Seasional occurrence of the invasive ctenophore *Mnemiopsis leidyi* in the western Dutch Wadden Sea

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**A B S T R A C T**

The ctenophore *Mnemiopsis leidyi* is an invasive species in northern European waters since 2006. This paper presents the first quantitative data for the western Dutch Wadden Sea based on weekly measurements year-round in 2009 of abundance and size distribution. Due to the short residence time of the water, the seasonal occurrence of this species in the western Dutch Wadden Sea is a reflection of its occurrence in the Dutch coastal zone of the North Sea. *M. leidyi* was present the whole year round with multiple peaks. Spawning started in May and was followed by an increase in density of 3 orders of magnitude, leading to the first peak in mid-June (highest mean density 360 ind m⁻³). After a decrease in July numbers increased again and a second peak occurred in mid-August (highest mean density 342 ind m⁻³) during which the highest density of 912 ind m⁻³ in a single haul was observed. At peak densities the population consisted almost entirely of small (<20 mm) ctenophores. Density and biomass remained high until October, decreasing to low levels in November. Predation by *Beroe gracilis* was observed, however the low densities suggested only a minor impact on *M. leidyi*. Predatory impact of *M. leidyi* on fish larvae in the Wadden Sea is likely to be restricted because most fish species spawn early in the year before the first peak of *M. leidyi*. Nevertheless, through competition for food with other zooplanktivores, the species could have a major influence on the Wadden Sea ecosystem.

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1. Introduction

Ctenophores are considered to be important predators and hence components of planktonic ecosystems (Mills, 1995). There are indications that gelatinous zooplankton blooms are increasing in magnitude and frequency (Gibbons and Richardson, 2009) as a consequence of new invasions and a range of anthropogenic factors such as habitat modification, eutrophication, climate change and overfishing (Mills, 2001). During the last decades one such invasion in the coastal waters of north-western Europe has been by the sea walnut *Mnemiopsis leidyi* A. Agassiz, 1865 (Costello et al., 2012).

*M. leidyi* is an opportunistic planktonic predator, feeding on a wide range of different zooplankton prey such as copepods and their nauplii, bivalve veligers, barnacle nauplii (Granbag et al., 2011; Javidpour et al., 2009a), fish larvae (Cowan and Houde, 1992) and eggs (Purcell et al., 1994). It is a simultaneous hermaphrodite, and this feature along with its high fecundity and very high growth rates allow it to increase very rapidly in numbers and biomass under favorable conditions (Purcell et al., 2001) and to form large blooms, which can exert a large predation pressure on zooplankton communities and thus cause a decrease in food availability for other zooplanktivorous animals.

In the 1980s the first invasion of *M. leidyi* to waters outside its native range was in the Black Sea, most likely via ballast water of oil tankers. After its first sighting in 1982 the *M. leidyi* population remained at relatively low levels until 1989, when its density and biomass exploded following recruitment failure in the dominant zooplanktivorous fish species, the anchovy *Engraulis encrasicolus* (Bilio and Niermann, 2004) due to overfishing. This lack of competition combined with climate induced enhanced carrying capacity led to a competitive advantage of *M. leidyi* over pelagic fish, which contributed to further anchovy stock depletion (Oguz et al., 2008). The collapse of pelagic fish stocks had a large impact on fisheries in the region (Knowler, 2005). A few years later, the natural predator of *M. leidyi*, *Beroe ovata*, was also introduced in the Black Sea and subsequently *M. leidyi* blooms decreased in frequency and magnitude (Shiganova et al., 2001). In recent years, *M. leidyi* blooms have been observed outside the Black Sea along the Mediterranean Sea coasts of Spain and Israel (Fuentes et al., 2010).

In north-western Europe, the number of reports of *M. leidyi* increased when molecular identification confirmed the presence of the species (Faasse and Bayha, 2006). By then it had been sighted in coastal waters off Sweden (Hansson, 2006), Germany (Javidpour et al., 2006) and the Netherlands (Faasse and Bayha, 2006; Tulp, 2006). Its presence
in northwestern European coastal waters has now also been reported from Denmark (Tendal et al., 2006), Germany in the North Sea (Boersma et al., 2007) as well as in the Baltic Sea (Javidpour et al., 2006), Poland (Janas and Zgrundo, 2007) and Norway (Oliveira, 2007).

