Research Article

Invasion along the French Atlantic coast by the non-native, carnivorous planktonic comb jelly *Mnemiopsis leidyi*: can an impact on shellfish farming be expected?

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Abstract

The distribution range of the American comb jelly *Mnemiopsis leidyi* has expanded across Europe for several decades, particularly in the eastern Atlantic and Mediterranean Sea. This study aims to assess its expansion along the French Atlantic coast, mainly in the Bay of Biscay and Iroise Sea, since the first record in 2014. *Mnemiopsis leidyi* is now clearly established along 500 km of coastline, from the coast of Lorient to Arcachon Bay, which is the southernmost colonised area in the eastern Atlantic to date. It will likely colonise the Spanish Gulf coast in the near future through natural dispersal via currents, as has occurred between the Gironde estuary and Arcachon Bay. We quantify that this species now colonises nearly 45% of the French coastline. The invaded area includes the main estuaries of the Seine, Loire, Gironde and Rhône rivers, where *M. leidyi* populations may constitute reservoirs for colonising other harbours through merchant vessel traffic via ballast water. Finally, the Marennes-Oléron Bay and Arcachon Bay are the two main spat-producing regions for the Pacific oyster *Magallana gigas* in France. As *M. leidyi* consumes bivalve larvae, the potential economic and ecological impacts on this shellfish industry are discussed.

Key words: alien species; gelatinous plankton; invasion dynamics; ballast water

Introduction

The ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 is a gelatinous plankton species native to the eastern coasts of the Americas. Its range extends from the NE USA coast to Argentina (Gesamp 1997). It was introduced in the early 1980s in the Black Sea and Azov Sea probably through shipping via ballast water (Pereladov 1988; Jaspers et al. 2021). *Mnemiopsis leidyi* has been partially responsible for several economic and ecological disasters in areas where it has invaded, especially for fisheries of zooplanktivorous fish, such as anchovies and the Mediterranean horse mackerel (Purcell et al. 2001; Shiganova et al. 2001; Oguz et al. 2008).

This species has many life-history traits that ensure its success in colonizing new habitats (Costello et al. 2012; Jaspers et al. 2018b; Shiganova 2020). Its reproduction is optimized due to a high reproductive rate that can exceed 14,000 eggs per individual per day (Kremer 1976a, b; Malej et al. 2017), a rapid sexual maturity with larvae able to reproduce (Martindale 1987) and a capacity for self-fertilization (Sasson and Ryan 2016). Finally, it has strong ecological plasticity for most environmental parameters such as temperature, salinity and oxygen (Costello et al. 2012). In theory, a single individual can start a new population if conditions are favorable.

The reasons outlined in the previous paragraph explain why *M. leidyi* is listed among the 100 worst invasive species in the world (Lowe et al. 2000). Its establishment is considered as one of the most dramatic environmental events to have taken place in the Black Sea (Kideys 2002). Although already widespread, Carboneras et al. (2018) identified *M. leidyi* as a high priority species for risk assessment in the European Union to be included in EU Invasive Alien Species (IAS) list (EU regulation 1143/2014). Despite its "massive" impact (according to the EICAT classification (Hawkins et al. 2015), *M. leidyi* has yet to be added to the list of IAS of Union concern.

The species has spread from the Black Sea to both the eastern and western basins of the Mediterranean Sea and Adriatic Sea (Costello et al. 2012). A second introduction in Europe probably took place in the Wadden Sea in the early 2000s (Faasse and Bayha 2006), after which individuals then spread southward until they reached the northern coast of France (Reusch et al. 2010; Ghabooli et al. 2013; Jaspers et al. 2018a). In France, *M. leidyi* is present in the English Channel, North Sea (Antajan et al. 2014) and most Mediterranean lagoons (Marchessaux and Belloni 2021). Its expansion along the French Atlantic coast continues since it has been frequently reported for several years in the Bay of Biscay (Jaspers et al. 2018a). However, it is still absent from the Atlantic coasts of Spain and Portugal.

