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Colonization of the Mediterranean Sea by the Lessepsian invasive jellyfish *Cassiopea andromeda* (Forskål, 1775) – a systematic review

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Abstract

The colonization of the Mediterranean Sea by *Cassiopea andromeda* underscores the complex interaction of biological, environmental, and anthropogenic factors influencing the spread of invasive species. This study describes the dispersal of *C. andromeda* across the Mediterranean basin and updates its current distribution. Starting from the initial introduction via the Suez Canal, we uncovered key stages of colonization across the Mediterranean, and discussed the role that salinity, dispersal vectors, and local genetic adaptations might have had in shaping its distribution. Through a comprehensive review of historical records, environmental parameters, and life cycle constraints, we identify three distinct colonization periods: a slow initial colonization, a rapid expansion phase, and a restricted westward spread, culminating in its appearance in the Mar Menor coastal lagoon in southwestern Mediterranean. Our findings suggest that salinity could have acted as a modulator of the spread velocity, delaying colonization in suboptimal conditions and potentially driving local adaptations. This work highlights the synergistic effects of anthropogenic activities and environmental stressors on the spread of marine invasives, providing insights to develop management strategies for *C. andromeda* and other invasive species in coastal ecosystems.

Keywords: Invasion; Non-Indigenous species; Salinity; Tropical jellyfish; Upside-down jellyfish.

Introduction

The Mediterranean Sea is a biodiversity hotspot, hosting over 17000 recorded species and exhibiting a high endemism rate (Coll *et al.,* 2010). However, it is also home to a significant number of non-indigenous species (NIS) whose spread is considered a cause of biodiversity loss, ecosystem functioning alteration, and economic damage (Zenetos *et al.,* 2017; Crocetta *et al.,* 2021). The number of NIS in the Mediterranean Sea increased notably after the completion of the Suez Canal in the second half of the 19th century. Following this construction, the term “Lessepsian migrant” was coined to refer to those Red Sea species which passed through the Suez Canal and established themselves in the Eastern Mediterranean Sea (Por, 1971). This migration was originally proposed as unidirectional given that only a few Mediterranean species reached the Red Sea despite their entrance to the Suez Canal (Por, 1971, 1978).

The underlying reason for the unidirectionality is derived from the Atlantic origin of the recent Mediterranean Sea fauna, mainly composed of temperate and subtropical species (Coll *et al*., 2010). Until the construction of the Suez Canal, the Eastern Mediterranean, given its tropical-like conditions, was inhabited by an impoverished fauna from the Western Mediterranean and was considered a zoogeographical *‘cul-du-sac’* (Por, 1971). This zoogeographical end was then artificially reconnected with the Red Sea, a typical tropical sea leading to a colonization of the Levantine basin by Red Sea species. Conversely, the Red Sea, being species-rich and home to well-adapted tropical organisms, presented strong competition for potential Anti-Lessepsian migrants.

In these migrations, the Suez Canal acts as a filtering system for the organisms unable to tolerate salinity changes along the route: from the hypersaline Red Sea (salinity around 43, and up to 60 in certain coastal lagoons), the Suez Canal (≈ 70 after its completion, and progressively decreasing until 45 by 1960), to the Levantine basin (≈ 39). Additionally, the 140 km route presents only a few locations, such as the Great Bitter Lake or Lake Timsah, that can be used as intermediate donor regions throughout their spread (Por, 1971, 1978; Fedele *et al.*, 2022).

The class Scyphozoa experienced similar barriers, with the Mediterranean scyphozoan species being considered rare or with irregular abundances in the Levant Sea (Galil *et al.,* 1990). Consequently, the opening of the Suez Canal and the little competition on the Mediterranean side facilitated the colonization by several Indo-Pacific species, including *Cassiopea andromeda* (Forskål, 1775), *Phyllorhiza punctata* von Lendenfeld, 1884, *Rhopilema nomadica* Galil, 1990 (Galil *et al.,* 1990), *Marivagia stellata* Galil & Gershwin, 2010 (Galil *et al.*, 2010), and *Cotylorhiza erythraea* Stiasny*,* 1920 (Galil *et al.*, 2017). However, establishment rates of scyphozoans were slower compared to the other taxa. In fact, there were not any scyphozoan jellyfish species included among the Lessepsian migrants by the author who coined the term (Por, 1978), to whom the lack of success of the euryhaline *C. andromeda* in colonizing the Mediterranean Sea, after being capable of settling in the Suez Canal, remained unexplained. Por (1978) probably ignored the records of *C. andromeda* in Cyprus (Maas, 1903) and Greece (Schäfer, 1955), but these were anecdotal, and the species did not settle in the Mediterranean Sea until the decades of 1970-1980 in Lebanese waters (Lakkis, 2013). The first documented appearances of *P. punctata* (1965), and *R. nomadica* (1977), though contemporaneous to Por's writings, were only published much later (Galil *et al.,* 1990; Lotan *et al.*, 1994).

The colonization route of the Mediterranean Sea by *R. nomadica* was initially suggested by Daly-Yahia *et al.* (2013) and further developed by Balistreri *et al.* (2017) and Edelist *et al.* (2020). Similarly, the colonization and expansion of *P. punctata* was analyzed by Fernández-Alías *et al.* (2024a). However, a comprehensive analysis of the spread of *C. andromeda* throughout the Mediterranean Sea was still lacking. In this study we compile the records of *C. andromeda* across the Mediterranean Sea, analyze the colonization process, the environmental niche occupied by the species in the Red Sea, Mediterranean Sea, Suez Canal and the Mar Menor coastal lagoon, the westernmost location where juveniles have been found, and discuss the mechanisms that have been involved in its spread.

Material and Methods

Mediterranean biogeography

A biogeography dataset including all the records of *Cassiopea andromeda* from the Mediterranean Sea and the Suez Canal until September 2024 has been constructed by integrating a systematic review on previous literature with the observations registered in jellyfish sightings and general biodiversity databases and those from our monitoring system in Mar Menor (See next section)

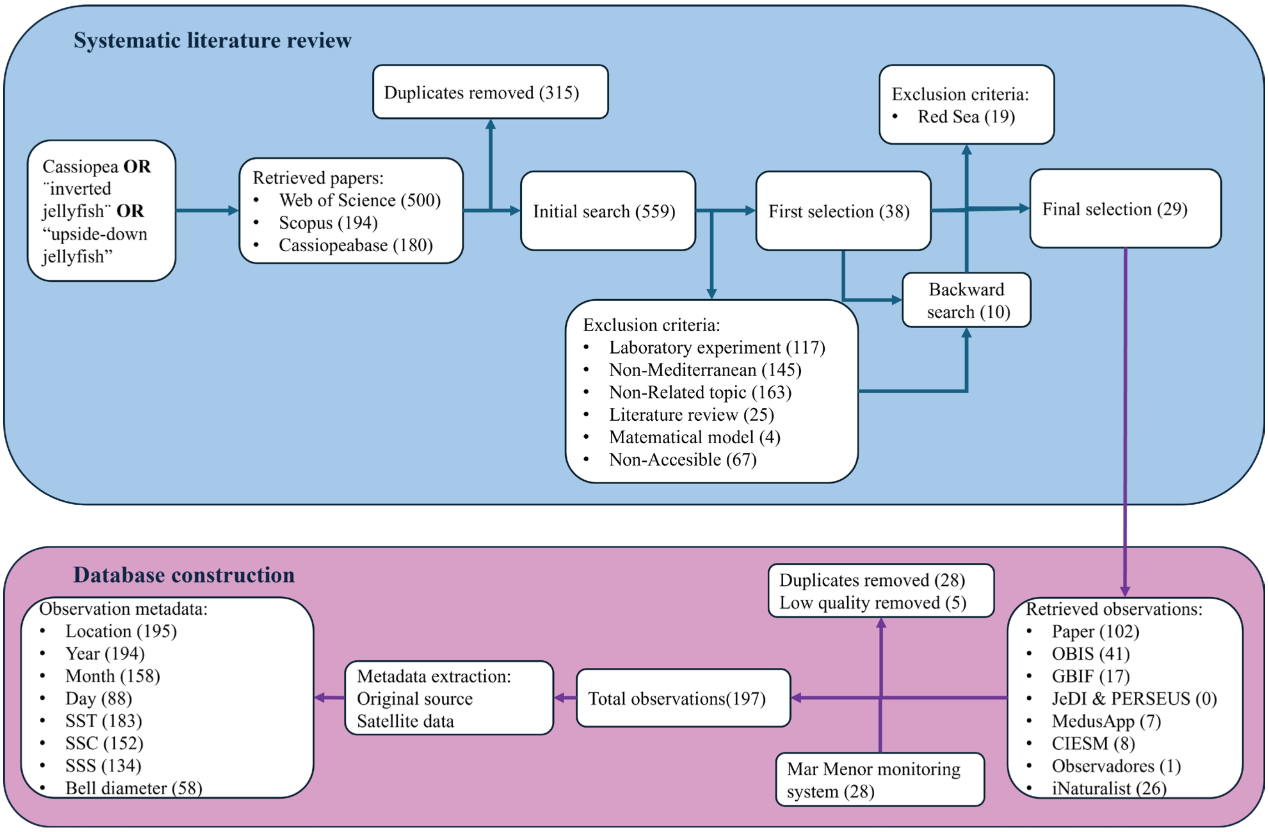

Fig. 1: Methodology overflow for the systematic review and the database construction. The numbers in brackets indicate manuscripts for the systematic review and observations for the database construction.

