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Trophic ecology of *Mnemiopsis leidyi* in the southern North Sea: a biomarker approach

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Abstract The non-indigenous ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 was first observed in the southern North Sea in 2006 and has since then frequently been encountered. Knowledge on the diet, trophic position and interactions with other components of the pelagic food web will largely contribute to assess the impact of this species on the ecosystem. Using both stable isotope (SI) and fatty acid (FA) analysis, this study revealed spatial and temporal variation in the trophic ecology of *M. leidyi* in different ecosystems in the southern North Sea. Based on the isotopic composition, spatial differences were largely driven by variation at the base of the food web rather than diet changes of *M. leidyi* in the different ecosystems. Temporal variation in *M. leidyi* SI composition was also influenced by shifting baseline values and driven by seasonal changes in the associated plankton communities. This study provides first data on the FA composition of *M. leidyi* as compared to FA concentrations of two indigenous ctenophores. Total FA concentration in *M. leidyi* was three to four times lower compared to *Pleurobrachia pileus* and *Beroe* sp., categorising it as a lipid-poor organism. Trophic interactions between *M. leidyi* and two co-occurring ctenophores (*P. pileus* and *Beroe* sp.) showed considerable resource differentiation, which could be the result of competition or different diets. A mixture of zooplankton was identified as potential food sources for *M. leidyi*. FA markers supported the carnivorous diet of *Beroe* sp., but its SI composition did not confirm the predatory relation with *M. leidyi*.

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Introduction

Invasions of non-indigenous species in coastal waters and inland seas are common and form a major threat to marine ecosystems worldwide (Ruiz et al. 1997; Briggs 2007; Katsanevakis et al. 2013). To evaluate the impact of non-indigenous species, one can focus on their (increase in) abundance and spatial or temporal distribution patterns. However, non-indigenous species can also alter the overall functioning and balance of the ecosystem (GESAMP 1997; Scheffer et al. 2001; Streftaris et al. 2005). Food web studies offer a quantitative and integrative framework to evaluate changes in both ecosystem structure and functioning (Thompson et al. 2012).

The non-indigenous ctenophore, *Mnemiopsis leidyi* A. Agassiz 1865, was observed for the first time in the southern North Sea in 2006 and has since then frequently been encountered in coastal waters, ports and estuaries in France, Belgium and the Netherlands, particularly from late summer until early winter (Faasse and Bayha 2006; Van Ginderdeuren et al. 2012; van Walraven et al. 2013; Antajan et al. 2014). In addition to its distribution patterns, knowledge of the diet, trophic position and interactions

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with other components of the pelagic food web will largely contribute to assess the impact of this non-indigenous species on the southern North Sea ecosystem.

Jellyfish in general (i.e. ctenophores and pelagic cnidarians) are usually positioned at the third trophic level in the pelagic food web, feeding on primary consumers like herbivorous crustaceans (Pauly et al. 2009). Therefore, they are often pooled into one single trophic category in ecosystem models (Condon et al. 2012) and can be seen as direct competitors with planktivorous fish (Sommer et al. 2002; Brodeur et al. 2008). However, jellyfish encompass a broad range of species, including predators of other gelatinous zooplankton (e.g. *Beroe gracilis*; Greve and Reiners 1988). Therefore, it is essential to evaluate their trophic diversity at the species level (Nagata et al. 2015). Furthermore, the diet of *M. leidyi* depends on a number of parameters such as ontogeny and food availability, both related to sampling area and period. Adult *M. leidyi* have a broad zooplanktivorous diet, including fish eggs and larvae (Purcell and Arai 2001; Purcell 2009), while *M. leidyi* larvae feed on the smaller microplanktonic fraction of the pelagic food web (Rapoza et al. 2005; Sullivan 2010).

Several techniques have been used to investigate the trophic ecology of jellyfish (reviewed in Pitt et al. 2009). Traditionally, gut content analyses and grazing experiments are performed to study feeding ecology. However, these techniques only allow to document the food items that were recently consumed, giving a diet snapshot, rather than what is actually assimilated (Pitt et al. 2009). Moreover, small or partly digested prey may be difficult to identify. Biochemical tracers, such as stable isotopes (SIs) and fatty acids (FAs) offer several advantages because they provide an analysis of the diet integrated over time and allow to identify contributions from different food sources based on the ‘you are what you eat’ principle (DeNiro and Epstein 1976; Peterson and Fry 1987; Pitt et al. 2009).

The SI composition can identify shared resources (potentially leading to competition) and predation interactions. For example, Kellnreitner et al. (2013) showed that juvenile herring was more enriched in ^{13}C and ^{15}N than *M. leidyi* and concluded based on experiments that competition rather than predation by *M. leidyi* occurred. Furthermore, Hamer et al. (2011) also reported potential competition with the indigenous ctenophore *Pleurobrachia pileus*, while Frost et al. (2012) confirmed *Beroe* sp. (an indigenous ctenophore) as a predator of *M. leidyi*, based on SI analysis.

Comparing FA concentrations and analysing the specific FA composition of organisms help to determine whether an organism is carnivorous or omnivorous and to elucidate the main energy flow at the base of the food web (e.g. Dalsgaard et al. 2003; El-Sabaawi et al. 2009; Pitt et al. 2009). Several studies have been conducted on the FA composition of gelatinous zooplankton (e.g. Falk-Petersen et al. 2002; Nichols et al. 2003; Ju et al. 2004). However, for *M. leidyi* only the total lipids have been determined for the tropical Caribbean Sea by Kremer and Reeve (1989) and by Anninsky et al. (2005) for the Black Sea. To our knowledge, no data on the FA composition of *M. leidyi* have been published yet.

A combination of both SI and FA analyses can give an even better insight into the food web. Such a combined approach was used by Ying et al. (2012) to elucidate the diet and trophic position of three jellyfishes *Aurelia aurita*, *Stomolophus meleagris* and *Cyanea nozakii* in the Yellow Sea. In our study, we performed both SI and FA analyses and investigated (1) spatial, temporal and ontogenetic patterns in the trophic ecology of the non-indigenous ctenophore *M. leidyi* and examined (2) the trophic interactions of this species with co-occurring (native) ctenophores and potential food sources in the southern North Sea food web.

Materials and methods

Study area

The study area covers different systems in the southern North Sea, with locations in Belgian and Dutch coastal waters, major ports in northern France and Belgium, and three estuarine systems (Westerschelde, Oosterschelde and Grevelingen) in the southern part of The Netherlands (Fig. 1; Table 1). The 16 locations are known to be inhabited by *M. leidyi* (Vansteenbrugge et al. 2015).

Sample collection

Sampling occurred between July and December 2012 (always at the beginning of the month) at these 16 locations, when *M. leidyi* was most abundant (Vansteenbrugge et al. 2015). This sampling strategy allowed us to evaluate both spatial and temporal patterns in the trophic ecology of *M. leidyi*. Zooplankton samples were collected using vertical WP2 net hauls (mesh size 200 μm; diameter 0.57 m) and undulating CalCOFI net tows (mesh size 1000 μm; diameter 1 m), deployed from different research vessels at sea and in the estuaries. The port locations (Zeebrugge P1, Oostende P2 and Dunkerque P4) were sampled using a hand-held dip net (mesh size 200 μm; diameter 0.20 m), deployed from moored pontoons. Phytoplankton (as basal food web component) was sampled by means of a Niskin bottle at sea and in the estuaries (closed at 3 m depth) and by means of a beaker in the ports (at the surface).

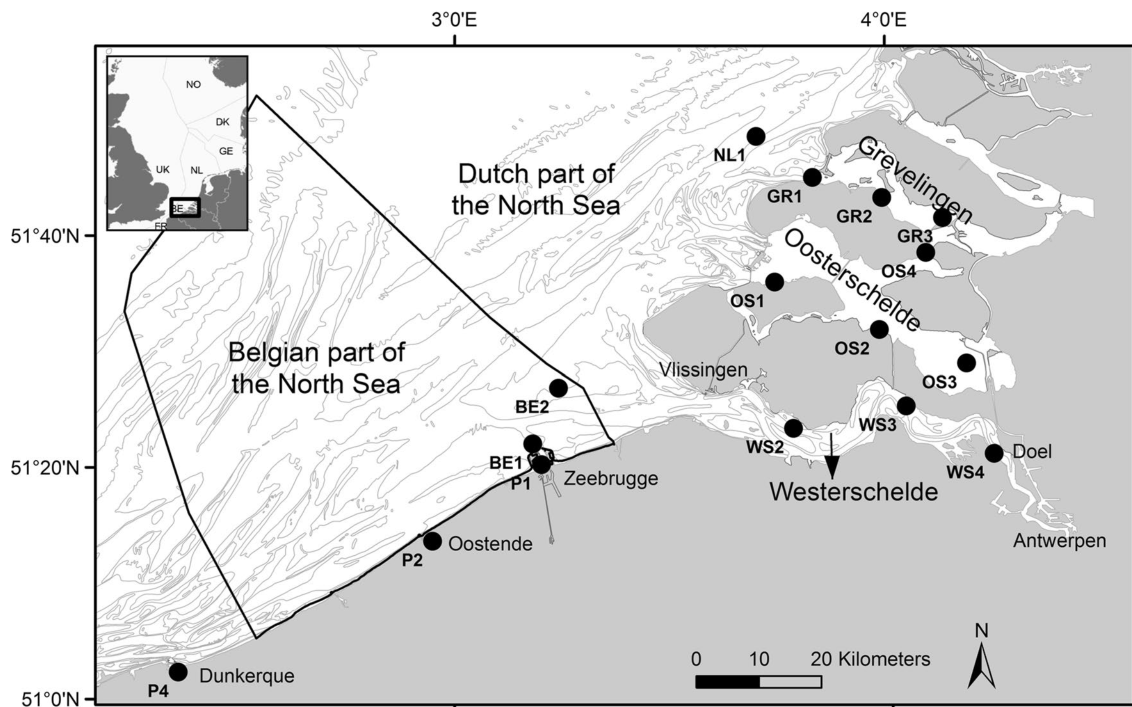

Fig. 1 Study area with 16 locations situated in different systems (ports, estuaries and coastal waters) in the southern North Sea (see Table 1); *inset* North Sea EEZs with indication of the study area

