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Patterns of invasive ctenophore *Mnemiopsis leidyi* distribution and variability in different recipient environments of the Eurasian seas

A review

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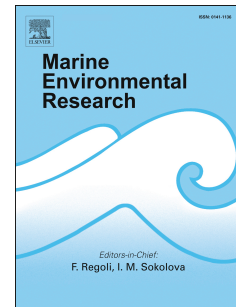
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Patterns of invasive ctenophore *Mnemiopsis leidyi* distribution and variability in different recipient environments of the Eurasian seas: a review

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Abstract

Harmful invader ctenophore *Mnemiopsis leidyi*'s expansions in the Eurasian Seas, its spatio-temporal population dynamics depending on environmental conditions in recipient habitats have been synthesized.

M. leidyi found suitable temperature, salinity and productivity conditions in the temperate and subtropical environments of the semi-enclosed seas, in the coastal areas of open basins and in closed water bodies, where it created autonomous populations. *M. leidyi* changes its phenology depending on seasonal temperature regime in different environments.

We assessed ranges of sea surface temperature, sea surface salinity and sea surface chlorophyll values, sufficient for *M. leidyi* general occurrence and reproduction based on comprehensive long-term datasets, contributed by co-authors. This assessment revealed that there are at least two eco-types (Southern and Northern) in the recipient seas of Eurasia with features specific for their donor areas. The range of thresholds for *M. leidyi* establishment, occurrence and life cycle in both eco-types depends on variability of environmental parameters in their native habitats.

Key words: invasive ctenophores; *Mnemiopsis leidyi*; distribution patterns; phenology; native habitats; recipient Eurasian seas

1. Introduction

Blooms of gelatinous zooplankton have become frequent due to increasing anthropogenic disturbance of environment such as eutrophication, overfishing, and rising temperature. As a result, in regions that previously supported many trophic levels and had productive fisheries, particularly in coastal waters, estuarine and semi-enclosed seas, simpler ecosystems dominated by gelatinous Cnidaria or Ctenophora now prevail. Trends in gelatinous populations reveal ecosystems where jellies share preys with adult or larval fishes (Shiganova and Bulgakova, 2000; Oguz *et al.*, 2008; Boero, 2013). Strong populations of gelatinous species in native habitats increase the possibility of their spreading to other parts of the World Ocean. Shipping, aquaculture and canals connecting previously separated waters facilitate invasions, where population explosions may occur, leading to disturbance of ecosystem services (Galil *et al.*, 2018; Olenin *et al.*, 2016; Shiganova, 2010). Understanding the reasons that facilitate blooms, dispersal and impact of gelatinous invasive species is crucial to develop long-term management against biodiversity loss and marine ecosystem degradation.

The lobate ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 is native to estuaries and bays along temperate and subtropical coastal waters of North and South America where it occurs at a wide range of temperature and salinity (Harbison *et al.*, 1978; Kremer, 1994; Purcell *et al.*, 2001; Costello *et al.*, 2012, Mianzan, 1999; Oliveira *et al.*, 2016). Since the early 1980s *M. leidyi* has penetrated in new areas with ballast waters due to shipping intensification, global expansion of its routes and basins connectivity extension (Seebens *et al.*, 2019). Factors facilitating *M. leidyi* establishment include climate warming and increasing disturbance of marine environments. In particular, the closed and semi-enclosed seas of Eurasia provide favorable conditions for the establishment of new populations.

Genetic studies have clarified the invasion history of *M. leidyi* in Eurasia. Despite some differences in conclusions, all studies confirm multiple invasions: *M. leidyi* was introduced from the Gulf of México to the Black Sea in ballast waters and subsequently spread throughout Ponto-Caspian basin and the Mediterranean Sea. An influx from USA coastal waters (Narragansett Bay) was the donor of populations in the North and Baltic Seas (Ghabooli *et al.*, 2011; Ghabooli *et al.*, 2013; Reusch *et al.*, 2010; Bolte *et al.*,

2013, Bayha *et al.*, 2014). In both regions, *M. leidyi* was introduced from coastal or estuarine areas, with no evidence of an invasion from open Atlantic areas (Bayha *et al.*, 2014).

Since its invasion in the Black Sea in the early 1980s (Vinogradov *et al.*, 1989), the geographic range of *M. leidyi* expanded over Eurasia by shipping and dispersal, demonstrating its ability to colonize the new recipient ecosystems. As a consequence, a number of observations and monitoring programs have been launched to track its expansion and ecology in new areas. Several review papers summarize the knowledge on invader dispersal and compare its effect on recipient and native habitats, including pattern of distribution, biology, and ecology (Purcell *et al.*, 2001; Shiganova *et al.*, 2001b; Costello *et al.*, 2012). Recent studies in the Mediterranean, Baltic and North seas have provided new insights in some aspects of its biology or were devoted to new records of *M. leidyi* (Oliveira, 2007; Galil *et al.*, 2009; Boero *et al.*, 2009, Fuentes *et al.*, 2009; Javidpour *et al.*, 2006; Faasse & Bayha, 2006; Boersma *et al.*, 2007; Tendal *et al.*, 2007, Malej *et al.*, 2017). In other cases, aspects of its ecophysiology were described for the recipient environments (Fuentes *et al.*, 2010, Javidpour *et al.*, 2009a; Jaspers *et al.*, 2011; Jaspers *et al.*, 2012; Jaspers *et al.*, 2013; Lehtiniemi *et al.*, 2011, Riisgård *et al.*, 2010; Haraldsson *et al.*, 2013, Antajan *et al.*, 2014). Here, we use comprehensive datasets on *M. leidyi* occurrence, to assess the scale of expansion and biogeographic patterns observed throughout the Eurasian seas. In addition, we provide a quantitative assessment of ctenophore life history in the recipient Eurasian ecosystems and compare the results with native North American populations. We review the current understanding of adaptive development strategies of this ctenophore in different, sometimes contrasting, recipient environments.

The goal of this paper is to show that the ecological plasticity permits the species to adapt to different environments and thus enable the wide distribution of *M. leidyi* in variable recipient ecosystems. Possible phenotypic developments might include different seasonal variability of annual cycle, and changing seasonal patterns of areas of distribution (including source, refugia and sink areas). We suggest that in spite of global existence of one valid species there are at least two ecotypes among introduced and established *M. leidyi* mega-populations: a southern (Black, Caspian, Azov, Marmara, Mediterranean seas and adjacent areas), and a northern (Baltic, North Sea and adjacent Atlantic areas) with ecology specific for their donor area. We

hypothesize that the range of thresholds for *M. leidyi* establishment, occurrence and life cycle in both eco-types depends on variability of these parameters in their donor areas.

2. Material and methods

2.1. Environmental parameters of recipient areas

The studied areas are divided into Southern and Northern eco-regions. The Southern recipient seas include brackish Black, Azov and Caspian seas, the more saline Sea of Marmara, the highly saline Mediterranean with its adjacent Atlantic areas, and Red Sea. The Northern recipient seas include the brackish Baltic Sea, the saline North Sea and adjacent Atlantic areas. All these ecosystems undergo the major structural and functional changes over the recent decades due to the climate and anthropogenic disturbances. Each of these ecosystems has been invaded by *M. leidyi* (Vinogradov et al., 1989; Studenikina et al., 1991; Shiganova, 1993; Ivanov et al., 2000; Shiganova et al., 2001a, b; Javidpour et al., 2006; Faasse & Bayha, 2006; Boersma et al., 2007, Tendal et al., 2007; Oliveira, 2007; Boero et al., 2009; Fuentes et al., 2009; Galil et al., 2009; Cruz et al., 2018).

The Black, Azov and Caspian Seas (Ponto-Caspian) merged to a single basin several times, most recently in the Pliocene. They were re-connected by the Volga-Don Canal built in 1952. The Black Sea and Sea of Azov are also part of the Mediterranean basin, connected via the Bosphorus Strait and the Sea of Marmara. Most of the Black, Azov and Caspian seas are temperate with a continental climate with some areas freezing in winter. These seas are characterized by relatively low species diversity and high productivity, in particular the Sea of Azov and the northern Caspian (Table 1). The Caspian Sea is an inland water body with limnological features (Dumont, 1998; Kosarev, 2006) and specific, mainly autochthonous, biota (Mordukhai-Boltovskoi, 1960; Kasymov, 1987). Physical geography and bottom topography divide the Caspian in Northern, Middle, and Southern regions, which have different climatic features.

The Mediterranean Sea is divided into three sub-basins: Western (Alboran, Balearic, Ligurian and Tyrrhenian Seas), Central (Ionian and Adriatic Seas) and Eastern (Levantine and Aegean Seas) (Table 1) with different circulation patterns (Iudicone et al., 2003). The Mediterranean shallow shelf, particularly its bays and lagoons, is subjected to stress from heavily populated drainage areas, intensive shipping, unsustainable fisheries and a rapidly growing aquaculture. The Mediterranean Sea, being a highly saline and

warm oligotrophic basin, has the highest number of non-native species due to a continuous influx through the Suez Canal (Galil *et al.*, 2018).

The North Sea is an arm of the Atlantic Ocean between Great Britain and north-west Europe. It is relatively shallow basin, featuring a large-scale cyclonic gyre, which influences also the Skagerrak, an outlet to the Atlantic Ocean from the Baltic Sea. The northern part of the North Sea is deeper and reveals seasonal stratification. Hydrodynamics of the North Sea also may be affected by estuaries and fjords (Brown *et al.*, 1999).

The Baltic Sea is a non-tidal basin isolated from the North Sea by geographical (narrow straits) and environmental (low temperature and salinity) barriers (Table 1). It connects with the North Sea via the Danish Straits. Human impacts (overfishing, eutrophication) and blooms of cyanobacteria in the Baltic proper, affecting up to one sixth of the whole sea area particularly in late summer, as well as natural factors (i.e. broad salinity-temperature gradients) have made the Baltic Sea vulnerable to invasion by non-native species (Paavola *et al.*, 2005).

Table 1. Background hydrological and productivity conditions in studied seas

Location	Depth (m), maximum/mean	Winter T, (°C)	Summer T, (°C)	Salinity	Chl A (mg m ⁻³), (min-max)/ mean	Zooplankton (mg C m ⁻³ ; mg m ⁻³ ; mg DW m ⁻³) (min-max)/mean	References
Black Sea	2245/1271 Oxygenated layer depth: 60-200	0-10	24-27	12-22.3	All sea: (0.47-1.62)/0.56±0.01 NW: (1.06 - 1.9)/1.5±0.4	(0.5-130) mg C m ⁻³	Shiganova <i>et al.</i> , 2004a
Sea of Azov without Sivash	14.5/7	-0.8 - 1.2	24-30	0.1-14	(2 - >3)	(67-143) mg C m ⁻³	Mirzoyan <i>et al.</i> , 2006
Caspian Sea All North Middle South	1025/208 15-20/4.4 770/192 1025/345	0-11 5.0-6.0 10-10.7	22-28 25-27 24-25 25-30	0.1-13 0.1-11 12.6-13 12.6-13	3.31±1.1 6.8± 2.09 2.1± 0.86 2.4± 1.59	(0.32-105) mg C m ⁻³ (60.6-105) mg C m ⁻³ (2.3-19.6) mg C m ⁻³ (5.4-17.8) mg C m ⁻³	Kosarev, 2006; Shiganova <i>et al.</i> , 2004b; Kopelevich <i>et al.</i> , 2014
Sea of Marmara	1335	8-15	24-29	18-29	(1-2.5)	(1.94-109.2) mg C m ⁻³	Isinibilir, 2011
N. Aegean Sea coastal waters	300/30	12 -18	24-27	33-39	(0.02-0.5)/0.32	(2.1-25.6)/6.7 mg m ⁻³	Siokou-Frangou <i>et al.</i> , 2010
S. Aegean Sea Gokava Bay	350/100	14.4-17.1	24-29	37-39.6	(0.08-0.7)	7338 ind.m ⁻³ (May) 3178 ind.m ⁻³ (Sept.)	N. Gülsahin, pers.com.
Levant Basin Israel coast	4433/1500	17.5-23	26-31	39.3-40	(0.04 - 0.16)	(0.5-8.7) mg C m ⁻³	Herut <i>et al.</i> , 2011
N. Adriatic Sea	55/30	6-10	24-28	28-39	(0.1 - 4)/2	(1.3-129.3) mg DW m ⁻³	Giani <i>et al.</i> , 2012; Mozetič , <i>et al.</i> , 2012
NW Mediterranean S. Catalan Coast	6.5/3.1	10-12	25-30	35-36	(0.096-1.28)/0.29	No data	M. Marambio, pers. comm. http://data.nodc.noaa.gov/las/getUI.do
Berre Lagoon, France	9.5/7	3.4-16	15-28.2	3-35	(1.5-110)	(13-357) mg DW m ⁻³	Gaudy & Vicas, 1985; Delpy <i>et al.</i>

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Ligurian Sea	2850/2300	13-15	23-26	37-39	(0.1-0.8)	(0.5-25) mg C m ⁻³	Berline et al., 2011 Vandromme et al., 2011
Mediterranean all	5068/1500	6-17	17- 28.5	31-39.9	(0.005-4.16)	(0.4-34.5) mg C m ⁻³	
W. Baltic Sea Kiel Fjord	23/13	<1	18-21	8-24	(1.1-9.7)/5.4	(0.5-230)/130 mg C m ⁻³	J. Javidpour, pers. comm.
Baltic Sea Great Belt Limfjorden	4.9	<1	17-22	19-24	(5-27 µg Chl l ⁻¹) (2-10 µg Chl l ⁻¹)	(2.8-8.1) mg C m ⁻³	Riisgård & Vicas, 2014
North Sea	50-400	-1 - 5	15-21	32-34.5 10-25	0.22-5.64 (0.83)	No data	http://data.nodc.noaa.gov/las/getUI.do

2.2. Sampling methods and data sets.

Long-term data sets were mostly collected by similar nets (Table 2) and provide information on seasonal variability and spatial distribution from the beginning of ctenophore establishment up to present time.

Table 2. Sampling locations, methods of collections and data sources

Location (time span)	Number of cruises, stations, observations	Number of gelatinous plankton samples	Net type	Number of zooplankton samples	Net type	Data provider
Northeastern Black Sea (1992-2017)	373	4086	Net Bogorov-Rass, mesh size 500 µm	4086	Juday net, mesh size 200 µm	Shiganova T.
Sea of Azov (1989-2015)	78	4467	Net Bogorov-Rass, mesh size 500 µm	4467	Juday net, mesh size 200 µm	Mirsoyan Z.
Sea of Marmara all (1992)	1	76	Net Bogorov-Rass, mesh size 500 µm	76	Juday net, mesh size 200 µm	Shiganova T.
Sea of Marmara (2000-2015)	303	132	WP-2, mesh size 200 µm	272	WP-2, Mesh size 200 µm	Isinibilir M.
Caspian Sea Northern, Middle, Southern (2000-2015)	56	460	Bogorov-Rass net or its smaller modification, mesh size 500 µm	338	Juday net, mesh size 200 µm	Shiganova T.
NE Aegean Sea, Greece (1999-2014)	27	108	WP-3, mesh size 500 µm	28	WP-2, mesh size 200 µm	Siokoi-Frangou I. Christou E. Shiganova T.
Aegean Sea, Gokova Bay Turkey (2011-2012)	336	266	WP-2, mesh size 200 µm	95	WP-2, mesh size 200 µm	Gülsahin N.
Levant basin, Israeli coast (2009-2013)	Semi- quantitative Sampling	Visual observations	NA	Visual observations	NA	Angel D.
Levant basin, Israeli coast (2012, 2014)	Semi- quantitative Sampling	Visual observations	NA	45, 17	NA	Galil B.
NW Mediterranean, Catalan coast, Ebro River delta (2010-2012)	19	90 + hand collection	Bongo net, 300-500µm Neustonic net, 100µm	58	Bongo net, 300-500µm	Marambio M. Fuentes V.

