



Mediterranean biogeography, colonization, expansion, phenology, and life cycle of the invasive jellyfish *Phyllorhiza punctata* von Lendenfeld, 1884

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ABSTRACT

There is a widespread belief concerning the increase in the number and intensity of jellyfish blooms, which is partly attributed to the expansion of species that form these blooms. However, the mechanisms of spread for these invasive species beyond human-mediated transportation are still not well understood. In this study, we have compiled a comprehensive dataset of Mediterranean Sea records (1965–2022) for the invasive, bloom-forming species *Phyllorhiza punctata* von Lendenfeld, 1884, in order to illustrate its spread throughout the Mediterranean basin, the role of coastal lagoons as stepping stones in this process, and its life cycle within Mediterranean waters. The first detection of *P. punctata* in the Mediterranean Sea dates back to 1965, but detections from the 20th century are scarce and widely spaced in time. Since the beginning of the 21st century, the species has spread across nearly the entire Mediterranean Sea. We have identified focal points of expansion in specific semi-enclosed environments such as coastal lagoons or embayments, which act as stepping stones in the colonization process. *P. punctata* rapidly colonizes these semi-enclosed environments within a short period of time. On a larger spatial scale, an approximate four-year interval is observed between different focal points of expansion. Moreover, in the Mar Menor coastal lagoon in Spain, the presence of a long-term monitoring system has allowed for a description of the colonization and spread mechanisms from the initial observation until the first exportation of individuals to the Mediterranean Sea. The seasonality of *P. punctata* populations remains consistent across the Mediterranean Sea, with the ephyrae being released after the increase in sea surface temperature in spring, and the medusae remaining in the water column from mid-summer until late autumn or early winter.

1. Introduction

The seasonality of jellyfish species, with regular, and yet unpredictable, massive blooms has arisen an increasing interest towards jellyfish blooms and bloom forming species (Pitt et al., 2018; Fernández-Alfías et al., 2021). Despite considering that, in certain ecosystems and conditions, jellyfish dynamics can help on the water quality maintenance (Pérez-Ruzafa et al., 2002; Fernández-Alfías et al., 2020, 2022), jellyfish blooms are generally considered a disturbance to human activities (Purcell et al., 2007). There is a general belief regarding the increase in number and intensity of the jellyfish blooms that is partly promoted by the expansion of the jellyfish bloom forming species, such as *Phyllorhiza punctata* von Lendenfeld (1884); Purcell et al. (2007); Richardson et al. (2009). Expanding their distribution range requires jellyfish species to reach suitable settlement areas within the limited

time of the pelagic phase (Dawson et al., 2005). Those areas might be spaced beyond their swimming capacities and different translocation vectors have been proposed to cover the gaps between colonized areas, including translocation through ballast water (ephyrae and medusae), hull-fouling organisms (benthic polyps and cysts), aquarium trade, or the opening of communication channels (Graham and Bayha, 2008; Purcell et al., 2007; Richardson et al., 2009; Duarte et al., 2013; Bayha and Graham, 2014; Killi et al., 2020).

The Mediterranean Sea is a biodiversity hotspot, but also a sensitive confined environment facing challenges such as habitat degradation, climate change, and biodiversity and community composition changes (Dailianis et al., 2016). In terms of jellyfish colonization, 13.5% of the total jellyfish species detected in the Mediterranean Sea are non-native, being the percentage of non-native scyphozoan detected species greatly superior (Killi et al., 2020). Within the phylum Cnidaria, the bloom

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forming species are concentrated in the class Scyphozoa (Hammer and Dawson, 2009), which also accounts, in general terms, for a higher invasiveness risk in the Mediterranean Sea (Killi et al., 2020). As mentioned above, ship translocation has been proposed as an important vector for the expansion of jellyfish species (Purcell et al., 2007; Richardson et al., 2009), posing confined environments such as harbours or coastal lagoons as primary colonization sites. Due to their environmental characteristics, these confined environments are also among the most suitable habitats to host jellyfish blooms (Fernández-Álías et al., 2021). Therefore, it is not surprising that *P. punctata*, a bloom-forming jellyfish species found in coastal lagoons (Rippingale and Kelly, 1995), accounts for one of the highest risks of invasiveness in the Mediterranean Sea (Killi et al., 2020).

The type location of *P. punctata* is Port Jackson, Australia (von Lendenfeld, 1884), and its 'native' distribution range is considered to be the Indo-Pacific, including Australian coastal lagoons, the Philippines archipelago, and Thailand (Rippingale and Kelly, 1995; Graham et al., 2003). During the 20th century, this species expanded its distribution range being successful in reaching and invading eastern Pacific (Larson and Arneson, 1990), trespassing the Panama Canal to colonize tropical Atlantic waters (García, 1990), and the Gulf of Mexico (Graham et al., 2003). The first detection of *P. punctata* in the Mediterranean Sea dates from the year 1965 in the coast of Israel (Galil et al., 1990). Before the beginning of the 21st century, only this, and a second observation in Egypt in 1986 (Atta, 1991), were performed, but since the year 2005, a spread of the species throughout the Mediterranean Sea has been reported (Abad-Navandi and Kikinger, 2007; Galil et al., 2009; Madkour et al., 2021; Kaminas et al., 2022). While an arrival of *P. punctata* to the Mediterranean Sea by ship through the Suez Canal seems clear (Mizrahi et al., 2021), the mechanisms for its expansion remain undescribed. Moreover, previous studies addressing the Mediterranean biogeography of *P. punctata* are incomplete given the absence of a detailed, systematic review of the previous literature or the neglect collection of the observations deposited on the main biodiversity and jellyfish databases (Madkour et al., 2021; Kaminas et al., 2022).

In this work we provide the detailed colonization process of *P. punctata* in the Mar Menor, a southwestern Mediterranean coastal lagoon, from its first detection until its life cycle closure. We also perform a systematic review of the distribution of this species in the Mediterranean Sea based both on literature and jellyfish databases, suggest a mechanism for its expansion throughout the Mediterranean basin, and reconstruct its life cycle by complementing the previous observations on the benthic stages with field observations, thermal niche calculation, and growth parameters modeling.

2. Material and methods

2.1. Mediterranean biogeography

A biogeography dataset gathering all the existing observations of *P. punctata* within the Mediterranean Sea and its margins (Red Sea and Gulf of Cadiz) until December 2022 has been elaborated. To develop it, an adaptation of PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analysis) (Moher et al., 2009) has been carried out by combining searches in scientific papers and jellyfish sighting databases. The search algorithm (Phyllorhiza OR "spotted jellyfish" OR "australian jellyfish" OR "spotted australian jellyfish") was used in SCOPUS and Web of Science (WOS) databases yielding 70 and 71 results respectively. 87 papers were kept after the removal of duplicates. The papers were selected under two inclusion criteria: i) the study place is located within the Mediterranean Sea or its margins (Gulf of Cadiz and Red Sea), and ii) sightings of the spotted Australian jellyfish are provided. A total of 15 papers met both criteria.

SCOPUS and WOS search algorithms provide the papers for which the term is included in the categories 'Abstract', 'Title' and 'Keywords'. On the contrary, Google Scholar performs the search on those categories

and the main text, but it can also provide papers that do not include the term used for the searching algorithm but terms that are considered synonyms, or related results. This searching engine does not have enough precision to be used alone in systematic reviews, but it can be a great addition to professional searching engines (Boeker et al., 2013; Haddaway et al., 2015). Therefore, an additional search on that platform under the algorithm ("Phyllorhiza punctata" AND "Mediterranean") was performed. This search yielded 700 papers, from which only 6 were finally selected, under the criteria described above, for their inclusion in the dataset. The observations provided from those 21 papers were extracted.

The observations of *P. punctata* recorded in the main biodiversity and jellyfish datasets (Jellyfish Dataset Initiative (JeDI), Ocean Biodiversity of Information System (OBIS), Global Biodiversity Information Facility (GBIF), MedusApp, JellyWatch, Observadores del Mar, The Mediterranean Science Commission (CIESM), The Policy Oriented Marine Environmental Research in the Southern European Seas (PERSEUS), Jellyfish Sightings Along the Italian Coast 2009–2017, and the Informative Campaign on the Presence of Jellyfishes along the Valencia Community Coast (2010–2021), limiting the geographical extent to the Mediterranean Sea and its margins, were retrieved and manually inspected before their inclusion in the dataset. Finally, we supplemented the dataset with our observations from the Mar Menor monitoring system described below and removed duplicated observations. When provided, sea surface temperature (SST), salinity (SSS), and chlorophyll *a* (SSC) concentration were collected from the original source and assigned to its associated observation. When not provided, SST and SSC were assigned based on the monthly average 0.1° satellite data collected from the NASA Earth Observation (NEO) server (<https://neo.gsfc.nasa.gov/>, accessed 16th February 2024). Environmental parameters of the Mar Menor coastal lagoon were collected *in situ*.

To depict the expansion of *P. punctata* inside the Mediterranean Sea, the yearly isolines of expansion have been calculated from the year of the first observation in each location with the kriging method in Surfer software. Finally, to provide insights into the ecology of *P. punctata*, the selected papers were screened in search of indications of the presence of symbiotic zooxanthellae in the detected individuals. When it is not indicated in the text, but a picture is provided, the absence of colour to dark brown scale of zooxanthella concentration described in Bolton and Graham (2004) is used to assign a categorical presence/absence of zooxanthellae in the different populations (Table S1).

