



Phenology of scyphozoan jellyfish species in a eutrophication and climate change context

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ABSTRACT

The uprising interest in gelatinous zooplankton populations must cope with a lack of robust time series of direct abundance observations in most of the ecosystems because of the difficulties in sampling small, fragile organisms, and of the dismissal of jellyfish as a nuisance. Most of the hypotheses about their dynamics are built on a few species and ecosystems and extended to the whole group, but the blooms are registered mainly for the members of the Class Scyphozoa that dwell in temperate, shallow waters. Within the scyphozoans, our knowledge about their phenology relies mainly on laboratory experiences. Here we present a long-term analysis of the phenology and life cycle of three scyphozoan species in an ecosystem affected by eutrophication in a climate change context. We have found that the phenology is directed by temperature, but not modified by different thermal and ecological regimes.

1. Introduction

In recent decades, an interest in gelatinous zooplankton populations (Pitt et al., 2018; Fernández-Alías et al., 2021) has raised, promoted by a perception of an increase in the abundance and intensity of their massive proliferations also called blooms (Brotz et al., 2012). The interferences of blooms with human activities, the claims that anthropogenic effects can benefit gelatinous zooplankton populations, and the services that jellyfish can provide, such as the maintenance of the water quality through eutrophication processes, are tickling scientists' interest (Pérez-Ruzafa et al., 2002; Purcell et al., 2007, 2013; Richardson et al., 2009). However, there is a general lack of robust time series of direct gelatinous plankton abundance observations in most of the ecosystems (Mitchell et al., 2021). By the year 2012, only about thirty-seven time series longer than 10 years were available for gelatinous plankton researchers (Condon et al., 2013) to test hypotheses such as climate change and eutrophication roles on the increase in gelatinous plankton proliferations. The combined analysis of those datasets is convoluted given the multiple metrics and methodologies used to retrieve the original data (Condon et al., 2013), and the necessity of gathering all the groups (scyphozoan jellyfish, ctenophores, salps, etc.) into a 'gelatinous plankton' group.

However, this group is heterogeneous, given the deep genetic divergences within it (Khalturin et al., 2019) and that massive occurrences of these organisms are not randomly distributed but concentrated in the Scyphozoa class, which have a metagenic life history (Hamner and Dawson, 2009), and within this class, on large species that dwell in temperate, shallow waters (Fernández-Alías et al., 2021).

The existence of metagenic life history for most scyphozoan species makes the phenological studies and the transitions between phases key points for understanding population dynamics. Despite the uprising interest in the topic (Pitt et al., 2018), phenology field studies are still scarce given the intrinsic difficulties of finding the first pelagic developmental stages, which are fragile and small-sized. The benthic stage, known as scyphistoma, has not so often been found in the field (Marques et al., 2019; van Walraven et al., 2020), only a few exceptions do report ephyra stage dynamics (Fernández-Alías et al., 2020; Leoni et al., 2021b) and, to our knowledge, there is no study about planulae settlement in the field. The data on the adult populations (medusa) is also limited as their fragile bodies can be broken by the fishing gears during the sampling, and as there has existed a dismissal of jellyfish as a nuisance in fisheries or even in the scientific surveys that evaluated economically interesting fish stocks (Mitchell et al., 2021).

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Consequently, most of the knowledge on the phenology of scyphozoan species is based on laboratory studies. The clearest evidence retrieved from experimental designs is that temperature plays a major role in the life cycle, particularly in triggering the strobilation process (Fuchs et al., 2014). However, when considering *Aurelia* spp., the most studied genus (Pitt et al., 2018), asymmetrical effects of the temperature can be found. For example, *Aurelia aurita* (Linnaeus, 1758) benefit from a long, cold winter to undergo strobilation (Loveridge et al., 2021), while *Aurelia coerulea* von Lendenfeld, 1884, shows earlier strobilation and higher ephyra production with warmer winters (Zang et al., 2022). This difference in the response can be sharper when different genera are considered, as it happens between *Nemopilema nomurai* Kishinouye, 1922, and *Cyanea nozakii* Kishinouye, 1891, the two major giant jellyfishes from East Asia, with strobilation temperatures between 22 and 25 °C for the first, and 10–13 °C for the latter (Feng et al., 2015). The second factor that should be considered is food availability (Goldstein and Steiner, 2020), given that polyps can compensate for the physiological stress when fed with prey enriched in highly unsaturated fatty acids (Chi et al., 2019), and that the quality and quantity of the food can modulate the intensity of strobilation under the appropriate thermal regime (Schiariti et al., 2014; Goldstein and Steiner, 2020) or enhance the survivorship through the ephyra to medusa transition (Chambel et al., 2016; Miranda et al., 2016).

The effect of temperature as the director factor of the species seasonality suggested by laboratory experiments is also reflected in short-term field studies (Fernández-Alfías et al., 2020; Gueroun et al., 2020). However, in long-term field studies, there are irregularities (years without the presence of any jellyfish, but without major differences in the temperature regime) that might conceal the effect of seasonality over the adult populations, but the years when they are present, they maintain a regular seasonal pattern (van Walraven et al., 2015; Stone et al., 2019). This reflects that temperature by itself is essential but not enough for the proper development of jellyfish populations (Fernández-Alfías et al., 2021). The irregularities registered in long-term time series and the asymmetrical response of the different scyphozoan species put at stake the old assumptions of the increase in jellyfish proliferations because of climate change and eutrophication (Purcell et al., 2007, 2013; Richardson et al., 2009; Brotz et al., 2012; Fernández-Alfías et al., 2021), and reflects the necessity of performing phenology studies on long-term time series including multiple scyphozoan species.

The main drivers hypothesized to increase the number and intensity of massive proliferations of gelatinous plankton are fishing activities, shore construction, and eutrophication embedded in a global warming context (Richardson et al., 2009). All those factors are gathered in coastal lagoons (Pérez-Ruzafa et al., 2019b), and semi-enclosed environments, which are also prone to host jellyfish blooms (Fernández-Alfías et al., 2021).

We have monitored the pelagic populations (ephyra and medusa stages) of three scyphozoan species, *Aurelia solida* Browne, 1905, *Cotylorhiza tuberculata* (Macri, 1778) and *Rhizostoma pulmo* (Macri, 1778), in the Mar Menor coastal lagoon, in different projects from 1997 until 2021. The existence of such a long time series, including three different jellyfish species in a semi-enclosed ecosystem prone to register blooms and affected by anthropic pressure and eutrophication in a global warming scenario has allowed us to analyze the phenology of those species and to test if their phenological responses were affected by different regimes of thermal anomaly and the different stages of the eutrophication process (low and high chlorophyll *a* concentration regime).

2. Material and methods

2.1. Study site and studied species

The Mar Menor is a hypersaline lagoon with a surface area of 136.1 km² and 4.4 m of mean depth, located on the southeast coast of Spain.

The lagoon has been occupied by dispersed human populations for centuries, but despite the fishing activities carried out in its waters, its functioning was mainly directed by natural factors (Pérez-Ruzafa et al., 1987). However, during the last century, and with a particular increase since 1970, the lagoon has been exposed to strong anthropic pressure. The habitat has been deeply modified by the construction of harbors, rock dams, and artificial beaches as a response to the touristic demand. The most noticeable actuation of that decade, in terms of ecological functioning, was the dredging and widening of El Estacio channel for the construction of a harbor between the coastal lagoon and the Mediterranean Sea (Pérez-Ruzafa et al., 1991). This modification has increased the water exchange between both water bodies, reduced the salinity and water residence time in the lagoon, and eased the colonization of the lagoon by Mediterranean species (Pérez-Ruzafa et al., 2005, 2012). In the decade of 1980, the agricultural regime of the drainage basin was transformed from dry farming to an irrigated regime. This transition was coupled with an increase in the nutrient input to the lagoon and the start of a eutrophication process that, after 30 years of ecosystem resilience, led to a series of dystrophic crises and mass mortalities of organisms (Pérez-Ruzafa et al., 2019a; Fernández-Alfías et al., 2022).

Before the increase of the anthropic pressure, *A. solida* (unpublished own data), reported in previous works as either *A. aurita* (Pérez-Ruzafa, 1989) or *Aurelia* sp. Lamarck, 1816 (Fernández-Alfías et al., 2020, 2022), was the only component of the gelatinous macro-zooplankton recorded in the Mar Menor, but the decline in the salinity after the dredging and widening of El Estacio channel has allowed the entrance and proliferation of a variety of species. The observation of most of the gelatinous zooplankton species has been limited to a few individuals or aggregations in a particularly favourable season (Fernández-Alfías et al., 2022), but *C. tuberculata* and *R. pulmo* have settled in the lagoon and maintained regular populations for the last 35 years. The temporal segregation of *C. tuberculata*, *R. pulmo*, and *A. solida* medusa populations as well as the lack of predators for the adult stages allowed their coexistence in Mar Menor (Fernández-Alfías et al., 2020).

2.2. Sampling design

Spatial and temporal medusa and ephyra abundance, chlorophyll *a* concentration, and sea surface temperature (SST) in the Mar Menor coastal lagoon have been monitored, from February 1997 to December 2021, using a sampling station network that spatially covered the whole lagoon (Fig. 1). Surveys were conducted weekly (February–November 1997 for the medusa stage and February–December 1997 for the ephyra stage), monthly (August 2006 – December 2012), and biweekly (July 2016 – December 2021). During the last sampling period (2016–2021) ephyra samples were collected monthly. A total of 20 sampling stations were first established in 1997. In 2009, three new sampling stations (EN1, ES1, and MA1) were added on the inner side of the inlets between the lagoon and the Mediterranean Sea. Also, in 2017, three coastal stations were added to the regular surveys (5', 9', and 12'). See Table S1 for a sampling and data summary.

