# NOBANIS - Invasive Alien Species Fact Sheet

## *Mnemiopsis leidyi*

**Author of this species fact sheet:** Viktoras Didžiulis, Catalogue of Life, School of Biological Sciences, Harborne Building, University of Reading, UK, RG6 6AS, viktorasdi@gmail.com

**Bibliographical reference – how to cite this fact sheet:**
Didžiulis, V. (2013): NOBANIS – Invasive Alien Species Fact Sheet – Mnemiopsis leidyi. – From: Online Database of the European Network on Invasive Alien Species – NOBANIS www.nobanis.org, Date of access x/x/200x.

## Species description

**Scientific name:** *Mnemiopsis leidyi* Agassiz, 1865 (Ctenophora, Tentaculata, Bolinopsidae)
**Synonyms:** *M. Gardeni* L. Agassiz, 1980 (as stated by Seravin 1994)
**Common names:** sea walnut (GB), mnemiopsis (LT), amerikankampamaneetti (FI), amerikansk kammanet (NO, SE), Amerikansk lobemanet (NO), amerikansk ribbegople (DK), Meerwalnuss (DE), Amerikaanse langlobribkwal (NL).

**Fig. 1.** *Mnemiopsis leidyi* (from Wikimedia Commons at http://commons.wikimedia.org/wiki/File:Mnemiopsis_leidyi_-_Oslofjord,_Norway.jpg)

**Species identification**
*Mnemiopsis leidyi* is an actively hunting lobate ctenophore (comb jelly) with a translucent body reaching 12 cm in length (NIMPIS 2002).
The ctenophore's body is laterally compressed, with large oral lobes (in adult form, larvae don't have lobes but a round body shape and tentacles), making four deep, noticeable furrows that characterize the genus. Two oral lobes are extensions of the ctenophore body. Four smaller lobes (auricules) are situated under the two oral lobes. It has eight (four long and four short) rows of small, but numerous, ciliated iridescent bioluminescent combs that may emit greenish light in dark (NIMPIS 2002). *M. leidyi* has inner structures of the lobes originating from a position at the same level as the apical organ, not far from the top of the animal, while these structures in the similar genus *Bolinopsis* originate from a much lower level, almost halfway down between the top and the mouth side. (Hansson 2006).

The species is hermaphrodites, with ovaries and testes situated along the eight meridional canals of the gastrovascular system and fixed in gastrodermis between the ctenes.

**Native range**
*M. leidyi* is originally distributed along the American coast of the Atlantic, from Narragansett Bay, USA to the Valdez Peninsula, Argentina (GESAMP 1997).

## Alien distribution

**History of introduction and geographical spread**
In the early 1980's, *M. leidyi* was introduced into the Black Sea (Purcell et al. 2001) and in the mid 1990's the invasion continued to the Caspian Sea (likely transported in the ballast waters via the Volga Don Channel) (Kideys 2002, Bilio and Niermann 2004). In August 2005, the species was photographed in Nissum Fjord, western Jutland (Denmark) (Tendal et al. 2007). In November 2005 *M. leidyi* specimens were photographed by divers in the Oslofjorden, Norway (Oliveira 2007). In 2006 it was recorded in Kiel Bay (Javidpour et al. 2006) and along the west coast of Sweden (Hansson 2006) as well as on the Dutch and German North Sea coast (Boersma *et al.* 2007, Kube *et al*. 2007). The relatively large size and density of observed populations in Dutch estuaries (Faase and Bayha 2006) and in Kiel Bay (Javidpour et al. 2006 indicates 92 individuals per cubic meter) indicate that the actual introduction into the North and Baltic Sea might have taken place earlier. In early spring of 2007 it was also identified in the Danish straits, and it spread throughout Danish waters over the summer (Tendal *et al.* 2007). In Danish waters, densities of up to 800 small (<15mm) individuals per cubic meter were recorded in August and September (Riisgård *et al.* 2007). In August, 2007 the specimens were observed in the Gulf of Finland and the Bothnian Sea (Lehtiniemi et al. 2007) and on the 3rd October, same year, was observed in the Gulf of Gdansk, Poland (Janas & Zgrundo 2007). In the Bornholm Basin it was found in high densities in 2007 (Huwer et al. 2008).

