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PRIMARY RESEARCH PAPER

Potential pathways of invasion and dispersal of *Mnemiopsis leidyi* A. Agassiz 1865 in the Baltic Sea

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Abstract The rapid spread of *Mnemiopsis leidyi* across the entire Baltic Sea after its first observation in 2006 gave rise to the question of its invasion pathway and the possible vector of its transport. To investigate pathways of *M. leidyi* invasion, the years 2005–2008 have been simulated by a three-dimensional coupled sea ice-ocean model of the Baltic Sea. In addition, a Lagrangian particle-tracking model has been utilized to test possible transport routes of this invader for 2006/2007. Based on the model, we exclude advection from the Kattegat as the main area of origin of *M. leidyi* and further spreading through the entire Baltic Sea. To explain the dispersion of *M. leidyi* in 2007 an earlier invasion already in 2005 is most probable. Alternatively, an invasion originating from main harbors with high ship traffic could also be a potential pathway. Drift simulations with drifter release in the main harbors are in good agreement with the observed distribution pattern of *M. leidyi*.

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Introduction

In aquatic systems, invasive species occur at an alarming rate and cause a global concern by their potential ecological and economic consequences (Mack et al., 2000; Occhipinti-Ambrogi & Savini, 2003; Reusser & Lee, 2008). This increase is an outcome of mainly anthropogenic drivers such as biotic homogenization due to intensified human transport vectors (e.g., ballast water of ship traffic) and weakening of recipient ecosystems resistance to invasion due to overexploitation and environmental changes (Carlton, 1999; Jackson et al., 2001). For an invader to be successful, a number of sequential stages including transport and introduction, establishment in the new habitat, spread and potential impacts on other species are required (Catford et al., 2009). Dispersal capacity of an invasive species is considered as a critical process determining establishment success and ecological impact the species might have (Kot et al., 1996). A drastic decline in zooplankton densities and the collapse of pelagic zooplanktivorous fish was attributed to the *Mnemiopsis leidyi* invasion in the Black and Caspian Seas (Shiganova & Bulgakova, 2000, Roohi et al., 2008). The recent invasion of *M. leidyi* in the Baltic Sea (observed in 2006) has attracted a lot of attention (Javidpour et al., 2006, Haslob et al., 2007). This species expanded its distribution through the whole Baltic Sea in less than 6 months (Javidpour et al., 2009). In 2005, 1 year before its discovery in the Baltic Sea, *M. leidyi* was also reported in some Dutch estuaries (Faasse & Bayha, 2006). In 2006–2007 it was widely distributed in Danish waters (Tendal et al., 2007), and has further been observed in the Pommeranian Bay, Arkona and Bornholm Basins, the Bay of Gdansk as well as in the Åland Sea and Bothnian Sea (Fig. 1; Kube et al., 2007; Lehtiniemi et al., 2007; Janas & Zgrundo, 2007).

The North Sea, Kattegat and Skagerrak have been considered as a potential source for the dispersal of other ctenophore species, such as *Pleurobrachia pileus*, *Bolinopsis infundibulum*, and *Beroe* sp. into the Baltic Sea via advection (Schneider, 1987). Therefore, it was necessary to examine whether the dispersal pathways of *M. leidyi* are in agreement with this general view or if other sources of introduction such as ballast water could play a role. It is likely that organisms once introduced into a Baltic port may subsequently spread and reach other Baltic Sea regions (secondary introduction), either by natural drift or by internal ship traffic. Approximately 120 invasive species have been recorded in the Baltic Sea during the last 100 years, most of them introduced by shipping (Gollasch & Leppaekoski, 2007). The number of ship operations (voyages, excluding ferry traffic) in the Baltic including ship traffic from outside the Baltic region as well as internal transfers, is estimated to be high (150,000 per year, Gollasch & Leppaekoski, 2007). It is assumed that shipping activities will considerably increase in the future. The Baltic Sea is already one of the most heavily trafficked seas in the world, accounting for up to 15% of the world's cargo transportation (www.helcom.fi/shipping/navigation/en_GB/navigation/).