Berre Lagoon	8	136	Hand collections	No data	Hand collections	Lilley M. Lombard F.
Berre Lagoon (01.2010-12.2011)	38	+ visual observations				Delpy F.
Bages-Sigean lagoon (2011)	11					Bonnet D.
W. Mediterranean, Villefranche-sur- Mer, France coast (2013-2014)	Daily visual observations for 2 months	157 >1000 observed	No data	No data	Visual observations	Lilley M. Lombard F.
N. Adriatic, Piran coast (2003-2018)	Irregular/ selective sampling	No data	selective sampling & diving observations	528	WP2, mesh size 200 µm	Malej A.
W. Baltic Sea, Kiel Fjord (2006-2010)	350	350	WP-3, mesh size 1000µm	104	WP-2, mesh size 200µm	Javidpour J.

Monthly-mean values of Chl a (mg/m^3) based on SeaWiFS satellite measurements (1997-2010) were obtained from the National Oceanic and Atmospheric Association (<http://data.nodc.noaa.gov/las/getUI.do>).

3. Results

3.1. Distribution and variability of interannual and seasonal population development in the recipient Eurasian seas

M. leidyi is native to the estuaries and coastal waters of the temperate and subtropical parts of North and South America where it occurs in a wide range of temperature, salinity and productivity (Fig. 1) (Kremer, 1994; Purcell et al., 2001; Costello et al., 2012; Mianzan, 1999; Oliveira et al., 2016).

Interannual variability of sea surface temperature in the Eurasian Seas during 1980-2010 indicates enhanced warming after the late 1990s. Rising temperatures of the surface layer (Fig. 2) led to an increase of warm water species invasions, including *M. leidyi*.

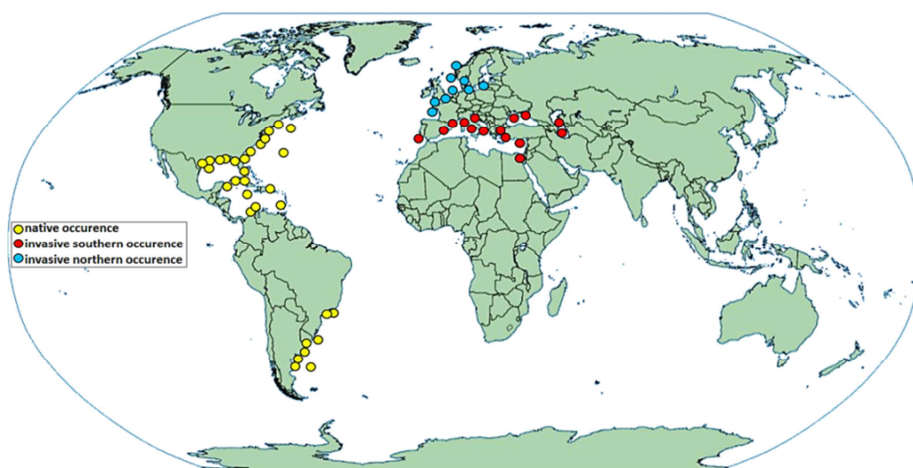


Fig. 1. *M. leidy* native locations along the Northern and Southern Atlantic coasts of America and its expansion in the recipient Eurasian areas (after GESAMP, 1997; Costello et al., 2012; Shiganova, 2009).

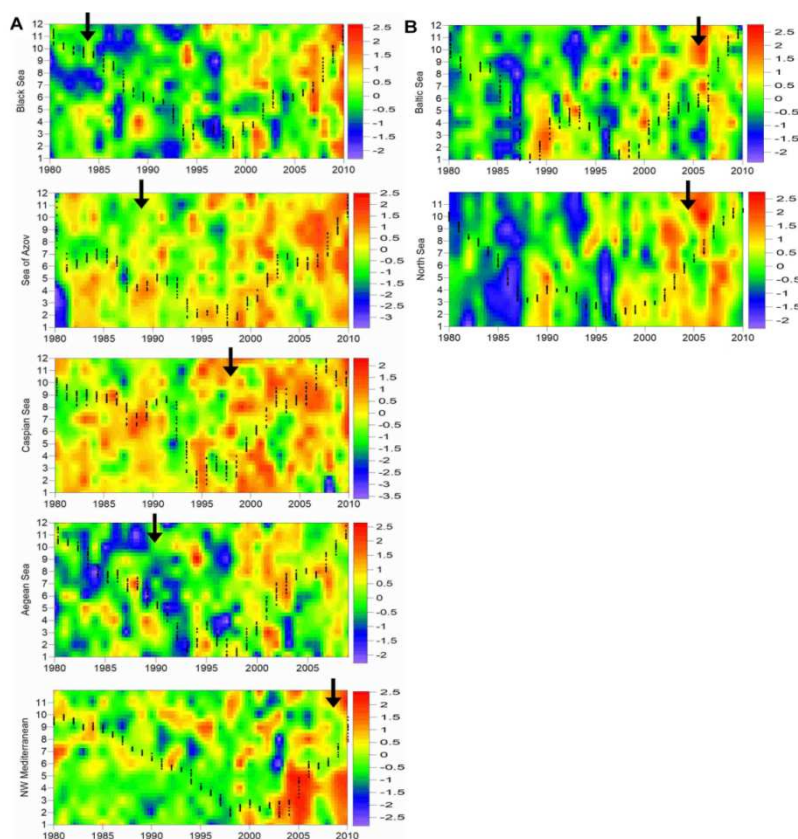


Fig. 2. Variability of SST anomalies in Southern (A) and Northern (B) seas. Arrows indicate the first report of *M. leidy*. The superimposed time series (dots) show some synchronism of the warming trends in Eurasian Seas since late 1990s.

In the early 1980s *M. leidy* was introduced into the Black Sea, successfully established there and begun spreading to colonize new areas (Fig. 3). The ctenophore's invasive success has been found in the source-sink dynamics that characterize *M. leidy* population seasonal distribution. The result of these interactions was a dynamic distribution pattern involving seasonal refugia under unfavorable conditions in the source area. Local current-driven dispersal in the sink area takes place with improving conditions there and growing population expansion around the sink area, while the population declines or disappears when suitable conditions are over. We assess the patterns of *M. leidy* distribution in all known recipient areas to analyze its seasonal and interannual variability and to identify its potential for continued expansion in new habitats.

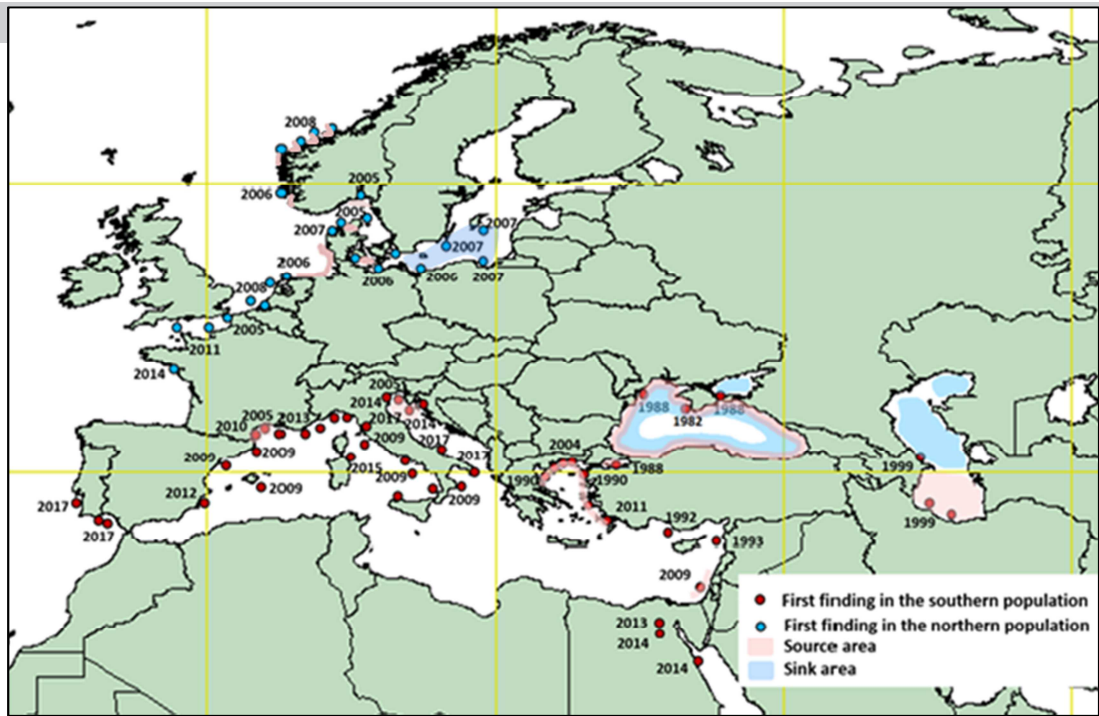


Fig. 3. Chronology of *M. leidyi* invasion and dispersal in the seas of Eurasia. Years indicate first finding in the area (sources: Pereladov, 1988; Vinogradov et al., 1989; Mutlu, 1999; Studenikina et al., 1991; Mirsoyan et al., 2006; Shiganova et al., 2001A; Shiganova, 1993; Shiganova & Malej, 2009; Galil et al., 2009; Boero et al., 2009; Lilley et al., 2014; Fuentes et al., 2010; Marambio et al., 2013; Javidpour et al., 2006; Boersma et al., 2007; Faasse & Bayha, 2006; Hansson, 2006; Oliveira, 2007; Tendal et al., 2007; Van Ginderdeuren et al., 2012; Antajan et al., 2014; Hosia & Falkenhaus, 2013; Delpy et al., 2012; Cruz et al., 2018; Zaghloul et al., in press).

3.2. Chronology of *M. leidyi* invasion in the Southern recipient seas and adjacent areas

3.2.1. The Black Sea

The Black Sea is a productive basin with high edible mesozooplankton biomass (Table 1), which generally has two seasonal peaks in spring contributed by cold-water Copepoda and late summer contributed by warm-water Copepoda including non-native *Acartia tonsa* in the western more brackish waters and Cladocera (Pasternak, 1993, Shiganova et al. 2014a). Among large gelatinous species there are two native scyphozoan *Aurelia aurita* (L) and *Rhizostoma pulmo* (Macri 1778) and one ctenophore *Pleurobrachia pileus* (O. F. Müller, 1776).

M. leidyi was first discovered in the Black Sea in early 1980s (Pereladov, 1988) with ballast waters from the northern Gulf of Mexico (Ghabooli et al., 2011). However, it could successfully establish only in the late 1980s when water temperature increased (Fig. 2) and spread throughout the Black Sea except the central areas of cyclonic gyres and freshened rivers mouths (Fig. 3). Its population reached high value (Fig. 4A) with the highest mean abundance of 304 ind. m⁻³ and biomass of 184 g WW m⁻³ in November 1989 in

the northeastern areas (Vinogradov et al., 1989) and 326 ind.m⁻³ in the Western Black Sea (Kamburska et al., 2006). Its source regions are the productive coastal waters where it is most abundant and intensively reproduces in warm months. From there due to the horizontal turbulent mixing reproductive aggregations spread in the open sea which is a sink area (Shiganova, 1998).

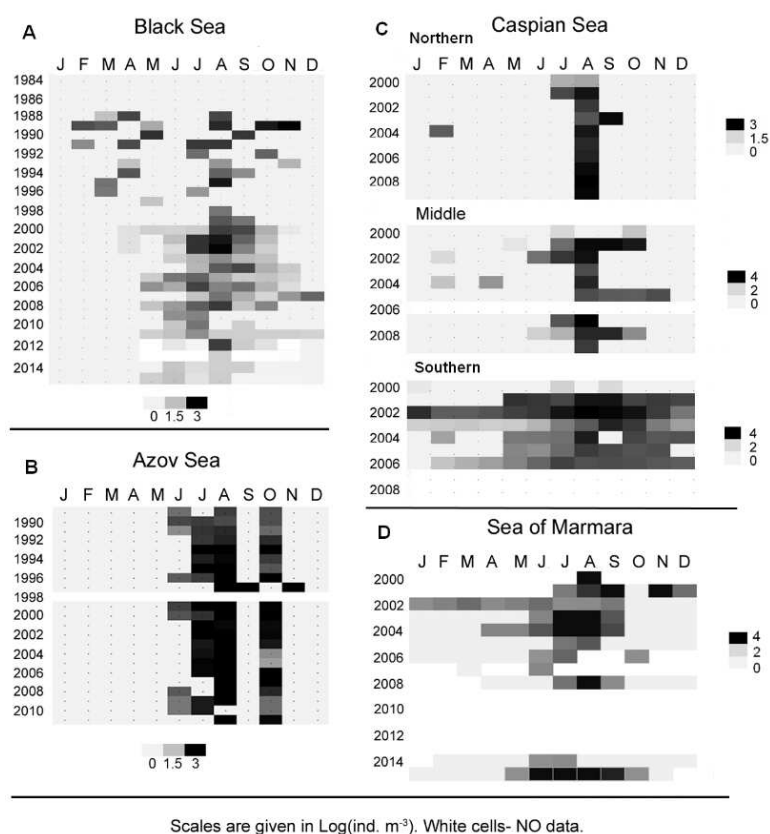


Fig. 4. Interannual and seasonal variability of *M. leidy* abundance. A - Black Sea (T. Shiganova's data), B - Sea of Azov (Z. Mirzoyan's data), C - Northern, Middle and Southern Caspian (T. Shiganova's data), D - Sea of Marmara (M. Işinibilir' data). White cells - no data.

In the 1990s before *Beroe ovata* arrival *M. leidy* seasonal and interannual abundance significantly changed depending on temperature. After cold winters its population diminished, while after warm winters its abundance remained rather high (Shiganova, 1998). Reproduction was starting in August. The highest abundances, biomass and reproduction rates were recorded in August-September (Fig. 4A), coinciding with temperatures 21-25⁰C (depending on year and area). That also coincided with the peak of warm-water zooplankton (Shiganova, 1998). In the late autumn, when the thermocline eroded, the entire population sank down to 50 m (video observations by Shiganova, 1993 and Mutlu, 1999) and continued feeding in case water temperature remained above 7-8 ⁰C. When temperature dropped below 5 ⁰C, *M. leidy* stayed in refugia coastal areas near the bottom at depths of 50-60 m, surviving on energy stored in its mesoglea (Reeve et al.

1989). At these temperatures, its movements slowed down, metabolism decreased, feeding stopped and individuals shrank in size, losing mesoglea (Zaika, 2005; Anninsky et al., 2005).

The *M. leidy* invasion in the Black Sea disrupted the ecosystem at all trophic levels both bottom up and top down and affected fisheries (Shiganova et al., 2004a). Estimated grazing rates on zooplankton, based only on daily metabolic demands, were 2.7- 43.8% of the zooplankton biomass daily in spring after warm winters and $41 \pm 67.8\%$ daily in summer. In warm years during the summer peak of *M. leidy*, its daily grazing demands were greater than the available standing zooplankton stock in the coastal waters (Shiganova et al., 2004a).

