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Contribution to the ICES/PICES Theme Session: ‘Interactions of Gelatinous Zooplankton within Marine Food Webs’

Pelagic population dynamics of *Aurelia* sp. in French Mediterranean lagoons

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The pelagic dynamics of the cosmopolitan scyphozoan *Aurelia* sp. was investigated in three French Mediterranean lagoons, Thau, Berre and Bages-Sigean, which harbour resident populations. The annual cycles showed a common univoltine pattern in all lagoons where the presence of pelagic stages in the water column lasted ~8 months. Field observations showed a release of ephyrae in winter time followed by pronounced growth between April and July, when individuals reached the largest sizes, before disappearing from the water column. Maximum abundance of ephyrae and medusae were registered in Thau. Medusae abundance attained a maximum of 331 ind 100 m⁻³ in Thau, 18 ind 100 m⁻³ in Berre and 7 ind 100 m⁻³ in Bages-Sigean lagoons. Temperature and zooplankton abundance appeared as leading factors of growth, where Bages-Sigean showed the population with higher growth rates (2.66 mm day⁻¹) and maximum size (32 cm), followed by Thau (0.57–2.56 mm day⁻¹; 22.4 cm) and Berre (1.57–2.22 mm day⁻¹; 17 cm). The quantification of environmental windows used by the species showed wider ranges than previously reported in the Mediterranean Sea, which suggests a wide ecological plasticity of *Aurelia* spp. populations in north-western Mediterranean lagoons.

KEYWORDS: ephyrae; medusae; *Aurelia* sp.; Mediterranean Sea; population dynamics; growth

INTRODUCTION

Jellyfish populations appear to be increasing in some coastal marine ecosystems at a global scale (Brotz *et al.*,

2012). Indeed, jellyfish proliferations have benefited from anthropogenic-related disturbances in the marine environment, such as habitat modification, eutrophication, climate

change and overfishing (Richardson *et al.*, 2009). As human population increases, the anthropogenic impact on the marine environment is likely to be enhanced, thereby promoting suitable conditions for an increasing frequency and magnitude of jellyfish blooms, leading to a gelatinous future (Pauly *et al.*, 2009; Purcell, 2012). The conspicuous blooms of gelatinous organisms may interfere directly or indirectly with human activities, such as fisheries, aquaculture, coastal industries and tourism, leading to increased economic losses globally (Purcell *et al.*, 2007). Such interference is particularly important in the Mediterranean Sea, where tourism and aquaculture represent important incomes for the coastal countries (Boero, 2013). The Mediterranean Sea is one of the most sensitive areas to the combined effects of anthropogenic disturbances (i.e. habitat modification and climate change) (Lejeune *et al.*, 2010), suggesting potentially favourable environments for jellyfish blooms.

A large number of jellyfish blooms in coastal areas and semi-enclosed seas are performed by scyphozoan species of the genus *Aurelia* (Mills, 2001), which occur in near-shore waters circumglobally between 70°N and 55°S (Dawson and Martin, 2001). In the Mediterranean Sea, *Aurelia* species inhabit coastal waters of western and central areas, as well as the Black Sea. They are common in the Adriatic Sea and in semi-enclosed lagoons, such as Mljet Island, Lake of Verano and Thau lagoon (Bonnet *et al.*, 2012; Boero, 2013), showing an increasing trend of recurrence of blooms in recent decades (Kogovšek *et al.*, 2010).

Aurelia spp. populations are recognized as highly diverse with contrasting dynamics. Growth is one of the most important indicators of population dynamics and is usually assessed in *Aurelia* spp. studies (e.g. Van der Veer and Oorthuysen, 1985; Olesen *et al.*, 1994; Uye and Shimauchi, 2005). However, in the jellyfish literature, growth rate calculations are heterogeneous, which hampers unbiased comparisons within species and even less between species. To date, researchers have calculated growth based on changes in bell diameter over time (Möller, 1980; Lucas and Williams, 1994; Palomares and Pauly, 2009), on wet weight (Hansson, 1997; Toyokawa *et al.*, 2000; Uye and Shimauchi, 2005; Aoki *et al.*, 2012) or dry weight (Lucas, 1996; Ishii and Båmstedt, 1998), with wet weight very often indirectly estimated from bell diameter (e.g. Toyokawa *et al.*, 2000). Jellyfish growth assessments must be carefully designed, since their characteristic high water content might conceal the real-life histories, such as abundance, growth, lifespan and timing of the different life stages (Lucas, 2001). Body weight has been showed as variable depending on salinity conditions, biasing growth estimations performed on the basis of weight (Hirst and Lucas, 1998). Instantaneous specific growth rate, commonly applied in the literature, based

on average body size within a population over time does not give independent values (Hansson, 1997). According to the latter author, the accuracy of a size estimate at one sampling occasion affects the estimate of instantaneous specific growth rate for both the preceding and the succeeding time interval. Consequently, there is a need to estimate growth rate over long-term periods based on individual bell diameter.

Aurelia aurita has long been considered as a cosmopolitan species, capable of local adaptation due to its phenotypic plasticity (Lucas, 2001). However, recent studies have addressed the biogeography of the genus *Aurelia* and reported that it is actually a species-complex embracing numerous locally adapted species (Dawson and Jacobs, 2001; Dawson and Martin, 2001; Schroth *et al.*, 2002; Dawson, 2003; Dawson *et al.*, 2005; Ki *et al.*, 2008). Our study was performed in three lagoons in the south of France, which are thought to be inhabited by *Aurelia* sp. 1 (Schroth *et al.*, 2002; Dawson, 2003; Dawson *et al.*, 2005), although further local molecular studies are required. Indeed, examination of isolated populations inhabiting Mediterranean coastal lagoons showed different cryptic species (e.g. Mljet lake, southern Croatia, is inhabited by *Aurelia* sp. 5) (Dawson and Jacobs, 2001). For this reason, we do not specify here which cryptic species are present in each of the lagoons studied until further taxonomic confirmation. The lack of biogeographic studies has led to misinterpretation of ecological data describing *Aurelia* spp. (Dawson and Martin, 2001) and, therefore, smaller spatial scale investigations over large areas should be performed and matched in order to fully understand the drivers of population dynamics of *Aurelia* spp. Even if this jellyfish species is the most studied in the world, population dynamics studies have been mainly focused on a specific location and very few have simultaneously considered multiple location comparisons.

In the Mediterranean Sea, despite the importance of jellyfish populations, such studies are scarce: Thau lagoon (Bonnet *et al.*, 2012); Adriatic Sea and adjacent coastal lagoons (Kogovšek *et al.*, 2012; Malej *et al.*, 2012) and Bizerte lagoon (Chakroun and Aloui-Bejaoui, 1995). Coastal lagoons offer ideal opportunities to study *Aurelia* spp. population dynamics. These ecosystems are very valuable, as they encompass ecosystem assets for human welfare. However, they are experiencing mounting threats from human activities, such as urbanization, agriculture and land-use, as well as industrial development and shipping (Newton *et al.*, 2014). Here we report a survey of *Aurelia* sp. in three lagoons of north-western Mediterranean Sea, with contrasting environments and levels of human pressure. We aimed to identify the patterns and environmental drivers of variability of *Aurelia* sp. pelagic populations within each lagoon and to compare

population dynamics between the different lagoons. Bell diameter datasets were also compiled from the literature to determine a growth rate comparable with the one computed in our study.

METHOD

Study site

A plankton sampling programme was carried out in three north-western Mediterranean lagoons: Thau, Berre and Bages-Sigean, located in the south of France (Fig. 1). Bimonthly sampling was conducted at three stations in Berre and Thau lagoons, from January to December 2010 and 2011. Station 1 of Thau lagoon was sampled from January 2013 to July 2014. In Bages-Sigean lagoon, sampling was performed only when *Aurelia* sp. medusae were detected by fishermen (May–September 2010, June–November 2011).