(Fig. 1). All the articles retrieved through the systematic review as well as the biogeography dataset are provided as Supplementary Information.

Systematic review

The systematic review followed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) methodology (Moher *et al.,* 2009). The search keywords combined with Boolean operators *Cassiopea OR "inverted jellyfish" OR "upside-down jellyfish"* were searched in the professional searching engines SCOPUS and Web of Science (WOS). The search was complemented by adding the papers recorded by CassiopeaBase (https://cassiopeabase.org/, accessed 24th September 2024), a specialized database for the *Cassiopea* genus. The search was conducted on the 24th September 2024, yielding 559 papers after duplicate removal.

During the initial screening, titles, abstracts, and materials and methods sections were analyzed, and the papers were classified into the following categories:

1. Selected: The study area includes the Mediterranean Sea, Suez Canal or Red Sea and the methodology involved specimen collection.
2. Laboratory experiment: The studied individuals were used for animal experimentation, but their origins could not be traced to a specific location.
3. Non-Mediterranean: The origin of the studied individuals could be traced to a specific location, but this was not from the Mediterranean Sea, Suez Canal nor Red Sea.
4. Literature review: The genus *Cassiopea* was involved in the manuscript, but no original observations were included in the paper.
5. Mathematical model: The genus *Cassiopea* was involved in the manuscript, but the mathematical model was constructed without using living organisms with traceable origins.
6. Non-related topic: This category included manuscripts involving scyphozoan genera other than *Cassiopea* or unrelated topics such as the shrub genus *Cassiope* or the constellation *Cassiopeia*.
7. Non-accessible: This includes documents from which no information could be recorded (i.e.,. grant proposals and conference abstracts), manuscripts not accessible from our institution and for which the corresponding author did not provide a reply after a month, and older manuscripts unavailable through SCOPUS, WOS, Google Scholar or the Biodiversity Heritage Library.

To ensure replicability of the systematic review, two authors (AFA and PRP) individually analyzed the papers. In case of discrepancies, the categorization was discussed, and if consensus was not reached, a third co-author provided an opinion.

At the second stage, the *Selected* and the *Literature review* papers were analyzed in detail to identify other record-containing manuscripts not detected by our searching string. The manuscripts with the Red Sea as study or collection area were also analyzed to identify any possible accidental introduction from the native location into the Mediterranean Sea and discarded afterwards. 10 papers were subsequently added through this backward search for a final selection of 29 manuscripts.

Database construction

We have considered three sources for the records: i) contained in a manuscript, ii) contained in an online database, iii) locally collected by our monitoring system. The observations of *C. andromeda* recorded in the main biodiversity and jellyfish datasets: iNaturalist, Ocean Biodiversity of Information System (OBIS), MedusApp, Observadores del Mar, Global Biodiversity Information Facility (GBIF, 2024), Jellyfish Dataset Initiative (JeDI), The Mediterranean Science Commission (CIESM), and The Policy Oriented Marine Environmental Research in the Southern European Seas (PERSEUS), limiting the geographical extent to the Mediterranean Sea and the Suez Canal, were retrieved and manually inspected before their inclusion in the dataset. The observations from the online databases were included either when the record included a picture that allowed identification at least up to genus level or when it had a previous expert validation. Observations from peer-reviewed publications were systematically considered as validated and our own observations were identified as described below. After the removal of duplicates and low-quality observations, we gathered a database with 197 records.

Then, we supplemented the dataset with the sea surface temperature (SST), salinity (SSS), and chlorophyll *a* (SSC) concentration for each observation. Preferentially, these data were collected from the original source and assigned to its associated observation. When not provided, SST, SSS and SSC were assigned based on the monthly average 0.1 degrees satellite data (0.5 for SSS) collected from the NASA Earth Observation (NEO) server (https://neo.gsfc.nasa.gov/ , accessed 30th October 2024). When available, we also collected information regarding the bell diameter of the observed organisms. Environmental parameters of the Mar Menor coastal lagoon were collected *in situ* (See next section). Additionally, we have included two Red Sea records (native location) where SST, SSS and bell diameter were available to compare them with the Mediterranean observations (Lampert *et al.,* 2011; Arossa *et al.*, 2021).

Database analysis

To analyze the spread of *C. andromeda* throughout the Mediterranean basin, we used two methods to calculate the dispersal rate. The first method assumes that a location where *C. andromeda* has been observed acts as a stepping-stone in the colonization process (Eq. 1). The second method, which is more restrictive, requires that at least one re-occurrence in a different year from the original record must be registered for a location to act as a stepping-stone (Eq. 2).

We define the dispersal rate as the distance covered by the species per year. To calculate the distances between the various locations, we constructed a triangular distance matrix using the cosine formula (Eq. 3). Following the factors influencing the dispersal of marine organisms (Carlton, 1996), which have already been demonstrated for scyphozoan jellyfish (Fernández-Alías *et al.,* 2024a), we implemented a rule for equations 1 and 2: the distance between two specific locations must be below the average distance between all locations (1204.66 km). This prevents unrealistic direct connections between easternmost and westernmost locations without the use of intermediate donor regions. Indirect introductions (e.g., ballast waters or hull fouling) are considered in the discussion.

Equation 1.

$$\text{Dispersal rate} = \frac{\text{Distance between locations}}{\text{First occurrence on the receptor} - \text{First occurrence in the donor}}$$

Equation 2.

$$\text{Dispersal rate}' = \frac{\text{Distance between locations}}{\text{First occurrence on the receptor} - \text{First reoccurrence in the donor}}$$

Equation 3.

$$\text{Distance} = \operatorname{acos}(\sin(\text{lat1}) \times \sin(\text{lat2}) + \cos(\text{lat1}) \times \cos(\text{lat2}) \times \cos(\text{lon2}-\text{lon1})) \times 6371$$

(global average Earth radius in km)

These equations allow for the determination of plausible origins of each population, and the locations to which they could be acting as stepping-stone in the dispersal of the species. The definition of the equations implies that possible origin and receptor populations are separated by less than 1204.66 km and either the first occurrence (Eq. 1) or the first reoccurrence (Eq. 2) in the donor location happened before the first appearance of the species in the receptor location. The triangular matrixes providing the results of the three equations between each pair of localities are provided as Supplementary Information.

Mar Menor monitoring system

Study site

The Mar Menor is a Mediterranean coastal lagoon located on the southeast of Spain, covering an area of 136.1 km^2 with an average depth of 4.4 m (Umgiesser *et al.,* 2014). Since the decade of the 1970s, this ecosystem has been exposed to a high degree of anthropogenic pressure, marked by coastal development, the growth of agriculture, and an increase in resident and tourist populations. In terms of ecological functioning, the dredging and widening of El Estacio channel to make it navigable and for harbor construction, and the transition of the agricultural regime from dry farming to irrigated stand out as the two most noticeable factors.

Modification of El Estacio inlet led to a smoothening in the physical conditions (temperature and salinity) and an increase in the water renewal rate. These changes favored the colonization of the ecosystem by a wide variety of organisms. Before the dredging and widening of El Estacio, *Aurelia solida* Browne, 1905 was the only representative of the class Scyphozoa in the Mar Menor coastal lagoon (Pérez-Ruzafa, 1989; Fernández-Alías *et al.,* 2023a), but several colonization events have occurred since. During the late 1970s and early 1980s, *Rhizostoma pulmo* (Macri, 1778) and *Cotylorhiza tuberculata* (Macri, 1778) were observed for the first time in the Mar Menor coastal lagoon, closing their life cycle within the Mar Menor ecosystem and starting to produce regular blooms by 1996 (Pérez-Ruzafa, 1997; Fernández-Alías *et al.,* 2023b). In 2017, *P. punctata* was observed for the first time, closing its life cycle by 2022 (Fernández-Alías *et al.*, 2024a). Also in 2017, *C. andromeda* was first observed in Mar Menor, but the species remained unnoticed until the summer of 2022, then reappeared during the summers of 2023 and 2024.

