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Research article

Abundance, horizontal and vertical distribution of the invasive ctenophore *Mnemiopsis leidyi* in the central Baltic Sea, November 2007

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Abstract

The distribution and abundance of the invasive ctenophore *Mnemiopsis leidyi* in the Bornholm Basin, an important spawning ground of several fish stocks, and in adjacent areas in the central Baltic Sea was studied in November 2007. The study showed that *M. leidyi* were relatively small (body length 18.6 ± 7.6 mm) and they were patchily distributed over a large part of the investigated area. Specimens were found on 68 and 59% of stations sampled with a Bongo net (n=39) and an Isaac-Kidd midwater trawl (n=51), respectively. Vertically, the highest densities of *M. leidyi* occurred at 40 to 60 m around the halocline. Horizontally, the highest abundances were found north and west of Bornholm, but relatively high densities were also observed in the Slupsk Furrow. The mean abundance was 1.58 ± 2.12 ind. m^{-2}, the peak abundance was 8.92 ind. m^{-2}, and the average and peak population density were 0.03 ± 0.05 and 0.28 ind. m^{-3}, respectively. The abundances are low compared to densities recently observed in other areas of the Baltic region (e. g. Limfjorden, Åland Sea) and the estimated predation impact on zooplankton by *M. leidyi* was negligible in November 2007. However, because of the ctenophore's wide distribution in the central Baltic Sea, its ability for rapid population growth, and its potential influence on fish stocks by competing for food and by preying on fish eggs and newly hatched larvae, close monitoring of the future development of *M. leidyi* in the Baltic Sea is strongly recommended.

Key words: *Mnemiopsis leidyi*, comb jelly, ctenophora, invasive species, Baltic fish stocks, Bornholm Basin

Introduction

Several studies have recently described occurrences of the invasive lobate ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 in the Baltic Sea (Javidpour et al. 2006; Haslob et al. 2007; Janas and Zgrundo 2007; Kube et al. 2007; Lehtiniemi et al. 2007; Tendal et al. 2007). The ctenophore was accidentally introduced with cargo ballast water into the Black Sea in the early 1980s, where its explosive population growth coincided with a breakdown of, in particular, the anchovy fishery (Vinogradov et al. 1989; Mutlu 1999; Kideys 2002). Subsequently, it spread into adjacent waters of the Mediterranean and to the Caspian Sea (Kideys and Niermann 1993; Shiganova 1993; Shiganova et al. 2001). In autumn 2006 *M. leidyi* was observed, nearly simultaneously, at several locations in northern Europe, including the western Baltic Sea (Faasse and Bayha 2006; Javidpour et al. 2006; Boersma et al. 2007; Oliveira 2007; Tendal et al. 2007). Early in 2007, observations of *M. leidyi* in Danish waters and the Baltic Sea commenced to become numerous, and in many cases there were indications of mass occurrences (Tendal et al. 2007; Lehtiniemi et al. 2007). *M. leidyi* has been documented to overwinter in low abundances (1-4 ind. m^{-3}) in the southern Baltic Sea at temperatures below 10 ºC (Kube et al. 2007). This has given the ctenophore an opportunity to extend its distribution range from the south-western to the central Baltic Sea between autumn 2006 and spring 2007 (Kube et al. 2007). In August 2007, very high densities were registered in the central parts of a shallow Danish fjord system (Limfjorden) where some localities reached values above 200 ind. m^{-3}, and in one case (Skive Fjord) the density was measured to be 867 ± 121 ind. m^{-3} (Riisgård et al. 2007). These values considerably exceeded abundances reported from the northern Baltic Sea during spring and summer 2007 (Lehtiniemi et al. 2007) and even most values reported from the Black Sea during the period when the zooplankton and fish stocks collapsed in this area (Purcell et al. 2001b; Shiganova et al. 2001).

The strong focus on the mainly carnivorous *M. leidyi* is due to its predation impact on zooplankton and ichthyoplankton which may be detrimental to fish populations (Purcell et al. 2001b; Kideys 2002). Furthermore, *M. leidyi* has a great invasive potential due to its ability of rapid growth and reproduction, and its high tolerance of broad ranges of temperatures and salinities (Kremer 1994; Shiganova 1998; Purcell et al. 2001b). Individual growth rates and egg production in *M. leidyi* varies with size, food availability and temperature (Kremer 1994; Purcell et al. 2001b) and Kremer (1994) concluded that three factors act in a hierarchy to determine the abundance of *M. leidyi*: temperature, food availability and mortality (predation), in decreasing order of importance.

Most of the recent studies on *M. leidyi* in the Baltic Sea are restricted to coastal areas and report on independent, purely qualitative catches or sightings obtained by various methods on different dates over a broad time scale. Exceptions are the studies by Lehtiniemi et al. (2007) who described abundances of *M. leidyi* in the Gulf of Finland, the Åland Sea and the Gulf of Bothnia, and by Haslob et al (2007) who investigated *M. leidyi* abundances on a station grid in the Bornholm Basin. The Bornholm Basin is of great importance for several fish species in the Baltic Sea, especially for the eastern Baltic cod *Gadus morhua* Linnaeus, 1758, as this area presently represents the only spawning ground that supports successful reproduction of this stock (Hinrichsen et al. 2007; Köster et al. 2005). Haslob et al. (2007) observed that the vertical distribution of *M. leidyi* showed an overlap with the water layers where cod eggs and, to a lesser degree, sprat eggs are neutrally buoyant. They hypothesized that this overlap may result in reduced recruitment success of these fish stocks due to predation by *M. leidyi* on fish eggs, as well as by competition for zooplankton food, influencing the survival success of fish larvae.

