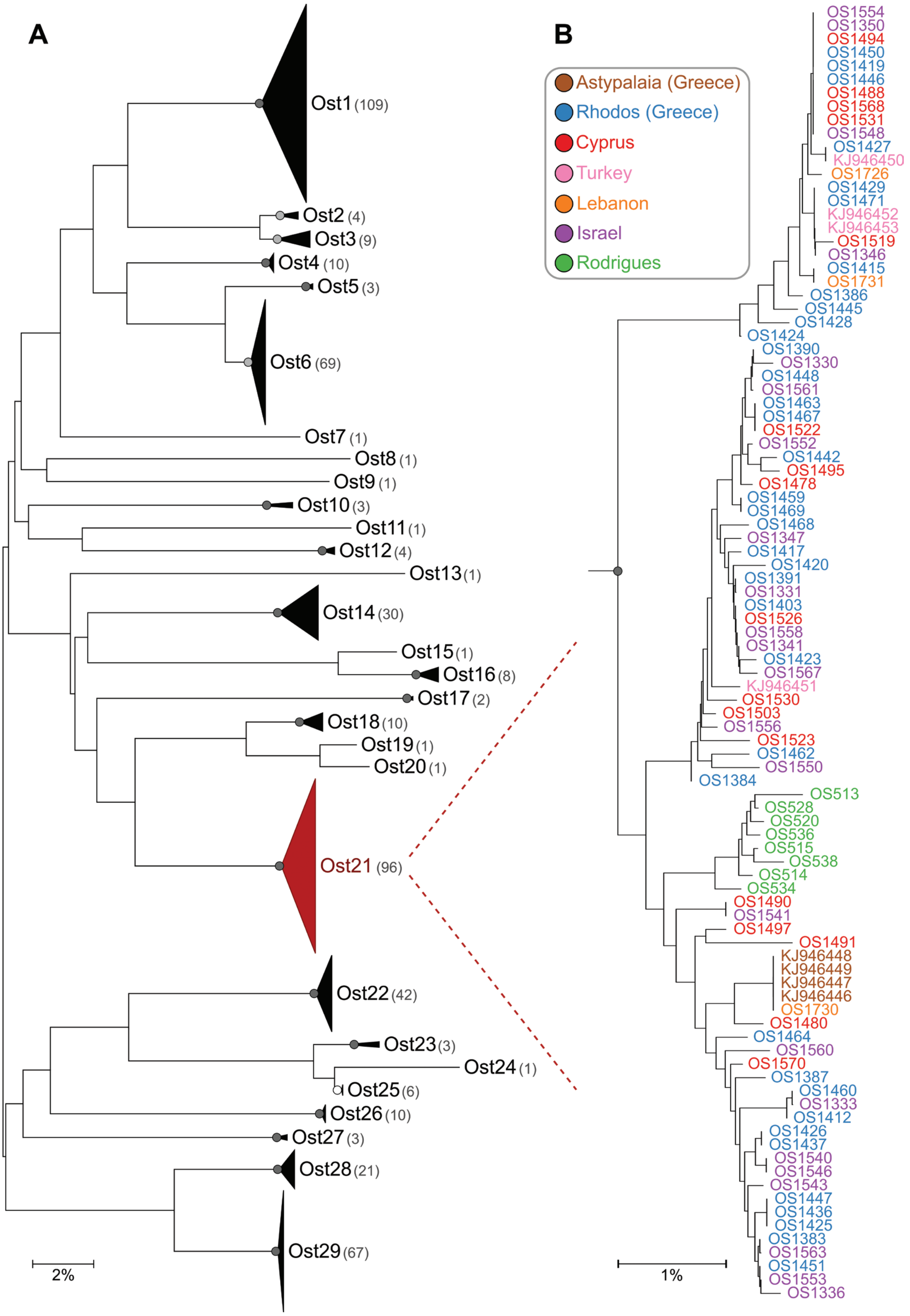

Figure 1. Neighbour-Joining (NJ) phylogenetic tree, based on the Ostreinae dataset (DS1) under the K2P evolutionary model. **A.** Complete NJ tree; **B.** Uncollapsed clade of the MOTU "Ost21" with sequences coloured, based on their respective geographical origin as reported in the legend. Bootstrap support values (BS) based on 1000 replicates are reported on nodes as dark grey (BS ≥ 95), light grey (95 > BS ≥ 80) or white (BS < 80) circles. Putative species clusters were collapsed, based on the results of the species delimitation analysis (Assemble Species by Automatic Partitioning; ASAP). All specimen of *Dendostrea* cf. *crenulifera* from the Mediterranean Sea and Rodrigues belong to the cluster "Ost21", that has been highlighted in red.

Phylogeographic structure and genetic diversity

The dataset DS2 included 96 sequences and 649 aligned positions (base pairs, bp). The phylogenetic network includes 51 haplotypes over 96 sequenced specimens, with 43 haplotypes found only in the Mediterranean Sea and eight haplotypes found exclusively in Rodrigues (Fig. 2 and Suppl. material 1). Mediterranean haplotypes cluster in three groups, Rodrigues haplotypes forming a single cluster (indicated with distinct colours in Fig. 2). These four haplogroups showed shallow phylogenetic divergence that does not reflect geographic distance: two Mediterranean clusters and the Rodrigues cluster are separated by seven mutational steps one from each other, whereas they are separated by 13 mutational steps from the third Mediterranean cluster (green in Fig. 2).