The change in the agricultural regime led to a higher nutrient input to the coastal lagoon, initiating a process of eutrophication. This process was marked by an initial resilience stage (1970-2016) in which the nutrient input was directed towards the benthic compartment (phanerogams and macroalgae) or removed by the coordinated action of *A. solida, R. pulmo*, and *C. tuberculata.* The medusa populations of the different species segregated in time extending the top-down control over the phytoplankton compartment (Pérez-Ruzafa *et al.*, 2019a; Fernández-Alías *et al.*, 2020). Since 2016, the ecosystem has alternated between jellyfish and phytoplankton blooms, which could also be coupled with hypoxia and mass mortality events if they prevented the light from reaching the bottom of the lagoon (Pérez-Ruzafa *et al.,* 2019a; Fernández-Alías *et al.,* 2022).

Monitoring system

The jellyfish blooms and the ongoing eutrophication event raised social concerns and led to the establishment of a monitoring system that has operated, with variable periodicity, since 1997. The monitoring system records physicochemical and biological parameters including sea surface temperature (SST), sea surface salinity (SSS), sea surface chlorphyll *a* (SSC), and medusa and ephyra abundance among others (see Pérez-Ruzafa *et al.*, (2019a) and Fernández-Alías (2024) for further details on the design and evolution of the monitoring system).

Since 2016, the physicochemical and the medusa stage are fortnightly monitored in a network of 31 stations, separated less than 3 km from each other, with a design including 3 coastal stations (E05', E09', and E12'), 20 stations distributed across the lagoon (E01-E20), 3 placed in front of the inner mouth of the inlets (EN1, ES1, and MA1), and 5 in the adjacent Mediterranean Sea (SPP, EN2, ES2, MA2 and CP) (Fig. 2). SST, SSC, and SSS are measured using a multiparametric probe YSI EXO 2 and averaged for the upper 1.8m of the water column. Medusa abundance is estimated from visual censuses, linearly

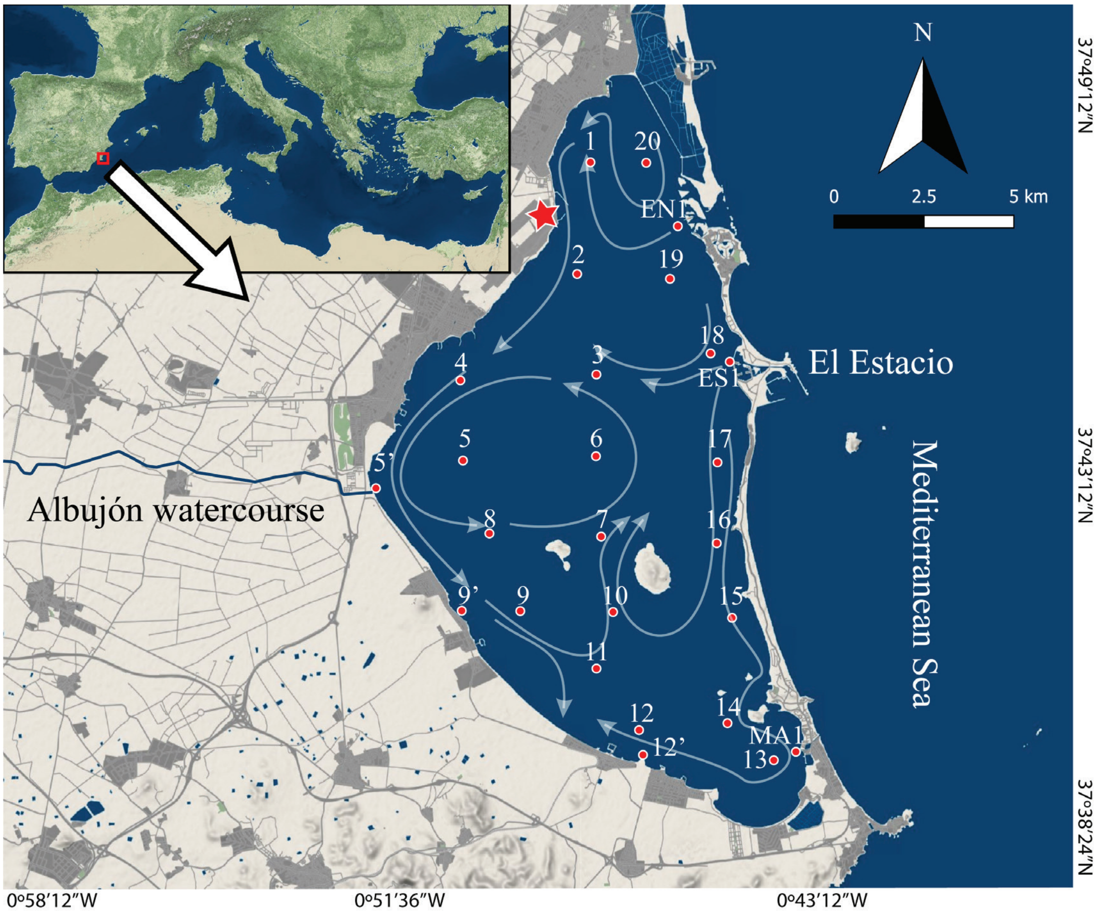

Fig. 2: Monitoring system's sampling stations and main currents of the Mar Menor coastal lagoon.

sailing for 5 minutes, by two operators, one on each side of the boat at 1.5-2.5 knots. The ephyra stage is sampled in all the sampling stations, except the three coastal ones, by means of a horizontal tow of a plankton net (mesh size 500 µm) equipped with a digital flowmeter, at 0.5-2 m depth, for seven minutes. Ephyra sampling is conducted only in the campaign of the first fortnight of each month. Medusa and ephyra abundances are standardized to individuals/100m^3 (ind/100m^3) following the methodology described in Fernández-Alías *et al.* (2020).

Given the benthic distribution of the medusa stage of *C. andromeda*, they are usually undetected through the visual censuses conducted from boat during our regular surveys. To prevent the information gap, we collaborated with the Department of Zoology and Physical Anthropology at the University of Murcia and with the NGO "Asociación Hippocampus". These groups provided observations of the species recorded through their regular coastal net trawls to monitor benthic fish populations (72 net trawls per year since 2015; for further details see Zamora-López *et al.,* 2023 and Guerrero-Gómez *et al.,* 2024) or through their underwater visual censuses (≈100 censuses per year since 2011; for further details see Vivas *et al.,* 2024) respectively. The department of Zoology and Physical Anthropology at University of Murcia provided a single record of a juvenile of the species, 23rd October 2024 at our E14 (Fig. 2), while Asociación Hippocampus provided 2 sightings of juveniles on early July 2023 at our E20. Based on their observations, three dives were done to collect individuals at the medusa stage. These dives occurred on the 6th and 8th of July 2023 (E20) and on the 20th of September 2024 (E19). The regular monitoring campaigns are also complemented by weekly scans of social networks and local newspapers to register any anomalous observation not captured by our monitoring system.

Species identification

A total of 74 individuals were collected using plankton net tows, immediately fixed in formaldehyde-sea water (3% v/v), and transported to the laboratory for their identification. An additional 24 individuals were hand-collected during the dives, measured alive to the closest millimeter, fixed in absolute ethanol, and carried to the laboratory for photography.

The identification of the species was carried out based on the descriptions of Forskål (1775) and Mayer (1910) for the medusa stage and Straehler-Pohl & Jarms (2010) for the ephyra stage. The medusa stage differs from the other scyphozoans registered on the Mar Menor coastal lagoon (Fernández-Alías *et al.,* 2022) in the shape of the umbrella (flat *vs* hemispherical), the presence of milky white spots on the exumbrella, and club shaped vesicles on the oral arms. The ephyra stage differs from the other scyphozoans registered in the ecosystem on the number of marginal lappets (16 to 21 *vs* 8). All the individuals were identified under a dissection microscope, photographed and their bell diameter measured with a digital caliper.

Given the cryptic character of the genus *Cassiopea* and the risk of misidentification (Holland *et al*., 2004; Gamero-Mora *et al*., 2022; Muffett & Miglietta, 2023), we also performed the molecular identification of 5 individuals collected on the 8th July 2023 and 5 individuals collected on the 20th September 2024. DNA extractions were carried out using the kit QIAamp DNA Mini Kit (QIAGEN), following the manufacturer's instructions. The DNA concentration was measured with a NanoDrop2000 Spectrophotometer (Thermo Scientific, Willmington, DE, USA) and adjusted to 10 ng/µl. Two different mitochondrial genetic markers, cytochrome *c* oxidase subunit I (hereafter COI), and ribosome RNA 16S (hereafter 16S), were amplified and sequenced. In both cases, the PCR mixture consisted of 1 µl template DNA, 1x reaction buffer, 0.2mM dNTPs, 0.5 µM primer (forward and reverse), and 0.4U of Taq polymerase (MyTaq DNA polymerase by Bioline). COI was amplified using the primers 'LCO1490-JJ2' and 'HCO2198-JJ2' (Gamero-Mora *et al*., 2022) following the procedure described in Maggio *et al*. (2019). 16S was amplified using the primers 'C&B1' and 'C&B2' (Cunningham & Buss, 1993) following the procedure described in Gamero-Mora *et al*. (2022). The size of the PCR products was checked in an agarose gel (0.8%) and both strains were sequenced at the University of Murcia facilities. Electropherograms were manually inspected and edited using SnapGene (www.snapgene.com). Sequences' identity was confirmed by BLASTn against the nucleotide database (Genbank) of the National Center for Biotechnology Information (NCBI, www.ncbi.nlm.nih.gov) after the entries correction by Muffett & Miglietta (2023). Accession numbers to the sequences deposited on Genbank are PV596173-PV596182 for COI and PV596185-PV596194 for 16S.