2.2. Mar Menor monitoring system

The Mar Menor is a hypersaline coastal lagoon, located on the southeast coast of Spain, with a total surface of 136.1 km², and an average depth of 4.4 m. This ecosystem has been exposed to increasing anthropic pressure, enhanced since the 1970s, and characterized by an increase in the resident and temporal (tourism) population, coastal development, and high input of nutrients. The two main modifications in terms of ecological functioning are the change of the agricultural regime from dry farming to irrigated, and the dredging and widening of El Estacio channel (Pérez-Ruzafa et al., 1991, 2005a, 2005b). The transition in the agricultural regime led to an ongoing eutrophication process marked by frequent dystrophic crises since the year 2016 (Pérez-Ruzafa et al., 2019a; Fernández-Álías et al., 2022). The modification of the inlet resulted in smoother temperature and salinity conditions, increased the water exchange between the Mediterranean Sea and the Mar Menor coastal lagoon, and enabled the colonization of the lagoon by numerous species. In the case of the class Scyphozoa, *Rhizostoma pulmo* (Macri, 1778) and *Cotylorhiza tuberculata* (Macri, 1778) were registered for the first time in the ecosystem in 1979 and 1980 respectively, and by the year 1996 both species had closed their life cycle inside the lagoon and had started to bloom regularly (Pérez-Ruzafa, 1989, 1996, 1997).

The simultaneous occurrence of eutrophication and jellyfish blooms

led to the establishment of a monitoring system that has operated, with variable periodicity, in different periods since 1997 (see Pérez-Ruzafa et al. (2002, 2005a; 2019a) for further details on the evolution of the monitoring system). Since 2016, a network of 31 sampling stations has been biweekly monitored with a design that includes 26 stations inside the lagoon (20 in the middle of the lagoon, 3 coastal stations, and 3 in the inner part of the inlets), and 5 in the Mediterranean Sea (3 in the outer part of the inlets, and 2 as control stations to the north and south of the Mar Menor) (Fig. 1). During each sampling event at each station, biological and environmental parameters were measured. Sea surface temperature (SST), salinity (SSS), and chlorophyll *a* concentration (SSC) were measured using a multiparametric probe YSI EXO 2 and averaged for the upper 1.8 m of the water column. Medusa abundance was estimated from visual censuses, linearly sailing for 5 min, by two operators, one on each side of the boat at 1.5–2.5 knots. Medusa individuals were sorted into ten size classes based on their umbrella diameter, with 5 cm intervals from 0–5 cm to 45–50 cm. The ephyra stage was collected using a horizontally towed plankton net (500 μm mesh size) for 7 min equipped with a digital flowmeter with a monthly periodicity, coincident with the campaign of the first fortnight of the month. We have considered the individuals collected by the plankton net to be in the ephyra stage when the diameter of the disk was below 2 cm, and before a

complete fusion of the rhopalial lappets and the development of the oral arms have occurred (Rippingale and Kelly, 1995; von Montfort et al., 2023). All the individuals in the ephyra stage were sorted into a single class. Medusa and ephyra abundances were standardized to individuals/100 m^3 (ind/100 m^3) following the methodology described in Fernández-Álías et al. (2020). This study presents the environmental and biological data collected from January 2021 to December 2022, the period in which *P. punctata* closed its life cycle inside the coastal lagoon. In August 2021, to capture the development of a dystrophic crisis (Fernández-Álías et al., 2022), an additional sampling campaign was conducted and the ephyra stage was collected in both fortnights. In August 2022, following the first bloom of *P. punctata* within the ecosystem, ephyra collection was carried out in both sampling campaigns.

2.3. Life cycle: pelagic stages

2.3.1. Growth and mortality

The growth of *P. punctata* through the year 2022 in the Mar Menor coastal lagoon was determined using the length frequency dataset and the Von Bertalanffy Growth Function (VBGF) (Bertalanffy, 1938). The VBGF is expressed as (Eq.1) $L(t) = L_{\infty}(1 - e^{-K(t-t_0)})$, where: $L(t)$ represents

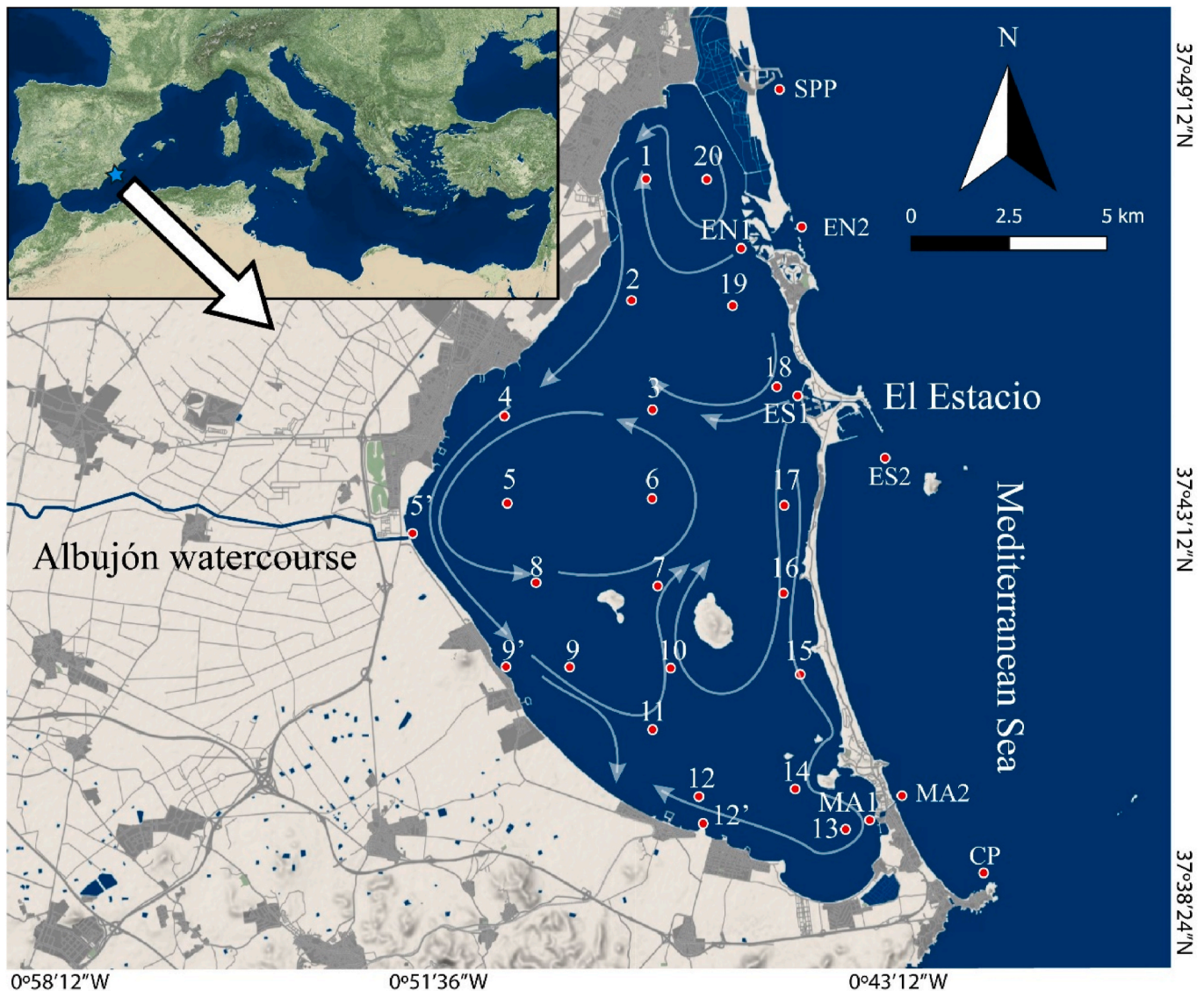


Fig. 1. Monitoring system's sampling stations and main currents of the Mar Menor coastal lagoon.

the length at a certain age (cm), L_∞ is the asymptotic length (cm), K is growth rate (year^{-1}), t is the age (year), and t_0 is the theoretical age at length 0.

The calculation of the growth and mortality parameters was performed using the Electronic Length Frequency Analysis (ELEFAN) method (Brey and Pauly, 1986) implemented in the ‘TropfishR’ package (Mildenberger et al., 2017) in R software (R Development Core Team, 2011). The theoretical age at length 0, t_0 , is a mathematical artefact used to improve the curve fitting (Moreau, 1987). It got no biological meaning as it yields a negative time when the estimated length is 0 cm. However, in the case of jellyfish, when estimating the growth parameters for the adult phase, t_0 can be considered the strobilation period in which the newly formed ephyrae are released (Fernández-Alfás et al., 2020). The calculation of t_0 is derived from the parameter t_{anchor} provided by TropfishR package, which represents the day in a numeric format ranging from 0 to 1 and is translated into the exact date to ensure that the curve is anchored during the strobilation period.

In fact, the day in which the VBGF is anchored, when it is previous or simultaneous to the first ephyra detection, can be considered as the onset of the strobilation (Fernández-Alfás et al., 2020). Similarly, the first day in which ephyrae are detected is indicative of a close in time strobilation event as their long-lasting survivorship without reaching the medusa stage is unlikely (Fernández-Alfás et al., 2020, 2023). To calculate how much time takes for an ephyra to reach the medusa stage we have considered the difference (in days) between the anchoring day of the VBGF and the first medusa detection (calculated transition time), and between the first ephyra and the first medusa detection (observed transition time) (Fernández-Alfás et al., 2020).