In this study, we provide first estimations of potential pathways of *M. leidyi* invasion to the Baltic Sea. We focus on two questions: first, is the potential source of invasion via circulation and water mass exchange with the North Sea, or second, via the release of ballast water in major harbors?

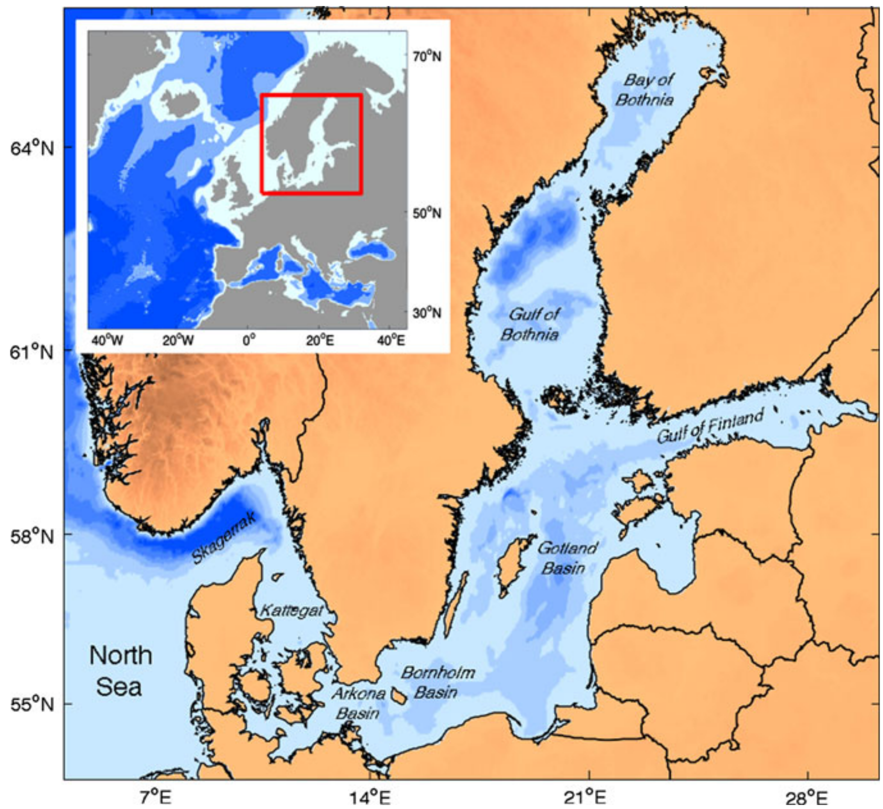

Fig. 1 Map of the Baltic Sea, areas of investigation

Materials and methods

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 (BSIOM; Lehmann & Hinrichsen, 2000; Lehmann et al., 2002). The horizontal resolution is 5 km (eddy-permitting), and 60 vertically 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 Kattegat and Skagerrak (Fig. 1). 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 realistic atmospheric conditions taken from the Swedish Meteorological and Hydrological Institute (SMHI Norrköping, Sweden) meteorological database (Lars Meuller, pers. comm.) which covers the whole Baltic drainage basin on a regular grid of 1° × 1° with a temporal increment of 3 h. The database, which for modeling purposes is further interpolated onto the model grid, includes surface pressure, precipitation, cloudiness, air temperature, and water vapor mixing ratio at 2-m height and geostrophic wind. In addition, runoff data are specified for 42 individual rivers distributed around the Baltic and the Kattegat. BSIOM was 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 were 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 model 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., 2003a, b).

Tracking of potential pathways of invasion; spread via North Sea water exchange

The years 2005–2006 were simulated by BSIOM, and the main drift routes calculated by a Lagrangian particle-tracking model, in which neutrally buoyant artificial particles represent a ''sample population'' of *M. leidyi*. In a preliminary back-tracking experiment drifters were released at positions where *M. leidyi* was observed during 2006 and 2007. This back-tracking experiment indicated that only the observations of *M. leidyi* in Kiel Bight potentially originated from the Kattegat and observations in the Mecklenburg Bight originated mainly from Arkona Sea. For the winter 2005/2006 the NAO winter index was negative which indicated a weak influence of the NAO on the Baltic Sea winter circulation (Lehmann et al., 2002). During summer 2006 mainly easterly winds prevailed. Thus, atmospheric conditions in 2006 were favorable for outflow of Baltic Sea waters to the Kattegat. This suggests that *M. leidyi* probably may have been introduced to the Baltic Sea earlier than 2006, thus we extended the investigation period into 2005.

