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Research Article

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). Consequenly, 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

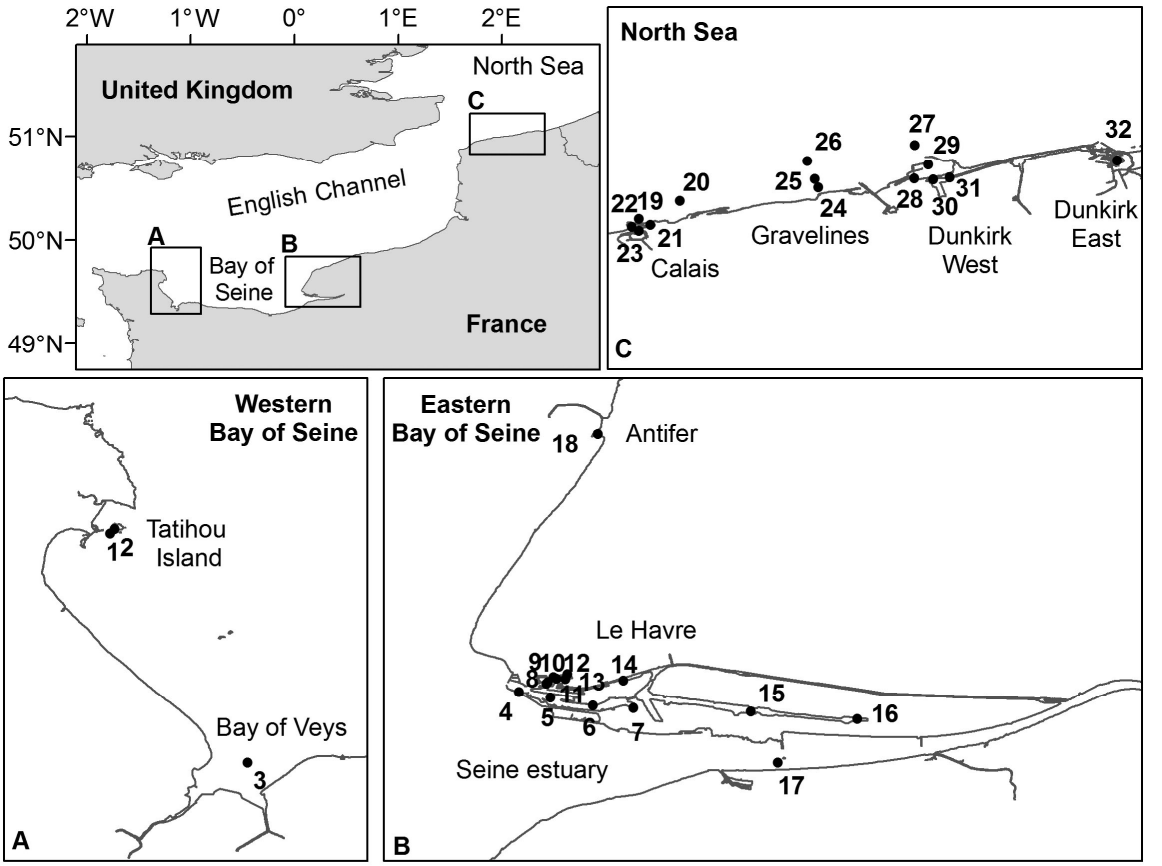

Figure 1. Sampling site records of *Mnemiopsis leidyi* in the Eastern English Channel – North Sea ecosystem; (A) Western Bay of Seine; (B) Eastern Bay of Seine; (C) French coasts of the North Sea.

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 m^3 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).

