Aquatic Invasions (2007) Volume 2, Issue 2: 137-145
doi: http://dx.doi.org/10.3391/ai.2007.2.2.9

Research Article

Mnemiopsis leidyi in the Baltic Sea – distribution and overwintering between autumn 2006 and spring 2007

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Received: 24 May 2007 / Accepted: 4 June 2007

Abstract

In autumn 2006 the first observations of the West Atlantic comb jelly *Mnemiopsis leidyi* in Northern Europe were reported from the North Sea, the Skagerrak and the south-western Baltic Sea. Here we report on the further spread of this invasive ctenophore from the south-western towards the central Baltic Sea up to the south eastern Gotland Basin during autumn/winter 2006 and spring 2007. The abundances were generally low (max. 4 ind. m^{-3}). While *M. leidyi* was located in the entire water column in Kiel Bight, it was found exceptionally below the halocline in the deep stratified central Baltic basins. Data of a weekly sampling program at a near shore sampling location in Mecklenburg Bight between January and May 2007 showed that up to 80 % of the individuals were juveniles, smaller than 1 mm total body length and that *M.* leidyi survived the winter in the Southern Baltic Sea, even if abundances dropped down to <1 ind. m^{-3} in February. A first assessment of the physiological demands of this species versus the environmental conditions of the Baltic Sea showed that the successful establishment of this ctenophore is probable in the south-western and central Baltic Sea.

Key words: invasive species, ctenophores, *Mnemiopsis leidyi*, Baltic Sea, overwintering, distribution range

Introduction

The number of species introductions into the Baltic Sea has been increasing since the end of the last century, with the highest rates observed during the last 40 years (Leppäkoski et al. 2002, Gollasch and Nehring 2006). The origins of non-indigenous species in the Baltic Sea were mainly the Ponto-Caspian region, the North-Western Atlantic and the Indo-Pacific, from were almost 50% of the introduced species reached the Baltic Sea via ballast water transport (Gollasch and Nehring 2006, Galil et al. 2007). For example, the calanoid copepod *Acartia tonsa* (Dana, 1849) was introduced by ballast water from North America and established in the Baltic Sea in the twenties of the last century (Berzins, 1939). During last two decades three Ponto-Caspian species of predatory cladocerans were introduced with ballast water of ships into the eastern Baltic Sea: *Cercopagis pengoi* (Ostroumov, 1891), *Evadne anonyx* Sars, 1897 and *Cornigerius maeoticus* (Pengo, 1879) (Ojaveer and Lumberg 1995, Panov et al. 2007).

While most of the introduced species can be considered as "additive" due to their rather low impact on native ecosystems (Reise et al. 1999), some are known to cause severe ecological alterations in the receiving habitats such as changes of the habitat structure, food web composition and species diversity (e.g. Diederich et al. 2005).

An invader with an especially bad reputation is the comb jelly *Mnemiopsis leidyi (*A. Agassiz 1865). This lobate ctenophore originates from Western Atlantic coastal waters and estuaries and was accidentally introduced into the Black Sea in the early 1980s, where it showed an explosive population growth (Vinogradov et al. 1989). Subsequently it has spread into the adjacent Sea of Azov (Vinogradov et al. 1989), Sea of Marmara (Shiganova 1993), Mediterranean Sea (Kideys and Niermann 1993) and Caspian Sea (Ivanov et al. 2000) within 20 years after its introduction from eastern American coast. This carnivorous species feed at high rates on zooplankton, fish eggs, ichthyoplankton and fish larvae (Purcell et al. 2001). Young stages are able to fulfil their growth requirements with microprotistant prey (Rapoza et al. 2005, Sullivan and Gifford 2004). *M. leidyi* have reached densities up to 300 ind. m^{-3} in the Black Sea region and coincided with a drastic decrease in zooplankton biomass, changes in zooplankton species composition and a breakdown of the commercially important anchovy *Engraulis encrasicholus* Günther, 1868 fishery in this area (Volovik et al. 1993, Vinogradov et al. 1995, Shiganova 1998). This collapse probably resulted from multiple factors, among which overfishing, food competi-tion and predation on the early life stages of the anchovy by *M. leidyi* played a prominent role (Bilio and Niermann 2004).