SST, chlorophyll *a*, ephyra and medusa abundances were recorded on each sampling occasion and station. Chlorophyll *a* and SST were recorded with two different multiparameter probes, a WTW Multiline F/Set3 before 2016 and a YSI EXO2 ever since. We consider SST as the average temperature of the upper 1.8 m of the water column. Ephyrae were collected by horizontally towing a plankton net (500 µm mesh size) equipped with a digital flowmeter for 7 min at 1.5–2.5 knots (≈ 90 m³ filtered water volume per tow). Zooplankton samples for ephyra identification were fixed with formalin-seawater (3 % v/v) after collection. Once in the laboratory, ephyrae were counted and identified to species level under a dissection microscope following Mayer (1910) and Russell (1970). Medusa abundance was estimated by visual censuses performed by two operators, one on each side of the boat, linearly sailing for 5 min at 1.5–2.5 knots. The water volume monitored through the visual censuses was calculated as a prism function (length x height x width) where

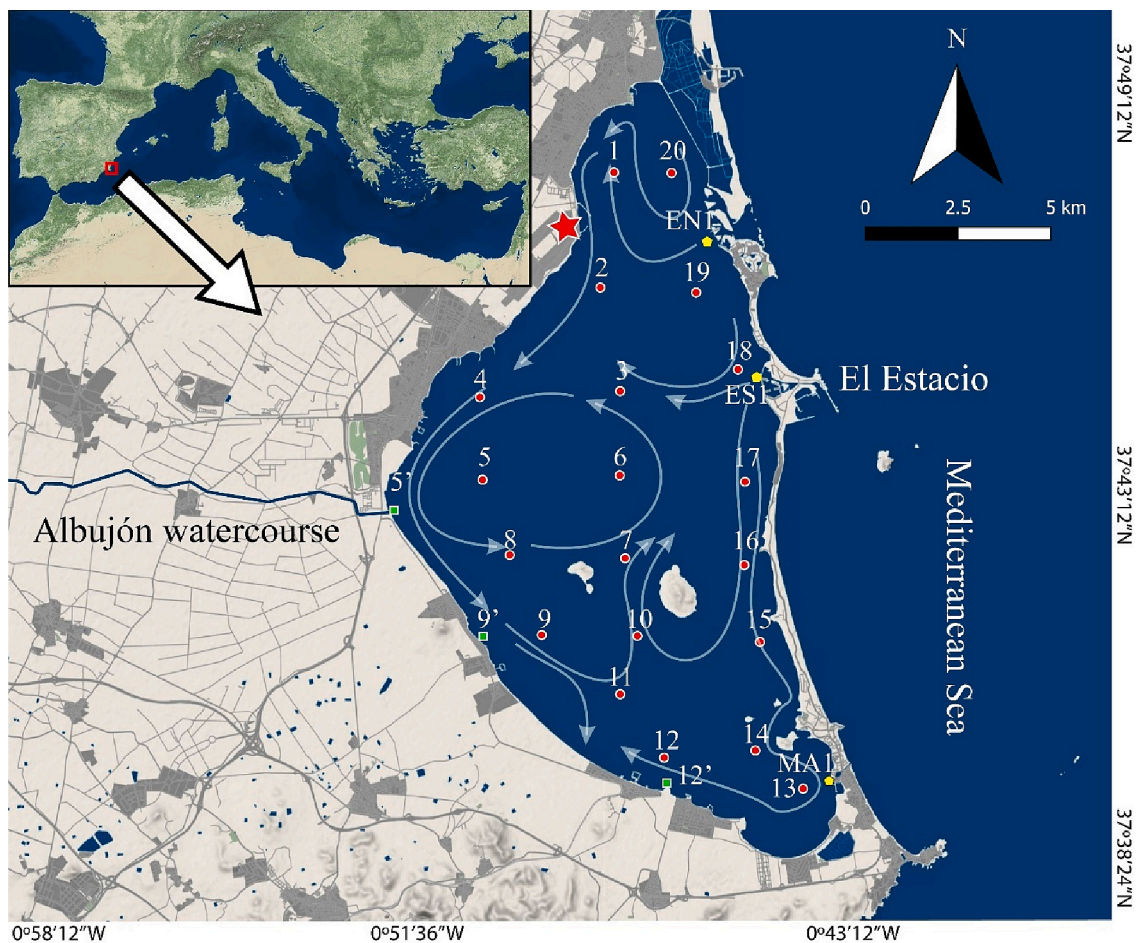


Fig. 1. Sampling stations and main currents in Mar Menor. Red points indicate the original sampling stations. Yellow points indicate the stations added in the inlets in 2009. Green squares indicate the coastal stations added in 2017. The red star indicates the location of San Javier's meteorological station.

Modified from Fernández-Álías et al., 2022. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the length is the sailed distance, height is the maximum estimated depth that allows species and size identification (2 m) or the water transparency measured with a Secchi disk whenever it was lower, and width is the horizontal distance from the boat side used for the transect (5 m). The jellyfishes were sorted into 4 different size classes of 10 cm length for *C. tuberculata* and *R. pulmo* (0-10 cm, 10-20 cm, 20-30 cm, >30 cm) and 5 cm in the case of *A. solida* (0-5 cm, 5-10 cm, 10-15 cm, >15 cm). Both ephyra and medusa abundances were standardized to individuals/100m³. The dataset consists of 257 sampling campaigns with a total of 5351 jellyfish visual censuses and 4112 plankton net tows.

2.3. Determination of thermal anomaly and ecological periods

The existence of large gaps in our dataset prevents the use of SST for the calculation of the thermal anomaly periods. Thus, we have retrieved the air temperature from San Javier's meteorological station (4 m over sea level) provided by the Spanish Meteorological Agency (AEMET) daily from 1st January 1997 until 31st December 2021 (Fig. 1). The correlation between SST and air temperature has been determined by a linear regression model in R (Fig. S1a). Remote SST measurements have been retrieved from the MODIS-Aqua dataset (<https://neo.gsfc.nasa.gov/>), with a monthly frequency (July 2002 – December 2021), at 0.1 degree resolution, and were used as a secondary proxy for *in situ* SST. The correlation between satellite measurements and *in situ* SST has been determined by a linear regression model in R (Fig. S1b).

Using the air temperature and remote SST as proxies for the *in situ*

SST, we have removed the seasonality and calculated the monthly temperature anomaly. Then, the thermal anomaly periods were determined using the functions *breakpoint* and empirical fluctuation process type OLS-CUSUM (*efp*) from the 'strucchange' package in R software (Zeileis et al., 2002, 2003; Zeileis, 2006).

The ecological status of the Mar Menor coastal lagoon has been evaluated in different works and two different statuses through the eutrophication process can be distinguished in our dataset: one of homeostasis maintenance or pre-crises (1997–2015) and the other with frequent dystrophic crises mainly characterized by an elevated chlorophyll *a* level (2016–2021) (Pérez-Ruzafa et al., 2019a; Mercado et al., 2021; Fernández-Álías et al., 2022).

2.4. Spatiotemporal variability of the species

For the temporal component, ephyrae and medusae abundances for each species, from 1997 until 2021, were standardized to individuals/100m³. For the spatial component, two horizontal distribution maps, one for each ecological period, of each jellyfish species were elaborated by the kriging method in Surfer software. To do so, abundances in each sampling station during each period were averaged and standardized on a 0–100 % scale of the maximum recorded abundance (MRA). Yearly distribution maps, on the same principle, are provided as supplementary material.

2.5. Blooming indicator index

Semiquantitative indicators to assess jellyfish blooming intensity had been proven useful when used with spatial coverage (Lee et al., 2021), and abundance or text mining (Leoni et al., 2021a) as input data. Here, a blooming indicator index (BI) was developed for each species of the Mar Menor coastal lagoon based on a combination of both abundance and spatial coverage through an algebraic addition of its transformed components (Eq. (1)).

$$BI = Ab + SC \quad (1)$$

The abundance component (Ab) can have values of 0 (abundance <1 % of the maximum recorded abundance (MRA)), 1 (1–25 % MRA), 2 (25–50 % MRA), 3 (50–75 % MRA) and 4 (>75 % MRA). The spatial coverage component (SC) is an indicator of the percentage of sampling stations in which a given species was present, holding a value of 0 for the absence of the species and increasing in 1, up to a value of 4, whenever a 25 % interval is surpassed. Thus, the BI ranges from 0 (absence of jellyfish) to 8 (the abundance and spatial coverage are higher than the percentile 75).

2.6. Phenology of the species

To study the phenology of the species, a multistep approach based on the association of each jellyfish stage and medusa class size to a particular frame of an environmental variable was developed. First, the association of each stage and class size to a thermal range by applying a modification of the Cumulative Frequency Distribution (CFD) method from Perry and Smith (1994) was determined. In simple, this methodology plots an unweighted CFD of a given environmental variable and a CFD of the same environmental variable weighted by the abundance of the species. Alike slopes from both curves denote an even distribution of the species throughout the studied variable frame while a steeper slope in a particular range reflects an association of the species to that interval of the environmental variable.

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

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

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

Eq. (2) indicates how the CFD for the environmental variable is constructed, being “n” the total number of observations, “ x_i ” the value of the environmental factor and “ $I(x_i)$ ” an indicator function (Eq. (3)) where “t” represents an index covering the whole range of the environmental variable at a step size appropriate for the desired resolution. In our study, the minimum recorded SST being 9.19 °C and the maximum 31.5 °C, we have set the step size of “t” to 1 °C ranging from 9 °C to 32 °C. Thus, $I(x_i)$ for a given “t” would be the number of data, number of censuses or net tows in our study, for which the environmental variable lay on that step. Eq. (4) indicates how the weighed CFD is constructed, “ y_i ” being the summatory of abundances of the species within the given environmental interval.

To test whether the differences in the slope indicate a significant association to a particular temperature or thermal range, the maximum absolute difference between $f(t)$ and $g(t)$, $D_{\max} = \max|g(t) - f(t)|$, is tested against bootstrapped reconstructions of $f(t)$ and $g(t)$. In each iteration, “ x_i ” and “ y_i ” are shuffled before the reconstruction of $f(t)$ and $g(t)$ and each resulting pair of $|g(t) - f(t)|$ is compared against D_{\max} value. We have performed 1000 iterations of the curve and, having 23 temperature steps, 23,000 comparisons. A significant association of the species to a particular environmental frame implies that the abundances are higher through that interval and that the D_{\max} value is necessarily

higher than the random differences obtained from the reconstructions of the curve. The null hypothesis would be that there is no difference between D_{\max} and the randomly obtained differences between pairs and, thus, an absence of association to any environmental range.

This procedure was applied for all the developmental stages and class sizes of each species in every period, this is to say: the complete dataset, the two different eutrophication periods, and the three different thermal periods determined. The first thermal period ends between December 2006 and September 2008 (June 2007 as the most probable date). Given the gaps of our dataset (Table S1), for the statistical analysis, only the data from 1997 were considered into the period 1, and 2006 and 2007 data were included in the period 2. The second period ends between October 2010 and May 2011 (March 2011 as the most probable date). Given the seasonality of the species, for the statistical analysis, the year 2011 was considered in the period 3.

Secondly, following the principle of the thermal association, we have tested if this association significantly differs between two periods within each developmental stage. This has been performed, within each stage, by calculating the maximum difference between the $g(t)$ of two different periods and testing it against the differences obtained in bootstrapped reconstructions of the curves. The null hypothesis indicates that the association to temperature is alike between the two compared periods, while the alternative hypothesis indicates a significant modification in the thermal association.

Finally, to test if the transition in the ecological status from a low to a high chlorophyll *a* concentration regime did modify the phenology of the species, the association between the jellyfish abundance, in medusa and ephyra stages, and chlorophyll *a*, for each species, in all the described periods were tested. The chlorophyll *a* concentration ranges from a minimum of 0 µg/l to a rare maximum, recorded only in two stations during a dystrophic crisis, of 107 µg/l. All the chlorophyll *a* intervals below a concentration of 25 µg/l have been sampled at least on 2 occasions, but from that concentration on, we have intervals with one or zero samples. Consequently, a step size of 1 µg/l was set up for chlorophyll *a* concentrations below 25 µg/l and all the data over that value were gathered in a final interval.