*Leidyia* has most likely been present earlier in northern Europe, in the past mistakenly identified as *Bolinopsis infundibulum* O.F. Müller, 1776. In Dutch waters for example, *Leidyia* was probably present as early as 2002 (Holsteijn, 2002) and maybe even from 1992 in Lake Grevelingen (Faasse and Ligthart, 2007). Despite its presence and the possible influence it may have on ecosystems and especially on zooplanktivorous fish stocks (Purcell and Arai, 2001), no investigations were carried out so far on *Leidyia* in the Dutch Wadden Sea which is an important nursery ground for various fish species (Zijlstra, 1972).

Previous studies on gelatinous zooplankton in Dutch coastal waters were only carried out in the 1980s (Kuipers et al., 1990; Miller and Daan, 1989; Van der Veer and Oorthuysen, 1985; Van der Veer and Sadée, 1984). Therefore, a year-round quantitative sampling program was set up in 2009. This paper presents information on the seasonal occurrence of *Leidyia* in the western Dutch Wadden Sea and discusses the factors influencing its population dynamics in this estuarine area and its potential role as predator on the zooplankton community, including fish and bivalve larvae.

### 2. Material and methods

#### 2.1. Field sampling

All samples were taken in the Marsdiep and Vlie basin in the western Dutch Wadden Sea in various 5–15 m deep tidal gulies during January to December 2009 (Fig. 1). In principle, two or more ebb and flood tides were sampled weekly during daytime and during each tide about 5 hauls were made from anchored vessels. Nets and flow meters were the same as used in previous studies on gelatinous zooplankton in the area (Van der Veer and Oorthuysen, 1985; Van der Veer and Sadée, 1984).

Oblique hauls were made with nets made of polyamide plankton gauze (Monodur 2000, 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$^{-2}$. The maximum depth, average depth and duration of each haul were measured with a Suunto D3 dive computer attached to the net frame. The amount of water passing through the net was registered with a Savonius type flow-meter mounted in the mouth of the net. Porosity and mesh area of the net (definitions according to Smith et al., 1968) were large enough to prevent any serious clogging and overflow even during the spring bloom of the algae *Phaeocystis pouchetii* (see Van der Veer and Sadée, 1984). The general reduction of water flow through the net was about 10% and independent of current velocity. Haul duration varied depending on current velocity, mesoplankton density and density of the alga *Phaeocystis* sp. Haul duration ranged between 3 min at high current velocities and 67 min at very low current velocities, and hence volume filtered per haul differed between 32 and 1099 m$^{-3}$. In addition, water temperature and salinity were measured at the surface once during the haul with a handheld conductivity meter (accuracy ± 0.1 unit).

Depending on volume, the catch was placed directly in a 1 mm sieve after net wash down, or in the case of > 5 l emptied in a 60 l bucket and then washed down above the sieve. Small samples were sorted freshly on board, otherwise the sample or a subsample was fixed and preserved using the slightly modified method of Adams et al. (1976) (see Appendix A). For this, the sample or a subsample of maximum 500 ml was put in an 800 ml glass jar, which was then filled up with the 10 g/l trichloroacetic acid (TCA)-seawater fixation solution. Subsequently, the samples were transported to the lab. In summer, the fixed samples were stored in a styrofoam box with ice for cooling. In the laboratory the TCA-fixed samples were transferred on the day they were caught to a 1% solution of 10 ml preservation stock solution of 5 ml propylene glycol and 45 ml 40% formaldehyde and 990 ml seawater. For this, samples were 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 a 5% solution of 50 ml preservation stock...
solution and 950 ml seawater. Samples were stored at a constant temperature of 4 °C.

