Population dynamics and relationship with environmental conditions of three scyphozoan jellyfishes in the Mar Menor lagoon (Spain)

Dinámica poblacional y relación con las variables ambientales de tres medusas de la clase Scyphozoa en la laguna del Mar Menor (España)

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<u>Population dynamics and relationship with environmental conditions of three scyphozoan jellyfishes in the Mar Menor lagoon (Spain)</u>

El Dr. Ángel Pérez Ruzafa y el Dr. José Carlos Hernández Pérez autorizan la lectura del Trabajo Fin de Máster "*Population dynamics and relationship with environmental conditions of three scyphozoan jellyfishes in the Mar Menor lagoon (Spain)*" realizado bajo nuestra dirección y presentado por Alfredo Fernández Alías para su defensa ante el tribunal calificador.

En …..….. a ……….. de enero de 2020   En …….. a ……….. de enero de 2020

Fdo. Ángel Pérez Ruzafa   Fdo. José Carlos Hernández Pérez

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Abstract:

Blooms of jellyfishes are perceived to have increased during the last decades causing interference with human activities of both recreational and professional type. Those blooms seem to hold correlation with human impacts and climate change parameters such as overfishing, the increase of temperature, eutrophication and habitat modification. In this study we perform the first simultaneous analysis population dynamics of three scyphozoan jellyfishes, *Cotylorhiza tuberculata* (Macri, 1778)*, Aurelia* sp. and *Rhizostoma pulmo* (Macri, 1778). Moreover, the effect of the nutrient input, temperature, salinity, ichthyoplankton and chlorophyll *a* have been studied for the three species. Temperature and its seasonal cycle have been determined to be a key factors regulating the populations, triggering the strobilation process either by an increase of temperature (*C. tuberculata*) or by a decrease of it (*Aurelia* sp.) and indicating that not all the species of jellyfish may be benefited from the climate change.

Keywords: Population Dynamics, Von Bertalanffy Growth Function, Scyphozoan, Jellyfishes, Environment.

Resumen:

Existe la percepción de que las proliferaciones de medusas han aumentado en abundancia durante las últimas décadas, causando interferencias con actividades humanas tanto de tipo recreacional como profesional. Estas proliferaciones parecen tener correlación con parámetros indicativos de impactos humanos y del cambio climático: sobrepesca, aumento de temperatura, eutrofización y modificaciones del hábitat. En este estudio se lleva a cabo el primer análisis simultáneo de dinámica poblacional de tres medusas de la clase Scyphozoa: *Cotylorhiza tuberculata* (Macri, 1778), *Aurelia* sp. y *Rhizostoma pulmo* (Macri, 1778). Además, el efecto de la entrada de nutrientes, temperatura, salinidad, abundancia de ictioplancton y concentración de clorofila *a* ha sido estudiado para las tres especies. Se ha determinado que la temperatura y su ciclo estacional son factores clave afectando a las poblaciones, disparando el proceso de estrobilación bien por aumento de temperatura (*C.tuberculata*) o por un descenso de esta (*Aurelia* sp.) e indicando que no todas las especies podrían verse beneficiadas por el cambio climático.

Palabras clave: Dinámica poblacional, Función de crecimiento de Von Bertalanffy, Medio ambiente, Medusa y Scyphozoa.

1. Introduction

Since 1970 jellyfishes' blooms are perceived to have been intensified in occurrence and abundance (Purcell, 2005; Brotz *et al.*, 2011). These blooms cause interference with human activities such as tourism, by stinging and even causing the death of swimmers, fisheries, by clogging and collapsing fishing nets, stinging fishermen, killing farmed fish and predating on fish' larvae, and with scientific activities, by causing interference with acoustic probe (Richardson *et al*., 2009). However, jellyfishes have also provided services to humanity having been used as food in Asia (Hsieh, Leong & Rudloe, 2001) and providing, in the field of molecular biology, the green fluorescent protein (Zimmer, 2005) and medicines (Sugahara *et al*., 2006; Ohta *et al.,* 2009) or regulating phytoplankton populations and maintaining the water quality in eutrophication process (Pérez-Ruzafa *et* al., 2002) but being, probably, these benefits overwhelmed by the negative effects caused by them on tourism and fishing activities.

Even if there still exists controversy about if the jellyfish abundance increment is something to be expected as part of an oscillating cycle lasting around 20y (Condon *et al.*, 2013), positive correlations between the climate change and the anthropic effect with the increase of gelatinous plankton have been reported (Purcell, Uye & Lo*,* 2007; Richardson *et al.,* 2009; Lynam *et al.,* 2011, Holst *et al*., 2012; Suchman, *et al.,* 2012).

The increase of temperature, generally, correlates positively with the abundance of jellyfishes within the waters (Purcell *et al.,* 2005), rendering the mild winters longer strobilation periods, higher ephyra production per polyp, a higher percentage of strobilated polyp (Holst *et al*., 2012) and improving the asexual reproduction rates (Purcell *et al*., 2012). However, and even if zooplankton tends to duplicate or triplicate its abundance with a 10ºC temperature increase (Richardson *et al*., 2009), some species (*e.g. Mastigias sp.*) are reported to undergo reductions in abundance in warmer waters (Dawson, 2005).

The habitat modification promoted by the construction, among other structures, of harbours has provided a solid settlement place for cnidarians (Purcell, 2012) easing the benthonic stage of their life cycle. It has also been accompanied by the introduction of alien species in the ballast waters contained in the ships, and whose exchange near shore liberates specimens from larva to adult stage (Graham & Bayha, 2008).

An elevated concentration of nutrients correlates with a higher medusa abundance as has been seen in zones under upwelling phenomena (Suchman *et al*., 2012). This effect

can also be appreciated in eutrophicated areas where the nutrient inputs drives to a high phytoplankton concentration and, subsequently, to increases in the jellyfish's predation over the lower trophic levels of the area (Pérez-Ruzafa *et* al., 2002; Purcell *et al*., 2005; Richardson *et al*., 2009). Moreover, the eutrophication involves an increase in the turbidity and the generation of low oxygen concentration. Both factors imply advantages of medusa over epipelagic fishes, being the first non-visual feeders while the second are visual feeders (Purcell, Uye & Lo, 2007) and being the jellyfishes tolerant to hypoxia conditions (Purcell *et al*., 2001).

Mar Menor lagoon is a hypersaline lagoon in which interior dwell three different scyphozoan species (*Cotylorhiza tuberculata* (Macri, 1778), *Aurelia* sp. (Linnaeus, 1758) and *Rhizostoma pulmo* (Macri, 1778)). The diversity of jellyfishes paired with the anthropic pressure and the oscillation of temperature (10-30 ºC) experienced every year makes it an ideal place to study the connection between the environmental variables and the jellyfish dynamics.

Before the dredging and widening of the Estacio channel only one species of jellyfish has been found in the Mar Menor lagoon, the moon jellyfish referred as *Aurelia aurita* (Linnaeus, 1758), but whose genetics remains unstudied and due to the pool of species that comprises the *Aurelia* genus and which have been traditionally missassigned, and not being this specie present in the Mediterranean sea (Scorrano *et al*., 2017), it will be referred from now on as *Aurelia* sp.. Since the dredging and widening of the channel, two allochthonous jellyfishes can be seen in dense blooms during the summer, *Cotylorhiza tuberculata* (Macri, 1778) and *Rhizostoma pulmo* (Macri, 1778), reaching combined population abundances up to 45 million individuals within the whole lagoon (Pérez-Ruzafa *et al.,* 1987, 2002). Here, the three scyphozoan jellyfish species are considered for the analysis.

Aurelia spp., the more cosmopolitan of the three, is distributed worldwide being thus its life cycle, from strobilation to planulae settlement and polyp formation, the most studied one (Di Camillo *et al*., 2010; Henroth & Gröndahl, 1983; Lucas, 1996; Miyake, Iwao & Kakinuma, 1997; Möller, 1980; Omori, Ishii & Fujinaga, 1995; Schneider, 1994; Tokoyama, Furota & Terazaki, 2000). However, the results show an extremely high interpopulation variability, exemplified by the strobilation process induction by a wide range of temperatures (Lucas, 2001), due to the pool of species which comprises the genus (Dawson & Martin, 2001; Ramšak, Stopar & Malej, 2012; Scorrano *et al*., 2017).

These studies, nevertheless, share the fact that, after reaching sexual maturity, jellyfishes undergo a degradation process which might be induced by parasitic invasion propitiated by the gastric filament extrusion during the gamete release (Spangenberg, 1965). However, starvation has also been reported to induce medusa shrinkage (Hamner & Jensen, 1974) and a combination of energetic investment in reproduction and parasitic invasion might be the cause of the size regression and death.

Within the Mar Menor lagoon, for *Aurelia* sp., only the strobilation temperature has been studied and determined to occur around 14ºC sea temperature (Purcell *et al*., 2012) indicating, presumably, a winter to spring occurrence of the adult pelagic phase.

C. tuberculata, is the species that that reach the highest abundances within the Mar Menor lagoon (Pérez-Ruzafa *et al*., 2002). Its life cycle was first studied in the Bay of Vlyho, Greece (Kikinger, 1992), which share similarities with the Mar Menor lagoon (temperatures seasonally oscillating from 13 to 30 ºC and slow renovation of waters). In this study, author found that an abrupt increase in temperature can trigger strobilation, summer medusa occurrence, 8 to 10 weeks from strobilation until the appearance of young jellyfish individuals, and six months since strobilation until 40cm bell diameter is reached.

C. tuberculata is also the most studied jellyfish in Mar Menor because its massive outbursts cause an interference with the touristic activities, making the authorities react with an intensive fishery that extract up to 4000 tons in 2003 (ECOS, 2004) being it also reported that the removal was highly ineffective as it was overwhelmed by the population growth rate and high fecundity of survivors (Pérez-Ruzafa, 1997; Ruiz *et al*., 2012). Under laboratory conditions, *C. tuberculata* has been determined to strobilate at temperatures superior to 20ºC (Purcell *et al.,* 2012), being it favored by a sudden increase of the temperature (Pérez-Ruzafa, 1997; Prieto *et al*., 2010) and to complete the transition from ephyra to medusa stage in a higher percentage when the water temperature increases (Astorga *et al.,* 2012). This is coherent with its summer appearance within the lagoon and with the model suggested by Ruiz *et al*., 2012. However, and being observations registered by the newspapers and the experiments under laboratory conditions numerous, a fully description of the seasonal cycle inside the lagoon has not been carried out yet.

The life cycle of *R. pulmo* at the lagoon was first described by Fuentes *et al.,* 2011. The ephyras were registered near the Albujon wadi and expanded afterwards to the central area. It reaches the peak of abundance during July and August, but adult individuals are

reported to survive through the winter (Pérez-Ruzafa *et al.*, 2002). Its strobilation temperature has been determined to be optimal between 14-21ºC (Purcell *et al.*, 2012).

With this study we provide the first simultaneous modeling of three jellyfish life cycles and relevant environmental variables such as: temperature, salinity, cholophyll *a* and nutrients concentration or ichthyoplankton abundance. The three scyphozoan jellyfish studied are: *Aurelia* sp*.*, autochthonous from the lagoon, *Cotylorhiza tuberculata* and *Rhizostoma pulmo*, both only present since the widening of El Estacio channel (Pérez-Ruzafa, 1989), and having strong proliferations after starting the eutrophication process in Mar Menor lagoon during the mid 1990s (Pérez-Ruzafa *et al.,* 2002).

2. Objectives

- Study the distribution and seasonal cycle from the Scyphozoan in the Mar Menor lagoon (*Cotylorhiza tuberculata* (Macri, 1778)*, Aurelia* sp*.* and *Rhizostoma pulmo* (Macri, 1778))..
- Analyze the effect of several environmental variables (temperature, salinity, nutrients, suspended solids, chlorophyll *a* concentration and ichthyoplankton abundance) over the jellyfish population dynamics using Canonical Detrended Correspondence Analysis (DCCA).
- Determine the growth parameters of the three scyphozoan using Von Bertalanffy Growth Function and estimate mortality using Ricker (1975) and Beverton & Holt (1957) methods.

