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A. Nowaczyk, V. David, Mario Lepage, A. Goarant, E. de Oliveira, et al.. Spatial and temporal patterns of occurrence of three alien hydromedusae, *Blackfordia virginica* (Mayer, 1910), *Nemopsis bachei* (Agassiz, 1849) and *Maeotias marginata* (Modeer, 1791), in the Gironde Estuary (France). *Aquatic Invasions*, 2016, 11 (4), pp.397-409. 10.3391/ai.2016.11.4.05 . hal-01400187

HAL Id: hal-01400187

<https://hal.science/hal-01400187>

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Research Article

Spatial and temporal patterns of occurrence of three alien hydromedusae, *Blackfordia virginica* (Mayer, 1910), *Nemopsis bachei* (Agassiz, 1849) and *Maeotias marginata* (Modeer, 1791), in the Gironde Estuary (France)

Antoine Nowaczyk^{1,2,*}, Valérie David^{1,2}, Mario Lepage³, Anne Goarant⁴, Éric De Oliveira⁴ and Benoit Sautour^{1,2}

¹Univ. Bordeaux, EPOC, UMR 5805, F-33400 Talence, France

²CNRS, EPOC, UMR 5805, F-33400 Talence, France

³IRSTEA, UR EPBX, F-33612 Cestas, France

⁴EDF-R&D, LNHE, 78400 Chatou, France

*Corresponding author

E-mail: a.nowaczyk@epoc.u-bordeaux1.fr

Received: 23 July 2015 / Accepted: 21 July 2016 / Published online: 29 August 2016

Handling editor: Philippe Gouletquer

Abstract

The species composition and seasonal abundance patterns of gelatinous zooplankton are poorly known for many European coastal-zone waters. The seasonal abundance and distribution of the dominant species of hydromedusae along a salinity gradient within the Gironde Estuary, Atlantic coast of France, were evaluated based on monthly surveys, June 2013 to April 2014. The results confirmed the presence of three species considered to be introduced in many coastal ecosystems around the world: *Nemopsis bachei* (Agassiz, 1849), *Blackfordia virginica* (Mayer, 1910), and *Maeotias marginata* (Modeer, 1791). These species were found at salinities ranging from 0 to 22.9 and temperatures ranging from 14.5 to 26.6 °C, demonstrating their tolerance to a wide range of estuarine environmental conditions. There was a clear succession of the three species that was influenced by temperature and salinity. *Blackfordia virginica* was the dominant hydromedusae during the warmest months and occurred at very high abundance (up to 634 individuals.m⁻³ corresponding to 21.40 g.m⁻³ as wet weight). The seasonal evolution of the size distribution indicated an extended period of release of medusae by hydroid polyps, and rapid growth, covering the whole period of occurrence for *B. virginica*. *Nemopsis bachei* also was present during the warmer months but only locally common. In contrast, *Maeotias marginata* only occurred in low numbers during autumn and had not been previously detected in the Gironde Estuary. Non-native jellyfishes clearly represent a prominent component of the Gironde Estuary, and additional work is needed to understand the potential impacts on the structure and functioning of entire zooplankton community.

Key words: high turbidity, macro tidal, numbers, biomass, size distributions, jellyfish, introduced species

Introduction

Blooms of jellyfishes and ctenophores occur worldwide, often having major effects on local food webs (Purcell et al. 2007; Richardson et al. 2009; Brotz et al. 2012). These blooms are natural features of pelagic ecosystems or induced by environmental perturbations such as the introduction of non-native species to an area (Richardson et al. 2009; Purcell 2012; Roux et al. 2013). Human activities such as fisheries, shipping, and aquaculture transfers promote the introduction of non-indigenous aquatic species, especially in strongly anthropogenically developed ecosystems such as many estuaries (Ruiz et al. 1997; Gollasch 2007; Purcell et al. 2007; Preisler et al.

2009). Among the introduction vectors, both ballast water and hull fouling are plausible dissemination mechanisms for jellyfish by medusa and polyp stages. Some gelatinous zooplankton species are highly adaptable, explaining their ability to efficiently colonize outside of their native range (Rees and Kitting 2002).

During August 2012, a bloom of hydromedusae occurred in the Gironde estuary (GE), one of the largest estuaries in Europe, clogging zooplankton and ichthyoplankton nets. Despite many early works focusing on mesozooplankton, mainly on copepods and mysids, such high densities of hydromedusa were unprecedented (e.g., David et al. 2005; Chaalali et al. 2013). In addition, due to the lower numerical abundances of this group compared to crustacean