The Bay of Biscay is the leading French region for bivalve exploitation, mainly the Pacific oyster *Magallana gigas* (Thunberg, 1793) and the blue mussel *Mytilus edulis* Linnaeus 1758, accounting for approximately 1400 shellfish farming companies (Agrest 2019). Considering that *M. leidyi* is a voracious species and an important zooplankton predator, it is also possible that its establishment represents an additional threat for this industry through the predation of bivalve larvae. In this context, the aim of this study was to document the spread of *M. leidyi* along the French Atlantic coast and to discuss its potential risks regarding socio-economic activities in the area.

Materials and methods

Study site

This survey was carried out along approximately 1,200 km of French Atlantic coastline (Figure 1). The coasts of the southern English Channel,

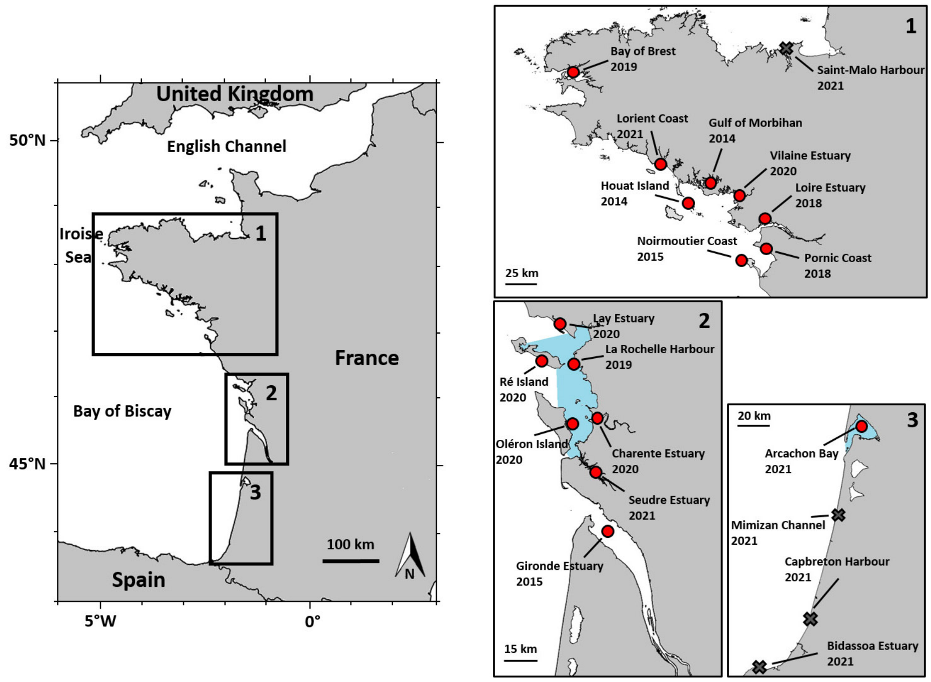

Figure 1. Sampling site records of *Mnemiopsis leidyi* presence (red circles) and absence (dark crosses) along the French Atlantic coast. Main oyster spat production areas are depicted in blue. The year under each site name corresponds to the date of the first record when the species was confirmed or to the most recent sampling date when the species as absent. See Table 1 for details.

Table 1. Records of *Mnemiopsis leidyi* in the Bay of Biscay and Iroise Sea listed from North to South. When several observations were made in the same area, only the first record is shown. See Table S1 for a full list of observations and details.