3. Materials and methods

3.1 Area of study

Mar Menor is a hypersaline lagoon with 135.8 km^2 surface area and 3.5m of mean depth, placed in the SE coast of Spain. Due to its conditions Mar Menor results an ideal place to study the connection between the jellyfish annual cycle and the climate change. The water temperature seasonally oscillates between 10ºC in winter and 31ºC during summer (Pérez-Ruzafa *et al.*, 2002), allowing thus the study on the temperature increment on invertebrate populations. Its natural characteristics have been anthropogenically modified during the last century due to the uprising of the tourism since the early 1950s and the widening of one of its communications with the Mediterranean Sea, the Estacio

channel, during the 1970s to improve the marine traffic (Pérez-Ruzafa *et al*., 1987). Moreover, Mar Menor lagoon got in its shoreline ten harbours which might provide artificial settlement for the medusa polyps as it happens in other places (Purcell, 2012). In this sense, previous studies have shown that the dredging and widening of the channel eased the invasion of the lagoon by two allochthonous medusa species, *C. tuberculata* and *R. pulmo* (Pérez-Ruzafa, 1989). It can be also used as a eutrophication model as the nutrient inputs experimented an increase since the agricultural activities started shedding nitrates to the lagoon through the main water course, El Albujón, in the 90s (Pérez-Ruzafa *et al*., 2002; García-Pintado *et al.,* 2007).

Twenty sampling stations, distributed over the whole lagoon, were considered for monitoring the environmental and abundance data. The lagoon was divided into five zones (Z1-Z5) based on the hydrodynamic conditions, and 4 sampling stations constituting each zone (Fig.1). The sampling was conducted weekly from February 25th, 1997, until November 19th, 1997.
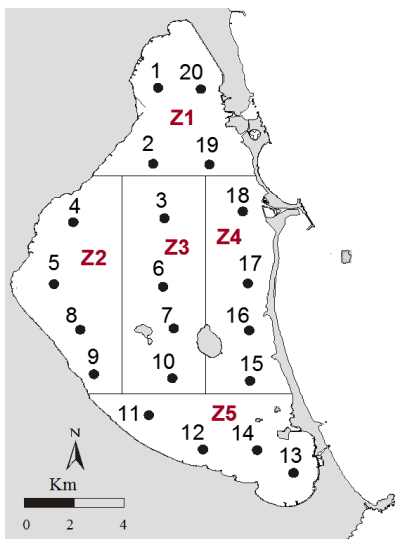

Fig. 1 Mar Menor lagoon sampling design

3.2 Sampling method

Adults jellyfishes were estimated by two methods. The first one consisted in a visual census from the boat and sorting the medusas by species and class size, divided in 5cm intervals from 0 up to 45cm. The second method consisted in a Bongo net, 0.5mm mesh size, towed at a velocity of 1 knot. The highest recorded number was considered to be the most accurate measure. All the measurements were standardized to number of jellyfishes per 100m^3 for analytical purposes.

Ephyras were sampled by a Bongo net, 0.5mm mesh size, and preserved in 5% formaldehyde-sea water until its analyses in the laboratory. Once in the laboratory, ephyras were sorted into their species and the abundance data were standardized to number of ephyra per $100m^3$ for analytical purposes.

The environmental variables: temperature, salinity, nutrients, and suspended solids and chlorophyll *a* concentration, were recorded for all the stations. Additionally, ichthyoplankton abundance was recorded. Salinity determination was done with a Beckman RS 7B salinometer. The water samples for nutrient analysis were taken at 1m depth with a Niskin bottle. Afterwards, they were kept in dark and at 4°C in field and stored at -28°C. Chlorophyll *a*, phosphate (PO_4^-), ammonia (NH_4^+) nitrite (NO_2^-) and nitrate (NO_3^-) were determined following the method described by Parsons *et al*. (1984). The ichthyoplankton was sampled by towing a Bongo net, 0.5mm mesh size, sub-superficially, 0.5-2m depth, and sailing at 1 knot for 7 minutes equipped with a flowmeter (General Oceanics 2030) in the net mouth. A 1 L collector was placed at the ending of the net which was later removed for the posterior count of the catch at the laboratory. All the samples were standardized to individuals/$1000m^3$.

3.3 Spatiotemporal distribution of jellyfishes

The spatiotemporal distribution was studied for each species, in the adult phase, individually, using a two-way PERMANOVA, performing 9999 permutations and doing the Monte Carlo tests. The design consists in two crossed factors, 'Season', with the levels Winter, Spring, Summer and Autumn, and 'Zone', with five levels (Z1-Z5). If a specie of jellyfish was absent during a month or a season those dates were excluded for its analysis.

The spatiotemporal distribution of the ephyras was studied for *C. tuberculata* and *R. pulmo* with one way PERMANOVA using 'Zone', with five levels (Z1-Z5), as a fixed factor for the whole period in which the ephyras are present in the lagoon. The analysis can not be the same that was applied for the adult phase due to the small period in which the ephyras are present in the lagoon. All the analysis were carried out in the statistical software PRIMER + PERMANOVA 6.0 (Clarke & Gorley, 2005).

3.3 Environmental effect on jellyfish population dynamics

Average environmental and abundance data for each zone and date were used to perform the site ordination for the species of jellyfish by applying Detrended Correspondence Analysis (DCA) with the 'Vegan package' (Oksanen *et al*., 2007). Since the first axis showed a gradient with a value higher than 2 in units of standard deviation, a Canonic Detrended Correspondence Analysis (DCCA) is recommended to explore the spatial variation of the different species of jellyfish in relation with the environmental parameters (Jongman *et al*., 1987). This analysis was performed using log (x +1) transformed data for the species abundance, detrended by 2nd order polynomial and applying Monte Carlo test for the canonical axes, all the calculations were made using CANOCO v 3.15 package (ter Braak, 1997).

3.4 Von Bertalanffy Growth Function parameters determination

The length frequency dataset recorded through 1997 was used to determine the parameters of the Von Bertalanffy Growth Function (VBGF, Bertalanffy, 1938), expressed as: $L(t) = L_\infty(1-e^{1-K(t-t0)})$, where: L(t) = Length at age, L_∞= Asymptotic length, K = growth rate (year^{-1}), t = age (year), t0 = theoretical length at age 0. Biologically, t0 got no meaning as it provides a negative time in which the specimen measured 0 cm, this is a mathematical artifact used to improve the adjustment of the curve (Moreau, 1987). In the case of jellyfishes, as we estimate the growth parameters for the adult phase, t0 corresponds with the strobilation period in which the newly formed ephyras are released.

The TropfishR package (Mildenberger, Taylor & Wolff, 2017) was used to implement the ELectronic LEngth Frequency ANalysis (ELEFAN) (Brey & Pauly, 1986) and determine K, L_∞ and t0. Two different methods are allowed by TropfishR were used to the determination. The first one, K and t0 determination after fixing L_∞ using the method described by Taylor (1958). The second, using a Response Surface Analysis (RSA) that explores different combinations of K and L_∞ within plausible intervals. t0 is calculated by the parameter given by TropfishR package, t_anchor, that provides the day in a numeric format, ranging from 0-1, and which was also translated into the exact date to ensure that the curve is anchored during the strobilation period.

Growth analysis was explored for each of the three species with both methods, and being the results obtained for both similar, only one of the methods is displayed. The

variation of L_∞ in the RSA method was used preliminary to identify the interval in which our species might be included, discarding afterwards the lengths which are shorter than the size seen on field, and testing ELEFAN with fixed lengths in search of a K and L_∞ combination which anchor our growth curve during the strobilation period. A fixed length is preferred for the representation as the whole variation of K is seen for a unique plausible value of infinite length. *Aurelia* sp. was represented with RSA as it clearly shows that the results for a narrow range of K-L_∞ combination could explain our dataset.

TropfishR was also used to determine different cohorts by applying the Bhattacharya method of resolution of a distribution into gaussian components (Bhattacharya, 1967).

The parameters of ts, which should be understood as a parameter to calculate the Winter Point (WP) by the equation WP = ts + 0.5, and seasonal oscillation (C), were not included for the analysis as the lifespans of all the species studied are approximately half a year, even if some isolated individuals are reported to survive overwinter (Kikinger, 1992; Pérez-Ruzafa *et al*., 2002; Pérez-Ruzafa *et al*., 2005; Fuentes *et al*., 2011). Agemax was fixed as 0.5 to prevent underestimation of the K parameter.

ELEFAN does not consider the shrinkage suffered by jellyfish during the late stages of their lifespan (Hamner & Jensen, 1974) nor the delay in growth experienced by injured individuals (Kikinger, 1992), but we think this ought to be considered as an unavoidable bias (Palomares & Pauly, 2009).

3.5 Mortality estimates

Total mortality rates (Z) were estimated applying two different routines from TropfishR. The first one calculates Z from the catch curve as described in Ricker (1975) and implemented in Gayanilo *et al*. (1995). The second implements the Beverton & Holt (1957) method through the Powell & Wetherall (P-W) plot (Powell, 1979; Wetherall, Polovina & Ralston, 1987).

We are conscious that P-W can be extremely biased since it does consider variability (inter-annual and intracohort) as zero, being it not provided with reliable infinite length nor K parameter and showing spurious correlation (Schwamborn, 2018). However, since our data only consider one year of sampling and comparing those results with the one provided from the length-converted catch curves might reinforce our

interpretation. The spurious correlation showed in mortality estimation by length-frequency datasets could not be avoided, making the results exploratory.

4. Results

4.1 Spatiotemporal distribution of jellyfishes

Aurelia sp. is present within the lagoon from February until mid June, *R. pulmo* is present all year round, being its peak of abundance in mid June and presenting four peaks of abundance during its season, by the time *Aurelia* sp. is disappearing, and *C. tuberculata* season starts in mid June, got its peak in August and disappear by late November (Fig.2A).
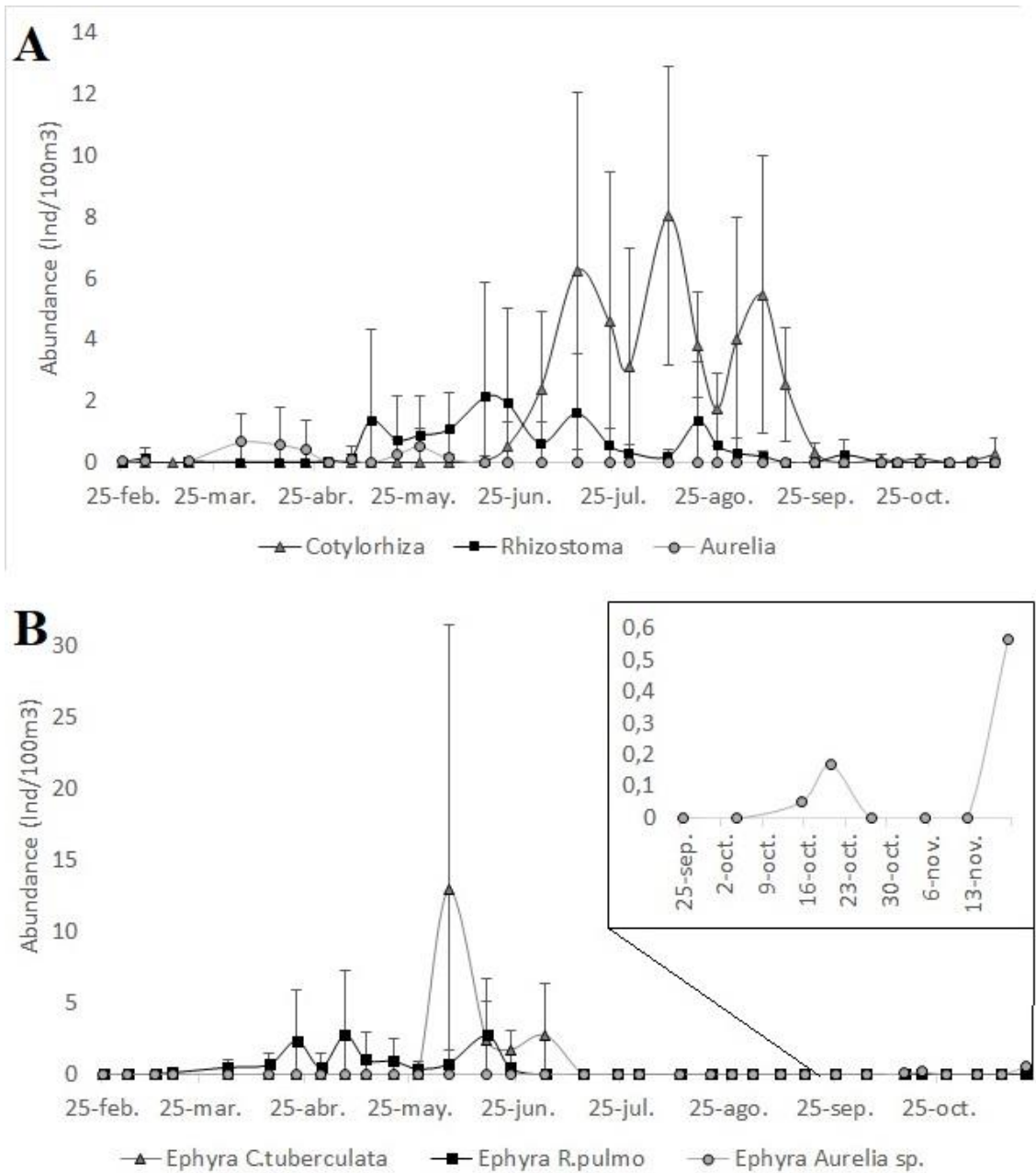
Fig. 2 *Spatiotemporal distribution from the three species of jellyfishes existing in the lagoon. A: Adult phase; B: Ephyra phase.*

For *R. pulmo,* four ephyra concentration peaks occurred during the period in which this jellyfish is present in the lagoon. *C. tuberculata* strobilated in early June, being the peak of ephyra detected by the 16th June. The ephyras of *Aurelia* sp. were found in the lagoon from mid October until late November, suggesting that the strobilation ought to start in early October continuing at least until November (Fig.2B).

