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Research Article

Presence of the introduced ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 in a lagoon system within the River Rhône delta (southeast France)Guillaume Marchessaux^{1,*}, Delphine Nicolas², Alain J. Crivelli², Silke Befeld³, Pascal Contournet² and Delphine Thibault¹¹Aix Marseille Univ, Univ Toulon, CNRS, IRD, MIO, Marseille, France²Tour du Valat, le Sambuc, F-13200, Arles, France³Société Nationale de Protection de la Nature, Réserve Naturelle Nationale de Camargue, La Capelière, 13200, Arles, France

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Abstract

The introduced ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 was observed in the Vaccarès Lagoon (River Rhône delta, southeast France) for the first time in 2016. Large blooms had been observed during the summer in 2016, with monthly zooplankton community monitoring carried out from November 2016 to October 2017. This was done to better understand the dynamics of this ctenophore within this brackish Lagoon. In parallel, we report the first record of *Mnemiopsis leidyi* in another Mediterranean lagoon near Camargue delta (Estomac Lagoon) in 2019.

Key words: invasive species, Mediterranean lagoons, introduced species, natural reserve**Introduction**

Non-indigenous species introduction in recipient ecosystems constitute a major source of biological pollution (Boudouresque and Verlaque 2002; Elliott 2003). As some of these species 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) (Gallardo et al. 2016).

The ctenophore *Mnemiopsis leidyi* has been ranked within the top 100 worst marine bio-invaders by the International Union for Conservation of Nature (IUCN; Lowe et al. 2000). 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. 2001a; Gallardo et al. 2016).

Mnemiopsis leidyi originates from estuaries and coastal waters along Atlantic coastlines from the Chesapeake Bay, USA, to Argentina (GESAMP 1997). Through ballast waters release, the species has spread the past 30 years over Eurasia (Costello et al. 2012; Jaspers et al. 2018a). *M. leidyi* was



Figure 1. French Mediterranean coastal systems where the ctenophore *Mnemiopsis leidyi* has already been observed.

Table 1. Locations of invaded lagoons in French Mediterranean coasts.

Date	Location	Latitude	Longitude	References
2005	Berre Lagoon	43.4592	5.1059	Delpy et al. 2012
2005	Bages-Sigean Lagoon	43.1054	2.9920	Delpy et al. 2016
2005	Biguglia Lagoon	42.6263	9.4649	Etourneau 2012
2009	Villefranche-sur-Mer bay	43.6994	7.3161	Fuentes et al. 2009
2009–2010	Salses-Leucate Lagoon	42.8584	2.9956	Delpy et al. 2016
2010	Le Grec Lagoon	43.5379	3.9433	Delpy et al. 2016
2011	Villepey Lagoon	43.4047	6.7171	Julien Caucat <i>pers. comm.</i>
2016	Vaccarès Lagoon	43.5353	4.6370	Present study
2019	Estomac Lagoon	43.4445	4.9536	Present study

observed with large wide ranges of temperature (0–31 °C), salinity (0.1–40 psu) and chlorophyll *a* concentrations (0.02–9.7 µg L⁻¹; Supplementary material Table S1) reflecting its high ecological tolerance. On the French Mediterranean coastlines, *M. leidyi* was first formally identified in the Berre Lagoon in 2005 (Figure 1, Table 1, Delpy et al. 2012). *Mnemiopsis* has been episodically present in six other Mediterranean lagoons (Figure 1, Table 1) but the first arrival of *M. leidyi* along French Mediterranean coastlines may have occurred much earlier.

Due to high productivity induced by brackish water, the Vaccarès Lagoon is in an emblematic French national reserve where high biodiversity is observed (i.e. birds nesting, fish nursery, etc.). But a lot of introduced invasive species are currently recorded (i.e. Louisiana crayfish *Procambarus clarkii*, *Ludwigia peploides*, Florida turtle *Trachemys scripta elegans*, etc.) and recently the ctenophore *Mnemiopsis leidyi*.

In this article, we report on the presence of *Mnemiopsis leidyi* in the Vaccarès Lagoon and on its variability in relation to environmental parameters. In order to better understand the ecology of *M. leidyi* within the Vaccarès Lagoon and to assess its environmental requirements, monthly monitoring was conducted from November 2016 to October 2017.

