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Expansion of *Mnemiopsis leidyi* in the French Mediterranean lagoons along the Gulf of Lion

Guillaume Marchessaux^{1,3,*}, Bruno Belloni^{2,3}

¹Université de Franche-Comté – Laboratoire Chrono-Environnement, UMR CNRS/UFC6249, F-25211 Montbéliard cedex, France

²GIS Posidonie, Aix-Marseille University, OSU Pythéas, 13288 Marseille, France

³See The Sea Production, 26 rue de Friedland, 13006 Marseille, France

* corresponding author : guillaume.gmarchessaux@gmail.com

Abstract

The ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 originates from estuaries and coastal waters along Atlantic coastlines from the Chesapeake Bay, USA, to Argentina. Through ballast waters, the species has spread the past 30 years over Eurasia. On the French Mediterranean coastlines, *Mnemiopsis leidyi* was first formally identified in the Berre Lagoon in 2005 and has been episodically present in other Mediterranean lagoons as Bages-Sigean, Vaccarès, and Estomac. Since 2010-2011 no update of the distribution of *Mnemiopsis leidyi* has been made. Since 2019, many records of *Mnemiopsis leidyi* have been reported in other French Mediterranean lagoons along the coast of the Gulf of Lion. In this context, a field survey on the French Mediterranean coast was conducted in July 2020 to measure the expansion of the *Mnemiopsis* population in coastal lagoons which are potential refuge habitats for this species. *Mnemiopsis leidyi* was present in 8 different areas: Or, Pérols, Vic, Ingril, Rhône-Sète Channel, Bages-Sigean, and Salses-Leucate. We were able to quantify for the first time the abundance and size structure of *Mnemiopsis* in the lagoons of Or, Pérols, Vic, Ingril, Rhône-Sète Channel, and Salses-Leucate. A decrease in the abundance of *Mnemiopsis leidyi* was observed from 1 ind m⁻³ (Ingril Lagoon) to 28 ind m⁻³ (Grec Lagoon) and 42 ind m⁻³ (Rhône-Sète Channel) between the North and the South along the Rhône-Sète Channel in parallel to the increase of salinity (from 20 to 41). The abundances measured in Bages-Sigean and Salses-Leucate lagoons were similar: 6 ind m⁻³ and 7 ind m⁻³ respectively.

Keywords: invasive species, Mediterranean lagoons, ctenophores, spatial distribution

1. Introduction

Non-indigenous species introduction in recipient ecosystem constitutes a major source of biological pollution (Elliott, 2003; Bourdouresque and Verlaque, 2002, 2012). As some become invasive, they often have strong ecological and economic impacts: modifying the diversity, the ecosystem functioning (e.g. competition, predation) and impacting human activities (e.g. fisheries, industrial complex, and tourism) (Katsanevakis et al., 2014a,b; Gallardo et al., 2016; Tsiamis et al., 2018).

The ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 has been ranked within the top 100 worst marine bio-invasers by the International Union for Conservation of Nature (IUCN; Lowe et al., 2004). This species originates from estuaries and coastal waters along Atlantic coastlines from the Chesapeake Bay, USA, to Argentina (GESAMP, 1997). Through ballast waters, the species has spread the past 30 years over Eurasia (Costello et al., 2012; Jaspers et al., 2018; Shiganova et al., 2019). *Mnemiopsis leidyi* appeared in the Black Sea in 1982, connected to the Gulf of Mexico seeding population, occurred in 1982 (Pereladov, 1988), the invader then rapidly spread through the whole Black Sea and the Caspian Sea and was found at the turn of the century in various Mediterranean basins (Shiganova et al., 2019 and references included). The second invasion into the North and Baltic seas was linked to the seeding population of the East Coast of the USA (Shiganova et al., 2019). *Mnemiopsis leidyi* was observed into large ranges of temperature (0 °C – 31 °C), salinity (0.1 - 40), and chlorophyll *a* concentration (0.02 – 9.7 µg L⁻¹) reflecting its wide ecological niche (Purcell et al., 2001). Due to high reproductive rates (Jaspers et al., 2015) and high predation rates on zooplankton communities (Purcell and Decker, 2005; Condon and

Steinberg, 2008), this ctenophore can strongly impact ecosystems both at ecological and economical levels (Purcell et al., 2001; Gallardo et al., 2016).

On the French Mediterranean coastlines, *Mnemiopsis leidyi* was first formally identified in the Berre Lagoon in 2005 (Fig. 1; Delpy et al., 2012) and has been episodically present in other Mediterranean lagoons as Bages-Sigean since 2005 (Delpy et al., 2016), Vaccarès since 2016, and Estomac since 2019 (Marchessaux et al., 2020b), but the first arrival of *Mnemiopsis leidyi* along French Mediterranean coastlines may have occurred much earlier. Indeed, for example, some fishermen from the Berre Lagoon reported observing *M. leidyi* in the late 1990s and early 2000s. (Marchessaux, 2019). Generally, French Mediterranean lagoons invaded by *Mnemiopsis leidyi* have brackish waters. Since the study of Delpy et al. (2016) conducted in the Berre and Bages-Sigean lagoons in 2010-2011 no update of the distribution of *Mnemiopsis leidyi* has been made. Since 2019, many records of *Mnemiopsis leidyi* have been reported in other French Mediterranean lagoons along the coast of the Gulf of Lion.

In this context, a field survey (MnemiOccitane project) on the French Mediterranean coast was conducted in July 2020 to measure the expansion of the *Mnemiopsis leidyi* population in coastal lagoons which are potential refuge habitats for this species as recently identified in the Berre Lagoon (Marchessaux et al., 2020a). The main objective of this study was therefore to update the biogeographic distribution of *Mnemiopsis leidyi* in the Gulf of Lion.

2. Materials and methods

2.1. Study areas and strategy

Coastal lagoons occupy about 50 % of the coastline along the Gulf of Lion, are numerous in the West part of the Rhône River, and less common on the Côte d'Azur, East part (De Wit et al., 2020). The study consisted of determining the presence/absence of *Mnemiopsis leidyi* in coastal lagoons in the western Gulf of Lion (Fig. 2). In total, 10 brackish and 4 marine water lagoons were sampled (Table 1). This study was performed in July (summer period) where *Mnemiopsis leidyi* showed the highest abundances in many Mediterranean lagoons (Bages-Sigean: Delpy et al., 2016; Berre: Marchessaux et al., 2020a; Vaccarès and Estomac: Marchessaux et al., 2020b).

Each lagoon had specific characteristics (i.e. depth, marine or brackish waters, connection with the sea, freshwater inputs, etc.). Coastal lagoons are characterized by permanent or temporary connections with the adjacent sea, via one or several inlets

(Kjerfve, 1994). Today, very few of the shallow lagoons (i.e., Grande Maire, Pissevache, and La Palme) shown in Figure 2 have natural moving inlets, which close off completely every year (Larue and Rouquet, 2016). For many (i.e. Ponant, Or, Grec, Pérols, Vic, Ingril, Bages-Sigean, and Salses Leucate lagoons), inlets have been modified by humans by the construction of hard-substrate artificial inlet banks. This has fixed the locations of the inlets and resulted in a permanent connection of the lagoons with the sea.

The Palavas lagoon complex in the North sector of the Gulf of Lion currently comprises lagoons (Grec, Pérols, Vic, Ingril) that have been created through the compartmentalization of the original Mergueil Lagoon by the creation of the Rhône-Sète Channel since the 18th century. This artificial channel has separated four permanent lagoons (Pérols, Vic, Ingril) from the coastline, and exchanges with the sea occur via this canal.

Prior to sampling, the strategy was to meet with sociological actors of the lagoons studied (i.e. managers of natural areas, reserves and natural parks, fishermen). Due to their activities, these actors were familiar with the lagoons, and the species populations found there. The announced theme of the meeting with sociological actors was about jellyfish in general. First, a series of pictures of different species of gelatinous zooplankton founded in the Mediterranean Sea was shown to the sociological actors (*Pelagia noctiluca*, *Rhizostoma pulmo*, *Aurelia* sp., *Cotylorhiza tuberculata*, *Veleva veleva*, *Gonionemus vertens*, *Mnemiopsis leidy*). The sociological actors had to identify the species already observed in the lagoons without the interviewer intervening. This made it possible to avoid any influence on the actors' choices. After identification, the same questions were asked (since when you have been observing *Mnemiopsis leidy*? do you observe a seasonality in the dynamics of *Mnemiopsis*? have you observed a long-term evolution?). In fact, their testimonies provided information on the presence/absence of *Mnemiopsis leidy* in the different lagoons. A total of 16 sociological actors were interviewed (Supplementary Table S1).