2.2. Laboratory measurements

Samples were sorted in black sorting trays and of each individual the distance from the mouth to the statocyst was determined. Ctenophores in length <10 mm were measured submerged in a petri dish using a stereo microscope with a measuring eyepiece. Larger ctenophores were measured using a vernier caliper. Subsampling of large densities of small (≤5 mm length) ctenophores was done using a Folsom plankton splitter. Individuals >2 cm have been considered as adults (c.f. Rapoza et al., 2005).

Measurements on preserved individuals were corrected for shrinkage and converted into fresh length and fresh wet mass (see Appendix A).

2.3. Data analysis

M. leidyi densities were log transformed to stabilize the variance. Analysis of the raw data was not possible due to high levels of autocorrelation, therefore we calculated weekly averages for density, temperature, and salinity and used these for further analyses.

Scatter plots of M. leidyi density versus time and versus the covariates showed non-linear patterns and therefore generalized additive models were applied (Wood, 2006). These models assume homogeneity, normality and independence of residuals. To verify these assumptions, residuals of the models were inspected for temporal correlation using the auto-correlation function. Normality and homogeneity of variance of the residuals were also verified using histograms and plots of residuals versus fitted values (Zuur et al., 2009). All calculations were carried out in R version 2.14.1 (R Development Core Team, 2012). The GAM was applied with the gam function in the mgcv package (Wood, 2006).

To investigate whether the relationship of abiotic factors temperature and salinity differed between the start and end of the season, the year was split into two periods (per) (weeks 3–26 and weeks 28–49). Model selection was performed using stepwise backwards selection. In the full model, the base 10 logarithm of M. leidyi density \( D \) was estimated by a model with intercept \( \alpha \), different smoother \( f \) for temperature and salinity, which also differed per period and an error term \( \epsilon \):

\[
\log(D)_{\text{per}} = \alpha + f(\text{temperature})_{\text{per}} + f(\text{salinity})_{\text{per}} + \epsilon
\]  

The relationship between temperature, salinity and start of spawning was investigated by determining the presence or absence of M. leidyi juveniles of ≤5 mm in length (hereafter called "larvae") for every sampling week. Only data from the first half of the year (weeks 3–26) was used because in the second half of the year this size class was present in all but one week. Logistic regression was used to model the probability of M. leidyi larvae presence \( p \) in relation to water temperature \( t \) and salinity \( s \). These models assume that the data are distributed according to a binomial distribution and that residuals are homogenous and independent. Model selection was performed using stepwise backwards selection. \( \logit(p) \) was estimated by a model with an intercept \( \alpha \), a parameter for temperature \( (\beta_t) \) and salinity \( (\beta_s) \) and error term \( \epsilon \).

\[
\logit(p) = \alpha + \beta_t \times \text{temperature} + \beta_s \times \text{salinity} + \epsilon
\]  

Data analysis was carried out using R (R Development Core Team, 2012) and SigmaPlot® 11.0.

3. Results

3.1. Abiotic factors

Seawater temperature ranged from 1.7 °C in February to maxima of 18–21 °C in May–August, followed by a decrease again to 4.1 °C in December (Fig. 2). Salinity was very variable over the sampled period and also between tidal phases. Salinity decreased from 30 in January to a minimum of 15 in April, after which it increased again to varying levels >22, except for one week in June and December. Salinity was generally higher during flood than during ebb tide, except in late summer/autumn (Fig. 2).

Fig. 2. Mean surface water temperature (SST) and salinity (SSS) of all sampling stations per week during flood and ebb tides in 2009.

Fig. 3. Mean density ± SE (ind m⁻²) of Mnemiopsis leidyi in the western Wadden Sea in 2009. All stations and hauls together.
3.2. Ctenophore data

*Mnemiopsis leidyi* was present the whole year round with lowest densities in February (Figs. 3 and 4). Catches were highly variable with fluctuations of orders of magnitude even within a single tide. Numbers remained low (at or below 1 ind m$^{-3}$) until mid-May. The first increase occurred in June, with a mean density of 360 ind m$^{-3}$. Hereafter, numbers decreased to a minimum of 0.7 ind m$^{-3}$ at the end of July, followed by a second increase with a mean density of 342 ind m$^{-3}$ at the end of August. A week later, there was a 20-fold decrease in density. The highest density in a single haul was 921 ind m$^{-3}$ at the end of August. This peak lasted only one week, after which it decreased again. The highest observed wet mass in a single haul was 204 ml m$^{-3}$ on October 29th.