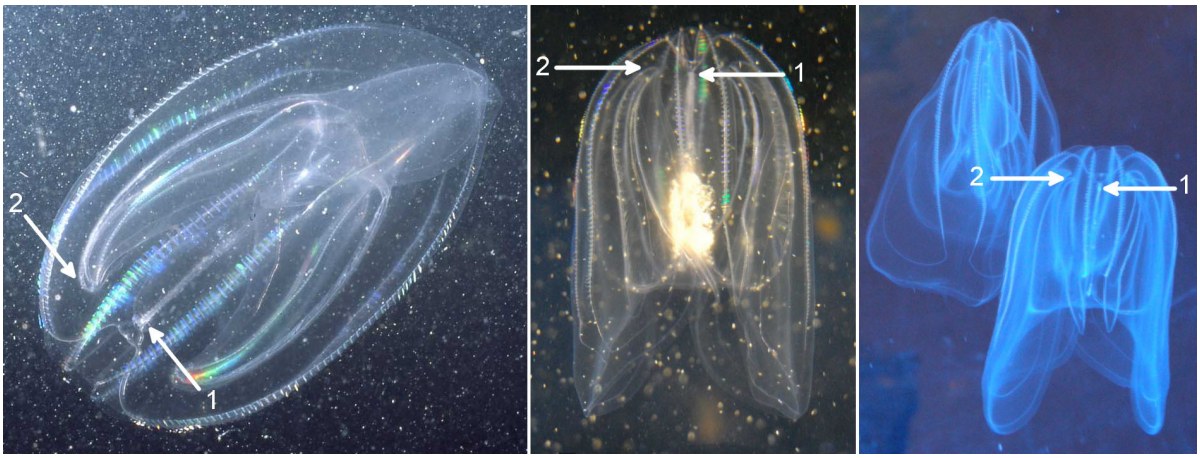

Figure 2. *Mnemiopsis leidyi* (A) from the Eastern Bay of Seine (Le Havre harbour) – photograph by G. Breton on the 25.09.2005; (B) from the Western Bay of Seine (Tatihou Island; Length 4–5 cm) – photograph by F. Chevallier on the 26.09.2011; (C) from the French coasts of the North Sea (Dunkirk Harbour; Length 6 cm) – photograph by J.M. Brylinski in kreisel tank. Arrows indicate the position of the statocyst (1) and lobes insertion (2), near the aboral end of the body in *M. leidyi*, a distinctive characteristic of the species.

Results

All observed specimens collected during this study were lobate individuals, and no cyddipid 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

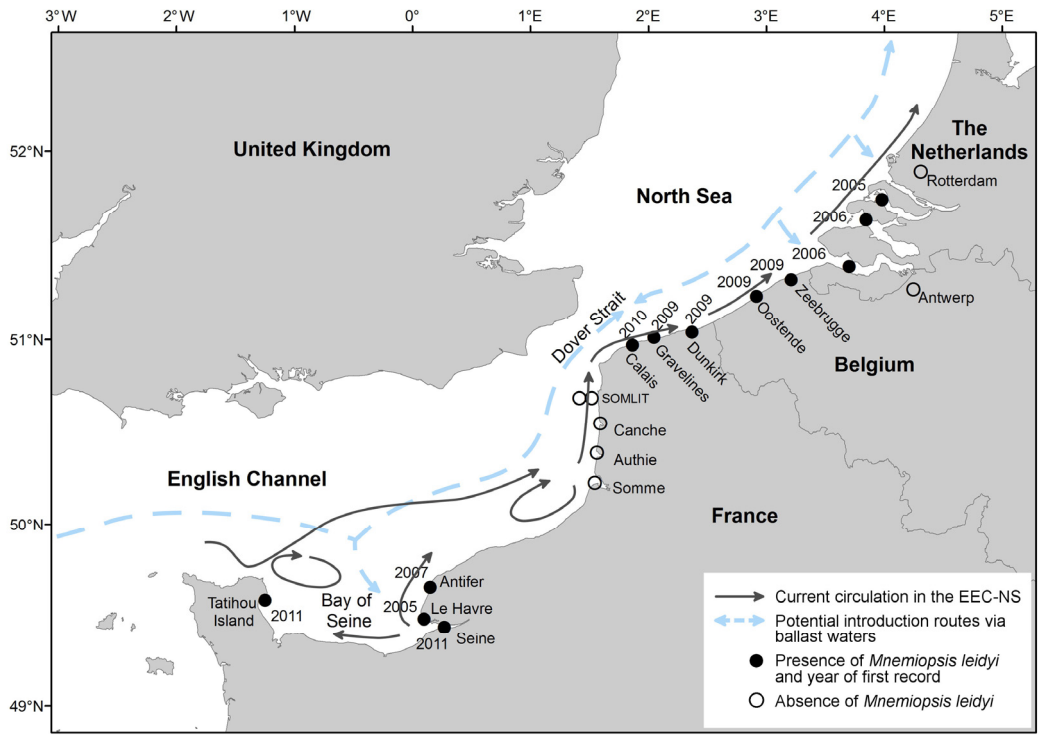

Figure 3. *Mnemiopsis leidyi* records and possible introduction and spreading vectors in the English Channel – North Sea ecosystem. Current circulation is based on Edwards (1968), Otto et al. (1990) and Lazure and Desmare (2011).