To adjust the growth curve, we did not consider seasonal growth oscillations as the lifespan of *P. punctata* is approximately half a year. However, we have manually set the parameter ‘agemax’ to 0.5 to prevent the underestimation of the K parameter.

Before determining the growth parameters, we tested the absence of different cohorts using the Bhattacharya method of resolving a distribution into Gaussian components (Bhattacharya, 1967). As this method revealed the existence of a single cohort (Fig. S1), there was no need to reconstruct separated populations before applying the ELEFAN method.

Two different procedures provided by TropfishR were used for the determination of the parameters. First, a Response Surface Analysis (RSA) was conducted, testing different combinations of K ($0.5\text{--}6 \text{ year}^{-1}$) and L_∞ ($42.5\text{--}52.5 \text{ cm}$). This analysis revealed a high probability area ($K = 1.2\text{--}1.7$) for each of the different L_∞ (Fig. S2). Secondly, we discarded all models with an asymptotic length lower than the maximum size recorded in the field. We then tested five different models in 1 cm increments for lengths immediately greater than the largest size class ($48.5\text{--}52.5 \text{ cm}$). Finally, we constructed an average model with the best fit for each size class. The total mortality rate (Z) was estimated from the catch curve as described in Ricker (1975) and implemented by Gayanilo et al. (1995).

2.3.2. Thermal association

The association of each jellyfish stage (ephyra and medusa) to a particular thermal range was determined by applying a modification of the Cumulative Frequency Distribution (CFD) method described by Perry and Smith (1994) on the whole dataset. In simple, this method compares two CFD plots. The first one is a cumulative frequency distribution of an environmental variable without considering the abundance of the studied species. In this case, we plot an unweighted CFD of the SST. The second one is a cumulative frequency distribution where different intervals of an environmental variable are given a weight in accordance with the abundance of the species within the given interval. Similar slopes in both curves indicate an even distribution of the species across the thermal range, while a steeper slope in a particular range reflects an association of the species with that temperature interval.

$$f(t) = \frac{1}{n} \sum_{i=1}^n I(x_i) \quad (\text{Eq. 2})$$

$$I(x_i) = \begin{cases} 1, & x_i < t \\ 0, & \text{otherwise} \end{cases} \quad (\text{Eq. 3})$$

$$g(t) = \frac{1}{n} \frac{\sum_{i=1}^n y_i \times I(x_i)}{\sum_{i=1}^n y_i} \quad (\text{Eq. 4})$$

$$D_{\text{max}} = \max |g(t) - f(t)| \quad (\text{Eq. 5})$$

Equation (2) indicates how the CFD for the environmental variable is constructed. In this equation, ‘ n ’ represents the total number of observations, ‘ x_i ’ denotes the value of the SST and ‘ $I(x_i)$ ’ is an indicator function (Equation (3)) where ‘ t ’ represents an index covering the entire range of the SST at an appropriate step size for the desired resolution. In our study, the minimum recorded SST is $9.54 \text{ }^\circ\text{C}$, and the maximum SST is $32.45 \text{ }^\circ\text{C}$. Therefore, we have set the step size of ‘ t ’ to $1 \text{ }^\circ\text{C}$ ranging from $9 \text{ }^\circ\text{C}$ to $33 \text{ }^\circ\text{C}$. Thus, $I(x_i)$ for a given ‘ t ’ corresponds to the number of data points, number of net tows for the ephyra stage, or number of censuses for the medusa stage, where the SST falls within that step. Equation (4) indicates how the weighed CFD is constructed. In this equation, ‘ y_i ’ represents the sum of abundances of the species within the specified environmental interval.

Significant differences in the slope between both CFDs are tested by comparing the maximum absolute difference between $f(t)$ and $g(t)$, denoted by D_{max} (Equation (5)), against bootstrapped reconstructions of $f(t)$ and $g(t)$. In each iteration, ‘ x_i ’ and ‘ y_i ’ are shuffled before reconstructing $f(t)$ and $g(t)$. The resulting pairs of $|g(t) - f(t)|$ are then compared against D_{max} value. We performed 1000 iterations of the curves, each with 24 temperature steps, resulting in a total of 24000 comparisons. If there is a significant association of the species with a particular environmental range, it implies that abundances are higher within that interval, and the D_{max} value will be higher than the random differences obtained from the curve reconstructions. The null hypothesis would be that there is no difference between D_{max} and the randomly obtained differences between pairs, indicating an absence of association with any environmental range.

The thermal association of the early developmental stage of scyphozoan species (ephyra) can be an indicator of strobilation, considering that the occurrence of a strobilation event within a close timeframe is more plausible than an extended survival of the ephyra stage (Fernández-Alfás et al., 2023). Similarly, the association between the medusa stage and a specific thermal frame indicates the ephyra to medusa transition.

3. Results

3.1. Mediterranean biogeography

A total of 154 *P. punctata* observations inside the Mediterranean Sea have been retrieved from literature and jellyfish databases, with the registers, in chronological order, from Israel (since 1965), Egypt (1985), Greece (2005), Italy (2009), Turkey (2010), Syria (2011), Tunisia (2012), Spain (2012), Lebanon (2015), Libya (2015), Malta (2016), Cyprus (2022), and Morocco (2022) (Table S2). Additionally, 30 observations from the Atlantic coast of Spain (Cadiz) have been registered since 2018 (Fig. 2A). The ephyra stage has been found in four semi-enclosed habitats: bay of Vlyho (Greece), Bizerte lagoon (Tunisia), Mar Menor coastal lagoon (Spain), and Sülüngur lake (Turkey). Those semi-enclosed habitats and surrounding areas dominate the detection spots, including commercial harbors, coastal lagoons, salt marshes, semi-enclosed bays, estuaries, and deltas (Table 1). The expansion of the species has not followed a linear direction from east to west, and the

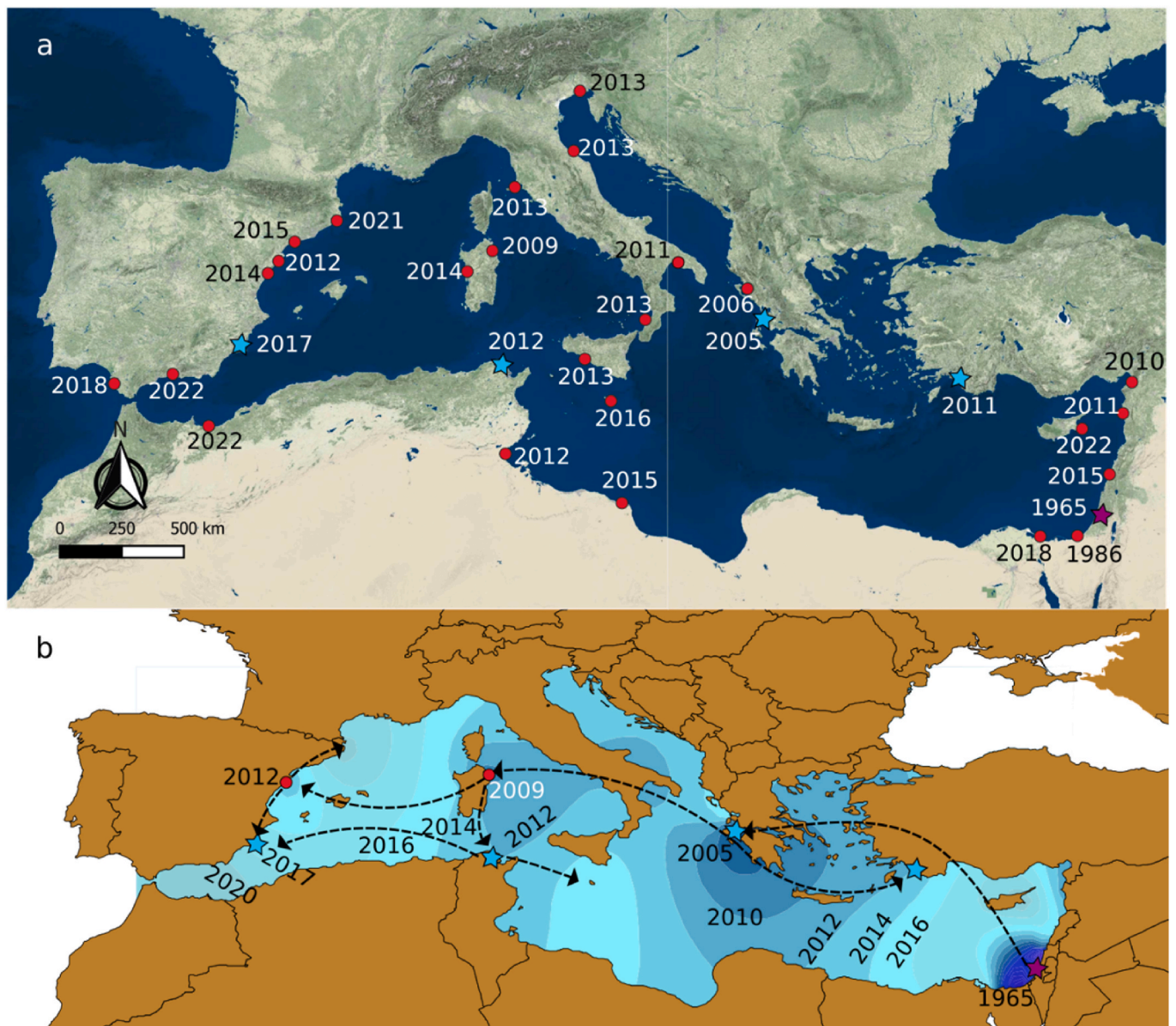


Fig. 2. *Phyllorhiza punctata* distribution in the Mediterranean Sea is indicated by the following symbols: red points represent locations where the medusa phase has been observed, blue stars indicate locations where both the ephyra and medusa phases have been recorded, and a purple star signifies the first Mediterranean register, and indicates the presence of adult individuals with developed gonads. The distribution is further visualized through two components: A) First register by location, and B) Yearly distribution isolines calculated by kriging and arrows indicating the possible dispersal pathways. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

yearly isolines revealed locations acting as a focus of expansion where the species established colonies, completed their life cycle, and began releasing particles into the surrounding area (Fig. 2B). The first focus corresponds to the coast of Israel, followed by Vlyho Bay, the north-eastern coast of Sardinia, Bizerte lagoon, and the Ebro Delta.