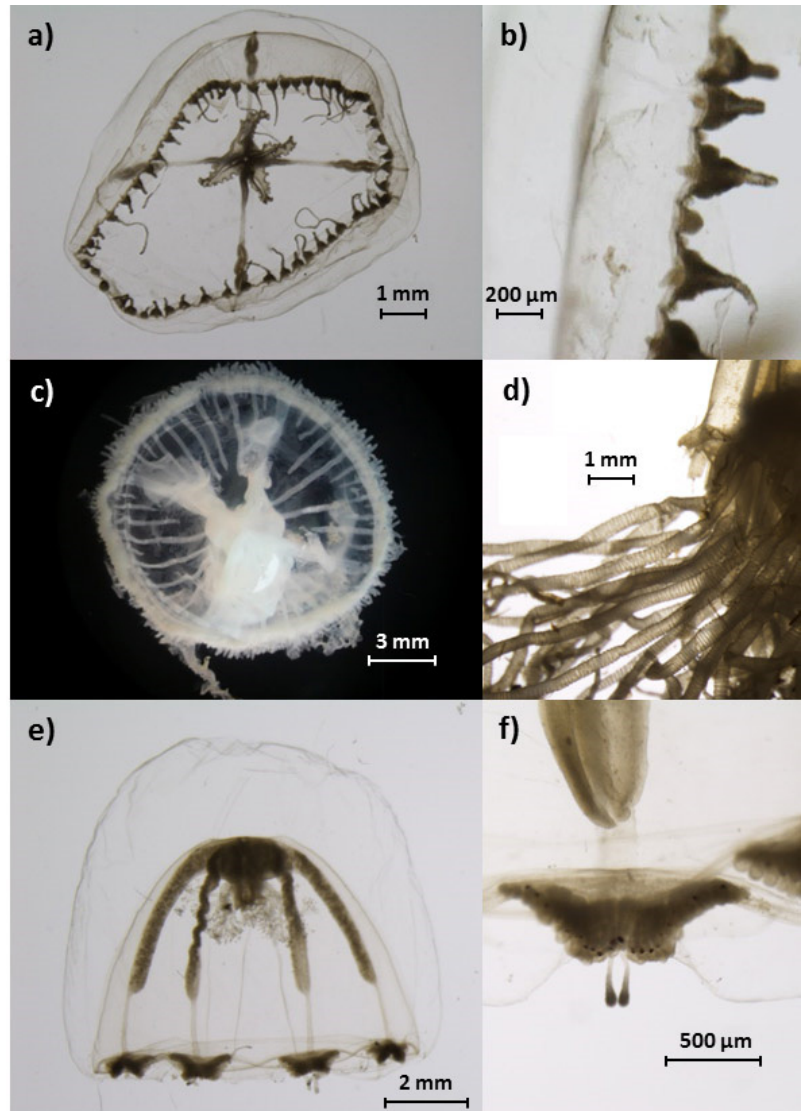


Figure 1. Oral view of *Blackfordia virginica* from the Gironde estuary (a) and details of tentacles showing oval diverticula into the bell margin (b). Oral view of *Maeotias marginata* (c) and details of tentacles with nematocyst rings (d). Lateral view of *Nemopsis bachei* (e) and details of one group of marginal tentacles showing ocelli and a median pair of club-shaped tentacles. Photomicrographs: A Nowaczyk.

zooplankton in the estuary, studies focusing on jellyfishes are scarce and jellyfish diversity is poorly known. As an example, only Tiffon (1956) reported the presence of *Nemopsis bachei* (Agassiz, 1849), a non-indigenous species, in the GE.

A recent study, based on a snapshot survey during July 2012, did report the species composition of the gelatinous plankton present during summer in the Gironde Estuary (David et al. 2016). With regards to non-native jellyfishes, *N. bachei* and *Blackfordia virginica* (Mayer, 1910), were abundant in some locations while another non-native species (Figure 1), *Maeotias marginata* (Modeer, 1791), was not detected. Indeed, the present study is the first record for *M. marginata* in the Gironde Estuary. Because

sampling only occurred in July, species that bloom at other times would not be detected, and that may have been the case for *M. marginata* because it has been present in the adjacent Loire Estuary for decades (Denayer 1973).

Nemopsis bachei mainly occurs in the North Atlantic Ocean and in the China Sea (Mendoza-Becerril and Marques 2013). This species appears to be native to the eastern coast of the USA from Cape Cod to Florida. It has been reported regularly from Chesapeake Bay since 1930 (Cronin et al. 1962; Cowan et al. 1992; Purcell and Nemazie 1992; Marshalonis and Pinckney 2007, 2008). In the Eastern Atlantic Ocean, it is mainly reported along the west coast of Scotland (Haeckel 1879) and in the North

Sea (ICES 2006; Dumoulin 1997; Frost et al. 2010; Vansteenbergue et al. 2015). It also is possible that this species was introduced from Northern Europe to North America (Faasse and Ates 1998) or is native to both sides of the Atlantic Ocean.

The original range of *Blackfordia virginica* also is uncertain. It is considered as a Ponto-Caspian species; however, some authors (Zaitsev and Oztürk 2001) consider this species to originate from the eastern coast of the USA, which is where this species was first described by Mayer (1910). This species is the most common of the three species included in our study and has been introduced worldwide. *B. virginica* is regularly found in temperate and tropical estuaries, including those on: the western coast of the USA (Mills and Sommer 1995; Mills and Rees 2000; Harrison et al. 2013; Wintzer et al. 2013); South America (Bardi and Marques 2009; Freire et al. 2014; Genzano et al. 2006; Paranagua 1963); Asia (Kramp 1958; Vannucci et al. 1970; Zang 1982; Sai-Sastry and Chandramohan 1989); and probably in Africa (Buecher et al. 2005). It is also recorded in Europe from Portugal (Moore 1987; Chicharo et al. 2009; Marques et al. 2015) and more recently from The Netherlands (Faasse and Melchers 2014).

Maotias marginata was first described from specimens collected in the Netherlands (Modeer 1791) and later reported from the Sea of Azov, the Black Sea, and the Danube Estuary (Ostroumoff 1896; Borcea 1928; Naumov 1960). Nevertheless, this species is considered as a Ponto-Caspian invader by most authors (Mills and Rees 2000; Väinölä and Oulasvirta 2001). *M. marginata* is recorded from coastal waters on Atlantic and Pacific coasts of the USA (Calder and Burrell 1969; Mills and Sommer 1995), China (Xu et al. 1985), and, more recently, the Baltic Sea (Väinölä and Oulasvirta 2001; von Numers 2013) and Portugal (Muha et al. 2012).

The three non-native species (Figure 1) included in the present study were also reported in another French estuary, the Loire Estuary, located 200 km north of the GE; in 1968 for *N. bachei* and in 1971 for the other two species (Denayer 1973). Since these reports, no additional information has been reported from the Loire Estuary.

In response to both to the lack of knowledge of these three species along the French Atlantic coast, and the high biomasses recently observed in the GE, we initiated a field study to evaluate aspects of the biology of jellyfishes in the GE. Specifically, this study examined the seasonal and spatial variation in numerical abundance, biomass, and size distributions of medusae of *N. bachei*, *B. virginica*, and *M. marginata* and compared these patterns with those described in other ecosystems.

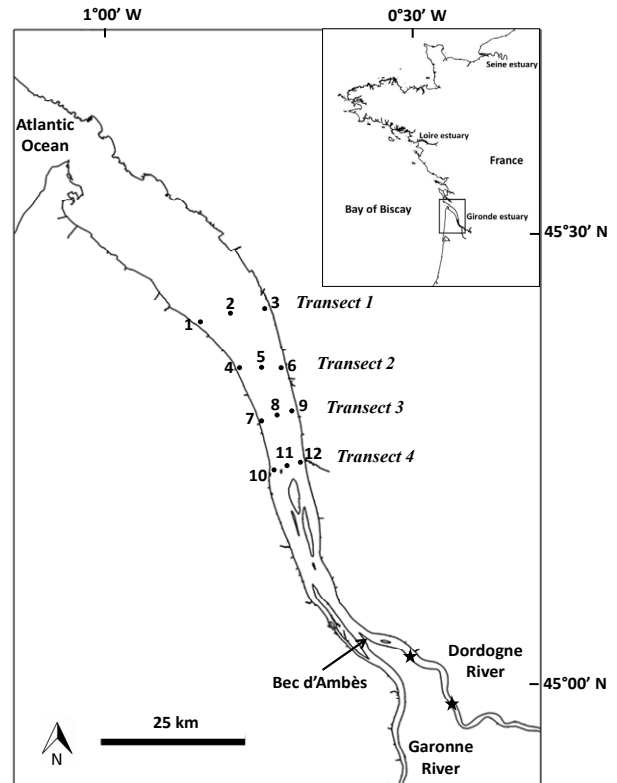


Figure 2. Location of the twelve sampling stations in the Gironde Estuary sampled monthly, June 2013 to April 2014. Black stars indicate two supplemental sampling stations in 2011 and 2012.