Thau lagoon is a semi-enclosed coastal lagoon (43°23'59.10"N; 3°36'37.15"E) with an area of 75 km² and connected to the Mediterranean Sea by three narrow channels (Canal de Sète, Canal des Quilles and the Grau de Pisses-Saumes) (Fig. 1). It is a shallow environment with a mean depth of 4 m and maximum depth of 24 m. Thau lagoon has a weak tidal range (<1 m) and a high water mass residence time (1–4 months; Fiandrino *et al.*, 2012). One of the most important economic activities is extensive mussel and oyster production, with an estimated standing stock of 15 000 tons, occupying 20% of the lagoon's surface (Mongruel *et al.*, 2013). Although connected to the sea, there is no advection of *Aurelia* sp. from the Mediterranean waters and both pelagic and benthic phases of *Aurelia* sp. occur inside the lagoon (Bonnet *et al.*, 2012; Marques *et al.*, 2015).

Berre is one of the largest coastal lagoons in Europe, with 155 km² and a mean depth of 7 m (43°27'49.10"N; 5°05'33.86"E). The lagoon is connected to Mediterranean Sea by one channel (Chenal de Caronte) and is composed of two main areas, the main lagoon and the Väine lagoon in the east (Fig. 1). Among the surveyed lagoons, Berre is under the highest anthropogenic pressure. The surrounding area is highly industrialized with large urban cities (i.e. Marseille), which result in large inputs of organic and inorganic pollutants. Moreover, the development of the hydroelectric power plant in 1966 (northern area of the lagoon) resulted in a drastic modification of the environment with the production of important freshwater inputs.

Bages-Sigean lagoon is the smallest and shallowest lagoon considered in this study (43°05'12.72"N; 3°00'35.30"E). It covers an area of 38 km² with a mean and maximum depth of 1.3 and 2.9 m, respectively. Bages-Sigean is included within a protected area (Parc Naturel Régional

de la Narbonnaise en Méditerranée) and is considered as the least human impacted lagoon in this study. In the northern part, the lagoon is supplied with freshwater inputs coming from small rivers and the Robine Canal, being connected to Mediterranean Sea in the south by the single channel of Port-la-Nouvelle (Fig. 1). This lagoon has long been exploited by local traditional fisheries (e.g. eels and sea bass).

In situ collections

Environmental parameters such as temperature, salinity, chlorophyll *a* concentration and zooplankton abundance were monitored. Temperature and salinity were recorded sub-surface (<0.5 m) with multi-parametric probes (EC 300 VWR International/WTW model 350i in Thau and Bages-Sigean; CTD SBE19 + Seabird for Berre).

At each sampling station, water samples (150 mL) were collected in triplicate in order to quantify chlorophyll *a* concentration. Water was filtered on Whatman GF/F filters and stored at –30°C until extraction and measurement by spectrofluorimetry (Thau and Bages-Sigean; LS 50B Perkin Elmer) or fluorimetry (Berre; Turner Design – TD 700).

In 2010 and 2011, metazooplankton was collected by near surface horizontal tows in Thau and Bages-Sigean lagoons due to the shallow depth at these stations (4.8 and 1.8 m, respectively), using a modified WP2 plankton net (1.2-m long, 50-cm opening area and 80-µm mesh size). In Berre lagoon, vertical hauls (from bottom to surface) were performed with a modified WP2 net (1.2-m long, 50-cm opening area and 80-µm mesh size) as the lagoon is deep enough (depth ranging from 6.9 m at station 1 to 9.5 m at Station 3). All samples were preserved in 4% buffered formaldehyde for further analysis in the laboratory. Zooplankton abundance was determined under a dissecting microscope.

The metazooplankton monitoring has started again in Thau at Station 1 since 2013 with a classical WP2 plankton net (2.5-m long, 54-cm opening area and 200-µm mesh size).

Gelatinous organisms were collected using a modified Nansen net (2-m long, 100-cm aperture and 700-µm mesh size) with a large plexiglass collector, in order to keep the organisms in good condition. Due to shallow waters, horizontal sub-surface hauls were performed in all the lagoons. The net was towed for from 2 to 6 min at an approximate speed of 2 ms⁻¹. A flowmeter set up at the entrance of the net indicated the volume filtered by the nets. Due to low concentrations, abundances were expressed as the number of organisms per 100 m³. In the laboratory, all *Aurelia* sp. individuals were identified. Bell diameter (Bd; cm) and abundance (ind 100 m⁻³) of ephyrae (Bd < 1 cm) and

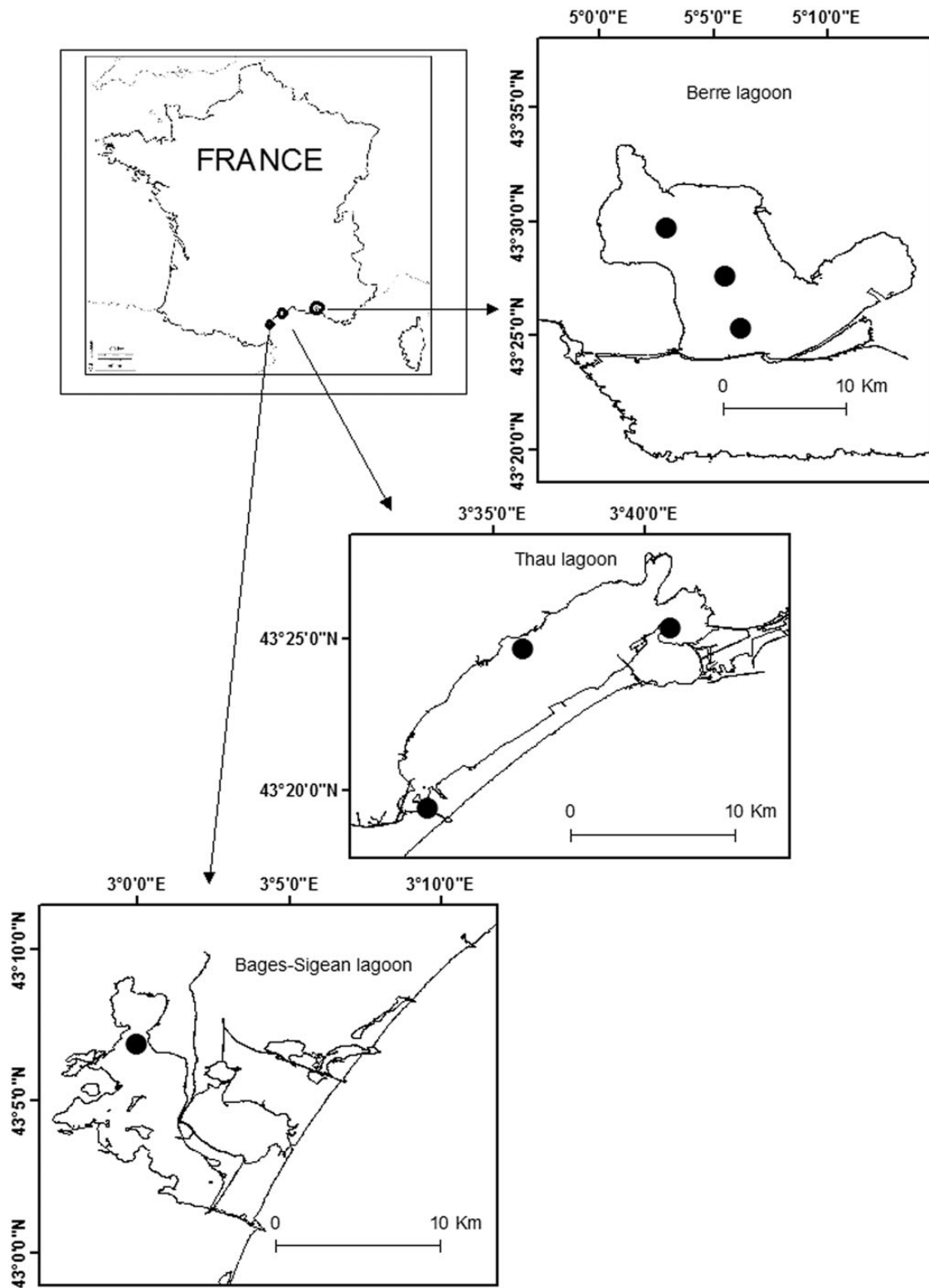


Fig. 1. Map of the three surveyed lagoons including sampling stations within each lagoon (black dots).

medusae ($Bd > 1$ cm) were determined under a dissecting microscope with an eyepiece graticule or a ruler to measure large specimens. Bell diameter was corrected for formalin shrinkage according to Möller (Möller, 1980).