In 2008 it was discovered that what had been identified as *M. leidyi* in northern Baltic waters was actually an Arctic species, *Mertensia ovum* (Fabricius, 1780), but because only larval and juvenile individuals had been found, the species was misidentified (Gorokhova et al. 2009). So far there have been no reports on occurrence of *M. leidyi* along the Eastern coastline of the Baltic Sea (Lithuania, Latvia, Estonia or Russia including the Kaliningrad).

**Pathways of introduction**

Faasse and Bayha (2006) suggest that ballast water transfer is the pathway of introduction, as two of the largest European ports (Antwerp and Rotterdam) are close to the Dutch estuaries, where the species was observed for the first time. However, Oliveira (2007) discusses that the possibility of natural oceanic transport by the North Atlantic Current (NAC) should not be discarded. A recent study indicates this may be possible because the Global Climate Change surface water temperature of the North Atlantic, including the NAC and the North Sea, was more than 1°C warmer in the last five years than the historical mean with temperatures averaging above 9°C (Hughes and Holliday 2006). The increased temperature might have facilitated the transport of living individuals of *M. leidyi* to the recipient regions in Europe (Oliveira 2007). It is now known that it is introduced from the American coast to the Baltic Sea (Reusch et al. 2010)

**Alien status in region**

In the North Sea and in areas of its native distribution the occurrence of *M. leidyi* seems to be restricted mainly to inshore habitats, which is its natural habitat in its natural range. In the Baltic Sea a rapid spreading is occurring. Although it has yet to be observed and reported in a few remaining countries around the Baltic Sea, considering the rapid proliferation of this species elsewhere, this is very likely to happen within a few years. In the Netherlands, *M. leidyi* has been observed in large numbers in the inland marine water bodies Lake Grevelingen, Westerschelde, Oosterschelde and Wadden Sea (A. Gittenberger, personal communication).

Every summer it occurs in large numbers in the central part of Limfjorden in Denmark. It is not known where they spend the winter, but possibly they re-invaded from the south-eastern part of the North Sea in 2009. In both 2008 and 2009, the predation of *M. leidy* (together with *Aurelia aurita* – a native jellyfish in the Baltic) on zoo plankton resulted in half times on about 1 day, which is reflected in the absence of copepods and dominance of ciliates in Skive Fjord (Riisgaard et al 2010). There are no official monitoring programmes in Denmark, but a public reporting study has given good information about the prevalence in the inner Danish waters.

| Country | Not found | Not established | Rare | Local | Common | Very common | Not known |
|---|---|---|---|---|---|---|---|
| Austria | X | | | | | | |
| Denmark | | | | | | X | |
| Estonia | X | | | | | | |
| European part of Russia | X | | | | | | |
| Finland | | | | X | | | |
| Faroe Islands | X | | | | | | X |
| Germany | | | | | X | | |
| Greenland | | | | | | | X |
| Iceland | X | | | | | | |
| Ireland | X | | | | | | |
| Latvia | X | | | | | | |
| Lithuania | X | | | | | | |
| Netherlands | | | | | X | | |
| Norway | | | | X | | | |
| Poland | | X | | | | | |
| Slovakia | X | | | | | | |
| Sweden | | | | X | | | |

**Table 1.** The frequency and establishment of *Mnemiopsis leidyi*, please refer also to the information provided for this species at www.nobanis.org/search.asp. Legend for this table: **Not found** –The species is not found in the country; **Not established** - The species has not formed self-reproducing populations (but is found as a casual or incidental species); **Rare** - Few sites where it is found in the country; **Local** - Locally abundant, many individuals in some areas of the country; **Common** - Many sites in the country; **Very common** - Many sites and many individuals; **Not known** – No information was available.