Location	Date of first record	Latitude	Longitude	Number of organisms observed	References
Bay of Brest	2019	48.356916	−4.507798	1 individual	This study
Lorient Coast	2021	47.697297	−3.454945	1 individual	This study
Morbihan Gulf	2014	47.577500	−2.749400	> 10	Le Roux 2018; Jaspers et al. 2018a
Vilaine Estuary	2020	47.405756	−2.490371	> 500	Marchessaux and Belloni 2021
Houat Island	2014	47.400666	−2.992555	2 individuals	Jaspers et al. 2018a
Loire Estuary	2018	47.332457	−2.008227	> 500	Marchessaux and Belloni 2021
Pornic Coast	2018	47.105201	−2.093434	> 500	This study
Noirmoutier Coast	2015	46.991671	−2,308722	2 individuals	Jaspers et al. 2018a
Lay Estuary	2019	46.305833	−1.284722	> 150	This study
La Rochelle, commercial harbour	2019	46.157778	−1.217771	5.8 ind.100m^{-3}	This study
Ré Island	2020	46.176389	−1.395833	> 150	This study
Oléron Island	2020	45.921389	−1.180028	0.7 ind.m^{-3}	This study
Charente Estuary	2020	45.951667	−1.066667	> 50	This study
Seudre Estuary	2021	45.710556	−0.975833	> 500	This study
Gironde Estuary	2015	45.516400	−0.957800	5 individuals	Jaspers et al. 2018a
Arcachon Bay	2021	44.751389	−1.123889	> 500	This study

Iroise Sea and northern Bay of Biscay have numerous bays and small coastal rivers, whereas the southern part of the Bay of Biscay is mainly a straight, sandy linear coast with far fewer bays and rivers. The main estuary is the Gironde Estuary, which is the confluence of the Dordogne and Garonne rivers. It is considered one of the main European estuaries, with a width of 12 km at its mouth and a mean annual discharge of 1,000 m^3 s^{-1} (Sottolichio and Castaing 1999). The second main estuary is the Loire, the longest French river of about 1,000 km, with a mean annual discharge of