Observations of *P. punctata* indicate seasonal pattern for the species, with the first observations in June–July, a peak in August–September, and a decline in the number of observations, disappearing during the winter months (Fig. 3A). Half of the *P. punctata* occurrences are registered on a narrow SST range, ranging from 23.78 to 26.99 °C (25.5 °C median SST, 24.92 °C average SST), the whiskers extend the SST range to 19.41–31.36 °C, with atypical values settling the minimum SST in 12.41 °C. In contrast, the registers occurred within a wide range of SSS due to its presence from estuaries and deltas to salt marshes (Table 1). In the case of SSC, half the occurrences are concentrated between 0.2 and 0.69 µg/l SSC, but the upper half extends until an SSC of 8.74 µg/l, with

atypical values reaching up to 15.32 µg/l (Fig. 3B).

3.2. Mar Menor monitoring system

SST and SSS exhibit a seasonal cycle influenced by global radiation, air temperature and rainfall. Maximum SST is reached during July and August (maximum 31.48 ± 0.09 °C, Mean \pm Standard Error, 28th July 2022) and the minimum in January (minimum 10.02 ± 0.07 °C, 18th January 2021). SSS oscillated between a minimum of 40.21 ± 0.04 in April 2022, after a particularly accentuated rainy period, and a maximum of 44.12 ± 0.07 in October 2022 (Fig. 4A). Mar Menor coastal lagoon is prone to experiencing a dystrophic crisis, characterized by a chlorophyll bloom, during the summer months (Fernández-Alfás et al., 2022). The last one occurred in August–September 2021 reaching a maximum SSC of 14.91 ± 2.04 µg/l on the 25th August 2021. No chlorophyll bloom was recorded during 2022, with SSC remaining below 2.3

Table 1
Semienclosed habitats in which *Phyllorhiza punctata* has been recorded: country, location, type of habitat, and original source.

Country	Location	Semienclosed habitat	Original source
Egypt	Port Said	Harbor, coastal lagoon, delta	Madkour et al. (2021)
	El-Arish	Harbor, coastal lagoon	Atta (1991)
Greece	Bay of Vlyho	Sheltered bay	Abed-Navandi and Kikinger (2007)
	Igoumenitsa	Harbor, coastal lagoon	Abed-Navandi and Kikinger (2007)
Israel	Ashdod	Harbor	Galil et al. (2009)
	Haifa	Harbor	Galil et al. (2009)
Italy	Tel Aviv	Estuary and Harbor	GBIF
	Isola d'Elba	Harbor	GBIF, OBIS, Jellyfish sighting along the Italian coast 2009–2017
	Marano Lagoon	Coastal lagoon	GBIF, OBIS, Jellyfish sighting along the Italian coast 2009–2017
	Pessaro	Estuary and harbor	GBIF, OBIS, Jellyfish sighting along the Italian coast 2009–2017
	Porto Cesareo	Coastal lagoon and Harbor	GBIF
	Sardinia	Sheltered bay, harbor, coastal lagoon	Boero et al. (2009)
Libya	Al Dafiniyah	Harbor	Rizgalla and Crocetta (2020)
Malta	Malta	Salt marsh	Deidun et al. (2017)
Morocco	Saïdia	Estuary and harbor	GBIF
Spain	Ebro Delta	Delta	Barrado et al. (2014)
	Mar Menor	Coastal lagoon	Fernández-Alfás et al. (2022)
	Cádiz	Marsh	Enrique-Navarro and Prieto (2020)
	Torre Vieja	Salt marsh and harbor	Observadores del Mar
Syria	Lattakia	Harbor	Durgham (2011)
Tunisia	Bizerte lagoon	Coastal lagoon	Guéron et al. (2015)
Turkey	Sütlüçür lake	Coastal lagoon	Killi (2020)

$\mu\text{g/l}$ (Fig. 4B).

In 2021, a single ephyra of *P. punctata* was collected the 5th of May at the E02 (Fig. 1) and five medusae were detected through visual censuses between October and December (Fig. 4B). The first bloom of this species in the Mar Menor occurred in 2022, being the appearance of the ephyra stage coincident with an increase in the SST at a rate of 0.11 °C/day (Fig. 4). The ephyra stage was observed from June until October with a maximum of 3.52 ± 1.12 ind/100 m³ in September, while the medusa stage was recorded from the 2nd August 2022 (1 individual) until the 10th January 2023 (4 individuals) with a maximum abundance of 3.58 ± 2.95 ind/100 m³ September 6th, 2022.

The bloom of *P. punctata* started in the northern part of the Mar Menor coastal lagoon, with the ephyrae and medusae confined to the ecosystem. Over time, the medusae become distributed throughout the coastal lagoon, and eventually, some of them were transported through the communication channels to the Mediterranean Sea, where they were detected (Fig. 5). The ephyra stage has not been detected in any sample collected in the Mediterranean Sea.

3.3. Life cycle: pelagic stages

3.3.1. Growth

The Bhattacharya method of resolution of a distribution into Gaussian components revealed the existence of a single cohort of *P. punctata* in the Mar Menor during the year 2022 (Fig. S1). The RSA revealed a maximum probability area for K values between 1.2 and 1.7 year⁻¹ (Fig. S2). After excluding the L_∞ equal or below the maximum

detected size class (47.5 cm) the most probable value of K was determined to be 1.24 year⁻¹ (Table 2). L_∞ was determined to be 50.5 cm with the VBGF anchored on the 2nd of August, approximately two weeks after the beginning of the ephyra peak on the 17th of July. The transition from ephyra to medusa is calculated to take from 17 to 27 days in the VBGF and 37 days in the Mar Menor coastal lagoon monitoring system. Mortality (Z) has been estimated to be 6.11 ± 0.4 year⁻¹ corresponding to a survival rate (S) after the end of the season of 0.2%.

3.3.2. Thermal association

The stages of *P. punctata*, ephyra and medusa, do not exhibit a random distribution across the recorded temperature range in the Mar Menor coastal lagoon (Fig. 6). It has been observed that these stages are associated with specific SST range. The ephyra stage is associated with the interval 27 to 30 °C with a p-value of 0.015, while the medusa stage is linked to the interval 22 to 27 °C with a p-value of 0.025 (Fig. 6; Table 2).

4. Discussion

4.1. Mediterranean biogeography

Previous attempts to gather reports of *P. punctata* lacked a systematic review process with defined inclusion and exclusion criteria and omitted the scientific and citizen science data collected in the main databases. As a result, the distribution of the species in spatial and temporal scales was inaccurately represented. Previous sighting collection attempts were limited to 15 (Madkour et al., 2021) and 30 reports (Kaminas et al., 2022), in contrast to the 154 sightings collected in this study (Table S2).

P. punctata was first detected in the Mediterranean Sea in the coast of Israel in 1965 (Galil et al., 1990). It has been proposed that the species arrived in the Mediterranean Sea through shipping, originating from the native Australian population (Mizrahi et al., 2021). After the initial detection, a second sighting occurred in Egypt in 1986 (Atta, 1991). There was then a two-decade gap until the species reappeared in Israel in 2005 (Galil et al., 2009), and the ephyra stage was observed for the first time in Greece (Abed-Navandi and Kikinger, 2007). Since then, the species has expanded throughout almost the entire Mediterranean Sea (Fig. 2A).

We have considered the year 2012 as the date of *P. punctata*'s arrival in Spain, even though there were reports of a bloom in the summer of 2010 mentioned in the literature (Brotz and Pauly, 2012; Galil, 2012). Brotz and Pauly (2012) claimed that 6 Spanish beaches in the Valencia Community were closed after more than 100 swimmers were stung during the summer of 2010, citing an Australian newspaper as the original source of the report (Anonymous, 2011). However, this detection was incorrect, as the closure of the Spanish beaches in 2010 was a result of the massive arrival of specimens of *Pelagia noctiluca* (Forsskål, 1775) (Ambrojo and Ruiz, 2010). Furthermore, there have been no reports of *P. punctata* in Spain after an intense jellyfish sampling effort conducted by the Spanish national government between 2007 and 2010 (Ministerio de Medio Ambiente y Medio Rural y Marino, 2011) or by the monitoring system directed by the Valencia Community regional government (Instituto de Ecología Litoral, 2011). The first confirmed detection from the Spanish Coast was published in Barrado et al. (2014) and previously presented at a congress in April 2013 (ISRSE35, 2013), where pictures of a proliferation of *P. punctata* in the Ebro Delta are provided. Considering Barrado et al. (2014) states that pictures were taken in 'last October', and that ISRSE35 was held in April 2013, we have assigned those pictures to October 2012.