However, in 1997 the predatory of *M. leidy* ctenophore *B. ovata* sensu Mayer 1912 arrived in the Black Sea with ballast waters and the ecosystem began to recover (Shiganova et al. 2001a; 2004a; 2018; Finenko et al., 2003). Appearance of *B. ovata* in the surface layer during the annual reproduction peak of *M. leidy* had a significant effect on its population, and within two weeks only a few *M. leidy* individuals remain in the water column (Shiganova et al., 2014a). Therefore, since the arrival of *B. ovata*, *M. leidy* occurs in sizable amount (i.e. ≥ 5 ind. m^{-3}) only during early and middle summer (Fig. 4A). *M. leidy* is now almost absent in winter, early spring and late autumn. Impact on zooplankton biomass by *M. leidy* lasts for 5-13 weeks between late spring and mid-summer, i.e. much shorter than during *M. leidy* occurrence without *B. ovata* (Shiganova et al., 2014a). In recent years with increasing temperature *M. leidy* starts to reproduce in May, *B. ovata* appears in water column also in May-June or earlier. Therefore it grazes the *M. leidy* population before it can reach high abundances. Warmer water temperature in August ($> 27^{\circ}C$ since 2012) also reduces the abundance of *M. leidy* by suppressing intensity of its reproduction (Shiganova et al., 2018).

3.1.2. The Sea of Azov

The sea is highly productive with abundant zooplankton (Table 1). There are two seasonal peaks of zooplankton, in spring and summer. In recent years non-native *Acartia tonsa* arrived from the Black Sea and contributes to zooplankton biomass in summer (Mirzoyan et al., 2006). There are no native large gelatinous species in the Sea of Azov. *Aurelia aurita* arrived in the 1970s from the Black Sea when salinity increased and disappeared again when salinity decreased below 11 in the late 1980s (Mirzoyan et al., 2000). Recently, with a new increase of salinity, *A. aurita* appeared again (Mirzoyan, pers. comm.).

The Black Sea is a source of *M. leidyi* for the Sea of Azov, where it enters via the Kerch Strait every spring or early summer with the northward currents associated with the seasonally prevailing southern wind. Since *M. leidyi* cannot survive the winter temperatures of the Sea of Azov, the entire population dies out every autumn at temperatures below 3⁰ C (Studenikina et al., 1991).

After re-introduction the following year, *M. leidyi* gradually occupies the whole sea in June or July. Early introduction (April-May) causes a peak of abundance in July-August at temperatures of 24-26⁰C, whilst the peak occurs in September-October when arrival is delayed (until late June) (Mirzoyan et al., 2006). The peak of abundance also depends on zooplankton concentrations in the north-eastern Sea of Azov and on temperature in May-June. If zooplankton concentration (1180-1220 mg.m⁻³) and temperature are high (>25⁰C) *M. leidyi* can reach abundance and biomass much higher than in the Black Sea: maximum values were recorded in 1999 and 2002 with 2890 ind. m⁻³ and 119 g wet mass. m⁻³. If zooplankton concentration and temperature are lower (260-470 mg. m⁻³), *M. leidyi* values could be low as those recorded in 1992-1993 with 56 ind.m⁻³ and 56.9 g m⁻³, and in 2003 with 57 ind.m⁻³ and 51.2 g m⁻³ (Fig. 4B) (Mirzoyan et al., 2006). Before 2005 it never spread into the low salinity Taganrog Bay, but since that time it began to spread further, in the eastern part of the bay, surviving at salinities as low as 3.5 (Mirzoyan et al., 2006), probably due to gradual adaptation. During recent years salinity began to increase again. A particular increase was recorded in last years since 2013 (up to 12.92-14.13 in the sea and up to 9 in Taganrog Bay). Therefore, *M. leidyi* can penetrate now throughout the whole sea and most of the bay (Mirzoyan data).

M. leidyi impact on the Sea of Azov ecosystem has been stronger than in the Black Sea because of the small shallow sea which did not provide potential prey any refugia. Most trophic levels are the potential food, including fish eggs, fish larvae and larvae of zoobenthic species (Mirsoyan et al., 2006; Nadolinsky, 2006, Rogov et al., 2000; Frolenko, 2006).

Arrival time of *M. leidyi* also affects its grazing rate in the Sea of Azov. Late colonization (late June) means that its daily food demands comprise only 20 % d⁻¹ of the available prey biomass during first month, but by August during the peak of *M. leidyi* when prey concentration has already been grazed down, food demand comprises up to 100% d⁻¹ of available zooplankton. Early colonization implies greater demands in zooplankton, amounting to about 100% d⁻¹ already in July, and its estimated daily demands are in excess of

266 available zooplankton biomass from July or August. *M. leidy* continues its development under food deficit
267 (Shiganova et al., 2001a).

268 *B. ovata* first arrived in the Sea of Azov from the Black Sea in 1999 (Shiganova et al., 2001b). Its
269 seasonal pattern of penetration is similar to that of *M. leidy*, but it arrives only by the end of summer or
270 early autumn, depending on its development in the Black Sea. *B. ovata* gradually occupies the Sea of Azov.
271 Therefore, the effect of recovery of the ecosystem is much lower than in the Black Sea (Mirsoyan et al.,
272 2006).

273 3.2.3. Caspian Sea

274 The Caspian Sea is a productive closed basin. The seasonal zooplankton stock increases in April,
275 dominated by non-native species *Acartia tonsa*, *Pleopis polyphemoides* and larvae of *Amphibalanus*
276 *improvisus* introduced from the Black Sea. *Acartia tonsa* replaced native zooplankton species, in particular
277 *Eurytemora grimmeri*, and became dominant in all regions of the Caspian within a few years of introduction
278 (Shiganova et al., 2004b).

279 *M. leidy* and *Aurelia aurita* were introduced with ballast waters from the Black Sea to the Middle
280 Caspian in 1999 (Ivanov et al., 2000). *M. leidy* has expanded even faster in the Caspian than in the Black
281 Sea (Shiganova et al., 2004b). Long-term observations indicate its continuous presence in the Southern
282 Caspian Sea where temperature is 7.4-15.0 °C in winter (Shiganova et al., 2004b; Roohi et al., 2010; Bagheri
283 et al., 2012) and salinity is 12.6-13. Its population size is primarily determined by temperature in the
284 previous winter and winter zooplankton concentrations in the Southern Caspian (Shiganova et al., 2004;
285 Roohi et al., 2010). With spring warming and zooplankton development *M. leidy* intensity of reproduction
286 and growth accelerates, and increased total population in May or earlier during last years starts to spread
287 northward. The Middle and Northern Caspian are the sink areas where *M. leidy* lives, grows and reproduces
288 only during the warm seasons. Considering that northward Ekman transport velocity along the eastern coast
289 of the Caspian Sea is 10-30 cm/s (Dobrovolskii & Zalogin, 1982), we can roughly estimate the time required
290 for *M. leidy* to disperse from the southernmost area due to current advection. So, it takes from 16 to 46 days
291 depending on wind-driven velocity to reach the Middle Caspian from the south (about 400 km) and 12- 34
292 days to be carried from the Middle to the Northern Caspian (about 300 km). The whole way from the south

to the north takes from 28 to 80 days depending on the current velocity. It means that *M. leidy* could reach the Northern Caspian during the optimal season for creating reproductive population.

When *M. leidy* first colonized the Southern Caspian Sea, it reached population sizes up to 500 ind. m^{-3} during the peak of development in August-October 2001 (Shiganova et al., 2004b). Its abundances reached 302 ind. m^{-3} in the Middle Caspian in 2008 and 327 and 259 ind. m^{-3} in August and September 2009 respectively in the North-Western Caspian Sea (Fig. 4C). Meanwhile, in the Southern Caspian abundance became lower since 2012. This shift in a peak of abundance from the South to the Middle and Northern Caspian probably results from an earlier seasonal warming in recent years (Shiganova et al., in press), which facilitates earlier northward dispersal. Peaks of abundance occur in August-October in the Middle Caspian and in August- September in the Northern Caspian at 25-26 $^{\circ}\text{C}$. The salinity tolerance of *M. leidy* has also changed. Until 2009 it could only live at salinities >4.0 and reproduce at salinities >6 , but since 2009 *M. leidy* has been found in an area with salinities of 3.5 (Shiganova, 2011). In addition, it could not survive in the north-eastern Caspian with low zooplankton biomass and high concentration of particulate organic matter (Shiganova et al., 2003), but now it is recorded in this area since 2010. *M. leidy* is most abundant in the upper layer above the seasonal thermocline, although in coastal areas it may occur in the entire water column. Larger individuals are usually found deeper (Shiganova et al., 2003; Bagheri et al., 2012). In the deep waters of the Middle Caspian some individuals are found below the thermocline at 25-50 m (Kamakin et al., 2010).

Impacts on the Caspian ecosystem were observed for all trophic levels including the commercially important small pelagic fishes as anchovy *Clupeonella engrauliformes* and big-eye kilkas *C. grimmi* and their consumers, piscivorous fishes including sturgeons, and seal (Shiganova et al., 2004b; Shiganova, 2011). The estimated daily food demands of *M. leidy* in the Caspian coastal waters of Iran during its peak comprises about 100% d^{-1} of prey biomass from July to the end of October (Shiganova estimation). In winter and spring, estimated food demands range from 12 to 29% d^{-1} .

In contrast to the Black Sea, *B. ovata* has not been recorded in the Caspian Sea and unrestricted *M. leidy* blooms continue every year. Thus, ecosystem impacts within the Caspian, including biodiversity loss and in fishery landings reductions are expected to keep increasing.

321 The Sea of Marmara that connects the Black Sea to the Aegean Sea is a productive basin, particularly
322 in the bays (Table 1). *Acartia clausi* and *Penilia avirostris* are the main mesozooplankton species, the non-
323 native *Acartia tonsa* also occurs but in small numbers. The most abundant native macrogelatinous species
324 are *Aurelia aurita* and *Rhizostoma pulmo*. The former often is accounting for 55% of the total gelatinous
325 zooplankton (Isinibilir et al., 2015).

326 *M. leidy* arrived from the Black Sea with the upper Bosphorus current, probably when it spread
327 throughout the Black Sea in 1988 (Fig. 3). However, it was recorded and described only in October 1992
328 (Shiganova, 1993). Subsequently it occurred throughout the year in the upper layer of the Sea of Marmara
329 prior to the arrival of *B. ovata* with a peak of abundance and reproduction in the summer-early autumn
330 (Fig.4D). *M. leidy* abundance ranged from 1.62 ind. m⁻³ to 27 ind. m⁻³ (Shiganova, 1993; Kideys &
331 Niermann, 1994; Isinibilir & Tarkan, 2001; Isinibilir et al., 2004). Although it may reproduce in the whole
332 Sea of Marmara, the highest rates were recorded in the bays, particularly in the highly polluted Izmir Bay,
333 peaking in August-September (Isinibilir, 2012). This area probably serves as a source for the *M. leidy*
334 population in the Sea of Marmara.

335 *B. ovata* spread also from the Black Sea and first was found near the Bosphorus in 1999 (Tarkan
336 et al., 2000). Its biomass ranged within 6-35 g.m⁻³ during *M. leidy* blooms. Pattern of interactions of the two
337 ctenophores are similar to the Black Sea, where *B. ovata* appears in the water column when *M. leidy*
338 reaches its seasonal peak (Isinibilir et al., 2015).

339 *M. leidy* affected the whole ecosystem of the Sea of Marmara (Isinibilir, 2012). However, after the
340 appearance of *B. ovata* in last years (2014-2015), mean abundances of *M. leidy* (Fig 4D) and *B. ovata* were
341 very low in the whole sea. Thereby *B. ovata* effectively controls *M. leidy* population in the Sea of Marmara
342 and, when it declines *M. leidy* seasonal abundance, *B. ovata* almost disappears from water column (Isinibilir
343 et al., 2015).

344 3.2.5. The Aegean Sea

The Aegean Sea is oligotrophic, with zooplankton abundance ranging from 1.7 to 438 ind. m⁻³ and wet biomass from 1 to 59 mg. m⁻³ (Table 1). The high values are found in coastal embayments and bays, with the maximum in Saronikos Gulf (Siokou-Frangou et al., 2004).

3.2.5.1. Northern Aegean Sea

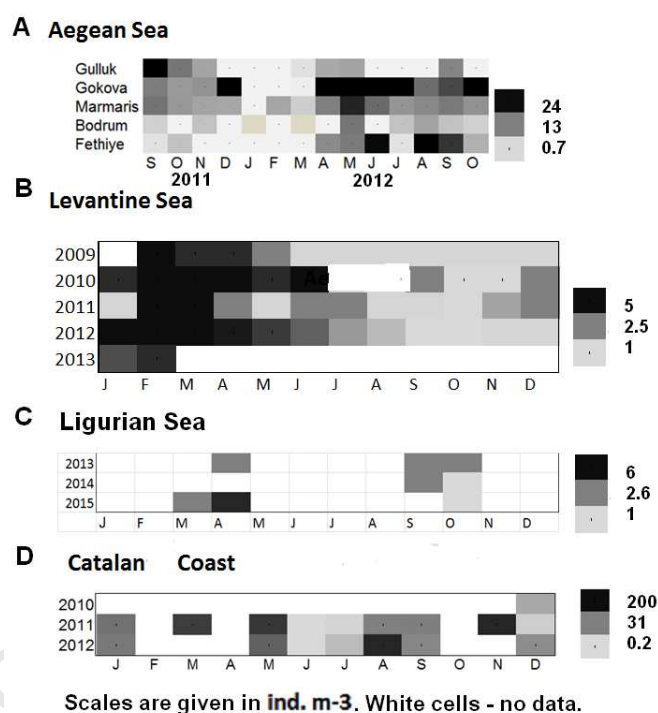
The Black Sea provided a source of *M. leidy* for the northern Aegean Sea via the Sea of Marmara. In addition, *M. leidy* was introduced, probably with ballast waters, into the Saronikos and Elefsis Gulfs in 1990 (Shiganova et al., 2004c). During 1991-1998 *M. leidy* abundance was low 0.05-3 ind. m⁻² in the areas, influenced by the Dardanelles Strait (Shiganova et al., 2001a). *M. leidy* was also recorded in the coastal waters of Gokceada Island (north-eastern Aegean Sea), influenced by the Black Sea currents. Here its values were also low with maximum of 8.3 ind.100 m⁻³-28 g.100 m⁻³, probably due to oligotrophic conditions with low zooplankton biomass (Shiganova et al., 2004c). Therefore, the northern Aegean Sea was considered as a sink area for *M. leidy* when it first occurred in the areas influenced by outflow of Black Sea water. No impact of *M. leidy* on the mesozooplankton was detected during first years after colonization, probably due to its low abundance (Shiganova et al. 2001a). *M. leidy* development and reproduction peaked in spring and early summer, ceasing in the hot summer months (Shiganova et al., 2004c). After 2002, *M. leidy* abundance began to increase (Siapatis et al., 2010), which was perceived as an evidence for a self-sustaining population establishment. The main reason was probably the increasing zooplankton biomass prey associated with warming (Siokoi-Frangou et al., 2010). *M. leidy* reached higher abundances in bays and lagoons of the northern Aegean Sea, which probably became source areas for the subsequent northern Aegean population. Highest abundances were recorded in Thermaikos and Strymonikos Gulfs influenced by high river runoffs with reduced salinity and terrigenous nutrient input (Siapatis et al., 2010). Recently (2014-2015) *M. leidy* is regularly found almost throughout the year with June peaks in a semi-enclosed Maliakos Gulf (Christou unpublished data), which is an evidence of a self - sustaining population there. Thus, during last decade *M. leidy* have established populations in the bays and coastal waters of the Northern Aegean Sea providing a potential source for other Mediterranean areas.