A 3D plot of *M. leidyi* density versus water temperature and salinity (Fig. 6) showed that the highest densities are reached at the highest water temperatures and at salinities >15. The smoothing function for salinity was not a significant factor in the GAM analysis of weekly averages of *M. leidyi* density in relation to abiotic factors, so the simplest model was:

$$\log(D)_{\text{per}} = \alpha + f(\text{temperature})_{\text{per}} + \varepsilon. \quad (3)$$

Water temperature was significant in both periods (Table 1). A plot of fitted values of the model using different smoothers for each period (Fig. 7) showed a clear positive relationship between water temperature and *M. leidyi* density in the first half of the year. The temperature effect increased at around 12 °C and leveled off at around 17 °C. The fitted model for the second half of the year showed a more complicated relationship between water temperature and *M. leidyi* density, where twice the temperature effect became negative and then positive again. At temperatures <8 °C the confidence interval was very wide.

With respect to the start of spawning, all parameters were significant except salinity (Table 3) and the remaining model was:

$$\text{logit}(p) = \alpha + \beta_1 \times \text{temperature} + \varepsilon. \quad (4)$$

The probability of *M. leidyi* larval presence (ctenophores <5 mm) increased with water temperature and was close to 100% at temperatures >15 °C (Fig. 8).

A few other ctenophore species were found: *Pleurobrachia pileus* (O. F. Müller, 1776) numbers started to increase at the end of March, and a first peak occurred in mid-May with a mean density of

![Fig. 4. Mean length distribution of three different size groups (bars) of Mnemiopsis leidyi of all sampling stations in the western Wadden Sea in 2009, together with total density (black dots; right axis).](image)

![Fig. 5. Mean biovolume of Mnemiopsis leidyi (wet mass; ml m$^{-3}$) in the western Wadden Sea in 2009. All stations and hauls together.](image)

![Fig. 6. 3D graph of Mnemiopsis leidyi density ind m$^{-3}$ versus water temperature and salinity per haul for all stations in 2009.](image)

Table 1

<table>
<thead>
<tr>
<th>Estimate</th>
<th>Std. error</th>
<th>t value</th>
<th>p-value</th>
</tr>
</thead>
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<td>(Intercept)</td>
<td>0.54</td>
<td>0.09</td>
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<td>S(temperature):period 1</td>
<td>4.56</td>
<td>25.4</td>
<td>&lt;0.001</td>
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<tr>
<td>S(temperature):period 2</td>
<td>7.56</td>
<td>9.11</td>
<td>&lt;0.001</td>
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</table>

$R^2$(adj) = 0.85 Deviance explained = 89.3% AIC = 68.15.
2.7 ind m⁻³. Over the next two weeks the numbers decreased to a mean density of 0.3 ind m⁻³ in the beginning of June before increasing again to 3.5 ind m⁻³ at the end of June, which coincided with the first peak in M. leidyi. Hereafter, numbers decreased; after mid-July the species was absent with only a few individuals sampled at the end of August (Fig. 9). Beroe gracilis Künne, 1939 was present only in summer with a mean peak density of 0.3 ind m⁻³ in mid-June, coinciding with the first peak density of M. leidyi and the second peak density of P. pileus. After the beginning of July it had almost disappeared. The individuals caught on June 16 were examined alive in the lab under a dissection microscope, and in one individual an ingested juvenile of Chrysaora hysoscella was found.

3.3. Scyphozoans

The abundance of scyphozoans was remarkably low. Aurelia aurita L. 1758, Chrysaora hysoscella L. 1767 and Cyanea lamarckii Péron and Lesueur, 1810 were almost absent. Rhizostoma octopus L. 1758 was found in different areas. The most abundant scyphomedusa, present from mid-June until the beginning of September, with a maximum density of 0.02 ind m⁻³ in the end of August.