Material and methods

Study site

The Gironde Estuary (GE), in southwestern France (45°20'N; 0°45'W), is formed by the confluence of the Dordogne and the Garonne Rivers. The GE is 76 km long from the confluence of the two rivers (Bec d'Ambès) to the Atlantic coast (Figure 2). The surface area is 625 km² at high tide. The Gironde is a macrotidal estuary (spring tides of 4.5 to 5 m) with semi-diurnal tidal regime (Sottolichio and Castaing 1999). It is well-mixed estuary and is characterized by an extensive maximum turbidity zone (MTZ), due to a strong marine influence and a long residence time of water, which migrates seasonally according to the river flow and tidal cycles (Allen et al. 1980; Lanoux et al. 2013). The salinity limit zone is located from the seaward opening to around 30 km, where the salinity is never below 0.5 (Savoie et al. 2012), and can extend beyond 100 km (Etcheber et al. 2011; Lanoux et al. 2013) depending upon tide and discharge. The mean annual discharge is about 1000 m³.s⁻¹ (Sottolichio and Castaing 1999); however, there is substantial seasonal variation in freshwater discharge

with a maximum in January–February (mean $1500 \text{ m}^3 \cdot \text{s}^{-1}$) and a minimum in August–September (mean $250 \text{ m}^3 \cdot \text{s}^{-1}$). The GE is characterized by a very high turbidity with an annual mean suspended particulate matter concentration $>500 \text{ mg} \cdot \text{L}^{-1}$; exceeding $1 \text{ g} \cdot \text{L}^{-1}$ in surface water and $10 \text{ g} \cdot \text{L}^{-1}$ in bottom water in the MTZ (Jouanneau and Latouche 1981). As a consequence, primary production is greatly reduced compared to other estuaries, and mainly limited to the upstream area (Irigoiien and Castel 1997). Nevertheless, there is high production of crustacean zooplankton that exhibits strong seasonal variation (Castel 1993; David et al. 2005).

Sampling strategy

Jellyfishes were sampled monthly at 12 stations along the salinity gradient from June 2013 to April 2014, except during February 2014 (Figure 2; Supplementary material, Table S1). The sampling stations were distributed along four transects (three stations / transect: one station near each shore and one in the middle of the estuary). The distances between transects were about 7 km, and the distances between stations varied from 2.3 to 5 km, depending on the width of the estuary.

Sampling was conducted each month during two consecutive days in order to perform all plankton hauls between mid-flood tide and high tide. Hauls were done using a single modified WP2 net (56 cm diameter mouth opening; net 3.43 m long; 500 μm mesh size) ending by a cod end of 6 L. The net was towed horizontally behind the boat just below the surface, against the current at a speed of $0.5\text{--}1 \text{ m} \cdot \text{s}^{-1}$ for 5 minutes. Filtered volumes were estimated using a digital flowmeter, model 2030R (General Oceanics Inc., Florida, USA) fixed at the mouth of the net, allowing the estimation of abundances and biomass per cubic meter. Temperature and salinity were also recorded at each sampling station using a YSI 6600 probe (YSI Inc., Yellow springs, Ohio, USA).

The total volume of living *N. bachei* and *B. virginica* was estimated on the survey boat immediately after sampling using the displacement volume method. Organisms were kept in a bucket, sieved in order to eliminate seawater, and then put in graduated cylinders (10 to 1000 mL, depending on amount of organisms) to estimate the volume. As *M. marginata* is clearly recognizable compared to the other two species, it was removed from the raw samples and the measures were performed separately. Jellyfishes (total volume or 250 mL subsample after sieving, depending on the amount of organisms) were then fixed and preserved in a 4% buffered formalin solution in seawater.

Laboratory analysis

Organisms were identified and counted using a dissecting microscope (Leica MZ6). Bell diameters were measured using an ocular micrometer on formalin-preserved specimens for *N. bachei* and *B. virginica*, less than three months after sampling, and on fresh specimens using a Vernier caliper (onboard the survey boat) for *M. marginata*. Data on individual sizes were pooled from all sampling stations for a given month. Stations where less than 30 individuals were collected were considered as non-representative.

Wet weight (WW) and volume of each species were measured on identified and preserved organisms. The proportion of the volume for each species, estimated by the displacement volume method, was calculated for *N. bachei* and *B. virginica* separately and these ratios were applied to the pooled volume measured for these living animals. Although the formalin preservation decreases the volume of jellyfishes, we assume that the ratios obtained from living and preserved organisms were the same according to previous tests. The volume and wet weight relationship was then estimated from these measures and corresponded to $1 \text{ mL} = 1 \text{ g WW}$ for the studied species.

Specimens of *N. bachei*, *B. virginica* and *M. marginata* preserved in 4% buffered formalin solution (MNHN-IK-2014-259, MNHN-IK-2014-261, MNHN-IK-2014-263, respectively) and 75% alcohol solution (MNHN-IK-2014-260, MNHN-IK-2014-262, MNHN-IK-2014-264, respectively), from the Gironde estuary, were deposited at the Muséum National d'Histoire Naturelle, Paris.

Statistical analysis

Spatial and temporal variations of abundances of the three jellyfish species were performed using Permutational Analyses of Variance (PERMANOVA test, plug-in for PRIMER 6.1; PRIMER-E, Plymouth Marine Laboratory, Plymouth, UK) to test the factors temperature and salinity. As temperatures were very similar at the 12 sampling stations for any given month (coefficient of variation $<4\%$), the monthly mean temperature value was used as a proxy for the “temporal effect”. For each month, sampling stations were classified into three categories of salinity according to the Venice system (McLusky 1993): oligohaline (<5), mesohaline (5–15), and polyhaline (>15) water masses. The raw data were square-root transformed and a Euclidean distance matrix was used for each univariate index. Both factors and their interaction were tested on 9999 permutations of residuals under a reduced model.

Results

Water characteristics

The seasonal pattern in surface water temperatures was similar for the four transects (Figure 3A), with a maximum of 26.5 °C during summer (August) and a minimum of 6.7 °C during winter (December). The temperature variability between and within transects for any given month was low (coefficient of variation <4 %), unlike the variation seen for salinity (Figure 3B). The surface salinity varied from 0 during the high river-flow period (June) to 22.9 during the low river-flow period (October). For each month, a salinity gradient was observed from upstream (transect 4) to downstream (transect 1). Surface salinity at transect 1 was generally 1.5 times higher than at transect 2.

