

Spreading and physico-biological reproduction limitations of the invasive American comb jelly *Mnemiopsis leidyi* in the Baltic Sea

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Abstract Hydrodynamic drift modeling was used to investigate the potential dispersion of *Mnemiopsis leidyi* from the Bornholm Basin in the Baltic Sea where it has been observed since 2007 further to the east and north. In the brackish surface layer dispersion is mainly driven by wind, while within the halocline dispersion is mainly controlled by the baroclinic flow field and bottom topography. Model runs showed that the natural spreading via deep water currents from the Bornholm Basin towards north and east is limited by topographic features and low advection velocities. Based on the information on ranges of salinity and temperature, which limit survival and reproduction of this ctenophore within the Baltic Sea, areas have been identified where the American comb jelly, *M. leidyi* could potentially survive and reproduce. While, we could show that *M. leidyi* might survive in vast areas of the northern Baltic Sea its reproduction is prevented by low salinity (<10 psu) and temperature (<12°C). Thus, due to the combined effect of low salinity and temperature, it is not probable that *M. leidyi* could

establish permanent populations in the central or northern Baltic Sea. However, it seems that in the southern parts of the Baltic Sea environmental conditions are suitable for a successful reproduction of *M. leidyi*.

Keywords Ctenophore · Physical factors · Reproduction · Survival · Drift modelling · Alien species

Introduction

Aquatic invasive species have been identified globally as one of the major threats to marine ecosystems, causing biodiversity loss and adverse environmental, economic and social impacts (Leppäkoski et al. 2002; Occhipinti-Ambrogi and Savini 2003). The most important global pathway for introductions is ship traffic including transfers by both ballast water (for free-swimming organisms) and sediments (for resting stages and benthic organisms) and ship fouling (for sessile organisms) (Molnar et al. 2008). Shipping is very effective in species transport due to its easy overcome of natural dispersal barriers e.g. too saline or cold water in the open ocean. It is important to note that over 80% of all marine introductions have been unintentional and 31% have happened via ballast waters of ships (Molnar et al. 2008). After establishment a non-indigenous species may also spread further from the primary site of introduction

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via a combination of natural dispersal and human-associated transport mechanisms. Currents and related drifts are among important natural dispersal pathways, which transport particles and organisms both vertically and horizontally, and may serve as a pathway for secondary spread of alien species as well.

The study area of this paper, the Baltic Sea (Fig. 1a), is one of the largest brackish seas in the world. It is a semi-enclosed basin connected to the main Atlantic Ocean only via the Danish Straits. The water exchange through these straits is limited, and as

a consequence of the positive freshwater balance the Baltic Sea water mass is brackish, with mean salinity of about 7 psu—one-fifth of the salinity of normal ocean waters. Inflowing highly saline water masses enter the Baltic Sea through the Danish Straits, move further to the east, sink, and fill deepwater pools. As a result, the Baltic Sea water body has a permanent two-layer structure: the upper brackish layer and the more saline bottom layer, separated by a permanent halocline. The depth of the halocline is usually 40–80 m (Fig. 1b). The Baltic Sea lies between maritime temperate and continental sub-Arctic climate zones. In winter it is partly ice-covered. During spring and summer a seasonal thermocline develops which separates a warm mixed layer from the old winter water body (for hydrographical details see Leppäranta and Myrberg 2009).

All euryhaline and eurythermal species are potential invaders to the Baltic Sea. Since most originate from warmer areas, global warming can be expected to increase future invasions (e.g. Paavola et al. 2005). However, the ability of these species to survive and reproduce in low salinity is a key factor to determine their invasion success. About 120 alien species have been recorded in the Baltic Sea (Baltic Sea Alien Species Database, http://www.corpi.ku.lt/nemo/alien_species_search.html). One of the recent invaders is the American comb jelly, *Mnemiopsis leidyi* A. Agassiz 1865, which has caused large ecosystem perturbations in the Black Sea and the adjacent areas (Vinogradov et al. 1989). It is a voracious predator capable of very rapid reproduction in optimal conditions, and thus it has been under suspicion to cause crashes of commercially important fish stocks by eating their young as well as competing for plankton food with them (e.g. Shiganova et al. 2003). This species originates from the estuaries and coastal regions of the east coast of North, Central and South America (Purcell et al. 2001). It has been unintentionally introduced with ballast water to the Black Sea in 1982 (Vinogradov et al. 1989) and later, in 1999, to the Caspian Sea (Ivanov et al. 2000). The first records of *M. leidyi* in northern European waters were made in 2005 in Oslofjorden, Norway (Oliveira 2007), then later in the North Sea, off the western coast of the Netherlands (Faasse and Bayha 2006), and on the Swedish west coast, in the Skagerrak and in the Kiel Bight, southern Baltic Sea in autumn 2006 (Javidpour et al. 2006; Hansson 2006). In 2006–2007