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).

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; Kesaulya 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 (such as *Aurelia aurita* (Linnaeus, 1758) and *Chrysaora hysoscella* (Linnaeus, 1767); Javidpour et al. 2009; Hosia and Titelman 2001), ctenophores (such as *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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References

Antajan E, Delesmont R, Dewarumez J-M, Lefebvre A, Luczak C, Warembourg C (2010) Surveillance écologique et halieutique du site de Gravelines, Novembre 2008 - Octobre 2009. IFREMER Technical report, 151 pp

Amara R (2002) Localisation et diagnostic de l'état de santé des nourriceries d'espèces d'intérêt halieutique en Manche orientale. Rapport de contrat LT 98040, Ministère de l'Aménagement du Territoire et de l'Environnement, 124 pp

Amara R, Lagardere F, Desaunay Y, Marchand J (2000) Metamorphosis and estuarine colonisation in the common sole, *Solea solea* (L.): implications for recruitment regulation. *Oceanologica Acta* 23 (4): 469–484, http://dx.doi.org/10.1016/S0399-1784(00)00134-1

Baker LD, Reeve MR (1974) Laboratory culture of the lobate ctenophore *Mnemiopsis mccradyi* with notes on feeding and fecundity. *Marine Biology* 26: 57–62, http://dx.doi.org/10.1007/BF00389086

Boersma M, Malzahn AM, Greve W, Javidpour J (2007) The first occurrence of the ctenophore *Mnemiopsis leidyi* in the North Sea. *Helgoland Marine Research* 61: 153–155, http://dx.doi.org/10.1007/s10152-006-0055-2

Bolte S, Fuentes V, Haslob H, Huwer B, Thibault-Botha D, Angel D, Galil B, Javidpour J, Moss AG, Reusch TBH (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, http://dx.doi.org/10.3354/meps10321

Brylinski JM, Lagadeuc Y, Gentilhomme V, Dupont JP, Lafite R, Dupeuble PA, Huault MF, Auger Y, Puskaric E, Wartel M, Cabioch L (1991) Le "fleuve Côtier": un phénomène hydrologique important en Manche Orientale. Exemple du Pas de Calais. *Oceanologica Acta* 11: 197–203

Colin SP, Costello JH, Hansson LJ, Titelman J, Dabiri JO (2010) Stealth predation and the predatory success of the invasive ctenophore *Mnemiopsis leidyi*. *Proceedings of the National Academy of Sciences of the United States of America* 107: 17223–17227, http://dx.doi.org/10.1073/pnas.1003170107

Costello JH, Sullivan BK, Gifford DJ, Van Keuren D, Sullivan LJ (2006) Seasonal refugia, shoreward thermal amplification, and metapopulation dynamics of the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. *Limnology and Oceanography* 51: 1819–1831, http://dx.doi.org/10.4319/lo.2006.51.4.1819

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, http://dx.doi.org/10.1007/s10750-012-1037-9

Otto L, Zimmerman JTF, Furnes GK, Mork M, Saetre R, Becker G (1990) Review of the physical oceanography of the North Sea. *Netherlands Journal of Sea Research* 26: 161–238, http://dx.doi.org/10.1016/0077-7579(90)90091-T

Dauvin JC, Ruellet T, Desroy N, Janson AL (2007) The ecological quality status of the Bay of Seine and the Seine estuary: use of biotic indices. *Marine Pollution Bulletin* 55: 241–257, http://dx.doi.org/10.1016/j.marpolbul.2006.04.010

Dumoulin E (2007) De Leidy's ribkwal *Mnemiopsis leidyi* (A. Agassiz, 1865) al massaal in het havengebied Zeebrugge-Brugge, of: exoten als de spiegel van al tè menselijk handelen. *De Strandvlo* 27(2): 44–60

Edwards C (1968) Water movements and the distribution of hydromedusae in British and adjacent waters. *Sarsia* 34: 331–346

Engell-Sørensen K, Andersen P, Holmstrup M (2009) Preservation of the invasive ctenophore *Mnemiopsis leidyi* using acidic Lugol's solution. *Journal of Plankton Research* 31: 917–920, http://dx.doi.org/10.1093/plankt/fbp030