The phylogeographic pattern within the Mediterranean has no geographic structure, with the three haplogroups co-occurring on all sampling regions (Türkiye, Rhodes, Cyprus, Israel) and being syntopic in most sampling sites (Fig. 2). This observation is supported by the AMOVA, which revealed no significant structure either at the regional or population levels (Table 2).

Haplotype diversity was remarkably high both in Rodrigues (observed h = 1 and N = 8) and in the eastern Mediterranean Sea, both as a whole (observed: h = 0.968 and N = 43; estimated: h = 0.969 and H = 7.227) and for single Eastern sampling regions (observed: h ranged from 0.833 to 0.978 and N from 1 to 19; estimated: h ranged from 0.945 to 0.979 and H from 6.446 to 7.413), as reported in Table 3. Nucleotide diversity was relatively high in the eastern Mediterranean Sea as a whole ($\pi = 1.463 \times 10^{-2}$) as well as for single Mediterranean sampling regions (π ranged from 1.377×10^{-2} to 1.591×10^{-2}) as compared to Rodrigues ($\pi = 0.480 \times 10^{-2}$; Table 3).

The haplotype accumulation curves do not reach an asymptote for any region (Cyprus, Rhodes and Israel/Lebanon), nor for the eastern Mediterranean as a whole (Fig. 3). In the Mediterranean Sea, 28 out of the 43 haplotypes found are singletons (> 50%) and the Chao1 estimator revealed an asymptotic value of haplotype richness of 98.32 (Fig. 3), suggesting that the true haplotype diversity of *Dendostrea* sp. is likely higher than estimated.

Morphological assessment

Despite molecular data indicating that the assayed oysters from the Mediterranean, Rodrigues and Île d'Ambre belong to two distinct MOTUs ("Ost21" for Mediterranean and Rodrigues and MOTU "Ost14" for Île d'Ambre), morphological assessment indicates that oysters from these three regions are morphologically very similar, with only slight differences that have no diagnostic value (Fig. 4). Indeed, the majority of shells analysed here have a large attachment area, the margin is irregularly toothed and the ribs are low, rounded and often obscure. This is the form more typical of *Dendostrea sandvichensis* that currently includes *D. crenulifera* from the Red Sea. The Mediterranean and Rodrigues shells are very variable, but the expression of the external ribbing is very poor in both, whereas the Île d'Ambre shells are often distinctly ribbed. Some shells have a reddish-black margin in both populations, but not in Île d'Ambre. The crenulations are numerous and angulate in both, whereas the Île d'Ambre shells appear to have more rounded crenulations.

