Flexible filter feeders
van Walraven, Lodewijk

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Chapter 9

Synthesis

Lodewijk van Walraven
The objective of this dissertation was to qualify and quantify the role of gelatinous zooplankton in Dutch coastal waters in the past, present and near future, with a focus on the invasive ctenophore *Mnemiopsis leidyi*. In this final chapter I will put our results in a bigger perspective, highlight the main findings and give suggestions for future studies.

In the first part, we reviewed the currently available knowledge on gelatinous zooplankton in the area. We performed additional sampling campaigns in the western Wadden Sea area and analysed available long-term time series. The introduction of the invasive ctenophore *Mnemiopsis leidyi* was the most important change in the gelatinous zooplankton community. This species and its impact on the pelagic ecosystem of Dutch coastal waters were thus the main focus of the second part of the manuscript.

The preceding chapters addressed the following research questions:

- 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?

**Main findings**

We show that changes have occurred in gelatinous zooplankton species composition and seasonal patterns in Dutch coastal waters (Chapter 2, 4 and 5). The Scyphomedusae have decreased in abundance, but this could not be linked to changes in environmental conditions because of large variation in catches. Seasonal patterns of some species are shifting to an earlier appearance or later disappearance as seasonal water temperatures increase. Scyphozoan polyps found in nearshore and offshore areas all belonged to *Aurelia aurita* and showed population subdivision. The location of the other species’ polyps remains unknown.

The overall importance of gelatinous zooplankton as predators has increased because of the introduction of *Mnemiopsis leidyi*. This species is now the most abundant gelatinous zooplankton species in nearshore and inshore Dutch coastal waters in summer and autumn. The year-round presence of *M. leidyi* in Dutch coastal waters, as well as the pattern of dispersion towards other north-western European areas suggests that Dutch coastal waters are a major source region for *M. leidyi* in north-western Europe. The finding of a genotype of *M. leidyi* that can
spawn at low salinity levels suggests that *M. leidyi* from Dutch waters can spread to a wider range of environments than assumed.

Changes in seasonal seawater temperature will likely change the phenology of most gelatinous zooplankton species, with increasing winter and spring temperatures leading to an earlier appearance and possibly bloom formation of Scyphozoa and *Mnemiopsis leidyi*. The increased overlap of the potential spawning window of *M. leidyi* with the zooplankton spring bloom could lead to a major increase in *M. leidyi* bloom magnitude and frequency and thus grazing pressure of the species on the zooplankton.

**Long term trends**

One limitation of the time series on jellyfish catches in the NIOZ kom-fyke that we analyse in Chapter 2 is that it is only a single station. A comparison of abundance trends in kom-fyke and ANEMOON foundation beach surveys (Fig. 9.1) shows that overall trends are similar and that also in the beach surveys there is a lot of variation between years. In both series *Aurelia aurita* is the most abundant species, followed by *Rhizostoma octopus*, *Chrysaora hysoscella* and *Cyanea* sp. A decrease in *A. aurita* abundance is seen in both series. *C. hysoscella* seems to be increasingly found in the beach surveys in recent decades but this trend is not seen in the kom-fyke data. There also appear to be several years where *C. hysoscella* was absent in the kom-fyke but present in the beach surveys. *Cyanea* sp. abundances in the beach surveys seem to be less variable in the most recent decade than in the years before but no clear trend is visible, similar to the kom-fyke surveys. *R. octopus* abundance shows a decrease in both time series. It seems thus that the general trends observed in the kom-fyke catches are also seen in the beach surveys of stranded jellyfish along the Dutch coast, but the absence of a species in the kom-fyke catches does not mean it was not present along Dutch shores in that year. The most common species of scyphomedusae, *Aurelia aurita* and *Rhizostoma octopus* have decreased in abundance in both time series.
Figure 9.1: Standardised \( \frac{N}{N_{\text{max}}} \) mean abundance of scyphomedusae in ANEMOON foundation beach-combing surveys at eight stations along the Dutch coast 1978–2013 (top row) and in NIOZ kom-fyke catches (bottom row). Abundance in the beach-comb surveys is scored in abundance classes (0, 1-9, 10-99, 100-999), so for comparison the average daily catches in the kom-fyke were log-transformed (base 10). Beach survey data is used with permission of the ANEMOON foundation.
No continuous long-term time series for gelatinous zooplankton other than scyphomedusae existed in Dutch coastal waters. Gelatinous zooplankton species composition, seasonal patterns and abundance in the Wadden Sea was studied in the early 1980s. For this thesis the 1980s sampling programme was repeated in 2009, initially for a single year and focused on *Mnemiopsis leidyi* (Chapter 4) but later extended to 2012 (Chapter 5). Compared to the 1980s, the abundance of most native gelatinous zooplankton species either showed no clear trend or had decreased.

**Importance of gelatinous zooplankton taxa as predators of zooplankton**

Scyphomedusae are the most conspicuous gelatinous zooplankters found in coastal waters, but how important are they as predators of zooplankton? In Fig. 9.1, Chapter 2 and Chapter 5 we show that the abundance of the main species of scyphomedusae, *Aurelia aurita* and *Rhizostoma octopus*, has decreased. The zooplankton clearance rates estimated for the most common species of Scyphomedusa, *Aurelia aurita*, in the western Wadden Sea were several orders of magnitude lower than those of *Mnemiopsis leidyi* and often also of *Pleurobrachia pileus* (Fig. 5.6). Scyphomedusae and hydromedusae are thus of minor importance as predators compared to ctenophores. *M. leidyi* is thus by far the most important species of gelatinous zooplankton in Dutch coastal waters, which is why the rest of this thesis focused mainly on this species.

**Impact of *Mnemiopsis leidyi* on ecosystems in Dutch coastal and inshore waters: present and future.**

**Predation by *Mnemiopsis leidyi***

**Impact on holoplankton**

As described in Chapter 5 the introduction of *M. leidyi* has lead to an increase in grazing pressure of gelatinous zooplankton compared to the 1980s, especially in late summer and autumn, a period when in the 1980s grazing pressure by gelatinous zooplankton was very low. This means that, rather than outcompeting local species, it appears that *M. leidyi* has found an empty or under-utilised niche in the Wadden Sea pelagic ecosystem.

