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Research Article

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Does the Invasive Predator *Mnemiopsis leidyi* A. Agassiz, 1868 Control Copepod Abundances in the Seine Estuary?

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Abstract
The indigenous ctenophore Pleurobrachia pileus *(O.F. Müller, 1776) was common in the coastal waters of the English Channel in the early 1990s and showed very abundant populations in the downstream part of the Seine estuary. In 2005, the non-indigenous ctenophore* Mnemiopsis leidyi *A. Agassiz, 1868, a species native to the Western Atlantic, was reported for the first time in Europe in Norwegian fjords and in Le Havre harbour (Seine estuary, France). More recently, in 2017, both* Pleurobrachia pileus *and* Mnemiopsis leidyi *were recorded during suprabenthos and zooplankton sampling in the Seine estuary along a downstream-upstream transect. Both species show more abundant populations in May than in September. Conversely, copepods show a spatial distribution depending on the ctenophore distribution, with low copepod abundances in the downstream part of the estuary being associated with high ctenophore abundances, while high copepod abundances are recorded where ctenophores are absent or display low abundances. We propose that the intense predation of ctenophores on copepods is related to changes in hydrological conditions over the two last decades. This may explain the dramatic decline of copepod abundance in the Seine estuary, which could have a negative effect on its nursery role.*

Keywords: *Mnemiopsis leidyi*; Non-Indigenous Species; *Pleurobrachia pileus*

Introduction

Invasive species have been identified as posing a major threat to marine ecosystems, leading to biodiversity loss and adverse environmental, economic and social impacts [1, 2]. *Mnemiopsis leidyi* A. Agassiz 1865 is known to be an invasive species in several parts of the world [3]. In the Black Sea, *M. leidyi* can reach a density of 304 individuals per m^3 and has had a major impact on the ecosystem functioning of this semi-enclosed sea. In combination with other anthropogenic pressures (overfishing and eutrophication), the invasion of *M. leidyi* has caused the collapse of local fisheries and the economy [4-6]. *M. leidyi* is a perfect competitor of indigenous species (e.g. native copepods) with its wide range of environmental tolerance (7) in terms of salinity (0-40), temperature (0-32°C) and low oxygen concentration (< 1.0 mL.L^{-1}) [7-10]. *M. leidyi* is a zoo-planktivorous species, feeding mainly on small copepods, barnacle nauplii, cladocerans, bivalve veligers, larvae and fish eggs [11-14]. In the Black Sea, Azov Sea and Marmara Sea, zooplankton show a dramatic decline after each bloom of *M. leidyi* [15]. The recent introduction of *M. leidyi* along the Emilia-Romagna Adriatic coast has significantly reduced the zooplankton biomass [16]. The plasticity of its diet, combined with its rapid growth and reproduction, mean that *M. leidyi* has a high population turnover [14].

Certainly introduced from the Atlantic coast of North America in the ballast waters of commercial vessels, *Mnemiopsis leidyi* appeared in Northern Europe (Norwegian fjords) in 2005 [17]. Then, this invasive species spread along the coasts of Denmark, Germany the Netherlands and Belgium following hydrodynamic circulation and/or by maritime traffic [18-22]. In the English Channel, the first observation of *M. leidyi* was in Le Havre harbour in 2005 and populations of this species are now well established in the Bay of Seine [3].

The first data on the near bottom and suprabenthic communities of the Seine estuary were obtained from a station just in front of the Seine estuary, where two series of samples were collected in June 1992 [23]. The most abundant taxa of the near-bottom meso- and macrozooplanktonic fauna at this station are represented by copepods and the ctenophore *Pleurobrachia pileus* (O.F. Müller, 1776). Abundant *P. pileus* populations were observed in the Seine estuary until the mid-1990s [24]. From the early years 2000 until around 2015, this ctenophore remained present but with very low abundances [25].

Renewed zooplankton and suprabenthos sampling in 2017 showed a return to high abundances of *Pleurobrachia pileus* coupled with the presence of the NIS *Mnemiopsis leidyi* in the lower part of the Seine estuary. Conversely, the copepods showed a dramatic decline in the marine and polyhaline downstream parts of the estuary, while an abundant population remained in the mesohaline zone.