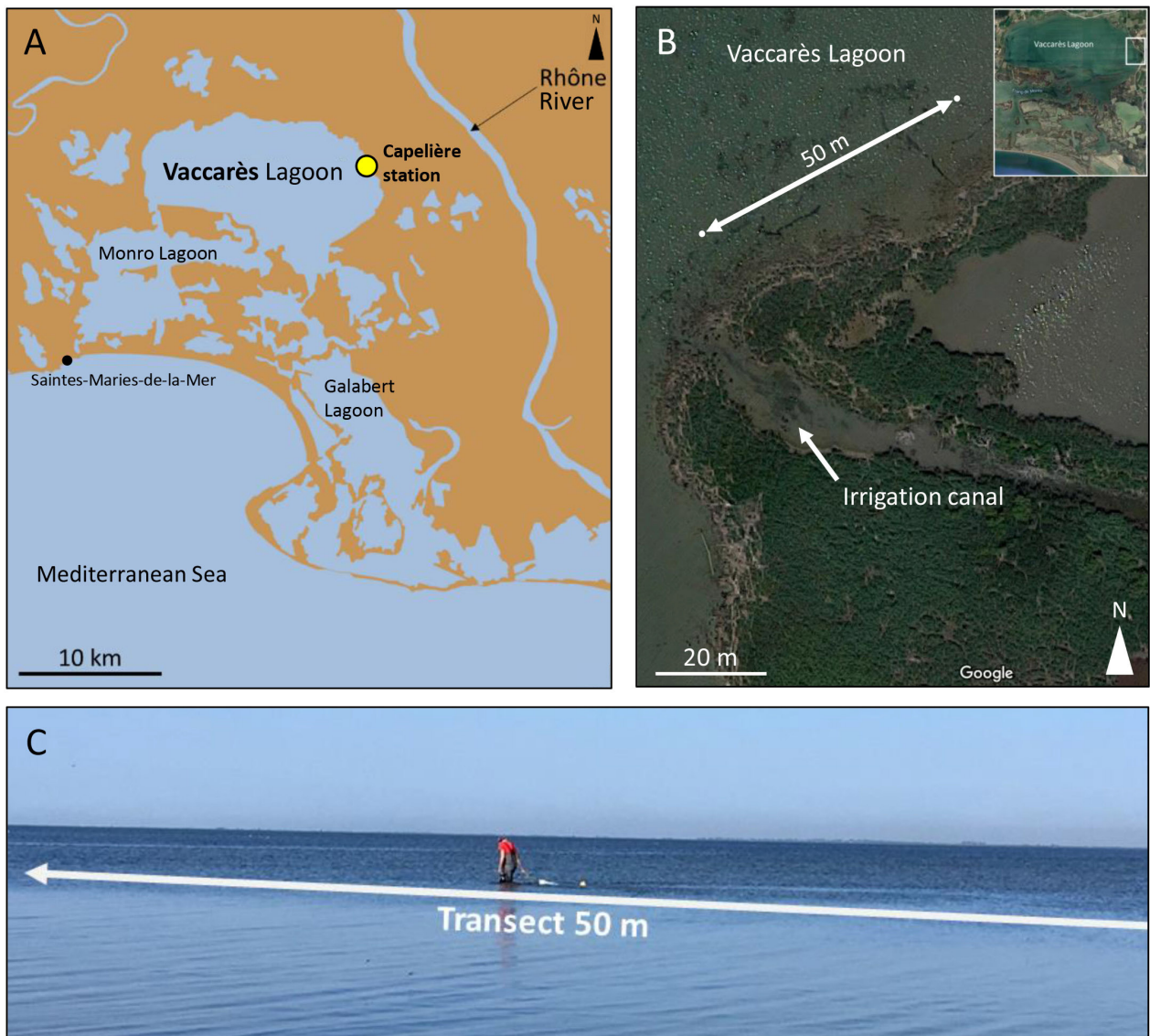


Figure 2. (A) Map of the network of lagoons in the National Natural Reserve of Camargue, sampling station, (B) aerial view of the sampling site (source: Google Earth), and (C) picture of sampling location. Yellow circle: sampling station “Capelière”. Photo by Bruno Belloni.

Materials and methods

The Vaccarès Lagoon, 6 500 ha, 2 m maximum depth, is in the center part of the Rhône River delta (South of France). It includes a protected area the National Natural Reserve of Camargue, which is managed by the National Society of Nature Protection (SNPN). Nonetheless, it is contaminated by agricultural runoff, especially during spring and summer seasons. Connections with the sea are distant (more than 5 km) and limited to narrow passages equipped with sluices.

Given the difficulty to access to the banks of the Vaccarès Lagoon (restricted access, siltation, quicksand, bird nesting areas) and the prohibition of motorboats, only the Capelière station was studied (Figure 2A; 43.5353°N; 4.6370°E).

From November 2016 to October 2017, once a month (except in July 2017), sampling of the zooplankton component was conducted (Table 2).

Table 2. Parameters measured during monthly monitoring of *Mnemiopsis leidyi* in the Vaccarès Lagoon In 2016–2017. T: temperature (°C), S: salinity (psu), Chl: chlorophyll *a* concentration ($\mu\text{g L}^{-1}$), P/A: presence (= 1) / absence (= 0) of *Mnemiopsis*.