To provide further context for the ensembled sequences from this study, we provide an haplotype network with all the available sequences of *C. andromeda*'s 16S and COI genetic markers available for the Mediterranean Sea and the Red Sea at the repositories of Genbank and 'The Barcode of Life Datasystem' (BOLD; https://boldsystems.org/). The retrieved sequences include 20 from Almería, Spain, 8 for COI (Accession numbers: PV533755 - PV533762) and 12 for 16S (Accession numbers: PQ154578 - PQ154589) (Marambio *et al*., unpublished), 9 from Saudi Arabia, 5 for COI (Accession numbers: PQ013077 - PQ013081) and 4 for 16S (Accession numbers: PQ012677 - PQ012680) (Aljbour & Agusti, 2024), and 1 from Egypt (COI; AY319458) (Holland *et al*., 2004). The central Mediterranean Sea is only represented by Palermo, but the sequences obtained by Maggio *et al*. (2019) are not available either in GenBank nor in BOLD and could not be included in the haplotype network. We have also included the 'Florida haplotype' (COI: OP503345; 16S: OP503932; Muffett & Miglietta, 2023) to provide a broader context. The retrieved sequencies, along with the Mar Menor ones were aligned in MEGA7 (Kumar *et al*., 2016) and trimmed to the length of the shortest sequence. The haplotype network was constructed in R using the package 'pegas' (Paradis, 2010).

Results

Mediterranean biogeography

A total of 197 observations of *C. andromeda* have been recorded in the Mediterranean Sea and the Suez Canal (Supplementary Material). The species was observed inside the Suez Canal for the first time in 1886 (Lake Timsah, Egypt). Its expansion followed an east-to-west pathway, with the first observations in the Mediterranean occurring in Cyprus (1903), Greece (1955), Lebanon (1966), Israel (1988), Turkey (2001), Malta (2009), Syria (2012), Italy (2013), Tunisia (2013), Spain (2017) and Libya (2021) (Fig. 3A; Table 1). All the observations were made at shallow depths (0 to 20 m), and 75.63 % of the observations were recorded in semi-enclosed environments (bays, coastal lagoons and harbors) (Supplementary Material).

The representation of the first observation by place alongside reoccurrences suggests that *C. andromeda* has covered the distance between the Suez Canal and the Alboran Sea in three stages, i) Eastern Mediterranean Sea: colonization of the Levantine Sea and the Aegean Sea (1900-2012), ii) Central Mediterranean Sea: colonization of the Ionian Sea, Adriatic Sea, and Tyrrhenian Sea (2013-2016), and iii) Western Mediterranean Sea: trespass of the Balearic basin and arrival to Spain (2017-2024) (Fig. 3B).

The dispersal rate increased throughout the spread of *C. andromeda* across the Mediterranean basin, with peaks of 897.34 km/year (Ancona, Italy, 2023) and 313.11 km/year (Mugla, Turkey, 2012), depending on whether locations are considered to act as stepping-stones at first occurrence or first reoccurrence, respectively (Table 1). Both approaches indicate that the dispersal rate remained below 15 km/year prior to 1980 and below 40 km/year prior to 2000. As expected, the more restrictive equation (Eq. 2) limits the number of stepping-stones and connections between locations. The most noticeable changes are:

- Cyprus reduces its contribution from being a major stepping-stone to having a local effect.
- Malta explained the colonization of Tunisia and Italy when stepping-stones were considered based on the first occurrence of the species. However, this contribution disappears under the restrictive equation.
- The arrival of the species in Malta, northern Italy, Tunisia, and Spain remains unexplained when using the restrictive equation, as no possible origin exists within a 1204.66 km radius.

The restrictive equation reveals a spread pattern consistent with the main currents of the Mediterranean Sea. The key locations acting as major stepping-stones would have been Lake Timsah (Egypt), Beirut (Lebanon), Lake Ölüdeniz (Turkey), Paros Island (Greece), and La Cala, Palermo (Italy). The dispersal rates between these locations are estimated as follows:

- 6.01 to 6.09 km/year (Lake Timsah to Beirut)
- 6.37 to 6.42 km/year (Lake Timsah to Lake Ölüdeniz)
- 18.95 to 21.48 km/year (Beirut to Lake Ölüdeniz)
- 35.41 to 50.58 km/year (Lake Ölüdeniz to Paros Island)

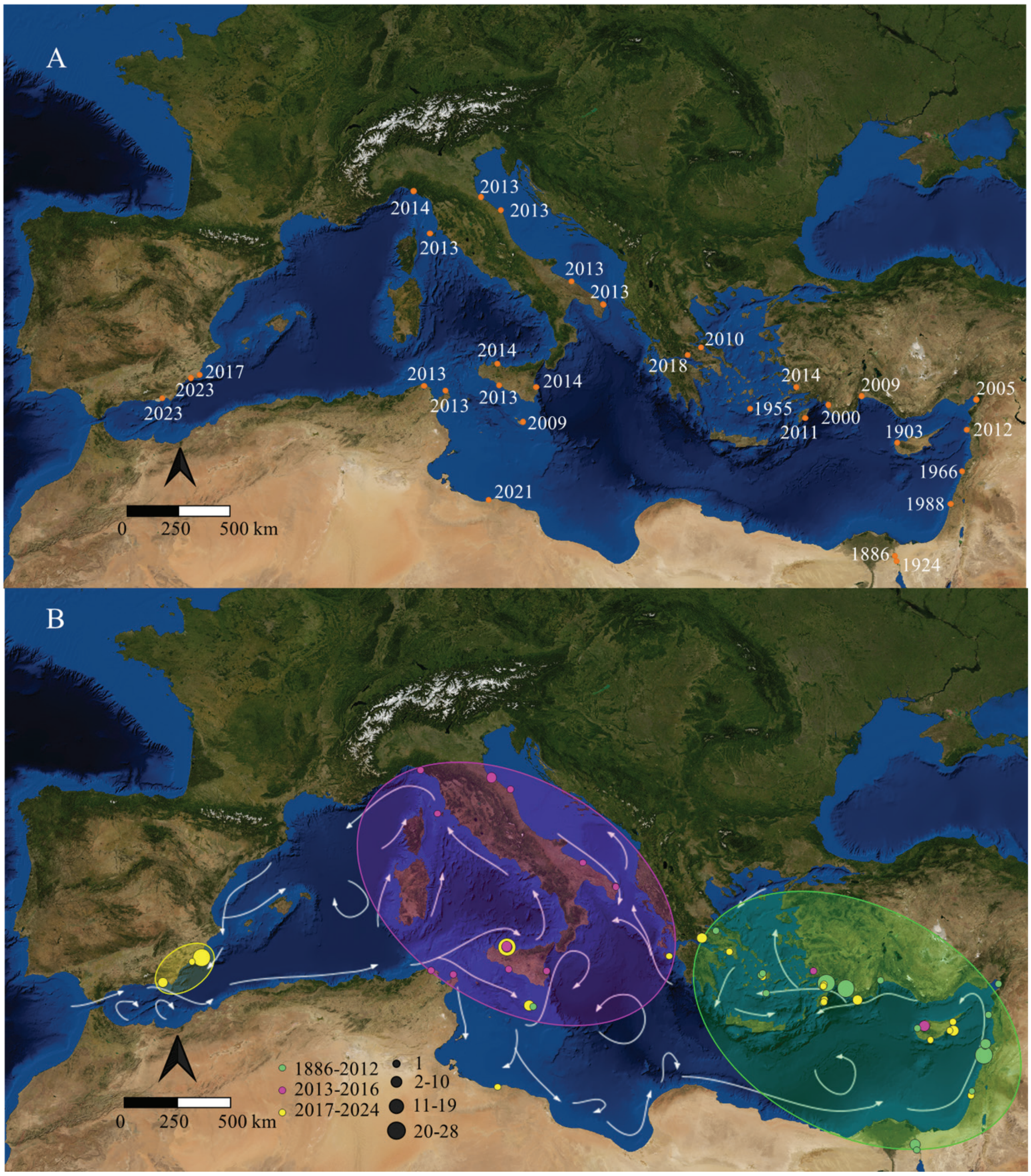

Fig. 3: Mediterranean distribution of *Cassiopea andromeda*. A) Date of the first record by location. B) Number of occurrences by period. White arrows indicate the main currents redrawn from Pascual *et al.* (2017).

