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Research Article

Species composition and predation pressure of the gelatinous zooplankton community in the western Dutch Wadden Sea before and after the invasion of the ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865

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Abstract

The ctenophore *Mnemiopsis leidyi* A. Agassiz, 1865 is a successful, recent, macroplanktonic invader in European coastal waters, including the Dutch Wadden Sea. It occurs year-round in substantial numbers. The effect of *M. leidyi* on structure of the gelatinous zooplankton community in the Dutch Wadden Sea was studied by comparing data from before and after its introduction. Gelatinous zooplankton species composition in the western Wadden Sea was largely the same between 1980–1983 and 2009–2012. Only the hydromedusa *Eutonina indicans* (Romanes, 1876) was absent in recent years while *Cosmetira pilosella* Forbes, 1848 and *Margelopsis haeckelii* Hartlaub, 1897 were rare species observed only in 2009–2012. *M. leidyi* was present since 2006, with high densities every year in summer and autumn. Predation pressure by scyphomedusae, ctenophores, and hydromedusae on fish larvae and zooplankton in 1980–1983 was low because of low densities and a temporal mismatch between gelatinous zooplankton and their prey. Despite the decrease in abundance of scyphomedusae in recent decades, the introduction of *M. leidyi* and its large annual blooms have increased the overall importance of gelatinous zooplankton as predators in the western Wadden Sea, whereby *M. leidyi* is responsible for most of the predation pressure on mesozooplankton in the area. Rather than outcompeting local species, *M. leidyi* appeared to fill in a previously unoccupied niche in the pelagic western Dutch Wadden Sea in late summer and autumn.

Key words: sea walnut, non-native species, plankton surveys, competition, ctenophores, hydromedusae, scyphomedusae

Introduction

The invasion of non-native organisms can have major effects on the structure and functioning of local communities and ecosystems (Elton 1958; Williamson 1996). The most frequent vectors of marine invasions are shipping and aquaculture (Molnar et al. 2008). Many organisms that get transported to other areas do not survive the journey, or perish because environmental conditions in the new environment are outside of their tolerance range. Of the ones that do survive, few establish themselves and even fewer become truly invasive (Williamson 1996). Often, however, there is a period in which an introduced organism is present in low abundance.

During this "lag" period, many introduced species go undetected. These lags can be caused by slow initial population growth, unsuitable environmental conditions, or a fitness deficit where the organism has to adapt to the new environment (Crooks et al. 2001). There are many different hypotheses as to why and how an introduced species becomes invasive (Ricciardi et al. 2013); including: propagule pressure; the number of individuals introduced; release from competition, predation, or parasitism; changes in environmental conditions; or the existence of an "empty" niche in the introduction area.

Assessing the effects of an invasive species requires detailed knowledge of the state of the ecosystem before the invasion (Blossey 1999). For

example, detailed knowledge on the ecosystem structure and function of lakes in the United States prior to invasion by the zebra mussel *Dreissena polymorpha* (Pallas, 1771) allowed a detailed assessment of changes in food web organisation and ecosystem activity (Miehls et al. 2009a, b).

In the Wadden Sea, an important fuelling station for migrating birds and an important nursery area for various fish species (Wolff 1983), several successful invasions of bivalve species have been observed, e.g., the sand gaper *Mya arenaria* Linnaeus, 1758, Pacific oyster *Crassostrea gigas* (Thunberg, 1793) and razor clam *Ensis directus* (Conrad, 1843) (Beukema and Dekker 1995; Wolff 2005; Troost 2010; Dekker and Beukema 2012). In 2006, the occurrence of an invasive ctenophore, *Mnemiopsis leidyi* A. Agassiz, 1865 was confirmed in Dutch coastal waters including the Wadden Sea (Faasse and Bayha 2006; Tulp 2006). *M. leidyi* is one of the recent successful invasive species in northern European waters. It has been reported from Sweden (Hansson and Kiørboe 2006), Germany (Javidpour et al. 2006; Boersma et al. 2007), Denmark (Tendal et al. 2007), the Baltic Sea (Javidpour et al. 2006), Poland (Janas and Zgrundo 2007), and Norway (Oliveira 2007). *M. leidyi* is an opportunistic planktonic predator, feeding on a wide range of zooplankton prey such as copepods and their nauplii, bivalve veligers, barnacle nauplii, fish larvae and eggs (Cowan and Houde 1992; Purcell et al. 1994; Javidpour et al. 2009; Granhag et al. 2011); therefore, competition with other gelatinous zooplankton species that have similar diets is possible.

For the western Wadden Sea, data on the gelatinous zooplankton species composition and seasonal patterns prior to the *Mnemiopsis leidyi* invasion are available. Substantial quantitative published and unpublished baseline information exists from several macroplankton surveys conducted during the 1980s (van der Veer and Sadée 1984; van der Veer 1985; van der Veer and Oorthuysen 1985; Daan 1986; Kuipers et al. 1990). During that period, a variety of hydromedusae and scyphomedusae species were present, and the most abundant gelatinous zooplankton species was the ctenophore *Pleurobrachia pileus* (O. F. Müller, 1776), which is preyed upon by *Beroe gracilis* Künne, 1939 (van der Veer and Sadée 1984). At present, *Mnemiopsis leidyi* has established itself as a macroplanktonic invader in the Dutch Wadden Sea, with a year-round occurrence in substantial numbers (van Walraven et al. 2013). In the period 2009–2012, macroplankton samples were taken using similar methods in the same area as during the 1980–1983 studies. The goal of this paper was to investigate the potential impact of the invasion by *M. leidyi* on the gelatinous zooplankton community in the Dutch Wadden Sea by comparison of the patterns in the 1980–1983 period with those in recent years (2009–2013). The specific goals were to evaluate:

1. whether the introduction of *M. leidyi* was followed by a shift in species composition, seasonal pattern of occurrence, and abundance of the gelatinous zooplankton community;
2. whether the introduction of *M. leidyi* increased competition for food and, if so, during which periods of the year; and
3. the current and possible future ecological impact of *M. leidyi* in the Wadden Sea system.

Material and methods

Sampling

Surveys were conducted in the western Dutch Wadden Sea (Figure 1) during 1982–1983 and 2009–2012. All samples were collected in tidal gullies ranging from 5–15 m in depth at current velocities >20 cm s^{-1} from an anchored ship or from a jetty. For 1982 and 1983, complete data sets were available and the data from these years were used as a baseline against which to compare the 2009–2012 species composition, seasonal patterns, and abundance of gelatinous zooplankton. Water temperature and salinity during the two sampling periods were obtained from a nearby station from which surface water temperature and salinity were measured daily (van Aken 2008a, b). In 2009–2012, water temperature and salinity were also measured at the surface once during each zooplankton net-haul with a hand-held conductivity meter (WTW cond 330i, WTW, Welheim, Germany, accuracy ± 0.1 unit).

