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Research Article

Temporal abundance and population parameters of the invasive medusa *Blackfordia virginica* Mayer, 1910 (Hydroidomedusae: Blackfordiidae) in Pueblo Viejo lagoon, Mexico

Alberto Ocaña-Luna[1,*], Marina Sánchez-Ramírez[1] and Alejandro Islas-García[2]

[1]*Laboratorio de Ecología, Departamento de Zoología, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional. Prolongación de Carpio y Plan de Ayala s/n, Colonia Santo Tomás, Alcaldía Miguel Hidalgo, C. P. 11340, Ciudad de México, México*

[2]*Grupo de Ciencia y Tecnología Ambiental Aplicada, Facultad de Ciencias Químicas, Universidad La Salle, Avenida Benjamín Franklin 45, Colonia Condesa, Alcaldía Cuauhtémoc, 06140, Ciudad de México, México*

Author e-mails: *ja_ocanaluna@hotmail.com* (AOL), *masachezra@ipn.mx* (MSR), *alejandro.islas@lasalle.mx* (AIG)

**Corresponding author*

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Abstract

The sex ratio, size at first maturity, morphological variations and abundance of the invasive species *Blackfordia virginica*, were analysed in the lagoon of Pueblo Viejo. Zooplankton were collected with a 505 µm net throughout the lagoon during October and December 1992, March, April, June and August 1993, and March 2009. Data were recorded simultaneously for salinity and temperature. A female/male sex ratio of 0.95:1.00 and a minimum size of gonadic maturity of $\overline{X}$= 5.25 ± 0.17 mm umbrella diameter were recorded. *Blackfordia virginica* presented 33 types of morphological variations. The number of marginal tentacles (53–104) increased with size (2.5–13.0 mm). Medusae were collected in this lagoon only in March and April 1993, with average densities of 1,946.75 and 2,508.83 ind/100 m^3 respectively. These medusae were recorded at temperatures of 19.0–28.0 °C and salinities of 11.0–21.0 PSU. The density of *B. virginica* was highly correlated with salinity (r_s = 0.796, n = 114, P < 0.001). The high density of specimens, the wide range of sizes, and the presence of both mature females and males as juveniles indicate that this species can reproduce and develop in this lagoon system. The absence of medusae in March 2009 indicates that the species is not a resident in the system in response to the oligohaline conditions (0.0–7.0 PSU) that are characteristic during June to October.

Key words: non-indigenous species, Leptomedusae, gonadic maturity, sex proportion, morphological variations

Introduction

The hydromedusae *Blackfordia virginica* Mayer, 1910 belongs to the family Blackfordiidae (Bouillon and Boero 2000). It was described by Mayer (1910) from specimens collected in an estuary near the mouth of Chesapeake Bay, and was re-described by Moore (1987) using material collected from the estuary of the River Mira, south-west Portugal. Thiel (1935) considered that *B. virginica* was most probably indigenous to the Black Sea, and was transported by boat to the east coast of North America prior to 1910. The widespread but localized records of *B. virginica* suggest that the hydroid