This procedure allows the determination of thresholds for ephyra appearance (strobilation), for the appearance of juvenile medusa stages (ephyra to medusa transition) and the thermal limit tolerance for the adult specimens. Also, when it is applied to long-term datasets where different thermal or ecological periods can be distinguished, the inter-period comparisons are testing if the global warming and eutrophication processes are affecting the phenological responses of the species. By integrating the information, the life cycles of the three species in the Mar Menor coastal lagoon were reconstructed. The reconstruction of the life cycle and the presence of thresholds was complemented with box and whiskers plots for SST and average umbrella size of the jellyfish populations on classical descriptors (Lee et al., 2021; Leoni et al., 2021a). Those descriptors are the days of the first, start, peak, end, and last observations from the year population, corresponding to the accumulated >0, ≥15, ≥50, ≥85, and 100 % of the year population's BI. For *C. tuberculata* and *R. pulmo*, the box and whiskers plots were constructed with the values of SST and average umbrella size from all the registered populations (1997–2021). In the case of *A. solida*, the populations from the years 2006–2011 were excluded from these plots as they were either absent or experienced mass mortality at the ephyra stage or the 0–5 cm class size.

3. Results

3.1. Thermal anomaly and ecological periods

The empirical fluctuation process shows that there is a structural change in the accumulated thermal anomaly as it surpasses the boundaries ($p < 0.05$) of the null hypothesis of ‘no structural change’ (Fig. 2). Breakpoint analysis on air temperature anomaly confirms that a

Thermal anomaly periods

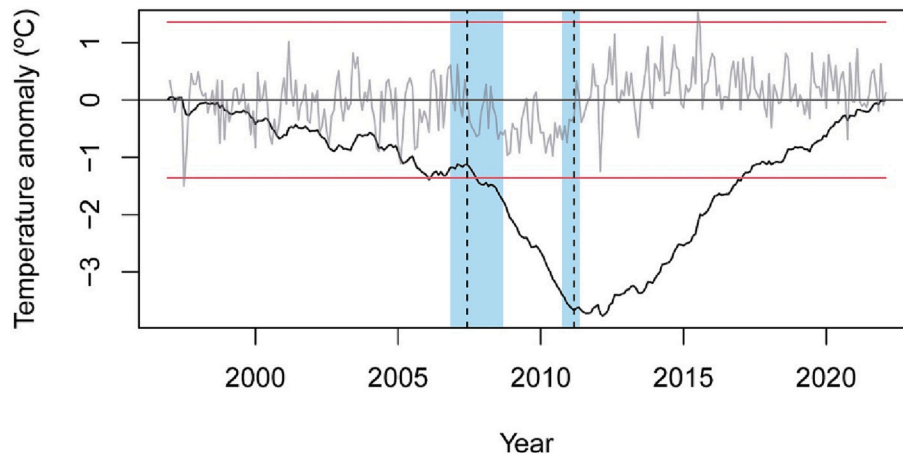


Fig. 2. Thermal anomaly periods. Horizontal lines indicate the monthly thermal anomaly (grey), accumulated thermal anomaly by OLS-CUSUM (black) and $p < 0.05$ boundaries of the empirical fluctuation process (red). Vertical dashed lines are used to indicate the breakpoints and blue shaded areas are used to indicate the confidence intervals of the breakpoints. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

structural change has occurred and reveals the existence of three different thermal anomaly periods through the period 1997–2021. The first period, extended from January 1997 until June 2007 (December 2006 – March 2007 as the confidence interval), is characterized by a negative increase in the accumulated thermal anomaly. The second period, finishing in March 2011 (October 2010 – May 2011 as the confidence interval), was characterized by a sharp negative increase in the accumulated thermal anomaly. The third period was characterized by a positive increase in the accumulated thermal anomaly (Fig. 2). Satellite SST anomaly analysis provide similar results and is only included as supplementary material.

Ecologically, two periods can be distinguished by a change from a low to a high chlorophyll *a* concentration regime. Before 2016, monthly average chlorophyll *a* concentration over 2 $\mu\text{g/l}$ was only registered in 14.7 % of the sampled months with a maximum of 6.2 $\mu\text{g/l}$ in April

2010. Since 2016, phytoplankton blooms increased in frequency (chlorophyll *a* concentration over 2 $\mu\text{g/l}$ was registered on 54.1 % of the sampled months) and intensity (21.2 % of the sampled months surpassed the average concentration registered in April 2010) (Fig. 3). Consequently, two different ecological statuses through the eutrophication process of the Mar Menor can be highlighted in our dataset: one of homeostasis maintenance or pre-crises (1997–2015) and other with frequent dystrophic crises (2016–2021) (Pérez-Ruzafa et al., 2019a; Mercado et al., 2021; Fernández-Alfás et al., 2022).

3.2. Jellyfish spatiotemporal and bloom variability

The three monitored scyphozoan species have shown different spatiotemporal and blooming patterns both in the medusa and the ephyra stages with important interspecies and interannual variability.

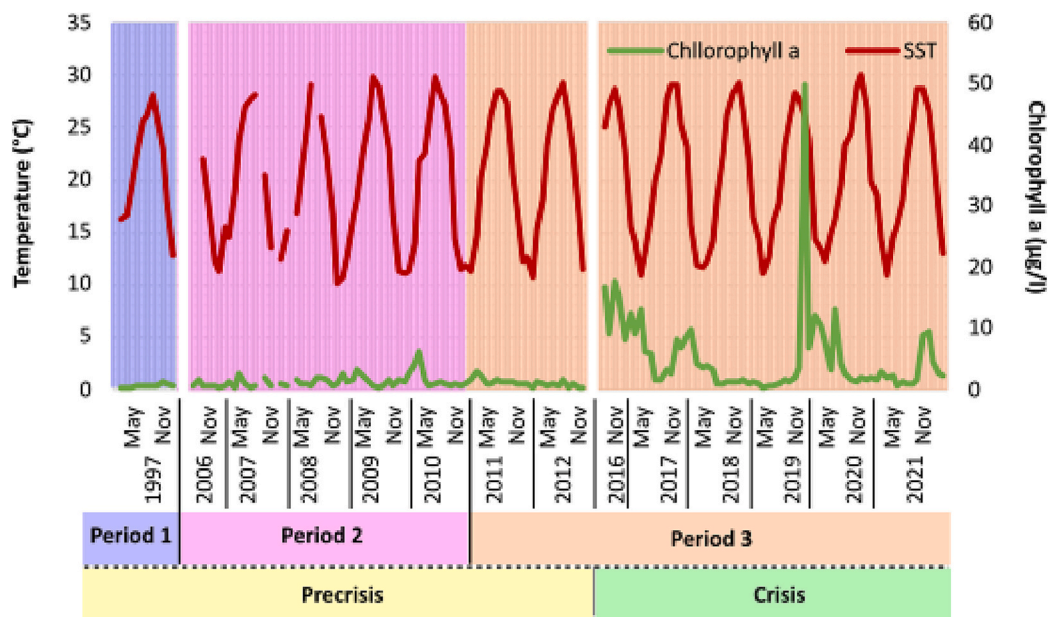


Fig. 3. Chlorophyll *a* and SST dynamics with thermal anomaly periods (blue, purple, and orange shaded areas corresponding with each of the three thermal anomaly periods) and ecological periods (yellow and green shaded areas corresponding with the pre and dystrophic crisis period respectively). Vertical white areas indicate discontinuities in the dataset. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Regarding the temporal pattern, we observed the segregation of the three species during the year. *A. solida* occurs in the water column from January to June, being replaced afterwards by *C. tuberculata*, which is present from June until December. *R. pulmo* is capable of overwintering and can be present all year round, but higher abundances were observed from May until August (Figs. 4, 6).

In terms of abundance, before 2016, *C. tuberculata* has been the most common species, with maximum recorded abundances of 151.8 ind/

100m³ for the ephyra stage (August 2011) and 146.1 ind/100m³ for the medusa stage (September 2011). However, this jellyfish has suffered a reduction in abundance since the beginning of the dystrophic crisis period. A similar trend has been found for *R. pulmo*, being the maximum abundances for the ephyra (9.6 ind/100m³) and the medusa stages (3.4 ind/100m³) registered in January 2009 and May 2012 respectively, with a reduction in its presence since the beginning of the dystrophic crisis period. In the case of *A. solida* the opposite tendency can be observed.