## Ecology

### Habitat description

*M. leidyi* lives and reproduces in wide salinity and temperature ranges (Baker and Reeve 1974, GESAMP 1997) inhabiting both coastal and estuarine waters (GESAMP 1997). Although it is known more as a coastal ctenophore (GESAMP 1997, Mianzan 1999), there are some specimen records in oceanic waters, including localities inside the inflow of the Gulf Stream (Harbison et al. 1978). *M. leidyi* may occur in temperatures from -0.7 to 35 °C and in salinities between 3.4-70 ppt, but for shorter periods of time, slightly lower or higher values are tolerated (Miller 1974, Hansson 2006). In low salinity areas, they die at higher temperatures (Shiganova et al. 2001). The maximum depth where the species has been observed is 80-110 m, but maximum densities have been found between 40-60 m (Huwer et al 2008).
*M. leidyi* has a broad food spectrum, which includes fish eggs and larvae, different kinds of smaller holoplanktonic animals, pelagic larvae and even protozoan plankton. In areas with dense populations of this ctenophore, it may locally affect populations of species with late summer or autumn larvae (Burrell and Van Engel 1976, Bullard et al. 1999). It often consumes excess food, which it then regurgitates and is able to eat up to ten times its body weight in food per day (NIMPIS 2002). *M. leidyi* survives food shortages for as long as 3 (or more) weeks reducing body size during starvation and in North America it has been observed hundreds of kilometres offshore where food is scarce (NIMPIS 2002).

### Reproduction and lifecycle

The species breeds at temperatures between approx. 9-23°C when plenty of food is available (GESAMP 1997). Spawning occurs during the night, where it releases eggs and sperm into the water where fertilisation takes place and it is reported to be able to reproduce all year (NIMPIS 2002). The number of eggs depends on food availability and temperature.

The species is a simultaneous hermaphrodite able to perform self-fertilisation (Oliveira and Migotto 2006), which means that a single individual should in theory be capable of establishing a new population. As many other Ctenophores it is able to reproduce sexually in larval stage (paedogenesis). However sexual maturity of larvae is followed by regression of gonads and subsequent re-maturing of adults (dissogony) (Planka 1974).

For the first 30 hours the embryo develops swimming freely within the egg envelope. Then it breaks the envelope and hatches into the cydippid stage (Mayer 1912). At this stage it is indistinguishable from *Pleurobrachia pileus* at the same stage, which in the eastern Atlantic and the Baltic is a native ctenophoran species; hence this stage is called “Pleurobrachia stage”. At this stage it is also indistinguishable from an Arctic ctenophore *Mertensia ovum*, which also occurs in the northern Baltic (Gorokhova et al. 2009, Gorokhova and Lehtiniemi 2010).When the animal reaches 5 mm in length the oral lobes start to develop and when it reaches 10 mm its outline becomes similar to that of the adult *Bolinopsis* (another ctenophore species), therefore this juvenile stage is called

“Bolinopsis stage”. Gradually lateral furrows extend upward to the apical organ and the *M. leidyi* acquires its own characteristic shape (NIMPIS 2002).

**Dispersal and spread**
Being native in the central West Atlantic Ocean (like many other marine aliens) and starting its cross-ocean journey somewhere in the 1980's, the species has now, a little more than 20 years later efficiently expanded its range to the North East Atlantic, Black Sea, Sea of Marmara, Caspian Sea, Aral Sea, Mediterranean, and the North and the Baltic Seas. Although its first invasion into the Black Sea was certainly mediated by shipping and ballast water, it is presently known that its most recent spread to the North and Baltic Seas was caused by shipping from its native region (Reusch et al. 2010).

