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Guillaume Marchessaux, Mireille Harmelin-Vivien, Mélanie Ourgaud, D. Bănaru, Loic Guilloux, et al.. First overview on trophic relationships of the invasive ctenophore *Mnemiopsis leidyi* in a Mediterranean coastal lagoon (Berre Lagoon, France): benthic–pelagic coupling evidenced by carbon and nitrogen stable isotope composition. *Regional Studies in Marine Science*, 2021, 41, pp.101570. 10.1016/j.rsma.2020.101570 . hal-03362598

HAL Id: hal-03362598

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First overview on trophic relationships of the invasive ctenophore *Mnemiopsis leidyi* in a Mediterranean coastal lagoon (Berre Lagoon, France): benthic–pelagic coupling evidenced by carbon and nitrogen stable isotope composition

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ARTICLE INFO

Article history:

Received 1 May 2020

Received in revised form 8 October 2020

Accepted 26 November 2020

Available online xxxx

Keywords:

Mediterranean lagoon

Pelagic ctenophores and cnidarians

C and N isotope composition

ABSTRACT

The ctenophore *Mnemiopsis leidyi*, ranking among the 100 most damaging bioinvaders in the world, is a major predator of zooplankton, known to alter the biodiversity and functioning of the ecosystems in which it has been introduced. This first survey on the trophic relationships of *M. leidyi* in a Mediterranean lagoon (Berre, South of France) was performed through stable isotope analyses. Carbon and nitrogen isotope composition was used (1) to determine the types of prey ingested by this ctenophore and (2) the influence of individual size on its isotope composition, and (3) to make assumptions to explore its trophic relationships with the native jellyfish *Aurelia* sp.. The two gelatinous species ingested mainly (79% to 97% of the diet) planktonic prey (copepods, cirriped nauplii, gastropod larvae and cladocerans), but also preyed upon benthic organisms (mainly harpacticoid copepods and the amphipod *Monocorophium insidiosum*) in lower proportions (2.5% to 21%). Size-related changes in *M. leidyi* diet were evidenced with an increase in trophic level and benthic prey consumption in the larger individuals. These two gelatinous organisms probably play an important and underestimated role in the benthic–pelagic coupling in coastal lagoons by transferring benthic organic matter to the pelagic food webs.

1. Introduction

Coastal lagoons play a major role in coastal biodiversity and human societies supporting high biological productivity, economic and socio-cultural activities, etc. (Lemée et al., 2019). However, they are very sensitive to environmental changes such as nutrient over-enrichment, contamination, habitat destruction, and non-indigenous species introductions (Audouit et al., 2019). Non-indigenous species (NIS) introductions in new ecosystems constitute a major source of biological pollution (Elliott, 2003; Boudouresque and Verlaque, 2012) and are often considered as invasive strong ecological and economic impacts, altering the diversity and functioning of ecosystems, and negatively impacting human activities such as fisheries, industry and tourism (Stref-taris et al., 2005; Gallardo et al., 2016). Understanding invasive

NIS impacts on ecosystem functioning requires the determination of their position and trophic relationships within the food web (Byrnes et al., 2007). The ctenophore *Mnemiopsis leidyi* Agassiz 1865 is ranked among the 100 worst bio-invaders in the world by IUCN (Lowe et al., 2000), with the source populations located in estuaries and coastal waters of the eastern seaboard of the Americas, from Chesapeake Bay on the east coast of the USA through the Gulf of Mexico to the coast of Argentina (GESAMP, 1997). This species has spread for the past 30 years through Eurasia following two main pathways (Ghabooli et al., 2011, 2013; Bayha et al., 2015). The first one connected the Gulf of Mexico seeding population to the Black Sea where in 1982 *M. leidyi* was first reported (Pereladov, 1988). It then spread rapidly to the Caspian Sea, and to various waters of the Mediterranean basin (see Shiganova et al., 2019, for a review). The second invasion linked the east coast of the USA to the North Sea and the Baltic Sea (Javidpour et al., 2006; Oliveira, 2007; Van Ginderdeuren et al., 2012; Antajan et al., 2014). Along the French Mediterranean

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<https://doi.org/10.1016/j.rsma.2020.101570>

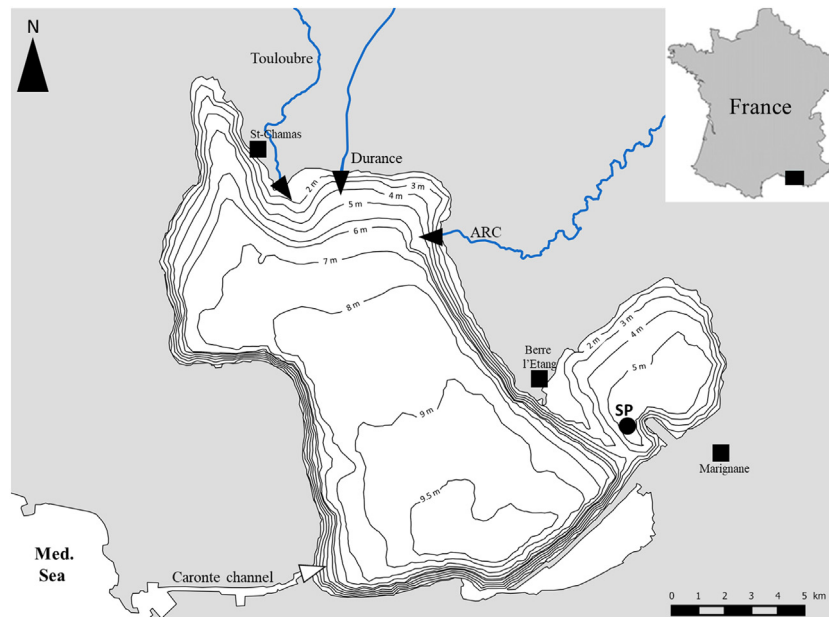


Fig. 1. Study area and sampling station. SP: sampling station. Black triangles: freshwater inputs (Touloubre, Durance (EDF powerplant), Arc) and white triangle: connection to the sea (Caronte Canal, south-west). Med. Sea: Mediterranean Sea.

coasts, *M. leidyi* was reported from early 2000 in several coastal lagoons, from Bages-Sigean in the west to Berre Lagoon in the east (Delpy et al., 2016; Marchessaux, 2019) and in Corsica (Shiganova et al., 2019).