The following forward-tracking experiment was designed to track the dispersion of *M. leidyi* from potential areas of origin. We selected five geographically distinct sections through the main basins of the Baltic Sea and released drifters between the surface and the bottom every 3 m, respectively. Sections have been chosen for Kattegat, Arkona Basin, Gotland Basin, Gulf of Finland, and Bothnian Sea (Fig. 2a–e). Drifters release started from January 1, 2005 and was repeated in 15-day interval. Although the fate of individual drift tracks depends on the currents they are exposed to, time and location of their release, we obtained similar drift tracks when launching drifters at different dates during the period January–March 2005. All drift calculations were ended on December 31, 2006.

Tracking of potential pathways of invasion; spread via ballast water

In the next experiment, we tested the hypothesis that the main pathway of invasion happened through ballast water transport released in major harbors and subsequent dispersion by internal circulation of the Baltic Sea. Drifters were released at the surface close to the main harbors at different time stamps (every 1st and 15th day of each specific month) from July to December 2006. This period from late summer to early winter was the period of high density of *M. leidyi* in the western Baltic Sea (Javidpour

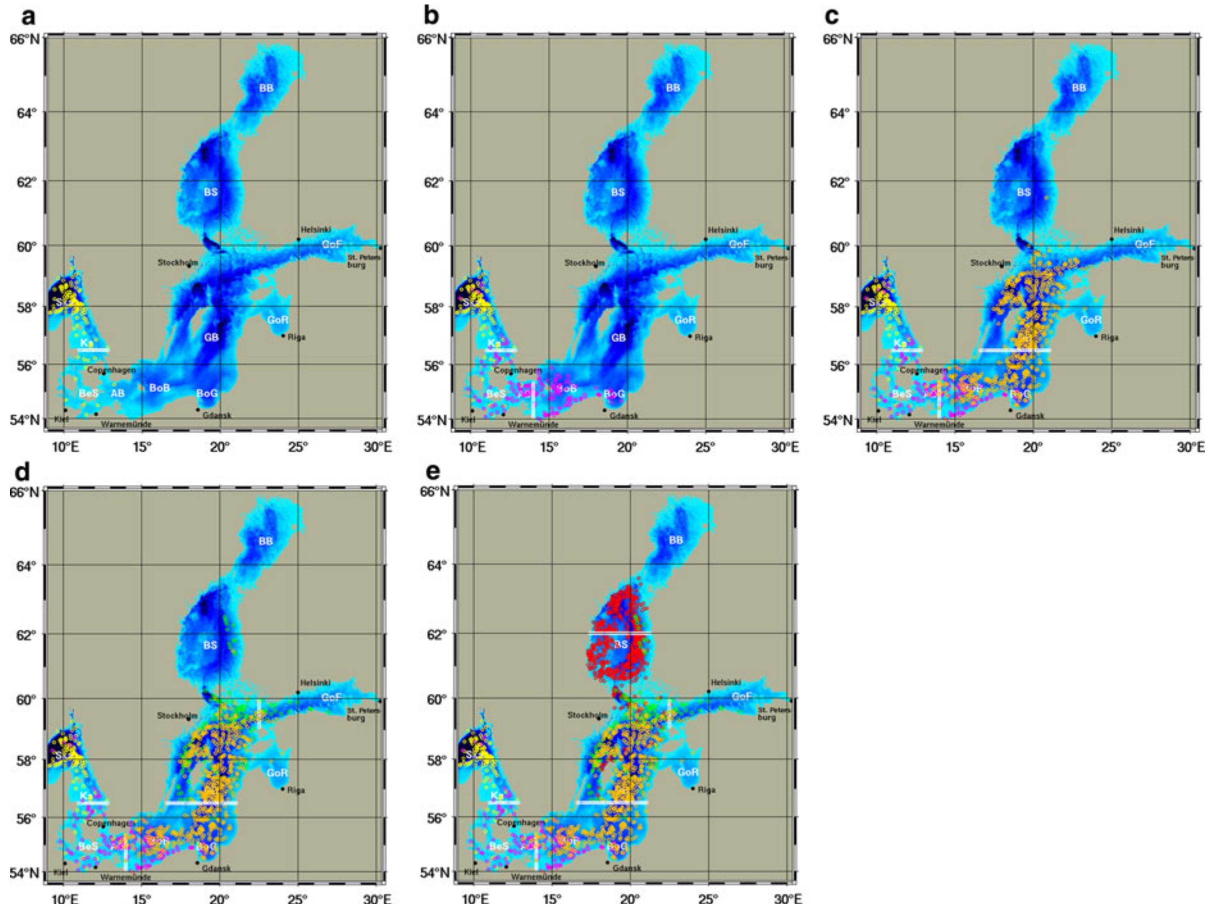

Fig. 2 **a–e** Pattern of dispersal of *M. leidyi* in the Baltic Sea by using the Lagrangian particle-tracking model. Launching positions of drifters (*white circles*) released in January 2005 and end positions (*colored circles*) in December 2006. Colors denote sub-basins of origin: **a** yellow = Ka, **b** cyan = AB, **c** orange = GB, **d** green = GoF, **e** red = BS. Ska = Skagerrak, Ka = Kattegat, BeS = Belt Sea, AB = Arkona Basin, BoB = Bornholm Basin, BoG = Bay of Gdansk, GB = Gotland Basin, GoR = Gulf of Riga, GoF = Gulf of Finland, BS = Bothnian Sea, BB = Bothnian Bay (Color figure online)

et al., 2009). All calculations of drifter routes were extended to March 2008. For this experiment drifters were not allowed to leave the layer in which they were launched. In a further experiment a sinking vertical velocity was specified. During winter period of 2007 *M. leidyi* were observed close to the bottom or residing within the halocline in 60- to 70-m depth (Haslob et al., 2007; Kube et al., 2007). We