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ORIGINAL PAPER

Variability of growth rates and thermohaline niches of *Rhizostoma pulmo*'s pelagic stages (Cnidaria: Scyphozoa)

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Abstract

In recent decades, an increase in the abundance and frequency of bloom events has been reported for the scyphozoan *Rhizostoma pulmo* in the Mediterranean Sea. Understanding such events requires a thorough assessment of the species' population dynamics through environmental windows allowing species development. The semi-enclosed coastal lagoon of Bages Sigean, France (43°05′12.72″N; 3°00′35.3″E) offers an exceptional framework for investigating the population dynamics of the species, and how its growth rates and environmental niches vary over time. Three cohorts starting in April, May and June 2019 were identified, while the overall population growth reached the maximum biomass (10.2 g m^{-3}) in July. Bell diameter and total length were identified as the best morphological proxies of biomass estimation. The abundances of the two most abundant copepods' species appear to drive *R. pulmo*'s dynamics in the lagoon. Based on multinomial analysis and using the von Bertalanffy model, different growth rates for juveniles (4.7 and 2.4 mm day^{-1}) and adults (1.8 and 0.9 mm day^{-1}) were determined for the first two cohorts. Thermohaline niches varied during ontogeny, but also among populations in three coastal Mediterranean lagoons: Bages Sigean (France), Mar Menor (Spain) and Bizerte (Tunisia), shedding light on the metapopulation dynamics of *R. pulmo* inhabiting the Mediterranean Sea. The pressing need for understanding the dynamics of jellyfish abundances and their impacts on ecosystems, calls for increased efforts on monitoring these populations and their life history traits to parametrize and build reliable ecosystem models.

Keywords Barrel jellyfish · Population dynamics · Mediterranean Sea · Morphological traits · Biomass estimations

Introduction

Jellyfish blooms are conspicuous natural events in coastal marine ecosystems, but over the last decades, their frequency and intensity have increased in middle latitudes (Graham et al. 2014). Identifying drivers of jellyfish population dynamics and quantifying favourable environmental windows throughout their life cycle is necessary to understand the variability of these bloom events. They are also required parameters to model population dynamics and to improve ecosystem models, which have long oversimplified the role of jellyfish. In particular, for jellyfish with metagenetic life cycles, semi-enclosed ecosystems provide substrates for benthic stages and refuges for pelagic stages from the advection by currents (Marques et al. 2015a), which favour the populations' development. Coastal lagoons may be considered as large mesocosms to survey ecological processes that are difficult to assess in open sea conditions, i.e., population growth, and to identify the environmental conditions these organisms face during the ontogeny (Bonnet et al. 2012; Marques et al. 2015b; Fernández-Alías et al. 2020).

Rhizostoma pulmo (Macri, 1778) is one of the most abundant and biggest jellyfish inhabiting coastal areas and semi-closed lagoons in the Mediterranean and Black Seas (Fuentes et al. 2011; Leoni et al. 2021). Research on *R. pulmo* ecology has been scarce (Pérez-Ruzafa et al. 2002; Daly Yahia et al. 2003; Lilley et al. 2009), although in recent years, the population dynamics, ecological role and biogeography of the species have gained interest (e.g., Fuentes et al. 2011; Ben Faleh et al. 2017; Basso et al. 2019; Dönmez

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and Bat 2019; Fernández-Alías et al. 2020). At the basin scale, the species has shown an increase in abundance and frequency of blooms in the last decades (Leoni et al. 2021). These massive blooms constitute a potential food resource and open the possibility for developing a Mediterranean jellyfish fishery (Leone et al. 2019).

The current knowledge on the wide distribution of the species in the Southern Mediterranean seas points towards a metapopulation composed by at least three genetically distinct populations (Ben Faleh et al. 2017), probably linked with the Mediterranean hydrographic provinces. Restricted ecological niches may explain those geographically distinct populations (Kingsford et al. 2000; Ramšak et al. 2012; Dawson et al. 2015; Ben Faleh et al. 2017). Hutchinson (1957) defined the ecological niche as the range of tolerance of a species when all environmental factors are considered, including interspecific competition and dispersal. In particular, the realized niche represents the fundamental niche modified by external factors such as competition that can narrow the breadth, or dispersion, that can expand it (Helaouët et al. 2011). Temperature (Lucas et al. 2014) and salinity (Zhang et al. 2012) are well-known key factors shaping jellyfish species' geographic distribution. As observed for other ectotherm animals (Gilbert and Lattanzio 2016), these environmental niches may vary during jellyfish ontogeny (e.g., ephyrae and medusae, Bonnet et al. 2012; Marques et al. 2015b), suggesting that they may be more size dependent than species-specific. In this context, characterization of environmental niches shed light on the ecological partitioning of the species and metapopulation dynamics and can help to understand the ecological role of each stage of development of the species.

Environmental conditions additionally shape growth patterns in marine populations (Bhaud et al. 1995). Determining the population growth rate and its interaction with the environment, is critical for stock assessment in harvested populations (Sparre and Venema 1998), including bloom-forming jellyfish (López-Martínez et al. 2020). Nevertheless, these data are still scarce in jellyfish fisheries (Omori and Nakano 2001). Scyphozoa' growth estimation is challenging due to technical limitations on their collection, manipulation or fixation (Purcell 2009). Growth estimations have been realized rearing individuals under laboratory conditions (e.g., Astorga et al. 2012; Acevedo et al. 2013), though they are restricted to small size species or early medusae stages. In the field, however, studies are far less numerous (López-Martínez et al. 2020).

Bell diameter frequency distribution is usually the most used proxy to estimate the population growth (Houghton et al. 2006; Palomares and Pauly 2009) and indirectly the population biomass (Nogueira and Haddad 2006). Recently, a new approach based on statoliths size and number (Sötje et al. 2017) has emerged to assess the growth of scyphomedusae in the field. Lately, jellyfish cohorts monitoring together with multi-model inference approaches have proven valuable to estimate population dynamics and growth of the harvest medusae *Stomolophus meleagris* (López-Martínez et al. 2020). These authors showed that the von Bertalanffy model provides the best growth estimation of multi-cohorts jellyfish species, supporting the use of this model to assess jellyfish growth (Palomares and Pauly 2009). Some efforts have been made to synthesize growth rates estimations of scyphozoan species (Palomares and Pauly 2009; Uye and Brodeur 2017), although all together the species of the Subphylum Medusozoa have not been considered.

In a global change scenario, determining environmental niches and growth rates is critical to understand jellyfish species' plasticity under changing marine ecosystems. Here, we assess a field survey of *R. pulmo* in Bages Sigean lagoon (France), a small semi-enclosed lagoon connected to the Mediterranean Sea, that is inhabited perennially (1) to evaluate underlying factors shaping the species' population dynamics and (2) to determine thermohaline niches of the species' pelagic life-stages (ephyrae, juveniles and adults) in Bages Sigean, and for ephyrae and medusae from Mar Menor (Spain) and Bizerte (Tunisia) lagoons. Using multimodal analysis and the von Bertalanffy model, we assessed (3) the species' population growth and mortality rates. Additionally, (4) we addressed our results in a broader context to identify growth patterns in the Medusozoa and (5) we performed a comparative multi-trait assessment to determine the best morphological proxy to estimate *R. pulmo* biomass.

Materials and methods

Study Area

The study was performed in the Bages Sigean lagoon (Fig. 1), on the French Mediterranean coast (43°05′12.72″N; 3°00′35.3″E). It is a small (38 km^2) and shallow lagoon (mean depth 2 m, maximum 4 m) connected to the Mediterranean Sea by a unique and narrow channel (Port La Nouvelle, 60 m width). The main freshwater and nutrients inputs come from the northern coast of the basin. Two main areas can be distinguished: the northern area, characterized by low salinity values (from 15 to 29) and the southern area with higher salinity values (from 20 to 35) (Fiandrino et al. 2017). Therein, many economic activities coexist, including artisanal fisheries (e.g., eels and sea bass), sport (e.g., kitesurf, sailing) and tourism. The lagoon is included in a protected area (Parc Naturel Regional de la Narbonnaise en Méditerranée).