The arrival and establishment of a large population of *M. leidyi* disturbed local environmental conditions both at the ecological (high predation pressure, competition with native planktivores) and economic level (i.e. clogging nets, catch reduction; Vinogradov et al., 1995; Purcell et al., 2001; Marchessaux, 2019). The diet of *M. leidyi* depends on different parameters such as ontogeny, size, food availability and season. Adults have a broad meso-zooplanktivorous diet, including fish eggs and larvae (Purcell and Arai, 2001; Purcell, 2009), while larvae feed on microplankton (Rapoza et al., 2005; Sullivan, 2010).

Gelatinous species in general (pelagic ctenophores and cnidarians) are often grouped into a single trophic category in ecosystem models (Pauly et al., 2009; Condon et al., 2012) and are considered as direct competitors of planktivorous fish (Sommer et al., 2002; Brodeur et al., 2008). However, they cover a wide range of species and diets, including predators of other gelatinous zooplankton (Greve and Reiners, 1988). It is therefore essential to assess trophic diversity at the species level (Nagata et al., 2015). Several techniques have been used to study the trophic ecology of gelatinous zooplankton, such as traditional gastrovascular cavity content analyses (Larson, 1987; Hansson, 2006) and grazing experiments (Mazlum and Seyhan, 2007; Rowshantabari, 2012), which indicate which prey was lately ingested, and more recently biochemical tracers, such as stable isotopes (SI) and fatty acids, which provide an integrated view of the assimilated food sources (Pitt et al., 2009; Vansteenbrugge et al., 2016). Fractionation from one trophic level to the next is assumed to be generally from 0.1 to 1‰ for $\delta^{13}\text{C}$ and from 2 to 4‰ for $\delta^{15}\text{N}$, which allows the use of stable isotopes to determine the trophic position of organisms within the food web (e.g. Peterson and Fry, 1987; Layman et al., 2012; Glibert et al., 2019). They also provide a way to quantify the contributions of different food sources if they statistically differ (Parnell et al., 2010; Phillips et al., 2014). SI composition of prey can identify common resources, which can provide a basis for hypotheses regarding competition or predation interactions among consumer organisms (Hamer et al., 2011; Frost et al., 2012; Kellnreitner et al., 2013). A recent modeling study of the growth of

M. leidyi indicates that variations in food quantity and quality may induce rapid changes in its population dynamics (Alekseenko et al., 2019; Marchessaux et al., 2020), but only planktonic prey were included in the biogeochemical model used. However, some studies demonstrate that, in coastal environments, jellyfish and ctenophores are able to prey on benthic organisms when they emerge from the sediment at night (Pitt et al., 2008) or benthic organic matter (Cui et al., 2012; Javidpour et al., 2016), playing therefore a role in the benthic–pelagic coupling.

The present study is a first attempt at elucidating the feeding relationships of *Mnemiopsis leidyi* with planktonic and benthic compartments in Berre Lagoon (Mediterranean Sea) through a stable isotope approach, which was never explored before in this coastal lagoon. Its aims were to (1) provide the C and N stable isotope composition of *M. leidyi* and its main food components, (2) evidence the variations of C and N isotope composition with individual size, (3) quantify the respective contributions of pelagic and benthic sources of prey in its diet, and (4) consider the eventual trophic relationships between *M. leidyi* and the jellyfish *Aurelia* sp.

2. Materials and methods

2.1. Study area

Berre Lagoon is the largest (surface area 155 km², total volume of 0.98 x 10⁹ m³, average depth 7 m) semi-enclosed brackish lagoon located near Marseille, southeast France. Inflows of freshwater into the lagoon are all situated in the northern part with two natural rivers (Touloubre and Arc), and the wide industrial channel of the Durance supplying several hydroelectric powerplants, the nearest located at Saint-Chamas (Fig. 1). These freshwater inputs participate to the high variability of the environmental parameters of the Berre Lagoon ecosystem, where temperature and salinity in particular largely fluctuate over the year (Table 1). Berre Lagoon is connected to the Mediterranean Sea in its southwestern part through the Caronte channel. Low-amplitude (~30 cm) semi-diurnal tides are observed. Berre Lagoon is composed of two sub-basins: the larger basin (~9 m maximum depth) and the Vaine basin (~5 m maximum depth), separated by a sand shoal (~1.5 m depth). Extensive *Zostera noltii* meadows are observed particularly in the Vaine basin.

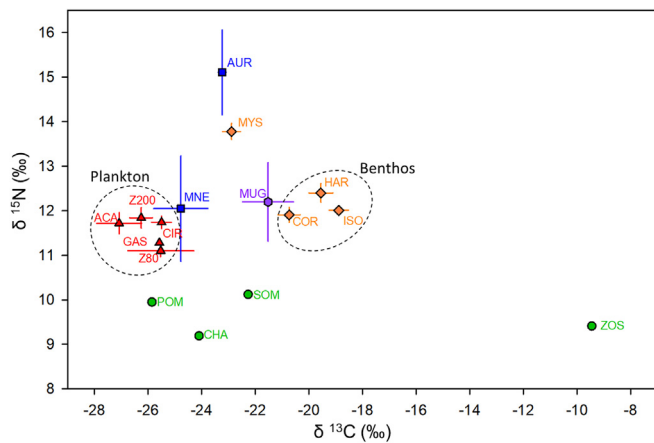


Fig. 2. Biplot of mean (\pm SD) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (‰) isotope values in the jellyfish food web of Berre Lagoon in April 2016. ACA: *Acartia tonsa*; AUR: *Aurelia* sp. (80–160 mm); CHA: *Chaetomorpha linum*; CIR: cirriped nauplii; COR: juveniles of *Monocorophium insidiosum*; GAS: gastropod larvae; HAR: harpacticoids; ISO: isopods; MNE: *Mnemiopsis leidyi* (10–20 mm); MUG: juveniles of *Mugil* sp.; MYS: mysids; POM: particulate organic matter; SOM: surface sediment; Z80: zooplankton 80–200 μm ; Z200: zooplankton 200–500 μm ; ZOS: *Zostera noltii*.