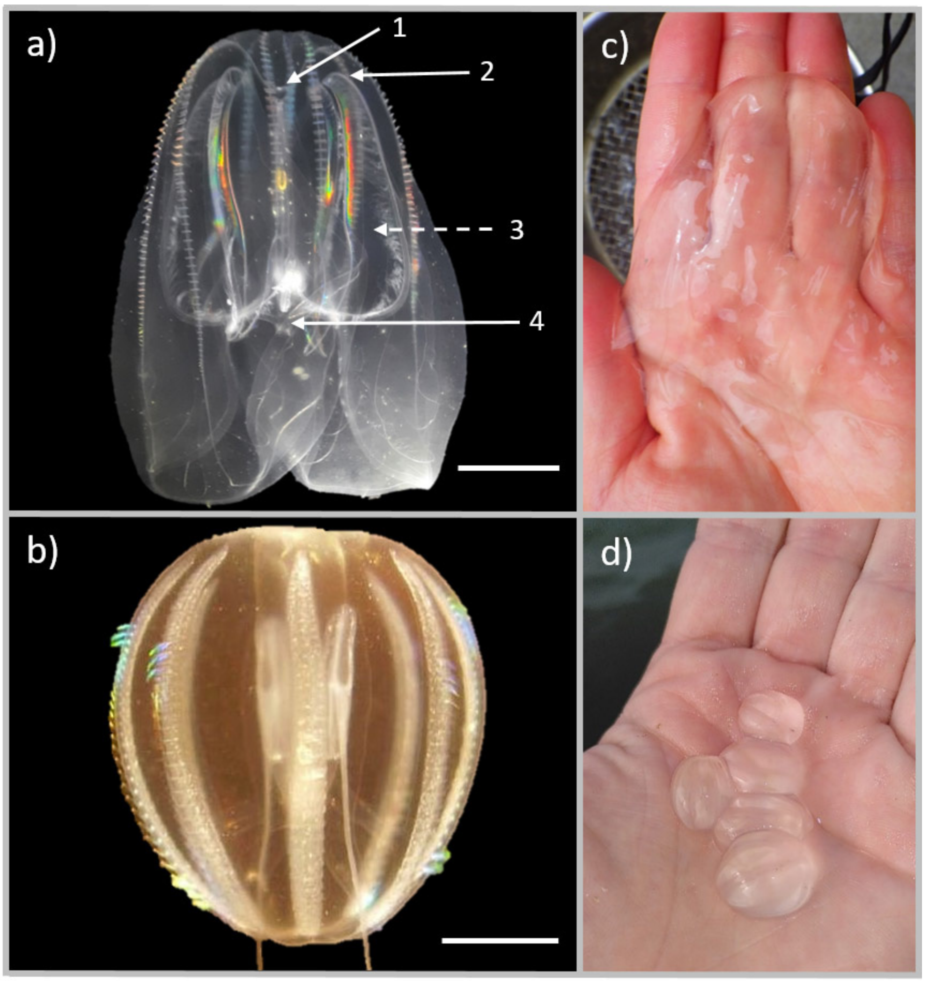

Figure 2. *Mnemiopsis leidyi* (a, c) and *Pleurobrachia pileus* (b, d) in water (a, b) and out of water (c, d). Scale bar 1 cm (a) and 5 mm (b). (1) statocyst; (2) termination of the lobes for *M. leidyi* and (3) for *Bolinopsis* sp. (4) mouth. Photographs: A. Nowaczyk (a, d); D. Vincent (b); C. Massé (c).

850 $m^3 s^{-1}$ (Hydro-Portail 2022). Finally, Arcachon Bay is the largest semi-enclosed estuarine lagoon in Europe, with an area of 155 km^2.

Mnemiopsis leidyi *identification*

Mnemiopsis leidyi A. Agassiz, 1865 is a species of lobate ctenophore, reaching up to 12 cm. The positions of the statocyst and the aboral termination of the lobes differentiate *M. leidyi* from other lobed ctenophores (Figure 2a). On the French Atlantic coasts, it can be confused with a rarely occurring lobate ctenophore species *Bolinopsis infundibulum* (O.F. Müller, 1776). Its lobes terminate near the mouth, whereas for *M. leidyi* the lobes extend to the statocyst (see fig. 2 in Faasse and Bayha 2006). There is also another indigenous ctenophore species that is sometimes very abundant in this area, *Pleurobrachia pileus* (O. F. Müller, 1776). It is easily distinguishable as it is rounded, without lobes, includes a pair of retracting tentacles and rarely exceeds 2.5 cm (Figure 2b). Out of the water, *P. pileus* looks like a "gelatinous marble" (Figure 2d), whereas *M. leidyi* is more difficult to grasp and has an "egg-white like texture" (Figure 2c). In this survey, only individuals larger than 1 cm were identified, excluding juvenile and larval stages.

Data sources

Multiple data sources were used in this study, such as photographs taken during scuba diving sessions or observations from zooplankton samplings. First, we compiled published data regarding *M. leidyi* distribution and records along the Atlantic coasts. Then, contacts were made with different groups of people working in the field such as staff from nature reserves and marine natural parks, fishermen, oyster farmers, public aquarium technicians as well as researchers. Photographic citizen science databases were also used as a final data source, relying on scuba diving observations by amateur naturalists (BioObs 2022; iNaturalist 2022). Further observations were collated from plankton samplings in the context of the French Non-Indigenous Species Monitoring Programme for the Marine Strategy Framework Directive (MSFD). Since 2019, oblique plankton net tows (lasting 5 minutes) were carried out each summer using a WP3 net (1 m^2 opening area – 500 µm mesh size) in Saint Malo Harbour, the Marennes-Oléron Bay (from the Lay estuary to the Seudre estuary) and in Arcachon Bay. Additionally oblique tows of 5 minutes were carried out in the Mimizan Channel, Capbreton Harbour and Bidassoa estuary with a modified WP2 plankton net (0.25 m^2 opening – 500 µm mesh size) in June, July and September 2021. Observations from existing long-term monitoring surveys (e.g. SOMLIT) and particularly from mesozooplankton monthly sampling in the Arcachon Bay and Gironde estuary were also used. Identifications were always carried out on freshly caught individuals as recommended in Antajan et al. (2014). Abundance from net plankton samples was expressed as ind. m^{-3}, whereas for scuba diving observations, abundance was expressed as an approximate number given that one record corresponds to the observation of at least 1 individual *M. leidyi* (see Supplementary material Table S1 for corresponding sources).