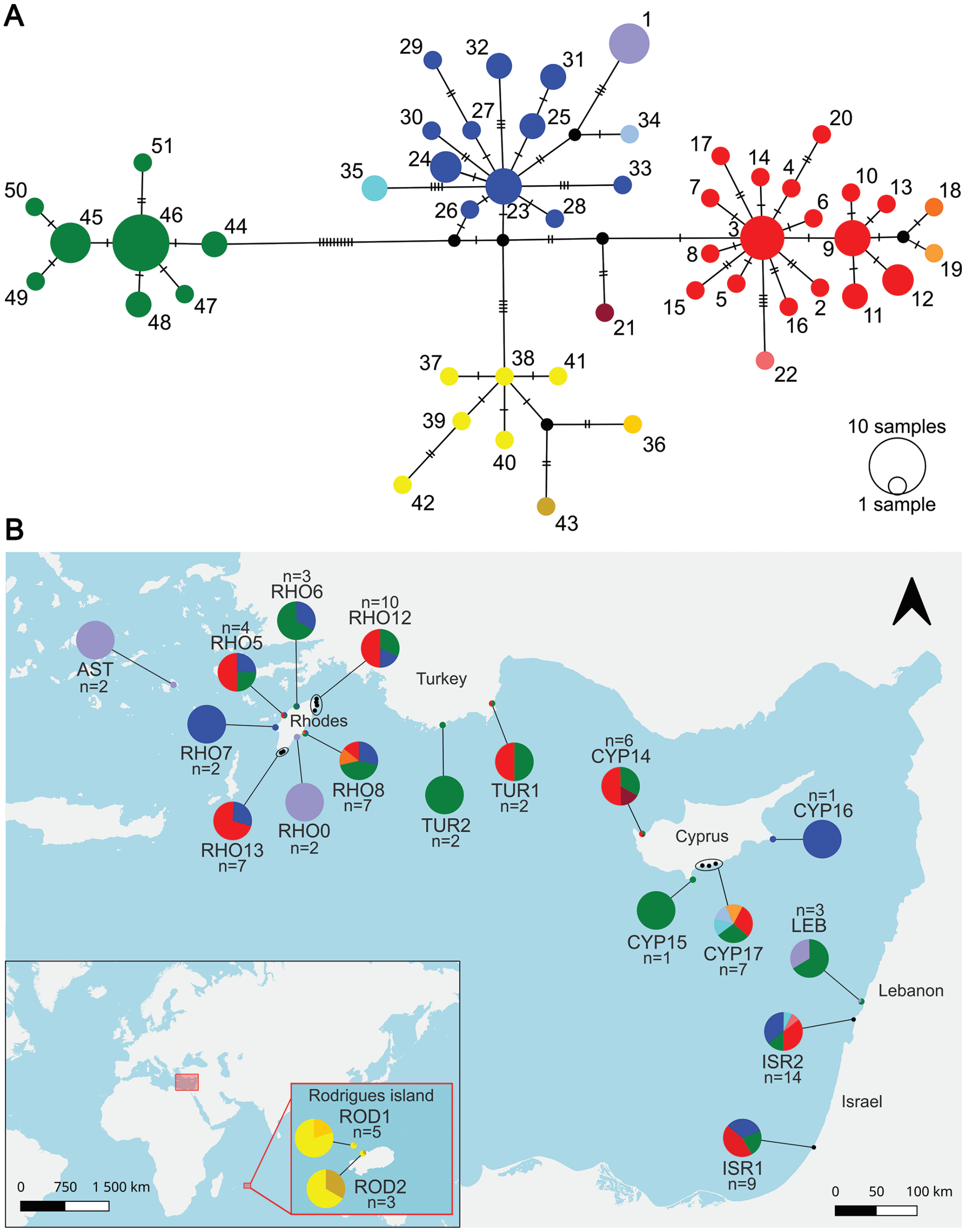

Figure 2. Phylogeography of *Dendostrea* cf. *crenulifera* from the Mediterranean Sea and Rodrigues. **A.** Median-Joining (MJ) haplotype network, based on the MOTU "Ost21" dataset (DS2). The four closely-related haplogroups within the MJ network are coloured; **B.** Their geographical distribution is reported on the map. Sampling sites closer than 8 km were shown as a single sample in the map, but a single site haplotype map is available in Suppl. material 2. The colouring of haplogroups is independent from the colouring of the sequences' origin used in Figs 1, 3. For each locality, the sampling size is reported (n).

In Mediterranean and Rodrigues shells, simple chomata are sparse and prominent, respectively, on the posterior dorsal margin. On the contrary, in Île d'Ambre shells, simple chomata are prominent all along the shell. Pustular (lophine) chomata are present between crenulations and on posterior margin only in the Mediterranean shells, whereas are sparse or absent in Rodrigues and Île d'Ambre shells.

Table 2. Analysis of molecular variance (AMOVA) for the COI sequences of *D.* cf. *crenulifera* (MOTU “Ost21”). To focus on the phylogeographic structure in the Mediterranean Sea, only the sequences from the Mediterranean Sea were considered, excluding the sequences from Rodrigues from this analysis.

Source of variation	DF	Variance components	% of variation	*p-value*
Between regions	5	0.024	2.44	0.020
Between sites within regions	21	0.018	1.85	0.258
Within sites	55	0.933	95.71	0.033
Total	81	0.975	100	

Table 3. Observed and estimated genetic diversity of *Dendostrea* cf. *crenulifera* (MOTU “Ost21”). Statistics were computed for each sampling regions and for the whole Mediterranean. To allow inter-population comparisons, haplotype richness, Nei’s diversity and nucleotide diversity indexes of each sampling region were estimated using a rarefaction analysis with 1000 iterations (standard resample size, n = 8). The 95% confidence intervals were computed, based on the bootstrap method with 1,000 replicates and are presented between brackets.

Regions	Observed diversity				Estimated diversity (n = 8)		
	n	N	*h*	π (*10^2)	H	*h*	π (*10^2)
Mediterranean Sea	82	43	0.968	1.463	7.227 (7.176–7.281)	0.969 (0.966–0.972)	1.467 (1.452–1.484)
Astypalaia	2	1	–	–	–	–	–
Türkiye	4	3	0.833	1.443	–	–	–
Rhodes East	26	19	0.978	1.456	7.413 (7.373–7.454)	0.979 (0.977–0.981)	1.456 (1.440–1.474)
Rhodes West	9	7	0.944	1.434	6.446 (6.417–6.473)	0.945 (0.943–0.946)	1.434 (1.428–1.439)
Cyprus	15	12	0.943	1.591	6.899 (6.846–6.954)	0.946 (0.942–0.950)	1.580 (1.570–1.591)
Israel and Lebanon	26	19	0.972	1.377	7.256 (7.209–7.301)	0.972 (0.970–0.974)	1.367 (1.350–1.383)
Rodrigues	8	8	1	0.480	–	–	–

n: sample size; N: number of haplotypes; H: estimated haplotype richness; *h*: Nei’s haplotye diversity; π: nucleotide diversity.

Discussion

Results of this study resolved the long-standing taxonomic ambiguity surrounding the small tropical oysters colonising the Mediterranean Sea. Based on genetic data, we inferred the invasion stages of this NIS, from its initial arrival to its post-establishment spread in the Mediterranean Sea.

