Non-indigenous upside-down jellyfish *Cassiopea andromeda* in shrimp farms (Brazil)

Jorge Thé [1]*, Edgar Gamero-Mora[2], Marcus V. Chagas da Silva[1], André C. Morandini[2,5], Sergio Rossi[1,3,4], Marcelo Soares[1] [3 4]

✉ Jorge Thé
jorgethe22@gmail.com

1. Instituto de Ciências do Mar (LABOMAR), Universidade Federal do Ceará (UFC), Fortaleza, Brazil
2. Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo (USP), São Paulo, Brazil

3. Institut de Ciència i Tecnologia Ambientals (ICTA), Universitat Autònoma de Barcelona (UAB), Barcelona, Spain.
4. DiSTeBA, Campus Ecotekne, University of Salento, 73100 Lecce, Italy
5. Centro de Biologia Marinha, Universidade de São Paulo, São Sebastião, Brazil

ABSTRACT

Invasive species are one of the biggest threats to coastal areas. Jellyfish, when found in aquaculture systems, may cause major economic damage; they are already present in many aquaculture facilities in the Mediterranean, Yellow Sea, and Bohai Sea. Herein, for the first time, we describe the occurrence of the upside-down jellyfish (genus *Cassiopea*) in shrimp (*Litopenaeus vannamei*) farms. The observed specimens were collected on the equatorial Southwestern Atlantic coast (Northeast Brazil) for identification by genetic sequence data (COI). The results indicate that the jellyfish in aquaculture systems are similar in terms of morphology and genetics to those found in natural environments in Bermuda, Egypt, Hawaii, Florida, and elsewhere in Brazil (Rio de Janeiro) and are related to specimens originally inhabiting the Red Sea (*Cassiopea andromeda*). In addition, we report the northward expansion of *C. andromeda* along the Brazilian equatorial margin. Only female jellyfish were observed, which suggests that the maintenance and spread of the non-indigenous population occur by asexual reproduction. The high abundance and presence of juvenile and adult animals may have major economic impacts on a high-value industry, given the potential of the population to spread to shrimp farms located in tropical mangroves.

Keywords: Aquaculture; Biological invasions; Jellyfish blooms; *Litopenaeus vannamei*; Invasive species

INTRODUCTION

Invasive species are one of the major threats in several coastal communities (Carlton, 1989; Carlton, 2001; Paul & Kar, 2016; Soares et al. 2018), being responsible for ecological, economical, and social impacts, such as the loss of biodiversity and biomass, and damage to ecosystem goods and services (Bellard et al., 2016; Gallardo et al., 2016; Vilà & Hulme, 2018; Walsh et al., 2016). Jellyfish have high invasive potential due to the ability of their planktonic and benthic (polyp) stages to survive under drastic environmental changes; however, worldwide, there are only five species for which there are confirmed reports of biological invasion (Bayha & Graham, 2014). Besides being a threat to the coastal ecosystem function (Graham et al., 2003; Paul & Kar, 2016), jellyfish can cause significant economic problems by impacting aquaculture systems (Purcell, et al., 2013; Dong et al., 2017).

The occurrence of jellyfish species in aquaculture activities, such as fish and shrimp farming, was reported along the Chinese coast, with species from the Bohai and Yellow Seas such as *Rhopilema esculentum* (Dong et al., 2009), *Aurelia aurita, Cyanea nozaki, Nemopilema nomurai* (Dong et al., 2010), *Aurelia* sp. (Dong et al., 2017), *Aurelia coerulea* (Dong et al., 2018), and *Phyllorhiza* sp. (Dong et al., 2019), as well as in the Mediterranean Sea, with the presence of *Pelagia noctiluca* (Bosch-Belmar et al., 2016, 2017).

Jellyfish blooms in aquaculture systems have already been seen in China, where *Phyllorhiza* sp. was detected (Dong et al., 2019). In the Mediterranean Sea, the mauve stinger (*Pelagia noctiluca*) was detected in fish farms, reducing the growth rates and even causing the death of European seabass (*Dicentrarchus labrax*) (Baxter et al., 2011). In the British Isles, including Ireland, the jellyfish species *Aurelia aurita* and *Pelagia noctiluca* were also reported to cause the death of many fish in salmon farms (Doyle et al., 2008; Marcos-López et al., 2014; Mitchell et al., 2013; Purcell et al., 2013). Aquaculture activities provide artificial substrates that can be used as settling areas for proliferating polyps, contributing to the increase in the number of possible medusae (Lo et al., 2008; Richardson et al., 2009; Dong, Liu and Keesing, 2010; Purcell et al., 2007; Purcell, 2012; Duarte et al., 2013; Dong et al., 2018).

