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Invasion of Danish and Adjacent Waters by the Comb Jelly *Mnemiopsis leidyi*—10 Years After

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Abstract

The invasive ctenophore *Mnemiopsis leidyi*, which comes from North America's east coast, was observed in Danish waters for the first time in 2007. Since then, the new invader has every summer spread in Danish and adjacent waters (*i.e.* North Sea, Limfjorden, Skagerrak, Kattegat, Belt Sea, Baltic Sea). The invasive comb jelly has apparently come to stay, as it has no effective enemies. Possible harmful effects of *M. leidyi* which feeds voraciously on zooplankton, fish eggs and larvae, have so far not been thoroughly studied in Danish waters, although dedicated attempts have been made in Limfjorden and in the central Baltic Sea. Over the last 10 years, the Danish national environmental monitoring program did not include gelatinous zooplankton, but new initiatives have been recently taken. A brief overview of our current knowledge on the impact of *M. leidyi* in Danish waters is given here.

Keywords

Invasive Ctenophore, Alien Comb Jelly, *Mnemiopsis leidyi*, Predation Impact, Zooplankton, Limfjorden, Baltic Sea, Kattegat, Great Belt, Hydrography

1. Introduction

In the last 10 years, we have witnessed a full-scale experiment in Danish and adjacent waters, where the alien invasive comb jelly *Mnemiopsis leidyi* now spreads every summer. This ctenophore comes from North America's east coast [1] [2] and has so far no effective enemies in Danish waters. Apparently it has come here to stay. Although *M. leidyi*'s natural predator, another ctenophore, *Beroe ovata*, was observed as a new species in Danish waters in 2014 [3], it has not yet, due to a low number of individuals, caused any documented changes in the abundance and distribution of *M. leidyi*. The biological and environmental factors controlling its sporadic occurrence are still poorly understood. Possible harmful effects of *M. leidyi* which feeds voraciously on zooplankton, fish eggs and larvae [4], have so far not been thoroughly studied in Danish waters, nor have possible competition for zooplankton with planktivorous fish (herring and sprat) been studied. The Danish national environmental monitoring program does not yet include occurrences and possible environmental damages caused by jellyfish and other gelatinous zooplankton. During the last 10 years and after the arrival of *M. leidyi* to the Danish waters, its possible adverse impacts have largely been ignored by the environmental authorities. Here, I give a brief overview of our current knowledge, as I see it.

2. The First Observations

In autumn 2006, *Mnemiopsis leidyi* was observed for the first time in large numbers in the Dutch Wadden Sea, where it had probably been transported by the ballast water in ships [5]. It then spread northwards and up along the west coast of Denmark, into Limfjorden and further north up around the tip of Denmark into the inner Danish waters, where the ctenophore was then coincidently observed in Kiel Bight (western Baltic) in October 2006 [6]. The new comb jelly was first observed in Danish waters in 2007 by Tendal *et al.* [7], in the Little Belt in February, and in the Great Belt in mid March. During the summer and autumn of 2007, the new comb jelly was observed everywhere in the inner Danish waters, and the phenomenon was extensively covered by the media. Based on more than 150 e-mails with photos from biologists, fishermen, divers, boaters and beach visitors, Tendal *et al.* [7] made a map showing that *M. leidyi* in the late summer of 2007 occurred all over the inner Danish waters (**Figure 1**), and often in large numbers as in Limfjorden (**Figure 2**), where it was quantified for