After its introduction to the Black Sea, *M. leidyi* reproduced intensively causing explosive blooms during 1988-1990, with a total biomass of 800 million tons of wet weight during the summer of 1989 (Vinogradov et al. 1989). *M. leidyi* thus displayed the typical population dynamics pattern of a new coloniser and soon afterwards its abundance and biomass have dropped from ~1000 up to 4600 WW g/$m^2$ (Vinogradov et al. 1989) or 100 – 400 individuals per cubic meter (Zaika et al 1990) or to moderate levels in 1991 and fluctuated within a range of 200 – 500 WW g/$m^2$ (Shiganova et al. 1998, Mutlu et al. 1994, Vinogradov et al. 1992) or up to 27 individuals per cubic meter (Purcell et al 2001). In its native range abundances vary in between 1 and 12 individuals per cubic meter (Purcell et al 2001).

## Impact

**Affected habitats and indigenous organisms**
As stated in multiple sources, feeding mainly on copepods, fish eggs, small fish and fish larvae it has a potential for big impacts on pelagic marine ecosystems; substantial reductions in abundance of fish and zooplankton have been attributed to spread of this species in the Black and Caspian Seas (Shiganova et al 1998; Shiganova et al 2001). In areas with dense populations of this ctenophore, it may locally affect populations of species with late summer or autumn larvae (Burrell and Van Engel 1976, Bullard et al. 1999, Purcell et al. 2001).

It directly competes with *Aurelia aurita* (native jellyfish in the Baltic). *M. leidyi* has a faster generation time and higher production rate and can outcompete *Aurelia* as they occupy the same layer in the water column and compete for the same planktonic food items (Mutlu et al 1991).

**Genetic effects**
Not known.

**Human health effects**
Recently, larvae of the parasitic sea anemone *Edwardsiella lineata* have been found in *M. leidyi* in Sweden. This is the first finding of the sea anemone larvae in the introduced range of *M. leidyi*. The larvae can cause a rash called “sea bather's eruption” in persons swimming in the sea due to specific stinging cells (also called nematocysts). The potential consequences for *M. leidyi* populations are discussed, but in its native range *E. lineata* causes lower and sometimes negative growth rates in *M. leidyi* populations (Selander et al. 2009).

**Economic and societal effects (positive/negative)**
Feeding mainly on a broad spectrum of planktonic organisms, fish eggs and larvae (Burrell and Van Engel 1976), *M. leidyi* populations grow rapidly when food is abundant (Purcell et al. 2001). In the early 1980's, it was introduced into the Black Sea, where it quickly established and exploded in abundance. The absence of predators combined with favourable environmental conditions allowed *M. leidyi* to spread into the adjacent Sea of Azov as well as Marmara and Aegean Seas (GESAMP 1997, Shiganova et al. 2001, Kideys 2002). During the population explosions in the Black Sea in 1989 and 1995 anchovy fisheries collapsed in the region (Shiganova et al. 2001) causing an estimated loss of $250 million (NIMPIS 2002). *M. leidyi* populations are still affecting the environment of the Caspian Sea, due to the absence of the predator *B. ovata* there (Stone 2005). In the Limfjord (DK) scyphomedusae, *Cyanea capillata* and *C. lamarcki*, have been observed to feed on *M. leidyi* (Riisgård *et al.* 2007). Expected to threaten sole, plaice and herring fisheries in the Baltic (Faasse and Bayha 2006, Oliveira 2007). It has also been predicted to affect reproduction of cod in the Baltic because *M. leidyi* tend to aggregate near the halocline where Baltic cod spawning also occurs (Haslob *et al.* 2007).

## Management approaches

**Prevention methods**
Control of ship ballast waters. However, if it spreads with oceanic currents, this will not prevent *M. leidyi* from invading new areas.

**Eradication, control and monitoring efforts**
Biological control – another Northwest Atlantic ctenophore, *Beroe ovata*, preys upon *M. leidyi.* When *B. ovata* was introduced into the Black Sea, both spread and environmental impact of *M. leidyi* has been greatly reduced (Gordina et al. 2005). There are two native species of Beroe, *B. gracilis and B. cucumis*, in the North Sea and inner Danish waters (Riisgård et al. 2007), which may be expected to be able to feed on *M. leidyi*. However, their life cycles may not be well adapted to year-round reproduction of *M. leidyi*. *B. ovata* cannot survive in salinities lower than 10 PSU.