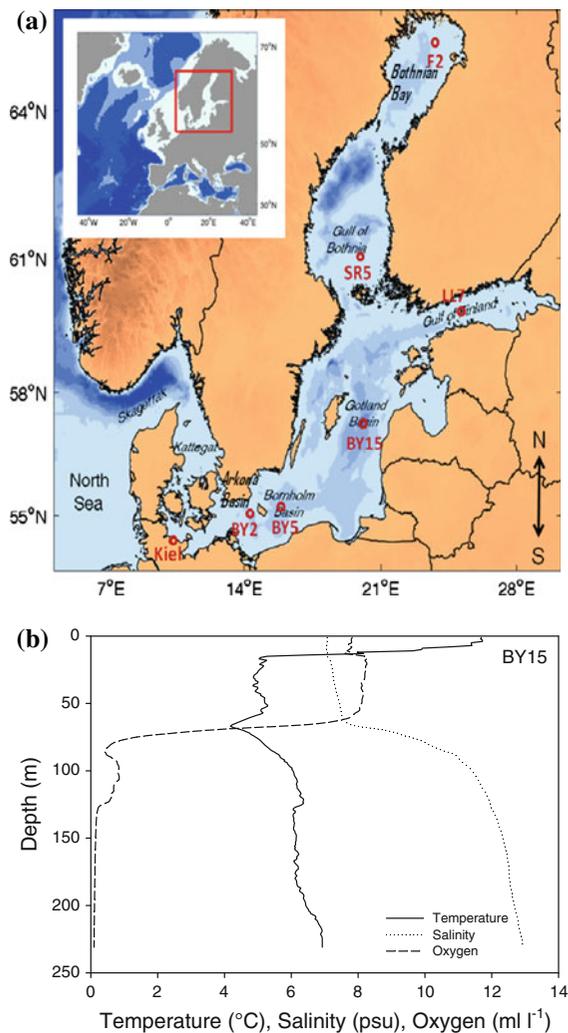


Fig. 1 **a** The Baltic Sea area. The stations for Temperature-Salinity plots (red symbols and labels) are included in the map. **b** The typical temperature, salinity and oxygen profiles in the Baltic Sea during summer stratification (station BY15, central Baltic Sea, in May 2007)

it was widely distributed in the Danish waters (Tendal et al. 2007). The species is easily identified from other ctenophores when the lobes have been developed, which are characteristic for adult specimens. However, small individuals i.e. cydippid stage larvae are difficult to identify to species level without applying genetic methods (Gorokhova et al. 2009; Reusch et al. 2010). This identification problem led to confusion to widely think that *M. leidy* had spread to almost the whole Baltic Sea (e.g. Lehtiniemi et al. 2007). However, based on genetic analyses the species occurring in the central and northern Baltic Sea was proven to be an arctic comb jelly (*Mertensia ovum*) (Gorokhova et al. 2009). In light of the new accumulating genetic evidence it seems most probable that *M. leidy* has not been found, until now, north or east of the Bornholm Basin and the Bay of Gdansk (Figs. 1, 2, Lehtiniemi unpubl.).

M. leidy is known to have a wide tolerance for environmental conditions, including salinities of 2–38 psu, temperatures between 2 and 32°C and low oxygen levels, which enable effective spreading to new areas (Purcell et al. 2001; Fuentes et al. 2010). Although showing wide tolerance to these physical parameters, *M. leidy* is clearly close to the limit of its occurrence in such conditions where both salinity and temperature are near the lowest tolerance limits. It has been shown in the Chesapeake Bay that it tolerates lower salinities (even 2 psu) during summer when temperatures are higher compared with winter situation when it needs over 6 psu salinity to survive in cold temperatures (Purcell et al. 2001).

To be able to establish permanently, *M. leidy* should be able to reproduce, which requires better environmental conditions compared with the conditions in which it survives. It is reported from other regions of the world ocean that reproduction occurs in temperatures above 12°C and in salinities above 6 psu although egg production increases remarkably in warmer temperatures (Purcell et al. 2001).

The aim of this study is to identify potential areas where *M. leidy* could disperse by natural drifting from the southern Baltic Sea. In addition, based on reproduction experiments done in different salinities in the laboratory as well as on environmental thresholds for survival from the literature, we estimated areas in the Baltic Sea where the species could potentially (1) survive and (2) reproduce with respect to hydrographic conditions.

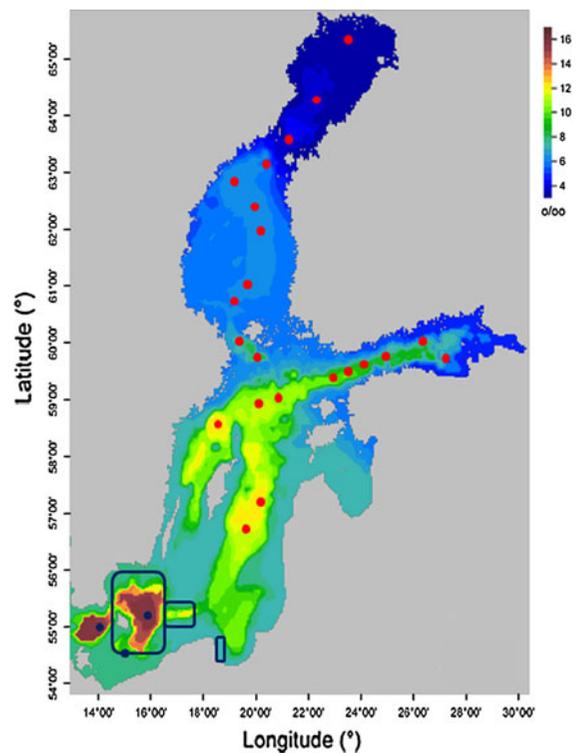


Fig. 2 Bottom salinity measured onboard R/V Aranda in June 2009 and *Mnemiopsis leidy* observations. The northern and easternmost areas (blue squares; Haslob et al. 2007; Janas and Zgrundo 2007; Huwer et al. 2008; Schaber et al. 2011) and stations (blue dots; observations done onboard R/V Aranda February 2010) where *M. leidy* has been observed and stations where it has not been observed (red dots) in the Baltic based on genetic analyses or observations of adult *M. leidy* individuals with lobes

Materials and methods

Drift model

Baltic sea ice-ocean model (BSIOM)

The numerical model, used in this study, is a general three-dimensional coupled sea ice-ocean model of the Baltic Sea (Lehmann and Hinrichsen 2000; Lehmann et al. 2002). The horizontal resolution used is 5 km (eddy-permitting), and vertically 60 levels are specified, which enables to resolve the upper 100 m with levels of 3 m thickness. The model domain comprises the Baltic Sea, including the Kattegat and the Skagerrak. At the western boundary, a simplified North Sea basin is connected to the Skagerrak, to take up sea-level elevations and to provide characteristic