Table 1

Variability of environmental parameters in the Berre Lagoon with mean values during the present study, and minimum–maximum values between 2010 and 2017 (Marchessaux et al., 2020).

Water parameters	Mean \pm SD (April 2016)	Min–Max (2010–2017)
Temperature ($^{\circ}\text{C}$)	16.5 \pm 0.3	0.3 – 28.2
Salinity	17.4 \pm 0.8	14.6 – 33.7
Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	1.1 \pm 0.8	0.2 – 37.1
Oxygen ($\mu\text{mol L}^{-1}$)	245.1 \pm 2.4	1.7 – 385.6

2.2. Sampling and sample preparation

Sampling was done at a station located in the Vaine basin (latitude: 43.446, longitude: 5.187; depth: 4 m) (Fig. 1), on 20 April 2016. Samples for benthic (sediment organic matter – SOM, macrophytes, invertebrates and juveniles of teleostean fish) and for pelagic (particulate organic matter – POM, zooplankton, the ctenophore *Mnemiopsis leidyi*, and the cnidarian *Aurelia* sp.) compartments were collected by divers or nets.

Benthic compartments: SOM was collected by divers by scraping the surface sediment with a sterile 1 L plastic bottle (\sim 500 g of matter). Four independent replicates were performed. In the laboratory, bottle contents were sieved on a 200 μm mesh sieve to remove large sediment particles and kept in polyethylene bags. Several individuals of the seagrass *Zostera noltii* and the green alga *Chaetomorpha linum* were collected by divers. In the laboratory, rhizomes, and damaged parts of the macrophytes were discarded and epiphytes gently removed by scraping the leaves. The clean leaves were rinsed with ultrapure water and placed in polyethylene bags.

Pelagic compartment: Four water samples (POM) were collected \sim 1 m below the surface using a sampling bottle. Between 2 to 4 L of water were first sieved through a 80 μm mesh silk to remove detritus and zooplankton organisms, and filtered on pre-combusted (450 $^{\circ}\text{C}$ for 5 h) and pre-weighed GF/F filters (porosity: 0.7 μm). Then filters were stored in hermetically sealed boxes. Zooplankton was collected using a vertical 80 μm mesh net (1.2 m long, 30 cm opening area), the content of the cod-end was then sieved onto a column of three sieves of decreasing size (500 μm , 200 μm and 80 μm) and each sieve content was then collected onto pre-weighed and pre-combusted GF/F filters. A second net sample was kept in a large volume of water

until the return to the laboratory. Different groups and taxa were then sorted directly under a dissecting microscope: *Acartia tonsa* (copepod Calanoida), harpacticoid copepods, cirriped nauplii, mysids, *Monocorophium insidiosum* (amphipod), isopods, and gastropod larvae. About 300 to 500 individuals from each taxa were sorted, placed together on pre-combusted GF/F filters, rinsed with ultrapure water and kept in hermetically sealed boxes. Cnidarians and ctenophores were collected with a dip net, rinsed with ultrapure water, measured (nearest mm) and individually placed in polyethylene bags. To minimize bias in C and N isotope analysis related to the presence of prey in their digestive tract, zooplankton and gelatinous organisms were conditioned only three hours after sampling, enabling gut clearing. Juveniles of teleostean fish (*Mugil* sp.) were caught with a landing net and measured (nearest mm). Dorsal white muscle samples without skin were individually placed in polyethylene bags. All samples were stored in a freezer at -20°C before being freeze-dried for 24 h, then stored in a dry place. Numbers of samples analyzed are given in Table 2.

2.3. Stable isotope analysis

Before stable isotope analysis, all freeze-dried samples were ground using a mortar and pestle and sieved on a steel sieve (60 μm) to obtain a homogeneous fine powder. Several compartments (POM, SOM, macrophytes, crustaceans, micro- and meso-zooplankton, gastropod larvae), susceptible to contain carbonates, were split into two subsamples. One sub-sample was acidified to remove carbonates, as they are enriched in ^{13}C (Lorrain et al., 2003) and was used for measurements of $\delta^{13}\text{C}$ values. The other subsample was used for measurements of $\delta^{15}\text{N}$ values of the organisms without any prior treatment. SOM decarbonation was done with 1% HCl solution abundantly poured onto the sample until cessation of bubbling. POM samples were acidified by three successive rinses of filters with 1% HCl and then rinsed thoroughly with ultrapure water. For macrophytes, crustaceans, zooplankton and gastropod larvae, acidification was carried out by exposure to HCl fumes for four hours. All samples were then rinsed three times with ultrapure water and dried in an oven (60 $^{\circ}\text{C}$). Non-acidified samples were placed in tin microcapsules, while decarbonated samples were conditioned in silver microcapsules. The mass of material analyzed was about 0.5 mg for crustaceans, gelatinous organisms and teleosteans, and 1 mg for POM and SOM. Stable isotope analyses (C and N) were carried out at the stable isotope facility of the Littoral Environnement et Sociétés (LIENSs) stable isotope facility (CNRS – University of La Rochelle), using an elemental analyzer (Flash EA 1112, Thermo Scientific) coupled with an isotope ratio mass spectrometer (Delta V Advantage with a ConFlo IV interface, Thermo Scientific).