Table 1 Overview of sampling locations in the southern North Sea (FR = France; BE = Belgium; NL = The Netherlands), with shaded areas representing sampling period, letters representing sampled taxa used for stable isotope analyses, and letters in bold representing taxa also used for fatty acid analyses; M = *M. leidyi*, B = *Beroe* sp., P = *P. pileus*, z = zooplankton, c = copepods, m = mysids, p = phytoplankton

Area	Station code*	Coordinates WGS84		Description	2012					
		Lat	Long		July	August	Sept.	October	Nov.	Dec.
Dunkerque port (FR)	P4	51.04°N	2.37°E	Dock connected with canal through sluice				M		
Oostende port (BE)	P2	51.23°N	2.95°E	Semi-enclosed basin			**M**,z,p	M,c,p	M,c,p	z,p
Zeebrugge port (BE)	P1	51.34°N	3.20°E	Navy dock	B,p	M,B,P,z,p	**M**,**B**,p	B,c,p	c	c,p
Belgian part of the North Sea	BE1	51.37°N	3.18°E	Coastal location				M,B,m		
	BE2	51.45°N	3.24°E	Coastal location	P,B,z,m,p	M,P,z,p	**M**,P,z,p	M,B,P,z,m,p	M,B,z,m,p	B,z,p
Westerschelde (NL/BE)	WS2	51.39°N	3.78°E	Lower estuary			M,**P**	M		M
	WS3	51.42°N	4.04°E	Middle estuary			M,**P**	M		
	WS4	51.35°N	4.24°E	Upper estuary			**M**			
Oosterschelde (NL)	OS1	51.6°N	3.74°E	Lower estuary, sea connected		M		M		
	OS2	51.53°N	3.98°E	Middle estuary		M		M		
	OS3	51.48°N	4.18°E	Upper estuary		M		M		
	OS4	51.64°N	4.09°E	Upper estuary, sluice connected to GR				M		
Grevelingen (NL)	GR1	51.75°N	3.83°E	Lower estuary, no connection				M		
	GR2	51.72°N	3.99°E	Middle estuary				M		
	GR3	51.69°N	4.13°E	Upper estuary, sluice connected to OS				M		
Dutch part of the North Sea	NL1	51.81°N	3.7°E	Coastal location				M,B,P,c,m		

* All locations sampled with WP2 and CalCOFI net, except the ports (P1, P2 and P4) which were sampled with a hand-held dip net

Sample processing

From the zooplankton samples, the ctenophores *M. leidyi*, *P. pileus* (as a potential competitor) and *Beroe* sp. (as a potential predator) were isolated, morphologically identified and measured (oral–aboral length, ±1 mm). All *M. leidyi* specimens were grouped into length classes to investigate ontogenetic variation in the trophic ecology. The smallest length class of *M. leidyi* (0–10 mm) represented mainly transitional stages (Rapoza et al. 2005), while the

larger specimens were categorised into 4 classes (11–20, 21–35, 36–55 and >55 mm) based on the length–frequency distributions. For both *M. leidyi* and *P. pileus*, the gastrointestinal canal was removed with a scalpel, to avoid measuring the signal from the ingested prey items (Feuchtmayr and Grey 2003; D'Ambra et al. 2014), and the remaining tissue was stored in 10-mL tubes and frozen at −20 °C for SI analysis and at −80 °C for FA analysis (Table 1). As no −80 °C freezer was present on board, samples were first preserved on dry ice. For *Beroe* specimens (not identified to species level), the entire individuals were stored and frozen, but no visible prey items were present in the gut.

The remaining zooplankton (as potential food source; collected from both WP2 and CalCOFI nets or hand-held dip net) from the samples was washed with deionised water over a 200-μm sieve and stored at −20 °C in sealed petri dishes. Although zooplankton samples were collected during the entire sampling period, only the samples from the Belgian part of the North Sea and the ports of Oostende and Zeebrugge were used for SI analyses (Table 1). For phytoplankton, up to 250 mL water per sample was filtered on pre-weighted, pre-combusted glass fibre filters (GF/F, Whatman, Ø 25 mm). These filters were stored in sealed petri dishes at −20 °C.

Stable isotope analyses

The use of SI analysis is based on the presence of different ratios of the common, light isotope to the heavy, rare isotope in food sources (Peterson and Fry 1987). The most commonly used isotopic ratios are those of carbon and nitrogen. SI ratios are expressed in conventional δ notation (‰) according to the following equation:

$$\delta X = \left[\left(R_{\text{sample}}/R_{\text{standard}}\right) - 1\right] \times 1000,$$

where X is ^{13}C or ^{15}N and R is the corresponding $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio relative to the Vienna Pee Dee Belemnite standard for carbon and atmospheric nitrogen (N_2) for nitrogen. Through fractionation, $\delta^{13}C$ and $\delta^{15}N$ values generally increase through the food chain (Vander Zanden and Rasmussen 2001; Post 2002). $\delta^{13}C$ reflects the origin of the food source (e.g. terrestrial or marine primary production), while $\delta^{15}N$ is mainly used to infer the relative or absolute trophic position (food web complexity) (Vander Zanden and Rasmussen 2001; Tykot 2004).

The frozen ctenophore samples (*M. leidyi*: $n = 267$; *P. pileus*: $n = 32$; *Beroe* sp.: $n = 59$; Table 1; Online Resource 1) were rinsed with deionised water to reduce the salt and were individually transferred to tin capsules (8 × 5 mm; Elemental Microanalysis). For the smallest length class (0–10 mm), several individuals were pooled together per sample. After drying (60 °C, overnight), the tin capsules were folded and placed in a sterile and sealed 96-multiwell. Similarly, the most abundant zooplankton species were selected from the thawed petri dish and transferred to tin capsules. Some were filled with mysids (15 samples), others with copepods (18 samples) or a mix of zooplankton species (including chaetognaths, copepods, mysids, decapod zoea and megalopa larvae, 45 samples). The phytoplankton filters (17 in total) were treated with dilute (10 %) HCl for 2 h to remove the carbonates, prior to drying (4 h, 60 °C), and then folded and placed into silver capsules (8 × 12 mm, Elemental Microanalysis). Multiwell plates containing all capsules were shipped to UC Davis Stable Isotope Facility (USA) for dual SI analyses (C, N) using a continuous flow isotope ratio mass spectrometer (Europa Integra). The C:N ratio for our target species *M. leidyi* was 4:1, and average weights for carbon were 232.39 ± SD 124.68 μg and 55.82 ± SD 28.44 μg for nitrogen.

Fatty acid analyses

The FA trophic marker concept relies on the fact that primary producers are characterised by certain FAs in their tissues, which may be transferred with little or no modification in their structure to their consumers (Copeman and Parrish 2003). As such, they provide knowledge on prey–predator relationships but also on the base of the food web (Dalsgaard et al. 2003; Pitt et al. 2009). Thus, the FA profile of *M. leidyi* will reflect the FA profile of its prey and the overall composition of its diet.