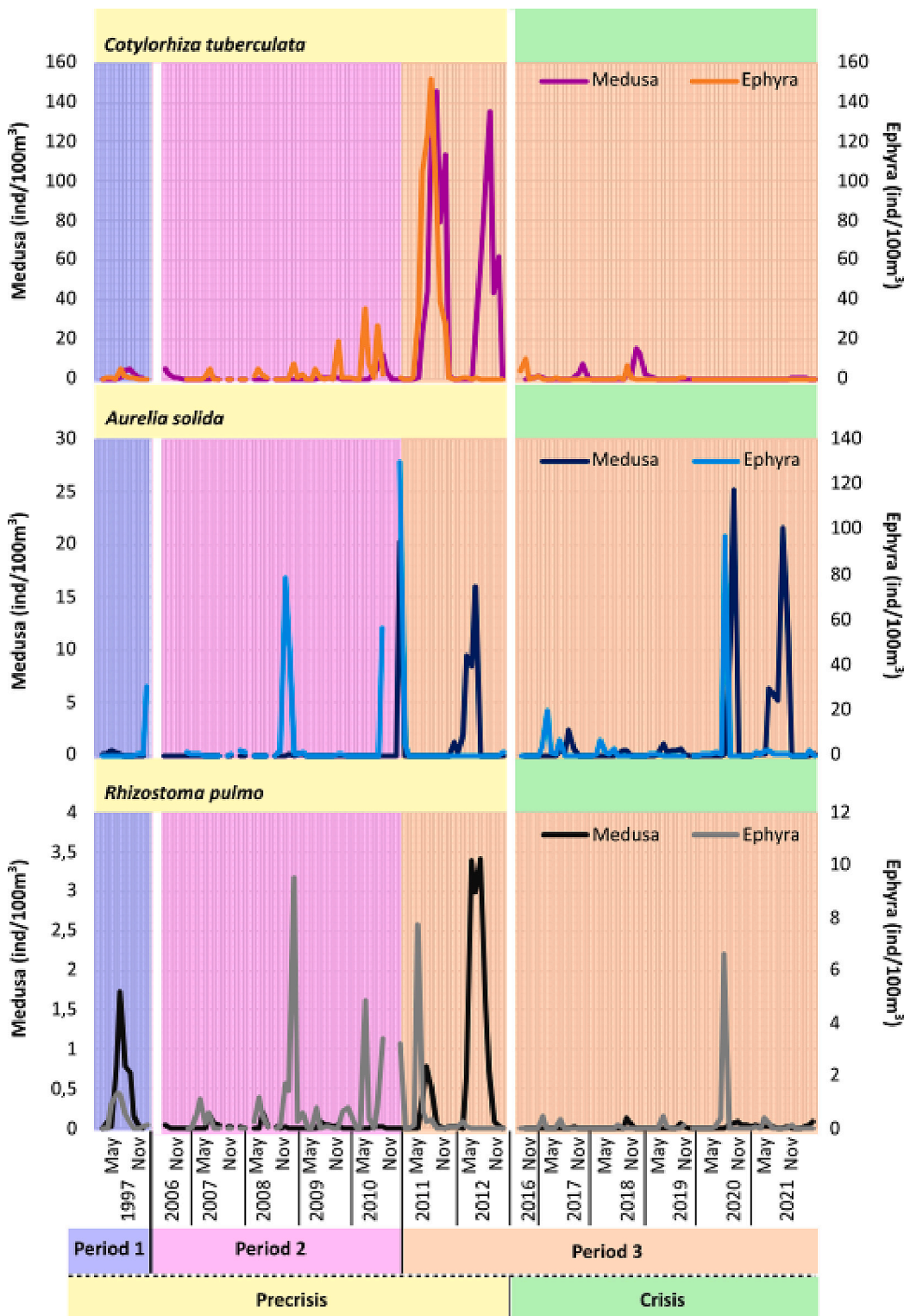


Fig. 4. Jellyfish, medusa and ephyra stages, dynamics of *C. tuberculata*, *A. solida* and *R. pulmo* with thermal anomaly periods (blue, purple, and orange shaded areas corresponding with each of the three thermal anomaly periods) and ecological periods (yellow and green shaded areas corresponding with the pre and dystrophic crisis period respectively). Vertical white areas indicate discontinuities in the dataset. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

This jellyfish did develop a low abundance population in 1997 and has been almost absent in the water column between 2006 and 2010. The individuals from 2011 were detected only on the 12th of January, having all the individuals an umbrella diameter lower than 5 cm and disappearing afterwards. Interestingly, the maximum abundance of the ephyra stage ($200 \text{ ind}/100\text{m}^3$) was recorded in that month. Ever since the beginning of the third thermal period, *A. solida* has yearly developed an adult population with a maximum recorded abundance on the medusa stage of $25.2 \text{ ind}/100\text{m}^3$, registered in June 2020 (Fig. 4).

The horizontal distribution maps show spatial segregation between the three species of jellyfish. *C. tuberculata* occupied the whole lagoon, but with a preference for the central and inner shore of the lagoon, and without a reduction in the habitat despite the reduction in the abundance. *A. solida*, present mainly between the islands in the precrisis period, has extended its habitat towards north during the dystrophic crises period. *R. pulmo*, occurring in the whole lagoon before the dystrophic crises period, but with a preference for the inner and southern shores, has its habitat reduced to those areas and the outer shore since the arrival of that period (Figs. 5; S3).

Our blooming indicator index integrates information about abundance, temporal and spatial patterns. From it, we retrieve that the blooming pattern has also been different between the three species. *C. tuberculata* and *R. pulmo* major blooms were concentrated before the beginning of the dystrophic crises period. Ever since, only a major bloom of *C. tuberculata* was recorded in the summer of 2018, while the presence of *R. pulmo* has been limited to minor blooms. On the contrary, *A. solida* blooms have increased in frequency and intensity since the beginning of the third thermal anomaly period and the dystrophic crises period (Fig. 6). The first two years of the third thermal anomaly period, 2011

and 2012, are key years in this change of the blooming pattern, being both years for which major blooms of the three species have been recorded.

3.3. Phenology of the species and variability between periods

Here we present the SST and the average size of the population on the day of the first (>0 % year accumulated BI), start (≥ 15 % year accumulated BI), peak (≥ 50 % year accumulated BI), end (≥ 85 % year accumulated BI), and final (100 % year accumulated BI) observation of each species. Also, we present the thermal association of the different life cycle stages for each species in the period 1997–2021 (Table 1), the comparison of the thermal association between the different periods for each species at the ephyra and medusa stages (Table 2). The thermal association of each stage and class size within each period is provided as supplementary material (Table S2).

Attending to the main descriptors of jellyfish populations, the first observations (>0 % year accumulated BI) of *C. tuberculata* medusae were mainly registered between 26.5 and 29.5 °C with an average umbrella size of the population between 5 and 12.8 cm. The beginning of the population (≥ 15 % year accumulated BI) was registered between 27.2 and 29.3 °C at sizes in the range of 6.8–15 cm. The peak of the population (≥ 50 % year accumulated BI) was reached after a decline in temperature (25.3 – 28.2 °C) and an increase in size (9.9–20.8 cm). The end of the population (≥ 85 % year accumulated BI) got placed between 16.4 and 25.0 °C at sizes of 13.1–24.9 cm. The final observations (100 % year accumulated BI), depending on the longevity of the adults and a late transition of ephyra to medusa take place at sizes in the range of 5 to 25 cm with temperatures between 12.6 and 20.5 °C (Fig. 7ab).

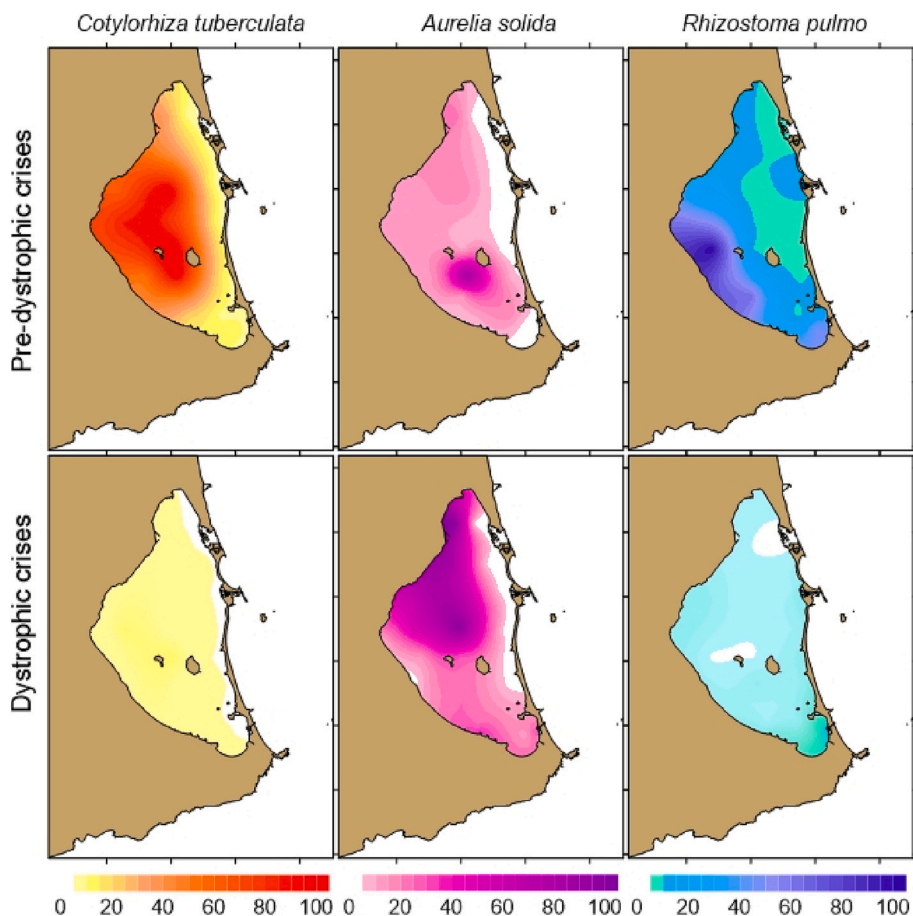


Fig. 5. Horizontal distribution map of *Cotylorhiza tuberculata*, *Aurelia solida*, and *Rhizostoma pulmo* during the precrisis and dystrophic crises period. Abundances are standardized in a 0–100 % scale of the maximum recorded abundance.

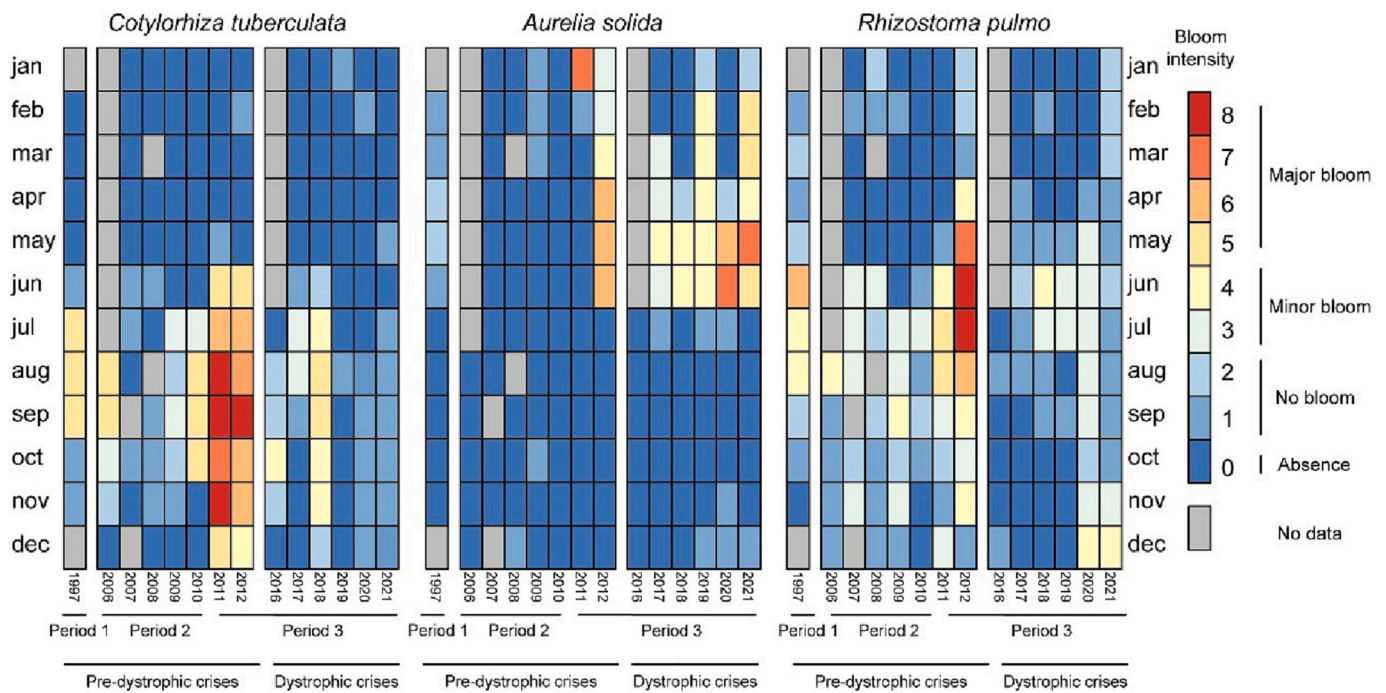


Fig. 6. Blooming indicator index for the scyphozoan species of the Mar Menor coastal lagoon and its evolution. 0: Absence of jellyfishes, 1–2: No bloom, 3–4: Minor bloom, 5–8: Major bloom.