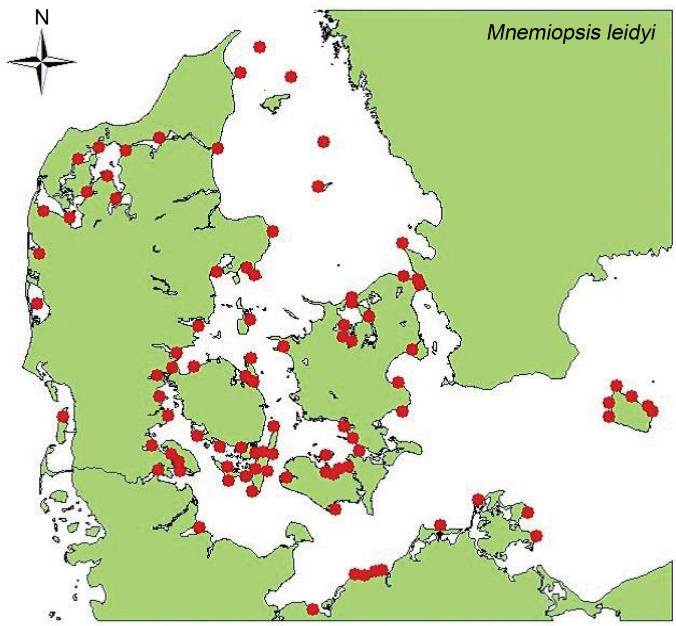

Figure 1. Observations of *Mnemiopsis leidyi* in inner Danish and adjacent waters in 2007. From: Tendal *et al.* [26].

