AQUACULTURE FACILITIES PROMOTE POPULATIONAL STABILITY THROUGHOUT SEASONS AND INCREASE MEDUSAE SIZE FOR THE INVASIVE JELLYFISH *Cassiopea andromeda*

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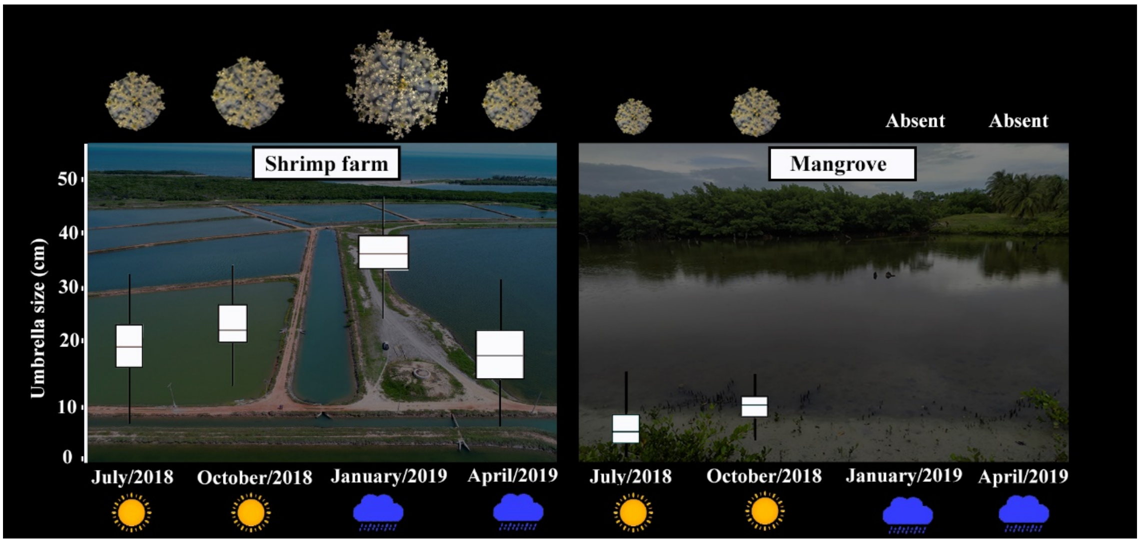
GRAPHICAL ABSTRACT



ABSTRACT

Cassiopea jellyfish have successfully invaded several marine ecosystems. We investigated if *Cassiopea andromeda* grows larger (umbrella size) and if their populations are more stable in shrimp farms than in mangroves in the Brazilian coast. Our results show that jellyfish abundance is higher in the shrimp farm during the rainy season and in the mangrove during dry season. The population is stable during both seasons in the shrimp farm, but unstable in the mangroves, as jellyfish are absent during rainy season. Shrimp farm-associated jellyfish are three times larger than those in the mangroves, regardless of season. We recorded the largest (49.2 cm of umbrella diameter) ever *C. andromeda* individual in the shrimp farm. Unlike the mangroves, the shrimp farm provides environmental intra-annual stability that promotes jellyfish growth and population persistence. Therefore, *C. andromeda* populations can be seasonally dynamic and artificial environments such as aquaculture facilities may facilitate the invasion process.

Keywords: estuary; mangrove; nutrients; Scyphozoa; shrimp farm; size distribution

1. INTRODUCTION

Cassiopea spp. ("upside-down jellyfish") are mixotrophic, benthic animals that acquire energy by both heterotrophic feeding, and photosynthate translocation performed by their symbiotic dinoflagellates (Symbiodiniaceae) (Ohdera et al., 2018). Because of their trophic plasticity, diversity of reproductive strategies (they display a metagenetic life cycle, with polyps performing asexual reproduction and producing medusae, while medusae reproduce sexually and generate polyps – see Morandini et al., 2016), and resilience to physico-chemical variations, *Cassiopea* spp. have successfully invaded many tropical and subtropical shallow ecosystems worldwide, such as mangroves, seagrass beds and hypersaline estuaries (Stoner et al., 2011; Heins et al., 2015; Morandini et al., 2017). Although there has been some confusion regarding the identification of *Cassiopea* species in the past, it is thought that this genus first invaded the Mediterranean through the Red Sea, before spreading to the Western Atlantic Ocean (Graham and Bayha, 2008; Bayha and Graham, 2014; Morandini et al., 2017).