Ctenophore samples (*M. leidyi*: $n = 45$; *P. pileus*: $n = 9$; *Beroe* sp.: $n = 7$; Table 1; Online Resource 1) were freeze-dried overnight before FA extraction. Hydrolysis of total lipid extracts and methylation to FA methyl esters (FAMEs) was achieved by a modified one-step derivatisation method after Abdulkadir and Tsuchiya (2008) as in De Troch et al. (2012). The boron trifluoride-methanol reagent was replaced by a 2.5 % H_2SO_4-methanol solution (2.5 mL) to prevent loss of polyunsaturated fatty acids (PUFAs) (Eder 1995). The fatty acid non-adecanoic acid C19:0 (20 μL, Fluka 74208) was added as an internal standard for later quantification. FAMEs were isolated through centrifuging the samples (Eppendorf Centrifuge 5810R; 3 min at 1000 rpm), heating in water for 1.5 h (80 °C), adding hexane (1.25 mL) and deionised water (1.25 mL) and centrifuging a second time. The FAMEs thus obtained were analysed using a gas chromatograph (HP 6890N) with a mass spectrometer (HP 5973). The samples were run in splitless mode, and 1 μL was injected per run at an injection temperature of 250 °C on a HP88 column (Agilent J&W, USA). The oven temperature was programmed at 50 °C for 2 min, followed by a first ramp to 175 at 25 °C min^{-1} and a second ramp to 230 at 2 °C min^{-1} with a 4-min hold. The FAs were identified by comparison with the retention times and mass spectra of authentic standards and a mass spectral

library (WILEY275), using MSD ChemStation software (Agilent Technologies). Quantification of individual FAs was accomplished using external standards (Supelco # 47885, Sigma-Aldrich Inc., USA) through linear regression of the chromatographic peak areas and the corresponding known concentrations of the standards (ranging from 25 to 200 mg mL^{-1}). Shorthand FA notations A:$B\omega X$ were used, where A represents the number of carbon atoms, B the number of double bonds and X gives the position of the double bond closest to the terminal methyl group (Guckert et al. 1985). FA concentrations were expressed as µg g DW^{-1}.

Data analyses

To visualise the SI composition in bi-plots, different samples were averaged (±standard deviation) per sampling event (station and date). In case different length classes were present, they were represented separately. PERMANOVA (Permutational ANOVA, Primer version 6.1.14 with PERMANOVA add-on software version 1.0.4) was used to investigate spatial and temporal variation in the SI and FA data sets. A PERMDISP test was performed to test the homogeneity of multivariate dispersion for each factor. PERMANOVA is a good tool to investigate variation in these unbalanced data sets, especially when using the type III partial analysis for sums of squares, which assures that the order in which terms are fit does not matter (Anderson et al. 2008).

Multivariate analyses of the SI composition combined $\delta^{13}C$ and $\delta^{15}N$ data per *M. leidyi* individual (or replicate for the smallest length classes) using the Euclidean distance similarity matrix (Clarke and Gorley 2006). To analyse spatial and temporal variation in the trophic ecology of *M. leidyi*, the smallest length class (<10 mm) was excluded to maximise the degrees of freedom. We looked for significant differences (P value <0.05) based on the factors 'area', 'month' and 'area × month' and further used pair-wise tests to locate the differences either within 'area', 'month' or within 'month per area'. Monte Carlo corrections were applied when the number of permutations was too low (<100) (Anderson et al. 2008). To further investigate spatial variation, we focussed on the month October, as most areas (all, except for the port of Zeebrugge, P1) were represented in this month (Table 1). Significant differences for $\delta^{13}C$ and $\delta^{15}N$ were identified separately for the factor 'area' using one-way ANOVA and several pair-wise Wilcoxon tests, applying Bonferroni correction for multiple pair-wise tests (assumptions for parametric tests were met) in R v 3.1.3 (R Core Team 2015). To further investigate temporal variation, we focussed on the BPNS, as most months (all except for July and December) were represented in this area (Table 1). Similarly, significant differences for $\delta^{13}C$ were identified for the factor 'month' using one-way ANOVA and several pair-wise Wilcoxon tests, applying Bonferroni correction for multiple pair-wise tests (assumptions for parametric tests were met) in R. To identify significant differences for $\delta^{15}N$ for the factor 'month', parametric assumptions were not met and therefore a nonparametric Kruskal–Wallis test and several Mann–Whitney U tests were performed in R, applying the Bonferroni correction for multiple pair-wise tests. To test for ontogenetic variation in the trophic ecology of *M. leidyi*, we focussed on an area and month where most length classes were represented (Westerschelde, September; 5 length classes) and again performed one-way ANOVA and multiple pair-wise Wilcoxon tests (including Bonferroni correction; parametric assumptions were met) in R to identify the differences between the length classes for $\delta^{13}C$ and $\delta^{15}N$ separately.

FA data of *M. leidyi* were only available for a few locations (WS3, WS4, BE2, P1 and P2; Table 1), all sampled during September, and limited to three length classes (21–35 mm: $n = 19$, 36–55 mm: $n = 17$ and >55 mm: $n = 9$). Two-way PERMANOVA and pair-wise tests (applying Monte Carlo corrections) were used to analyse significant spatial and ontogenetic differences ($P < 0.05$) within the factors 'area' (WS = locations WS3 and WS4 representing Westerschelde estuary; BE = locations BE2, P1 and P2 representing coastal and port samples), 'length class' and 'area × length class', based on a Bray–Curtis similarity matrix.

To investigate trophic interactions of *M. leidyi* with other components of the planktonic food web, we first focused on the interspecific variation of the ctenophore species in the BPNS: *M. leidyi*, *P. pileus* and *Beroe* sp. The combined $\delta^{13}C$ and $\delta^{15}N$ isotopic composition of all three ctenophores was compared by performing multivariate analyses in PERMANOVA (factor 'species') using the Euclidean distance similarity matrix (Clarke and Gorley 2006). This allowed us to determine whether their position in the bi-plot/food web differed significantly ($P < 0.05$). For the pair-wise tests, Monte Carlo corrections were applied when the number of permutations was too low (<100) (Anderson et al. 2008). A PERMDISP test was performed to test the homogeneity of multivariate dispersion for the factor. Subsequently, we compared the ctenophores in terms of isotopic niche width. To define the isotopic niche space of a species in a community, convex hulls can be used (Layman et al. 2007). However, this metric is sensitive to small sample sizes (Jackson et al. 2011). Therefore, Jackson et al. (2011) suggested to calculate standard ellipse areas (SEAs), using a Bayesian approach and in particular the SEAc metric as it specifically corrects for small samples sizes. Standard ellipses contain about 40 % of the data and are based on a bivariate normal distribution, while the convex hulls are based on the full extent of the data (Jackson et al. 2011). To compare the niche area among species, estimates of the

uncertainty around the SEAc ellipses are calculated using Bayesian inference based on 100,000 posterior draws (i.e. bivariate equivalents to standard deviations in univariate analysis; Jackson et al. 2011). The probability that ellipses of two species are significantly different can then be determined. All these calculations were performed using the SIBER (Stable Isotope Bayesian Ellipses in R) routine in the SIAR package for R v3.1.3 (Parnell et al. 2010; Jackson et al. 2011; R Core Team 2015).

Secondly, we focused on each month (July–December) separately and also considered the potential food sources of the ctenophores. Again, multivariate analyses in PERMANOVA (factor 'species') were performed, and the combined $\delta^{13}C$ and $\delta^{15}N$ isotopic composition of all species were compared (applying Monte Carlo corrections for pair-wise testing and PERMDISP). Ellipses and convex hulls were drawn on the bi-plot to visualise potential niche partitioning. Standard ellipse areas were calculated for all taxa and compared for the three ctenophore species.

Both multivariate and univariate tests were performed on the FA data. Due to the limited data (no samples with all three taxa co-occurring), one-way PERMANOVA was executed (factor 'species') for the FA composition of *Beroe* sp. (P1: $n = 7$) and *P. pileus* (WS2 and WS3: $n = 9$; Table 1) versus *M. leidyi* separately. Univariate nonparametric tests (KW and pair-wise MWU tests with Bonferroni correction) were performed to further compare concentrations of the specific fatty acids between the three ctenophores. Finally, the concentrations of some fatty acids were combined to calculate specific trophic and dietary FA markers for the three ctenophores: 15:0 + 17:0, 18:2ω6, DHA/EPA and D/F (the ratio of all diatom markers over all flagellate markers), respectively, reflecting a bacterial, detritus and dinoflagellate or diatom-based food web (Kaneda 1991; Budge and Parrish 1998; Dalsgaard et al. 2003). Next to these food web markers, also the ratio of polyunsaturated over saturated FAs (PUFA/SFA), and the ratios DHA/EPA and 18:1ω9/18:1ω7 were calculated, indicating a carnivorous or an omnivorous diet (Budge and Parrish 1998; Stevens et al. 2004). Again significant differences were explored using univariate nonparametric tests (KW and pair-wise MWU tests with Bonferroni correction).