*Mnemiopsis leidyi* densities and clearance rates estimated for *Mnemiopsis leidyi* in the western Wadden Sea in this thesis are some of the highest among invaded areas in north-western Europe, similar to those observed in Limfjorden *Riisgård et al.* (2012) and the eastern Wadden Sea *Kellnreitner et al.* (2013). Clearance rate estimates in this study are likely conservative, as mentioned by Purcell (2009); *Riisgård et al.* (2012) who used the same parameters. Several studies report higher clearance rates (*Colin et al.*, 2010; *Granhag et al.*, 2011). Actual grazing pressure of *Mnemiopsis leidyi* on zooplankton in the area might thus be higher.
Impact on bivalve larvae

In its native range, unlike scyphomedusae (Purcell, 1991a), *Mnemiopsis leidyi* is a known predator of bivalve larvae and can at peak densities remove an average of 20–89% of bivalve larvae from the water column (McNamara et al., 2010). In invaded areas, *M. leidyi* has been shown to feed on bivalve larvae as well (Granhag et al., 2011). It is thus interesting to see whether bivalve larvae are consumed by *M. leidyi* in the Wadden Sea as well. D-stage bivalve larvae cannot be identified to species level morphologically and to investigate species composition and seasonal patterns of bivalves in the plankton, species specific primers are used (Philippart et al., 2014). We developed a stomach content extraction method and combined this with molecular identification of bivalve larvae in extruded stomach contents (Box 5) to show that *M. leidyi* does indeed consume bivalve larvae in the Wadden Sea.

If clearance rates on bivalve larvae are comparable to those for copepods, *M. leidyi* grazing pressure on bivalve larvae would be significant during the periods of highest grazing rates in August–October (Fig. 5.6). The impact of ctenophore predation on bivalve larvae settlement will differ for different bivalve species, as each has a different spawning period (Philippart et al., 2014). *Macoma balthica*, *Cerastoderma edule*, *Mya arenaria* and *Mytilus edulis* peak spawning happens several months before the *M. leidyi* densities start to increase but peak spawning of *Crassostrea gigas* and *Ensis directus* overlaps with the period of highest *M. leidyi* grazing rates. Interestingly, these species are also invasive in the area.

Right now the highest densities and thus clearance rates of *Mnemiopsis leidyi* take place in summer and autumn. However, as discussed above, increasing temperatures could lead to earlier reproduction and bloom formation of *M. leidyi*, increasing the overlap with peak spawning of bivalves and with the general peak in mesozooplankton food availability (Fransz et al., 1991). The exceptional year of 2009 with blooms of *M. leidyi* already in June (Chapter 4) shows that this is indeed possible.

Top-down control of *Mnemiopsis leidyi* by predation?

Escape from natural predators, the “enemy release hypothesis” is a frequently given reason for why invasive species can rapidly increase in distribution and abundance in invaded areas (Keane and Crawley, 2002). It is not applicable to all invasions (Jeschke et al., 2012). When investigating whether enemy release contributed to the success and extent of an invasion, three arguments have to be considered (Keane and Crawley, 2002). Firstly, top-down control by predators is has to be an important regulating factor for the population. Secondly, predators need to have a greater impact on native than on invasive populations and thirdly, the invaders have to be able to increase their abundance and distribution in response to relaxed predation.

In the native range of the species, *Mnemiopsis leidyi* is predated upon by several predators (Purcell et al., 2001; Arai, 2005; Costello et al., 2012), the majority of which are also gelatinous animals (so-called “intraguild predation”, Purcell, 1991b;
The main predators of *M. leidyi* along the Atlantic coast of the US are the Scyphomedusa *Chrysaora quenquecirrha* (Purcell and Cowan Jr, 1995; Purcell *et al.*, 2001) and the ctenophore *Beroe ovata* sensu Mayer (Kremer and Nixon, 1976; Purcell and Arai, 2001). In the Chesapeake Bay area abundances of *C. quenquecirrha* and *M. leidyi* are often inversely related, suggesting predatory control of the ctenophores by the medusae (reviewed in Purcell *et al.*, 2001) and predation rates of *C. quenquecirrha* on *M. leidyi* can exceed the population growth potential of *M. leidyi* (Condon and Steinberg, 2008; Costello *et al.*, 2012). Similar predatory control may occur by the ctenophore *Beroe ovata*, but since it is less tolerant of lower salinities than *M. leidyi* the latter is sheltered from predation in the more shoreward, low saline areas (Purcell *et al.*, 2001).

In western Europe, *Mnemiopsis leidyi* is predated upon by native species of Scyphomedusae (*Cyanea capillata*, Hosia and Titelman, 2011) and ctenophores (*Beroe gracilis*, Hosia *et al.*, 2011). *B. gracilis* is smaller in size relative to *M. leidyi* but it can consume parts of larger prey by ingesting and biting off parts of the lobes of *M. leidyi* (Fig. 1.2). These predators occur in Dutch waters as well, along with other Scyphomedusae and *Beroe cucumis* (Chapter 5). In Chapter 5 we show that densities of native *Beroe* ctenophores did not show a clear increase after the introduction of *M. leidyi*. This suggests that predation by *Beroe* species is at present not controlling the *M. leidyi* population. As *Chrysaora hysoscella* is such an important predator of *Mnemiopsis leidyi* in the native range, it is interesting to see whether the native *Chrysaora* species in Dutch coastal waters, *Chrysaora hysoscella*, could control the *M. leidyi* population in a similar way. The cnidome (types of nematocysts that the species possesses) is similar for both species (Morandini and Marques, 2010) suggesting similar diets.

In Chapter 2 we show that last occurrence of *Chrysaora hysoscella* was related to summer seawater temperature and that the species is present longer in recent decades as average seawater temperatures have increased. Fig. 2.2 shows an increase in *C. hysoscella* catches in summer and autumn in the kom-fyke. In Fig. 9.1 yearly average *C. hysoscella* abundance in beach surveys seems to be increasing as well. The seasonal pattern of *M. leidyi* and *C. hysoscella* overlaps as well (see Fig. 5.4 in Chapter 5) so it is possible that the scyphomedusa is predating on the ctenophore but based on $\delta^{15}$N stable isotope analysis in Chapter 8 the trophic level of both species is almost equal and $\delta^{15}$N and $\delta^{13}$C ratios are mainly overlapping, suggesting that both species have similar diets.

In the Black Sea area *Beroe ovata* appeared more than a decade after the *Mnemiopsis leidyi* invasion, and *M. leidyi* biomass decreased after its introduction (Finenko *et al.*, 2003; Shiganova *et al.*, 2003), suggesting that predation by *Beroe ovata* is controlling the *M. leidyi* population to some extent. Where gelatinous predators are absent, such as in the Caspian Sea, the introduction of *M. leidyi* did have a bigger impact on the ecosystem (Roohi *et al.*, 2008, 2010). In this area a possible deliberate introduction of *B. ovata* was considered (Stone, 2005). Species identification of *Beroe* species is difficult and was found impossible for smaller specimens (Appendix B). As of 2015 *Beroe ovata* has only been observed at a single location in north-western Europe, in the Great Belt, Denmark (Shiganova *et al.*, 2014). *Beroe cucumis* specimens caught in the sampling performed for this
thesis were frequently examined for the presence of anastomosing diverticulae, the distinguishing feature of *B. ovata*, but these were never observed.