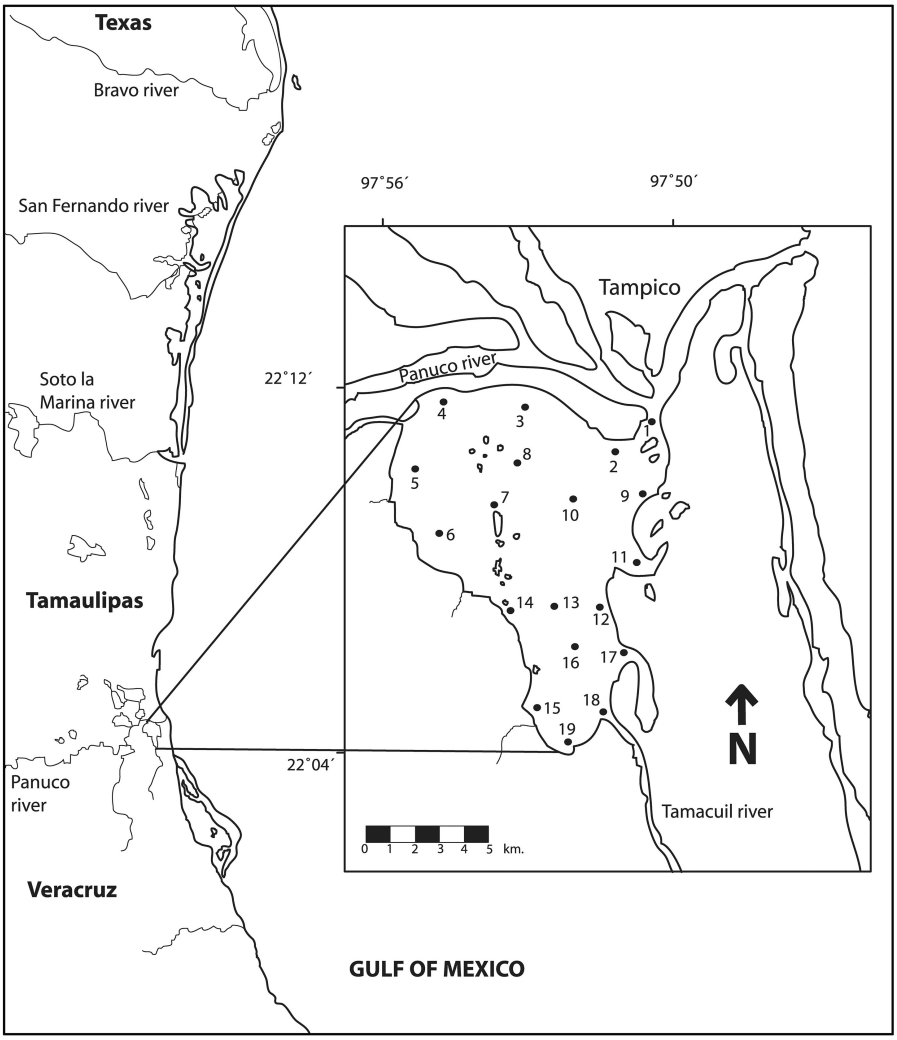

Figure 1. Study area and sampling stations. Pueblo Viejo Lagoon, Veracruz, Mexico.

stage may be transported passively by boats (Valkanov 1935). The species has also been recorded as introduced in northern San Francisco Bay (Mills and Sommer 1995).

The species has a wide distribution. It is found at present in the southwestern and northern Atlantic Ocean, the Mediterranean Sea, and the Indo-Pacific Ocean (Bouillon 1999). In South America, it has been recorded in Pernambuco, the Jaboatão River estuary (Paranaguá 1963/4), Antonina Bay (Nogueira Júnior and de Oliveira 2006), Cananéia Channel, Guaratuba Bay and Batitonga Bay, Brazil (Bardi and Marques 2009), as well as in Argentina-Uruguay in the Río de la Plata estuary (Genzano et al. 2006).

It has also been recorded along the Mexican Pacific coast in the Chantuto-Panzacola lagoon system, Chiapas (Álvarez-Silva 1999), and in the southern Gulf of Mexico in the lagoons of Tamiahua and Alvarado, Veracruz (Signoret-Poillón 1969).

The study area of this project, Pueblo Viejo lagoon, is located in the northern region of the state of Veracruz, between 22°05′ and 22°13′N, and between 97°50′ and 98°00′W. The northern area of the lagoon is connected to the Pánuco River (Figure 1) approximately 10.0 km upriver from the Gulf

Table 1. Geographic position of sampling stations, ranges of salinity and temperature (°C) of superficial water, and density of *Blackfordia virginica* (number of individuals/100 m^3). Pueblo Viejo Lagoon, Veracruz, Mexico.