The single previous study on gelatinous zooplankton in the lagoon during 2010–2011 (Bonnet 2013) did not report

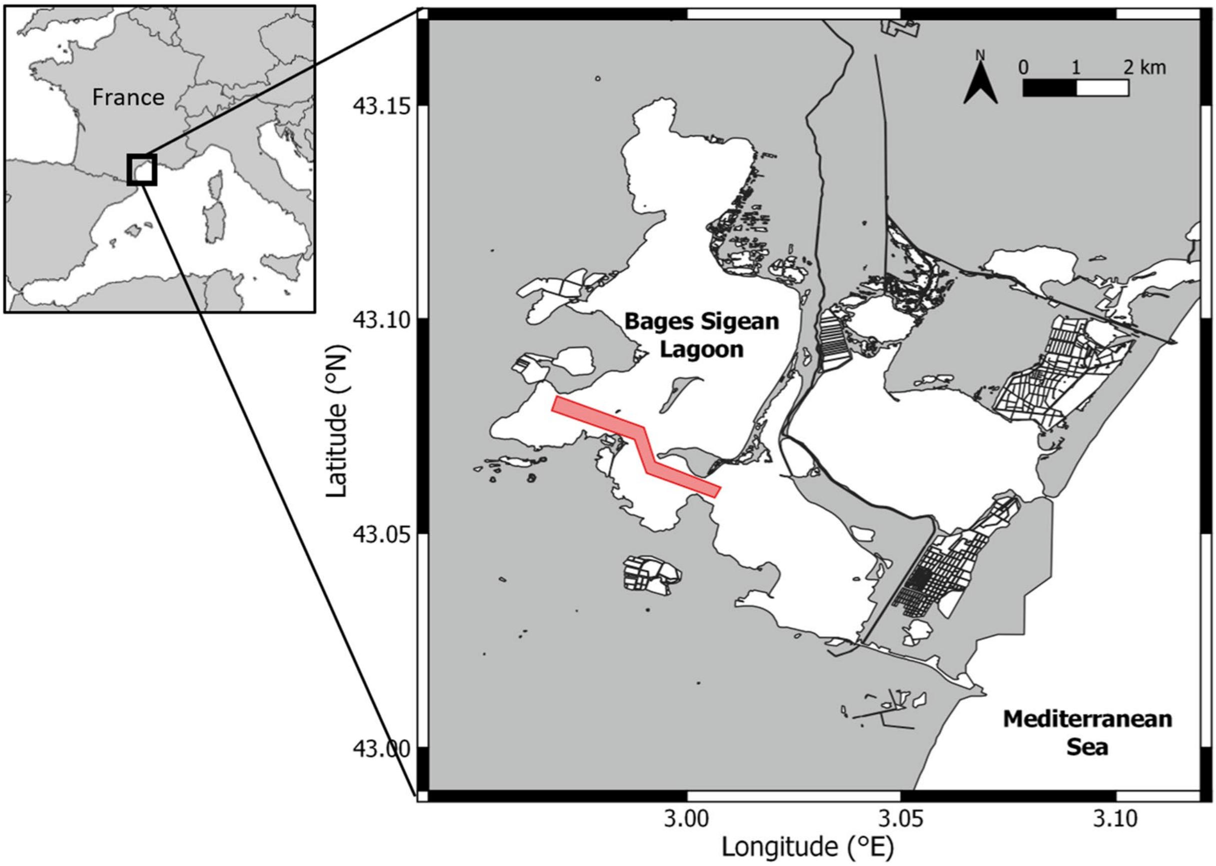

Fig. 1 Map of Bages Sigean lagoon (Aude, France). Sampling area is indicated as a red polygon

the presence of *R. pulmo*, which inhabits Bages Sigean lagoon since 2014 only (Stéphane Marin, pers. comm).

In situ monitoring

A bimonthly sampling was performed from February to November 2019 ($n = 16$) during daytime (between 09:00 and 12:00 AM). Due to weather conditions, only one sampling was carried out in some months (February, March, September, October and November). The sampling area (Fig. 1, red polygon) was chosen based on previous exchanges with fishermen, who indicated the presence of the species every year in this zone since 2014.

Environmental parameters

Environmental parameters were measured twice at each sampling date to characterize the physical environment. Salinity and temperature data were recorded in sub-surface (< 0.5 m) with a multiparameter probe (Hanna HI 9829) and visibility with a Secchi disk. Water samples (150 mL) were collected in triplicate and stored in darkness and fresh conditions to estimate chlorophyll *a* concentration afterwards. Back to the laboratory, water triplicates were filtered on Whatman GF/F filters and stored at − 30 °C until extraction and measurement by spectrofluorimetry (LS 50B Perkin Elmer).

Zooplankton composition analysis

Zooplankton was collected with plankton nets towed horizontally under the sub-surface due to the shallow depth in the area. Mesozooplankton and macrozooplankton samples were performed with 200-µm (0.54 m diameter × 2.5 m length) and 700-µm (0.78 m diameter × 2 m length) mesh nets, respectively, and were fixed in formalin 4%. The volumes filtered by the nets were determined using flowmeters. Zooplankton organisms were identified and counted in a Bogorov chamber under a stereomicroscope Leica using taxonomic guides (Trégouboff and Rose 1978; Hecq et al. 2014) and their abundances were estimated from subsamples and expressed as the number of individuals per cubic meter.

Medusae stage of development

Based on Fuentes et al.'s (2011) criteria of development, ephyrae of stages 2, 4, 6 and 7 were identified in the lagoon. Regarding medusae stages, size classes were determined and juveniles were defined as individuals without gonads and adults as individuals with gonads. Although gonads started to appear on some individuals of 12 cm of bell diameter (BD), they were present in all individuals > 15 cm. We therefore used 15 cm as the size threshold to distinguish juveniles from adults' specimens.

Medusae abundance estimations

R. pulmo undergo a wide range of size, from ephyrae (from 1 mm) to adults with *ca*. 40 cm of BD, weighting up to 2 kg. Two sampling methods were combined to better estimate the abundance of *R. pulmo* pelagic stages and to capture this heterogeneity of size. Ephyrae and juvenile medusae were collected by a 700-µm zooplankton net with a flowmeter and abundances were estimated and expressed as the number of individuals per cubic meter. In the sampling area (Fig. 1), two stations within a distance of 3 km were sampled at each date to have a better representation of the abundances. An average of both values was then calculated. For adults, this monitoring was coupled with a non-intrusive count from the boat in the same area (Fig. 1). Medusae were identified and counted simultaneously by two observers on each side of the boat, along 1 km transects twice. The exact length of each transect (L) was defined by GPS coordinates of departure and arrival points. On each side of the boat, a 3 m wide band (w) was considered as the maximum visibility distance, and depth visibility (d) was based on Secchi disk measurements. All samplings were performed under calm weather conditions, and detectability at Secchi depth was assumed to be 100%. Individuals counted (n) were attributed to three size categories: < 15 cm, 15–30 cm and > 30 cm BD. Counts for adults (BD > 15 cm) were then converted in terms of individuals per cubic meter (X) based on the formula:

$$X = n/(w \times L \times d)$$

Biometrical measurements and biomass estimations

In parallel to net collections, more than 400 specimens were randomly collected by dip nets and conserved in big containers on board with seawater to be measured on land. Each specimen was gently dried with paper and weighted with a balance (precision ± 0.1 g). We further performed a multi-traits assessment to determine the best allometric estimation for the wet weight (WW). Morphological measurements: bell diameter (BD), total length (TL), bell height (BH), manubrium diameter (M) and oral arms' length (OA) were recorded on each medusa collected (Fig. 2). Those measurements were taken with an ichtyometer (precision ± 0.1 cm) and a digital caliber (precision ± 0.01 cm). To estimate the growth rates of the species, calculations were based on BD measurement.

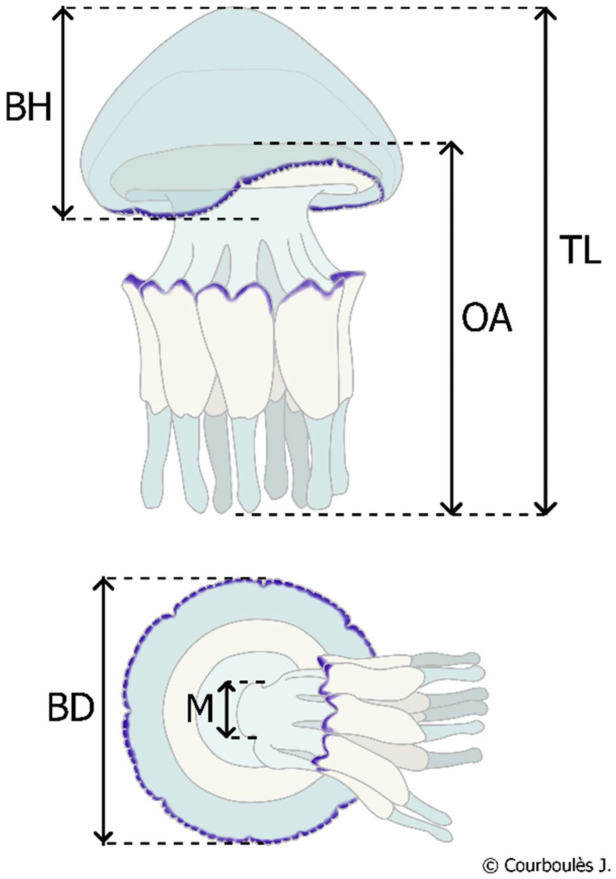

Fig. 2 Morphological measurements recorded on each *Rhizostoma pulmo* medusa collected: bell height (BH), total length (TL), oral arms' length (OA), bell diameter (BD) and manubrium diameter (M). (Illustrator: Justine Courboulès)

Biomass estimation (g m^{-3}) of juveniles (BD < 15 cm) was obtained from specimens caught with the 700-µm net and weighted. For adults (BD > 15 cm), biomass estimation was performed using the individual data from dip nets. Once the number of specimens by category (15–30 cm and > 30 cm) was obtained from visual counts, the same number of organisms from dip nets for each size category was aleatory chosen and its individual weight (g) was considered to estimate the biomass per cubic meter (g m^{-3}).