The present study explores the potential inverse correlation between copepod abundances in the Seine estuary and the presence of the invasive *Mnemiopsis leidyi* population associated with the indigenous *Pleurobrachia pileus.* We explore the hypothesis of an intensive predation of Ctenophores on copepods resulting from changes of hydrological conditions over the two last decades.

Methods

Seine Estuary

The Seine estuary is located on the northern coast of France, open to the Bay of Seine and the eastern part of the English Channel (Figure 1). The tidally influenced section of the Seine is 160 km long from the mouth upstream to the Poses dam. It is the third largest estuarine ecosystem in France after the Gironde and Loire on the Atlantic coast [26]. Freshwater input into the estuary is primarily from the Seine River, which has a catchment area of approximately 77,000 km^2 feeding the discharge of 14 x 109 m^3 of water per year, with monthly and inter-annual variations (Figure 2) [27].

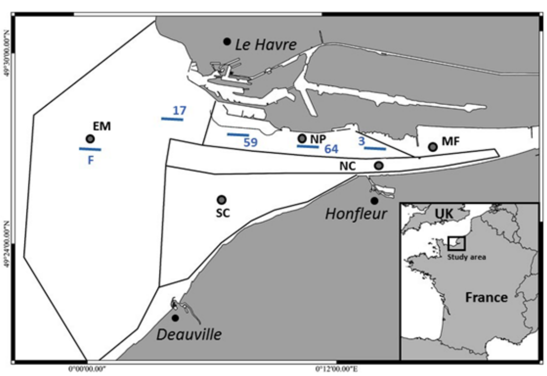

Figure 1. Map showing locations of zooplankton and suprabenthic locations (in black) in the Seine estuary in the five zones. Estuary Mouth (EM), North Port 2000 Channel (NP), South Channel (SC), Navigational Channel (NC) and Mud Flat (MF) and showing locations of suprabenthic locations in the North Channel of the Seine during the Port 2000 survey (in blue).

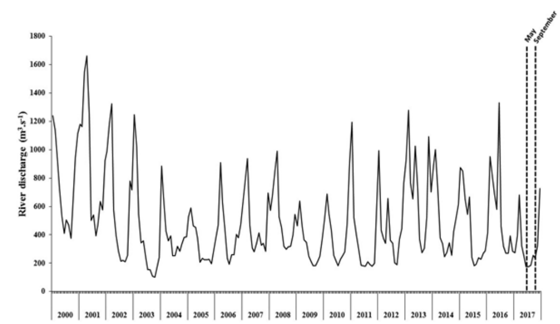

Figure 2. Monthly averaged flow of the Seine from 2000 to 2017 with sampling dates (May and September) in 2017 (dotted lines).

Sampling Strategy

The data come from a scientific project dedicated to fish nurseries in the Seine estuarine ecosystem (https://www.seine-aval.fr/projet/capes/), with results from suprabenthic and zooplankton samples collected in five different zones in the Seine estuary: Estuary Mouth (EM), North Port 2000 Channel (NP), South Channel (SC), Navigation Channel (NC) and Mud Flat (MF) (Figure 1).

The suprabenthos was sampled using a sledge filtering the water at 0.10–0.40 m above the sea bottom. The sledge was equipped with a WP2 zooplankton net (0.5 mm mesh size), with a flow meter at its centre to measure the volume of water filtered. The sampling duration (i.e. the time during which the sledge remains in contact with the seabed) was 5 min at a speed of approximately 1.5 knots.

The zooplankton was sampled using a WP2 zooplankton net (0.2 mm mesh size), with a flow meter at its centre to measure the volume of water filtered (Table 1). The sampling strategy involves collecting a total of three oblique samples per station from the seabed to the surface at a speed of approximately 1 m.s^{-1} for a total of 30 samples during the study.

Table 1: Seawater characteristics of the five zones in the Seine estuary during May and September 2017. (S: Surface; B: Bottom); Volumes filtered correspond to zooplanktonic samples.