One of the non-indigenous species (NIS) of jellyfish found in natural environments is from the genus *Cassiopea*, also known as upside-down jellyfish. This benthic medusa is commonly found in shallow waters (Ohdera et al., 2018) and is considered invasive in several coastal areas of the Caribbean and the Eastern Mediterranean Sea (Holland et al., 2004). Migotto et al. (2002) first recorded the genus *Cassiopea* (as *C. xamachana*) in the Southwestern Atlantic (Brazil). However, Morandini *et al.* (2017) identified a NIS population of *Cassiopea andromeda* based on morphology and a molecular marker (COI) and hypothesized that it has inhabited the Brazilian coast for more than 500 years. This species is considered native to the Red Sea, where it can aggregate in large numbers in natural ecosystems such as seagrass beds, coral reefs, lagoons, and mangrove habitats (Holland et al. 2004, Niggl and Wild 2010). Although it is considered invasive or non-indigenous in many coastal environments worldwide, *Cassiopea* has never been reported in aquaculture ponds (Bayha & Graham 2014; Ohdera et al. 2018).

Here, we report the occurrence of the NIS *Cassiopea andromeda* in shrimp farms in Northeast Brazil. This record is important because it shows a northward expansion of the invasion of *C. andromeda* in the Western Equatorial Atlantic (Brazilian coast), and it is the first mention in the literature of the presence of a species of *Cassiopea* in aquaculture systems anywhere in the world.

MATERIALS AND METHODS

The field activities were conducted on shrimp farms located in the municipality of Acaraú, Ceará State (NE Brazil) (Figure 1). The study area is located in the Brazilian Equatorial Margin (Figure 1), western equatorial Atlantic Ocean, under oligotrophic conditions and a semi-arid climate. In this area, the rainfall pattern is defined by two seasons: rainy (January to May) and dry (June to December) (Barroso et al. 2018), with low intra-annual and interannual variation in sea temperature (26-30º C) (Soares et al. 2019).

The study area is also subject to the continuous subequatorial atmospheric circulation of the trade winds, which are persistent and intense throughout the year (Gomes et al. 2014). Moreover, the study area is of special interest owing to the occurrence of an easterly flowing equatorial current that links the western equatorial Atlantic and the Amazon coast at this tropical latitude (Soares et al. 2017). The shrimp farms are generally found in coastal areas (Queiroz et al., 2013), where there are shallow and hypersaline estuaries characterized by freshwater-deprived conditions (e.g., multiple dams and severe droughts) and mangrove forests (Barroso et al. 2018).

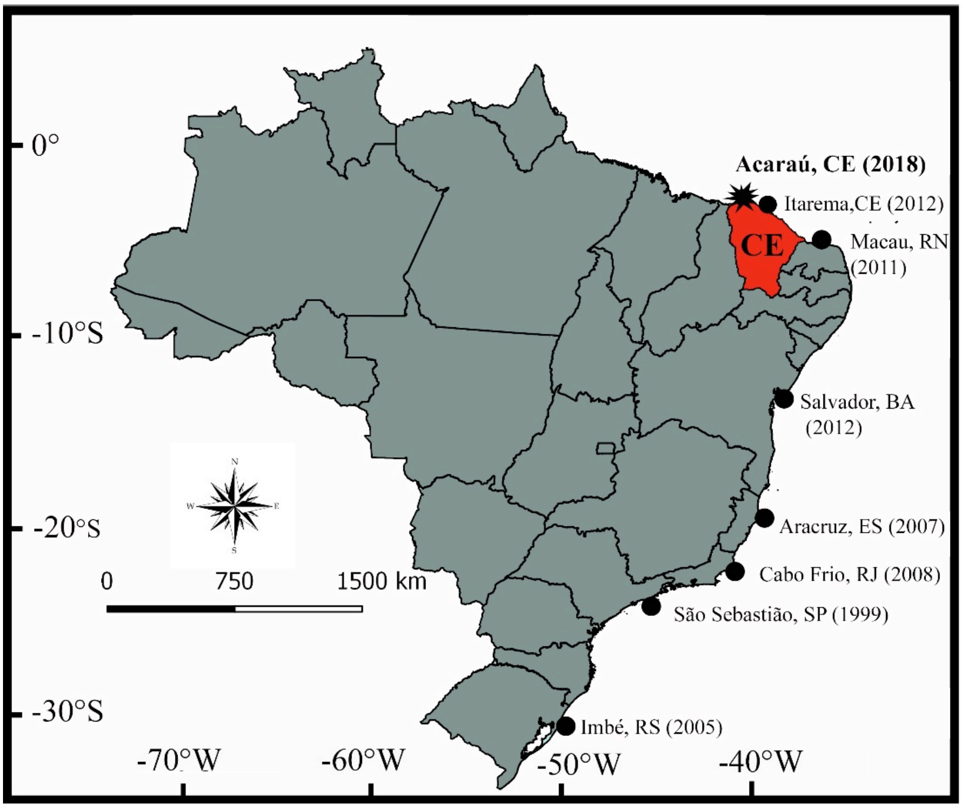

Figure 1. Map showing previous reports of the presence of *Cassiopea andromeda* (circles) along the Brazilian coast (Morandini et al. 2017) and the new record (star) of the presence of this jellyfish at shrimp farms on the Ceará (CE) coast.