Cotylorhiza tuberculata

In the case of *C. tuberculata* no significative differences were found for the ephyra stage of *C. tuberculata* even if they were more concentrated in Z3 (Fig. 3A) where they have a sudden and massive appearance in mid June, probably corresponding to a single strobilation event, reaching a density of 166.6 ephyra /100m^3 in station 7 in the center of the Mar Menor. Previously, some isolated ephyra were sampled in one occasion in March and in April.

C. tuberculata adults got an unequal distribution within the lagoon. They first appear in spring in the Z3, spreading to other zones during the summer, but being very scarce in Z2 ($p = 0$), and retreating to the central area (Z3) in autumn ($p = 0.04$) (Fig. 3B, Table S1).
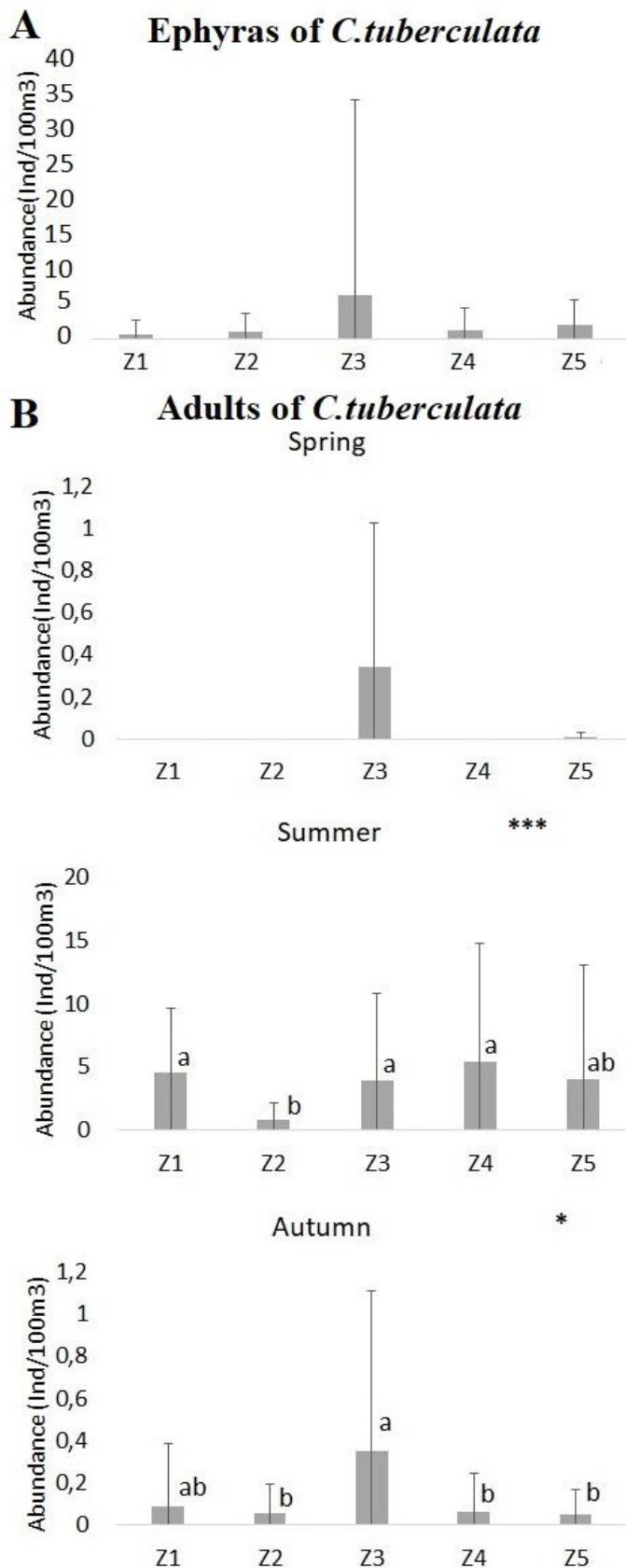
Fig. 3 *Cotylorhiza tuberculata spatial distribution during the different seasons. A: Ephyra phase; B: Adult phase.*

Aurelia sp.

During the winter season *Aurelia* sp. adults were more frequent in Z2 and Z3, closely followed by Z1 (p = 0.04) and completely absent in the eastern (Z4) and southern (Z5) part of the lagoon. During the summer season, this jellyfish dominated the central area (Z3, p = 0.005) (Fig. 4, Table S1).
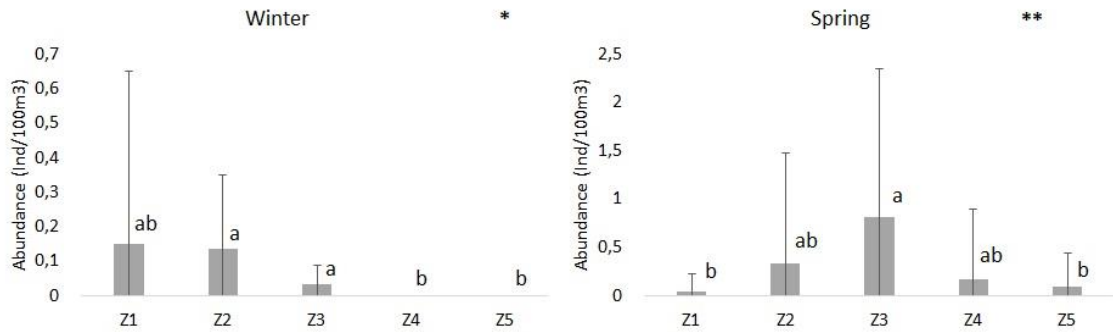

Fig. 4 *Aurelia sp. adults' spatial distribution*

The ephyras of *Aurelia* sp. first appear in the inner coast of the lagoon at densities lower than 0.5 ephyras/100m³. It could not be ruled out that this species might have some strobilation peak in December or January, months that have not been sampled in this work.

Rhizostoma pulmo

R. pulmo showed multiple strobilation events, starting in March but with higher peaks in April and May (Fig. 2B). The ephyras first appear in different points of the western coast of the lagoon, being significantly more abundant in Z2 (p = 0) (Fig. 5A, Table S1).

R. pulmo adults showed concentrations of 0.1-0.3 individuals/m³ during the winter season, being this species is present in Z1 and Z2 (p = 0.01). During spring and summer, when the highest abundances were reached, *R. pulmo* remained mainly in Z2 (p = 0.007) and no significative differences between zones for the autumn period (Fig. 5B, Table S1).
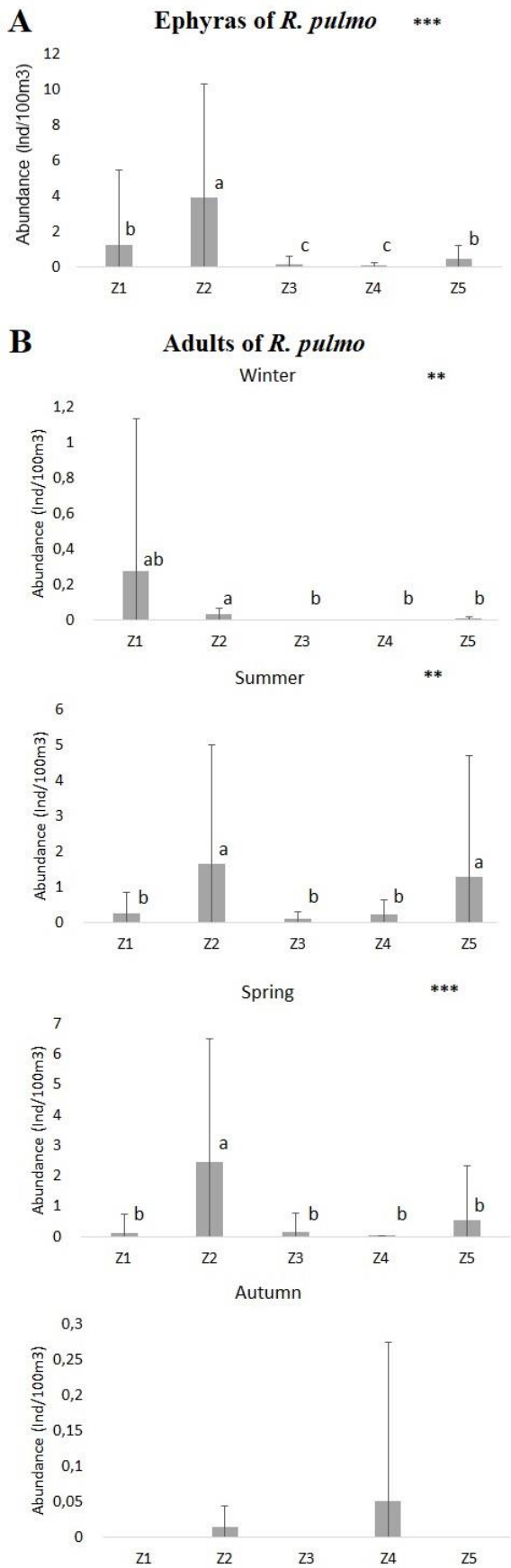
***Fig. 5** Rhizostoma pulmo spatial distribution during the different seasons. A: Ephyra phase; B: Adult phase*

4.2 Environmental effect on jellyfish population dynamics

The temperature oscillated from a minimum of 16.15˚C in February to a maximum of 28.9˚C in August being it reduced afterwards to 16.75˚C in November. The salinity was low at the beginning of the sampling period after a torrential rainfall (36.66) but got a soon recovery to values over 40 (Fig. 6).
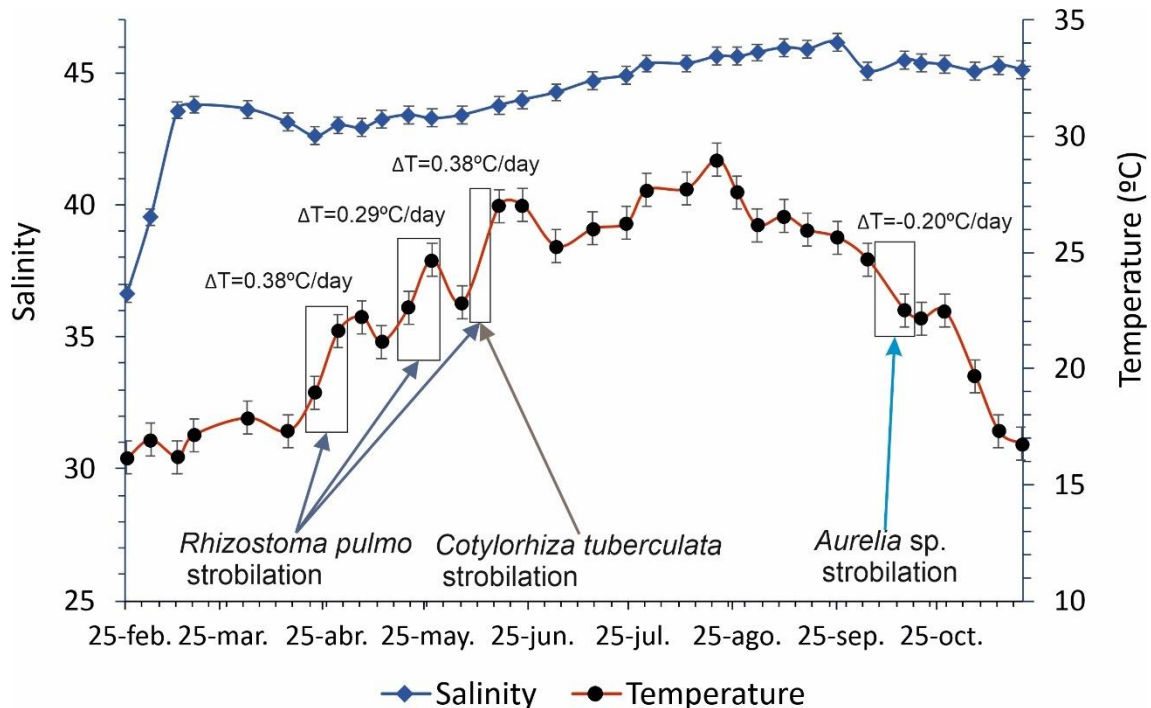

Fig. 6 *Temperature and salinity records from Mar Menor lagoon through 1997 indicating the daily rate of increasing or decreasing temperature in the peaks of strobilation for each jellyfish species.*

The nitrogen compounds showed a higher mean concentration in the water column during the spring and the beginning of the summer season, having the ammonia a peak on March the 17th of 6.04μM and the nitrate an average concentration superior than 2μM from mid April until the end of July. On the contrary, nitrite remained with an average concentration below 0.15μM for the whole sampling period (Fig. 7A).