Spatial and temporal variation of jellyfish

Medusae were present into the water column from June to November. A clear seasonal succession of the three species (Figure 4) was observed with *Nemopsis bachei* appearing first, then *Blackfordia virginica*, and finally *Maeotias marginata*. These three species were found along the four transects for at least a period of one month. Numerical abundance varied widely in space and time.

Nemopsis bachei

Nemopsis bachei was recorded during every month from June to October and was the only hydromedusae collected during June and July (Figure 4). It was first located in the upstream area in low densities and spread throughout the estuary but was never located at all sampling stations in any given month. Higher abundances were generally located upstream, reaching 4.3 individuals.m⁻³ (station 3) and 0.76 g WW.m⁻³ in August (Figure 5).

Bell diameters ranged from 0.4 mm to 11.6 mm (Figure 6). A clear unimodal size distribution appeared with 86 and 92 % of the population ranging from 4.0 to 9.0 mm in August and September, respectively. Small medusae (< 3.0 mm) were absent in September while in October there were no medusae larger than 4.6 mm. These small sizes explain the low biomasses recorded in October, which did not exceed 0.008 mg WW.m⁻³, while numerical abundances were in the same range as seen during the previous month.

Although *N. bachei* occurred across a wide range of salinities (0.0 to 22.9), this species was most numerous in the polyhaline water mass (Figure 7) and at water temperatures between 16.7 and 26.4 °C. The effect of temperature on abundance variation was

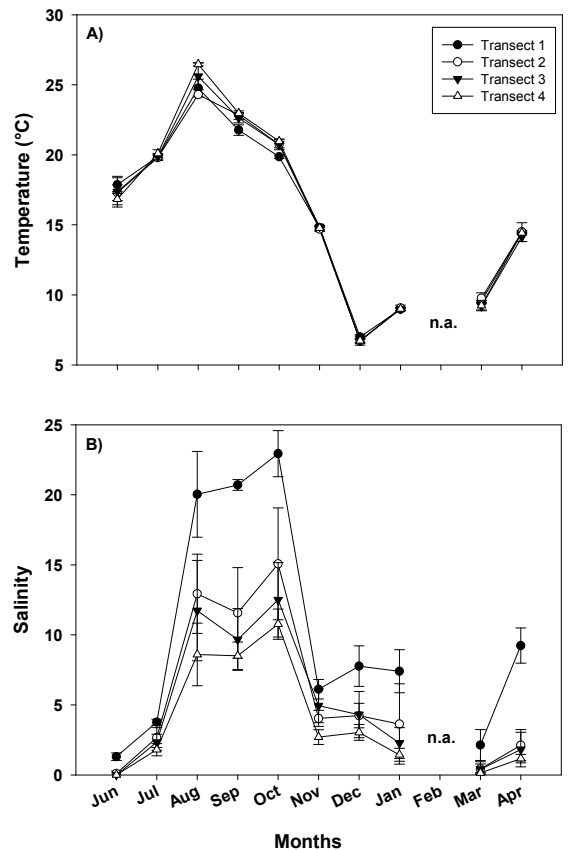


Figure 3. Seasonal pattern of mean (\pm SD) surface water temperature (A) and salinity (B) with from June 2013 to April 2014 at each transect (3 values / transect).

not statistically significant unlike salinity and the interaction term (Table 1).

Blackfordia virginica

Blackfordia virginica occurred during a short period during the warm months (Figure 4). This species appeared in the entire study area in August with high abundances and biomasses (maximum of 637 ind.m⁻³ corresponding to 21.40 g WW.m⁻³) even though it had been absent four weeks earlier. Consequently, it dominated the jellyfish assemblage at all sampling stations in August and September, contributing on average to 89 and 87 % of the total numerical abundance and 81 and 78 % of the total biomass, respectively. In October, its abundances decreased and it contributed to less than 30 % of the total abundance, excepting for one station (83 %, station 11).

Small individuals (<3.0 mm) were observed during the entire occurrence period and medusae ranging from 1.0 to 2.0 mm dominated the community each

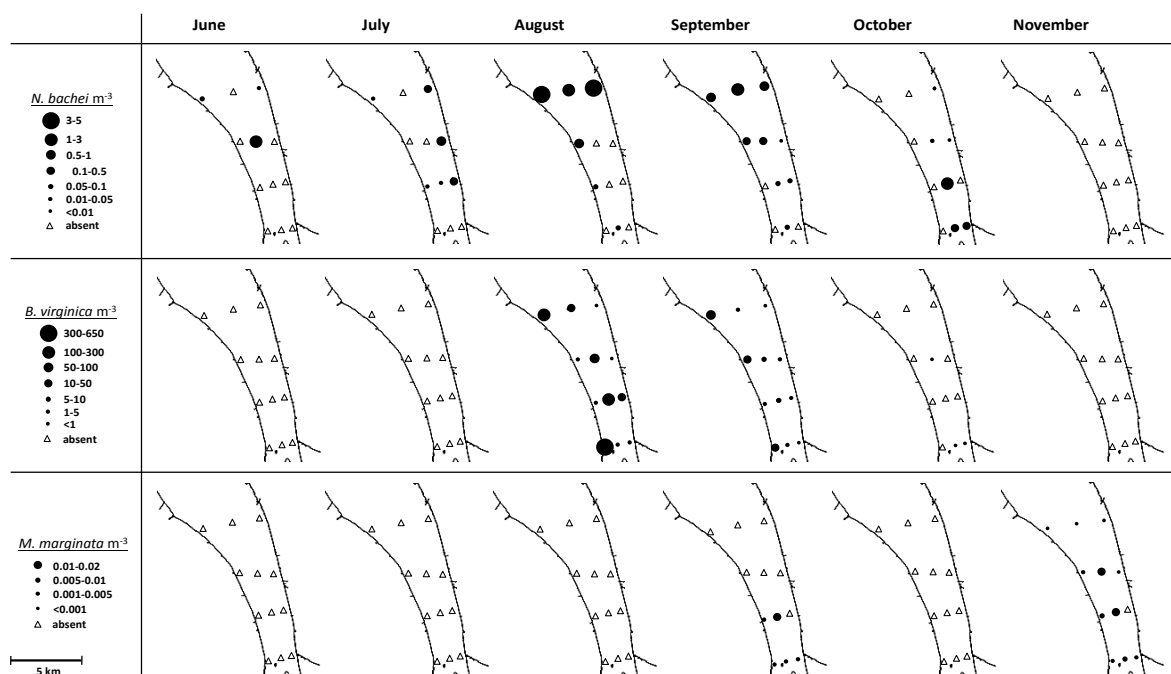


Figure 4. Spatial and temporal distributions of abundances (ind.m⁻³) for *Nemopsis bachei*, *Blackfordia virginica* and *Maeotias marginata* medusae during their periods of occurrence from June 2013 to April 2014 in the Gironde estuary. Station names are given in Figure 2.

month. The size distribution in August and September were similar apart from some medusae larger than 11.0 mm occurring in September (3.8 % of the total population), which included the largest individual measured (bell size of 14.3 mm) (Figure 6). In October, the size distribution was clearly different with only medusae <3.3 mm being present, and a clear peak in the 1.0–2.0 mm size class. The smallest bell diameter observed was 0.4 mm.