Results

Spatial, temporal and ontogenetic variation in *M. leidyi* stable isotope composition

The SI composition of *M. leidyi* samples collected at different stations of the same area clearly clustered together, and significant differences were observed for the factors 'area', 'month' and the interaction 'area × month' (pseudo-$F = 71.92$, 11.31 and 5.11, respectively; $P = 0.0001$). Table 2 presents the results from the pair-wise tests for the factor 'months for area', and Fig. 2a visualises the variation in the SI composition of *M. leidyi* with indication of the spatial differences. The samples from Dunkerque (DK) were significantly different from the rest, with the most depleted $\delta^{13}C$ and $\delta^{15}N$ values. The samples from the Westerschelde (WS) largely clustered together in the bi-plot and were characterised by low $\delta^{13}C$ values and highest $\delta^{15}N$. Another clear group consists of the Oosterschelde (OS) and Grevelingen (GR) samples (no significant differences in pair-wise tests), with high $\delta^{13}C$ values and relatively low $\delta^{15}N$ values. All other *M. leidyi* samples are situated between the WS and OS/GR samples in the bi-plot, stretching along the $\delta^{13}C$ axis, but with comparable $\delta^{15}N$ values (i.e. more enriched in ^{15}N than OS/GR but more depleted than WS). In this group, samples from the port of Zeebrugge (P1) were most depleted in $\delta^{13}C$, followed by the samples from the Belgian and Dutch coastal zone (BPNS and DPNS) and the port of Oostende (P2), with the latter being most enriched in ^{13}C. PERMDISP tests for both 'area' and 'month' were significant ($F = 3.75$; $P = 0.003$ and $F = 19.19$; $P = 0.0001$, respectively), indicating that the significant PERMANOVA results could also be explained by the dispersion of the samples within 'area' or 'month'. Therefore, we focussed on the month October (PERMDISP $F = 2.53$; $P = 0.06$), to present only spatial variation (Fig. 2b). Significant differences in $\delta^{13}C$ were found (one-way ANOVA $F = 76.82$; $P < 0.001$) between samples from Dunkerque, Oostende and the Westerschelde with all other areas ($P < 0.05$). Significant differences in $\delta^{15}N$ were found (one-way ANOVA $F = 56.28$; $P < 0.001$) between samples from Dunkerque and all other areas ($P < 0.001$). The Oosterschelde samples also differed significantly in $\delta^{15}N$ from all areas ($P < 0.03$) except for Grevelingen ($P = 0.99$), while samples of the latter only differed with those of the BPNS and Westerschelde ($P < 0.001$). The $\delta^{15}N$ values from the Westerschelde, BPNS, DPNS and Oostende did not differ significantly ($P > 0.05$).

We focussed on the BPNS to investigate the temporal variation (PERMDISP $F = 5.29$; $P = 0.03$), as these samples were collected with the highest temporal resolution (Table 1; Fig. 2c). August was most depleted in ^{13}C and ^{15}N, while we observed gradual enrichment in both ^{13}C and ^{15}N for the other months. Significant differences were found for the factor 'month' for both $\delta^{13}C$ and $\delta^{15}N$ (one-way ANOVA $F = 9.06$; $P < 0.001$ for $\delta^{13}C$; KW $df = 3$; $P < 0.001$ for $\delta^{15}N$). The bi-plot confirmed the significant pair-wise differences for $\delta^{13}C$ between samples from August with October and November ($P = 0.03$ and $P = 0.0001$, respectively) and between September and November ($P = 0.007$). Significant differences for $\delta^{15}N$ were found between samples from August with October

Table 2 Pair-wise testing showing significant differences in the stable isotope composition of *M. leidyi* (both $\delta^{13}C$ and $\delta^{15}N$) for the factor 'area × month' ($P < 0.05$ marked in bold)

	August			September				October							November	
	BPNS	P1	OS	WS	BPNS	P2	P1	WS	BPNS	P2	DPNS	OS	GR	P4	BPNS	P2
(A)																
Westerschelde estuary (WS)																
Belgian part North Sea (BPNS)				**0.0001**				**0.0015**								
Port Oostende (P2)				**0.0001**	**0.0001**			**0.0008**	**0.0077**						**0.0340**	
Port Zeebrugge (P1)	**0.0130**			**0.0001**	**0.049**	**0.0001**										
Dutch part North Sea (DPNS)								**0.0005**	0.1385	**0.0084**						
Oosterschelde estuary (OS)	**0.0001**	**0.0001**						**0.0001**	**0.0001**	**0.0001**	**0.0029**					
Grevelingen estuary (GR)								**0.0001**	**0.0001**	**0.0002**	**0.0054**	0.2093				
Port Dunkerque (P4)								**0.0001**	**0.0001**	**0.0005**	**0.0011**	**0.0001**	**0.0001**			

	Westerschelde estuary		BPNS				Port Oostende			Port Zeebrugge		Oosterschelde	
	September	October	August	September	October	November	September	October	November	August	September	August	October
(B)													
August													
September			**0.04**							**0.0001**			
October	0.8366		**0.0009**	**0.0001**			**0.0003**					0.0006	
November			**0.0007**	**0.0002**	0.0535		0.1244	**0.009**					

(A) Differences within 'month' for 'area' and (B) differences within 'area' for 'month' (samples of December were not present in this analysis as in this month only specimens smaller than 10 mm were collected, which were not included here to maximise the degrees of freedom)

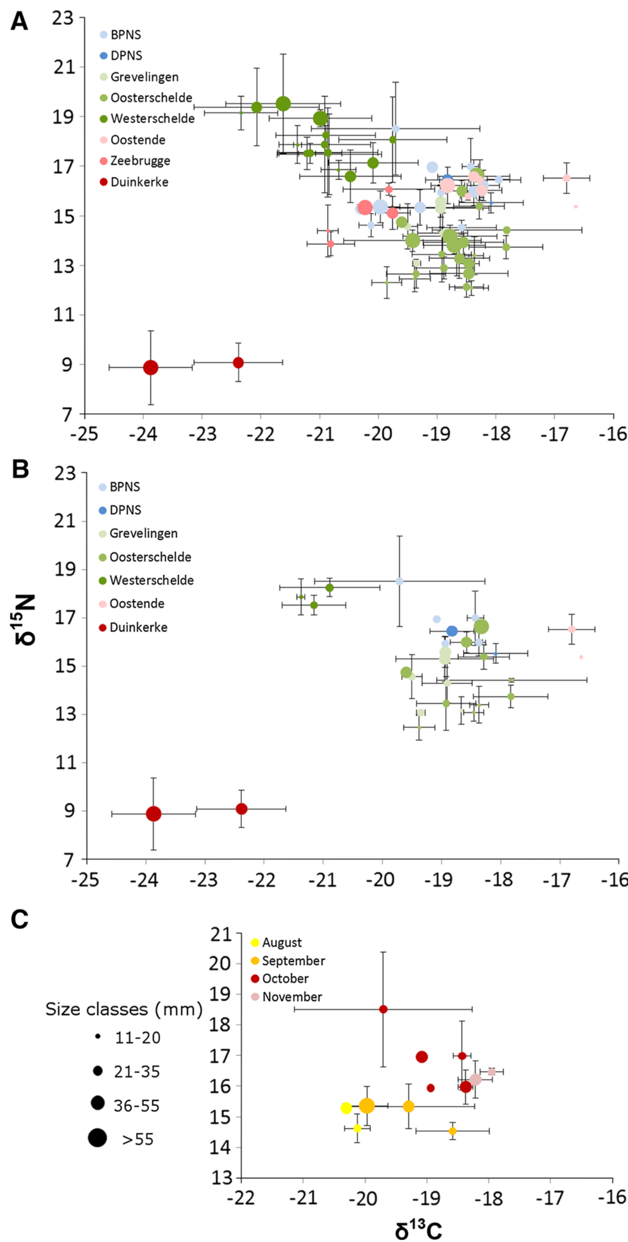

Fig. 2 **a** SI composition for all *M. leidyi* samples, indicating spatial variability; **b** spatial variability in SI composition for *M. leidyi* samples from October over all sampled areas (except for Zeebrugge, where no samples were available); **c** temporal variability in SI composition for *M. leidyi* samples from the Belgian part of the North Sea (BPNS) over all sampled months (except for December, when no samples were available); samples were averaged (±standard deviation) per sampling event, but with indication of different length classes (*note* the different scale on the *y* axis)

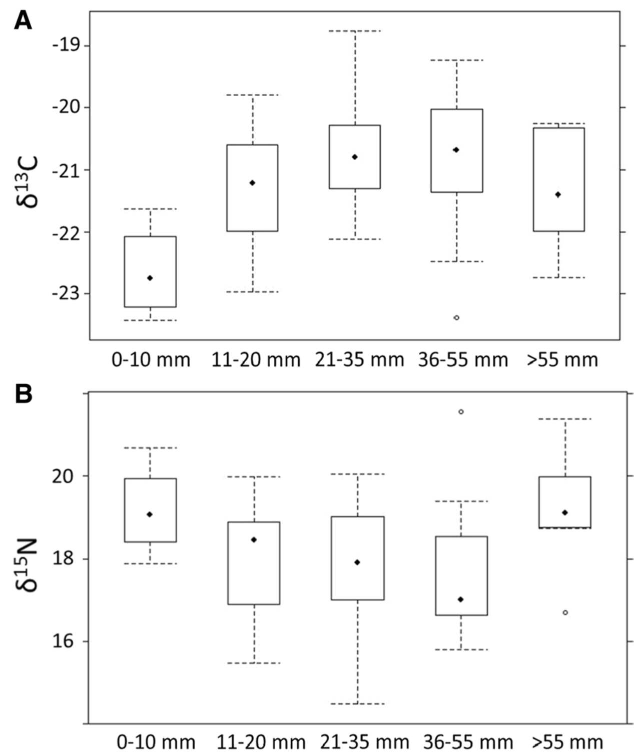

Fig. 3 Ontogenetic variation in $\delta^{13}C$ (**a**) and $\delta^{15}N$ (**b**) for *M. leidyi* samples from the Westerschelde estuary in September with indication of the median (*black dot*), the lower and upper quartiles (25 and 75 %) and the minimum and maximum values

and November ($P = 0.01$ and $P = 0.007$, respectively) and between samples from September with October and November ($P = 0.007$; $P = 0.005$, respectively).