The phosphate got a peak mean concentration of 5μM on April the 14th being it reduced to mean concentrations below 0.2μM afterwards. The chlorophyll *a* got its concentration augmented as the sampling period went by reaching the maximum concentrations, 1.45μg/L, during October (Fig. 7B).
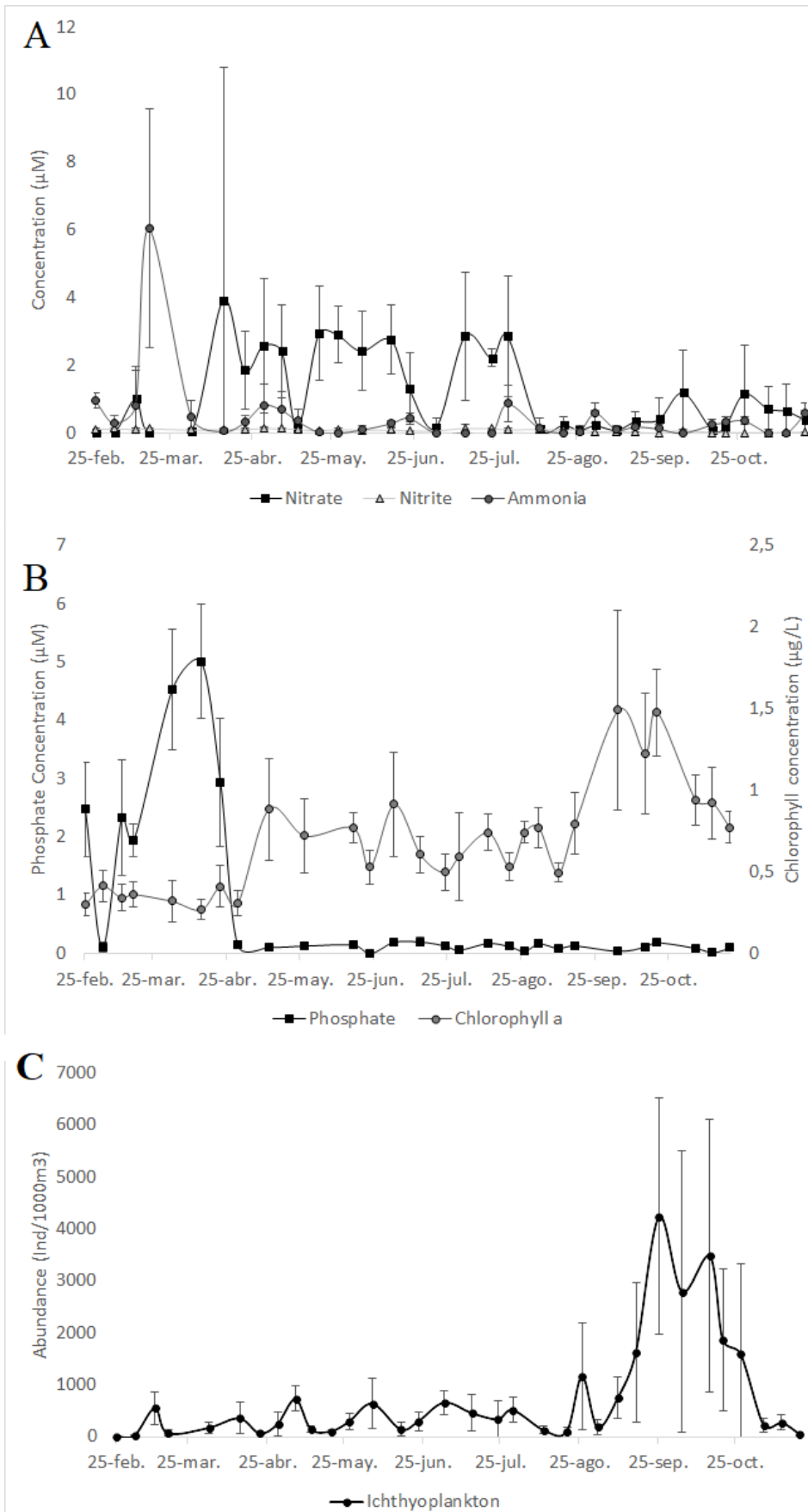
Fig. 7 *Data referred to Mar Menor lagoon through 1997. A: Nitrogen compounds concentration; B: Phosphate and chlorophyll a concentration; C: Ichthyoplankton abundance.*

Ichthyoplankton abundance showed seasonality with a high concentration period, September and October, when the number of individuals reached up to 4234 individuals/1000m^3 while the abundance oscillates from 13 to 600 individuals/1000m^3 during the rest of the year (Fig. 7C)

When analyzing the relation between environmental variables and jellyfish abundance it can be seen a negative relation between *Aurelia* sp. and temperature, positive relation between phosphate and *Aurelia* sp., nitrite and nitrate with *R. pulmo*, and *C. tuberculata* being explained by salinity and temperature. On the other hand, ammonia and the Redfield N to P ratio seems to have no effect over none of the species (Fig. 8).

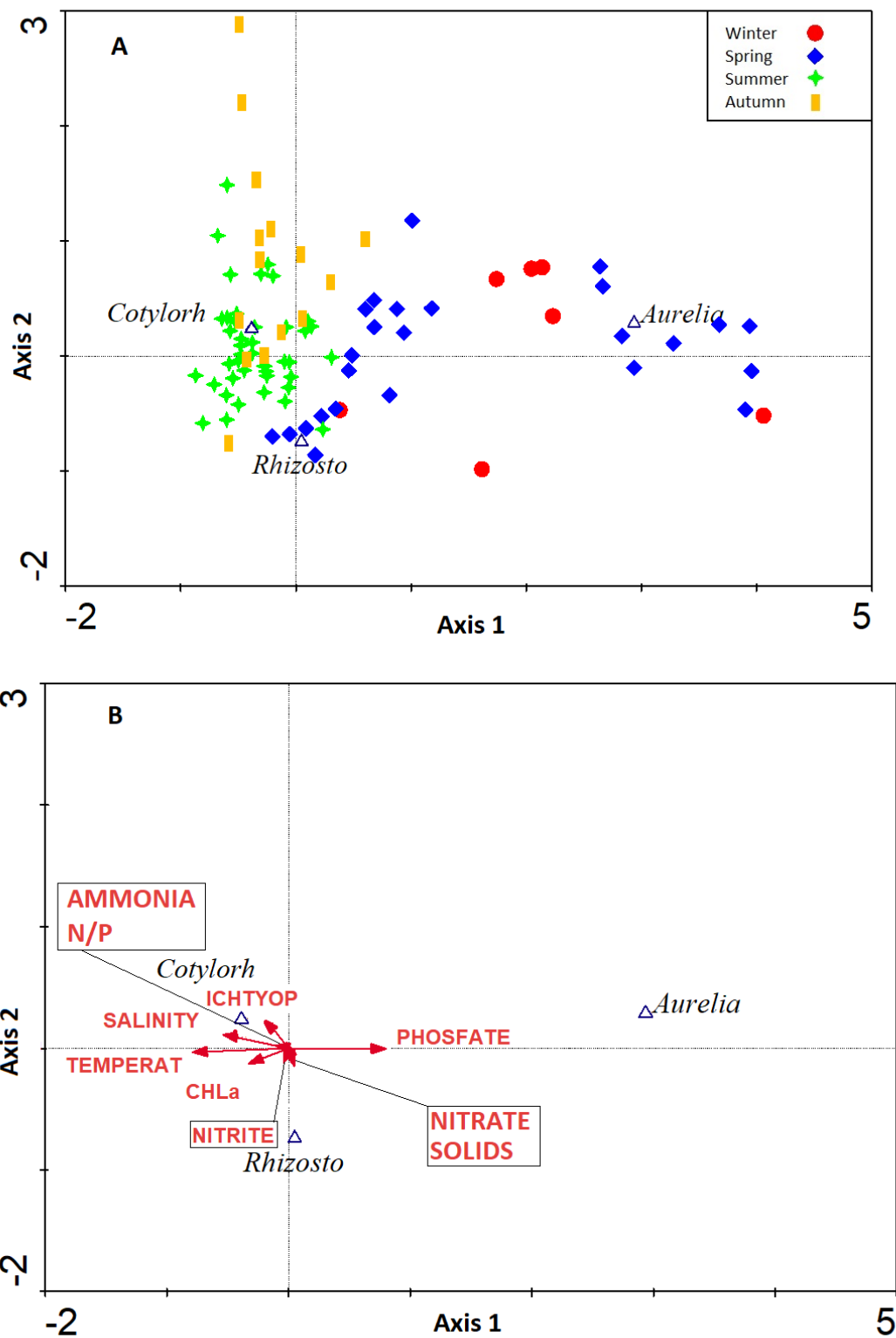**Fig. 8** *Ordination of species + samples (A) and species + environmental variables (B) in the representation of the two canonical axes (p = 0.0001; 88.1% of variance explained) of the redundancy analysis (DCCA) performed on the jellyfish species matrix using environmental data as explanatory variables.*

4.3 Growth and mortality estimates

4.3.1 Growth

The growth analysis of *C. tuberculata* shows: $L_\infty = 42.1$, $K = 2.36$, t_anchor $= 0.44$ = 9th June and t0 = -0.02. The peak score is highly probable to be accurate since no other peak is detected for this infinite length value. The growth analysis for *Aurelia* sp. shows a narrow range of plausible values for L_∞ (40-45cm) and K (1.2-1.35 year^{-1}) having it maximum score value for $L_\infty = 43.33$ and $K = 1.25$, which shows t_anchor $= 0.88 = 19$th November and t0= -0.27 (Fig. S1).

The growth analysis for *R. pulmo* needed of a first stage of cohort separation since four peaks of ephyra and jellyfish abundance were detected consecutively on time. The cohort analysis was done by the Bhattacharya method (Bhattacharya, 1967) and it suggest the existence of 4 successive cohorts during the time period in which *R. pulmo* is present in the lagoon (Fig. S2). The cohorts started in the 20th May, 16th June, 14th July and 26th August. Those cohorts grew at a high speed reaching their maximum size within 20 days since the first determination of the cohort. The individuals from each specific cohort rapidly disappear, being it expected to find isolated adults who survive, but being it impossible to determine the cohort in which they belong.

The growth analysis for each individual cohort throws similar results for all of them, being the K value in a range from 3 to 3.5 year^{-1} when the anchoring of the VBGF is fitted within the strobilation period for each cohort being it highly reduced when the anchoring parameter is not regarded and being the L_∞ in the range [44.44, 47.32]cm (Table S2).