Statistical analysis

Objective 1. Environmental drivers of *R. pulmo* population dynamics

Generalize Lineal Models (GLM) were run to assess the relevance of potential environmental drivers (i.e. temperature, salinity, chlorophyll *a* concentration and mesozooplankton and macrozooplankton abundances) on *R. pulmo*'s abundances seasonal changes. Explanatory variables were selected with a limit of $p = 0.05$ and models with and without interactions were selected based on the Akaike's Information Criteria (AIC). Models were fitted in R `stats´ through the function *glm*.

Objective 2. Thermohaline niches of each stage of development

We used a nonparametric test of association between environmental factors (i.e. temperature, salinity) and the abundance of each pelagic developmental stage of *R. pulmo* (ephyrae, juveniles and adults). The approach encompasses a cumulative frequency method and a Monte Carlo randomization (Paramo et al. 2003). It is based on the maximum absolute difference between the cumulative frequency distribution (CFD) of an environmental factor and the abundance weighted CFD of that environmental factor. First, the relative CFD was calculated for temperature and salinity. Then, the CFD for each environmental variable was weighted by the abundance of each *R. pulmo* pelagic stage. The comparison of unweighted and weighted CFD indicates the association of the population with the environmental variable. If the density of the population is randomly distributed in relation to the environmental variable, the cumulative pattern will increase similarly in the two curves and they will not be significantly different. In turn, if the population is related with a specific range of the environmental variable, the slope of the weighted CFD should be steeper than the unweighted environmental variable (Molinero et al. 2009). This allows testing, by a randomization procedure, the degree of association between the species abundance and environmental factors. The same analysis was performed to estimate the thermohaline niche of the medusae stage pooling together juveniles and adults' abundances.

To have a broader picture of *R. pulmo* niche, we compiled data from previously reported locations, Mar Menor lagoon, Spain (Fernández-Alías et al. 2020) and Bizerte lagoon, Tunisia (Gueroun 2016) to compute the thermohaline niche of ephyrae and medusae stages. The estimations of abundances of *R. pulmo*'s ephyrae and medusae in both lagoons were performed following the methodology used in the present study (Gueroun 2016; Fernández-Alías et al. 2020).

Objective 3. Growth and mortality rates

Identifications of cohorts: Size frequency histograms of BD size classes of 0.5 cm were created for each month from specimens caught by dip nets and counted by the visual method. To avoid bias in the frequency distribution of jellyfish caught by dip nets and the in situ distribution observed visually from boat, the size classes of jellyfish were compared by a nonparametric Wilcoxon test.

Cohorts were determined by multimodal analyses by matching monthly frequency distribution of 0.5 cm BD class to log-normal distributions according to the presumed number of cohorts (López-Martínez et al. 2020) based on maximum-likelihood estimation for grouped data. If the distributions significantly represented the data ($p < 0.05$), then the number of estimated cohorts was retained. This technique is classically recommended to analyze the size frequency distribution of a population with overlapping age groups, to identify the distributions that best fit to the size frequency histograms. This was performed using the *mix* function of the 'mixdist' package (Macdonald and Du 2018). Once the cohorts were identified, the specimens were grouped by cohort and treated independently for subsequent analyses.

Growth rate estimations: The von Bertalanffy growth model (VBGM) has been used in numerous studies to quantify the growth of fish (e.g. Ogle and Isermann 2017), crustaceans (Indarjo et al. 2020) and mollusks (Ford et al. 2020). It has been also demonstrated to be an appropriated way to estimate jellyfish growth (Palomares and Pauly 2009; Fernández-Alías et al. 2020). For *R. pulmo*, once the number of cohorts was defined, a von Bertalanffy function (Beverton and Holt 1957; Ogle 2013) was estimated for each cohort as:

$$L_{(t)} = L_{\infty}(1 - (1 - e^{-k(t-t_0)})$$

where $L_{(t)}$ is the length at age t, L_{∞} is the asymptotic length at which growth is zero, k is the growth coefficient (in month or year), t is the age at size $L_{(t)}$ and t_0 is the age at which the organisms would have had zero size (initial condition parameter).

Starting parameters values for the model (k and L_{∞}) were estimated individually for each cohort following the methodology in Ogle (2013). Typically, this equation is utilized when both age and body size are known. Here, the age of the jellyfish was considered by month during one year. Once the cohorts were defined, specimens were monthly grouped and the initial values estimated using the BD as size, with the function *vbStarts* of the `FSA´ package. Then, these values were used to fit the model. This was performed with the `FSA´ and `nlstools´ packages

(Baty et al. 2015; Ogle et al. 2021). Once the VBGM was obtained for each cohort, growth curves were fitted between the age (in months) and the BD. Somatic growth rates (mm of BD per day) were determined from the average of the slopes obtained for each month. In addition, the same method was used to estimate the growth rate for juveniles and adults of each cohort independently.

Literature review: To gain further perspective on jellyfish growth, a literature review of growth rate estimations (mm of BD per day) of Medusozoa species was made through a search on Google Scholar. The terms used were: 'Jellyfish growth rate', 'Medusae growth rate' or the name of each Class/Order followed by 'growth rate'. Available data of BD were assembled from different studies and growth rates were uniformly re-calculated as a linear regression fitted to BD data from all individuals collected. Both medusae and ephyrae were considered (as different groups when possible) when a continuous period was available. *Aurelia* spp.'s growth rates reviewed by Marques et al. (2015b) were included in the analysis, but not showed in details in the synthesis.

Growth rates were compared among taxonomic Orders by an ANOVA test. The effect of individual mean size on the growth rate values was evaluated with a Linear Model (LM) fitted between the mean BD and the estimated growth rate.

Mortality rates estimations: Mortality is a key component to understand the jellyfish population dynamics. Mortality rates were estimated using the Chapman–Robson method (Chapman and Robson 1960). This method assumes that the catches at each age on the descending limb of the catch curve follow a geometric probability distribution. The catch of jellyfish at each age is proportional to the number of jellyfishes observed by age, considering the age as months. This distribution was used to derive a maximum-likelihood estimator for the survival parameter of the distribution, used later to estimate mortality. This analysis was carried out with the function *chapmanRobson* of the 'FSA' package (Ogle et al. 2021).

Objective 4. Biomass assessment

To determine the reliability of allometric relationships to estimate the WW, nonlinear regressions were fitted between individual WW and morphological measurements. The selection of the best trait was based on the best fitted curve (r^2), but also considering the easiest measurement to acquire in the field.

All the analyses were performed using the open source software R 3.6.0 (R Core Team 2020) and plots were created with the 'ggplot2' package (Wickham 2016). The map was performed using the open source software QGis 3.4.4 (QGIS Development Team 2009).