North Sea water masses due to different forcing conditions (Lehmann 1995; Novotny et al. 2005). The coupled sea ice-ocean model is forced by meteorological data taken from the Swedish Meteorological and Hydrological Institute (SMHI Norrköping, Sweden) database (Lars Meuller, pers. comm.) which covers the whole Baltic drainage basin on a regular grid of $1^\circ \times 1^\circ$ with a temporal increment of 3 h. The database, which for modelling purposes is further interpolated onto the model grid, includes surface pressure, precipitation, cloudiness, air temperature and water vapour mixing ratio at 2 m height and the geostrophic wind. Additionally, runoff data are specified for 42 individual rivers distributed around the Baltic and the Kattegat (Bergström and Carlsson 1994). BSIOM has been run for the period 2005–2008 starting from an existing model run covering the period 1979–2005. Three-dimensional fields of temperature and salinity as well as the current field have been extracted as daily averages from the model to be further used in a Lagrangian particle tracking model (Hinrichsen et al. 1997). Thus, circulation and drift track models are operated subsequently. The advantage of an offline subsequent processing of the drift track model is that drifters can be released freely within the 3-d model fields and drift tracking can be forward or backward. This model system has been proven to be useful in a number of drift studies (e.g. Hinrichsen et al. 2003; Lehmann and Javidpour 2010).

Drifters were released only at those positions where *Mnemiopsis leidyi* was reported to occur in May and November 2007 (Haslob et al. 2007; Huwer et al. 2008; Fig. 2). In May the comb jellies occurred mainly within the halocline (Haslob et al. 2007; Schaber et al. 2011). Therefore, drifters were released at 60, 65, 70, 75, 80 and 85 m depths once a day from 24 to 27 of May 2007. There were 11 positions in the Bornholm Basin and Stolpe Channel where *Mnemiopsis* has been observed. To increase the number of drifters, 5 drifters were released at each position at a distance of about 5 km from each other. Drifters were tracked until the end of November 2007. Another set of drift model runs was conducted by releasing drifters in November 2007, again only at those positions where the comb jelly was recorded, every 4th day from 3 to 15 November. Due to the reported vertical occurrence pattern of the majority of the population at that time of the year drifters were

released every 5th meter from 20 to 80 m depth (Huwer et al. 2008). Drifters were tracked until the end of December 2007. In total 330 drifters were released for each experiment in May and 741 in November.

Temperature-Salinity (TS) as regulating physical factors

To estimate the potential for *Mnemiopsis leidyi* survival and reproduction we collected information from literature on the tolerance limits of survival from around the world (Table 1). In the Baltic Sea (Bornholm Basin) *M. leidyi* has been observed in temperatures $> 4^\circ\text{C}$ and in salinities > 7 psu (Table 1, references therein). Tolerance experiments conducted in the laboratory also suggest that *M. leidyi* should survive in temperatures above 3°C and in salinities over 4.5 psu (Table 1; Sarpe et al. 2007). Therefore we chose to use tolerance limits of 3°C and 4.5 psu for *M. leidyi* survival in our estimations in the Baltic Sea area. Reproduction experiments conducted in the southern Baltic have shown that *M. leidyi* reproduces in temperatures above 12°C (Sarpe et al. 2007). The salinity tolerance limits for reproduction were not available from the literature. Thus we conducted laboratory experiments to study this (see below).

To identify typical temperature and salinity conditions of the different sub-basins of the Baltic Sea (stations marked in Fig. 1a) we used TS-diagrams (modified from Leppäranta and Myrberg 2009). The TS-diagrams are drawn from physical data collected at HELCOM monitoring stations of all sub-basins of the Baltic Sea and in Kiel Fjord from bottom to surface covering all seasons. These data show the long-term hydrographic conditions at stations, which are representative in the respective sub-basins. Generally, TS-curves in the Baltic are hook-shaped and express more continuous stratification than pure water masses. A vertical alignment of TS-values in a TS-diagram represents temperature stratification, whereas a horizontal alignment stands for salinity stratification. In the TS-curves high salinities are linked to advection of water masses from the North Sea. Those saline (i.e. having large density) water masses are warmer than the ambient Baltic waters as well. Such stratified water masses situate at the near-bottom layer in the Baltic Sea due their large density.

Table 1 Salinity and temperature ranges in areas where *Mnemiopsis leidyi* (*M. leidyi* in the table) occurs (west and northeast coasts of Atlantic, Black and Caspian Seas, Mediterranean and southern Baltic) and where it does not occur in the Baltic Sea as well as in potential source and recipient areas

Characteristics of the area	Area	<i>M. leidyi</i> occur	Salinity psu		Temperature °C		References
			Annual min–max	Min where <i>M. leidyi</i> obs	Annual min–max surface	Min where <i>M. leidyi</i> obs	
Area of <i>M. leidyi</i> origin	Chesapeake Bay, USA	Yes	3–25	3	1–25	2	Purcell et al. (2001)
Area of <i>M. leidyi</i> origin	Bay of Biscayne, USA	Yes	14–45		7–32	7	Purcell et al. (2001)
Invaded area	Black Sea	Yes	18–22.3	2	0–27	4	Purcell et al. (2001)
Invaded area	Caspian Sea	Yes	0.1–11	4.2	0–28		Purcell et al. (2001), Shiganova et al. (2003)
Invaded area	Mediterranean	Yes	36–38		18–26		Fuentes et al. (2010)
Invaded area	Southern Baltic Sea	Yes	7.0–25	7	3–26	4	HELCOM data; Kube et al. (2007), Haslob et al. (2007)
Potential source area	Gothenburg port, SWE	Yes	13.1–18.2				Gollasch and Leppäkoski (2007)
Potential source area	Rotterdam port, NETH	Yes	27–33		0–25		Rijkswaterstaat waterbase ^a
Invaded area, laboratory experiments	Southern Baltic Sea			4.5		3	Sarpe et al. (2007)
Potential area of invasion	Northern Baltic Sea	No	2.5–12	–	–1–26	–	HELCOM data