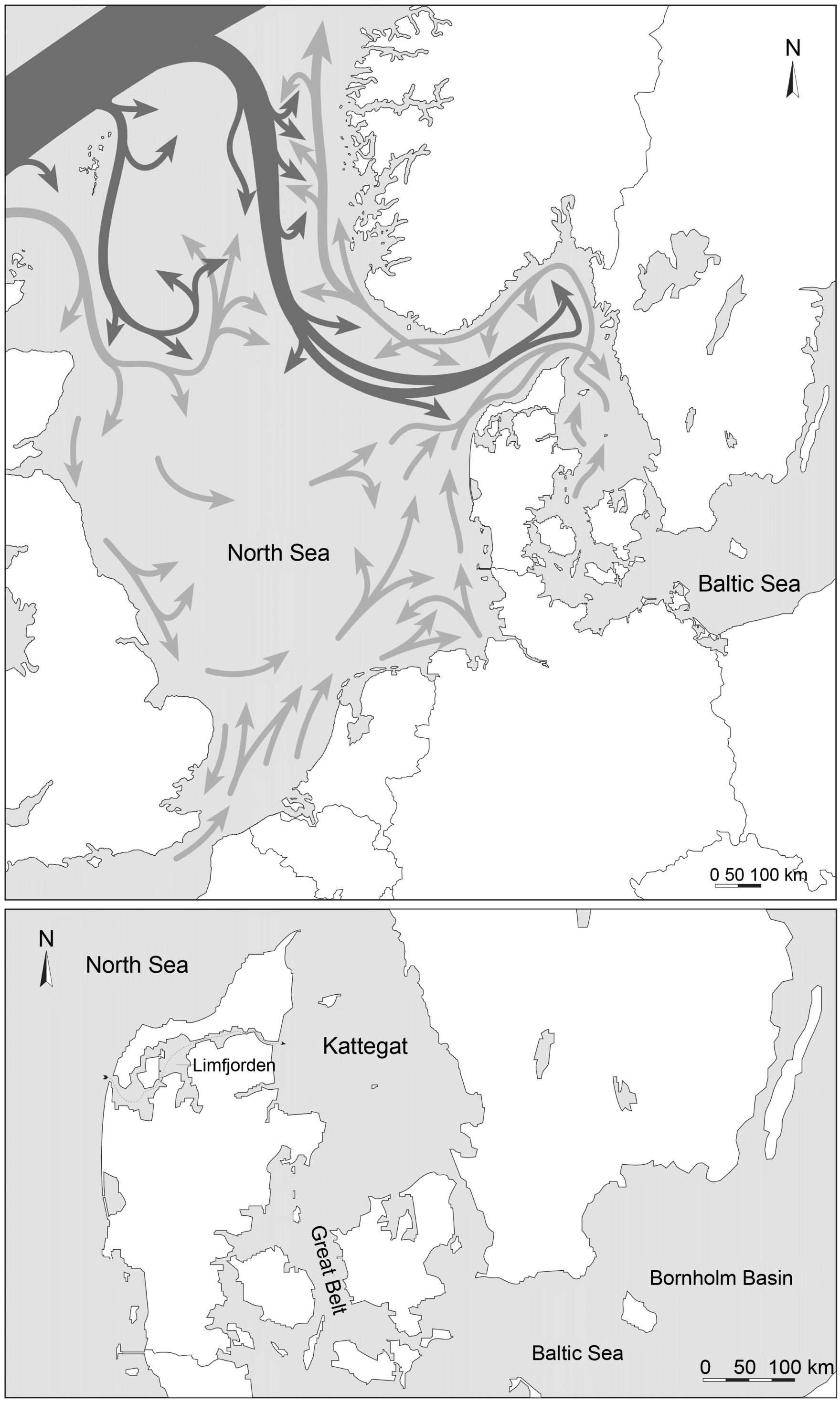

Figure 2. (Upper panel) Directions of main surface currents in the North Sea. Dark grey arrows indicate flow of Atlantic water and light grey arrows indicate water of other types. The northward directed coastal currents from the English Channel and up along the Dutch and Danish west coasts ensure that *Mnemiopsis leidyi* re-invades Limfjorden and possibly other Danish and adjacent waters from the North Sea every summer. (Lower panel) Water exchange in Limfjorden is mainly caused by strong westerly winds inducing intrusions of North Sea water. The path of water exchange between the North Sea in the west and Kattegat in the east is indicated by a broken line. Adapted from Caveen *et al.* [8].

the first time [9]. The situation continued in the following years, but due to the Danish national monitoring program not including jellyfish and other gelatinous zooplankton, we have today no comprehensive overview of the development of the new comb jelly's presence in the Danish waters, apart from quantitative studies Limfjorden and the western and central Baltic Sea, as it appears from the following sections. However, the many scattered observations that I know of (own observations in Danish waters and harbours, and e-mails with photos from many interested citizens) indicate that *M. leidyi* still occur every summer and spread ubiquitously in the inner Danish waters.

3. Studies in Limfjorden

Mass occurrence of *Mnemiopsis leidyi* was first observed in Limfjorden in 2007 [9], but it probably arrived the previous year [7]. Every year since, *M. leidyi* has apparently re-invaded Limfjorden (which is actually a sound) from the North Sea via Thyborøn Canal. This invader is transported by water masses partly originating from the English Channel [10] [11], the Belgian part of the North Sea [12] [13], and the western Dutch Wadden Sea, where it is present year round [14] [15] [16]. The hypothesis of *M. leidyi* being brought into Limfjorden from the North Sea has not been directly proved, but a number of strong indications support this interpretation. Thus hydrographic observations and model calculations made by Riisgård *et al.* [17] indicated, along with previous studies [18] [19], that re-invasion of *M. leidyi* from the North Sea seeded the autumn population in Limfjorden in mid-September 2011. *M. leidyi* has frequently exerted a significant predation impact on the zooplankton biomass in Limfjorden during late summer [9] [17] [18] [19] [20] [21]. In most years *M. leidyi* has thrived extremely well in Limfjorden, with maximum densities and specific bio-volumes in August-September in central parts (**Table 1**). In late summer 2007, *M. leidyi* was

Table 1. *Mnemiopsis leidyi*. Maximum densities (D) recorded in Skive Fjord (an inner branch of Limfjorden). L = oral-aboral body length; B = specific bio-volume of the ctenophore population; $t_{1/2}$ = estimated half-life of zooplankton (copepods), cf. Riisgård *et al.* [9], Equation (3) therein. Mean ± S.D. indicated.