Results

Environmental conditions

Mean depth of the sampling area was 1.8 ± 0.1 m. Temperature showed a typical seasonal cycle in the lagoon, with highest values recorded in August (27.2 °C) and lowest in November (7.2 °C) (Fig. 3a). Salinity displayed an increasing trend during the year, reaching values higher than previously reported (Fiandrino et al. 2017) in the lagoon

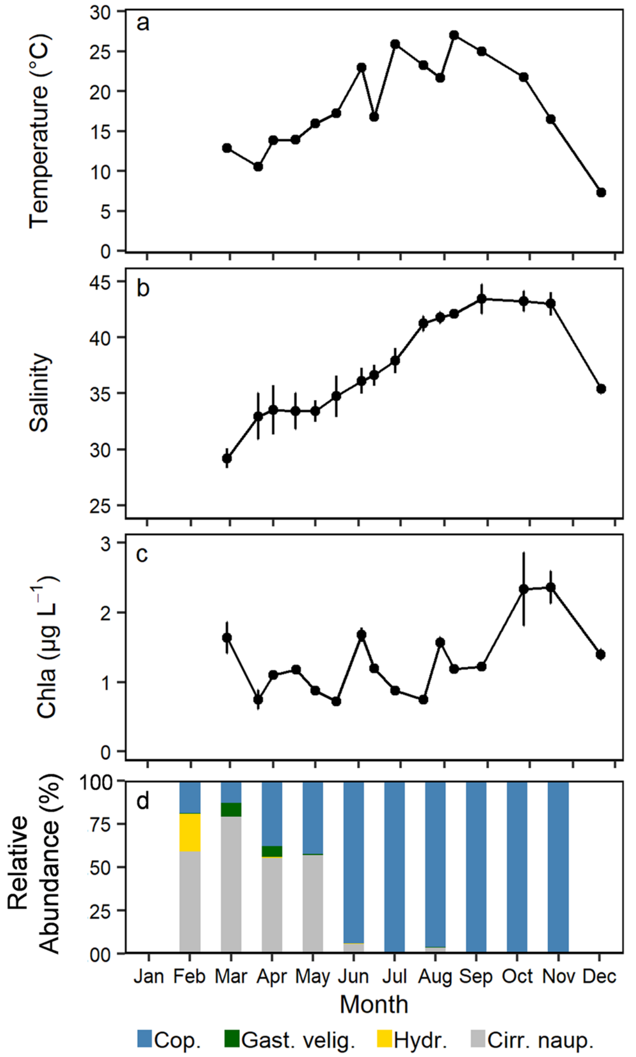

Fig. 3 **a** Average seasonal cycles of temperature (°C), **b** salinity and **c.** chlorophyll a (µg L^{-1}) during 2019 in Bages Sigean lagoon (France). Curves represent the mean and error bars the standard error by sampling date. **d** Monthly relative abundance (%) of the main mesozooplankton groups (Cop. = Copepoda, blue; Gast. velig. = Gastropoda veliger larvae, green; Hydr. = hydromedusae, yellow; Cirr. naup. = Cirripedia nauplii, grey)

during summer (44.7 in August) and minimum values in winter (28.3 in February) (Fig. 3b). Chlorophyll *a* showed a main seasonal peak in autumn (2.4 µg L^{-1} in October) and a noticeable monthly variability. Three smaller peaks were also observed in February, June and July and the minimum value was measured in March (0.7 µg L^{-1}) (Fig. 3c).

Zooplankton composition

Zooplankton abundance displayed a marked seasonal variability (data not shown). The copepods *Acartia clausi*, *Paracalanus parvus* and *Pseudocalanus elongatus* and the cirripeds nauplii contributed at least to 80% of the total mesozooplankton abundance (Fig. 3d). We therefore used these taxa for posterior statistical analysis as representative of the mesozooplankton community.

A temporal succession in the gelatinous zooplankton community was observed. This community showed a dominance of the small (less than 1 cm of BD) hydromedusae *Rathkea octopunctata*, *Odessia maeotica, Ptychogena crocea* and *Podocoryne minima* during Spring. They all disappeared in May when the scyphomedusae *R. pulmo* and *Aurelia coerulea* abundances increased (data not shown).

Objective 1. *R. pulmo* population dynamics and its environmental drivers

The visual counting was performed for 2 km (*L*) with a 1.2 m visibility depth (*d*). Total abundance of *R. pulmo* pelagic stages presented three peaks: a maximum in April and two smaller in June and July (Fig. 4a). Ephyrae occurred from April to June, with a maximum abundance in June (6.1 ind 100 m^{-3}). Juveniles appeared from April to September, with a peak in April (17.5 ind 100 m^{-3}), and adults from May to October, rising a peak at the end of June (1.0 ind 100 m^{-3}) (Fig. 4b). *R. pulmo* total biomass (g m^{-3}) was estimated for the medusae stages (juveniles and adults) and presented three peaks (June, July and September), with a maximum in July (10.2 g m^{-3}) (Fig. 4c). When the last adults were observed, the bottom of the lagoon was full of dead medusae (V. Leoni personal observation). In November, no individual occurred.

The temporal variability of *R. pulmo* abundance was positively correlated to the abundance of the copepods *A. clausi* and *P. elongatus*, with an explained variance of 51% (GLM, $p < 0.05$) (Fig. 4d). Environmental parameters (temperature, salinity or chlorophyll *a*) did not show any significant correlations with *R. pulmo* abundance.

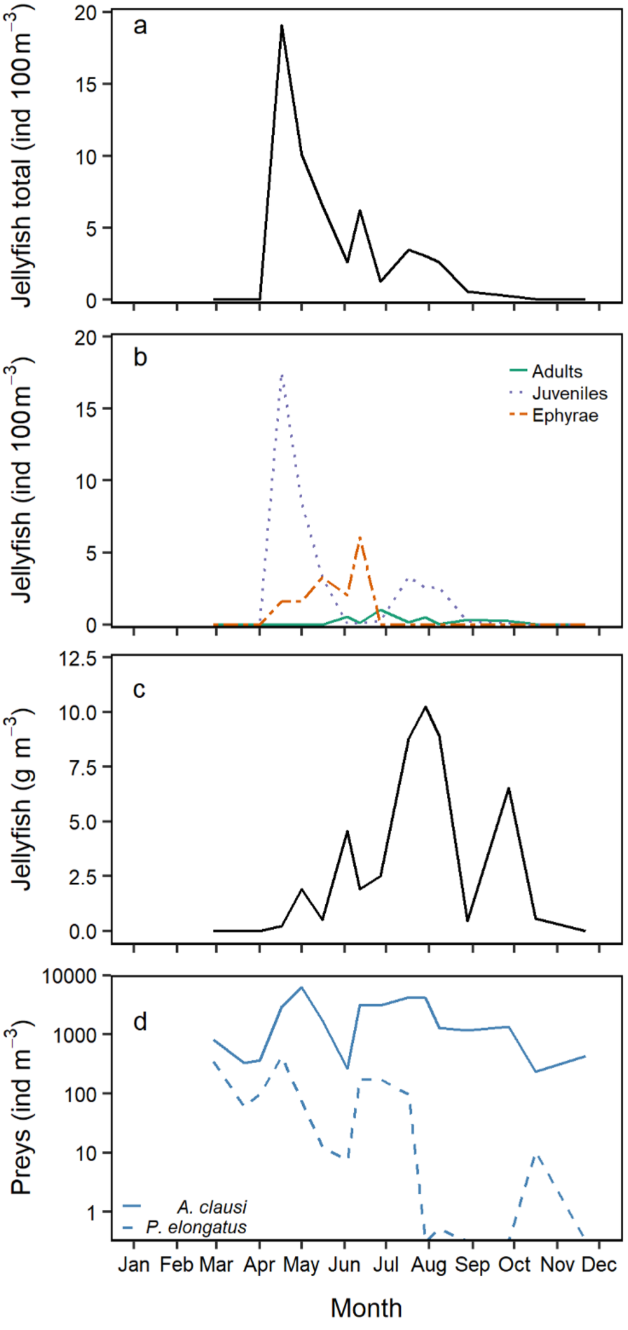

Fig. 4 **a** Temporal variability of the total abundance (ind 100 m^{-3}) of the three pelagic stages of *Rhizostoma pulmo.* **b** Abundance for each developmental stage (ephyrae in dashed orange line; juveniles < 15 cm in dotted purple line; adults > 15 cm in continuous green line). **c** Temporal variability of the medusae total biomass (g m^{-3}) (juvenile and adults together). **d** Abundance of the two copepods species (*Acartia clausi*: continuous blue line and *Pseudocalanus elongatus*: dashed blue line) showing a significant correlation with *R. pulmo* total abundance (Note that *Y* axis is represented in logarithmic scale). Data were collected in Bages Sigean lagoon (France) during 2019

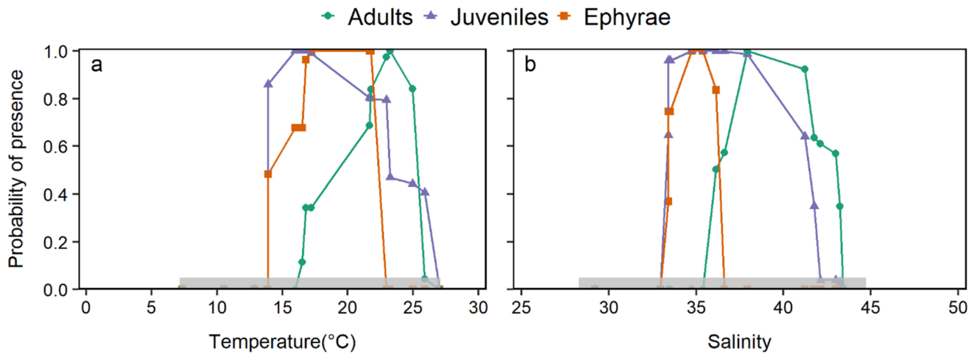

Fig. 5 **a** Environmental niche of temperature and **b** salinity of ephyrae in orange, juveniles in purple and adults medusae of *Rhizostoma pulmo* in green in Bages Sigean lagoon (France) during 2019. Grey bars represent the range of the environmental variable during the study period

Objective 2. Thermohaline niches of each stage of development

Niches of salinity and temperature in Bages Sigean differed among the three pelagic stages of development of *R. pulmo* (Fig. 5). Ephyrae showed the narrowest thermal window (13.9–21.8 °C), with the highest probability of occurrence at 20.2 °C. In contrast, juveniles occurred in a largest range of temperature (from 13.9 to 25.9 °C) and their maximum probability of presence was at a lower temperature (16.8 °C) than ephyrae. The maximum probability of adults' occurrence was at 23.2 °C, a warmer temperature than for juveniles or ephyrae. Adults were present between 16.5 and 25.9 °C. Regarding salinity, ephyrae occurrence was associated to a narrow range (33.4–36.1) and juveniles showed a noticeable wider range (33.4–41.8). However, both ephyrae and juveniles displayed a maximum of probability of occurrence at a salinity of 35.1. Similarly, as for temperature, adults were found at higher salinities (36.1–43.2), with a maximum at 37.9.