^a http://www.rijkswaterstaat.nl/water/scheepvaartberichten_waterdata/historische_waterdata/

In the TS-profile this becomes visible as a hook-shaped profile. TS-curves illustrate well how the halocline separates the advected lower layer and vertically mixed upper layer from each other. If the hook falls horizontal and the TS-line is L-shaped, then the lower water is isothermal but stratified in salinity. We chose TS-diagrams to show the combined effect of temperature and salinity for *M. leidy* survival and reproduction. We added the temperature and salinity tolerance limits for *M. leidy* survival and reproduction on the TS-diagrams to show the potential areas where *M. leidy* could possibly survive and/or reproduce.

Reproduction experiments

Experiments to determine egg production (as number of laid eggs) as well as hatching success of larvae at different salinities were conducted at the Leibniz Institute of Marine Sciences in Kiel, Germany. Lobate individuals of 2 ± 0.5 cm were collected by vertical net sampling from Kiel Fjord during summer 2008. Active and healthy specimens were chosen for fecundity experiments. We manipulated five levels of salinity (5, 10, 15, 20 and 30 psu) representative of the Baltic Sea salinity gradient, which changes from 30 psu in the west to <5 in the north. At least 10 individuals for each salinity treatment were placed in a glass bottle containing 10 l of membrane filtered seawater ($0.2 \mu\text{m}$) and were acclimated gradually from ambient salinity (15 psu) to other salinities. *M. leidy* is an osmoconformer that needs a few hours to re-establish its equilibrium buoyancy (Yazdani Foshtomi et al. 2007), thus acclimation time of 1 day is supposed to be sufficient. To avoid introducing starvation as confounding factor into the experiment, individuals were fed with natural mesozooplankton twice during the period of acclimation.

Six actively swimming specimens from each salinity treatment were chosen and incubated individually in 2 l culture flasks for the reproduction experiment. Experimental jars were placed in culture cabinet in dark conditions and allowed to reproduce for 36 h under an ambient temperature of 18°C . After 36 h of incubation the adult was removed with a large pipette or hose and the water was filtered and scanned for eggs.

To get a closer look at the development time from egg to larva 20 eggs from each salinity treatment

were taken randomly and incubated in a cell culture for 1 week at 18°C . As animals incubated at the lowest and highest salinities did not produce sufficient numbers of eggs, we introduced eggs of neighboring salinities into 5 and 30 psu treatments. The development from eggs to larvae was monitored daily for 6 days with a binocular microscope.

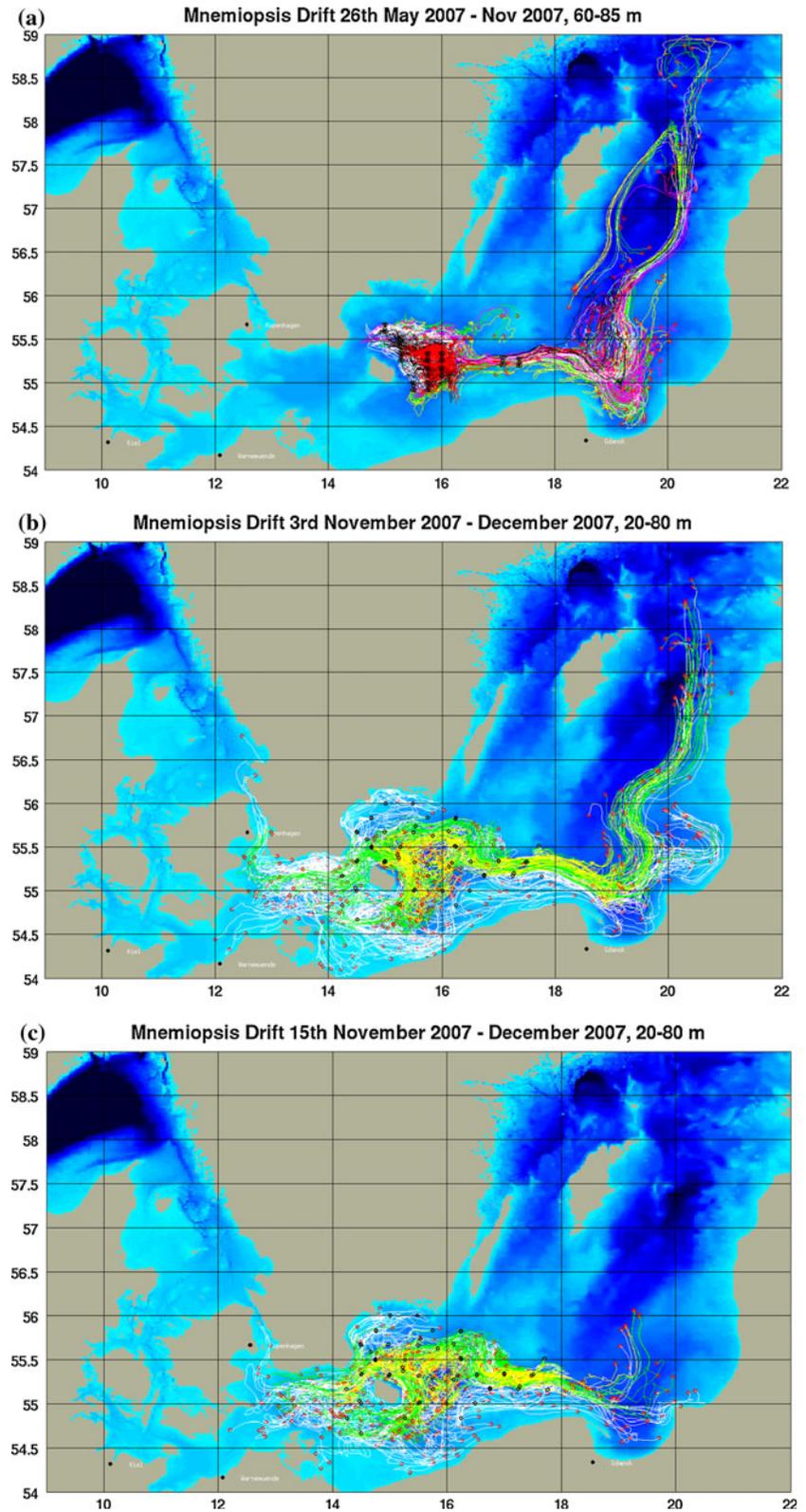
The data was transformed to fulfil the requirements for parametric tests. One-way analysis of variance was conducted to compare means among salinity treatments.