Taxonomic identification of Mediterranean Dendostrea

Since the first record of *Dendostrea* in the Mediterranean Sea (Çeviker 2001), several names have been applied: *D. folium* (Linnaeus, 1758), *D. frons* (Linnaeus, 1758) and *D. crenulifera* (G.B. II Sowerby, 1871) with the latter updated to *D. sandvichensis* (G.B. II Sowerby, 1871) following Huber (2010) (MolluscaBase 2024). Crocetta et al. (2015) summarised records of non-indigenous oysters in the Mediterranean and suggested a close relationship between Mediterranean *Dendostrea* and a sequence

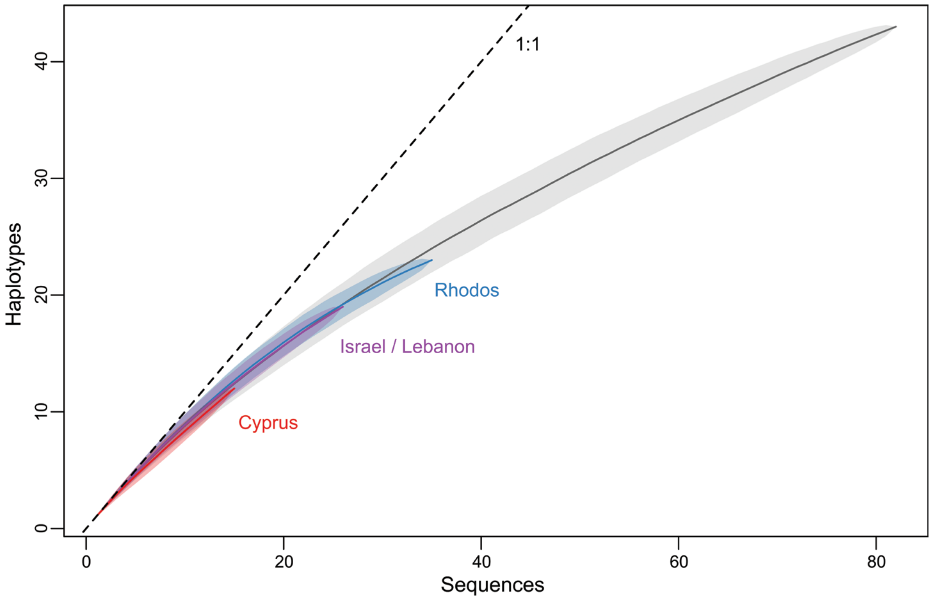

Figure 3. Haplotype accumulation curves of the entire Mediterranean Sea (yellow), Rhodes (blue) and Cyprus (red).

registered in GenBank under the name *Dendostrea folium*. Consequently, recent papers (e.g. Ragkousis et al. (2023)) record it as *D. folium*, while others remain undecided (e.g. Moussa and Khafage (2023)). MolluscaBase (2024) currently indicates that *D. frons* is distributed in both the Caribbean and the Mediterranean.

Such a taxonomic uncertainty, alongside the nomenclatural complexity of oysters, arises from the challenging and often unreliable morphological identification of those species (Lam and Morton 2003; Raith et al. 2015; Salvi and Mariottini 2017; Guo et al. 2018). The issue is compounded by the limited availability of reference sequences in public databases that could serve for molecular identification (Liu et al. 2011; Crocetta et al. 2015). For this reason, DNA barcoding analyses by Crocetta et al. (2015) were not able to assign Mediterranean specimens to a known species. Their 16S sequences were closely related (genetic distance = 3–3.7%) to a sequence registered as *Dendostrea folium* from the South Pacific Ocean (accession AF052069), although this sequence was very divergent (7.6%) from — and did not cluster with — another GenBank sequence from the north-eastern Indian Ocean assigned to *D. folium* (accession EF122380), suggesting conflicting identification of these vouchers. At the COI marker, the closest match was with two unidentified oysters from the western coast of the Malay Peninsula (accession JF9115513-4), but again with a high genetic distance (13–14%). The high genetic distance between the non-indigenous oysters in the Mediterranean and GenBank sequences of Indo-Pacific specimens indicates they are distinct species (Crocetta et al. 2015).

In this study, we resolved the taxonomic uncertainty surrounding the Mediterranean *Dendostrea* by using an extended molecular dataset, including specimens from the western Indian Ocean. Molecular data unambiguously indicate that the Mediterranean populations are conspecific (mean K2P-distance = 1.74%) with oysters from the Indian Ocean island of Rodrigues, identified as *Dendostrea crenulifera* (Oliver et al. 2004). Our study also corroborates the challenging morphological identification of these oysters. Mediterranean specimens show a very high plastic shell morphology, as noted by Crocetta et al. (2015), overlapping with the morphological variation of