Sampling in the 1980s took place weekly at one or more of several stations in the Marsdiep tidal basin from February to December in 1982 and from April to December in 1983 (Figure 1). Oblique hauls were made with plankton nets made of polyamide plankton gauze (2-mm mesh size) with an opening of 0.7 m^2, a length of 5 m, a porosity of 0.59, and a total surface area of 12 m^2 (definitions according to Smith et al. 1968). A flow meter mounted in the opening of the net was used to estimate the volume of water filtered. Samples collected in the 1980s were preserved in a 4% formaldehyde solution and photographed submerged in seawater in a flat basin with a black background. Organisms were identified, counted, and the lengths of a subsample of ca. 100 organisms were measured from a projection of the slide photographs using a ruler. More details on sampling methodology can be found in van der Veer

Figure 1. Stations in the western Wadden Sea sampled in this study, together with the years for which the station was sampled. Dark grey represents land, light gray intertidal area, white is subtidal. For details see supplementary material Tables S1–S4.
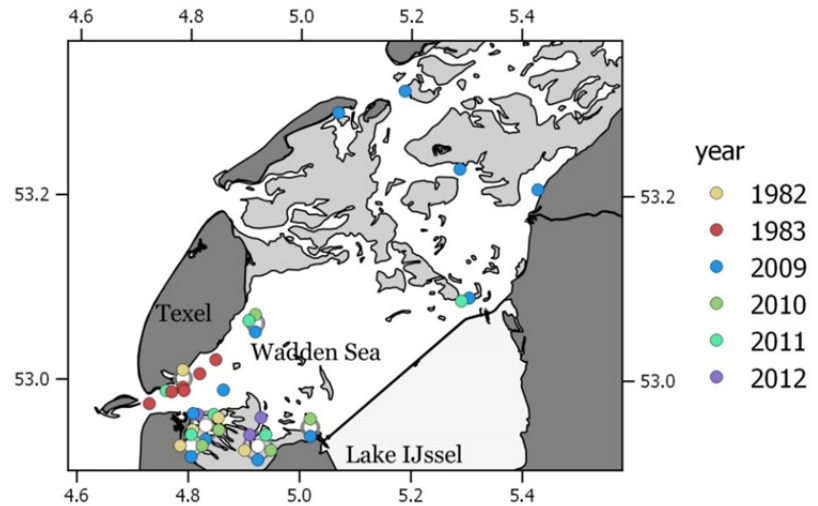
and Sadée 1984 (1982 data) and Kuipers et al. 1990 (1983 data). Raw data on ctenophores, scypho-medusae, and hydromedusae from this period were derived from van der Veer and Sadée 1984; Kuipers et al. 1990; and unpublished data (H. van der Veer and R. Daan). For 1982, colour-slide images of the original samples were available and used to confirm the species identifications for that period.

Recent sampling was done from January–December in 2009, during the second half of the year in 2010, from April–August in 2011, and from April–October in 2012 (Figure 1 and supplementary material Table S1). Sampling frequency varied from weekly to monthly depending on availability of the research vessels in the sampling area as most of the sampling was carried out when the vessels were at station waiting for non-related research to be carried out on the tidal flats. After collection, the cod end of the net was emptied in a bucket and the contents were either identified to species level, counted, and individual sizes measured directly on board using a submerged 1 mm sieve directly after collection or, when high numbers of juvenile ctenophores occurred, fixed on board using the trichloroacetic acid (TCA) method (Adams et al. 1976), applied for fixation of quantitative samples as described in van Walraven et al. (2013). Sampling protocol and methods corresponded with those during the period 1982–1983, except for 2012. In 2012, the gear was changed from a 2-mm mesh size to a 1-m diameter net with 1 mm mesh size, a circular opening of 0.78 m², and a length of 5 m. Water flow through the net was estimated using a flow meter mounted in the net opening.

For each haul, all individuals were identified to species level based on Greve (1975) for ctenophores,

Holst (2012a) for scyphomedusae and on Russell (1953), Cornelius (1995a, b) and Schuchert (2012) for hydromedusae. For each species, number per sample were converted into densities (individuals m⁻³). For each date, the mean (± SE) number per haul (as ind. m⁻³) was then calculated. Sizes were measured to the nearest mm on a measuring board with 1 mm scale except for large scyphozoa which were measured to the nearest cm and juvenile ctenophores, which were measured to the nearest mm submerged in a petri dish using a binocular microscope and ocular micrometer.

Predation estimates

Potential for competition for food with other gelatinous zooplankton by *Mnemiopsis leidyi* was studied by estimating and comparing the species-specific prey consumption rates in a manner similar to that used in Limfjorden, Denmark (Riisgård et al. 2012). For each of the four most abundant species in the period 2009–2012, the daily clearance rate for an average sized individual F_{ind} was estimated using predator size-clearance rate relationships for copepods and/or copepodites obtained from several published sources (Table 1). This was done for all years. If needed, animal biovolume was estimated from measured lengths using allometric relationships from other studies (Table 2).

Population clearance rates F_{pop} of the four most abundant species were calculated by multiplying individual clearance rate for an average-sized individual F_{ind} with the population density (D, ind m⁻³). Assuming that population clearance rates F_{pop} are independent of temperature and prey density and that

Table 1. Size–clearance rate relationships used in clearance rate estimation F_{ind} = clearance rate per individual (l^{-1} ind d^{-1}), V = live volume in ml, D = diameter in mm, L = polar length in mm, H= bell height in mm.

Nr.	Species	Relationship	Reference
1	*Pleurobrachia pileus*	$F_{ind}=0.2L^{1.9}$	Møller et al. (2010)
2	*Mnemiopsis leidyi*	$F_{ind}=2.64V$	Riisgård et al. (2012)
3	*Aurelia aurita*	$F_{ind}=0.0073D^{2.1}$	Møller and Riisgård (2007)
4	*Sarsia tubulosa*	$F_{ind}=e^{2.75ln(H)-0.95}*24/1000$	Hansson and Kiørboe (2006)

Table 2. Biometric conversions for gelatinous zooplankton used in this study. V = live volume in ml, D = diameter in mm, OA = Oral−Aboral length in mm, TL = total length in mm, WW = wet weight in g, DW = dry weight in mg.

Species	Conversion	Reference
Pleurobrachia pileus	$TL=1.25D$	van der Veer and Sadée (1984)
Pleurobrachia pileus	$TL_{fresh}=TL_{form.fixed}/0.80$	van der Veer and Sadée (1984)
Pleurorachia pileus	$TL_{fresh}=TL_{TCAfixed}/0.81$	van Walraven et al. (2013)
Mnemiopsis leidyi	$OA_{fresh}=OA_{TCAfixed}/0.81$	van Walraven et al. (2013)
Mnemiopsis leidyi	$V_{fresh}=0.0226OA_{fresh}^{1.72}$	Riisgård et al. (2007)

the water is well mixed, the time it takes for a population of a predator species to reduce the concentration of a prey species by half ($t_{0.5}$) was estimated following Hansson et al. (2005) and Riisgård et al. (2012) as follows:

$$t_{0.5} = \frac{ln2}{F_{pop}} \qquad (1)$$

If the half-life time was longer than three weeks, it was considered negligible as half-life time then exceeds the average generation time for copepods (Riisgård et al. 2012). Data analyses and modelling were perfomed using R (R Core Team 2014). Figures were made using the ggplot2 package (Wickham 2009).

Results

Environmental conditions

The average water temperature values were remarkably consistent between years. Mean weekly water temperature typically showed a minimum in January– February and a maximum in July–August (Figure 2). The lowest single observed winter water-temperature was −1.5 °C in January 1982 but winter water temperatures usually exceeded 2 °C. The highest single observation of summer water-temperature was 22.0 °C in July 1983 but the average seldom exceeded 19 °C.

Salinity was quite variable between months and between years, most weekly averages ranged between 24 and 31. The lowest values (<23) were observed in January–February 1982 with the next lowest values (<24) being observed during May to July 1983.

Species composition

Seventeen species of gelatinous zooplankton were caught: 4 ctenophores, 5 scyphomedusae, and 8 hydromedusae (Table 3). Three species of hydromedusae were only observed on one or two days in some of the years during the 2009–2012 period: *Aequorea vitrina* Gosse, 1853 was caught every year in very low numbers with a maximum of 3 individuals per year. For *A. vitrina*, the earliest observation in the year was on 8 April 2010 and the last on 14 August 2012. Fourteen individuals of *Cosmetira pilosella* Forbes, 1848 were caught on 11 August 2011. A single specimen of *Margelopsis haeckelii* Hartlaub, 1897 was collected on 21 June 2011.