M. leidyi has a great invasive potential due to its ability of rapid population growth (Kremer 1976) and its broad ecophysiological plasticity regarding environmental factors such as temperature and salinity (Kremer 1994). In native habitats, *M. leidyi* density fluctuations are mainly controlled by food availability and predators (Kremer 1994) and temperature as well (Feigenbaum and Kelly 1984).

In autumn 2006 *M. leidyi* was observed for the first time at several locations in Northern Europe almost synchronously (Annex 1). It was found in the North Sea (Faasse and Bayha 2006, Boersma et al. 2007), at the Swedish west coast (Hansson 2006) and in the western Baltic Sea (Javidpour et al. 2006). Assuming *M. leidyi* establishes in the Baltic Sea, it is the fifth ctenophore species together with the widespread “sea gooseberry” *Pleurobrachia pileus* (O. F. Müller, 1776) and three marine species that occur occasionally as a result of saline water inflows from the Kattegatt into the western Baltic Sea (*Bolinopsis infundibulum* (O. F. Müller, 1776*)*, *Beroe cucumis* Fabricius, 1780, *Beroe gracilis* Künne, 1939 (Greve 1975). Whereas all the native ctenophores do not seem to play any important role in the Baltic Sea ecosystem, the impact of *M. leidyi* is not yet clear.

The aim of this report is to show the expanding distribution range of *M. leidyi* from the south-western Baltic Sea to the central Baltic Sea between summer 2006 and spring 2007. We discuss the potential invasive capacity of *M. leidyi* in the Baltic Sea ecosystem regarding to its known ecological demands in native environ-ments.

Materials and Methods

First sampling of *M. leidyi* was conducted at Kühlungsborn Pier (Mecklenburg Bight, (54°09,21'N; 11°45,47'E) with a weekly sampling starting at the 16th of January 2007. Horizontal plankton hauls were taken by hand in the upper 1 m of the water column with a WP-2 net (mesh size 400 µm). The volume filtered was calculated from the distance of the tows (each tow 300 m). The collected samples were brought to the lab alive and determined and counted immediately by using a stereomicroscope. Each individual was measured to the nearest 0.1 mm for specimens <5 mm and to the nearest 1.0 mm for specimen >5 mm, except for the first sampling date (16 Jan) when only specimens >5 mm were counted. Salinity and water tempera-ture were measured at each sampling date.

During regular HELCOM monitoring cruises of the Baltic Sea Research Institute Warnemünde (IOW) in February, March and May 2007, plankton samples were taken at 8 stations in the south-western and central Baltic Sea: Kiel Bight, Mecklenburg Bight, Kadet Furrow, Darss Sill, Arkona Basin, Bornholm Deep, South Eastern Gotland Basin and Gotland Deep (for coordinates and water depth see Annex 2). Vertical WP-2 net (mesh size 200 µm) hauls were taken below and above the halocline, according to the temperature and salinity profiles measured by CTD casts at each sampling site.

During monitoring cruises of the German Oceanographic Museum Stralsund (DMM), samples were taken in the Pomeranian Bight in December 2006 and in the Kadet Furrow in March 2007 (for coordinates and water depth see Annex 2). The WP-2 net (mesh size 200 µm) was hauled vertically through the entire water column. Salinity and temperature were measured by CTD.