Year	Date	D (ind. m^{-3})	L (mm)	B (ml·m^{-3})	$t_{1/2}$ (d)	References
2007	8 August	867 ± 121	5 ± 3	312	0.8	[9]
2008	10 September	196 ± 118	5 ± 3	78	3.4	[18]
2009	26 August	66 ± 13	9 ± 5	66	4.0	[18]
2010	18 August	3.2 ± 0.2	40 ± 8	41	6.3	[17]
2011	17 November	41 ± 3.8	4.7 ± 0.3	13	19.6	[17]
2012	2 October* 28 November*	- -	- -	- -	- -	[21]
2013	23 September	54 ± 12	6.1 ± 2.5	47.9	2.1	[21]
2014	23 September	255 ± 117	5.8 ± 1.6	-	2.2	[20]

*In 2012, the ctenophore *Pleurobrachia pileus* was numerous and very few *M. leidyi* were observed.

found in every net sample from 9 locations in Limfjorden, and the population densities were high, up to more than 800 individuals m^{-3} in Skive Fjord, an inner branch of the fjord-system, but body lengths were small (5 to 15 mm). The specific bio-volumes were very high in the central parts of Limfjorden (*i.e.*, Thisted Bredning: 102 $ml \cdot m^{-3}$, Løgstør Bredning: 113 $ml \cdot m^{-3}$, Junget Øre: 228 $ml \cdot m^{-3}$, Skive Fjord: 312 $ml \cdot m^{-3}$) and were even greater than those from the Black Sea, where the greatest mean bio-volume was approximately 184 $ml \cdot m^{-3}$ in the autumn of 1989, when the zooplankton and fish stocks collapsed [4].

Mnemiopsis leidyi relies on a holoplanktonic life cycle and is a self-fertilizing hermaphrodite, releasing eggs and sperm in the ambient water where fertilization occurs [22] [23] [24]. High fecundity and rapid generation times during the whole season may explain why *M. leidyi* occurs in large numbers in Limfjorden. The incoming water from the North Sea is of decisive importance for the yearly re-invasion by *M. leidyi* from the warmer southwestern North Sea, which in cold winters seems to serve as a refuge. In this way Limfjorden functions as a nursery for *M. leidyi,* which subsequently disperse into Kattegat (**Figure 2**), adjacent waters and the western Baltic Sea [17] [20].

Compared to previous years, 2012 was atypical due to only a very few small individuals of *Mnemiopsis leidyi* were observed in Limfjorden [21]. In mid-September 2012, the hydromedusa *Aequorea vitrina* and the scyphozoan jellyfish *Rhizostoma octopus* appeared in Limfjorden, with relatively high salinities indicated that a large volume of high-saline North Sea water had been pushed in through Thyborøn Canal by westerly winds. Therefore Riisgård & Goldstein [21] suggested that mainly *Pleurobrachia pileus* (and not *M. leidyi*) had been brought into Limfjorden from the North Sea in 2012 (**Table 1**). The density of *P. pileus* was 157 ± 45 ind. m^{-3} and the estimated half-life of zooplankton was only 1.5 d showing that this ctenophore controlled the zooplankton biomass, and possibly outmatched *M. leidyi* in this year.

Herring (*Clupea harengus)* and sprat (*Sprattus sprattus*) are pelagic fish species in Limfjorden, and because they feed on zooplankton, they will in certain areas and periods compete with large numbers of *Mnemiopsis leidyi* for the same limited amount of food [20] [21] [25]. However, no studies have so far attempted to determine the degree of interspecific competition for zooplankton between the comb jellies and the planktivorous fish. The short estimated half-lives of zooplankton (a few days, or shorter; **Table 1**) along with a conspicuous reduction of the zooplankton biomass [17] [18] [19] [20] potentially caused by *M. leidyi*, suggest very poor feeding conditions for juvenile herrings in Limfjorden.

4. Observations in Kattegat and Great Belt

Only few sporadic observations of *Mnemiopsis leidyi* have been made in the Kattegat and Great Belt, which connect the North Sea with the Baltic Sea (**Figure 2**). *M. leidyi* was observed in Great Belt for the first time in early spring 2007.