We display the VBGFs for the different species using $K = 3.1$ as a value which can explain every *R. pulmo* cohort (Fig. 9).
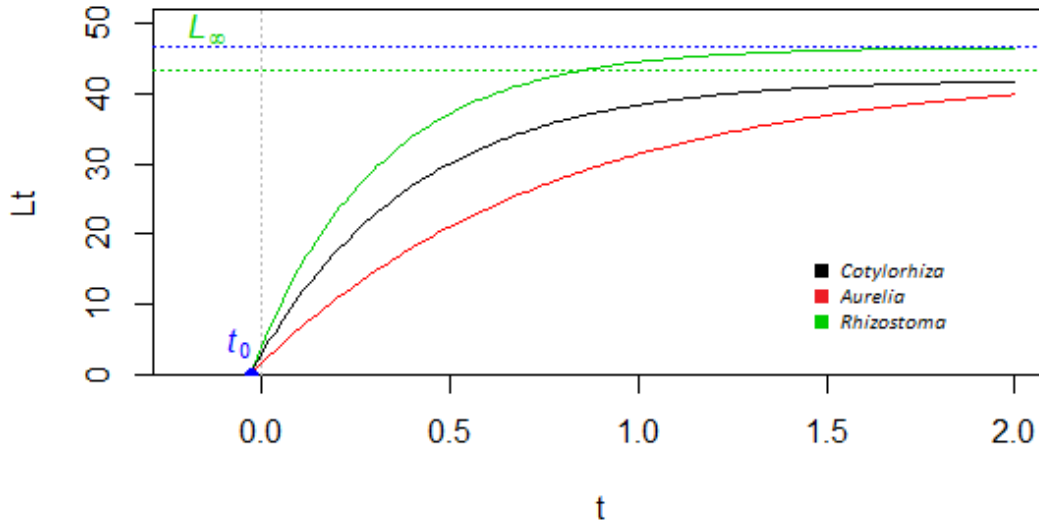
Fig. 9 *VBGF for the different species of jellyfishes present in Mar Menor lagoon. Green dashed line: Asymptotic length for C. tuberculata and Aurelia sp. Blue dashed line: asymptotic length for R. pulmo.*

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4.3.2 Mortality

The mortality analysis of *C. tuberculata,* independently of the method applied, shows an extreme value of Z (10.76 +/- 0.83) which indicates a total death of the population every end of the season (S = 0.002% = 2 out of 10^6). The study of mortality for *Aurelia* sp. by the both methods applied shows a total mortality rate (Z) of 1.68+/- 0.11, indicating a survival rate (S) of 18.63%. The mortality for the combined cohorts of *R. pulmo* shows a mortality of 7.8 +/- 0.63, indicating a low survival rate (0.04%) (Fig. 10).
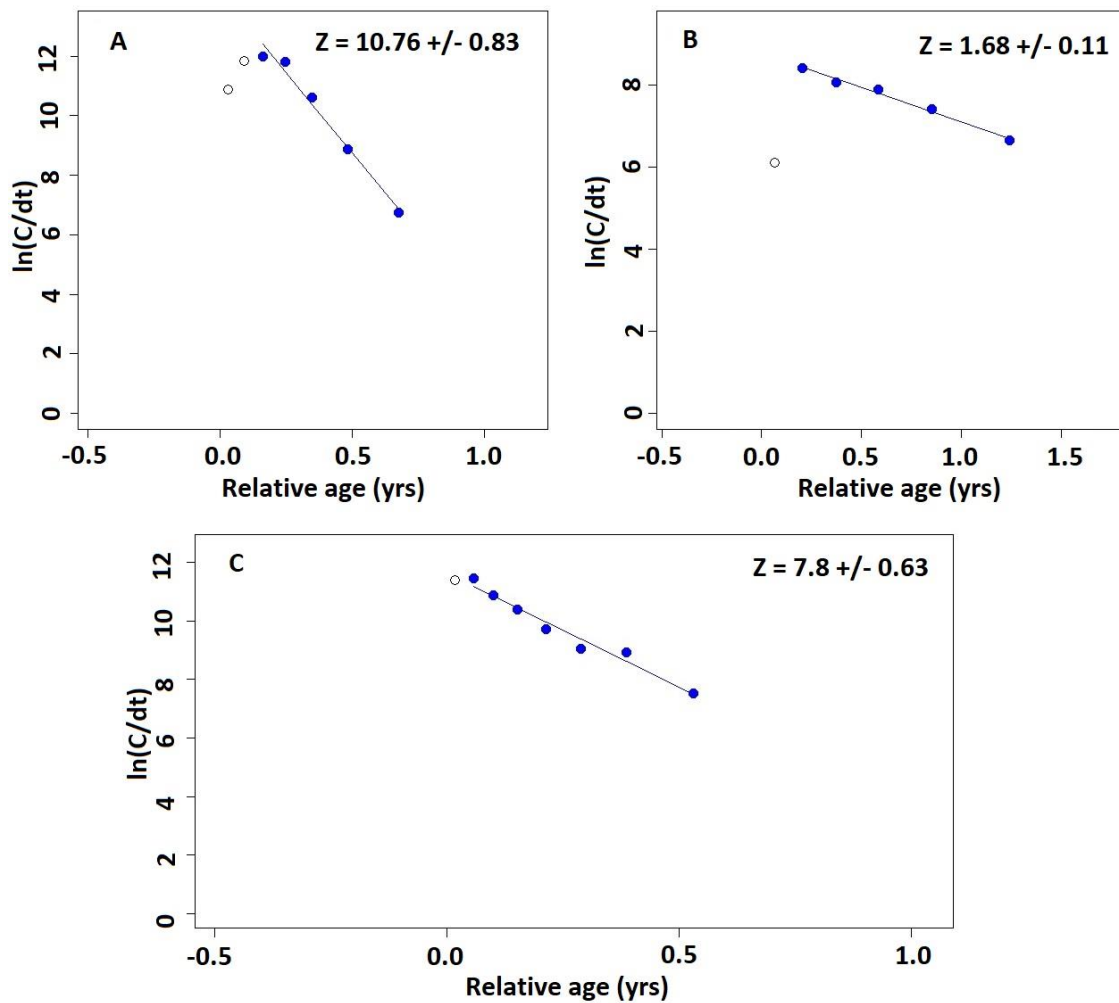
Fig. 10 *Mortality estimation from length-converted catch curves. A: C.tuberculata mortality; B: Aurelia sp. mortality; C: R.pulmo mortality*

5. Discussion

5.1 Spatiotemporal distribution

The results obtained show that the biological cycles of the species have a regular pattern and that they are repeated almost identically to what was observed in the previous year 1996 (Pérez-Ruzafa, 1996, 1997; unpublished data). This suggests strobilation trigger mechanisms that allow temporary segregation of species. The three species of jellyfish showed a succession in its peak of abundance. *Aurelia* sp. has the lowest densities. It dominates the lagoon during the winter season and it reaches its maximum in April with 0.84 individuals / $100m^3$ and practically disappears at early June, being replaced by *R. pulmo* during spring and *C. tuberculata* in the summer, whose seasonality

holds a great resemblance with the population from Bay of Vlyho, Greece (Kikinger, 1992). However, the seasonality found for *Aurelia* sp. does not exactly match with none of the populations reviewed by Lucas (2001), being the most similar one, both for the ephyra release and the *Aurelia* sp. adult population, the population from Kagoshima Bay, being it just a little bit longer lasting in both phases (Miyake *et al.*, 1997). This might be explained due to the high variability found within the genus *Aurelia* all over the world (Lucas, 2001; Dawson & Martin, 2001; Ramšak, Stopar & Malej, 2012) and probably to climatic differences in the seasonal temperature and light pattern. The seasonality of *R. pulmo* is quite similar to the one described for the north-eastern Spanish coast during the years 2007-2009, starting the peak in June and lasting until August with a sharp descend in September (Fuentes *et al.,* 2011).

      C. tuberculata bloomed at the beginning of the summer season leading to a domination of the lagoon during those months with an average density in its peak of 8.3 individuals/m^3, a maximum of 12.39 ind/m^3 in Z3 and 39 ind/m^3 in S5. However, the distribution was unequal during the summer season, being its density reduced in Z2 especially and slightly in Z5. These regions were occupied however by *R. pulmo* during the summer months showing a spatial segregation of both species despite the fact that wind and hydrodynamic conditions would be the same for both species. The presence of *C. tuberculata* in the central part of the lagoon since mid June can be explained because the ephyras are detected since that time, indicating a relatively close in time strobilation and a faster development from the ephyra to the adult phase than the recorded in the Bay of Vlyho, were it took eight to ten weeks to perform the transformation (Kikinger, 1992). The preference of the ephyras in the central area (Z3) suggest that either the hydrodynamic force displace them there or that the benthic phase is settled in the middle of the lagoon, given that jellyfishes have been seen swarming with the gonads active in the area close to the central islands (Pérez-Ruzafa personal observation).

      Aurelia sp. also showed a preference for some regions of the lagoon, being it more abundant in the central, southern and western zones during all the period in which it was present in Mar Menor. Ephyras of *Aurelia* sp. for the cohort of 1997 were not detected since from the beginning of the sampling period it was present in the lagoon, but it can be assumed that the strobilation period might not differ significantly from the year period in which they strobilated in 1997, from mid October until late November.

      In the case of *R.pulmo* the isolated individuals found during the winter season can be considered as survivors from 1996 because the strobilation during 1997 did not start

until mid March with the first concentration peak registered in April the 29th. Including that peak, in four different sampling days the ephyra density was higher than 1.4 individuals/m^3, being the abundance during the first three peaks higher than 2 individuals/m^3. This suggests the existence of, at least, 4 different cohorts, which were afterwards confirmed by the application of Bhattacharya method (Bhattacharya, 1967), being it coherent with the polydisc strobilation performed by *R.pulmo* (Fuentes *et al*., 2011). During the months of winter and spring, being the abundance superior in the last one, the jellyfishes reached the highest densities in Z2, expanding its coverage area to Z5 during the summer period. The ephyras were also found in higher densities in Z2 suggesting that the polyps ought to be settled in the area, mainly characterized by sandy bottoms with more or less isolated patches of *Cymodocea nodosa* (Ucria) Ascherson, 1870 meadow. Both data support that the whole cycle of the jellyfish is completed within the lagoon (Pérez-Ruzafa. 1997; Fuentes *et al*., 2011). The higher densities recorded in these areas regarding the rest of the lagoon can be consequence of the higher primary production registered in Z2 due to the presence of a nutrient input through the Albujon wadi (Pérez-Ruzafa *et al*., 2002, 2005). The observed temporal and spatial segregation of ephyras appearance and adult abundance is also maintained in spawning time and probably localization.

5.3 *Environmental effect on jellyfish population dynamics*

C. tuberculata spatiotemporal distribution is mainly explained by hydrographical conditions, mainly temperature and salinity associated to seasonal patterns, being the species absent until the increase of temperature triggers the strobilation and remaining the jellyfish abundance reduced at Z2, where the input of freshwater through the Albujon wadi causes a reduction in the salinity. The effect of an abrupt increase of temperature as a strobilation trigger has been previously observed in the Mar Menor (Prieto *et al*., 2010) and Greece (Kikinger, 1992) while the relationship between high temperature and *C. tuberculata* abundance was modelized in Ruiz *et al*., 2012.

Aurelia sp. showed a positive relation with phosphate, but the peak of phosphate seems to be cause of an external and marked event which is not part of the lagoon dynamic (Pérez-Ruzafa *et al*., 2002), being the positioning of the species better explained by the low temperature of the occurrence months given the existence of a gene in the population of *Aurelia aurita* from Kiel fjord, where the strobilation period takes place at the same

temperature that in Mar Menor lagoon, that induces strobilation when the temperature is reduced (Fuchs *et al*., 2014).

The positive correlation between the nitrites and nitrates with *R. pulmo* alongside the distribution of this jellyfish species surrounding the Albujon wadi, responsible of the nutrient input (Pérez-Ruzafa *et al*., 2002, 2005), indicates a preference of the species for the high productivity zones; fact explained given that *R. pulmo* predates mainly over diatoms and tintinnids (Pérez-Ruzafa *et al*., 2002). Temperature seems to not have any correlation with *R. pulmo* which can be explained because its peak appeared before the maximum temperatures are reached and due to the wide range of temperatures (14-21 °C) in which this species can strobilate (Fuentes *et al*., 2011). Even though, the appearance of *R. pulmo* during the winter period, in which the temperature reaches its minimum, is anecdotical.

The positive relation observed between chlorophyll *a* with the species: *C. tuberculata* and *R. pulmo,* should not be interpreted as a bottom-up effect, even if diatoms constitute a part of the diet of both species, but as a more complex interaction; both jellyfishes predates on copepods, which mainly feed on small diatoms, and the removal of those by the jellyfishes allows the diatoms to increase its concentration, an effect that is lately continued by ichthyoplankton (Pérez-Ruzafa *et al*., 2002). The absence of correlation between any of the species with the Redfield ratio can be explained because the primary productivity is limited mainly by the phosphate (Pérez-Ruzafa *et al*., 2005).

The effect of the climate change over the different species of jellyfishes seems to not be uniform given that, even if *C.tuberculata* and *R.pulmo* positively correlates with temperature and nutrient input correspondingly, *Aurelia sp*. is negatively correlated with an increase of temperature, something that has already been observed for some species of jellyfish (*e.g., Mastigias sp.*) (Dawson, 2005).