Public information about comb jelly observations were collected by distributing a *Mnemiopsis* – observation - questionnaire to local newspapers and diving centres. The questionnaire showed photographs of *M. leidyi* including a species description. Volunteers were asked to report the occurence of *M. leidyi* from

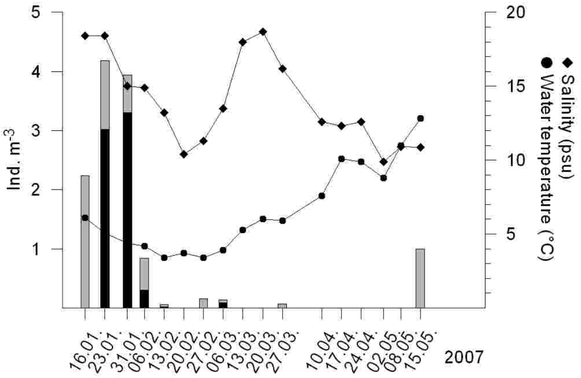

Figure 1. Abundance of *M. leidyi* (bars), salinity (squares) and water temperature (dots) at Kühlungsborn Pier during weekly sampling from January 2007 until May 2007. Black bars indicate the abundance of juveniles < 5 mm, grey bars indicate the abundance of adults > 5 mm. The sampling location is indicated in Figure 3 by dot "7".

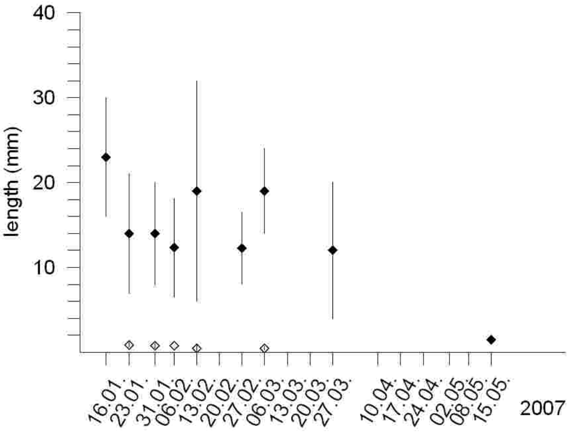

Figure 2. Length of *M. leidyi* > 5 mm (filled squares) and < 5 mm (open squares) at Kühlungsborn Pier during weekly sampling from January 2007 until May 2007 (Mean±SD).

diving observations as well as from bioluminescence observations from the shore. The latter method is appropriate to record *M. leidyi* since no other species are known to cause this phenomenon at the southern Baltic Sea coast in winter.

Results

At Kühlungsborn Pier *M. leidyi* was most abundant in January 2007 but did not exceed 4 ind. m^{-3} (Figure 1). The population density dropped in February to less than 1 ind. m^{-3} and remained very low until May. Up to 80 % of the ctenophores were juveniles in the cydippae stage with a maximum total length <1 mm. The total length of older individuals ranged between 5 and 35 mm (Figure 2). The water temperature ranged between 3 and 10 °C and the salinity fluctuated between 10 and 18 PSU during the study period (Figure 1).

Data from the sampling cruises of the IOW and the DMM gave evidence that *M. leidyi* broadened its distribution range from the south-western Baltic Sea north-eastwards (Figure 3, Annex 2). In December 2006, low densities (0.2 ind. m^{-3}) were observed in the Pomeranian Bay. During monitoring cruises in February, March and May 2007, *M. leidyi* was sampled in Kiel Bight (south-western Baltic Sea), in the Kadet Furrow (southern Baltic Sea), in the Bornholm Basin and in the South Eastern Gotland Basin. In Kiel Bight the abundance was higher in the near bottom water layer (4 ind. m^{-3}) than in the upper 10 m of the water column (1.2 ind. m^{-3}; Annex 2). However, CTD data did not show a clear stratification of the water body at Kiel Bight sampling station (max. depth 20 m). In contrast, a strong stratification of high saline deep water and lower saline surface water layers was observed in the Bornholm Deep and in the South Eastern Gotland Basin. The halocline was detected in approximately 60 m water depth. *M. leidyi* was exclusively found below the halocline (Annex 2).