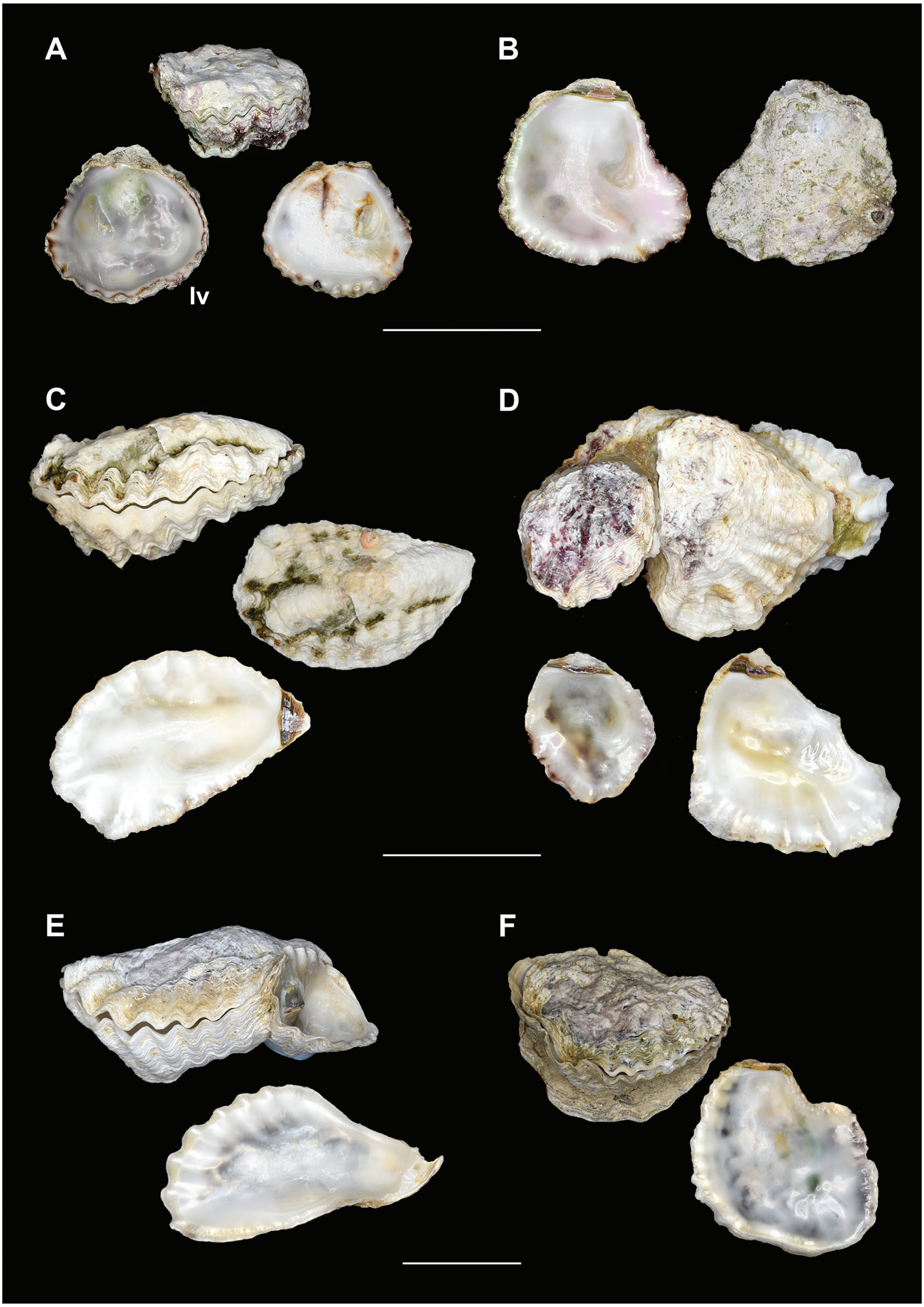

Figure 4. Shells of *D.* cf. *crenulifera*. *D.* cf. *crenulifera* from the Mediterranean Sea: **A.** OS1412; **B.** OS1403. *Dendostrea* cf. *crenulifera* from Rodrigues: **C.** NMW.Z.1999.073.05; **D.** NMW.Z.1999.073.30/31. *Dendostrea sandvichensis* from Île d'Ambre: **E.** NMW.Z.1999.73.63; **F.** NMW.Z.1999.73.66. Single upper valves are reported for each specimen. One single lower valve (lv) is shown for OS1412.

populations from both Rodrigues and Île d'Ambre. However, the latter belong to a distinct species, phylogenetically very divergent (mean K2P-distance = 19.4%). Île d'Ambre specimens are assigned to *D. sandvichensis* because they share haplotypes with specimens from the type locality of this species. Currently, *D. sandvichensis* includes *D. crenulifera* (WoRMS (2025)); the type locality of *D. sandvichensis* is Hawaii, while that of *D. crenulifera* is the Red Sea. Our results indicate that these are two distinct species rather than synonyms. Mediterranean and Rodrigues specimens are referred conservatively as *D.* cf. *crenulifera*, pending the analyses of sequences from samples collected at the type locality in the Red Sea. A detailed nomenclatural assessment of these species is provided elsewhere (Oliver et al. 2025).