- 216.61 to 348.82 km/year (Paros Island to La Cala, Palermo)

Mar Menor monitoring system

The first record of the species within the Mar Menor coastal lagoon corresponds to several individuals (> 10 individuals) with a bell diameter below 1 cm at 4 m depth. It was recorded by the NGO 'Asociación Hippocampus' on the 22nd July 2017 in the proximity of the island El Barón (close to E10 in our monitoring system) (Rubio, 2017). The species remained undetected from the initial observation until the 14th June 2022, when we collected some ephyrae in our monitoring system. Including that date, the ephyra stage has appeared in 23 plankton net tows, with maximum abundances for a sampling station of 2.36 ind/100m^3 in 2022 (E01), 24.01 ind/100m^3 in 2023 (E20), and 3.64 ind/100m^3 in 2024 (E19). The medusa stage has been observed only in four occasions apart from the initial record, one time by seine net trawl (one individual, E13, 23rd October 2024, Guerrero-Gómez pers. comm.), and three times by dive (<1 ind/m^2, Fernández-Alías and Oliver, pers. obs.). All the observations have been recorded close to the communication channels between the two water bodies, in the areas of the coastal lagoon with higher communication with the Mediterranean Sea (Fig. 4). Notably, no sightings of *C. andromeda* have been recorded in the adjacent Mediterranean Sea.

All the records from the Mar Menor coastal lagoon correspond to either ephyrae or early juveniles of *C. andromeda* with bell diameters between 0.82 mm and 2 cm. The ephyrae are characterized by the presence of an average of 17 tuning-fork-like rhopaliar lappets, over 16 spatula-like velar lappets, gastric canals extended to the tip of the lappets, the presence of mouth tentacles, and the inclusion of zooxanthellae (Fig. 5A-J).

The medusa stage is characterized by its flat, circu-

Table 1. Distance covered per year by *Cassiopea andromeda* (dispersal rate) during the colonization of the Mediterranean Sea.

				Stepping-stone at first observation			Stepping-stone at first re-occurrence		
Country	Locality	1st obs	2nd obs	Number of possible origins	Number of possible receptors	Dispersal Rate (km/y)*	Number of possible origins	Number of possible receptors	Dispersal Rate (km/y)*
Egypt	Lake Timsah	1886	1887	0	22	6.60	0	22	6.73
Cyprus	Chrysochou Bay	1903	2013	Lake Timsah	24	5.24	Lake Timsah	10	104.89
Egypt	Great Bitter Lake	1924		2	20	9.21	Lake Timsah	0	-
Greece	Nea Kameni	1955		3	32	14.16	Lake Timsah	0	-
Lebanon	Beirut	1966	1970	4	18	11.04	Lake Timsah	18	12.19
Israel	Neve Yam	1988		5	17	25.70	2a	0	-
Turkey	Lake Ölüdeniz	2000	2003	6	21	38.00	2a	21	56.07
Turkey	Sarsala Bay	2000		6	22	39.94	2a	0	-
Turkey	İskenderun	2005		8	15	77.43	3b	0	-
Malta	San Pawl il-Baħar	2009	2018	Nea Kameni	21	183.13	0	4	152.27
Turkey	Antalya	2009	2021	9	18	136.24	3b	5	270.29
Greece	Paros	2010	2011	11	22	185.38	3b	20	257.29
Greece	South Evoikos	2010		7	27	220.31	Lake Ölüdeniz	0	-
Greece	Rhodes	2011	2021	12	16	210.42	3b	5	237.44
Turkey	Mugla	2011	2012	12	16	208.08	3b	15	313.11
Syria	Latakia port	2012		14	9	106.88	4	0	-
Cyprus	Morphou	2013	2014	15	10	106.55	5	9	72.07
Italy	Bari	2013		8	11	325.88	3d	0	-
Italy	Isle Elba	2013		2	10	298.18	0	0	-
Italy	Lido Rossello	2013		4	9	182.57	Paros	0	-
Italy	Rímini	2013		2	8	349.13	0	0	-
Italy	San Foca	2013		9	11	327.43	3d	0	-
Italy	Settecannoli	2013		4	8	175.94	Paros	0	-
Italy	Torre dell'Orso	2013		9	11	327.29	3d	0	-
Tunisia	Bizerte Bay	2013		2	11	254.83	0	0	-
Tunisia	Haouaria	2013		2	12	226.50	0	0	-
Italy	Augusta	2014		16	6	98.32	2e	0	-
Italy	Genova	2014		10	4	164.93	0	0	-
Italy	La cala, Palermo	2014	2017	12	5	105.69	Paros	5	262.79
Turkey	Asin Bay	2014		20	9	99.70	6	0	-
Cyprus	Protaras	2017	2019	17	7	224.98	7	4	131.11
Spain	Mar Menor	2017	2022	4	2	19.41	0	2	116.47
Cyprus	Iskele	2018		18	4	103.20	7	0	-
Cyprus	Lemescos	2018		18	5	116.70	7	0	-
Greece	Itea	2018	2024	25	6	155.04	6	0	-
Lybia	Janzour	2021		15	3	675.76	2	0	-
Greece	Athens	2022		33	5	639.27	12	0	-
Cyprus	Ayia Napa	2023		22	Sdot Yam	288.58	10	0	-
Greece	Aegeou	2023		26	2	704.63	10	0	-

Continued

Table 1 continued

				Stepping-stone at first observation			Stepping-stone at first re-occurrence		
Country	**Locality**	**1st obs**	**2nd obs**	**Number of possible origins**	**Number of possible receptors**	**Dispersal Rate (km/y)***	**Number of possible origins**	**Number of possible receptors**	**Dispersal Rate (km/y)***
Italy	Ancona	2023		18	Zakynthos	897.34	2e	0	-
Spain	Aguadulce, Almería	2023	2024	3	0		Mar Menor	0	-
Spain	Isla Plana, Murcia	2023		5	0		Mar Menor	0	-
Greece	Zakynthos	2024		31	0		9	0	-
Israel	Sdot Yam	2024		22	0		10	0	-

The number of possible origins and receptors was determined from Eqs. 2 and 3. In cases where only one possible origin or receptor existed, its name has been specified. a: Lake Timsah and Beirut; b: Lake Timsah. Beirut and Lake Ölüdeniz; c: Paros and Mugla; d: Paros. Mugla and Lake Ölüdeniz; e: La Cala and San Pawl il-Baħar; *The dispersal rate is the average distance by year that the species would have had to cover from this location to the possible receptors.

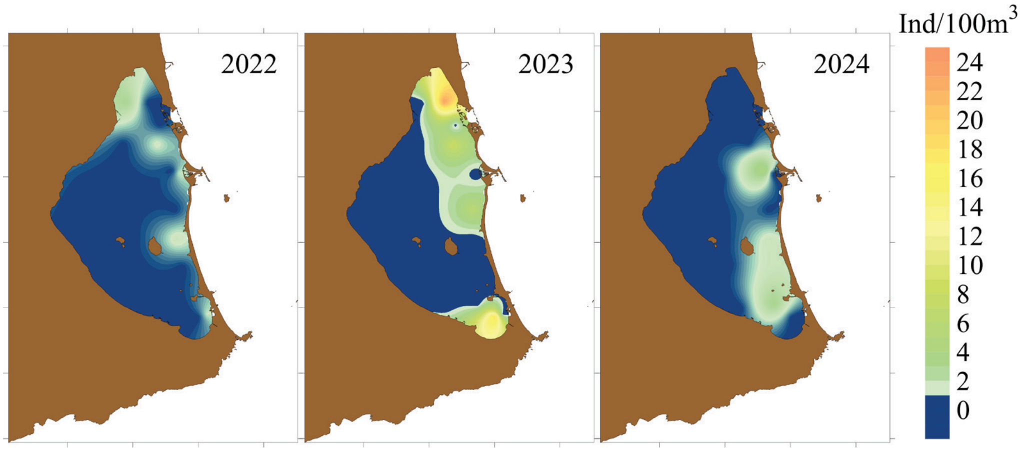

Fig. 4: Horizontal distribution of the ephyra stage of *Cassiopea andromeda* in the Mar Menor coastal lagoon. Represented abundances (individuals/100 m^3) correspond to the maximum observed for each sampling station during the indicated year.