When comparing ontogenetic niche partitioning among areas, we found that *R. pulmo* occurs at higher temperature (13.0–29.0 °C) and salinity (39.5–45.9) ranges in Mar Menor, compared with Bages Sigean and Bizerte lagoons (Fig. 6). Medusae from Bages Sigean and Bizerte showed similar thermal windows and a maximum probability of presence at close temperatures (mean around 19.8 °C in Bizerte and at 17.2 °C in Bages Sigean, Fig. 6c). Although the salinity range of medusae occurrence in Bages Sigean was the widest, the maximum probability of occurrence was at lower salinity (35) than in Bizerte (37.2) (Fig. 6d).

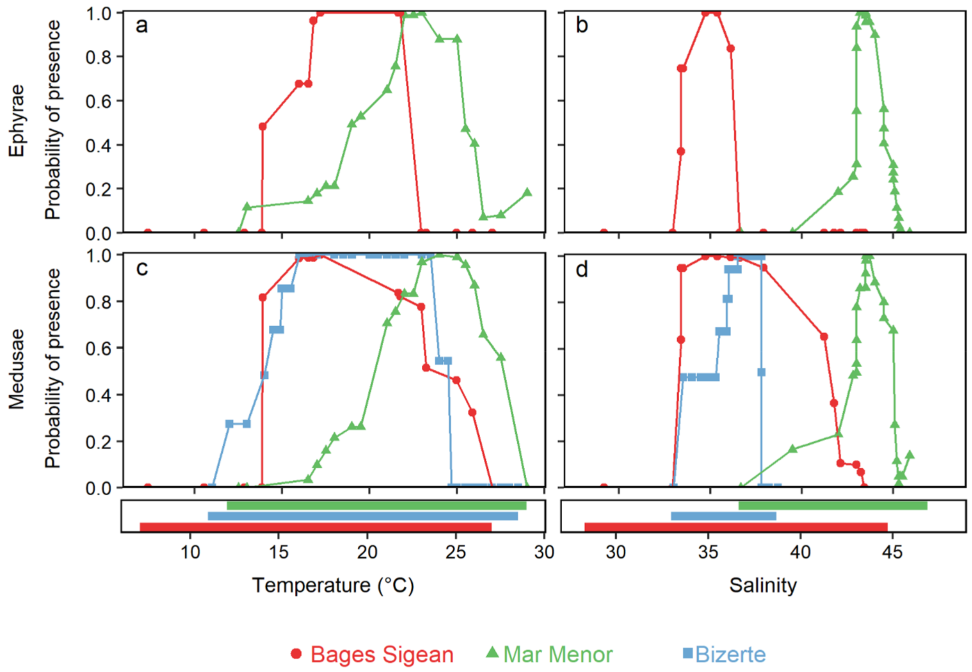

Fig. 6 **a-b** Thermohaline niche for ephyrae and **c-d** medusae of *Rhizostoma pulmo* in three coastal Mediterranean lagoons: Bages Sigean lagoon in red (France, 2019), Mar Menor lagoon in green (Spain, 1997) and Bizerte lagoon in blue (Tunisia, 2012–2014). Horizontal lines represent the range of the environmental variable (temperature or salinity) during the study period for each region

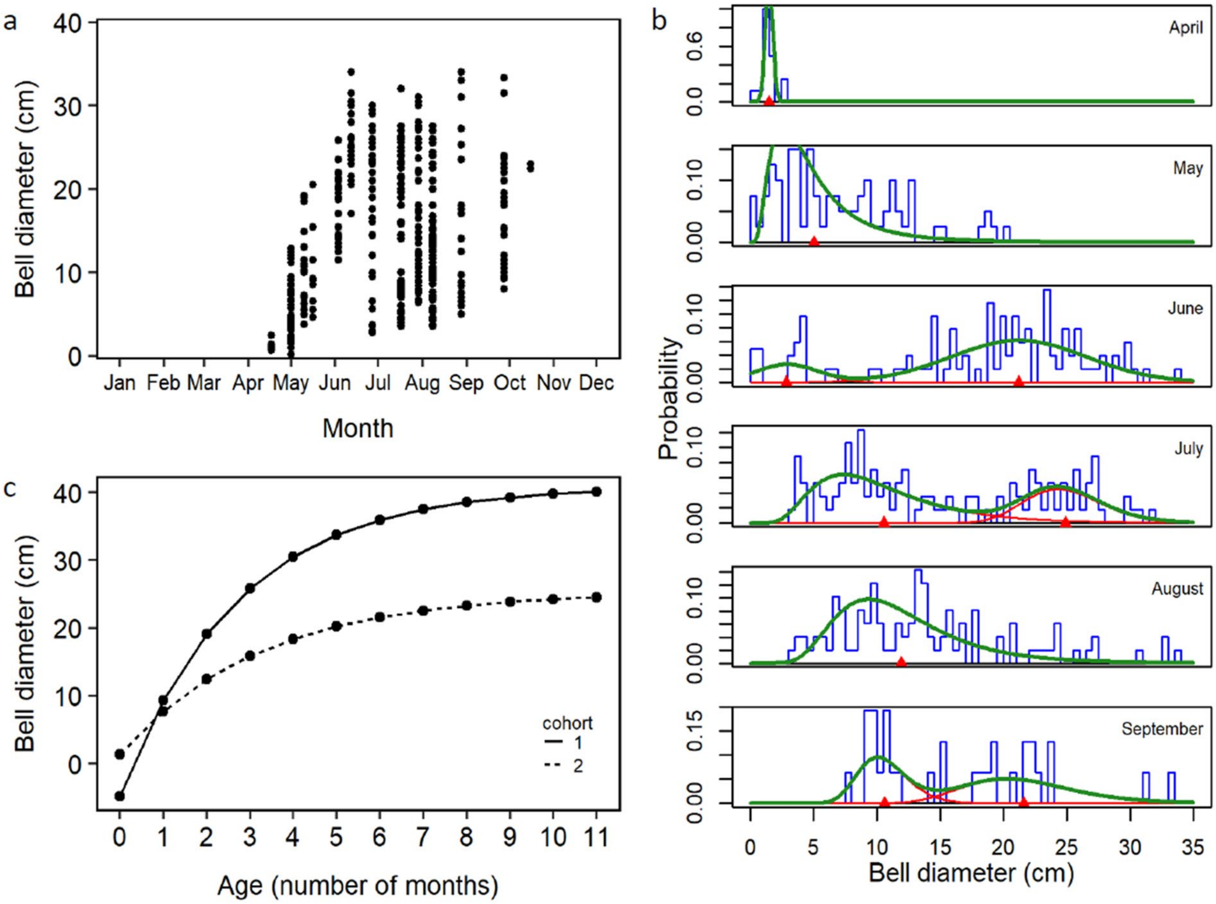

Fig. 7 **a** Individual bell diameter (cm) of *Rhizostoma pulmo*. **b** *R. pulmo* size class distribution multinomial analysis in Bages Sigean lagoon (France) from April to September 2019. Blue lines show the observed bell diameter frequencies and green lines show theoretical modal groups of the species. Red symbols indicate a significant mode identified. **c** Growth curves described by the von Bertalanffy growth model for two of the three cohorts identified for *R. pulmo* in Bages Sigean lagoon

Table 1 Growth parameters estimated by von Bertalanffy growth model for the different cohorts of *Rhizostoma pulmo* in Bages Sigean and Mar Menor lagoons.