Most of the lagoons studied were shallow (~ 1 m). It was often difficult if not impossible to sample by boat. Given the difficulty to access to the banks of the lagoons (restricted access, siltation, quicksand, bird nesting areas, natural reserves), all the samples were taken by feet. To make the data collected comparable, the same protocol was used.

2.2. Physical and chemical parameters

The temperature was measured with a digital thermometer (*Vellman*®) and salinity with a refractometer (*Atago*® *Master-S*). To measure the chlorophyll *a* concentration, water

samples were collected at the surface with 2 L plastic containers and kept in the dark. Volumes of 50 or 100 mL of water were filtered separately on GF/F (0.7 μm porosity). Filters were kept frozen (- 20 °C until further analysis). Chlorophyll *a* was extracted using acetone (90 %) in the dark and at - 20 °C overnight. The acidification method was used to measure chlorophyll *a* concentration according to Lorenzen (1967) using a spectrometer (Turner®).

To present the physical and chemical context of the lagoons studied, additional monitoring data (temperature, salinity, chlorophyll *a*) from monitoring programs extracted from the French database “Survall” which among others hosts the data of the Réseau Suivi Lagunaire (RSL) monitoring program (IFREMER, <https://wwz.ifremer.fr/surval/>, period: 2000-2019) for all lagoons except for Pissevaches Lagoon where data were extracted for the Forum Interrégional des Lagunes Méditerranéennes (FILMED) monitoring program (Pôle-Relais Lagunes Méditerranéennes, period: 2018-2019).

2.3. Morphological species identification

The most important morphological characteristic of *Mnemiopsis leidyi* is the extent of the oral lobes with a translucent body up to 12 cm in length (NIMPIS, 2002) (Fig. 3). Two oral lobes are extensions of the body of the ctenophore. Four small lobes (auricles) are located under the two oral lobes. The oral lobes of *Mnemiopsis leidyi* extend over almost the whole body and reach the statocyst (the apical sensory organ), whereas in the similar species *Bolinopsis vitrea*, the oral lobes end between the mouth and the statocyst (Hansson, 2006). The extent of the oral lobes was checked for each lobed ctenophore.

2.4. Zooplankton and *Mnemiopsis leidyi*

Based on the information given by the sociological actors of the lagoons, 100 m long line transects parallel to the banks were carried out (Table 1) on different sampling stations to detect the presence/absence of *Mnemiopsis leidyi* and quantify its abundance. Initially, visual observation was made along the transect. Secondly, whether in the presence or absence of *M. leidyi*, a conical plankton net (80 μm mesh, 30 cm opening area, 1,2 m long) was used to sample zooplankton and *M. leidyi* when it was present. It is important to note that the number of transects carried out was conditioned by the difficulty of access to the shores of lagoons (restricted access, siltation, quicksand, protected areas, bird nesting areas, prohibition of motor boats).

Due to the shallowness of the sites, the conical net was tracked by feet as describe in Marchessaux et al. (2020b). The samples were performed along a 50 m linear transect

parallel to the shore, delimited by two wooden sticks (Marchessaux et al., 2020b). In 1 m depth when it was possible, the operator was placed on the left side of the net to limit the influence of his movements (Supplementary Figure S1); a round trip was performed to cover a distance of 100 m long. This operation was replicated (14.1 m³ sampled). A total of 17 samples were analyzed.

After sampling, individuals of *Mnemiopsis leidyi* were isolated from zooplankton, and washed with filtered lagoon water. The total number of individuals *M. leidyi* sampled in the net were counted, and 30 ctenophores were freshly measured. Individuals were directly placed on a plastic plate consisting of a ruler and were photographed using a Nikon D60 (Fig. 3). At the laboratory, after calibration and for greater accuracy, the ImageJ software was used to measure the size (oral-aboral length).

The samples of zooplankton were preserved in buffered sea water-formalin solution (4 % final concentration) for further zooplankton taxonomic identification. At the laboratory, the zooplankton compartment was divided into 3 groups: copepods (nauplii, copepodites and adults), meroplankton (larvae of veliger, gastropods, Zoe, polychaeta, and barnacles), holoplankton (rotifers, cladocerans) and benthos (amphipods). The number of organisms was counted, and abundances determined (ind.m⁻³).

2.5. Statistical analysis

The graphs presented in this article were made using Sigmaplot 12.5 software. To test the differences in oral-aboral length of *Mnemiopsis leidyi* in different lagoons, Analyses of Variance (ANOVA) were calculated using Sigmaplot 12.5 software. If the overall ANOVA results were significant, Bonferroni pair-wise comparisons ($p < 0.05$) were performed to test among combinations.

To link the presence/absence of *Mnemiopsis leidyi* with environmental data (biotic and abiotic) of lagoons studied, a principal component analysis (PCA) was performed using R software. The data matrix included environmental data (temperature, salinity, chlorophyll concentration) and abundance data for zooplankton and *Mnemiopsis leidyi*. After the transformation of the data into $\log(n+1)$, the latter were normalized (Shapiro-Wilk test). The PCA was thus traced as well as the circle of correlations allowing to identify the factors influencing the presence/absence of *Mnemiopsis leidyi* in lagoons.

3. Results

3.1. Environmental parameters

The temperature of the Mediterranean lagoons studied showed ranges of values typical of temperate areas with a minimum temperature observed (January to March; 0.3 – 10 °C) in winter and maximum values in summer (July to September; 22 – 30.9 °C) (Fig. 4A). During our study in July 2020, the temperature did not show significant differences between the lagoons, was between 20.0 °C (Ingril Lagoon) and 30 °C (Mateille Lagoon), and was in the same ranges than long-term monitoring data (Fig. 4A).

All the lagoons had brackish water (except Ingril, Thau, and Gruissan-Grazel) with significant variations in salinity ranging from 0.1 (winter, Ponant) to 57.1 (summer, La Palme) (Fig. 4B). The salinity of marine lagoons varied from 28.7 to 44.5 (mean: 38.22 ± 3.03 ; Ingril), 32.9 to 40.9 (mean: 37.97 ± 1.68 ; Thau), and from 17.3 to 48.3 (mean: 36.87 ± 4.95 ; Gruissan-Grazel). In July 2020, the minimum salinity measured was 10 in La Palme Lagoon while the maximum ($S = 40$) was observed in the Ingril Lagoon. The salinity was in the same ranges as long-term monitoring.

The concentration of chlorophyll *a* showed significant difference from one lagoon to another (Fig. 4C). The lagoons of Or, Grec, Pérols and Canet and the Rhône-Sète Channel had the widest ranges of chlorophyll concentrations: from 1.29 to 567.58 $\mu\text{g L}^{-1}$, 0.23 – 103.79 $\mu\text{g L}^{-1}$, 0.23 – 273.67 $\mu\text{g L}^{-1}$, 0.07 – 157.79 $\mu\text{g L}^{-1}$, and 0.23 – 227.40 $\mu\text{g L}^{-1}$ respectively. In contrast, the other lagoons showed lower values and less variation: 0.62 – 56.71 $\mu\text{g L}^{-1}$ (Ponant); 0.22 – 50.8 $\mu\text{g L}^{-1}$ (Vic); 0.16 – 20.54 $\mu\text{g L}^{-1}$ (Ingril); 0.44 – 12.70 $\mu\text{g L}^{-1}$ (Thau); 0.30 – 24.48 $\mu\text{g L}^{-1}$ (Gruissan-Grazel); 0.15 – 23.58 $\mu\text{g L}^{-1}$ (Bages-Sigean); 0.16 – 14.02 $\mu\text{g L}^{-1}$ (La Palme), 0.24 – 12.77 $\mu\text{g L}^{-1}$ (Salses-Leucate). The concentration of chlorophyll *a* measured in July 2020 were low and ranged from $0.38 \pm 0.12 \mu\text{g L}^{-1}$ (Gruissan-Grazel) and $2.01 \pm 0.81 \mu\text{g L}^{-1}$ (Ponant), 3.10 $\mu\text{g L}^{-1}$ (Grec) and $6.56 \pm 2.44 \mu\text{g L}^{-1}$ (Canet). For the other lagoons, chlorophyll *a* concentration was comprised between 0.39 $\mu\text{g L}^{-1}$ (Ingril) and 1.80 $\mu\text{g L}^{-1}$ (Vic).