Additionally to the plankton field surveys public information were collected since September 2006 by distributing a *Mnemiopsis* – observation - questionnaire in diving centres and newspapers. Replies show the occurrence of *M. leidyi* in autumn 2006 and winter 2006/07 along the German Baltic Sea coast from Wismar Bay (Wohlenberger Wiek) to the east coast of Rügen Island (Sassnitz and Göhren, Figure 4, Annex 3). The probably very first observation of *M. leidyi* in Mecklenburg Bight (near Kühlungsborn, water depth 24 m) was already made in June 2006 by scientific divers of the University of Rostock but interpreted as *Bolinopsis infundibulum* (Annex 3). A video sequence taken during this dive for other purposes show however that these lobed ctenophores have probably been *M. leidyi* (Figure 5).

Unfortunately no data from previous zooplankton samples are available because this fragile species is easily damaged in ordinary net sampling and disintegrates in the fixation

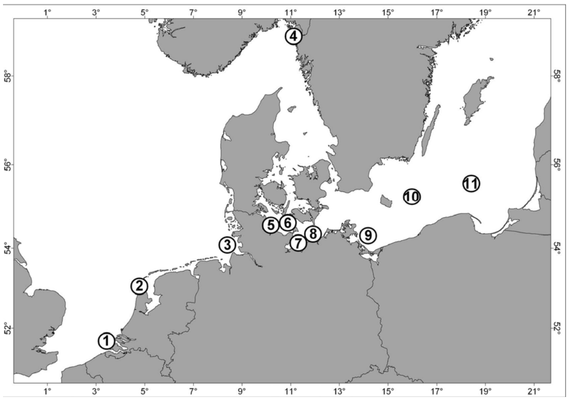

Figure 3. Summary of *M. leidyi* records from late summer 2006 to spring 2007 (according to the literature and to this study). 1 – South-western Dutch estuaries, 2 – Dutch Wadden Sea, 3 – Helgoland, 4 – Tjärnö, 5 – Kiel Fjord, 6 – Kiel Bight, 7 – Kühlungsborn Pier, 8 – Kadet Furrow, 9 – Pomeranian Bay, 10 – Bornholm Deep, 11 – South Eastern Gotland Basin. Location numbers refer to Annex 1 and 2 .

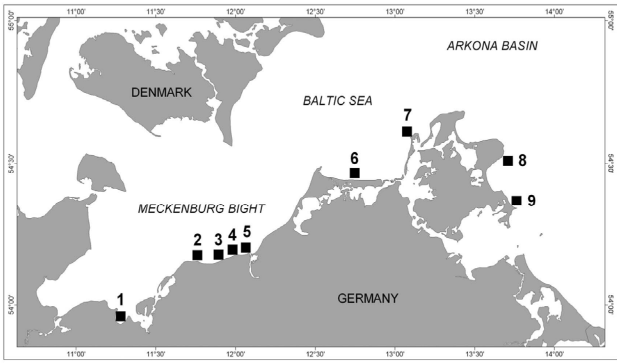

Figure 4. Public observations of *M. leidyi* along the German Baltic Sea coast from Wismar Bay to the eastern coast of Rügen Island. Numbers refer to column 1 in Annex 3 .

Figure 5. Snap shot from a video sequence of a lobed ctenophore from 29 June 2006, observed by scientific divers near Kühlungsborn, Mecklenburg Bight (54°17,334N; 11°46,257E) in 24 m water depth. This record was probably misinterpreted as *Bolinopsis infundibulum* during the observation, but later determined as *M. leidyi* by the video sequence. Photograph G. Niedzwiedz.

solutions (Purcell 1988, Hosia 2007). Therefore the abundance is likely underestimated specially at low concentrations.

