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Ocean current connectivity propelling the secondary spread of a marine invasive comb jelly across western Eurasia

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Abstract

Aim: Invasive species are of increasing global concern. Nevertheless, the mechanisms driving further distribution after the initial establishment of non-native species remain largely unresolved, especially in marine systems. Ocean currents can be a major driver governing range occupancy, but this has not been accounted for in most invasion ecology studies so far. We investigate how well initial establishment areas are interconnected to later occupancy regions to test for the potential role of ocean currents driving secondary spread dynamics in order to infer invasion corridors and the source–sink dynamics of a non-native holoplanktonic biological probe species on a continental scale.

Location: Western Eurasia.

Time period: 1980s–2016.

Major taxa studied: 'Comb jelly' *Mnemiopsis leidyi*.

Methods: Based on 12,400 geo-referenced occurrence data, we reconstruct the invasion history of *M. leidyi* in western Eurasia. We model ocean currents and calculate their stability to match the temporal and spatial spread dynamics with large-scale connectivity patterns via ocean currents. Additionally, genetic markers are used to test the predicted connectivity between subpopulations.

Results: Ocean currents can explain secondary spread dynamics, matching observed range expansions and the timing of first occurrence of our holoplanktonic non-native biological probe species, leading to invasion corridors in western Eurasia. In northern Europe, regional extinctions after cold winters were followed by rapid recolonizations at a speed of up to 2,000 km per season. Source

areas hosting year-round populations in highly interconnected regions can re-seed genotypes over large distances after local extinctions.

Main conclusions: Although the release of ballast water from container ships may contribute to the dispersal of non-native species, our results highlight the importance of ocean currents driving secondary spread dynamics. Highly interconnected areas hosting invasive species are crucial for secondary spread dynamics on a continental scale. Invasion risk assessments should consider large-scale connectivity patterns and the potential source regions of non-native marine species.

KEYWORDS

biological invasions, gelatinous zooplankton, invasion corridors, invasive species, jellyfish, marine connectivity, *Mnemiopsis leidyi*, range expansion, source populations, source–sink dynamics

1 | INTRODUCTION

The rate of species translocations and the successful establishment of non-native organisms in new recipient habitats is increasing (Seebens et al., 2017), impacting biodiversity and ecosystem functioning worldwide (Molnar, Gamboa, Revenga, & Spalding, 2008). The transport and release of organisms via ballast water in cargo ships is regarded as a primary vector for long-distance translocations of non-native species in the marine environment (Molnar et al., 2008; Seebens, Schwartz, Schupp, & Blasius, 2016), and the invasion probabilities of ecosystems have subsequently been calculated based on shipping activity and the matching of environmental characteristics (e.g., Keller, Drake, Drew, & Lodge, 2011; Seebens et al., 2016). However, it has also been shown that ocean currents are essential for the transport, hence for connectivity of marine plankton organisms from differing subpopulations (Gaylord & Gaines, 2000) at regional (Grosholz, 1996; Wasson, Zabin, Bedinger, Diaz, & Pearse, 2001) and global scales (Dawson, Sen Gupta, & England, 2005; Van Gennip et al., 2017; Villarino et al., 2018; Wood, Paris, Ridgwell, & Hendy, 2014). Therefore, transport via ocean currents should also be considered for the dispersal of invasive species (Grosholz, 1996; Wasson et al., 2001), as documented for lionfish in the Caribbean (Cowen, Paris, & Srinivasan, 2006; Johnston & Purkis, 2011). However, it remains a challenge to link ocean currents to observational data (Pineda, Hare, & Sponaugle, 2007), especially following the range expansion of a non-native species in real time over large spatial scales, and to identify previously unknown source areas.

Biophysical models have been used to infer connectivity patterns by following the trajectories of particles over time, which are assumed to represent the drifting plankton species in question (e.g., David et al., 2015; Dawson et al., 2005; Lee et al., 2013). However, model outcomes are highly dependent on background information, such as release area, depth strata of occurrence, drift duration and small-scale model accuracy, where conclusions can vary significantly depending on such input parameters (Simons, Siegel, & Brown, 2013). In the present study, we apply a general ocean current modelling approach that is not dependent on a priori assumptions about the biological properties of our species in question. Average current directions and velocities are used as a proxy for general circulation patterns, combined with an estimation of the stability of these current patterns. This new approach, which has so far been applied only at a regional scale (Lehmann & Hinrichsen, 2000), is used as an indication of the persistence and potential large-scale connectivity between areas. We evaluate estimated connectivity patterns against empirical observations using the comb jelly *Mnemiopsis leidyi* A. Agassiz, 1865, a holoplanktonic gelatinous zooplankton organism that is dispersed by prevailing ocean currents throughout its life, as a biological 'probe'. With this approach, we aim to test for the role of ocean currents for the secondary spread dynamics of marine invasive species in general.

Mnemiopsis leidyi is an ideal candidate for use as a biological 'probe' species owing to its ability to cope with varying biotic and abiotic conditions, allowing this versatile and adaptable species to tolerate an increased environmental envelope. Additionally, greater public awareness has led to comprehensive but as yet unsynthesized knowledge about its distribution. Native to the east coast of the Americas (Costello, Bayha, Mianzan, Shiganova, & Purcell, 2012), two independent invasion events have introduced *M. leidyi* populations to southern and northern areas of western Eurasia (e.g., Bayha et al., 2015; Reusch, Bolte, Sparwel, Moss, & Javidpour, 2010). In the Black Sea, *M. leidyi* were first recorded during the 1980s (Pereladov, 1988), whereas in northern Europe, *M. leidyi* were first observed a quarter of a century later, in 2005 (e.g., Faasse & Bayha, 2006). With the associated large-scale ecosystem changes attributed to the high abundance of *M. leidyi* in the Black Sea (Kideys, 2002), it was considered among the most severe invasive non-native species worldwide (Lowe, Browne, Boudjelas, & De Poorter, 2000). It is therefore of concern that *M. leidyi* populations have recently reached exceptionally high abundances in particular regions of Northern Europe (Riisgård, Bøttiger, Madsen, & Purcell, 2007; van Walraven, Langenberg, & van der Veer, 2013), leading to documented changes in food web structure and function (Tiselius & Møller, 2017). As a result of its high reproductive capacity, with earlier maturation in invaded compared with native habitats (Jaspers, Marty, & Kiørboe, 2018) and simultaneous self-fertilization (Jaspers, Costello, & Colin, 2015), *M. leidyi* is prone to rapid population increase and is therefore extremely responsive over large spatial scales within short time frames. Although salinity has been shown to restrict establishment in certain regions of northern Europe (Jaspers, Møller, & Kiørboe, 2011) and that winter temperatures < 4 °C may lead to a die-off of southern invasive subpopulations (Shiganova et al., 2001), the factors governing the range occupancy and spread dynamics of *M. leidyi* populations remain unresolved.

