SHORT COMMUNICATION

The invasive ctenophore *Mnemiopsis leidyi* overwinters in high abundances in the subarctic Baltic Sea

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We report successful overwintering of the invasive ctenophore Mnemiopsis leidyi in the Baltic Sea, demonstrated by the highest abundances ever observed in the northern parts of this subarctic brackish-water ecosystem.

The invasive ctenophore *Mnemiopsis leidyi* has had tremendous ecological and economic effects in a range of habitats, such as the brackish Black and Caspian Seas (Knowler, 2005), virtually changing the structure of the entire zooplankton community as well as contributing to a collapse of several fisheries (Vinogradov *et al.*, 1989; Purcell *et al.*, 2001; Finenko *et al.*, 2006). *Mnemiopsis leidyi* first invaded the southern Baltic Sea in autumn 2006 (Hansson, 2006; Javidpour *et al.*, 2006) and currently occupies the whole Baltic area, exclusive only of the northernmost basin of the Gulf of Bothnia (Bothnian Bay) and the eastern end of the Gulf of Finland. The capability of this ctenophore to tolerate a wide range of abiotic conditions led to speculation about its potential to sustain viable populations and to survive through the winter in the northern Baltic Sea. This is a subarctic brackish-water ecosystem characterized by scarce pelagic food, surface temperatures of 0–2°C and partial ice-cover (Myrberg *et al.*, 2006). While *M. leidyi* has been observed to overwinter in the southern Baltic Sea (Kube *et al.*, 2007), this study demonstrates successful overwintering and high abundances of the invader in cold low-saline waters of the northern Baltic Sea.

Distribution and abundance of *M. leidyi* were surveyed during January 2008. The study was carried out on a regular HELCOM monitoring cruise on board R/V Aranda (Finnish Institute of Marine Research). The ctenophore sampling was performed with a 500 μm mesh WP-2 plankton net with a cod end (100 μm mesh size). The samples were collected from both the southern, central and northern Baltic Sea (Fig. 1), excluding the easternmost Gulf of Finland, where the occurrence was monitored in December 2007 (Lehtiniemi *et al.*, 2007). Three replicate tows from the bottom to the surface at a rate of 0.5 m s^{-1} were taken at each station. Ctenophores were counted from unpreserved samples with 10–60× magnification immediately after collection, and a subsample of at least 50 specimens from 10 stations were measured for length (aboral–oral dimension, including lobes) and assigned to size classes to the closest 0.5 mm. The counts per tow were converted to abundances (ind. m^{-2}) by dividing the values by the towed area (0.25 m^2).

To define the vertical distribution of *M. leidyi* as well as potential food resources (micro- and zooplankton) in winter, additional sampling was performed in March

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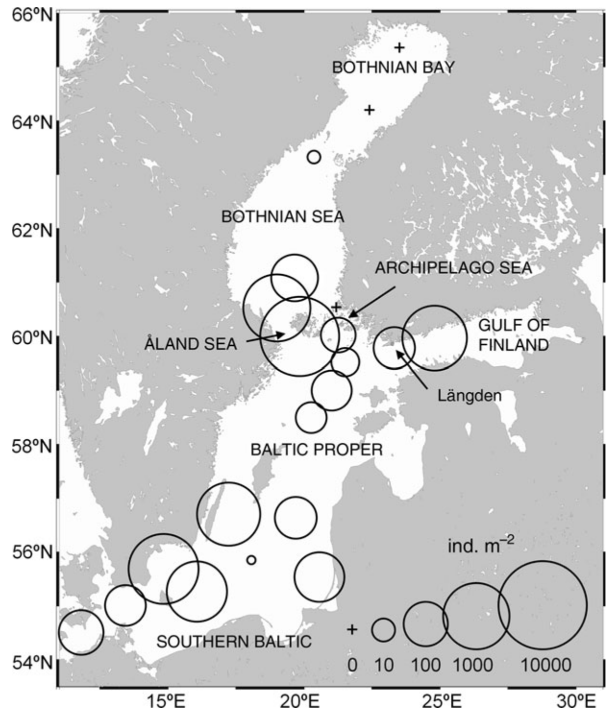

Fig. 1. Occurrence and abundances of *Mnemiopsis leidyi* in the Baltic Sea in January–March 2008. The diameter of the circle denotes the abundance in ind. m^{-2} on a logarithmic scale.