Station	Northern latitude	Western longitude	Density October	December	March	April	June	August
1	22.20°	97.85°	0.00	0.00	12.00	580.00	0.00	0.00
2	22.19°	97.86°	0.00	0.00	0.00	154.38	0.00	0.00
3	22.20°	97.90°	0.00	0.00	30.51	43.76	0.00	0.00
4	22.19°	97.93°	0.00	0.00	11.66	93.33	0.00	0.00
5	22.17°	97.93°	0.00	0.00	4.81	6.10	0.00	0.00
6	22.16°	97.92°	0.00	0.00	589.87	495.60	0.00	0.00
7	22.16°	97.90°	0.00	0.00	661.26	159.35	0.00	0.00
8	22.18°	97.90°	0.00	0.00	24.04	415.47	0.00	0.00
9	22.18°	97.85°	0.00	0.00	615.84	2666.67	0.00	0.00
10	22.17°	97.87°	0.00	0.00	43.80	93.11	0.00	0.00
11	22.15°	97.86°	0.00	0.00	1025.79	4566.31	0.00	0.00
12	22.13°	97.87°	0.00	0.00	4509.55	7063.12	0.00	0.00
13	22.13°	97.89°	0.00	0.00	1309.63	7418.58	0.00	0.00
14	22.13°	97.90°	0.00	0.00	1095.14	2274.83	0.00	0.00
15	22.09°	97.89°	0.00	0.00	62.07	5061.95	0.00	0.00
16	22.11°	97.88°	0.00	0.00	3299.77	4538.14	0.00	0.00
17	22.11°	97.85°	0.00	0.00	20656.72	3561.69	0.00	0.00
18	22.09°	97.86°	0.00	0.00	1080.29	6191.26	0.00	0.00
19	22.08°	97.87°	0.00	0.00	8.70	2284.06	0.00	0.00
mean			0.00	0.00	1946.75	2508.83	0.00	0.00
Sd			0.00	0.00	4826.48	2600.70	0.00	0.00
T (°C)			22.5–25.0	22.0–26.0	19.0–28.0	26.0–28.0	27.0–31.0	27.0–30.0
S			0.0–2.0	5.0–18.0	11.0–18.0	18.0–21.0	0.0–7.0	1.0–3.0

of Mexico. Hydrologic conditions in the lagoon vary drastically throughout the year. Surface salinity varies from 0.0 to 7.0 PSU in the rainy season and from 5.0 to 21.0 PSU in the dry season, and temperature varies from 19.0 to 31.0 °C annually.

An analysis of population parameters and variations in the abundance of *B. virginica* in this lagoon throughout an annual cycle will enable us to understand how this non-native species develops in a system with conditions that vary between oligohaline and polyhaline.

Materials and methods

Zooplankton were collected during six field trips in October and December 1992, and March, April, June and August 1993, at 19 sampling stations that were located with a Sony GPS (precision 100.0 m) (Table 1). A later field trip took place in March 2009. Samples were collected by circular trawling for five minutes from the water surface to a depth of 50.0 cm, using a 505 μm mesh size conical net with a 50.0 cm diameter opening bearing a flowmeter (General Oceanics) to calculate the volume of filtered water. Samples were fixed with 4% formalin and neutralised with sodium borate. Surface salinity and temperature were measured *in situ* with an Atago SMill/E refractometer and a mercury thermometer, respectively.

Lab work included separating the medusae and identifying them using the taxonomic criteria of Mayer (1910) and Moore (1987). All the *B. virginica* specimens in the samples were quantified, except for the very abundant samples for which sub-samples were obtained with a Folsom splitter.

Reproduction

A sample of 446 specimens with mature gonads, collected in March and April of 1993 at the stations 13 and 17, respectively, stations with high abundance, and well-preserved specimens of a wide range of umbrella diameter sizes, were selected in order to establish the sex ratio and minimum size of sexually mature individuals.

Morphological variations

All specimens collected at all sampling stations were analysed in order to detect morphological variations. They were grouped according to the type of variation: the number of radial canals, the bifurcation of the radial canals, the number of gonads and the number of manubria. A sample of 50 specimens was selected to establish the variation in the number of marginal tentacles throughout development. The size of the medusae (umbrella diameter) was analysed with respect to the number of marginal tentacles.

Temporal abundance

Density data of *B. virginica* were calculated using the volume of filtered water and expressed as number of ind/100 m^3. The r_s coefficient of Spearman's range correlation (Zar 1999) was applied to determine the relationship between the density and the salinity and temperature of the surface water in the lagoon.

Results

Reproduction

With respect to the sex ratio, 117 females and 106 males of *B. virginica* were identified in March, with a female/male ratio of 1.1:1.0, whereas in April, there were 100 females and 123 males, with a female/male ratio of 0.8:1.0. Considering both months, there were 217 females and 229 males, and the total female/male ratio for the population in the lagoon was 0.95:1.0. The umbrella diameter size of sexually mature individuals was recorded at $\overline{X}$= 5.25 ± 0.17 mm.