5.2 Growth and mortality estimates

C. tuberculata show a fast growth (K = 2.36 year $^{-1}$; L_∞ = 42.1cm) reaching, thus, higher values than the previously reported for the species (K =0.73 year^{-1}; L_∞ = 39.0cm) (Palomares & Pauly, 2008). Those differences might be explained by the addition of the parameter "age max = 0.5" that consider the short lifespan of the species and which was not taken into account when the dataset from Kikinger (1992) was analyzed, although the combined effect of the high temperatures that reach the waters of the lagoon and the high

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biological productivity after the start of an eutrophication process should not be ruled out (Pérez-Ruzafa et al., 2002, 2005). Our results fixed the VBGF on June the 9th (t_anchor = 0.44; t0 = -0.02) and, given that the ephyra peak was recorded on June the 16th, it seems a plausible date for the strobilation, represented in the VBGF as t0, to take place. The mortality calculated by both methods (Catch curve and Powell-Wetherall plot), $Z = 10.76$, indicates a survival rate of 0.002% over the winter season. The low survival rate appreciated concords with the appearance of isolated adult individuals through the winter period after reaching peaks population exceeding the 10 individuals/m^3 during the summer season (Kikinger, 1992; Pérez-Ruzafa et al., 2002, 2005; Fuentes et al., 2011). This low survival rate makes the reproductive success a key point for the continuity of the species within the ecosystem and might be the explanation for the swarming behaviour showed by the adults of *C. tuberculata* (Kikinger, 1992; Hamner & Dawson, 2009). Even considering that our mortality data could be biased (Schwamborn, 2018) they explained the little to zero appearance of *C. tuberculata* in the majority of the sampling stations from the lagoon when its season is over.

The literature for *Aurelia* spp. reflects a wide disparity for the L_∞ (11.1-37.4cm) and K (0.45-3.83 year^{-1}) parameters (Palomares & Pauly, 2008) which might hold relationship with the differences in the strobilation induction, either by low or high temperatures, reported worldwide (Lucas, 2001) and/or with the existence of cryptic or siblings species constituting the previously known as *Aurelia aurita* (Dawson & Martin, 2001; Ramšak, Stopar & Malej, 2012, Scorrano et al., 2017). In our study the parameters were determined to be $L_\infty = 43.33$cm and $K = 1.25$ year^{-1}, being the VBGF anchored on the 19th of November, which matches with a point of the ephyra phase detection for 1997 (it extended from October the 15th until November the 19th). For the comparison of our data only the European populations are considered as it is more likely that closer populations are more interrelated than those which are separated. Genetically, different clades are present within the European seas (Ramšak, Stopar & Malej, 2012), which have been now identified as a pool of different *Aurelia* species including *A. coerulea*, *A.relicta*, *A.solida* and *A.aurita* (Scorrano et al., 2017), but unfortunately, growth parameters have only been determined for populations from the *A.aurita* clade Borealis (Palomares & Pauly, 2008), which comprises the North and the Black seas. Even considering only this clade L_∞ still got the same range of values while K range is slightly reduced (0.62-3.70 year^{-1}). Those divergences suggest that every single population ought to be managed individually and that environmental factors might play a key role for the development of

Aurelia spp. The mortality was estimated to be $Z = 1.68 +/- 0.11$. This value seems to us highly underestimated since the survival rate obtained is 18.63% and no individuals were found after June, but it might be seen as the mortality rate during the lifespan and resulting in a massive mortality afterwards which can not be reflected by the catch curve with higher sizes due to the regression in size suffered after the planulae release (Hamner & Jensen, 1974) induced by the starvation consequence of the extrusion of the gastric filaments (Spanenberg, 1965). The total disappearance which indicates a complete mortality of the jellyfishes is confirmed by the fortnight variation in the abundance ($p = 0.04$).

The analysis *R. pulmo* growth parameters for the four successive cohorts, determined by Bhattacharya method for resolution of a distribution into Gaussanian components (Bhattacharya, 1967), gives a high degree of similarity between them, being L_∞ estimated to range between 44.44-47.1cm and K between 3.0-3.5 year^{-1} for those t0 which matches the ephyra peaks for each cohort. The value of K makes *R. pulmo* the one with the fastest growth in the lagoon, which combined with the fact of a polydisc strobilation (Fuentes *et al*., 2011), allows this species to develop multiple cohorts in a single season. The mortality is estimated to be $Z = 7.8 +/- 0.63$, providing thus a survival rate of 0.04% which seems plausible considering that, even if it can be found all year round, the concentration during the summer peak is 900 folds the winter minimum. The fact of being the only one of the jellyfish lagoon species whose appearance during the whole year is not an exception but a regular thing might be explained by its higher survival rate. The longer survival from a part of the adult population might explain the absence of a swarming behaviour (Hamner & Dawson, 2009), given that the reproductive success during the peak of the season should not be as determinant for the continuity of the species as it is in *C. tuberculata* and *Aurelia* sp.

6. Conclusions

(1). *Aurelia* sp. has the lowest densities. It dominates the lagoon during the winter season and it reaches its maximum in April with 0.84 individuals / 100m^3 and practically disappears at early June, being replaced by *R. pulmo* during spring and *C. tuberculata* in the summer.

(2). Temperature is the main driven factor to explain the strobilation of jellyfishes, promoting it either being both, high or low, indicating that not all the species might be benefited from climate change.

(3). Salinity seems to be a key factor explaining the spatial distribution of jellyfishes within Mar Menor lagoon.

(4). Jellyfishes plays a key role in the trophic net of Mar Menor lagoon, being the chlorophyll and ichthyoplankton abundance peaks explained by the medusa species succession through the year.

(5). Nutrients concentration contribute to the reach of the highest jellyfish abundances as well as in the upwelling areas.

(6). Jellyfishes are fast growth species which can reach their maximum size and complete the pelagic adult phase in less than a year.

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8. References

Astorga, D., Ruiz, J., & Prieto, L. (2012). Ecological aspects of early life stages of Cotylorhiza tuberculata (Scyphozoa: Rhizostomae) affecting its pelagic population success. In *Jellyfish Blooms IV* (pp. 141-155). Springer, Dordrecht.

Beverton, R. J. H. & Holt, S. J. (1957). On the dynamics of exploited fish population. *Fish Investigation*. London, Ser., 2 (19): 533 p

Bertalanffy, L. V. (1938). A quantitative theory of organic growth (inquiries on growth laws. II). *Human biology*, *10*(2), 181-213.

Bhattacharya, C. G. (1967). A Simple Method of Resolution of a Distribution into Gaussian Components. *Biometrics*, *23*(1), 115–135. https://doi.org/10.2307/2528285

Brey, T., & Pauly, D. (1986). Electronic length frequency analysis: a revised and expanded user's guide to ELEFAN 0, 1 and 2.

Brotz, L., Cheung, W. W., Kleisner, K., Pakhomov, E., & Pauly, D. (2012). Increasing jellyfish populations: trends in large marine ecosystems. In *Jellyfish Blooms IV* (pp. 3-20). Springer, Dordrecht.

Clarke, K. R., & Gorley, R. N. (2005). PRIMER: Getting started with v6. *PRIMER-E Ltd: Plymouth, UK.*

Condon, R. H., Duarte, C. M., Pitt, K. A., Robinson, K. L., Lucas, C. H., Sutherland, K. R., … Graham, W. M. (2013). Recurrent jellyfish blooms are a consequence of global oscillations. *Proceedings of the National Academy of Sciences*, *110*(3), 1000–1005. https://doi.org/10.1073/pnas.1210920110

Dawson, M. N., & Martin, L. E. (2001). Geographic variation and ecological adaptation in Aurelia (Scyphozoa, Semaeostomeae): some implications from molecular phylogenetics. In *Jellyfish Blooms: Ecological and Societal Importance* (pp. 259-273). Springer, Dordrecht.

Di Camillo, C. G., Betti, F., Bo, M., Martinelli, M., Puce, S., & Bavestrello, G. (2010). Contribution to the understanding of seasonal cycle of Aurelia aurita (Cnidaria: Scyphozoa) scyphopolyps in the northern Adriatic Sea. *Journal of Marine Biological Association of the United Kingdom*, *90*(6), 1105–1110. https://doi.org/10.1017/S0025315409000848

ECOS (2004) Poblaciones de medusas en el Mar Menor. Murcia: CARM. 12 p.

Fuchs, B., Wang, W., Graspeuntner, S., Li, Y., Insua, S., Herbst, E. M., ... & Domazet-Lošo, T. (2014). Regulation of polyp-to-jellyfish transition in Aurelia aurita. *Current Biology*, *24*(3), 263-273.

Fuentes, V., Straehler-Pohl, I., Atienza, D., Franco, I., Tilves, U., Gentile, M., ... & Gili, J. M. (2011). Life cycle of the jellyfish Rhizostoma pulmo (Scyphozoa: Rhizostomeae) and its distribution, seasonality and inter-annual variability along the Catalan coast and the Mar Menor (Spain, NW Mediterranean). *Marine Biology*, *158*(10), 2247-2266.

García-Pintado, J., Martínez-Mena, M., Barberá, G. G., Albaladejo, J., & Castillo, V. M. (2007). Anthropogenic nutrient sources and loads from a Mediterranean catchment into a coastal lagoon: Mar Menor, Spain. *Science of the Total Environment*, *373*(1), 220-239.

Gayanilo, J. F., P. Sparre & D. Pauly, 1995. FAO/ICLARM Stock Assessment Tools (FiSAT) User's Guide. Report No. 8. FAO, Rome.

Graham, W. M., & Bayha, K. M. (2008). Biological invasions by marine jellyfish. In *Biological invasions* (pp. 239-255). Springer, Berlin, Heidelberg.

Hamner, W. M., & Jenssen, R. M. (1974). Growth, Degrowth, and Irreversible Cell Differentiation in Aurelia aurita. *American Zoology*, *14*, 833–849.

Hernroth, L., & Gröndahl, F. (1983). On the biology of Aurelia aurita (L .) 1 . Release and growth of Aurelia aurita (L .) ephyrae in the Gullmar Fjord , Western Sweden , 1982 – 83. *Ophelia*, *22*(2), 189–199. https://doi.org/10.1080/00785326.1983.10426595

Holst, S. (2012). Effects of climate warming on strobilation and ephyra production of North Sea scyphozoan jellyfish. In *Jellyfish Blooms IV* (pp. 127-140). Springer, Dordrecht.

Hsieh, Y. P., Leong, F. M., & Rudloe, J. (2001). Jellyfish as food. In *Jellyfish Blooms: Ecological and Societal Importance* (pp. 11-17). Springer, Dordrecht.

Jongman, R. G. H., Ter Braak, C. J. F., & Van Tongeren, O. F. R. (1987). Data Analysis in Community and Landscape Ecology, –Pudoc, Wageningen, 299pp.

Kikinger, R. (1992). Cotylorhiza tuberculata (Cnidaria: Scyphozoa) - Life History of a Stationary Population. *Marine Ecology*, *13*(4), 333–362.

Lucas, C. H. (1996). Population dynamics of Aurelia aurita (Scyphozoa) from an isolated brackish lake, with particular reference to sexual reproduction. *Journal of Plankton Research*, *18*(6), 987–1007.

Lucas, C. H. (2001). Reproduction and life history strategies of the common jellyfish, Aurelia aurita, in relation to its ambient environment. *Hydrobiologia*, (451), 229–246.

Lynam, C. P., Lilley, M. K. S., Bastian, T., Doyle, T. K., Beggs, S. E., & Hays, G. C. (2011). Have jellyfish in the Irish Sea benefited from climate change and overfishing? *Global Change Biology*, *17*(2), 767–782. https://doi.org/10.1111/j.1365-2486.2010.02352.x

Mildenberger, T. K., Taylor, M. H., & Wolff, M. (2017). TropFishR: an R package for fisheries analysis with length-frequency data. *Methods in Ecology and Evolution*, *8*, 1520–1527. https://doi.org/10.1111/2041-210X.12791

Miyake, H., Iwao, K., & Kakinuma, Y. (1997). Life History and Environment of Aurelia aurita. *South Pacific Study*, *17*(2), 273–287.

Möller, H. (1980). Population Dynamics of Aurelia aurita Medusae in Kiel Bight, Germany (FRG). *Marine Biology*, *60*, 123–128.

Ohta, N., Sato, M., Ushida, K., Kokubo, M., Baba, T., Taniguchi, K., ... & Mochida, J. (2009). Jellyfish mucin may have potential disease-modifying effects on osteoarthritis. *BMC biotechnology*, *9*(1), 98.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, M. H. H., Oksanen, M. J., & Suggests, M. A. S. S. (2007). The vegan package. *Community ecology package*, *10*, 631-637.

Omori, M., Ishii, H., & Fujinaga, A. (1995). Life history strategy of Aurelia aurita (Cnidaria, Scyphomedusae) and its impact on the zooplankton community of Tokyo Bay. *ICES Journal of Marine Science*, *52*(3–4), 597–603.

Palomares, M. L. D., & Pauly, D. (2008). The growth of jellyfishes. In *Jellyfish Blooms: Causes, Consequences, and Recent Advances* (pp. 11-21). Springer, Dordrecht.

Parsons, T. R., L. Maita & C. M. Lalli. (1984). A Manual of Chemical and Biological Methods for Seawater Analysis. Pergamon Press, New York.