In the northern Aegean Sea, two *B. ovata* individuals were collected from swarms of *M. leidy* in the northern Evvoikos Gulf in November 2004 (Shiganova et al., 2007). *B. ovata* has not been observed to

372 impact *M. leidy* populations in the region, probably due to low concentrations of *M. leidy* or a lack of
 373 observations.

374 3.2.5.2. The southern Aegean Sea

375 *M. leidy* was first observed along the Turkish coast of the southern Aegean Sea in 1992-1993, when
 376 a few ctenophores (2 ind.100 m⁻³) were found off Kusadasi (Kideys and Niermann, 1994). Gökova Bay
 377 between the Aegean and Levantine seas is likely to be a separate sink of *M. leidy* population that originated
 378 in the northern Aegean Sea (Gülşahin, 2013; Gülşahin and Tarkan, 2014). In 2011-2012 within Gökova Bay,



379
 380 Fig. 5. Seasonal and interannual variability of *M. leidy* abundance in the Mediterranean areas: A - Aegean
 381 Sea (N. Gulsahin data); B - Levantine Sea (D. Angel data); C - Villefranche coast, Ligurian Sea (F.
 382 Lombard, M. Lilley data); D - Catalan Coast (M. Marambio data). White cells –no data.

383 *M. leidy* was studied in several small embayments Marmaris, Bodrum and Fethye, where salinity is 36.45-
 384 39.5, winter temperatures are 14.3-17.4 °C and summer (July-August) temperatures 24.5-29.0 °C and low
 385 productivity predominates (Table 1; Fig. 5A) (Gülşahin and Tarkan, 2014). Zooplankton reaches peak in
 386 May and September with the abundance up to 7338 ind.m⁻³ and 3178 ind. m⁻³ respectively (Table 1). *M.*
 387 *leidy* appears in March - April and its abundance increases in May at temperatures 23.43-26°C, peaking in
 388 late spring and autumn every year with the exact timing depending on location, when temperatures are not
 389 higher than 26.5°C (or 18.5°C in November) (Fig. 5A). Maximal biomass of 39.3 g. m⁻³ was observed in
 390 Gökova Bay in October 2012, which was facilitated by seasonal peaks of zooplankton (Gülşahin, 2013).

Beroe mitrata (Moser, 1907) (identification by T. Shiganova), native to the Mediterranean, probably

arrived in Gökova Bay from the northern Aegean Sea with the currents from the north and it is regularly observed in Gökova Bay and several sub-bays. Abundance of *Beroe mitrata* depends on the concentration of *M. leidy* with peaks at the same time or one month later. In general, the distribution of *M. leidy* is limited by zooplankton biomass and the distribution of *Beroe mitrata* (Gülşahin, 2013).

3.2.6. Levantine Sea

The Levantine Sea is ultra-oligotrophic, with high salinity and temperature in summer (Table 1). *M. leidy* was first found in the Mersin Bay in spring 1992 (Kideys and Niermann, 1994) and near Latakia in October 1993 (Shiganova, 1997). Since both locations were in the vicinity of ports, and population did not exist after the first findings, it is reasonable to assume that *M. leidy* had been introduced with ballast water (Shiganova et al., 2001b). In 2009 large swarms (Fig. 5 B) were observed along the Israeli Mediterranean coast up to a depth of 20 m and inside the ports (Galil et al., 2009). In 2009- 2013 *M. leidy* was regularly observed along the Israeli coast (pers. obs. D. Angel, B. Galil) from late winter to early summer (May-June or, in some years, July), in large swarms. *M. leidy*'s abundance was relatively low with 1.7-3 ind.m⁻³; however, in winter 2012 its mean abundance rose to 6.9 ind. m⁻³ and maximum abundance reached 10 ind.m⁻³ (Fig 5B). As a rule, *M. leidy* was absent during August-October due to high temperature (Table 1), before re-appearing in November- December with low abundances (0. 75-1.5 ind.m⁻³) (Fig. 5B). In 2014, *M. leidy* abundance significantly increased (pers. obs. B. Galil). *M. leidy* has obviously established a self-sustaining population off the Israeli coast with a definite seasonality, its swarms commonly coinciding with the spring zooplankton peak. It might reduce the local zooplankton stock and moderate the size of the early summer swarms of the equally voracious invasive scyphozoan *Rhopilema nomadica* Galil, 1990 (Galil, 2007). Reproduction rates were not studied but probably occur during peak of abundance in spring and autumn.

B. ovata sensu Mayer was first recorded along the Mediterranean coast of Israel outside the port of Ashdod in June 2011. Like *M. leidy*, it may have been transported to Israel with ballast waters from the Black Sea (Galil et al., 2009, 2011). Following the swarming of *M. leidy* in 2009, and to a lesser degree in 2011-2014, *B. ovata* established a local population, though it remained unrecorded until summer 2011 (Galil

et al., 2011). This species has been regularly collected in winter- spring and late autumn from 2009 and up to 2017 (Galil obs.). *B.cucumis* sensu Mayer was recorded in December 2011, January and December 2012, and February, April and May 2013 (Galil and Gevili, 2013). Thus, both the invasive *B. ovata* and the Mediterranean *Beroe* spp. appeared in swarms of *M. leidyi*, and preyed on it (Galil et al., 2011; Galil and Gevili, 2013). Identification of both species *Beroe* off the Israeli coast is confirmed by genetic analyses (Ghabooli and Shiganova identification).

3.2.7. Adriatic Sea

The northern Adriatic is the northernmost area of the Mediterranean Sea, and strongly influenced by rivers discharge. It is one of the most productive regions of the Mediterranean Sea (Harding et al., 1999), although Trieste Gulf is moderately eutrophic (Table 1) (Malej et al., 1995). Mean mesozooplankton dry mass was around 20 mg m⁻³ in 1989-2002, decreasing to < 10 mg m⁻³ in 2003-2010 (Mozetič et al., 2012) (Table 1).

In October 2005, a swarm of *M. leidyi* was recorded in the shallow (depths < 30 m) Gulf of Trieste, in the northernmost part of the Adriatic Sea, together with native *B. cucumis* sensu Mayer, *B. forskalii* Chun and non-native *B. ovata* from the Black Sea. Ballast waters from the Black Sea provided the source for both *B. ovata* and *M. leidyi*, through regular shipping between the port in Koper and various Black Sea ports (Shiganova and Malej, 2009). In spite of monitoring, *M. leidyi* was not observed in the middle and southern Adriatic Sea, supporting the hypothesis of the ballast waters was the introduction vector in the Gulf of Trieste. Continuous observations during the following years proofed that *M. leidyi* had not built a population in the northern Adriatic despite favorable environmental and trophic conditions. We suggest that the presence of two native and one non-native predatory *Beroe* species prevented establishment of *M. leidyi* after its first arrival. In addition, low propagule pressure was probably also important. This 'natural experiment' suggests that presence of native predators can control *M. leidyi*.

In July-December 2016 large-scale blooms of *M. leidyi* were observed in different locations in the northern Adriatic, at temperatures 13 -29 °C and salinities 11-38. Blooms were recorded in the coastal waters near Pula, Rovinj, in the Gulf of Trieste, in Marano-Grado lagoon, Venice lagoon and lagoons in the Po delta, Veneto-Emilia Romagna-Marche regions and offshore waters along a transect from Rovinj. In

addition, in 2016 *M. leidy* was recorded in the south Adriatic lagoons Lesina and Varano, where they were introduced via artificial tidal canals. Each bloom was composed of individuals of variable sizes and presence of cydippid larvae and juveniles (most numerous in autumn) indicating successful reproduction. Large individuals showed morphological characteristics typical for the other Mediterranean *M. leidy* (Malej et al., 2017). The vector of arrival is not clear yet but most probable could be ballast waters again.

During 2017 *M. leidy* was present in the open northern Adriatic from April and was very abundant in summer-early autumn, while in late autumn its abundance dropped (Pagliaga, pers. comm.). In the Gulf of Trieste *M. leidy* occurred in low abundances in June, in very high abundance in summer, and occurred till November (Kogovšek, pers. com.). It was also detected in the Neretva channel in the eastern part of the southern Adriatic although only sporadically and with few individuals (Lučić, pers. comm.). In October 2017 *M. leidy* was very abundant in lagoons: Lesina with abundance of 80.7 ± 47.8 ind. m^{-3} and in Varano 94.6 ± 129.8 ind. m^{-3} . Its maximal abundance was recorded in the western site of the Varano Lagoon 168.9 ± 167.1 ind. m^{-3} , while the minimum in the eastern site (20.4 ± 24.4 ind. m^{-3}). Thus, *M. leidy* expanded to the southern Adriatic Sea, establishing populations in productive lagoons.

In 2018 *M. leidy* was observed in all the previously mentioned Adriatic locations and spread further. It was also recorded by fishermen in large numbers in the lagoon of Grado (V. Tirelli, pers. comm.).

3.2.8. Italian coastal areas of the Ligurian, Tyrrhenian Sea and Ionian Seas

In May-June 2009 the first records of *M. leidy* were made in the Ligurian, Tyrrhenian and one record in the Ionian Seas of Italy (Boero et al., 2009). The large distribution area of *M. leidy* and high abundance suggest that the species invaded or dispersed in this area during the summer 2009. Ctenophores were recorded during observations in the framework of the CIESM Jellywatch campaign in the summer 2009. *M. leidy* was observed in the area continuously throughout the summer and declined in late autumn. When the swarms started to dissolve, numerous specimens of the fish *Sarpa salpa* (L., 1758) were seen to feed upon the spent ctenophores (Boero et al., 2009). That was first large-scale occurrence *M. leidy* in the western Mediterranean. Its wide expansion was probably facilitated by local currents, but ballast waters as a vector is also possible.

There were no further observations in those areas until October 2015, when, during a survey campaign on fishing of European eel in Sardinia, a massive bloom of *M. leidy* was observed in the eutrophic S'Ena Arrubia Lagoon (Diciotti et al., 2016). Subsequent sampling at three stations in the lagoon was conducted with a fyke net in order to estimate the abundance of *M. leidy* and to consider its impact on fishing. The abundance, 2.83 ind. m⁻³ consisted of small adults (18-62 mm total length). The high number of *M. leidy* (6837 individuals *per* fyke net) damaged fishing operations, reducing catches and affecting the performance of fishing gears. Most probably a separate *M. leidy* population had established in Arrubia Lagoon.

From June to October 2017 *M. leidy* was first reported in the Fiora River (Latium, Italy) (Macali & Tiralongo, 2018). Environmental parameters were T = 28.9 °C; pH = 6.74; salinity = 1.85 at 1 m depth; flow = 0.44 m/sec; average depth = 1, 75 m. DNA analysis, with the use of the COI mitochondrial marker (see Ghabooli et al., 2013) confirmed its identification. It seems that the establishment of a self-sustained population of the *M. leidy* in Fiora River is not possible due to low salinity. However, the perspective of high numbers of *M. leidy* occurrence during the dry season may pose concerns about its future impacts on freshwater species (Macali & Tiralongo, 2018).

3.2.9. Ligurian Sea (Villefranche coast)

In April-May 2013 *M. leidy* was first recorded in the coastal waters of Villefranche-sur-Mer in abundance up to 16.7 ind.m⁻³ and in Port of Monaco on the French Riviera, southern France but for only six weeks in April-May, and for only two weeks at high abundance when temperature was 17 °C and salinity 39 (Fig 5C) (Lilley, Lombard and Shiganova observation). Individuals were predominantly large (mean 8.5 cm, range 1.6-12 cm total length, mean wet weight 26.8 g, maximum wet mass 80 g). Nevertheless, juvenile individuals and a few cydippid larvae were also found, suggesting local reproduction. Adult individuals produced egg strings and reproduced in the laboratory. Appearance of *M. leidy* in these waters might be explained by current transport. The southeastern coast of France is influenced by the Northern, Ligurian or Liguro-Provençal currents. These currents have been shown to transport zooplankton around the western Mediterranean basin (Qiu et al. 2010), including gelatinous zooplankton, with localized wind events providing onshore transport (Berline et al. 2013). The currents may also have been responsible for the wide

distribution of *M. leidy* between the coasts of Italy and Spain in 2009 (Boero et al. 2009; Fuentes et al. 2010). In 2014-2015 *M. leidy* was regularly recorded in spring and autumn (visual counting during observation by F. Lombard) (Fig. 5C) during the zooplankton bloom, but was absent during the highest summer temperatures where the sea surface reaches 27 °C in the Ligurian coast. We concluded that *M. leidy* had become established in the French Riviera but its source area is not known yet.

Among predators, high densities of *Pelagia noctiluca* were observed along French Riviera 10-30 km offshore during an overnight survey on Apr 17, 2013 prior to the bloom of *M. leidy* and their considerable numbers were also observed in the Bay of Villefranche. *Pelagia noctiluca* is known to prey on *M. leidy* (Tilves et al., 2013) and occurs year-round close to the study area, being driven off-shore by favorable winds and a near-shore current (Ferraris et al., 2012; Berline et al., 2013). During *M. leidy* occurrence, both off- and in-shore, high abundance of *P. noctiluca* was observed in the same area and it is likely that *P. noctiluca* contributed to a rapid decrease in the ctenophore population.

The native *Beroe cucumis* sensu Mayer was recorded simultaneously with *M. leidy* in March-April 2015 (F. Lombard observation).

3.2.10. Lagoons of French Mediterranean coast

Along the French Mediterranean coast, *M. leidy* was first observed in Berre (D. Thibault, observation) and Bages-Sigean lagoons (D. Bonnet observation) in 2005. Later it was found in Le Grec in 2010 (D. Banaru observation), in Biguglia and Urbino (Corsica) in 2012 (S. Etourneau observation).

The first finding in 2005 was most probably introduction with ballast waters and it was the first record of *M. leidy* in the Western Mediterranean. Genetic analyses have shown that it could be a direct introduction from North America (Ghabooli et al., 2013).

Berre and Bages-Sigean lagoons are semi-enclosed, shallow basins with temperature and salinity variations linked to anthropogenic freshwater inputs. *M. leidy* successfully established self-sustaining populations in the Berre and Bages-Sigean Lagoons (Fig. 6 A, B).

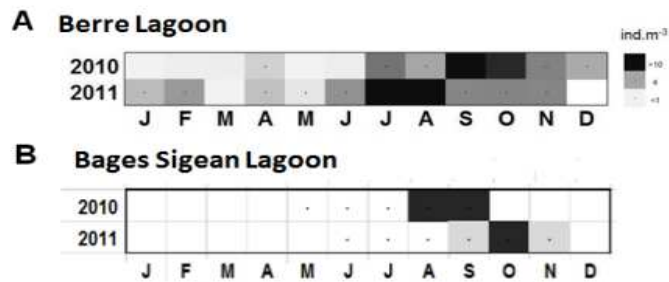


Fig. 6. Seasonal and interannual distribution *M. leidy* in French Lagoons: A- Berre lagoon; B - Bages Sigean lagoon. White cells –no data.