specified for each drifter a sinking rate of 1 m day^{-1} when the sea surface temperature dropped below 10°C. When released during the warm season drifters followed the surface circulation, and with the surface cooling during autumn and winter, drifters slowly migrated downward. The sinking rate was reset to zero when the environmental temperature reached 5.5°C, which was the mean temperature of halocline waters observed in 2007. Thus, drifters were able to move gently downward and stopped sinking when reaching halocline waters.

Results

Tracking of potential pathways of invasion; spread via North Sea water exchange

Figure 2 shows the results of the forward-tracking experiment when drifters were launched in different areas of the Baltic Sea. Only start and end positions of the different drifter routes are shown to provide a clear image of the areas of dispersal (starting positions marked by white circles and end positions marked by different colors). Drifters which were launched in the Kattegat (yellow circles, Fig. 2a) mainly end up in the Skagerrak. Some of them reached Kiel Bight and Mecklenburg Bight during 2006 which principally can explain the invasion of *M. leidyi* from the Kattegat to the western Baltic Sea in autumn 2006 (Javidpour et al., 2006; Kube et al., 2007). However, drifters were not able to reach Mecklenburg Bight, when released in early 2006 (not shown). Drifters which were launched in the Arkona Basin (cyan circles, Fig. 2b) could be found in the Skagerrak and Kattegat as well as in the Belt Sea and along the southern coast of the Baltic Sea to the Bay of Gdansk. If we assume that *M. leidyi* had already been introduced to the Arkona Basin in 2005, all detection records in Mecklenburg and Kiel Bight as well as in the Danish waters could be explained. Released drifters in the Gotland basin (orange circles, Fig. 2c) were distributed over the Baltic Proper to the western Baltic Sea. Some of them reached the Gulf of Riga and the Bothnian Sea as well as the entrance of the Gulf of Finland. Drifters which were launched at the entrance of the Gulf of Finland (green circles, Fig. 2d) mainly reached the northern Gotland Basin, the inner Gulf of Finland and the Bothnian Sea. Drifters which were released in the Bothnian Sea (red circles, Fig. 2e) were strongly circulating in the Bothnian Sea or scattered further to the south in the northern Gotland Basin, but no drifters reached Bothnian Bay.