We hypothesize that ocean current connectivity can explain secondary spread dynamics and invasion corridors of *M. leidyi* across large spatial

scales. To test this hypothesis, we applied an interdisciplinary approach including ocean current modelling, original field investigations and literature occurrence data, statistical analyses and molecular population genetics. The range expansion of *M. leidyi* was reconstructed based on a comprehensive occurrence database, with 12,400 records throughout western Eurasia covering the past 35 years. A dramatic range contraction and subsequent recolonization observed during the early 2010s allowed for disentanglement of the effect of winter temperature on the distribution of *M. leidyi* in Northern Europe. We hypothesize that cold winter conditions caused a range contraction and that two cold winters in a row exacerbated the impact. We used this natural experiment as a proof of concept for the role of ocean currents in secondary spread dynamics and applied population genetic analyses to verify source regions for recolonization events. The identification of *M. leidyi* source areas and their connectivity are important to (a) predict secondary spread through ocean currents, (b) identify potential barriers to its current spread, (c) identify high-risk areas for further invasions and (d) assess possible mitigation strategies for non-native marine species in general.

2 | METHODS

2.1 | Geo-referenced distribution data

To reconstruct the distributional range and timing of the first occurrence of the non-native comb jelly *M. leidyi*, we compiled a database using 12,400 geo-referenced unpublished (60%) and published (40%) observations from western Eurasia (see Supporting Information Appendices S1 and S2). Unpublished data were collected as presence/absence records by the authors and their institutes as part of dedicated gelatinous zooplankton or ichthyoplankton surveys, zooplankton investigations, and diving observations by citizen science projects with photographic documentation or other confirmed sightings evaluated by experts using morphology and/or DNA analyses. Published data were based on a comprehensive literature review using the Web of Science and Google Scholar search engines for the search terms 'Mnemiopsis*' or 'ctenophore*' or 'comb*', filtered with 'invasive*' or 'non-native*' and applying forward and backward citation search. Additionally, the bibliographies of all co-authors were searched (Supporting Information Appendix S1: Reference list). Data were extracted from the publications using Web Plot Digitizer (https://automeris.io/WebPlotDigitizer/) or were supplied directly by the authors. A detailed methodology section for all individual data points is given in Supporting Information Appendix S2, Table S1. All confirmed data from 1982 to 2016 are visualized with regions of presence and absence indicated by colour code (Figure 1). Consecutive confirmed presence observations are used as the border for occurrence regions (ArcGIS, v.10.1). For Northern Europe, we have presence/absence data for a series of stations/investigation areas that have been covered at the same time of the year using

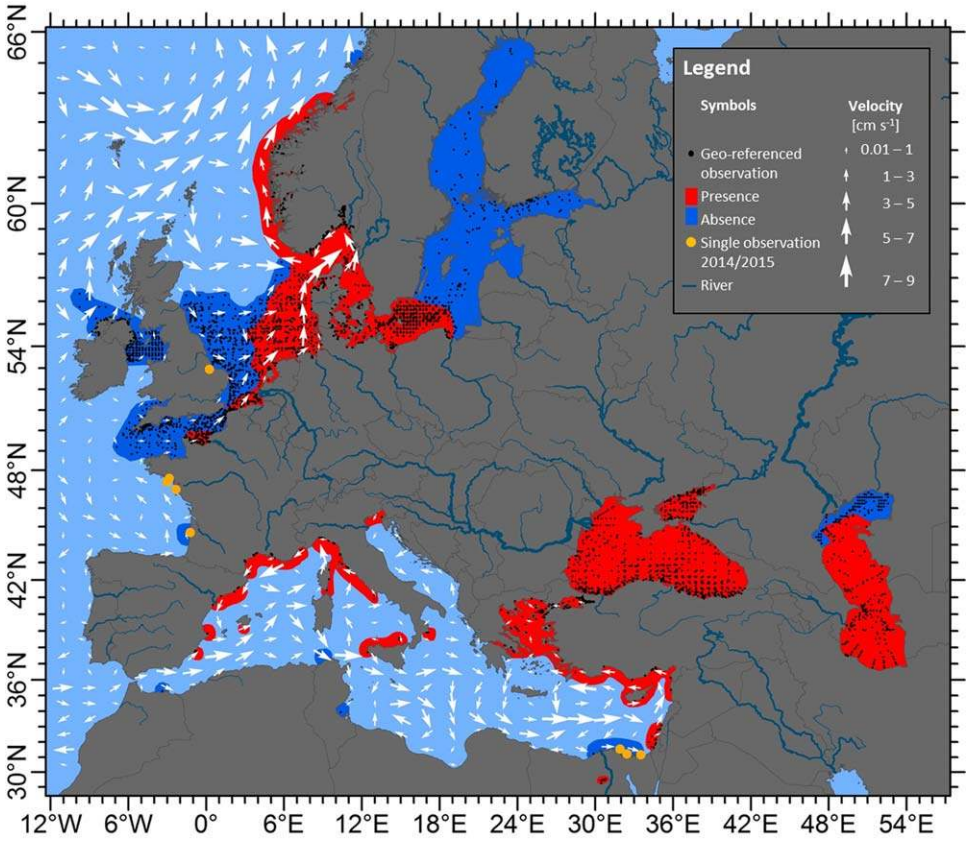

FIGURE 1 Distribution of *Mnemiopsis leidyi* throughout western Eurasian waters for the period from 1990 to the present (November 2016) based on 12,400 geo-referenced observations (black dots), with regions of presence (red) and absence (dark blue) highlighted. Average current speed and direction (white arrows) are shown to depict general circulation patterns (excluding Baltic, Caspian and Black Seas) generated from the CMEMS model. Single observations of a few animals or environmental DNA during 2014–2015 are indicated (orange dots); see Supporting Information Appendix 2, Table S1 for reference

comparable methodologies. These time-series data have been used to examine large-scale source–sink dynamics, range expansions and recolonization events of *M. leidyi* (see section 2.3 Statistical analyses of winter temperatures; Supporting Information Appendix S2, Table S1; Appendix S3, Figure S1).