Date	Latitude	Longitude	T	S	Chl	P/A
25 Nov. 2016	43.5353	4.6370	14	19	–	1
14 Dec. 2016	43.5353	4.6370	9	20	3,99	1
12 Jan. 2017	43.5353	4.6370	3	18	5,12	1
17 Feb. 2017	43.5353	4.6370	10	18	4,37	1
23 Mar. 2017	43.5353	4.6370	16	20	1,89	0
6 Apr. 2017	43.5353	4.6370	17	20	1,47	0
12 May 2017	43.5353	4.6370	17	20	6,69	0
15 June 2017	43.5353	4.6370	27	20	7,39	0
18 Aug. 2017	43.5353	4.6370	29	18	4,35	0
14 Sept. 2017	43.5353	4.6370	19	12	7,07	0
12 Oct. 2017	43.5353	4.6370	18	25	1,90	0

Due to the shallowness of the site and to the prohibition of motorboating, sampling was conducted by feet. Zooplankton and ctenophore were sampled using a conic net (80 μm mesh, 30 cm opening area, 1.2 m long). The operator was placed on the left side of the net to limit the influence of his movements. A round trip along a 50 m linear transect parallel to the banks, delimited by two sticks, was performed (Figure 2B, C). This operation was replicated (14.1 m^3 sampled). A total of 20 samples were analysed. Ctenophores were isolated and washed with filtered lagoon water. The total number of *M. leidyi* were counted, the whole sample was then preserved in buffered sea water-formalin solution (4% final concentration) for further zooplankton taxonomic identification. Just before each zooplankton transect, temperature was measured with a digital thermometer and salinity with a refractometer. 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 25 or 50 mL of water were filtered separately on GF/F (0.7 μm porosity). Filters were kept frozen ($-20\text{ }^\circ\text{C}$ until further analysis). Chlorophyll *a* was extracted using acetone (90%) and held in the dark at $-20\text{ }^\circ\text{C}$ overnight. The acidification method was used to measure chlorophyll *a* concentration according to Lorenzen (1967).

The Capelière station has long-term monitoring data for temperature, salinity, and chlorophyll *a* using the same method as previously mentioned. Monthly measures were provided by the SNPN from 2008–2016 for temperature/salinity and from 2008–2015 for chlorophyll *a*.

To identify which parameters influenced the ctenophores presence/absence, a principal component analysis (PCA) was performed using R 3.5.0, on monthly data for the sampling period 2016–2017. Groups of data were obtained by a hierarchical agglomerative clustering analysis

Additionally, in 2019, after a report by a naturalist (T. Mosca *pers. comm.*), ctenophore identifications were conducted in June 2019 by Guillaume Marchessaux in the Estomac Lagoon (southeast France). Individuals were sampled using a landing net, temperature and salinity were measured as explained above.

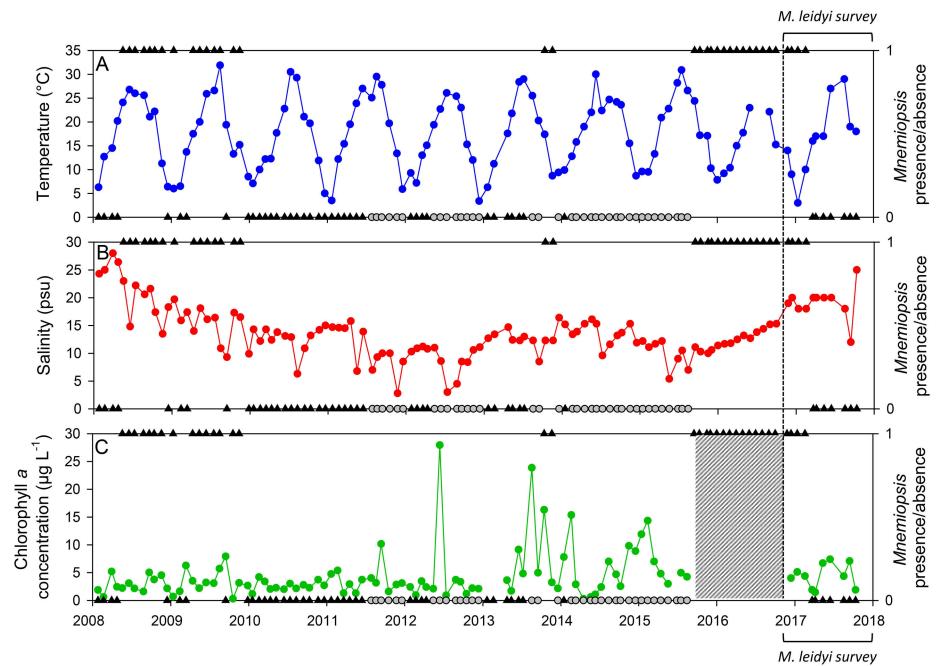


Figure 3. Monthly evolution of (A) temperature, (B) salinity and (C) chlorophyll *a* concentration ($\mu\text{g L}^{-1}$) in the Vaccarès Lagoon between January 2008 and 12 October 2017. Grey rectangle: no data. Black triangle: presence/absence of ctenophores. Grey circle: no data. Data between 2010–2016 produced by the SNPN/RNNC.

Results

The water temperature varied similar to established Mediterranean seasonal pattern with low temperatures in winter ($3\text{ }^{\circ}\text{C}$) and high temperatures in summer ($30\text{ }^{\circ}\text{C}$, Figure 3A, Table S1). During 2017, the minimum of $3\text{ }^{\circ}\text{C}$ was recorded in January and the maximum of $29\text{ }^{\circ}\text{C}$ in August (Figure 3A, Table 2).