4.1.1. Semienclosed habitats as stepping-stones in the expansion of *P. punctata*

The perception of a global increase in jellyfish blooms is partly promoted by the translocation of bloom forming species, and the subsequent expansion from its native habitat to new locations (Purcell et al.,

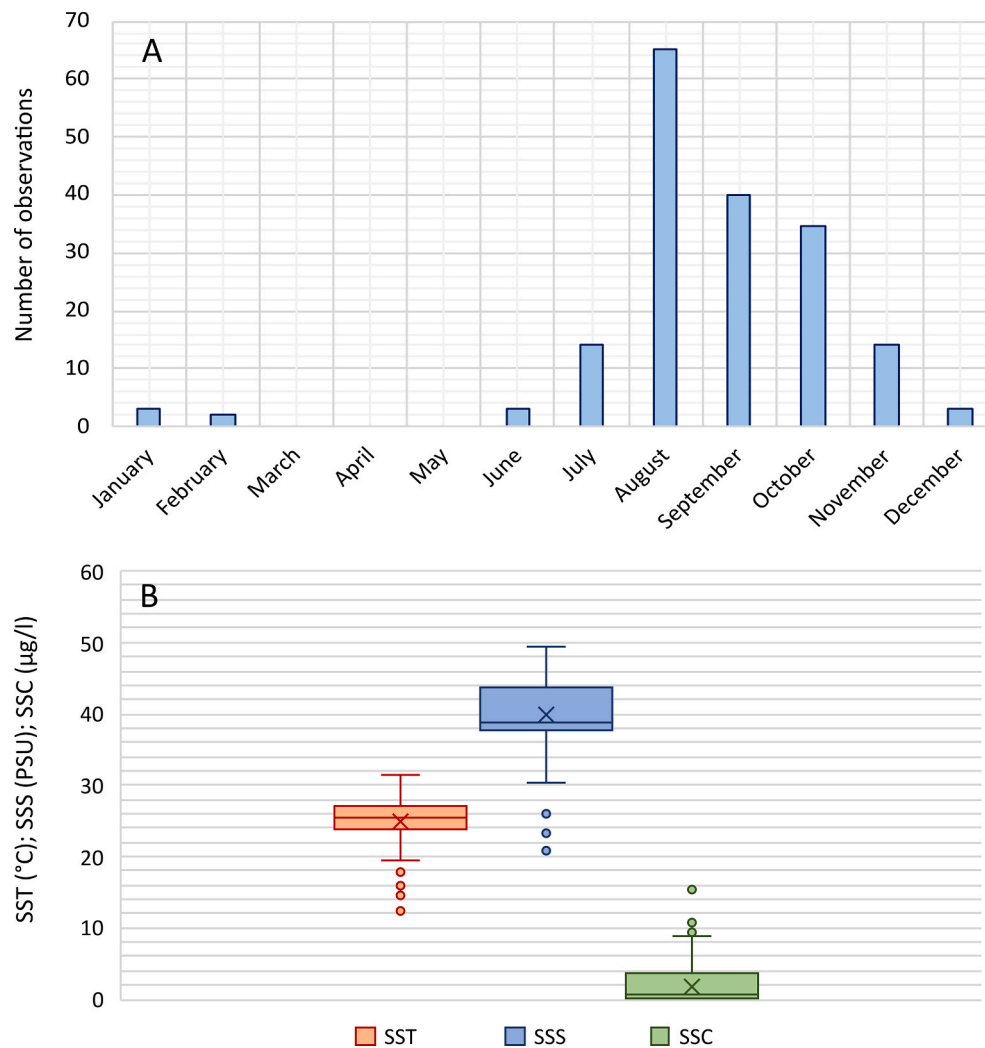


Fig. 3. A: Number of *Phyllorhiza punctata* observations each month in the Mediterranean Sea. B: Boxplot of the environmental parameters from each observation of *P. punctata* in the Mediterranean Sea. SST: Sea surface temperature, SSS: sea surface salinity, SSC: sea surface chlorophyll *a*.

2007; Richardson et al., 2009). The main anthropic-mediated vectors proposed for the spread of the species are ballast water (ephyrae and medusae), hull-fouling organisms (benthic polyps and cysts), aquarium trade, or the opening of communication channels (Graham and Bayha, 2008; Purcell et al., 2007; Richardson et al., 2009; Duarte et al., 2013; Bayha and Graham, 2014). In the case of *P. punctata*, vessel transportation has also been suggested as a means of dispersal beyond its native distribution range (Larson and Arneson, 1990), as well as the Mediterranean Sea introducing vector (Abed-Navandi and Kikinger, 2007; Deidun et al., 2017; Mizrahi et al., 2021). On the contrary, advective currents have been proposed as a possible dispersal vector for its arrival to the eastern part of Australia (Rippingale and Kelly, 1995), and even to cover the 1000 km gap from the Caribbean to the Mississippi Bight (Graham et al., 2003; Johnson et al., 2005).

The lack of detections of *P. punctata* in the Red Sea, along the genetic studies, suggest that this species arrived in the Mediterranean Sea directly transported from Australia by ship (Mizrahi et al., 2021). However, once in the Mediterranean, its spread pattern (Fig. 2B) suggests that factors beyond direct ship transport are also at play. Carlton (1996) proposed six non-exclusive factors for the dispersal of marine organisms, including: i) changes in the donor region that increase the abundance of the invasive species in its natural habitat, ii) new, intermediate donor regions, iii) environmental changes that increased the probability of colonization in the receptor region, iv) adequate invasion windows, v) stochastic inoculation events, and vi) changes in the

dispersal vector.

The yearly isolines of propagation of *P. punctata* in the Mediterranean Sea suggest that semienclosed habitats act as stepping-stones, like the intermediate donor regions proposed by Carlton (1996), in the colonization process (Fig. 2B). It should be noted that those areas are more likely to host jellyfish blooms (Fernández-Alfás et al., 2021), and *P. punctata* is a species known for forming blooms in its native habitats such as estuaries and lagoons (Rippingale and Kelly, 1995). This species has a long history of invading such ecosystems in the Pacific Ocean (Larson and Arneson, 1990), Atlantic Ocean (Graham et al., 2003; Haddad and Nogueira Júnior, 2006), and the Mediterranean Sea (Abed-Navandi and Kikinger, 2007; Gueroun et al., 2015; Killi, 2020). Moreover, in the Mediterranean Sea, the ephyra stage has only been found in Vlyho Bay (Abed-Navandi and Kikinger, 2007), Bizerte lagoon (Gueroun et al., 2015), Sülüngür lake (Killi, 2020), and Mar Menor coastal lagoon (this study) indicating that the reproduction is occurring within these ecosystems.

The three last factors proposed by Carlton (1996) for the dispersal of marine organisms, in the case of coastal lagoons and other semienclosed environments, can be explained by the confinement theory (Pérez-Ruzafa and Marcos, 1992, 1993; Pérez-Ruzafa et al., 2019b). This theory incorporates a random component of colonization, where lagoon communities are shaped by the probabilities of species colonization, as well as the balance and energy costs resulting from adaptation, reproduction, population growth rates, and competition with other species.