		Volume filtered m3	Salinity		Temperature		Oxygen		Turbidity	
			S	B	S	B	S	B	S	B
May	EM	5.3 ± 2.5	23.3	30.7	15.6	14.7	3.6	3.8	15.8	14.1
	SC	12.2 ± 11.4	23.3	30.7	15.6	14.7	3.6	3.8	15.8	14.1
	NP	4.1 ± 4.0	29.4	30.7	15.4	14.9	5.6	5.9	2.8	6.9
	NC	6.7 ± 1.8	24.6	26.1	15.6	15.6	5.0	5.3	11.4	33.8
	MF	11.6 ± 3.6	11.2	11.2	18.5	18.5	2.5	2.5	76.7	76.7
September	EM	36.3 ± 29.8	31.7	31.9	17.2	17.2	5.5	5.6	2.4	9.1
	SC	88.1 ± 11.6	30.9	31.4	17.1	16.9	5.6	5.6	3.8	10.7
	NP	37.2 ± 19.3	21.6	25.7	16.2	16.8	6.0	5.8	73.1	214.0
	NC	34.7 ± 19.4	23.4	26.6	16.7	16.8	5.9	5.8	29.5	77.8
	MF	29.8 ± 29.8	9.4	9.4	16.8	16.8	3.5	3.5	214.0	214.0

The zooplankton and suprabenthos were sampled at two seasons, i.e. summer sampling on 24 May (EM, NP, SC and NC) and 9 June (MF) and autumn sampling on 20-21 September 2017, with three replicates in each zone. Thus, a total of 60 samples were analysed, with 15 samples per season and per gear. In each sample, all organisms were washed, the ctenophores sampled with the sledge and the WP2 zooplankton net were identified and counted, while all copepods from the 30 planktonic samples were counted as a single taxa.

Regarding the environmental parameters, the freshwater discharge of the Seine is obtained from data acquired at the dam of Poses (http://seine-aval.crihan.fr). At each sampling station, a CTD Seabird 25 was used to determine the hydrological conditions (salinity, turbidity, oxygen concentration and temperature).

Historical data of *Pleurobrachia pileus* are derived from the Port 2000 construction survey in the North Channel of the Seine estuary. In this area, the suprabenthos was sampled at four stations (F; 17; 59; 64 and 3) (Figure 1) from 2001 to 2015. The suprabenthos was sampled using a new version of the Macer-GIROQ sledge, which consisted of four 0.18 m2 boxes (0.6 × 0.3 m), designed to filter the water column at four layers above the sea bottom: 0.10–0.40 m (box 1), 0.45–0.75 m (box 2), 0.80–1.10 m (box 3) and 1.15–1.45 m (box 4) (Dauvin et al., 2010). Each box was equipped by a WP2 zooplankton net (0.5 mm mesh size), including a Tsurimi- Seiki-Kosakusho (TSK) flow meter at its center to measure the volume of water filtered. The sampling duration (i.e., the time during which the sledge remains in contact with the seabed) was 5 min at a sledge speed of approximately 1.5 knots. At each sampling date, a CTD Seabird 25 was used to determine the hydrological conditions at each station (salinity and turbidity). Data are available for seven sampling periods (each extending in most cases from September-October to March of the following year). For each station and each sampling period, we give the mean abundance for the four boxes expressed per 100 m^3.

Statistical Analysis

Two-way ANOVA was used to test seasonal (May versus September) and spatial (EM; FP; NP; NC; MF) changes in the seawater parameters (salinity, temperature, oxygen, turbidity) and abundance of three taxa: Copepoda, *Mnemiopsis leidyi* and *Pleurobrachia pileus.*

Prior to each ANOVA, a Shapiro-Wilk normality test and a Bartlet test for homogeneity of variances were performed. The post-hoc Tukey Honestly Significant Difference test was applied when ANOVA showed significant differences. All analyses were performed using R software.

Results

Hydrological Characteristics

During the period 2010-2017, an important variability of inter-year freshwater inputs was observed in the Seine estuary (Figure 2). A series of four main episodes occurred during the years 2000-2017, the first period (2000-2003) is characterized by winter peaks of > 1,200 $m^3.s^{-1}$ and a maximum of 1,600 $m^3.s^{-1}$, while the second period (2004-2010) is associated with low freshwater input, which increases again during the third period 2011-2016) with winter peaks of > 1,000 $m^3.s^{-1}$. The last period (2017) corresponds to a return to low freshwater inputs. The maximum annual freshwater discharge was 903 $m^3.year^{-1}$ in 2001, falling to a minimum (328 $m^3.year^{-1}$) in 2009. During the sampling year of 2017, the annual freshwater discharge was 332 $m^3.year^{-1}$.