Considering the low density of native predators, the lack of an increase in *Beroe gracilis* densities following the *Mnemiopsis leidyi* introduction and the absence of *Beroe ovata* we consider the current potential for top-down control of *M. leidyi* populations in Dutch coastal waters to be low.

**Parasites of *Mnemiopsis leidyi***

Aside from predator release, the lack of parasites in invasive populations can also contribute to the abundance and spread of invaders (Torchin *et al.*, 2003).

The most conspicuous parasite of *Mnemiopsis leidyi* is the endoparasitic larva of the sea anemone *Edwardsiella lineata*. Infection by the parasite causes decreases in growth and fecundity. In the native range of *M. leidyi* prevalence of *E. lineata* can be very high and it has been suggested that the decline of the *M. leidyi* population in US waters in fall can be partly attributed to *E. lineata* infection (Bumann and Puls, 1996). While the parasite has been found in *M. leidyi* off the Swedish west coast in 2007 (Selander *et al.*, 2010), in five years of sampling (2009–2013) we have never observed *Edwardsiella* parasites in *M. leidyi* in Dutch coastal waters, making top-down control of the *M. leidyi* population in the area by these parasites currently unlikely.

**Dutch estuaries as a source for *Mnemiopsis leidyi* in Europe**

Figure 9.2: (a) Final concentration of particles (N m\(^{-3}\)) relative to an assumed initial concentration of 1.0 (N m\(^{-3}\)) for the eastern Scheldt July simulation, Delft model; (b) similar for the western Scheldt. Reproduced from van der Molen *et al.* (2015).
In *van der Molen et al.* (2015) we investigated dispersal of *Mnemiopsis leidyi* from the Dutch Delta area to the North Sea using two different hydrodynamic models. Dispersal from the Eastern Scheldt and Western Scheldt areas was investigated using a high resolution 3-D particle tracking model: the Delft3D model. A homogeneous particle distribution as well as a particle distribution based on in-situ observations of ctenophore density in September 2012 were used as starting conditions. When the model was ran for three months, a clear pattern of retention in the back of the estuaries could be seen (Fig. 9.2) but part of the particles are also dispersed into the North Sea. This means that there is enough retention in the area to retain an overwintering population.

Long-distance transport from this area was investigated with a lower resolution model for the North Sea area, the GETM–ERSEM–BFM (3-D General Estuarine Transport Model–European Regional Seas Ecosystem Model–Biochemical Flux Model) with particle tracking (General Individuals Transport Model – GITM). The GETM-ERSEM model reproduction model coupled to a biogeochemical model

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**Figure 9.3:** Density of particles on the model grid (number of particles per grid cell). (a) on day 1 of the simulation (1 June 2008); (b) on day 61 (31 July 2008); (c) on day 121 (29 September 2008); (d) on day 240 (25 January 2009). Reproduced from *van der Molen et al.* (2015).
modeled survival and reproduction of particles using *Mnemiopsis leidyi* physiological parameters from literature data, and the GITM model modeled the transport of the particles. The simulation was started on 31 July 2008 and ran for 240 days to simulate transport from the bloom period over the winter. This simulation showed that the majority of particles were transported to the north-east as far as the west coast of Denmark. This matches very well with observations of *M. leidyi* in the North Sea in winter described in David et al. (2015). The simulation suggests that the Dutch estuaries are a source of *M. leidyi* for coastal areas to the north-east such as the Wadden Sea, German Bight, Limfjorden, Skagerrak and Kattegat. It is likely that the same holds true for the Wadden Sea as well, as in Chapter 4 and 5 we show that *M. leidyi* is present year-round in this area.

Dutch coastal waters are likely not the sole source for *Mnemiopsis leidyi* in areas to the northeast, as the species is observed in more southern locations as well: the Belgian North, several Belgian ports (Van Ginderdeuren et al., 2012; Vansteenbrugge et al., 2015a,b) and also in the French part of the eastern English Channel and the ports of Le Havre (Antajan et al., 2014).

Habitat suitability of the open North Sea area for *M. leidyi* survival and reproduction was investigated in two concurrent studies (Collingridge et al., 2014; David et al., 2015). Both these studies predict highest survival and abundances in nearshore areas, in the German Bight, west of Denmark and Collingridge et al. (2014) also in Skagerrak and Kattegat.
Figure 9.4: Results of DEB model simulations. (a) grey: carbon mass at stage transitions at $f = 1$. Below are presented the ages at each stage transition for three different ingestion levels ranging from 1 to 0.3. (b) Age at puberty as function of temperature. (c–d) Reproduction rate at puberty and at ultimate mass respectively as function of temperature. (a–d) Simulations are for three ingestion levels: $f = 1$ (solid line), $f = 0.45$ (dashed line) and $f = 0.3$ (dotted line). Reproduced from van der Molen et al. (2015).
Survival, growth and reproduction of *M. leidyi* in the southern North Sea area

**The role of food and temperature**

In van der Molen et al. (2015) the Dynamic Energy Budget (DEB) model that was parametrised in Chapter 6 was used to predict survival and reproduction of both adult and juvenile *Mnemiopsis leidyi* in the North Sea. Using the food density and temperature experienced by a particle in the GETM-ERSEM-GITM model simulation (Fig. 9.3) it is shown that larger ctenophores are more sensitive to decreases in food availability than smaller ctenophores but produce much more eggs under favourable food conditions. This relationship is also clear when the DEB model is used to predict age at stage transition and reproductive rates as a function of water temperature for three different food levels (Fig. 9.4). 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. This delay in stage transitions at lower temperatures and food levels has not yet been documented experimentally or in the field and would be an interesting topic for future studies.

In the native range of the species, the timing of *Mnemiopsis leidyi* blooms is changing as a result of warmer winter and/or spring temperature conditions (Condon and Steinberg, 2008; McNamara et al., 2010; Robinson and Graham, 2014); blooms are occurring earlier at increased temperatures. Water temperatures in Dutch coastal waters have increased in the last decades (Van Aken, 2010) and if this increase continues, the phenology of *M. leidyi* will likely shift to earlier blooms in the year.

**The role of salinity**

Models can be used to predict growth, reproduction, survival and risk of invasion for invasive species in new areas. These often use data from several different sources and populations of origin to estimate model parameters, assuming that the phenotypic response to differing environmental conditions is the same among populations. Examples for *Mnemiopsis leidyi* are Salihoglu et al. (2011), Collingridge et al. (2014) and Augustine et al. (2014a). In Chapter 7 we show that this assumption is not correct for *M. leidyi* as we have found a novel genotype of *M. leidyi* that reproduces at salinities lower than assumed possible in previous studies. This emphasises the importance of validating model assumptions with physiological rate measurements from the populations which are studied since they may show a different environmental tolerance window.