Berre lagoon, northwest of Marseille is among the largest coastal lagoons in Europe (155 km², ~7 m deep) (Delpy et al., 2016). It has been under intense anthropogenic pressure for several decades. The massive urbanisation of the surrounding area (1973-1990) and main freshwater inflow from the man-made Durance river bypass channel supplying hydroelectric power plant results in a lower salinity. At that time zooplankton was mainly represented by non-native *Acartia tonsa* and *Brachionus plicatilis*. In 2006 legislation was passed restricting the number of freshwater releases and with increasing salinity the zooplankton became more diverse in 2008-2011. *A. tonsa* is still present, but less abundant, while the native *Aurelia aurita* became a common species in the lagoon (Delpy et al., 2012). In Berre lagoon, *M. leidy* was present all year around during observations in 2010 and 2011 with small size individuals in low abundance ($0.1 \pm 0.2 \text{ ind.m}^{-3}$) in winter, which were probably shrunken adults because of low temperature ($5-7^{\circ}\text{C}$). Small size adults (oral-aboral lengths of (1-2.5 cm) were also present from January to March and from April to June, with individuals in a wider range of sizes (1-6 cm). In the warmest months (August and September) followed marked increase of abundance ($7.5 \pm 6.0 \text{ ind.m}^{-3}$). In autumn (October-November), when the population was mainly composed of small individuals (1.0-3.0 cm), abundance decreases to $3.9 \pm 0.2 \text{ ind.m}^{-3}$ (Delpy et al., 2016). Based on the size classes it is assumed that reproduction and growth of *M. leidy* occurred in spring, summer and early autumn (Fig. 6A).

Bages-Sigean lagoon is the smallest (37 km²) and shallowest (2.0 m average depth) of these lagoons. In the northern part, it is supplied by freshwater from small rivers and the Robine Canal. The southern part of the lagoon is connected to the Mediterranean Sea by a single channel in Port la-Nouvelle. In Bages-Sigean Lagoon during surveys *M. leidy* was observed in August and September 2010 ($63.5 \pm 59.3 \text{ ind. m}^{-3}$), and in August - November 2011 ($6.1 \pm 13.4 \text{ ind. m}^{-3}$) (Fig. 6B). Its abundance was up to 50 times higher

than in the Berre lagoon (Fig. 6B). Maximum abundance was recorded in August 2010 (113.9 ± 11.5 ind. m^{-3}) reducing to 20.1 ± 23.0 ind. m^{-3} in August-October 2011 (20.1 ± 23.0 ind. m^{-3}). There were no samplings in winter and spring 2010-2011. Seasonal variations of its abundances observed in both lagoons could be associated with environmental conditions such as salinity and biological production related to brackish and eutrophic waters (Delpy et al., 2016).

In Bages-Sigean lagoon, *M. leidy* smaller individuals (1-3 cm) were recorded in August, September and November (Delpy et al., 2016). This indicates that reproduction probably occurs in August, September and continues in November.

Few predators have been recorded in the lagoons. *B. ovata* was recorded in Berre lagoon but with a few individuals. It was observed for the first time in October 2012 (identification by T. Shiganova); its abundance was ~ 0.01 ind. m^{-3} and reached 0.35 ind. m^{-3} in November 2012 before disappearing (Delpy et al., 2016). Most likely *B. ovata* was co-introduced with *M. leidy* and was found when salinity was 26, which is optimal for this species (Shiganova et al., 2004a). However, in the following years *B. ovata* did not occur regularly and was never found in Bages-Sigean (D. Bonnet, obs.) in spite of *M. leidy* occurrence, probably due to variable salinity.

Aurelia aurita competes with *M. leidy* for food (Delpy et al., 2012) and occurs in both lagoons in low abundances. However, the population dynamics of both species are different: with *Aurelia aurita* blooming in spring and *M. leidy* in summer-autumn (D. Bonnet obs.).

Thus, *M. leidy* was established in Berre and Bages-Sigean lagoons and created autonomous populations, which are absent in the adjacent coastal areas.

3.2.11. Catalan coast of Spain

M. leidy was first recorded along the Catalan coast and along the entire coast from Cap de Creus to Alcanar in summer 2009 (Fig. 3; 5D) in large swarms observed from early July to late August. In addition, it was recorded in Denia (Valencia) and in Cabrera (Balearic Islands) areas. It was observed at salinities 34-38.2 and temperatures 22-25°C from May to September in the coastal Catalan waters (Fuentes et al., 2009). The shelf waters were characterized by high spatial variability of environmental conditions due to freshwater inputs from continental runoff (Salat et al., 2002). *M. leidy* was reported along the coast and was not found

in estuaries. It created a self-sustaining population in the coastal Catalan waters, where reproduction now occurs almost year-round. Peak reproduction occurs in winter (December-January) when the temperature is about 10-12 °C, and continues until May. During summer (July-August), when temperature is between 27-30 °C, no reproduction was observed in 2010 and 2011 (Fig. 5D) but it occurred during the summers of 2012 and 2013 at lower temperatures. Size ranges from 0.4 to 18.0 mm in winter, with a mean of 2.6 mm and mainly adults 25.0-120.0 mm, mean 58.0 mm in summer. In autumn, there is a wide diversity of size 2.0-70.0 mm with a mean size of 35.0 mm.

Among its predators *Beroe spp.* were recorded only in spring and early summer along the Catalan coast. At the beginning of July 2009, both *M. leidy* and *Pelagia noctiluca* were present in the coastal waters and *P. noctiluca* preyed upon *M. leidy* (Tilves et al., 2013).

3.2.12. Mar Menor lagoon, Iberia, Spain

Mar Menor lagoon is a shallow lagoon with an average depth of 3.5 m and is hypersaline (42-47) (Velasco et al., 2006). Water temperatures range here is 10-32 °C (Pérez-Ruzafa et al., 2004). The lagoon is separated from the Mediterranean Sea by La Manga, a 20-km-long and 100-900 m-wide sand-bar, which has five shallow inlets, including the Estacio Channel (Pagès, 2001).

In summer 2012, *M. leidy* was observed in the area 37° 38'-37° 50' N and 0° 43'-0° 57' W, located in the SE Iberian Peninsula, with an average abundance of 0.234 ind. m⁻³ in early August, declining to 0.082 ind. 100 m⁻³ by early September. The population contained only adults (total length 19-79 mm), which increased in size during the summer. The Mar Menor lagoon is anthropogenically-disturbed and may be favorable for this species occurrence. *M. leidy* was recorded also in 2013, but was absent later. No evidence of reproduction was observed and this location is probably a temporal sink area for *M. leidy* occurrence (Marambio et al., 2013).

3.2.13. Portuguese coast

In April 2017 *M. leidy* was recorded in three important fish nursery areas along the Portuguese coast – the Ria Formosa lagoon, and the Sado and Guadiana estuaries. The water temperature there ranged in 17.4-19.9 °C and salinity in 34.9-35.3 (Crus et al, 2018). The collected specimens were still in their larval stage and had similar sizes (range: 0.8-6.5 mm; average: 2.6 ± 1.2 mm; $t = 1.79$, d. f. = 24, $p = 0.086$). The

maximum average abundance of zooplankton (5743 ± 2326 ind. m^{-3}) was recorded on April 11, 2017. The total zooplankton abundance in the Ria Formosa lagoon appears to be high enough to sustain population growth and there was a negative correlation between total abundance of zooplankton and the abundance of *M. leidyi* through the tidal cycle on this sampling date ($r = 0.61$, $p < 0.05$) (Crus et al, 2018).

Although ballast water is an efficient introduction vector, dispersion of propagules by currents from adjacent regions could also be cause of the its introduction in Portuguese coastal waters (Crus et al, 2018).

A scyphozoan, *Catostylus tagi* (Haeckel, 1869) is the only putative predator of *M. leidyi* in Portuguese ecosystems. However, its predation pressure seems to be restricted to summer, and it probably would not be high enough to control *M. leidyi* populations.

3.2.14. Lakes of the Fayum, Egypt

In 2013, *M. leidyi* was first recorded in a true lake, Birket Qarun in the Fayum, Egyptian Desert, by fishermen finding substantial jelly accumulations in their nets. Because the original inoculum must have been small, this pushes the likely date of the introduction back to around 2010 or earlier. In 2014, *M. leidyi* greatly expanded in numbers and was also recorded in lake El Rayan II, south of Birket Qarun. In spring 2014, there was a bloom of *M. leidyi* at two survey stations with abundances up to 40 ind. m^{-3} (mean size was 30-40 mm, with few specimens up to 60 mm). Both lakes are saline, with Birket Qarun currently more concentrated than seawater (El Shabrawy and Dumont, 2009).

The Fayum lakes (Birket Qarun and Rayan lakes) are fed by Nile water, first pumped up to irrigate the agricultural areas surrounding them, and then drained to the lake(s) since they are situated in a depression below sea level. As soon as the ancient permanent link with the Nile was severed, salinity in Birket Qarun started rising. Around the beginning of the 20th century, the lake became mesohaline. At present it is hypersaline with salinity 40-45. Most probably *M. leidyi* was brought to the lakes with mullet fries from aquaculture facilities in the Nile Delta. So, *M. leidyi* has now crossed yet another barrier, that between the sea and two true land-locked lakes, Birket Qarun and Lake El Rayan II (El-Shabrawy and Dumont, 2016).

3.2.15. Red Sea

M. leidyi was recorded for the first time in the Egyptian waters of the northern Red Sea during

surveys conducted along Hurghada coast (between latitudes 27°14.362' and 27° 8.371' N, and longitudes 33°51.235' and 33° 51.235' E.), conducted from August 2014 to July 2015. In spite of long-term surveys *M. leidyi* was recorded only in May (Zaghloul et al., in press).

3.3. Chronology of *M. leidyi* invasion in the Northern recipient seas and adjacent areas

3.3.1. The North Sea

The North Sea is a relatively shallow basin, dynamically governed by large-scale cyclonic gyre. Salinity range is 32-35. In the open sea and in the west, seasonal changes of surface salinity are insignificant (Brown et al., 1999). The temperature ranges within -1 - + 5 °C in winter and 15-21 °C in summer (Table 1).

M. leidyi was discovered first in 2005 in several locations far from each other (Fig 3; 7): in Skagerrak in Oslo (Norway) and Tjarno (Sweden) Fjords (Oliveira, 2007; Hansson, 2006) and along the coasts of the Eastern English Channel and the North Sea: Western and Eastern Bay of Seine and French coasts of the North Sea (Antajan et al., 2014) (Figs. 7, 8A), which suggest independent simultaneous introductions with ship ballast waters.

In 2006 *M. leidyi* was discovered in Skagerrak Gullmar Fjord (Sweden) (Vergara-Soto et al., 2010) and in Kattegat in Helsingør (Tendal et al., 2007) and Horsens Fjords (Denmark) (Jaspers et al., 2017). In addition in 2006 *M. leidyi* was recorded further north in Bergen (Norway) (Hansson 2006), and to the south in several locations in Nissum Fjord (Denmark) (Tendal et al., 2007).

Further to the south *M. leidyi* was reported in Helgoland (Germany) in 2006 (Boersma et al. 2007), in Dutch coastal waters (Faasse and Bayha 2006, Van Walraven et al., 2013), and in the two different estuaries, in the Wadden Sea and in the northern and the southwestern estuaries (the Grevelingen, Oosterschelde and Westerschelde), often in extremely large aggregations. With the high shipping traffic in Dutch ports, ballast water transport may be an important vector for *M. leidyi*, resulting in its further invasions elsewhere (Van Ginderdeuren et al., 2012). In addition, to the south in 2006 *M. leidyi* was recorded in Belgian coastal waters (Dumoulin, 2007) and in 2007 in Zeebrugge (Belgium) (van Ginderdeuren et al., 2012).

These results suggest that there were multiple and simultaneous introductions in the main harbors, presumably by large ships arriving in the major European ports of Calais, Dunkirk and Le Havre (France),

Rotterdam (Netherlands), Antwerp, Zeebrugge (Belgium) and Hamburg (Germany) from the northern USA coastal waters (e.g., Narragansett Bay) (Antajan et al., 2014). It acted as the primary vector of the North Sea *M. leidyi* populations introduction (Reusch et al., 2010; Bolte et al., 2013). Local shipping promoted regional distribution as it was observed along the Belgium and Dutch coasts (Faasse and Bahya, 2006; Van Ginderdeuren et al., 2012). Current advection serves as a vector responsible for secondary *M. leidyi* spreading (Fig.7) (Lehmann and Javidpour, 2010; Schaber et al., 2011; Van Ginderdeuren et al., 2012).

In following years, observations were irregular; however, swarms of *M. leidyi* were reported in fjords of Bergen and Flødevigen between 2013 and 2016, at salinity 28.91 and temperature 13 °C, and in Fanafjorden and Outer Sotra in early October of those years (Figs. 7, 8B). Presence of several size classes and small individuals points at local reproduction (Ringvold et al., 2015). In other regions of Norway, *M. leidyi* was recorded in Oslofjord (September-October 2010), along the southern Norwegian coast and northward from Bergen up to Trondheimsfjord (2009-2012) (Fig. 7) (Hosia et al., 2013). Our analysis of *M.leidyi* distribution and current patterns allow assuming that Swedish coast population could be a source for *M.leidyi* dispersal along the Norwegian western coast.

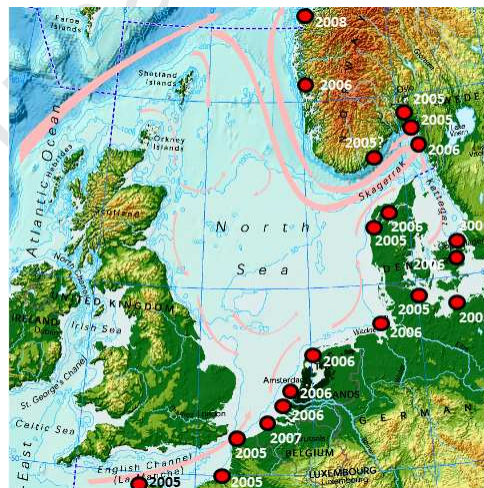


Fig. 7. Distribution of *M. leidyi* (red circles) and currents pattern (arrows) in the North Sea. Years indicate first record.

In the western Dutch Wadden Sea, located further south, *M. leidyi* was recorded in a very high abundance also in 2009 and this location becomes an important source area, seeding the whole Dutch coastal zone. In the Wadden Sea temperature ranges from 1.7 °C in February to maximum of 18–21 °C in May–August, with a decrease to 4.1 °C in December. Salinity significantly varies both seasonally from 30 in January to 15 in April and with tidal phases. Salinity is generally higher during flood than during ebb tide,

except in late summer/autumn. *M. leidy* is present during the whole year with multiple peaks. Its spawning started in May and reached a peak in mid-June (highest mean 360 ind. m⁻³). A second peak occurred in mid-August (mean density 342 ind. m⁻³ with the highest abundance of 912 ind. m⁻³ in a haul). At peaks the population almost entirely consists of small (<20 mm) individuals (Van Walraven et al., 2013).