Ontogenetic variation was investigated for the five length classes present in the Westerschelde samples from September (PERMDISP $F = 0.39$; $P = 0.86$). $\delta^{13}C$ values were significantly different for the factor 'length class' ($F = 3.43$; $P = 0.02$; Fig. 3). Pair-wise testing identified significant differences between the smallest length class (0–10 mm) and length class 3 (21–35 mm; $P = 0.01$) and 4 (36–55 mm; $P = 0.03$). For $\delta^{15}N$, no significant differences were found ($F = 2.16$; $P = 0.09$). Although within-group variation was quite large, length class 1 (0–10 mm) was most depleted in ^{13}C compared to the other length classes and most enriched in ^{15}N together with length class 5 (>55 mm) compared to the length classes 2–4 (11–55 mm).

Spatial and ontogenetic variation in *M. leidyi* fatty acid profiles

The concentrations of 15 fatty acids were determined. The FA profiles of *M. leidyi* were not significantly different for the factor 'area' (WS vs. BE; pseudo-$F = 2.50$; $P = 0.06$) nor the interaction 'area × length class' (pseudo-$F = 1.56$; $P = 0.16$). Only some significant ontogenetic differences were noted (factor 'length class'; pseudo-$F = 7.33$; $P = 0.0001$), due to differences between medium-sized individuals (21–35 mm) and larger individuals (36–55 mm and >55 mm, $P = 0.0004$ and 0.0001, respectively). See Online Resource 2 for detailed differences per FA.

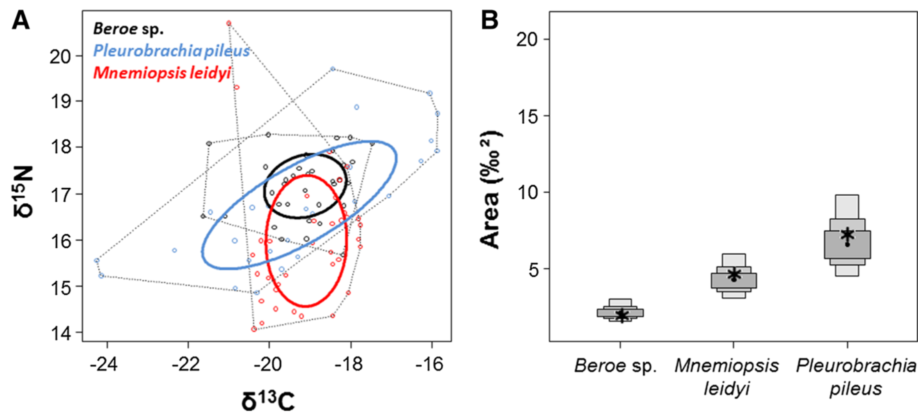

Fig. 4 **a** Variation in δ^{13}C and δ^{15}N values for *Beroe* sp., *M. leidyi* and *P. pileus* from the BPNS. Bivariate ellipses (approximately 40 % credibility interval) and convex hulls, demonstrating the overlapping isotopic niche areas of the three ctenophore species. **b** Surface ellipse area (SEA) measurements per species calculated using Bayesian inference based on 100,000 posterior draws. Measures of uncertainty and central tendency showing 95, 75 and 50 % credibility intervals from light to *dark grey*, respectively [*black dots* mode based on SEA; *asterisk* mode based on SEAc (corrected for small sample size)]

Trophic interactions of *M. leidyi* with co-occurring native ctenophores and potential food sources in the planktonic food web of Belgian coastal waters based on SI and FA analyses

First, trophic interactions between *M. leidyi* and co-occurring native ctenophores in the BPNS were investigated (Fig. 4a). Variation in δ^{13}C and δ^{15}N values as indicated by the ellipses and convex hulls demonstrated common isotopic niche areas among the three ctenophore species. However, the isotopic composition differed significantly with ctenophore species (pseudo-$F = 3.76$; $P = 0.009$), and more specifically between *Beroe* sp. and *M. leidyi* ($P = 0.0001$). Furthermore, based on probability estimates using Bayesian methods, the niche width of *P. pileus* (7.06 ‰^{2}) was significantly larger compared to *M. leidyi* (4.47 ‰^{2}; $P = 0.04$) and *Beroe* sp. (2.13 ‰^{2}; $P < 0.0001$) (Fig. 4b). Additionally, the niche width of *M. leidyi* was significantly larger than *Beroe* sp. ($P = 0.002$).

As samples were collected in the BPNS over a period of six months, temporal variation could be present in the data set (partly reflected by PERMDISP $F = 13.46$; $P = 0.0001$). To identify potential temporal differences, we analysed the data on a monthly basis and also considered the trophic interactions between these ctenophores and potential food sources. The three ctenophores clustered highest in the food web, followed by mysids and zooplankton (Fig. 5). At the base, phytoplankton samples were present over a broad range of δ^{13}C values.

In July, resource differentiation was observed between *Beroe* sp. and *P. pileus* and their niche width did not differ significantly ($P = 0.50$; Fig. 6). In fact, both species had significantly different isotopic compositions (PERMANOVA pair-wise test $P = 0.003$). Considering fractionation levels of 0.4–0.8 ‰ for δ^{13}C and 3.4 ‰ for δ^{15}N (Vander Zanden and Rasmussen 2001; Post 2002), predation interactions could be identified for *P. pileus* and mysids on zooplankton and to a lesser extend for *Beroe* sp. on *P. pileus* and zooplankton on phytoplankton. In August, samples of *P. pileus* and *M. leidyi* were positioned closely together in the bi-plot, which could be pointing to common isotopic niche areas (both feeding on zooplankton). However, their isotopic composition was significantly different ($P = 0.003$). Niche widths did not differ significantly between both ctenophores ($P = 0.25$). Furthermore, a clear shift in δ^{13}C was observed for *P. pileus* compared to July. The enrichment in ^{13}C of *P. pileus* samples continued in September. This resulted in even more resource differentiation between *P. pileus* and *M. leidyi*. Significant differences in isotopic composition for the two ctenophores were found ($P = 0.001$), but niche widths did not differ significantly ($P = 0.34$). In October, samples were available from all three ctenophore species. As in September, resource differentiation was present between *P. pileus* and *M. leidyi*, but also with *Beroe* sp. On the other hand, *M. leidyi* and *Beroe* sp. shared an isotopic niche area, which was supported by the non-significant differences in their isotopic composition ($P = 0.33$). The niche width of *M. leidyi* seemed larger than in September (with extension towards more enriched δ^{15}N values) and was significantly larger than the niche width of *Beroe* sp. ($P = 0.002$), but not compared to the one of *P. pileus* ($P = 0.70$). On the other hand, the niche width of *Beroe* sp. was significantly different from *P. pileus* ($P = 0.02$). From the bi-plot, it is unclear what *Beroe* sp. and *M. leidyi* fed on. *P. pileus* probably fed on the sampled zooplankton. In November, the niche width of *M. leidyi* decreased and was not longer significantly different from the one of *Beroe* sp. ($P = 0.43$), but isotopic composition pointed to resource differentiation between