2.2 | Hydrodynamic modelling

We modelled general surface ocean currents for the upper 50 m of the water column, concomitant with supporting evidence that *M. leidyi* frequently occurs at this depth stratum (Haraldsson et al., 2013). The velocity and direction of ocean currents were calculated using outputs from the ocean general circulation model (OGCM), provided through the Copernicus Marine Environment Monitoring Service (CMEMS, http://marine.copernicus.eu) for the period 1 January 2007 to 31 December 2014. We used a global configuration (ORCA12) at 1/12° horizontal resolution (grid sizes: Mediterranean Sea *c.* 10 km; North Sea *c.* 8 km) and 50 vertical levels, based on the NEMO model (Madec, 2008). The model was forced by 3-hourly winds and corresponding heat and freshwater fluxes from the European Centre for Medium-Range Weather Forecasts (ECMWF) operational atmosphere model. Numerical models naturally contain errors not only because of their physical simplifications and numerical limitations but also because of the nonlinear character of the ocean. To overcome this, a range of ocean observations (from satellite to *in situ* data) were assimilated using a Kalman filter approach, leading to a realistic representation of the upper ocean.

The calculated average current velocities allow a general estimate for connectivity between regions, hence the existence of characteristic persistent circulation patterns. However, no direct information about their variability or event-driven changes in flow regimes can be evaluated. Therefore, current stabilities (Lehmann & Hinrichsen, 2000) were calculated using:

$$B = \frac{\left(\bar{u}^{\,2} + \bar{v}^{\,2}\right)^{0.5}}{\frac{1}{n}\sum_{i=1}^{n}\left(u_i^2 + v_i^2\right)^{0.5}} \quad (1)$$

where $\bar{u} = \frac{1}{n}\Sigma\, u$ and $\bar{v} = \frac{1}{n}\Sigma\, v$ are the average components of the flow, and n is the number of current observations at the location under consideration. The vectorial mean value of individually observed current vectors and the arithmetic mean velocity are obtained by averaging the speeds. This estimate is a measure of the variability of the general current patterns; hence, it is a proxy for connectivity between regions. High stabilities (values close to one) indicate strong evidence for persistent circulation patterns and, consequently, strong connectivity between neighbouring areas; vice versa, low stability values ($< .3$) indicate high variability of currents; hence, low connectivity between areas (Figure 2). For display purposes, current velocities and directions were averaged with 2° longitudinal and 1° latitudinal resolution for all regions except the highly dynamic Skagerrak (resolution: 1° longitudinal; 1° latitudinal).

Additionally, we calculated temperature anomalies and average current velocities (in metres per second) for the coldest winter months in Northern Europe (January–March) based on data for the years 2007–2015. We did so because cold winter conditions have been shown to lead to population die-offs for southern invasive subpopulations (Shiganova et al., 2001), and overwintering adults are responsible for establishing the next generation (Costello, Sullivan, Gifford, Van Keuren, & Sullivan, 2006). Average winter temperatures for the upper 50 m were obtained from the CMEMS model (see above) for all but the Baltic Sea, for which BSIOM data were used (Supporting Information Appendix S3).

2.3 | Statistical analyses of winter temperatures

To investigate the effect of winter temperature on the distribution of *M. leidyi* in northern Europe, datasets from 13 selected monitoring stations/regional sampling programmes covering the entire distributional range (English Channel, 49.5 °N to Bergen, 60 °N and the central Baltic Sea 15.8 °E) were compiled and included in all statistical analyses (Supporting Information Appendix 3, Figure S1). These data consist of consecutive presence/absence observations during the *M. leidyi* high-abundance season (summer/autumn) for the years 2007–2015 and represent all comprehensive datasets available in Northern Europe. For statistical analyses, this information has been condensed to one value per station per year, representing either the presence (one) or the absence (zero) of *M. leidyi*. We used two expressions of winter temperature conditions as independent variables: the average winter temperature of the preceding winter (model 1) and the average winter temperatures of the two preceding winters (model 2). The latter model was chosen to investigate our hypothesis that two cold winters in a row might have a cumulative impact on the probability of *M. leidyi* occurrence. We included the same number of years for 1- and 2-year average winter temperatures in model 1 and model 2, respectively (years 2008–2015, $n = 104$). The probability of the presence/absence of *M. leidyi* has been analysed using generalized linear models assuming binomial distributions (SAS v.9.3). Owing to collinearity between the two expressions of winter conditions, their effects on the probability of occurrence were tested separately, using the odds ratios as an estimate for likelihood of occurrence. Hence, parameter estimates for the logistic regression were also used to estimate the odds ratio for temperature, which quantifies how much a 1 °C increase will increase the likelihood of encountering *M. leidyi*. Additionally, we estimated the critical winter temperature, which is the temperature at which there is a 50% likelihood of encountering *M. leidyi* (Supporting Information Appendix S3). This is meaningful only for stations where both presence and absence were recorded. We include station as a fixed factor in the model together with the temperature estimate (Supporting Information Appendix S3).

2.4 | Molecular analyses

In order to identify the source of individuals involved in a recolonization event in Northern Europe during 2014, animals were collected in Belgium, Bergen (Norway), Kiel (Germany) and the Bornholm Basin (central Baltic Sea) during summer/autumn 2014. DNA was extracted from GFF or coffee filters, and seven microsatellite loci (Reusch et al.,