***Aurelia* sp. growth**

Two different stages of *Aurelia* sp. life cycle were identified: ephyrae ($Bd < 1$ cm) and medusae (from 1 cm to maximum Bd). For each year, *Aurelia* sp. growth was calculated using the slope of a regression line, fitted to Bd data from all individuals collected by stage.

Data regarding *Aurelia* sp. growth were gathered from the literature (Table I). Available data of mean Bd were assembled from different studies and growth rates were uniformly re-calculated as previously described. Only medusae were considered (i.e. Bd between 1 cm and the maximum reported) when a continuous period of time was available.

Onset of growth was determined as the date at which the first medusae were recorded in each year.

Statistical analysis

Since datasets were not normally distributed, non-parametric ANOVA (Kruskal–Wallis sum rank tests) were performed with the ‘*pgirmess*’ package (Giraudoux, 2014) in R (R Core Team, 2014) to identify differences in environmental variables within and among lagoons, according to similar time periods. As Bages-Sigean was monitored from May to September in 2010 and June to November in 2011, environmental conditions were compared over the same study period both in Thau and Berre lagoons. When testing inter-annual variability of zooplankton abundance in Thau lagoon, only the subset sample comprising organisms $> 200 \mu\text{m}$ was considered. Differences of ephyrae and medusae abundances between lagoons and over time were assessed by pairwise comparison using Wilcoxon rank-sum test with continuity correction. The same test was also applied to evaluate differences between total abundance of ephyrae and medusae for each year within each lagoon.

Generalized linear models (GLMs) were run to test the relationships between Bd and the environmental factors (biotic and abiotic) as predictors. This allowed the individual effects and their interactions to be assessed. Since the Bages-Sigean lagoon dataset was too small, a correlation matrix was done. Linear models or GLMs were performed in order to assess correlations between several variables: correlations between abundances of *Aurelia* sp. (total abundance or by stage, i.e. ephyrae and medusae) and environmental parameters or Bd were tested.

Habitat association curves were assessed using the same years, 2010 and 2011, in the three lagoons. To do so, we obtained this from the maximum absolute difference between the cumulative frequency distribution (CFD) of abiotic and biotic variable (i.e. temperature, salinity, chlorophyll *a* concentration and zooplankton abundance) and the abundance-weighted CFD of that variable. After determining the maximum absolute difference between the two CFD curves, we compared it with the distribution of the maximum absolute differences from 1000 randomizations of the Monte Carlo resampling for *Aurelia* sp. and the abiotic (biotic) variable. A similar approach has been used to depict the habitat association of fish (Perry and Smith, 1994), copepods (Molinero *et al.*, 2009) and jellyfish (Bonnet *et al.*, 2012).

All statistical analyses were performed using the software R 3.1.1 (R Core Team, 2014) and Statistica v.10 (StatSoft, Inc.).

RESULTS

Environmental parameters

The observed range of variability of environmental conditions is displayed in Fig. 2. No significant difference of environmental conditions was observed between Bages-Sigean and the two other lagoons in 2010 (from May to September) whereas salinity and chlorophyll *a* were significantly different ($P < 0.01$) with Thau and with Berre respectively in 2011 (June–November period). Over the study period (from January 2010 to December 2011), and between years independently, salinity, chlorophyll *a* concentration and zooplankton abundance were significantly different ($P < 0.01$) between Thau and Berre lagoons. Temperature was not significantly different ($P > 0.05$) both over the study period and the 2 years independently.

***Aurelia* sp. abundance**

Abundances of ephyra and medusa stages of *Aurelia* sp. in each lagoon are presented in Fig. 3. The timing of occurrence of both life stages appeared relatively similar between lagoons. In Thau and Berre, ephyrae first appeared in November and remained in the water column until early-spring (March–April), when they gave rise to medusae. Medusae were present until May–June in Thau and Berre, while in Bages-Sigean, this stage happened later in the year (May–August). Medusae further disappeared in the three lagoons until the next generation of ephyrae had emerged again at the end of the year. Our results suggest that *Aurelia* sp. pelagic stages lifespan in both lagoons ranges as a maximum from 7 to 8 months (November–May/June; Bages-Sigean lagoon not included), as previously suggested

Table I: Literature review of *Aurelia* sp. maximum abundances, size and growth rate

Region	Location	Species	Max. ab. ephyrae (ind m ⁻³)	Max. ab. medusae (ind m ⁻³)	Maximum Bd (cm)	Growth rate (mm day ⁻¹)	<i>n</i>	Months (years)	<i>T</i> (°C)	Ref.
Northeastern Atlantic	Limfjorden, Denmark	<i>Aurelia aurita</i>	2.2 ± 1.4	14.8 ± 0.8	12.9 ± 3.4	0.63–1.14	3–4	April–July (2009)	20.5–22	1
	Kertinge Nor and Kerteminde Fjord, Denmark	<i>Aurelia aurita</i>	304 ± 129	248 ± 292	5.4	0.40–0.56	4–7	June–September (1991) May–June (1992)	n.a.	2
	Southampton Water, UK	<i>Aurelia aurita</i>	8.71	2.80	14.1	0.42–2.37	3–6	May–June (1990, 1991, 1993) March–May (1992)	10–16	3
	Horsea Lake, UK	<i>Aurelia aurita</i>	–	24.90	10.5	0.19	7	March–September (1994)	5.8–18.6	4
	Kiel Bight, Germany	<i>Aurelia aurita</i>	0.07	0.16	44	1.9–2.4	3–4	May–August (1978) June–August (1979)	n.a.	5
	Kiel Bight, Germany	<i>Aurelia aurita</i>	–	0.23	~30	2.20–3.05	6–7	May–August (1982, 1984) April–August (1983)	11.4–16.7	6
	Vågsbøpollen, Norway	<i>Aurelia aurita</i>	–	22.00	11.8	1.24	6	May–June (1996)	11–15	7
	Wadden Sea, Netherlands	<i>Aurelia aurita</i>	–	0.49	29	1.75–3.38	6–13	May–July (1981) April–August (1982)	n.a.	8
North-western Pacific	Tapong Bay, Taiwan	<i>Aurelia aurita</i>	328.00	14.50	29.7	0.80	5	May–October (2001)	27.5–33	9
	Tokyo Bay, Japan	<i>Aurelia aurita</i>	2.40	1.60	28.4	1.0–1.4	3–8	April–August (1991) March–May (1992)	12–25	10
	Inland Sea, Japan	<i>Aurelia aurita</i>	–	–	27.3 ± 4	2.02–2.56	4–5	April–July (1990, 1991) May–June (1992)	15–25	11
	Kogoshima Bay, Japan	<i>Aurelia aurita</i>	–	–	23	1.38	6	February–July (1994)	15–28	12
	Mikawa Bay, Japan	<i>Aurelia aurita</i>	–	0.91	32.6	0.96	4	March–July (2008)	11.6–22	13
Mediterranean Sea	Thau lagoon, France	<i>Aurelia</i> sp.	2.00	3.30	11.33	2.45	4	April–May (2010)	13–16	14
	Thau lagoon, France	<i>Aurelia</i> sp.	14.70	3.30	22.38	0.59–2.35	2–4	April–May (2010, 2011) April–June (2013) March–May (2014)	13–20	Ts
	Berre lagoon, France	<i>Aurelia</i> sp.	0.43	0.18	17.00	1.68–2.22	2–3	March–May (2010) April (2011)	7–17	Ts
	Bages-Sigean lagoon, France	<i>Aurelia</i> sp.	–	0.07	31.90	2.66–2.67	2	May–June (2010) June–July (2011)	14–28	Ts

Maximum abundances (Max. ab.) of ephyrae and medusae, as well as maximum bell diameter (Bd) represent the highest reported values.