**Information and awareness**
*M. leidy*i presents a serious economic and ecological threat, therefore it is in focus of scientific and popular publications related to the general topic of invasive alien species and their spread.

**Knowledge and research**
Because of its potential threat to fishery resources of the North and Baltic Sea new occurrences of the species are published as soon as they become noticed. So far there is no definitive information as to how much the species actually impacts ecosystems in its new invaded range throughout North European waters, however large impacts on abundance of zooplankton and fish have already been attributed to *M. leidyi* in the Black and Caspian seas (Shiganova et al 1998; Shiganova et al 2001) and therefore are likely elsewhere.

**Recommendations or comments from experts and local communities**
*M. leidyi* occurs only in the western and southern Baltic Sea (Gorokhova et al. 2009). Thus, it would be important to prevent further introduction of specimens from ballast waters and thus to rapidly apply IMO guidelines for ballast water treatment.

Although *M. leidyi* tolerates wide range of salinities it is not likely to establish in the northernmost parts of the Baltic Sea (Bothnian Bay) where both salinity and temperature are low.

In Germany and Denmark, for example, there are no coordinated monitoring programmes to document the spreading and impacts of *M. leidyi* in the long run (and of all other alien species). Thus, it is still a challenge to act on alien species. Therefore, existing management initiatives and instruments as well as the implementation of new and relevant programmes, must be carefully applied (Nehring and Klingenstein 2008).

## References and other resources

**Contact persons**

Sandra Kube (DE) E-mail:: sandra.kube@uni-rostock.de

Stefan Nehring (DE), AeT umweltplanung, Bismarckstraße 19, D-56068 Koblenz, Germany Phone: +49 261 1330398; E-mail: nehring@aet-umweltplanung.de

Prof. Hans Ulrik Riisgård (DK) Marine Biological Research Centre, University of Southern Denmark. E-mail: hur@biology.sdu.dk

Dr. Ole S. Tendal (DK) Zoological Museum, University of Copenhagen. E-mail: ostendal@snm.ku.dk

Arno Põllumäe (EE) Estonian Marine Institute, University of Tartu,10a Mäealuse Street,Tallinn, 12618, Estonia. Phone +3725212535, fax +3726718976, E-mail: Arno.Pollumae@ut.ee

Maiju Lehtiniemi (FI), Finnish Environment Institute, P.O.Box 140, 00251 Helsinki, Finland, e-mail: maiju.lehtiniemi@ymparisto.fi

Adriaan Gittenberger (NL), GiMaRIS, E-mail: gittenberger@gimaris.com]

Elena Gorokhova(SE), Department of Applied Environmental Science, Stockholm University, Sv. Arrhenius v. 8, SE-11418 Stockholm, Sweden, e-mail: elenag@itm.su.se

Urszula Janas (PO) Institute of Oceanography University of Gdansk Al. M. Pilsudskiego 46 81-378 Gdynia E-mail: oceju@univ.gda.pl

Mariusz Sapota (PO) Institute of Oceanography University of Gdansk Al. M. Pilsudskiego 46 81-378 Gdynia. E-mail: ocems@univ.gda.pl

Melanie Josefsson (SE) Swedish Environmental Protection Agency, SE 106 48 Stockholm, Sweden. Phone: +46 18 67 31 48, E-mail: Melanie.Josefsson@snv.slu.se

**Links**

Aquatic Invasions: http://www.aquaticinvasions.ru

Alien species in Swedish waters, Fact sheet on *Mnemiopsis leidyi*
http://www.frammandearter.se/0/2english/pdf/Mnemiopsis_leidyi.pdf

The Baltic Sea Portal
http://www.itameriportaali.fi/en/tietoa/tulokaslajit/en_GB/kampamaneetti/

Global Invasive Species Database:
http://www.issg.org/database/species/ecology.asp?si=95&fr=1&sts=sss&lang=EN

Aquatic alien species in German inland and coastal waters - database: http://www.aquatic-aliens.de

## References


Baker, L. D and and Reeve, M.R., 1974. Laboratory culture of the lobate ctenophore *Mnemiopsis mccradyi* with notes on feeding and fecundity. IMar. Biol.26: 57-62.