Results

The earliest Atlantic French records of *M. leidyi* that could be verified with photographs provided by scuba divers were from the northern Bay of Biscay, precisely in the Gulf of Morbihan and Houat Island in 2014 (Figure 1 and Table 1). The following year, the species was caught for the first time further south in the Gironde estuary during a monthly zooplankton survey that has been running since the 1980s. Since then, its presence has been recurrent every year, and its range in the estuary has expanded (Nowaczyk, *study in progress*). During periods of high abundance in summer, it was often found stranded in the intertidal zone (Figure 3a). The year 2015 could also correspond to the first observations in the Marennes-Oléron Bay, located 70 km further north. Indeed, although its presence in this bay was officially confirmed in 2019 with a zooplankton net sample (Table S1), earlier observations were made by biologists from the La Rochelle aquarium

Figure 3. *Mnemiopsis leidyi* stranded in the Gironde Estuary (a), swimming in Arcachon Bay (b) and collected in the Charente Estuary (c). Photographs: A Nowaczyk.

in 2015 but not fully verified by a taxonomic specialist. These individuals, at the time, were identified as *Bolinopsis* sp. which was most likely a misidentification.

Six years later, in May 2021, *M. leidyi* colonised Arcachon Bay, 100 km south of the Gironde estuary. These two ecosystems are separated by a linear sandy beach with no suitable areas for colonisation (e.g. no harbours, estuaries, etc). This introduction was peculiar in that *M. leidyi* was restricted to semi-enclosed ponds (i.e. natural swimming pools, former fishponds) in the back of the bay. Abundances in the ponds reached several individuals per cubic meter (Figure 3b). Then, for the first time in August and September 2021, 10 individuals were collected at the entrance of Arcachon Bay during fortnightly zooplankton surveys which have been running since 1996 (Somlit stations), indicating its probable expansion in this bay.

Further south, dedicated sampling carried out in summer 2021 in the Mimizan Channel, Capbreton Harbour, and Bidassoa estuary did not collect *M. leidyi*. To our knowledge, the Arcachon Bay is the most southerly region of the eastern Atlantic colonised by *M. leidyi* to date. Currently, the species can be found along 450 km of coastline in the Bay of Biscay.

North of the Bay of Biscay, *M. leidyi* was identified in the Iroise Sea from a single individual photographed in the Bay of Brest by a diver, one each in 2019 and 2020. Since 2021, it has been frequently reported in this region, particularly at the end of summer (Table S1).

Citizen observations of this species usually occur when concentrations are already high, whereas small individuals often go undetected and require the use of zooplankton nets. For example, in the Charente estuary, an abundance of 115 ind. m^{-3} in July 2021 was estimated using WP3 net samplings. Only 15 individuals larger than 1 cm were collected, while 99.8% were juveniles < 1 cm (Figure 3c).

The Bay of Biscay is the last known French coastline to be colonised by *M. leidyi*. It has now colonised the four major French estuaries (Seine, Loire, Gironde and Rhône) and has spread discontinuously over 45% of the French coastline (Figure 4). Interestingly, *M. leidyi* has never been recorded between the Bay of Seine and the Bay of Brest. During the summers of 2020