Isotope composition is expressed in the δ notation (‰) as deviations from international standards (Vienna Pee Dee belemnite for carbon and atmospheric N_2 for nitrogen, Peterson and Fry, 1987): $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, with X is ^{13}C or ^{15}N and R the isotopic ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Carbon/Nitrogen (C/N) atomic ratios were also computed. Calibration was done using reference materials (USGS-24, IAEA-CH6, IAEA-600, USGS-61, USGS-62 for carbon; IAEA-N2, IAEA-NO-3 and IAEA-600, USGS-61, USGS-62 for nitrogen). Analytical precision based on the analyses of USGS-61 and USGS-62 used as laboratory internal standard was $<0.10\text{‰}$ and $<0.15\text{‰}$ for carbon and nitrogen, respectively. As lipids are depleted in ^{13}C compared to the other biochemical components, a high lipid content may have a significant effect on $\delta^{13}\text{C}$ values of organisms (De Niro and Epstein, 1977; Logan et al., 2008) and a correction should be applied for zooplanktonic organisms presenting a C/N ratio >5 (Smyntek et al., 2007). *Mnemiopsis leidyi* $\delta^{13}\text{C}$ values were thus corrected for lipids according

Table 2

Mean (\pm standard deviation) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (‰) values of the different compartments analyzed in the Berre Lagoon food webs (NW Mediterranean). The letters indicate whether the differences are significant between the compartments (Kruskal–Wallis ANOVA, $p < 0.05$). N = number of samples.

Compartments	Codes	N	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$			C / N					
Organic matter sources														
POM	POM	4	-25.9	\pm	0.1	a,b	9.9	\pm	0.4	a,b	3.9	\pm	1.0	a,b
SOM	SOM	4	-22.3	\pm	0.0	d,e	10.1	\pm	0.1	a,b	8.3	\pm	0.1	a,b
<i>Zostera noltii</i>	ZOS	3	-9.5	\pm	0.2	e	9.4	\pm	0.2	a	24.4	\pm	0.7	b
<i>Chaetomorpha linum</i>	CHA	3	-24.1	\pm	0.1	b,c,d,e	9.2	\pm	0.1	a	8.1	\pm	0.2	a,b
Zooplankton														
Zooplankton 80–200 μm	Z80	15	-25.5	\pm	1.2	a,b	11.1	\pm	0.1	a,b	2.8	\pm	0.8	a
Zooplankton > 200 μm	Z200	15	-26.3	\pm	0.4	a	11.8	\pm	0.2	c	3.7	\pm	0.6	a,b
<i>Acartia tonsa</i>	ACA	7	-27.1	\pm	0.8	a	11.7	\pm	0.2	b,c	4.0	\pm	0.2	a,b
Cirripeds nauplii	CIR	4	-25.5	\pm	0.4	a,b,c	11.7	\pm	0.1	b,c	4.7	\pm	0.7	a,b
Gastropod larvae	GAS	1	-25.6				11.3				4.0			
Gelatinous zooplankton														
<i>Aurelia</i> sp. (80–160 mm)	AUR	9	-23.2	\pm	0.1	c,d,e	15.1	\pm	0.9	e	4.2	\pm	0.1	a,b
<i>Mnemiopsis leidyi</i> (10–20 mm)	MNE	18	-24.8	\pm	1.0	b,c,d	12.0	\pm	1.2	c,d	5.4	\pm	2.2	a,b
Benthic invertebrates														
<i>Monocorophium insidiosum</i>	COR	4	-20.7	\pm	0.4	e	11.9	\pm	0.2	c,d	4.7	\pm	0.3	a,b
Harpacticoids	HAR	3	-19.6	\pm	0.4	e	12.4	\pm	0.2	c,d,e	4.3	\pm	0.0	a,b
Isopods	ISO	3	-18.9	\pm	0.4	e	12.0	\pm	0.1	c,d	4.1	\pm	1.0	a,b
Mysids	MYS	3	-22.9	\pm	0.3	c,d,e	13.8	\pm	0.2	d,e	3.6	\pm	0.1	a,b
Teleosteans														
<i>Mugil</i> sp. Juveniles	MUG	6	-21.5	\pm	0.9	e	12.2	\pm	0.9	c,d	3.8	\pm	0.2	a,b
Kruskal–Wallis ANOVA			H = 82.8 $p < 0.001$				H = 73.1 $p < 0.001$				H = 31.3 $p < 0.005$			

to the equation given by Post et al. (2007), as done by D'Ambra et al. (2014, 2018) for *Aurelia* sp.. Mean change in $\delta^{13}\text{C}$ values (*M. leidyi* $\Delta\delta^{13}\text{C} = 1.9\text{‰}$) due to lipid correction was close to the value given by Logan et al. (2008) for marine invertebrates ($\Delta\delta^{13}\text{C} = 1.3\text{‰}$).

2.4. Data analysis

Differences in mean stable isotopic values and C/N ratio among food web components or organism size classes were tested using nonparametric Kruskal–Wallis ANOVA, followed by post-hoc Dunn tests of comparison of means. A hierarchical clustering analysis, using Euclidean distance and Ward criterion, enabled the grouping of species of similar isotope composition. The relationships between the logarithm of individual size and $\delta^{15}\text{N}$ value in *M. leidyi* and *Aurelia* sp. were tested by Pearson's linear correlation. The respective contributions of the different sources of organic matter ingested by *M. leidyi* and *Aurelia* sp. were determined with Bayesian mixing models using the SIAR (Stable Isotope Analysis in R) package (Parnell et al., 2010) although these models are called into question below (Stock et al., 2018). SIAR models estimate probability distributions of the contribution of different sources to consumers. The Bayesian approach of mixing models takes into account the variability in stable isotope values of sources and provides a probability distribution associated with contribution values, but it is sensitive to the choice of the trophic enrichment factor (TEF) applied (Phillips et al., 2014; Bond and Diamond, 2011). The TEF values used for the gelatinous organisms were selected following Vansteenberghe (2015): $\Delta\delta^{13}\text{C} = 1.6 \pm 0.6\text{‰}$ and $\Delta\delta^{15}\text{N} = 3.5 \pm 0.6\text{‰}$, for *M. leidyi*. SIAR models were run with two prey categories (Plankton and Benthos) according to the results of a previous study on the gastrovascular cavity contents of *M. leidyi* (Marchessaux et al., submitted). However, as different authors testified from predation on ctenophores by jellyfishes (Purcell and Cowan, 1995; Breitbart and Burrell, 2014), three prey categories (Plankton, Benthos and *Mnemiopsis*) were also considered as potential prey for *Aurelia* sp. in SIAR models.