Morphological variations

The analysis of the *B. virginica* specimens showed that 45 out of 9,738 (0.46%) individuals presented morphological variations in March, whereas 468 out of 22,479 individuals (2.08%) did so in April. These individuals represent 1.59% of the population.

The morphological variations observed in the 513 individuals of *B. virginica* that presented variations during the year included 33 types of variations, with the most common occurring in the number of radial canals and in the number of gonads. Individuals were observed to have from two to six radial

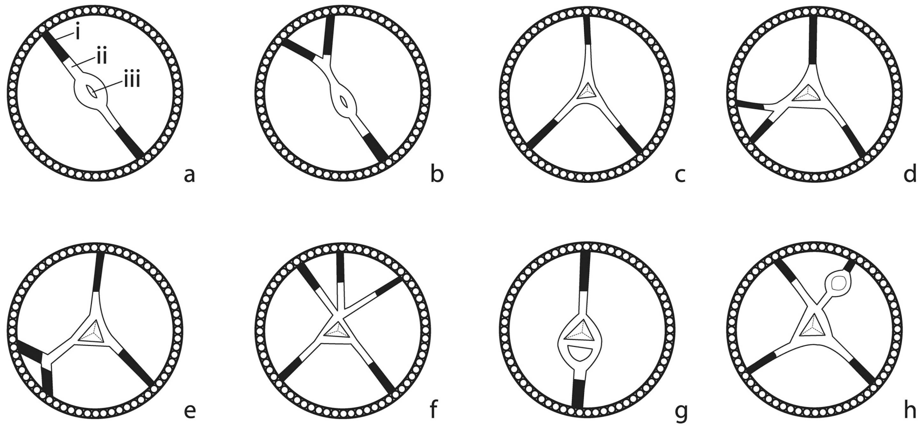

Figure 2. Variations with two and three radial channels of *Blackfordia virginica.* Pueblo Viejo Lagoon, Veracruz. Mexico. i) gonad, ii) radial canal, iii) manubrio.