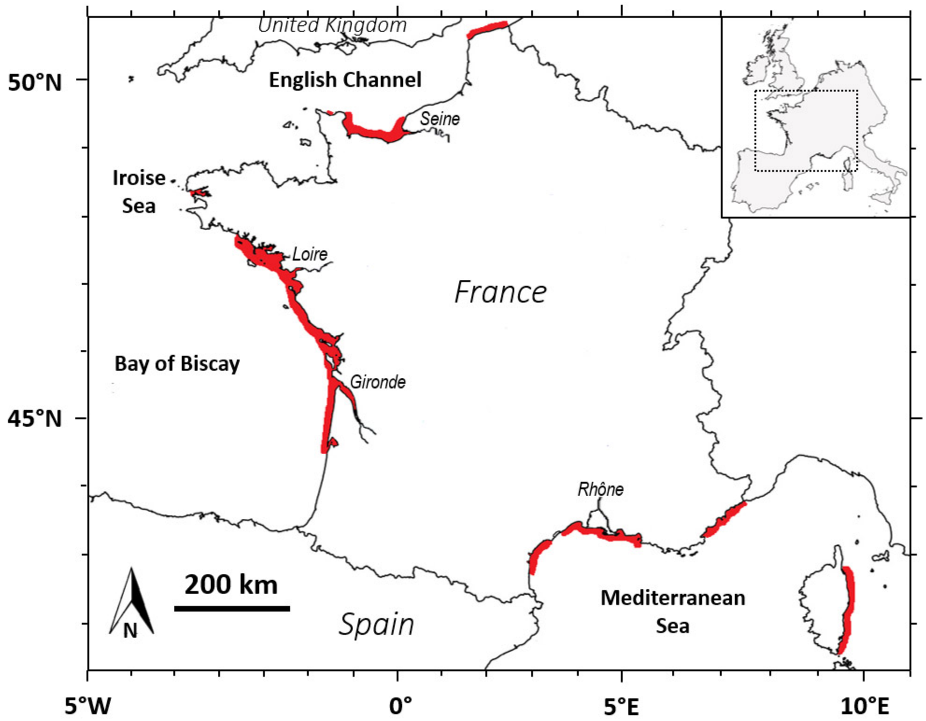

Figure 4. Distribution of *Mnemiopsis leidyi* along the French coast (from Antajan et al. 2014 for the English Channel; Marchessaux and Belloni 2021 for the Mediterranean Sea; this study for the Iroise Sea and Bay of Biscay).

and 2021, additional zooplankton sampling carried out in Saint-Malo Harbour confirmed its absence in this area.

Discussion

One of the difficulties in studying non-indigenous species is acknowledging, with certainty, the actual period of its arrival in a given region. Monitoring for introduced species may incur significant financial efforts due to intensive sampling strategies or the use of complementary techniques like eDNA (Dias et al. 2017), which was recently used to sample for *M. leidyi* in coastal waters of the United Kingdom (Créach et al. 2021). Therefore, although it is possible that *M. leidyi* was introduced earlier in the Bay of Biscay, the first confirmed record of its presence occurred in 2014 (Jaspers et al. 2018a), a decade after it was first recorded along the French coasts of the English Channel (Antajan et al. 2014).

The spread of this species from one area to the other could be explained by advection processes and natural currents, which act as vectors of secondary spread (Schaber et al. 2011; Jaspers et al. 2018a). Several elements, however, do not support the hypothesis of *M. leidyi* naturally spreading southeastward from the English Channel (e.g. Antajan et al. 2014). Firstly, surface currents are predominantly oriented northwards both in the English Channel, including the Bay of Seine (Bailly du Bois and Dumas 2005), and in the Bay of Biscay (Koutsikopoulos and Le Cann 1996; Charria et al. 2013). Moreover, *M. leidyi* shows a strong geographical discontinuity between the Bay of

Seine and the north of the Bay of Biscay. *Mnemiopsis leidyi* is only present in the Bay of Brest in the Iroise Sea and has not yet been found offshore in the Iroise Sea, despite regular sampling efforts carried out by the Iroise marine natural park since 2010. Finally, strong hydrodynamics and, in particular, haline and thermal fronts in this region (Le Boyer et al. 2009) may limit the connectivity between English Channel and Bay of Biscay populations as exemplified by Ayata et al. (2010) for organisms with bentho-pelagic life cycles.