The Hydromedusae *Clytia hemisphaerica* (Linnaeus, 1767) and *Eucheilota maculata* Hartlaub, 1894 were present, often in high numbers, throughout the sampled period. These species could not be distinguished from each other on the scanned slide photographs from 1981–1982 and were grouped together under "Leptothecata". The black spots on the outer wall of the stomach of *E. maculata* (Cornelius 1995b) were visible in most, but not all TCA-fixed samples (Adams
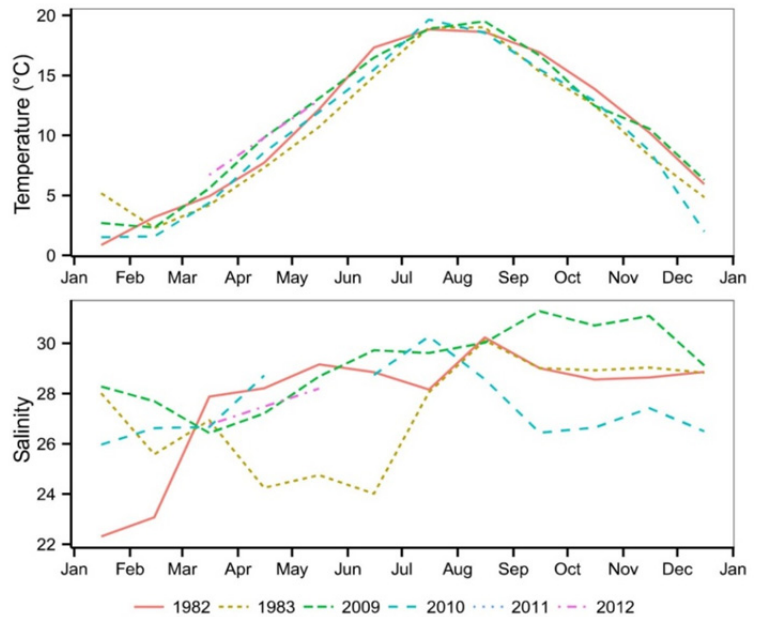
Figure 2. Monthly surface seawater temperature and salinity at the Royal Netherlands Institute for Sea Research jetty in the western Wadden Sea for the studied years.

Table 3. Overview of gelatinous zooplankton species caught in the surveys, per year. *other years uncertain.

Species	Authority	Years present					
Hydromedusae		1982	1983	2009	2010	2011	2012
Aequorea vitrina	Gosse, 1853	x	x	x	x	x	x
Clytia hemisphaerica	Linnaeus, 1767	x	x			x	x
Eucheilota maculata	Hartlaub, 1894	x	x	x	x	x	x
Cosmetira pilosella	Forbes, 1848						
Eutonina indicans	Romanes, 1876	x	x				
Margelopsis haeckelii	Hartlaub, 1897					x	
Nemopsis bachei	L. Agassiz, 1849	x	x	x	x	x	x
Sarsia tubulosa	M. Sars, 1835	x	x	x	x	x	x
Scyphomedusae							
Aurelia aurita	Linnaeus, 1758	x	x	x	x	x	x
Chrysaora hysoscella	Linnaeus, 1767	x	x	x	x	x	x
Cyanea capillata	Linnaeus, 1758			x	x	x	
Cyanea lamarckii	Péron and Lesuer, 1810	x	x	x	x	x	x
Rhizostoma octopus	Linnaeus, 1758	x	x	x	x	x	x
Ctenophores							
Beroe cucumis	Fabricius, 1780					x*	
Beroe gracilis	Künne, 1939	x	x	x	x	x	x
Mnemiopsis leidyi	A. Agassiz, 1865			x	x	x	x
Pleurobrachia pileus	O. F. Müller, 1776	x	x	x	x	x	x

et al. 1976). If absent, the presence and number of marginal cirri at each tentacle bulb was used as a distinguishing feature. The thecate hydroid *Eutonina indicans* could be distinguished by its elongated gastric peduncle, also in photographs of formaldehyde-preserved samples taken in 1982. Abundant athecate hydroids on the 1982 slide photographs that were previously identified as *Bougainvillia ramosa* (Van

Beneden, 1844) (now accepted as *Bougainvillia muscus* (Allman, 1863)) were reassigned to *Nemopsis bachei* L. Agassiz 1849 for this study based on the presence of ribbon-like folds that extended along the radial canals more than two-thirds towards the bell margin (Schuchert 2012). In the fixed samples (2009–2012), these structures were sometimes missing, in this case the species was identified based on the presence of

the two small capitate tentacles at the tentacle bulbs (Schuchert 2012). No individuals of *B. mucus* were detected in any of our samples.

Five species of scyphomedusae were found: *Aurelia aurita* (Linnaeus, 1758), *Chrysaora hysoscella* (Linnaeus, 1767), *Cyanea capillata* (Linnaeus, 1758), *Cyanea lamarckii* Péron and Lesueur, 1810 and *Rhizostoma octopus* (Linnaeus, 1758). All species were observed in all years in both periods except for *C. capillata,* which was only found in 2009–2012.

With respect to the ctenophores, *Mnemiopsis leidyi*, as expected, was only found in 2009–2012. Of the other species, the cydippid ctenophore *Pleurobrachia pileus* was present in all years as was its predator, the beroid *Beroe gracilis*. *Beroe cucumis* Fabricius, 1780 was identified from the samples in 2011. Because small (<20 mm) individuals of the two *Beroe* species were very difficult to distinguish, especially from the fixed samples and photographs, their abundances were combined as *Beroe* spp.

Most hydromedusae species were caught at sizes >1 mm. The five most abundant species, *Eutonina indicans*, *Sarsia tubulosa* (M. Sars, 1835), *Nemopsis bachei*, *Clytia hemisphaerica* and *Eucheilota maculata* (the last two combined here as Leptothecata) showed distinct seasonal patterns (Figure 3). *S. tubulosa* was the first species appearing, generally in April with an earliest observation on 24 March 2011; it reached peak abundance in May and was never caught after June. *E. indicans* showed a similar seasonal pattern as *S. tubulosa* but was only observed in the 1980s. The combined leptothecates group appeared in June and peaked generally in mid-summer. They remained present until the end of the year. *N. bachei* was also a summer species; in most years its peak abundance was reached in July. In 2009 and 2011, however, *N. bachei* was already observed at the end of April. Two other species (*Cosmetira pilosella* and *Margelopsis haeckelii*) were only observed during a single month (August and June 2011), respectively.

There were strong seasonal patterns in abundance of scyphomedusae (Figure 4). *Cyanea capillata* was not observed in the 1980s, and infrequent observed in April/May 2009–2011. *Aurelia aurita* and *Cyanea lamarckii* appeared at about the same time around March with the abundances of both species peaking in late April/early May. *Chrysaora hysoscella* and *Rhizostoma octopus* appeared next, peaking in August/September. Peak abundances of *A. aurita* were an order of magnitude lower in 2009–2012 than in 1982 and 1983. When species of Scyphomedusae appeared in the catches, they had a minimum size of 4 or 5 mm.

The ctenophore *Pleurobrachia pileus* was always present early in the year, often present at the start of the sampling period (Figure 5). In 1982 and 1983, there were two peaks in abundance: a spring peak in May and a smaller autumn peak in October/November. In 1982 and 1983, *P. pileus* was the most abundant gelatinous zooplankton species. The timing and magnitude of the spring bloom remained relatively constant throughout the sampled period. In 2009–2012, the timing of the spring bloom was the same as in the 1980s but the peak densities were an order of magnitude lower than those in the 1980s. In recent years, the autumn bloom was much less pronounced or absent. In most years, the predatory *Beroe* species peaked approximately one month after the *P. pileus* peak, in June. In 2011, *Beroe* reached its highest densities in autumn. *Beroe cucumis* was only observed in 2011, at which time large beroid ctenophores were collected that had the branching of the gastrovascular system characteristic of *B. cucumis* (Greve 1975). In 2009 and 2012, *Beroe* larger than 30 mm (the published maximuml length for *B. gracilis* Greve (1975)) were also observed but the branches where not visible. *Mnemiopsis leidyi* was absent in the 1980s but present in all recent years. In most years, it was present in low densities throughout the year, and bloomed in August–October at densities an order of magnitude higher than those of *P. pileus*. The year 2009 was an exception with the *M. leidyi* bloom already underway in June.