For the 2017 sampling year, the salinity in the downstream part of the Seine estuary (Figure 1) can be classified into three main categories: two stations (EM and SC) in marine waters (>30 psu), NP and NC in the polyhaline zone (18-30 psu) and MF station in the mesohaline zone (5-18 psu) in May and September (Table 1). Although there is no significant temporal variability in salinity (result test, Tables 1 and 2), a spatial gradient can be observed in the Seine estuary, ranging from a marine (EM) to a mesohaline (MF) system with the lowest salinity recorded at MF (Tables 1 and 2).

The temperature ranges from a minimum of 14.7 °C at EM and SP in May to a maximum of 18.5 °C at MF, also recoded in May, with no significant seasonal differences between the zones (result test., Tables 1 and 2). The oxygen concentration ranges from 2.5 mL.L^{-1} at MF in May to 6.0 mL.L^{-1} at NP in September. No seasonal variation is observed in oxygen concentration, but the highest values are found at NC and NP, and the lowest at MF (Tables 1 and 2). The turbidity ranges from 2.4 NTU at EM in September to 214 at NP and MF during September, with no seasonal variation. However, the turbidity at NC and NP is significantly different from the value recorded at MF (Tables 1and 2).

Zooplankton Variability

During the study period, a total of 6,894 copepods were collected, along with 3,576 ctenophores (3,490 individuals of *Pleurobrachia pileus* and 86 individuals of *Mnemiopsis leidyi*). For all three taxa, seasonal differences are observed in their abundances (Tables 2 and 3), with a higher copepod abundance during May in the upper part of the estuary. The mean abundance of copepods varies from 44 ± 16 individuals per 100 m^3 at MF in September to 15,410± 6,992 individuals per 100 m^3 at MF in May (Table 2). For both sampling dates, copepod abundances are lower in EM and SC and higher in NP, NC and MF (Tables 2 and 3).

Table 2: Mean abundances with standard deviation (numbers of individuals per 100 m^3) in the five sectors of the Seine estuary in May and September 2017 for the zooplanktonic samples.

		Copepoda	*Mnemiopsis leidyi*	*Pleurobrachia pileus*
May	**EM**	428 ± 416	188 ± 64	4,453 ±812
	SC	243 ± 52	62 ± 36	594 ± 92
	NP	6,051 ± 7,789	0	2,479 ± 158
	NC	3,751 ± 1,430	0	142 ± 26
	MF	15,410 ± 6,992	0	0
September	**EM**	159 ± 14	1 ± 2	129 ±56
	SC	146 ± 62	6 ± 6	0
	NP	196 ± 290	12 ± 2	555 ± 75
	NC	145 ± 144	0	407 ± 13
	MF	44 ±16	0	0

For *Mnemiopsis leidyi*, the mean abundance varies between 0 ± 2 individuals per 100 m^3 at EM in September to a maximum of 188 ±64 individuals per 100 m^3 at EM in May (Table 2), the values being higher at EM than at NC, NP or MF (Table 3). *M. leidyi* is found in the lower estuary at EM and SP in May (Figure 3) and at EM, SC and NP in September (Figure 4). This species is absent from the upper part of the Seine estuary (NP, NC and MF) in May and also at NC and MF in September (Figures 3 and 4).

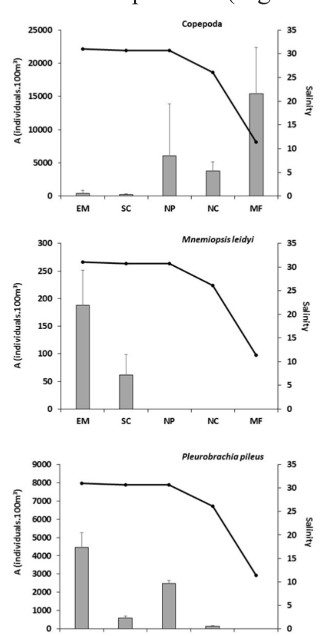

Figure 3: Histogram showing mean abundances with standard deviation (numbers of individuals per 100 m^3) in the five zones of the Seine estuary for Copepoda, *Mnemiopsis leidyi* and *Pleurobrachia pileus* in May 2017 in link with the measured salinity (dark line).