Tracking of potential pathways of invasion; spread via ballast water

The rapid spreading of *M. leidyi* all over the Baltic Sea also could be achieved through the release of ballast water. Figure 3 shows the resulting drift tracks where drifters have been released close to the main harbors on October 15, 2006. Drift tracks have been calculated until March 2008. Drifters which were released in the western harbors (e.g., Kiel port, Copenhagen, and Gothenborg) dispersed over the western Baltic Sea but did not reach the Baltic proper and central Baltic Sea. However, drifters which were originated from the southern and central Baltic ports like Swinoujscie, Gdansk and Klaipeda were transported far away from the harbors to the deep basins. The same pattern was observed for drifters which were launched at Helsinki and Tallinn. Drifters of the northern ports like Turku and Sundsvall were transported within the Bothnian Sea but did not enter the Bothnian Bay. Drifters released in the Bothnian Bay were mainly circulating in deeper parts whereas only one reached the Kvarken archipelago.

Discussion

We have provided the first model simulations to show the general pattern of dispersion of *M. leidyi* via ocean circulation and release by ballast water and subsequent dispersal. The more or less complete distribution of *M. leidyi* over the Baltic Sea in 2007 could partly be explained by the circulation within the Baltic Sea basins (i.e., invasion through the Kattegat). The output from the simulation particle-tracking model strongly suggests that *M. leidyi* range expansion after its first observation is unlikely to be via passive dispersal by the western Baltic currents to the central or from the central Baltic to the northern parts. Recently, Gorokhova et al. (2009) reconsidered identification of specimens collected at the northern Baltic Sea sites (e.g., Lehtiniemi et al., 2007). Gorokhova et al. reported *Mertensia ovum* which naturally distributes in the Arctic and its marginal seas and indicated that *M. leidyi* does not occur in the northern Baltic Sea. In general, in the Baltic Sea distinct circulation patterns exist which comprise the main basins with less water mass exchange between them (Lehmann & Hinrichsen, 2000; Lehmann et al., 2002). This is also reflected by the calculated drift patterns (Fig. 2). Regardless to the recent changes in species distributions of *M. leidyi*, our model supports the new finding of Gorokhova et al. (2009) that a complete dispersion of *M. leidyi* throughout the Baltic Sea via internal circulations was not possible.

This study has demonstrated the potential introduction of a pelagic invasive species via ballast water and subsequent long distance distribution in the Baltic Sea. As shown by the model (Fig. 3) it is likely that organisms once introduced into one Baltic port may subsequently spread and reach other Baltic regions by internal circulation and surface drift. This supports the recent reports of *M. leidyi* spatial distribution in which a concentration of individuals in deeper parts of the central Baltic was found (Haslob et al., 2007). Further analysis of the population spread