Blackfordia virginica occurred during the warmer months when the water temperature ranged from 20.6 to 26.6 °C. Statistically, temperature showed the only significant effect on abundance (Table 1). Nevertheless, this jellyfish never occurred in the oligohaline water masses (Figure 7) as it was only recorded in salinities between 6.8 and 22.9.

Maeotias marginata

Maeotias marginata occurred in September and November in very low abundances first in the upstream area and then in the entire study area, however, with very low abundance and biomass values (Figure 4).

This species was larger than the two previous species with bell diameters ranging from 0.7 to 7.5 cm (Figure 6). Its average size was slightly higher in November than in September (2.1 vs 2.4 cm)

explaining partially that biomass values were two to three times higher during this month (Figure 5).

Maeotias marginata was never found in polyhaline water masses (Figure 7) and occurred at salinities ranging from 2.3 to 11.8 and temperatures of 14.5 to 23 °C. Statistically, the temperature and salinity-temperature interactions had significant effects on abundance (Table 1).

Discussion

Gelatinous zooplankton community in the GE

Three non-indigenous jellyfish species (*Nemopsis bachei*, *Blackfordia virginica* and *Maeotias marginata*) were found in the GE during our study. In addition, some native species were also collected: *Eucheilota maculata* (Hartlaub, 1894) (1 individual) and *Liriope tetraphylla* (Chamisso and Eysenhardt, 1821) (2 individuals) in September and October, respectively. Two additional species, *Rhizostoma pulmo* (Macri, 1778) and *Pleurobrachia pileus* (O.F. Müller, 1776), were regularly identified during July 2012 but further downstream and outside of our study area (David et al. 2016). In meso- and oligohaline water masses, these non-indigenous species have settled in an unoccupied ecological niche as no other gelatinous zooplankton lives in this part of the

estuary. Due to the high abundances and biomasses measured in this study, the non-native species could, at times, be competitors for copepod prey with the native jellyfishes (Purcell and Nemazie 1992; Wintzer et al. 2013; Marques et al. 2015) or potentially control the abundances of fish larvae (Chicharo et al. 2009).

Introduction of three non-indigenous jellyfish species in the GE

Although the presence of these three non-indigenous jellyfish species was already documented in the Loire estuary (Denayer 1973), this was the first study to describe a seasonal cycle of abundance in an estuary of the French Atlantic coast. The occurrence of *N. bachei* in the GE is not a result of a recent introduction since this species was already well-established in 1953 (Tiffon 1956). The introduction of *B. virginica* seems to be more recent and *M. marginata* was reported for the first time in the GE in the present study.

Our historical samples (since 1985) were used to identify the potential introduction period of these species (Supplementary material, Table S2). While there were shortcomings in the sampling methods (small volume filtered (around 10 m³), use of a 200 µm mesh size, only a small subsample was archived), they provide some useful information. A single specimen of *M. marginata*, measuring 4 cm in diameter, was identified in August 2003. In contrast, over one hundred *B. virginica* and thirty *N. bachei* were found in the oldest archived samples from summer 1985, including juveniles (diameter <3.0 mm – absence of gonads) and adults (Bardi and Marques 2009). These limited data indicates *B. virginica* was already well established in the estuary by 1985. Moreover both *B. virginica* and *N. bachei* occurred regularly in subsequent summer samples, confirming these populations persisted.

The vector of introduction of non-native jellyfishes to the GE is unclear but transport by seawater circulation from the Loire Estuary located north of the GE is possible. Available information indicates presence of *N. bachei* in 1968 and *B. virginica* and *M. marginata* in 1971 (Denayer 1973). While these species were never identified in coastal waters of the Bay of Biscay, current patterns do not exclude this possible source. Waters flowing from the Loire Estuary are usually advected to the right, resulting in northerly directed water currents along the French west coast in most months. However, during spring and summer (corresponding to the occurrence period of these hydromedusae), river discharges are low and north-westerly winds could generate southerly

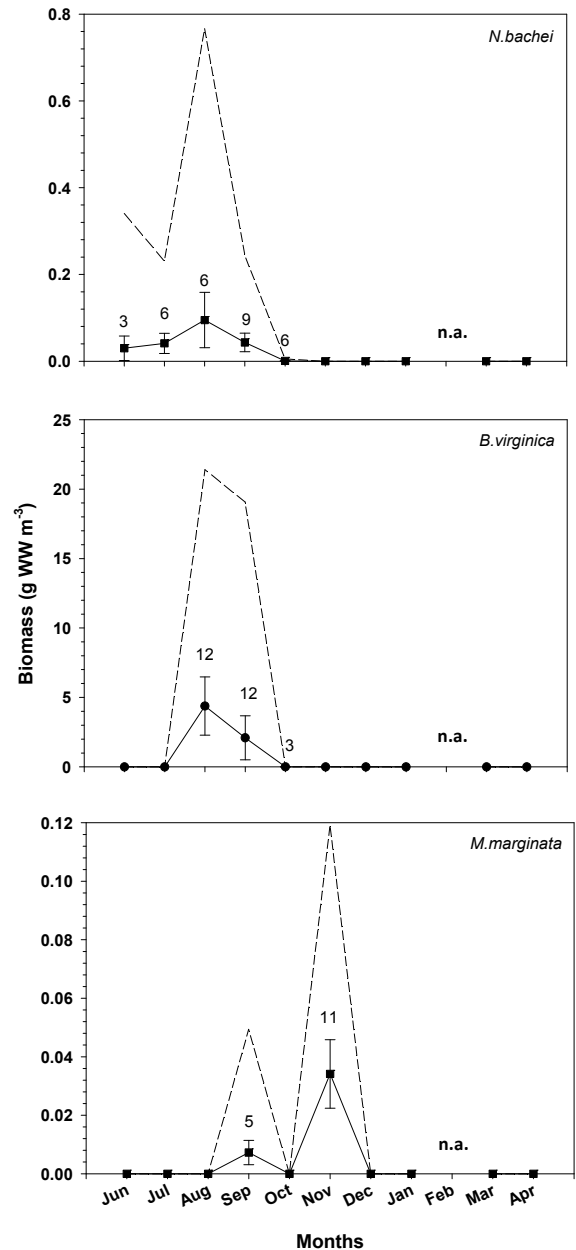


Figure 5. Monthly wet biomass (g.m⁻³) of *Nemopsis bachei*, *Blackfordia virginica* and *Maeotias marginata* in the Gironde estuary from June 2013 to April 2014. Black line: mean ± SD; dotted line maximum observed value; the number of stations where jellyfishes were present (n_{max} = 12) is indicated above the curve.

