The invasive ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 along the English Channel and the North Sea French coasts: another introduction pathway in northern European waters?

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**Abstract**

The presence of *Mnemiopsis leidyi* A. Agassiz, 1865 along the French coasts of the Eastern English Channel and the North Sea (EEC-NS) was established via morphological observation and molecular evidence. The earliest records were from surveys carried out in autumn 2005 in Le Havre harbour (Bay of Seine, EEC) and coincided with the historical introduction of the species in other Northern European waters. Since 2009, the species has also been frequently observed along the French coast of the North Sea. Results indicate *M. leidyi* has established a self-sustaining population in the Bay of Seine, which may act as a source population for northern European harbours via commercial shipping.

**Key words:** ctenophore, invasive species, *Mnemiopsis leidyi*

**Introduction**

The voracious zooplanktivore *Mnemiopsis leidyi* A. Agassiz, 1865 is a lobate ctenophore native to the Atlantic coasts of North and South America (Gesamp 1997). This eurythermic and euryhaline species can tolerate a wide range of environmental conditions (Kremer 1994; Purcell et al. 2001). These features, together with its regeneration (Henry and Martindale 2000) and reproductive ability (self-fertile hermaphrodite with high fecundity and rapid growth rates), explain the success of *M. leidyi* as an invasive species (Baker and Reeve 1974; Costello et al. 2006; Jaspers et al. 2011). The establishment of *M. leidyi* had severe ecological and economic impacts in the Black Sea in the 1980’s (Shiganova 1998) and in the Caspian Sea in the late 1990’s (Roohi et al. 2010). Consequently, recent (since 2005) discoveries of this species in Norwegian fjords (Oliveira 2007; Hosia et al. 2011), the Baltic Sea (Hansson 2006; Javidpour et al. 2006; Kube et al. 2007), Danish territorial waters (Tendal et al. 2007), the German Bight (Boersma et al. 2007), the Netherlands (Faasse and Bayha 2006) and in Belgian coastal waters (Dumoulin 2007; Van Ginderdeuren et al. 2012), has alarmed the scientific community, especially as these northern European waters are amongst the world's most important fishing grounds. However, work by Hamer et al. (2011) concludes that the densities of *M. leidyi* currently observed in northern waters do not represent a threat to eggs and fish larvae, although they might compete with larval fishes for small plankton prey and it is unknown whether the species represents an immediate ecological threat. In this context, the aim of this article is to document the first records of *M. leidyi* along the French coasts.
of the Eastern English Channel–North Sea ecosystem (EEC-NS), and discuss possible invasion routes from its native range.

**Methods**

Sample sites were located along the French coast between the western part of the Bay of Seine (BoS) and the North Sea (Figure 1A–C). A variety of sampling devices and observations were used depending on the sampling location (Table 1S). Scuba diving observations by amateurs were the source of most *M. leidyi* records in the BoS (mainly in Le Havre Harbour). Photographs taken by divers (Figure 2A–C) permitted morphological identification of *M. leidyi* based on the position of the oral lobes extending to the apical statocyst (sense organ) over nearly the entire body length (Faasse and Bayha 2006; Oliveira and Migotto 2006).

Within research monitoring surveys, two types of plankton nets were used along the French coast of the North sea for quantitative estimate of *M. leidyi*, a WP2 net (opening area 0.25m² and 200 µm mesh size; Fraser 1968a) and a WP3 net (opening area 1.0 m² and 1.0 mm mesh size; Fraser 1968b). The *M. leidyi* record from the Seine estuary represents specimens collected during a bottom trawl survey (280 × 40cm aperture, 20 mm mesh size).

When available, abundance and approximate sizes are provided in Table 1S of supplementary material. When actual numbers per m³ were not available, abundance was expressed as less than ten (+), sparse (++) or common (+++). Freshly caught individuals from all sites were observed and identified alive, and some of them were preserved in 70–100 % ethanol and stored at 4°C for further genetic analyses (following Van Ginderdeuren et al. 2012; see superscript in Table 1S).
Results

All observed specimens collected during this study were lobate individuals, and no cydipid larvae were recorded. The earliest records of *M. leidyi* that we could verify with photographs provided by divers (Figure 2A) were from Le Havre Harbour (Figure 1B and Table 1S, N° 8, 12 and 13) in September and October 2005. Since then, there have been frequent observations of individuals (ranging from 3 to 8 cm in length) reported during diving sessions in the same area (Figure 1B and Table 1S N° 4 to 16). Some individuals collected in 2011 (Figure 1B and Table 1S, N° 9 and 10) were genetically identified and confirmed our initial morphological identification (E. Antajan, unpublished data). In Le Havre Harbour, the greatest numbers of *M. leidyi* were recorded during July to October; however, a few individuals were still observed in winter (Figure 1B and Table 1S, N° 13).