Over the last four decades, Northeast Brazil experienced an intense development of industrial shrimp farming (*Litopenaeus vannamei*), making this area one of the main shrimp producers in Latin America (Meireles et al., 2007). By the end of the 1990s, shrimp farming had become an important food export industry, supported by government assistance, public-bank financing, academic collaboration, and legislative permissiveness, especially with respect to farming in the mangrove forests. Shrimp farms in northeastern Brazil are mostly located in estuarine areas that include mangrove ecosystems (Soares et al. 2017). The farms may be installed in mangrove forests where the trees have been cut to accommodate the installation of aquaculture facilities or they are constructed, under environmental licensing, in old salt pond facilities (Queiroz et al., 2013).

Biological sampling and environmental data collection occurred in July 2018 (end of rainy season). We measured the pH, salinity, and water temperature using a multiparameter probe (YSI 6602). To calculate the density of jellyfish, three belt transects (BTs) of 20 × 2 m (40 m^2) were made. On these BTs, we randomly distributed quadrats of 50 × 50 cm and took images of the benthic jellyfish to analyze the size structure of the population. We also used a drone to photograph the area inside the shrimp farms (Figure 2C and 2D). The data from the BTs and photo-quadrats were collected at the border of the circulating canal at a depth of 50 cm (Figure 2B). The images were analyzed using the software program IMAGE J to count the number of specimens in the area and assess the main morphometric features within the population (density, abundance, and umbrella diameter). The diameter of the umbrella was measured from the images obtained and using the quadrats of 50 × 50 cm as a scale. The images obtained from both the drone camera and hand-held camera were analysed were analyzed using the IMAGE J program.

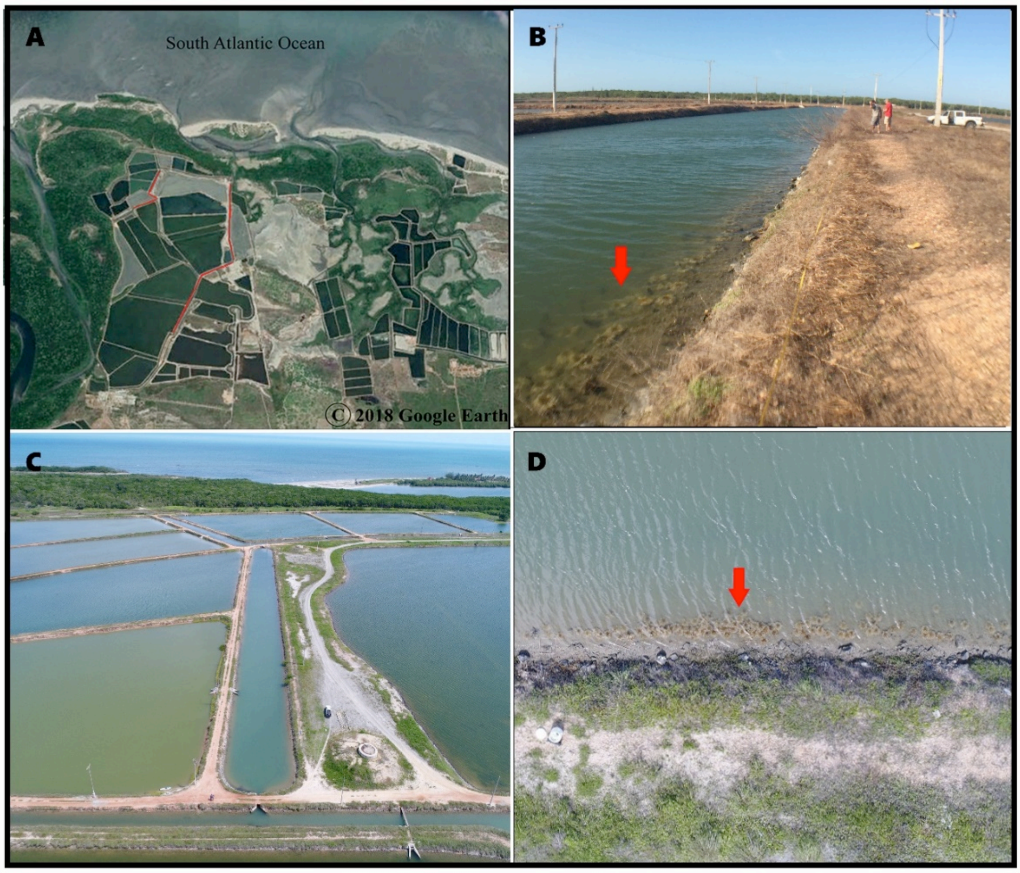

Figure 2. Shrimp farms and the study site (delimited by red lines) in Acaraú, Northeast Brazil (A). Closer view of the flooding canal where the jellyfish were collected; some specimens can be seen on the margin (red arrow) (B). View of the flooding canal where the sampling was performed (C). Closer view of the flooding canal with visible specimens (red arrow) (D). Image sources: A, Google Earth; B, field survey; C and D, aerial views captured using a drone.