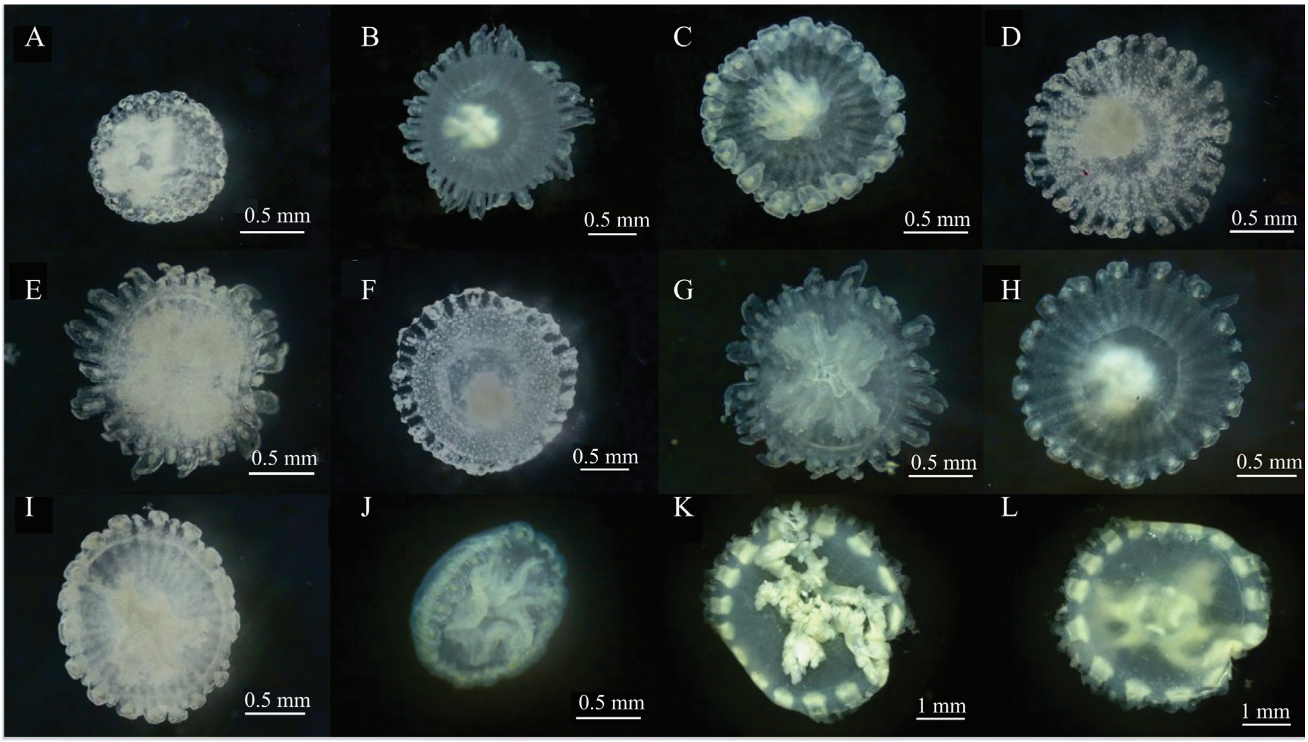

Fig. 5: Ephyra (A-J) and medusa (K-L) stages of *Cassiopea andromeda* collected in the Mar Menor coastal lagoon. Photo credits: Paloma Ramos-Pérez.

lar umbrella, with presence of milk white spots along the edge of the exumbrella, at the base of the rhopalia. The oral arms are flat, and feature club-shaped vesicles hanging from them (Fig. 5K-L).

Mar Menor vs Mediterranean observations

We identified two main differences between our observations from the Mar Menor coastal lagoon and those from other Mediterranean locations. The first one is related to the size of the recorded individuals. In the case of the Mar Menor, all our records correspond to either ephyrae or early juveniles with bell diameters not exceeding 2 cm, sizes only found for the first individuals that were measured in the Mediterranean Sea. In contrast, all the other records from the Mediterranean basin refer to medusae with bell diameters that can reach up to 30 cm (Table 2). However, size data is not reported for most records, being available for only 58 out of the 197 registers from our assembled database, 29 of which correspond to the Mar Menor observations.

The second notable difference is related to the salinity in which the species have been observed. Within the Mar Menor coastal lagoon, *C. andromeda* has been observed in salinities between 40.33 and 47.37 (N = 29), while for the rest of the Mediterranean locations the salinity range of the observations varies from 33.27 to 39.1 (N = 106). The observations from all locations have been made within similar temperature and chlorophyll *a* ranges (Supplementary Material). The scatter plots of temperature *vs* salinity, and salinity *vs* bell diameter highlight the distinction between Mar Menor and Mediterranean observations. The population of the Red Sea develops in conditions analogous to Mar Menor, but the size of the medusae aligns more closely to those from the other Mediterranean locations (Fig. 6).

The haplotype network analysis revealed that there is one dominant haplotype for both genes in the Spanish Mediterranean coast, being it the only one found in the Mar Menor

Table 2. Bell diameter of the different *Cassiopea andromeda* individuals registered across the Mediterranean Sea.

Reference	Date	Country	Bell diameter (cm)
Schäfer (1955)	1955	Greece	0.2 to 3
Lakkis (2013)	1966 – 1987	Lebanon	Up to 20 cm
Çevik *et al.* (2006)	20/07/2005	Turkey	5
Çardak *et al.* (2011)	11/2009	Turkey	8.3
Schembri *et al. (*2010)	20/03/2009	Malta	3 to 11
Gülşahin & Tarkan (2012)	07/2011	Turkey	15 to 28
Özbek & Öztürk (2015)	13 to 18/10/2014	Turkey	2 to 3
De Rinaldis *et al.* (2021)	11/2017 to 12/2017	Italy	13.5 to 17.5
Cilliari *et al.* (2022)	06/2017 to 4/2018	Italy	5 to 20
Rubio (2017)	22/07/2017	Spain	<1
Yokeş *et al.* (2018)	9/01/2018	Malta	2 to 10
Mammone *et al.* (2023)	15/05/2017 to 20/04/2018	Italy	6 to 21.50
Deidun *et al.* (2018)	09/01/2018	Malta	2 to 10
This study	14/06/2022	Spain	0.18 to 0.33
This study	15/06/2022	Spain	0.21
This study	13/07/2022	Spain	0.16
This study	23/08/2022	Spain	0.19
This study	25/08/2022	Spain	0.18
This study	07/07/2023	Spain	0.21 to 0.4
This study	03/05/2023	Spain	0.20
This study	05/06/2023	Spain	0.15 to 0.36
This study	03/07/2023	Spain	0.08 to 0.25
This study	01/08/2023	Spain	0.12 to 0.19
This study	04/06/2024	Spain	0.18 to 0.24
This study	03/07/2024	Spain	0.15 to 0.21
MedusApp	15/08/2024	Spain*	5 to 10
This study	20/09/2024	Spain	0.4 to 2

*Only Spanish location outside the Mar Menor, corresponding to the harbor of Aguadulce (Almería).

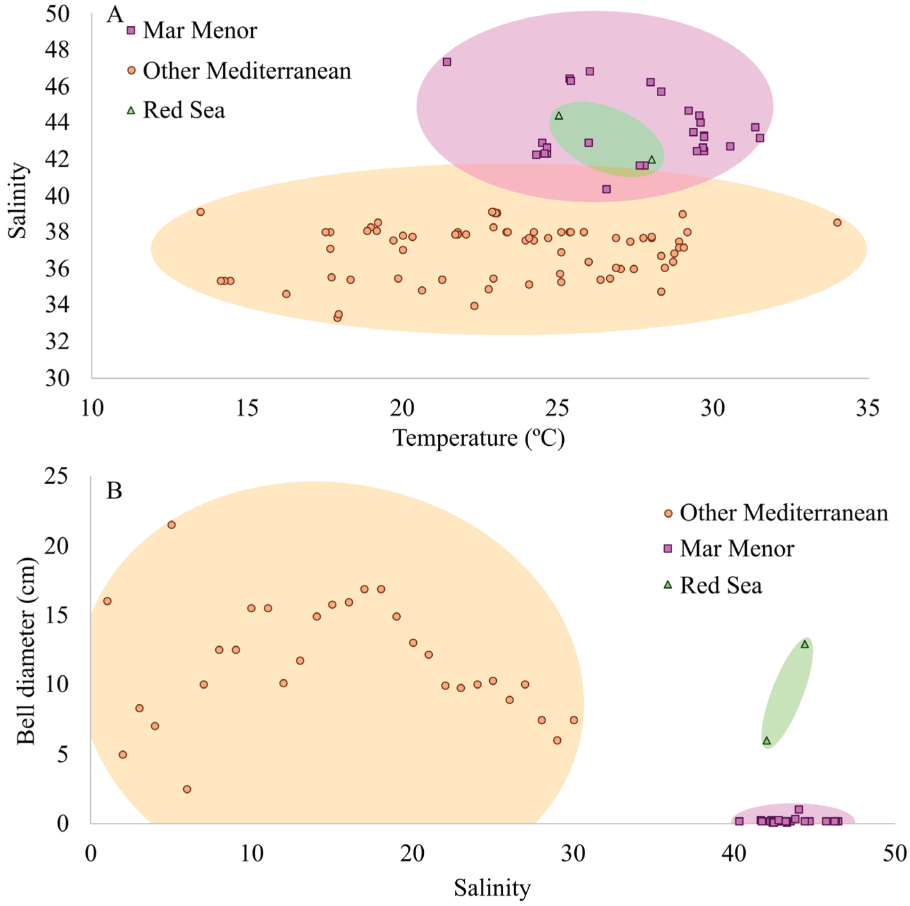

Fig. 6: A: Temperature *vs* salinity scatter plot of the different *Cassiopea andromeda* records across the Mediterranean Sea. B: Salinity *vs* bell diameter scatter plot. Three groups have been represented, i) Mar Menor records, ii) other Mediterranean locations, and iii) Red Sea (native distribution area).