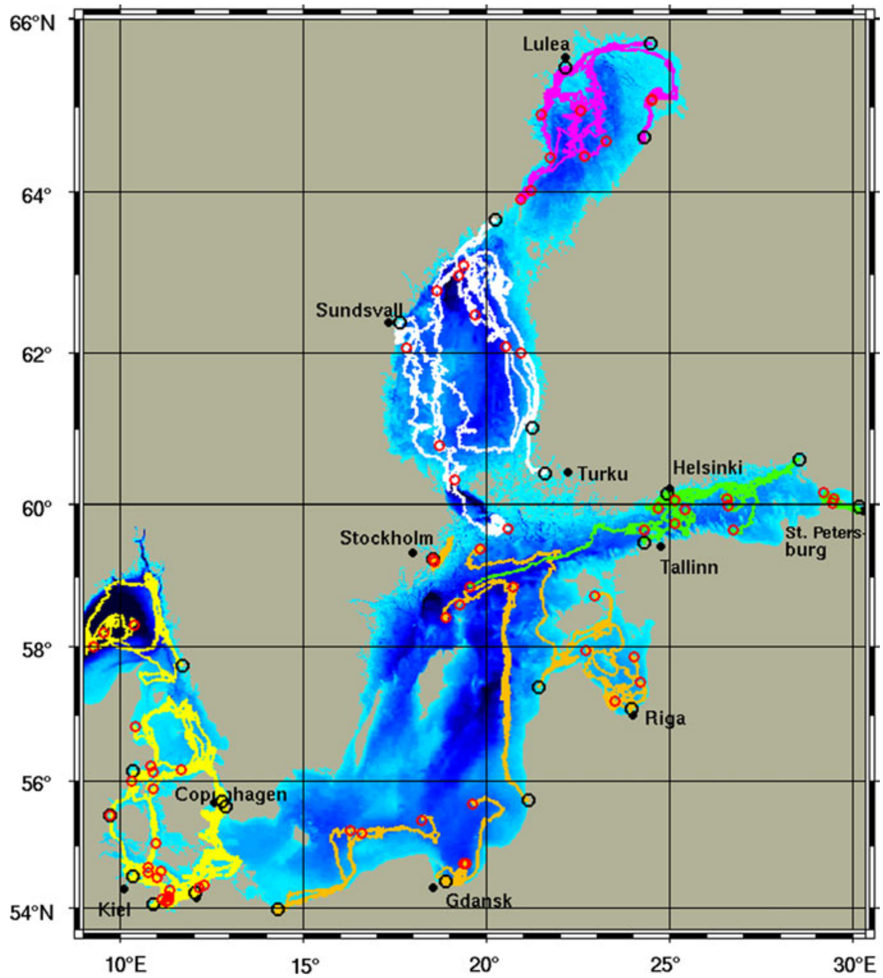

Fig. 3 Pattern of dispersal of *M. leidyi* over the Baltic Sea by using a Lagrangian particle-tracking model. Launching positions of drifters (*black circles*) close to the main harbors released in October 2006, and end positions (*red circles*) in March 2008. Different colors of drift tracks denote sub-basin of origin

should consider biological characteristics of different population sources of *M. leidyi*. Both life history and the spatio-temporal pattern of the environment are critical determinants of spread rate (Elton, 1958). The ability to reproduce at low temperature and salinity, or secondary spread by offspring can be a particularly important factor influencing spread rate. While juveniles are the stage most likely to disperse, reduced reproduction can lead to slower rates of geographical range expansion (Lockwood et al., 2007). *M. leidyi* shows a wide tolerance range for salinity and temperature which might explain its successful distribution (Purcell et al., 2001), however, the environmental conditions in which it reaches the highest density in the Baltic Sea is narrow. *M. leidyi* was found in high abundance mostly in the south-west Baltic where generally winter temperatures and salinity are higher compared to the northern and eastern areas of the Baltic Sea (Javidpour et al., 2009).

There are many biological models for estimation of expansion rates of non-native species (for review, see Kinlan & Hasting, 2005). Most of those models rely on assumptions about population parameters (growth rate, offspring size, demography, and adaptation) and environmental conditions which limit those biological variables. The flexibility of the particle-tracking model used here, and the fact that it is independent of the biological features of the invader in the new habitat (which is still unknown), provided a general insight of patterns of spread of *M. leidyi* in this area. Given the fact that *M. leidyi* is a holoplanktonic organism, the pattern obtained by the tracking method can be useful to evaluate potential routes of any pelagic invader in the Baltic Sea. Our model can be a helpful tool to understand the biogeography of the species in terms of large scale distribution and in mapping and explaining its static features, rather than precisely mimicking the population dynamics process. If the population dynamics of *M. leidyi* in the Baltic Sea, which is still widely unknown, could be included into our drift tracking model, the results of the simulation would be more specific for this invader.