Bilio M. and Niermann U., 2004. Is the comb jelly really to blame for it all? *Mnemiopsis leidyi* and the ecological concerns about the Caspian Sea. Marine Ecology Progress Series 269: 173–183

Boersma, M., Malzahn, A.M., Greve, W., Javidpour, J., 2007. The first occurrence of the ctenophore *Mnemiopsis leidyi* in the North Sea. Helgoland Marine Research 61:153-155.

Bullard S.G., Lindquist N.L. and Hay M.E., 1999. Susceptibility of invertebrate larvae to predators: how common are postcapture larval defenses? Marine Ecology Progress Series 191: 153-161

Burrell Jr V.G. and Van Engel W.A., 1976. Predation by and distribution of a ctenophore, *Mnemiopsis leidyi* A.
Agassiz, in the York River estuary. Estuarine, Coastal and Shelf Science 4: 235–242

Faasse M.A. and Bayha K.M., 2006. The ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 in coastal waters of the Netherlands: an unrecognized invasion? Aquatic Invasions 1(4): 270–277

GESAMP (IMO/FAO/UNESCO-IOC/WMO/WHOI/IAEA/UN/UNEP Joint Group of Experts on the Scientific Aspects of Marine Pollution), 1997. Opportunistic settlers and the problem of the ctenophore *Mnemiopsis leidyi* invasion in the Black Sea. GESAMP reports and studies No. 58. International Maritime Organization, London.

Gordina A.D., Zagorodnyaya JuA, Kideys A. E. and Satilmis A. E, 2005. Summer ichthyoplankton, food supply of fish larvae in the Black Sea during 2000 and 2001. J. mar. Biol. Ass. U.K. 85: 537-548.

Gorokhova, E., Lehtiniemi M., Viitasalo-Frösen, S. and Haddock, S. H. D. 2009. Molecular evidence for the occurrence of ctenophore Mertensia ovum in the Northern Baltic Sea and implications for the status of *Mnemiopsis leidyi* invasion. Limnol. Oceanogr. 54 (6): 2025-2033

Hansson H.G., 2006. Ctenophores of the Baltic and adjacent Seas – the invader *Mnemiopsis* is here! Aquatic Invasions 1(4): 295–298

Harbison G.R., Madin L.P. and Swanberg, N.R. 1978. On the natural history and distribution of oceanic ctenophores. Deep-Sea Research 25: 233–256

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

Hughes S. L. and Holliday N. P. (eds) (2006) ICES Report on Ocean Climate 2005. ICES Cooperative Research Report 280: 1–49

Huwer, B., Storr-Paulsen, M., Riisgård, H.U. and Haslob, H. 2008. Abundance, horizontal and vertical distribution of the invasive ctenophore *Mnemiopsis leidyi* in the central Baltic Sea, November 2007. Aquatic Invasions 3(2): 113-124 (available online)

Javidpour J., Sommer U. and Shiganova T., 2006. First record of *Mnemiopsis leidyi* A. Agassiz 1865 in the Baltic Sea. Aquatic Invasions 1(4): 299-302

Janas, U. and Zgrundo, A. 2007. First record of *Mnemiopsis leidyi* A. Agassiz, 1865 in the Gulf of Gdansk (southern Baltic Sea). Aquatic Invasions 2(4): 450-454

Jensen, Kathe R. (2010): NOBANIS – Invasive Alien Species Fact Sheet – *Mnemiopsis leidyi* – From: Identification key to marine invasive species in Nordic waters – NOBANIS www.nobanis.org, Date of access: 9/11/2010.