The population density in Great Belt remained low, ranging from 0.004 to 0.034 ind. m^{-3} in the period 18 April to 18 June 2007, although the mean body length increased from 1.1 ± 0.4 cm to 4.6 ± 1.3 cm [7].

During late 2008 and 2009, the population dynamics of *Mnemiopsis leidyi* and the indigenous moon jellyfish, *Aurelia aurita*, were studied in the fjord system Kerteminde Fjord/Kertinge Nor that connects with the adjacent Great Belt [27]. The population density of *A. aurita* was always highest in the innermost part of the fjord system, the shallow cove of Kertinge Nor, while the density of *M. leidyi* was always highest in the outermost Kerteminde Fjord, indicating recruitment of the ctenophore from the Great Belt. During November 2008 the density of small 3 to 5 mm *M. leidyi* in Kerteminde Fjord reached a maximum of 590 ind. m^{-3}. In Kertinge Nor, the first *A. aurita* ephyrae appeared in March 2009, and by the end of May the medusae had obtained a maximum umbrella diameter of only 30 mm likely due to food limitation. The estimated half-life of zooplankton caused by *A. aurita* was less than one day from May to September 2009 [27]. This extremely high predation impact explains why *M. leidyi* could be outcompeted by *A. aurita* in Kertinge Nor.

Haraldsson *et al.* [28] studied the seasonal population dynamics of *Mnemiopsis leidyi* from May 2009 until April 2010 along a transect of 8 monitoring stations from Skagerrak into the Baltic Proper. Throughout the year, *M. leidyi* was found at 5 of the 8 stations, and the ctenophore never extended further east than the southern Gotland basin. *M. leidyi* was present in Skagerrak and Kattegat from July to March, and the population densities were larger in Skagerrak and Kattegat (1.16 ± 1.70 ind. m^{-3}) than in the Baltic Proper (0.02 ± 0.04 ind. m^{-3}). The highest densities of up to 13.4 ind. m^{-3} were recorded in Kattegat in October 2009. Haraldsson *et al.* [28] suggested that transport of *M. leidyi* by advection from "presumably the North Sea" was the main cause for the ctenophore's occurrence in the Baltic Proper where low salinity prevents reproduction and local recruitment [29].

Between mid-December 2011 and mid-January 2012, an unusual mixture of ctenophores was observed in the inlet to Kerteminde Fjord (Great Belt), namely the native species *Pleurobrachia pileus* and *Bolinopsis infundibulum* along with their predator *Beroe cucumis*, and further, *Mnemiopsis leidyi* along with two other non-native predators on zooplanktivorous ctenophores, *B. ovata* and *B. gracilis* [3]. The presence of the mixture of ctenophores in the Great Belt correlated with replacement of Baltic Sea water with Kattegat water. *B. ovata* is known as the natural predator of *M. leidyi* and may be expected to follow the spreading of its natural prey. So far, however, the distribution and densities of *M. leidyi* in Limfjorden [20] [21] and other Danish waters do not seem to have changed since the arrival of its natural predator.