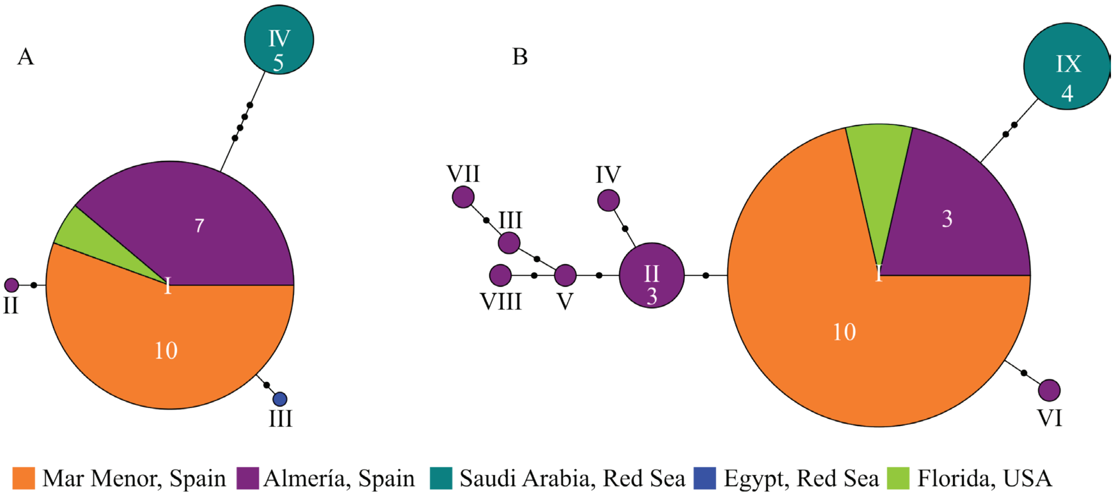

Fig. 7: Haplotype network for *Cassiopea andromeda* within the Mediterranean and Red Seas. A: COI haplotype network; B: 16S haplotype network. Roman numbers identify the haplotype while Arabic numbers indicate the number of sequences for a locality and haplotype.

coastal lagoon, and being coincident with the ‘Florida haplotype’. Considering the whole Spanish Mediterranean coast, other haplotypes were found in Almería, particularly for the 16S gene, where 8 haplotypes were sequenced out of 12 individuals. Red Sea individuals exhibit a single haplotype, separated from the ‘Florida’ and ‘Spanish’ haplotypes by 4 mutations in COI and 2 mutations in 16S (Fig. 7).

Discussion

Expansion across the Mediterranean basin

The first colonization events of the Suez Canal and the Levantine Sea by species of the Red Sea are difficult to be confirmed due to a lack of consistent and organized scientific efforts during the first century after the completion of the canal (Por, 1978). The first works on general biology, with samples taken from 1882 to 1887, reported the entrance of *C. andromeda* from the Red Sea to the Suez Canal, and the presence of this species in Great Bitter Lake and Lake Timsah (Keller, 1888). Although the precise timing of the first introduction event remains unclear, it can reasonably be assumed that the species entered the canal shortly after its construction.

The first stage of the Mediterranean Sea colonization by *C. andromeda*, the settlement on the Levantine Sea, took around one century. This species was first observed at the beginning of the 20th century in Cyprus (Maas, 1903), and half a century later, very young specimens (2 to 30 mm) were reported in Nea Kameni, Greece (Schäfer, 1955). However, those observations were not followed by a re-occurrence in the country until the twenty-first century, suggesting that the species failed to establish itself during initial attempts.

Lebanon became the first location with consistent re-occurrences, with numerous records between 1966 and 1982. These observations were part of a monitoring system by the University of Lebanon conducted between 1965 and 2007 and subsequently uploaded to OBIS, from which we retrieved data on dates and locations. However, we carefully considered these observations since Lakkis (2013), owner of the dataset, consider 1987 as the first observation from Lebanese waters, a record not uploaded to OBIS. Nevertheless, we included earlier records, as by the year 1987, individuals from all sizes, up to 20 cm bell diameter, could be found on Lebanese waters (Lakkis, 2013), indicating a successful settlement on the area. The species then appeared in Israel in 1988 (Galil *et al.* 1990), and in Turkey, where several populations established early in the twenty-first century (Özgür & Öztürk, 2008; Gülşahin & Tarkan, 2012; Gülşahin *et al.,* 2016).

The colonization process accelerated in the later part of the first stage and during the second dispersal period, with the species spreading between Turkey, Greece and the Central Mediterranean Sea at rates that can largely exceed 100 km/year (Table 1). In the Central Mediterranean Sea, blooms of *C. andromeda* have been reported in Tunisia (Ounifi-Ben Amor *et al.,* 2015), Malta (Schembri *et al.,* 2010; Deidun *et al.,* 2018) and Italy, where several studies, including the genetic identification of the species, have been carried out on Palermo's population (Cillari *et al.,* 2018, 2022; Maggio *et al.,* 2019; De Rinaldis *et al.,* 2021; De Domenico *et al.,* 2025). The settlement on the Eastern and Central Mediterranean Sea is further confirmed by the appearance of the species in other Mediterranean countries such as Syria (Siokou *et al.,* 2013) and Lybia (Crocetta *et al.,* 2021), and re-occurrences in previously colonized countries (Katsanevakis, 2011; Zenetos *et al.,* 2011; Özbek & Öztürk, 2015; Mammone *et al.,* 2023).

The final dispersal stage, the arrival to the Western Mediterranean, particularly to the Spanish coast and the Mar Menor coastal lagoon, began in 2017. We are inclined to think that Italy, and particularly Palermo, where there is a settled population of the species, is likely to have acted as a stepping stone in the process. However, the lack of sequences from the Central Mediterranean Sea (those produced by Maggio *et al.* (2019) are unavailable in online repositories), and the shared haplotype between Spain and Florida's coastal waters suggest some uncertainties about the origin of this population (Fig. 7). In any case, the arrival of the species to this location seems to have necessarily occurred by ship transportation as no intermediate donor region appears when re-occurrences and a maximum distance between locations are considered a requirement for two locations to be connected (Table 1).

The three periods we propose are distinguished by different dispersal rates: a slow initial entrance to the Mediterranean, followed by a rapid expansion, and difficulties achieving the adult size in the Mar Menor coastal lagoon (Tables 1, 2). To analyze the plausible dispersal vectors allowing the current distribution of the species within the Mediterranean basin we should consider its limited swimming capabilities and duration of each life stage. The polyp (sessile and benthonic) and the medusa (semi-sessile and benthonic) are unlikely to play significant roles in dispersal by their own means. For the planula and the ephyra stages, *Cassiopea* spp. planulae got a swim speed of 0.15 cm/s (Fitt & Hofmann, 2020), and those scyphozoan planulae settle during the first 10 days after being released (Gambill *et al.,* 2018). Rhizostomeae ephyra swim, on average, at 0.8 cm/s (von Montfort *et al.,* 2023) and remain in the water column, before reaching the medusa phase, from 10 to 60 days (Fernández-Alías *et al.,* 2023b).

Under ideal conditions (negligible current effects and perfectly directed swimming), the maximum dispersal distance would be 42.8 km/year (1.3 km as a planula and 41.5 km as an ephyra). This estimate falls well short of the distances the species must have covered annually after the first dispersal phase (Table 1). Therefore, only small-scale movements can be achieved by the own means of the species, while its spread throughout the basin likely resulted from a synergistic interaction between its swimming capabilities, ocean currents, and anthropogenic vectors. This is further supported by the lack of plausible origins to the records of Malta, north Italy, Tunisia, and Spain when at least one re-occurrence is considered necessary for a location to act as a stepping-stone (Table 1).