Pérez Ruzafa, A. (1989). Estudio ecológico y bionómico de los poblamientos bentónicos del Mar Menor (Murcia, SE de España).

Pérez-Ruzafa A, 1997. Estudio de la dinámica de las poblaciones de medusas en el Mar Menor, problemática asociada y búsqueda de soluciones. Final report of the Ecología y Ordenación de Ecosistemas Marinos Costeros Research Group, Department of Ecology and Hydrology, University of Murcia, Spain.

Pérez-Ruzafa, A., Marcos, C., Pérez-Ruzafa, I. M., & Ros, J. D. (1987). Evolución de las características ambientales y de los poblamientos del Mar Menor (Murcia, SE de España). *Anales de Biología*, *12* (Biología ambiental, 3), 53–65.

Pérez-Ruzafa, A., Gilabert, J., Gutierrez, J. M., Fernandez, A. I., Marcos, C., & Sabah, S. (2002). Evidence of a planktonic food web response to changes in nutrient input dynamics in the Mar Menor coastal lagoon, Spain. *Hydrobiologia*, 359–369.

Pérez-Ruzafa, A., Fernández, A. I., Marcos, C., Gilabert, J., Quispe, J. I., & García-Charton, J. A. (2005). Spatial and temporal variations of hydrological conditions, nutrients and chlorophyll a in a Mediterranean coastal lagoon (Mar Menor, Spain). *Hydrobiologia*, *550*(1), 11-27.

Powell, D. G. (1979). Estimation of mortality and growth parameters from the length frequency of a catch [model]. *Rapports et Proces-Verbaux des Reunions (Denmark)*.

Prieto, L., Astorga, D., Navarro, G., & Ruiz, J. (2010). Environmental Control of Phase Transition and Polyp Survival of a Massive-Outbreaker Jellyfish, *5*(11). https://doi.org/10.1371/journal.pone.0013793

Purcell, J. E. (2005). Climate effects on formation of jellyfish and ctenophore blooms: a review. Journal of the Marine Biological Association of the United Kingdom 85(3):461-476. [nudibranch p. 465]. [cbfd0e528452fc6608c7. *Journal of Marine Biological Association of the United Kingdom*, *85*, 461–476. Retrieved from http://journals.cambridge.org/download.php%5Cneqfile%5Cle/MBI/MBI85_03/S0025315405011409a.pdf&code%5Clee7fb79f222de

Purcell, J. E. (2012). Jellyfish and Ctenophore Blooms Coincide with Human Proliferations and Environmental Perturbations. *Annual Review of Marine Science*, *4*(1), 209–235. https://doi.org/10.1146/annurev-marine-120709-142751

Purcell, J. E., Breitburg, D. L., Decker, M. B., Graham, W. M., Youngbluth, M. J., & Raskoff, K. A. (2001). Pelagic cnidarians and ctenophores in low dissolved oxygen environments: a review. *Coastal and Estuarine Studies*, 77-100.

Purcell, J. E., Uye, S. I., & Lo, W. T. (2007). Anthropogenic causes of jellyfish blooms and their direct consequences for humans: A review. *Marine Ecology Progress Series*, *350*, 153–174. https://doi.org/10.3354/meps07093

Purcell, J. E., Atienza, D., Fuentes, V., Olariaga, A., Tilves, U., Colahan, C., & Gili, J. M. (2012). Temperature effects on asexual reproduction rates of scyphozoan species from the northwest Mediterranean Sea. In *Jellyfish Blooms IV* (pp. 169-180). Springer, Dordrecht.

Ramšak, A., Stopar, K., & Malej, A. (2012). Comparative phylogeography of meroplanktonic species, Aurelia spp. and Rhizostoma pulmo (Cnidaria: Scyphozoa) in European Seas. In *Jellyfish Blooms IV* (pp. 69-80). Springer, Dordrecht.

Richardson, A. J., Bakun, A., Hays, G. C., & Gibbons, M. J. (2009). The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends in Ecology and Evolution*, *24*(6), 312–322. https://doi.org/10.1016/j.tree.2009.01.010

Ricker, W. E. (1975). *Computation and interpretation of biological statistics of fish populations* (Vol. 191, pp. 1-382). Ottawa: Department of the Environment, Fisheries and Marine Service.

Ruiz, J., Prieto, L., & Astorga, D. (2012). A model for temperature control of jellyfish (Cotylorhiza tuberculata) outbreaks: A causal analysis in a Mediterranean coastal lagoon. *Ecological Modelling*, *233*, 59–69. https://doi.org/10.1016/j.ecolmodel.2012.03.019

Schwamborn, R. (2018). How reliable are the Powell–Wetherall plot method and the maximum-length approach? Implications for length-based studies of growth and mortality. *Reviews in Fish Biology and Fisheries*, *28*(3), 587-605.

Schneider, G. (1994). Population dynamics and the trophic role of Aurelia aurita medusae in the Kiel Bight and western Baltic. *ICES Journal of Marine Science*, *51*(4), 359–367.

Scorrano, S., Aglieri, G., Boero, F., Dawson, M. N., & Piraino, S. (2017). Unmasking Aurelia species in the Mediterranean Sea: an integrative morphometric and molecular approach. *Zoological Journal of the Linnean Society*, *180*(2), 243-267.

Spangenberg, D. B. (1965). Cultivation of the Life Stages of Aurelia aurita under Controlled Conditions. *Journal of Experimental Zoology*, (159), 303–318.

Suchman, C. L., Brodeur, R. D., Daly, E. A., & Emmett, R. L. (2012). Large medusae in surface waters of the Northern California Current: variability in relation to environmental conditions. In *Jellyfish Blooms IV* (pp. 113-125). Springer, Dordrecht.

Sugahara, T., Ueno, M., Goto, Y., Shiraishi, R., Doi, M., Akiyama, K., & Yamauchi, S. (2006). Immunostimulation effect of jellyfish collagen. *Bioscience, biotechnology, and biochemistry*, *70*(9), 2131-2137.

Taylor, C. C. (1958). Cod growth & temperature. *ICES Journal of Marine Science*, *23*(3), 366–370. https://doi.org/10.1093/icesjms/23.3.366

ter Braak, C.J.F., 1997. Update notes: Canoco v. 3.15. Wageningen: Agricultural Mathematics Group DLO.

Toyokawa, M., Furota, T., & Terazaki, M. (2000). Life history and seasonal abundance of Aurelia aurita medusae in Tokyo Bay, Japan. *Plankton Biology & Ecology*, *47*(1), 48–58.

Wetherall, J. A., Polovina, J. J., & Ralston, S. (1987). Estimating growth and mortality in steady-state fish stocks from length-frequency data. In *ICLARM Conf. Proc* (Vol. 13, pp. 53-74).

Zimmer, M. (2005). *Glowing genes: a revolution in biotechnology*. Prometheus Books.

Glossary and abbreviations

Bloom: Rapid increase from the abundance of jellyfishes induced by a dense strobilation event.

C: Seasonal oscillation. The presence of a Winter Point might modify slightly the VBGF providing months of fast growth and months of low to zero growth. The C parameter is used to perform the adjustment of the curve.

DCA: Detrended Correspondence Analysis. Ordination method applied to a single data matrix used when a gradient is observed when other methods, such as PCA or CA, are applied.

DCCA: Canonical Detrended Correspondence Analysis. Ordination method applied to two data matrix, one explaining the species abundance and the other the environmental variables, applied when the axis of the DCA analysis got a length superior to 2 in standard deviation units.

ELEFAN: ELectronic LEngth Frequency ANalysis. Analysis performed to determine the parameters from the VBGF.

Ephyra: Intermediate state of the jellyfishes, newly released from the benthic polyp stage and previously to the transformation into the adult jellyfish stage, being completely planktonic.

K: Growth rate. It can be considered as the fraction of the maximum length reached by the species during a natural year. Measured in year^{-1}.

L∞: Asymptotic length or maximum length which can be expected for the species. Measured in centimeters.

L(t): Average length of the species at the moment 't' of its life. Measured in centimeters.

P-W: Powell & Wetherall plot for the estimation of mortality.

RSA: Response Surface Analysis. Mathematical analysis performed by TropFishR testing a defined range of L∞ and K in which to fit the VBGF. A colored map with isoscore lines is obtained from the analysis. White color indicates the highest score.

Strobilation: Release of the ephyras from the benthic polyp phase of the jellyfishes.

SX: Sector and number selected to divide the Mar Menor lagoon with analytical purposes.

Swarm: Jellyfishes aggregation not induced by water currents or winds but by its own means.

t0: Interval of time between the moment in which the species represented in the VBGF got a length of 0 and the detection of it by the fishing gear selected expressed as a fraction of a year, being it considered as 1, and holding negative value. Even if it has no biological

meaning for fish fisheries, it can be considered the strobilation moment for jellyfishes to make the VBGF parameters more precise.

VBGF: Von Bertalanffy Growth Function. Equation widely applied as a method of describing organic growth.

WP: Winter Point. Point in which the growth from the species ceases or it is reduced due to the low temperatures.

ZX: Zone and number selected to divide the Mar Menor lagoon with analytical purposes.

t_anchor: Anchoring point from the VBGF. By expressing a whole natural year as 1, the fraction indicates the moment in which the length is 0. It can be converted into a date by using TropFishR.

Z: Total mortality rate. It can be related with the survival rate by using the equation:
$$\text{`}S=e^{-Z}\text{'}$$