See the text for growth rate calculation. References: (1) Riisgård *et al.*, 2012; (2) Olesen *et al.*, 1994; (3) Lucas and Williams, 1994; (4) Lucas, 1996; (5) Möller, 1980; (6) Schneider, 1989; (7) Ishii and Båmstedt, 1998; (8) Van Der Veer Oorthuysen, 1985; (9) Lo and Chen, 2008; (10) Toyokawa *et al.*, 2000; (11) Uye and Shimauchi, 2005; (12) Miyake *et al.*, 1997; (13) Aoki *et al.*, 2012; (14) Bonnet *et al.*, 2012.

Ts, this study; n.a., not available.

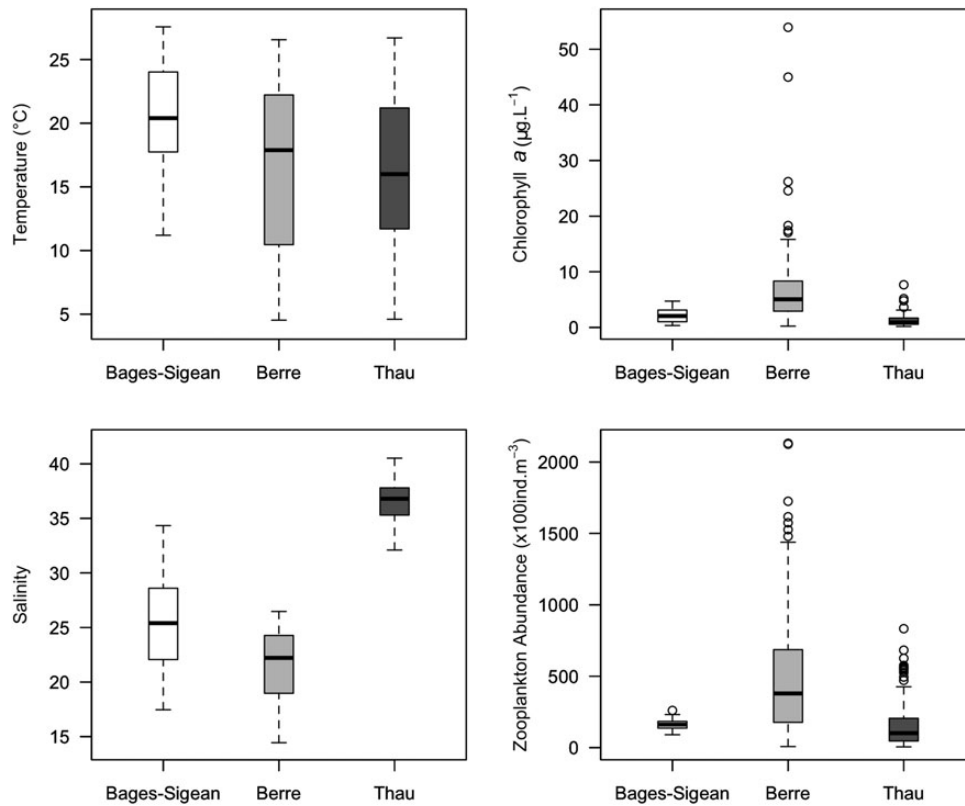


Fig. 2. Environmental conditions for Bages-Sigean, Berre and Thau lagoons (all stations combined) during their respective monitoring in 2010 and 2011. Central boxes show data between the 25th and the 75th percentiles with the median (50th percentile) represented as a line and the mean as a square. The whiskers extend as far as the minimum and maximum values not considered as outliers. Outliers are represented by circles and defined as values lower or higher than 1.5 times the interquartile differences (75th–25th percentiles values).

(Bonnet *et al.*, 2012). In the three lagoons, the whole life cycle of *Aurelia* sp. was considered to occur inside the lagoons, since no advection happened from and to the Mediterranean Sea (Bonnet *et al.*, 2012; Delpy, 2013).

The abundance of both *Aurelia* sp. pelagic life stages did not differ significantly between the different stations (Kruskal–Wallis test; $P > 0.05$) and, therefore, spatial variability within each lagoon was not explored further. When considering ephyrae abundance, spatial (between lagoons) and temporal (within lagoons) variability was observed (Wilcoxon test, $P < 0.05$). In Thau, maximum annual peaks ranged from 3 to 1472 ind 100 m^{-3} , where the maximum abundance was, for instance, 30 times higher in 2014 than in 2010. In Berre, the most important ephyrae abundance was observed in 2010 (43 ind 100 m^{-3}). The abundance of medusae revealed significant differences between lagoons (Wilcoxon test, $P < 0.001$). Within each lagoon, inter-annual variability was observed in Thau and Berre (Wilcoxon test, $P < 0.05$), but not in Bages-Sigean. Maximum annual peaks of medusae ranged from 3 to 331 ind 100 m^{-3} in Thau, from 4 to 18 ind 100 m^{-3} in Berre and from 5 to 7 ind 100 m^{-3} in Bages-Sigean lagoon.

When considering the data set within each lagoon, ephyrae abundance was not correlated with any environmental variable (GLM, $P > 0.05$; results not shown). Nevertheless, medusae abundance and total *Aurelia* sp. abundance (i.e. ephyrae and medusae together) were significantly correlated with temperature and zooplankton abundance in Thau (temperature: $t = 2.55$, $P = 0.03$; zooplankton: $t = 2.76$, $P = 0.02$) and Berre lagoon (temperature: $t = -2.25$, $P = 0.03$; zooplankton $t = 2.08$, $P = 0.05$), respectively. In Thau lagoon, in 2014 the abundance of ephyrae was significantly much higher than medusae (Wilcoxon test, $P < 0.01$). In Berre, significant differences between ephyrae and medusae abundances were only recorded in 2011, with ephyrae being also more abundant (Wilcoxon test, $P = 0.05$).

Aurelia sp. growth

In Thau and Berre lagoons, *Aurelia* sp. populations displayed a typical pattern of slow initial growth followed by exponential increase in Bd and shrinkage towards the end of its life cycle (Fig. 4). Descriptive values of growth

are presented in Table II. Ephyrae growth showed very low values ranging from 0.001 to 0.08 mm day⁻¹. Bd suddenly increased reaching up to 22.38, 17.00 and 31.90 cm for Thau, Berre and Bages-Sigean lagoons, respectively, with similar maximal growth rate ~2.5 mm

day⁻¹ for the three lagoons. In Thau lagoon, maximum growth rate (2.53 mm day⁻¹) was recorded in 2013, which led to a maximum registered Bd of 22.38 cm. In contrast, 2014 had the lowest values of medusae growth rate (0.57 mm day⁻¹) and maximum Bd (5.7 cm);