Faasse MA, Bayha KM (2006) The ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 in coastal waters of the Netherlands: an unrecognized invasion? *Aquatic Invasions* 1: 270–277, http://dx.doi.org/10.3391/ai.2006.1.4.9

Fraser JH (1968a) Smaller mesozooplankton, report of Working Party No. 2. In: Tranter DJ (ed), Standardization of zooplankton sampling methods at sea, Part II. Monogr. Oceanogr. Methodol. 2, Zooplankton Sampling. UNESCO (United Nations Educational, Scientific, and Cultural Organization) Press, Paris, pp 153–159

Fraser JH (1968b) Larger mesozooplankton, report of Working Party No.3. In: Tranter DJ (ed), Standardization of zooplankton sampling methods at sea, Part II. Monogr. Oceanogr. Methodol. 2, Zooplankton Sampling. UNESCO (United Nations Educational, Scientific, and Cultural Organization) Press, Paris, pp 160–163

Fuentes VL, Angel DL, Bayha KM, Atienza D, Edelist D, Bordehore C, Gili JM, Purcell JE (2010) Blooms of the invasive ctenophore, *Mnemiopsis leidyi*, span the Mediterranean Sea in 2009. *Hydrobiologia* 645: 23–37, http://dx.doi.org/10.1007/s10750-010-0205-z

GESAMP (IMO/FAO/UNESCO_IOC/WMO/WHO/IAEA/UN/UNEP Joint Group of Experts on the Scientific Aspects of the Marine Environmental Protection) (1997) Opportunistic settlers and the problem of the ctenophore *Mnemiopsis leidyi* invasion in the Black Sea. GESAMP reports and studies No 58. International Maritime Organization, London

Ghabooli S, Shiganova TA, Zhan A, Cristescu MC, Eghtesadi-Araghi P, MacIsaac HJ (2011) Multiple introductions and invasion pathways for the invasive ctenophore *Mnemiopsis leidyi* in Eurasia. *Biological Invasions* 13: 679–690, http://dx.doi.org/10.1007/s10530-010-9859-8

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, http://dx.doi.org/10.1371/journal.pone.0081067

Graham WM, Pagès F, Hamner WM (2001) A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia* 451: 199–2012, http://dx.doi.org/10.1023/A:1011876004427

Grattepanche J-D, Breton E, Brylinski J-M, Christaki U (2011) Succession of primary producers and micrograzers in a coastal ecosystem dominated by *Phaeocystis globosa* blooms. *Journal of Plankton Research* 33: 37–50, http://dx.doi.org/10.1093/plankt/fbq097

Hamer HH, Malzahn AM, Boersma M (2011) The invasive ctenophore *Mnemiopsis leidyi*: a threat to fish recruitment in the North Sea? *Journal of Plankton Research* 33: 137, http://dx.doi.org/10.1093/plankt/fbq100

Hansson HG (2006) Ctenophores of the Baltic and adjacent Seas–the invader *Mnemiopsis* is here! *Aquatic Invasions* 1: 295–298, http://dx.doi.org/10.3391/ai.2006.1.4.16

Henry JQ, Martindale MQ (2000) Regulation and regeneration in the ctenophore *Mnemiopsis leidyi*. *Developmental Biology* 227: 720–733, http://dx.doi.org/10.1006/dbio.2000.9903

Hosia A, Titelman J (2011) Intraguild predation between the native North Sea jellyfish *Cyanea capillata* and the invasive ctenophore *Mnemiopsis leidyi*. *Journal of Plankton Research* 33: 535–540, http://dx.doi.org/10.1093/plankt/fbq106

Hosia A, Titelman J, Hansson LJ, Haraldsson M (2011) Interactions between native and alien ctenophores: *Beroe gracilis* and *Mnemiopsis leidyi* in Gullmarsfjorden. *Marine Ecology Progress Series* 422: 129–138, http://dx.doi.org/10.3354/meps08926

Ivanov VP, Kamakin AM, Ushivtzev VB, Shiganova T, Zhukova O, Aladin N, Wilson SI, Harbison GR, Dumont HJ (2000) Invasion of the Caspian Sea by the comb jellyfish *Mnemiopsis leidyi* (Ctenophora). *Biological Invasions* 2: 255–258, http://dx.doi.org/10.1023/A:1010098624728

