Summary

Gelatinous zooplankton are an understudied group in many areas. The arrival of a notorious invasive species, the ctenophore *Mnemiopsis leidyi* in Dutch coastal waters instigated a series of sampling programmes and triggered a renewed interest in the ecology of this diverse group of animals. The main goal of this thesis is to investigate the present spatial and temporal distribution of gelatinous zooplankton species in Dutch coastal waters. How are these influenced by the many environmental changes observed in the area?

The thesis is divided into two parts: a first part focused on investigating changes in gelatinous zooplankton species composition, seasonal patterns and abundance and a second part focused on gaining insight in the mechanisms that make *M. leidyi* such a successful invasive species.

Questions asked at the start of the study were: What is the present spatial and temporal distribution of gelatinous zooplankton species in Dutch coastal waters? How are these influenced by the many environmental changes observed in the area in the past? What are the bottom-up and top-down controlling mechanisms of gelatinous zooplankton in Dutch coastal waters? What is the grazing pressure on the zooplankton community, and is there much competition with fish? How will projected climatic and other anthropogenically induced changes influence gelatinous zooplankton populations and their importance in Dutch coastal waters?

Gelatinous zooplankton in Dutch coastal waters

As a first step, available studies and data on gelatinous zooplankton in Dutch coastal waters were reviewed. In the Marsdiep area of the western Wadden Sea, the NIOZ Royal Netherlands Institute for Sea Research has operated a kom-fyke fish trap, a type of passive fishing gear. From 1960 onwards the catch of this kom-fyke was recorded each day for the spring, autumn and sometimes summer season. Catches of jellyfish in the kom-fyke were also counted and recorded. This unique 50 year time series was analysed in Chapter 2 where changes in phenology, abundance and species composition of Scyphozoan jellyfish are related to changing environmental conditions. All species appeared earlier in the year in recent decades, which at least for one species (*Aurelia aurita*) was related to increasing winter temperatures. Abundance trends could not be related to changing environmental conditions because of high variation in the data, which could imply that population
regulating mechanisms operate mainly during the sessile polyp stages.

The location of these sessile polyp stages of Scyphozoans is unknown for many species which is why in Chapter 3 the distribution, species composition and population structure of jellyfish polyps is investigated by sampling a variety of different natural and artificial substrates in the southern North Sea and identify them using molecular markers. Unfortunately all polyps that were found in nearshore and offshore areas belonged to *Aurelia aurita* and thus the location of the other species’ polyps remains unknown. The high number of *A. aurita* polyp samples did allow us to perform the first study on population structure of Scyphozoans based on polyps and not medusae. *A. aurita* polyps showed population subdivision whereby polyps from the central North Sea differed from those in the other areas.

The most recent quantitative sampling programmes focused on gelatinous zooplankton in both the Dutch Wadden Sea as well as the estuaries of Zeeland dated from the 1980s, which is before *Mnemiopsis leidyi* was present. In 2009 the 1980s sampling programme in the Marsdiep area of the western Wadden Sea was repeated using similar methods and stations. In Chapter 4 we show that nowadays *Mnemiopsis leidyi* is present in high densities in the area. Following this, the western Wadden Sea monitoring programme was continued in 2010–2012 and species composition, seasonal patterns and zooplankton grazing pressure are compared with those in the 1980s in Chapter 5. Because of the introduction of *M. leidyi* the overall importance of gelatinous zooplankton as predators has increased. *M. leidyi* is now the most abundant gelatinous zooplankton species in near-shore and inshore Dutch coastal waters. In the 1980s grazing pressure on the zooplankton by gelatinous predators was low in summer and autumn but in 2009–2012 high densities of *M. leidyi* exerted a high grazing pressure on the zooplankton, with a peak in September. This is a major change in the Wadden Sea pelagic ecosystem, which has likely occurred in the estuaries of Zeeland as well. It appears that *M. leidyi* has found an empty or under-utilised niche in the Wadden Sea pelagic ecosystem.

**The invasion success of *Mnemiopsis leidyi* investigated**

In Chapter 6 modelling and data analysis is combined to study the energy budget of *M. leidyi* over its full life-cycle using Dynamic Energy Budget (DEB) theory and literature data to investigate the response of different life stages to changes in food and temperature. An analysis of data obtained at temperatures ranging from 8 to 30 °C suggests that the optimum thermal tolerance range of *M. leidyi* is higher than 12 °C. Furthermore *M. leidyi* seems to undergo a so-called metabolic acceleration after hatching. Intriguingly, the onset of the acceleration appears to be delayed and the data do not yet exist which allows determining what actually triggers it. It is hypothesised that this delay confers a lot of metabolic flexibility by controlling generation time.