3.2. Zooplankton abundance and *Mnemiopsis leidyi*

The abundance of zooplankton showed large variations from one lagoon to another (Fig. 4D). The minimum abundance was observed in La Palme Lagoon (1 300 ind m^{-3}) while two maximum abundances were measured in Grande Maire Lagoon (124 264 ind m^{-3}), and Canet Lagoon (761 667 ind m^{-3}). Copepods dominated the zooplankton community in the lagoons of Pérols (78 %), Vic (94 %), Thau (67 %), Grande Maire (99 %), Pissevache (80

%), Mateille (99 %), and Canet (62 %). On the contrary, meroplankton larvae were dominants in the lagoons of Ponant (53 %), Or (72 %), Grec (86 %), Ingril (63 %), Gruissan-Grazel (52 %), Bages-Sigean (99 %), La Palme (81 %) and Salses-Leucate (86 %) and in the Rhône-Sète Channel (93 %). The other groups (i.e. holoplankton and benthos) represented between 0 % and 1 % of the community of lagoons studied.

Mnemiopsis leidyi was observed in 7 lagoons and in the Rhône-Sète Channel (Fig. 5) which corresponded to the testimonies of sociological actors collected, except for the Grec Lagoon, Pérols Lagoon, Vic Lagoon, and Ingril Lagoon where the sociological actors had never observed *Mnemiopsis leidyi*. On the other hand, *Mnemiopsis leidyi* was not observed in the Thau, Gruissan-Grazel, Grande Maire, Pissevache, La Palme, and Canet in July 2020.

The sociological actors described the temporal dynamics of *Mnemiopsis leidyi* over the seasons. *Mnemiopsis* was observed all year round in the Or, Pérols, Grec, Bages-Sigean and Salses-Leucate lagoons, but presents significant variability according to the season, and from one year to another in terms of abundance. On the other hand, *Mnemiopsis leidyi* was observed punctually in the Grande Maire Lagoon between February and April according to the fisherman when the lagoon was connected to the sea by a natural channel dug by marines' storms.

The abundance of *Mnemiopsis leidyi* was variable and ranged from 1 ind m⁻³ (Ingril Lagoon) to 28 ind m⁻³ (Grec Lagoon) and 42 ind m⁻³ (Rhône-Sète Channel) (Fig. 6A). A decrease in the abundance of *Mnemiopsis leidyi* was observed between the North (Or Lagoon – Rhône-Sète Channel) and the South (Ingril Lagoon) along the Rhône-Sète Channel; *Mnemiopsis* was absent at the connection between the channel and the Thau Lagoon. The abundances measured in Bages-Sigean and Salses-Leucate lagoons were similar: 6 ind m⁻³ and 7 ind m⁻³ respectively.

The length of the oral-aboral axis of *Mnemiopsis leidyi* also showed differences between the lagoons (Fig. 6B). Individual were significantly smaller (ANOVA, Bonferroni test, $p < 0.05$) in the Or (1.88 ± 0.42 cm), Bages-Sigean (1.18 ± 0.38 cm) and Salses-Leucate (1.81 ± 0.37 cm) lagoons than the other lagoons: Rhône-Sète Channel (2.04 ± 0.56 cm), Grec Lagoon (2.76 ± 0.92 cm), Perols Lagoon (2.45 ± 0.57 cm), Vic Lagoon (2.40 ± 0.37 cm), and Ingril Lagoon (2.42 ± 0.65 cm).

The hierarchical clustering performed on collected data dissociates 5 groups according to the abundances of *Mnemiopsis leidyi* and lagoons environmental parameters in July 2020 (Fig.7). PCA showed that when *Mnemiopsis leidyi* was present in the lagoons (i.e. Or, Rhône-Sète Channel, Grec, Pérols, Vic, Ingril, Salses-Leucate, Bages-Sigean), the abundance of zooplankton decreased significantly. An effect of salinity was observed on

Mnemiopsis leidyi abundance with lowest abundances measured in the Ingril Lagoon (1 ind m⁻³; salinity = 40). However, no relationship was observed between abundances of *M. leidyi* and chlorophyll *a* concentration and temperature. Canet and La Palme lagoons were respectively isolated from the other lagoons because they presented extremes values (minimum or maximum) of zooplankton abundance (La Palme: 1 300 ind m⁻³; Canet: 761 667 ind m⁻³) and chlorophyll *a* concentrations (La Palme: 0.50 µg L⁻¹; Canet: 6.56 µg L⁻¹).

4. Discussion

4.1. *Mnemiopsis leidyi* and environmental parameters

From the Gulf of Mexico, the ctenophore *Mnemiopsis leidyi* has invaded many habitats in Europe (Shiganova et al., 2019, and references included) with very different characteristics (Table 2). Coastal and estuarine areas are suitable habitats for the maintenance of *Mnemiopsis leidyi* (Kremer, 1994; Costello et al., 2006). The success of the invasion of *Mnemiopsis leidyi* lies mainly in its life cycle (Sasson and Rayan, 2016) with high reproductive rates allow it to establish a sustainable population in invaded areas (Graham and Bayha, 2008; Jaspers et al., 2011; Lehtiniemi et al., 2012). Successful expansion of *Mnemiopsis leidyi* is often associated with disturbed ecosystems, such as in the Black Sea, where introductions were favored by overfishing and anthropogenic pollution (Shiganova et al., 2001). In the 1980s, *Mnemiopsis leidyi* was introduced into the Black Sea where overfishing had severely reduced small pelagic fishes' stocks (i.e. anchovy, sprat, and Mediterranean horse mackerel). *Mnemiopsis leidyi* has contributed to the decline in stocks of these commercial species (Cucu 2002). In the Berre Lagoon (France) its introduction followed several decades of intense anthropogenic pressure (i.e. increased freshwater and silt inputs from a hydropower plant, chemical pollution, and urbanization) (Delpy et al., 2012; Marchessaux et al., 2020a).

Mnemiopsis leidyi has many of the characteristics typical of invasive species (i.e. high reproductive, growth and feeding rates), making it one of the 100 most invasive species in the world (Lowe et al., 2007). Table 2 illustrates the ability of *Mnemiopsis leidyi* to invade a wide variety of ecosystems. The establishment of sustainable populations depends on abiotic (i.e. temperature and salinity) and biotic (i.e. food availability) factors (Costello et al., 2012). *Mnemiopsis leidyi* can survive over wide ranges of temperature (0-32 °C) and salinity (1-46) confirming its eurythermal and euryhaline potential (Purcell et al., 2001). In general, *Mnemiopsis leidyi* proliferates in highly productive and eutrophic environments, both in native areas (76 mg Chl_a L⁻¹ in Chesapeake Bay (Condon and Steinberg, 2008)) and in

invaded areas (40 mg Chla L⁻¹ in the Caspian Sea (Roohi et al., 2008, 2010; Roohi & Sajjadi, 2011)). However, it is necessary to have zooplankton biomass greater than 3 mgC m⁻³ (Kremer, 1994; Purcell et al., 2001) for *Mnemiopsis leidyi* populations to be able to survive.

The lagoons studied were highly variable in terms of temperature, salinity, chlorophyll a concentration, and zooplankton abundance, confirming the high tolerance of *Mnemiopsis leidyi* to the variability of environmental windows. During our study, we were able to update the distribution of *Mnemiopsis leidyi* along the French Mediterranean coasts and quantify for the first time the abundance and size of individuals in the Or, Grec-Perols, Vic, Ingril and Salses-Leucate lagoons where *Mnemiopsis leidyi* was never observed or studied (Fig. 5). As reported in the literature, salinity and temperature are determining factors for the maintenance of ctenophores. In our study, the records of *Mnemiopsis leidyi* at temperatures ranging from 20.0 °C to 30 °C and salinity from 20 to 41 were consistent with the eurythermal and euryhaline tolerances of this ctenophore (Purcell et al., 2001). *Mnemiopsis leidyi* has indeed been shown to survive in salinity from 1 to 46 (Kremer et al., 1994; Purcell et al., 2001). Different studies showed the effects of salinity and chlorophyll and, to a lesser extent, the temperature on the Berre (Marchessaux et al., 2020a) and Bages-Sigean (Delpy et al., 2016) populations. As observed by Delpy et al. (2016), salinity appeared to be a limiting factor in the abundance of *Mnemiopsis leidyi* in the Bages-Sigean Lagoon. Even though *M. leidyi* has been shown to survive in extreme salinity and temperature ranges, reproduction rates under low salinity levels (< 10) have been reported extremely low and both low salinity and low temperature may explain its limited range expansion in Northern Europe (Jaspers et al., 2011, 2013b). This would explain why we have observed a decrease in abundance of *Mnemiopsis leidyi* in the Palavas lagoon complex between the North (Or Lagoon – Rhône-Sète Channel) and the South (Ingril Lagoon) along the Rhône-Sète Channel. In the Vaccarès Lagoon, ctenophore presence appeared promoted when the salinity is over 20 (Marchessaux et al., 2020b) but for large ranges of salinity (10 – 30) in the Berre Lagoon (Delpy et al., 2016, Marchessaux et al., 2020a).