5. Occurrence in the Central Baltic Sea

The distribution and abundance of *Mnemiopsis leidyi* in the central Baltic Sea

(Bornholm Basin, **Figure 2**), which is the most important spawning ground for especially Eastern Baltic cod (*Gadus morhua*), but also sprat (*Sprattus sprattus*) [30], has been studied rather intensely [30] [31] [32] [33]. In November 2007, Huwer *et al.* [30] found that individuals of *M. leidyi* in the central Baltic were small (body length < 2 cm) and patchily distributed. The highest densities occurred at 40 to 60 m water depth around the halocline, and the highest abundances were found north and west of Bornholm, but they were low compared to the densities observed in Limfjorden [9], and the estimated predation impact on zooplankton by *M. leidyi* was negligible. Four months later the same area was investigated, and the highest population densities were now observed in somewhat deeper water (90% of specimens registered below 70 m) with higher temperatures, and an observed decrease in mean size from 18.6 ± 4.9 mm in November 2007 to 10.5 ± 7.6 mm in March 2008 was interpreted as the possible outcome of a new generation, although the smaller mean size could also have been caused by starvation during winter-time [31]. In a more recent study, Schaber *et al.* [32] investigated the seasonal changes in densities and distribution of *M. leidyi* in the central Baltic Sea from April 2007 to May 2010. A clear seasonal pattern was seen: highest densities in spring and autumn, and absence or only sporadic appearance of *M. leidyi* during summer. The vertical distribution of *M. leidyi* showed that it was mostly confined to water layers below the permanent halocline, and Schaber *et al.* [32] suggested that food limitation plays a major role in the decline of *M. leidyi* in the central Baltic Sea during summer, and while they considered a self-sustaining population unlikely, they stated that *M. leidyi* is "most likely re-introduced" every year. Schaber *et al.* [33] investigated the temporal and spatial overlap of *M. leidyi* and eggs and larvae of cod and sprat in order to assess the potential impact of the new invader on two of the most important Baltic fish stocks. The spatial overlap between *M. leidyi* and fish eggs and larvae was found to be low for most of the period observed, although situations with high overlaps were detected, for example for sprat larvae and cod eggs in spring, but on a general level it was concluded that *M. leidyi* "presently does not have a strong impact" [33].

6. Origin and Spreading

Recent genetic analyses have revealed some of the possible origins and spreading of *Mnemiopsis leidyi* [1] [34] [35] [36]. Thus, *M. leidyi* probably entered the Black Sea in ships' ballast water from the Gulf of Mexico in the 1980s; the subsequent spreading of *M. leidyi* into the Sea of Azov was probably via the natural connection between these seas, whereas further spreading into the Caspian Sea may have been with ballast water from the Volga-Don canal ([35] and references therein). The more recent spreading of *M. leidyi* to North European waters originated from New England, possibly Narragansett Bay, and an almost direct transport of individuals has been suggested to be responsible for the introduction of *M. leidyi* into the Baltic Sea, whereas the North Sea was either colonised secondarily from the Baltic Sea, or *M. leidyi* came directly with ballast water to e.g. Hamburg or Rotterdam harbours from the east coast of the USA [1]. Bolte *et al.* [36] studied the *M. leidyi* populations in the North and Baltic Seas by analysing genetic changes over 3 years (2008-2010) and found that there was apparently limited gene flow between the North Sea and the western Baltic Sea, and successful reproduction in both areas. But in the eastern central Baltic Sea (Bornholm Basin), the genetic diversity decreased during the study period, indicating that *M. leidyi* in this area is a sink population. However, the occurrence and spreading of *M. leidyi* in Danish and adjacent waters is still rather unknown as it appears from the following.

Figure 2 shows the directions of main surface currents in the North Sea. It may be assumed that the northward directed coastal currents from the English Channel up along the Dutch and Danish west coasts [5] [11] [16] [37] ensure that *Mnemiopsis leidyi* re-invade Limfjorden from the North Sea every year (via the Jutland current that flows northwards along the Danish west coast) through Thyborøn Canal [20], see **Figure 2**. Further, this northwards current also carries *M. leidyi* to e.g. Gullmarsfjorden [38] and the coastal waters at Tjärnö [39] on the Swedish west coast, and further northwards to Oslofjord [40] and Hardangerfjord [37] on the Norwegian west coast. A minor part of the more saline North Sea water, which mixes with Atlantic water in Kattegat, flows southwards below the less saline outflowing Kattegat water [41]. It is unknown to what degree *M. leidyi* in this way may be brought into the inner Danish waters [28], and likewise, it remains uncertain if *M. leidyi* may be brought into the Baltic Sea via the Kiel-Canal which connects the North Sea with the Kiel Bight [6] [42] [43], or if *M. leidyi* is occasionally released with ballast water from various ports or native habitats, resulting in mixed populations [11].

