

# The non-indigenous ctenophore *Mnemiopsis leidyi* in the southern North Sea: Ecological and socio-economic effects related to its trophic position and the current distribution of gelatinous zooplankton

Vansteenbrugge Lies

ILVO, Ankerstraat 1, 8400 Oostende, Belgium  
E-mail: [lies.vansteenbrugge@ilvo.vlaanderen.be](mailto:lies.vansteenbrugge@ilvo.vlaanderen.be)

In recent years, abundances of gelatinous zooplankton are thought to have increased all over the world, resulting in jellyfish-dominated ecosystems and food webs. This trend, also referred to as 'jellification', is mainly based on a few local case studies and media-driven public perception, because long-term jellyfish datasets are scarce. Sudden increases in jellyfish densities (blooms) are a common life cycle characteristic, mainly driven by natural fluctuations in the climate. However, certain anthropogenic pressures, such as overfishing, eutrophication, non-deliberate transport of non-indigenous species can be correlated with varying jellyfish abundances. Moreover, gelatinous zooplankton blooms can directly interfere with anthropogenic activities, for example by clogging and rupturing of commercial fishing nets, by stinging beach tourists or by killing fish in sea farms. To be able to manage and reduce the potential problems and economic costs related to jellyfish outbreaks, understanding the mechanisms driving these outbreaks is imperative.

In the 1980s, the ctenophore *Mnemiopsis leidyi* A. Agassiz 1865, indigenous to the Atlantic coast of North and South America, was introduced in the Black Sea through ballast water of ships. The densities of this invasive species rapidly increased in the Black Sea, and in addition to overfishing and eutrophication led to a collapse of the major fisheries, causing vast ecological and socio-economic losses. Consequently, the first observations of *M. leidyi* in northern European marine waters in 2005, and the subsequent sightings of this non-indigenous ctenophore in Belgian marine waters in 2007 caused the appropriate concern. This PhD thesis, as part of the Interreg Iva 2 Seas MEMO project, aimed to assess the structural and functional role of the non-indigenous ctenophore *Mnemiopsis leidyi* in the southern North Sea. More specifically, we focussed on (1) the current distribution of *M. leidyi* in Belgian marine waters, the adjacent ports and the Westerschelde estuary, related to other gelatinous zooplankton, (2) the trophic ecology and interactions of *M. leidyi* in the planktonic food web, (3) the potential ecological and socio-economic effects of the presence of *M. leidyi* and other gelatinous zooplankton in these waters, and (4) the overall threat of *M. leidyi* and the implications for non-indigenous species' management.

After a general introduction (**Chapter 1**) on jellyfish and gelatinous zooplankton, the potential introductory pathways of invasive species and the life cycle characteristics of *M. leidyi*, the data and results are presented in seven chapters. Different approaches were used to tackle the research questions and objectives, including field studies, experimental and laboratory work, database analyses and public questionnaires. In this PhD study, the term 'gelatinous zooplankton' was narrowed down to the planktonic medusa phase (jellyfish) of the phylum Cnidaria (classes Hydrozoa and Scyphozoa) and the phylum Ctenophora.

In the southern North Sea, long-term data on gelatinous zooplankton are scarce, which is partly driven by the difficulties to sample and preserve these often 'fragile' organisms, *M. leidyi* in particular. Therefore, in **Chapter 2**, methodological issues concerning sampling and preservation were investigated. We focused on two different types of plankton nets: a WP2 net (mesh size 200  $\mu\text{m}$ ) and ring trawl net (mesh size 1000  $\mu\text{m}$ ). Based on their different mesh size and way of deployment (vertical versus undulating trawl), we evaluated whether they can be compared in terms of *M. leidyi* density and size distribution. *Mnemiopsis leidyi* densities from 245 sampling events were analysed according to net type and revealed that WP2 nets do not provide a good estimate of its presence compared to ring trawl nets. Moreover, when *M. leidyi* was present in both nets, much larger density estimates were found by the WP2 net ( $45.2 \pm 114.0 \text{ ind.m}^{-3}$  for WP2 net versus  $12.8 \pm 28.5 \text{ ind.m}^{-3}$  for ring trawl net). The ring trawl net gave a good overview of adult population structure, but may underestimate some of the small ctenophores. Consequently, both the filtered volume and the mesh size largely determine the catch. We also tested different preservation solutions and methods with respect to morphological and genetic identification of *M. leidyi* and in function of stable isotope analyses. From our experiments it became clear that unpreserved samples are preferred for any type of analysis. However, in many situations, direct identification in the field is not possible and preserving the sample is inevitable. Then, short-term preservation in

Lugol's solution or RCL2® may provide a good alternative, but shrinkage was observed in both preservatives. For stable isotope analyses, different preservation methods resulted in significant differences in both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , which should be considered when comparing different isotopic compositions. The findings and recommendations formulated in this study should be considered in future *M. leidy* monitoring. Zooplankton samples collected during this PhD were analysed on board and *M. leidy* was morphologically identified and measured alive (except for Tentaculata larvae which were genetically identified).