2008 from the Tvärminne Zoological Station, University of Helsinki, SW coast of Finland. Samples were taken with a vertically towed 200 μm mesh WP-2 plankton net equipped with a closing mechanism from a 60 m deep coastal station, Längden (Fig. 1). The use of a smaller mesh size in March than in January (200 μm instead of 500 μm) may have slightly overestimated the numbers of small specimens in March compared with those in January. Three tows were taken with depth intervals of 20–0 m, 40–20 m and 55–40 m. Additionally, two continuous hauls from the bottom (~55 m) to the surface were taken. For the total abundance determination, the data from the three stratified and the two continuous hauls were combined to obtain three replicates (from the bottom to the surface). Due to heavy weather conditions, the upper end of the net could not be rinsed before collecting the samples, which may have resulted in an underestimation of the total abundances. The net was rinsed, however, in between the tows. The samples were placed in 3 L buckets and transferred to the laboratory for microscopic examination. *Mnemiopsis leidyi* was counted and measured for length from the unpreserved samples, as described earlier, after which the samples were preserved in Lugol's solution for zooplankton counting with an inverted microscope with 50× magnification. To determine microplankton abundance in the water column, water samples from depths of 3, 10, 17, 23, 30, 37, 43, 50 and 57 m were collected with a 5 L Limnos sampler and pooled into three samples (0–20 m, 20–40 m and 40–60 m). From each pooled sample, a 1 L subsample was preserved in Lugol's solution and examined with an inverted microscope with 50–100× magnification.

The abundance data of *M. leidyi* were converted to biomass (wet weight and carbon content) values using the following equations:

$$\text{Wet weight (g)} = 0.0011k^{2.34} \quad (1)$$

$$\text{Carbon content (mg)} = 0.0017k^{2.0138} \quad (2)$$

where k is the median length (mm) of each size group (Kideys and Moghim, 2003; Sullivan and Gifford, 2004).

Carbon content values for zooplankton were obtained from Viherluoto and Viitasalo (Viherluoto and Viitasalo, 2001), for ciliates from Putt and Stoecker (Putt and Stoecker, 1989) and for other microplankton (mainly dinoflagellates and diatoms) from Menden-Deuer and Lessard (Menden-Deuer and Lessard, 2000).

An estimate of total ingestion (I) of microplankton was calculated using the carbon content (C) obtained from equation (2) (Sullivan and Gifford, 2004):

$$I = 0.4\,\mu\text{g C}\,\mu\text{g}^{-1}\,\text{C day}^{-1} \quad (3)$$

This estimate represents the smallest ctenophore size category (1 mm) used by Sullivan and Gifford (Sullivan and Gifford, 2004), and was selected due to the dominance of small individuals (95% ≤2 mm) in our data as well as the fact that this estimate was obtained from grazing experiments with the lowest prey C content (59 μg C L^{-1}), which best corresponds to the situation in our study.

Theoretical clearance rates (c) on microplankton were estimated using the equation (Sullivan and Gifford, 2004):

$$c\ (\text{mL ind.}^{-1}\,\text{h}^{-1}) = 9.36k + 4.54 \quad (4)$$

The difference in ctenophore abundances between stations with and without a distinctive halocline was tested with a Student's *t*-test. Correlation between the depth of the station and the abundance and biomass of *M. leidyi* at each station (excluding stations with no ctenophores) were tested using the Pearson's correlation test. The abundance and biomass data were log-

Table I: Sampling stations, hydrographic conditions, abundance and biomass of Mnemiopsis leidyi in the Baltic Sea