Besides the global anthropogenic modification of marine systems due to high transport rates of invasive species by ballast water, the ecological niche of aquatic members can change due to accelerating climate change worldwide (Dulvy et al., 2008). A recent meta-analysis found that climate change has already been associated with an average 6.1 km per decade pole-ward shift in species' ranges (Parmesan & Yohe, 2003). Indeed temperature of the Baltic Sea has increased by about 1–1.5°C since the late 1980s (Hinrichsen et al., 2007; MacKenzie & Schiedek, 2007). A predictive understanding of future shifts in population distribution, as well as previous changes that have led to the current establishment of the species will require detailed knowledge of long-term processes determining distribution pattern across the Baltic Sea as well as the evolutionary adaptive processes in different populations along the salinity gradient within the Baltic Sea.

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References

Carlton, J. T., 1999. The scale and ecological consequences of biological invasions in the world's oceans. In Sandlund, O. T. S. P. & A. Viken (eds) Invasive Species and Biodiversity Management. Kluwer, Dordrecht: 195–212.

Catford, J. A., R. Jansson & C. Nilsson, 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. Diversity & Distributions 15: 22–40.

Dulvy, N. K., S. I. Rogers, S. Jennings, V. Stelzenmuller, S. R. Dye & H. R. Skjoldal, 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. Journal of Applied Ecology 45: 1029–1039.

Elton, C. S., 1958. The Ecology of Invasions by Animals and Plants. Methuen, London, UK.

Faasse, M. A. & K. M. Bayha, 2006. The ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 in coastal waters of the Netherlands: an unrecognized invasion? Aquatic Invasions 1: 270–277.

Gollasch, S. & E. Leppaekoski, 2007. Risk assessment and management scenarios for ballast water mediated species introductions into the Baltic Sea. Aquatic Invasions 2: 313–340.

Gorokhova, E., M. Lehtiniemi, S. Viitasalo-Frösen & H. D. Haddock, 2009. Molecular evidence for the occurrence of ctenophore Mertensia ovum in the northern Baltic Sea and implications for the status of the *Mnemiopsis leidyi* invasion. Limnology and Oceanography 54: 2025–2033.

Haslob, H., C. Clemmesen, M. Schaber, H. H. Hinrichsen, J. O. Schmidt, R. Voss, G. Kraus & F. W. Köster, 2007. Invading *Mnemiopsis leidyi* as a potential threat to Baltic fish. Marine Ecology Progress Series 349: 303–306.

Hinrichsen, H. H., A. Lehmann, M. A. St. John & B. Brügge, 1997. Modelling the cod larvae drift in the Bornholm Basin in summer 1994. Continental Shelf Research 17(14): 1765–1784.

Hinrichsen, H. H., U. Böttcher, F. W. Köster, A. Lehmann & M. A. St. John, 2003a. Modelling the influences of atmospheric forcing conditions on Baltic cod early life stages: distribution and drift. Journal of Sea Research 49: 187–201.

Hinrichsen, H. H., A. Lehmann, C. Möllmann & J. O. Schmidt, 2003b. Dependency of larval fish survival on retention/dispersion in food limited environments: the Baltic Sea as a case study. Fisheries Oceanography 12(4/5): 425–433.

Hinrichsen, H. H., A. Lehmann, C. Petereit & J. Schmidt, 2007. Correlation analysis of Baltic Sea winter water mass formation and its impact on secondary and tertiary production. Oceanologia 49(3): 381–395.

Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner & R. Warner, 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629–637.

Janas, U. & A. Zgrundo, 2007. First record of *Mnemiopsis leidyi* A. Agassiz 1865 in the Gulf of Gdańsk (southern Baltic Sea). Aquatic Invasions 2: 450–454.

Javidpour, J., U. Sommer & T. A. Shiganova, 2006. First record of *Mnemiopsis leidyi* A. Agassiz 1865 in the Baltic Sea. Aquatic Invasions 1: 299–302.

Javidpour, J., J. C. Molinero, J. Peschutter & U. Sommer, 2009. Seasonal changes and population dynamics of the ctenophore *Mnemiopsis leidyi* after its first year of invasion in the Kiel Fjord, Western Baltic Sea. Biological Invasions 11: 873–882.