The salinity in the Vaccarès Lagoon strongly varies over the years, depending highly on freshwater inflow (precipitations and especially agricultural pumping during the spring and summer seasons) and water management. Between 2008 and 2016, salinity have varied from 2.8 psu (November 2011) to 28 psu (March 2008; Figure 3B). During 2016–2017, the salinity remained between 12 psu (September 2017) and 25 psu (October 2017) but is generally stable between November 2016 and August 2017 ($19 \pm 1\text{ psu}$) (Figure 3B, Table 2), decreased in September ($S = 12\text{ psu}$) and an increase of 25 psu in October 2017.

Chlorophyll *a* concentration has remained low, especially during winter ($4.5 \pm 2.1\text{ }\mu\text{g Chla L}^{-1}$), except during some annual blooms such as in 2012 ($27.9\text{ }\mu\text{g Chla L}^{-1}$; 13 June 2012), 2013 ($23.8\text{ }\mu\text{g Chla L}^{-1}$; 18 August 2013), 2014 ($15.3\text{ }\mu\text{g Chla L}^{-1}$; 19 February 2014) and 2015 ($14.3\text{ }\mu\text{g Chla L}^{-1}$; 12 February 2015; Figure 3C, Table S2).

Zooplankton abundance, assessed during the 2016–2017 monitoring, ranged from $622\text{ individuals m}^{-3}$ (Nov. 2016) to $14\,710\text{ individuals m}^{-3}$ (Apr. 2017, Figure 4, Table 2). The diversity of the zooplanktonic community is low with only 6 identified species/genus of copepods (*Euterpina acutifrons* (Harpacticoids), *Harpacticus littoralis* (Harpacticoids), *Metis* spp. (Harpacticoids), *Eurytemora velox* (Calanoid), *Acartia* sp. (Calanoid) and

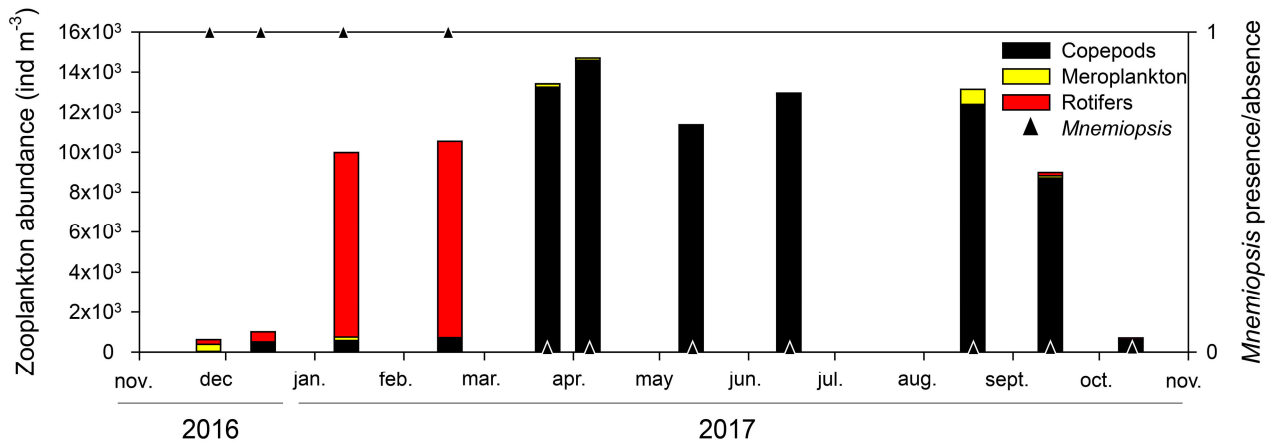


Figure 4. Evolution of zooplankton abundance (ind m^{-3}) and the contribution of each major zooplankton group between 25 November 2016 and 12 October 2017. Black triangle: presence/absence of ctenophores.