Results

Spread via drift

The spread of drifters gives a very detailed view (Fig. 3) of how deep water currents at the depth of 60–85 m in May and 20–80 m in November transport particles and freely floating organisms or in other words, tracks of drifters reflect the prevailing circulation in the corresponding depth ranges. On average drifters stay in the depth range in which they have been launched. Drifters which have been released in May 2007 in the Bornholm Basin resided mainly in the basin, but a part drifted through the Stolpe Channel into the Bay of Gdansk and the southern part of the eastern Gotland Basin (Fig. 3a). Those which have been released in the Stolpe Channel partly reached the Gdansk Basin and partly moved to the north into the eastern Gotland Basin, some of them recirculating in the central eastern Gotland Basin. It took about 6 months to reach the most northern positions. It is interesting to note that none of the drifters released in the Stolpe Channel entered the Bornholm Basin. In November drift patterns were much more dispersive, due to stronger winds and increased turbulence, and because drifters were released in shallower depths where the impact of the wind on the circulation is the strongest. Drifters, which have been launched in the Bornholm Basin partly ended up in the Arkona Basin but also in the Bay of Gdansk. Drift tracks starting in the Stolpe Channel revealed similar patterns as in May (Fig. 3b). It is interesting to note that the lengths of the drift routes were considerably shorter for those drifters, which have been released in the middle of

Fig. 3 Patterns of dispersal of *Mnemiopsis leidyi* in the central Baltic Sea by using the Lagrangian particle-tracking model. Launching positions of drifters (*black circles*) released in 26th of May 2007 (**a**) and 3rd of November 2007 (**b**) and **c** 15th of November in the area where *M. leidyi* has been observed and end positions (*red circles*) in December 2007. Colors denote drifters launched in different depths, **a** 60 m (*yellow*), 65 m (*green*), 70 m (*magenta*), 75 m (*white*), 80 m (*black*), 85 m (*red*) and in **b** and **c** 20–40 m (*white*), 45–60 m (*green*), 65–80 m (*yellow*). In May the drifters were launched from 60–85 m and in November from 20–80 m depths according to the observations on the major parts of the *M. leidyi* populations (Haslob et al. 2007; Huwer et al. 2008)



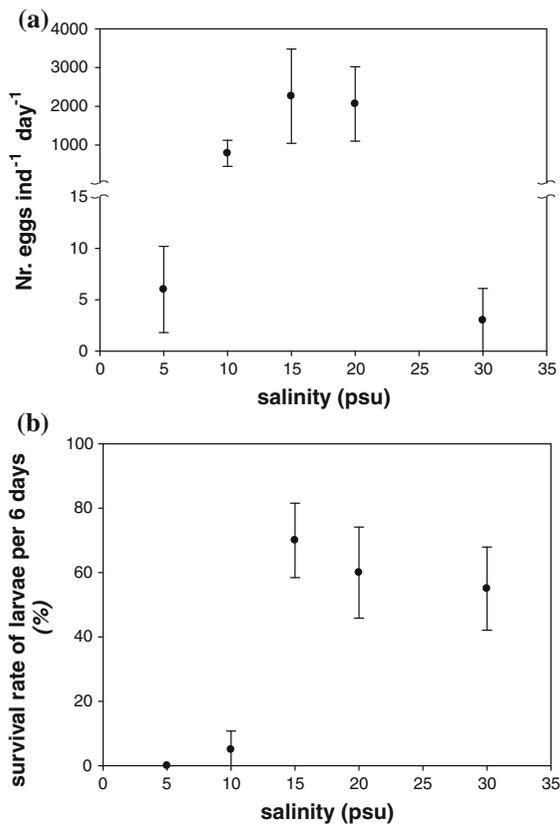


Fig. 4 Egg production (number of eggs produced by one ctenophore per day) and larval survival (percentage of larvae survived per 6 days) of *Mnemiopsis leidyi* in 18°C in different salinities from 5 to 30 psu. Average \pm SD

November 2007 compared with those released earlier in this month (Fig. 3c).