The increase in abundance and size of these invasive jellyfish is usually observed in coastal environments under anthropogenic pressure (Stoner et al., 2011; Zarnoch et al., 2020). Typical examples of artificial causes for intense jellyfish blooms include climate change, eutrophication, overfishing, coastal construction, and introduction of alien species (Purcell et al., 2007; Purcell, 2012; Richardson et al., 2009; Stoner et al., 2016). This occurs because *Cassiopea* spp. populations are largely influenced by intra-annual variations in environmental conditions, such as temperature, salinity and nutrient concentration (Fitt and Costley, 1998; Stoner et al., 2011; 2014; Freeman et al., 2016; Aljbour et al., 2017; 2019).

Temperature is a critical factor in *Cassiopea* spp. life cycle and invasion success because it modulates several stages of development for both asexual and sexual reproduction, including strobilation, larval settlement and metamorphosis (Fitt and Costley, 1998; Hofmann et al., 2003; Newkirk et al., 2018). In addition, temperature affects symbiont concentration in the jellyfish tissue because warmer conditions may induce bleaching (McGill and Pomory, 2008; Lampert, 2016; Newkirk et al., 2018; Klein et al., 2019). Salinity is also an important modulator of *Cassiopea* spp. populations because it is a regulatory mechanism for asexual reproduction (Fitt and Costley, 1998; Newkirk et al., 2018). In addition, prolonged exposure to lower salinities may cause high mortality episodes (Klein et al., 2016a). Besides temperature and salinity, variations in other environmental parameters may also play a relevant role in the physiology and ecology of *Cassiopea* jellyfish. For instance, increase in nutrients, chlorophyll-*a* (chl-a), and organic matter often enhance both heterotrophic feeding and the photoautotrophy performed by their endosymbionts (Welsh et al., 2009; Stoner et al., 2011; 2016; Lampert, 2016; Freeman et al., 2017; Ohdera et al., 2018; Djeghri et al., 2020). Therefore, fluctuations in all of these parameters due to natural conditions and/or human activities may stimulate either an increase or decrease in *Cassiopea* spp. populations during the invasion process.

Urban development, agriculture, aquaculture activities, and their associated consequences constitute major human pressures to estuaries and mangroves worldwide (Lacerda, 2006; Suárez-Abelenda et al., 2014). These activities produce a large amount of nitrogen and phosphorus, which leads to eutrophication events (Diaz et al., 2017; Barcellos et al., 2019). Recently, it has been detected that the jellyfish *Cassiopea andromeda* has invaded shrimp farms on the Brazilian semiarid coast, located in the western Atlantic Ocean (Thé et al., in press). Shrimp farming is an economic activity of great importance worldwide, that is often performed at or near mangroves (Sousa et al., 2006; Nóbrega et al., 2013; Queiroz et al., 2013; FAO, 2018; Barcellos et al., 2019). However, investigations comparing *Cassiopea* spp. non-indigenous populations in aquaculture farms and nearby mangroves have not been conducted. The Brazilian semiarid coast presents high and stable temperatures, oligotrophic waters, and low rainfall rates (Barroso et al., 2018; Fernandez et al., 2019; Soares et al., 2019). Therefore, it provides a unique opportunity to assess the intra-annual variations in size, spatial distribution, abundance and seasonal frequency of the invasive *C. andromeda* in both shrimp farms and mangroves. We investigated *C. andromeda* populations in the semiarid mangrove and shrimp farm facilities to determine differences in medusae umbrella size and populational stability, while also monitoring key environmental conditions to determine the effects of seasonality for both habitats. In this way, *C. andromeda* was investigated to determine if it displays larger umbrella size and if populations are more stable in a shrimp farm than in the mangrove.