The first records of *M. leidyi* in the North Sea were made in September 2009 (Antajan et al. 2010, Figure 1C; N° 24 to 27). Specimens of *M. leidyi* were also collected during 2010, 2012 and 2013 in the two nearby harbours of Calais (N° 19 to 23) and Dunkirk (N° 28 to 32). *M. leidyi* was recorded from these sites from September to December at temperature ranging from 5.5 to 20.2°C and salinity between 29.7 and 34.9.

In January 2011, the launch of the European MEMO project (InterReg IVa-2 seas, *Mnemiopsis Ecology and Modelling: Observation of an invasive comb jelly in the North Sea*) was accompanied by a major public communication effort and has led many reports by citizens of the presence of the species in the BoS (Figure 1A–B and Table 1S, N° 1 to 3 and 18). Following the collection of *M. leidyi* in the Seine estuary during a bottom trawl survey (Figure 1B and Table 1S, N°17), the Somme, Canche and Authie estuaries (Figure 3), and a long-term monitoring station (SOMLIT stations) were also surveyed to assess whether *M. leidyi* had spread northward. However, no *M. leidyi* were detected at any of these four sites.

Discussion

*Mnemiopsis leidyi* has been present along the French coast since at least 2005. Earlier occurrence is possible; however, the routine monitoring surveys along the French coasts of the North Sea (e.g. Calais, Dunkirk and Gravelines) use a formalin solution to preserve zooplankton samples immediately after collection. This causes *M. leidyi* to disintegrate and makes species identification, counting, and measuring practically impossible (Kube et al. 2007; Engell-Sørensen et al. 2009; Sullivan and Gifford 2009). Purcell (1988) presented an identification method for formaldehyde-preserved samples based on identification of *M. leidyi* tentacle bulbs. This method was tested on 2005–2009 formalin-fixed samples but given the very low number of individuals (< 2 ind.m⁻³) and the large amount of particulate matter in the
samples, tentacle bulbs were impossible to detect. Since our 2009 record of *M. leidyi* in non-preserved samples (Figure 1C and Table 1S, N° 24–26), zooplankton sampling techniques were reconsidered and collected samples were first examined while specimens were alive before sample preservation. This new strategy resulted in additional records in the North Sea, and we recommend a systematic visual inspection of still living material for ctenophores and similar taxa prior to sample preservation in future zooplankton surveys.

Our first record of *M. leidyi* in 2005 in Le Havre Harbour coincides with the first record of *M. leidyi* in the northern part of the North Sea - Oslo fjord in Norway (Oliveira 2007). Although the North Atlantic Current has previously been considered as a potential introduction vector of *M. leidyi* in the North Sea (Oliveira 2007), it could not explain our simultaneous record in the Bay of Seine (BoS) because this current does not extend into the English Channel (Otto et al. 1990). Instead, our results suggest there were multiple and simultaneous introductions of the species in the main harbours of Northern Europe, presumably by means of ballast water (Vinogradov et al. 1989; Ivanov et al. 2000; Oliveira et al. 2007; Fuentes et al. 2010 and references therein).

Large ships crossing the Strait of Dover towards the North Sea regularly stop in the Calais and Dunkirk harbours and can also visit the large European harbours such as Le Havre (France), Rotterdam (Netherlands), Anvers, Zeebrugge (Belgium) and Hamburg (Germany; Figure 3). The introduction pattern of *M. leidyi* by cargo ships in the EEC-NS would, therefore, result from trans-Atlantic (e.g. East coast of Mexico and USA) and local ship transits as was observed along the Belgium and Dutch coasts (Wolff 2005; Faasse and Bahya 2006; Van Ginderdeuren et al. 2012) and in the Mediterranean Sea (Bolte et al. 2013; Ghabooli et al. 2013).

Advection processes and natural transport (drift, internal circulation) have previously been identified as vectors of secondary spread for *M. leidyi* (Lehmann and Javidpour 2010; Schaber et al. 2011; Van Ginderdeuren et al. 2012). Therefore, it is possible that *M. leidyi* introduced along the French coast of the North Sea originated from adjacent regions (e.g. Belgium or BoS).