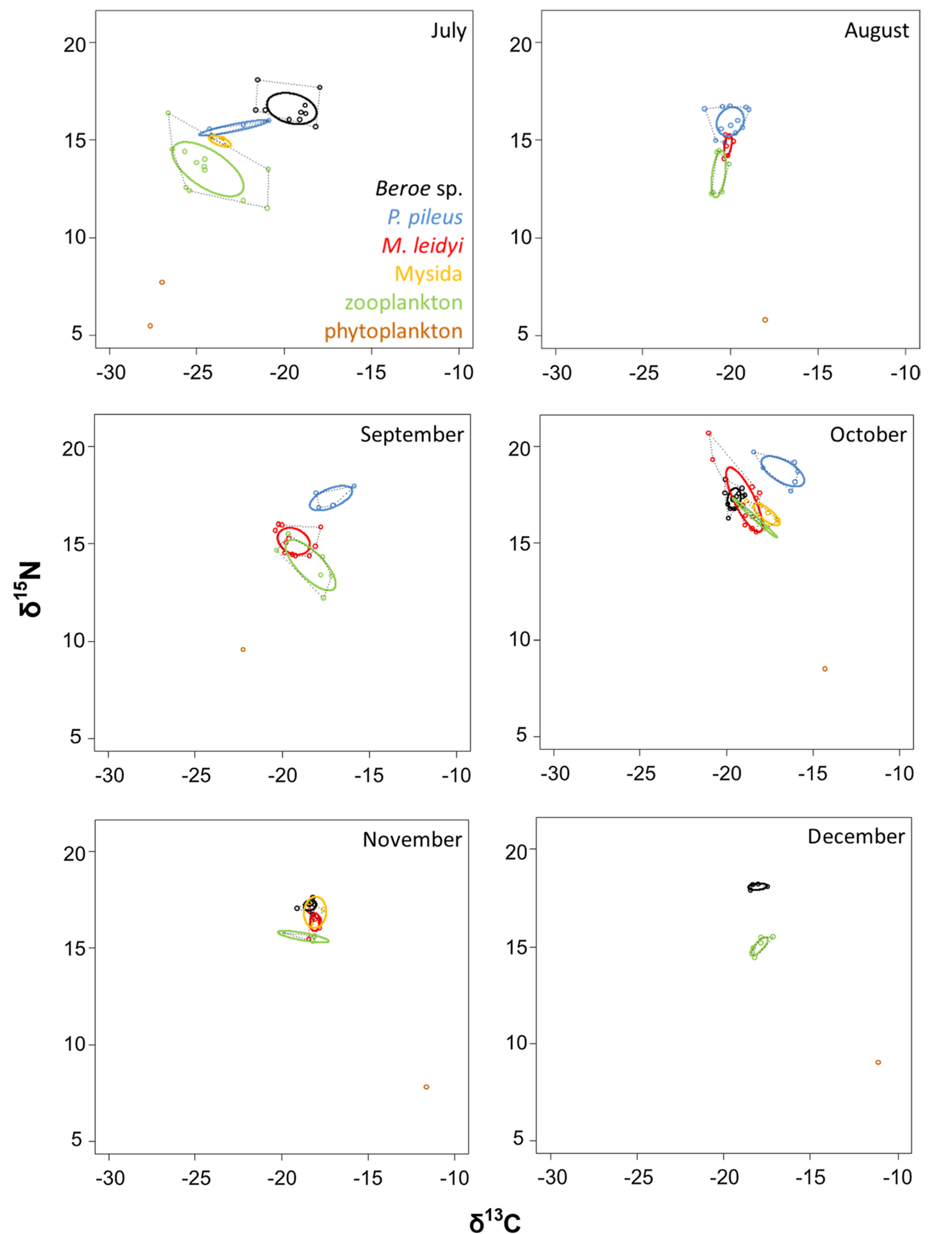

Fig. 5 Variation in the monthly isotopic composition (δ^{13}C and δ^{15}N) of *M. leidyi*, two native ctenophores and potential food sources in the Belgian part of the North Sea. Bivariate ellipses (approximately 40 % credibility interval) and convex hulls, demonstrating common isotopic niche areas or resource differentiation

both species ($P = 0.0001$). The niche area of mysids on the other hand showed considerable overlap with that of the two ctenophore species ($P = 0.17$ for *Beroe* sp. and $P = 0.18$ for *M. leidyi*). In December, only a limited amount of samples was available. *Beroe* sp. remained at the same position in the bi-plot, while zooplankton showed a substantial decrease in its niche width.

Note that the small number of replicates for each taxon resulted in a large range in Bayesian SEA estimates (e.g. phytoplankton samples; Fig. 6). PERMDISP values were not significant for all months ($P > 0.05$), except for August ($F = 5.99$; $P = 0.02$).

The most abundant fatty acids in the three ctenophores were DHA, 16:0, EPA and 18:0 (Table 3). *Beroe* sp. had significantly higher concentrations compared to *M. leidyi* (Table 3; PERMANOVA, pseudo-$F = 10.97$; $P = 0.0001$) for all but one FA (ALA) (MWU tests with Bonferroni correction, $P < 0.02$). Similarly, FA profiles of *P. pileus* differed significantly from *M. leidyi* (PERMANOVA, pseudo-$F = 6.01$; $P = 0.005$), more specifically in concentrations of 16:1ω7 (MWU, $P = 0.003$), 18:1ω9 ($P = 0.02$), 18:1ω7 ($P = 0.03$), 18:2ω6 ($P = 0.001$), ARA ($P = 0.006$) and EPA ($P = 0.0009$). *M. leidyi* had the lowest total average FA concentration (2150 ± 2050 µg g DW^{-1}), being four times lower than *Beroe* sp. (9442 ± 6254 µg g DW^{-1}) and three times lower than *P. pileus* (7001 ± 6343 µg g DW^{-1}). The species-specific analysis on the selected trophic and dietary FA markers showed significantly higher values for *Beroe*

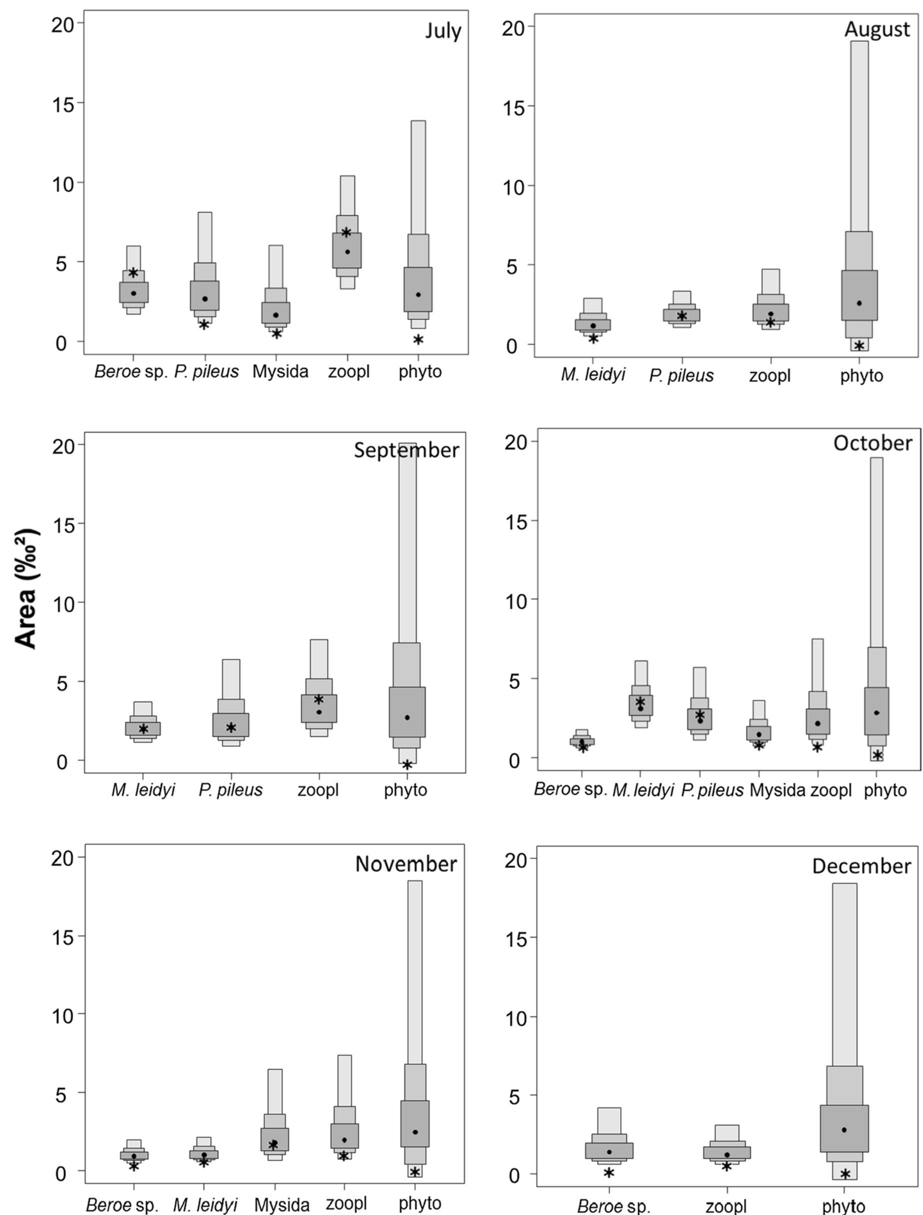

Fig. 6 Surface ellipse area (SEA) measurements per species/species group (zoopl = zooplankton; phyto = phytoplankton) calculated using Bayesian inference based on 100,000 posterior draws. Measures of uncertainty and central tendency showing 95, 75 and 50 % credibility intervals from light to dark grey, respectively (*black dots* mode based on SEA; *red squares* mode based on SEAc (corrected for small sample size); note that the modes do not always overlap as a result of small sample sizes, which also results in much uncertainty, e.g. for phytoplankton)

sp. compared to *M. leidyi* for 15:0 + 17:0, PUFA/SFA and 18:1ω9/18:1ω7 (Fig. 7). The other ctenophore *P. pileus* differed significantly from *M. leidyi* in 18:2ω6, DHA/EPA, PUFA/SFA and D/F. *Beroe* sp. differed significantly from *P. pileus* for DHA/EPA, 18:1ω9/18:1ω7 and D/F.