2. MATERIALS AND METHODS

2.1. Study area

Field surveys were performed in two adjacent habitats on the Brazilian semiarid coast (Ceará state) in the western Atlantic Ocean (Fig. 1A-B): water channels inside a shrimp farm in Acaraú (Fig. 1C-D, 2° 50' 9.00" S/40° 7' 13.30" W); and the mangroves at Itarema (Fig. 1E-F, 2° 53' 2.83" S/39° 54' 42.17" W). Sites were approximately 20 km apart. The shrimp farm has supply channels for pumping seawater from the ocean into the farms. The semiarid mangrove is in a shallow (3-m deep) bar-built estuary. The estuarine lagoon area between the coast and the barrier sandy beach is a protected area of low hydrodynamics.

Climate in the area is tropical semiarid, marked by high sea surface temperature, with low intra-annual variability (minimum of 26 °C and maximum of 30 ºC), and little rainfall (500–1000 mm.year^{-1}) (Soares et al., 2017). Ninety percent of the rainfall takes place during rainy season in the summer and autumn. In the dry period, because of low rainfall, high irradiance, and higher evaporation rates, a hypersaline condition (as high as 38–63) is common in the shallow-water mangroves and surrounding estuaries (Barroso et al., 2018; Valentim et al., 2018). Four intra-annual surveys were conducted at each of the two habitats on July/2018 and October/2018 (dry season), and January/2019 and April/2019 (rainy season), at a depth of 1–2 m.

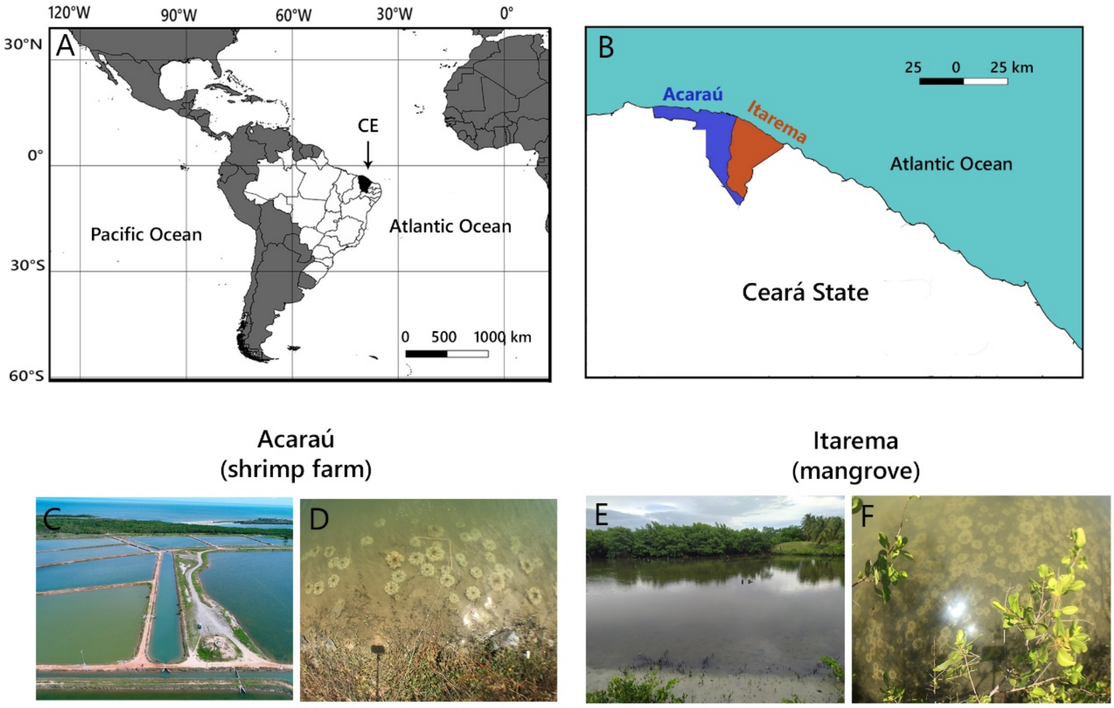


Figure 1. The population structure of the invasive jellyfish *Cassiopea andromeda* was surveyed at two habitats on the Brazilian coast (Ceará state) (A-B) in the Western Atlantic Ocean: seawater channels inside a shrimp farm in Acaraú (C-D) and the adjacent semiarid mangroves at Itarema (E-F).