To determine the sex of the specimens, the gonads (n = 40 jellyfish) were exposed by cutting away the oral arms (Schiariti et al., 2012) and observing the lower part of the umbrella under the microscope (following the protocol described by Kienberger et al., 2018). For molecular identification, samples of different tissues (oral arms, umbrella margin, and gonads) of ten specimens were preserved in 90% ethanol prior to analysis. The same ten specimens were preserved in 4% formaldehyde solution in seawater for morphological observations.

DNA extraction, amplification, sequencing and assembling

A protocol using ammonium acetate was used to extract DNA from the umbrella tissue (Fetzner 1999), but DNA samples from four of the ten available specimens were sequenced. A 700-bp fragment, including the standard barcoding region of cytochrome *c* oxidase I (COX1), was amplified (Hebert et al., 2003). One microliter of the extracted DNA was used as a template, with the final PCR reaction volume being 25 µl. The primers used were FishF1–5′ -TCAACCAACCACAAAGACATTGGCAC-3′ and med-cox1-R-5′ -TGGTGNGCYCANACNATRAANCC-3′ (Lawley et al. 2016; Ward et al. 2005). The PCR thermal program consisted of an initial denaturation step of 3 min at 95°C, followed by 35 cycles of 30 s at 95°C, 40 s at 54°C, and 50 s at 72°C, with a final extension of 7 min at 72°C. The PCR products were visualized on 2% agarose gels and purified using AmPure XP. Products were labeled using the BigDye Terminator V.3.1 Cycle Sequencing Kit (Applied Biosystems, Inc.) using the same primers and annealing temperature as those used in the PCR reaction. Dye-labeled DNA was sequenced bidirectionally using an ABI 3730 sequencer at the Biosciences Institute, Botany Department, University of São Paulo (USP).

Sequence identification and phylogenetic analysis

Sequences were assembled and edited using Geneious^{TM} 6.1.8. and analyzed using the BLAST server against the sequences within the NCBI databases. Sequence identification was performed based on BLAST scores and percent identity. *Cassiopea andromeda* sequences obtained from our specimens (two from the shrimp farm, MN384761 and MN384762, and two from the surrounding mangrove, MN384763 and MN384764) and those retrieved from GenBank were aligned using MAFFT and visualized and edited in BioEdit. Aligned sequences were submitted to TNT v.1.5

(Goloboff and Catalano, 2016) to be analyzed under parsimony as the optimality criterion using “New Technology” searches (Goloboff, 1999; Nixon, 1999). Node support was assessed by Goodman-Bremer support values (Goodman et al., 1982; Bremer, 1994; Grant and Kluge, 2008). *Cassiopea frondosa* was used as the outgroup (GenBank accession number AY319467; Holland et al. 2004).

RESULTS

The water temperature and salinity were recorded as 27.8°C and 39 ppt, respectively. The density of individuals found was 1.75 specimens/m^2, and the mean umbrella size was 19.5 ± 5.94 cm ($n = 211$). We observed both young and adult specimens in the shrimp farm populations (Figure 4A) but curiously, only females were found (Figure 4B). In case of some young specimens, it was not possible to check the sex due to undifferentiated gonadal tissues.

The specimens sampled from the shrimp farm could be clearly identified as belonging to the genus *Cassiopea* based on the general morphology (upside-down habit). With regard to color pattern (greenish to brownish), number of oral arms and rhopalia (7–10 oral arms; 14–20 rhopalia), and bell diameter (2–25 cm), our specimens were comparable to those from other populations in Brazil.

The COX1 data obtained from the four specimens were identical, and the results of the BLAST search with GenBank sequences are shown in Table 1 (using only one sequence for comparison). The specimens collected correspond to *C. andromeda* (*sensu* Holland et al. 2004), being related (~ 99%) with other *C. andromeda* sequences including those from the Red Sea (the type locality of *C. andromeda*), Bermuda, Brazil, French Polynesia, Mexico, and the United States of America (Table 1). The phylogenetic hypothesis obtained (Figure 3) was poorly resolved, with mostly polytomic branching patterns, and the Goodman–Bremer support values were weak. *Cassiopea andromeda* from the Ceará coast (NE Brazil) are more related to specimens from Bermuda, Brazil, Egypt, and the United States. However, the dataset was not variable enough to show full resolution within the *C. andromeda* subclade.

Table 1. Comparison of BLAST results of *Cassiopea* sp. samples from shrimp farms on the Ceará coast (this study) and those reported in previously published studies.