What will be most interesting is how the DEB model parameters (Chapter 6) will differ when they are estimated for low salinities and for different populations. The studies used as source data in Chapter 6 were all performed at saline conditions and as we show in Chapter 7, growth, mortality, reproduction and age and size at puberty are different at a salinity of 8 compared to a salinity of 33. This would also
allow one to investigate which process is actually influenced by salinity: are the maintenance costs increased, the energetic cost per unit of volume or something else? One way of doing this is to treat salinity the same way as toxicants and apply the DEBtox model as described in Jager et al. (2006).

In Chapter 7 we introduce the ratio between total length (TL) and oral-aboral length (OA) as a measure for the onset of metamorphosis in M. leidy (Fig. 7.6) and show that this differs for different salinity levels. It would be interesting to compare TL/OA ratios of different M. leidy populations at different salinity levels.

## Suggestions for research & management

### The missing polyps

In Chapter 3 we present a first survey of distribution and species composition of scyphozoan polyps in the southern North Sea area. Unexpectedly, all polyps found belonged to Aurelia aurita. The location of the polyps of the other four species of Scyphomedusae in the area is one of the most interesting questions that still remains. The analysis of polyp population differentiation, where high genetic diversity was found between Dogger Bank samples and other southern North Sea areas, will be interesting to expand to a larger area and to compare genetic differentiation in polyps with those in medusae to be able to link specific medusae aggregations to their polyp origin. Even though in our study only Aurelia aurita polyps were found, it cannot be excluded that in previous work polyps of other species were present and it is recommended that any future study on field-sampled polyps includes species identification based either on molecular identification or on the traditional method of rearing, strobilation and identification of ephyrae.

### Sampling methodology

Recommendations for sampling, preservation and identification of Mnemiopsis leidy that originated from this thesis are included in Vansteenbrugge (2015). The fixation method using Trichloroacetic Acid that we used for our sampling campaign allows fixation and preservation of M. leidy and storage of samples for longer periods (Appendix A) as well as easier identification of smaller ctenophores (Appendix B). It will be useful when ship-time is limited and detailed measurements of ctenophore length distribution are required. The method could be improved by finding a substitute for the formaldehyde that is still being used in preservation after Trichloroacetic Acid fixation.

### Monitoring

What is missing in this thesis is an assessment of zooplankton prey densities before and after the M. leidy introduction. No baseline data on zooplankton density and species composition was available for comparison, and within the scope of this study...
it was not possible to do a detailed study of the non-gelatinous mesozooplankton as well.

The EU Water Framework Directive 2000/60/EG stipulates ecological and chemical parameters that EU member states have to monitor in inshore and nearshore waters. The Netherlands has implemented this directive in the “Kaderrichtlijn Water” regulations for monitoring of surface waters. Phytoplankton is included for all water body categories but zooplankton is not (Anonymous, 2014b) and thus there has been very little zooplankton monitoring effort, both qualitatively and quantitatively, in Dutch waters. Every year a monitoring plan for physical, chemical and biological parameters is made, the “Monitoring Waterstaatkundige Toestand des Lands Milieumeetnet Rijkswateren” (MWTL) plan (Anonymous, 2014a). Zooplankton is only monitored in inland, fresh waters but this includes the North Sea canal. The current monitoring protocol only samples surface waters (a bucket sample in waters with currents and a 1.5 m long tube sample for stationary waters) as described in de la Haye (1996) and will thus miss any organisms that are in deeper layers in stratified systems like the North Sea Canal. Sampling volume is 45 L, which might be sufficient for mesozooplankton but will under sample most gelatinous zooplankton species.

As zooplankton are a critical component of pelagic food webs for which monitoring is now lacking in the Netherlands, we argue that yearly monitoring of species composition and density of zooplankton, preferably in every season, should be included in the MWTL programme for fresh, brackish and saline areas. In stratified systems all different water layers should be sampled, at least in the seasons when stratification is occurring. Areas which receive high ballast water loads, such as the ports of Amsterdam and Rotterdam, should receive additional attention.

In the Netherlands, many water bodies were closed off from the sea by man-made barriers and became fresh, the main example being Lake IJssel which was closed off from the Wadden Sea in 1932. In the south of the Netherlands several areas were closed off from the North Sea, one of them being the Lake Grevelingen. After the lake was closed off from the North Sea by the Brouwersdam, water quality issues prompted the construction of a small opening in the Brouwersdam in order to re-salinise the lake (Bannink et al., 1984). Gelatinous zooplankton monitoring in Lake Grevelingen shows *M. leidyi* densities similar to those in the western Wadden Sea (L. van Walraven unpublished data). Several smaller and larger water bodies are or will be re-salinised in the near future. Lake Oostvoorne near the port of Rotterdam was recently re-salinised, and blooms of *M. leidyi* are observed as well (L. van Walraven personal observation). Other semi-enclosed areas, like the Volkerrak-Zoommeer, will likely be good habitat for *M. leidyi* as well when they are re-salinised, and these areas should be monitored for *M. leidyi* presence and abundance.
Appendix
Appendix A

The use of trichloroacetic acid fixation and propylene phenoxyetol conservation in quantitative sampling of ctenophores

Lodewijk van Walraven, Victor T. Langenberg, Henk W. van der Veer

This chapter was published as an appendix to Van Walraven et al. (2013).
Introduction

Lobate ctenophore species are notoriously difficult to sample due to their fragility and preservation in traditional media such as buffered formaldehyde solution or ethanol is difficult. A method which has largely been unnoticed or possibly considered as too labor intensive (Purcell, 1988) is a method developed for preservation of individual specimens from samples by Adams et al. (1976). This method consists of fixation using a trichloroacetic acid (TCA) solution and subsequent preservation in a seawater solution containing propylene phenoxetol, propylene glycol and formaldehyde. In 2009, we tested this method for preservation and fixation of field samples and subsequently applied it with some modifications successfully for a year-round quantitative sampling programme of the ctenophores Mnemiopsis leidyi, Pleurobrachia pileus and Beroe gracilis in the western Wadden Sea (this study). This appendix describes the use of this modified fixation method and its advantages and disadvantages.

Materials and methods

Original fixation and preservation method for single specimens

The fixation and preservation method for individual ctenophores was the result of an investigation of some eighty reagents by the SCOR Working Group 23 project (Adams et al., 1976). For fixation a solution of 1 g tri-chloracetic acid or 1 g p-toluenesulphonic acid in 99 ml sea water is used. For preservation, a solution of 5 ml propylene phenoxetol, 45 ml propylene glycol and 50 ml 40% formaldehyde is prepared. The original protocol includes the following steps:

1. separate the ctenophores from other plankters and place them in a beaker with sea water;

2. drain the sea water away from the ctenophores by using bolting silk;

3. pour the ctenophores gently into the fixative;

4. fix for 30 minutes during which the specimens change slightly from transparency to translucency;

5. remove the fixative and replace it with a 1% preservation/sea water solution;

6. preserve for 5–7 days;

7. transfer from a 1% to a 5% preservation/sea water solution and store between 5 and 20 °C.
Modified protocol for fixation and preservation of quantitative samples

In applying the method of Adams et al. (1976) for quantitative samples, the following criteria were used when testing different modifications:

1. fixation and preservation of all species occurred;

2. after shrinkage fresh length and mass could be reconstructed;

3. stomach analysis could be performed on preserved individuals.