2.2. Data collection

2.2.1 Environmental parameters

A multiparametric probe (AK87, AKSO) was used to measure temperature, salinity and pH. For both habitats, measurements were performed once during each of the four surveys, at a depth of 0.5 m. Surface water samples were also collected for quantification of chlorophyll-a (chl-a) and nutrients. For chl-a analyses, samples were filtered in glass fiber filters of 0.7 µm (nominal pore size, Macherey-Nagel), and frozen at -20 °C (Parsons et al., 1984). Chlorophyll-*a* was extracted with 90% acetone (for 24 hours, in the dark, at 4 °C), and readings were performed on a spectrophotometer (wavelengths of 630, 647, 664, 665 and 750 nm). Absorbance values were converted to chl-a concentration, according to the equations of Jeffrey and Humphrey (1975).

Unfiltered water samples were used for quantification of total nitrogen (TN) and total phosphorus (TP) according to the procedures of UNESCO (1983). Nutrient and chl-a analyses were performed in quadruplicates.

2.2.2. Population structure

The unusual lifestyle of *C. andromeda* facilitates investigation and measurements using photographs because, unlike other jellyfish species, they rarely swim and mostly remain relaxed on the benthic surface. To investigate the individual size, abundance, and spatial distribution of *C. andromeda* jellyfish populations in the shrimp farm and semiarid mangrove, we performed three replicated 20-m transects within a single site for each habitat. During each of the four surveys, 40 quadrats (0.5 x 0.5 m) were photographed for each transect. The quadrats were equal (0.5 x 0.5m) with always the same size throughout the sampling along the year. Image J was calibrated photo by photo using the known quadrat sizes (0.5m x 0.5m).

Cassiopea andromeda individuals were classified as mature or immature based on morphological characteristics and gonad presence (refer to Campbell, 1974 and Schiariti et al., 2012). Ten individuals were collected during each of four surveys at each of the two habitats. We then removed the oral disc and visually assessed the gonadal tissue. Immature specimens displayed indistinguishable gonads, a small number (less than 15) of appendages in the developing oral arms, and a small umbrella size (less than 7.0 cm). Mature specimens presented brown gonads with visible gametes, a higher number of oral appendages (> 15) and measured 7.0 cm or more in umbrella diameter. Histological preparations to discern between different developmental stages of the gonads were not made.

2.3. Data sampling

The presence of *C. andromeda* in the shrimp farm and semiarid mangrove was quantified by analyzing the photoquadrats on ImageJ 1.51k software. The mean size of the umbrella of *C. andromeda* specimens at both sites was also calculated with the use of ImageJ 1.51k.

The spatial distribution of *C. andromeda* in the shrimp farm and mangrove was also quantified using the Morisita index to determine if upside-down jellyfish display a random, uniform or aggregated (patchy) distribution in both habitats (Morisita, 1959; Amaral et al., 2014; Hayes and Castillo, 2017). The Morisita index (Iδ) was applied to the populations in shrimp farm and mangroves assessed during each of the four surveys, according to the formula (Equation 1).

$$I\delta = n \times \Sigma X^{2} \text{-} N/N(N\text{-}1), \qquad \text{(Eq. 1)}$$

where n: number of sample units; N: total number of individuals counted in all n sample units; ΣX^2: sum of the square of the number of individuals per sample unit. If dispersion is random, Iδ = 1.0; if it is perfectly uniform, Iδ = < 1.0; and the aggregate pattern is given by Iδ > 1.0, with the maximum aggregation being Iδ = n (when all individuals are found in 1 sample unit).