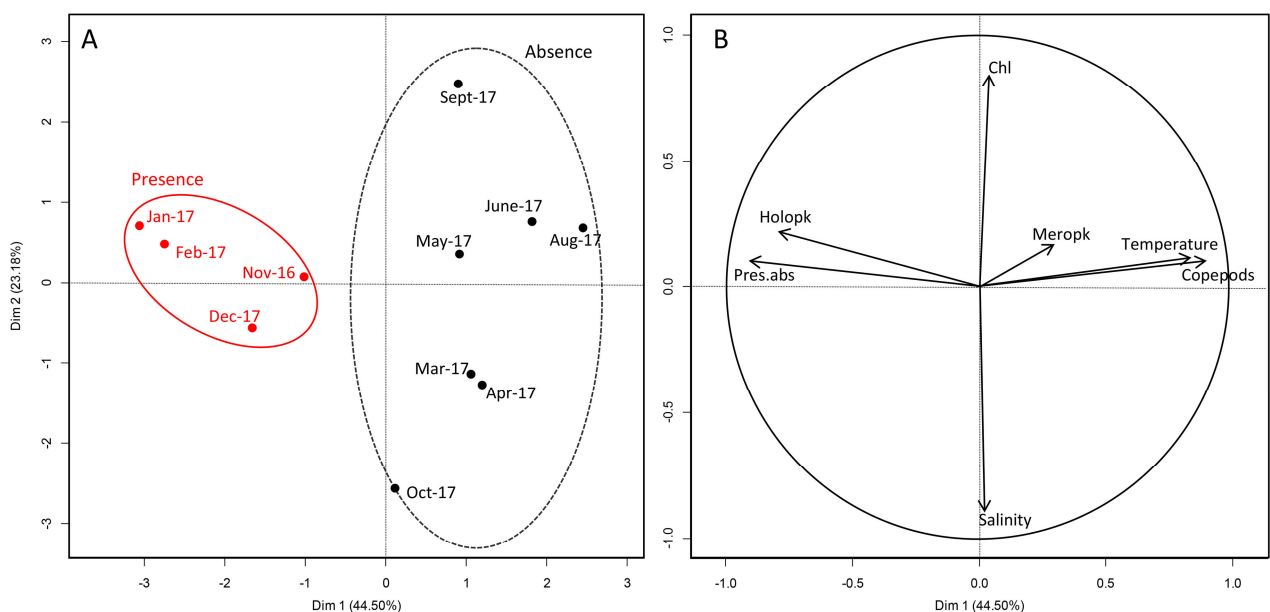


Figure 5. Principal components analysis (PCA) on data from 2016–2017. (A) Projection of individuals and (B) correlation circle. Chl: chlorophyll *a* concentration ($\mu\text{g L}^{-1}$), copepods: copepods abundance (ind m^{-3}), holopk: holoplankton abundance (ind m^{-3}), meropk: meroplankton abundance (ind m^{-3}), Pres.abs: presence/absence of *M. leidyi*, Salinity (psu), Temperature ($^{\circ}\text{C}$).

Thermocyclops sp. (Cyclopoid), 3 species/genus of rotifers (*Asplanchna* sp., *Hexarthra fennica*, *Notommata* sp.) and other reported taxa such as bivalves larvae, gastropods larvae, annelids larvae, eggs and fish larvae. Rotifers were mostly abundant during the winter, while copepods represented between 80.0% and 99.6% of the zooplankton community during the spring, summer and fall seasons.

M. leidyi has been observed between December 2016 and February 2017 (Table S2). Nonetheless, the presence of *M. leidyi* was reported present throughout all 2016, based on Tour du Valat scientific surveys and fishermen observations.

The hierarchical clustering performed on collected data dissociates two groups according to the presence or absence of *M. leidyi* in 2016–2017 (Figure 5). PCA showed that when *M. leidyi* was present in the Vaccarès

	January	February	March	April	May	June	July	August	September	October	November	December
1993			X	X	X		X	X	X	X		X
1994	X	X	X	X		X	X	X	X	X	X	X
1995	X	X	X	X	X	X			X	X		
1996	X	X	X	X	X	X	X	X	X	X	X	X
1997	X	X	X	X	X	X	X	X	X	X	X	X
1998	X	X	X	X	X	X	X	X	X	X	X	X
1999	X	X	X	X	X	X	X	X	X	X	X	X
2000	X	X	X	X	X	X	X	X	X	X	X	X
2001			X	X	X	X			X	X		
2002				X	X	X			X	X	X	
2003												
2004												
2005	X	X	X	X	X	X	X	X	X	X	X	X
2006	X	X	X	X	X	X	X	X	X	X	X	X
2007	X	X	X	X	X	X	X	X	X	X	X	X
2008	X	X	X	X	X	X	X	X	X	X	X	X
2009	X	X	X	X	X	X	X	X	X	X	X	X
2010	X	X	X	X	X	X	X	X	X	X	X	X
2011	X	X	X	X	X	X						
2012	X	X	X	X								
2013	X	X	X	X	X	X			X	X		
2014	X	X	X	X	X	X						
2015	X	X	X	X	X	X	X	X	X	X	X	X
2016	X	X	X	X	X	X	X	X	V	V	V	V
2017	V	V	V	V	V	V	V	V	V	V	V	V
2018	V	V	V	V	V	V	V	V	V	V	V	V
2019	V	V	V	V	V	V	V	V	V	V	V	V

Absence
 Presence
 No datas

V Confirmed observation from scientific sampling program
 X Unconfirmed observation by fishermen

Figure 6. Presence/absence of *M. leidyi* in scientific fishing nets at the Capelière within the Vaccarès Lagoon. Data produced by the Tour du Valat Research Institute laboratory (1993–2019).

Lagoon, the abundance of copepods decreased significantly primarily with holoplankton (i.e. rotifers) during winter periods. However, no correlation was observed with salinity and chlorophyll *a* concentration.

Discussion

In this study, we report the introduction of the invasive ctenophore *M. leidyi* in the Vaccarès Lagoon, which has been confirmed *in situ* by Guillaume Marchessaux for the first time in 2016. Our data from November 2016 to October 2017 showed that *Mnemiopsis* presence/absence was very variable in the Vaccarès Lagoon.

At the Capelière station, a long-term fish scientific survey had been initiated in 1993, using traditional passive fishing gear, called “capechade”, composed of a pound net and several fyke nets of 6 mm mesh size, that are commonly used by fishermen in lagoons. Through this survey the first observation was reported of gelatinous individuals that may correspond to *M. leidyi* in 1996 (Figure 6, Table S2). Unfortunately, no sample is available to confirm this report. However, since the first report, Tour du Valat has reported monthly on the presence or absence of the supposed *M. leidyi*, based on scientific surveys and fishermen observations. Fishermen and scientists described the gelatinous individuals with several details (presence of lobe, cilia, rainbow colors and body transparency) which tend to confirm that the individuals may have always corresponded to *Mnemiopsis leidyi*. Furthermore, any other species of gelatinous zooplankton (i.e. cnidarian, etc.) has been observed in the Vaccarès Lagoon.