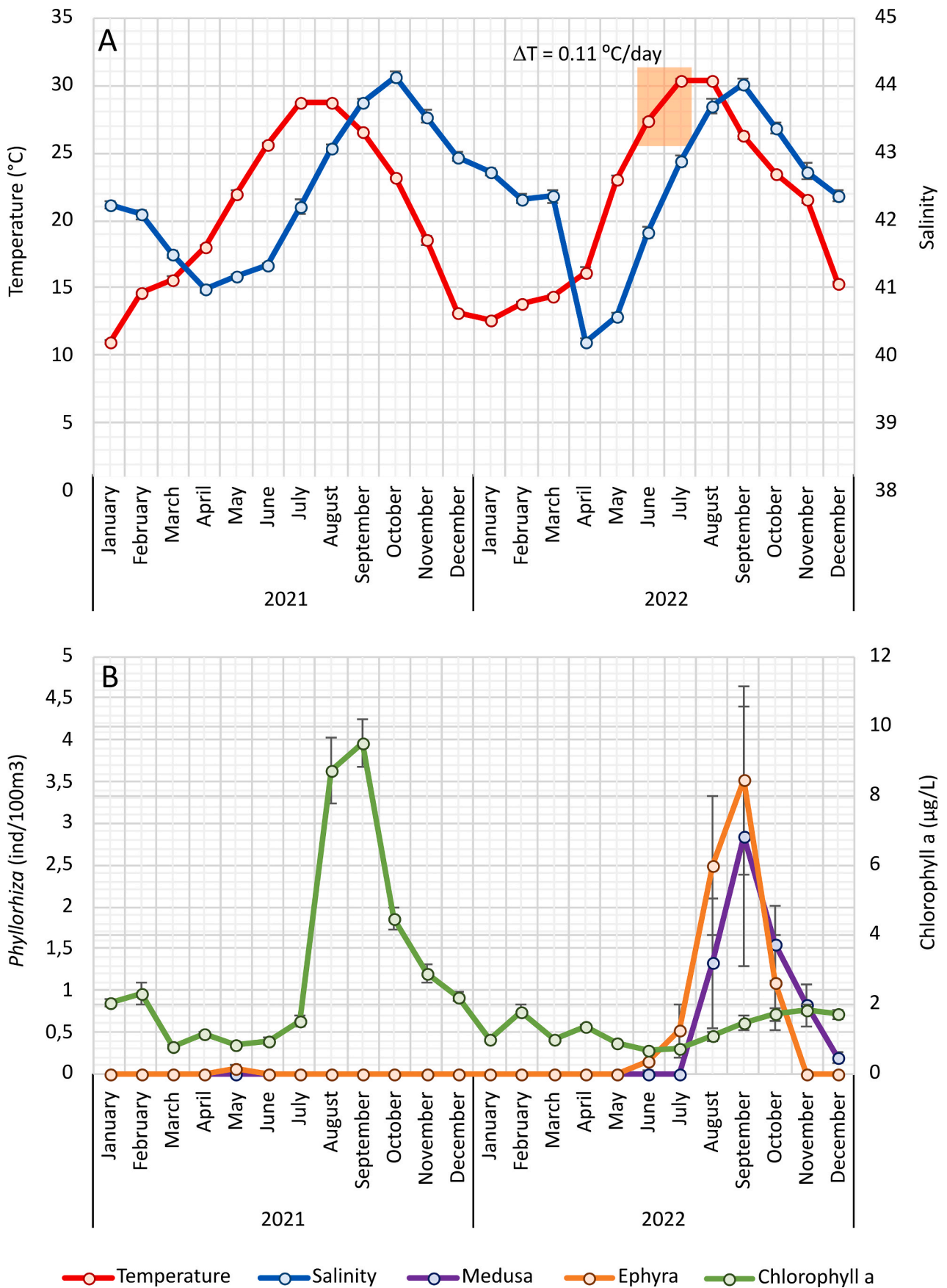


Fig. 4. Environmental and biological parameters within the Mar Menor coastal lagoon. Error bars indicate standard error. A: Sea surface temperature, and sea surface salinity; B: Sea surface chlorophyll a concentration, and *Phyllorhiza punctata* (ephyra and medusa phases) abundance.

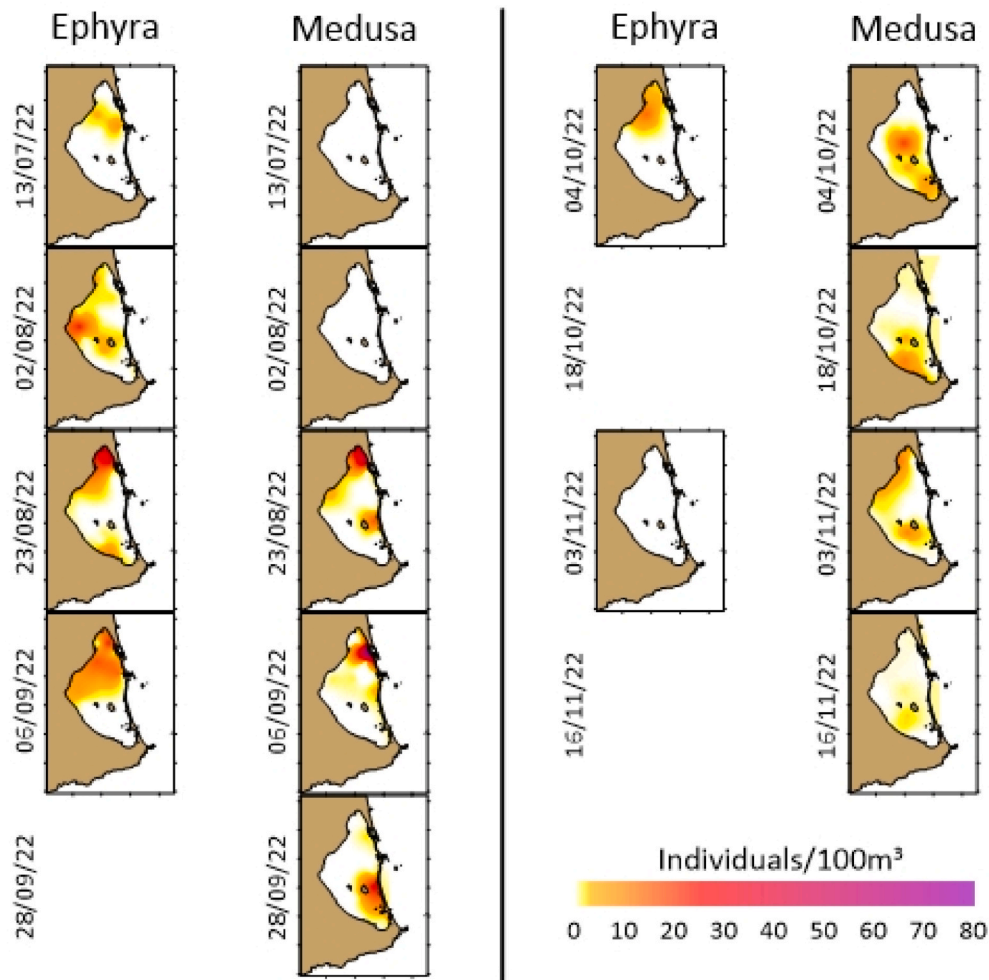


Fig. 5. Horizontal distribution of the 2022 bloom of *Phyllorhiza punctata* (ephyra phase in the left column, and medusa phase in the right column) in the Mar Menor coastal lagoon and the surrounding area of the Mediterranean Sea. The absence of ephyra collection on a specific date is indicated by the lack of a map in the ephyra column.

Table 2

Von Bertalanffy Growth Function parameters and temperature association of the *Phyllorhiza punctata* population from the Mar Menor coastal lagoon.

	L _∞ (cm)	K (year ⁻¹)	t ₀	Z (year ⁻¹)	Strobilation day	Ephyra peak (start)	Medusa peak (start)	Ephyra to medusa (days)	
					Calculated	Real	Real	Calculated	Real
Value	50.5	1.24	-0.06	6.11 ± 0.4	2nd August	17th July	23rd August	21	37
Minimum and maximum	48.5 to 52.5	1.2 to 1.3	-0.073 to -0.048	5.81 to 6.69	27th July to 6th August			17 to 27	
Thermal association	Ephyra 27-30 °C			p-value 0.015		Medusa 22-27 °C		p-value 0.025	

These factors are influenced by hydrodynamics, salinity, water characteristics, substrate, trophic conditions, and the range and predictability of environmental fluctuations, among others (Pérez-Ruzafa and Marcos, 1993). Furthermore, low colonization rates, arising from communication channel restrictions, barriers posed by differences in salinity and temperature compared to the open sea, and the inherent randomness of the process, prevent homogenization within the system. This allows for a wide range of diversity, adaptation to change, and significant differences in species composition among lagoons. Thus, lagoon ecosystems exhibit high heterogeneity, with the primary source of variability appearing to be the random component imposed by restricted connectivity during the colonization process (Pérez-Ruzafa, 2015).

In the case of *P. punctata*, its euryhalinity (Rippingale and Kelly,

1995; Rato et al., 2021) enables its entry into semienclosed ecosystems with varying salinity regimes, ranging from estuarine to salt marshes conditions (Table 1; Fig. 3B). The colonization process in the Mar Menor coastal lagoon began in 2017, with *P. punctata* closing its life cycle, blooming, and exporting individuals to the Mediterranean Sea by the summer of 2022 (Figs. 5 and 7). Similarly, the expansion from Vlyho Bay (Greece) to the northeast coast of Sicily (Italy), and subsequently to Ebre Delta (Spain) and Bizerte Lagoon (Tunisia) took place in three to four year steps (Fig. 2B), suggesting the existence of approximately a 4 years step in the colonization process.

It has been argued that the previous colonization processes of the Mar Menor coastal lagoon by other scyphozoan species were facilitated by the dredging and widening of El Estacio channel for the construction