These criteria were applied in a three-step procedure: first different concentrations were tested for optimal fixation and preservation. Next, shrinkage and reconstruction of fresh mass was determined and finally, regurgitation was measured.

Ctenophores were caught using the method and gear as described in Van der Veer and Sadée (1984) in tidal gullies in the western Wadden Sea, the Netherlands. The whole sample or a subsample was examined on a 1mm sieve and if possible macroalgae such as Ulva lactuca were removed. The sample or a subsample of maximum 500 ml was put in a 800 ml glass jar, which was then filled up with the fixation solution. Solutions were prepared on board by adding different quantities of 100 g/l TCA-seawater solution to ambient seawater. In summer, the fixated samples were stored in a styrofoam box with ice for cooling.

In the lab the TCA-fixed samples were transferred on the day they were caught to sea water containing 1% preservation stock solution by volume. For this, samples were put on and drained in a sieve of ca. 0.5 mm mesh size, returned in the jar and subsequently the preservation solution was added. After 5-8 days the samples were transferred to sea water with 5% preservation stock solution. Samples were stored at a constant temperature of 4 °C.

Ctenophores of 10 mm or smaller in length were measured submerged in a petri dish using a stereo microscope with a measuring eyepiece. Larger ctenophore lengths were measured using a Vernier caliper. For Pleurobrachia pileus and Beroe gracilis the length measurement taken was the polar length, for Mnemiopsis leidyi the distance from the mouth to the statocyst.

Live ctenophores were fixed and preserved individually in glass jars to study shrinkage. Length and weight was measured prior to fixation, when transferred from the 1% to the 5% preservation solution. After preservation length and weight were measured twice with intervals of multiple months. Measurements were taken as described above.

Wet mass was determined by putting individual ctenophores on a drain for 20 sec to remove adhesive water. Ash Free Dry Mass (AFDM) was determined by first drying for 2 to 3 d at 60 °C in a ventilated stove, weighing and incinerating for 2 h at 520 °C. The weight loss after incineration was considered to represent AFDM.
Data analysis

All data were stored in a Microsoft Access database. Data analysis was carried out using R (R Core Team, 2014) and SigmaPlot 12.0. The allometric relationship

\[ V = a \times l^b \]  

between the fresh volume (V; ml) and oral–statocyst length before and after fixation (l; mm), was estimated using the non-linear least squares function of R.

Results and discussion

When the TCA solution was added the effect could be observed almost instantly. Structures such as the comb rows, meridional canals, oral lobes and walls of the stomodaeum became increasingly opaque white (Fig. A.3). This property greatly increased the visibility, especially when sorting in black sorting trays.

The fixation and preservation method worked in preserving ctenophores individually as well as together with hydromedusae, crustacean- or ichthyoplankton in a single sample. When samples contained large quantities of plant- peat- or macroalgae fragments or high quantities of crustaceans, often only the mouth, stomodaeum and statocyst complex of the *M. leidyi* ctenophores were left after preservation. Overall ca. 95% of ctenophores could be measured in preserved samples. Large samples of ctenophores smaller than 5 mm length could be subsampled using a Folsom plankton splitter without major damage to the specimens. Of the first 30 *M. leidyi* that were individually fixed, only one could not be measured on the last measuring moment 475 days after fixation in total 7 out of 128 (5.5%) *M. leidyi* disintegrated or were too damaged to measure. One Pleurobrachia pileus had disintegrated and all Beroe gracilis could be measured. Relationships between lengths and weights of fresh and fixed *M. leidyi* are shown in Fig. A.1.

A significant allometric relationship between fixed and fresh lengths and fresh weights of individually fixed ctenophores could be estimated for *M. leidyi* (Fig. A.1; Table A.1) and *P. pileus* (Table A.1). Mean shrinkage by volume as measured when transferring the samples from the 1% to the 5% stock solution was 55% for large *M. leidyi* (n = 8, sd = 4.9) and 54% for small *M. leiuydi* (n = 80, sd = 13.1). Percentage of shrinkage was highly variable in small ctenophores.

Mean shrinkage by length was 16% (n = 88, sd = 13.0) post-fixation and 19% (n = 53, sd = 19.8) measured on the second measuring moment. Mean shrinkage by length of fixed *P. pileus* measured on the first measuring moment was 19% (n = 12, st.dev=7.8) and also 19% (n=12, sd = 9.7) measured on the second measuring moment. Mean shrinkage by length of fixed *B. gracilis* after the first and second measuring moment was respectively 26% (n = 20, sdv = 7.0) and 28% (n = 18, sd = 9.1).

There was a positive relationship between ash free dry weight and fresh ctenophore volume (Fig. A.2) for ctenophores weighing less than 20 g (*afdm = 0.0088 * freshweight*). For the ctenophores weighing more than 20 g the sample size was too low to see a clear relationship.
Table A.1: Parameter estimates and standard errors and p-values of the estimated length (fixed or fresh) - fresh volume relationship $V = a \times l^b$.

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>estimate</th>
<th>SE</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. leidy$\text{f}_{\text{fresh}}$</td>
<td>128</td>
<td>a 0.0145</td>
<td>0.0030</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>M. leidy$\text{f}_{\text{fresh}}$</td>
<td>128</td>
<td>b 2.0000</td>
<td>0.0580</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>M. leidy$\text{f}_{\text{fixed}}$</td>
<td>128</td>
<td>a 0.0079</td>
<td>0.0013</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>M. leidy$\text{f}_{\text{fixed}}$</td>
<td>128</td>
<td>b 2.3202</td>
<td>0.0481</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>P. pileus$\text{f}_{\text{fixed}}$</td>
<td>89</td>
<td>a 0.0011</td>
<td>0.0003</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>P. pileus$\text{f}_{\text{fixed}}$</td>
<td>89</td>
<td>b 2.6809</td>
<td>0.1075</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>B. gracilis$\text{f}_{\text{fixed}}$</td>
<td>20</td>
<td>a 0.0022</td>
<td>0.0019</td>
<td>0.273</td>
</tr>
<tr>
<td>B. gracilis$\text{f}_{\text{fixed}}$</td>
<td>20</td>
<td>b 2.2282</td>
<td>0.3281</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

No regurgitation was observed in 10 individuals of M. leidy after 10 minutes following addition of the TCA solution to a Petri dish containing the specimen. Food was observed moving towards the mouth opening, but not expelled. After the final preservation step however the stomodaeum wall had turned from translucent to opaque and was often disintegrated into small particles making stomach content analysis difficult or impossible. Only larger crustacean zooplankton prey items such as cyprid larvae and copepods could be distinguished, and in one instance a 6mm long goby larva.