3. Results

3.1. Stable isotope composition of food web components

Stable isotope values of planktonic (POM, micro- and mesozooplankton, ctenophores and cnidarians) and benthic (SOM, macroalgae, seagrasses, crustaceans and juvenile fish) components analyzed in Berre Lagoon ranged from -27.1‰ to -9.5‰ for $\delta^{13}\text{C}$ values and from 9.2‰ to 15.1‰ for $\delta^{15}\text{N}$ values (Table 1). At the base of the food web, the wide range of $\delta^{13}\text{C}$ values ($\Delta\delta^{13}\text{C} = 14.6\text{‰}$) clearly distinguished the seagrass *Zostera noltii* (ZOS) from the other carbon sources (*Chaetomorpha linum* (CHA), POM and SOM), which presented much lower $\delta^{13}\text{C}$ values (from -25.9‰ to -22.3‰). All these organic matter (OM) sources presented low $\delta^{15}\text{N}$ values (from 9.2‰ to 10.1‰). The range of $\delta^{15}\text{N}$ ($\Delta\delta^{15}\text{N} = 5.9\text{‰}$) between the base of the food web and *Aurelia* sp. (AUR: 15.1‰) suggested the existence of two trophic levels between them.

The hierarchical clustering separated two groups of potential prey for gelatinous organisms, which presented significantly different carbon and nitrogen compositions (Fig. 2): benthic prey ($\delta^{13}\text{C} = -19.8 \pm 0.9\text{‰}$ and $\delta^{15}\text{N} = 12.1 \pm 0.3\text{‰}$) and planktonic prey ($\delta^{13}\text{C} = -26.1 \pm 1.0\text{‰}$ and $\delta^{15}\text{N} = 11.5 \pm 0.4\text{‰}$). The group of benthic organisms (hereafter Benthos) included harpacticoid copepods (HAR), isopods (ISO), and the amphipod *Monocorophium insidiosum* (COR), and displayed significantly higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (ANOVA, $F = 317.30$, $p < 0.001$ and $F = 18.53$, $p < 0.001$ for C and N respectively) than the group of planktonic prey (hereafter Plankton) composed by microzooplankton 80–200 μm (Z80), mesozooplankton >200 μm (Z200), *Acartia tonsa* (ACA), cirriped nauplii (CIR) and gastropod larvae (GAS). Among planktonic organisms, Z80 and GAS presented close C and N isotope composition with the lowest $\delta^{15}\text{N}$ values ($< 11.5\text{‰}$), while ACA, CIR and Z200 exhibited higher, while not significantly, $\delta^{15}\text{N}$ values ($> 11.5\text{‰}$). Juveniles of the teleost fish *Mugil* sp. (MUG) had a similar isotope composition to the group of benthic prey, but due to their size (> 5 cm) were not potential prey for gelatinous organisms and were thus excluded from the Benthos prey group. Mysid shrimps (MYS), abundant in *Zostera* seagrass meadows, displayed a $\delta^{13}\text{C}$ value ($-9.5 \pm 0.2\text{‰}$) intermediate between

those of Plankton and Benthos, and a significantly higher $\delta^{15}\text{N}$ value (Table 1, Fig. 2), but were never observed in *M. leidy* gastrovascular cavity (GM pers. obs.). *M. leidy* (MNE) was positioned close to the Plankton group with slightly higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, while *Aurelia* sp. (AUR) presented the highest $\delta^{15}\text{N}$ values ($\delta^{15}\text{N} = 15.1 \pm 0.9\text{‰}$) observed among the organisms analyzed (Fig. 2).

3.2. Size- and species-related variations

Three size classes were distinguished among MNE individuals collected, which were all of small size: 10 mm, 15 mm and 20 mm, which significantly differed in their stable isotope composition (Fig. 3): individuals from the 20 mm size class were significantly more enriched in ^{13}C than the two smaller classes (-23.2‰ vs. $< -25.0\text{‰}$, KW-ANOVA, $H = 9.44$, $p = 0.009$) and individuals from the smallest 10 mm size class were significantly more depleted in ^{15}N than the two largest ones (10.2‰ vs. $> 12.0\text{‰}$, $H = 8.84$, $p = 0.012$). A significant positive linear correlation was observed between $\delta^{15}\text{N}$ value and the logarithm of size in the two species ($r = 0.70$, $p = 0.001$, $N = 18$ and $r = 0.77$, $p = 0.015$, $N = 9$, for *M. leidy* and *Aurelia* sp., respectively).

Two categories (Plankton and Benthos) with statistically different stable isotope composition were identified as potential prey for both *M. leidy* and *Aurelia* sp. and used in SIAR models. Results testified to a zooplanktonic based diet for the two gelatinous organisms, but also to the assimilation of a small proportion of benthic organisms (Fig. 4). A mean proportion of 97.5% (93.6–100%, 95% Bayesian credible interval) of Plankton was found in MNE diet, with a low but significant proportion of Benthos (mean 2.5%; 0.3–6.4%) (Fig. 4a). SIAR model with two prey categories indicated that AUR mainly preyed on plankton (79.2%; 68.6–89.9%) but ingested also a small quantity of benthic organisms or some prey influenced by benthic OM (20.8%; 10.1–31.4%) (Fig. 4b). When MNE was included in the SIAR model as a third prey category for AUR, the mean proportions of assimilated prey in AUR tissues were 47.9% (26.1–71.8%, 95% Bayesian credible interval) for Plankton, 12.1% (10.2–66.5%) for Benthos and 39.9% (18.8–22.0%) for MNE.