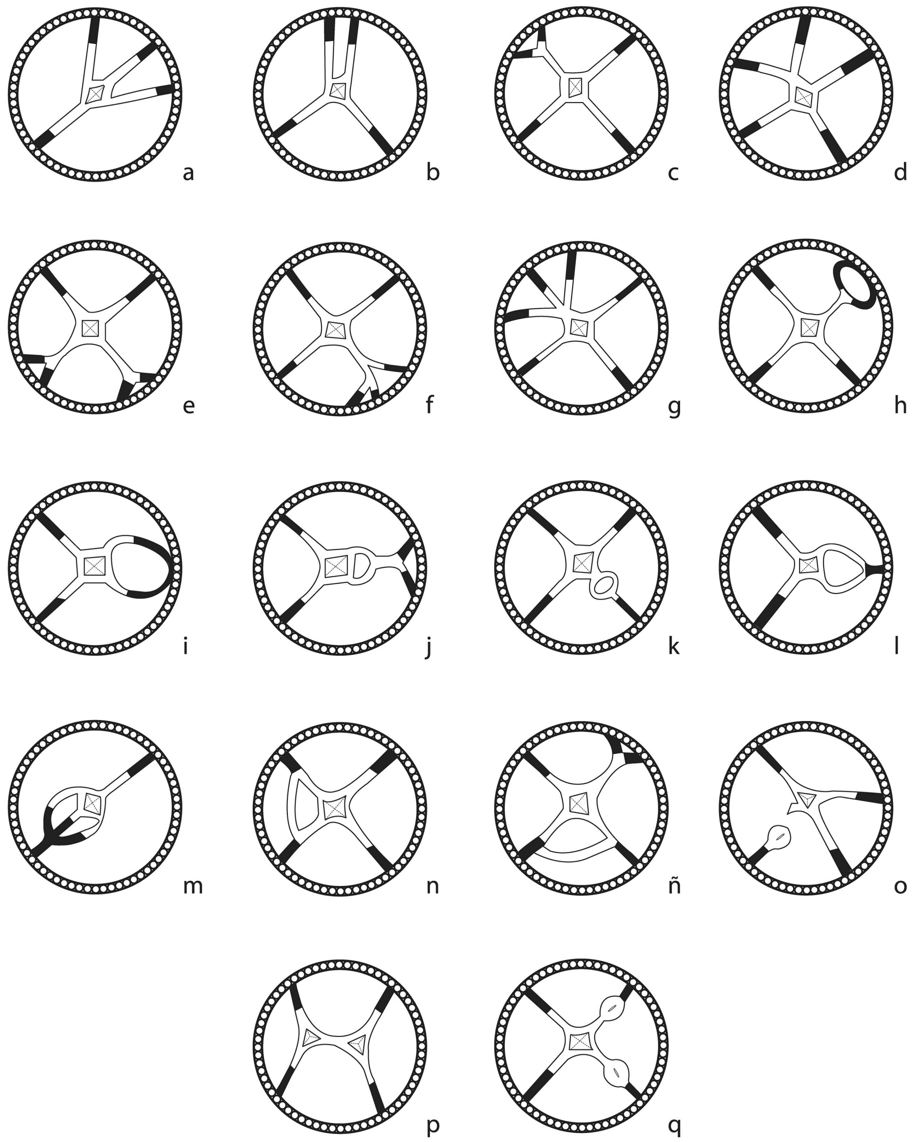

Figure 3. Variations with four radial channels of *Blackfordia virginica,* Pueblo Viejo Lagoon, Veracruz, Mexico.

canals and from two to eight gonads (Figures 2–4). The most frequent variations were observed in individuals with four radial canals (Figure 3).

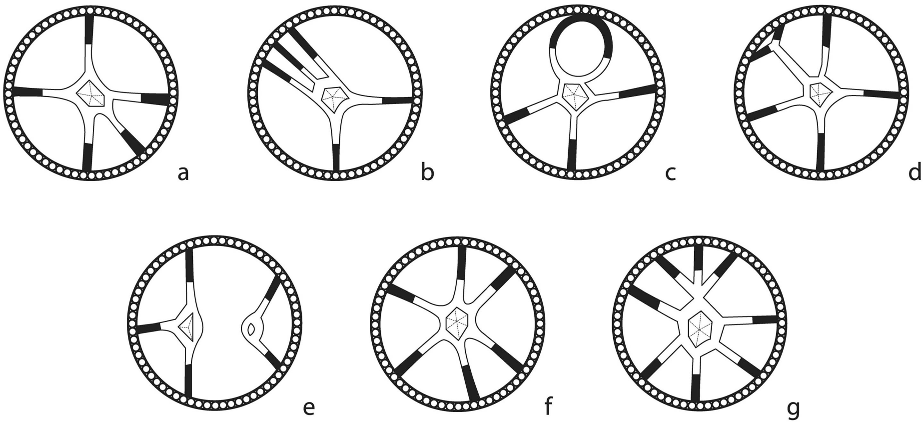

Figure 4. Variations with five and six radial channels of *Blackfordia virginica,* Pueblo Viejo Lagoon, Veracruz, Mexico.

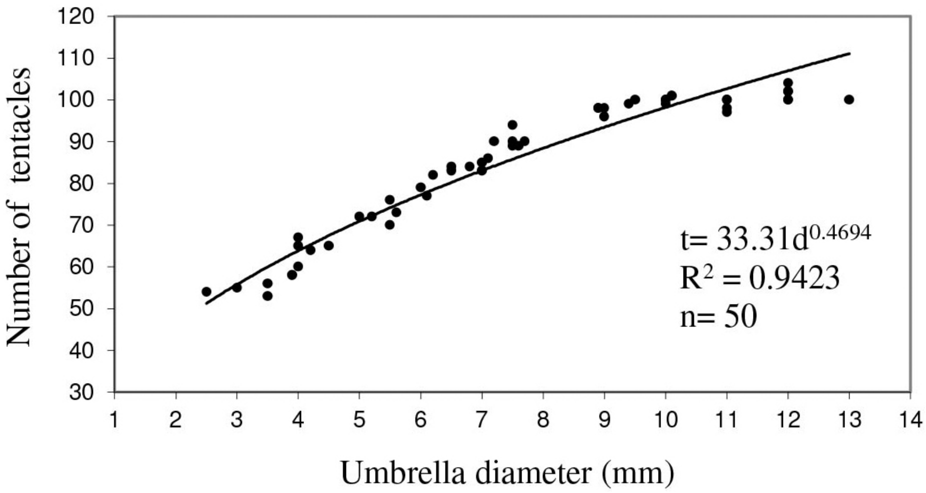

Figure 5. Relationships between number of tentacles and umbrella diameter of *Blackfordia virginica*. Pueblo Viejo Lagoon, Veracruz, Mexico.