7. Monitoring and Management

More in-depth knowledge about *Mnemiopsis leidyi* is of importance, not only for a general understanding of how this invasive ctenophore influences the pelagic dynamics in marine ecosystems, often causing strong trophic cascades [38], but also for marine monitoring programs. Existing monitoring programs that routinely use phyto- and zooplankton as parameters to assess the environment have so far not been sufficiently aware of the role of the often extremely high number of *M. leidyi* in especially eutrophicated and overfished areas. As it appears from the present review of observations in Limfjorden, *M. leidyi* may often significantly reduce the zooplankton biomass (see, [18] Figure 4 therein; [17] Figure 5 therein; [20] Figure 7 therein). Therefore, variations in both phyto- and zooplankton abundance may remain incomprehensible without complementary knowledge about the predation impact of *M. leidyi* on zooplankton, which may be strongly reduced releasing the grazing impact on the phytoplankton which subsequently bloom [19] [38]. One consequence of this is that environmental and fishing monitoring programs should include observations of *M. leidyi* (and other gelatinous zooplankton) to allow for an assessment of their effects, as emphasised by Riisgård *et al.* [19] [21]. So far, none of the Danish environmental vessels have been put into action for monitoring the spreading and development of *M. leidyi* populations and indicative of this lack of responsibility is the fact that without a generous charge-free aid of the Danish Naval Homeguard probably no quantitative studies would have been possible in Limfjorden (**Figure 3**).

In 2012, Denmark adopted the Ballast Water Management Convention, which will enter into force in September 2017 (www.dnvgl.com/bwm). This will mark a milestone towards stopping the dispersal of *Mnemiopsis leidyi* and other invasive species in Danish waters. Thus in the future, ships must efficiently treat their ballast water to avoid discharge of living organisms transported over long distances. Knowledge of source populations and spreading ways of *M. leidyi* is necessary for understanding its invasion success and predation impact, but such knowledge is also a prerequisite for rational monitoring and effective management of ballast water. Now, 10 years after invasion into Danish waters by *M. leidyi*, such desirable knowledge is still absent. Marine invasive species are monitored by the Danish Environmental Protection Agency according to the national monitoring program, called NOVANA, which has conventional plankton monitoring stations for both the Water Framework Directive (EU directive 2000/60/EC) and the Marine Strategy Framework Directive (EU directive 2008/56/EC). So far however, *M. leidyi* has not been recorded in the monitoring databases [44]. But from mid-2017 NOVANA will be supplemented with marine