Kinlan, B. P. & A. Hasting, 2005. Rates of population spread and geographic range expansion. In Sax, D. F., J. J. Stachowicz & S. D. Gaines (eds) Species Invasions, Insights into Ecology, Evolution, and Biogeography. Sinauer Associates, Sunderland, MA: 480 pp.

Kot, M., M. A. Lewis & P. vanden Driessche, 1996. Dispersal data and the spread of invading organisms. Ecology 77: 2027–2042.

Kube, S., L. Postel, C. Honnef & C. B. Augustin, 2007. *Mnemiopsis leidyi* in the Baltic Sea – distribution and overwintering between autumn 2006 and spring 2007. Aquatic Invasions 2: 137–145.

Lehmann, A., 1995. A three-dimensional baroclinic eddy-resolving model of the Baltic Sea. Tellus 47: 1013–1031.
Lehmann, A. & H. H. Hinrichsen, 2000. On the wind driven and thermohaline circulation of the Baltic Sea. Physics and Chemistry of the Earth, Part B: Hydrology, Oceans and Atmosphere 25: 183–189.
Lehmann, A., W. Krauss & H.-H. Hinrichsen, 2002. Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. Tellus 54A: 299–316.
Lehtiniemi, M., J. P. Pääkkönen, J. Flinkman, T. Katajisto, E. Gorokhova, M. Karjalainen, S. Viitasalo & H. Björk, 2007. Distribution and abundance of the American comb jelly (*Mnemiopsis leidyi*) – a rapid invasion to the northern Baltic Sea during 2007. Aquatic Invasions 2: 445–449.
Lockwood, J. L., M. F. Hoopes & M. P. Marchetti, 2007. Invasion Ecology. Blackwell publishing, Oxford, UK: 304 pp.
Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout & F. A. Bazzaz, 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10: 689–710.
MacKenzie, B. R. & D. Schiedek, 2007. Daily ocean monitoring since the 1860s shows record warming of northern European seas. Global Change Biology 13(7): 1335–1347.
Novotny, K., K. G. Liebsch, R. Dietrich & A. Lehmann, 2005. Combination of sea-level observations and an oceanographic model for geodetic applications in the Baltic Sea. In Sanso, F. (ed.), A Window on the Future of Geodesy, Vol. 128 of Springer Series of IAG Symposia. Springer, New York: 195–200.
Occhipinti-Ambrogi, A. & D. Savini, 2003. Biological invasions as a component of global change in stressed marine ecosystems. Marine Pollution Bulletin 46: 542–551.
Parmesan, C. & G. Yohe, 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421: 37–42.
Purcell, J. E., T. A. Shiganova, M. B. Decker & E. D. Houde, 2001. The ctenophore *Mnemiopsis leidyi* in native and exotic habitats: U. S. estuaries versus the Black Sea basin. Hydrobiologia 451: 145–176.
Reusser, D. A. & H. Lee, 2008. Predictions for an invaded world: a strategy to predict the distribution of native and non-indigenous species at multiple scales. ICES Journal of Marine Science 65: 742–745.
Roohi, A., Z. Yasin, A. E. Kideys, A. T. S. Hwai, A. G. Khanari & E. Eker-Develi, 2008. Impact of a new invasive ctenophore (*Mnemiopsis leidyi*) on the zooplankton community of the Southern Caspian Sea. Marine Ecology 29: 421–434.
Schneider, G., 1987. Role of advection in the distribution and abundance of *Pleurobrachia pileus* in Kiel Bight. Marine Ecology Progress Series 41: 99–102.
Shiganova, T. A. & Y. V. Bulgakova, 2000. Effects of gelatinous plankton on Black Sea and Sea of Azov fish and their food resources. ICES Journal of Marine Science 57: 641–648.
Tendal, O. S., K. R. Jensen & H. U. Riisgård, 2007. Invasive ctenophore *Mnemiopsis leidyi* widely distributed in Danish waters. Aquatic Invasions 2: 46–455.