The second hypothesis for the spread of *M. leidyi* is that one or more new introduction events took place, probably via ballast water discharge as already demonstrated by genomic analysis in the North sea (Jaspers et al. 2021). Indeed, about 3,000, 900 and 700 merchant vessels annually transit the Loire, Gironde and Brest Bay estuaries, respectively (BPA 2022; PB 2022; PNM 2022). These estuaries may then serve as locations for further spread of *M. leidyi* into adjacent areas. This is probably the case for the Arcachon Bay population, as it is likely that this population was started from a population in the Gironde estuary. These two regions are not connected through merchant vessel traffic and are separated by a linear sandy coastline of about 100 km with no other estuaries, bays or harbours. Under certain conditions, notably dominant northwest winds associated with low river flows, the direction of the Seine, Loire and Gironde plumes reverse, particularly during the summer (Lazure and Jegou 1998; Ellien et al. 2004; Charria et al. 2013). Based on biogeochemical circulation models and the use of salinity as a proxy to visualise the movement of water mass originating from the Gironde estuary, a southward deviation of the plume was observed in mid-July 2020 which then entered Arcachon Bay a fortnight later (MARC 2022). This water mass has higher primary and secondary production than coastal waters (Sautour et al. 1996; Labry et al. 2001) and can potentially transport and allow for the survival of *M. leidyi*. Moreover, this period corresponds to high abundances of *M. leidyi* in the Gironde estuary (Nowaczyk, study in progress) and precedes the first record of *M. leidyi* in Arcachon Bay by few months. Genetic analyses would clarify the invasion history of *M. leidyi* along the French Atlantic coast, as has been previously carried out on this species in the Mediterranean Sea and Northern Europe (Reusch et al. 2010; Ghabooli et al. 2011, 2013; Bayha et al. 2015).

Marchessaux and Belloni (2021) reported, on the basis of citizen science observations only, that *M. leidyi* had not been reported from the coastal zone of the Bay of Biscay. Nevertheless, our study shows that *M. leidyi* is now clearly established in this area (Figure 1 and Table S1) and has colonised more than 500 km of coastline including different habitats such as estuaries, lagoons, channels and harbours. Some of these habitats may provide refuge areas in winter, allowing the species to colonise new habitats later (Costello et al. 2006). Given that coastal currents can be directed southwards in the Bay of Biscay during the summer (Lazure and Jegou 1998; Charria et al. 2013), a period corresponding to the maximum abundance of this species, it is likely that *M. leidyi* will reach the Adour, Nivelle and Bidassoa estuaries in the near future and then extend to the northern coast of Spain. This expansion pattern with much lower and slower rates than those observed in other areas (e.g. North Sea to the Central Baltic Sea and western Norway; Jaspers et al. 2018a) can, in fact, allow animals to 'slowly but surely' extend their distribution area.

During its development, *M. leidyi* feeds on a wide diversity of prey taxa covering a wide range of prey sizes, ranging from microplankton during its larval phase to mesozooplankton several millimeters in length (e.g., copepods or small amphipods) when it becomes lobate (Purcell et al. 2001; Sullivan and Gifford 2004; Granhag et al. 2011; Marchessaux et al. 2021). Although it is an opportunistic feeder, it captures bivalve veligers more efficiently compared to other mobile prey such as copepods (Larson 1987; Madsen and Riisgård 2010). *Mnemiopsis leidyi* populations can exert significant grazing pressure on veliger stocks by ingesting up to 95% of the bivalve larval stock per day (McNamara et al. 2010). It could, therefore, represent a significant threat to bivalve populations (Purcell et al. 1991; McNamara et al. 2010).