Since its first possible appearance in 1993, *M. leidyi* presence in the Vaccarès Lagoon has rather been chaotic, being totally absent during relative long periods (from 1998 to 2000, 2005 and 2010), and sometimes present all year round (in 2015, Figure 6, Table S2). *Mnemiopsis* has been present all of 2016 (Figure 6) but absent in 2017 and early 2018. Last observations showed that *Mnemiopsis* was present between June 2018 and December 2018, and in October and November 2019 (Figure 6, Table S2).

In our study, given the difficulties of access to the lagoon and high-water turbidity, it was difficult to quantify ctenophores abundances. We suggest to attach plankton net on sticks to sample passively zooplankton and ctenophores and longer sampling periods (1 hour for example) a biggest net (Regent net, 70 cm opening area for example) to quantify ctenophores abundances. Additionally, even if rotifers measured $\sim 100 \mu\text{m}$, the use of the $80 \mu\text{m}$ meshed net could be not appropriate to quantify these organisms. Then, we suggest use of $60 \mu\text{m}$ meshed net in future studies.

As reported in the literature, salinity and temperature are determining factors for the maintenance of ctenophores. The records of *M. leidyi* at temperatures ranging from 3 to 29 °C and salinity from 5 to 25 psu are consistent with the eurythermal and euryhaline tolerances of this ctenophore. *M. leidyi* has indeed been shown to survive in salinity from 5 to 40 psu (Kremer 1994; Purcell et al. 2001b). Even though *M. leidyi* has been shown to survive in extreme salinity and temperature ranges, reproduction rates under low salinity levels (< 10 psu) have been reported. Extremely low salinity and low temperature may explain its limited range expansion in Northern Europe (Jaspers et al. 2011, 2018b). In the Vaccarès Lagoon, ctenophore presence appeared to increase when the salinity is over 20 psu (Figure 3B).

To compare with other Mediterranean lagoons, chlorophyll *a* concentrations measured in our monthly study ($1.5\text{--}7.4 \mu\text{g L}^{-1}$) were lower than observed in the Berre Lagoon ($0.9\text{--}24.6 \mu\text{g L}^{-1}$; Delpy et al. 2016) and in the same range as Bages-Sigean Lagoon ($0.3\text{--}4.7 \mu\text{g L}^{-1}$; Delpy et al. 2016). In our study, chlorophyll *a* concentration did not influence ctenophores presence/absence as observed by Delpy et al. (2016). *Mnemiopsis leidyi* was observed in the Vaccarès Lagoon for chlorophyll *a* concentration from $3.9 \mu\text{g L}^{-1}$ to $5.12 \mu\text{g L}^{-1}$, whereas it was absent in our sampling for chlorophyll range from $1.5 \mu\text{g L}^{-1}$ to $7.1 \mu\text{g L}^{-1}$. In our results, chlorophyll *a* concentration does not influence *Mnemiopsis* present/absence. More data will be needed to confirm this hypothesis especially as *Mnemiopsis* is an omnivorous organism, then phytoplankton could play an important role in its growth (Deason and Smayda 1982).

The presence of this gelatinous zooplankton species may have a strong impact on zooplankton community function as it has been observed in the Black Sea (Shiganova et al. 2019). The presence of this introduced species and its high predation pressure in a national protected area could have a negative impact on the biodiversity (e.g. fish, mussels, etc.) (Shiganova et al.



Figure 7. Photographs of *Mnemiopsis leidyi* in the Estomac Lagoon in June 2019. Photos by Guillaume Marchessaux.

2019 and references within). In the Berre Lagoon and in the Black Sea meroplankton and rotifers were more predated by ctenophores than copepods (Rapoza et al. 2005; Marchessaux 2019). In the Vaccarès Lagoon it would be the reverse: low abundances of copepods were observed in the lagoon when *M. leidyi* was present suggesting a potential high ctenophores predation pressure on copepods.

In the Berre Lagoon, the population of *M. leidyi* was maintained during the 2010 to 2017 despite variable conditions: temperatures ranging from 3 to 28 °C, salinities from 10 to 30 psu, and a quantity of carbon available around 3 mgC L⁻¹ or more (Delpy et al. 2012, 2016; Marchessaux 2019). In the Vaccarès Lagoon, *M. leidyi* does not seem to be permanently established in the Camargue. The introduction pattern of *M. leidyi* by cargo ships result from trans-Atlantic (e.g. East coast of Mexico and USA) and local ship transits

Table 3. Locations of surveys conducted in June 2019 in Estomac Lagoon (south France).