To compare with other Mediterranean lagoons, chlorophyll a concentrations measured in our study (0.38 µg L⁻¹ – 6.56 µg L⁻¹) were lower than observed in the Berre Lagoon (0.9 – 24.6 µg L⁻¹; Delpy et al., 2016; Marchessaux et al., 2020a) and in the same range than Bages-Sigean Lagoon (0.3 – 4.7 µg L⁻¹; Delpy et al., 2016). *Mnemiopsis leidyi* was observed in the Vaccarès Lagoon for chlorophyll a concentration from 3.9 µg L⁻¹ to 5.12 µg L⁻¹, whereas it was absent in sampling for chlorophyll range from 1.5 µg L⁻¹ to 7.1 µg L⁻¹ (Marchessaux et al., 2020b). More futures data need to be produced to confirm the influence

of chlorophyll especially as *Mnemiopsis* is an omnivorous organism, then phytoplankton could play an important role in it maintain (Deason and Smayda, 1982).

The relatively small size of adults in French Mediterranean lagoons is typical of the populations present in brackish waters (Huerter et al., 2008) and in the Caspian, Sea of Azov, Baltic seas (Shiganova, 2020). Data presented in the literature show a wide variation in the maximum adult size of *Mnemiopsis leidyi*. In our study, adults were small (between 1 and 5 cm). The size of individuals was larger in the lagoons in the northwestern Gulf of Lion (Rhône-Sète Channel: 2.04 ± 0.56 cm; Grec 2.76 ± 0.92 cm; Pérols: 2.45 ± 0.57 cm; Vic : 2.40 ± 0.37 cm; Ingril: 2.42 ± 0.65 cm) than in Or (1.88 ± 0.42 cm), Bages-Sigean (1.18 ± 0.38 cm) et Salses-Leucate (1.81 ± 0.37 cm) lagoons. There are no data prior to our study in these lagoons except for Bages-Sigean where maximum sizes of 4.5 cm were measured in August 2010-2011 (Delpy et al., 2016). In the Berre and Estornac Lagoons the maximum oral-aboral length measured were respectively ~ 4.5 cm (total length: ~ 7 cm) in July 2016 (Marchessaux, 2019) and 7 cm (total: 10 cm) In June 2019 (Marchessaux et al., 2020b). However, these data are similar to those reported in the Caspian Sea (Finenko et al., 2006) and Narragansett Bay (Kremer and Nixon, 1976). During proliferation in the Berre Lagoon, individuals of 2-3 cm made up the size structure of the adult population in 2010-2011 (Delpy et al., 2016), while individuals of 1 – 1.5 cm were observed in 2017 for an abundance of 45 ind m⁻³ (Marchessaux, 2019). These data are similar to what was observed in Bages-Sigean where 1 – 2 cm individuals dominated the size structure in August and September (Delpy et al., 2016), in the Dutch Wadden Sea (~ 2 cm; Van Walraven et al., 2013). Salinity can also limit the development of large individuals as observed in Narragansett Bay (S = 23-32) (Kremer, 1994; Sullivan et al., 2001); the Baltic Sea (S = 8-16) (Storr-Paulsen and Huerter, 2008) and the Black Sea (Mullu, 1999). For salinities (S ~ 34 , in Argentina) Mianzan et al. (2010) found organisms up to 14 cm, similarly at Villefranche-sur-Mer (S ~ 30) organisms, ~ 15 cm were observed (Delpy et al., 2016). Maximum sizes of *Mnemiopsis leidyi* were observed in the north-western Black Sea (18 cm - Shiganova, 1997; 12 cm - Weisse et al., 2002).

4.2. Expansion of *Mnemiopsis leidyi* in the French Mediterranean lagoons

Introduced via the ballast water of international commercial ships, *Mnemiopsis leidyi* is an invasive species that has managed to spread in most European coastal waters, particularly in estuaries and lagoons that are conducive to its establishment. *Mnemiopsis leidyi* has a high tolerance to variations in environmental conditions, high phenotypic

variability, and a capacity for rapid population growth (Javidpour et al., 2006; Costello et al., 2006, 2012).

The introduction pattern of *Mnemiopsis leidyi* by cargo ships result from trans-Atlantic (e.g. East coast of Mexico and USA) and local ship transits within the Mediterranean Sea (Bolte et al., 2013; Ghabooli et al., 2013). As no maritime traffic occurs in many lagoons (i.e. Or, Grec, Pérols, Vic, Ingril, Bages-Sigean, Salses-Leucate) its presence may probably result from regular reintroductions. Advection processes and natural transport (drift, internal circulation) are certainly a vector of secondary spread of *Mnemiopsis leidyi* from closed lagoons such as the Berre Lagoon as observed by Jaspers et al. (2018a). Currents and artificial canals between lagoons may be vectors of *Mnemiopsis leidyi* expansion. Our study also showed dispersion of *Mnemiopsis leidyi* within the vast interconnected network of lagoons located on the French Mediterranean coast, notably via the Rhone-Sète Channel whose mouth is at the harbor of Sète.

During our study, *Mnemiopsis leidyi* was present in 8 different areas: Or, Pérols, Vic, Ingril, Rhône-Sète Channel, Bages-Sigean, and Salses-Leucate. We were able to quantify for the first time the abundance, and size structure of *Mnemiopsis leidyi* in the lagoons of Or, Pérols, Vic, Ingril, Rhône-Sète Channel and Salses-Leucate. Based on the testimonies of sociological actors, *Mnemiopsis leidyi* would be present all year round in the lagoons of l'Or, Pérols, Vic, Ingril, Rhône-Sète Channel, Bages-Sigean and Salses-Leucate. In the Berre Lagoon (East of the Gulf of Lion), *Mnemiopsis leidyi* has been present all year round since the early 2000s thanks to the presence of a refuge area (Marchessaux et al., 2020a).

The success of the sustainability of *Mnemiopsis leidyi* resides in the presence of refuge areas that offer optimal conditions for the wintering of *Mnemiopsis leidyi* (Costello et al., 2006). In the Berre Lagoon the presence of a refuge area in the sub-basin of Vaine allows the maintenance of the population of *Mnemiopsis leidyi* all year round (Marchessaux et al., 2020a). This area offers optimal environmental conditions (presence of semi-permanent gyre, temperature: 3.5 – 27.1 °C; Salinity: 18.8 – 27.8; available carbon: 2.0 – 854.5 $\mu\text{gC L}^{-1}$) for the maintenance of *Mnemiopsis leidyi* populations in winter conditions. In the western lagoons of the Gulf of Lion, the presence of refuge areas would explain the maintenance of the populations all year round, particularly in the Or, Grec, Pérols, Bages-Sigean, and Salses-Leucate as suggested by Delpy et al. (2016).

In Bages-Sigean, the winter absence of *Mnemiopsis leidyi* was observed in 2010-2011 by Delpy et al. (2016) and a reappearance in August. However, in our study, we observed individuals in our samples in early July 2020. During the sociological interviews, fishermen from Bages-Sigean explained that they have been seeing *Mnemiopsis leidyi* year-

round (low abundance in winter and high abundance in summer) since 2019. The fishermen are on the lagoon all year round and their testimony gives a reliable idea of the dynamics of *Mnemiopsis leidyi*. It would, therefore, seem that the population of *Mnemiopsis leidyi* in the Bages-Sigean Lagoon has adapted to the environment of the lagoon and finds favorable conditions for its maintenance all year round, but we do not have much data on the long-term evolution of the environmental conditions in these lagoons. The same pattern was also observed in Salses-Leucate Lagoon, but no data were measured before this study on the dynamics of *Mnemiopsis leidyi*.