2.4. Data and statistical analyses

To determine if jellyfish umbrella size varies seasonally for mangrove versus shrimp farms, as well as between seasons (January, April, July, and October), a two-way ANOVA and post-hoc comparisons (Tukey's HSD) were conducted. All analyses were conducted using R software (version 3.1.1), with the 'vegan' package (Oksanen et al., 2016).To describe the spatial and temporal intra-annual variability of the abiotic factors, and environmental variables (temperature, salinity, pH, chl-a, TN and TP), a principal component analysis (PCA), and a cluster analysis were performed. The environmental data were transformed and standardized for further use in the PCA analysis. The grouping analysis was based on Euclidean distance, and complete linkage, with the data previously transformed by log (x + 1). The statistical software PAST v. 3.20 (Hammer et al., 2001) was used for PCA analysis, and the software PRIMER v. 6.0 (Clarke and Gorley, 2006) was used for cluster analysis and dendrogram construction. The significance level for all statistical analyses was considered at $p < 0.05$.

3. RESULTS

3.1. Environmental data

Salinity and pH values varied similarly in both habitats, with minimum values in the rainy period (April/19) and maximum values in the dry period (October/2018) (Table 1). In the dry period (July and October), and January, waters were hypersaline, both in the shrimp farm and semiarid mangroves. Temperatures reached slightly higher values in the mangroves than in the shrimp farm (34 ºC and 31.5 ºC, respectively) (Table 1). Nutrients (TN and TP) in the shrimp farm were unexpectedly lower than in the mangroves (Table 1). The exception was the April/2019 (rainy season) survey, where similar values of TP and TN were found in the shrimp farm and mangrove. A similar intra-annual trend was also observed for chl-a (Table 1).

Table 1. Six environmental parameters (temperature, salinity, pH, total nitrogen-TN, total phosphorus-TP and chlorophyll-*a*) were evaluated in water channels inside a shrimp farm, and on semiarid mangroves containing invasive *C. andromeda* jellyfish populations. Both habitats are located on the tropical Brazilian coast in the Western Atlantic Ocean. The parameters were evaluated during dry (July 2018 and October 2018) and rainy (January 2019 and April 2019) seasons.

Site	Month /Year	C°	Salinity	Chlorophyll-*a* (µg L^{-1})	pH	TN (µM)	TP (µM)
Shrimp farm	Jul/2018	27.8°	39.9	1.70	7.9	18.38 ± 1,73	1.05 ± 0,043
	Oct/2018	31.5°	46.2	0.76	8.4	13.30 ± 0,94	0.31 ± 0,046
	Jan/2019	31.1°	43.2	1.46	8.2	15.70 ± 0,30	0.31 ± 0,046
	Apr/2019*	28.6°	31.6	13.2	8.0	42.78 ± 0,61	1.81 ± 0,112
Mangrove	Jul/2018	31.7°	38.9	5.08	8.0	52.84 ± 3,71	2.76 ± 0,094
	Oct/2018	31.8°	46.9	3.26	7.9	42.28 ± 2,29	1.87 ± 0,046
	Jan/2019	34°	44.5	2.18	8.3	64.70 ± 0,80	2.13 ± 0,230
	Apr/2019*	30.4°	24.4	2.45	8.1	42.06 ± 0,84	1.79 ± 0,032

* Most intense rainy period in the last 11 years old (FUNCEME 2019).

3.2. Population structure

A greater number of jellyfish was found in the mangroves during dry season (Fig. 2). A total of 546 individuals were counted in the mangroves on July/2018, and 158 for October/2018; 207 and 119 were counted for the shrimp farm on those dates, respectively. However, zero jellyfish were detected in the semiarid mangroves during the rainy season, while the shrimp farm recorded 170 and 58 individuals for January/2019 and April/2019, respectively (Fig. 2) (XXX). For both habitats, populations display an aggregated spatial distribution pattern (Table 2).