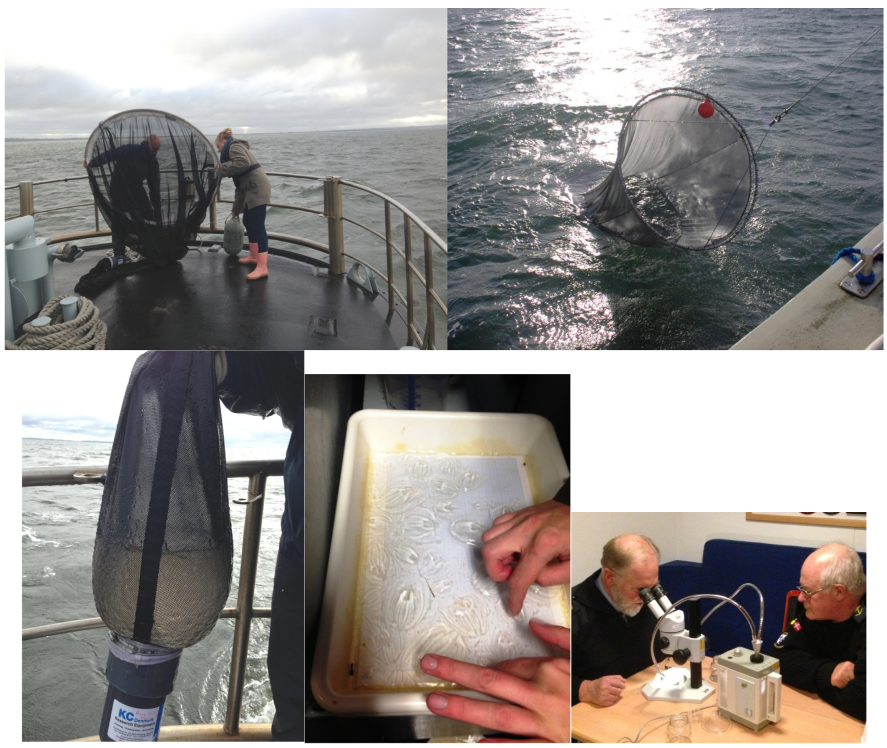

Figure 3. *Mnemiopsis*-research cruise in Limfjorden with the Danish Naval Homeguard in September 2014. Photo: Hans Ulrik Riisgård.

sampling for investigation of a number of invasive species, among these *M. leidyi*, by detecting environmental DNA (*i.e.*, eDNA; [45]) using species-specific setups that are capable of distinguishing between eDNA shed from invasive species and other sympatric species. The method (described by Thomsen *et al.* [46], Sigsgaard *et al.* [47]) will involve development and validation of multiple species-specific setups that can detect some 20 invasive species in Danish waters. Furthermore, the NOVANA program will begin to monitor high-risk harbors for introductions of invasive species by using both conventional methods and screening for eDNA (Ulrik Christian Berggreen and Steen Wilhelm Knudsen, pers. comm.). This commendable initiative may hopefully soon help to disclose some of the many possible ways of spreading *M. leidyi* in Danish and adjacent waters.

8. Conclusion

Ten years after the arrival of the alien invasive *Mnemiopsis leidyi* in Danish waters, we still have no overview of its presence and the factors controlling it. In Limfjorden, *M. leidyi* thrives extremely well and the fjord-system (actually a sound) functions as a nursery for *M. leidyi,* spreading into the Kattegat and adjacent waters. Predation by *M. leidyi* causes marked reductions in zooplankton biomass and presumably poor feeding conditions for juvenile herrings and sprats in Limfjorden, but no studies have so far documented the effect of this interspecific competition for zooplankton. Only few sporadic observations of *M. leidyi* have been made in Kattegat and Great Belt. In the central Baltic Sea (Bornholm Basin), the predation impact on zooplankton by *M. leidyi* seems to be negligible; food limitation may explain its decline during summer, and it is likely re-introduced every year. *M. leidyi*'s natural predator, *Beroe ovata*, was observed in Danish waters for the first time in 2014, but it has not yet caused documented changes in the number and distribution of *M. leidyi*. The coastal current of North Sea water up along the Danish west coast ensures that *M. leidyi* every year re-invade Limfjorden, but this current also carries *M. leidyi* to the Swedish and Norwegian coasts, and a minor part of the water enters the Kattegat below the Baltic outflow water. But the importance of this entry of *M. leidyi* into inner Danish waters is still unknown. Likewise, it remains uncertain if *M. leidyi* is brought into the Baltic Sea via the Kiel-Canal, or if *M. leidyi* is occasionally released with ballast water from various ports. Danish environmental vessels have not been put into action for monitoring the spreading and development of *M. leidyi* populations, and without the aid of the Danish Naval Homeguard probably no studies would have been possible in Limfjorden and Great Belt. Knowledge of source populations and spreading methods of *M. leidyi* is needed for understanding its invasion success. Such knowledge is also a prerequisite for rational monitoring and effective management of ballast water. Nevertheless, the Danish national monitoring programme still does not include gelatinous zooplankton, but from mid-2017 the monitoring programme (NOVANA) will be supplemented with marine sampling for investigation of invasive species, among these will be *M. leidyi*, by detecting environmental DNA (eDNA).

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