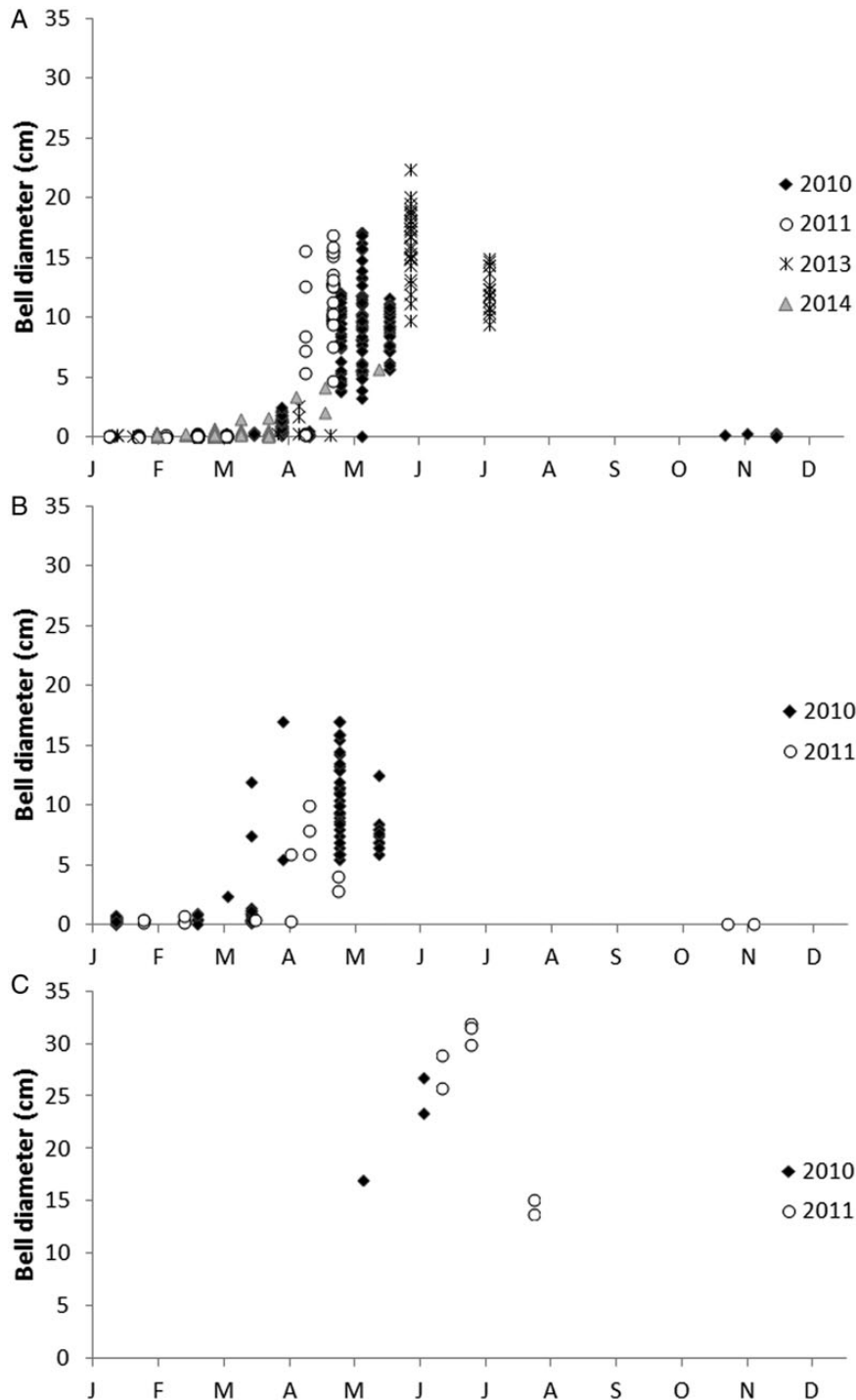


Fig. 4. Bell diameter (cm) of all *Aurelia* sp. individuals in Thau (A), Berre (B) and Bages-Sigean (C) lagoons during the study period.

however, measurements were performed on only a few organisms ($n = 6$) compared with other years. Larger individuals were though observed in Thau lagoon in 2014 but were not collected during our surveys. In Berre lagoon, highest growth rate was observed in 2011 (2.22 mm day^{-1} , $n = 4$), but bigger individuals were detected in 2010 (17.0 cm). Among the different lagoons, Bages-Sigean had the fastest growth (2.66 mm day^{-1}) and harbours the biggest individuals (31.9 cm). However, results have to be interpreted carefully as few individuals were collected for measurements (2010: $n = 3$; 2011: $n = 5$). Medusae can shrink at the end of their life cycle and this might reflect the amount of energy that they invest in the reproduction process (Albert and Walsh, 2014; Fu et al., 2014; Fuchs et al., 2014). The highest shrinking rate was registered in Bages-Sigean (5.19 mm day^{-1} , $n = 5$) and the lowest in Thau (0.56 mm day^{-1} , $n = 92$).

Table II: Growth rate per stage, maximum bell diameter (Max. Bd) and growth onset of *Aurelia* sp. for each year in Thau, Berre and Bages-Sigean lagoons

Lagoon	Year	Growth rate (mm day^{-1})			Growth onset (Julian days)
		Ephyrae (n)	Medusae (n)	Max Bd (cm)	
Thau	2010	0.08 (115)	2.02 (131)	17.07	98
	2011	0.004 (158)	1.33 (14)	16.93	110
	2013	0.01 (6)	2.53 (31)	22.38	107
	2014	0.02 (350)	0.57 (6)	5.70 ^a	77
Berre	2010	0.01 (111)	1.57 (43)	17.00	70
	2011	0.001 (7)	2.22 (4)	10.00	102
Bages-Sigean	2010	–	2.66 (3)	26.72	139
	2011	–	2.66 (5)	31.90	179

^aLarger medusae were observed in Thau lagoon in 2014 but were not collected.

Table III: Estimates of generalized linear models (A) and correlation matrix (B) used to assess correlation between bell diameter and environmental variables in bold: significant correlations (P -value < 0.05)

Lagoon	Variable	Estimate	Std. error	t-value	Pr ($> t $)
A					
Thau	(Intercept)	-0.04	0.11	-0.35	0.73
	Temperature	0.65	0.13	4.79	<0.001
	Salinity	0.08	0.14	0.58	0.57
	Chlorophyll <i>a</i>	0.17	0.15	1.15	0.26
	Zooplankton	-0.07	0.12	-0.60	0.56
	(Intercept)	0.00	0.19	0.00	1.00
Berre	Temperature	0.41	0.22	1.89	0.09
	Salinity	-0.24	0.20	-1.19	0.26
	Chlorophyll <i>a</i>	0.02	0.20	0.12	0.91
	Zooplankton	0.52	0.21	2.42	0.04
	Variable	Temperature	Salinity	Chlorophyll <i>a</i>	Zooplankton
B					
Bages-Sigean	Bell diameter	0.90	-0.95	0.29	0.87

GLMs (Table IIIA) revealed significant positive correlations between Bd and temperature in Thau lagoon ($t = 4.79$, $P < 0.001$), whereas in Berre there was a significant correlation with zooplankton abundance ($t = 2.42$, $P < 0.05$). In Bages-Sigean, the available data did not allow the GLM to be run. Therefore, a correlation matrix was performed indicating that temperature and salinity were the main driving forces (Table IIIB, $P < 0.05$, $n = 5$). However, this analysis is only indicative owing the lack of sufficient data. For both ephyrae and medusa, the Bd was not significantly correlated with the abundance of *Aurelia* sp. in the lagoons.

Growth onset represents the time at which exponential growth was triggered (Table III and Fig. 4). In Thau and Berre lagoons, the results revealed that this transition to adult stage occurred in March–April. However, none of the environmental parameters could significantly explain growth onset.

Environmental windows

The annual pattern of temperature followed the typical trend in temperate regions, with lower values in winter months and higher values in summer months. Temperature ranged from 4.6 to 26.70°C in Thau and 4.53 to 26.56°C in Berre (Fig. 5). In Bages-Sigean, temperature ranged from 11.2 to 27.57°C, minimum annual temperatures are not presented since the winter season was not included in our study period. Ephyrae were present within a colder temperature window than medusae and with a narrower range in Thau, when compared with Berre lagoon. In contrast, medusae occurred in warmer waters, especially in Bages-Sigean where, unlike in Thau and Berre, the highest probability of occurrence was associated with temperatures above 20°C.