Study area	Cohort	k (year^{-1})	L_∞ (cm)	t_0	Reference
Bages Sigean lagoon (France, 2019)	1	4.47	40.95	0.02	Present study
	2	3.76	25.31	− 0.01	
	3	NA	NA	NA	
Mar Menor lagoon (Spain, 1997)	1	3.19	46.36	− 0.04	Fernández-Alías et al. (2020)
	2	3.44	46.36	− 0.08	
	3	3.10	46.36	− 0.07	
	4	3.00	46.36	− 0.13	

L_∞ is the asymptotic size at which growth is zero. k is the growth coefficient (year^{-1}). The parameter t_0 is included to adjust the equation for the initial size of the organism and is the time at which the organism would have had zero size (initial condition parameter)

Objective 3. *R. pulmo* growth and mortality rates

For most sampling dates, a wide range of medusae size was observed in the lagoon (Fig. 7a), indicating the probable existence of more than one cohort during the year. Multinomial analysis showed the presence of three cohorts of *R. pulmo* overlapping during 2019. The first cohort occurred from April to September, the second from May to October, and the third from June to October. Graphically, the multinomial analysis showed modal progressions through time from April to September 2019 (Fig. 7b).

The growth parameters estimated with VBGM are presented in Table 1. Figure 7c depicts the fitted growth curves of VBGM for the two first cohorts, as there were not enough individuals collected to parameterize the third cohort. The projected growth curve on the age-length data showed a pronounced curvature in the youngest medusae. Even so, the

Table 2 Literature review of growth rates (mm per day) of jellyfish species

Class	Order	Species	Growth rate range (mm day^{-1})	Nb. of cohorts per year	Strobilation type (nb. ephyrae release)	Medusae size (min–max) in mm	Stage	Study area	Reference
Scyphozoa	Rhizostomeae	*Catostylus mosaicus*	4.81 (max)	1 to 3	Mono/polydisc	20.0–250.0	Young medusae	Botany Bay and Lake Illawarra, New South Wales (Australia)	Pitt and Kingsford (2003)
		Cephea cephea	0.71	–	–	2.0-45.0	Young medusae	Laboratory conditions (28 °C) (Japan)	Sugiura (1966)
		Cotylorhiza tuberculata	5.40	1	Monodisc	1.5–350.0	Ephyrae + Medusae	Vlyho Bay (Lefkada, Greece)	Kikinger (1992)
			5.00–5.10	2		1.5–400.0	Ephyrae + Medusae	Vlyho Bay (Lefkada, Greece)	Kikinger (1992)
			0.08	–		2.1–13.0	Young medusae	Laboratory conditions (20 °C) (Spain)	Astorga et al. (2012)
		Mastigias papua	2.90	–	Monodisc	–	Medusae	–	Sugiura (1964)
		Nemopilema nomurai	0.92	1	Polydisc (3–7)	2.2–18.0	Ephyrae + Metaephyrae	Laboratory conditions (22–28 °C) (East Asia)	Kawahara et al. (2006)
			3.77			18.0–110.0	Young medusae	Laboratory conditions (22–28 °C) (East Asia)	
		Phyllorhiza punctata	2.00	1 or 2	Monodisc	10.0–400.0	Medusae	Laguna Joyuda (Puerto Rico)	Garcia (1990)
			0.74	–		1.5–46.0	Ephyrae + Medusae	Vlyho Bay (Lefkada, Greece)	Abed-Navandi and Kikinger (2007)
		Rhizostoma pulmo	1.50–2.30	3	Polydisc (8 -18)	6.7–340.0	Medusae	Bages Sigean lagoon (France)	Present study
		Rhizostoma octopus	2.90	–	Polydisc (1–12)	–	Medusae	–	Thiel (1966); Krüger (1968)
		Rhizostoma luteum	0.68	–	Monodisc	4.0–19.4	Ephyrae	Laboratory conditions (17 °C)	Kienberger et al. (2018)
			2.41			19.4–164.0	Medusae	Laboratory conditions (17 °C)	
			–	1 (potentially 3)		–	Medusae	La Herradura (Spain)	

Table 2 (continued)

Class	Order	Species	Growth rate range (mm day^{-1})	Nb. of cohorts per year	Strobilation type (nb. ephyrae release)	Medusae size (min–max) in mm	Stage	Study area	Reference
		Rhopilema nomadica	1.89	–	Polydisc (5–6)	2.0–170.0	Ephyrae + Medusae	Laboratory conditions (NA) (Israel)	Lotan et al. (1994)
		Stomolophus meleagris	3.10	3	Polydisc (1–3)	4.2–160.0	Ephyrae + Medusae	Gulf of California (Mexico)	López-Martínez et al. (2020)
	Semaeostomeae	*Aurelia* sp.[a]	0.19–3.38	–	Polydisc	–	Medusae	Synthesis multisite report	Marques et al. (2015b)
			0.59–2.67	1		10.0–31.9	Medusae	Thau lagoon (France)	Marques et al. (2015b)
		Cyanea	0.40–0.80	1	–	20.0–70.0	Medusae	Niantic River, Waterford (USA)	Brewer (1989)
		Pelagia noctiluca	0.09	2	Holoplanktonic	0.5–10.0	Ephyrae	Gulf of Trieste (Adriatic Sea)	Malej and Malej (1992)
			0.25	–		1.1–1.5	Ephyrae	Laboratory conditions (13.5 °C) (Gulf of Trieste, Adriatic Sea)	Avian (1986)
			0.28–0.30	1		20.0–145.0	Medusae	Straits of Messina (Central Mediterranean Sea)	Rosa et al. (2013)
Cubozoa	Chirodropida	*Chiropsalmus* sp.	1.00	3 to 4	Monodisc	3.0–71.0	Medusae	Port Douglas, North Queensland (Australia)	Gordon et al. (2004)
		Chiropsalmus quadrigatus	0.77	–	Monodisc	18.0–110.0	Medusae	Matagorda Bay, Texas (USA)	Guest (1959)
		Chironex flackeri	3.20	–	–	0.6–190.0	Medusae	Cape York (Australia)	Gordon and Seymour (2012)
	Carybdeidae	*Carybdea marsupialis*	0.08	–	–	2.0–20.0	Medusae	Laboratory conditions (NA) (17.2-25.1°C) (Spain)	Acevedo et al. (2013)

Table 2 (continued)

Class	Order	Species	Growth rate range (mm day^{-1})	Nb. of cohorts per year	Strobilation type (nb. ephyrae release)	Medusae size (min–max) in mm	Stage	Study area	Reference
Hydrozoa	Limnomedusae	*Craspedacusta sowerbii*	0.28	–	–	1.0–11.1	Medusae	Laboratory conditions (29 °C)	Marchessaux and Bejean (2020)
			0.12	–	–	0.6–5.0	Medusae	Laboratory conditions (21–30 °C) (Panama)	Folino-Rorem et al. (2016)
	Leptomedusae	*Clytia* spp.	0.27 (max)	–	Colony	2.0–10.0	Medusae	Laboratory conditions (15 °C) (France)	Matsakis (1993)
		Clytia hemisphaerica	0.25–0.37	–	Colony	1.0–2.5	Medusae	Laboratory conditions (18–20 °C)	Lechable et al. (2020)
			1.19	–	Colony	2.5–12.0	Medusae	Laboratory conditions (18–20 °C)	

[a] Data from *Aurelia* spp. previous review by Marques et al. (2015b) are not included in details in this table

growth curve for the second cohort showed a lower asymptotic value compared to the first one. On average, medusae grow 2.3 mm day^{-1} for the first cohort, and 1.5 mm day^{-1} for the second cohort. Regarding each developmental stage separately, juvenile growth rates were much higher than those determined for adults, with 4.7 and 2.4 mm day^{-1}, for the first and second cohorts, respectively. Adults' growth rates were 1.8 and 0.9 mm day^{-1}, for the first and second cohorts, respectively. Moreover, the L_∞ was higher for the first cohort than the second cohort (Table 1). The monthly mortality rates were 52.6% and 61.3% for the first and second cohorts, respectively.

A literature review on the growth rate of jellyfish species (Table 2) revealed a heterogeneity between taxonomic groups, the Scyphozoan being the most studied species. Differences among Classes, but also among Orders of each Class have been identified (Fig. 8a), with Rhizostomeae species presenting the highest growth rates. If the mean BD is considered to explain this variability (Fig. 8b), an increase of the growth rate is revealed with an increase of the size of the jellyfish. We observed also that Rhizostomeae species are the largest jellyfishes for which growth has been studied.

Objective 4. Biomass assessment

Significant relationships were obtained between WW and all morphological parameters measured (Table 3). In fact, all the morphological traits considered in the present study are good indicators to estimate the biomass of *R. pulmo*. In particular, the BD and the TL of the individuals presented both the best fit (r^2).