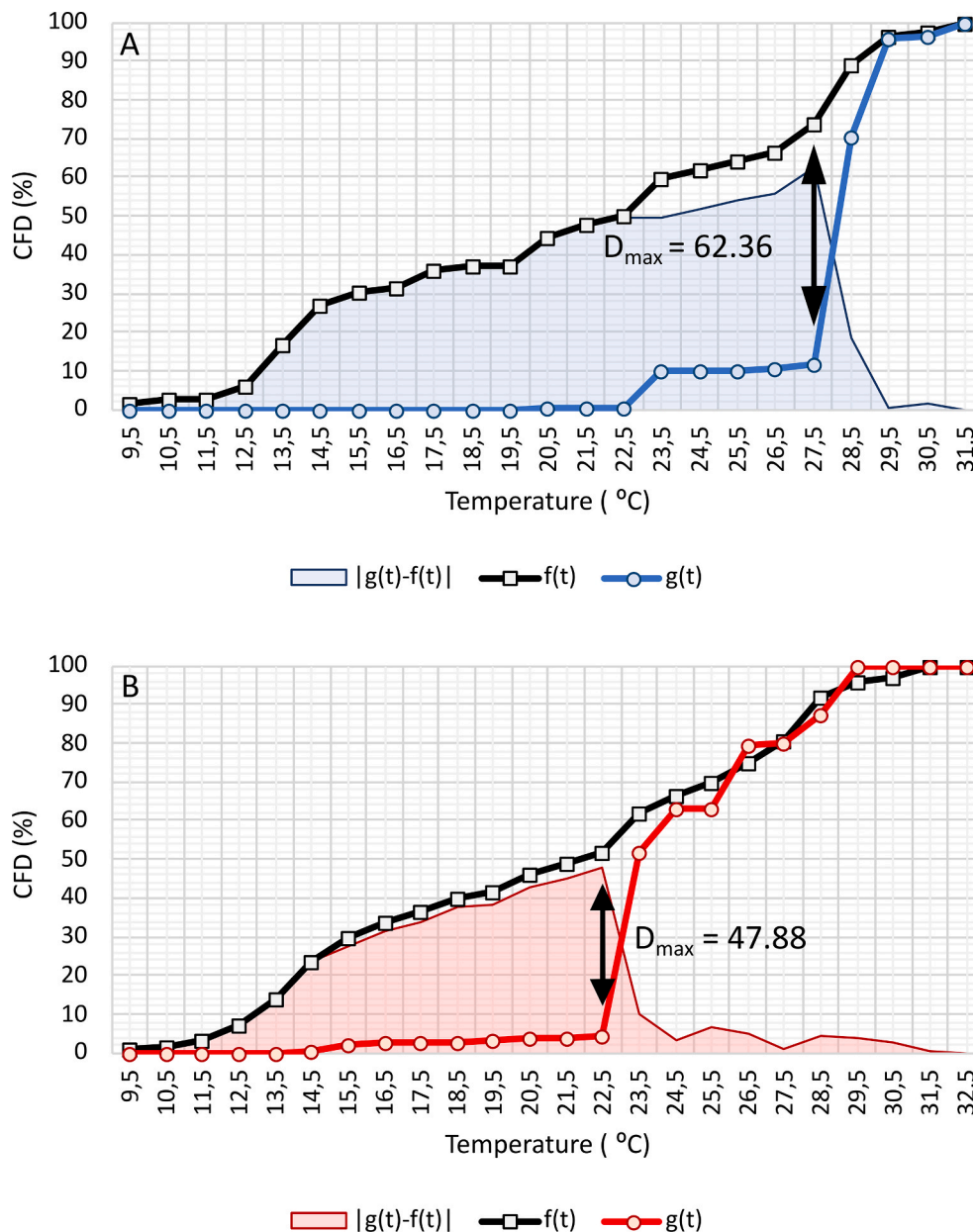


Fig. 6. Cumulative Frequency Distribution (CFD) of the Mar Menor's sea surface temperature (SST), denoted as $f(t)$, and SST weighted by the abundance of *Phyllorhiza punctata*, denoted as $g(t)$. The shaded area indicates the absolute difference between both distributions, $|g(t) - f(t)|$. D_{max} indicate the maximum difference between the two distributions, which is used to calculate the p-value of the thermal association through bootstrap reconstruction of the curves. A (blue): ephyra stage, B (red): medusa stage. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

of a commercial harbor, reducing the water renewal time and increasing the availability of hard substrate (Pérez-Ruzafa and Coord, 1997; Fernández-Alfás et al., 2023), which is a requirement for the polyps to settle (Duarte et al., 2013). In this case, this factor seems to have also played a role since the first appearance of the ephyrae during the *P. punctata* 2022 bloom occurred in the inner part of El Estacio (Fig. 5). Thus, it is likely that the polyps have settled in this commercial harbor, but this might not be an exclusive location since the coastline of the lagoon has been deeply modified by the construction of up to ten harbors, and several dams which might explain the coverage of the lagoon by the ephyrae (Fig. 5). This colonization of the Mar Menor coastal lagoon has been faster compared to *R. pulmo* and *C. tuberculata*, where a 15-year gap existed between the initial detection and the first bloom (Pérez-Ruzafa, 1989, 1996, 1997).

4.2. Life cycle

Considering previous literature, we have paid special attention to the temperature and salinity conditions in the Mar Menor coastal lagoon to elucidate whether one factor directs *P. punctata*'s seasonality on its own, or whether both actuate in a coordinated manner. Usually, temperature depends mostly on seasonal variations, while salinity is also affected by rainfall and runoffs. In the Mar Menor coastal lagoon, temperature shows the expected seasonal regularity and a quite homogeneous spatial distribution, while salinity shows a very heterogeneous spatio-temporal variability and therefore it is less correlated with the seasonal productivity in the lagoon (Pérez-Ruzafa et al., 2005a). In the study period, the salinity dropped from 42.23 to 40.98 between January and April 2021, being the ephyrae detected in May. In 2022, the salinity dropped sharper, from 42.36 to 40.21 between March and April, because of a higher accumulated rainfall (Fig. 4). However, the first ephyra detection

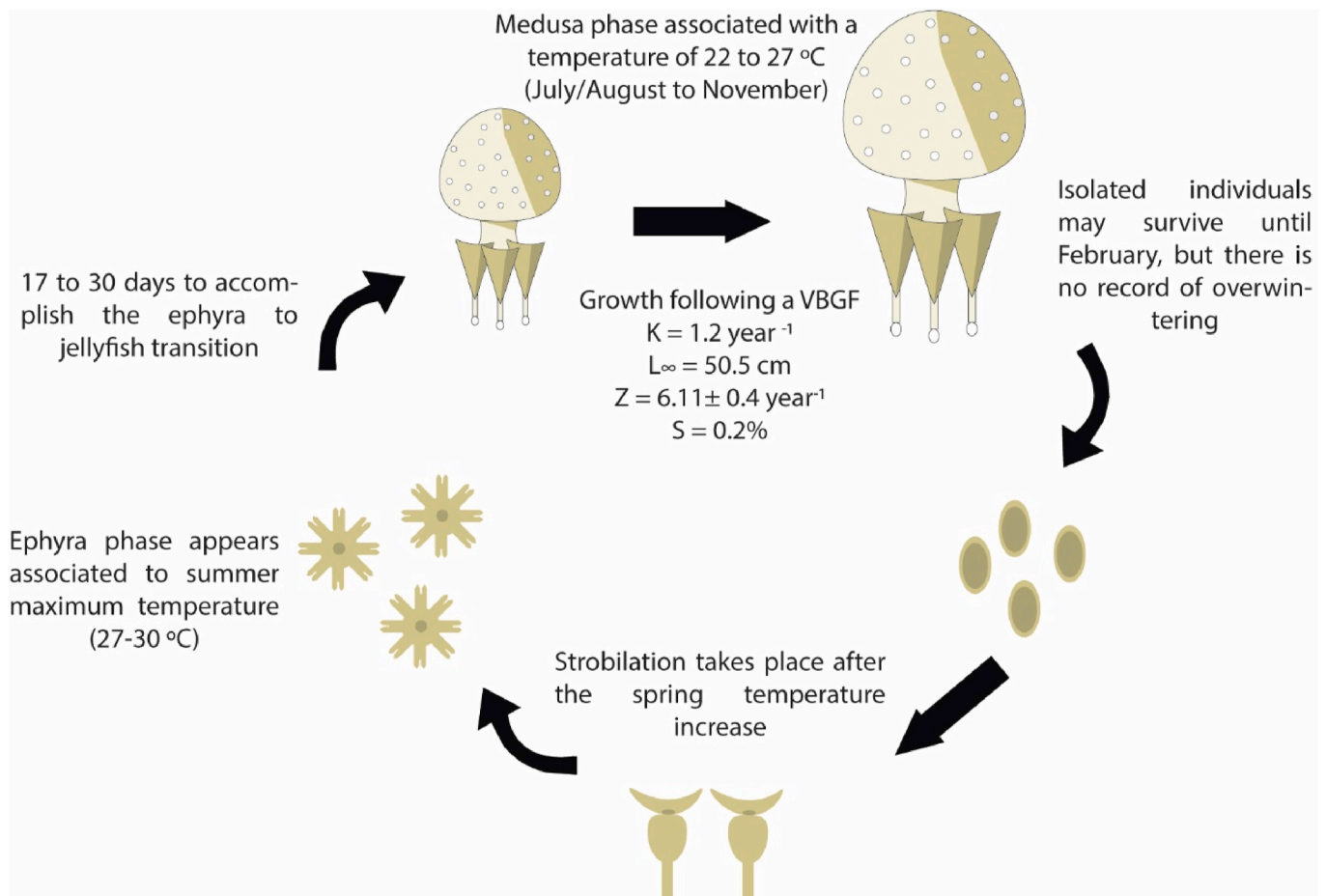


Fig. 7. *Phyllorhiza punctata* life cycle in the Mediterranean basin. We have adjusted the coloration of the jellyfish to enhance the contrast with the background and highlight the white crystalline inclusions known as spots or 'punctae'.

was in June, when the salinity was in the process of recovering (41.82). Our dataset only includes two seasons of ephyra appearance, one after a decline in the salinity (2021) and a second after a recovery of the same (2022), making it difficult to elucidate the role of the salinity. On the contrary, the ephyrae detection on both years occurred after a temperature increase. This result suggests that, in this ecosystem, the phenology of the species is directed by temperature, which is also a factor that allows the species to anticipate the adequate conditions for its development (including the seasonality and productivity of the system) (Fernández-Alfás et al., 2024). Moreover, the seasonality of *P. punctata* seems to be consistent throughout the Mediterranean basin, where it also seems to be mainly influenced by temperature (Figs. 3 and 4B; Abed-Navandi and Kikinger, 2007; Gueroun et al., 2015). This might contrast with tropical ecosystems, such as Laguna Joyuda coastal lagoon in Puerto Rico, or Swan-Canning estuary in Australia, where the salinity has been pointed out to act coordinately with temperature, photoperiod and rainfall pattern regulating the life cycle of *P. punctata* (García, 1990; Rippingale and Kelly, 1995; Palomares and Pauly, 2009). However, these studies refer to an absence of the medusa phase when the sea surface salinity is lower, but the salinity at suitable depths for polyp development is much more stable, and the role of a temperature increment to trigger the strobilation is also pointed out (Rippingale and Kelly, 1995).