The present study investigated the horizontal and vertical distribution as well as abundances of *M. leidyi* in the Bornholm Basin and surrounding areas in November 2007. To our knowledge, this study represents the first extensive and systematic investigation on the distribution of *M. leidyi* in the central Baltic Sea on such a broad scale.

Materials and Methods

Samples of *M. leidyi* were collected during a cruise with the Danish research vessel 'DANA' from November 1st to 18th, 2007. The investigation covered an area from approximately 14.15° E to 18.15° E and 54.30° N to 56.15° N. The sampling was conducted with three different gears to obtain a coverage of the horizontal and vertical distribution of *M. leidyi*: an Isaac-Kidd midwater trawl (IKMT), a Multinet (5 nets), and a Bongo net. Corresponding ambient hydrographic conditions (salinity, temperature, oxygen concentration) were recorded at the sampling stations with a CTD (Sea-Bird plus).

Sampling with the Isaac-Kidd midwater trawl (mesh size 4 mm in the cod end) was conducted to investigate the horizontal and vertical distribution of *M. leidyi*. Hauls were taken on a regularly-spaced station grid with a distance of approximately 13.5 nautical miles between sampling stations. The duration of a haul was 30 min, and the gear was equipped with a flowmeter to measure the volume of filtered water. On stations with a bottom depth shallower than 35 m, one haul was made with the gear undulating between the surface and 5 m above the sea floor.

On stations deeper than 35 m, a two-layer sampling strategy was adopted to investigate the vertical distribution of *M. leidyi*. Thus, two hauls were taken; during the first haul, the gear was undulating between 5 and 25 m above the sea floor, while the second haul covered the remaining part of the water column, undulating between 25 m above the bottom and the surface. The decision of conducting two hauls at stations deeper than 35 m was based on the depth range at which the halocline was found in the study area (35-50 m), as previous studies by Haslob et al. (2007) and Kube et al. (2007) found *M. leidyi* exclusively below the halocline. Altogether, 91 IKMT hauls were taken on 51 stations.

To get a finer resolution of the vertical distribution of *M. leidyi* than obtained with the two-layer sampling strategy using the IKMT, hauls with an opening/closing Multinet (mesh size 335 µm, aperture 0.25 m^2) were taken on three stations. The vertical distribution of *M. leidyi* was resolved in steps of 5 or 10 m. The gear was towed, undulating in each depth range for approximately 5 to 6 min.

To assess abundances of *M. leidyi*, hauls with a Bongo net were taken on a total of 39 stations. The Bongo net (60 cm mouth diameter) was equipped with 500 µm mesh size nets, cod ends with 335 µm mesh size, and a flowmeter. This gear was towed in a double oblique haul integrating the entire water column, from 5 m above the bottom to the surface. The numbers of specimens from the two nets were combined. Counts of *M. leidyi* were standardised to individuals per m^2 by accounting for the filtered water volume and the maximum depth of the tow.

Specimens of *M. leidyi* were sorted from the samples, counted and the body oral-aboral length of each individual was measured to the nearest 1.0 mm with the aid of a sliding caliper. All samples were analysed within 30 min after capture. Individuals caught with Bongo and Multinet were generally less damaged than individuals captured with the IKMT, probably due to the different mesh sizes and haul durations.

A comparison of *M. leidyi* length distributions caught with the IKMT and with the Bongo net reflected that the catchability for smaller individuals (<10 mm) was lower with the IKMT (Figure 1), due to the relatively large mesh size of this gear. Generally, the catchability of the IKMT gear was smaller than the catchability of the Bongo net.

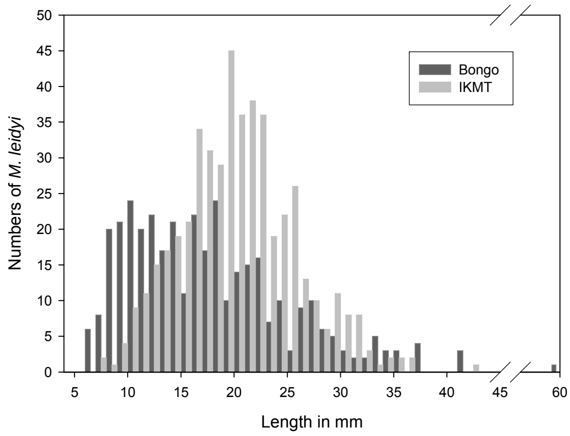

Figure 1. Mnemiopsis leidyi. Size distribution of ctenophores sampled with Isaac-Kidd midwater trawl (IKMT) and Bongo net.