Table 1

Temperature presence and association ranges of each species and life stage with pvalue of the association in the complete dataset (1997–2021). The medusa column gathers the data from the four size classes of each species. Numbers in bold indicate a significant association with the indicated thermal frame.

	Ephyra	Medusa
<i>Cotylorhiza tuberculata</i>		
Temperature presence range (°C)	9.7–30.1	10.3–31.5
Temperature association (°C)	27–29	25–30
pvalue	0.018	0.004
<i>Aurelia solida</i>		
Temperature presence range (°C)	9.2–29.0	9.5–29.5
Temperature association (°C)	10–17	
pvalue	0.004	0.167
<i>Rhizostoma pulmo</i>		
Temperature presence range (°C)	9.3–29.6	9.5–31
Temperature association (°C)		23–29
pvalue	0.175	0.005

In the case of *A. solida* we have constructed the box and whiskers plot without including the populations from period 2 and that from 2011 given the significantly different behaviour exhibited (Table 2). The first observation of the species is registered between 12.5 and 17.5 °C with an average size of the population of 2.5–9.3 cm. The start is registered with temperatures of 14.0–20.7 °C at sizes of 3.1–9.7 cm. The population peaks at temperatures between 17.9 and 23.6 with sizes between 11.0 and 14.5 cm. The decline of the population is marked by a reduction in size coupled with the increase in SST during the summer. Thus, the end of the population and final observation show sizes of 7.4–12.8 cm and 3.0–10.5 cm respectively at temperatures of 23.4–26.1 °C (end) and 27.0–29.3 °C (final) (Fig. 7cd).

The first appearance of *R. pulmo* is registered between 18.8 and 25.7 °C with average sizes of 5–14.8 cm. The start of the population takes place within an SST of 22.3–27.9 °C and at sizes of 13.87–22.78 cm. The peak of the population, with an average size of the species

between 15.3 and 22.5 cm, occurs at an SST of 25.7–29.0 °C. The end of the population occurs between 13.4 and 28.1 °C with average sizes of the population of 13.7–25.8 cm. The final observation is registered with SST of 11.6–26.2 °C at sizes of 15–34.2 cm (Fig. 7ef).

All three jellyfish species show high plasticity, being detected in a wide thermal range during the ephyra stage and in all the class sizes of the medusa stage. Despite this plasticity, some association with thermal ranges exist. *C. tuberculata*'s ephyra stage is associated with the range of 27–29 °C and the medusa stage is associated with the range of 25–30 °C (Table 1) without significant differences between periods (Table 2). The ephyra stage of *A. solida* is associated with an SST range of 10–17 °C while for the medusa stage, no significant association is found (Table 1). This species, in the medusa stage, exhibited a significantly different behaviour during the thermal anomaly period 2 (Table 2). During that period, the ephyrae were not particularly associated with any thermal range (Table S2), but the pattern did not differ significantly from the other periods. On the contrary, the transition from ephyra to medusa and the medusa development did not occur, as strobilation peaks did not lead to medusa formation and, when the transition occurred, the medusae never reached the second-class size (Fig. 4; Table S1). Also, for the ephyra stage, it should be noted that they have mostly been recorded after the decrease of temperatures during the autumn (Figs. 4, 6), but one important strobilation event took place in April 2020 with the temperatures increasing during spring, slightly modifying the strobilation pattern during the dystrophic crises period (Table S2). For *R. pulmo* only the medusa stage showed an association with SST between 23 and 29 °C (Table 1). When comparing both periods, no significant differences were detected at the medusa stage, but the ephyra stage exhibited a significantly different behaviour during the crises period, being associated during that period with 12–20 °C (Table 2; Table S2).

3.4. Chlorophyll a and jellyfish blooms

Since the beginning of the sampling period, the amount of data collected in which the chlorophyll a concentration held values below 2 µg/l has followed a decreasing trend. During the first thermal period and before the dystrophic crises period, the percentage of collected data with

Table 2
Comparison of the thermal association between periods for ephyra (below diagonal) and medusa (above diagonal) stages within each species.

<i>Cotylorhiza tuberculata</i>							
	Medusa	Complete	Period1	Period2	Period3	Precrises	Crises
Ephyra							
Complete			0,233	0,4	0,534	0,598	0,35
Period1		0,125		0,24	0,194	0,265	0,142
Period2		0,057	0,037		0,4	0,48	0,352
Period3		0,379	0,092	0,056		0,5	0,428
Precrises period		0,782	0,124	0,048	0,366		0,296
Crises period		0,086	0,087	0,279	0,057	0,093	
<i>Aurelia solida</i>							
	Medusa	Complete	Period1	Period2	Period3	Precrises	Crises
Ephyra							
Complete			0,058	0	0,705	0,198	0,405
Period1		0,315		0	0,061	0,107	0,072
Period2		0,265	0,153		0,002	0,016	0,002
Period3		0,355	0,313	0,142		0,194	0,44
Precrises period		0,642	0,326	0,25	0,42		0,098
Crises period		0,069	0,052	0,189	0,082	0,048	
<i>Rhizostoma pulmo</i>							
	Medusa	Complete	Period1	Period2	Period3	Precrises	Crises
Ephyra							
Complete			0,186	0,304	0,422	0,67	0,171
Period1		0,098		0,321	0,092	0,266	0,153
Period2		0,232	0,029		0,251	0,308	0,244
Period3		0,353	0,133	0,245		0,362	0,274
Precrises period		0,667	0,154	0,228	0,312		0,13
Crises period		0,002	0	0,064	0,035	0,002	

a value of chlorophyll *a* below 2 µg/l exceeded 85 % of the total collected data. However, since the beginning of the dystrophic crises period, only a 45.93 % of the data lay within the 0–2 µg/l chlorophyll *a* concentration interval. When the data on jellyfish are looked upon this reduction did not occur on the medusa phase of any species, being 89 % of the CFD already reached during the first two steps of its construction, in all the species, during the dystrophic crises period. In the case of the ephyrae, a reduction, similar to that occurring with the chlorophyll *a*, is found for *A. solida* and *R. pulmo* (Table 3).

The CFD analysis of association to a chlorophyll *a* concentration range showed that the interval of 0–2 µg/l was the most probable for every species and stage to be associated with, but none of them showed a significant association with the interval (Fig. 8). Nevertheless, it should be noted that there exists a tendency towards a significant association of the medusa phases and *C. tuberculata*'s ephyrae with this interval revealed by a sharp reduction of the *p*value coupled with the reduction in the amount of data with chlorophyll *a* concentration below 2 µg/l. In the case of *C. tuberculata*, between the precrises and the dystrophic crises period, the reduction in the *p*value is 0.348 for the medusa phase and 0.370 for the ephyra stage, while the medusa phase of *A. solida* and *R. pulmo* show a reduction of 0.262 and 0.245 respectively (Fig. 8).

3.5. Life cycle

We have reconstructed the life cycle of each species in the Mar Menor coastal lagoon, focusing on our additions, by combining all the previously displayed data (Fig. 9). For this purpose, we have considered that the detection of ephyrae in the water column is indicative of a close in

time strobilation event.

The ephyrae of *C. tuberculata* appear in the Mar Menor after a major strobilation event in late spring and summer, between 24 and 29 °C. Eventually, the strobilation is extended until autumn or early winter (Fig. 5; Table 1). However, the autumn-winter strobilation does not lead to an ephyra to medusa transition, existing a threshold for the appearance of juveniles of medusa at 25–29 °C, being this transition precluded by the decrease in temperature (Figs. 6a, 7a; Table 1). During the summer SST peak, the medusae undergo continuous growth before the release of the planulae and the massive medusa mortality during the late autumn and early winter (Figs. 6a, 7a).

The polyps of *A. solida* strobilate mainly from 10 to 19.5 °C. This strobilation is triggered by the decrease in temperatures occurring between November and December with an exception in 2020. During that year, the strobilation started in late autumn and early winter but got a peak in April when the temperatures began to rise in spring (Figs. 4, 5). Other minor strobilations have been recorded at 22.5 °C and 26.5–28.5 °C without being followed by an ephyra to medusa transition. We have detected a threshold for this transition, being impeded when the SST surpasses 19.5 °C (Fig. 7b; Table S2). Also, it should be noted that, despite the absence of differences in strobilation between the different periods, massive mortalities at ephyra or 0–5 cm class size can prevent the development of the population (Figs. 5, 6b; Tables 2, S2). The medusae grow during spring until the SST reaches 21.7 °C. Afterwards, the release of the planulae takes place, and the medusae undergo a reduction in size and massive mortality between 24.5 and 29 °C.

In the case of *R. pulmo*, the strobilation occurs throughout the year, but the transition from ephyra to medusa only takes place when the SST