Discussion

The West Atlantic ctenophore *M. leidyi* is well known for its great invasive capacity and its significant ecological impact on zooplankton communities across its native as well as invaded distribution range. As an invader, this species has a rather bad reputation and therefore attracted great attention shortly after its discovery in Northern Europe (Faasse and Bayha 2006, Boersma et al. in press, Hansson 2006, Javidpour et al. 2006). Data about the abundance of this new northern European invader are still rare. Javidpour et al. (2006) reported quite high densities of up to 100 ind. m^{-3} in Kiel Bight in October/November 2006, which is a quarter of the maximum abundance *M. leidyi* reached in the Black Sea in the 1980s (Vinogradov et al. 1989). The abundances of *M. leidyi* recorded in our present study for the southern and central Baltic Sea are much lower (max. 4 ind. m^{-3}). However, our data clearly show that *M. leidyi* survived the winter in the Baltic Sea and extended its distribution range from the south-western to the central Baltic Sea as far as the Gotland Basin between summer 2006 and spring 2007.

A critical point of evaluating the invasive potential and the subsequent ecological impact of

M. leidyi in the Baltic Sea is to understand its population dynamics and the factors that control the species abundance throughout the distribution range. Investigations of *M. leidyi* in North America and in the Black Sea concerning these matters reveal that the species' ecophysiological capacity regarding temperature and salinity, the food availability and the occurrence of predators may mainly control the distribution limits and the abundance of *M. leidyi* (Kremer 1994, Purcell et al. 2001).

M. leidyi is euryhaline, tolerating salinities from <2 to 38 PSU and eurytherm in a range between 0 and 32°C (Purcell et al. 2001). The highest reproductive potential was recorded at temperatures between 24°C and 28°C, but reproduction starts already at 12°C (Purcell et al. 2001). In accordance with this great ecophysiological capacity *M. leidyi* occurs in the western Atlantic over a wide latitudinal gradient (Kremer 1994). Libby et al. (2001) described mass occurrences of *Mnemiopsis* in fall 2000 in Boston habor at 42°21'N which is probably the northern distribution limit in North America and a potential donor area. The temperature and salinity ranges may not differ much from that what Kremer (1994) recorded from Narragansett Bay (41°35'N) nearby. This temperate estuary has an annual temperature range of 1 - 25°C, and a salinity range between 21 and 32 PSU. The occurrence of *M. leidyi* in Northern Europe at latitudes up to 57°N in the Baltic Sea clearly exceeds the native northern distribution limit of this species. However, the temperature range in the Baltic Sea is comparable to the conditions in Narragansett Bay. Our data show that *M. leidyi* occurred in the central Baltic Sea during the winter month below the halocline, were temperatures do not drop below 4°C (Annex 2). The stratification of the water column in the Baltic Sea due to salinity and temperature differences in the surface and bottom water layers might provide an overwintering refuge for *M. leidyi*. Thus, low sea surface temperatures in the Baltic Sea in winter do probably not limit the further distribution of *M. leidyi* in the southern and central basins. The mesohaline conditions of the Baltic Sea are even not expected to limit spreading of *M. leidyi* within the salinity gradient from the south-western to the north-eastern region of the Baltic Sea since M. leidyi seems not to be limited by salinities <2 PSU (Purcell et al. 2001). It is however assumed that low salinities in combination with low temperatures might cause higher mortalities, reduced growth rates and subsequently reduced population density increases in summer (Shiganova 1998). Thus, the reproduction of *M. leidyi* may be limited in the north-eastern parts of the Baltic Sea, where both, temperature and salinity range at the physiological tolerance limit of this species.