However, we assume that the catchability of the IKMT is equal amongst hauls, and that IKMT stations are comparable with each other. A direct calculation of abundances per filtered volume from IKMT catches would largely underestimate true abundances of ctenophores. Assuming that the Bongo net has a catchability of 1, we compared Bongo catches to IKMT catches at those stations that were sampled with both gears. Only individuals >10 mm were considered in this analysis. One outlier was excluded (Bongo n=61, IKMT n=3), which may be due to a small scale patchiness in the distribution of *M. leidyi*. The analysis resulted in a significant linear relation between IKMT and Bongo catches ($P<0.001$, $r^2=0.72$), and we used this relationship to convert IKMT data to abundance estimates (ind. m^{-2}).

Results

While the size distributions of *M. leidyi* in the catches using the Multinet and the Bongo net were similar (cod end mesh size was 335 µm in both gears), the size distribution of *M. leidyi* retained in the IKMT and Bongo nets differed due to the different mesh sizes. *M. leidyi* between 6-59 mm (average 18.6 mm ± 7.6 SD) and 8-43 mm (average 21 mm ± 5.7 SD) were retained in the Bongo net and the IKMT, respectively (Figure 1). Although the IKMT was able to catch some *M. leidyi* <10 mm, the catchability of this gear for smaller specimens was lower in comparison to the Bongo net. Thus, for the comparison of IKMT catches to Bongo net catches, only specimens >10 mm were considered.

The IKMT catches showed highest numbers of *M. leidyi* to occur in the deep hauls (Figure 2) where 70% of specimens were caught, whereas 30% were caught in the shallow hauls. A peak in the deep-haul density of *M. leidyi* was observed in the area north of Bornholm (Figure 2b),

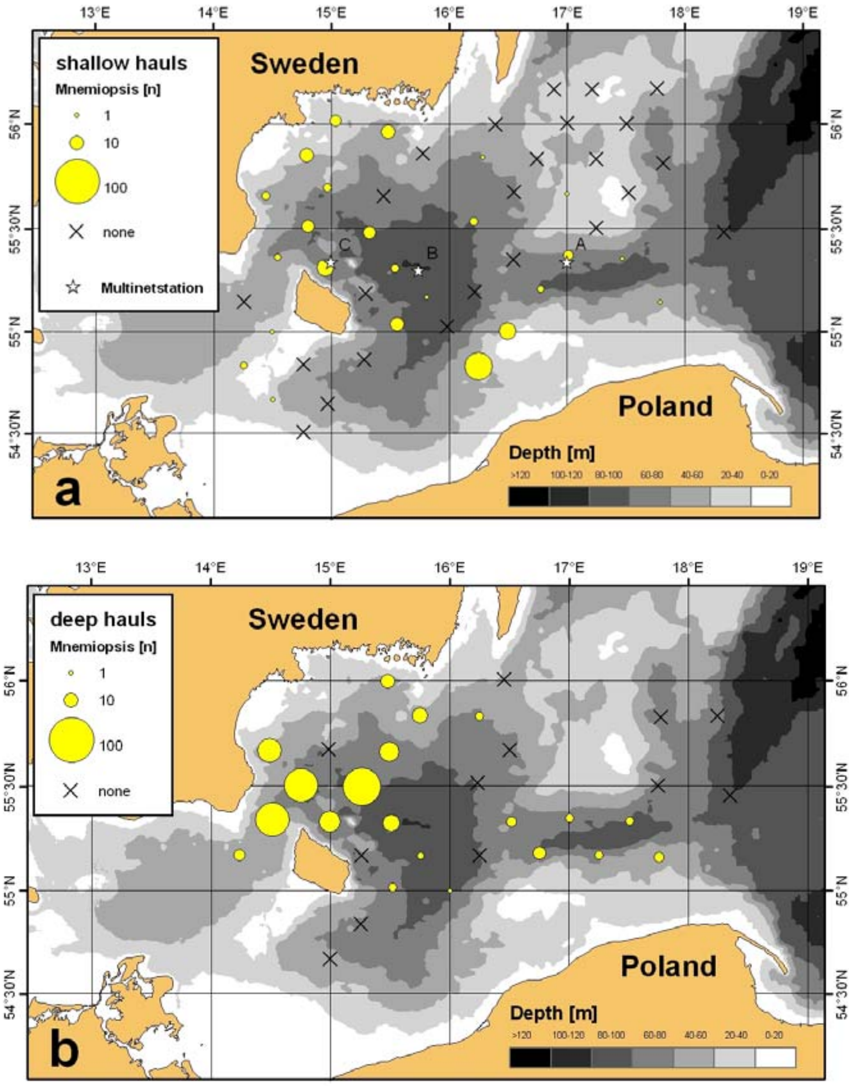

Figure 2. Mnemiopsis leidyi. Horizontal distribution of numbers of ctenophores per haul sampled with Isaac-Kidd midwater trawl (circles) and stations without ctenophores (crosses) in (a) shallow, and (b) deep hauls. Figure 2a also depicts the positions of Multinet stations A, B and C (white stars).

although a relatively large number of specimens were also caught by shallow hauls taken close to the coasts of Sweden, Bornholm and Poland (Figure 2a).

The results from the three Multinet stations support the observation from the IKMT catches that highest densities of *M. leidyi* mainly occurred at larger depths (Figure 3). In comparison with the CTD data, the vertical distribution of Multinet catches shows that the highest *M. leidyi* densities were found close to the halocline, and at two stations (A and C) *M. leidyi* was not observed above 35 m, but it was found at low oxygen levels down to 0.29 ml l^{-1}.