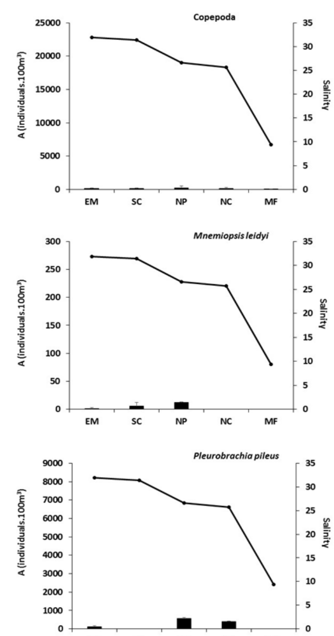

Figure 4: Histogram showing mean abundances with standard deviation (numbers of individuals per 100 m^3) in the five zones of the Seine estuary for Copepoda, *Mnemiopsis leidyi* and *Pleurobrachia pileus* in September 2017 in relation with the salinity (dark line) for the zooplanktonic samples.

Table 3: Two-way ANOVA for the seawater parameters (Salinity, Temperature, Oxygen, Turbidity) and the abundance of Copepoda, *M. leidyi* and *P. pileus* with Tukey on the five zones.

			Df	F	p	Tukey test
	Salinity	Season	1	0.004	0.95	
		Station	4	35.8	< 0.01	MF ≠ EM ; SC ; NP ; NC
	Temperature	Season	1	38.8	< 0.01	
		Station	4	18.4	< 0.01	MF ≠ EM ; SC ; NP ; NC
	Oxygen	Season	1	392.0	< 0.001	
		Station	4	300.1	< 0.001	MF ≠ NC; NP
	Turbidity	Season	1	14.8	< 0.001	
		Station	4	11.2	< 0.001	MF ≠ EM; SC
		∑	10			
A Zooplankton	**Copepoda**	Season	1	17.0	< 0.001	
		Station	4	5.1	< 0.01	EM; SC ≠ NP; NC; MF
	M. leidyi	Season	1	29.7	< 0.001	
		Station	4	18.0	< 0.001	EM ≠ NC; MF; NP
	P. pileus	Season	1	184.8	< 0.001	
		Station	4	82.8	< 0.001	EM ≠ NC; MF; NP
A Suprabenthos	***M. leidyi***	Season	1	4.0	0.05	
		Station	4	5.4	< 0.01	EM; SC ≠ NC; MF; NP
	P. pileus	Season	1	18.8	< 0.001	
		Station	4	5.0	< 0.01	MF ≠ EM ; SC ; NP ; NC
		∑	20			

The abundance of *Pleurobrachia pileus* varies from 129 ± 56 individuals per 100 m^3 at EM in September to 4,453 ± 812 individuals per 100 m^3 at EM in May (Table 2). Differences are observed between the two sampling periods, with higher abundances at EM than at NC, NP or MF (Tables 2 and 3). *P. pileus* was not present at the upper station (MF) on both dates and at SC in September (Figures 3 and 4).

The abundances of copepods, as well as the ctenophores *M. leidyi* and *P. pileus*, are lower in September than in May (Table 2). However, for both sampling periods, the presence and abundance of both ctenophores and copepods shows an inverse distribution pattern (Figures 3 and 4).

Suprabenthic Faunal Variability

During the study period, a total of 23,400 *Pleurobrachia pileu*s and 26 *Mnemiopsis leidyi* were collected with the suprabenthic sledge. For *M. leidyi*, no seasonal abundance difference can be observed (Tables 3 and 4); however, for *P. pileus*, the maximum abundance is observed in May (Tables 3 and 4). For *Mnemiopsis leidyi*, the mean abundance varies from 1 ± 1 individuals per 100 m^3 at SC in September to 4 ± 2 individuals per 100 m^3 at EM in September (Table 4), and are only present at EM and SC (Tables 3 and 4). For *Pleurobrachia pileus*, abundances vary from 36 ± 16 individuals per 100 m^3 at EM in September to 2,850 ± 1,716 individuals per 100 m^3 at EM in May (Table 4). Abundance are higher in May than in September, and do not differ significantly between the four stations where this species is present (EM; NC; NP and SC) (Tables 3 and 4). *P. pileus* is not present at the upper station (MF) for both sampling periods (Table 4).