Reproduction and larval survival experiments

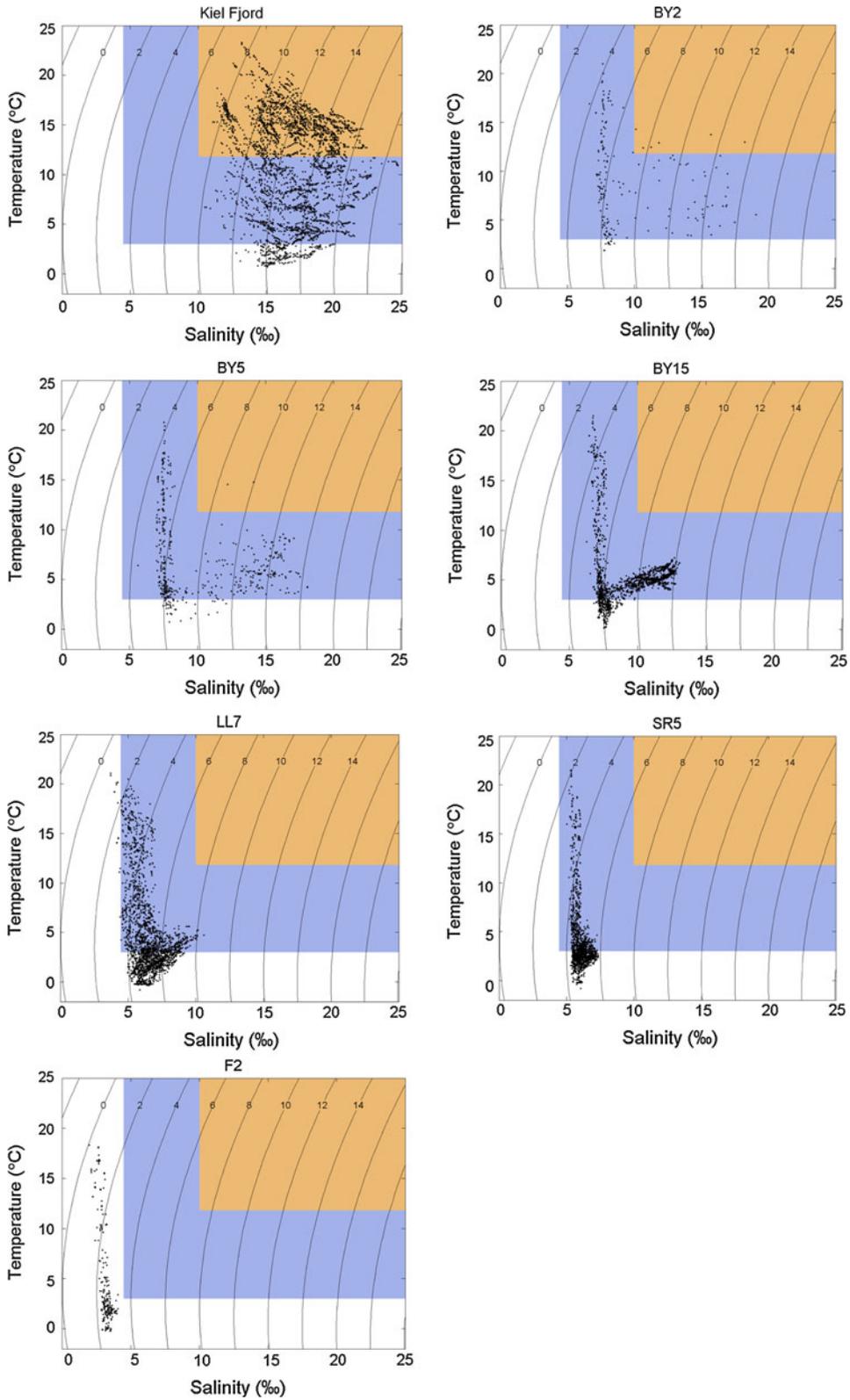
The reproduction experiments conducted in different salinities show that *M. leidyi* produces eggs at a high rate (Max. \sim 3500 eggs) in salinities from 10 to 20 psu (Fig. 4a). Although in 10 psu salinities the production rate is lower than in 15 and 20 psu salinities, it is not significantly different (Tukey HSD test: $P > 0.05$). In salinity treatments of 5 or 30 psu some eggs were produced, however the rate of reproduction was negligible (on average 6 eggs at 5 psu and 3 eggs at 30 psu). Larval survival was also high in higher salinities ranging from 15 to 30 psu, 10 psu being the lowest salinity where larvae survived. In 5 psu no larvae survived (Fig. 4b).

Fig. 5 Temperature-Salinity plots for stations from different sub basins of the Baltic Sea (starting from the southern and westernmost stations in Kiel Fjord in upper left corner and ending to the northernmost station F2 in lower right corner). For station locations see Fig. 1. Black dots show temperature and salinity measurements taken by CTD on board research vessels Aranda (Finnish Institute of Marine Research, 1979–2007) (redrawn from Leppäranta and Myrberg 2009) and Polarfuchs (Leibniz Institute of Marine Research, IFM-GEOMAR, Kiel Fjord; 2004–2009). The lines in the background indicate isolines of the density of the sea water. The light blue indicates the temperature and salinity ranges where *Mnemiopsis leidyi* could survive and light orange indicates the ranges for reproduction

Physical factors limiting survival and establishment

The hydrographic conditions (temperature and salinity) enabling *M. leidyi* to survive and/or reproduce in the Baltic Sea are marked in the Temperature-Salinity (TS) diagrams for stations in all sub-basins of the sea (Fig. 5). The required environmental conditions (temperature $> 3^\circ\text{C}$ and salinity > 4.5 psu) for survival are met on all studied stations and sub-basins except in the northernmost basin, the Bothnian Bay (station F2), where all TS measurements fall outside the survival range. On the stations in Kiel Fjord and on BY2 and BY5 (Fig. 5) in the Arkona and Bornholm Basins, respectively, almost all TS measurements coincide with the survival conditions required. In these areas *M. leidyi* has been observed every year since 2007 (Huwer et al. 2008; Javidpour et al. 2009; Schaber et al. 2011) including present observations (own observations February 2010, see Fig. 2). In the Gotland Basin (BY15) and the Gulf of Finland (LL7) part of the TS measurements fall outside the physical survival range. However, large part of the water column (large part of the TS measurements) are still in that range, which should enable survival in those areas. In the Bothnian Sea (SR5) observed salinity range is very narrow, and close to the limits of survival for *M. leidyi*. In addition, temperature is most of the time near the lower limit for survival as well.