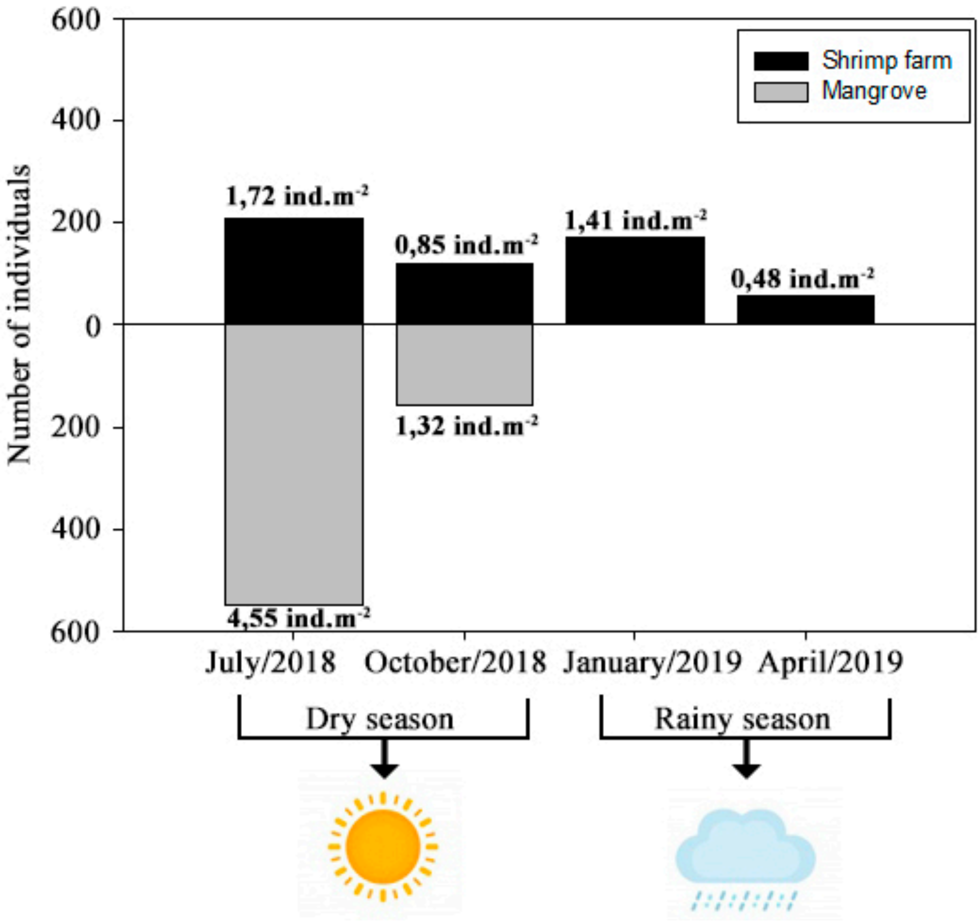


Figure 2. Number of individuals and population density (individuals per m^2) of the invasive jellyfish *Cassiopea andromeda* evaluated during the dry and rainy seasons in a shrimp farm and mangroves, both located on the tropical Brazilian coast (Western Atlantic Ocean).

Table 2. The Morisita Index (Iδ) was applied to investigate whether *Cassiopea andromeda* populations display a random (Iδ = 1.0), uniform (Iδ < 1.0) or aggregated (Iδ > 1.0) distribution pattern in a shrimp farm and in a semiarid mangrove, both located in the tropical Brazilian coast (Western Atlantic Ocean). (-): no jellyfish detected.

Sites	Month/Year	Iδ	Distribution
Shrimp farm	July/2018	3.6	Aggregated
	October/2018	1.71	Aggregated
	January/2019	1.98	Aggregated
	April/2019	2.73	Aggregated
Mangrove	July/2018	1.22	Aggregated
	October/2018	2.04	Aggregated
	January/2019	-	-
	April/2019	-	-

Cassiopea andromeda umbrella size was 8.2 ± 3.4 cm in the mangroves, and 24.7 ± 5.8 cm in the shrimp farm (Figs. 3 and 4). The results of Two-Way ANOVA on umbrella size showed significant differences between the mangrove and shrimp farm (df=1; F=4679.49; p< 0.0016), as well as between the months (df=3; F=517.68; p< 0.0016), as well as identified significant interactions between these two factors (df=1; F=10.12; p<0.0015). The Tukey multiple comparisons of means between the months (January, April, July, October) showed significant differences in all comparions; the only exception is between April and July in the shrimp farm when the umbrella diameter showed similar mean sizes (F=4.08; p=0.1239) (Figura 4). The smallest size class (0–7 cm) was recorded only in the dry period, and for the mangrove only (Fig. 3). This pattern explains the abundance of small-sized jellyfish (Fig. 3) in this estuarine habitat during the dry period (Fig. 2). Smaller jellyfish were present during dry and rainy seasons at the shrimp farm. Larger jellyfish were predominant during both seasons at the shrimp farm (Fig. 3). Adult jellyfish were only seen in the semiarid mangroves in the dry period (Figs. 3 and 4).