Generally, *M. leidyi* was widely distributed in the study area being present in 68% of the Bongo net stations and 59% of the IKMT stations (Figures 2 and 4). The horizontal distribution of *M. leidyi* sampled with the Bongo net revealed highest abundances north and west of Bornholm, and relatively high densities were observed in the Slupsk Furrow which connects the Bornholm Basin to the Gdansk Deep further to the east (Figure 4). However, no *M. leidyi* were observed in the southwestern part of the investigation area and in the northeastern part, in the region around the Middelbanke with very shallow water. The maximum abundance of *M. leidyi* caught at the Bongo net stations was 8.92 ind. m^{-2} (0.28 ind. m^{-3}), with mean densities of 1.58 ± 2.12 ind. m^{-2} (0.03 ± 0.05 ind. m^{-3}).

The horizontal distribution and abundance estimates obtained from the IKMT catches (Figure 5) are largely in concordance with the results from the Bongo net samplings. Again, highest abundances were observed in the area north of Bornholm. However, abundances in the Slupsk Furrow were somewhat lower than observed by the Bongo net sampling, while the IKMT sampling suggested a second, smaller abundance peak at the southeastern edge of the Bornholm Basin, an area that was not covered by the Bongo net sampling. The observation that no *M. leidyi* occurred in the southwestern and northeastern parts of the investigated area was also confirmed by the IKMT sampling. However, the maximum values of abundance estimates from the IKMT sampling were lower compared to the Bongo net sampling (maximum 4.42 ind. m^{-2} for the IKMT and 8.92 ind. m^{-2} for the Bongo net sampling). It should be kept in mind, though, that the abundances obtained by means of the IKMT samplings only included ctenophores >10 mm body length.

Using equations given by Riisgård et al. (2007), the population filtration rate of *M. leidyi* with mean body length (18.8 mm) and peak density (0.28 ind. m^{-3}) found in the present study was estimated to be $F_{pop} = 2.3 \times 10^{-3}$ m^3 d^{-1}, and subsequently the half-time of zooplankton (copepods) was found to be $t_{1/2} = 300$ d.

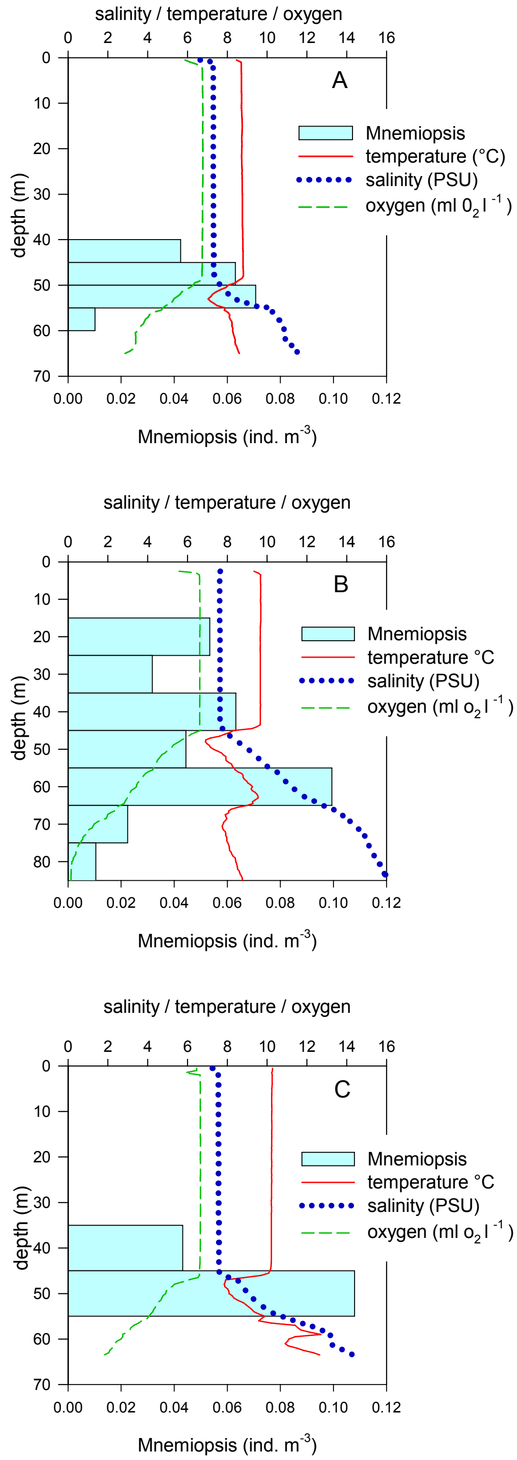

Figure 3. Mnemiopsis leidyi. Vertical distribution of ctenophores sampled with Multinet on three stations (A, B, C, see Figure 2a) in relation to temperature, salinity and oxygen concentration as determined by CTD measurements.