Prey consumption

Potential food consumption was estimated for the four most abundant species: the hydromedusae *Sarsia tubulosa*, the scyphomedusae *Aurelia aurita*, and the ctenophores *Pleurobrachia pileus* and *Mnemiopsis leidyi*. The other species were only present for brief periods or in much lower abundances.

During 1981–1983, *Pleurobrachia pileus* had the highest water-column clearance rates. Consistent with the trends in abundance, clearance rates showed a peak in spring (Figure 6). Year-to-year differences in clearance rate were large. Maximum rates in spring varied between 0.2 and 0.8 m^3 per m^3 per day with average ($\pm$ SE) rates in spring of 0.099 ± 0.176 m^3 per m^3 per day. Clearance rates of *A. aurita* were an order of magnitude lower than those of *P. pileus,* with highest average rates during summer of 0.003 ± 0.004 m^3 per m^3 per day and clearance rates in *S. tubulosa* were even lower than those of *A. aurita*, with highest average rates in spring of 0.001 ± 0.002 m^3 per m^3 per day. Any impact of gelatinous zooplankton on the rest of the plankton community was restricted to the first half of the year, after July the combined clearance rate of the three species became very low.
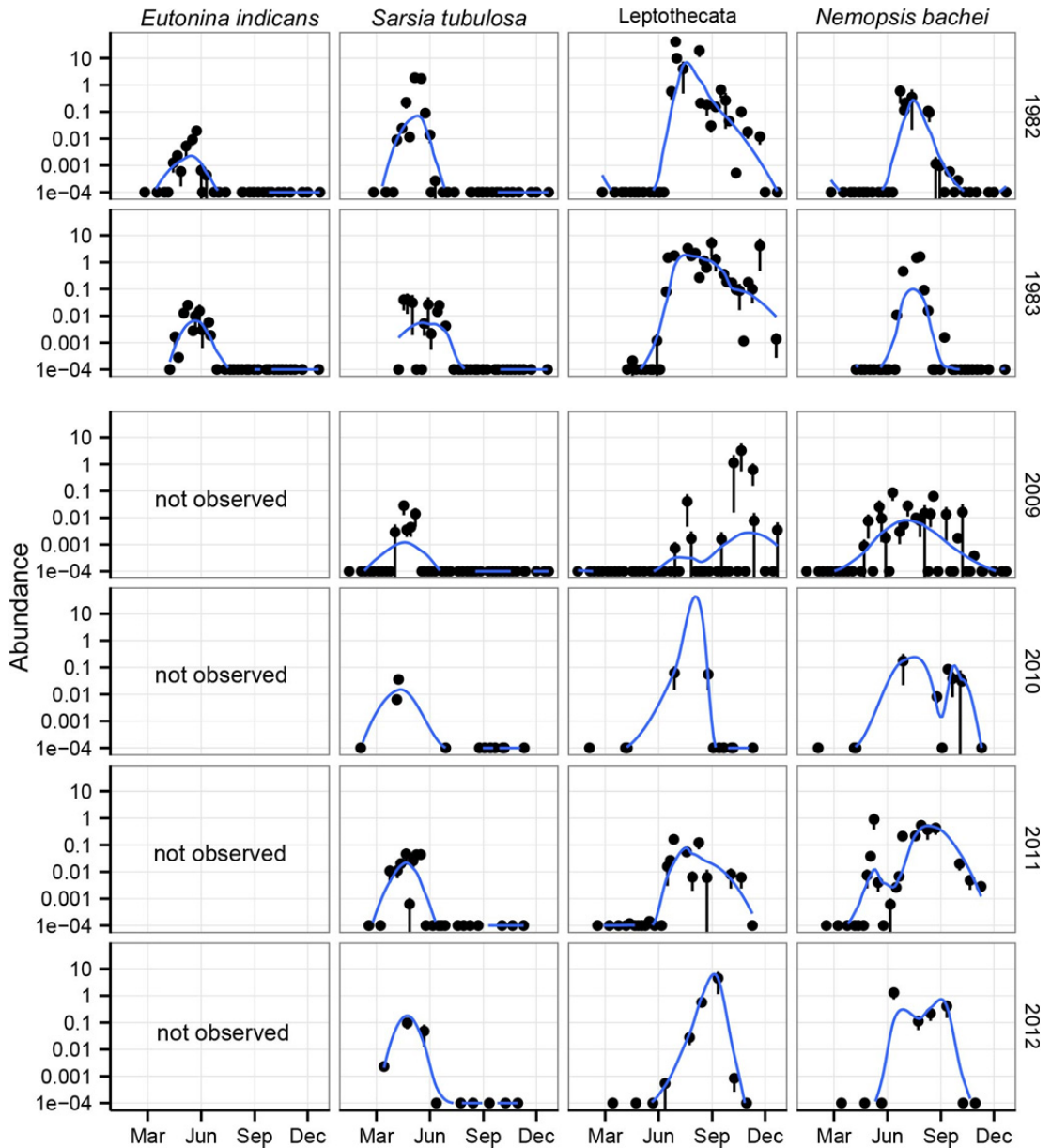
Figure 3. Abundance of Hydromedusae: mean weekly densities ($1e^{-4} + n\ m^{-3}$) with standard errors for *Sarsia tubulosa*, *Eutonina indicans*, Leptothecata (*Clytia hemisphaerica* and *Eucheilota maculata*), and *Nemopsis bachei* averaged over all stations. The y axis is a log scale. A small number ($1e^{-4}$) was added to every value to enable plotting of zero values (species absent) on the log scale. A LOESS smoother (span = 0.6) was added to aid interpretation. Source data including sample sizes are available in supplementary material Table S2.

Period 2009–2012

For *Pleurobrachia pileus, Aurelia aurita* and *Sarsia tubulosa,* clearance rates during 2009–2012 were lower than those during 1981–1983 (Figure 6). Highest clearance rates of *Pleurobrachia pileus* occurred in spring with average rates of $0.013 \pm 0042\ m^3$ per m^3 per day. Clearance rates of *A. aurita* were highest in summer