The Bay of Brest is one of the two last catchment areas for the flat oyster *Ostrea edulis* in France, with a production of 21.5 t per year (CRC 2022). Since the 2000s there has also been a small production of Pacific oyster *Magallana gigas* spat in the Bay (CRC 2022). The recent observations of *M. leidyi* in the Bay of Brest (i.e. September 2019 and 2021) followed peaks of abundance in Pacific and flat oyster larvae, generally observed at the end of August in this area (ECUME 2022). The bays of Arcachon and Marennes-Oléron are the two main Pacific oyster breeding basins in France. Arcachon Bay produces more than 70% of French Pacific oyster spat. In 2012, 80% of the companies practiced natural oyster seed collection (Agrest 2019), and the sale of spat constitutes 25% of the annual income of the Arcachon oyster industry (Auby and Maurer 2004).

France is the first European country where, since the 1970s, the main pathway for marine alien species is aquaculture, which is responsible for about 50% of introductions, mainly through the import and culture of *M. gigas* from the Pacific area (Nunes et al. 2014). However, this industry was not responsible for the introduction or spread of *M. leidyi*, as the transport of oyster stocks occurs out of water, a lethal condition for this species.

In the Gironde Estuary, the maximum abundances of *M. leidyi* occur during the summer (Nowaczyk, study in progress) as is the case in other areas in northern Europe (van Walraven et al. 2013). Unfortunately for oyster farmers, this period also corresponds to the greatest period of oyster reproduction. If the abundances of this ctenophore became high, it is likely to pose a novel constrain on the survival of oyster larvae. While numerous successive oyster spawning events were observed, the abundances of medium and large veliger larvae were abnormally low in Marennes-Oléron Bay in summer 2020 and Seudre estuary in summer 2021 (Bouquet et al. 2020, 2021), which could indicate possible predation by *M. leidyi*. This larval predation risk does, however, seem to be more moderate for other commercialized bivalves such as mussels, clams and cockles since their reproduction occurs during the spring, a period when the abundance of *M. leidyi* remains moderate. Although direct predation and effects of *M. leidyi* on bivalve larvae population dynamics could not be inferred from the present study, the presence of *M. leidyi* in shellfish farming ecosystems constitutes an additional potential pressure on the life cycle of bivalves, cumulating with other existing pressures (e.g. disease, pollution, unfavourable temperature, HABs and associated toxins) (Rico-Villa et al. 2009; Pardon et al. 2016; Gamain et al. 2017; de Lorgeril et al. 2018) and could therefore have economic repercussions on oyster farming.

Conclusions

This survey assessed the expansion of *M. leidyi* along the French Atlantic coastline of the Bay of Biscay by combining citizen science observations by scuba diver amateurs and results from *in situ* zooplankton sampling undertaken within the framework of existing networks (e.g. SOMLIT, MSFD monitoring programme for Descriptor 2 – Non Indigenous Species). Our results demonstrated the wide distribution of the species in French coastal waters from Arcachon Bay to the Bay of Brest. Although the species has yet to be confirmed in the southern part of the Bay of Biscay as well as in northern Brittany, *in situ* surveys and observations should be maintained to monitor potential spread. Additional information is also needed from offshore waters to gain a better understanding of its distribution patterns at larger scales and should rely on scientific campaigns. Whether the species constitutes a new pressure on shellfish farming activities is a question that should be addressed via long-term and regular monitoring in the main shellfish farming areas where it has already been observed. Finally, a genetic study remains is needed to elucidate the phylogeography of *M. leidyi* and determine whether its presence is due to an expansion of the Northern European population or to new introductions events.

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Authors' contribution

A.N. and C.M. designed and performed research; A.N., D.V., A.C., E.A. and C.M. investigated and collected data; A.N. and C.M. analyzed data; A.N. wrote the paper with contribution from D.V., A.C. and C.M.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Records of *Mnemiopsis leidyi* in the Bay of Biscay and Iroise Sea.

This material is available as part of online article from:
http://www.reabic.net/journals/bir/2023/Supplements/BIR_2023_Nowaczyk_etal_SupplementaryMaterial.xlsx