4. Discussion

In 2006 M. leidyi was observed in Dutch coastal waters from August to December (Faasse and Bayha, 2006) but this study shows that in 2009 M. leidyi appeared to be present year-round at least in the western Dutch Wadden Sea. This area is relatively well mixed with only weak vertical salinity stratification (Postma, 1954; Zimmerman, 1976). Approximately 70% of the water in the western Wadden Sea is renewed every week by sea water from the North Sea and fresh water from Lake IJssel (Zimmerman, 1976). Ridderinkhof et al. (1990) estimated the mean turnover time for the Marsdiep basin as 17 tidal cycles (ca. 8.5 days), and that of the Vlie tidal basin as 13 tidal cycles (6.5 days). Nevertheless, particles such as sediment can accumulate in these basins by a mechanism of being swirled up and transported more during the generally stronger flood tides than being washed back with the relatively weaker ebb flows (Postma, 1961; Van Straaten and Kuenen, 1958). This mechanism can also result in an import and accumulation of planktonic organisms, especially small ones such as barnacle (de Wolf, 1973) and flatfish larvae (Rijnsdorp et al., 1985; Van der Veer, 1986). A similar mechanism might apply for ctenophores (de Wolf, 1989).

M. leidyi exhibited multiple peaks in the western Wadden Sea in contrast to other areas in the northern part of its native range, where it exhibits one annual peak in biomass, which generally occurs in late summer and autumn (Table 2). The more irregular and short nature of M. leidyi peaks in the western Wadden Sea may support the view that in the Wadden Sea it is a sink population (Costello et al., 2012). In the Kiel Bight the M. leidyi population also exhibited the same seasonal patterns as observed in this study: multiple short peaks (Javidpour et al., 2009a). The high variation in densities of

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**Table 2**

<table>
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<th>Area</th>
<th>Highest means of:</th>
<th>Reference</th>
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</thead>
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<tr>
<td></td>
<td>Density (ind m⁻³)</td>
<td>Biovolume (ml m⁻³)</td>
</tr>
<tr>
<td>Narragansett Bay</td>
<td>100</td>
<td>544</td>
</tr>
<tr>
<td>Chesapeake Bay</td>
<td>76</td>
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</tr>
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<tr>
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<td>Wadden Sea</td>
<td>613</td>
<td>140</td>
</tr>
</tbody>
</table>

**Table 3**

Model results of the logistic regression model describing the relation between probability of M. leidyi larvae < 5 mm in length presence and water temperature.

<table>
<thead>
<tr>
<th>Estimate</th>
<th>Std. error</th>
<th>z value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>−4.88</td>
<td>2.02</td>
<td>−2.41</td>
</tr>
<tr>
<td>Temperature</td>
<td>0.53</td>
<td>0.20</td>
<td>2.65</td>
</tr>
</tbody>
</table>

M. leidyi in catches made even within a single tide suggests that even in the turbulent and well-mixed channels of the Wadden Sea M. leidyi has a very patchy distribution. This is in line with previous observations on a range of different zooplankton species in the Wadden Sea (de Wolf, 1989).

Density and biomass remained relatively constant throughout the winter until March, when the density stayed constant but the bio-volume in terms of wet mass increased, suggesting a period of growth, but no spawning, as can also be seen in the length distribution. The analysis of weekly averages of M. leidyi density in relation to abiotic factors reveals a significant relationship of ctenophore density with temperature. In the first half of the year ctenophore density increases exponentially with increasing temperature above ca. 13 °C, and levels off at temperatures >17 °C. The second half of the year shows a different, more complicated pattern which is not possible to interpret using temperature alone. Here the temperature effect becomes negative two times. Probably other factors such as food availability (which was not measured) play a role here. A positive relationship between M. leidyi abundance and temperature is also observed in other areas, such as the Baltic Sea (Javidpour et al., 2009b) and North American temperate waters (Kremmer, 1994).

The presence of small ctenophores <5 mm in length was also significantly related to water temperature and was close to 100% probability at temperatures > 15 °C (Fig. 9). The first ctenophores <5 mm were caught at a water temperature of 8 °C. This fits with the observation that in Narragansett Bay low egg production was observed at temperatures as low as 6 °C (Costello et al., 2006).