with average rates of $0.0001 \pm 0.0005\ m^3$ per m^3 per day and clearance rates for *S. tubulosa* were highest in summer with average rates of $0.0001 \pm 0.0002\ m^3$ per m^3 per day. The main difference between both periods was the additional high clearance rate by *Mnemiopsis leidyi*. *M. leidyi* was the most important gelatinous zooplankton species in terms of predation pressure on the zooplankton. *M. leidyi* population
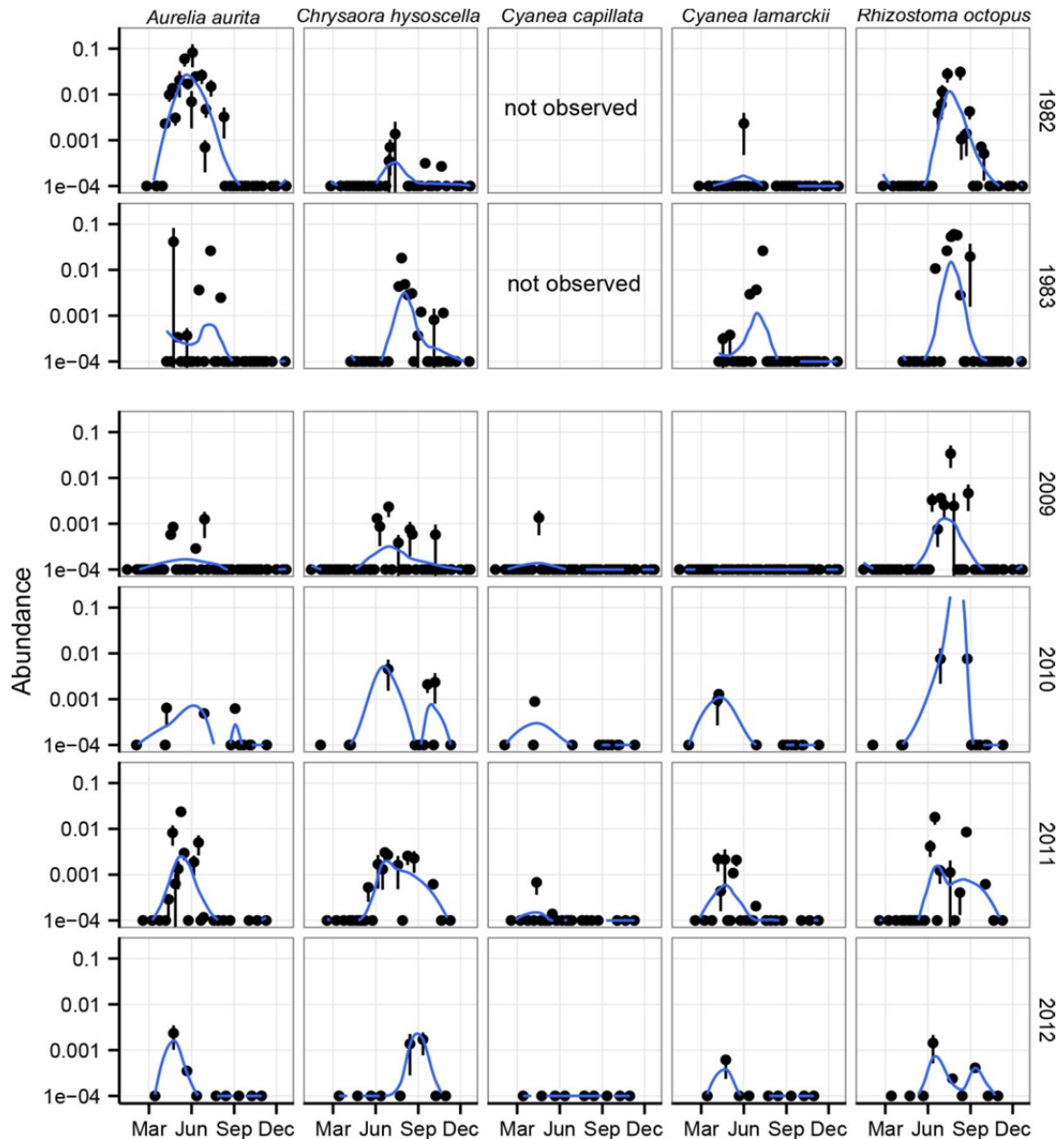
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Figure 4. Abundance of Scyphomedusae: mean weekly densities ($1e^{-4}$ $+$ n m^{-3}) with standard errors for *Aurelia aurita, Chrysaora hysoscella, Cyanea capillata, Cyanea lamarckii* and *Rhizostoma octopus* averaged over all stations. The y axis is a log scale. A small number ($1e^{-4}$) was added to every value to enable plotting of zero values (species absent) on the log scale. A LOESS smoother (span = 0.6) was added to aid interpretation. Source data including sample sizes are available in supplementary material Table S3.

clearance rates were highest in late summer–autumn and in 2009 also in spring. The periods of high daily clearance rates of *M. leidyi* were often of a short duration of one or a few days. The highest maximum clearance rate F_{pop} of *M. leidyi* was slightly higher than 1.0 m^3 per m^3 per day. Estimated zooplankton half-life times showed the same trend.

Using the clearance rate estimates, zooplankton half-life time was longer than three weeks for all

species studied except for *Rhizostoma octopus, Pleurobrachia pileus,* and *Mnemiopsis leidyi* with that of *R. octopus* being lower than three weeks only on a single day; hence, it was not shown (Figure 7). In spring 2011 and 2012, *P. pileus* was still the most important zooplankton predator, but the introduction of *M. leidyi* has caused there to be even higher total predation rates in summer and autumn. For most of the period investigated, the *M. leidyi* population had
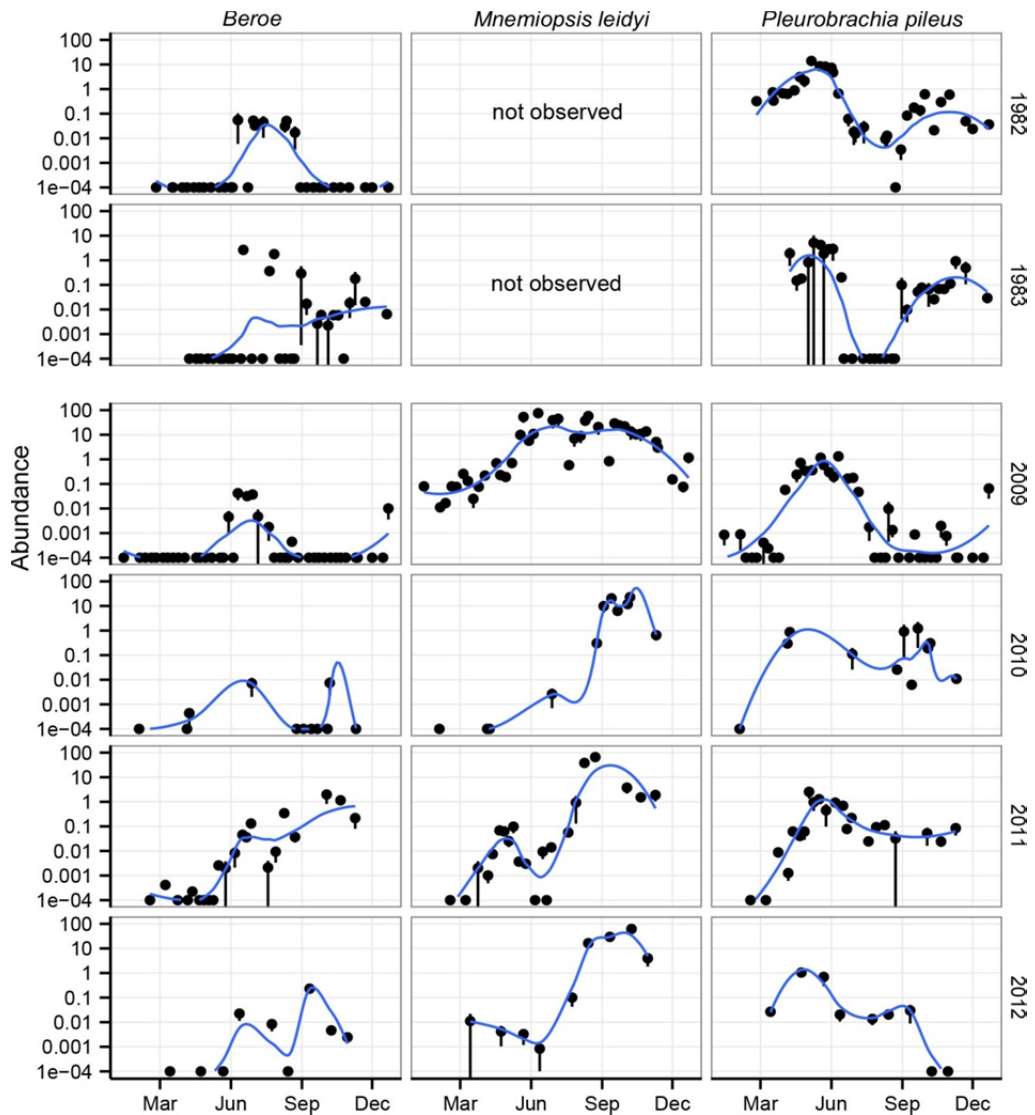
Figure 5. Abundance of ctenophores: mean weekly densities ($1e^{-4+}$ n m^{-3}) with standard errors for *Pleurobrachia pileus*, *Mnemiopsis leidyi* and *Beroe* spp. averaged over all stations. The y axis is a log scale. A small number ($1e^{-4}$) was added to every value to enable plotting of zero values (species absent) on the log scale. A LOESS smoother (span = 0.6) was added to aid interpretation. Source data including sample sizes are available in supplementary material Table S4.

the highest predation rate of any species studied. Contrary to the 1981–1983 period, in 2009–2012 the combined impact of gelatinous zooplankton was not restricted to the first half of the year but was highest in the second half of the year, mainly in late summer to early autumn.