4. Discussion

4.1. Isotopic composition of jellyfish food webs in Berre Lagoon

The carbon and nitrogen isotope composition of *M. leidy* and *Aurelia* sp. indicated that their food resources were mainly based on planktonic POM, and in a lower proportion on benthic SOM and macroalgae, while the seagrass *Zostera noltii* was not used as a food source directly (Fig. 2). The high $\delta^{13}\text{C}$ value of *Z. noltii* in Berre Lagoon (-9.5‰) is similar to that (-9.7‰) reported for this seagrass by Carlier et al. (2009) in Salses-Leucate, a lagoon located in the southwestern part of the French Mediterranean coast. POM includes phytoplankton, but also microzooplankton, bacteria, detritus, and fecal pellets, among other elements (Lienart et al., 2017). In coastal waters POM presents generally lower $\delta^{13}\text{C}$ and higher $\delta^{15}\text{N}$ values than phytoplankton, mainly due to the influence of terrestrial detritus in its composition, as observed in the Gulf of Lions (Harmelin-Vivien et al., 2008). Berre Lagoon is exposed to high freshwater inputs and thus presents a low $\delta^{13}\text{C}$ value (-25.9‰), close to those of the Rhône River POM (-27.4‰ to -26.6‰ ; Harmelin-Vivien et al., 2010). Low $\delta^{13}\text{C}$ ($< -24\text{‰}$) and relatively high $\delta^{15}\text{N}$ ($> 9\text{‰}$) values for POM, as observed in Berre Lagoon, were reported in other highly anthropized French Mediterranean lagoons subject to river inputs or with restricted connections with restricted exchanges with the sea, such as Mauquo (Vizzini et al., 2005; Dierking et al., 2012) and Canet (Carlier

et al., 2009). In other French and Italian lagoons subject to lower river inputs or benefiting from more extensive connections with the sea, slightly higher $\delta^{13}\text{C}$ (-23‰ to -18‰) and lower $\delta^{15}\text{N}$ (2‰ to 6‰) values were observed for POM (Carlier et al., 2007; Vizzini and Mazzola, 2008). In all the studied Mediterranean lagoons, SOM had higher (or similar) $\delta^{13}\text{C}$ values than POM, as observed in Berre Lagoon, highlighting a similar origin, while varying $\delta^{15}\text{N}$ values were more related to the degree of human impact. SOM was composed of settled POM, microphyto- and meio-benthos, and a wide range of detritus (detrital macroalgae, seagrasses and terrestrial plants, fecal pellets, etc.) (Cresson et al., 2012). In Berre lagoon, the higher $\delta^{13}\text{C}$ value of SOM was also probably due to the influence of *Z. noltii* detritus.

Two groups of potential prey items for ctenophores and jellyfishes with statistically different stable isotope values were individualized in Berre Lagoon. The pelagic group (Z80, Z200, the copepod *A. tonsa*, cirriped nauplii and gastropod larvae) included planktonic organisms relying on POM and phytoplankton as carbon sources, as observed by Vansteenbrugge et al. (2016) in the North Sea. Microzooplankton (Z80) and gastropod larvae displayed the lowest $\delta^{15}\text{N}$ values as they mainly fed on pico- and nanophytoplankton, heterotrophic protozoans and bacteria (Calbet and Landry, 2004; Vargas et al., 2006). Mesozooplankton (Z200), cirriped larvae and the invasive copepod *A. tonsa* exhibited slightly higher $\delta^{15}\text{N}$ values, while not statistically different (Table 2), as they fed on larger cells (diatoms, chlorophytes, dinoflagellates, tintinnids and rotifers) (Gaudy and Pagano, 1987; Saiz et al., 2014).

The second group of potential prey items included benthic organisms such as harpacticoid copepods, the amphipod *Monocorophium insidiosum* and isopods, which presented significantly higher $\delta^{13}\text{C}$ values than planktonic prey, and slightly higher $\delta^{15}\text{N}$ values. Vizzini and Mazzola (2003) also recorded higher $\delta^{13}\text{C}$ values in harpacticoid copepods and *Monocorophium* amphipods than in planktonic calanoid copepods in Sabaudia Lagoon. These high $\delta^{13}\text{C}$ values were in accordance with a consumption of benthic OM (SOM, benthic diatoms and macrophytes detritus) by these compartments (Nair and Anger, 1979; Arrontes, 1990). As observed in Berre Lagoon, rather high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were recorded for mysids in different Mediterranean lagoons and in the North Sea coastal areas (Persic et al., 2004; Vizzini and Mazzola, 2008; De Clippele, 2012). The positioning of these crustaceans at a higher trophic level than planktonic and benthic smaller crustaceans was in accordance with their predatory feeding behavior (Rudstam et al., 1989).

The $\delta^{13}\text{C}$ values (-26 to -22‰) observed for *M. leidy* in Berre lagoon were similar to those measured by Vansteenbrugge et al. (2016) in the port of Dunkirk (-24 to -22‰), but lower than those generally recorded in the coastal and estuarine sites of the North Sea (-22 to -16‰) (Hamer et al., 2011; De Clippele, 2012; Vansteenbrugge et al., 2016; Van Walraven et al., 2018). The $\delta^{15}\text{N}$ values for this ctenophore (9 to 13‰) in Berre Lagoon were lower than those reported by these authors in the North Sea (12 to 21‰), probably owing to the small size of the individuals collected. However, similar C and N isotopic composition was recorded for *Aurelia* sp. in Berre Lagoon ($\delta^{13}\text{C} = -23$ to -23.5‰ ; $\delta^{15}\text{N} = 13$ to 16‰) and the North Sea ($\delta^{13}\text{C} = -24$ to -18.5‰ ; $\delta^{15}\text{N} = 11$ to 15‰) for individuals of similar size (Javidpour et al., 2016; Van Walraven et al., 2018).