Kideys A.E., 2002. Fall and rise of the Black Sea ecosystem. Science 297: 1482–1483

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

Lehtiniemi, M., Pääkkönen, J.-P., Flinkman, J., Gorokhova, E., Karjalainen, M., Viitasalo, S. and Björk, H. 2007: Distribution and abundance of the American comb jelly (*Mnemiopsis leidyi)* – A rapid invasion to the Northern Baltic Sea during 2007. Aquat Invasions 2(4):445-449.

Madsen, C.V., Riisgård, H.U. (2010) Ingestion-rate method for measurement of clearance rates of the ctenophore *Mnemiopsis leidyi*. Aquatic Invasions (in press)

Mayer, A.G., 1912. Ctenophores of the Atlantic coast of North America. Carnegie Institution, Washington, USA.

Mayer A.G. 1900. Description of new and little-known medusae from Western Atlantic. Bulletin of Museum of Comparative Zoology 37: 1-12.

Mianzan H.W. 1999. Ctenophora. In: Boltovskoy D. (ed.) South Atlantic Zooplankton. Backhuys, Leiden, The Netherlands, pp 561–573

Miller R.J., 1974. Distribution and biomass of an estuarine ctenophore population, *Mnemiopsis leidyi* (A. Agassiz).

Chesapeake Sci. 15: 1-8
Mutlu, E., 1999. Distribution and abundance of ctenophores and their zooplankton food in the Black Sea. II. Mnemiopsis leidyi. Marine Biology 135:603-613.
Mutlu, E., Bingel, F., Gucu A. C., Melnikov V. V., Niermann, U., Ostrovskaya N. A., Zaika V. E., 1994. Distribution of the new invader *Mnemiopsis sp*. and the resident *Aurelia aurita* and *Pleurobrachia pileus* populations in the Black Sea in the years 1991-1993. ICES J. of Mar. Sci., 51: 407-421.
Nehring, S., Klingenstein, F., 2008. Aquatic alien species in Germany - Listing system and options for action. Neobiota 7: 19-33.
NIMPIS (2002). *Mnemiopsis leidyi* reproduction & life cycle. National Introduced Marine Pest Information System (Eds: Hewitt C.L., Martin R.B., Sliwa C., McEnnulty, F.R., Murphy, N.E., Jones T. & Cooper, S.). Web publication <http://crimp.marine.csiro.au/nimpis>, Date of access: 5/6/2008
Oliveira O.M.P. and Migotto A.E ., 2006. Pelagic ctenophores from the São Sebastião Channel, southeastern Brazil. Zootaxa 1183: 1–26
Oliveira, O.M.P. 2007. The presence of the ctenophore *Mnemiopsis leidyi* in the Oslofjorden and considerations on the initial invasion pathways to the North and Baltic Seas. European Research Network on Aquatic Invasive Species. Aquatic Invasions (2007) 2(3): 185-189.
Planka H.D. 1974 Ctenophora. Reproduction of marine invertebrates. Eds. Glese A.C. Pearse J.S. V.1.p.201-265.
Purcell J.E., Shiganova T.A., Decker M.B. and Houde E.D., 2001. The ctenophore *Mnemiopsis* in native and exotic habitats: U.S. estuaries versus the Black Sea basin. Hydrobiologia 451: 145–176
Reusch, T.B., Bolte, S, Sparwel, Moss, M. G. and Javidpour, J. 2010: Microsatellites reveal origin and genetic diversity of Eurasian invasions by one of the world's most notorious marine invader, Mnemiopsis leidyi (Ctenophora). Molecular Ecology. doi: 10.1111/j.1365-294X.2010.04701.x
Riisgård, H.U., Bøttiger, L., Madsen, C,V., Purcell, J.E. (2007). Invasive ctenophore *Mnemiopsis leidyi* in Limfjorden (Denmark) in late summer 2007 - assessment of abundance and predation effects. Aquatic Invasions 2(4): 395-401. (available in pdf)