Mnemiopsis leidyi was occasionally observed in the lagoon of Grande Maire by fishermen. The Grande Maire lagoon is punctually connected to the sea via a natural channel that forms in winter under the action of sea storms. In this configuration, the lagoon is connected to the sea and becomes saline. On the other hand, in spring and summer, the natural channel closes, thus isolating the lagoon, which desalinates under the action of freshwater coming in from the rivers. According to the fishermen we met, *Mnemiopsis leidyi* enters the Grande Maire lagoon when it is connected to the sea in winter. On the other hand, more regular monitoring should be carried out according to the seasons to determine whether *Mnemiopsis leidyi* is present in this lagoon especially because fishermen saw only the adult forms. The sometimes-particular functioning of the lagoons can influence the maintenance or not of *Mnemiopsis leidyi* populations. In the Vaccarès Lagoon in the Camargue, *Mnemiopsis leidyi* is not observed all year round since the lagoon is not always connected to the sea, the connection to the sea being managed manually by humans via canals (Marchessaux et al., 2020). In fact, just like the Grande Maire lagoon, the Vaccarès Lagoon desalinates in winter when it is isolated from the sea, *Mnemiopsis leidyi* is not or hardly observed there.

Finally, some lagoons such as Thau, Mateille, and Grazel-Guissan have specific hydrographic characteristics (i.e. marine waters, presence of other native gelatinous species). The absence of *Mnemiopsis leidyi* in the Thau Lagoon is probably due to external control preventing the development of a population, e.g. inadequate temperature and salinity conditions for reproduction and/or potential food competition with a resident population of jellyfish *Aurelia* sp. as shown by Riisgård et al. (2010). The coastal areas of the Gulf of Lion, and by extension the entire French Mediterranean coast, may be threatened by the introduction of *M. leidyi*. Its presence has already been detected in coastal stations off Villefranche-sur-Mer in 2012 and Marseille in 2013 (Delpy et al., 2016) but also in fishermen's fishing nets in Agde. During favorable environmental periods (i.e. summer and autumn in temperate waters), it can be conducted outside its regions of origin and spread along the coasts using local currents (Costello et al., 2012).

This study showed that the expansion of *Mnemiopsis leidyi* along the French Mediterranean coast continues even beyond the Mediterranean Sea. In fact, the French citizen science *Mnemiop'See* program, led by the organization See The Sea Production, has made it possible to collect new data on the distribution of *Mnemiopsis leidyi* in France. While *Mnemiopsis leidyi* had never been observed on the French Atlantic coast, its presence was reported in the Loire Estuary (28 September 2018; longitude: 47.332457; latitude: 2.008427; temperature: 16 °C; salinity: 13; total length: 1 – 3 cm; number of individuals observed: 1 000) and in the La Vilaine Estuary (18 July 2020, longitude: 47.405756; latitude: -2.490371; temperature: 18 °C; total length: 4 – 6 cm, number of individuals observed: 50) (Fig.8).

5. Conclusion

The distribution area of *Mnemiopsis leidyi* continues to expand along the French coasts and this study provided an overview of the distribution of *Mnemiopsis leidyi* along the French Mediterranean coasts. Based on these observations, it is necessary to monitor *Mnemiopsis leidyi* in the Palavas lagoon complex, Bages-Sigean and Salses-Leucate lagoons to understand the temporal dynamics and the sociological and ecological impacts of the proliferation of *Mnemiopsis leidyi*. A study is currently underway to quantify the impact of *Mnemiopsis leidyi* on professional fishing in the French Mediterranean lagoons. Finally, another study of large-scale currents will be carried out to understand the connectivity between the lagoons of the Gulf of Lion.

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Conflict of Interest.

The authors declare that they have no conflict of interest.

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Table 1. Sampling stations and characteristics of the lagoons.

Site	Date	Longitude	Latitude	Surface (km ²)	Maximum depth (m)	Number of transects (100 m)	Connection with the sea?	Source of long-term monitoring data
Ponant	6 July 2020	43.565454	4.122044	2.8	4 m	3	Yes	RSL 2000–2019
	6 July 2020							
Or	6 July 2020	43.553003	3.970823	30	1.2 m	1	Yes	RSL 2000–2019
	6 July 2020							
Rhône-Sète Channel 1	6 July 2020	43.574063	4.082531	Length: 98 km	2.5 m	1	Yes	RSL 2000–2019
	6 July 2020							
Grec	6 July 2020	43.545218	3.962791	270	0.5 m	1	Yes	RSL 2000–2019
	6 July 2020							
Pérois	6 July 2020	43.551714	3.955359	717	0.8 m	1	No	RSL 2000–2019
	7 July 2020							
Vic	7 July 2020	43.483343	3.807646	1250	1.7 m	1	No	RSL 2000–2019
	7 July 2020							
Ingril	7 July 2020	43.441742	3.790557	1085	1.1 m	1	Yes	RSL 2000–2019
	7 July 2020							
Thau	7 July 2020	43.344117	3.532186	70.12	4 m	2	Yes	RSL 2000–2019
	9 July 2020							
Grande Maire	9 July 2020	43.270004	3.341792	4.1	1.0 m	4	Partially, during winter	No data
	9 July 2020	43.281308	3.338484					
Pissevaches	9 July 2020	43.191170	3.199316	9.05	1.0 m	2	Partially, during winter	FILMED 2018–2019
	9 July 2020							
Mateille	9 July 2020	43.132126	3.135865	2.5	7 m	2	Yes	No data
	9 July 2020							
Gruissan-Grazel	9 July 2020	43.109163	3.090031	1.45	1.2 m	2	Yes	RSL 2000–2019
	10 July 2020							
Bages-Sigean	10 July 2020	43.142795	3.002607	55	4 m	3	Yes	RSL 2000–2019
	10 July 2020	43.125286	2.994181					
La Palme	10 July 2020	42.967826	2.999978	6	1 m	2	Partially, during winter	RSL 2000–2019
	10 July 2020							
Salses-Leucate	10 July 2020	42.800983	2.996367	54	9.0 m	3	Yes	RSL 2000–2019
	10 July 2020	42.837074	3.023089					
Canet	10 July 2020	42.677609	3.029257	7.82	1.1 m	5	Yes	RSL 2000–2019
	10 July 2020	42.659516	3.032313					

Table 2. Environmental ranges of invaded areas by *Mnemiopsis leidyi*.