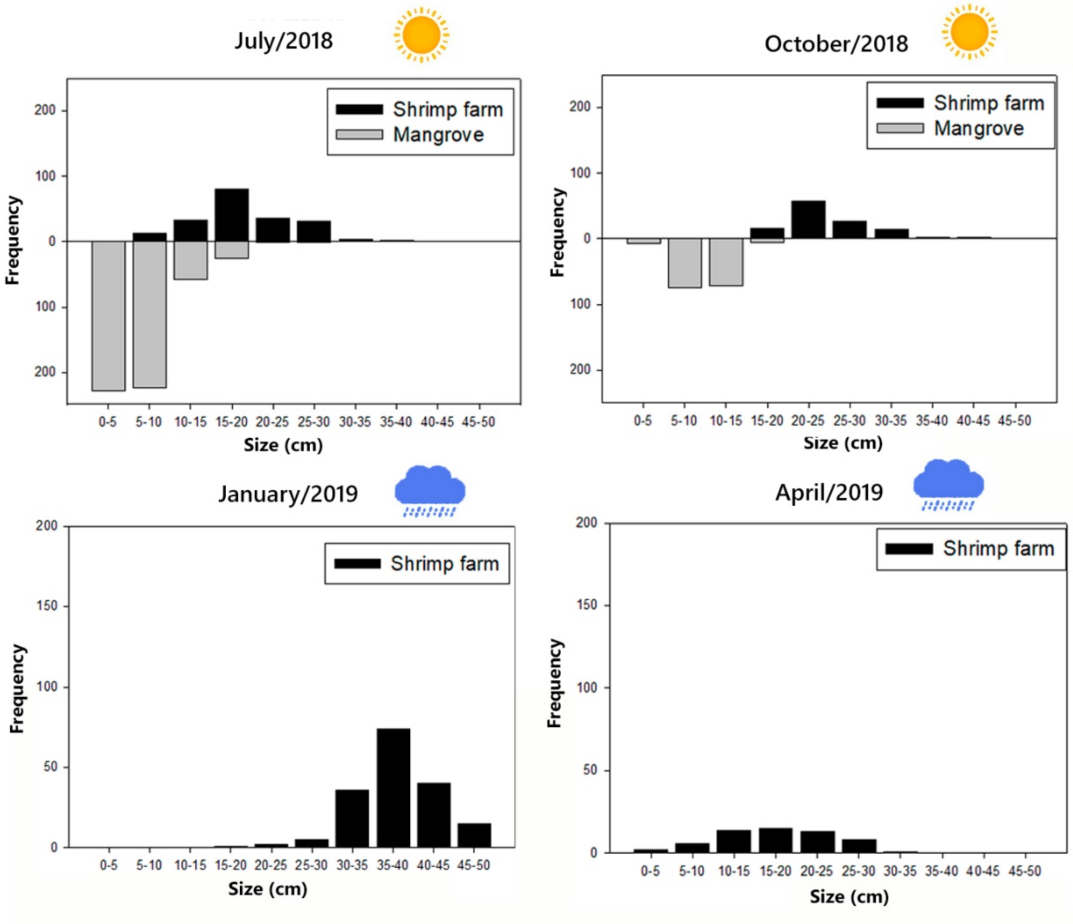


Figure 3. Size class frequency of the umbrella diameter (cm) of the invasive jellyfish *Cassiopea andromeda* in a shrimp farm and in semiarid mangroves located on the tropical Brazilian coast in the Western Atlantic Ocean. Data were produced during both dry and rainy seasons.