Although *Mnemiopsis leidyi* can tolerate a broad range of temperatures and salinities in its native range, low salinity limits its range expansion in parts of
northern Europe. Large *M. leidyi* blooms have been observed in the brackish North Sea Canal near Amsterdam in the Netherlands, at salinities considered too low for successful reproduction. In Chapter 7 the influence of salinity as a factor limiting the spread of *M. leidyi* in invaded areas is studied in a common-garden experiment where *M. leidyi* from the low salinity Amsterdam population and a nearby marine population were acclimatised and raised at two salinity levels. This experiment shows that *M. leidyi* can complete its entire life cycle at a salinity of 8, albeit with much higher mortality than at a salinity of 33. Genotyping of the animals surviving at the end of the experiment revealed high differentiation between sub-populations of origin. Within the Amsterdam sub-population high genetic differentiation was found. This is the first observation of a low salinity genotype of *M. leidyi* in Europe, which could spread to yet uninvaded areas where environmental parameters were previously thought to be limiting.

In Chapter 8 competition between *Mnemiopsis leidyi* and other zooplanktivorous species in the Wadden Sea is qualified by estimating diet overlap of fish, scyphozoans, hydromedusa, ctenophores, crustaceans and cephalopods of the western Wadden Sea using Stable Isotope Analysis. A cluster analysis showed that average $\delta^{13}$C and $\delta^{15}$N ratios of the invasive *M. leidyi* were similar to those of fish species of intermediate trophic level such as the glass goby *Aphia minuta*, the herring *Clupea harengus* and the horse mackerel *Trachurus trachurus*. Diet overlapped with that of most other gelatinous zooplankton species as well, such as the compass jellyfish *Chrysaora hysoscella*, the sea gooseberry *Pleurobrachia pileus* and the hydroid *Nemopsis bachei*. $\delta^{15}$N of *M. leidyi* was positively related to ctenophore size, suggesting that small ctenophores occupy a lower trophic level than large ones. At the beginning of the bloom period in August when almost the entire population consisted of larvae and juveniles there was no overlap in isotopic niche of *M. leidyi* with that of any other pelagic zooplanktivore. The period of high diet overlap with other consumers is also the period in which *M. leidyi* is least abundant. This suggests that at present, *M. leidyi* is not a significant competitor for other gelatinous zooplankton and fish species. During the bloom period of *M. leidyi* the abundance of competing species is low, suggesting that *M. leidyi* is using an unoccupied niche.

**The future of Dutch gelatinous plankton**

This thesis increases our understanding of gelatinous zooplankton phenology, abundance and species composition in Dutch coastal waters and provides tools such as the Dynamic Energy Budget model of *Mnemiopsis leidyi*, the application of fixation and preservation of *M. leidyi* in quantitative sampling and a common garden experiment to study the phenotypical response of different *M. leidyi* populations to differing environmental conditions. These tools can be applied in the study of gelatinous zooplankton in other areas as well.

Our study on sampling, identification and population structure of Scyphozoan polyps (Chapter 3) would be interesting to expand to a wider area and different habitat types as the location of polyps other than those of *Aurelia aurita* remains
unknown.

In **Chapter 9** an application of the Dynamic Energy Budget (DEB) model parametrised in Chapter 6 is presented. Using ecological modelling we show that *M. leidyi* ctenophores can be transported from the southern North Sea to the central North Sea and German Bight and subsequently, the DEB model predicts survival and reproduction of *M. leidyi* in the conditions experienced along the transport trajectory. This shows that Dutch coastal waters can be a source of *M. leidyi* for other western and northern European waters. The application of the DEB model yields some interesting predictions: larger *M. leidyi* ctenophores are more sensitive to decreases in food availability than smaller ctenophores but produce much more eggs under favourable food conditions, and at lower temperatures and lower food levels the predicted age at puberty (the moment allocation of energy to maturation stops and allocation to reproduction starts) is greatly increased. This could be a survival strategy for *M. leidyi* used to survive periods of low food availability. Both these predictions could be tested experimentally. The experiment of **Chapter 7** shows that reproduction, growth and metamorphosis of *M. leidyi* are different at lower salinity levels. Consequently, DEB parameters will likely also differ.

Concluding, the results in this thesis show that the introduction of *Mnemiopsis leidyi* in Dutch coastal waters has not yet had a large impact on the populations of native zooplanktivorous fish and plankton. However, as *Mnemiopsis leidyi* reproduction and growth is strongly related to temperature, climate induced warming could cause shifts in its phenology and blooms in periods or areas where temperature was previously limiting. Similarly, the finding of a *M. leidyi* genotype able to live at lower salinity levels could lead to blooms in unexpected locations. This means that continued monitoring of *M. leidyi* presence and abundance is important. Unfortunately, monitoring of zooplankton in Dutch coastal waters is lacking in coastal as well as inshore waters and blooms of *M. leidyi* or introductions of other invasive species are currently going unnoticed.