Riisgård, H.U., Tendal, O. (2010) Invasive comb jellies (*Mnemiopsis leidyi*) in Danish waters. Pool32Mag, vol:2, p. 212-225 (E-publication in fly fishing e-magazine): published 25 September 2010 online, see link www.poll32mag.blogspot.com).
Riisgård, H.U., Madsen, C.V, Barth, C., Purcell, J.E. (2010). Population dynamics and possible competition between the indigenous scyphozoan *Aurelia aurita* and the invasive ctenophore *Mnemiopsis leidyi* in Limfjorden (Denmark). Mar. Ecol. Prog. Ser. (submitted).
Riisgård, H.U., Barth, C., Madsen, C.V. (2010). Predation impact by the jellyfish *Aurelia aurita* eliminates the invasive ctenophore *Mnemiopsis leidyi* in a shallow cove (Kertinge Nor, Denmark). Aquatic Invasions (published online).
Selander, E., Møller, L.F., Sundberg, P. and Tiselius, P. 2009. Parasitic anemone infects the invasive ctenophore *Mnemiopsis leidyi* in the North East Atlantic. Biological Invasions 12(5), 1003-1009
Seravin L.N., 1994. The systematic revision of the genus *Mnemiopsis* (Ctenophora, Lobata). II: Species attribution of *Mnemiopsis* from the Black Sea and the species composition of the genus *Mnemiopsis*. Zoologičeskij žurnal 73 (11): 19-34
Shiganova T.A., Mirzoyan Z.A., Studenikina E.A., Volovik S.P., Siokou-Frangou I, Zervoudaki S, Christou E.D.,
Skirta A.Y. and Dumont H.J., 2001. Population development of the invader ctenophore *Mnemiopsis leidyi* in the Black Sea and other seas of the Mediterranean basin. Marine Biology 139: 431–445
Shiganova, T. A., Kıdeys, A. E., Gücü, A. C., Niermann, U., Khoroshilov, V. S., 1998. Changes in species diversity and abundance of the main components of the Black Sea pelagic community during the last decade. In: NATO TU Black Sea project: Ecosystem Modeling as a Management Tool for the Black Sea, Symposium on Sci. Results, L. Ivanov & T. Oguz (eds.), Kluwer Acad. Publ. Vol. 1: pp. 171-188.
Stone R, 2005. Attack of the killer jellies. Science 309: 1805–1806
Tendal, O.S., Jensen, K.R. and Riisgård, H.U. 2007. Invasive ctenophore *Mnemiopsis leidyi* widely distributed in Danish waters. Aquatic Invasions 2(4): 455-460 (download)
Vinogradov, M. E., Shushkina, E. A., Musaeva E. I., Nikolaeva, G. G., 1992. Vertical distribution of the Black Sea mesoplankton in winter 1991. In: Winter state of the open Black Sea ecosystem (ed. Vinogradov, M. E.). Moscow, IO RAN: 103-119, (in Russian)
Vinogradov, M. Ye., Shushkina, E. A., Musayeva, E. I., Sorokin, P. Yu., 1989. A newly acclimatised species in the Black Sea: The ctenophore Mnemiopsis (Ctenophora: Lobata). Oceanology 29(2): 220-224.
Zaika, V. E. & N. K. Revkov, 1994. Anatomy of gonads and regime of spawning of ctenophore *Mnemiopsis sp.* in the Black Sea. Zool. Zhurnal 73: 5-10 (in Russian)
Zaika, V.Ye. & Sergeyeva, N.G. (1990): Morphology and Development of *Mnemiopsis mccradyi* (Ctenophora, Lobata) in the Black Sea. Hydrobiological Journal 26: 1-6 [English version].

**Date of creation/modification of this species fact sheet:** 06-06-2013