Discussion

Semi-enclosed coastal lagoons can be considered as large mesocosms, offering unique opportunities to study jellyfish dynamics. Here, we provide evidence of a bottom–up control on the population dynamics of *R. pulmo* in Bages Sigean lagoon, which is further shaped by multiple recruitment pulses on a yearly basis. In addition, we also show different thermohaline niches for western Mediterranean populations of *R. pulmo*.

Population dynamics of *Rhizostoma pulmo* in coastal Mediterranean lagoons

Multiple recruitment pulses have been described in many scyphozoan (Calder 1982) and cubozoan species (Table 2). However, the underlying causes of such patterns are still far from understood (Houghton et al. 2007). In the present study, we identified three abundance peaks of *R. pulmo* ephyrae during one year. This multi-cohort pattern agrees with previous observations in Mar Menor, where four ephyrae abundance peaks were detected (Fernández-Alías et al. 2020). Under laboratory conditions, thermal shocks stimulates scyphostomae strobilation in some species (Holst 2012; Marques et al. 2019). For *R. pulmo*, empirical observations have shown that only one thermal shock may induce more than one strobilation event (Anaïs Courtet, Paris Aquarium, pers. comm.), with the possibility that the same scyphostoma strobilates twice (Purcell et al. 2012). We suggest that multi-strobilation may be a common feature for some species (Calder 1982; Houghton et al. 2007) including *R. pulmo*, whilst interannual variability in the number of cohorts (Kikinger 1992) has been associated to the delta of temperature prior scyphostomae strobilation.

The seasonal dynamics of *R. pulmo* in Bages Sigean during 2019 was characterized by a peak of medusae abundance during spring (April) and a disappearance during winter (November). This trend supports previous observations in Mar Menor during 1997 (Fernández-Alías et al. 2020). In both lagoons, first ephyrae appeared at the beginning of spring (April) and medusae seemed to grow inside the lagoons throughout the year, as all pelagic stages were observed. Fuentes et al. (2011) recorded a quite similar seasonal distribution during three consecutive years (2007, 2008, 2009) on the Catalan coast (Spain). On both French and Spanish Mediterranean coasts, seasonal patterns of temperature, salinity and chlorophyll *a* concentration are similar, which may explain the quasi-synchronous annual pattern of *R. pulmo* in the lagoons. Despite a similar seasonality, *R. pulmo* abundances seem to exhibit marked variability. Maximum abundance detected in Bages Sigean during 2019 was 19.1 ind 100m^3, while in 1997 in Mar Menor it was 2.6 ind 100m^3 (Fernández-Alías et al. 2020), but interannual abundance variability are also to be considered (D'Ambrosio et al. 2016). In the Southern Mediterranean coast, *R. pulmo* was observed in the bay of Bizerte (Tunisia) mainly during summer–autumn months: in September 1994, May, September and October 1995 (Daly Yahia et al. 2003) and from September to November 2013 (Gueroun 2016). In 2014, the species appeared in Bizerte lagoon during winter–spring months (January to April), which probably corresponds to some individuals capable of entering in the lagoon to withstand the winter. In all cases, *R. pulmo* was observed at low abundances (< 1 ind 100m^3) therein and in specific months, which suggests that the species is transported from adjacent areas.

The thermal window of *R. pulmo* medusae in the Mediterranean Sea in the last decade, based on medusae semi-quantitative data and satellite temperature data, was identified between 15 and 22 °C (Leoni et al. 2021). Our results support the reported range, but also showed that at local scales, the width of the thermal niche is larger, with a potential thermal niche from 13 to 29 °C, although major abundances were found at temperatures > 15 °C. The ability of *R. pulmo* to dwell a wide range of temperatures is probably due to the capacity of temperate ectothermic species to tolerate changing temperatures as observed for marine copepods (Molinero et al. 2009).

Except for the low winter temperature measured in the shallow Bages Sigean lagoon, temperature values were comparable in the three lagoons. However, we have shown that the species presents different realized niches in the three evaluated geographic regions: Tunisia, Spain and France (Fig. 6). For *R. pulmo*, at least three genetically distinct populations have been identified in Tunisia, North Adriatic and Western Mediterranean (coast of Spain and Italy) Sea (Ben Faleh et al. 2017). Population genetic differentiation among distant areas has been also observed for others scyphozoan species (Kingsford et al. 2000; Ramšak et al. 2012; Dawson et al. 2015; Glynn et al. 2015). In those distinct jellyfish populations, physiological adaptation to temperature variability has been observed (Dawson et al. 2015; Gotoh et al. 2017). Here, the niche variation we observed on *R. pulmo* is likely indicative of local adaptation and phenotypic plasticity of *R. pulmo* populations from the Western Mediterranean. Future biogeography studies of this species should include not only the French population, but also those from other ecoregions of the Mediterranean to identify its potential divergence.

Ontogenetic variations in the thermohaline niche were also revealed, as observed in *A. coerulea* in Thau lagoon (Bonnet et al. 2012; Marques et al. 2015b). The maximum ephyrae abundance was reached in June, in concurrence with a peak of temperature. This agrees with laboratory observations, where *R. pulmo* scyphistomae produced more buds and ephyrae under warm (21 to 28 °C) than cold conditions (14 °C) (Purcell et al. 2012). The widest range of temperature observed for young medusae in Bages Sigean is probably due to the continuous ephyrae production under different environmental conditions. This underlines that plasticity in juvenile stages is probably higher than in mature sexual medusae. The detection of juveniles' abundance peak (April 17) before ephyrae abundance peak (June 12) (Fig. 4b) was probably due to a combination of a fast growth rate (4.7 mm day^{-1}) of early pelagic stages, and a low-frequency sampling (April sampling occurred in April 1 and 17), which did not allow to capture the ephyrae short-term dynamics. Moreover, the use of fixed sampling stations for monitoring free-living species, transported with current generated by the winds in the area, may explain the lack of ephyrae detection prior to the peak of juveniles. Overall, adults in Bages Sigean were observed under warmer waters conditions than younger stages, which agrees with summer blooms reported for many Mediterranean jellyfish species (Boero 2014). Salinity ranges differ between lagoons, but the optimal salinity values for ephyrae in Bages Sigean and medusae from Bages Sigean and Bizerte were similar. In Bages Sigean and Mar Menor, ephyrae presented a different but restricted range of salinity, probably because of their short period of development, as new released ephyrae of approximately 1 mm should grow only 9 mm before developing into a small medusae.

Despite that drivers of jellyfish population dynamics are still not well understood, increasing evidences on the role of food availability have been provided by in situ monitoring (Lucas 1996; Buecher et al. 2001; Rosa et al. 2013; Marques et al. 2015b; Goldstein and Riisgård 2016). For *R. pulmo*, bottom–up processes appeared to be main drivers of the pelagic population dynamics in Bages Sigean, in agreement with previous research in Mar Menor (Fernández-Alías et al. 2020) and Bizerte (Addad et al. 2008) lagoons, or for the Rhizostomeae *Nopilema nomurai* in Dalian Sea, China (Xie et al. 2021). In Bages Sigean, copepods play a key role in shaping *R. pulmo* abundances. In this regard, increasing knowledge on the diet of the species (Pérez-Ruzafa et al. 2002; Dönmez and Bat 2019) is required to evaluate not only the role of plankton community in the dynamics of the species, but also the feeding pressure of *R. pulmo* on the ecosystem.

The voracious food-consumption of scyphomedusae (Acuña et al. 2011), together with the fast growth rates (several mm per day, Table 2), induces rapid development of large individuals in short periods of time. The growth coefficients (K in years^{-1}) of *R. pulmo* varied from 3.76 to 4.47, but are consistent with those reported for other scyphozoans: *S. meleagris* (3.97 to 5.79), *Phyllorhiza punctata* (4.69), *C. hysoscella* (4.30) and *A. aurita* (3.83) (Palomares and Pauly 2009; López-Martínez et al. 2020). However, Fernández-Alías et al. (2020) reported lower values (3.00 to 3.44) for *R. pulmo* in Mar Menor, probably due to the fact that they used a different method for cohort identification and defined a unique L_∞, whilst we defined a specific value for each cohort. In Bages Sigean, *R. pulmo* growth varied between cohorts and during ontogeny. We suggest that this difference may be partly due to the overlapping between adults from the first cohort with juveniles of the second cohort, which could induce competition for food. This, together with the natural seasonality of the zooplankton community in the lagoon, might limit their growth rate but also the maximum size raised by adults from the second cohort. In addition, growth can be reduced in adult stages (> 15 cm) when resources are reallocated to reproduction (Lucas and Lawes 1998). *R. pulmo* start to present gonads when their BD is larger than 15 cm. Based on age estimations derived from our study, medusae could reach sexual maturity within 1 to 2 months, as estimated for *Catostylus mosaicus* (Pitt and Kingsford 2003).