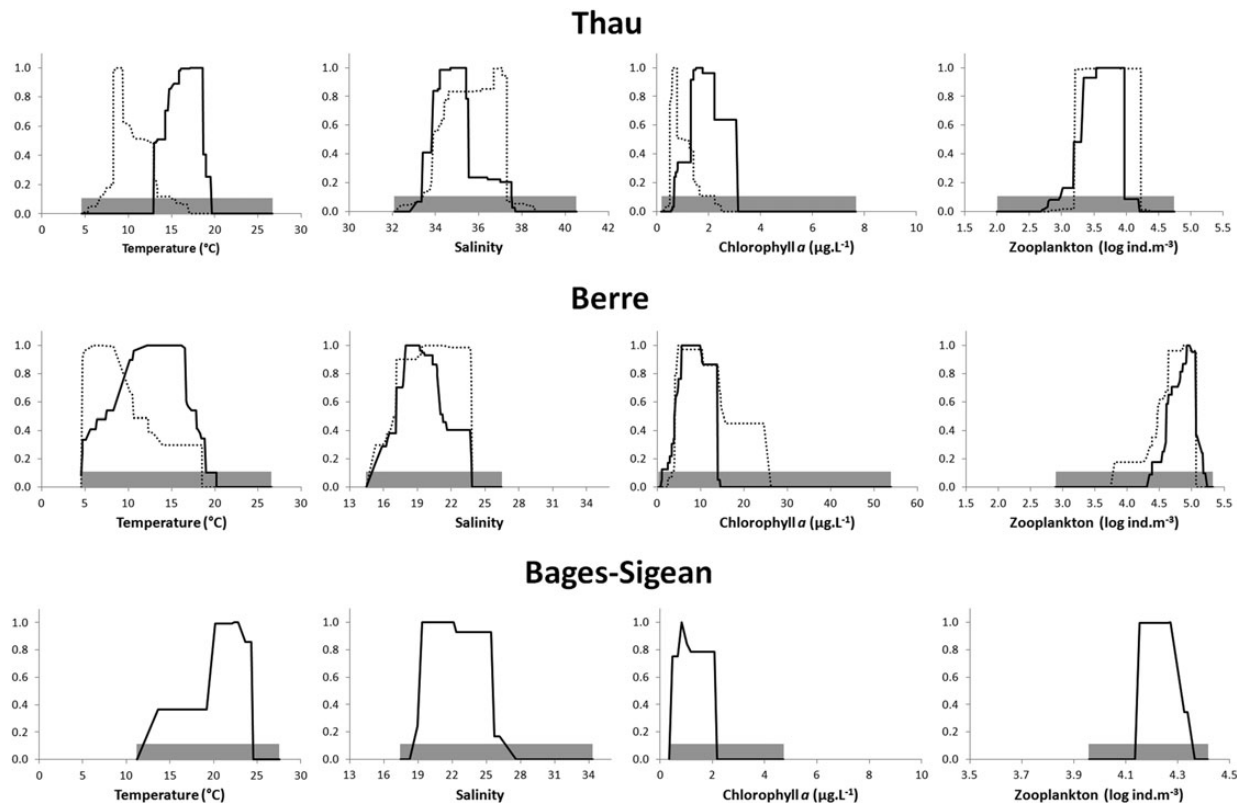


Fig. 5. Environmental windows of occurrence probability of ephyrae (dashed line) and medusae (continuous line) in Thau, Berre and Bages-Sigean lagoons. Grey bar represents the range of the environmental variable during the study period.

Salinity showed significant differences among lagoons (Kruskal–Wallis test, $P < 0.001$). Thau is characterized by marine conditions (32.1–40.5), while Berre is strongly influenced by freshwater inputs leading to a brackish environment (14.4 and 26.5) (Fig. 2). Bages-Sigean, despite the lack of a complete annual trend, showed the highest variability (17.5–34.4) (Fig. 2). We found that, in these contrasting environments, both life stages of *Aurelia* sp. inhabit a wide range of salinity conditions, from 14 (in Berre) to 38 (in Thau). However, larger probabilities were found in the range of 19–25 (Bages-Sigean), 18–22 (Berre) and 34–37 (Thau) (Fig. 5).

Chlorophyll *a* concentration and zooplankton abundance showed a high annual variability in all lagoons (Fig. 2), with significant differences between them (Kruskal–Wallis test, $P < 0.001$). Berre was the most productive with chlorophyll *a* ranging from 0.24 to 53.93 $\mu\text{g L}^{-1}$ and zooplankton from 776 to 213 079 ind m^{-3} . Peaks of chlorophyll *a* concentration and zooplankton abundance were 4–11 times higher than in the other lagoons. In Thau and Bages-Sigean, chlorophyll *a* ranged from 0.2 to 7.7 and 0.34 to 4.73 $\mu\text{g L}^{-1}$, respectively, while zooplankton varied from 99 to 55 826 and 9058 to 26 057 ind m^{-3} , respectively. Within each lagoon,

significant trends were observed over time. In Berre, chlorophyll *a* was higher in 2011 (Kruskal–Wallis test, $P < 0.05$), with peak values up to 3.4 times higher than in 2010. In Thau lagoon, zooplankton abundance varied over time and showed significant differences between years (Kruskal–Wallis test, $P < 0.001$). In Bages-Sigean, significant differences in these variables were not observed. Regardless of the range, *Aurelia* sp. seemed to inhabit waters with low of chlorophyll *a* concentrations. In contrast, high abundances of zooplankton, within the range of each lagoon, appeared to foster the occurrence of *Aurelia* sp. (Fig. 5).

Potential inter-specific competition with other zooplankton carnivorous taxa

Although the environmental conditions were the main influence on *Aurelia* sp. population dynamics, we do not exclude potential inter-specific competition with other gelatinous carnivores, i.e. the ctenophore *Mnemiopsis leidyi*. In fact, the examination of the annual pattern of the invasive *Mnemiopsis leidyi* showed large seasonal overlapping with *Aurelia* sp. in Berre lagoon, whereas the overlapping was limited to a few weeks in Bages-Sigean

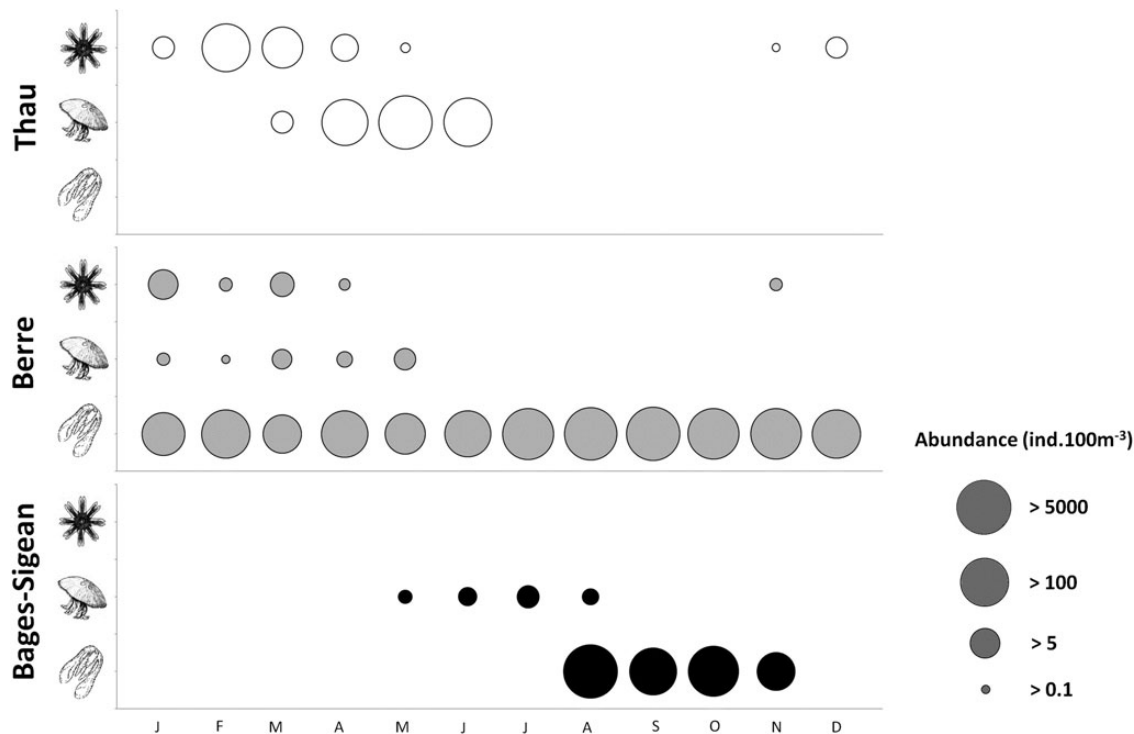


Fig. 6. Mean abundance (logarithmic scale) of *Aurelia* sp. ephyrae and medusae, as well as *Mnemiopsis leidyi* in Thau, Berre and Bages-Sigean lagoons.

lagoon, while in Thau lagoon the species was absent (Fig. 6). Although there is no experimental evidence that *M. leidyi* may outcompete *Aurelia* sp., the high abundances of the new invader observed in Berre and Bages-Sigean lagoons, which reached up to 1998 and 12 197 ind 100 m⁻³, respectively, as well as the high ingestion rate of *M. leidyi* may result in potential competition/predation upon young *Aurelia* sp. medusae.