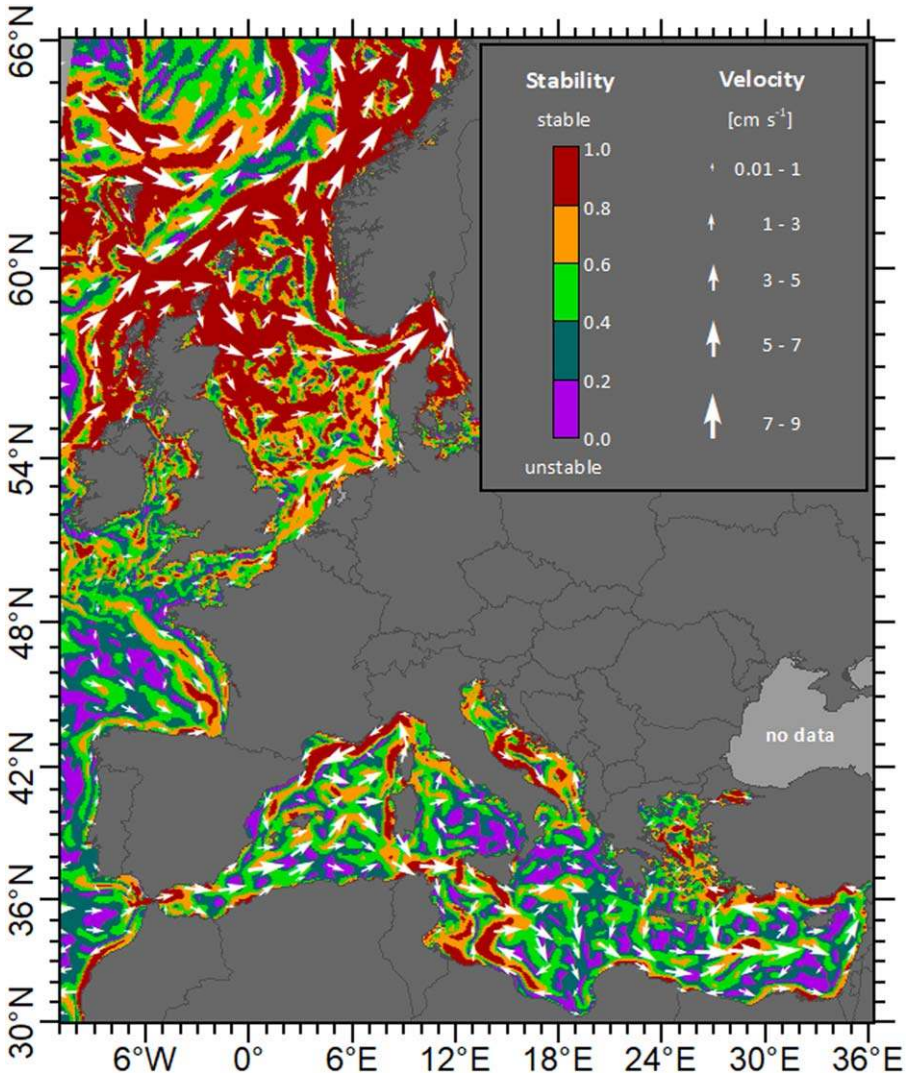

FIGURE 2 Stability of ocean currents (colour code), ranging from one (very stable, orange/red) to zero (unstable, pink), and ocean current directions and velocities (arrow, in metres per second; see Figure 1) for the upper 50 m of the water column (CMEMS ocean model, 2007–2014 mean)

2010) were used for genotyping. The analyses were supplemented with samples from two locations in the Baltic Sea (Kiel, Germany; Bornholm Basin, central Baltic) before the range contraction (2008–2010) and were re-analysed along with the newly extracted 2014 samples (Supporting Information Appendix S3). General ITS1 primers, previously used for ctenophore species identification, were used for species verification in the North Sea following published protocols (Reusch et al., 2010; Supporting Information Appendix S3). The sequence data are deposited at GenBank (accession numbers: KY204070–KY204083; Supporting Information Table S3).

3 | RESULTS AND DISCUSSION

Mnemiopsis leidyi has been present in west Eurasian waters since the early 1980s. First observed in the Black Sea, *M. leidyi* quickly spread and established populations throughout adjacent waters, including the eastern Mediterranean Sea and the Caspian Sea (Table 1). In Northern Europe, the first sightings of *M. leidyi* were made a quarter of a century later compared with the South. During 2005, *M. leidyi* was first sighted in the extended North Sea area, ranging from northern France to south Norway, and by 2008 animals were recorded throughout large areas of Northern Europe (Table 2). The two invasions have been regarded as independent initial ballast-water-mediated translocations, with the invasive Black Sea population stemming from the Gulf of Mexico region, whereas the northern invasion can be traced genetically to the native northeast U.S. coast population (e.g., Bayha et al., 2015; Reusch et al., 2010).

3.1 | Ocean currents and secondary spread

Hydrodynamic modelling shows strong connectivity via ocean currents in the North Sea area (Figure 1). Stable surface currents interconnect the English Channel, the Southern North Sea and Norway by a persistent flow (stability $>$ .6, range: 0–1; Figure 2). This current connects the Dutch and German coasts via the German Bight off Helgoland

TABLE 1 Chronology of first *Mnemiopsis leidyi* records during the southern invasion into western Eurasia

Year	Region	Reference
1982	Black Sea	Pereladov (1988) as cited by Shiganova et al. (2001)
1988	Sea of Azov	Studenikina, Volovik, Miryozan, and Luts (1991)
1991–1992	Sea of Marmara	Shiganova (1994)[a]
1990	Aegean Sea	Shiganova et al. (2001)
1992	E Mediterranean Sea: Mersin, Turkey	Uysal and Mutlu (1993)
1993	Syria	Shiganova (1997)
1993	Turkey: entire coast	Kideys and Niermann (1994)
1995–1999	Caspian Sea	Ivanov et al. (2000); see Bilio and Niermann (2004)
2005	France: Berre Lagoon	This study (Supporting Information Appendix 2, Table S1)
2005	N Adriatic Sea	Shiganova and Malej (2009)
2009	Italy: Tyrrhenian and Ligurian Seas	Boero et al. (2009)
2009	Corse	Fuentes et al. (2010)
2009	Spain: Balearic coast	Fuentes, Atienza, Gili, and Purcell (2009)
2009	Israel: entire coast	Galil, Kress, and Shiganova (2009)
2015	Egypt	This study (Supporting Information Appendix 2, Table S1)

[a]No monitoring before this time point; probable presence of *M. leidyi* since 1989 (see Supporting Information Table S1).