GenBank ID	Max and Total Score	Query Cover	E value	Percent identity	GenBank accession	Collection locality	Reference (DOI)
Cassiopea andromeda	1245	100%	0	99.42%	JN700934.1	Tiahura, Moorea, French Polynesia, France	10.1093/gbe/evr123
Cassiopea andromeda	1175	96%	0	98.64%	KC464458.1	Cabo Frio, Brazil	10.1017/S0025315416000400
Cassiopea sp.	1112	89%	0	99.51%	MF742169.1	Richardson's Bay, Bermuda	10.3354/meps12521
Cassiopea andromeda	1112	89%	0	99.51%	HF930521.1	Subarea 51.1, Western Indian Ocean	10.1016/j.foodres.2013.10.003
Cassiopea xamachana	1088	87%	0	99.50%	AY319463.1	Walsingham Pond, Bermuda	10.1007/s00227-004-1409-4
Cassiopea xamachana	1083	87%	0	99.33%	AY319464.1	Richardson's Bay, Bermuda	10.1007/s00227-004-1409-4
Cassiopea andromeda	1079	87%	0	99.16%	AY319458.1	El Ghardaqa, Red Sea, Egypt	10.1007/s00227-004-1409-4
Cassiopea xamachana	1077	87%	0	99.00%	AY319468.1	Key Largo, Florida Keys, USA	10.1007/s00227-004-1409-4
Cassiopea andromeda	1077	87%	0	99.00%	AY319453.1	Kainaone fishpond, Moloka'i, Hawaii, USA	10.1007/s00227-004-1409-4
Cassiopea xamachana	1066	87%	0	98.66%	AY319466.1	Walsingham Pond, Bermuda	10.1007/s00227-004-1409-4
Cassiopea xamachana	1066	87%	0	98.66%	AY319465.1	Richardson's Bay, Bermuda	10.1007/s00227-004-1409-4
Cassiopea andromeda	1053	87%	0	98.16%	AY319454.1	Kainaone fishpond, Moloka'i, Hawaii, USA	10.1007/s00227-004-1409-4
Cassiopea	1046	84%	0	99.31%	AY319449.1	Oahu, Hilton Leeward, Hawaii,	10.1007/s00227-004-1409-4

andromeda						USA	
Cassiopea andromeda	1044	84%	0	99.13%	AF231109.1	Oahu, Waikiki Beach, Hilton Lagoon, Hawaii, USA	10.1007/s00227-004-1409-4
Cassiopea andromeda	1042	83%	0	99.48%	KC464459.1	Cabo Frio, Brazil	10.1017/S0025315416000400
Cassiopea andromeda	1040	84%	0	99.13%	AY319451.1	Oahu, Hilton Leeward, Hawaii, USA	10.1007/s00227-004-1409-4
Cassiopea andromeda	1035	84%	0	98.96%	AY319450.1	Oahu, Hilton Leeward, Hawaii, USA	10.1007/s00227-004-1409-4
Cassiopea sp.	1033	82%	0	99.47%	MF742172.1	Walsingham Pond, Bermuda	10.3354/meps12521
Cassiopea andromeda	1026	84%	0	98.62%	AY319448.1	Oahu, Hilton Leeward, Hawaii, USA	10.1007/s00227-004-1409-4
Cassiopea sp.	990	79%	0	99.45%	MF742168.1	Richardson’s Bay, Bermuda	10.3354/meps12521
Cassiopea sp.	985	79%	0	99.27%	MF742213.1	Moorea, French Polynesia, France	10.3354/meps12521
Cassiopea andromeda	983	79%	0	99.26%	KY610556.1	Baja California Sur, Isla San Jose, Mexico	10.1071/IS16055
Cassiopea andromeda	983	79%	0	99.26%	KY610555.1	Baja California Sur, Isla San Jose, Mexico	10.1071/IS16055
Cassiopea andromeda	983	79%	0	99.26%	KY610553.1	Baja California Sur, Isla San Jose, Mexico	10.1071/IS16055
Cassiopea andromeda	983	79%	0	99.26%	KY610552.1	Baja California Sur, Isla San Jose, Mexico	10.1071/IS16055
Cassiopea andromeda	983	79%	0	99.26%	KY610551.1	Baja California Sur, Isla San Jose, Mexico	10.1071/IS16055
Cassiopea sp.	981	79%	0	99.08%	MF742215.1	Moorea, French Polynesia, France	10.3354/meps12521
Cassiopea andromeda	977	79%	0	99.08%	KY610554.1	Baja California Sur, Isla San Jose, Mexico	10.1071/IS16055