Discussion

A comparison between the 1980s and the present is complicated by the fact that after the 1980s, some important biotic and abiotic characteristics of the

western Wadden Sea have changed. A reduction in riverine N and P inputs (van Raaphorst and de Jonge 2004) was followed by a decrease in primary production (Philippart et al. 2010), and the average annual seawater temperatures have risen from 10 °C to 11.5 °C, an increase that is observed in all seasons (van Aken 2008b). These and other factors have lead to changes in the timing and magnitude of phytoplankton blooms (Philippart et al. 2010) and a reduction of heterogeneity, trophic structure, and nursery function (Eriksson et al. 2010; van der Veer et al. 2011, 2015). Warmer winters are related to changes

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Figure 6. Mean monthly population clearance rates F_{pop} in m³ per m³ per day by *Sarsia tubulosa*, *Aurelia aurita*, *Pleurobrachia pileus,* and *Mnemiopsis leidyi* in the western Wadden Sea as estimated using the size–clearance rate relationship found in Table 1. For 1981, only data on *Aurelia aurita* and *Pleurobrachia pileus* were available.
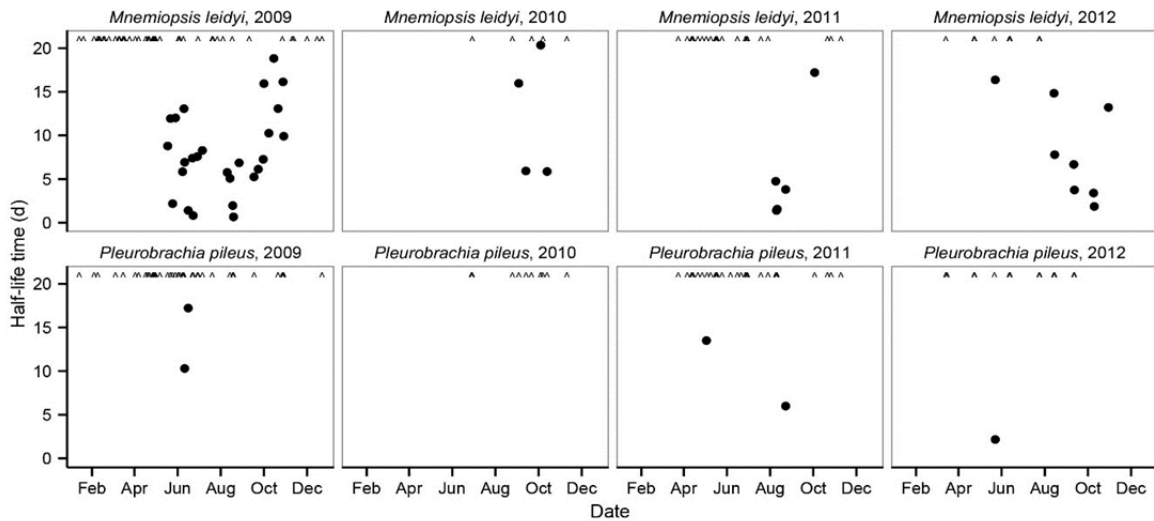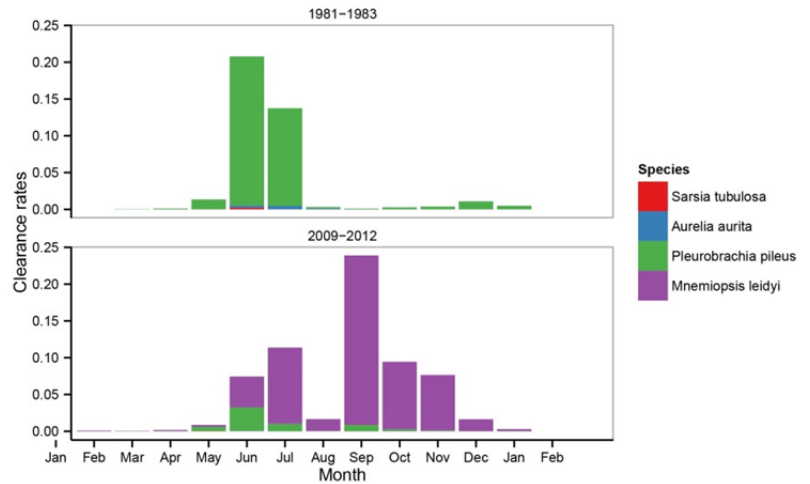

Figure 7. Mean daily zooplankton half-life times due to predicted consumption by *Mnemiopsis leidyi* and *Pleurobrachia pileus* in 2009–2012 estimated from the daily average F_{pop} for the species. Values of half-life times > three weeks are indicated by "^".

in phenology of various organisms such as spawning time in *Macoma balthica* (Philippart et al. 2003), earlier arrival of crustacean predators of bivalves (Dekker and Beukema 2014), and earlier arrival of Scyphozoa (van Walraven et al. 2015).

A large number of invasive species have been found in the Wadden Sea since the 1980s (Wolff 2005). All of these changes are known to influence gelatinous zooplankton abundance, seasonal pattern, and species composition (reviewed in Purcell 2012; Lucas and Dawson 2014). An analysis of 50 years of Scyphozoa catches in a kom-fyke, a passive fishing

gear, in the same area revealed that catches decreased following the decrease in primary production in the 1980s but these variables could not be linked to each other as abundances were highly variable (van Walraven et al. 2015). In the same study, phenology of Scyphozoa changed; *Aurelia aurita* appeared earlier in the year in response to increased winter seawater temperatures and *Chrysaora hysoscella* was present for a longer period in autumn following warmer summers. Similar changes in phenology in response to temperature changes may also have occurred in other gelatinous zooplankton taxa.

Species composition

A comparison of the species composition over time requires observations be obtained and identified in a similar way, preferably by standardised protocols. Sampling methods in this study were almost the same for both periods and species identification was done following the same procedure.

Several difficulties were encountered, however, during taxonomical identification of the samples. For example, van der Baan (1980a) had problems with high abundances of the thecate hydroid *Clytia hemisphaerica* dominating the catches and making it impossible to identify the small thecate hydroids to species level in the formaldehyde-fixed samples. In this study, the method used for analysing the 1982 catches (identifying, counting, and measuring from photographs) could not be used to identify most of the thecate hydromedusae to species level. For that, analysis of fresh or preserved samples using a dissection microscope is necessary.

Nemopsis bachei was originally found in the Netherlands only in the former Zuiderzee, before it was closed off and turned into a freshwater lake in 1932, with the last sighting in 1928 (Wagenaar Hummelinck 1954). In 1993, numerous medusae were caught in the Eastern Scheldt estuary and were first identified as *Bougainvillia* sp., but later concluded to be *Nemopsis bachei* based on the presence of the two small capitate tentacles on each tentacle bulb (Faasse and Ates 1998). In 2002, the species was also found in the Dutch Wadden Sea (Tulp 2002). The authors of the two papers argue that the species was likely present after 1932, but misidentified as *Bougainvillia* species. The findings in this study confirm that *N. bachei* was at least present in 1982 and 1983 in the western Wadden Sea.

Systematics within the genus *Beroe* are confusing (Bayha et al. 2004) and in need of revision. In 2011, large individuals of *Beroe cucumis* were observed for the first time in the surveys. *B. cucumis* has been observed before in the Wadden Sea (Holsteijn 2002). Another species of *Beroe*, *Beroe ovata* sensu Mayer, 1912, was observed in Danish waters in 2014 (Shiganova et al. 2014). The main difference between *B. cucumis* and *B. ovata* seems to be the lack of anostomosing diverticulae in the first species. Anostomosing diverticulae were never observed in *Beroe* from the western Wadden Sea by the authors of this study. Eastern Atlantic *Beroe cucumis* is likely a different species from that occurring in the Mediterranean Sea which has also been named *Beroe ovata* sensu Chun (Mills et al. 1996).