DISCUSSION

Life cycle

The life cycle of *Aurelia* sp. in the north-western Mediterranean coastal lagoons showed a typical pattern of temperate populations with a unique generation by year. *Aurelia* sp. showed a 1-year life cycle in Thau and Berre, with a lifespan ranging from 7 to 8 months. Ephyrae first appeared in early winter giving rise to adult individuals at the beginning of spring, when temperature increased. Medusae remained in the lagoons until late spring disappearing during summer and autumn. Such an annual cycle has previously been reported in Thau lagoon by Bonnet *et al.* (Bonnet *et al.*, 2012) and confirmed during our study. Univoltine populations with a

similar annual cycle have been reported elsewhere [reviewed in Lo and Chen (Lo and Chen, 2008)]. For instance, as in Thau and Berre, strobilation begin in November in the Northern Adriatic Sea (Malej *et al.*, 2012) and in the Kiel Bight (Baltic Sea, Germany), entering in the medusae stage in April (Möller, 1980). Strobilation is later in the Wadden Sea (The Netherlands; Van der Veer and Oorthuysen, 1985), in Southampton Water (UK; Lucas and Williams, 1994) and in the Inland Sea (Japan; Uye and Shimauchi, 2005), releasing ephyrae in January–March but growing to adult stage in similar periods. In all the latter reports, medusae reached their maximum size in June–August and disappeared in late Summer/Autumn, suggesting a lifespan concurrent with our results. However, large variability of population dynamics of *Aurelia* sp. is recognized. For instance, medusae are present all year round in other Mediterranean sites (e.g. Veliko Jezero, Kogovšek *et al.*, 2012) as well as in Tokyo Bay (Japan, Omori *et al.*, 1995), the Black Sea (Mutlu, 2001) or Tapong Bay (Taiwan, Lo and Chen, 2008) and different generation may overlap (Lucas, 1996; Lo and Chen, 2008).

Abundance appeared to be generally higher in enclosed and semi-enclosed ecosystems than in open environments (Ishii and Båmstedt, 1998). Consistent with this, we found that maximum abundances recorded in Thau lagoon

were higher than at sites more exposed to water exchange with the open sea (e.g. Kiel Bight, Tokyo Bay) (Möller, 1980; Schneider, 1989; Toyokawa *et al.*, 2000), although our results did not reach the high values reported for other semi-enclosed habitats, such as in Denmark (Olesen *et al.*, 1994) and Taiwan (Lo and Chen, 2008), where the values exceeded 300 ind m⁻³ (Table I). In contrast, Berre and Bages-Sigean lagoons showed values lower than expected for a semi-enclosed environment and even lower than in some open water environments such as the Wadden Sea (Van der Veer and Oorthuysen, 1985) and Tokyo Bay (Toyokawa *et al.*, 2000).

Among the three studied lagoons, Thau sustains the most abundant population, followed by Berre and Bages-Sigean (Fig. 3, Table I). Considering all the field data (all years and all stations), temperature and zooplankton abundance were the main drivers of medusae abundance in Thau and total *Aurelia* sp. abundance in Berre. However, other processes (predation, natural mortality, recruitment etc.) might also be responsible for the differences registered. Indeed, the abundance of *Aurelia* spp. medusae relies mainly on the ephyrae production by polyps and its recruitment success (Hernroth and Grondahl, 1985; Lucas *et al.*, 2012). Therefore, the abundance variability between lagoons and within each lagoon depends primarily on the benthic population dynamics and the environmental drivers acting at this stage (Boero *et al.*, 2008). A recent study showed that salinity at 15 significantly increased the duration of the planulae stage increasing morphological deformities of settled polyps and salinity at 20 caused delayed tentacle development of polyps (Conley and Uye, 2015). Hence, we hypothesize that survival of planulae, polyps and deformed ephyrae is affected in environments like Berre and Bages-Sigean, where salinity ranged from 15 to 27 and 18 to 34, respectively, explaining the low abundances observed there.

Few investigations have focused on environmental drivers triggering benthic population dynamics (e.g. Miyake *et al.*, 2002; Willcox *et al.*, 2008; Toyokawa *et al.*, 2011), although increasing coastal constructions were showed to promote the development of polyp populations (Holst and Jarms, 2007; Hoover and Purcell, 2009; Duarte *et al.*, 2012; Makabe *et al.*, 2014). This appears to be the case in Thau lagoon, where polyps are well established (Marques *et al.*, 2015) and where the highest abundances of *Aurelia* sp. were recorded. In Berre, we may expect to find *Aurelia* sp. polyps, as indicated by the presence of ephyrae (Toyokawa *et al.*, 2011) and considering the abundant coastal constructions in this lagoon. For Bages-Sigean, even if ephyrae dynamics were not surveyed, only few hard substrates are available (natural or artificial). Still, despite the lack of direct investigations on benthic populations, the hypothesis suggested above is consistent with the observed differences in abundance between lagoons.

Growth and environmental drivers

Growth patterns in Thau and Berre lagoons followed similar patterns to those previously reported by other authors (e.g. Schneider, 1989; Lucas and Williams, 1994; Olesen *et al.*, 1994; Uye and Shimauchi, 2005). During the ephyrae stage, growth remained low until the growth onset, after which bell diameter increased dramatically up to reaching their maximum size. Afterwards, a reduction of the bell diameter was observed for some years in the three lagoons.

Growth rates were calculated for two different stages: ephyrae and medusae (Table II). Ephyrae growth did not exceed 0.08 mm day⁻¹, which is consistent with previous reports (0.1 mm day⁻¹) (Lucas and Williams, 1994). The growth of ephyrae has been shown to be dependent not only on food availability, but also on prey size, quality and behaviour (Sullivan *et al.*, 1997; Båmstedt *et al.*, 2001; Rüssegård and Madsen, 2011) which together with temperature are the main drivers.

The transition between ephyra to medusa stage, i.e. growth onset, varies between lagoons and years. Such variability is common and can occur over small or large spatial and temporal scales (Lucas, 2001). In our study, the timing of the growth onset of *Aurelia* sp. was negatively correlated with the difference of temperature between January and the appearance of the first medusae in the field ($r = 0.97$, $P < 0.01$), suggesting a later transition to medusa stage with decreasing difference of temperature. The results of Fuchs *et al.* (Fuchs *et al.*, 2014), pointing out that metamorphosis of *Aurelia aurita* is initiated by temperature shift and regulated by secreted strobilation inducers (molecular process) support our hypothesis.

When considering the medusae stage, Thau and Berre appeared to promote parallel growth rates leading to relatively similar maximum individual size, while Bages-Sigean appeared to offer better conditions for *Aurelia* sp. growth and consequent largest individuals, achieving 32 cm (Table III). Intra-specific density-dependent mechanisms have been suggested for polyp population (Melica *et al.*, 2014) or adult size regulation (Lucas, 2001). However, in our study, no significant relationships between bell diameter and abundance were determined. Inter-annual variability of growth was observed in our survey, as previously reported elsewhere (e.g. Möller, 1980; Van der Veer and Oorthuysen, 1985; Schneider, 1989). Among different habitats, comparable values of growth with Thau and Berre lagoons were obtained for Southampton Water and the Wadden Sea, while the Inland Sea was the habitat with similar values as in Bages-Sigean (Table I). Overall, in the Northeastern Atlantic, *Aurelia* spp. appears to attain smaller sizes than in the North-western Pacific, with Mediterranean populations living in between. However, this is not straight

forward. For instance, the largest *Aurelia* spp. individual reported in the literature was found in Mijet Island (Mediterranean Sea) reaching 55 cm diameter (Benovic *et al.*, 2000). Furthermore, extreme values of maximum individual size may occur in a very small geographic area, e.g. in Kertinge Nor (5.4 cm) (Olesen *et al.*, 1994) and Kiel Bight (44 cm) (Möller, 1980), suggesting that general climate variability (i.e. latitudinal gradient of temperature) does not solely explain the difference in the growth of *Aurelia* spp.