4.2. Variation in ctenophore and jellyfish diet: planktonic vs. benthic prey

The two gelatinous organisms investigated in Berre Lagoon seemed to be positioned at different trophic levels, but this was mainly due to the considerable difference of size between the

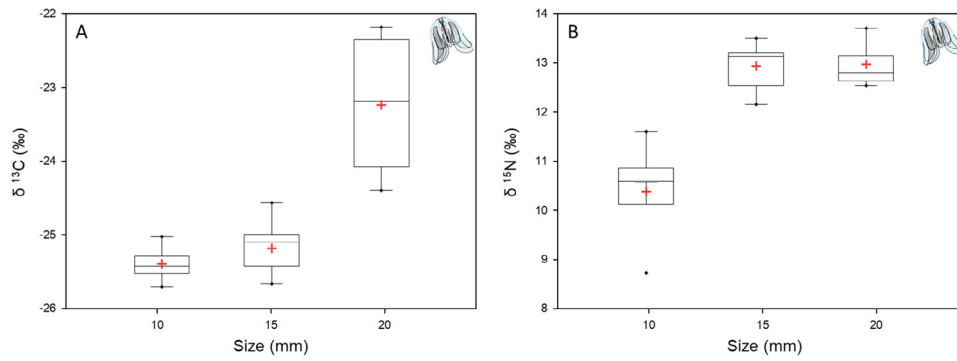


Fig. 3. Boxplot of mean (\pm SD) isotope values of *Mnemiopsis leidy*, (A) $\delta^{13}\text{C}$ (‰) and (B) $\delta^{15}\text{N}$ (‰), as a function of ctenophore size (mm). Number of individuals: 10 mm (N = 4), 15 mm (N = 10), 20 mm (N = 4). Horizontal bars represent median values and red crosses mean values.

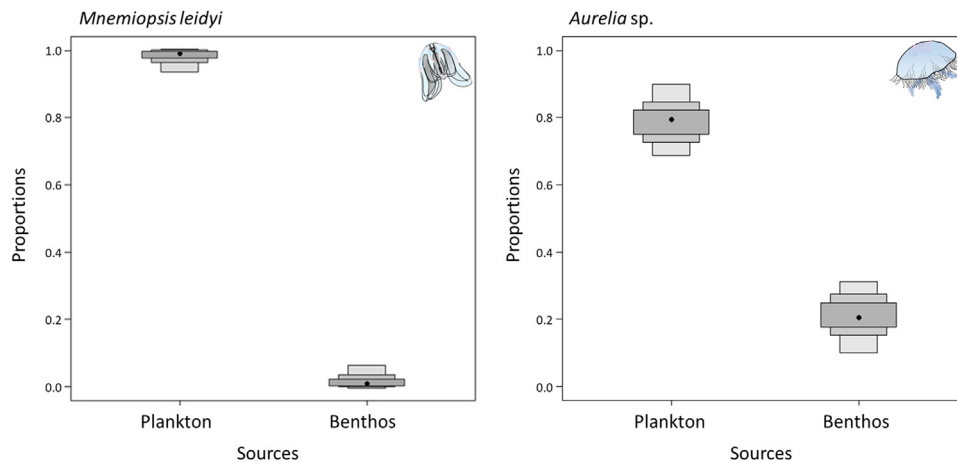


Fig. 4. Relative contributions of planktonic (Plankton) and benthic (Benthos) prey to the diets of *Mnemiopsis leidy* and *Aurelia* sp. from SIAR models. Points represent the mode of the distribution and boxes the 50%, 75% and 95% Bayesian credibility intervals from light to dark gray.

individuals analyzed in the two species. The small-sized (10 to 20 mm) *M. leidy* analyzed presented a lower $\delta^{15}\text{N}$ value (12.1‰) than the large-sized (80 to 160 mm) *Aurelia* sp. (15.1‰). However, a significant positive correlation between $\delta^{15}\text{N}$ value and size was observed in the two species in this lagoon, as recorded by Javidpour et al. (2016) for *Aurelia aurita* in the Baltic Sea, and Van Walraven et al. (2018) for *M. leidy* in the North Sea. But Vansteenbergue et al. (2016) observed unexpectedly higher $\delta^{15}\text{N}$ values in small (< 10 mm) than in large (11 to 55 mm) *M. leidy* individuals in the Westerschelde estuary. Higher $\delta^{15}\text{N}$ values (16.1‰ to 16.5‰) have been observed for large *M. leidy* (70–120 mm) in Berre Lagoon in a previous study (B. Hunt, pers. comm.), close to those observed here for *Aurelia* sp. of similar size (13.6‰ to 16.2‰; 80–160 mm), positioning the two species at a similar trophic level for similar sizes. Thus, the difference and narrow range of C and N isotope composition recorded for these two jellyfishes in this study most likely came from the low number and narrow size range of the individuals analyzed. In the future, it would be important to consider a wide range of ctenophore and cnidarian size classes in order to determine with precision their role in the food web functioning of Berre Lagoon.

Significant differences in both isotope compositions were observed among the three size classes of *M. leidy*, with the smallest size class presenting the lowest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Fig. 3). This suggested that 10 mm-sized *M. leidy* probably consumed phytoplankton (POM) and small microzooplanktonic organisms. Small ctenophores (10 mm) are reported to be omnivorous, consuming small prey items such as tintinnids, protists and copepod nauplii (Sullivan and Gifford, 2004; Rapoza et al., 2005), and

to be positioned at a low trophic level in the food webs. The largest *M. leidy* size class analyzed in the present study was only 20 mm long, but it presented significantly higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than the smaller ones, indicating a shift in their diet toward larger prey (micro- and mesozooplankton) and benthic crustaceans, as suggested by Vansteenbergue et al. (2016). This dietary pattern was confirmed by the results of the analysis of the gastrovascular cavity content of *M. leidy* in Berre Lagoon (Marchessaux et al., submitted), indicating that this ctenophore ingested mainly mollusk larvae (34%), copepods (29%), barnacle larvae (13%) copepod nauplii (11%) and the benthic amphipod *M. insidiosum*.