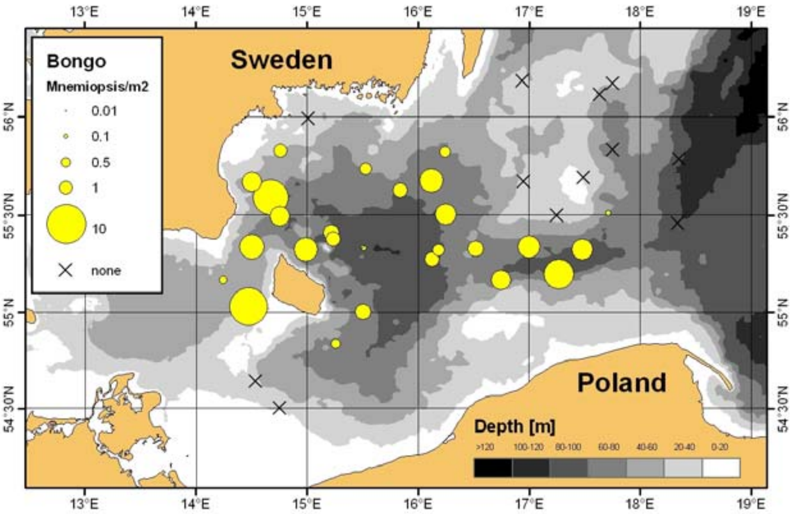

Figure 4. Mnemiopsis leidyi. Abundance of ctenophores (ind. m^{-2}) sampled with Bongo net

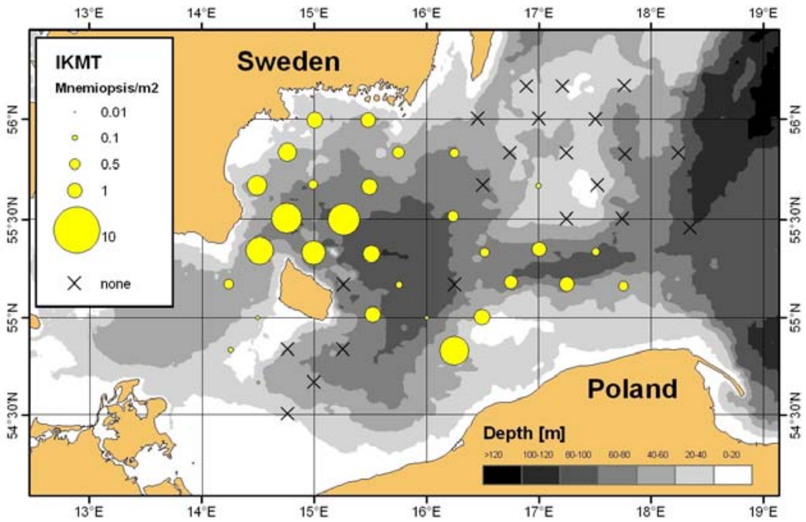

Figure 5. Mnemiopsis leidyi. Abundance of ctenophores (> 10 mm; ind. m^{-2}) sampled with Isaac-Kidd midwater trawl (IKMT).

Discussion

Hydrographic influence on distribution

Temperature appears to be of overriding importance in determining conditions suitable for population increase and expansion of *M. leidyi* (Kremer 1994; Mutlu 1999; Purcell et al. 2001b; Shiganova et al. 2001; Purcell and Decker 2005). In its native environment, reproduction occurs from spring through autumn at temperatures ≥12 °C, reproduction peaks at temperatures of 24–28 °C (Purcell et al. 2001b), and in the Sea of Azov Shiganova et al. (1998, 2001) did not find any specimens when the temperature dropped below 4 °C.

Lehtiniemi et al. (2007) found the highest densities of *M. leidyi* eggs (90 eggs m^{-3}) around the halocline at 80-60 m depth where the temperature ranged between 4.5-5 ºC. This indicates that although the optimal spawning temperature for *M. leidyi* in the Black Sea or in its native environment is high, *M. leidyi* may have adopted to the Baltic Sea environment and spawn now at lower temperatures. Besides, higher abundances of *M. leidyi* than previously recorded in the Black Sea and the Caspian Sea have been registered in a shallow Danish fjord system, at relatively low temperatures (11-19 °C) (Riisgård et al. 2007).

M. leidyi does not seem to be limited by salinities >2 PSU, but low winter temperatures, particularly in combination with low salinities, may prevent survival throughout the winter in some locations, e.g. the Sea of Azov (Purcell et al. 2001b). Data by Kube et al. (2007) show that *M. leidyi* occurred in the central Baltic Sea during the winter months below the halocline where temperatures do not drop below 4°C. Therefore, it seems reasonable to suggest that *M. leidyi* may use the Bornholm Basin as a refuge during winter, and to expand its distributional range in spring when temperature and food availability are increasing. It has been shown that *M. leidyi* also overwinters in the Gulf of Finland (Lehtiniemi et al. 2007), and it is therefore possible that other areas in addition to the Bornholm Basin act as winter refuges.

Lehtiniemi et al. (2007) suggested that the distribution and further expansion of *M. leidyi* in the northern Baltic Sea may be restricted by low salinity or low oxygen concentrations as they did not find the ctenophore at salinities <5 PSU, or on localities where oxygen was depleted at water depths below 60-70 m. In the present study, we found individuals of *M. leidyi* at oxygen levels down to 0.29 ml l^{-1} which is in accordance with laboratory experiments showing 100% survival in a 96 h incubation at an oxygen concentration of 0.5 ml l^{-1} (Purcell et al. 2001a). This suggests that in the Baltic Sea, salinity may exert a stronger influence than oxygen on the expansion and distribution of the ctenophore.