Location	Station	Latitude	Longitude	Date	Depth max (m)	Salinity (psu)	Temp. (°C)	Depth of the clines (m)	Abundance (ind. m^{-2})	Biomass (g ww m^{-2})
Bothnian Bay	F2	65°23.02	23°27.76	12 Jan 2008	74	3	0.5–3	T20	0	0
Bothnian Bay	F16	64°18.30	22°21.50	14 Jan 2008	42	3.5–5	0.5–1	HT15	0	0
Bothnian Sea	SR5	61°05.00	19°35.00	10 Jan 2008	110	5.5–6.5	3.5–5	T70	129.3	3.03
Bothnian Sea	F18	63°18.86	20°16.36	12 Jan 2008	92	5.5	3.5	–	2.7	No data
Åland Sea	F67	59°56.00	19°49.80	9 Jan 2008	190	6–7	4–6.5	–	3809.3	10.89
Åland Sea	F33	60°31.99	18°56.26	10 Jan 2008	120	5.5–6.5	3–5	–	1117.3	7.32
Archipelago Sea	IU2	60°35.01	21°07.80	17 Jan 2008	37	6.5	2.5	–	0	0
Gulf of Finland	LL7	59°50.79	24°50.27	31 Jan 2008	90	6–7	3–5	–	842.7	No data
Gulf of Finland	Längden	59°45.58	23°15.23	4 Mar 2008	60	6–6.5	2	–	73.3	0.03
Baltic Proper	Teili	59°26.00	21°29.81	8 Jan 2008	110	5	6.5	HT80	17.3	0.01
Baltic Proper	IU6	59°56.21	21°13.26	17 Jan 2008	110	6.5	4	–	37.3	No data
Baltic Proper	LL17	59°02.00	21°04.77	21 Jan 2008	150	7–11	4.5–5.5	H80	64.0	No data
Baltic Proper	F79	58°27.00	20°10.00	22 Jan 2008	95	7.5–10.5	5–5.5	H65	24.0	No data
Southern Baltic	BY10	56°38.00	19°35.00	23 Jan 2008	135	7–12	4–6	HT55	78.7	No data
Southern Baltic	6B	55°31.84	20°33.83	23 Jan 2008	55	7.5–10.5	5–6	HT55	178.7	No data
Southern Baltic	STB8	54°26.00	11°36.00	27 Jan 2008	18	18.5–21	4.5–5	–	105.3	1.18
Southern Baltic	BY1	55°00.00	13°18.00	28 Jan 2008	39	8.5–20	4–5.5	H25	68.0	0.23
Southern Baltic	HBP215	55°37.00	14°52.00	28 Jan 2008	70	7.5–8.5	4.5–9.5	HT50	1462.7	4.09
Southern Baltic	BY5	55°15.00	15°59.00	29 Jan 2008	80	7.5–16	4.5–10	HT50	545.3	2.03
Southern Baltic	BCSIII8	55°51.00	18°03.00	29 Jan 2008	46	7–9.5	4–5	HT45	1.3	No data
Southern Baltic	BCSIII2	56°42.00	17°07.00	30 Jan 2008	75	7–9.5	4–5	HT55	740.0	0.22

Depth max denotes the depth of the station, whereas depth of the clines specifies the upper depth of the halo- (*H*) and thermoclines (*T*).

transformed to normalize the distributions. All statistics were performed using SPSS 15.0 software.

At 11 stations out of 21, a halocline was detected at depths of 15−80 m (Table I). Neither halocline nor thermocline was observed at eight stations, indicative of a thoroughly mixed water column. Ctenophores were found at all stations except in the Bothnian Bay (two stations) and at a single station in the Archipelago Sea. No difference was found in ctenophore abundances between stations with and without a halocline ($t = 1.01$, $df = 16$, $P = 0.33$) At the stations where ctenophores occurred, the surface and deep-water salinity ranged between 5.0−18.5 psu and 5.0−21.0 psu, respectively, while the corresponding temperature ranges were 2.0−6.5°C and 2.0−10.0°C, respectively (Table I). In comparison, salinity and temperature in the Bothnian Bay were only 3−5 psu and 0.5−3.0°C. The present data show that *M. leidyi* does occur at very low temperatures (2°C), while it does not appear to tolerate salinities <5 psu. Although showing wide tolerance to these abiotic parameters (Purcell *et al*., 2001), *M. leidyi* seems to be close to the limit of its occurrence in conditions where both are low.