Supplementary material
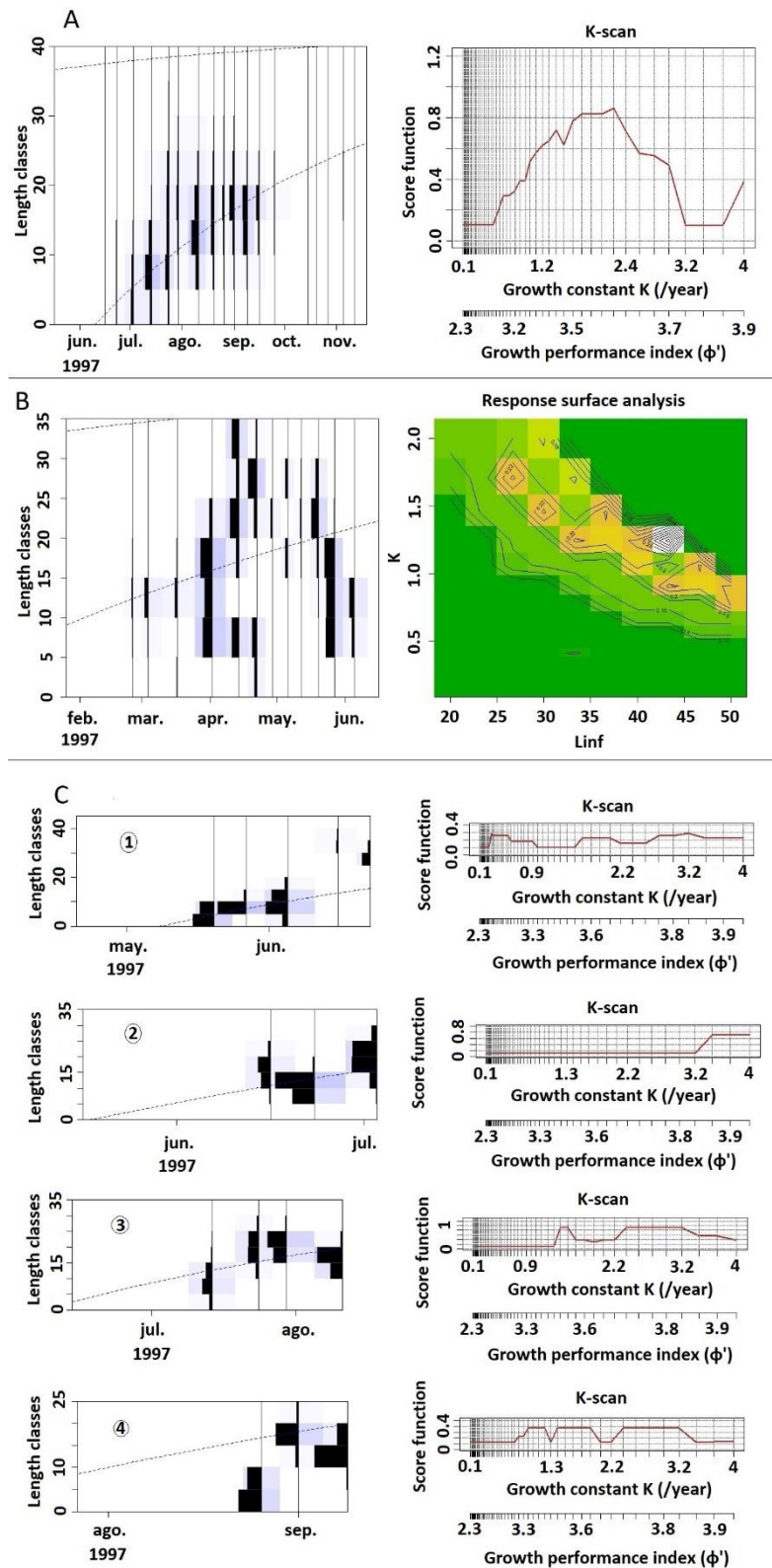
Fig. S1 *ELEFAN result for the growth analysis of the different species of jellyfishes. A: Analysis for C.tuberculata, left = VBGF, right = K Scan; B: Analysis for Aurelia sp., left = VBGF, right = RSA; C: Analysis for the different cohorts of R.pulmo, the number specifies the cohort, left images = VBGF, right images = K Scan*
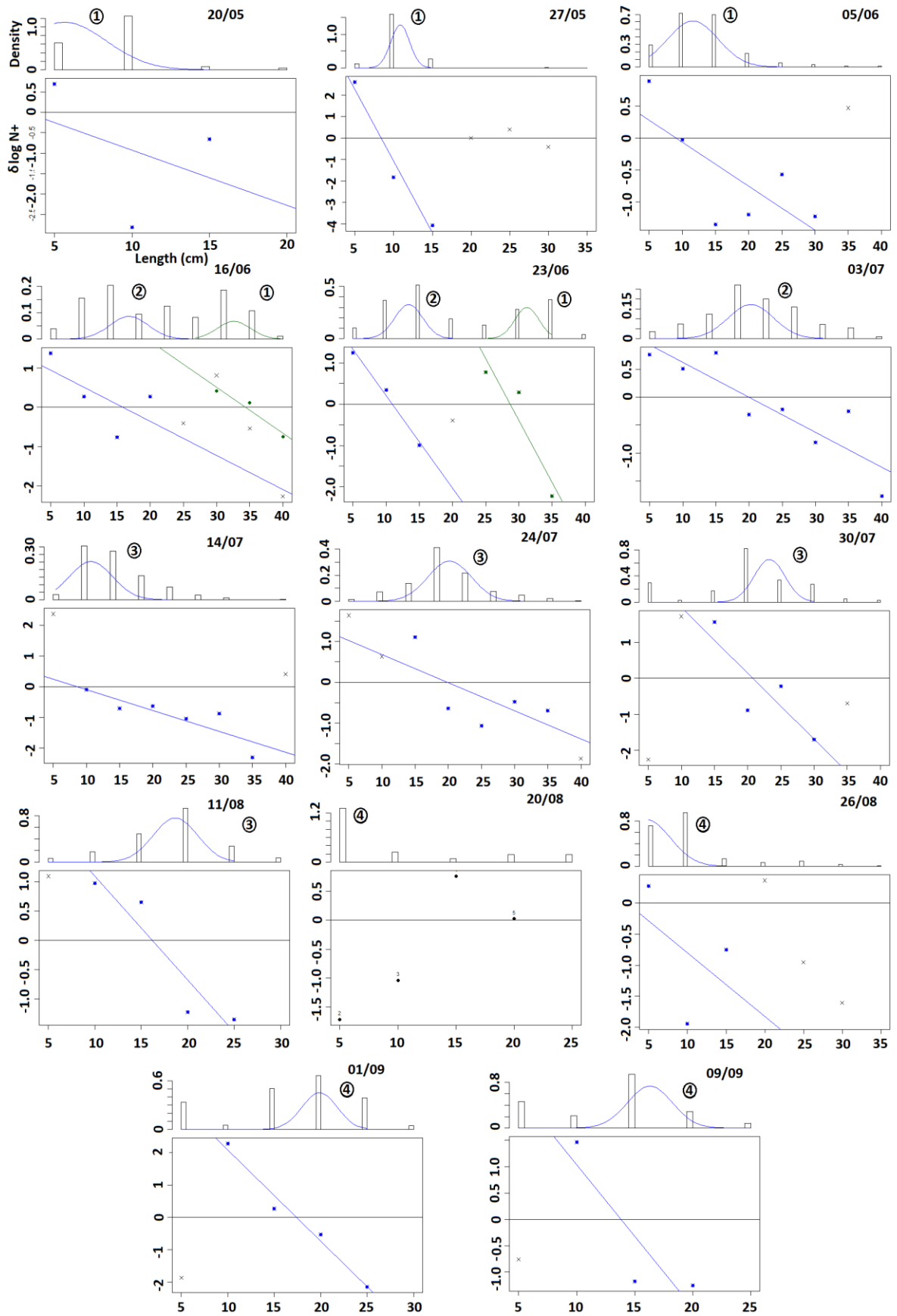
Fig. S2 *Bhattacharya method for cohort separation applied to the population of Rhizostoma pulmo existing in the lagoon through 1997. Circled numbers indicate the cohort number.*

Table S1. PERMANOVA results for the jellyfish spatiotemporal distribution analysis. Bolded results are considered significative. Zo: Zone; Sea: Season; Sec: Sector; Mo: Month; Qu: Fortnight; WIN: Winter; SPR: Spring; SUM: Summer; AUT: Autumn

Source	df	SS	MS	Pseudo-F	P(MC)
Cotylorhiza tuberculata					
Zo	4	40.782	10.196	0.37285	0.8316
Sea	2	1310	655.02	23.954	**0.0001**
ZoxSea	8	233.2	29.15	1.066	0.3862
Res	385	10528	27.345		
Total	399	12362			

Within level 'SPR' of factor 'Season'

Groups	t		P (MC)	
Z1, Z3	1		0.3661	
Z1, Z2	Denominator is 0			
Z1, Z5	1		0.3527	
Z1, Z4	Denominator is 0			
Z3, Z2	1		0.3473	
Z3, Z5	1		0.3712	
Z3, Z4	1		0.3596	
Z2, Z5	1		0.3532	
Z2, Z4	Denominator is 0			
Z5, Z4	1		0.3617	

Within level 'SUM' of factor 'Season'

| Groups	t		P (MC)	
Z1, Z3	0.54443		0.5966	
Z1, Z2	4.687		**0.0001**	
Z1, Z5	0.34833		0.7223	
Z1, Z4	0.52897		0.5968	
Z3, Z2	2.8257		**0.0059**	
Z3, Z5	9.289E-2		0.9257	
Z3, Z4	0.88646		0.3776	
Z2, Z5	2.2906		**0.0235**	
Z2, Z4	3.2074		**0.0017**	
Z5, Z4	0.71055		0.4808	

Ephyras of *Cotylorhiza tuberculata*

Groups	t		P(MC)	
Z1, Z3	1.1935		0.2388	
Z1, Z2	0.43698		0.6565	
Z1, Z5	2.0031		0.0489	
Z1, Z4	0.89269		0.3726	
Z3, Z2	1.1413		0.2559	
Z3, Z5	0.90621		0.3594	
Z3, Z4	1.0759		0.2838	
Z2, Z5	1.4974		0.141	
Z2, Z4	0.44657		0.655	
Z5, Z4	1.0198		0.3049	

Source	df	SS	MS	Pseudo-F	P(MC)
Rhizostoma pulmo					

Zo	4	61.108	15.277	4.7494	**0.0008**
Sea	3	48.51	16.17	5.0271	**0.0022**
ZoxSea	12	93.899	7.8249	2.4327	**0.0055**
Res	560	1801.3	3.2166		
Total	579	2112.5			

Within level 'WIN' of factor 'Season'

Groups	t	P(MC)
Z1, Z3	1.1054	0.2858
Z1, Z2	0.98614	0.3398
Z1, Z5	1.0887	0.2863
Z1, Z4	1.1054	0.2812
Z3, Z2	2.9067	**0.0083**
Z3, Z5	1	0.3282
Z3, Z4	Denominator is 0	
Z2, Z5	2.316	**0.0301**
Z2, Z4	2.9067	**0.0074**
Z5, Z4		0.3341

Whitin level 'SPR' of factor 'Season'

Groups	t	P(MC)
Z1, Z3	8.211E-2	0.93
Z1, Z2	3.6266	**0.0004**
Z1, Z5	1.4029	0.164
Z1, Z4	1.1651	0.249
Z3, Z2	3.6053	**0.0005**
Z3, Z5	1.3581	0.1748
Z3, Z4	1.2375	0.2151
Z2, Z5	2.7571	**0.0071**
Z2, Z4	3.8505	**0.0004**
Z5, Z4	1.8961	0.0615

Within the level 'SUM' of the factor 'Season'

Groups	t	P(MC)
Z1, Z3	1.7142	0.0933
Z1, Z2	2.7444	**0.0083**
Z1, Z5	2.0017	0.0524
Z1, Z4	0.40932	0.6849
Z3, Z2	3.0986	**0.0019**
Z3, Z5	2.3408	**0.0197**
Z3, Z4	1.6742	0.0988
Z2, Z5	0.5101	0.6075
Z2, Z4	2.8524	**0.0053**
Z5, Z4	2.1024	**0.0389**

Whitin the level 'AUT' of the factor 'Season'

Groups	t	P(MC)
Z1, Z3	Denominator is 0	
Z1, Z2	2.0113	0.0522
Z1, Z5	Denominator is 0	
Z1, Z4	1	0.3207
Z3, Z2	2.0113	0.0525

Z3, Z5	Denominator is 0			
Z3, Z4	1		0.3318	
Z2, Z5	2.0113		0.0508	
Z2, Z4	0.72106		0.4779	
Z5, Z4	1		0.3217	

Ephyras of *Rhizostoma pulmo*

Groups	t		P(MC)	
Z1, Z3	1.9567		0.0572	
Z1, Z2	2.8419		**0.0063**	
Z1, Z5	1.4155		0.1632	
Z1, Z4	2.1752		0.0333	
Z3, Z2	4.82		**0.0001**	
Z3, Z5	2.3831		0.0195	
Z3, Z4	1.5494		0.1238	
Z2, Z5	4.4304		**0.0003**	
Z2, Z4	4.979		**0.0001**	
Z5, Z4	3.8686		**0.0003**	

Source	df	SS	MS	Pseudo-F	P(MC)
Aurelia sp.					
Zo	4	3.5431	0.88577	1.2836	0.2749
Sea	1	2.3483	2.3483	3.4031	0.0724
ZoxSea	4	4.0272	1.0068	1.459	0.2184
Res	250	172.51	0.69005		
Total	259	190.66			

Within level 'WIN' of factor 'Season'

Groups	t		P(MC)	
Z1, Z3	0.79699		0.4382	
Z1, Z2	7.755E-2		0.9429	
Z1, Z5	1.0306		0.3108	
Z1, Z4	1.0306		0.3169	
Z3, Z2	1.6515		0.1115	
Z3, Z5	2.1455		**0.0412**	
Z3, Z4	2.1455		**0.0424**	
Z2, Z5	2.2477		**0.0034**	
Z2, Z4	2.2477		**0.0322**	
Z5, Z4	Denominator is 0			

Whitin level 'SPR' of factor 'Season'

Groups	t		P(MC)	
Z1, Z3	3.13		**0.0024**	
Z1, Z2	1.6174		0.1129	
Z1, Z5	0.81285		0.4210	
Z1, Z4	1.0489		0.2920	
Z3, Z2	1.5645		0.1233	
Z3, Z5	2.8733		**0.0054**	
Z3, Z4	2.394		**0.0196**	
Z2, Z5	1.2993		0.1963	
Z2, Z4	0.80163		0.4198	
Z5, Z4	0.57898		0.5606	

Table S2 Growth of the different cohorts from Rhizostoma pulmo under the different applied methods. Bold result indicates a discardable one since the low K value forces the curve to be anchored 2 months before the strobilation period.

Cohort	Method	L_∞	K value	t_anchor	t0	phiL	Score
1	L_∞ Fixed (Taylor,1958)	46.36	3.19	0.3482118 7th May	-0.0356	3.8360775	0.289
1	RSA	47.22	3.16	0.3490525 7th May	-0.00356	3.8479799	0.289
2	Taylor	46.36	3.44	0.3776643 18th May	-0.07945	3.8573317	0.714
2	RSA	44.44	3.5	0.3776643 18th May	-0.07945	3.8397030	0.714
3	**Taylor**	**46.36**	**1.39**	**0.2592752 4th April**	**-0.279**	**3.4753017**	**0.915**
3	Taylor	46.36	3.1	0.4305351 6th June	-0.104	3.8236485	0.915
4	Taylor	46.36	2.37	0.4553581 15th June	-0.197	3.7070352	0.369
4	Taylor	46.36	3.00	0.5004431 2nd July	-0.151	3.8094081	0.369