These results show that the method of Adams et al. (1976) for the preservation of single species also worked well for the preservation of field samples of ctenophores, allowing detailed quantitative measurements in the lab. Heavily damaged specimens could often still be measured because the mouth-stomodaeum-statocyst complex remained intact (Fig. A.3). This method, while being slightly more labour intensive than the method using Lugol’s solution proposed by Engell-Sorensen et al. (2009), could potentially be more effective as it does not have the disadvantages of the high variation in shrinkage and discoloration. The percentages of ctenophores that are still measurable are also higher using this method. The Lugol’s solution method has been shown to work also for larval ctenophores (Sullivan and Gifford, 2009), whether that is also the case for this method is still unknown. The fixed oral–statocyst length – fresh mass relationship for M. leidy and the other species can be used to accurately estimate the wet mass or bio-volume of live ctenophores. Overall, this method will be very useful for sampling ctenophore populations more efficiently and accurately. A further major improvement to the method would be finding a suitable replacement for the toxic formaldehyde used in preservation.
Figure A.1: Relationships between fresh length and fresh weight (a), fixed length and fresh weight (b), fresh- and fixed weight (c) and fresh and fixed length (d) of individual *Mnemiopsis leidyi*. 
Figure A.2: Relationship between ash free dry weight (afdw, g) and fresh weight of *Mnemiopsis leidyi* ctenophores with fitted regression lines.

Figure A.3: Photographs of preserved ctenophores: *Mnemiopsis leidyi*: (a) specimen of 8 mm oral–aboral length after 231 days in the preservation solution, (b) specimen of 16 mm oral–aboral length after 475 days in the preservation solution, (c) specimen of 34 mm oral–aboral length after 397 days in the preservation solution, (d) damaged preserved specimen of 32 mm oral-aboral length after 397 days in the preservation solution. Note that the statocyst-stomodaeum-mouth complex is still intact allowing measurement. (e) specimen of *Pleurobrachia pileus* 14 mm length after 397 days in the preservation solution. (f) specimen of *Beroe gracilis* of 16 mm length after 358 days in the preservation solution.
Appendix B

Identification key for ctenophora in Dutch coastal waters

This key can be used for the identification of ctenophores in Dutch coastal waters (excluding overseas territories).

The identification of ctenophores can be very difficult, especially when dealing with damaged specimens. This key for the identification of ctenophores found in Dutch coastal waters is based upon the experience obtained identifying ctenophores in North Sea, Wadden Sea and coastal waters of Zeeland in the period 2009–2014 and the ICES ID leaflet “ctenophora” (Greve, 1975).

Identification is best performed on submerged specimens, e.g. in a petri dish, with oblique lighting from a cold light source or transverse lighting using a light table. A binocular microscope is necessary.

Key

1. (a) Comb rows along the longitudinal axis of the body. Bilaterally symmetric.
   (b) No comb rows, radially symmetric. Scypho- or hydromedusa

2. (a) Larger than 5 mm
   (b) Smaller than 5 mm

3. (a) Spherical or spheroid. Two long finely branched tentacles.
4. (a) Oval, large mouth occupying the entire width of the animal.  
(b) Not oval, with two oral lobes.

5. *Beroe* species can be distinguished by the presence and characteristics of diverticulae, canals diverging from the meridional canals under the comb rows (Fig. B.1). These do not develop until the animal reaches a length of approximately 20 mm and thus *Beroe* specimens smaller than this can not be identified to species level.

(a) No diverticulae. Maximum length 35 mm.  

**NL: slanke meloenkwal Beroe gracilis**

(b) Diverticulae diverging from the canals under the comb rows. The diverticulae of parallel comb rows are never connected. Can be bigger than 35 mm.

**NL: grote meloenkwal Beroe cucumis**
(c) Diverticulae diverging from the canals under the comb rows. Some diverticulae of parallel comb rows are connected (anastomose). Can be bigger than 35mm.

*Beroe ovata* (not yet recorded in Dutch coastal waters)

6. (a) Oral lobes terminate near or past the statocyst (Fig. B.2).

**NL:** Amerikaanse ribkwal **EN:** Sea walnut *Mnemiopsis leidyi*

(b) Oral lobes terminate nearer to the mouth than to the statocyst (Fig. B.2). One comb row on each lobe has a black stripe (often not visible).

*Bolinopsis infundibulum*

![Diagram](image)

Figure B.2: *Bolinopsis infundibulum* and *Mnemiopsis leidyi* compared, with the distance from the statocyst to the termination of the oral lobe indicated.

7. (a) Tentacle bulbs present.

(b) No tentacle bulbs.

*Beroe*, not identifiable to species level at this size.

8. **Cydippid larvae.** Note: Cydippid stage ctenophores are very difficult to distinguish. The below characteristics are visible using a binocular microscope or similar magnification. Small individuals of the Arctic species *Mertensia ovum* found in the Baltic Sea together with *M. leidyi* are very similar to *M. leidyi* and require genetic indentification (*Gorokhova et al., 2009; Gorokhova and Lehtiniemi, 2010*). Especially samples of small ctenophores only, without larger specimens in the same sample should be treated with caution. Visibility of the comb rows is much better in TCA-fixed specimens (Fig. B.3) than in fresh specimens.
Appendix B

(a) Rounded tentacle bulbs. Comb rows thinner compared to *Pleurobrachia pileus* in direct comparison (Fig. B.3).

**NL:** Amerikaanse ribkwal **EN:** Sea walnut *Mnemiopsis leidyi*

(b) Elongated, non-round tentacle bulbs. Comb rows thicker compared to *Mnemiopsis leidyi* in direct comparison (Fig. B.3).

**NL:** Zeedruif **EN:** Sea gooseberry *Pleurobrachia pileus*

Figure B.3: Comparison of TCA-fixed cydippid stages of *Mnemiopsis leidyi* (top three individuals) and *Pleurobrachia pileus* (bottom three individuals) of different sizes. Viewed through a binocular microscope using transverse lighting.
Bibliography


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.
Samenvatting

Kwalachtigen zijn een onderbestudeerde diergroep in veel zeegebieden. In Nederlandse kustwateren was de vondst van de invasieve uitheemse ribkwal *Mnemiopsis leidyi* aanleiding voor de start van een serie nieuwe onderzoeken naar de ecologie van kwalachtigen in het gebied en een hernieuwde interesse in deze diverse diergroep. Het hoofddoel van dit proefschrift is om de huidige verspreiding, het voorkomen en de seizoenspatronen van kwalachtigen in de Nederlandse kustwateren in kaart te brengen. Hoe worden deze beïnvloed door de vele veranderingen in de omgeving in dit gebied?