Transport and introduction

Dendostrea cf. *crenulifera* possibly colonised the Mediterranean Sea through vessel-mediated introduction across the Suez Canal. As a brooding species, *Dendostrea* oysters release advanced-stage larvae with a brief planktonic phase before metamorphosis (Foighil and Taylor 2000). As a result, natural range expansions via marine currents are limited and unlikely to occur over long distances. A stepping-stone process via multiple short-distance dispersals could also be ruled out, based on genetic diversity data, i.e. lack of bottleneck signature (see below). These life history traits and genetic data restrict the transport of *D.* cf. *crenulifera* to anthropogenic vectors, such as ballast waters for larvae or hull fouling for adults, similar to many non-indigenous molluscs in the Mediterranean Sea (Galil 2008). Vessel-mediated vectors are believed to play a key role in maintaining high propagule pressure of NIS, such as *D.* cf. *crenulifera*, in the eastern Mediterranean Basin, due to the central position of the Suez Canal in the global maritime network and its intense traffic (Lockwood et al. 2005; Roman and Darling 2007; Nunes et al. 2014). Hull-fouling has been observed several times for *Dendostrea* specimens (e.g. Ulman et al. (2017)), whereas no evidence of ballast-water transport has been reported yet. The ballast-water-mediated introduction is less likely due to the short duration of the planktonic stage of *Dendostrea* cf. *crenulifera* compared to the shipping time between the Indian Ocean and the Mediterranean.

A scenario of shipping-driven introduction from the Red Sea or the western Indian Ocean implies that *D.* cf. *crenulifera* is most likely sampled in harbours and transported to other harbours of the eastern Mediterranean Sea, as there are more opportunities of transport and introduction between these highly-connected homogeneous habitats (Hufbauer et al. 2012; Blackburn et al. 2015; Daly et al. 2023; Prestes et al. 2024). Checklists of the past two decades support this assumption, with almost all first and additional detections signalled in artificial habitats in port areas (Çeviker 2001; Zenetos et al. 2009; Ulman et al. 2017; Gerovasileiou et al. 2017; Ragkousis et al. 2023).

Establishment and spread

The remarkably high genetic diversity observed in *D.* cf. *crenulifera* in the eastern Mediterranean Sea, together with multiple haplogroups lacking a phylogeographic structure (Fig. 2, Table 2), indicate high propagule pressure and significant establishment success underlying the introduction of this species within the eastern Mediterranean Sea. Three factors can explain this successful establishment: (i) an intense and continuous introduction of specimens from multiple genetic lineages;

(ii) individual or population traits promoting invasion (i.e. species invasiveness); and (iii) the increasing ecosystem invasibility of the eastern Mediterranean Sea.

High local genetic variability is predicted to facilitate the long-term establishment of marine non-indigenous species populations (Lee 2002; Wellband et al. 2017; Geburzi et al. 2020). The spread beyond the area of introduction is commonly characterised by sequential founder events, leading to a spatial pattern of decreasing genetic diversity from the invasion entry point (Slatkin and Excoffier 2012). These two assumptions highlight the so-called genetic paradox, which questions how introduced populations adapt to the new selection pressures of the recipient habitat despite reduced genetic diversity (Sax and Brown 2000). However, we found no evidence of a founder effect in any of the sampled populations of *D.* cf. *crenulifera* that show remarkably high and evenly distributed haplotype diversity (Fig. 3, Table 3) and relatively high nucleotide diversity compared to other non-threatened bivalves (> Q_3 = 1.31^{e-02}; Petit-Marty et al. (2021); Table 3). This suggests that the number of specimens involved in each introduction event (i.e. propagule size) and/or the number of releases (i.e. propagule number) is sufficient to counteract the effects of genetic, environmental and demographic stochasticity (Lockwood et al. 2005; Roman and Darling 2007; Lockwood et al. 2009; Blackburn et al. 2015). It is also important to consider vectors in the context of the corridors along which they act (Roman and Darling 2007). The vector-corridor combination of ballast water transport and the Suez maritime network appears particularly conducive to promoting repeated introductions from genetically diversified sources, enabling continuous recruitment at introduction sites driven by periodic releases from recurrent maritime routes (Roman and Darling 2007; Nunes et al. 2014). Along with the lack of phylogeographic pattern, our results suggest that the spread of *D.* cf. *crenulifera* does not follow a stepping-stone model, but rather a 'jump' dispersal model of independent and numerous shipping-mediated introduction events combined with secondary local natural expansions. Growing evidence from many marine non-indigenous species suggests that shipping-driven high propagule pressure is a common invasion scenario that promotes high local genetic diversity, thus overcoming the genetic paradox (Roman 2006; Roman and Darling 2007; Bernardi et al. 2010; Lawson Handley et al. 2011; Rius et al. 2015). For example, the Lessepsian mussel *Brachidontes pharaonis* exhibits a high local genetic diversity without phylogeographic structure in its non-native range, similar to *D.* cf. *crenulifera* (Shefer et al. 2004; Sirna Terranova et al. 2006; Battiata et al. 2024). The ballast water transport of this mussel subjected the eastern Mediterranean Sea to a high propagule pressure, causing the two allopatric mitochondrial lineages from the Red Sea to occur in sympatry in the introduced Mediterranean populations (Shefer et al. 2004). This multiple-introduction process from several genetically differentiated sources is observed in various other non-indigenous benthic species and likely underlies the spread of *D.* aff *crenulifera* (e.g. Simon-Bouhet et al. (2006); Rius et al. (2012); Zhan et al. (2012); Makino et al. (2018)). However, in the absence of population genetic data from the native range, we cannot rule out a single-source origin for *D.* aff *crenulifera*, under the hypothesis that the pattern observed in the Mediterranean – high genetic diversity and lack of phylogeographic structure – mirrors the one in the source area, especially if the propagule size is large enough to prevent the sampling effect and subsequent founder effects at each introduction site (Lockwood et al. 2009; Blackburn et al. 2015; Zeeman et al. 2020).