The salinity and temperature requirements for reproduction are much higher and therefore not met in most of the sub-basins (Fig. 5). The only areas where TS measurements lay inside the range enabling reproduction are in the western Baltic Sea: in the Kiel Bight. Also in the Arkona and Bornholm Basins a



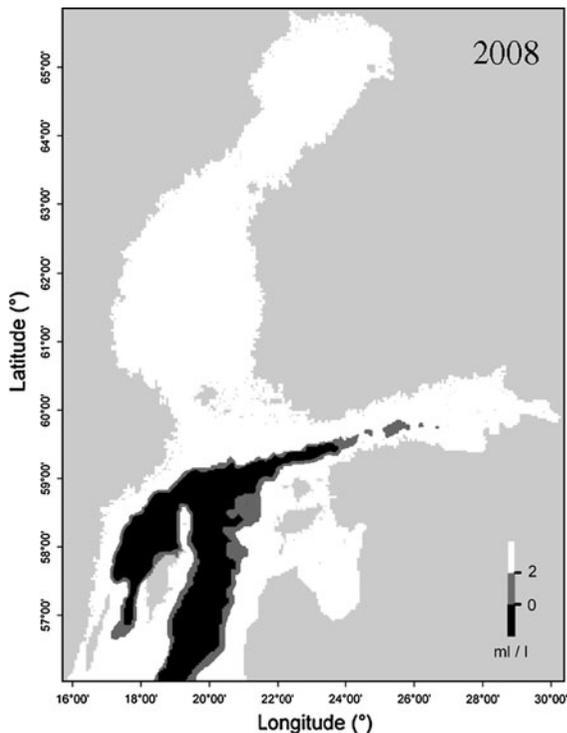


Fig. 6 Map showing hypoxic (grey: oxygen level between 0 and 2 ml l⁻¹) and anoxic (black: oxygen < 0 ml l⁻¹) areas in August 2008. Oxygen measurements are taken onboard R/V Aranda (Finnish Environment Institute) during HELCOM monitoring cruise

few TS measurements coincide with the requirements but most of the time salinity and temperature are too low for reproduction. In the central and northern Baltic all TS measurements are far from the needed conditions (Fig. 5). However, the required temperature for reproduction is found every year during summer above the thermocline in all sub-basins of the Baltic, but salinity is too low in this layer. Therefore the regulating factor for reproduction is mainly salinity in the southern, central and northern Baltic Sea.

One important factor, in addition to salinity and temperature, influencing survival of *M. leidy* is the oxygen content of the water. The strong stratification, which prevents mixing of the water column, causes deep-water hypoxia or even anoxia in the central Baltic Sea (Fig. 6). This most probably affects *M. leidy* survival (Breitburg et al. 2003) during slow drifting from the southern Baltic Sea via deep water currents (Fig. 3).

Discussion

Spreading possibilities

Mnemiopsis leidy has been observed in the Kattegat, Danish Straits, Bornholm Basin and Bay of Gdansk (Hansson 2006; Haslob et al. 2007; Javidpour et al. 2006, 2009; Kube et al. 2007; Huwer et al. 2008; Schaber et al. 2011). In the Bornholm Basin it is found in the deep water layers near the halocline (in 40–80 m depth) (Haslob et al. 2007; Huwer et al. 2008; Schaber et al. 2011; own observations February 2010). Based on the drift modeling we did, this is the most probable source population for secondary spread to other areas in the central and northern Baltic Sea. The deep-water currents transport particles through the Stolpe Channel to the Bay of Gdansk and eastern Gotland Basin. Our drift model runs showed that when floating particles were launched at the same time as the first observations of *M. leidy* were made in the Bornholm area (Haslob et al. 2007) they moved first towards the east into the Bay of Gdansk and then to north ending up in the Gotland Basin. This took about 6 months. There is not much published information on the longevity of *M. leidy* or other ctenophores but even in the cold waters of the Arctic Seas the life cycle is not more than 2–3 years (Siferd and Conover 1992; Lundberg et al. 2006). We assume that *M. leidy*, which is reported to spawn during summer when water is warm (e.g. Purcell et al. 2001; Costello et al. 2006), has a short life cycle (Baker and Reeve 1974), and probably does not live for more than a year. This would mean that adult specimens drifting in the deep water currents from the Bornholm Basin and Stolpe Channel towards north do not live long enough to survive the transport. If the life cycle is longer in colder environments like the Baltic Sea, as observed in other animals (e.g. Begon et al. 1990), some individuals might survive the drifting time and potentially invade the Gotland Basin and even more northern basins. In our experiments most of the drifters launched in the Bornholm Basin were circulating there and were retained in the basin. Only those which were launched in the Stolpe Channel reached northern parts of the eastern Gotland Basin, and only those can potentially reach the Gulf of Finland and the Bothnian Sea.

Another potential factor restricting the survival during transport is low oxygen levels or even anoxia

in deep waters over the central Baltic Sea. *M. leidy* is known to tolerate low oxygen conditions (Purcell et al. 2001), however it cannot survive in anoxic waters (Purcell and Decker 2005). Based on the drift model results, it is evident that drifters spread to areas in the central Baltic Sea, eastern Gotland Basin, where deep water areas suffer from oxygen depletion or even anoxia (Fig. 6), which would exert an additional stress on *M. leidy*. Low oxygen affects also negatively other biota, decreasing the amount of available food for the comb jellies during drifting.

Thus, it is unlikely that *M. leidy* could spread naturally to the northern parts of the Baltic Sea via currents from the North Sea or from the Bornholm Basin during our period of investigation. This is in line with a recent study of potential pathways of invasion and dispersal of *M. leidy* in the Baltic Sea by Lehmann and Javidpour (2010). They excluded an invasion solely by advection from the Kattegat to the central Baltic Sea. Nevertheless, it may still be transported across the central Baltic Sea in ships' ballast water. Thus, an invasion originating from the main harbors of the southern Baltic Sea could be a potential way for spread to the northern areas.