Table 4: Mean abundances with standard deviation (numbers of individuals per 100 m^3) in the five zones of the Seine estuary in May and September 2017 for the suprabenthic samples.

		Mnemiopsis leidyi	*Pleurobrachia pileus*
May	EM	0	2,850 ± 1,716
	SC	1 ± 2	1,185 ± 1,266
	NP	0	1,723 ± 67
	NC	0	59 ± 9
	MF	0	0
September	EM	4 ± 2	36 ± 16
	SC	1 ± 1	0
	NP	0	323 ± 74
	NC	0	108 ± 17
	MF	0	0

Suprabenthic *Pleurobrachia Pileus* Population from 2001 To 2015

Pleurobrachia pileus shows very large changes in spatio-temporal abundances in the lower part of the North Channel of the Seine estuary (Figure 5). There have been years without *Pleurobrachia* (such as 2001, 2008/2009 and 2015), as well as other years with low abundances (such as 2004/2005 and 2001/2012), and periods with high abundances, such as in 2003 (Table 5). The highest abundances are associated with the highest salinities (Table 5), especially in 2002 (Figure 5); in September 2003, however, all the stations with a salinity > 30 were colonised by *Pleurobrachia* (Table 5).

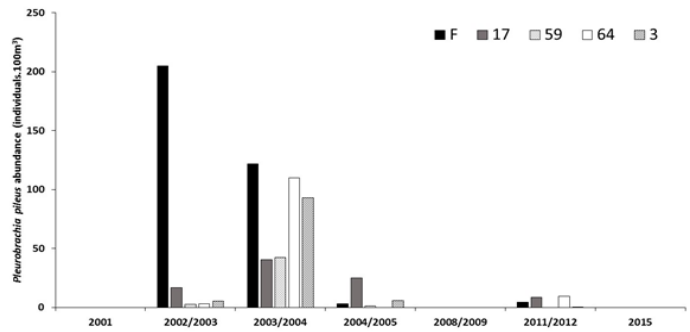

Figure 5: Spatio-temporal distribution of *Pleurobrachia pileus* abundances along the North Channel of the Seine estuary from suprabenthic samples collected between 2001 and 2015.

Table 5. Salinity and mean *Pleurobrachia pileus* abundance with standard deviation (number of individuals per 100 m^3) in the North Channel of the Seine estuary between 2001 and 2015.

		Salinity					*P. pileus* abundance				
		F	17	59	64	3	F	17	59	64	3
2001	September 2001	26.6	19.7	12.7	11.6	11.6	-	-	-	-	-
	December 2001	22.2	12.9	12.6	11.6	11.6	-	-	-	-	-
2002/2003	October 2002	26.6	20.6	15.5	17.7	16.5	6.2 ±6.1	0.8 ± 1.6	3.5 ± 3.9	6.0 ± 3.9	11.1 ± 15.7
	March 2003	30.9	30.4	29.1	26.7	25.6	403.7 ± 207.9	32.7 ± 23.8	2.0 ± 4.0	0.5 ± 0.9	-
2003/2004	September 2003	33.0	31.2	31.8	32.2	31.3	243.6 ± 179.4	80.9 ± 86.1	84.1 ± 25.6	218.5 ± 58.6	184.8 ±60.4
	March 2004	31.3	31.9	30.7	29.0	27.9	0.3 ±0.4	0.2 ± 0.5	0.6 ± 0.7	1.6 ± 0.6	1.5 ± 2.1
2004/2005	September 2004	22.7	12.9	13.9	15.0	16.7	6.4 ± 5.6	49.6 ± 11.1	2.6 ± 5.3	-	12.0 ± 16.0
	March 2005	29.5	27.2	27.8	25.7	24.7	-	-	-	-	-
2008/2009	September 2008	33.4	33.2	32.8	31.5	30.7	-	-	-	-	-
	February 2009	30.8	29.0	28.6	27.1	25.7	-	-	-	-	-
2008/2009	October 2011	31.8	31.5	30.9	29.0	26.8	-	-	-	-	-
	March 2012	28.5	28.8	28.5	23.9	22.5	9.1 ± 6.6	16.7 ± 11.1	-	18.5 ± 11.6	0.3 ± 0.6
2015	October 2015	31.2	31.4	28.6	18.4	17.9	-	-	-	-	-
	March 2015	28.3	31.3	31.8	29.3	27.4	-	-	-	-	-