The population dynamics of *M. leidyi* in the North American estuaries (Narragansett Bay, Chesapeake Bay) typically shows strong intra-annual fluctuations. Whereas abundances are extremely low during most time of the year, there is a rapid biomass increase in late summer/ early autumn which lasts for only 2 to 3 months (Deason and Smayda 1982). The explosive population development of *M. leidyi* is attributed to its high reproductive and regenerative capacity. The high biomass of *M. leidyi* in late summer has been shown to correlate with the zooplankton biomass (Deason and Smayda 1982) and the warmer water at this time (Feigenbaum and Kelly 1984). To evaluate the likelihood of this seasonal population dynamics scenario of *M. leidyi* for the Baltic Sea, the mesozooplankton dynamics has to be considered. A major prey item of *M. leidyi* in Narragansett Bay is the calanoid copepod *Acartia tonsa* (Kremer 1994). In the southern Baltic Sea, abundances of calanoid copepods achieve numbers above the annual mean generally in the period between May and October. Maximum annual densities of calanoid copepods ranged from 25000 to 36000 ind. m^{-3} between Kiel Bight and the central Baltic proper between the years 1995 and 2005 (Wasmund et al. 2006). In November 2006, the density of calanoid copepods reached 700 to 9000 ind. m^{-3} above and 500 to 2000 ind. m^{-3} below the halocline between Kiel Bight and the central Baltic proper (this study). The maximum annual densities of *A. tonsa* in Narragansett Bay reached 3000 to 5000 ind. m^{-3} which allowed *M. leidyi* abundances of 35 ind. m^{-3} (Costello et al. 2006). Consequently, *M. leidyi* would meet favourable food conditions in the southern and central Baltic Sea in the second half of the year.

Predation pressure has been documented to control the biomass of *M. leidyi* in Narragansett Bay (Kremer and Nixon 1976) and in the Black Sea (Shiganova et al. 2001). Especially the presence of the ctenophore genus *Beroe* is known to affect the density pattern of *M. leidyi*. In the moment, it is not clear to what extent it could be happen during a potential mass occurrence of *Mnemiopsis*. But anyway, the distribution of *Beroe cucumis* and *B. gracilis* in the Baltic Sea is restricted to areas with higher salinities west of Darss Sill.

The further development of the *M. leidyi* population in the Baltic Sea remains a subject of speculation. However, the first assessment of the physiological demands of this species versus the environmental conditions of the Baltic Sea showed that the successful establishment of this ctenophore is probable in the south-western and central Baltic Sea.

Acknowledgements

We wish to thank B. Buuk, S. Busch, U. Hehl, A. Postel and I. Topp for technical assistance. Thanks to all involved divers and volunteers, especially to G. Niedzwiedz, for reporting their observations and providing photographs. We are grateful to J. Javidpour, J. Nejstgaard, J. Kube, and V. Panov for their constructive discussions and contributions to the manuscript.

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Supplementary material

The following supplementary material is available for this article:

Annex 1. Published records of *M. leidyi* in autumn 2006 in the North Sea and Baltic Sea.

Annex 2. Abundance of *M. leidyi* in the south-eastern and central Baltic Sea.

Annex 3. Public observations of *M. leidyi* by divers and from the shore by bioluminescence in 2006 and 2007.

Annex 1. Published records of *M. leidyi* in autumn 2006 in the North Sea and Baltic Sea.

Location	Location in Figure 3	Date of observation	Abundance (n m^{-3})	Water temperature (°C)	Salinity (PSU)	Reference
North Sea Southwestern estuaries (Oosterschelde, Westerschelde, Grevelingen) Wadden Sea (Balgzand)	1 2	Aug – Nov 2006	no data	10-23	no data	Faasse & Bayha 2006
North Sea, Helgoland (54°11,18'N; 07°54,00'E)	3	Nov - Dec 2006	0.1	10	30-33	Boersma et al. in press
Skagerrak, Tjärnö (58°52'N; 11°06'E)	4	Aug – Oct 2006	no data	9-15	no data	Hansson 2006
Baltic Sea, Kiel Bight, Kiel Fjord (54°19,7'N; 10°09,5'E)	5	Oct – Nov 2006	30-100	10-15	20-23	Javidpour et al. 2006

Annex 2. Abundance of *M. leidyi* in the south-eastern and central Baltic Sea during regular sampling cruises of the Baltic Sea Research Institute (IOW) and the German Oceanographic Museum (DMM) in winter and spring 2007.