Consequently, our description of the life cycle (Fig. 7), based on the Mediterranean basin, focuses on the temperature parameter. For environments with fluctuating salinity, both temperature and salinity need to be considered. In tropical areas, where the temperature conditions for the strobilation and development of *P. punctata* occur throughout the

year, likely temperature and salinity act in a coordinate manner controlling the asexual reproduction, strobilation process and phenology of the species. If the description of the life cycle is to be used on those environments it should be considered that the polyps of *P. punctata* got a lower salinity tolerance limit of 10 (Rippingale and Kelly, 1995; Rato et al., 2021). However, there is a gap in knowledge regarding the lower salinity tolerance limit of the pelagic stages. We have estimated it around 20 since the lowest value of salinity for a record of this species is 20.74 in the Mediterranean basin (Fig. 3B), and the absence of the medusa phase has been reported below that limit in an Australian estuary (Rippingale and Kelly, 1995). Additionally, the polyp populations of *P. punctata* exhibit higher maturity and asexual reproduction rates at salinities of 20 and above (Rippingale and Kelly, 1995; Rato et al., 2021), making it plausible that strobilation is inhibited below this threshold.

P. punctata polyps colonize the substrate through free swimming buds with better performances when the food is available and the water is warm (Schiari et al., 2014). During the spring, after a temperature increase (from 16 to 24 °C), the ephyrae are released through monodisc strobilation (Rippingale and Kelly, 1995). The ephyra stage is linked with the summer temperature maximum (27–30 °C) (Table 2). The transition from ephyra to medusa stage takes from 17 to 37 days, showing consistency between models, laboratory, and field observations (Table 2; Abed-Navandi and Kikinger, 2007). We detected a single cohort in the Mar Menor coastal lagoon during the year 2022 (Fig. S1), which is consistent with the monodisc strobilation performed by *P. punctata* (Rippingale and Kelly, 1995).

The medusa phase is associated with an SST of 22–27 °C,

corresponding with the SST decrease occurring from August until November, and the growth of the individuals can be adjusted to a VBGF. Previous estimations of the VBGF for *P. punctata* show a great variability for both K value (2.3–4.69 year⁻¹), and L_∞ (38.3–57.5 cm) (Palomares and Pauly, 2009). The calculated infinite length for the species in the Mar Menor is within the same frame of those estimated for *P. punctata* in Laguna Joyuda, Puerto Rico (Palomares and Pauly, 2009), but the K value is 1–3 points below the estimations for the Puerto Rican lagoon. The variations higher than 1 point in the K value can be explained because the L_∞ from those models are below the sizes we have detected in the Mar Menor, and the decrease in the L_∞ is coupled with an increase in the K value (Fig. S2). For the latter model, K = 2.3 year⁻¹ and L_∞ = 57.5 cm (Palomares and Pauly, 2009), the differences in the K value can be explained by the shorter recruitment time in Laguna Joyuda (García, 1990). However, it is possible that the extended recruitment period of the Mar Menor coastal lagoon, even if it does not provide two different cohorts, slightly underestimate the K value. Based on the calculated model, the highest sizes would not be reached during the season, and other species with similar ecological traits, in this ecosystem, show higher K values (Fernández-Alfías et al., 2020). In the Mediterranean Sea, the disappearance of the medusa phase occurs during late autumn and winter, with no record of overwintering individuals (Fig. 3A; Table 2).

There are still certain gaps in knowledge regarding the scyphozoan jellyfish dynamics in general (Fernández-Alfías et al., 2024), and *P. punctata* in particular. In our monitoring system we have observed a bloom in 2022 and a lack of the same in 2021. It is noticeable that the minimum SST in 2021 was 10.95 °C, while in 2022 the minimum SST was 12.59 °C. In this line, we should consider that the minimum winter SST has been proven to affect the intensity of the blooms in *Aurelia aurita* (Linnaeus, 1758) (Loveridge et al., 2021), and that *P. punctata*'s polyps got higher an asexually reproduction rate in warm waters (Schiariti et al., 2014). Thus, the absence of a bloom in 2021 can be temperature related. However, the minimum thermal threshold for polyp survival in this species has not been defined and, in the context of colonization and eutrophication processes, there are other factors that can not be ruled out. On one hand, the numerical expansion of the scyphozoan populations in the pelagic stage is higher by several orders of magnitude than in the benthic phase (Fernández-Alfías et al., 2024), and it is possible that by 2021 the number of planulae and medusae that the Mar Menor has received was not enough to establish a large polyp population. It should be noted that *P. punctata* got a lower asexual reproduction rate than other scyphozoan species (Schiariti et al., 2014). On the other hand, it has been argued a chlorophyll *a* bloom, such as the one that occurred in 2021, prevented the appearance of the medusa phase of *C. tuberculata*, the other zooxanthellated scyphozoan species from the Mar Menor (Fernández-Alfías et al., 2022, 2023), and its effect over the strobilation of *P. punctata* is still unknown.

4.3. Ecological considerations

P. punctata is a facultative zooxanthellated jellyfish, capable of full development with or without zooxanthellae (Graham et al., 2003). The number of symbiotic zooxanthellae varies among the populations that possess them (Bolton and Graham, 2004). Zooxanthellated populations have been found in tropical, oligotrophic waters with small sized individuals (García, 1990; Rippingale and Kelly, 1995), while individuals from the turbid, and highly productive Gulf of Mexico showed an absence of zooxanthellae and bigger sizes (Graham et al., 2003; Bolton and Graham, 2004). Within the Mediterranean Sea, the different *P. punctata* populations show a high variability in the coloration, varying from no coloration, white or bluish in azooxanthellated individuals to an increasing intensity of brown according to the number of zooxanthellae (Table S1; Bolton and Graham, 2004; Cevik et al., 2011). In the case of Mar Menor coastal lagoon, we have found that some individuals exhibited a light brown coloration in the border of the umbrella and in the oral arms in the smallest class size (0–5 cm), while they were

completely white at larger sizes. This might imply a loss of the zooxanthellae throughout their ontogeny, or a change in the diet or in the grazing pressure to match the energetic requirements during its development (García and Durbin, 1993; Graham et al., 2003; Gueroun et al., 2015). Therefore, it is likely that *P. punctata* exerts a control over the pelagic trophic network on various levels, preying on the zooplankton fraction (García and Durbin, 1993; Gueroun et al., 2015), and competing with the phytoplankton for the nutrient availability (Fig. 4B; Djeghri et al., 2019). In both cases, the plankton fractions are maintained at low concentrations during the jellyfish bloom (Fig. 3B; 4B; García and Durbin, 1993; Gueroun et al., 2015).

The introduction and spread of *P. punctata* in the Mediterranean Sea have not resulted in significant economic losses in any location (Stamouli et al., 2017) except for some net fouling and clogging in the Bizerte lagoon (Gueroun et al., 2015). This contrasts with its introduction to the Gulf of Mexico, where the colonization of *P. punctata* has led to several million dollars in losses (Graham et al., 2003). In the Mar Menor coastal lagoon, the ongoing eutrophication process has led to a series of dystrophic crises marked high SSC and by fish mortalities during hypoxia/anoxia events. These crises have resulted in economic losses and raised social concerns (Fernández-Alfías et al., 2022). All the registered dystrophic crises have occurred during the summer months, in a context of absence of jellyfishes and high nutrient input (Fernández-Alfías et al., 2022). In the 2022 summer, the Mar Menor coastal lagoon experienced an additional 230 tons of nitrate shed compared to the previous year (CARM, 2023), yet a dystrophic crisis did not occur in 2022, unlike in 2021 (Fig. 4B; Fernández-Alfías et al., 2022). Furthermore, high SST is a requirement for the dystrophic crises to occur, and the summer of 2022 recorded the highest SST since the launch of the monitoring system. The top-down control that jellyfish blooms can exert in preventing dystrophic crises has already been demonstrated in the Mar Menor (Pérez-Ruzafa et al., 2002). Additionally, another factor to consider is that since the winter of 2021, the regional government of the Region of Murcia (CARM) has made significant efforts to remove the biomass of nitrophilic algae that had accumulated on the beaches. This removal prevented their decomposition and resulted in a significant reduction of nutrients in the ecosystem (Pérez-Ruzafa, 2023). Both circumstances, the proliferation of *P. punctata* and the removal of biomass, may have acted synergistically to prevent dystrophic crises. Therefore, it requires further study to determine if the presence of *P. punctata* can help maintain top-down control over phytoplankton and prevent dystrophic crises, as suggested by our observations (Fig. 4B).

CRedit authorship contribution statement

Alfredo Fernández-Alfías: Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization. **Jhoni Ismael Quispe-Becerra:** Investigation. **Manuel Rosendo Conde-Cañó:** Investigation. **Concepción Marcos:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Angel Pérez-Ruzafa:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2024.108699>.

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