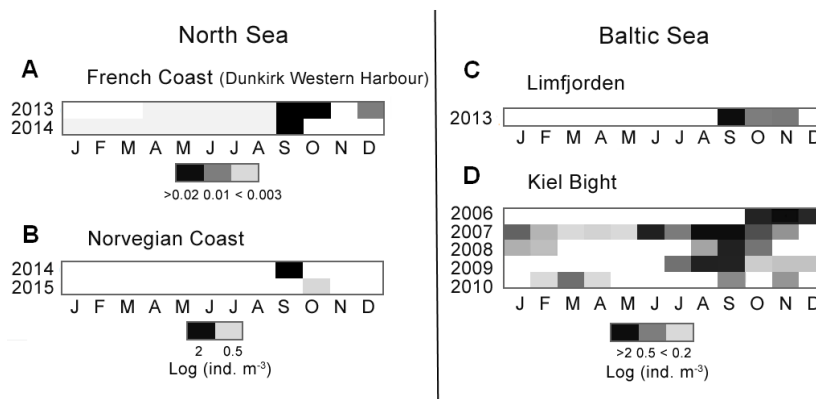


Fig.8. Interannual and seasonal variability of *M. leidy* abundance in the North and Baltic seas: A - French coast (Bastian et al., 2014), B - Norwegian Coast (Ringvold et al., 2015), C - Limfjorden (Riisgård and Goldstein, 2014), D - Kiel Bight (data Javidpour). White cells – no data.

The temperature tolerance of *M. leidy* in the North Sea is considerable, with individuals surviving the cold winters with temperatures below 2 °C at south-eastern coasts. Habitat modeling suggests its source population along the northern Dutch coast and in the German Bight (Lepparanta & Myrberg, 2009). In addition, our comparative analyses of first records with subsequent observations and their chronology in the North Sea allow us to assume that *M. leidy* established local populations in fjords and bays of Skagerrak and western coast of Norway.

Predators in the region are *Beroe* sp. (preliminary *B. norvegica*) and *Beroe gracilis* (Greve, 1975), and *Chrysaora hysoscella*, which co-occurred with *M. leidy* in the coastal areas, with inter-annual variation between 2011 and 2012 in summer, autumn and winter (spring was not sampled in 2012 in Dutch waters (Vansteenbrugge et al., 2015). Predation by *Beroe gracilis* was observed but had minor impact on *M. leidy*. Predatory impact of *M. leidy* on fish larvae in the Wadden Sea was restricted, but due to its high abundance, impact on zooplankton is hypothesized to be considerable (Van Walraven et al., 2013). In Norwegian coastal waters *B. gracilis* (Ringvold et al., 2015) and *Beroe* sp. (preliminary *norvegica*) were also observed over the

same timescale. In experiments in the North Sea water, *B. gracilis* consumed small-sized *M. leidy*, while larger individuals were partly bitten (Hosia et al., 2011).

3.3.2. The Baltic Sea

The Baltic Sea including Kattegat (Fig. 9) is one of the world's largest brackish basins. Its surface salinity varies from 20-22 in the southwestern part to 1-2 in the northernmost Bothnian Bay and the easternmost Gulf of Finland (Fig. 9) (Lepparanta and Myrberg, 2009). Differences in temperatures and salinities and their seasonal variability determine the occurrence or absence of *M. leidy*, its source and sink areas (Fig. 9). High populations of the southern North Sea is considered as a source of *M. leidy* reported in the Baltic Sea and some areas of the Kattegat and Skagerrak following the pattern of the currents in the regions (Fig. 7). *M. leidy* penetrated into the highly productive (Table 1) and saline (Fig. 9) southwestern part of the Baltic Sea, which is under strong influence of the North Sea currents (Fig. 7). It was first recorded in August 2005 in Danish fjords Felsted Kog and Nissum Fjord (Tendal et al., 2007). In early summer 2006 numerous *M. leidy* was found off Helsingør Harbor. In October 2006 the species appeared in Limfjorden (Fig. 8C), Isefjord (northern Zealand) and the northern part of Great Belt. Subsequently, numerous reports of *M. leidy* were received in the northern Little Belt and Kerteminde Bay in February-March 2007 where the abundance of small 3-5 mm *M. leidy* reached a maximum of 590 ind. m⁻³. In November 2008 (Riisgård, 2017).

In April-June 2007, the abundance of *M. leidy* was still low in the Great Belt, but reports indicated wide distribution of *M. leidy* in all inner Danish waters in July-September 2007, in areas like Limfjorden (Tendal et al., 2007). Limfjorden is one of the major Danish water systems and connects the North Sea via Thyborøn Canal in the west and to the Kattegat in the east. It is heavily eutrophicated and locally suffers from oxygen depletion in summer. Bottom-dwelling fish have disappeared, while jellyfish and ctenophores, including *Aurelia aurita* and *M. leidy*, increased. Inflowing water in Limfjorden usually originated from the Jutland Coastal Current that flows northwards along the Danish western coast, carrying mixed water masses from the English Channel and the southern North Sea (Riisgård and Goldstein, 2014).

In Limfjorden *M. leidyi* reached extremely high abundance with maximum in August-September.

High abundances up to $>800 \text{ ind. m}^{-3}$ were observed in the innermost part, showing relatively small individuals of 5 to 15 mm. In the central parts of Limfjorden the biomasses reached 300 ml m^{-3} .

Summarizing the pattern of *M. leidyi* distribution in Danish fjords, Riisgård (2017) hypothesized that with the northward coastal currents along the Dutch and Danish west coasts, *M. leidyi* re-invades Limfjorden and possibly other Danish and adjacent waters from the warmer southwestern North Sea every summer, which in cold winters, serve as a source and refugia for *M. leidyi*. Limfjorden in turn is most probably a source with the potential to seed the Kattegat and adjacent Danish waters being a sink area (Fig. 7).

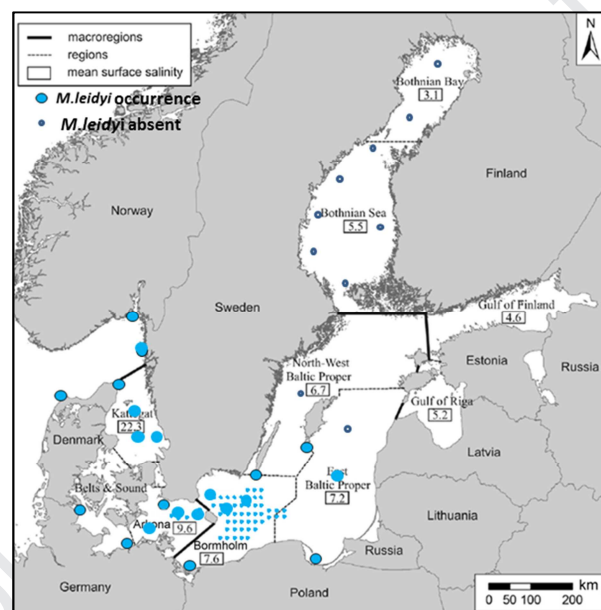


Fig. 9. Distribution of *M. leidyi* (blue dots) and salinity conditions in the Baltic Sea (after Tendal et al., 2007; Riisgård, 2017; Javidpour et al., 2006; Schaber et al., 2011; Jaspers et al., 2013; Haraldsson et al., 2013).

In July 2006 *M. leidyi* was recorded in Kiel Bight, when surface water temperature reached 22.6°C , which was 1.7°C higher than in July 2005 and 5°C higher than in October and November respectively. The salinity ranged from 13.1 to 22.2 (Fig.9). *M. leidyi* abundance was $29.5 \pm 12.7 \text{ ind. m}^{-3}$ in October, increasing to $92.3 \pm 22.4 \text{ ind. m}^{-3}$ in November (Fig 8D). More than 80 % of individuals were $\leq 5 \text{ mm}$ in total length, indicating reproduction (Javidpour et al., 2006). From August 2007 observations indicated successful establishment of *M. leidyi* in Kiel Bight, when a 5-fold higher abundance (505 ind. m^{-3}) was observed compared to 2006. In the most sampling areas about 85-90% of the population consisted of small larvae and juveniles of 10 mm lengths. During winter and spring, abundance dropped, and populations had a high

proportion of adults, which concentrated near the bottom for overwintering. In spring, after temperature rising and the development of the vertical water stratification, the whole population is migrating upward (Javidpour et al., 2009a). Thus, *M. leidyi* established permanent population in Kiel Bight, where its annual cycle is characterized by a main peak in August-September, when it occurs and reproduces in the upper warm layers. After November and through winter no reproduction occurs and the population decreased with temperature drops. As a response to low temperatures, a reduced new generation moves down to deep layers, where it takes refuge (Esser et al., 2004; Costello et al., 2006; Javidpour et al., 2009a).

However, from 2011 to spring 2014 *M. leidyi* was almost entirely absent in Kiel Bight, most probably due to cold winters in those years. Only few specimens were recorded sporadically. Since autumn 2014 *M. leidyi* has occurred again in Kiel Bight with a population outbreak in late summer. The similar pattern was observed in 2015-2016 with maximum density of over 200 ind. m⁻³ recorded in September 2015 (Javidpour data).

From the southwestern Baltic along the northern coast of Germany *M. leidyi* spread to the central Baltic Sea (the Bornholm and north Arkona Basin) in subsequent years (Huwer et al., 2008; Javidpour et al., 2006; Kube et al., 2007; Schaber et al., 2011). Observations indicated that there is no self-sustaining population of *M. leidyi* in the central Baltic Sea due to low salinity (Fig. 9). *M. leidyi* most likely re-introduces into the Bornholm Basin every year via lateral advection from the southwestern Baltic. It may live seasonally and reproduces in this area where salinity >7. These findings are important for further assessment of the impact of *M. leidyi* on the pelagic ecosystem of the central Baltic (Schaber et al., 2011; Jaspers et al., 2013). Investigations of the seasonal changes in abundance and distribution of *M. leidyi* in the central Baltic Sea from April 2007 to May 2010 (Schaber et al., 2011) indicated highest abundances in spring and autumn, and absence or only sporadic appearance of *M. leidyi* during summer. The vertical distribution of *M. leidyi* was mostly confined to water layers below the permanent halocline. Schaber et al. (2011) assumed that food limitation plays a major role in the decline of *M. leidyi* in the central Baltic during summer. Observation in northwestern Baltic proper, Bothnian basin showed absence of *M. leidyi* in the areas with salinity <7 (Haraldsson et al., 2013). So, in the low saline (7-8) Central Baltic *M. leidyi* was sporadically observed with

low abundance (mean 0.02 ind. m³ - 1.16 ind. m³) (Fig. 9). Probably, low salinity restricts reproduction and establishment of *M. leidy* there (Jaspers et al., 2011).

Bolte et al. (2013) studied *M. leidy* in the North and Baltic Seas by analyzing genetic changes over 3 years (2008-2010) and found limited gene flow between the North Sea and the southwestern Baltic Sea, and successful reproduction in both areas. In the eastern part of central Baltic Sea (Bornholm Basin), the genetic diversity decreased during the study, indicating that this area is a sink for *M. leidy*.

Dispersal models suggested that *M. leidy* undergoes wind driven dispersal in the brackish surface layer east- and northward from the Bornholm Basin, where *M. leidy* has been observed since 2007. However, in the northern Baltic survival is possible only in its southernmost part, like Pomeranian and Gdansk Bays (Janas et al., 2007; Jaspers et al., 2018). *M. leidy* is absent in the Gulf of Bothnian, Finland and Riga Bays and along Estonia, Latvia, Lithuania and Russian coast due to low salinity (3-6.5) (Fig. 9). Nevertheless, the observations of penetration and minor reproduction of *M. leidy* in the waters with salinity 6, observed in the Northern Caspian and Azov seas, in Narragansett Bay and Chesapeake Bay (Costello et al., 2012; Purcell et al., 2001; Shiganova et al., 2004 b), should be taken into consideration if the temperature continue to rise in the Baltic Sea (Fig. 2).

Thus, the environmental conditions for *M. leidy* reproduction are most favorable in the southwestern Baltic. It reaches high abundances in the disturbed and often eutrophicated Kiel Bight and Danish bays and fjords and adjacent waters.

Among predators should be mentioned *Cyanea capillata*, which occurs in Kiel Bight; it preyed on *M. leidy* in feeding experiments by Hosia et al. (2011) but 90% of encounters ended in escape. In addition, seasonal overlapping of these two species in the Kiel Bight is limited by the early autumn when *M. leidy* population is already diminished. Among predators in February 2016 in Kiel Bight *Beroe* sp. was recorded sporadically, but species-level identification was impossible (Javidpour, pers.obs).

In Danish fjords three species *Beroe*: *Beroe cucumis*, *B. gracilis* and *B. ovata* were observed, with the latter two species observed for the first time in the Baltic Sea (Shiganova et al., 2014b). *Beroe* spp. probably arrive from the North Sea, but at irregular intervals and therefore their effect on the *M. leidy* population size was not clearly seen (Riisgård, 2017).

800 **4.1 Summary of *M. leidyi* distribution patterns and seasonal dynamics in recipient and**
801 **native areas**

802 We have summarized current harmful invader *M. leidyi* expansion around the Eurasian seas and
803 patterns of its establishment and distribution. The Black Sea has been the first recipient and then donor area
804 of *M. leidyi* introduction in the most of the Southern seas (Ghabooli et al., 2011, 2013). Supposedly in late
805 1980s, *M. leidyi* has expanded from the Black Sea, with the currents eastward in the Sea of Azov, which
806 became a sink area, and with ballast waters was brought in the Caspian Sea and south-westward to the Sea
807 of Marmara and the eastern Mediterranean Sea. Anthropogenic and climatic changes of environmental
808 conditions made these locations physiologically favorable for *M. leidyi*. Since 2009 *M. leidyi* has become
809 widespread further throughout the Western Mediterranean and established, mainly in disturbed coastal
810 areas, bays, estuaries, and lagoons, which became sources for its continued expansion as far as estuaries of
811 southern Portugal (Cruz et al., in press). So, both local currents and shipping were the probable vectors for
812 *M. leidyi* transportation around the Mediterranean and other Southern Eurasian seas. However, it should be
813 taken into consideration that current advection covers a relatively short distance (e.g., particle travel for 300
814 km takes 350 days, with the typical mean current velocity 1 cm/s), which is much longer than the duration of
815 *M. leidyi* annual reproductive age. That may explain why it took long time (from 1990 to 2009) for *M.*
816 *leidyi* to spread throughout the Mediterranean Sea. Moreover, this is an overestimation since the eddy
817 dynamics patterns of the flow may slow down the current transportation. One more requirement for *M. leidyi*
818 during dispersal is to find somewhere on the way suitable conditions for reproduction and creation of a self-
819 sustaining population. Otherwise dispersed populations vanish with the advent of unfavorable conditions
820 such as a strong decrease or increase of temperature or extreme salinity or oligotrophic conditions with lack
821 of enough food. So, the currents can be only of local importance. The primary vector of the multiple
822 introductions is the ship ballast waters.

824 In the Northern region *M. leidyi* was first introduced in the North Sea (Reusch et al., 2010) where
825 it has been recorded in several locations since 2005. One of the main source areas, where it reaches very
826 high abundance became southeastern coastal areas and estuaries along the northern Dutch coast and in the
827 German Bight influenced by riverine inflow, where the environment allows overwintering (Lepparanta &

Myrberg, 2017). In addition, comparison of first records and subsequent observations in the North Sea provide us understanding that *M. leidyi* established local source populations in fjords and bays of Skagerrak and western coast of Norway as well.

From the Dutch areas with the northward coastal currents (Fig. 7) during spring warming *M. leidyi* spreads every year in the Baltic Sea, in Danish fjords and adjacent waters (Riisgård, 2017). In the Kiel Bight *M. leidyi* created permanent population originated from the North Sea with possible elimination during cold winters (as it happened in 2011-2014) and re-invaded from the North Sea again (Jaspers et al., 2018).