Although exploratory in this study and the subject of criticism, the mixing models SIAR allowed estimation of the contributions of the different food sources assimilated by the two gelatinous organisms. SIAR results indicated that planktonic prey dominated the diet of both species, particularly the copepod *A. tonsa*, cirriped nauplii, and gastropod larvae, clustered in the Plankton group. The isotope composition of the ctenophore close to that of its prey was mainly explained by a very rapid assimilation rate, particularly for small individuals such as those analyzed in this study (Kremer and Reeve, 1989; Reeve et al., 1989; Bumann and Puls, 1997). However, SIAR results indicated that both *M. leidy* and *Aurelia* sp. also assimilated benthic prey in addition to pelagic prey, even if in small proportions (from 2.5% to 21%; Fig. 4). The predation on benthic organisms by these two gelatinous organisms was confirmed by the analysis of their gastrovascular cavity content, within which harpacticoid copepods and small *Monocorophium insidiosum* were often recorded (Marchessaux,

2019; Marchessaux et al., submitted)). The predation on benthic organisms by pelagic ctenophores and cnidarians was due to specific behavior patterns of both predator and prey. *M. leidy* was observed swimming close to the bottom or among seagrasses when the wind was strong and the surface water rough, or at night (GM pers. obs.). Such behavior favored its predation on the small crustaceans (i.e. amphipods, harpacticoids) from the sediment, as observed by Pitt et al. (2008), or living in the *Zostera* canopy. In addition, juvenile *M. insidiosum*, which were among the most common amphipods found in the *Mnemiopsis* gastrovascular cavity, are known for being very active outside their tubes in contrast to the adults (Fricke et al., 2015). The predation on benthic crustaceans, such as the Malacostraca *Lucifer* and night emergent copepods, by the scyphozoan jellyfish *Catostylus mosaicus* in Australia was demonstrated by Pitt et al. (2008), providing evidence of benthic–pelagic coupling by jellyfishes in coastal areas. Evidence of assimilation of benthic OM by jellyfishes was also provided through the use of sulfur stable isotope ($\delta^{34}\text{S}$) in *Aurelia aurita* in the North Sea (Javidpour et al., 2016) and of fatty acids in *A. aurita* and two other jellyfish species in the Yellow Sea (Cui et al., 2012). Thus, pelagic cnidarians and ctenophores could play a major and underestimated role in benthic–pelagic coupling of food webs in coastal areas.

4.3. Ctenophore–jellyfish relationships: competition and/or predation?

Particulate Organic Matter (POM) was the main OM source for zooplankton and thus the major base line of the planktonic food web of Berre Lagoon. C and N stable isotope composition and gastrovascular cavity content indicated that *M. leidy* and *Aurelia* sp. mainly relied on the same planktonic prey for food (mollusk veliger larvae, particularly gastropod larvae, copepods, mainly *A. tonsa*, cirriped nauplii, the cladoceran *Pleopis polyphamoides*, and polychete larvae) (Marchessaux et al., submitted), being thus in potential competition when these resources decreased. Hamer et al. (2011) also reported potential competition between the invasive *Mnemiopsis* and the native ctenophore *Pleurobrachia pileus*.

But predation relationships among pelagic ctenophores and cnidarians have been reported by different authors (Krebs et al., 1997; Purcell and Cowan, 1995; Hosia et al., 2011; Tilves et al., 2012, 2016; Breitburg and Burrell, 2014), and Frost et al. (2012) confirmed *Beroe* sp. (an indigenous ctenophore) as a predator of *M. leidy*, based on isotope composition. In Berre Lagoon, the cnidarian *Aurelia* sp. was positioned at a higher trophic level than the ctenophore, probably owing to the small size of the *M. leidy* individuals analyzed, and SIAR results suggested that small *Mnemiopsis* could also represent potential prey for large *Aurelia* sp. Predation on *Aurelia* planula and ephyrae by *M. leidy* was observed in the Baltic Sea (Javidpour et al., 2009; Riisgård et al., 2010). It might be possible that the opposite is also true and that *Aurelia* adults were preying on the ctenophore eggs, larvae, and juveniles, as suggested here. However, this hypothesis needs to be thoroughly tested in situ and with experiments.

5. Conclusion

While exploratory, the present study highlighted a potential important predation role of the invasive ctenophore *Mnemiopsis leidy* and the native moon jellyfish *Aurelia* sp. on the same zooplanktonic organisms in Berre Lagoon. Our results evidenced that both *M. leidy* and *Aurelia* sp. preyed on and also assimilated benthic organisms (harpacticoid copepods, amphipods), while in lower proportions, which confirmed the results of the gastrovascular cavity content analysis (Marchessaux et al., submitted). The shallow mean depth of Berre Lagoon probably favored two

pathways of OM transfer (i.e. from both pelagic and benthic communities) in which pelagic ctenophores and cnidarians played an underestimated role. In the future, a more complete study of the functioning of the whole food web, up to fishes, should be carried out in this lagoon, including in particular an assessment of the seasonal and spatial variations of the C and N isotope composition of both the organisms and the organic matter sources.

CRedit authorship contribution statement

Guillaume Marchessaux: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft. **Mireille Harmelin-Vivien:** Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft. **Mélanie Ourgaud:** Investigation, Writing - review & editing. **Daniela Bănar:** Methodology, Writing - review & editing. **Loïc Guilloux:** Investigation, Writing - review & editing. **Bruno Belloni:** Investigation, Writing - review & editing. **Benoit Lebreton:** Investigation, Writing - review & editing. **Gaël Guillou:** Investigation, Writing - review & editing. **Delphine Thibault:** Writing - review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgment

We would like to thank Robert Arfi (MIO), Raphaël Grisel (GIPREB), Adrien Goujard (GIS Posidonie), Dorian Guillemain (MIO) and Elodie Rouanet (GIS Posidonie) for their help during *in situ* sampling. Thanks to Maria Jesus Ferrara-Guerrero (Universidad Nacional Autónoma de México), Maria-Elena Huidobro-Salas (Universidad Nacional Autónoma de México), José Luis Gama-Flores (Universidad Nacional Autónoma de México) and Marc Pagano (MIO) for their help in sample conditioning. We also thank the Microscopie et Imagerie Marine (MIM) and Service à la Mer (SAM) facilities in MIO. The project leading to this publication has received funding from the European FEDER Fund under project 1166-39417. Guillaume Marchessaux was supported by a PhD fellowship from the French Ministry of Higher Education and Research from 2015 to 2018. Thanks to Michael Paul, a native English speaker, for proof-reading the text.

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