In comparison with other Class of Medusozoa (Table 2), scyphozoan species show the fastest growth and the biggest BD. A great proportion of the variability of Medusozoan's growth rate was explained by the medusae size ($r^2 = 0.44$, Fig. 8b). Despite most of the studies have been realized on *Aurelia* spp., a greater diversification is observed in the studies on Order Rhizostomeae, with 11 species analyzed compared to 3 species of Semaeostomeae. In contrary, Hydromedusae and Cubomedusae showed similar rates, but less than 10% of these species have their growth rates estimated. The fast growth rates of scyphomedusae could explain their relatively short longevity (< 1 year) (Arai 1997). A maximum longevity of 7 months was identified for *R. pulmo* in Bages Sigean, as previously reported in the Mediterranean Sea (Leoni et al. 2021). Similar estimations have been made for Rhizostomeae species as *S. meleagris* (8 months) (López-Martínez et al. 2020) and *N. nomurai* (7 months) (Sun et al. 2015) and for the Semaeostomeae *A. coerulea* (7–8 months) (Bonnet et al. 2012; Marques et al. 2015b) and *A. solida* (6–7 months) (Gueroun et al. 2020). However, some species could live longer than one year in nature, like *C. mosaicus* (13 months) (Pitt and Kingsford 2003). Few individuals of *R. pulmo* were observed to survive winter conditions in Mar Menor where temperature did not drop under 10 °C (Fuentes et al. 2011), suggesting that its lifespan can be sometimes longer. In addition, some jellyfish species kept in captivity under optimal conditions may live for multiple years (e.g., *Cassiopiea* sp., 4 years; *A. aurita*, 2 years; Zahn 1981). In this regard, in situ mortality of medusae seems to be age-independent.

Seasonal declines in jellyfish abundance are typically observed in temperate regions (e.g., Lucas 1996). Therein, many factors could explain these massive mortality events, including the release of gametes (Omori et al. 1995), low temperatures and food availability. The sharp abundance decreases with massive stranded individuals observed in winter months could be triggered by the decrease of temperature. It is possible that medusae do not survive winter conditions in Bages Sigean where temperature typically decreases under 7 °C (PNRNM 2021), as the adults' thermal niche is the warmest among all life stages. If temperature minimum is the cause behind this mortality event, warming trend in the NW Mediterranean Sea (0.04 °C year^{-1}) (Salat and Pascual 2002) could induce a temporal expansion of these events if food availability is not limited for the population.

Jellyfish population biomass estimations

Jellyfish demographic features, such as BD frequency distribution, size at sexual maturity, growth rates, diameter–weight relationships, abundance and biomass, are crucial for resources management. Nevertheless, population biomass estimations are still missing for many jellyfish species (Lucas et al. 2014). Non-invasive technologies based on images (Cimino et al. 2018; Schaub et al. 2018; Raoult and Gaston 2018) provide new opportunities to monitor these

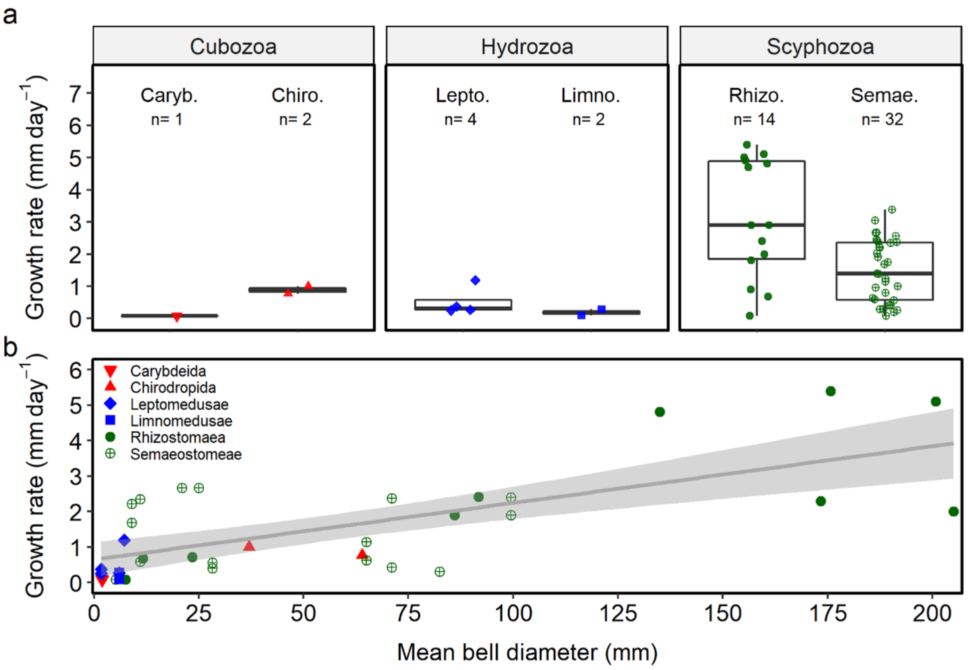

Fig. 8 **a** Growth rate (mm day^{-1}) for each Medusozoa Order (Caryb. = Carybdeidae, Chiro. = Chirodropida, Lepto. = Leptomedusae, Limno. = Limnomedusae, Rhizo. = Rizostomeae, Semae. = Semaeostomeae) by Class (Cubozoa, Hydrozoa and Scyphozoa). Dots represent each data (n). **b** Linear significant relationship between mean bell diameter (BD) and growth rate (GR) ($GR = 0.02 \times BD + 0.64$, $p < 0.01$, $r^2 = 0.44$). Grey area indicates the 95% confidence limits. Both analyses were performed with published data of jellyfish growth rates (literature review in Table 2)

Table 3 Relationships between wet weight (WW, in g) and morphological traits (in cm) measured in *Rhizostoma pulmo*

Morphological trait (cm)	*N*	Function	r^2
Bell diameter (BD)	485	$WW = 0.09 \times BD^{2.91}$	0.98
Total length (TL)	455	$WW = 0.19 \times TL^{2.63}$	0.97
Oral arm's length (OA)	258	$WW = 1.15 \times OA^{2.52}$	0.96
Bell height (BH)	384	$WW = 0.95 \times BH^{2.82}$	0.95
Manubrium diameter (M)	353	$WW = 47.81 \times M^{2.68}$	0.92

N number of specimens

populations covering large study areas. However, those methods require determining allometric relationships to estimate medusae biomass. Although BD is the most used morphological trait for biomass or growth rate estimations on Scyphomedusae (Nogueira and Haddad 2006), for some Rhizostomeae species, TL has proven to be more appropriate (López-Martínez et al. 2020). In these organisms, OA are an important fraction of the biomass of the medusae compared with the other groups. Here, we observed a tight correlation between all morphological traits considered and the WW (Table 3). Due to the swimming behavior of these medusae in parallel to the water surface (Raoult and Gaston 2018), and because measuring the BD can be a difficult task due to the bell consistency on the biggest specimens (i.e. hard collagen umbrella difficult to flatten), TL should be preferred on *R. pulmo* to obtain an accurate estimation of WW, and subsequently, of biomass (g m^{-3}).

Conclusion

We have shown that a bottom–up control shaped *R. pulmo*'s population dynamics in the Bages Sigean lagoon during 2019 and that the growth rate and environmental windows of the species presented ontogenetic variability. Experimental studies may provide complementary information (see Purcell et al. 2012) to understand the physiological responses of each stage of development under future scenarios of significant water temperature changes. These results stress the need to consider jellyfish ontogeny and differences among Medusozoans into food web models. At the Mediterranean basin scale, the variability of the realized thermohaline niche of *R. pulmo* among geographic regions sheds light on the plasticity of the species. These results may reflect genetic divergences of the studied populations, so future investigations should include genetic identification of these Mediterranean populations. As *R. pulmo* is currently in the spotlight as a potential fishery resource, the identification of distinct populations is crucial for its sustainable exploitation (González et al. 2020) to avoid overfishing on jellyfish stocks (Getino Mamet et al. 2019). In addition, the methodology we used to estimate growth rate for a multicohort species is recommended in jellyfish stocks assessment. We expect that the ecological information provided in the present study help to elucidate the biogeography and ecology of one of the most common species in the Mediterranean Sea.

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Authors contributions VL, JCM and DB designed the study. VL, JCM, MM and DB performed field sampling. MM and VL analyzed the data. VL, JCM, MM and DB interpreted the results. VL wrote the initial draft of the manuscript. JCM and DB made critical revisions and contributed to writing the manuscript.

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Data availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest We declare that we have no conflicts of interest.

Ethical approval The jellyfish *Rhizostoma pulmo* is a cnidarian (invertebrate) which is not an endangered or protected species and therefore, no permit was needed for sampling. Sampling and field study were realized in agreement with fishermen of the area and with the directive of the Natural Park.

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