The discovery of *M. leidy* in Belgian waters in 2007 created a unique opportunity to enhance our knowledge on the distribution of gelatinous zooplankton in the southern North Sea (**Chapter 3**). Monthly and seasonal CalCOFI ring trawl plankton net samples (mesh size 1000  $\mu\text{m}$ , undulating trawl) from the Belgian part of the North Sea and the adjacent Westerschelde estuary were gathered between March 2011 and February 2012. The gelatinous zooplankton in these samples consisted of three Scyphozoa, three Ctenophora and 27 Hydrozoa taxa, including three non-indigenous species: *M. leidy*, *Nemopsis bachei* and *Lovenella assimilis*. In an addendum (Addendum II), we also described the re-discovery of larval mantis shrimp (*Rissoides desmaresti*), which has not been observed in the Belgian part of the North Sea since 1913. Average gelatinous zooplankton densities reached up to 18 ind. $\text{m}^{-3}$  near the coast, gradually declining towards the open sea, while in the brackish Westerschelde, average densities remained below 3 ind. $\text{m}^{-3}$ . Gelatinous zooplankton densities were highest in summer and autumn, and the ctenophore *Pleurobrachia pileus* and the hydromedusa *Clytia* sp. were present year-round and at every location. Gelatinous zooplankton densities never outnumbered the non-gelatinous zooplankton densities from the CalCOFI net. Due to the larger mesh size (1000  $\mu\text{m}$ ) of this net, only the larger fraction of the zooplankton is captured. The spatial and temporal distribution patterns seemed to be mainly driven by temperature (season) and salinity (location). In terms of population dynamics, the predatory ctenophore *Beroe* sp. followed the three reproductive cycles of its prey *P. pileus*, but may profit from the high abundances of *M. leidy* in summer and autumn by reaching higher densities. This study provides a firm baseline to evaluate potential gelatinous zooplankton increases in the Belgian part of the North Sea and the Westerschelde estuary.

The analysis of the spatio-temporal distribution and population dynamics of *M. leidy* in the southern North Sea and its main coastal ports (**Chapter 4**) revealed that *M. leidy* occurred from August to December, but was never found more than 30 km offshore. Densities were generally low (average  $0.8 \pm 2.8$  ind. $\text{m}^{-3}$ ) compared to other invaded ecosystems in Europe (densities up to 867 ind. $\text{m}^{-3}$ ). Highest densities of *M. leidy* were found in the semi-enclosed basin in the port of Oostende (18.4 ind. $\text{m}^{-3}$ ) and the Westerschelde estuary (1.9 ind. $\text{m}^{-3}$ ). The presence of larvae and the sudden appearance of high numbers across the size distribution in August indicated that ports and estuaries may act as sources, populating the adjacent coastal (sink) areas. By means of a zero-inflated negative binomial regression model, the observed variation in *M. leidy* densities was related to temperature (highest densities when temperature starts to decrease), wave height (higher densities in low energetic systems) and dissolved oxygen concentrations (higher densities at low oxygen concentrations). Although *M. leidy* densities remained relatively low since its first appearance in Belgian waters in 2007, a permanent *M. leidy* population has established in the southern North Sea. As outbreaks may happen with only small changes in environmental parameters, further monitoring of this notorious non-indigenous species is recommended.

Knowledge on the diet of *M. leidy* and its interactions with other components of the pelagic food web will largely contribute to assess the impact of this non-indigenous species on the ecosystem. Using both stable isotope (SI;  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) and fatty acid (FA) analyses, we revealed spatial and temporal variation in the trophic ecology of *M. leidy* in different ecosystems in the southern North Sea (**Chapter 5**). Based on the isotopic composition, we found that spatial differences were largely driven by variation at the base of the food web rather than diet changes of *M. leidy* in the different ecosystems. Temporal variation in *M. leidy* SI composition was also influenced by shifting baseline values and driven by seasonal changes in the associated plankton communities. In this chapter, we provide the first data on the FA composition of *M. leidy* as compared to FA concentrations of two other (indigenous) ctenophores. The total FA concentration of *M. leidy* was three to four times lower compared to *Pleurobrachia pileus* and *Beroe* sp., categorising this non-indigenous ctenophore as a lipid-poor organism. Trophic interactions between *M. leidy* and the two co-occurring ctenophores (*P. pileus* and *Beroe* sp.) showed considerable resource differentiation, which could be the result of competition or both ctenophores could have different diets. A mixture of zooplankton was identified as potential food source for *M. leidy*. FA markers supported the carnivorous diet of *Beroe* sp., but its SI composition did not confirm it as a predator of *M. leidy*.