TABLE 2 Chronology of first *Mnemiopsis leidyi* recordings during the northern invasion into western Eurasia

Time	Location	Region	Reference
2005			
7	Dutch coast, The Netherlands	S North Sea	Faasse and Bayha (2006)
8	Nissum Fjord, Denmark	SE North Sea	Tendal, Jensen, and Riisgård (2007)
9	Le Havre, France	English Channel	Antajan et al. (2014)
10	Oslo Fjord, SE Norway	Skagerrak	Oliveira (2007)
2006			
6	Helsingør, Denmark	Kattegat	Tendal et al. (2007)
8–12	Horsens Fjord, Denmark	Kattegat[a]	This study
8–11	Tjärnö, Sweden	Skagerrak	Hansson (2006)
9/11/12	Eastern German coast	SW Baltic Sea[b]	Kube, Postel, Honnef, and Augustin (2007)
10/11	Kiel Bight, Germany	W Baltic Sea[c]	Javidpour, Sommer, and Shiganova (2006)
10–11	Gullmar Fjord, Sweden	Skagerrak	Vergara-Soto et al. (2010)
11	Helgoland, Germany	SE North Sea[d]	Boersma, Malzahn, Greve, and Javidpour (2007)
Autumn	Bergen, Norway	SW Norway	Hansson (2006)
2007			
2–5	Bornholm Basin	SC Baltic Sea	Kube et al. (2007)
2–3	SE Gotland Basin	SC Baltic Sea	Kube et al. (2007)
8	Zeebrugge, Belgium	S North Sea	van Ginderdeuren et al. (2012)
8/9	Limfjord, Denmark	N Denmark[e]	Riisgård et al. (2007)
9	Pomeranian Bay, Poland	S Baltic Sea[f]	This study
10/11	Gdansk Bay, Polish coast	SE Baltic Sea[g]	Janas and Zgrundo (2007)
2008			
9	Trondheim Fjord, Norway	Norwegian Sea	Hosia and Falkenhaug (2015)
2014			
	NE, Bay of Biscay, France	Bay of Biscay	This study
	Wash Bay, U.K.[h]	SE U.K.	Personal communication, Veronique Creach, CEFAS, U.K.

Note. Time is indicated as year and month of first occurrence. Densities (as *M. leidyi* per cubic metre): [a]380; [b]dense accumulations; [c]92; [d]0.1; [e]*c.* 1,000; [f]5; [g]*c.* 20; [h]confirmed by environmental DNA.

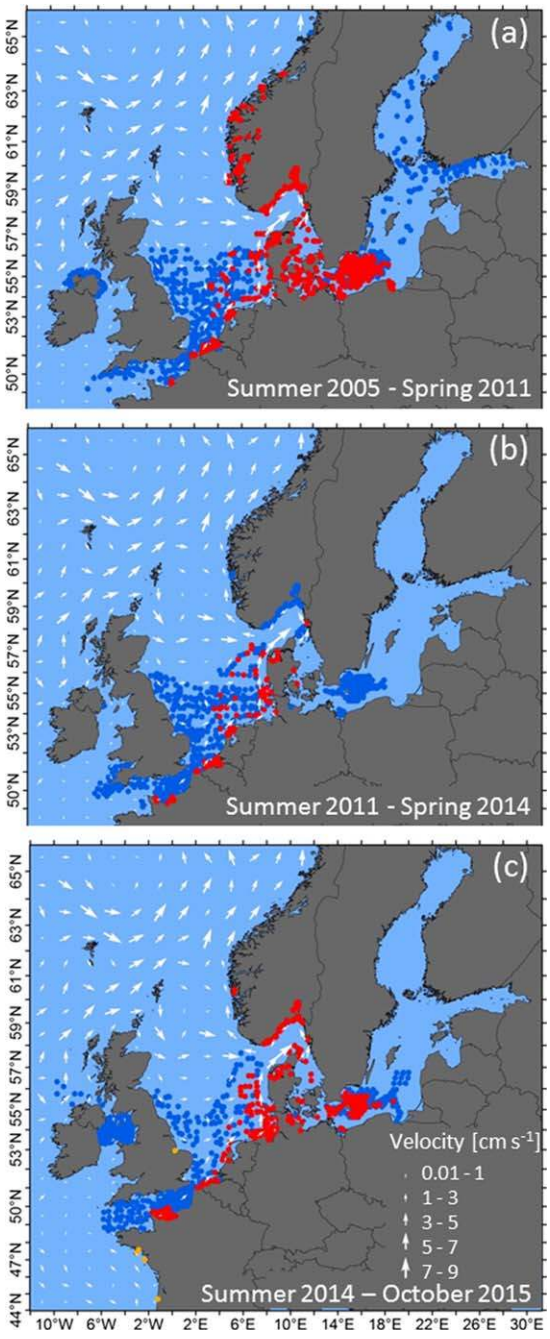

FIGURE 3 Distribution of *Mnemiopsis leidyi* throughout northern Europe for three time periods after first sightings in 2005 up to the present. (a) Maximal distribution during the initial invasion period up to spring 2011. (b) A cold period with major contraction of the distribution range from summer 2011 to spring 2014. (c) Realization of its previous distribution after one warm winter during 2013–2014 depicted for summer 2014–October 2015. Orange dots in (c) indicate sporadic sightings in 2014–2015

towards north-west Denmark, continuing with an anticlockwise gyre through the Skagerrak and then northwards along the western Norwegian coast (Figure 1). The first sightings of *M. leidyi* during 2005 (Figure 1; Table 2) match this overall current connectivity pattern.

A sudden range contraction in Northern Europe provided the opportunity for a natural experiment to test the hypothesis that the secondary spread of *M. leidyi* is realized by connectivity via ocean currents covering large spatial scales. During 2008–2010, populations existed along the entire distribution range in northern Europe up to mid-Norway (Figures 1–3a, and 4; Table 2; Supporting Information Table S1). However, after a series of cold winters in the early 2010s, the *M. leidyi* range contracted to a small core area in the southern North Sea and the English Channel outside U.K. waters (Figures 3b and 4; Supporting Information Table S1). The populations in these areas remained throughout the year (Supporting Information Table S1). After one exceptionally warm winter in 2013–2014 with positive temperature anomalies (Figure 5), the range occupancy of *M. leidyi* expanded to its pre-2010 distribution by summer/autumn 2014 (Figures 3c and 4). This swift recolonization suggests that the spread was caused by advection via currents characterized by high stability estimates, forming invasion corridors in Northern Europe (Figures 1–5; Supporting Information Table S1).

3.2 | Range limits attributable to winter temperatures and connectivity patterns

Observations gathered since 2007 from 13 regional monitoring stations in northern Europe (Figure 4; Supporting Information Appendix 3, Figure S1) were analysed to examine the relationship between winter temperatures and the occurrence of *M. leidyi*. Logistic regression revealed that the average winter temperature of the upper water column (0–50 m) in the preceding winter (model 1) and the cumulative effect of the two preceding winters (model 2) had a significant effect on the probability of *M. leidyi* occurrence ($p < .05$; Supporting Information Appendix 3, Table S3). The odds ratio estimate in the latter model is three orders of magnitude higher compared with the single-winter temperature effect (odds ratios: model 1 = 3.9; model 2 = 7,882). Hence, the cumulative winter temperatures of two cold winters in a row have a much stronger impact on the likelihood of *M. leidyi* occurrence (Supporting Information Appendix 3, Table S3). The parameter estimates from our logistic regression enabled us to estimate the temperature range above which there is a 50% or greater probability for the occurrence of *M. leidyi*. The critical temperature range for *M. leidyi* lies between 1.3 and 2.6 °C when considering the preceding winter temperature and between 1.4 and 2.7 °C when considering the average temperature of the two preceding winters (Supporting Information Appendix 3, Table S4). Hence, from 2011 to 2013, *M. leidyi* was restricted to localities in northern Europe (Figure 3b) that were characterized by higher winter temperatures (Figures 4 and 5; Supporting Information Appendix 3, Figure S2).