Date	Latitude	Longitude	Temperature	Salinity	Ctenophores size	Number of organisms
12 June 2019	43.4445	4.9536	26.2	30	7–10 cm	30
26 June 2019	43.4445	4.9536	27.7	29	> 10 cm	200

within the Mediterranean Sea (Bolte et al. 2013; Ghabooli et al. 2013). As no maritime traffic occurs in the Camargue area (i.e. natural reserve) its presence may probably result from regular reintroductions. Advection processes and natural transport (drift, internal circulation) are certainly a vector of secondary spread of *M. leidyi* from closed lagoons such as the Berre Lagoon as observed by Jaspers et al. (2018a). Currents and artificial canals between the Berre and other lagoons may be vectors of *M. leidyi* expansion.

Recently, January 2019 *M. leidyi* was observed in the Estomac Lagoon (Fos sur Mer, south France) near the Berre Lagoon but not connected to its (Thierry Mosca *pers. comm.*). In June 2019, ctenophores measured between 7 cm and 10 cm long (Figure 7, Table 3). The lagoon temperature was between 26.2 °C and 27.7 °C and salinity between 29–30 psu. In early June 2019, 30 individuals were observed but, 200 were identified by 26 June 2019.

In conclusion, the present study reports that the alien ctenophore *M. leidyi* has been present along the French lagoon ecosystems since at least 2005 (in the Berre Lagoon), and probably earlier. Long-term monitoring with population genetic investigations are needed to address source-sink dynamics of this species along the Mediterranean coastlines.

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References

- Bolte S, Fuentes V, Haslob H, Huwer B, Thibault-Botha D, Angel D, Galil B, Javidpour J, Moss AG, Reusch TB (2013) Population genetics of the invasive ctenophore *Mnemiopsis leidyi* in Europe reveal source-sink dynamics and secondary dispersal to the Mediterranean Sea. *Marine Ecology Progress Series* 485: 25–36, <https://doi.org/10.3354/meps10321>
- Boudouresque CF, Verlaque M (2002) Biological pollution in the Mediterranean Sea: invasive versus introduced macrophytes. *Marine Pollution Bulletin* 44: 32–38, [https://doi.org/10.1016/S0025-326X\(01\)00150-3](https://doi.org/10.1016/S0025-326X(01)00150-3)
- Condon RH, Steinberg DK (2008) Development, biological regulation, and fate of ctenophore blooms in the York River estuary, Chesapeake Bay. *Marine Ecology Progress Series* 369: 153–168, <https://doi.org/10.3354/meps07595>
- Costello JH, Bayha KM, Mianzan HW, Shiganova TA, Purcell JE (2012) Transitions of *Mnemiopsis leidyi* (Ctenophora: Lobata) from a native to an exotic species: a review. *Hydrobiologia* 690: 21–46, <https://doi.org/10.1007/s10750-012-1037-9>
- Deason EE, Smayda TJ (1982) Experimental evaluation of herbivory in the ctenophore *Mnemiopsis leidyi* relevant to ctenophore-zooplankton-phytoplankton interactions in Narragansett Bay, Rhode Island, USA. *Journal of Plankton Research* 4: 219–236, <https://doi.org/10.1093/plankt/4.2.219>
- Delpy F, Pagano M, Blanchot J, Carlotti F, Thibault-Botha D (2012) Man-induced hydrological changes, metazooplankton communities and invasive species in the Berre Lagoon (Mediterranean Sea, France). *Marine Pollution Bulletin* 64: 1921–1932, <https://doi.org/10.1016/j.marpolbul.2012.06.020>