The feeding ecology of *M. leidy* was further investigated as its invasive success is partly related to a broad and flexible planktivorous diet. In **Chapter 6**, we investigated the feeding rates and carbon assimilation of *M. leidy* by means of grazing experiments with a pelagic diatom species

*Phaeodactylum tricornutum* and three potential mesozooplankton prey species: nauplii from brine shrimp *Artemia salina*, a copepod *Acartia tonsa*, and eggs and larvae of European sea bass *Dicentrarchus labrax*. Clearance rates were on average  $0.2 \pm 0.1 \text{ L.mL}^{-1} \cdot \text{h}^{-1}$ , with no significant differences in clearance rates between prey type or prey size. The assimilation of carbon by *M. leidyi* for these different prey types was determined using  $^{13}\text{C}$  tracer experiments. Highest carbon assimilation was observed for *Acartia* and sea bass larvae (most efficiently assimilated), and lowest for the pelagic diatom *P. tricornutum*. To further elucidate the prey-dependent variation in carbon uptake, we investigated the effect of each prey type in terms of fatty acids as a proxy for food quality. The consumption of sea bass larvae, characterised by higher levels of DHA (an essential fatty acid), resulted in significantly higher FA concentrations in *M. leidyi*. As *M. leidyi* does not convert excess food into storage lipids, survival, growth and reproduction are likely enhanced by the higher food quality, which might contribute to its invasive success. As global warming may result in an earlier appearance of *M. leidyi* and thus temporal overlap with high quality prey such as fish larvae, a substantial impact on the ichthyoplankton community in the southern North Sea might be expected.

The third aim of this PhD study was to determine the potential ecological and socio-economic effects of the presence of *M. leidyi* in Belgian waters. For the latter, we needed to broaden our scope by focusing on the impact of all prevailing jellyfish on beach tourism in Belgium, as *M. leidyi* is too small and fragile, and thus rarely noticed by tourists (except for divers). In **Chapter 7**, we examined to what extent the main jellyfish messages in the Flemish media corresponded with the knowledge and perception in the tourism sector along the Belgian coast. We searched Flemish newspapers for jellyfish-related articles issued between January 2000 and September 2012 and executed questionnaires at the Belgian coast in the summer of 2012. The number of Flemish newspaper articles increased from less than 5 in 2000 to 27 articles in 2010. Almost 75 % of these articles reported on the causes and economic consequences of jellyfish blooms, and many articles mentioned the dramatic consequences of stinging, poisonous and invasive species. The analysis of the questionnaires showed that the perception of beach tourists on jellyfish is only partly driven by the general media (mainly related to the causes of jellyfish blooms), while personal experience (e.g. stinging, slimy organisms) was at least an equally important driver. As public perception is a key driver for certain policy decisions, integrated coastal zone managers should consider the provision of simple and good information concerning jellyfish (e.g. billboards or aquaria) at the beach. The results of this socio-economic study might serve as a baseline for future citizen science programs.

Finally, the main results of this PhD study were discussed in a broader perspective to manage the introduction and presence of non-indigenous or invasive species (**Chapter 8**). We performed a risk assessment for *M. leidyi* in the southern North Sea by means of the online Harmonia+ tool, which generates exposure (introduction, establishment and spread) and impact (on the environment and human activities) scores. An overall risk of 0.286 was calculated for the non-indigenous ctenophore *M. leidyi* in the southern North Sea, which is considered to be low. Up to 2012, *M. leidyi* showed a clear seasonal outbreak between summer and autumn. Relatively high densities (up to  $18 \text{ ind.m}^{-3}$ ) were only observed in the ports, which are considered to be of lower ecological value compared to the 'richer' coastal zone or Westerschelde estuary, where *M. leidyi* densities mostly remained below  $1 \text{ ind.m}^{-3}$ . The combination of periods with unfavourable environmental conditions, the diverse gelatinous zooplankton community (potential competition) and the presence of predators such as *Beroe* sp., probably has limited the success of *M. leidyi* in the southern North Sea. However, this PhD study (including the more recent observations in 2014) showed that the population of *M. leidyi* is fully established in the different southern North Sea ecosystems. Therefore, *M. leidyi* should remain under close observation by means of regular monitoring surveys, and management actions should not be postponed in order to safeguard the current ecosystem services. As such, trying to keep the population under control is most probably the only way forward for a proper management of this non-indigenous species. Ratification of the Ballast Water Convention by all countries around the world is another key issue to at least prevent the introduction of new species and to avoid potential re-introduction of *M. leidyi* in our waters. In light of the Marine Strategy Framework Directive, the early detection (and subsequent eradication) of non-indigenous species (many of them appearing in the water column as some sort of zooplankton stage), for example by means of automated sampling tools, needs to be promoted. This PhD study is a baseline for future (gelatinous) zooplankton monitoring in the Belgian part of the North Sea and Westerschelde estuary (and by extension the southern North Sea).