Although the average current velocity stability estimates in the North Sea are very high, the intensity of this connectivity varies between years. Warmer winters display a stronger connectivity and net transport than colder winters (Figure 5). Therefore, current-driven connectivity patterns during winter might also play an important role in the range expansions and population dynamics of *M. leidyi* in northern Europe. *Mnemiopsis leidyi* was observed simultaneously in large areas of northern Europe in 2005 (Table 2). However, *M. leidyi* first attained its maximal range occupancy in 2007 and 2008, when areas such as

Location / Year	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
Le Havre, France	+	+	+	+	+	+	+	+	+	+	+
Lake Grevelingen, Netherlands	+	+	+	+	+	+	+	+	+	+	+
Texel, Dutch Wadden Sea	-	+	+	+	+	+	+	+	+	+	+
Helgoland, German Bight	-	+	+	+	+	+	+	+	+	+	+
Hörnum Deep, Germany	-	-	+	+	+	+	+	+	+	+	+
Meldorfer Bight, Germany	-	-	+	+	+	+	+	+	+	+	+
Sylt, Germany	n.a.	n.a.	+	+	+	+	+	+	+	+	+
Bergen, Norway	n.a.	+	+	+	+	+	-	-	-	+	+
Kristian Sand, Norway	-	+	+	+	+	+	-	-	-	+	+
Oslo Fjord, Norway	+	+	+	+	+	+	-	-	-	+	+
Kristineberg, Sweden	n.a.	+	+	+	+	+	-	-	-	+	+
Kiel Bight, Germany	-	+	+	+	+	+	-	-	-	+	+
Bornholm Basin, Baltic Sea	-	-	+	+	+	+	-	-	-	+	+
Temperature bins (°C)	≤2	2-4.5	4.5-7	>7							

FIGURE 4 Spatio-temporal differences in occurrence of the invasive comb jelly *Mnemiopsis leidyi* across its distribution range throughout northern Europe. Presence (+) and absence (−) during summer/autumn are indicated for the years 2005–2015 at 13 monitoring stations (for references, see Supporting Information Appendix 2, Table S1; Appendix 3, Figure S1). Average meteorological winter temperatures of the upper 50 m of the water column are expressed by temperature bins (see key) from the CMEMS MERCATOR model output for all but the Bornholm Basin, where BSIOM data were used. n.a.: no data

the central Baltic Sea and the Norwegian Coast up to 63.5 °N were successfully colonized (Figure 4; Table 2). In these years, the current connectivity during winter was strong, along with a very high temperature anomaly during January–March (Figure 5a; Supporting Information Appendix 3, Figure S2). A similar situation occurred from January to March 2014 (Figure 5c), when *M. leidyi* recolonized large areas of northern Europe during one season (Figure 3c). In contrast, colder winters, as observed during 2011, displayed limited connectivity and much lower current speeds compared with warmer winters (Figure 5b).

3.3 | Molecular confirmation of connectivity patterns

To confirm whether populations in north-western Europe became extinct during colder winters, we conducted molecular analyses to describe the population structure and the degree of population differentiation before and after the cold snap. Before the cold period, the population structure showed a significant difference between the Baltic Sea and North Sea populations (Reusch et al., 2010). Re-analyses of existing samples before the cold-winter period and during the recolonization in 2014 showed that the distinct *M. leidyi* gene pool present in the Baltic Sea before 2011 became extinct and was replaced by a new, significantly different ($p < .0001$) North Sea genotype during 2014 (Table 3). In detail, the two Baltic Sea *M. leidyi* subpopulations showed significant population differentiation before and after the cold period (Kiel: 2010 *vs* 2014, $F_{ST} = .036$, $p < .0001$; and Bornholm Basin: 2010 *vs* 2014, $F_{ST} = .036$, $p < .0001$) and when comparing the Baltic Sea 2010 and North Sea 2014 subpopulations ($F_{ST} > .02$, $p < .03$). However, no population differentiation was found when comparing North and Baltic Sea locations during 2014 ($F_{ST} < .006$, $p > .3$). The observed lack of population structure throughout our northern European sampling sites suggests recolonization from a single source region and population during 2014, and it provides evidence that this spread was genuine and not an artefact from local populations during 2011–2013 (Figure 3; Table 3). It cannot be ruled out that animals observed in the Baltic Sea during 2014 were directly seeded via ballast water from the North Sea. However, this is unlikely, as the timing of reoccurrence in the extended Baltic Sea area (Supporting Information Appendix 2, Table S1) and the general circulation pattern (Figures 1 and 2) are in agreement in supporting current-mediated transport instead of ballast-water release. Therefore, the speed and the extent of the area that was reoccupied in 2014, together with the replacement of the pre-2010 gene pool in the Baltic Sea, support our findings that ocean current connectivity was the main vector behind this recolonization event.

3.4 | High-abundance areas as hubs for secondary spread

We found that *M. leidyi* populations with high abundances and year-round presence are characterized by warmer winter temperatures (Figure 4; Supporting Information Appendix 3, Figure S1). In addition, they show strong interconnectivity with other areas of Northern Europe via ocean currents (Figures 1 and 2). These areas can be regarded as high-abundance source areas for *M. leidyi*, and they include the southern North Sea and the English Channel outside U.K. waters and, more specifically, the Dutch Wadden Sea, The Dutch Delta area, regions within the southern English Channel and the south-eastern North Sea/German Bight (Figure 4; Supporting Information Appendix 2, Table S1). Assuming that *M. leidyi* drift with the prevailing currents from these high-abundance areas at an observed speed of *c*. 0.25 m/s (Figure 5c), *M. leidyi* can potentially recolonize different areas after drifting distances of up to 2,000 km during a season. This corresponds to the observed recolonization distances of *M. leidyi* realized during 2014 from the North Sea to the central Baltic Sea and western Norway. This indicates that strong current connectivity provides an invasion corridor along the continental southern North Sea, interconnecting large areas of northern Europe.