![Figure 3. Mnemiopsis leidyi records and possible introduction and spreading vectors in the English Channel – North Sea ecosystem. Current circulation is based on Edwards (1968), Otto et al. (1990) and Lazure and Desmare (2011).](image-url)
The spread of *M. leidyi* southward from the North Sea, where established populations are observed (Faasse and Bayha 2006; Van Ginderdeuren et al. 2012), is unlikely because the residual tidal transport is oriented northward; water masses typically drift from the English Channel to the North Sea (Otto et al. 1990; Brylinski et al. 1991; Figure 3). North-easterly winds can at times reverse the general circulation pattern and induce southward spreading of plankton organisms (Dauvin et al. 2007), but these conditions did not prevail during our sampling periods (autumn 2009-2010, 2012, 2013 and January 2010). Recurring records year-round in the BoS since 2005 suggest the existence of another potential, self-maintaining, source population (*sensu* Costello et al. 2012). However, a northward spread from the BoS is also unlikely as no *M. leidyi* were recorded in the main EEC estuaries (Somme, Canche and Authie) nor at the SOMLIT stations (Figure 3). Natural expansion from the Seine estuary would likely lead to *M. leidyi* spreading westward, which is consistent with the net seaward transport in the Seine estuary (Wang et al. 1995), the general water circulation pattern in the BoS (Le Hir et al. 1985; Lazure and Desmare 2011), and observations of *M. leidyi* in the western part of the BoS in autumn 2011 (Figures 1A and 3; N° 1 and 2 Table 1S). Thus, simple water drifting as a vector of *M. leidyi* spreading from the BoS to the French coast of the North Sea is unlikely, and records suggest the existence of distinct North Sea and a BoS populations. Although the BoS population seems to be self-sustaining, the absence of *M. leidyi* in winter or year-round in the North Sea (in 2011) suggests a regular pattern of elimination and re-inoculation more typical of a sink population (*sensu* Costello 2012).

Two main invasion pathways were identified for *M. leidyi* introductions in Eurasia (Ghabooli et al. 2011; Reusch et al. 2010; Costello et al. 2012). While specimens from the Gulf of Mexico invaded the Black Sea and then the Caspian Sea, specimens from the Baltic Sea seem to originate from Narragansett Bay (USA). Studies of *M. leidyi* population genetics would permit assessment of whether EEC-NS specimens are individuals imported from their native habitats or represent mixed populations resulting from water exchanges between the EEC-NS harbours during ship transit, as was demonstrated in the Mediterranean Sea (Fuentes et al. 2010; Ghabooli et al. 2013).

Our seasonal and spatial records of *M. leidyi* at temperature ranging from 5.5 to 20.2°C and salinity from 29.7 to 34.9 are consistent with its euryhaline and eurythermal nature (Kremer et al. 1994; Purcell et al. 2001). Records of *M. leidyi* are also consistent with its versatile opportunistic zooplanktivorous feeding behaviour, with it being able to exploit the high standing stocks of copepods (Grattepanche et al. 2010), fish larvae (Amara 2002; Amara et al. 2000), and bivalve larvae characterizing the EEC-NS French coastal waters. However, two characteristics of the EEC-NS ecosystem could represent limiting factors for *M. leidyi* spreading and survival. First, choppy sea conditions in the EEC-NS ecosystem (high turbulence and tidal mixing; Seuront et al. 1999, 2002; Kesauliya et al. 2008) can cause direct physical damage (Miller 1974; Graham et al. 2001; Mianzan et al. 2010) and decrease feeding efficiency of *M. leidyi* (Waggett and Costello 1999; Colin et al. 2010). Second, predation by cnidarians (*sensu* Aurelia aurita (Linnaeus, 1758) and Chrysaora hysoscella (Linnaeus, 1767); Javidpour et al. 2009; Hosia and Titelman 2001), ctenophores (*sensu* Beroe gracilis Künne, 1939 and B. cucumis Fabricius, 1780; Hosia et al. 2011; Van Ginderdeuren et al. 2012), or fish (Mianzan et al. 1996; Purcell et al. 2001; Schaber et al. 2011) may limit *M. leidyi* population size or even persistence.

In conclusion, the present study demonstrated that the alien invasive ctenophore *M. leidyi* has been present along the French coasts of the EEC-NS ecosystem at least since 2005. If the species has established a population in the BoS, its development and origins in North Sea French harbours (Calais and Dunkirk) are poorly understood. Long-term monitoring, along with population genetics investigations, are therefore needed to address source-sink dynamics of the species and potential establishment along the French coasts of the North Sea.

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The following supplementary material is available for this article:

Table 1S. Records of Mnemiopsis leidyi along the English coasts of the English Channel and the North Sea.

This material is available as part of online article from: http://www.aquaticinvasions.net/2014/Supplements/AI_2014_Antajanetal_Supplement.xls