Locations	Temperature (°C)	Salinity	Chla ($\mu\text{g L}^{-1}$)	Zooplankton ($\times 10^3 \text{ ind m}^{-3}$)	<i>Mnemiopsis leidyi</i> (ind m^{-3})	References
Native areas						
Chesapeake Bay (USA)	2.0 – 29.0	10.0 – 22.0	6.0 – 76.0	0.1 – 18.9	1.0 – 480.0	Condon & Steinberg (2008)
Narragansett Bay (USA)	5.0 – 28.0	23.0 – 31.3	0.5 – 25.0	0.8 – 2000.0	0.01–1450.0	Costello <i>et al.</i> (2006)
Biscayne Bay (USA)	18.0 – 32.0	14.0 – 45.0	–	–	–	Kremer (1994)
Nueces Estuary (USA)	7.0 – 31.0	20.0 – 38.0	–	–	–	Kremer (1994)
Gulf of Mexico Valdés Peninsula (Argentina)	8.8 – 15.5	33.2	–	–	–	Haraldsson <i>et al.</i> (2013)
Northern Europe						
Baltic Sea	0.0 – 18.5	7.2 – 33.4	0.0 – 8.4	1.0 – 21.0	3.0 – 1235.0	Haraldsson <i>et al.</i> (2013)
Kiel Bight (Germany)	4.9 – 17.2	11.0 – 22.0	–	1.0 – 22.0	0.5 – 505.0	Javidpour <i>et al.</i> (2009a,b)
Limfjorden (Denmark)	15.6 – 21.1	22.2 – 27.8	0.0 – 8.0	0.0 – 22.0	0.5 – 867.0	Riisgard <i>et al.</i> (2012a,b)
North Sea (Germany)	10.0	30.0 – 33.0	–	–	0.1	Boersma <i>et al.</i> (2007)
Wadden Sea (Netherlands)	1.7 – 22.0	15.0 – 22.0	–	–	0.7 – 613.0	Van Walraven <i>et al.</i> (2013)
North Sea (Belgium)	9.5 – 23.2	13.6 – 36.0	< 13.0	–	0.01 – 18.4	Vaansteenbrugge <i>et al.</i> (2015)
English Channel (France)	5.5 – 20.2	29.7 – 34.9	–	–	0.01 – 1.7	Antajan <i>et al.</i> (2014)
Eastern Europe						
Black Sea (Russia)	2.1 – 27.0	1.2 – 22.3	0.47 – 1.32	–	12.4 – 304.0	Shiganova <i>et al.</i> (2019)
Azov Sea (Russia)	24.0 – 26.0	1.1 – 16.3	–	–	–	Haraldsson <i>et al.</i> (2013)
Caspian Sea (Iran)	10.0 – 31.0	10.0 – 13.0	0.9 – 40.9	1.0 – 21.0	3.0 – 1235.0	Roohi <i>et al.</i> (2008, 2010)
Marmara Sea (Turkey)	8.0 – 28.0	10.0 – 25.0	2.7 – 11.7	2.0 – 49.5	0.7 – 12.1	Isinibilir (2012)
Aegean Sea (Greece)	15 – 29.1	27.1 – 35.8	–	–	0.01 – 5.3	Gülsahin (2013)
Mediterranean Sea						
Adriatic Sea (Italy)	13 – 20	11 – 38	0.2 – 9.7	–	–	Malej <i>et al.</i> (2017)
Levantine Basin (Israel)	18.0 – 31.5	39.1 – 39.8	–	0.0 – 2.6	–	Fuentes <i>et al.</i> (2010)
Mar Menor Lagoon (Spain)	27.5 – 31.3	42.3 – 45.6	–	–	0.08 – 1.2	Marambio <i>et al.</i> (2013)
Catalan Sea (Spain)	20.8 – 25.3	37.0 – 37.9	–	–	–	Fuentes <i>et al.</i> (2010)
Biguglia Lagoon (France)	6.9 – 28.4	5.1 – 21.7	2.3 – 24.9	–	> 85.0	Delpy <i>et al.</i> (2016)
Berre Lagoon (France)	0.3 – 26.0	15.6 – 29.5	0.19 – 37.1	0.17 – 159.28	0 – 940	Marchessaux <i>et al.</i> (2020a)
Vaccarès Lagoon (France)	2.0 – 29.0	12 – 25	1.90 – 7.39	0.62 – 14.71	0 – 17	Marchessaux <i>et al.</i> (2020b)
Estomac Lagoon (France)	27.7	30	–	–	–	Marchessaux <i>et al.</i> (2020b)
Or Lagoon (France)	27.0	25	1.39	32.40	14.1	This study
Rhône-Sète Channel (France)	26.1	20	0.70	10.50	42.5	This study
Grec Lagoon (France)	27.1	31	3.10	8.10	28.3	This study
Pérois Lagoon (France)	28.1	30	1.24	8.30	10.4	This study
Vic Lagoon (France)	21.6	38	1.80	11.90	10.4	This study
Ingril Lagoon	20.0	41	0.39	19.50	0.9	This study

(France)								
Bages-Sigean Lagoon (France)	9 – 27 (26.6)	17 – 35 (19)	0.7 – 5 (0.79)	11.8 – 30 (24.05)	6.1 – 114 (5.7)			Delpy <i>et al.</i> (2016) (this study)
Salses-Leucate Lagoon (France)	26.6	27	0.62	27.75	7.1			This study

Figure 1. Distribution of *Mnemiopsis leidyi* in French Mediterranean lagoons along the Gulf of Lion.

Figure 2. Sampling stations and RSL (Réseau Suivi Lagunaire) monitoring stations. Legends in red: deep lagoons (> 2 m); in blue: shallow (< 2 m) mesohaline lagoons; in purple: shallow (< 2 m) poly- and euhaline lagoons.

Figure 3. Pictures of *Mnemiopsis leidyi* taken in the Or Lagoon in July 2020 (Photograph: Guillaume Marchessaux).

Figure 4. Physico-chemical dynamics of lagoons studied. (A) Temperature (°C), (B) salinity, (C) chlorophyll *a* concentration ($\mu\text{g L}^{-1}$) and (D) Zooplankton abundances (ind m^{-3}) measured in July 2020. Boxplot: datas extracted from “Survall” database, RSL monitoring program (IFREMER, <https://www.ifremer.fr/surval/>), and from FILMED monitoring program for Pissevaches Lagoon, black lines: mean. Red triangles: data measured in July 2020.

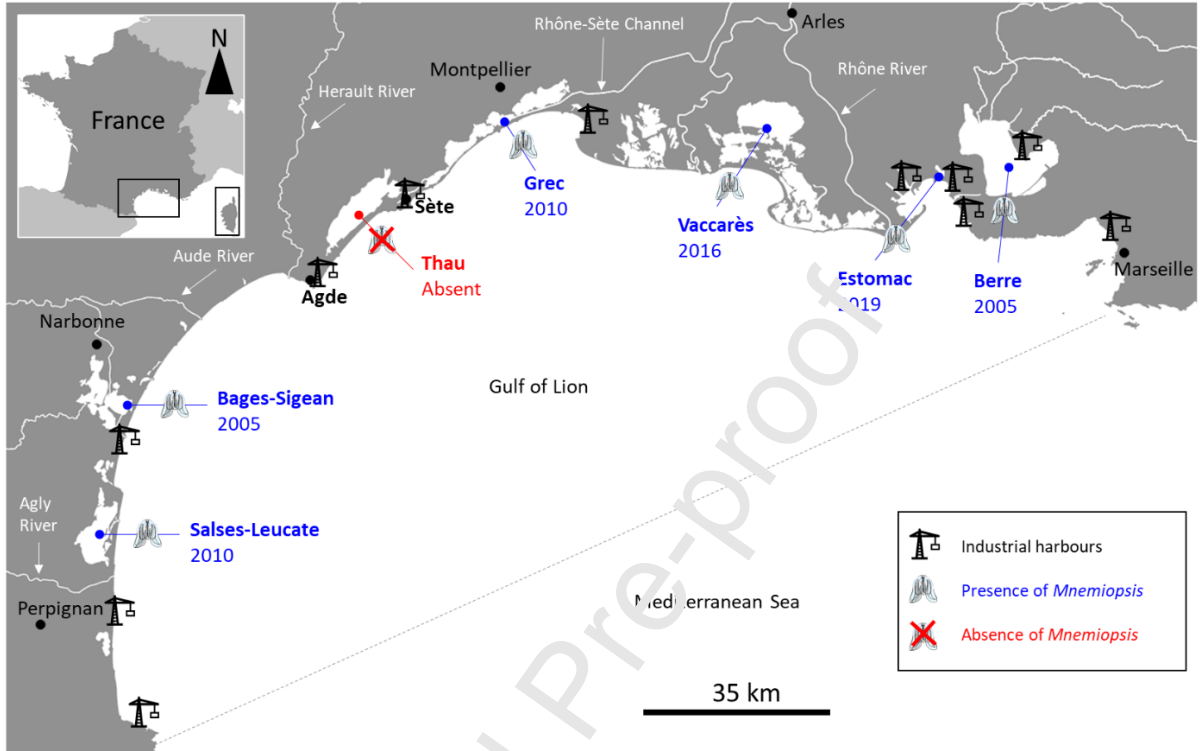
Figure 5. Revised distribution of *Mnemiopsis leidyi* in French Mediterranean lagoons.

Figure 6. Abundance (A) and oral-aboral length (B) of *Mnemiopsis leidyi* measured in July 2020.

Figure 7. Principal components analysis (PCA) on data from July 2020. (A) Projection of individuals and (B) correlation circle. Chlorophyll: chlorophyll *a* concentration ($\mu\text{g L}^{-1}$), Zooplankton: zooplankton abundance (ind m^{-3}), Mnemiopsis: *Mnemiopsis* abundance (ind m^{-3}), Temperature (°C). Colors represent hierarchical clustering.

Figure 8. Pictures of *Mnemiopsis leidyi* along the French Atlantic coast: Loire Estuary and Vilaine Estuary. Data collected from Mnemiop’See citizen program (See The Sea Production organization).

Figure 1.



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Figure 2.