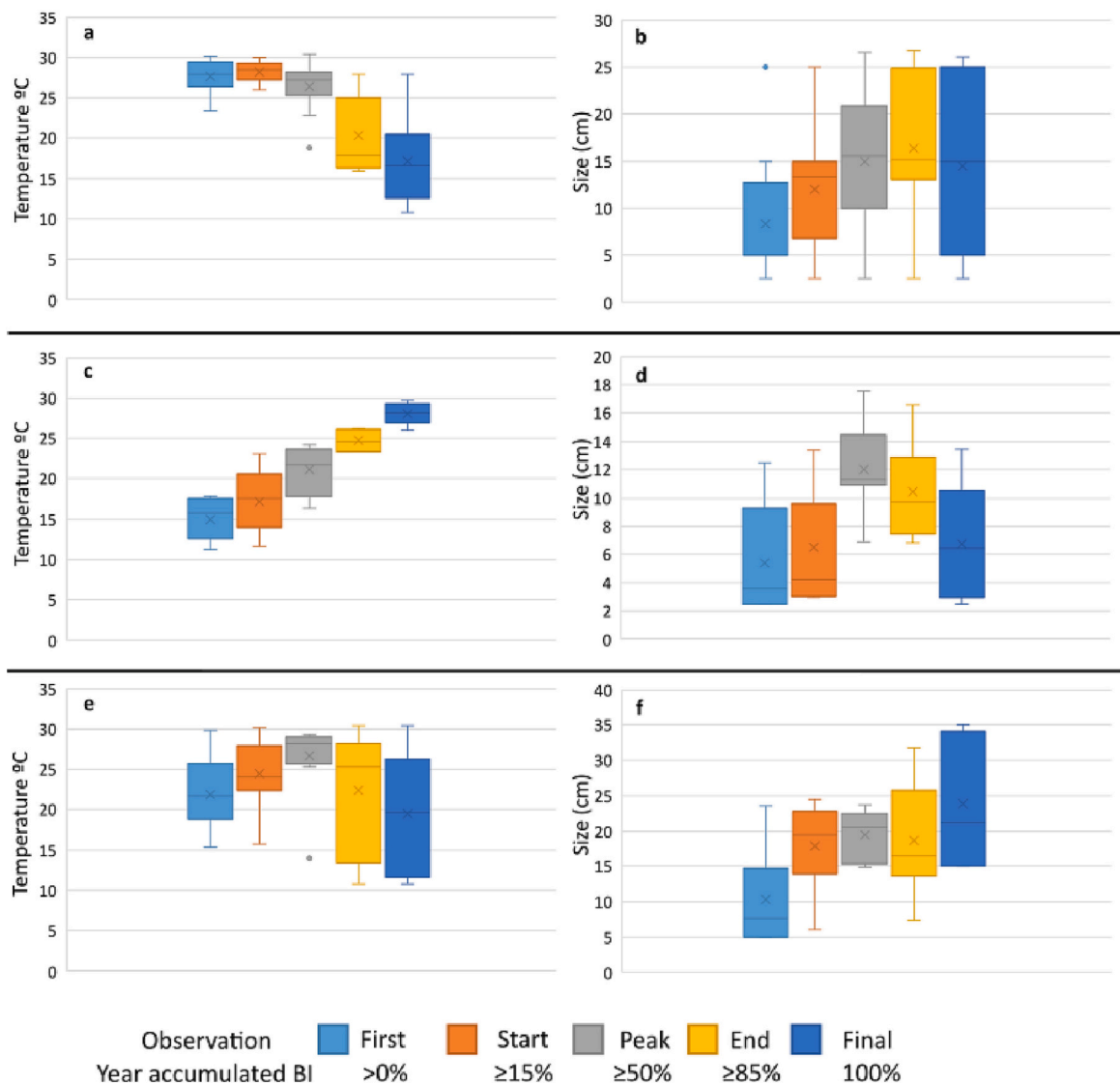


Fig. 7. Box and whiskers plot of SST (a, c, e) and average umbrella size of the individuals (b, d, f) during the development of the populations (first, start, peak, end, and final observations of the population) of *Cotylorhiza tuberculata* (a, b), *Aurelia solida* (c, d), and *Rhizostoma pulmo* (e, f) throughout the dataset (1997–2021). The *Aurelia solida*'s populations from 2006 to 2011 were excluded from the plots given the absence of medusae or the massive mortality at the class size 0-5 cm.

Table 3

Percentage of data whose chlorophyll *a* concentration was below 2 µg/l, f(2) in Eq. (2), (chlorophyll *a* column), and cumulative frequency distribution (CFD) of the jellyfish species, in medusa and ephyra stage, for that interval, g(2) in Eq. (4).

	Chlorophyll <i>a</i>	<i>Cotylorhiza tuberculata</i>		<i>Aurelia solida</i>		<i>Rhizostoma pulmo</i>	
		Medusa	Ephyra	Medusa	Ephyra	Medusa	Ephyra
Complete	69.51	97.35	98.41	96.19	97.93	98.40	95.25
Period 1	99.16	99.83	100	100	100	99.57	100
Period 2	80.33	99.77	98.98	92.71	99.67	99.28	93.87
Period 3	56.91	96.06	97.41	94.57	90.12	99.39	93.86
Precrises	85.31	98.53	98.97	99.83	99.84	96.39	97.37
Crises	45.93	91.79	84.56	90.77	51.13	89.93	68.29

surpasses 21 °C (Fig. 6c; Table 1). The medusae keep growing during the late spring and the summer. Most of the medusae disappear from the water column at the end of this season, but some individuals do overwinter, and the adults can be seen throughout the year.

4. Discussion

4.1. Spatiotemporal variability and blooming pattern

The gelatinous plankton assemblage of the Mar Menor coastal lagoon is composed of ten different species, but most of them do not settle in the ecosystem and are classified as marine stragglers or marine frequent

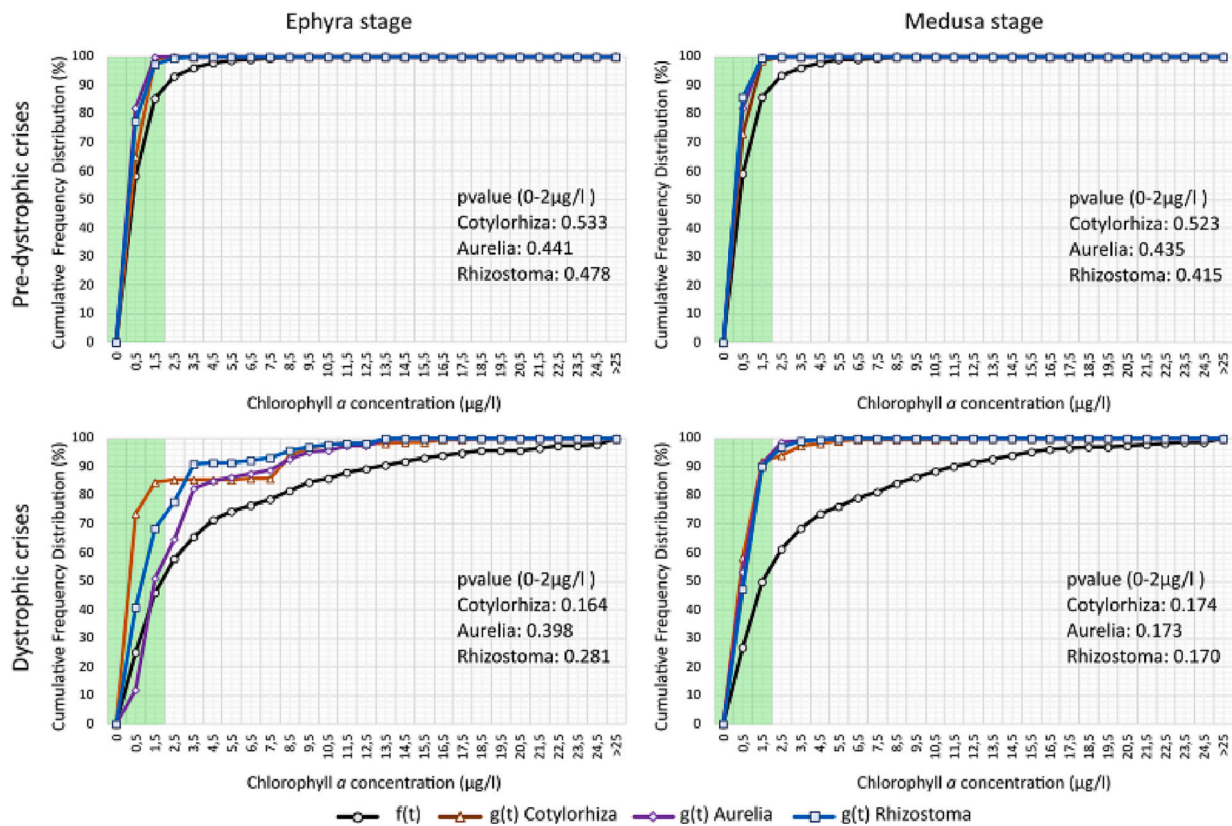


Fig. 8. Cumulative frequency distribution for the association between chlorophyll *a* concentration ($f(t)$) and the three studied jellyfish species ($g(t)$; ephyra and medusa stages), in the two distinguished ecological periods. Green shaded area indicates the most probable interval of association between the species and chlorophyll *a*. *p*-value indicates the probability of the association between jellyfish and the 0-2 µg/l chlorophyll *a* concentration limit. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

visitors *sensu* Pérez-Ruzafa et al. (2019b) (Fernández-Alfás et al., 2022). From that list, three species of Scyphozoan jellyfish, *C. tuberculata*, *A. solida*, and *R. pulmo*, are perennial in the Mar Menor coastal lagoon showing a temporal and spatial variability on their proliferation (Fernández-Alfás et al., 2020). The seasonality of the three species was first described for the years 1996 and 1997 (Pérez-Ruzafa, 1996, 1997; Fernández-Alfás et al., 2020), and, despite the existence of years without some species or despite the large interannual variability in the abundance (Fig. 4), the pattern is maintained throughout all the monitoring period (Fig. 6). These irregularities, including differences in abundance and the existence of years without any sighting of a given species, are common in long gelatinous zooplankton monitoring systems, but the seasonality of the species, when they proliferate, is kept from one year to another (van Walraven et al., 2015; Stone et al., 2019; Pestorić et al., 2021).

The abundance and blooming intensity of *C. tuberculata* and *R. pulmo* have increased from the 1990s until the year 2012 (Figs. 4, 6), and suffered continued decline since the moment in which the dystrophic crises of the Mar Menor started taking place (Fernández-Alfás et al., 2022). During the most important blooms, the populations reached maximum densities of 146.10 ind/100m³ (September 2011; Fig. 4) in the case of *C. tuberculata* and 3.41 ind/100m³ (July 2012; Fig. 4) in *R. pulmo*, corresponding with a population, for the whole lagoon, of about 875 million individuals of *C. tuberculata* and 20 million individuals of *R. pulmo*. This is an increase in the population of both species, compared to data from 1997 (Pérez-Ruzafa, 1997; Fernández-Alfás et al., 2020), of approximately 3000 %. The density of the populations during that period affected the fishing and tourism sectors and forced the installation of nets protecting bathing areas and the implementation of a massive jellyfish removal program by the local government. The massive removal program was proved inefficient given the

fertility and density of the species (Pérez-Ruzafa, 1997; Pérez-Ruzafa et al., 2002) and was finally suspended in 2014.

This period was followed by an 89.25 % reduction in the peak of maximum abundance since the beginning of the dystrophic crises period for *C. tuberculata* (99.95 % after 2019), and a 96.06 % reduction in *R. pulmo* (Figs. 4, 6). In the case of *A. solida*, the population either died at the ephyra stage or the 0-5 cm medusa class size or was absent between 2006 and 2011 (Figs. 4, 6), but the density during the peak of the population in 2012 was 21.43 times higher than in 1997. This trend continued during the dystrophic crises period, for a final increase in the density, between 1997 and the dystrophic crises period, of 5730 % (25.21 ind/100m³, about 150 million individuals in the whole lagoon; Figs. 4, 6).