The potential model presented the best adjustment ($R^2 = 0.94$) for the data series and indicated a potential type increase in the number of marginal tentacles with an increase in size (2.5–13.0 mm) (Figure 5). The data series recorded in this study includes a range of number of marginal tentacles of 53 to 104, juvenile samples (2.5 to 4.5 mm) with 53 to 65, and the sexually mature medusae (≥ 5.0 mm) umbrella diameter with 72 to 104 marginal tentacles.

Temporal abundance and environmental relationships

During the sampling year of 1992–1993, a total of 32,217 *B. virginica* individuals were collected only in March and April, with average densities of 1,946.75 and 2,508.83 ind/100 m^3 respectively (Table 1). The species was collected at temperatures of 19.0–28.0 °C and salinities of 11.0–21.0 PSU. It is important to note that the specimens were collected in March and April 1993 when salinity was higher, but were not present at other times of the year when salinity was lower (Table 1). The density of *B. virginica* medusae presented a strong correlation with salinity ($r_s = 0.796$, n = 114, $P < 0.001$) and there was not any correlation with the temperature ($r_s = 0.101$, n = 114, $P > 0.2$).

Discussion

Reproduction

A female/male sex ratio of 1.1:1.0 and 0.8:1.0 was found in March and April. In comparison, Álvarez-Silva et al. (2003) recorded a greater female/male ratio of 2.2:1.0 in the Chantuto-Panzacola lagoon system, Chiapas. In other invader hydromedusae, the sex ratio varies like in *Gonionemus* sp. A. Agassiz, 1862, mature medusae varied between sites, there were 0.0–1.4 female per male (Carman et al. 2019), while there are unisexual populations of female or male individuals of *Craspedacusta sowerbii* Lankester, 1880 (Aker and Muscat 1976) and only male individuals in *Maeotias inexpectata* Ostroumoff, 1896 (Mills and Sommer 1995).

This smallest sexually mature (female with eggs) *B. virginica* size found (≥ 5.0 mm umbrella diameter) is smaller than the ≥ 6.0 mm umbrella diameter one recorded by Mills and Sommer (1995) in the San Francisco Estuary. The presence of both mature females and males as juvenile in Pueblo Viejo lagoon may indicate that this species is able to reproduce in this system.

Morphological variations

Ten out of the 33 types of variations observed in this study have been documented previously. Álvarez-Silva et al. (2003) observed seven similar cases in the lagoon system of Chantuto-Panzacola, Chiapas, medusae with: two radial canals, one canal bifurcated; three radial canals, one canal bifurcated; four radial canals, three canals together; four radial canals, one canal with distal bifurcation; four radial canals, one canal bifurcated; four radial canals, two canals connected and with five radial canals. On the other hand, Signoret-Poillón (1969) recorded six similar cases in the lagoons of Tamiahua and Alvarado, Veracruz, medusae with: two radial canals; two radial canals, one bifurcated; three radial canals, one with distal bifurcation; four radial canals, one bifurcated; finally with five and six radial canals.

The *B. virginica* medusae in this system present marked morphological variations never before identified. Of 33 types of variations, 23 have not been reported previously. This contrasts with Genzano et al. (2006) who found only one specimen with abnormalities (with six radial canals) out of more than 20,000 specimens of *B. virginica* collected from the Río de la Plata estuary, Argentina-Uruguay. Nogueira Júnior and de Oliveira (2006) also found only two individuals in Antonina Bay, Paraná, Brazil with morphological variations represented by the presence of only three radial canals.