currents (Lazure and Jegou 1998). Thus there can be suitable environmental conditions for transport, and some of the species appear tolerant of full oceanic conditions. *B. virginica* in particular, may survive in oceanic waters as one specimen appears to have been collected in open waters off the coast of South Africa (Buecher et al. 2005); however, it has not been possible to confirm the identification. Transport

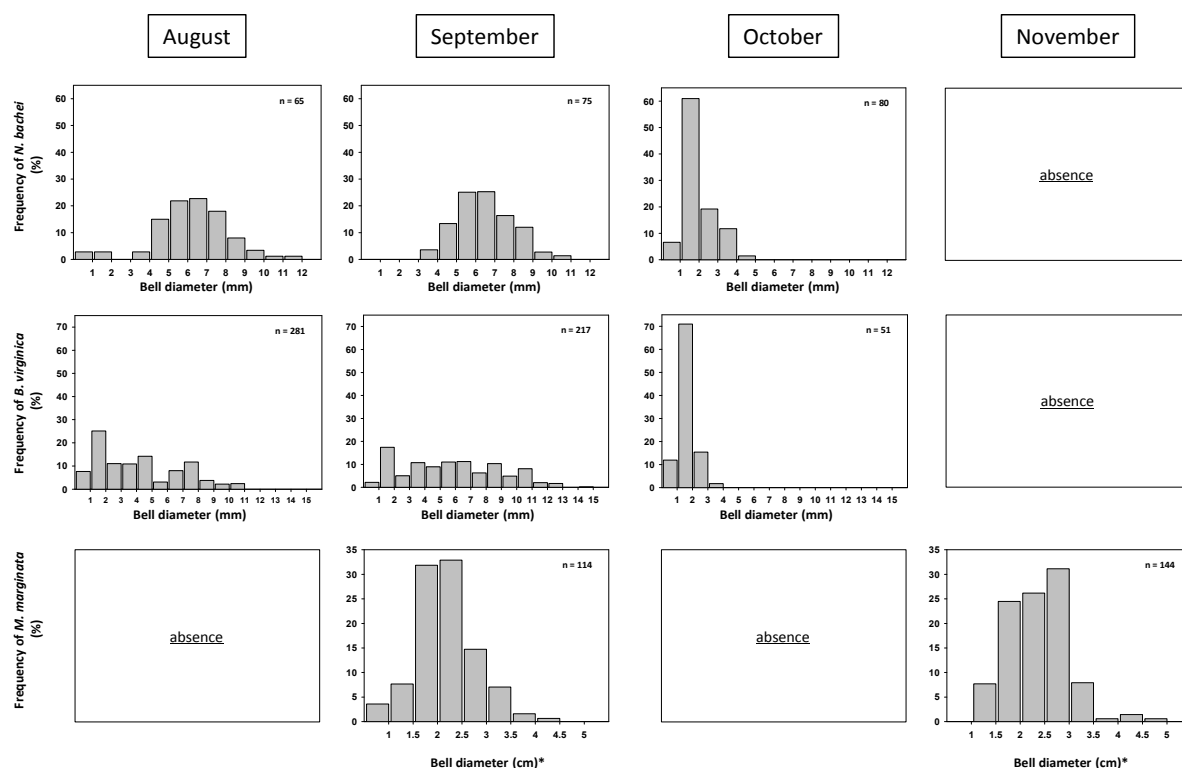


Figure 6. Bell diameters of *Nemopsis bachei*, *Blackfordia virginica* (mm) and *Maeotias marginata* (cm) in the Gironde estuary during their period of occurrences. *: measured on fresh specimens. No size distributions for June and July were available for *N. bachei* (< 30 individuals).

Table 1. Results of PERMANOVA tests performed on abundances of *Nemopsis bachei*, *Blackfordia virginica* and *Maeotias marginata* between temperature (Temp), haline water masses (HWM) and interactions (Temp X HWM). Bold values indicate significant differences: *: $p < 0.05$; **: $p < 0.01$. Res: residuals; df: degree of freedom; MS: mean square; F: F-statistic.

	df	<i>Nemopsis bachei</i>		<i>Blackfordia virginica</i>		<i>Maeotias marginata</i>	
		MS	F	MS	F	MS	F
Temp	5	0.317	1.866	58.098	4.598**	0.012	5.327**
HWM	3	0.516	3.034*	0.484	0.038	0.004	1.974
Temp X HWM	2	1.063	6.254**	1.692	0.134	0.0116	4.934*
Res	61	0.17		12.635		0.002	

by ballast water and hull fouling in cargo vessels is also a common vector for transfer of invasive species in aquatic ecosystem (Hewitt et al. 2009). It is obviously not excluded as a vector for the GE because more than 2,500 merchant vessels annually transit the area (BPA 2016).

Densities and biomasses of non-indigenous jellyfish species

Comparisons of densities and biomasses between studies are not straight forward due to differences in sampling methodology. Sampling gears often differ with regards type of net, mesh size, net mouth

diameter, and use of a flow meter. The sampling strategy (vertical, horizontal, or stepped oblique) also influences the abundance estimations due to the heterogeneous distribution within the water column. For example, *M. marginata* is considered as an epibenthic species, mainly feeding near the bottom (Mills and Sommer 1995), and our densities based on sub-surface samples likely are underestimates. In contrast, even though no clear pattern concerning the diel vertical distribution of *N. bachei* in the Chesapeake Bay was found, its vertical distribution were not homogenous throughout the water column (Purcell and Nemazie 1992), and it appeared more influenced by the salinity gradient than the prey

distribution (Frost et al. 2010). Even if our sampling strategy may be slightly underestimated some abundances, this does not affect the seasonal patterns and, therefore, comparisons with other studies.