Discussion

The American ctenophore *Mnemiopsis leidyi* was recently ranked among the 100 most invasive marine species in the world by the International Union for the Conservation of Nature (IUCN, https://www.iucn.org/fr). Along the French coast, the first occurrence of *M. leidyi* was recorded from the Vauban basin in the port of Le Havre in 2005 [3, 28]. This species was then observed along the French coasts of the North Sea (between Calais and Dunkirk) in

2009, and in the Bay of Seine in 2011 [3,28]. A survey of the autumn population from 2014 to 2018 shows maximum abundances in the Bay of Seine ranging from 200 to 450 ind.100 m^3. This autumn population is abundant offshore the Calvados coast and the western part of the Bay of Seine (Bay of Veys), but rare or absent at the mouth of the Seine estuary (https://wwz.ifremer.fr/lern/Le-LERN/).

The spring abundances measured in May 2017 are of the same order of magnitude as the maximum observed in other parts of the Bay of Seine; moreover, our observations in September 2017 confirm the low abundance of *M. leidyi* in the lower part of the Seine estuary at this period.

The Seine estuary and Le Havre harbour are known as hotspots of NIS detection, with at least 36 NIS recorded in this area [28,29]. In 2017, the mysid *Neomysis americana* (S.I. Smith, 1973) and the isopod *Synidotea laticauda* Benedict, 1897 were recorded for the first time in the EC in the Seine estuary [30-32]. Moreover, in Le Havre harbour (Vauban basin), three new NIS were recorded in 2019 for the first time in the EC: two amphipods of the genus *Aoroides* (*A. semicurvatus* Ariyama, 2004 and *A. longimerus* Ren & Zheng, 1996 and the isopod *Paranthura japonica* Richardson, 1909 along with another species (*Ianiropsis serricaudis* Gurjanova, 1936) which was recorded for the first time along the French coast of the EC [33- 35]. All these records confirm the importance of maritime transport, mainly from ballast waters, in controlling the introduction of NIS in the eastern part of the Bay of Seine via the port of Le Havre.

At the beginning of the 1990s (1991-1994), the ctenophore *Pleurobrachia pileus* (O.F. Müller, 1776) was very abundant at the mouth of the Seine estuary [23, 36]. The abundances were higher than reported for any other European shallow waters, with a mean spring abundance of 3,300 ind.100 m^3 in 1991 and 3,000 ind.100 m^3 in 1992 when it reached a maximum of 80,000 ind.100 m^3. In the Seine estuary, *P. pileus* shows passive tidal advection and active diel migration [36]. At the mouth of the estuary, high abundances are observed around low tide, and diel vertical migration is very important. However, many individuals remain aggregated near the bottom all the time (suprabenthic hauls). In the early 1990s, *P. pileus* with high abundances was collected in waters of salinity 15 to 33 psu in the marine downstream part of the estuary.

The spring 2017 survey shows *P. pileus* abundances of the same order of magnitude as those observed at the beginning of the 1990s: mean 4,200 ind.100 m^3 with a maximum of 5,243 ind.100 m^3 at the EM station.

Moreover, *P. pileus* shows strong long-term variability in abundance, with periods of very high abundance such as in 1990-1995, then in 2017, and period of presence with low abundances. A Before/During/After Control-Impact approach has been used to assess the effects of Port 2000 on the suprabenthos in the Estuary Mouth (EM) and North Channel (NP) of the Seine estuary (Figure 1) from September 2001 to October 2015 (Table 5). The results show a maximum abundance of *P. pileus* in March and September, remaining at around 100 ind.100 m^3. except in March 2003 when it reached 400 ind.100 m^3. Long-term monitoring over three decades reveals a succession of periods without *P. pileus* (such as in 2001, 2008 and 2015) and periods with blooms (such as in 1991, 1992 and 2017).