Het proefschrift bestaat uit twee delen: een eerste deel gefocused op het onderzoeken van veranderingen in soortensamenstelling, seizoenspatronen en voorkomen van kwalachtigen en een tweede deel gericht op het verkrijgen van inzicht in de mechanismen die van de ribkwal *Mnemiopsis leidyi* zo’n successvolle invasieve soort maken.

Vragen die aan het begin van het onderzoek werden gesteld waren: Wat is de huidige verspreiding in tijd en ruimte van kwalachtigen in de Nederlandse kustwateren? Hoe zijn deze beïnvloed door veranderingen in de omgeving? Door welke top-down en bottom-up processen worden kwalachtigen beïnvloed? Wat is de predatiedruk op de dierlijke planktongemeenschap en is er veel concurrentie met vissen? En hoe worden populaties van kwalachtigen in Nederlandse kustwateren beïnvloed door klimaatverandering en andere anthropogene invloeden?

**Kwalachtigen in Nederlandse kustwateren**

Aan het Marsdiep, een zeegat in de westelijke Waddenzee, beheert het NIOZ Koninklijk Nederlands Instituut voor Zeeonderzoek een kom-fuik, een passief vistuig. Sinds 1960 elke dag de vangst uit de kom-fuik geregistreerd, voornamelijk in het voor- en najaar maar soms ook in de zomer. Aantallen gevangen kwallen per soort in de fuik zijn ook genoteerd. Dit heeft een unieke tijdserie opgeleverd van meer dan vijftig jaar aan kwallenvangsten, die in **hoofdstuk 2** is gebruikt om veranderingen in fenologie, voorkomen en soortensamenstelling van kwallen in relatie tot omgevingsfactoren te onderzoeken. Hier laten we zien dat in de recente decennia alle soorten eerder in het jaar verschenen, wat voor de oorkwal *Aurelia aurita* gerelateerd was aan een toegenomen zeewater temperatuur in de winter. De kompaskwal *Chrysaora hysoscella* blijft ook tot later in het jaar nog aanwezig.
Door de grote dagelijkse variatie in vangsten konden patronen in het voorkomen van kwallen niet gerelateerd worden aan veranderingen in omgevingsvariabelen. Dit zou kunnen impliceer dat populatie-regulerende processen vooral optreden in het poliepstadia van de kwallen. Wel waren de vangsten in de fuiw in recente decennia een stuk lager dan in de jaren 80 en 90; een periode die gekenmerkt werd door een hoge mate van eutrofiëring van de Waddenzee.

Door een vestigingsplaats voor kwalpoliepen te bieden kunnen door mensen gebouwde structuren in zee bijdragen aan de vorming van kwallenbloeien. De locatie van de vastzittende poliepstadia van de schijfkwallen was onbekend voor veel soorten, ook in Nederlandse kustwateren. Daarom is in hoofdstuk 3 de verspreiding, soortensamenstelling en populatie structuur van kwalpoliepen onderzocht door het nemen van monsters van poliepen van verschillende substraten in de zuidelijke Noordzee en aangrenzende gebieden. Omdat poliepen van elke soort er vrijwel identiek uit zien werden de poliepen aan de hand van genetische verschillen op soortniveau geïdentificeerd. Helaas behoorden alle gevonden poliepen tot de oorkwal *Aurelia aurita* waardoor de locatie van de poliepen van de andere soorten nog steeds niet is gevonden. Het hoge aantal *A. aurita* monsters maakte het echter wel mogelijk om de eerste studie aan de populatiestructuur van kwallen die gebaseerd is op poliepen in plaats van medusen uit te voeren. *A. aurita* poliepen vormden verschillende populaties, waarbij poliepen uit de centrale Noordzee een andere populie vormden dan poliepen uit de kustgebieden.

De meest recente kwantitatieve monsterprogramma’s gericht op kwalachtigen in zowel het Waddengebied als in Zeeuwse wateren stammen uit de jaren 80, toen *Mnemiopsis leidyi* hier nog niet voor kwam. In 2009 is daarom het in de jaren 80 uitgevoerde monsterprogramma in en rond het Marsdiep herhaald met dezelfde methodes en op dezelfde plek. In hoofdstuk 4 laten we zien dat *M. leidyi* in hoge dichtheden voorkomt in dit gebied, vooral in de nazomer en het najaar. Dit monsterprogramma is vervolgd in 2010–2012 en in hoofdstuk 5 wordende soortensamenstelling, seizoenspatronen en predatiedruk op het dierlijk plankton vergeleken met die in de jaren 80. Door de introductie van *M. leidyi* is de rol van kwalachtigen als predatoren van het dierlijk plankton toegenomen. De soortensamenstelling is grotendeels hetzelfde, met één belangrijke uitzondering: *M. leidyi* is nu de meest algemene kwalachtige in Nederlandse kustwateren. In de jaren 80 was de predatiedruk van kwalachtigen op het dierlijke plankton laag, behalve in het voorjaar tijdens de voorjaarspiek van *Pleurobrachia pileus*. In 2009–2012 echter zorgden hoge dichtheden *M. leidyi* voor een hoge predatiedruk op het plankton ook in de zomer en het najaar. Op sommige dagen zou in theorie al het plankton in de waterkolom binnen een dag weggefilterd kunnen worden. Dit is een belangrijke verandering in het ecosysteem van het vrije water in de Waddenzee, die waarschijnlijk in Zeeuwse wateren ook is opgetreden. Het lijkt erop dat *M. leidyi* een on- of ondergebruikte niche heeft gevonden in het ecosysteem als predator van dierlijk plankton in nazomer en herfst.
Het succes van *Mnemiopsis leidyi* als invasieve exoot onderzocht

In hoofdstuk 6 wordt het energiebudget van *Mnemiopsis leidyi* gedurende de gehele levenscyclus onderzocht met behulp van de Dynamic Energy Budget (DEB) modelltheorie. Aan de hand van gegevens uit de literatuur over parameters als grootte, groei, voortplanting en respiratie is een DEB model geparameetriserd voor *M. leidyi*, wat daarna is gebruikt om de respons van verschillende stadia van *M. leidyi* op verschillen in voedselbeschikbaarheid en temperatuur te onderzoeken. Data verzameld bij temperaturen van 8 tot 30 °C suggereren dat de optimale tolerantiegrens qua temperatuur bij *M. leidyi* hoger ligt dan de 12 °C die eerder werd aangenomen. Verder lijkt *M. leidyi* zogenoemde metabolische acceleratie (een afwijking van het standaard Von Bertalanffy groeimodel) te ondergaan na het uitkomen van het ei. Deze acceleratie lijkt vertraagd te worden door een nog onbekende factor. De modellsimulaties suggereren dat *M. leidyi* door het vertragen of versnellen van de groei en het beïnvloeden van de generatietijd erg veel metabolische flexibiliteit heeft en zich aan kan passen aan zowel lage als hoge voedselbeschikbaarheid.