Maximum density of *B. virginica* in the GE was much higher than most maxima reported elsewhere. Wintzer et al. (2013) and Marques et al. (2015) compiled density reports for *B. virginica* in other systems. These values ranged from less than on average 1 ind.m^{-3} , in Antonina Bay (Brazil) (Nogueira Jr and De Oliveira 2006) to 232 ind.m^{-3} , in the Petaluma River (San Francisco Bay) (Wintzer et al. 2013). In contrast, a maximum abundance of 384 ind.m^{-3} was measured the GE in July 2012 (David et al. 2016; Appendix A), and we detected up to 637 ind.m^{-3} . To the best of our knowledge, the highest value on record is $1,689 \text{ ind.m}^{-3}$ in the Mira Estuary, Portugal (calculated from Marques et al. 2015). In contrast, our maximum estimates for *N. bachei* and *M. marginata* were well below values seen elsewhere. For example, *N. bachei* densities in Chesapeake Bay were 30 times higher (132 ind.m^{-3}) than those observed in this study (Cronin et al. 1962; Purcell and Nemazie 1992). There seems to be substantial inter-annual variation in the GE because up to 124 ind.m^{-3} were found during July 2012 surveys (David et al. 2016). Identifying the factors controlling such wide between-year variation will require additional, targeted, research. Similarly, we only detected a few specimens of *M. marginata* in our samples while abundances with $10\text{--}20 \text{ ind.m}^{-3}$ were reported in San Francisco Bay (Rees 1999). The current study was the first to detect *M. marginata* in the GE and if it truly is an autumn species, the July 2012 surveys (David et al. 2016) could not have detected it. Accounting for seasonal succession in presence of jellyfishes seems to be a common issue and only well-designed sampling, including taking season into account, is needed when looking for non-native species in coastal habitats.

Compared to numerical abundance data, there is little information on biomass exists in the literature for the three species detected in the GE. Maximum biomass reported for *B. virginica* in San Francisco Bay was 62 mg.m^{-3} dry weight (Wintzer et al. 2013), which converts to $\sim 1 \text{ g WW.m}^{-3}$ assuming jellyfish are 95 % water (de Lafontaine and Leggett 1989). Similarly, the maximum single weight reported for *N. bachei* in the North Inlet estuary (eastern coast of the USA) was $118 \text{ mg WW.ind}^{-1}$ with abundance of 0.33 ind.m^{-3} (Marshallon and Pinckney 2007, 2008) equals 0.04 g WW.m^{-3} . Thus our estimates of *B. virginica* and *N. bachei* biomass in the GE were ~ 20 times higher than in the San Francisco and North Inlet estuaries. No data were found concerning the biomass of *M. marginata* in other systems.

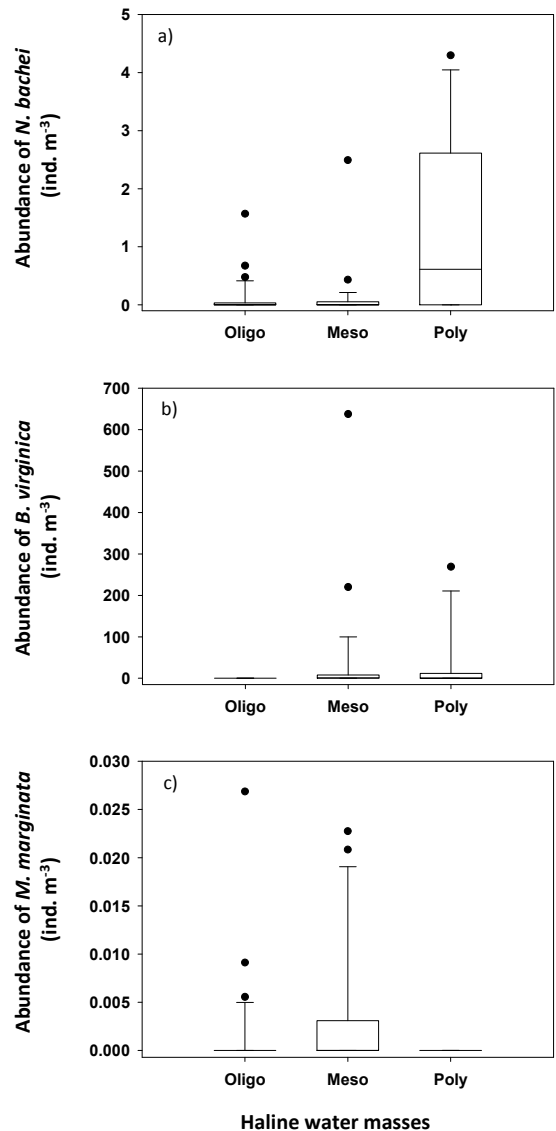


Figure 7. Box plot representing the abundances (ind.m^{-3}) of *Nemopsis bachei* (a), *Blackfordia virginica* (b) and *Maeotias marginata* (c) in the different haline water masses in the Gironde estuary during their periods of occurrence.

Spatio-temporal variation

In the present study, a strong spatial heterogeneity was observed in our monthly samples likely due, in part, to the complex hydrodynamic conditions in the GE. There is substantial variation in both tides and fresh water flows, which move the planktonic organisms upstream or downstream. For example, *M. marginata* was not detected in October, when salinities were the highest of the year, likely due to a strong marine inflow that transported this jellyfish upstream of our study area only to have tidal conditions relax and

have them re-appear in November. Such mechanisms, and year-to-year variation in when they occur (temporal aliasing) may explain studies where *B. virginica* and *M. marginata* were collected in high abundances in an area in one year but were absent the next (e.g., Rees 1999; Rees and Kitting 2002; Schroeter 2008). At a smaller spatial scale, interactions between complex water masses and resulting turbulence is a source of patchiness in the zooplankton community (Kimmerer et al. 2014), and this patchiness was apparent in our study as there was high variability in abundance estimates between adjacent stations.

Another potential factor in spatial heterogeneity relates to the polyp stage in the life cycle. For most of hydromedusae, polyps are attached to a hard substrate and the distribution of suitable hard surfaces will then determine the site of release of medusae. For example, Wintzer et al. (2011) was able to document locations of concentrations of polyps for *Moerisia* sp., *Cordylophora caspia* (Pallas, 1771), and *B. virginica*, in the San Francisco Estuary, and *B. virginica* polyps were associated with regions of high salinity (14.9–22.2), higher water transparency, low dissolved oxygen (2.3–6.3 mg.l⁻¹), and high temperature (20.0–23.1°C). The substrates of the GE consist principally of soft-sediments (sand and mud); hard substrate is scarce and mainly occurs downstream of our study area in areas of limestone cliffs and oyster reefs on the north shore. There is, however, additional potential habitat for polyps in the form of artificial structures such as buoys, dykes, and pontoons (Duarte et al. 2013). According to this and the observed distributions of medusae, we hypothesize that polyps of the three species probably were not located in the same area of the GE. *B. virginica* and *N. bachei* polyps might occur in the downstream area but *M. marginata* polyps might occupy an upstream area because this species was first located along the last transect and two months later in the entire study site, albeit with lower densities in downstream area.