In its native environment, *M. leidyi* encounters wide ranges of temperatures (2-32 °C) and salinities (2-38 PSU) (Purcell et al. 2001b). Nevertheless, both ctenophore size and size-specific egg production were less at low temperature (9 °C) and salinity (7 PSU) than at warmer temperatures and higher salinities tested in the laboratory (Purcell and Decker 2005). Thus, even though *M. leidyi* has been reported to tolerate low salinities, it probably has a preference for higher salinities. Accordingly, it can not be precluded that in the Baltic Sea, *M. leidyi* is actively or passively (via drift) distributing to areas or depths with higher salinities and/or temperatures where growth and reproduction are optimal. This possibility receives some support from the depth-stratified IKMT and Multinet samplings which showed a clear peak in abundances of *M. leidyi* in the deeper water layers of the Bornholm Basin where higher salinities are found. However, in contrast to the studies by Haslob et al. (2007) and Kube et al. (2007) who found *M. leidyi* exclusively below the halocline, the stratified samplings in the present study showed that in November 2007, the ctenophore was also distributed above the halocline, and in shallower, less saline coastal areas. The preference of the ctenophore for high saline water may possibly reflect an active search, and if this is true, an outbreak of *M. leidyi* in the central Baltic Sea may hitherto have been restricted by low salinities. This hypothesis receives further support by findings of Riisgård et al. (2007), who observed high densities of *M. leidyi* at salinities of 27-28 PSU.

Densities in the Bornholm Basin

In May 2007, Haslob et al. (2007) investigated the abundance of *M. leidyi* in the Bornholm Basin. They found abundances of up to 7.74 ind. m^{-2} in the central Basin. The *M. leidyi* abundances observed during the present study in November 2007 showed a similar range, with maximum abundances of 8.92 ind. m^{-2}. However, the horizontal distribution of *M. leidyi* exhibited differences between the two studies. While Haslob et al. (2007) found the abundance peak to be in the central Bornholm Basin in May 2007, we observed the highest abundances at the northwestern and southeastern edges of the Bornholm Basin.

In the late summer of 2007, Riisgård et al. (2007) found densities of mainly small (5 to 15 mm) *M. leidyi* to be between 18 and 867 ind. m^{-3} in Limfjorden, a shallow Danish fjord system. These densities even exceeded those observed in the Black Sea in 1989 when the zooplankton and fish stocks collapsed, and where the mean and maximum density was 12.4 and 304 ind. m^{-3}, respectively (Shiganova et al. 2001).

Lehtiniemi et al. (2007) reported abundances of 694 ind. m^{-2} and densities of 24 ind. m^{-3} for the northern Baltic Sea in September 2007. Compared to these high figures, the levels registered in the Bornholm Basin in November 2007 seem modest. However, as shown by Lehtiniemi et al. (2007), abundances may increase remarkably within a few weeks in some areas, which confirms the great potential of *M.*

leidyi to reproduce and reach outbreak levels within a short time.

Potential influence of the Baltic sprat stock on M. leidyi population dynamics

It is striking that high abundances of *M. leidyi* have been observed in areas west and north of the central Baltic (Riisgård et al. 2007; Lehtiniemi et al. 2007), while the abundance in the Bornholm Basin and the surrounding areas is low. An explanation for this could be competition for food (zooplankton) caused by the currently very large stock of sprat *Sprattus sprattus* (Linnaeus, 1758). Among other possible factors, Purcell et al. (2001b) identified low competition for food by heavily overfished zooplanktivorous fish stocks to be one of the main reasons for the population explosion of *M. leidyi* in the Black Sea. In the Baltic, however, the sprat stock has increased considerably since the late 1980s and has been on a high level in recent years (Figure 6, Möllmann and Köster 2002). Möllmann et al. (2005) have shown a decrease in Baltic sprat condition due to strong intra-specific competition for zooplankton at large stock size.

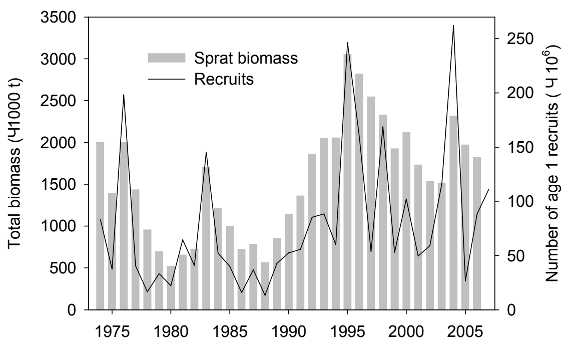

Figure 6. Time series of total sprat biomass and recruits at age 1 in the Baltic Sea (ICES subdivisions 22-32). Data from ICES (2007).

Accordingly, sprat may act as an important competitor for zooplankton in the central Baltic Sea, especially as sprat are migrating into the Bornholm Basin during spring and early summer for spawning (Aro 1989), i.e. periods likely to provide the best conditions for *M. leidyi* development. In addition to that, feeding sprat concentrate at depths between 50 m and the oxygen depleted deep water (Köster and Schnack 1994), i.e. the same depth range where the highest abundances of ctenophores have been found (Figure 3, Haslob et al. 2007).