In growth experiments, larva of M. leidyi reached a length of 2 mm after 5–12 days (Sullivan and Gifford, 2007), which is roughly the minimum length at which they were caught with our sampling gear. As the eggs hatch between 20 and 24 h after spawning (Purcell et al., 2001) and the first large batch of juveniles was observed in mid-May, spawning probably started 6–13 days earlier in the beginning of May. The mean water temperature in this period was 12.6 °C, which corresponds with observations on the start of spawning at ca. 12 °C in Chesapeake Bay (Purcell et al., 2001). Egg production can resume within 2–4 days when favorable conditions occur (U. Bannstedt, unpublished data cited in Purcell, 2001). The rapid increase in temperature in May preceding the first peak of M. leidyi in June might reflect such a period with favorable conditions. In both our models salinity was not a significant covariate. This might be because the minimum salinity observed (15) is still higher than that below which salinity becomes limiting to reproduction (Jaspers et al., 2011).

After each peak there was a rapid decrease in density, especially after the second one that only lasted one week. A possible cause might be predation. However, predators of M. leidyi larvae and juveniles such as A. aurita, C. hysocella or B. gracilis were either absent or present in very low numbers. Intraspecific predation by adults of M. leidyi on juveniles has also been observed in high larval densities and at high water temperatures in the Baltic Sea (Javidpour et al., 2009a,b) and this could be a factor contributing to the rapid decrease in density of larval and juvenile M. leidyi.

The highest mean density of M. leidyi recorded in this study was considerably higher than that observed in estuaries in its native range (Table 2), while the highest recorded mean bio-volume is almost equal or lower. The simultaneous occurrence of peaks in biomass with peaks in density in this study, is also observed in other studies in invaded areas in north-western Europe, such as the Limfjorden (Riisgård et al., 2007) and Kiel Bight (Javidpour et al., 2009a). At these peaks in biomass the population consists almost entirely of small (~20 mm in length) ctenophores. The large mesh size of 2 mm that was used for comparative reasons likely resulted in the loss of many of these small ctenophores. Thus our estimate of the density of M. leidyi during density peaks is likely even an underestimation of the actual density in the field.

The most recent studies on seasonal patterns of gelatinous zooplankton in the same area date back to the early 1980s. During that time P. pileus blooms occurred in spring with peak densities up to 17 ind m$^{-3}$ (Van der Veer and Sadée, 1984). No such bloom of P. pileus was found in 2009, the highest mean density observed was only 3.5 ind m$^{-3}$ in June. Scyphozoan density was so low that the filtering capacity of our sampling gear might be too low to sample them accurately, and a larger net such as an Isaacs–Kidd midwater trawl might be more suited to sample them. The small peak in B. gracilis density observed in 2009 occurred around the same time in the early 1980s, in early/mid June, after the first P. pileus bloom. B. gracilis is able to prey on especially small M. leidyi (Hosia et al., 2011). Several times ingested M. leidyi juveniles inside B. gracilis were observed during this study (pers. obs.), but any quantitative estimation of the predation role of B. gracilis on M. leidyi is not possible at present. In its native range, M. leidyi blooms are partially controlled by the ctenophore B. ovata Bruguiera, 1789, the scyphozoan Chrysaora quinquecirrha Decor and the butterfish Peprilus triacanthus Peck, 1804 (Purcell and Arau, 2001). These species do not occur in the Wadden Sea, and the local Chrysaora (C. hysocella) and Cyanea (C. lamarcckii and Cyanea capillata L. 1758) species, of which the latter is a known predator of M. leidyi (Hosia and Titelman, 2011) were only present in very low numbers. At present the impact of M. leidyi on the ecosystem of the Wadden Sea is still unknown. Recent field and experimental work suggest that in the North Sea, the direct impact of M. leidyi as predator on fish eggs might be restricted and that the indirect effects via competition for food could be more important (Hamer et al., 2011).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.seares.2013.02.003.

References