Recently Jaspers et al. (2018) hypothesized that *M. leidyi* could be transported by currents from the English Channel, the Southern North Sea and Norway towards north-west Denmark, continuing with an anticlockwise gyre through the Skagerrak and then northwards along the western Norwegian coast as far north as 64° N. However, the quoted rates of that re-colonization of up to 2000 km per season seem to be doubtful. For instance, to transport a particle over 2000 km during one season the mean current velocity should be 25 cm/s, which is unrealistic.

Our assessment has confirmed that invasion success is determined by the complex interaction of global shipping and local population dynamics as earlier described by Seebens et al. (2019).

We intently investigated seasonal and interannual variability of permanent and temporal occurrence of *M. leidyi* throughout the Eurasian recipient seas with sources, sinks and refugia areas. We have figured out temporal characteristics of development and reproduction of *M. leidyi* population during the year in studied areas based on authors' long-term data. We found that *M. leidyi* with its high physiological tolerance and capacity for adaptation demonstrated different patterns of spatial distribution and seasonal dynamics depending on environmental conditions. *M. leidyi* has adapted to local conditions, changing its phenology to maximize duration of seasonal development and areas of distribution in different Eurasian seas, including sources and sinks. In addition, we found out that physiological limitations and environmental restrictions of *M. leidyi* reproduction and its duration is different in Eurasian seas. The seasonal start and duration of reproduction depend on temperature, salinity and food availability, i.e. concentrations of microzooplankton for larvae and mesozooplankton for juveniles and adults.

Table 3. Periods of *M. leidy* reproduction (grey stripes) and peaks of abundance and reproduction (black stripes) and corresponding favorable environmental conditions: temperature (T), temperature of reproduction (T, R) salinity (S), peak of zooplankton (Z) in the recipient habitats

AREA/MONTH	J	F	M	A	M	J	J	A	S	O	N	D	T °C	T °C, R	S	Z	References
Black Sea (<2006)													5-25	21-25	12-22	+	Shiganova et al., 2004
Black Sea (>2006)													8-30	18-26	12-22	+	Shiganova et al., 2018
Sea of Azov													-0.8-30	18-26	6-14	+	Mirzoyan et al., 2006
Southern Caspian													10-30	10-30,5	12.6-13	+	Shiganova, 2011
Middle Caspian													5.8-26	18-26	12.1-12.6	+	Shiganova, 2011
Northern Caspian													3.8-28	23-27	6.1-10.0	+	Shiganova, 2011
Sea of Marmara													8-29	21-26	22-29	+	Isinibilir, 2012; Shiganova, 1993
Northern Aegean													12-27	21-25	33-39	+	Siapatis, 2014
Southern Aegean													14.5-29	18-26.5	37.3-39.6	+	Gulsahin, 2013
Levantine Sea													17.5-31	19.5-23.5	39.3-40.0	ND	Galil pers.com.
Northern Adriatic													6-29	17-28	11-38		Malej et al., 2017
Ligurian Sea													1-27	17-21.9	37.9-38.2	+	Lilley, Lombard pers.com.
Catalan Coast													10-30	10-25	34-38	ND	Marambio pers.com.
Berre Lagoon													3.4-28.2	10-25.2	15.9-26.2	+	Delpy et al., 2016
Bages-Sigean													9.6-27.1	18-27	18.9-34.3	+	Delpy et al., 2016
Portugal coast													17.2-22.2	17.4-20	34.9-35.3	+	Crus et al., 2018
Kiel Bight													3.5-22.2	13.1-22.2	14-20	+	Javidpour et al., 2009a
Danish Fjords													-0.5-24	12-24	19-34	+	Riisgård, et al., 2015- 17
Central Baltic													2-20	8.4-10.7(>)	7.8±0.3	+	Jaspers et al. 2011,2013
Kattegat													0-21	11.± 7-21	25±3	-	Jaspers et al. 2011; Haraldsson et al.,2013
Skagerrak													6-20	>9-20	25-29	-	Haraldsson et al.,2013
Wadden Sea													1.7-22	18-21	34-35	ND	Van Walraven et al., 2013

ND - no data

In temperate Southern seas (Black, Azov, most of Caspian and Marmara) reproduction reaches its peak in summer-early autumn depending on temperature and zooplankton concentration (Table 3). During last decade, reproduction tends to start earlier in May-June due to an earlier increase of spring and summer temperature (Fig. 2) and earlier development of warm water zooplankton species (Shiganova et al., 2014a; 2018).

In the subtropical conditions of the oligotrophic Mediterranean regions with hot summers, *M. leidy* increases seasonal abundance and reproduces in spring and autumn and sometimes in winter, which coincides with seasonal zooplankton development in these areas (Aegean Sea, Levantine Sea, Ligurian coast of France and Italy) (Fig. 5A, B and C; Table 3). In hot summer *M. leidy* disappears from water column and a reduced new generation occupies deep refugia (Shiganova et al., 2004c; Lombard et. al., obs.). In productive northern Adriatic Sea *M. leidy* reaches high abundances and high reproduction rate in late summer and autumn (Malej et al., 2017). Open parts of the Mediterranean Sea became sinks where *M. leidy* may spread with the local currents. Part of this dispersal is propagules potentially seeding populations in the

coastal zones, lagoons estuaries and bays. Another part is a sterile dispersal, where *M. leidyi* may survive temporally without reproduction.

In the Northern European seas seasonal dynamics are similar to those in temperate Southern seas (Table 3) but reproduction time and duration has not been studied in details. Probably, reproduction duration is shorter and the peak has to be in the warmest months in most of cases coinciding with peak of zooplankton abundance. In specific conditions of the Wadden Sea with flood and ebb tides reproduction was observed during two periods (May-June and mid-August) and remained high until October (Van Walraven et al. 2013) (Table 3).

Meanwhile, modeling assessment for the North Sea (Collingridge et al., 2014) indicated that reproduction might be possible for most of the year according to estimated environmental conditions (up to 212 days in 2011), but this is highly improbable in the Northern sites.

In the Baltic Sea *M. leidyi* reproduces most intensively in the productive Kiel Bight and Danish Fjords with a peak of abundance in late summer-early autumn (Fig. 8C, D; Table 3) with highest concentration in Limfjorden (Javidpour et al., 2006; 2009a; Riisgård and Goldstein, 2014). In Limfjorden *M. leidyi* probably re-invades from the North Sea every year as into sink area of south-eastern coastal populations of the North Sea. On the other hand, Limfjorden is probably a source area for other Danish fjords and adjacent waters (Riisgård, 2017). *M. leidyi* reproduction was observed also in the central Baltic Sea, but it was indicated that it is a sink area of southwest Baltic where *M. leidyi* may live seasonally and reproduce if salinity >7 (Schaber et al., 2011; Haraldsson et al., 2013).

Thus, in the disturbed areas of the North Sea (Dutch coastal waters including Wadden Sea) and the Baltic Sea (Kiel Bight, Limfjorden) *M. leidyi* could reach much higher abundances than in the most of the southern seas and amounts to abundance comparable with the Sea of Azov and the Caspian Sea (Figs. 4, 8).

Our general assessment suggests multiple and sometimes simultaneous *M. leidyi* introductions in the main harbors of Southern (Mediterranean areas) and Northern seas, presumably by large ships, and its subsequent local dispersal throughout the connected seas and water bodies.

The transfer of *M. leidyi* with aquacultures activities indicates a new vector of introduction to the hypersaline Fayum lakes of Egypt.

To summarize, we conclude that *M. leidyi* found suitable temperature, salinity and productivity conditions to create populations in the Black, Caspian and Azov Seas, including source and sink areas, in the coastal areas, bays and lagoons of the Mediterranean and in the coastal waters, fjords and estuaries of the Baltic and North seas. In the seas where it cannot persist during the full annual cycle, *M. leidyi* could find sink areas or suitable refugia to survive through the most unfavorable conditions (very low temperatures as sometimes in the Black, Baltic and North seas or very high temperature as in Southern Aegean, Levantine, Ligurian seas) and recover populations with improving conditions or re-introductions in the case of extinction. We showed the possibility of this species to establish autonomous populations in closed basins (isolated Caspian Sea, Egyptian land-locked lakes), where it may complete its annual cycle. In some regions populations are eliminated during sharp winter cooling in the sink areas (Sea of Azov, Northern and Middle Caspian) and re-builds again every year with arrival of a new generation from the source area (Black Sea; Southern Caspian). *M. leidyi* has been found throughout a wide range of environmental conditions, from temperate to subtropical regions, in brackish and marine and even hyperhaline waters. Environmental conditions shape its patterns of spatial distribution and phenology. There are at least two eco-types in the recipient seas of Eurasia. The temperature and salinity thresholds of establishment and life cycle of the southern (the Black, Caspian, Azov, Mediterranean Seas), and the northern (the Baltic and North Seas) reflect conditions in their donor areas (the Gulf of Mexico and Narragansett Bay).

Apart of that, we compared environmental conditions, time and rate of reproduction in the recipient Eurasian seas with the native locations in the Northern America from where they were introduced (Ghabooli et al., 2011; 2013; Reusch et al., 2010, Bayha et al, 2015). Native subtropical estuaries of Biscayne Bay, Florida are indicated as a donor for the Black Sea and consequently to the most of the Southern Eurasian populations (Ghabooli et al., 2013). In those estuaries temperature range is 18-32 °C and salinity ranges from mesohaline <20 to hypersaline >40 depending on season and location. *M. leidyi* does not reproduce in summer in high salinity and high temperatures, its peaks of abundance and reproduction is observed in spring, autumn and early winter (Table 4) (Kremer, 1994; Purcell et al., 2001). Similar environmental conditions and, consequently, seasonal dynamics and time of reproduction are observed in the Mediterranean Sea, where reproduction occurs in spring and autumn and in some areas in early winter

Table 4. Periods of *M. leidy* reproduction (grey stripes) and peaks of abundance and reproduction (black stripes) and corresponding favorable environmental conditions: temperature (T), temperature of reproduction (T, R) salinity (S), peak of zooplankton (Z) in the native habitats

AREA/MONTH	J	F	M	A	M	J	J	A	S	O	N	D	T °C	T °C-R	S	Z	References
Narragansett Bay, RI													1-25	10-23	21-32	+	Costello et al., 2012
Mid Chesapeake Bay, MD													2-30	12-29	5-16	+	Lonsdale, 1981; Olson, 1987; Purcell et al., 2001
Biscayne Bay, FL													18-32	18-28	14-45	+	Baker, 1973
Nueces Estuary, TX													10-30	10-30	20-38	+	Buskey, 1993
Rio de la Plata estuary, ARG													7.5-25	10-25	9-24	+	Mianzan et al., 1996; Sorarrain, 1998
Blanca bay, ARG													5-24	10-24	24-38	+	Mianzan & Sabatini, 1985; Mianzan, 1986
Nord Patagonic Tidal front, ARG													10-16	10-16	33	+	Mianzan et al., 1996, 2010; Mianzan pers. obs

In warm coastal waters of the Gulf of Mexico including subtropical waters of both St. Andrey Bay, Florida and the Nueces (Texas) Estuaries, the annual temperature range is 10-30 °C and salinity ranges 20-33. *M. leidy* is abundant there year-round with peaks in late summer in areas where zooplankton biomass is high (Table 4) (Kremer, 1994). Environmental conditions and seasonal dynamics similar to subtropical waters of Gulf of Mexico are observed in the Southern Caspian (Table 3).

In the colder waters such as Narragansett Bay, near the northern end of the geographical range for *M. leidy*, annual temperature ranges 1-25 °C with temperature >20 °C from June to September, salinity range 25-32 (Table 4). This area is indicated as a donor for the Northern seas populations (Reusch et al., 2010; Ghabooli et al., 2011). Minor eggs releases at temperatures as low as 6 °C, but 10 °C is a good approximation of a threshold for successful egg production and its rates increase with the temperature rise. Thus, temperature range for reproduction is 10-23 °C with some reproduction at 25 °C (Costello et al., 2012). Recipient Northern European seas have temperature close to that in Narragansett Bay. However salinity values are close to Narragansett Bay only in the North Sea, where *M. leidy* first established, and which is the main source area for both northern seas. The beginning of reproduction (April, at 14 °C) and the peak occurs earlier (July-August) than in the North and Baltic seas but at the same temperature, when waters become warmer.

In Chesapeake Bay *M. leidy* reproduction starts from mid-April to early June and it is most intensive between June and September (Table 4) at the temperatures of 12-29 °C and at salinity 6-16 (Kremer, 1994;

Purcell et al., 2001). The seasonal pattern and environmental conditions in Black, most of Caspian, and Azov seas are close to Chesapeake Bay, However, reproduction in all three seas are observed in summer. During recent years with temperature is rising in spring and summer *M. leidy* begin to reproduce in late spring (Fig 4, Table 3).

Based on the analyses of conditions in recipient and donor areas we identify the following constraints on *M. leidy* occurrence and reproduction and population growth:

Occurrence conditions. There are areas of occurrence of self-sustainable *M. leidy* populations with the possibility to reproduce in certain seasons. And there are areas, where it can spread and survive temporary without reproduction in the unfavorable conditions. Acceptable environmental conditions for *M. leidy* occurrence have been summarized in Fig 10A, C.

Acceptable water temperatures under which *M. leidy* occurs are variable and range between >3 and 30°C for southern seas and $1-24^{\circ}\text{C}$ (maximal temperatures) for northern sea recipient areas (Fig. 10A).

Acceptable salinity at which *M. leidy* occurs ranges between 3.5-45 in southern seas and 4.5-35 in northern seas (Fig 10A).

Surface chlorophyll concentration has been taken as indicator of ecosystem productivity and is similar to using the concentration of microplankton and mesozooplankton. According to field data, *M. leidy* requires a mean Chl level above $0.1\text{ mg}\cdot\text{m}^{-3}$ (Fig 10C).

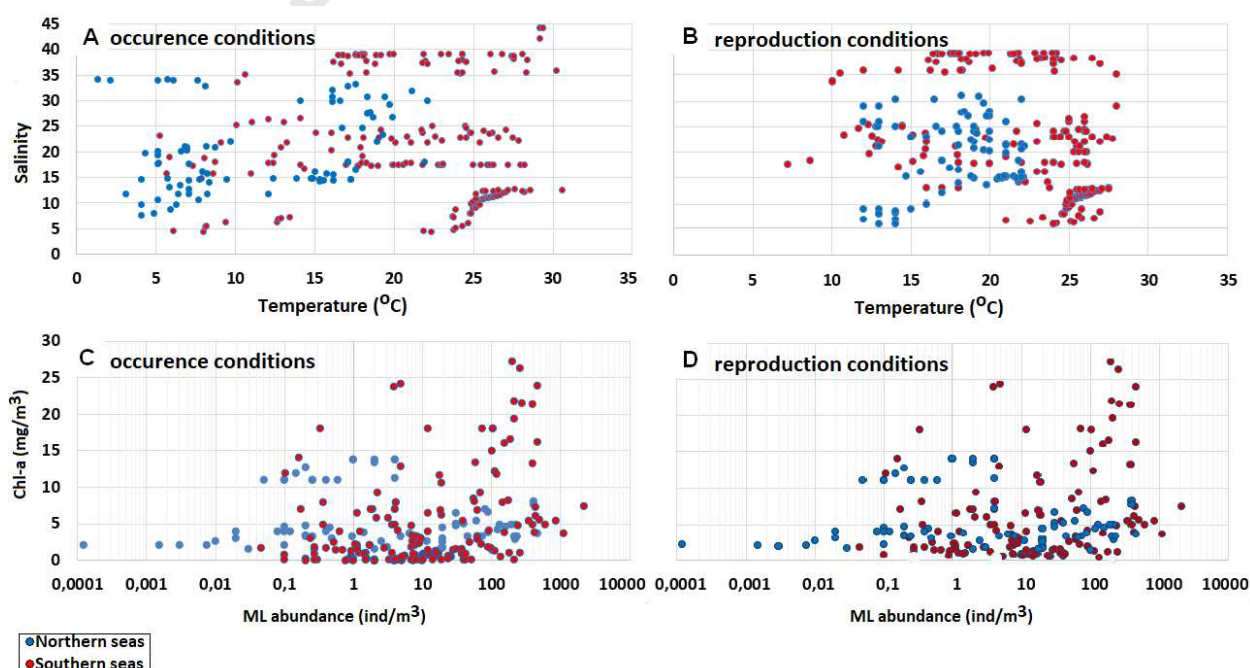


Fig.10. Ranges of SST, SSS and Chl values, sufficient for *M. leidy* general occurrence (A, C) and reproduction and population growth (B, D). Compiled from *in situ* data from various recipient basins.