Alhoewel *Mnemiopsis leidyi* bij een brede range van temperatuur en zoutgehalte kan overleven in zijn oorsprongelijke leefgebied, lijkt in veel gebieden waar de soort is geïntroduceerd de verspreiding gelimiteerd te zijn bij lage zoutgehaltes. Dit maakte het optreden van hoge dichtheden *M. leidyi* in het brakke Noordzeekanaal bij Amsterdam opmerkelijk, aangezien het zoutgehalte hier veelal te laag zou zijn om voortplanting van *M. leidyi* mogelijk te maken. In hoofdstuk 7 is de rol van zoutgehalte als limiterende factor voor de verspreiding van *M. leidyi* onderzocht in een “common-garden” experiment waarin ribkwallen afkomstig uit brak water bij Amsterdam en ribkwallen afkomstig uit zout water bij Texel werden geacclimatiseerd en opgekweekt bij twee verschillende zoutgehaltes: 8 en 33. Tijdens het experiment werden overleving, groei en voortplanting dagelijks gemeten. In dit experiment kon *M. leidyi* zijn hele levenscyclus voltooien bij een laag zoutgehalte van 8. Minder ribkwallen overleefden het experiment bij een zoutgehalte van 8 dan bij een zoutgehalte van 33. Genetische analyse van de ribkwallen die het experiment overleefden toont aan dat er duidelijke verschillen zijn tussen sub-populaties met verschillende afkomst. Binnen de Amsterdamse sub-populatie wordt hoge genetische differentiatie gevonden. Dit is de eerste waarneming van een *M. leidyi* genotype dat zich bij zulke lage zoutgehaltes kan voortplanten. Ribkwallen van dit genotype zouden zich kunnen verspreiden naar gebieden waar tot nu toe van werd aangenomen dat het lage zoutgehalte de voortplanting van *M. leidyi* belemmerde.

In hoofdstuk 8 is een kwalitatieve schatting gemaakt van voedselconcurrentie tussen *Mnemiopsis leidyi* en andere dierlijk plankton etende diersoorten in de Waddenzee. Aan de hand van Stabiele Isotopen Analyses (SIA) werd de overlap in dieet tussen vissen, kwallachtigen, kreeftachtigen en inkvissen onderzocht. Een clusteranalyse toonde aan dat gemiddelde δ¹³C en δ¹⁵N verhoudingen van *M. leidyi* hetzelfde waren als die van planktonetende vissoorten zoals de glasgrondel *Aphia minuta*, de haring *Clupea harengus* en de horsmakreel *Trachurus trachurus*. Ook
was er overlap met δ¹³C en δ¹⁵N verhoudingen van de kompaskwal Chrysaora hysoscella, de zeedruif Pleurobrachia pileus en de hydroidkwal Nemopsis bachei. δ¹⁵N van M. leidyi was positief gerelateerd aan de groote van de ribkwallen, wat suggereert dat kleinere ribkwallen op een lager troisch niveau zitten dan grote. Aan het begin van de bloeiperiode in augustus bestond vrijwel de hele M. leidyi populatie uit larven en juveniele ribkwallen en was er geen overlap met de stabiele isotopen niche van andere pelagische zooplankton eters. De meeste overlap tussen het dieet van M. leidyi men dat van andere soorten treedt op in perioden waarin de ribkwallen het minst talrijk zijn, wat suggereert dat M. leidyi op dit moment nog geen belangrijke voedselconcurrent is voor inheemse kwalsachtigen en vissoorten. Tijdens de periode waarin M. leidyi het meest algemeen is, is de dichtheid aan concurrense kwalachtigen laag. Dit suggereert dat M. leidyi een ongebruikte niche heeft opgevuld.

**Nederlandse kwalsachtigen in de toekomst**

Dit proefschrift is een belangrijke aanvulling op onze kennis over de fenologie, het voorkomen en de soortensamenstelling van kwalsachtigen in Nederlandse kustwateren. De ontwikkelde en geteste technieken zoals het Dynamisch Energie Budget (DEB) model, de fixatie- en preservatiemethode voor Mnemiopsis leidyi en het “common-garden” kweekexperiment kunnen ook toegepast worden bij onderzoek aan kwalsachtigen in andere gebieden.

Het zou interessant zijn als het onderzoek naar identificatie en populatiestructuur van kwalpoliepen (hoofdstuk 3) wordt uitgebreid naar meer gebieden en habitat-types aangezien de locatie van poliepen van andere soorten dan Aurelia aurita nog steeds een mysterie is.


Concluderend laten de resultaten van dit proefschrift zien dat de introductie van Mnemiopsis leidyi in Nederlandse kustwateren op dit moment nog weinig impact heeft op de populaties van andere plankton-etende vissen en kwalsachtigen. Echter, aangezien de voortplanting en groei van Mnemiopsis leidyi sterk afhankelijk is van de watertemperatuur zou opwarming van het water door klimaatverandering
verschuivingen in de seizoenspatronen van voorkomen van de ribkwallen kunnen veroorzaken. Daardoor kan de soort bloeien gaan vormen in jaargetijden waar nu nog temperatuur de limiterende factor is. Ook door de in dit proefschrift aangetoon-de lagere tolerantiegrens voor zoutgehaltes kan de soort op plekken opduiken waar dit niet wordt verwacht. Op dit moment is monitoring van het dierlijk plankton in Nederlandse kustwateren helaas vrijwel afwezig waardoor bloeien van *M. leidyi* en de introductie van andere potentieel schadelijke soorten waarschijnlijk niet, of te laat, opgemerkt zullen worden.
Lodewijk van Walraven was born on 25 March 1986 in Warnsveld (Zutphen), the Netherlands. Through holidays on the Frisian isles and camps and excursions of the Dutch youth association for nature and environmental study (JNM) he became interested in marine biology at a young age. After attending pre-university college in Zutphen he studied Marine Biology at the University of Groningen. For his MSc thesis he studied fisheries induced evolution in North Sea plaice at Wageningen IMARES, and the seasonal pattern of the invasive ctenophore *Mnemiopsis leidyi* in the western Wadden Sea at NIOZ Royal Netherlands Institute for Sea Research. After working one year as a research assistant at Royal NIOZ he started the PhD that resulted in this thesis at the same institute. At the moment he works at Royal NIOZ on the impact of sustainable energy (Reverse Electro Dialysis, RED) on the marine environment, and as sustainable fisheries researcher at Good Fish Foundation.
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