Some individual and population biological traits, along with their plasticity, facilitate the establishment of non-indigenous species. These traits characterise the so-called species invasiveness (Elton 1958; van Kleunen et al. 2010; Daly et al. 2023). High plasticity in traits relevant to invasion propensity can allow a broader range of ecological tolerance, which may be key to success in the early stages of invasion (e.g. Daly et al. (2023); Battiata et al. (2024); Kinnby et al. (2025)). *Dendostrea* cf. *crenulifera* shows a high phenotypic plasticity, typical of oysters and, in particular, of intertidal species (Gunter 1950). The high intraspecific variation in shell morphology is a response to variable environmental conditions, such as those experienced by oysters subjected to tidal regimes or diverse substrate types (Gunter 1950; Seilacher et al. 1985) and reflects the highly plastic feeding and growth physiology of bivalves (Bayne 2004). We have often found abundant populations of *D.* cf. *crenulifera* established in disturbed artificial habitats, such as small or large harbours. However, they can also be found established in natural areas. This suggests that, after settling in various harbours throughout the Mediterranean Sea, this species can spread locally to suitable natural areas through a post-introduction dispersal process likely driven by its ecological response to diverse intertidal-subtidal habitats reflected in its phenotypic plasticity (Nawrot et al. 2015).

To explain the successful introduction of *D.* cf. *crenulifera*, it is essential to consider both the species' invasiveness and the invasibility of the recipient ecosystem. The eastern Mediterranean Sea has experienced a significant decline in the native molluscan biodiversity and a process of tropicalisation due to increased salinity and sea-surface temperatures (Albano et al. 2021a, b). Over the past few decades, climatic and ecological conditions of the eastern Mediterranean Sea and the Gulf of Suez converged, becoming undistinguishable in some regions, such as the Levant coast (Albano et al. 2021a). The subsequent eradication of native species in shallow rocky habitats has reduced biotic resistance and facilitated establishment by avoiding competition for resources (Nawrot et al. 2015; Albano et al. 2021a; Steger et al. 2022, 2024; Daly et al. 2023). This combination of climatically suitable and taxonomically and functionally impoverished Levantine Basin might explain the high establishment success of *D.* cf. *crenulifera*, as well as its widespread distribution and local abundance (Daly et al. 2023).

Additionally, an earlier timing of introduction may have also contributed to the successful establishment of *D.* cf. *crenulifera* (Crooks 2005; Nawrot et al. 2015; Albano et al. 2018; Daly et al. 2023). Chances of detection of the earliest specimens of an introduced population of small-sized bivalves are slim and new records often occur during the later stages of invasion (Galil 2008; Albano et al. 2018, 2021b, 2024). This time lag between introduction and establishment/spread, followed by subsequent detections, is evident in *D.* cf. *crenulifera.* There was a 10-year gap between the first detection in 1998 (Çeviker 2001) and the second in 2008 (Zenetos et al. 2009), followed by an acceleration of first country detections in the following years (Zenetos et al. 2011; Crocetta et al. 2015; Ulman et al. 2017; Gerovasileiou et al. 2017; Ragkousis et al. 2023). The global trend of increasing sea surface temperature and salinity in the eastern Mediterranean Sea likely provided an 'opportunity window' (Johnstone 1986; Daly et al. 2023), facilitating the spread of this non-indigenous oyster in the past decade, similar to other NIS (Albano et al. 2021a, b). Along with the gradually increasing environmental suitability, the ever-increasing maritime traffic passing through the Suez Canal (Baccelli et al. 2015) may have resulted in increased propagule pressure of *D.* cf. *crenulifera* on the eastern Mediterranean Sea. Both factors likely increased the odds and opportunities for introduction and establishment, reducing detection time and promoting later stages of the invasion (Crooks 2005; Lockwood et al. 2009; Blackburn et al. 2015).