Discussion

Spatial, temporal and ontogenetic variation in trophic ecology of *M. leidyi*

Two types of trophic biomarkers, SI and FA, revealed spatial, temporal and ontogenetic variation in the trophic ecology of *M. leidyi* in the southern North Sea. The spatial variation in isotopic composition did not so much reflect geographical differences, but rather alterations at the base of the food web in the different systems. The δ^{13}C values of marine coastal organic matter are typically situated between −18 and −22 ‰ (Thornton and McManus 1994 and references therein). A similar range was noted in the samples of *M. leidyi* originating from the coastal areas (BPNS and DPNS), the Belgian ports (Zeebrugge and Oostende) and the Grevelingen (GR) and Oosterschelde (OS) (highly saline) estuaries. In contrast, *M. leidyi* samples from the Westerschelde estuary (WS) and port of Dunkerque (DK) were more depleted in δ^{13}C. Dunkerque receives riverine water through a sluice from the Canal de Bergues. This not only affects salinity but also affects the organic matter input in this system. Organic matter originating from

Table 3 Absolute (μg g DW^{-1}) and relative (%) concentrations of fatty acids in three ctenophore species in the southern North Sea

Fatty acid		*Beroe* sp. ($n = 7$)			*P. pileus* ($n = 9$)			*M. leidyi* ($n = 52$)		
Systematic name	ω reference	Mean	±SD	%	Mean	±SD	%	Mean	±SD	%
cis-4,7,10,13,16,19-docosahexaenoic acid	22:6ω3 (DHA)	4333.7	2908.0	45.9	2406.5	2163.0	34.4	974.6	951.7	45.3
Hexadecanoic acid	16:0	1818.7	1225.8	19.3	1352.1	1142.1	19.3	498.2	461.2	23.2
cis-5,8,11,14,17-eicosapentaenoic acid	20:5ω3 (EPA)	879.6	583.9	9.3	1573.5	1466.4	22.5	196.4	230.6	9.1
Octadecanoic acid	18:0	479.4	316.7	5.1	486.0	446.1	6.9	158.4	144.9	7.4
Tetradecanoic acid	14:0	259.4	167.2	2.7	216.2	191.9	3.1	77.2	67.2	3.6
*cis*7-octadecenoic acid	18:1ω7	134.8	99.0	1.4	141.6	123.0	2.0	43.0	48.1	2.0
Heptadecanoic acid	17:0	149.5	99.9	1.6	89.7	88.8	1.3	42.6	39.0	2.0
cis-5,8,11,14-eicosatetraenoic acid	20:4ω6 (ARA)	470.3	297.0	5.0	250.1	285.6	3.6	38.7	47.9	1.8
*cis*9-octadecenoic acid	18:1ω9	317.0	205.9	3.4	130.6	130.6	1.9	34.2	31.7	1.6
*cis*9-hexadecenoic acid	16:1ω7	218.1	136.9	2.3	178.6	146.6	2.6	30.0	32.2	1.4
Pentadecanoic acid	15:0	115.0	83.6	1.2	50.5	47.5	0.7	23.7	23.6	1.1
cis-11-eicosenoic acid	20:1ω9	116.5	76.8	1.2	24.7	22.9	0.4	9.6	14.2	0.4
cis/trans-9,12-octadecadienoic acid	18:2ω6	32.6	27.5	0.3	80.9	92.3	1.2	8.7	14.9	0.4
cis-9,12,15-octadecatrienoic acid	18:3ω3 (ALA)	25.0	27.7	0.3	14.2	19.5	0.2	8.7	15.3	0.4
Eicosanoic acid	20:0	92.8	73.9	1.0	5.9	7.8	0.1	6.1	8.8	0.3
	Total	9442.4		100.0	7001.0		100.0	2150.2		100.0

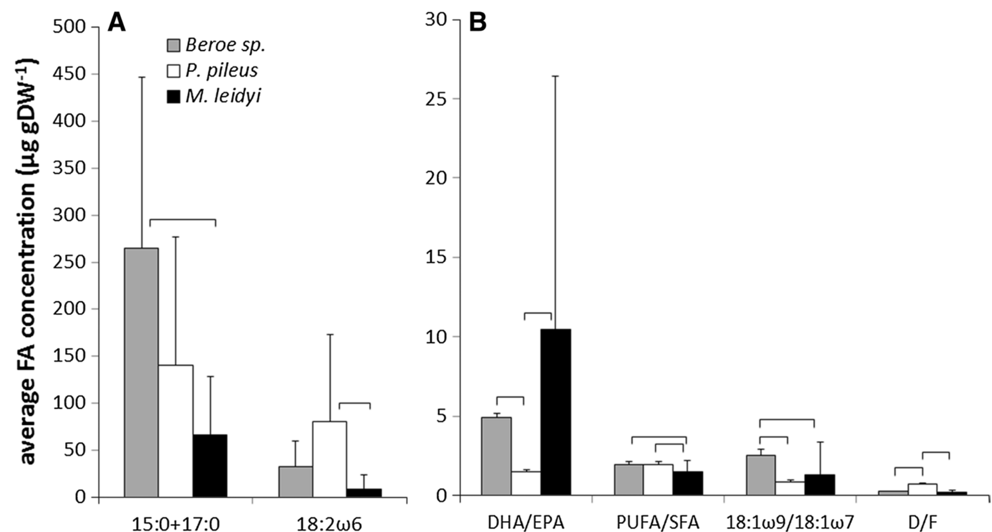

Fig. 7 Trophic and dietary fatty acid markers per ctenophore species: **a** average FA concentrations (±standard deviation); **b** FA biomarker ratios. Significant differences between species indicated by *brackets* (see "Materials and methods" for explanation of the FA names)

terrestrial, sewage estuarine or riverine sources is generally more depleted in $\delta^{13}C$ values, with values between −26 and −27 ‰ for terrestrial material (Thornton and McManus 1994), between −28 and −23 ‰ for sewage (Andrews et al. 1998) and between −30 and −40 ‰ for riverine sources (Hamilton et al. 1992). Also, the Westerschelde is influenced by a river (Schelde), but *M. leidyi* samples were collected in the polyhaline part of the estuary. These samples were probably more influenced by estuarine sources with $\delta^{13}C$ values between −21 and −24 ‰ (Middelburg and Nieuwenhuize 1998). Through incorporation by microorganisms, the depleted carbon is further transferred to higher trophic levels (Thornton and McManus 1994; Middelburg and Herman 2007). As such, the influence of the depleted resources was also reflected in *M. leidyi* $\delta^{13}C$ values of WS and DK.

Still, the diet of *M. leidyi* in the Westerschelde probably does not depend on the bacterial and terrestrial detritus-based food web alone. A higher proportion of odd-chained fatty acids 15:0 + 17:0 and 18:2ω6 would then be expected when compared to the marine (coastal) samples (Kaneda 1991; Fukuda and Naganuma 2001; Dalsgaard et al. 2003). However, this was not the case, as the FA profiles of *M. leidyi* specimens from the marine samples were not

significantly different from the estuarine samples. Perhaps, the smaller amount of FA samples ($n = 45$) compared to SI analysis ($n = 267$) might have obscured some of the spatial variation. However, most likely, *M. leidyi* also feeds on the phytoplankton-based food web in the Westerschelde (Heip et al. 1995).

The $\delta^{15}N$ values are generally used to determine trophic position in the food web (Minagawa and Wada 1984; McCutchan et al. 2003). However, the higher $\delta^{15}N$ values in the WS samples do not necessarily reflect a longer food chain. Again, an alteration in baseline values, this time for $\delta^{15}N$, seems more likely. At the riverine part of the Schelde, high concentrations of ammonium and a preferential uptake of ^{14}N by microorganisms have been observed. This results in more ^{15}N in the Westerschelde, which is even further enhanced by the long residence time of water (1–3 months) throughout the system (Mariotti et al. 1984; Middelburg and Herman 2007). The incorporation of this ^{15}N is reflected in the enriched SI values of higher trophic levels, including *M. leidyi*. When accounting for the effect of fractionation (3.4 ‰; Vander Zanden and Rasmussen 2001) per trophic level, the coastal (BPNS and DPNS) and Belgian port (Zeebrugge and Oostende) samples again reflected the marine origin at the basis of the food web in these systems, with a typical nitrogen isotopic range for marine organic matter between 8 and 10 ‰ (Sweeney and Kaplan 1980b; Mariotti et al. 1984). The more depleted $\delta^{15}N$ values in the OS and GR estuaries and surely in the DK samples could point to a considerable detritus and sewage ($\delta^{15}N = 1.5$–2.5 ‰) influence in those systems (Sweeney and Kaplan 1980a; Mariotti et al. 1984).