Location	Location in Figure 3	Date of observation	Sampling depth (m)	Abundance (n m^{-3})	Water temperature (°C)	Salinity (PSU)
Kiel Bight (54°36,00'N; 10°27,00'E)	6	06.02.2007 (IOW)	0-10 10-14	1.2 4.0	Surface layer: 4.7 Bottom layer: 5.1	Surface layer: 19.7 Bottom layer: 21.3
		23.03.2007 (IOW)	0-15	0	Surface layer: 5.0 Bottom layer: 5.1	Surface layer: 15.4 Bottom layer: 19.0
Kadet Furrow (54°28,00'N; 12°13,00'E)	8	07.02.2007 (IOW)	0-27	0	Surface layer: 4.5 Bottom layer: 5.5	Surface layer: 10.0 Bottom layer: 11.0
		14.03.2007(DMM)	0-22	4	Surface layer: 5.8 Bottom layer: 3.9	Surface layer: 11.4 Bottom layer: 17.3
		25.03.2007 (IOW)	0-21	0.1	Surface layer: 5.5 Bottom layer: 5.5	Surface layer: 18.0 Bottom layer: 19.0
		01.04.2007 (IOW)	0-21	0.01	Surface layer: 5.5 Bottom layer: 5.5	Surface layer: 18.0 Bottom layer: 19.0
		05.05.2007 (IOW)	0-14	0.02	No data	No data
Pomeranian Bay, Oderbank (54°23,80'N; 14°19,00'E)	9	19.12.2006 (DMM)	0-10	0.2	Surface layer: 6.4 Bottom layer: 7.0	Surface layer: 7.9 Bottom layer: 8.2
Bornholm Deep (55°15,00'N; 15°59,00'E)	10	09.02.2007 (IOW)	0-40 40-80	0 1	Surface layer: 4.3 Bottom layer: 9.4	Surface layer: 7.9 Bottom layer: 16.3
		13.02.2007 (IOW)	0-40 42-82	0 0.85	Surface layer: 4.3 Bottom layer: 9.4	Surface layer: 7.9 Bottom layer: 16.3
		27.03.2007 (IOW)	0-50 50-80	0 0.02	Surface layer: 4.3 Bottom layer: 9.3	Surface layer: 7.9 Bottom layer: 16.2
		31.03.2007 (IOW)	0-50 50-80	0 0.01	Surface layer: 4.3 Bottom layer: 9.3	Surface layer: 7.9 Bottom layer: 16.2
		10.05.2007 (IOW)	0-50 50-80	0 0.01	No data No data	No data No data
South Eastern Gotland Basin (55°33,00'N; 18°24,00'E)	11	10.02.2007 (IOW)	0-40 60-85	0 0.16	Surface layer: 4.3 Bottom layer: 5.9	Surface layer: 7.5 Bottom layer: 11.1
		30.03.2007 (IOW)	0-81	0	Surface layer: 4.5 Bottom layer: 5.8	Surface layer: 7.5 Bottom layer: 11.0

Annex 3. Public observations of *M. leidyi* by divers and from the shore by bioluminescence in 2006 and 2007. Numbers in column 1 refer to the map in Figure 4.

	Location	Observation dates	Observation Methods	Estimated abundance
1	Wohlenberger Wieck	24.12.2006 04.01.2007 18.02.2007	Observation of bioluminescence from the shore	single individuals
2	Kühlungsborn	29.06.2006 15.09.2006	Diving, Photo Figure 5	single individuals
3	Nienhagen	20.09.2006 29.11.2006	Diving	swarms
4	Stolteraa	17.09.2006 24.09.2006	Diving	swarms
5	Warnemünde	29.11.2006 29.12.2006	Observation of bioluminescence from the shore	single individuals
6	Zingst	23.11.2006 07.12.2006	Observation of bioluminescence from the shore	unknown
7	Hiddensee Island	30.09.2006	Diving	single individuals
8	Rügen Island, Sassnitz	20.12.2006	Diving	single individuals
9	Rügen Island, Göhren	06.01.2007	Diving	25-30 ind m^{-3}