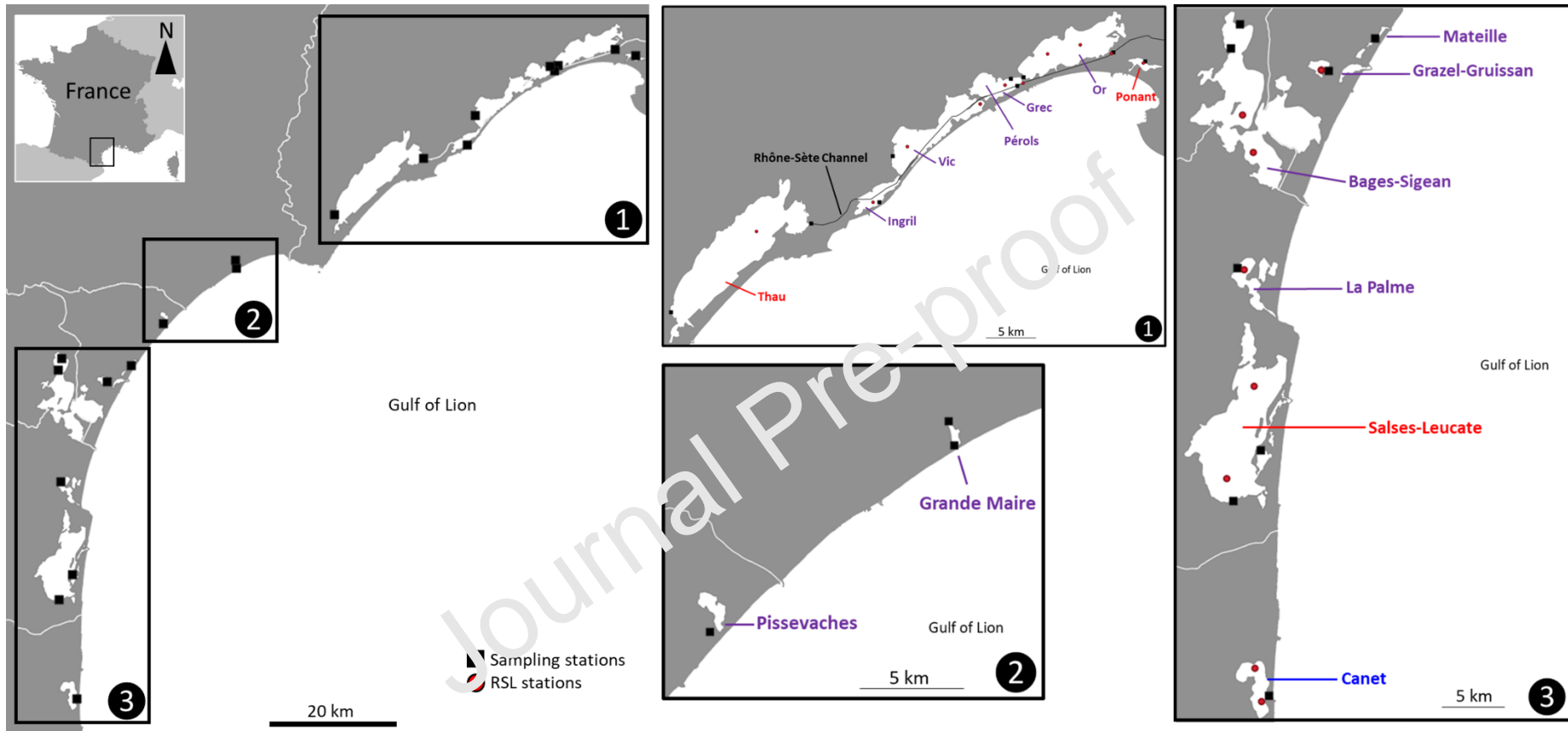


Figure 3.



Figure 4.

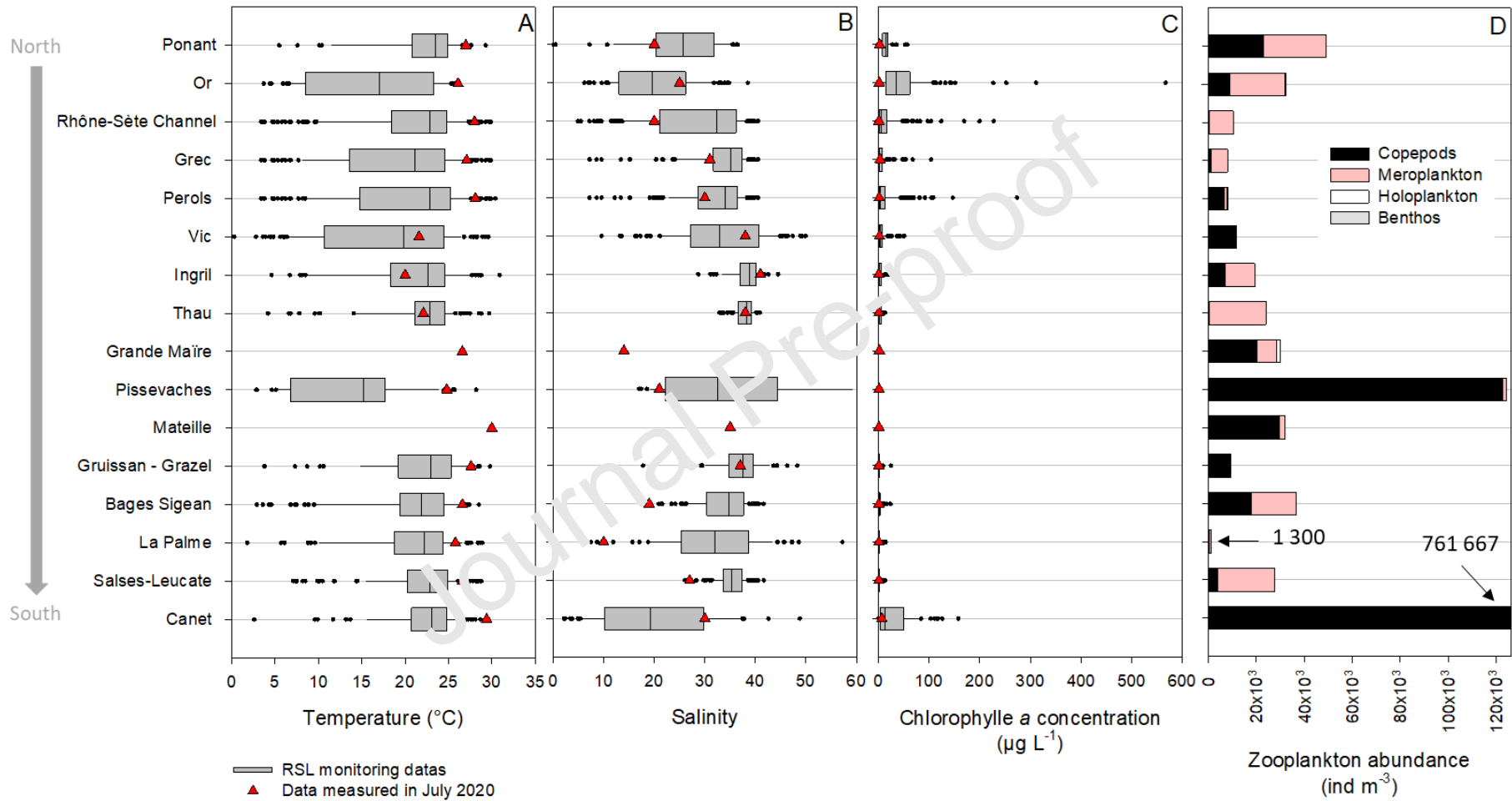


Figure 6.