Temporal variation in SI composition of *M. leidyi* has been observed in several areas (e.g. Hamer et al. 2011; van Looijengoed 2011; Nagata et al. 2015). Notwithstanding the short seasonal occurrence of *M. leidyi* in Belgian waters (Vansteenbrugge et al. 2015), we found temporal differences in SI composition. Both $\delta^{13}C$ and $\delta^{15}N$ values of *M. leidyi* tended to increase from August towards November, which can be explained by several simultaneously working processes. After the spring phytoplankton bloom, high amounts of suspended matter (dead phytoplankton cells) are present in the water column, enhancing microbial processes (Mariotti et al. 1984; Thornton and McManus 1994; O'Brien et al. 2011). This enriches the isotopic baseline and consequently the higher trophic levels including *M. leidyi*. Changes in phytoplankton and zooplankton species composition over time (O'Brien et al. 2011; Van Ginderdeuren et al. 2014) result in temporal variation in prey availability. Consequently, the diet composition of *M. leidyi* and lower trophic levels may change over time. Moreover, calanoid copepods from temperate regions (e.g. *Acartia tonsa*) may change from a herbivorous to a carnivorous diet to survive winter (Lonsdale et al. 1979). Such dietary shifts may also lead to enrichment in ^{15}N, reflected in the isotopic composition of higher trophic levels.

Some ontogenetic variation was observed both in SI and FA, but a clear enrichment as a result of ontogenetic shifts from larvae to adults was not fully confirmed by our results. Larvae of *M. leidyi* (<10 mm) feed on microplankton (including autotrophic and heterotrophic prey), normally resulting in more depleted $\delta^{13}C$ and $\delta^{15}N$ values (Sullivan and Gifford 2007; van Looijengoed 2011). This was not the case in our study and may partly due to the limited amount of samples. Rapoza et al. (2005) stated that after metamorphosis from the tentacular cydippid larvae to the lobate adult, the diet and consequently the $\delta^{15}N$ values in *M. leidyi* remained the same for all adults >30 mm. Both SI and FA profiles in our samples largely corroborated these findings for the adult length classes. The lower concentrations of FAs 15:0, 17:0 and 18:2ω6 might indicate that specimens between 21 and 35 mm were less dependent on a detritus or bacteria-based food web in comparison with the larger adults (Kaneda 1991; Fukuda and Naganuma 2001; Dalsgaard et al. 2003). However, length class does not always reflect adult age and smaller adults might have been poorly fed (shrinking; Anninsky et al. 2005).

Trophic interactions of *M. leidyi* with co-occurring ctenophores and potential food sources in the planktonic food web of Belgian coastal waters

Based on similar isotopic compositions and overlapping isotopic niches, the ctenophores *M. leidyi* and *P. pileus* seemed to share resources in the BPNS. Isotopic niche width was larger in *P. pileus*, indicating that this native ctenophore is more of a generalist than the non-indigenous *M. leidyi*. However, when considering temporal variation, niche overlap between these two species seemed to be avoided, and common isotopic niche areas were rare.

This resource differentiation could be explained by competition between the two ctenophores, which is supported by the fact that the isotopic niche of *P. pileus* seemed to enrich more in ^{13}C over time compared to *M. leidyi*, especially when the two species co-occur. However, this could also be the result of different diets. The food source of *P. pileus* would then be more enriched in ^{13}C, for example, as a result of changes at the base of the food web. The FA data supported this and showed that for the indigenous ctenophore *P. pileus*, the diatom-based (low DHA/EPA and high D/F ratios) and detritus-based (high 18:2ω6) food web seemed to be more important (Budge and Parrish 1998, Dalsgaard et al. 2003). In contrast, the FA profile for *M. leidyi* revealed an omnivorous diet (low 18:1ω9/18:1ω7 ratio) with a strong dependency on the dinoflagellate-driven food web, as can be derived from the high DHA/EPA and low D/F ratios (Budge and Parrish 1998; Stevens et al. 2004;

Dinasquet et al. 2012). This is further supported by the fact that both ctenophores exhibit different hunting mechanisms. *P. pileus* is an ambush predator and stretches its tentacles into a wide 'net' entangling highly mobile prey (Gibbons and Painting 1992; Costello and Coverdale 1998). The lobate *M. leidyi* on the other hand generates a feeding current through beating of the cilia on the four auricles, which directs prey towards its colloblasts (Waggett and Costello 1999; Colin et al. 2010). Additionally, *M. leidyi* captures prey when they collide with the inner surface of its oral lobes. The combination of both techniques supports a broader diet for *M. leidyi*, as it can catch less mobile microzooplankton as well as highly mobile mesozooplankton (Costello and Coverdale 1998; Waggett and Costello 1999).

In the eastern North Sea, Hamer et al. (2011) observed competition between these ctenophore species based on overlapping prey spectra (metazoan prey between 150 and 1000 µm), but also seasonal niche differentiation as *P. pileus* feeds on fish eggs at certain times of the year. Frost et al. (2012) identified mesozooplankton >300 µm as prey for *P. pileus* in the central North Sea, whereas *M. leidyi* was shown to have a variable diet ranging from microzooplankton and slowly swimming zooplankton to calanoid copepods (Javidpour et al. 2009; Granhag et al. 2011). This would imply that *M. leidyi* is more of a generalist (having a larger niche width) than *P. pileus*, which was not confirmed by our data (isotopic niche areas were not significantly different between *M. leidyi* and *P. pileus*).

The ctenophore *Beroe* sp. has been described as a predator of both *P. pileus* and *M. leidyi* (Greve and Reiners 1988; Hosia et al. 2011; Frost et al. 2012). However, this was not fully supported by our data and probably some temporal variation in the isotopic niches occurred. The isotopic composition between *Beroe* sp. and *M. leidyi* differed significantly over all samples of the BPNS (regardless the temporal variation) and *Beroe* sp. probably fed on *P. pileus* in July. However, in October $\delta^{15}N$ of *Beroe* sp. was lower than that of *P. pileus* and overlapped with *M. leidyi*. Hosia et al. (2011) showed that *M. leidyi* of 20 mm (oral–aboral length) or larger could only be partially consumed by *Beroe* sp. (handling error). Consequently, *Beroe* sp. probably fed on the smallest ctenophores or on small hydromedusae in the BPNS in October. Its carnivorous diet was corroborated by high proportions of the specific FA ratios DHA/EPA, PUFA/SFA and C18:1ω9/C18:1ω7 (Budge and Parrish 1998; Stevens et al. 2004).

The overall FA concentration in *M. leidyi* was considerably lower compared to the other ctenophores, which labels it as a lipid-poor species (Lee et al. 2006). *M. leidyi* has a low reserve capacity and is characterised by high turnover rates of reserve compounds and fast shrinkage (Lee et al. 2006; Augustine et al. 2014). Although *P. pileus* had three times higher FA concentrations than *M. leidyi* in our study, Lee (1974) labelled it also as a lipid-poor species. A more detailed analysis through fractionation of the lipids may elucidate what part of the FA is used for storage to clarify the interspecific differences.

We also aimed to investigate potential food sources of *M. leidyi*. In July, August and September, the sampled zooplankton could be identified as a food source for both *M. leidyi* and *P. pileus*. However, it is unclear what these ctenophores have been feeding on from October until December. Probably, the limited amount of zooplankton samples available and the fact that they represented a mixture of different taxa with a herbivorous, carnivorous or detritivorous diet influenced this outcome. Mysids showed niche overlap with *M. leidyi* and probably also feed on zooplankton (Mauchline 1980 as referred to in Verslycke et al. 2004). The large isotopic variation ($\delta^{13}C$) noted in the phytoplankton samples (primary producers) was probably the result of particulate organic matter also being retained on the glass fibre filters (Montoya et al. 1990; Thornton and McManus 1994). Consequently, the $\delta^{13}C$ and $\delta^{15}N$ values for the primary producers may be too low.

Using biomarkers to study trophic ecology of ctenophores

Biochemical markers such as SI composition and FA profiles have proven to be useful tools to elucidate planktonic food web ecology (e.g. Petursdottir et al. 2010; Ying et al. 2012; Nagata et al. 2015). Still, a number of studies showed that the SI outcome may differ, depending on several factors, such as the preparation and preservation of the samples (Pitt et al. 2009; Fleming et al. 2011), the species studied, its feeding strategy (herbivorous or carnivorous) or the body part that is retained for the analyses (Vander Zanden and Rasmussen 2001; Fleming et al. 2011; D'Ambra et al. 2014). In our study, we treated all samples in the same way to reduce this processing bias as much as possible. Also, the amount of salt (NaCl) might influence the identification of SI composition and FA concentrations (µg g DW^{-1}), as salt partly accounts for the dry weight (DW) of each sample. The amount of organic material for SI analysis was sometimes close to the border of detection. However, thanks to sufficient replicates, we could determine whether the obtained values from these small samples were comparable and reliable, which was mostly the case. For the FA samples, De Clippele (2012) conducted a small test to remove the salt in 11 *M. leidyi* samples (washing with deionised water and centrifugation to separate the salt form the samples) and concluded that the amount of salt was more or less the same in all 11 samples (av. 0.03 ± 0.01 g), meaning that this error did not influence the main results for the FA concentrations.

The advantages of simultaneously performing SI and FA analyses are clear. In summary, variation in *M. leidyi's* isotopic niche and FA profiles seemed to be influenced by the variation at the base of the food web, temporal shifts in the zooplankton community composition and/or different resource use. Trophic interactions between *M. leidyi* and the co-occurring native ctenophores showed considerable resource differentiation, while a mixture of zooplankton seemed to function as a food source for *M. leidyi*.

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