Thus, the competition for food exerted by the presently large Baltic sprat stock may so far have prevented the population of *M. leidyi* to reach outbreak levels in the central Baltic Sea.

Predation impact of M. leidyi on zooplankton and cod eggs in the central Baltic Sea

Based on the calculations of population filtration rate and the half-time of zooplankton ($t_{1/2}$ = 300 d), the predation impact of *M. leidyi* on zooplankton in the central Baltic Sea in November 2007 is regarded negligible. Nevertheless, it may become significant ($t_{1/2}$ = 20-30 d) if the *M. leidyi* population density increases 10 to 15 times which may be realistic during the productive period. In this regard, the fact that *M. leidyi* was found around the entire Bornholm Basin in November 2007 is of major concern. Besides, high abundances were reported from fjord areas in Denmark (Riisgård et al. 2007) and from the northern Baltic Sea (Lehtiniemi et al. 2007). It is possible that these areas will act as donor areas, allowing *M. leidyi* to spread into the important fish spawning ground in the Basin centre. Such an expansion from coastal to offshore waters was observed in the Black Sea. Here abundance and biomass of *M. leidyi* was initially highest in inshore areas, which warm up earlier and/or are subjected to higher eutrophication. Subsequent increases of temperatures in offshore waters caused the expansion of populations into the central parts of the Black Sea (Mutlu 1999).

Despite the low present predation impact by *M. leidyi* on zooplankton, the ctenophore may exert a significant predatory influence on Baltic cod eggs at relatively low abundances due to an overlap in their vertical distribution in the Bornholm Basin. Haslob et al. (2007) observed highest densities of *M. leidyi* in the Bornholm Basin at the same depth range where cod eggs are found, a result that was corroborated by the present study.

The recruitment success of eastern Baltic cod is strongly dependent on increased egg survival due to inflows of high saline, oxygen rich water from the North Sea (Köster et al. 2005). As discussed above, an outbreak of *M. leidyi* in the central Baltic Sea could so far have been restricted by low salinities. Thus, higher survival of cod eggs and larvae after inflow events may be counteracted by an intensified predation impact of *M. leidyi* whose abundances may simultaneously increase due to rising salinities.

Conclusion and recommendation

The abundances of *M. leidyi* in the central Baltic Sea observed in the present study are low compared to the mass occurrences recently reported from neighboring areas. However, the fact that *M. leidyi* is now spread over vast areas of the central Baltic Sea is of major concern due to the ctenophore's ability to survive through the winter in the Baltic Sea, its high potential for explosive population development and its possible negative influences on fish stocks. Therefore, close monitoring of the future development of *M. leidyi* in the Baltic Sea is strongly recommended.

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Annex 1

Sampling date, sampling position, sampling depth, and abundance of *Mnemiopsis leidyi* sampled with Bongo net

Date	Latitude °N	Longitude °E	Sampling depth [m]	Abundance [ind. m^{-2}]
03.11.2007	55°22.633	15°14.099	0-80	1.21
03.11.2007	55°24.675	15°12.972	0-80	1.53
04.11.2007	55°16.511	16°07.378	0-78	1.29
05.11.2007	55°19.224	16°11.115	0-70	0.92
06.11.2007	55°35.448	14°40.272	0-65	8.10
06.11.2007	55°40.170	14°30.191	0-44	2.34
06.11.2007	55°49.709	14°45.595	0-30	1.08
06.11.2007	55°59.524	15°00.573	0-30	0.00
07.11.2007	55°37.734	15°50.160	0-65	1.32
07.11.2007	55°44.319	15°31.756	0-55	0.76
07.11.2007	55°19.417	14°59.347	0-65	3.30
07.11.2007	55°20.329	14°29.930	0-50	3.71
08.11.2007	55°29.718	14°45.230	0-60	2.27
08.11.2007	55°10.126	14°14.721	0-40	0.35
08.11.2007	55°01.875	14°28.406	0-32	8.92
10.11.2007	54°38.456	14°32.145	0-30	0.00
10.11.2007	54°30.129	14°45.354	0-17	0.00
10.11.2007	54°50.331	15°15.416	0-62	0.55
10.11.2007	55°00.176	15°30.183	0-71	1.57
11.11.2007	55°40.664	16°06.986	0-60	3.43
11.11.2007	55°49.390	16°14.549	0-49	0.58
12.11.2007	56°06.819	17°38.346	0-40	0.00
12.11.2007	56°10.065	17°45.276	0-20	0.00
12.11.2007	56°10.838	16°56.419	0-23	0.00
13.11.2007	55°40.280	16°57.134	0-27	0.00
13.11.2007	55°29.973	17°14.964	0-27	0.00
13.11.2007	55°41.420	17°29.364	0-24	0.00
14.11.2007	55°49.901	17°45.364	0-55	0.00
14.11.2007	55°47.195	18°20.955	0-90	0.00
14.11.2007	55°27.465	18°20.305	0-80	0.00
15.11.2007	55°19.524	17°28.814	0-73	2.86
15.11.2007	55°30.742	17°42.738	0-61	0.14
15.11.2007	55°20.234	16°59.857	0-62	3.17
15.11.2007	55°19.743	16°30.960	0-52	1.41
16.11.2007	55°10.042	16°44.901	0-62	2.24
16.11.2007	55°11.868	17°16.169	0-77	5.53
16.11.2007	55°30.259	16°14.992	0-65	2.62