The widening and dredging of El Estacio channel in the decade of 1970 has increased the water exchange between the Mar Menor coastal lagoon and the Mediterranean Sea and eased the SST and salinity conditions in the Mar Menor. Those environmental conditions have allowed *R. pulmo* and *C. tuberculata* colonization of the lagoon (Pérez-Ruzafa et al., 2005, 2012) together with the construction of a commercial harbor in the channel (Pérez-Ruzafa et al., 1991), increasing the availability of hard substrate for polyps' settlement in the point of the highest water exchange (García-Oliva et al., 2018). In this line, *R. pulmo* and *C. tuberculata* were detected in the lagoon for the first time in 1979 and 1980 respectively, being still considered marine frequent visitors by 1989 (Pérez-Ruzafa, 1989). The first bloom of both species, when their classification was changed to lagoon populations, was recorded in the year 1993 (Pérez-Ruzafa, 1996, 1997). By the year 1997, *R. pulmo* was preferentially present in the inner and southern shores, and *C. tuberculata* in the central part and outer shore (Fernández-Alfás et al., 2020; Fig. S3). This partial spatial segregation was completed with *A. solida* occupying preferentially the central part of the lagoon

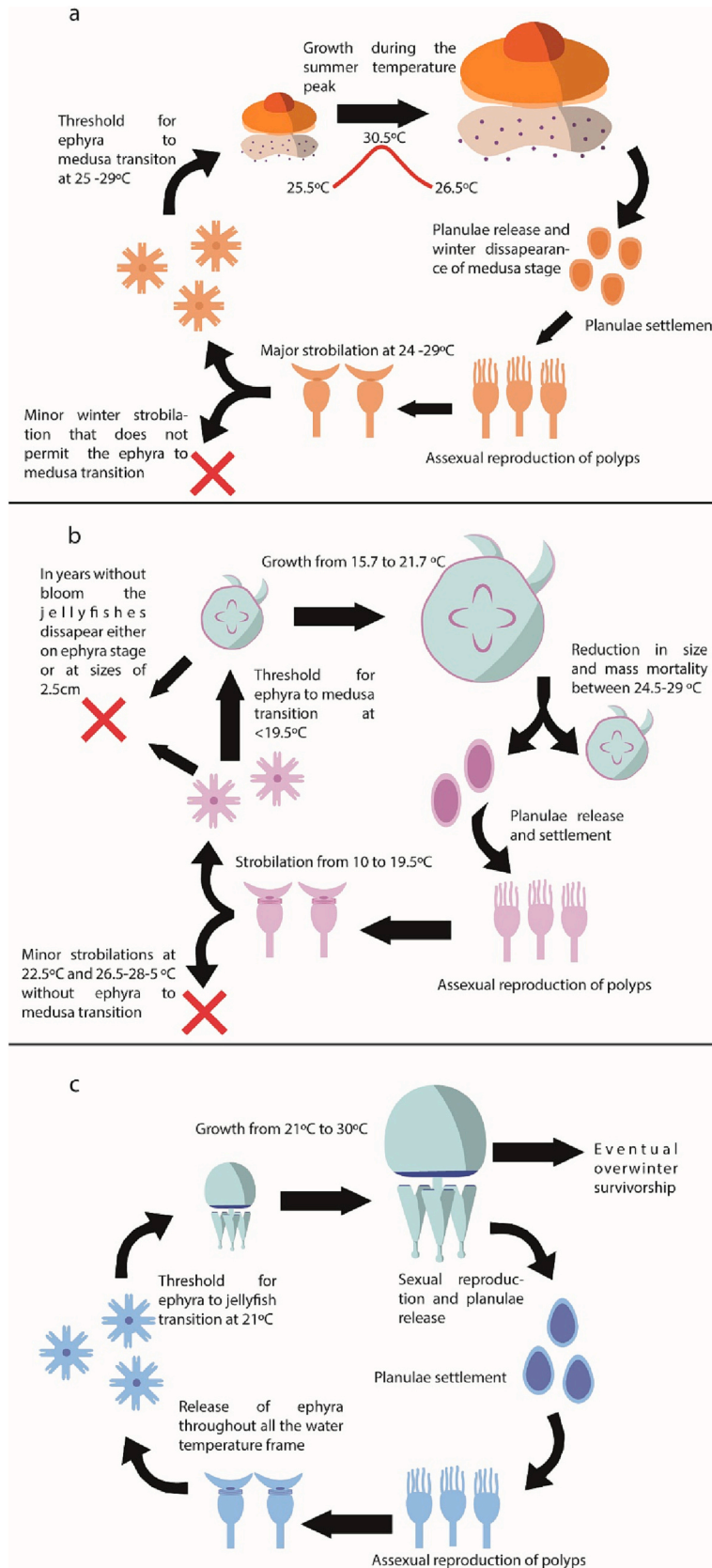


Fig. 9. Life cycle of a) *Cotylorhiza tuberculata*, b) *Aurelia solida*, and c) *Rhizostoma pulmo* in the Mar Menor coastal lagoon.

(Fernández-Alfías et al., 2020). During the pre-dystrophic crises period, *R. pulmo*, and *A. solida* maintain their previous distribution, while *C. tuberculata* moved to the central and inner shores (Fig. 5). The collapse of the population of *C. tuberculata* during the dystrophic crises period (Fernández-Alfías et al., 2022) was not followed by a reduction in its habitat as it occurred with *R. pulmo*. On the contrary, *A. solida* increased their occupation of the lagoon during this last period coupled with the increase in its abundance and blooming intensity (Figs. 4, 5, 6).

4.2. Life cycle

4.2.1. *Cotylorhiza tuberculata*

C. tuberculata is one of the most common bloom-forming species from the Mediterranean Sea (Enrique-Navarro et al., 2021) with settled populations inhabiting semi-enclosed ecosystems such as the Vlyho Bay in Greece (Kikinger, 1992) or the Mar Menor coastal lagoon in Spain (Pérez-Ruzafa et al., 2002; Fernández-Alfías et al., 2020). Since the first appearance of the medusa phase (June–July), the specimens keep growing through the summer and autumn, reaching their maximum sizes, up to 42.1 cm umbrella diameter, in <6 months (Figs. 7, 9; Kikinger, 1992; Fernández-Alfías et al., 2020). The planulae are released in late summer and autumn, with an optimum settling temperature between 23 and 25 °C (Kikinger, 1992; Astorga et al., 2012; Franco, 2016).

After the planula settlement, the polyps acquire zooxanthellae (Astorga et al., 2012), colonize the substrate by asexual reproduction and prepare themselves for the strobilation with the spring temperature rise (Kikinger, 1992; Prieto et al., 2010; Fernández-Alfías et al., 2020). The winter survival of the polyps can be a key point for the development of the blooms given that laboratory experiences yield high mortality at 9 °C or below (Prieto et al., 2010). In the Mar Menor, the polyps must stand the most critical temperatures (SST 9–10 °C) <15 days a year, so we can assume that the winters are not cold enough as to compromise the viability of the summer bloom (Fig. 3; Prieto et al., 2010).

During the winter, we found some ephyrae that did not lead to the appearance of the medusa phase (Figs. 4, 9), being its development inhibited at temperatures of 20 °C or below (Astorga et al., 2012). The major strobilation is registered when, being the food abundant and the polyps zooxanthellated (Kikinger, 1992; Prieto et al., 2010), an increase in the temperature is registered (approximately from 17 to 24 °C), being the ephyrae liberated and present in the water column until an SST of 29 °C (Table 1; Fig. 7; Kikinger, 1992; Prieto et al., 2010; Fernández-Alfías et al., 2020).

We have registered that the average time between the detection of the first ephyra and the first medusa is 68.36 ± 9.83 days (mean \pm standard error), with a minimum of 26 and a maximum of 139 days (Fig. 4), being coherent with the previous data of the Mar Menor and Vlyho Bay (Kikinger, 1992; Fernández-Alfías et al., 2020). The laboratory experiences indicate that the transition from ephyra to medusa can be even faster at high temperatures (Astorga et al., 2012) and that can explain the fact that we missed the ephyra peak or that this showed a lower abundance than the medusa one on the years 2012, 2017, 2018, 2020, and 2021 (Fig. 4). The years in which we registered an ephyra peak that could explain the medusa one, the reduction (mortality) of this went from a maximum of a 100 % (winter strobilation) to an average of 69.63 ± 14.16 %, and a minimum of 3.73 % (year 2011). Finally, we have found that the ephyra can reach the medusa stage once the SST surpasses 25 °C (Table 1; Fig. 7), being coherent with laboratory experiments (Astorga et al., 2012).

4.2.2. *Aurelia solida*

A. solida got a winter to early summer medusa phase in the Mar Menor, with a season that starts between December and March and finishes by the end of June (Figs. 4, 6) matching the observations from the Bizerte Lagoon (Gueroun et al., 2020). The medusae grow from their appearance, typically at SST 15.7 °C, until late April – early May

(21.7 °C) (Figs. 7, 9) before experiencing a reduction in size in a pattern alike the observations from the Bizerte Lagoon (Gueroun et al., 2020). During the growth, the medusae prey over a variety of zooplanktonic groups (Gueroun et al., 2020) and diatoms (Fig. S4), while preparing themselves for the sexual reproduction and planulae release. During the zooplankton sampling by Fernández-Alfías et al. (2022), we found planulae of *A. solida* from March until June 2021, when the average size of the medusa population reaches the maximum and starts the decrease in size. This reduction, first described in the ecosystem for the population of 1997 (Fernández-Alfías et al., 2020), has been maintained through the years (Fig. 7), observed in distinct geographic locations (Gueroun et al., 2020) and *Aurelia* spp.'s lineages (Möller, 1980; Toyokawa et al., 2000; Bonnet et al., 2012). As explanations for this reduction in size, the extrusion of the gastric filaments when the planulae are released and the subsequent loss of the ingestion ability (Spangenberg, 1965), genetic determination, and parasitism have been proposed (Möller, 1980).

The polyps of *A. solida*, and in general through the genus *Aurelia*, have shown great plasticity in terms of survival and asexual reproduction through a wide temperature and salinity window (Schäfer et al., 2021). The strobilation is, on the contrary, thermally restricted. Without thermal fluctuations, the strobilation of *A. solida* is almost negligible and the released ephyrae can be deformed (Schäfer et al., 2021). In the natural environment, where the temperature fluctuates through the year and within the day in semi-enclosed ecosystems, the strobilation of *A. solida* is registered when a decline in temperature occurs (Fernández-Alfías et al., 2020; Gueroun et al., 2020). In the Mar Menor coastal lagoon, the ephyra stage is typically present in the water column from November, following a 10 °C SST reduction between September and November (Fig. 4), until March, thus occurring between 10 and 17 °C (Fig. 3; Table 1). The ephyra to medusa transition takes between 11 and 153 days (average 71.5 ± 16.95 days; Fig. 4) in the Mar Menor, and 30–60 days in the Bizerte Bay (Gueroun et al., 2020). The mortality rate for the years in which the ephyra peak abundance is higher than the medusa one is between 74.01 and 100 % (average 92.17 ± 3.33 %).