Although species composition differed between years and between the two periods due to presence/ absence of rare species, the overall species composition was rather similar with the same species being abundant. The most significant difference, of course, was the presence of high densities of non-native *Mnemiopsis leidyi* in recent years. The first confirmed sightings in the western Wadden Sea are from 2006 (Faasse and Bayha 2006). It might, however, have been present earlier and misidentified as *Bolinopsis infundibulum* (O.F. Müller, 1776) in 2002 (Holsteijn 2002) or even present as early as 1992 (Faasse and Ligthart 2007). Although large catches of ctenophores were observed during summer in the fish catches of the Royal Netherlands Institute for Sea Research (NIOZ) fish trap long-term monitoring programme in some years before 2006 (H. Witte, NIOZ Royal Netherlands Institute for Sea Research, Texel, pers. comm.), the identity of these ctenophores is unknown.

Seasonal abundance

Hydromedusa

Russell (1953) mentions that the *Eucheilota maculata* usually occurs in late summer and autumn. Its hydroid is found in Dutch coastal waters (Cornelius 1995a; Vervoort and Faasse 2009). *Clytia hemisphaerica* medusae were released in spring and summer off Plymouth according to Russell (1953), and van der Baan (1980a) mention that the species was abundant near the lightvessel "Texel" from June to January, with peak catches in autumn. In this study, peak catches of small Leptothecata were observed in summer, with the highest densities found in 1982. *Eutonina indicans* was not observed in the recent years. It is found in the Wadden Sea and other Dutch coastal waters infrequently (Vervoort and Faasse 2009; Tulp 2001). Ates (2003) gives an overview of sightings of *E. indicans* in the Netherlands and also notes the sporadic occurrence of the species; often with no records for several decades.

Polyps of *Sarsia tubulosa* are known to occur in Dutch coastal waters, including the western Wadden Sea (Vervoort and Faasse 2009). The seasonal pattern of *S. tubulosa* in the western Wadden Sea was the same as described by Cornelius (1995a) in British waters.

This study confirmed that *N. bachei* was at least present in 1982–1983. Thiel (1967) assumed that *N. bachei* arrived in Europe in the mid 19th century from the Atlantic coast of North America attached to ship hulls, but the scarcity of sightings makes it impossible to confirm this. The solitary polyps of *N. bachei* are inconspicuous and have not been found in the field. However, since small medusae of 1 mm length are also found in the Wadden Sea, the polyp

is likely to be found in or near the area. According to Schuchert (2012), the reproductive season of the species is summer–autumn, but in this study it was already observed in April in 2009 and 2011 in relatively high spring temperatures.

Two species of hydromedusae were only observed in 2011. *Margelopsis haeckelii* is known from the Wadden Sea already, the medusae as well as the pelagic polyp stage (Vervoort and Faasse 2009). *Cosmetira pilosella* has not yet been recorded in the plankton of Dutch coastal waters, but several individuals were caught in 1961–1966 from the lightvessel "Texel" located approximately 20 nm offshore Texel island in the North Sea by van der Baan (1980a).

Scyphomedusae

Van der Baan (1980a) studied the seasonal patterns of ephyrae and medusae of scyphomedusae extensively based on plankton samples taken in 1961–1966 from the lightvessel "Texel". She found post-ephyrae (2–10 mm diameter) of *Cyanea lamarckii* from November–June in high densities, post-ephyrae of *Aurelia aurita* in some years in January but most years after March. Small post-ephyrae of *Chrysaora hysoscella* were much less numerous and post-ephyrae of *Rhizostoma octopus* were never observed, although van der Baan (1980b) mentions that they are often observed in the Wadden Sea.

The minimum size of all five scyphomedusae species found in this study was at or close to the size of newly released ephyrae found by Holst (2012b). This means that medusae are likely to be produced in or close to the western Wadden Sea and not only transported there by advection as is the case in the central Baltic Sea (Barz et al. 2006). Experimental work on polyps of the species observed here shows that they can survive in the environmental conditions encountered in the western Wadden Sea (Holst and Jarms 2010; Holst et al. 2007). Only for *Aurelia aurita* have the polyps been found in Dutch coastal waters (Lindeyer and Gittenberger 2011).

Ctenophores

For ctenophores, information on seasonal occurrence is present for the German Bight (Greve and Reiners 1988). The timing of the spring bloom of *Pleurobrachia pileus* in this study was similar to that in the adjacent German Bight. In most years there was a clear succession visible with *Beroe* peaking one month after the *Pleurobrachia pileus* bloom, as is also observed in the North Sea (Greve and Reiners 1988; Greve et al. 2004). Hosia et al. (2011) showed that *B. gracilis* can prey on invasive *M. leidyi*. If *B. gracilis* would be able to successfully prey and

reproduce on a diet of *M. leidyi* densities of the predator should be much higher in late summer–autumn, when high densities of *M. leidyi* occur. Figure 5 however does not suggest that *B. gracilis* has increased in the recent years. Only in 2011 there was a clear increase in *Beroe* density in autumn following the *M. leidyi* bloom. In that period *Beroe* densities were an order of magnitude higher than those of its prey *P. pileus*.

The seasonal pattern of *Mnemiopsis leidyi* in the western Wadden Sea normally includes blooms in summer and autumn, comparable to the seasonal pattern in Narragansett Bay and Long Island estuaries in the native range (Kremer 1994; McNamara et al. 2010). In several studies, *M. leidyi* reproduction was shown to be related to temperature (Costello et al. 2006; Robinson and Graham 2014) and increased winter survival of *M. leidyi* combined with early warming of the water in spring could lead to earlier blooms of *M. leidyi*, as has been observed in the species' native range as well (Costello et al. 2006; McNamara et al. 2010; Robinson and Graham 2014). This consequently means increased overlap with the annual zooplankton spring bloom, as well as spawning periods of bivalves (Philippart et al. 2014) and fish (van der Veer 1985). The seasonal pattern of *M. leidyi* in 2009 showed that earlier blooms have happened at least once already in the western Wadden Sea. As shown in van Walraven et al. (2013), salinity is unlikely to influence the seasonal pattern or abundance of *M. leidyi* within the range of salinity (22–32) observed in the Wadden Sea. In contrast, salinity can be much lower in Scandinavian waters and limits the establishment of *M. leidyi* (Haraldsson et al. 2013).

The introduction of *Mnemiopsis leidyi* does not seem to have affected species composition or seasonal occurrence of most other gelatinous zooplankton species; however, some impact on the abundance of the other ctenophores (especially *P. pileus)* cannot be excluded. During the 2009–2012 period, the size of the peak abundance of *P. pileus* in spring seemed to be much smaller than in the period 1982–1983, suggesting some form of species interaction. In Kertinge Nor, Denmark, high abundances of *Aurelia aurita* appear to limit the establishment of *M. leidyi* in a shallow cove (Riisgård et al. 2010). Densities of *A. aurita* in the Wadden Sea were much lower than in Kertinge Nor, so it is unlikely that *A. aurita* is limiting *M. leidyi* here.

Impact on the zooplankton

Information on the standing stock of zooplankton in the western Wadden Sea was not available for 1982

and 2009–2012; therefore, so it was not possible to compare changes in predation pressure with actual changes in zooplankton concentrations. The available data on gelatinous zooplankton abundance and density in the western Wadden Sea in the 1980s was used in several studies that investigated predation pressure on zooplankton by the most abundant species of ctenophores, scyphomedusa, and hydromedusa, all of which found that the impact of this predation to be low to moderate. Daan (1986) determined ingestion rates and growth rates of *Sarsia tubulosa* in experiments and used these to investigate growth and predation pressure of *S. tubulosa* in situ. He found that growth appeared to be optimal and predation impact on the zooplankton stocks was negligible. Hansson and Kiørboe (2006) estimated size-based clearance rates of *S. tubulosa* feeding on different prey types in the laboratory and used the data on *S. tubulosa* size and abundance from (Daan 1986) to estimate prey mortality rates in the field, and they reached similar conclusions. When the method of Hansson and Kiørboe (2006) is used to estimate clearance rates for *S. tubulosa* in 1982 and 2009–2012, a similar low impact on zooplankton stocks is found.