Conclusion

This study highlights the effectiveness of molecular methods for reliable identification of non-indigenous species and for the reconstruction of the invasion process. Mitochondrial data are particularly well-suited as an initial approach for both applications. COI, in particular, is the most commonly used barcode in animal studies and offers the largest reference library in public repositories, which is crucial for reliable species identification. In terms of invasion history, mitochondrial markers have the advantage of being highly susceptible to genetic drift, such as bottlenecks, due to the fourfold difference in effective population sizes between the haploid, uniparentally inherited mitochondrial genome and the nuclear genome (Hudson and Turelli 2003). By including specimens from the western Indian Ocean, we resolved the long-standing taxonomic uncertainty surrounding the small non-indigenous oysters invading the Mediterranean Sea, assigning them to *Dendostrea* cf. *crenulifera*. By combining data on geographic patterns of genetic diversity in the non-native range with species traits and characteristics (both biotic and abiotic), we gathered crucial information on dispersal mode, propagule pressure and temporal and spatial patterns of establishment, allowing us to dissect the invasion stages from arrival to post-establishment spread in the Mediterranean Sea.

The global trend of increasing sea surface temperature and salinity in the eastern Mediterranean Sea likely facilitated the spread of this non-indigenous oyster (Raitsos et al. 2010; Albano et al. 2021a). The invasibility of the eastern Mediterranean Sea is determined by dynamic processes that may vary over time (Daly et al. 2023). As global warming continues, an extended decline in native species is expected (Albano et al. 2021a), potentially creating suitable environmental conditions and empty niche opportunities for *D.* cf. *crenulifera* in the eastern Mediterranean Sea, as well as at the western invasion front towards the Aegean and central Mediterranean Seas. This could pose a threat to native Mediterranean species such as *Ostrea stentina* and *Ostrea edulis* (Daly et al. 2023).

Temporal data and molecular evidence suggest that ongoing propagule pressure facilitated the establishment and spread of this non-indigenous species, revealing a possible time lag between these two stages of the invasion. Such a time lag is well documented in other Lesspesian species. For example, in the mussel *Brachidontes pharaonis*, there was an extensive time lag between introduction and the climate-warming-driven spread 120 years later (Rilov et al. 2004). Whether the time lag observed for *D.* cf. *crenulifera* can be attributed to the genetic admixture of different evolutionary lineages in the Mediterranean and the introduction of adaptative genetic variation for new areas and habitats deserves further research. Additionally, further research in the Red Sea is necessary to validate the assignment of Mediterranean *Dendostrea* to *D. crenulifera* using topotypes and to precisely identify the source area(s), helping to distinguish between single vs. multiple source hypotheses. A good understanding of the introduction process is important for evaluating the impact on Mediterranean ecosystems and developing mitigation strategies.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Daniele Salvi and Matteo Garzia contributed to the study conception and design. All authors performed sample collection and preparation. Genetic data collection and analysis were performed by Matteo Garzia, Nathan Delcour and Daniele Salvi. The first draft of the manuscript was written by Nathan Delcour, Matteo Garzia and Daniele Salvi and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Detailed information on the 96 sequences of *Dendostrea* cf. *crenulifera* and *D. sandvichensis*

Authors: Nathan Delcour, Matteo Garzia, Daniele Salvi

Data type: ods

Explanation note: Information concerns the sequences of *Dendostrea* cf. *crenulifera* assigned to the MOTU “Ost21” (dataset DS2), and the sequences of *Dendostrea sandvichensis* from Île d’Ambre. Specimens and GenBank codes and coordinates of each sampling locality are reported. Inventory numbers (Inv. numb.) are provided for the dry shells deposited in the following collections: Roma Tre University (referent: Prof. Paolo Mariottini, “BAU”), the Malacological Collection of the University of L’Aquila (“OS”), the Stazione Zoologica Anton Dohrn (“SZN”), the Natural History Museum in Vienna (“112930-LM”) and the National Museum of Wales (“NMW”). Haplotype codes are reported only for the sequences used in the Median-Joining (MJ) network (see Fig. 2B of the main article). The locality codes refer to the site codes used in Suppl. material 2B. †: sequences retrieved from GenBank; ‡: sequences filtered out from the MJ analysis because they contain > 5% of ambiguous sites; §: sequences of specimens identified as *Dendostrea sandvichensis*.

Link: https://doi.org/10.3897/neobiota.101.154917.suppl1

Supplementary material 2

Phylogeography of *Dendostrea* cf. *crenulifera* from the Mediterranean Sea and Rodrigues

Authors: Nathan Delcour, Matteo Garzia, Daniele Salvi

Data type: png

Explanation note: **A** Median-Joining (MJ) haplotype network, based on the MOTU “Ost21” dataset (DS2). The four closely-related haplogroups within the MJ network are coloured and **B** their detailed geographical distribution is reported on the map, based on each sampling site. The colouring of haplogroups is independent from the colouring of the sequences’ origin used in Figs 1, 3. For each locality, the sampling size is reported (n).

Link: https://doi.org/10.3897/neobiota.101.154917.suppl2

Supplementary material 3

Neighbour-Joining (NJ) phylogenetic tree, based on the Ostreinae dataset (DS1) under the K2P evolutionary model

Authors: Nathan Delcour, Matteo Garzia, Daniele Salvi

Data type: pdf

Explanation note: **A** complete uncollasped NJ tree with GenBank accession numbers; **B** Putative species clusters, based on the results of the species delimitation analysis (Assemble Species by Automatic Partitioning; ASAP).

Link: https://doi.org/10.3897/neobiota.101.154917.suppl3