In our study, temperature (in Thau and possibly in Bages-Sigean) and zooplankton abundance (in Berre) were determined as the main drivers of bell diameter increase and consequently of growth (Table III). Similarly, temperature was shown to be responsible for higher growth rates of *A. aurita*, when food availability is not limiting (Hansson, 1997). Ishii and Båmstedt (Ishii and Båmstedt, 1998) showed for the first time that food availability can explain growth and maximum size of *A. aurita*, as also suggested by several authors (Olesen *et al.*, 1994; Lucas, 1996). Among the different lagoons assessed, Berre had the most abundant zooplankton population and therefore faster growth and bigger individuals would be expected. However, the values remained below the growth and size obtained in Bages-Sigean, where zooplankton abundance is the lowest in our study. A possible explanation might be related to the quality of zooplankton community. According to Båmstedt *et al.* (Båmstedt *et al.*, 2001), *A. aurita* may achieve proper development based on the most abundant prey, but bigger size range and higher nutritional quality promotes higher growth rate and larger individuals. Zooplankton diversity was quite different in the lagoons during *Aurelia* occurrence. For example in winter and spring, copepods represent a minimum of 86% contribution to the total zooplankton abundance in Thau (the main species being *Acartia clausi*) while in Berre cirripedes, polychaetes and bivalves make the main bulk of the zooplankton (*Acartia clausi* contributing up to 12% only). While the predation of *Aurelia* sp. was not directly assessed during our study, the role of prey quality is an important point to consider.

The decrease of bell diameter during medusa stage is well known (Möller, 1980; Van der Veer and Oorthuysen, 1985; Lucas and Williams, 1994), but usually not quantified. The shrinkage of *Aurelia* spp. is largely associated with releasing of planulae, representing the input of energy in the production of gametes and in the spawning process, which results in morphological degradation and death of adult medusae (Lucas, 1996; Hansson, 1997; Aoki *et al.*, 2012). Among the three lagoons, *Aurelia* sp. population from Bages-Sigean shrank with a rate of up to -5 mm day^{-1} , possibly as a mechanism of life history adjustment (Boero *et al.*, 2008), in order to overcome the lower abundance of the population.

Occurrence of *Aurelia* sp. and environmental windows

Kogovšek *et al.* (Kogovšek *et al.*, 2012) assembled information regarding the environmental windows that favour *Aurelia* spp. in different locations of the Mediterranean Sea and identified a common general pattern of temperature and salinity, ranging from 7 to 28°C and 32 to 38, respectively. Our results support the reported temperature window, though we suggest a much wider range of salinity used by the species. Temperature is the only physical parameter favouring differently the ephyrae and medusae stage in Thau and Berre lagoons (Fig. 4), confirming the main effect of temperature in *Aurelia* sp. growth within lagoons. Medusae are generally favoured by warmer waters, though in Berre, medusae were present at temperatures as low as 4.7°C, considerably lower than previous reports, i.e. in Bizerte (12.5–27.5°C) and Veliko Jezero (11.2–28°C) (Chakroun and Aloui-Bejaoui, 1995; Bonnet *et al.*, 2012; Kogovšek *et al.*, 2012). Salinity windows, on the other hand, equally favoured both life stages. However we reported a wider range when considering Berre and Bages-Sigean lagoons. Here, *Aurelia* sp. was present in environments with salinities up to 26, remaining below the minimum values previously reported (Kogovšek *et al.*, 2012). Outside of the Mediterranean Sea, comparable temperature and salinity windows to Thau and Berre were reported in Southampton Water (Lucas and Williams, 1994) and Kertinge Nor (Olesen *et al.*, 1994). Though, the ecological niche of *Aurelia* spp. in different habitats around the world should take into account its biogeography (Dawson and Martin, 2001). For instance, the Northeastern Atlantic appears to be inhabited by *Aurelia aurita* (Dawson *et al.*, 2005; Ki *et al.*, 2008), while in the Mediterranean Sea several cryptic species are present, such as *Aurelia* sp. 1 in France (Dawson, 2003; Dawson *et al.*, 2005), *Aurelia* sp. 5 in Veliko Jezero (Dawson and Jacobs, 2001; Dawson *et al.*, 2005; Ki *et al.*, 2008), *Aurelia* sp. 8 (Dawson *et al.*, 2005; Malej *et al.*, 2012) as well as *Aurelia* sp. 7 (Ki *et al.*, 2008) in the Adriatic Sea. Therefore, differences of environmental windows used by different populations of *Aurelia* species might reflect genotypic variation among them, which should be considered in further ecological studies.

Potential inter-specific competition with gelatinous zooplankton predators

Food limitation, as a consequence of competition with other organisms with overlapping diets, could result in low abundances, growth rates and small bell diameter in *Aurelia* spp. Inter-specific competition was previously suggested with bivalves (Bonnet *et al.*, 2012) and reported with

Pleurobrachia pileus (Lucas and Williams, 1994). Here we suggest a likely inter-specific competition with *M. leidyi* in Berre and Bages-Sigean lagoons (Fig. 5). *M. leidyi* is recognized to be among the worst marine invasive species, which is now established in European seas, including a number of Mediterranean ecosystems (Ghabooli et al., 2013). This ctenophore has a reputation of having strong impact on the pelagic community, either as a result of food competition or direct predation (Shiganova, 1998; Hamer et al., 2011). Competition between *M. leidyi* and *Aurelia* spp. has been previously hypothesized in Limfjorden (Denmark) (Riisgård et al., 2012), where both predators feed on the same broad spectrum of zooplankton. In Berre lagoon, *M. leidyi* was present all year round. However, when overlapping with *Aurelia* sp. occurrence, its abundance was lower and it increased after *Aurelia* sp. disappearance. As previously discussed, in Berre, *Aurelia* sp. growth occurred with high zooplankton abundances, but growth and maximum bell diameter were relatively low. In this lagoon, the zooplankton assemblage is characteristic of an anthropogenic impacted ecosystem, with more brackish species and a less diversity community (Delpy et al., 2012). Although the abundance was high, competition for specific prey types (Sullivan et al., 1994) should be considered in understanding the observed small maximum size attained by *Aurelia* sp. in this lagoon, as also suggested by Riisgård et al. (Riisgård et al., 2012) for the Limfjorden.

Future direction

Our study presents for the first time comparative estimates (same methods of calculation and a similar stage of development) of *Aurelia* spp. growth rates based on direct morphological measurements. However, new techniques are now available offering possible methods for jellyfish growth assessments, potentially overcoming the flaws of the currently used methods. For instance, RNA:DNA ratios and RNA content have previously been used for zooplankton growth quantification (e.g. Wagner et al., 2001). Likewise, methods based on enzyme activities are also attractive as potential indices of growth, since some enzyme activities are directly related to protein synthesis (e.g. Berges et al., 1990). For example, evaluating Aminoacyl-tRNA synthetases activity has been suggested as an index of growth in zooplankton (Yebrá and Hernández-León, 2004) and has been successfully employed with some organisms (e.g. *Calanus helgolandicus* and *Calanus finmarchicus*) (Yebrá et al., 2005, 2006). To our knowledge, biochemical methods have not been used to measure the growth of gelatinous organisms, although they may provide promising results for a better understanding of jellyfish ecology.

Our study further highlights the need for complementary studies embracing both molecular and ecological approaches. Here, comparisons were performed within *Aurelia aurita* species, since taxonomic confirmation of the populations studied is still lacking. However, the reported inter-population variation might be an outcome of their phylogenetic characteristics, which should be considered in future investigations. Understanding the role of genetic diversity and population structure among different ecosystems is crucial to distinguish the influence of environmental variability on the population dynamics of each cryptic species. Such knowledge is of greatest importance to eventually forecast *Aurelia* spp. blooms and prevent potentially negative impacts on the ecosystem as well as on goods and services.

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