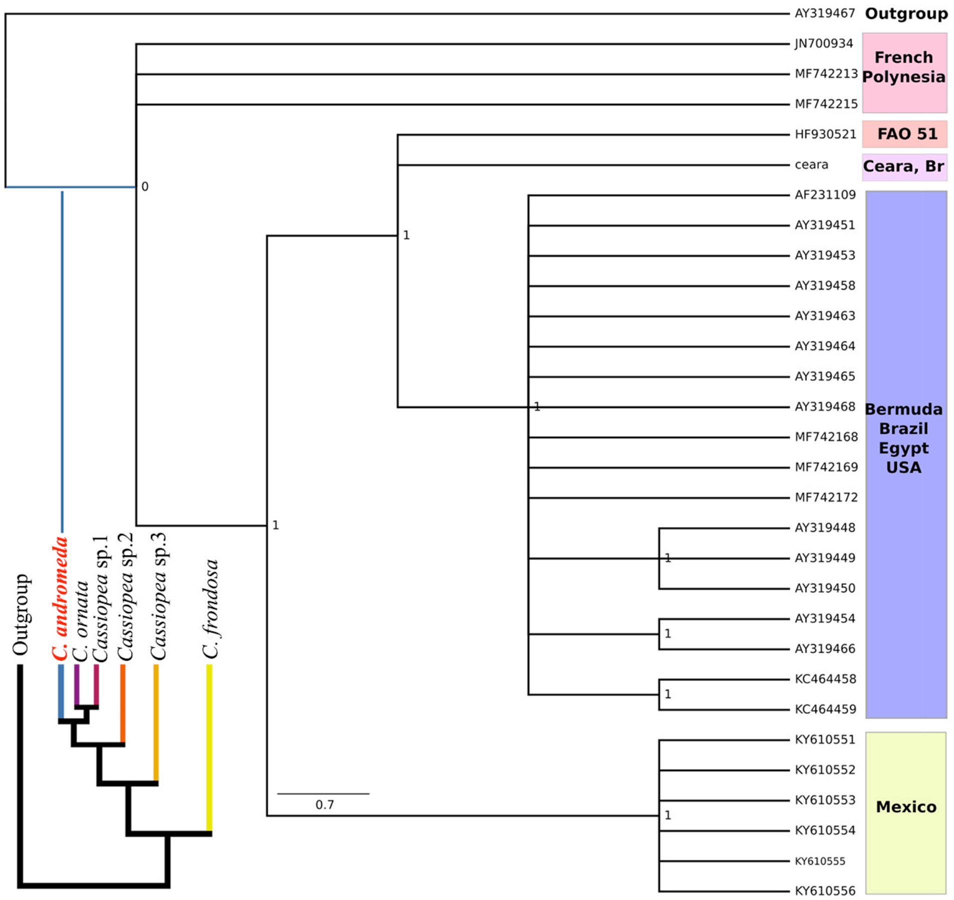

Figure 3. Phylogenetic hypothesis of *Cassiopea* spp. and *Cassiopea andromeda* based on the mitochondrial cytochrome *c* oxidase I gene. Lower left corner: simplified cladogram representation of *Cassiopea* spp. obtained by Holland et al. (2004), Morandini et al. (2017), and also recovered in this analysis (Ceara, Br = Ceará state, Brazil) based on the parsimony optimality criterion. Right panel: topology inferred using parsimony optimality criterion with 94 steps in length and Goodman–Bremer support values obtained based on a 442-bp fragment of the COX1 gene of *Cassiopea andromeda*, and *Cassiopea frondosa* (as an outgroup). More information about the OTU codes can be found in Table 1.