Jaspers C, Møller LF, Kiørboe 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: e24065, http://dx.doi.org/10.1371/journal.pone.0024065

Javidpour J, Sommer U, Shiganova T (2006) First record of *Mnemiopsis leidyi* A. Agassiz 1865 in the Baltic Sea. *Aquatic Invasions* 1: 299–302, http://dx.doi.org/10.3391/ai.2006.1.4.17

Javidpour J, Molinero JC, Lehmann A, Hansen T, Sommer U (2009) Annual assessment of the predation of *Mnemiopsis leidyi* in a new invaded environment, the Kiel Fjord (Western Baltic Sea): a matter of concern? *Journal of Plankton Research* 31: 729–738, http://dx.doi.org/10.1093/plankt/fbp021

Kesaulya I, Leterme SC, Mitchell JG, Seuront L (2008) The impact of turbulence on foam formation, seawater viscosity and chlorophyll concentration in the Eastern English Channel. *Oceanologia* 50: 167–182

Kremer P (1994) Patterns of abundance for *Mnemiopsis* in US coastal waters - a comparative overview. *Ices Journal of Marine Science* 51: 347–354, http://dx.doi.org/10.1006/jmsc.1994.1036

Kube S, Postel L, Honnef C, Augustin CB (2007) *Mnemiopsis leidyi* in the Baltic Sea: distribution and overwintering between autumn 2006 and spring 2007. *Aquatic Invasions* 2: 137–145, http://dx.doi.org/10.3391/ai.2007.2.2.9

Lazure P, Desmare S (2011) Courantologie dans la sous-région marine Manche, Mer du Nord. Ministère de l'Ecologie du Développement Durable des Transports et du Logement, DCSSM/EI/EE/MMN/1.1.6/2011, 7 pp

Le Hir P, Salomon JC, Le Provost C, Chabert d'Hieres G, Mauvais JL (1986) Approche de la circulation résiduelle en baie de Seine. In: Ifremer (ed), La baie de Seine (Greco-Manche), Actes de Colloques no 4, université de Caen, France, April 24–26, 1985, pp 63–72

Lehmann A, Javidpour J (2010) Potential pathways of invasion and dispersal of *Mnemiopsis leidyi* A. Agassiz 1865 in the Baltic Sea. *Hydrobiologia* 649: 107–114, http://dx.doi.org/10.1007/s10750-010-0233-8

Mianzan H, Mari N, Prenski B, Sanchez F (1996) Fish predation on neritic ctenophores from the Argentine continental shelf: A neglected food resource? *Fisheries Research* 27: 69–79, http://dx.doi.org/10.1016/0165-7836(95)00459-9

Mianzan HW, Martos P, Costello JH, Guerrero RA (2010) Avoidance of hydrodynamically mixed environments by *Mnemiopsis leidyi* (Ctenophora: Lobata) in open-sea populations from Patagonia, Argentina. *Hydrobiologia* 645: 113–124, http://dx.doi.org/10.1007/s10750-010-0218-7

Miller RJ (1974) Distribution and biomass of an estuarine ctenophore population, *Mnemiopsis leidyi* (A. Agassiz). *Chesapeake Science* 15: 1–8, http://dx.doi.org/10.2307/1350952

Oliveira OMP (2007) The presence of the ctenophore *Mnemiopsis leidyi* in the Oslofjorden and considerations on the initial invasion pathways to the North and Baltic Seas. *Aquatic Invasions* 2: 185–189, http://dx.doi.org/10.3391/ai.2007.2.3.5

Oliveira OMP, Migotto AE (2006) Pelagic ctenophores from the São Sebastião Channel, southeastern Brazil. *Zootaxa* 1183: 1–26

Otto L, Zimmerman JTF, Furnes GK, Mork M, Saetre R, Becker G (1990) Review of the physical oceanography of the North Sea. *Netherlands Journal of Sea Research* 26: 161–238, http://dx.doi.org/10.1016/0077-7579(90)90091-T

Purcell JE (1988) Quantification of *Mnemiopsis leidyi* (Ctenophora, Lobata) from formalin-preserved plankton samples. *Marine Ecology Progress Series* 45: 197–200, http://dx.doi.org/10.3354/meps045197