Dispersal factors throughout the Mediterranean Sea colonization

Sheltered ecosystems, harbors, and ship transport

The most commonly reported anthropogenic vectors for the expansion of scyphozoan jellyfish include ship-transportation, the opening of new shipping channels, and aquarium trade (Graham & Bayha, 2007; Bayha & Graham, 2014). For the genus *Cassiopea,* all the proposed factors contribute to explaining its current distribution, and some of them have already been demonstrated or proposed for the Mediterranean basin. The construction of the Suez Canal is the primary reason for its arrival in the Mediterranean Sea (Galil *et al.,* 1990). *Cassiopea* was the first genus of the class Scyphozoa to be widely available for its aquarium exhibition (Lange & Keiser, 1995). Additionally, the 'live rock' commerce can be a threat for the spread of the upside-down jellyfish in case of mismanagement (Bolton & Graham, 2006), and its display in the Malta aquarium has been proposed as a plausible reason for the first reappearance of *C. andromeda* in this country (Deidun *et al.*, 2018). Ship-transportation, both by hull fouling or ballast water, has been the proposed vector for the arrival of the genus to Hawaii, USA (Holland *et al.,* 2004; Graham & Bayha, 2007) and, while it has already been proposed as a spread vector within the Mediterranean Sea (Özgür & Öztürk, 2008), we prove here for the first time that it should have acted synergistically with *C. andromeda* natural dispersal capabilities. Furthermore, its presence in harbors and their surrounding area also suggests that ship-transportation has acted in shaping its distribution in the Mediterranean Sea.

Indeed, our systematic review shows that sheltered or semi-sheltered environments account for most of the records (75.63% with all records included, up to 87.65% excluding the ones we suggested to consider cautiously). This pattern is not exclusive from the Mediterranean Sea, as the native habitats for all the species of the genus *Cassiopea* are coastal lagoons, mangroves and, in general, sheltered shallow water ecosystems, and so are the locations colonized by species from the genus in Atlantic waters (Holland *et al*., 2004; Graham & Bayha, 2007; Morandini *et al*., 2017; Muffett & Miglietta, 2023). It is also important to notice that all the records we have collected have been made at warm temperatures and low chlorophyll *a* concentration (Fig. 6; Supplementary material) and, considering that the species from the *Cassiopea* genus are tropical and host zooxanthellae, the conditions for its development are also more likely to appear in sheltered shallow waters. Moreover, sheltered environments have been proved as suitable stepping-stones for the spread of other scyphozoan species within the Mediterranean Sea (Fernández-Alías *et al*., 2024a). This can be related with the productivity of these ecosystems, the scarcity of adult jellyfish predators, and the high level of ship connection between them.

The role of salinity

In addition to these traditional factors, salinity could have had a role modulating the species' dispersal across the Mediterranean basin. Salinity is known to affect the distribution and abundance of scyphozoan jellyfish species (Stone *et al.,* 2019; Fernández-Alías *et al*., 2021) by increasing the mortality rate at all life stages, reducing strobilation and asexual reproduction or causing abnormal development (Fernández-Alías *et al*., 2024b), but it has not been extensively studied for the *Cassiopea* genus.

Fitt *et al.* (1987), one of the few studies comparing the effect of different salinities on *C. andromeda*, evaluated the polyp formation from either axenic buds or planulae from the Red Sea population under three different scenarios: autoclaved Red Sea water (salinity of 43), autoclaved North Sea water (≈30), and artificial sea water (30 for bud experiments and 41 for planulae experiments). Fitt *et al.* (1987) obtained polyps only in the Red Sea water for the bud experiment and got a better performance under this condition for the planula experiment. The authors attributed these results to a thermostable compound naturally present in Red Sea water but surprisingly did not consider salinity as a factor, despite sodium chloride (NaCl) being a thermostable compound that varied among treatments.

To our knowledge, the effect of salinity in the ephyra development in *C. andromeda* remains unstudied despite its potential to act as a critical bottleneck in the scyphozoan life cycle (Fernández-Alías *et al.,* 2024b). In this line, our review allows us to hypothesize that salinity might induce stress for the ephyra and juvenile of *C. andromeda*. The species was one of the first to colonize the Suez Canal from the Red Sea (Por, 1978), but the process came to a temporary halt before settling in Lebanese waters a century later (Lakkis, 2013). Salinity in the Red Sea, in the locations where *C. andromeda* is found, exceeds 40 (Por, 1978; Lampert *et al.* 2011; Arossa *et al.,* 2021), and is in the same range as those within the Suez Canal, including Lake Timsah and Great Bitter Lake (Por, 1978). However, all the observations from the Mediterranean Sea, excluding those from the Mar Menor coastal lagoon, have been made at salinities below this threshold (Fig. 6). This osmotic stress could have been the reason for the lack of development of juveniles in Nea Kameni (Greece) during the first colonization attempts of the Mediterranean Sea by *C. andromeda* (Schäfer, 1955). Given that the process accelerated on the last decade of the 20th century and early in the 21st century, we suggest that a bottleneck occurred in the first stages of the colonization of the Mediterranean Sea, leading to a Mediterranean population better adapted to salinities below 40.

In the Mar Menor coastal lagoon, where the salinity also exceeds 40, even if re-occurrences have been registered, the species is still classified as a marine straggler *sensu* Pérez-Ruzafa *et al.* (2019b) as it is incapable of reaching an adult stage and sexually reproduce in the ecosystem. Indeed, observations in the Mar Menor have exclusively involved ephyrae or early juveniles with bell diameters not exceeding 2 cm (Figs. 5, 6). Nonetheless, the colonization process follows the typical pattern for a coastal lagoon, with initial observations occurring near channels where Mediterranean and lagoon waters mix (Fig. 4) (Sala-Mirete *et al.,* 2023a, b; Fernández-Alías *et al.,* 2024a). The existence of a single haplotype within the ecosystem might indicate that the population could be facing, in this particular location, an opposite effect that only allows to survive the scarce Mediterranean haplotypes that can still stand high salinity conditions, but this cannot be ascertained given the randomness of colonization processes (Pérez-Ruzafa *et al*., 2019b) and the sharing of haplotypes with distant populations such as the one from Florida (Muffett & Miglietta, 2023).

Over time, the original bottleneck effect we suggest may have selected alleles better suited for Mediterranean salinities, enabling the species to spread throughout the basin. This bottleneck would also explain why *C. andromeda* from the Mediterranean Sea is not capable of successfully colonizing high salinity ecosystems like the Maltese saltmarshes (Deidun *et al.,* 2018) or the Mar Menor coastal lagoon, despite these salinities falling within its natural range. Further studies on genetic connectivity across the Red Sea, Suez Canal, and Mediterranean Sea, along with bottleneck studies, and early stages laboratory experiments are required to confirm the role of salinity as modulator of the dispersal speed. So far, the change in the salinity conditions between the colonized ecosystems has been marked by a clear pattern: i) lack of development of the ephyra and juvenile specimens, and ii) delay in the colonization process when compared to with ecosystems with different salinities or to other invasive scyphozoan species (Fernández-Alías *et al.,* 2024a).

It is also worth noting that *C. andromeda* is mainly a coastal lagoon species. These ecosystems model the genetic and epigenetic characteristics of the species throughout the colonization processes as to optimize their biological strategies (Pérez-Ruzafa *et al.*, 2013). Coastal lagoons often exhibit exclusive haplotypes or rare alleles in higher proportion than the open sea, eventually leading to local adaptations (Vergara-Chen *et al.,* 2010, 2013; Pérez-Ruzafa *et al.,* 2019b). Such was the case of *Holothuria (Roweothuria) poli* Delle Chiaje, 1824 in the Mar Menor coastal lagoon, where a local population adapted to salinities of 42 to 46 could not survive within its own native Mediterranean salinity range of 37 to 39 (Pérez-Ruzafa *et al.,* 2019b). Consequently, we suggest that, after a bottleneck occurred in the first stages of the colonization of the Mediterranean Sea, the Mediterranean population is better adapted to salinities below 40, and facing difficulties to colonize hypersaline ecosystems, despite these being analogous to their native conditions.

Conclusion

The colonization of the Mediterranean basin by *Cassiopea andromeda* illustrates a polyhedric invasion process driven by a combination of natural dispersal, anthropogenic vectors, and environmental constraints. The historical review of its spread shows a progression from a slow initial settlement in the Eastern Mediterranean to a quick dispersal across the basin modulated by local ecological conditions. Salinity could have acted as a factor modulating the species' life cycle, with osmotic stress delaying its establishment in both hypersaline and hyposaline environments. This pattern is exemplified by its limited development in the Mar Menor coastal lagoon, where *C. andromeda* fails to reach adult stages despite multiple reoccurrences. The findings emphasize the importance of understanding the physiological and genetic responses of invasive species to environmental stressors. Future research should focus on the genetic connectivity between populations in the Red Sea, Suez Canal, and Mediterranean Sea, and stress experiments on distinct origin of polyp, ephyra and juvenile populations to better understand the role of bottlenecks and local adaptations in shaping invasion dynamics.

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Statements and Declarations

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Supplementary Data

The following supplementary information is available online for the article:
The retrieved and selected papers and *Cassiopea andromeda* records obtained using the PRISMA approach, the biogeography dataset analyzed in the manuscript, and the triangular matrices resulting from the application of equations 1 to 3.