- Delpy F, Albouy-Boyer S, Pagano M, Thibault D, Blanchot J, Guilhaumon F, Molinero JC, Bonnet D (2016) Identifying the drivers of abundance and size of the invasive ctenophore *Mnemiopsis leidyi* in Northwestern Mediterranean lagoons. *Marine Environmental Research* 119: 114–125, <https://doi.org/10.1016/j.marenvres.2016.05.026>
- Elliott M (2003) Biological pollutants and biological pollution—an increasing cause for concern. *Marine Pollution Bulletin* 46: 275–280, [https://doi.org/10.1016/S0025-326X\(02\)00423-X](https://doi.org/10.1016/S0025-326X(02)00423-X)
- Etourneau S (2012) Cartographie des peuplements et types de fonds de l'étang de Biguglia. Département de la Haute-Corse - Service de la réserve naturelle de l'étang de Biguglia, 35 pp
- Fuentes VL, Atienza D, Gili JM, Purcell JE (2009) First records of *Mnemiopsis leidyi* A. Agassiz 1865 off the NW mediterranean coast of Spain. *Aquatic Invasions* 4: 671–674, <https://doi.org/10.3391/ai.2009.4.4.12>
- Gallardo B, Clavero M, Sánchez MI, Vilà M (2016) Global ecological impacts of invasive species in aquatic ecosystems. *Global Change Biology* 22: 151–163, <https://doi.org/10.1111/gcb.13004>
- GESAMP (1997) Opportunistic settlers and the problem of the ctenophore *Mnemiopsis leidyi* invasion in the Black Sea. GESAMP Reports and Studies 58. International Maritime Organization, London, 84 pp
- Ghabooli S, Shiganova TA, Briski E, Piraino S, Fuentes V, Thibault-Botha D, Angel DL, Cristescu ME, MacIsaac HJ (2013) Invasion pathway of the ctenophore *Mnemiopsis leidyi* in the Mediterranean Sea. *PLoS ONE* 8: e81067, <https://doi.org/10.1371/journal.pone.0081067>
- Jaspers C, Møller L, Kjørboe T (2011) Salinity gradient of the Baltic Sea limits the reproduction and population expansion of the newly invaded comb jelly *Mnemiopsis leidyi*. *PLoS ONE* 6: 1–6, <https://doi.org/10.1371/journal.pone.0024065>
- Jaspers C, Møller LF, Kjørboe T (2015) Reproduction rates under variable food conditions and starvation in *Mnemiopsis leidyi*: significance for the invasion success of a ctenophore. *Journal of Plankton Research* 37: 1011–1018, <https://doi.org/10.1093/plankt/fbv017>
- Jaspers C, Huwer B, Antajan E, Hosia A, Hinrichsen H-H, Biastoch A, Angel D, Asmus R, Augustin C, Bagheri S, Beggs SE, Balsby TJS, Boersma M, Bonnet D, Christensen JT, Dänhardt A, Delpy F, Falkenhaus T, Finenko G, Fleming NEC, Fuentes V, Galil B, Gittenberger A, Griffin DC, Haslob H, Javidpour J, Kamburska L, Kube S, Langenberg VT, Lehtiniemi M, Lombard F, Malzahn A, Marambio M, Mihneva V, Møller LF, Niermann U, Isinibilir Okyar M, Özdemir ZB, Pitois S, Reusch TBH, Robbens J, Stefanova K, Thibault D, van der Veer HW, Vansteenberghe L, van Walraven L, Wozniczka A (2018a) Ocean current connectivity propelling the secondary spread of a marine invasive comb jelly across western Eurasia. *Global Ecology and Biogeography* 27: 814–827, <https://doi.org/10.1111/gcb.12742>
- Jaspers C, Marty L, Kjørboe T (2018b) Selection for life-history traits to maximize population growth in an invasive marine species. *Global Change Biology* 24: 1164–1174, <https://doi.org/10.1111/gcb.13955>
- Kremer P (1994) Patterns of abundance for *Mnemiopsis* in U.S. coastal waters: a comparative overview. *ICES Journal of Marine Science* 51: 347–354, <https://doi.org/10.1006/jmsc.1994.1036>
- Lorenzen C (1967) Determination of chlorophyll and phaeopigments: spectrophotometric equations. *Limnology and Oceanography* 12: 343–346, <https://doi.org/10.4319/lo.1967.12.2.0343>
- Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the world's worst invasive alien species: a selection from the global invasive species database (Vol. 12). Auckland, New Zealand: Invasive Species Specialist Group
- Marchessaux G (2019) Etude de l'anthroposystème emblématique de l'étang de Berre: approches écosystémique et sociologique de l'impact du cténaire invasif *Mnemiopsis leidyi*. PhD Thesis, Aix-Marseille University, France, 386 pp
- Purcell JE, Decker MB (2005) Effects of climate on relative predation by scyphomedusae and ctenophores on copepods in Chesapeake Bay during 1987–2000. *Limnology and Oceanography* 50: 376–387, <https://doi.org/10.4319/lo.2005.50.1.0376>
- Purcell JE, Graham WM, Dumont HJ (eds) (2001a) Jellyfish blooms: ecological and societal importance. Proceedings of the International Conference on Jellyfish Blooms, held in Gulf Shores, Alabama, USA, 12–14 January 2000. *Hydrobiologia* 451, 333 pp, <https://doi.org/10.1007/978-94-010-0722-1>
- Purcell JE, Shiganova TA, Decker MB, Houde ED (2001b) The ctenophore *Mnemiopsis* in native and exotic habitats: US estuaries versus the Black Sea basin. *Hydrobiologia* 451: 145–176, https://doi.org/10.1007/978-94-010-0722-1_13
- Rapoza R, Novak D, Costello JH (2005) Life-stage dependent, in situ dietary patterns of the lobate ctenophore *Mnemiopsis leidyi* Agassiz 1865. *Journal of Plankton Research* 27: 951–956, <https://doi.org/10.1093/plankt/fbi065>
- Shiganova TA, Sommer U, Javidpour J, Molinero JC, Malej A, Kazmin AS, Isinibilir MOI, Christou E, Siokou-Frangou I, Marambio M, Fuentes V, Mirsoyan ZA, Gülsahin N, Lombard F, Lilley MKS, Angel DL, Galil BS, Bonnet D, Delpy F (2019) Patterns of invasive ctenophore *Mnemiopsis leidyi* distribution and variability in different recipient environments of the Eurasian seas: A review. *Marine Environmental Research* 152: 104791, <https://doi.org/10.1016/j.marenvres.2019.104791>

Supplementary material

The following supplementary material is available for this article:

Table S1. Temperature (T, °C), salinity (S, psu), and chlorophyll *a* concentration (Chl, µg L⁻¹) ranges in invaded areas by *Mnemiopsis leidyi*.

Table S2. Parameters conditions and ctenophores presence/absence in the Vaccarès Lagoon between 1993 and 2019.

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