The number of marginal tentacles recorded in individuals with umbrella diameter from 2.5–13.0 mm individuals presented a range of 53 to 104. It must be mentioned that Mayer (1910) recorded over 80 marginal tentacles in the original species description from Chesapeake Bay. Álvarez-Silva et al. (2003) analysed 6.5–9.9 mm individuals of this species in the lagoon system of Chantuto-Panzacola, Chiapas, and recorded a range of 86 to 125 marginal tentacles. For individuals in southern Brazil, Nogueira Júnior and de Oliveira (2006) recorded between 68 and 128 marginal tentacles for 1.0–6.0 mm individuals and Bardi and Marques (2009) recorded from 50 to 142 marginal tentacles for 4.1–14.0 mm individuals. This species may thus present an ample range of number of marginal tentacles, as has been recorded for the different localities where it is distributed. The morphologic variations are frequent in the medusae, which may be caused by different factors like for example the abnormalities observed in the stauromedusa *Haliclystus auricula*, as presence of more body parts than normal may also be the result of regeneration injured tissue and may also reflect a lack of genetic variations in the population (Zagal 2008). This possibility has been also analyzed in populations of *B. virginica* in North America by Harrison et al. (2013), who observed low genetic diversity. Another cause of the symmetric disorder may be chemical pollutants in the water (as noted in Gadreaud et al. 2017). This may also be the case in Pueblo Viejo Lagoon since the location shows the highest concentrations of chemical pollution, which receives input from the River Pánuco (as reported by Botello and Calva 1998).

Temporal abundance and environmental relationships

This is a first record of *B. virginica* for Pueblo Viejo Lagoon, Veracruz. The species has been recorded previously for other lagoon systems of Veracruz, including Tamiahua and Alvarado (Signoret-Poillón 1969). The records in these three lagoons constitute the only records for the Mexican coast of the Gulf of Mexico.

The higher density of *B. virginica* recorded for Pueblo Viejo lagoon was 20,656.72 ind/100 m^3 at one single sampling station in March. This is the second highest value for density after the one recorded by Wintzer et al. (2013) (23,200 ind/100 m^3) in the Petalum River, California (USA), where they are also considered introduced. The great density reported for the species coincides with the greater productivity in the system during the months of March and April. De la Lanza-Espino and Cantú-Ramírez (1986) recorded maximum values of phytoplanktonic density (110071–346329 cells/L) during these months. The species has also been recorded in one locality in Aroor, Cochin, India for January, February, May and June (Vannucci et al. 1970) with an average density of 4,730 ind/100 m^3. A maximum density of 6,660 ind/100 m^3 was recorded in the Mira estuary, Portugal, by Moore (1987). Other records include those of Chícharo et al. (2009) of 3,170 ind/100 m^3 for the Guadiana estuary, Genzano et al. (2006) of 2,952 ind/100 m^3 for the Río de la Plata estuary during the summer, and Álvarez-Silva et al. (2006) of 6,680 ind/100 m^3 for the lagoon system of Chantuto-Panzacola, Chiapas.

Records of this species in rivers, estuaries and lagoon systems indicate it is euryhaline and eurythermic. It is normally associated with salinities of

20.0–30.0 PSU but can tolerate levels as low as 3.0 (Moore 1987). For example, specimens have been collected at temperatures of 17.0–20.0 °C and salinities of 14.0–17.0 PSU in San Francisco Bay, USA (Mills and Sommer 1995), as well as in southern Brazil (Nogueira Júnior and de Oliveira 2006; Bardi and Marques 2009) and in the Río de la Plata estuary, Argentina-Uruguay (Genzano et al. 2006) in salinities of 2.0–30.0 and 23.0–29.7 PSU and temperatures of 21.5–30.5 and 23.5–24.3 °C, respectively. It has also been collected in the lagoon system of Chantuto-Panzacola, Chiapas, in salinities of 15.0–32.0 PSU and temperatures of 31.0–33.0 °C (Álvarez-Silva et al. 2006). These last are the maximum values of salinity and temperature at which the species has been recorded to date. The euryhaline and eurythermic character of the species has enabled it to invade new environments and successfully establish itself. Recently Baumsteiger et al. (2018) noticed that a low salinity seems to reduce abundance of *B. virginica,* since it is much more abundant in the more saline Napa and Petaluma River estuaries, California. This fact is in line with observations carried out at the Pueblo Viejo Lagoon in March and Abril, where the average densities were of 1,946.75 and 2,508.83 ind/100 m^3, respectively, with salinities of 11 to 21 PSU. Therefore, salinity has a clear effect on the presence and abundance of medusae.