The predation pressure by *Aurelia aurita* on zooplankton in the western Wadden Sea was found to be low to moderate in 1981 and 1982 (van der Veer 1985; van der Veer and Oorthuysen 1985). As densities of *A. aurita* were lower in recent years, the clearance rates of the *A. aurita* population were also lower, as expected.

Predation on zooplankton by *Pleurobrachia pileus* was investigated using different methods in the 1980s. Specifically, van der Veer and Sadée (1984) estimated the food demand of P. pileus in the western Wadden Sea based on ctenophore abundance and observed growth (here an increase in mean diameter) in the field. They suggest that *P. pileus* is important as a predator in May, as in this month the *P. pileus* population would need to consume half of the zooplankton standing stock daily in order to sustain the observed growth rate. Following up, Kuipers et al. (1990) supplemented field sampling with digestion-time experiments and stomach content analysis of caught animals, which were used to estimate prey consumption rate. Based on this, they estimate a daily mortality rate of less than 0.01 for copepods and copepodites by *P. pileus* predation. This is more than an order of magnitude lower than the estimates of population clearance rate using the same data and the length–clearance rate relationship of Møller et al. (2010). A reason for this may be that Kuipers et al. (1990) based their consumption rates on stomach content analysis of field-caught ctenophores.

Stomach contents were very low in the study of Kuipers et al. (1990), with the majority of stomachs being empty. This suggests that regurgitation occurred during sample fixation (van der Veer 1985), capture, or handling (Larson 1987; Chandy and Greene 1995).

In the 1980s, the seasonal period of highest abundance of the most common species *A. aurita* and *P. pileus* showed little overlap with that of several potential prey species. The immigration of flatfish larvae was earlier (van der Veer 1985) and the start of the mesozooplankton bloom occurred when gelatinous predator densities were already decreasing again (Kuipers et al. 1990).

With *M. leidyi* present the seasonal pattern in zooplankton predation rates was different. While the seasonal pattern of *P. pileus* abundance in 2009–2012 was similar to that observed in the 1980s, the average abundance and thus clearance rate were much lower, making the species less important a predator in the recent period. Densities of other native zooplankton species were similar or even lower in 2009–2012 than in the 1980s, suggesting that they as well are less important as predators now as they were in the 1980s. Here it is shown that *M. leidyi* is now the most important zooplanktivorous predator in the area. Furthermore, the period of highest clearance rates and thus predation rates on zooplankton, has shifted from late spring to late summer and autumn (Figure 6). A recent study has shown that in spring as well as autumn, the Marsdiep area of the western Wadden Sea is an important habitat for zooplanktivorous fish species, including commercial species such as sprat *Sprattus sprattus* (Linnaeus, 1758), herring *Clupea harengus* Linnaeus, 1758, pilchard *Sardina pilchardus* (Walbaum, 1792), and anchovy *Engraulis encrasicolus* (Linnaeus, 1758), which are in turn an important food item for birds, fish, and mammals in the area (Couperus et al. 2016). High predation rates by *M. leidyi* in the autumn period might cause decreased food availability for zooplanktivorous fish and then have cascading effects through the food web.

In a nearby area (Limfjorden) invaded by *Mnemiopsis leidyi*, mesozooplankton was virtually absent at the highest combined clearance rates of *Aurelia aurita* and *M. leidyi* (Riisgård et al. 2012). In that area, mesozooplankton stocks did not show the annual peaks in abundance that were present in years previous to the introduction of *M. leidyi*. Clearance rates of *M. leidyi* in the western Wadden Sea were comparable to those found in Limfjorden and on several days even higher, suggesting a comparable predation pressure of the invasive ctenophores on mesozooplankton in this area. This is also reflected in the zooplankton half-life times we

Figure 8. Different relationships between *Mnemiopsis leidyi* oral-aboral length and individual clearance rates in liters per individual per day from other studies. Riisgård et al. (2012) is used in this study. For Colin et al. (2010) who used total lengths instead of oral-aboral length, oral length was assumed to be 60 % of total length.
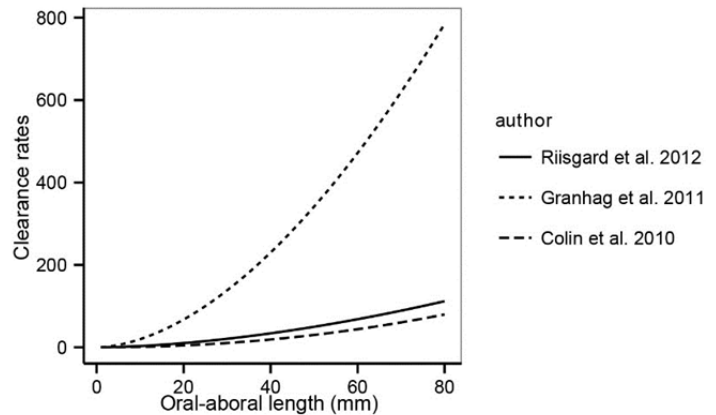
estimated, which were often less than three weeks, which is an average generation time for copepods (Gillooly 2000). On the days with the shortest half-life times, it is likely that *M. leidyi* was controlling the zooplankton stocks. Outside of summer and autumn, however, the predation pressure on the zooplankton community by *M. leidyi* likely was low.

As Purcell (2009) and Riisgård et al. (2012) note, their clearance rate estimates for *M. leidyi* are likely conservative. The relationship between clearance rate and total length of Colin et al. (2010) leads to slightly lower estimated clearance rates for a given length when oral-aboral length is assumed to be 60% of total length (L. van Walraven, unpublished data). When using the relationship between oral-aboral length and clearance rate of Granhag et al. (2011), clearance rates are up to 7 times higher, depending on ctenophore size (Figure 8). Actual predation pressure of *M. leidyi* on zooplankton in the area might be even higher than estimated here.

Larval and juvenile *M. leidyi* feed mainly on microzooplankton (Sullivan and Gifford 2004), but growth rates of microzooplankton-fed *M. leidyi* decrease when the larvae reach a length of 4–5 mm (Sullivan and Gifford 2007). By feeding on micro-zooplankton-feeding mesozooplankton, adult *M. leidyi* can decrease competition for their juveniles as well (McNamara et al. 2013).

The introduction of *M. leidyi* has lead to an increase in predation pressure of gelatinous zooplankton compared to the 1980s, especially in late summer and autumn, a period when in the 1980s predation 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 temporal niche in the Wadden Sea pelagic ecosystem. The concept of invasive species occupying a previously-vacant niche is well known

in invasion ecology (Wilson and Turelli 1986; Hierro et al. 2005) under different names (Catford et al. 2009). In the Wadden Sea, one of the main examples of an invasive species occupying an empty niche is the introduced razor clam *Ensis directus*. This species occupies exposed parts of the intertidal zone that emerge infrequently. This habitat used to have a low density and biomass of macrozoobenthos, but could be used by *E. directus*, which is well adapted to frequent digging and moving in sand (Beukema and Dekker 1995; Dekker and Beukema 2012). Something similar might be happening with *M. leidyi*; it seems to have found and occupied an under-used niche in the area as a zooplanktivore in summer and autumn.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Occurrence of all species caught in pelagic plankton hauls in the western Wadden Sea 2009–2012.

Table S2. Mean weekly densities (n m^{-3}) with standard errors of Hydromedusae averaged over all stations in 1982, 1983 and 2009–2012.

Table S3. Mean weekly densities (n m^{-3}) with standard errors of Scyphomedusae averaged over all stations in 1982, 1983 and 2009–2012.

Table S4. Mean weekly densities (n m^{-3}) with standard errors of Ctenophores averaged over all stations in 1982, 1983 and 2009–2012.

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