Irrespective of intensive sampling effort, *M. leidyi* has not yet been found in the western North Sea (Supporting Information Table S2),

along the U.K. coast of the English Channel, the Irish and Celtic Seas, around Northern Ireland or in the eastern and northern Baltic Sea (Figure 1). Apart from the low-saline eastern and northern Baltic Sea, where salinity probably restricts establishment (Jaspers et al., 2011), these areas lie outside the highly interconnected high-abundance regions hosting *M. leidyi* aggregations with permanent year-round populations (Supporting Information Appendix 2, Table S1). It cannot be ruled out that episodic event-driven reversion of the general current circulation patterns can lead to the seeding of *M. leidyi* in those areas. For example, high-stability estimates of the southward-directed current along the eastern U.K. coast are reduced south of 52.5 °N (Figures 1 and 2). In this region, recent records using environmental DNA indicate the first presence of *M. leidyi* (Table 2), although monitoring activities with net sampling have not yet confirmed the presence (Supporting Information Appendix 2, Table S1). Also, despite the short distance across the English Channel and the close vicinity to high-abundance areas along the continental coast, *M. leidyi* have not been confirmed in U.K. waters (Figure 1). These regions again lie outside the strongly interconnected areas, similar to the Bay of Biscay, where *M. leidyi* were first observed in a few localities after 2014 (Figure 3; Table 2; Supporting Information Appendix 2, Table S1). Thus, ocean currents can both facilitate connectivity and act as a barrier to range expansion (Gaylord & Gaines, 2000). Consequently, expansions into less well-interconnected areas, as highlighted in the present study, might take much longer, in the order of 10–20 years (Figure 3; Table 2).

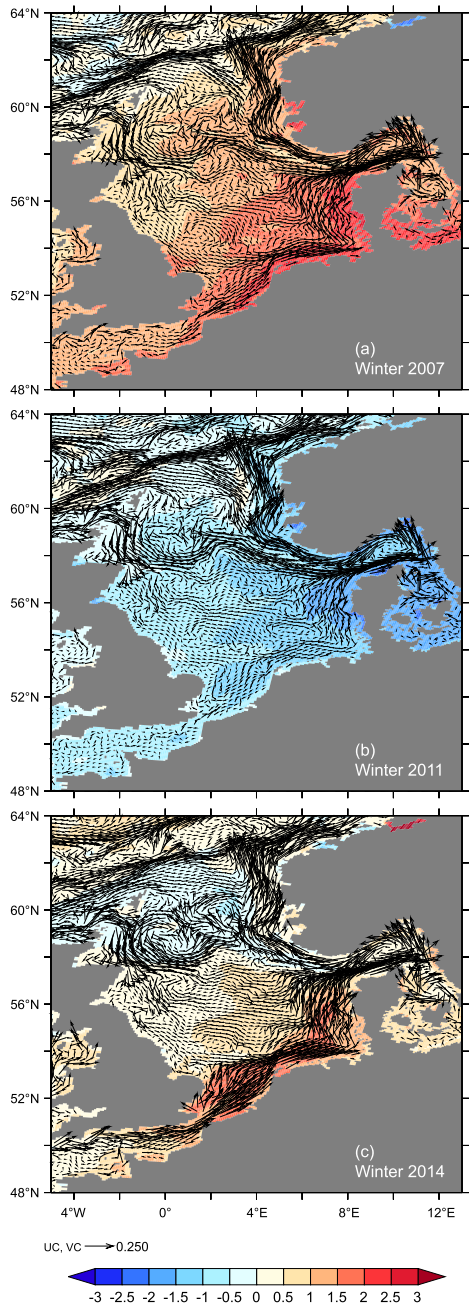

FIGURE 5 Temperature anomalies and current characteristics in northern Europe for representative cold and warm winters. Temperature anomalies (red = above, blue = below 2007–2014 average; in degree Celsius), current velocities and directions (black arrows; in metres per second) averaged for meteorological winter periods (January–March) for characteristic warm (a, c) and cold (b) winter periods in northern Europe. Data source: CMEMS model

TABLE 3 Pairwise F_{ST} matrix of *Mnemiopsis leidyi* microsatellite allele frequencies within Northern Europe, with significant differences

	BB10	BB14	Ki10	Ki14	Be14	No14
BB10	–					
BB14	.036***	–				
Ki10	.002	.031***	–			
Ki14	.030***	.006	.036***	–		
Be14	.034***	.003	.034***	.000	–	
No14	.021*	.000	.023**	.002	.006	–

Note. Structure analyses confirm two significant clusters grouping together the Baltic Sea before 2010 compared with all 2014 samples. Locations: Central (BB) and SW (Ki) Baltic Sea; SW North Sea, Belgium (Be); and Bergen, Norway (No), covering the years 2010 (10) and 2014 (14), with $^{*}p < .03$, $^{**}p < .01$, $^{***}p < .0001$, adjusted $\alpha = .03$.

3.5 | Correlation of Southern invasion history with ocean current connectivity

Mnemiopsis leidyi has established year-round populations in the Black and Caspian Seas (Supporting Information Appendix 2, Table S1), with maximal abundances of > 1 individual/L documented for the latter area (Bagheri, Niermann, Mansor, & Yeok, 2014; Roohi et al., 2010). The invasion history in the South suggests that, aided through ocean currents, *M. leidyi* spread from the Black Sea to the Sea of Azov in 1988. Owing to the positive water balance of the Black Sea, *M. leidyi* spread via surface water run-off into the Sea of Marmara, and onwards to the Aegean and the Eastern Mediterranean Seas (Table 1). *Mnemiopsis leidyi* was reported in high numbers in the Sea of Marmara in 1992, and within 2 years its presence was confirmed in the entire northeastern Mediterranean Sea (Table 1). The southern Aegean Sea is interconnected with the north-eastern Mediterranean Sea through a stable anticlockwise surface water gyre (upper 50 m) with a very persistent net

surface water transport in the central eastern Mediterranean Sea (Levantine Sea; Figures 1 and 2). The observed sequence of occurrence suggests transport by prevailing surface currents from the Aegean Sea through the central Levantine Sea to the coast of Syria, expanding north-west with the stable coastal current along the Turkish coastline (Figures 1 and 2; Table 2). An alternative hypothesis might suggest that *M. leidyi* spread from the Aegean Sea along the coastline of Turkey to Syria. However, owing to the very stable anticlockwise coastal current along the south-eastern Mediterranean coastline, the current-mediated dispersion of *M. leidyi* to the southwest is expected to be limited (Figures 1 and 2). Consequently, there is a 15-year gap before first sightings off Israel, and likewise, southwest propagation of *M. leidyi* to the Egyptian coast was first realized in 2015 (Table 1). Until now, and irrespective of monitoring activities, *M. leidyi* has not been observed in other areas along the North African coast off Tunisia and Morocco (Figure 1; Supporting Information Appendix 2, Table S1). This is in accordance with the major eastward current along the African coast, which shows high stability and little entrainment of waters from the Mediterranean coast off Europe where *M. leidyi* is present (Figures 1 and 2; Supporting Information Appendix 2, Table S1). However, discharge of ballast water and the seeding of animals in western areas (e.g., Morocco) make the entire African coastline prone to invasions by *M. leidyi* (Figures 1 and 2).