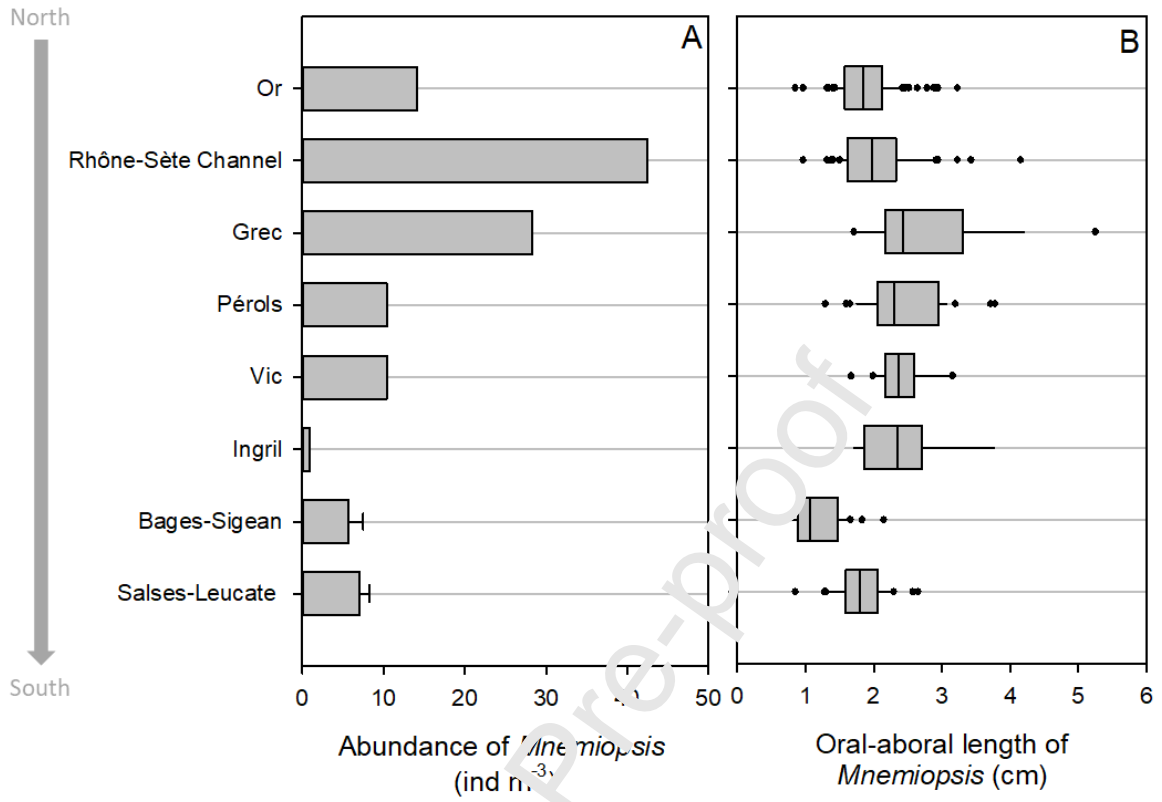


Figure 7.

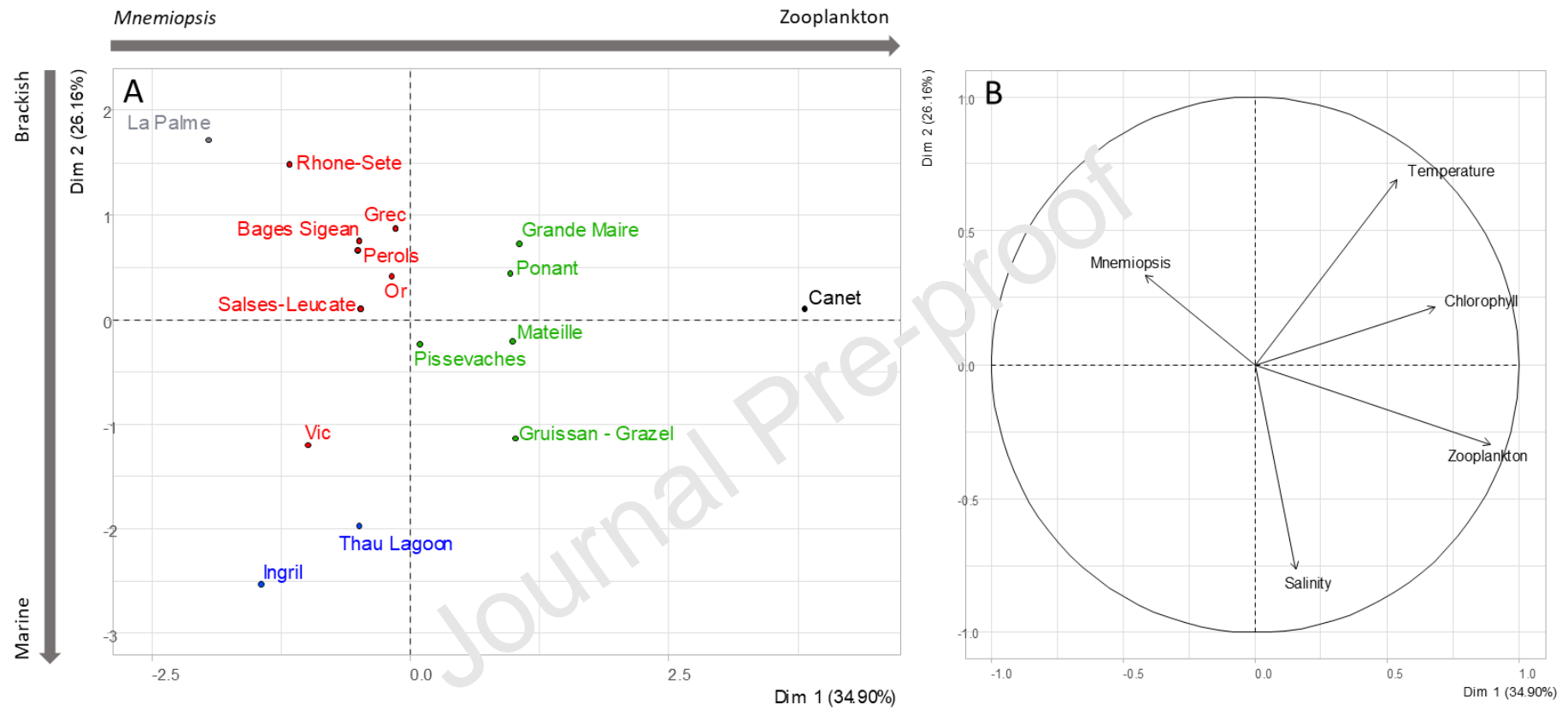
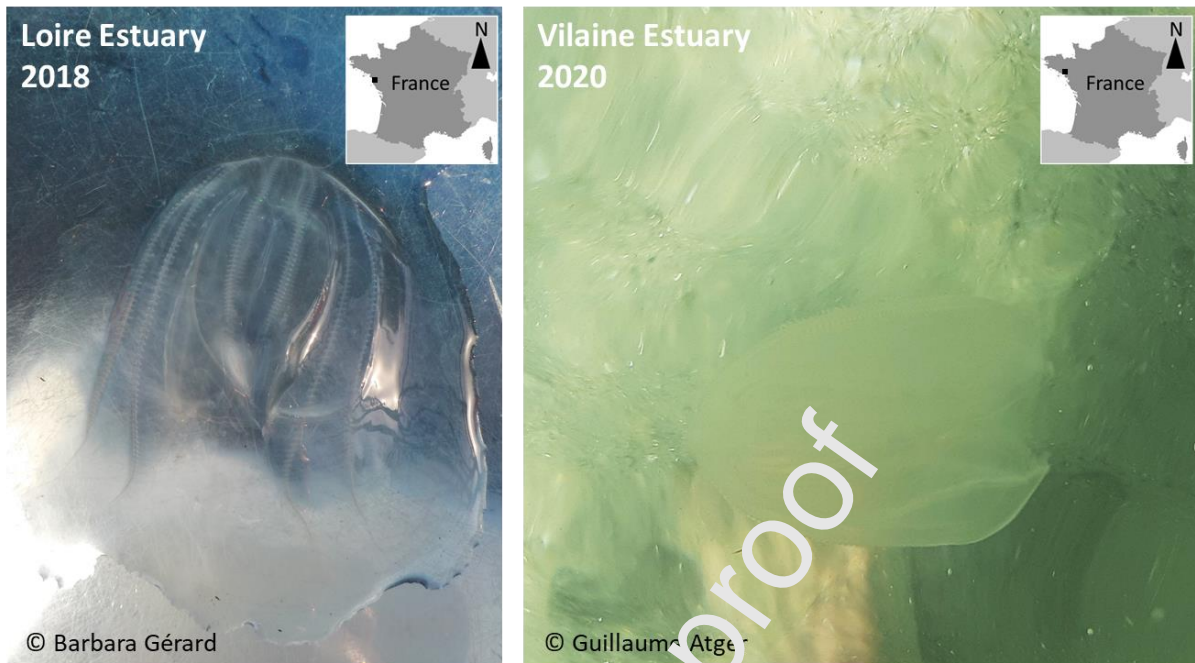


Figure 8.



Highlights

- Since 2019, many records of *Mnemiopsis leidyi* along the coast of the Gulf of Lion
- Field survey on the French Mediterranean coast was conducted in July 2020 to measure the expansion of the *Mnemiopsis*
- *Mnemiopsis leidyi* was present in 8 different areas: Or, Pérols, Vic, Ingril, Rhône-Sète Channel, Bages-Sigean, and Salses-Leucate