Survival and reproduction

Although *Mnemiopsis leidy* is known to live in a vast range of environmental conditions (e.g. Vinogradov et al. 1989; Purcell et al. 2001; Riisgård et al. 2007; Shiganova and Malej 2009; Roohi et al. 2010; Fuentes et al. 2010) the combination of physical conditions close to the tolerance limits may prevent the species to invade and establish. We have shown that *M. leidy* may spread further north as a secondary spread from the present occurrence area in the Bornholm Basin if we assume that individuals have a multi-year life cycle and are able to pass the central Baltic area suffering from oxygen depletion. Although *M. leidy* can survive hypoxic waters (Breitburg et al. 2003) its zooplankton prey most probably cannot avoid the area (Kolesar et al. 2010), which further hampers survival of the ctenophores during drifting. The invasion is also possible via ship's ballast water from the southern Baltic ports (e.g. Port of Gothenburg; Lehmann and Javidpour 2010). Hydrographical factors (mainly temperature and salinity) should not limit its survival in the central and northern parts of the Baltic Sea because

conditions over survival thresholds (salinities > 4.5 psu and temperatures > 3°C; laboratory tests: Sarpe et al. 2007; USA: Purcell et al. 2001; southern Baltic: Haslob et al. 2007; Kube et al. 2007; Janas and Zgrundo 2007, see Table 1) are widely found in these regions. Temperature-Salinity plots indicate that *M. leidy* could survive in all other areas of the Baltic Sea except the northernmost parts of the Gulf of Bothnia and easternmost parts of the Gulf of Finland where both salinity and temperature are too low and their combined effect can limit the survival. *M. leidy* may occur at lower salinities if temperature is higher (Purcell et al. 2001), which means that the most suitable part of the water column in the central and northern Baltic for this species would be in the surface layers during summer (higher temperature although lower salinity compared to the bottom waters, better food availability; Ojaveer et al. 1998; Schulz et al. 2007). During summer it would also be possible to survive in the near-bottom waters but during winter-time the combined effect of very low temperature (if not at freezing point) in the surface waters and low salinity in the whole water column are too harsh for *M. leidy* to survive (Javidpour et al. 2009).

The highest abundances of *M. leidy* have been observed in salinities between 16 and 20 psu and in temperatures between 14 and 17°C in the western Baltic Sea (Javidpour et al. 2009) and above 13.5 psu salinities in the Bornholm Basin (Schaber et al. 2011). These conditions are optimal and therefore also reproduction should occur when these conditions are met if enough food is available (Shiganova et al. 2003; Costello et al. 2006). Our laboratory experiments support this by showing that the highest egg production rates as well as larval survival rates were observed in 15–20 psu salinities and 18°C. We have shown that these conditions are found only in the western parts of the Baltic Sea during summer time (Fig. 5). This indicates that the probability of *M. leidy* reproduction is very low in the southern parts (Arkona and Bornholm Basins) of the Baltic as Schaber et al. (2011) proposed and even lower in the central or northern parts of the sea. Although eggs were produced in 10 psu salinities the larval survival rate was very low in 10 psu. Only a few surviving larvae could not sustain a permanent population. This indicates that in the Arkona and Bornholm Basin, reproduction may take place only irregularly as environmental conditions above the tolerance limits

for reproduction are only seldomly met in these areas. The best, and in many parts of the world the only time, for reproduction is summertime due to annual temperature variations (Purcell et al. 2001; Costello et al. 2006). In the Baltic Sea, sufficient temperatures for reproduction are only found above the thermocline during summer. However, strong stratification prevents to a large extent mixing of the deeper and saltier waters with this fresher and warmer water, making the surface waters too fresh for *M. leidy* reproduction in all sub-basins east and north of the Arkona Basin. In the Gulf of Bothnia and the eastern Gulf of Finland, the stratification is not so pronounced, which could allow mixing of the water column. However, in these areas the salinity is in any case so low that *M. leidy* survival is not very probable.

Food availability is very important for *M. leidy* reproduction as well (Baker and Reeve 1974; Costello et al. 2006). Although the species can survive in low prey concentrations it needs to attain high feeding rates for effective egg production (Purcell et al. 2001 and references therein). In the central and northern Baltic Sea the salinity stratification would restrict *M. leidy* survival to near or below halocline waters where the availability of zooplankton prey is very low (Ojaveer et al. 1998; Schulz et al. 2007). Thus reproduction would be even less probable in those waters.

For an invasive species it is important to establish permanent populations in the invaded areas. That is the only way to spread further and cope with changing physical conditions. Our results show that *M. leidy* would not be able to reproduce in the central or northern basins of the Baltic Sea although it would be able to survive in case it would spread there. Thus, the only areas which may have permanent populations of *M. leidy* are found in the westernmost parts of the Baltic Sea. However, *M. leidy* is observed in high abundances in the Bornholm Basin as well (Schaber et al. 2011) although the populations are not probably reproducing there but advecting from the more western areas. Further studies should be done in these areas where the populations attain high abundances and impacts on the food web may be seen in order to understand the level of threat this species poses to the ecosystem functioning.

Summary

We have shown that the probability for a spreading of *Mnemiopsis leidy* from the Bornholm Basin to the central or northern parts of the Baltic Sea via currents is very low due to the combination of low drift speed near the halocline and large anoxic areas in the central Baltic. The survival of the species—if it would anyhow spread to the north—would be possible although the sub-optimal combination of low salinity, low temperature and low food availability would lower the survival rate. We hypothesize that the only real possibility for *M. leidy* introduction would be via ballast waters of ships coming e.g. from the southern Baltic. These populations would be already adapted to Baltic salinities which make the survival more probable even in the northern basins. The higher requirements of temperature and salinity for reproduction make effective reproduction possible only in the western parts of the Baltic Sea. In the central and northern Baltic Sea the species could not reproduce and thus establish permanent populations.

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