Purcell JE, Shiganova TA, Decker MB, Houde ED (2001) The ctenophore *Mnemiopsis* in native and exotic habitats: US estuaries versus the Black Sea basin. *Hydrobiologia* 451: 145–176, http://dx.doi.org/10.1023/A:1011826618539

Reusch TBH, Bolte S, Sparwel M, Moss AG, Javidpour J (2010) Microsatellites reveal origin and genetic diversity of Eurasian invasions by one of the world's most notorious marine invader, *Mnemiopsis leidyi* (Ctenophora). *Molecular Ecology* 19: 2690–2699, http://dx.doi.org/10.1111/j.1365-294X.2010.04701.x

Roohi A, Kideys AE, Sajjadi A, Hashemian A, Pourgholam R, Fazli H, Khanari AG, Eker-Develi E (2010) Changes in biodiversity of phytoplankton, zooplankton, fishes and macrobenthos in the Southern Caspian Sea after the invasion of the ctenophore *Mnemiopsis leidyi*. *Biological Invasions* 12: 2343–2361, http://dx.doi.org/10.1007/s10530-009-9648-4

Schaber M, Haslob H, Huwer B, Harjes A, Hinrichsen HH, Koster FW, Storr-Paulsen M, Schmidt JO, Voss R (2011) The invasive ctenophore *Mnemiopsis leidyi* in the central Baltic Sea: seasonal phenology and hydrographic influence on spatio-temporal distribution patterns. *Journal of Plankton Research* 33: 1053–1065, http://dx.doi.org/10.1093/plankt/fbq167

Seuront L, Schmitt F, Lagadeuc Y, Schertzer D, Lovejoy S (1999) Multifractal analysis as a tool to characterize multiscale inhomogeneous patterns. Example of phytoplankton distribution in turbulent coastal waters. *Journal of Plankton Research* 21: 877–922, http://dx.doi.org/10.1093/plankt/21.5.877

Seuront L, Gentilhomme V, Lagadeuc Y (2002) Small-scale nutrient patches in tidally mixed coastal waters. *Marine Ecology Progress Series* 232: 29–44, http://dx.doi.org/10.3354/meps232029

Shiganova TA (1998) Invasion of the Black Sea by the ctenophore *Mnemiopsis leidyi* and recent changes in pelagic community structure. *Fisheries Oceanography* 7: 305–310, http://dx.doi.org/10.1046/j.1365-2419.1998.00080.x

Sullivan LJ, Gifford DJ (2009) Preservation of the larval ctenophore *Mnemiopsis leidyi* A. Agassiz (Ctenophora, Lobata). *Journal of Plankton Research* 31: 921–926, http://dx.doi.org/10.1093/plankt/fbp031

Tendal OS, Jensen KR, Riisgård HU (2007) Invasive ctenophore *Mnemiopsis leidyi* widely distributed in Danish waters. *Aquatic Invasions* 2: 455–460, http://dx.doi.org/10.3391/ai.2007.2.4.19

Van Ginderdeuren K, Hostens K, Hoffman S, Vansteenbrugge L, Soenen K, De Blauwe H, Robbens J, Vincx M (2012) Distribution of the invasive ctenophore *Mnemiopsis leidyi* in the Belgian part of the North Sea. *Aquatic Invasions* 7: 163–169, http://dx.doi.org/10.3391/ai.2012.7.2.002

Vinogradov ME, Shushkina EA, Musayeva EI, Sirokin PU (1989) New invader in the Black Sea – ctenophore *Mnemiopsis leidyi* (Agassiz). *Ocean Science* 29: 293–299

Waggett R, Costello J (1999) Capture mechanisms used by the lobate ctenophore, *Mnemiopsis leidyi*, preying on the copepod *Acartia tonsa*. *Journal of Plankton Research* 21: 2037, http://dx.doi.org/10.1093/plankt/21.11.2037

Wang Z, Thiebaut E, Dauvin J-C (1995) Spring abundance and distribution of the ctenophore *Pleurobrachia pileus* in the Seine estuary: advective transport and diel vertical migration. *Marine Biology* 124: 313–324, http://dx.doi.org/10.1007/BF00347135

Wolff WJ (2005) Non-indigenous marine and estuarine species in the Netherlands. *Zoologische Mededelingen Leiden* 79: 1–116

The following supplementary material is available for this article:

Table 1S. Records of *Mnemiopsis leidyi* along the French 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_Antajan_etal_Supplement.xls