4.2.3. *Rhizostoma pulmo*

The barrel jellyfish, *R. pulmo*, is a common jellyfish in coastal areas and semi-enclosed basins in the Mediterranean and Black Sea (Fuentes et al., 2011; Leoni et al., 2021a, 2021b). The medusa phase can be present all year round, being capable of surviving through the winter (Figs. 4, 6; Fernández-Alfías et al., 2020; Pestorić et al., 2021), but the peak of the population is registered between April and August (Leoni et al., 2021b). The appearance of juveniles is associated with a minimum temperature of 21 °C (Table 1; Fig. 9) but can occur with values from 18.78 °C in the Mar Menor (Fig. 7) and they keep growing until maximum sizes that can exceed the 40 cm umbrella diameter are reached (Fernández-Alfías et al., 2020; Leoni et al., 2021b). We have registered a great dispersion in the sizes and SST during the final observation of the year population (Fig. 7), explained by the existence of multiple cohorts with different growth and mortality rates (Fernández-Alfías et al., 2020; Leoni et al., 2021b).

The analysis of the gonad-somatic index and the survival ability of *R. pulmo* suggested a longer reproductive period than the other two species that undergo complete mortality after the sexual reproduction (Fernández-Alfías et al., 2020). After settling on hard substrates, the polyps asexually reproduce and colonize the substrate through podocyst formation (Fuentes et al., 2011; Schiariti et al., 2014). The strobilation is triggered by temperature changes (Fernández-Alfías et al., 2020), which in semi-enclosed environments with high variability occur multiple times and, given the polydisk strobilation strategy of the polyps (Fuentes et al., 2011), yield multiple cohorts (Fernández-Alfías et al., 2020; Leoni et al., 2021b).

In our long-term analysis, we have found that the ephyra recruitment can occur through all the temperature frame, not being this stage particularly associated with any temperature, but the transition from

ephyra to medusa is temperature regulated, existing a threshold for the transformation at approximately 21 °C (Table 1; Fig. 9). The required time for the transition from ephyra to medusa is difficult to assess given the continuous recruitment of ephyrae, and the possibility of missing the ephyra peak in the sampling (Leoni et al., 2021b), but assuming that one peak of ephyra abundance is indicative of a close in time strobilation, the transition has been estimated to take between 27 and 53 days (Fernández-Alfás et al., 2020).

4.3. Factors operating over seasonality and bloom intensity

4.3.1. The role of temperature on the scyphozoan seasonality

Climate change, and more specifically, temperature, has been the most reported factor involved in the blooms of scyphozoan species (Pitt et al., 2018; Fernández-Alfás et al., 2021). However, the temperature and the thermal amplitude regulate the life cycle, but temperature by itself does not guarantee the development of a bloom (Fernández-Alfás et al., 2021). In this line, the overamplification of the statements present in the three most influential reviews on the gelatinous zooplankton status could have enhanced the perception of the ocean warming increasing the jellyfish abundance in the seas (Pitt et al., 2018), and the role of temperature needs to be revised and redefined.

Our analysis revealed that the seasonality is directed by temperature, being the different stages and class sizes of the scyphozoan species linked to specific thermal ranges (Tables 1, S2). Moreover, this association is not modified by changes in the thermal anomaly regime (Table 2), implying that the global warming trend recorded in the oceans (Ramanathan and Feng, 2009) will increase the scyphozoan blooms only if an expansion of the blooming-species that dwell or tolerate warm waters occur and if the thermal amplitude allows the proper development of their life cycle (Fernández-Alfás et al., 2021). On the other side, from the lack of modification of the thermal association in our dataset, it can be expected that the associations between temperature and strobilation or the presence of medusa phase for the different species and ecosystems found in short-term studies and laboratory experiments (e.g. Fuchs et al., 2014; Leoni et al., 2021b; Loveridge et al., 2021) are maintained in time. In other words, the thermal association analyses allow the description of the life cycle of a given scyphozoan species within the studied ecosystem. However, and in agreement with the previous observations (Fernández-Alfás et al., 2021), the maintenance of the thermal association fails to explain the interannual variability and the change in the blooming intensity pattern. This implies that, in general terms, the intensity of the bloom is independent of the phenological response of the species, and different factors need to be discussed.

Even though, there still exist non studied, but plausible, effects of temperature over jellyfish dynamics. For example, there is evidence supporting variations in the strobilation intensity related to the warming speed (Zang et al., 2022), and high mortality of polyps after strobilation (Prieto et al., 2010), but remains a gap in knowledge the effect of short time events, such as heatwaves or cooldowns, over polyp dynamics, if an 'out of season' strobilation might be triggered, and the latter development of ephyra stage when the event is over, or if the 'out of season' strobilation might compromise the 'on time' strobilation.

4.3.2. The role of the trophic state and eutrophication

While the temperature regulates the life cycle, and the transition between the different stages (Table 1; Fig. 9), food availability, both in quantity and quality, enhances the survivorship in the ephyra to medusa transition (Chambel et al., 2016; Miranda et al., 2016), modulates the strobilation intensity (Schiariti et al., 2014; Goldstein and Steiner, 2020), and sustains the population (Girón-Nava et al., 2015). However, the distribution of blooming and non-blooming scyphozoan species seems unaffected by chlorophyll *a* concentration, and complex bottom-up and top-down control interactions might be affecting the intensity of the blooms (Fernández-Alfás et al., 2021).

Our association analysis between jellyfish abundance and chlorophyll *a* concentration indicates an absence of a significant association between both variables (Fig. 8). Even though, the important reduction in the *p*-value registered since the change in the trophic status in 2016 (Pérez-Ruzafa et al., 2019a; Mercado et al., 2021; Fernández-Alfás et al., 2022) indicates that an extension of the periods of elevated chlorophyll *a*, if the medusa phase keeps appearing mainly with low chlorophyll *a* concentration, would link this stage with the 0–2 µg/l chlorophyll *a* concentration interval. Here, it should be considered that the crises are short and spatially restricted (Pérez-Ruzafa et al., 2019a; Fernández-Alfás et al., 2022), making this low chlorophyll *a* concentration interval over-represented and making it difficult to reach a significant *p*-value by the CFD method (Table 3). There are two possible explanations for the reduction of the *p*-value: the proliferation of jellyfish acts as a top-down control for the phytoplankton, or the jellyfish are incapable of blooming in a bottom-up controlled scenario.

The top-down and the bottom-up control equilibrium, between jellyfish and different phytoplankton groups, is fragile, particularly in ecosystems where a eutrophication process is developing (Boero et al., 2008; Fernández-Alfás et al., 2021, 2022). During the first stages of those processes, the primary production is still directed towards the benthic system (Pérez-Ruzafa et al., 2020), and complemented by the top-down control exerted by the jellyfishes (Pérez-Ruzafa et al., 2002). In fact, there is a synergy between both compartments. In the Mar Menor coastal lagoon, before the dystrophic crises period, the bottom of the lagoon was covered by macroalgae and seagrass meadows that fixed nutrients and were suitable for the settlement of the polyps of *C. tuberculata* (Astorga et al., 2012; Pérez-Ruzafa et al., 2012), and altogether with this species, which added nutrient fixation through the symbiotic zooxanthellae and predated over the phytoplankton, out-competed this group (Kikinger, 1992; Pérez-Ruzafa et al., 2002; Enrique-Navarro et al., 2021). However, in the year 2016, a major phytoplankton bloom prevented the light to reach the bottom of the lagoon (Pérez-Ruzafa et al., 2019a) and caused the death of the benthic meadows below 3 m depth (Belando et al., 2017). This year was also marked by a reduction in the abundance of *C. tuberculata* (Figs. 4, 6), probably induced by the same factor given the necessity of its polyps to possess light-dependent zooxanthellae to strobilate (Kikinger, 1992; Prieto et al., 2010). The disappearance of the meadows did not, however, reduce the availability of natural hard substrate for the polyps to settle on as it was coupled with the mortality of benthic organisms such as mollusks (Sánchez-Fernández, O., personal communication) whose empty shells can be used for the settlement (Astorga et al., 2012; Franco, 2016; van Walraven et al., 2020). Thus, the change in the pattern of dominance in the gelatinous zooplankton fraction, from *C. tuberculata* to *A. solida* (Fig. 6), cannot be directly linked to the disappearance of meadows. However, the following dystrophic crises were marked by the presence of hypoxia patches in the bottom layers of the water column (Fernández-Alfás et al., 2022), yielding environmental conditions where the benthic phase of *A. solida* is benefited over that of *R. pulmo* and *C. tuberculata* (Ishii et al., 2008). Also, those dystrophic crises, likely to happen during the summer season (Fernández-Alfás et al., 2022), when the polyps of *C. tuberculata* are expected to strobilate (Figs. 4, 6, 9; Table 1), can prevent the light to reach the bottom of the lagoon and inhibit the strobilation if the viability of the zooxanthellae is comprised.

The temporal segregation of the blooms of *A. solida* and phytoplankton, together with the possibility of a bloom from the latter preventing the proliferation of *C. tuberculata* seems to indicate that the system is bottom-up controlled (Fernández-Alfás et al., 2022), but, at the same time, *C. tuberculata* and *R. pulmo* medusae mainly prey upon diatoms in the Mar Menor (Pérez-Ruzafa et al., 2002), we have found *C. tuberculata* ephyrae with the guts filled with diatoms from the genus *Coscinodiscus* C.G. Ehrenberg, 1839 (Fig. S4), and diatoms of the same genus trapped in the gastric filaments of a mature *A. solida* (Fig. S4). Thus, there exists an equilibrium between both kinds of ecological control of the trophic network in which small variations in the system

alter which group is benefited. Those variations include, among others, predation pressure over polyps, ephyra, and planula stages (Ishii et al., 2004; Takao et al., 2014; Kuplik et al., 2015), or the lack of success in the ephyra to medusa transition (Astorga et al., 2012). In our study, we have found ephyra peaks that are not followed by a medusae population (Fig. 4), indicating ephyra mortality (natural or by predation), the lack of success in the transition from ephyra to medusa, and an interruption of the life cycle. The completion of the life cycle of the scyphozoan is required for the maintenance of the populations as the scyphistoma can experience high mortality rate after strobilation (Prieto et al., 2010) or have their potential to asexually reproduce and strobilate reduced after several generations of asexual reproduction (Chi et al., 2022). Thus, the mortality at the ephyra stage could not only compromise the year's bloom but also the subsequent ones.

CRedit authorship contribution statement

Alfredo Fernández-Álías: Conceptualization, Formal analysis, Investigation, Data Curation, Writing – Original draft, Writing – Review & Editing, Validation; **Juan Carlos Molinero:** Formal analysis; **Jhoni-Ismael Quispe-Becerra:** Investigation; **Delphine Bonnet:** Investigation, Writing – Original draft; **Concepción Marcos:** Conceptualization, Formal analysis, Supervision, Writing – Original draft, Project administration, Funding acquisition, Validation; **Angel Pérez-Ruzafa:** Conceptualization, Formal analysis, Data Curation, Supervision, Writing – Original draft, Project management and administration, Funding acquisition, Review, Editing & Validation.

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.marpolbul.2023.115286>.

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