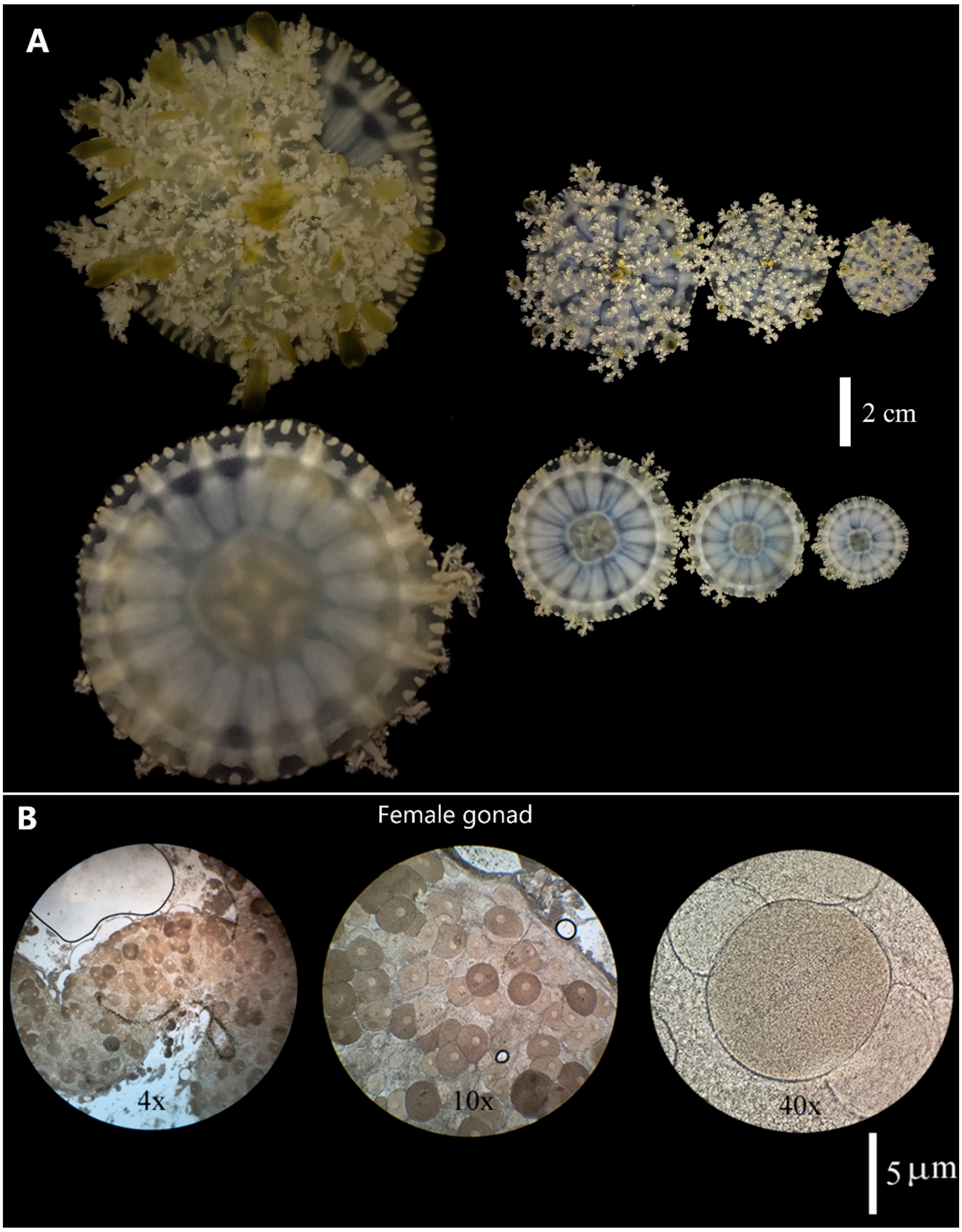

Figure 4. (A) Oral and aboral view of different specimens of the non-indigenous species *Cassiopea andromeda* from the shrimp farms (Ceará coast, NE Brazil). (B) Different amplification views (4×, 10×, and 40×) of the female gonads of *C. andromeda* from the shrimp farm.

DISCUSSION

Morphological identification of the specimens sampled was inconclusive. This was somewhat expected due to the high variation in morphology and few characteristic features of species belonging to the genus *Cassiopea* (Morandini et al., 2017). However, the genetic analyses confirmed the first record of the non-indigenous (NIS) upside-down jellyfish *Cassiopea andromeda* in shrimp (*Litopenaeus vannamei*) farms globally.

For the first time, our study a bloom of *C. andromeda* in aquaculture facilities (shrimp farms) and the northernmost record of the species on the Brazilian coast (Figure 1). This NIS species has expanded its range 24 km to the west, compared to the first report of its presence in mangroves in the Ceará state (from Morandini et al. 2017). Interestingly, we found only females from the cultivation and flooding canals of the shrimp farm. The presence of a single sex in the study population reinforces the hypothesis of Morandini et al. (2017) that the species arrived in Brazil through fouling on ship hulls and is establishing and expanding its population through asexual reproduction.

We adopt the term NIS for this *Cassiopea andromeda* population in our study considering that it is not established, i.e., there appear to be no breeding between males and females. In addition, we have no information about the ecological and socioeconomic impacts of this species on mangroves and the shrimp farm in this region. This demonstrates the importance of future studies regarding these possible impacts. The presence of this NIS in shrimp farms in this region of Brazil can be explained by two mechanisms. First, the arrival of the population in the northeastern Brazil probably occurred by the transport of polyps or larvae attached to ship hulls, ballast water tanks, or even on some farm material (e.g., pumps or hoses). Secondly, the local expansion of the population in the localities of Acaraú and Itarema (Figure 1) may have occurred by short-term dispersion by larvae in the estuarine area which enabled to reach on the shrimp farms and mangroves. The establishment of the population and its expansion on the shrimp farm and nearby areas such as mangroves require further investigation. Genetic analyses may indicate if the species first invaded the mangroves and then expanded to the shrimp farms or the other way around. Additionally, the availability of natural substrates (mangrove roots and leaves) in the surroundings of the aquaculture ponds also favors the invasive process in the shallow-water estuaries.