The total abundances of *M. leidyi* ranged between 1 and 3809 ind. m^{-2} (Fig. 1 and Table I), the maximum value being the highest ever found in the northern Baltic Sea, and 6-fold greater than that (619 ind. m^{-2}) observed in autumn 2007 (Lehtiniemi *et al*., 2007). Despite different sampling methods, these values are also two orders of magnitude higher than those recently observed in the southern Baltic (Huwer *et al*., 2008). While the abundances in the north were higher in the sampling performed in January 2008 than in August−September 2007, temperature and salinity conditions had not changed radically, implying that hydrographic parameters did not preclude larval survival and thereby growth of *M. leidyi* populations. Compared with the size distribution in the ponto-Caspian region, the Baltic specimens were small, ≤10 mm in the north (>59°N) and ≤40 mm in the south (<57°N). Overall, 95% of all

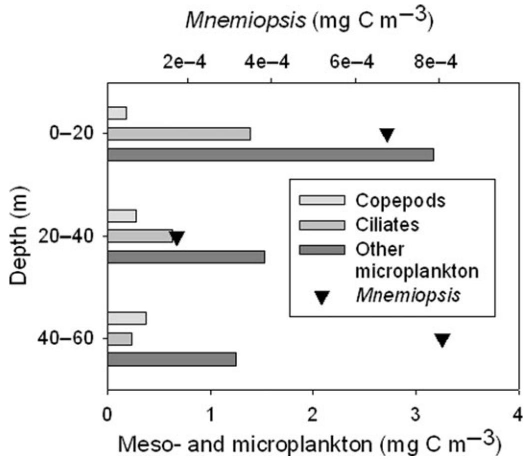

Fig. 2. Vertical distribution and biomass of *Mnemiopsis leidyi*, copepods and microplankton in Längden, SW coast of Finland, March 2008.

specimens were ≤2 mm, resulting in low biomass. The maximum biomass (10.9 g ww m^{-2}) co-occurred with the maximum abundance in the Åland Sea (Table I).

Previous studies in the Baltic Sea have shown that *M. leidyi* occurs deep in the water column, near the halocline (60–80 m) (Haslob *et al.*, 2007; Lehtiniemi *et al.*, 2007; Huwer *et al.*, 2008). In this study, however, the vertical distribution data from Längden showed that under well-mixed conditions, the ctenophores occurred in all water layers (Fig. 2). Although the total ctenophore biomass correlated positively with the depth of the station ($r = 0.65$, $P = 0.04$, $n = 10$), indicating preference for deep waters, no correlation was observed between the abundance and the station depth ($r = 0.28$, $P = 0.26$, $n = 18$). All ctenophores in Längden were larval stages <1 mm. The zooplankton community was mainly composed of copepods, the total biomass varying between 0.2 and 0.3 mg C m^{-3} in the different water layers, while the microplankton community was dominated by dinoflagellates, the total biomass being 1.5–4.6 mg C m^{-3} (Fig. 2 and Table II). In summer, the biomass is typically one to two orders of magnitude higher (Uitto, 1996). The most abundant taxa were *Acartia* spp., *Centropages hamatus*, *Eurytemora affinis*, *Temora longicornis*, *Scrippsiella* sp. and *Myrionecta rubra* (Table II). In an experimental study by Sullivan and Gifford (Sullivan and Gifford, 2004), *M. rubra* was a positively selected prey item over a span of microplankton taxa, suggesting that suitable prey were present in the water column. Using equation (3), *M. leidyi* in Längden (total biomass 0.03 g ww m^{-2} and 30.4 μg C m^{-2}) could ingest 0.1–0.3 μg C m^{-3} day^{-1} in the three different depth strata,

Table II: Biomasses of microplankton and mesozooplankton as means over three depth layers (0–20, 20–40 and 40–60 m) in Längden, Gulf of Finland