Areas along the European coast of the Mediterranean Sea were colonized much later, with the first records from the northern Adriatic Sea and southern France in 2005 and from Italy and Spain during 2009 (Table 1). Although surface water exchange along the European coast from east to west is limited, low current stability estimates indicate unstable flow fields, with occasional water transport from the Greek west coast to the southern coast of Italy (Figures 1 and 2). This might explain the observed delay in colonization and secondary spread, even though direct transport via ballast-water discharge from the Black Sea cannot be ruled out. Especially in lagoon systems along the north-western Mediterranean Sea, *M. leidyi* reaches high abundances in, for example, the Berre and Bages-Sigean Lagoons, France, and Mar Menor, Spain (Boero et al., 2009; Delpy et al., 2016; Marambio et al., 2013). Year-round populations also exist along the open Mediterranean coastline (e.g., in the Balearic Sea off Dénia, Spain) and in river deltas such as the Spanish Ebro Delta (Supporting Information Appendix 2, Table S1). For the Ebro river delta, abundances of $>$ 100 individuals/m^3 were reached in 2011 and 2012 (Supporting Information Appendix S2, Table S1). Although this is an order of magnitude lower in comparison with high-abundance areas in northern Europe and the Caspian Sea (Bagheri et al., 2014; Riisgård et al., 2007; Roohi et al., 2010; van Walraven et al., 2013), the occurrence of year-round populations since first recording indicates that *M. leidyi* is established especially along the Spanish Mediterranean coastline. However, additional high-abundance areas are likely to be detected, for example, along the Italian coast.

4 | CONCLUSIONS AND PERSPECTIVES

By using an invasive zooplankton species as a biological 'probe' to address the role of current-driven dispersal of planktonic organisms, we show that geographical and temporal sequences of first occurrences are in agreement with prevailing current circulation patterns. This is supported by molecular analyses documenting recolonization at a speed of up to 2,000 km during one season after regional extinctions throughout northern Europe. Such recolonizations are realized from high-abundance areas, where persistent *M. leidyi* populations are present year-round, characterized by warmer winter temperatures and high interconnectivity. Our findings support the importance of ocean current connectivity as a highly effective mechanism for the dispersal of non-native species, similar to the spread of invasive lionfish in the Caribbean (Cowen et al., 2006), rather than a series of ballast-water release events.

So far, invasion risk assessments have been based on shipping intensity, trade activities and environmental match (Keller et al., 2011; Seebens et al., 2016), focusing on ballast water as a primary invasion vector. Release of ballast water has taken place in various regions and has prompted the development of populations of *M. leidyi* and other organisms, such as crustaceans, bivalves and gastropods, in, for example, San Francisco Bay or Chesapeake Bay in the U.S.A. (as reviewed by Ruiz, Carlton, Grosholz, & Hines, 1997). However, the present study provides compelling evidence that the secondary spread dynamics via ocean connectivity should also be considered in risk assessments. Lately, it has been highlighted that management actions to mitigate invasion impacts should focus on invasion vectors and pathways (e.g., by pre-border control of ballast water; Ojaveer et al., 2015). We posit that an integrated management strategy should also take secondary spread dynamics into account to detect high-risk areas based on the strength of connectivity between regions. Connectivity patterns could further inform the design of monitoring programmes. This is especially pressing, because, even for data-rich terrestrial systems, it has been highlighted that more distribution data are necessary to obtain reliable information about species range expansions and shifts attributable to global change (Duputie, Zimmermann, & Chuine, 2014). In particular, the propagule dispersal of planktonic organisms is likely to change globally owing to climatically induced changes in ocean circulation (van Gennip et al., 2017). Therefore, interdisciplinary efforts and cross-border monitoring initiatives are needed to face future challenges associated with global change.

New international initiatives have led to the ratification of the International Maritime Organization's ballast water management convention, which came into force in autumn 2017 (http://www.imo.org/en/MediaCentre/PressBriefings/Pages/22-BWM-.aspx). Even though it is expected that this convention is likely to reduce dramatically the propagule pressure or even prevent species translocations altogether, it remains to be seen how efficient this instrument will become. Irrespectively, our results highlight that initial ballast-water-mediated long-distance translocations into highly interconnected areas are of major concern. Examples of highly interconnected areas are the southern North Sea and the English Channel outside U.K. waters, which harbour some of the largest ports in the world (Seebens et al., 2016). On the one hand, we fight a losing battle to eliminate already established non-native species in such high-abundance areas from which recurrent re-seedings of animals over large areas can be expected. On the other

hand, new ballast-water-induced introductions should be avoided by all means necessary to prevent the colonization of new highly interconnected areas (e.g., along the northwest African coastline) and to avoid introducing new genotypes into existing ones. Understanding the synergies between initial ballast-water-induced introductions and secondary spread mechanisms via ocean currents could allow for management mitigation strategies and conservation efforts to be more effective.

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DATA ACCESSIBILITY

All data are available from the Pangaea database (https://doi.org/10.1594/PANGAEA.884403) and GenBank (accession numbers KY204070–KY204083).

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BIOSKETCH

The paper is a result of a collaborative research initiative, and its initiation dates from October 2010, when an international workshop about the invasion dynamics of *Mnemiopsis leidyi* throughout Europe was held at the National Institute of Aquatic Resources, DTU Aqua in Copenhagen. This event brought together researchers from Europe and stimulated discussions to improve our understanding about the range occupancy of *M. leidyi* in non-native habitats. Since then, this consortium has been growing and now includes marine ecologists, fishery biologists, modellers and physical and biological oceanographers throughout western Eurasia.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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