Such blooms of *P. pileus* are known in the southern part of the North Sea; Schlüter et al. suggested that changes of abundances in this species could be correlated with inter-annual changes in spring temperatures [37]. Moreover, in this area, the long periods of *P. pileus* abundances are correlated with a decline in the autumn abundance of copepods. Such long-term changes of *P. pileus* in the English Channel including the Bay of Seine remain to be analysed.

In 2017, both ctenophores species *M. leidyi* and *P. pileus* were more abundant in the lower part of the Seine estuary, but *P. pileus* was able to colonize the navigation channel of the Seine river further upstream than *M. leidyi*.

Copepod abundances were very low in September (50-200 ind.100 $m^{3)}$, without any downstream-upstream gradient, while late spring abundances were higher especially in the polyhaline (4,000-6,000 ind.100 m^3) and mesohaline (15,400 ind.100 m^3) zones. These spring values are very low compared to those recorded in spring 1996 by Mouny and Dauvin : ~ 20,000 ind.100 m^3 in the polyhaline zone and 500,000 ind.100 m^3 in the mesohaline zone, and from bottom planktonic hauls in the EM zone: 600-26,500 ind.100 m^3 [23, 38]. The spatio-temporal changes could be the consequences of two main factors.

1. During the two last decades, there has been a marinization of the downstream part of the Seine estuary with a significant increase of salinity mainly in the North channel (NP) and the navigation channel (NC). The changes of plankton fauna from estuarine to marine type components are associated with a strong decrease in suprabenthic species [24]. During the same period, the highly abundant population (up to 200,000 ind.m^3 in the 1990s; Mouny and Dauvin, 2002) of the oligohaline copepod *Eurytemora affinis* migrated upstream in the freshwater part of the Seine estuary as far as Rouen which is located at 120 km from the estuary mouth (Seine-Aval project SARTRE, unpublished data) [38].

2. Predation of the indigenous ctenophore *Pleurobrachia pileus* as well as the non-indigenous ctenophore *Mnemiopsis leidyi* on the copepods has led to their declining population linked with hydrological changes in the Seine Estuary. [39]. Has studied the species composition and predation pressure of the zooplankton community in the western Wadden Sea (the Netherlands) before and after the invasion of the ctenophore Mnemiopsis leidyi. *M. leidyi* has been present in the Wadden Sea since 2006, with high densities every year in summer and autumn [39]. During 1980-1983, predation pressure by scyphomedusae, ctenophores and hydromedusae on fish larvae and zooplankton was low because of the low densities of these predators. However, during the period 2009-2012, *M. leidyi* was responsible for most of the predation pressure on mesozooplankton in this area. A strong decrease of zooplankton abundances and biomass has been observed after each bloom of *M. leidyi* in the Black Sea, Azov Sea, Marmara Sea and Adriatic Sea [15,16]. Such temporal predation changes have probably also occurred in the Seine estuary in relation to the appearance of high abundances of *M. leidyi*, Although the abundance of *P. pileus* has

remained of the same order of magnitude, the competition between these two ctenophores should be enhanced along with the decrease of copepod abundances over the two last decades.

Moreover, modelling studies highlight differences in trophic functioning linked to different areas of the Seine estuary (estuary mouth, North Channel, South channel, navigation channel, and intertidal mud flats) [40]. Results show that the North and Central Navigation channels display a functioning related to a high level of stress, while the South Channel shows the highest system activity. In a second study, [40]. modelled the trophic web for the North Channel before and after Port 2000 construction (2002-2005), analysing the dynamics of the three inner estuarine habitats of the Seine estuary (North, South and Navigation Channels) [41]. Again, results show that the South Channel is the least stressed habitat of the estuary. In the future, it should be interesting to *M. leidyi.*

Conclusion

This paper addresses an abundance comparison of two ctenophores (*P. pileus* and *M. leidyi*) with copepod abundance in the Seine estuary. Results highlighted that copepods show a spatial distribution depending on the ctenophore distribution, with low copepod abundances in the downstream part of the estuary being associated with high ctenophore abundances, while high copepod abundances are recorded where ctenophores are absent or display low abundances. Thus, the introduction of *M. leidyi* has lead to an increase in predation pressure of copepods. The intense predation of the both ctenophores on the copepods has led to declining copepod population linked with hydrological changes in the Seine Estuary.

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