The estuarine environments have a wide range of salinity profiles due to the influx of freshwater and tidal action (Azhikodan and Yokoyama, 2016). However, the studied shallow-water estuary is located on the equatorial coast and has thermal stability (ranging from 26–30°C) (Soares et al. 2019) and sometimes, the higher salinities of the hypersaline estuaries (Barroso et al. 2018), which favor the occurrence of *Cassiopea andromeda*. In addition, there is a large amount of food available for both the pelagic and benthic fauna in this estuarine area due to the high levels of organic matter and phytoplankton productivity (Barroso et al., 2018).

The high abundance and presence of young and adult individuals of the NIS *C. andromeda* (Figure 4) in the shrimp farm can be attributed to the location of the aquaculture infrastructure in a mangrove area. Such an environment is ideal for the life cycle of the species, given that it comprises shallow and transparent waters and also high levels of available organic matter (Fitt & Costley, 1998; Fleck & Fitt 1999). The medusae are gathered only at the edge of the channel, where presumably light harvesting by the photosynthetic endosymbionts is possible. The aquaculture activities promote the eutrophication of the estuarine waters due to the input of phosphorus, nitrogen, and surplus organic matter, which favors phytoplankton growth (Barcellos et al., 2019).

The eutrophication can further favor the establishment of *Cassiopea* populations by providing nutrients for the symbiotic algae Symbiodiniaceae and plankton for heterotrophic feeding (Ohdera et al., 2018). Thus, the mixotrophic strategy of the jellyfish is an advantage in this estuarine environment. On the other hand, *Cassiopea* may also impact the ecological processes in this tropical shallow-water environment. High densities of *Cassiopea* may increase the benthic ammonium uptake and oxygen production but reduce nitrate uptake in a tropical lagoon (Zarnoch et al. 2020), which suggests that the *Cassiopea* population can significantly alter the biogeochemical cycles in the mangroves and shrimp farms.

The genetic marker COX1 confirmed the first record of *Cassiopea andromeda* in the shrimp farm industry globally. Different genetic markers have been used to answer specific questions about the systematics of medusozoans. Slowly evolving genes have been shown to be appropriate for inferring relationships among scyphozoan jellyfish families (e.g., 18S and 28S) (Bayha et al. 2010). COX1 has been reported as useful for revealing diversity in genera such as *Aurelia*, *Cassiopea*, and *Cyanea*, having been used to demonstrate that taxa such as *Aurelia aurita*, *C. andromeda*, and *Cyanea capillata* do not comprise a single taxonomic unit as previously assumed (Dawson & Jacobs 2001; Holland et al. 2004; Dawson 2005; Scorrano et al. 2017).

COX1 has also been employed in biogeographic, population genetics, and phylogeographic studies of scyphozoans; thus, it was useful in distinguishing two reciprocally monophyletic clades of *Catostylus mosaicus* showing evidence of early evolution (Dawson et al. 2005). On the contrary, researchers using COX1 and internal transcribed spacer 1 sequences observed neither geographic clusters nor genetic structure in the jellyfish *Rhizostoma pulmo* in the Mediterranean Sea (Ramšak et al. 2012). Similar to the case of *R. pulmo* (Ramšak et al. 2012), we saw no evidence of geographical clustering of the subclades of *C. andromeda* using COX1 (with our parsimony hypothesis), and neither did we not obtain a good resolution, nor well-supported clades. Although they have different life habits (pelagic and epibenthic), both species lack differences in their genetic structure at these geographical scales. The wide distribution and drifting/swimming abilities of *R. pulmo* enable population connectivity for this species within the Mediterranean Sea; in the case of *C. andromeda*, the reduced mobility, combined with human-mediated distribution via maritime transport and invasive mechanisms can explain the population connectivity.

Seasonal studies aimed at understanding the reproductive patterns, population structure, and factors favoring the increase in abundance and size of this NIS jellyfish in aquaculture facilities are urgently needed. The possible presence of *Cassiopea* jellyfish in other Brazilian shrimp farms should also be investigated. This can be carried out through a citizen's science approach (Embling et al. 2015; Deidun et al. 2018); digital images could be distributed to farms along the coast, and scientists would then validate the presence (or absence) of *Cassiopea* jellyfish. Moreover, considering the possible biogeochemical and ecological impacts of this NIS jellyfish (Ohdera et al. 2018; Zarnoch et al. 2020), further studies could evaluate the positive, negative, or neutral effects of such species on the shrimp farms and mangroves.

The high abundance and presence of juvenile and adult animals may have major economic and ecological impacts on a high-value industry and mangroves. The tropical mangroves—in which the farms are located—could act as a bridge for the further spreading of the population of NIS jellyfish. Accordingly, other important issues to be addressed are the ecological, social, and economical consequences of the expansion of *C. andromeda* to farms producing the shrimp *Litopenaeus vannamei,* which is considered a valuable aquaculture resource globally (FAO 2018).

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