These results highlight the difficulties to understand the links between environmental conditions and population responses of both medusae and polyps. Nevertheless, hydromedusae and many members of the zooplankton community are able to colonize suitable estuarine habitats by making use of vertical migration during appropriate times in the tidal cycle (Wooldridge and Erasmus 1980; Kimmerer et al. 2002; David et al. 2016). In the GE, the zooplankton distribution is mainly driven by the salinity along the upstream-downstream gradient (Chaalali et al. 2013) affecting the community composition as classically observed in estuaries (Telesh and Khlebovich 2010). In this study, *N. bachei* and *B. virginica* were mainly

observed in the meso- and polyhaline water masses. *N. bachei* was previously considered as characteristic of the polyhaline water masses, while *B. virginica* was considered as characteristic of the mesohaline water masses (David et al. 2016). Our results confirm the affinity of these two species for high salinities, and they are able to survive in full seawater (30–36; Cronin et al. 1962; Vannucci et al. 1970; Moore 1987; Buecher et al. 2005; Marshalonis and Pinckney 2008; Freire et al. 2014). In contrast, *Maeotias marginata* was never found in polyhaline water masses during our study, which corresponds to published reports of its distribution in oligo- and mesohaline zones (Mills and Sommer 1995; Mills and Rees 2000; Schroeter 2008).

At the lower end of the scale, some individuals tolerate near freshwater (salinities close to 0 or equal to 0) conditions. For example, in July 2011, we collected *N. bachei* and *B. virginica* in the Dordogne River (Figure 1) with 0.46 ind.m⁻³ and 213 ind.m⁻³ respectively (we used a pump and sieved at 63 µm mesh size; Supplementary material, Table S2). This was the first observation of *B. virginica* and *N. bachei* in freshwater. Taken together, these results and published reports confirm that *B. virginica* and *N. bachei* are tolerant to a wide range of temperature and can survive in waters corresponding to almost freshwater and seawater (Cronin et al. 1962; Vannucci et al. 1970; Moore 1987; Buecher et al. 2005; Marshalonis and Pinckney 2008; Mendoza-Becerril and Marques 2013; Freire et al. 2014). *Maeotias marginata* was found in the Garonne River at a salinity of 1.1 in September 2013 (0.23 × 10⁻³ ind.m⁻³) (ichthyoplankton trawl, 21 m² opening surface, mesh size reducing from 18 mm to 1 mm in the cod end (Table S2). In other systems, *M. marginata* was found at a salinity of 0.9 but, under laboratory conditions, it survives in good condition in freshwater for at least five days (Mills and Rees 2000).

B. virginica: GE vs others systems

(Marques et al. 2015) conducted concurrent surveys (using 200 µm net) in the Mira Estuary (Portugal), which allows comparison between the two estuaries under the influence of the same seasonal pattern of Atlantic Ocean inflow. There were some noteworthy differences. In the GE, *B. virginica* occurred during a short and distinct period corresponding to warmer months while it occurred from May to December in the Mira estuary, corresponding to both a wider temperature range (12.0 to 23.6 °C) and wider salinity range (12.0 to 27.5); although some of that may be due to the downstream location of the sampling station in the Mira Estuary. Similarly, in San Francisco Bay, *B. virginica* occurred for two months

in the Napa River and for more than six months in the nearby Petaluma River (Wintzer et al. 2013). Hence, wide variation in seasonal occurrence appears to be a characteristic of this species.

The size structures of the two populations were different in the Mira and Gironde estuaries. Large individuals (e.g., 14.0 to 20.0 mm) were prominent in all samples in the Mira and Guadiana Estuaries (Chicharo et al. 2009; Marques et al. 2015), and large size may be characteristic of these populations. In our study, only one bell diameter corresponding to this large size class was observed. Also, individuals >6.0 mm were observed at the end of the period of occurrence in the Mira estuary while it was the small size class (1.0–2.0 mm) that was dominant at the end of the period of occurrence in the GE. It is interesting that the population in the Napa River (Mills and Sommer 1995) showed a similar seasonal pattern to the GE in terms of population size distributions. At present, these differences population size distributions among study locations cannot be explained.

Is B. virginica invasive

We have investigated the question of whether *B. virginica* might act as an invasive species because this species dominated the hydromedusae community when it was present in the GE, rapid growth seems to be a characteristic of the species, and there is an extended period of production of medusa from the polyps. The appearance of large numbers of medusa in the GE was abrupt from zero in July to high abundance in August over the whole study area. However, medusae <3.0 mm were present during the entire period of occurrence – a size that corresponds to juveniles lacking gonads (Genzano et al. 2006). This extended period of release of medusa during the warmer months is also observed in other locations (Mills and Sommer 2009; Wintzer et al. 2013). In addition, individual growth was rapid because a full size-range of individuals was present. Similar rapid growth was observed in the Mira estuary where, during the initial period of the medusa seasonal cycle, only small individuals occurred (<6.0 mm) and 25 days later all size classes were present (Marques et al. 2015). Rapid growth was also observed in the San Francisco Estuary where bell diameters increased from 0.4 to >10.0 mm in two weeks (Rees and Kitting 2002).

In summary, because the polyps continuously produce large numbers of medusa, which grow rapidly and are widely distributed when the environmental conditions allow their development, *B. virginica* might be considered as an invasive species in the GE. Consequently, further investigations are needed

to evaluate their impact in the food web in this estuary, which is an important spawning and nursery area of many fishes.

Acknowledgements

We thank the crew of the *M/V Esturial* (J.-F. Bigot and B. Ballion) and S. Bons for their assistance during sampling on board the survey boat. We are also grateful to Editor-in-Chief, John Mark Hanson, and the anonymous reviewers for their helpful comments and suggestions. The COLMATAGE program (Caractérisation et Observation des géLatineux MACroplanToniques Associés à la GirondE) has been carried out with financial support from Electricité de France Company (EDF) and the framework of Cluster of Excellence COTE.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Occurrence of non-native jellyfishes (abundance and biomasse) at 12 sampling stations from June to November 2013 in the Gironde estuary (France).

Table S2. Occurrence of non-native jellyfishes in the Gironde estuary and rivers from archived samples.

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http://www.aquaticinvasions.net/2016/Supplements/AI_2016_Nowaczyk_et_al_Supplement.xls