Annex 2

Sampling date, sampling position, sampling depth, and abundance of *Mnemiopsis leidyi* (> 10 mm) sampled with Isaac-Kidd midwater trawl (IKMT)

Date	Latitude °N	Longitude °E	Sampling depth [m]	Abundance [ind. m^{-2}]
03.11.2007	55°10.154	15°15.641	0-57	0.00
03.11.2007	54°50.289	14°45.716	0-35	0.00
04.11.2007	54°40.037	14°59.855	0-55	0.00
04.11.2007	55°10.094	16°15.107	0-55	0.00
04.11.2007	54°59.992	16°00.052	0-55	0.06
05.11.2007	54°49.856	16°14.982	0-35	3.97
05.11.2007	55°00.168	16°29.620	0-25	1.19
05.11.2007	55°19.494	15°30.716	0-60	1.29
05.11.2007	55°29.824	15°15.773	0-60	4.42
05.11.2007	55°40.400	14°59.128	0-60	0.34
06.11.2007	55°40.290	14°29.462	0-45	1.80
06.11.2007	55°50.160	14°45.373	0-30	1.62
06.11.2007	55°59.903	15°00.429	0-30	1.17
06.11.2007	55°59.784	15°28.938	0-40	0.98
07.11.2007	55°50.198	15°44.828	0-40	0.65
07.11.2007	55°19.908	14°59.441	0-60	2.68
07.11.2007	55°20.560	14°30.618	0-40	3.46
08.11.2007	55°30.229	14°45.059	0-55	4.36
08.11.2007	55°10.171	14°14.376	0-40	0.35
08.11.2007	55°00.023	14°29.814	0-20	0.06
10.11.2007	54°50.036	14°15.118	0-20	0.12
10.11.2007	54°40.119	14°30.190	0-30	0.04
10.11.2007	54°30.329	14°45.986	0-15	0.00
10.11.2007	54°50.254	15°15.360	0-50	0.00
10.11.2007	55°00.887	15°31.317	0-50	1.08
10.11.2007	55°10.112	15°45.294	0-55	0.22
11.11.2007	55°40.171	16°30.433	0-55	0.00
11.11.2007	55°49.960	16°14.953	0-50	0.39
12.11.2007	56°00.212	17°00.173	0-30	0.00
12.11.2007	56°10.117	17°46.062	0-20	0.00
12.11.2007	56°00.042	17°30.538	0-32	0.00
12.11.2007	56°09.883	17°12.700	0-21	0.00
12.11.2007	56°09.930	16°53.650	0-23	0.00
13.11.2007	56°00.186	16°27.377	0-45	0.00
13.11.2007	55°50.070	16°44.729	0-38	0.00
13.11.2007	55°50.023	17°14.884	0-27	0.00
13.11.2007	55°39.964	16°59.988	0-27	0.09
13.11.2007	55°30.084	17°14.942	0-28	0.00
13.11.2007	55°40.347	17°31.448	0-26	0.00
14.11.2007	55°49.657	17°46.254	0-55	0.00
14.11.2007	55°49.881	18°14.904	0-55	0.00
14.11.2007	55°27.272	18°20.979	0-55	0.00
14.11.2007	55°09.721	17°45.346	0-40	0.41
14.11.2007	55°20.000	17°30.333	0-60	0.31
15.11.2007	55°30.083	17°45.006	0-60	0.00
15.11.2007	55°20.819	17°00.085	0-55	0.87
15.11.2007	55°19.984	16°31.040	0-50	0.34
16.11.2007	55°10.770	16°45.075	0-60	0.78
16.11.2007	55°10.239	17°15.011	0-60	0.86
16.11.2007	55°30.919	16°14.296	0-50	0.46
16.11.2007	55°39.926	15°29.452	0-60	1.22

Annex 3

Sampling date, sampling position, sampling depth, and density of *Mnemiopsis leidyi* sampled with Multinet (A, B and C refer to locations in Figure 2a)

Multinet A	**Date**	**Sampling depth [m]**	**Density [ind. m^{-3}]**
	15.11.2007	0-10	0.000
		10-20	0.000
Latitude °N	**Longitude °E**	20-30	0.000
55°20.333	16°59.969	30-35	0.000
		35-40	0.000
		40-45	0.042
		45-50	0.063
		50-55	0.071
		55-60	0.010
Multinet B	**Date**	**Sampling depth [m]**	**Density [ind. m^{-3}]**
	11.11.2007	5-15	0.000
		15-25	0.053
Latitude °N	**Longitude °E**	25-35	0.032
55°17.806	15°44.944	35-45	0.063
		45-55	0.044
		55-65	0.099
		65-75	0.022
		75-85	0.010
Multinet C	**Date**	**Sampling depth [m]**	**Density [ind. m^{-3}]**
	07.11.2007	0-15	0.000
		15-25	0.000
Latitude °N	**Longitude °E**	25-35	0.000
55° 20.135	15°00.031	35-45	0.043
		45-55	0.108