Species/taxon	mg C m^{-3}
Dinoflagellata	
Scrippsiella sp./*Woloszynskia* sp.	1.12
Dinoflagellata >30 μm	0.03
Dinoflagellata 30 μm	0.04
Dinoflagellata 25 μm	0.08
Dinoflagellata 20 μm	0.18
Dinoflagellata 15 μm	0.03
Dinoflagellata 10 μm	<0.01
Dinoflagellata <10 μm	<0.01
Gymnodinium vestificii	0.01
Amphidinium longum	0.01
Peridiniella catenata	0.14
Dinophysis acuminata	0.03
Dinophysis rotundata	<0.01
Protoperidinium granii	<0.01
Gyrodinium sp. 60–70 μm	0.01
Gyrodinium sp. 100 μm	0.03
Total Dinoflagellata	1.71
Diatoma	
Skeletonema costatum	0.02
Melosira sp.	<0.01
Achnantes taeniata	0.01
Thalassiosira sp.	0.22
Chaetoceros sp.	<0.01
Chaetoceros wighamii	<0.01
Chaetoceros holsaticus	<0.01
Nitzchia sp.	<0.01
Tabellaria sp.	0.01
Navicula sp.	<0.01
Total Diatoma	0.26
Cryptophyceae	
Teleaulax acuta	0.01
Ciliata	
Myrionecta rubra	0.39
Mesodinium pulex	<0.01
Askenasia stellaris	0.02
Lacrymaria rostrata	0.02
Urotricha sp.	<0.01
Strombidium conicum	0.17
Strombidium emergens	0.04
Strombidium sp. 40–50	0.02
Strombidium sp. 25–30	0.01
Strombidium sp. <25 μm	<0.01
Tintinnopsis beroidea	<0.01
Tintinnopisis lobiancoi	0.01
Tintinnidium fluviatile	0.01
Ciliata sp. 60 μm	0.05
Ciliata sp. small	<0.01
Total Ciliata	0.75
Copepoda	
Centropages hamatus	0.04
Pseudocalanus acuspes	0.01
Acartia spp.	0.09
Eurytemora affinis	0.02
Temora longicornis	0.06
Limnocalanus macrurus	<0.01
Total Copepoda	0.21

while the mesozooplankton community totaled 200–350 μg C m^{-3}, ciliates 240–1380 μg C m^{-3} and other microplankton 1250–3170 μg C m^{-3}. These calculations indicate that food was not the limiting factor in Längden. It is possible that the low *M. leidyi* abundances at the sampling site were either due to the low temperature (2°C), late sampling date (March) or strong wintertime currents (Myrberg *et al*., 2006), leading to a patchy distribution.

In addition to Längden, potential ingestion rates of the *M. leidyi* population were estimated for the two stations in the Åland Sea with the highest ctenophore biomasses in January, F67 (biomass 10.9 g ww m^{-2}) and F33 (7.3 g ww m^{-2}). These calculations yield a total ingestion of 5910 μg C day^{-1} (F67) and 2980 μg C day^{-1} (F33), being high compared with the wintertime food conditions in Längden. Unfortunately, no data on micro- and zooplankton in the Åland Sea could be collected due to strong winds, which precludes conclusions on potential food limitation. The clearance rate estimates [given by equation (4)] of the ctenophore population feeding on microplankton prey were 1510 and 530 L m^{-2} day^{-1} for the same two stations, converting to 1.5 and 0.5 m^3 m^{-2} day^{-1} or 1.5% and 0.5% of the water column daily (assuming all ctenophores were within the uppermost 100 m). It should be noted that these estimates are only suggestive and should be interpreted carefully. However, they indicate a low population clearance capacity compared with that (up to 60%) calculated by Sullivan and Gifford (Sullivan and Gifford, 2004) for the native *M. leidyi* population in Narragansett Bay, NW coast of USA.

It must be emphasized that the winter of 2008 was ice-free and very mild, and in more adverse winters low temperatures together with scarce food could restrict the abundance of *M. leidyi* populations. However, the present study demonstrates that this ctenophore is capable of surviving and sustaining high population abundances during the Baltic winter. Future studies should examine which factors control further dispersal and increase of the Baltic *M. leidyi*. For example, growth of *M. leidyi* populations is often found to be food limited (Purcell *et al*., 2001), but whether this is the case also for the overwintering deep-water ctenophores in the northern Baltic Sea remains to be studied.

SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt.oxfordjournals.org.

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