This species, hypothesized to be native to the Black Sea (Harrison et al. 2013), may have been introduced into Pueblo Viejo lagoon after the dormant stages of the polyps or the fertilised eggs were transported by ships. Calder and Burrell (1969) proposed this introduction mechanism and pointed out that the polyps are more tolerant and can survive adhered to crusts of fouling organisms on a ship's hull. Although it is unlikely that the polyps of brackish water hydrozoans can remain active during transoceanic voyages, the dormant stages of the polyps or the fertilised eggs may well be able to survive. This type of invasion is a consequence of intense shipping and of the opening of new transportation routes, and results in brackish habitats being increasingly affected by non-indigenous species. In connection with this Cohen (2006) points out that this species has been transported as hull fouling or in ballast water tanks through the Panama Canal. Explanations as to why brackish systems are prone to introductions of alien species include, among others, that the wide salinity gradients in brackish systems provide a greater range of opportunities for the establishment of non-indigenous species (Paavola et al. 2005).

The presence and great abundance of this species in the lagoon in March and April 1993 most probably results from a marine water mass that immigrates from the Gulf of Mexico into the Pánuco River estuary, as is evidenced by the greater than average salinities recorded throughout the year. This marine influence was described by Castillo-Rivera and Kobelkowsky (1993), who mentioned that the greatest effect takes place in the area of the lagoon inlet during March, April and May. The connection of the lagoon to the Pánuco River estuary, one of the largest rivers of the Gulf of Mexico, may have favoured the immigration of *B. virginica* into the lagoon from other regions, as its mouth is located at the port of Tampico and at a distance of 30 km from one of the most important ports of Mexico, the port of Altamira. Significant maritime activities are carried out in this region with the arrival of ships from the east coast of the United States, northern Europe, the Mediterranean Sea, New Zealand, Australia, South America, the Caribbean, South Africa and the Far East (SCT 2007).

Blackfordia virginica was introduced into Pueblo Viejo lagoon in 1993, where in this study it was recorded in March and April with the greatest abundance values registered for its worldwide distribution range. It presented a wide range of sizes, adults of both sexes, and a great morphological variability (this last as a possible response to the environmental heterogeneity). The species may not be established in the system as no individuals were observed in March 2009. Additionally, the conditions in this brackish system (11.0–21.0 PSU) in March and April favoured the development of medusae during this short period of the year, after being transported by ships arriving at the ports of Tampico and Altamira. The medusae entered Pueblo Viejo lagoon on the tidal current when the flow of the Pánuco River was low (from January to May, with an average monthly discharge of 121.58–173.2 m^3 sec^{-1}). In contrast, the maximum flow (from June to December, with an average monthly discharge of 239.87–1383.87 m^3 sec^{-1}) (Las Adjuntas Station, 1965–1979) (SAGE 2018) generates oligohaline conditions that prevent the establishment and invasion of *B. virginica*.

The lower Pánuco basin area has been subjected to severe floods (e.g., 1955, 1990, 1993, 1999, 2003, 2007 and 2011) causing serious devastation; the maximum flow in the river is often associated with the increase in tropical cyclone activity within the Gulf of Mexico (e.g., September). As an example of the size of the extreme discharges that can be drained into the Pánuco River during the event of 1993, the estimated flow was 5836 m^3 sec^{-1} (Pedrozo-Acuña et al. 2013). As a consequence, salinity decreased and *B. virginica* did not remain in the area. This is in concordance with observations made at Gironde Estuary, Portugal and San Francisco Estuary, USA, where this species increases in population when the water reaches higher salinity values, > 6 PSU in Gironde Estuary and 8 PSU in San Francisco Estuary (Baumsteiger et al. 2018; Nowaczyk et al. 2016).

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Authors' contribution

AOL and MSR – research conceptualization; AOL and MSR – sample design and methodology; AOL, AIG and MSR – investigation and data collection; AIG and MSR – data analysis and interpretation; MSR – funding provision; MSR – original draft; AOL and MSR – writing, review and editing.

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