Reproduction conditions. Areas with environmental conditions favorable for reproduction and growth of *M. leidy* self-sustaining population, which includes source and sink areas summarized in Fig 10B and D.

The range of water temperature favorable for *M. leidy* reproduction and population growth is $12^{\circ}\text{C} < \text{SST} < 27^{\circ}\text{C}$ for the Southern seas. Below 11.8°C , *M. leidy* stops active reproduction. However, in productive areas of the Southern Caspian and Northern Adriatic reproduction was recorded at higher temperature, such as 29°C and 28°C respectively (Fig 10B). In the Northern seas, temperature favorable for reproduction ranges between $10\text{--}24^{\circ}\text{C}$ (Fig 10B). In the Northern Caspian, in Narragansett Bay and Chesapeake Bay minor reproduction is recorded at 6°C (Costello et al., 2012; Purcell et al., 2001).

Water salinity for *M. leidy* reproduction and growth of a population is in the range 6-40 (Fig 10B).

Productivity conditions, favorable for *M. leidy* reproduction starts from $\text{Cl} \geq 0.5 \text{ mg} \cdot \text{m}^{-3}$ (Fig. 10D). The data array on *M. leidy* occurrence, reproduction and population growth, compiled in this study, were also used to generate a model that successfully accounts for past and current patterns and uses this capability to predict future invasive patterns (Shiganova et al., 2019).

4.2. Impact

M. leidy's impact on zooplankton was considerable in temperate southern seas (Black, Azov, and in some years in the Sea of Marmara and its bays). In these seas bottom up and top down impact on the most of trophic levels was observed before *B. ovata* arrived (Shiganova et al., 2004 a, b). Now these ecosystems are recovering, but still there is an impact during the summer peak of *M. leidy*. However, its effect is getting shorter with each year. There is no predator in the Caspian Sea and ecosystem disruption at all trophic levels increases from year to year (Shiganova, 2011). High impacts were found in the Baltic in Kiel Fjord and Limfjorden (Javidpour et al. 2009a; Riisgård and Goldstein, 2014). In the North Sea *M. leidy* impact on zooplankton seems considerable in regions such as the Dutch coastal areas and the Wadden Sea (Van Walraven et al., 2013). This is the result of much higher abundances than recorded in native regions, where the highest biomass estimated in the Narragansett Bay was up to $100 \text{ ml} \cdot \text{m}^{-3}$ (Kremer, 1994). Therefore, the dramatic expansion of *Mnemiopsis leidy* in the seas of Eurasia and in saline lakes is alarming, in

combination with enlargement of eutrophicated areas, a growing aquaculture sector and decreasing fish stocks. The only positive factor is the increasing dispersal of the invasive *B. ovata*, which follows *M. leidyi* to new areas and the active migration of native *Beroe spp.* into areas of *M. leidyi* blooms.

4. 3. Prey

Food for juveniles and adults of *M. leidyi* includes mesozooplankton, meroplankton, small pelagic fish and fish eggs (Costello et al., 2012).

It is important to stress out that in all brackish seas (north-western Black Sea; Sea of Azov, Caspian and Baltic Seas, parts of the Sea of Marmara and coastal waters of brackish Mediterranean lagoons) the main food is the non-native copepod *Acartia tonsa* and in most of them also larvae of the non-native barnacle *Amphibalanus improvises*. Both species were introduced in the Black, Baltic and Caspian seas and to Berre Lagoon (Gomoiu and Scolka, 1996; Gubanova, 2000, Delpy, 2012) probably from the Atlantic coast of America. From the Black Sea they were introduced into the Sea of Azov and Caspian Sea (Shiganova, 2009). Interestingly, the same fast growing, warm water copepod *A. tonsa* is also a *M. leidyi* prey in coastal waters of America (Kremer, 1994).

Unusual prey consumption was observed seasonally in Kiel Bight. In winter, the diet was mostly composed of slow-moving mesozooplankton like larval *Amphibalanus improvisus* (on average, 82% of total prey found in the gut). In contrast, the relative abundance of crustacean zooplankton in the diet was low: copepods reached 6% and cladocerans 1% of total prey (Javidpour et al, 2009). In August, ctenophore larvae larger than 5 mm were dominant in the gastrovascular cavity of adults and contributed up to 76% of the total while copepods ranked second in prey captured (23%). In late summer, *M. leidyi* fed mostly on planulae of *Aurelia aurita* (57% in September and 72% in October), while the relative share of copepods was only 14%. Predation of *M. leidyi* on planulae of *Aurelia aurita* and on own larvae, which were observed in the Kiel Bight (Javidpour et al, 2009), has not been observed in other habitats to date.

4.4. Predators and competitors

Our results show that in the most temperate seas, coastal waters, lagoons, fjords and estuaries *Aurelia aurita* is the main native competitor of *M. leidyi* (Table 5), which abundance was suppressed by *M. leidyi* as more successful competitor in most of areas. However, in the northern Adriatic periods of

occurrence of *A. aurita* and *M. leidy* do not overlap: *A. aurita* is most abundant from March to June, while *M. leidy* (since 2016) appears later in summer and is most abundant in autumn. In contrast, occurrence of *Cotylorhiza tuberculata* overlaps with *M. leidy* as well as *Rhizostoma pulmo* (which also have a peak of abundance of largest individuals in late autumn).

In Southern semi-enclosed seas with *M. leidy* populations, its predator *Beroe ovata* sensu Mayer follows it shortly and these ecosystems are gradually recovering (Black Sea, the Sea of Marmara, and Azov). Invading *B. ovata*, native *B. cucumis* sensu Mayer and *B. forskalii* control the populations of *M. leidy* in the Levantine Sea. Their presence completely stopped the establishment of *M. leidy* in the northern Adriatic in 2005 (Shiganova and Malej, 2009).

Table 5. Native and non-native gelatinous species in studied areas

Location	Native gelatinous competitors	Invasive gelatinous competitors	Native predators availability	Invasive predators availability	Reference
Black Sea	<i>Aurelia aurita</i> (L) <i>Rhizostoma pulmo</i> (Macri) <i>Pleurobrachia pileus</i> (Müller)	No	No	<i>Beroe ovata</i>	Shiganova, 2009
Sea of Azov	No	No	No	<i>Beroe ovata</i>	Mirzoyan et al., 2006
Caspian Sea	No	<i>Aurelia aurita</i>	No	No	Ivanov et al., 2000
Sea of Marmara	<i>Aurelia aurita</i> <i>Rhizostoma pulmo</i>	No	No	<i>Beroe ovata</i>	Isinibilir et al., 2015
N. Aegean Sea coastal waters	<i>Aurelia aurita</i>	No	Temporary <i>Beroe forskalii</i> , <i>B. sensu cucumis</i>	<i>Beroe ovata</i>	Shiganova et al., 2004
S. Aegean Sea Gokava Bay	<i>Aurelia aurita</i> <i>Cotylorhiza tuberculata</i> <i>Cestum veneris</i>	No	<i>Beroe mitrata</i>	No	Gülşahin and Tarkan, 2014
Levant Basin Israel coast	No	<i>Rhopilema nomadica</i> Galil, 1990	Temporary <i>Beroe forskalii</i> , <i>B. sensu cucumis</i> <i>Beroe mitrata</i>	<i>Beroe ovata</i>	Galil et al., 2009, 2011
N. Adriatic Sea	Temporary <i>Aurelia aurita</i> <i>Bolinopsis vitrea</i> (L. Agassiz), <i>Leucothea multicornis</i> (Quoy&Gaimard)	No	Temporary <i>Beroe forskalii</i> , <i>B. sensu cucumis</i> <i>Pelagia noctiluca</i>	Temporary <i>Beroe ovata</i>	Shiganova and Malej, 2009
NW Mediterranean S. Catalan Coast	No data	No	<i>Pelagia noctiluca</i> <i>Beroe spp</i>	No	Tilves et al., 2013
Berre Lagoon	<i>Aurelia aurita</i>	No	No	Temporary <i>Beroe ovata</i>	Delpy et al., 2012
Bages-Sigean	<i>Aurelia aurita</i>	No	No	No	Delpy et al., 2016

lagoon		Journal Pre-proof			
Ligurian Sea	<i>Bolinopsis vitrea</i> (L. Agassiz, 1860), <i>Leucothea multicornis</i> (Quoy&Gaimard)	No	<i>Pelagia noctiluca</i> <i>B. sensu cucumis</i> Mayer	No	Lilley M. Lombard F. pers.comm.
W. Baltic Sea Kiel Fjord	<i>Aurelia aurita</i>	No	No	Temporary <i>Beroe sp.</i>	Javidpour et al., 2009
Baltic Sea Great Belt Limfjorden	<i>Aurelia aurita</i>	No	<i>Beroe gracilis</i> <i>B. cucumis</i>	<i>B. ovata</i>	Riisgård, 2017
North Sea	<i>Aurelia aurita</i>	No	<i>Beroe gracilis</i> <i>B. cucumis</i> <i>Chrysaora hysoscella</i>	No	Van Walraven et al., 2013

B. ovata was recorded in the Limfjorden simultaneously with native *Beroe cucumis* (redefined preliminary as *B.norvegica*) and *Beroe gracilis*, which arrived from the North Sea to prey on *M. leidyi*. All of them control *M. leidyi* abundance temporally (Shiganova et al., 2014b; Riisgård and Goldstein, 2014). In the North Sea in Norwegian coastal waters *B. gracilis* and *Beroe sp.* (redefined preliminary as *B.norvegica*) were first recorded in swarms of *M. leidyi* (Ringvold et al., 2015; Hosia and Falkenhaus, 2013; Johansson et al., 2018). Generally, *B. ovata* tends to follow *M. leidyi* into new areas. However, it may create a self-sustaining population and predator-prey cycles with *M. leidyi* where both have a permanent occurrence. Native *Beroe* species both in the Mediterranean and the North seas migrate into *M. leidyi* blooms and feed on it. In recipient areas, *Beroe ovata* plays a more significant role than in native Florida and Narragansett Bay, where *B. ovata* does not occur regularly (Shiganova et al., 2014b). In the southern Aegean Sea (Gökova Bay) *M. leidyi* is controlled regularly by native *B. mitrata* (identification by Shiganova).

Among other predators, *Pelagia noctiluca* has the potential to limit *M. leidyi* population growth in coastal waters of the Mediterranean (Tilves et al., 2013). In the Baltic and North Seas *Cyanea capillata* may be an important predator (Hosia et al., 2011).

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AREA/MONTH	J	F	M	A	M	J	J	A	S	O	N	D	T ⁰ C	T ⁰ C,R	S	Z	References
Black Sea (<2006)													5-25	21-25	12-22	+	Shiganova et al., 2004
Black Sea (>2006)													8-30	18-26	12-22	+	Shiganova et al., 2018
Sea of Azov													-0.8-30	18-26	6-14	+	Mirzoyan et al., 2006
Southern Caspian													10-30	10-30,5	12.6-13	+	Shiganova, 2011
Middle Caspian													5.8-26	18-26	12.1-12.6	+	Shiganova, 2011
Northern Caspian													3.8-28	23-27	6.1-10.0	+	Shiganova, 2011
Sea of Marmara													8-29	21-26	22-29	+	Isinibilir, 2012; Shiganova,1993
Northern Aegean									ND	ND	ND		12-27	21-25	33-39	+	Siapatis, 2014
Southern Aegean													14.5-29	18 -26.5	37.3-39.6	+	Gülşahin, 2013
Levantine Sea													17,5-31	19.5-23.5	39.3-40.0	ND	Galil pers.com.
Northern Adriatic													6-29	17-28	11-38		Malej et al., 2017
Legurian Sea													1-27	17-21.9	37.9-38.2	+	Lilley, Lombard, Shiganova unpublished
Catalan Coast													10-30	10-25	34-38	ND	Marambio pers.com.
Berre Lagoon													3,4-28.2	10-25.2	15.9-26.2	+	Delpy et al., 2016
Bages-Sigean													9,6-27,1	18-27	18.9-34.3	+	Delpy et al., 2016
Portugal coast													17.2-22.2	17.4-20	34.9-35.3	+	Crus et al, in press
Kiel Bight													3.5-22.2	13.1-22.2	14-20	+	Javidpour et al., 2009a
Danish Fjords													-0.5-24	12-24	19-34	+	Riisgård, et al., 2015- 17
Central Baltic													2-20	8.4-10.7(>)	7.8±0.3	+	Jaspers et al. 2011,2013
Kattegat													0-21	11.± 7-21	25±3	-	Jaspers et al. 2011;

																Haraldsson et al.,2013
Skagerrak												6-20	>9-20	25–29	-	Haraldsson et al.,2013
Wadden Sea												1.7-22	18-21	34-35	ND	Van Walraven et al., 2013

AREA/MONTH	J	F	M	A	M	J	J	A	S	O	N	D	T ⁰ C	T ⁰ C-R	S	Z	References
Narragansett Bay, RI													1-25	10-24	25-32	+	Costello et al., 2012
Mid Chesapeake Bay, MD													2-30	12-29	5-16	+	Lonsdale, 1981; Olson, 1987; Purcell et al., 1994
Biscayne Bay, FL													18-32	18-28	14-45	+	Baker, 1973
Nueces Estuary, TX													10-30	10-30	20-38	+	Buskey, 1993
Rio de la Plata estuary, ARG													7.5-25	10--25	9-24	+	Mianzan et al., 1996; Sorarrain, 1998
Blanca bay, ARG													5-24	10-24	24-38	+	Mianzan & Sabatini, 1985; Mianzan, 1986
Nord Patagonic Tidal front, ARG													10-16	10-16	33	+	Mianzan et al., 1996, 2010; Mianzan pers. obs

- Harmful invader *M. leidy*'s expansions in the Eurasian Seas have been synthesized
- Ranges of sea surface temperature, salinity and chlorophyll values were assessed
- These ranges sufficient for *M. leidy* occurrence and reproduction were used
- Two eco-types (Southern and Northern) in the recipient seas of Eurasia were revealed
- Thresholds in both eco-types depend on environmental parameters in native habitats

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