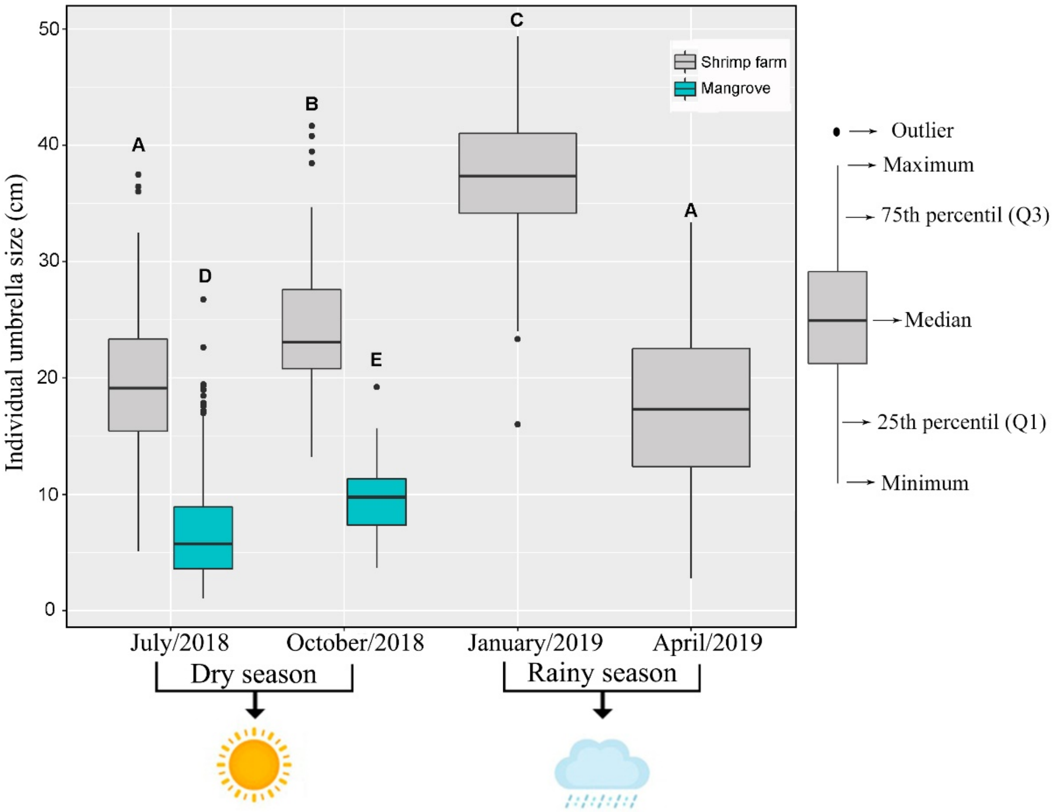


Figure 4. Seasonal variation in the umbrella size of the invasive jellyfish *Cassiopea andromeda* in a shrimp farm and in semiarid mangroves located on the tropical Brazilian coast in the Western Atlantic Ocean. Data were produced during dry (July/2018 and October/2018) and rainy seasons (January/2019 and April/2019). Different letters above the box plots indicate statistically different groups assessed with the use of a two-way analysis of variance and Tukey's multiple comparison test.

Cluster analysis and PCA revealed two distinct groups (Figs. 5 and 6). In the PCA, the first two axes explained most of the variation in the environmental data (76%) (Fig. 5). Axis 1 (42%) was negatively correlated with temperature (r = -0.15), pH (r = -0.35), and salinity (r = - 0.41), and positively correlated with TN (r = 0.42), TP (r = 0.53) and chl-a (r = 0.45). On the other hand, axis 2 (34%) was negatively correlated with chl-a (r = -0.14), and positively correlated with temperature (r = 0.67), salinity (r = 0.23), TN (r = 0.50), TP (r = 0.32) and pH (r = 0.33). Group I was characterized by higher values of TN, TP and chl-a, and generally smaller jellyfish. Group II presented the exact opposite trend, and was composed of shrimp farm samples only (Figs. 5 and 6).

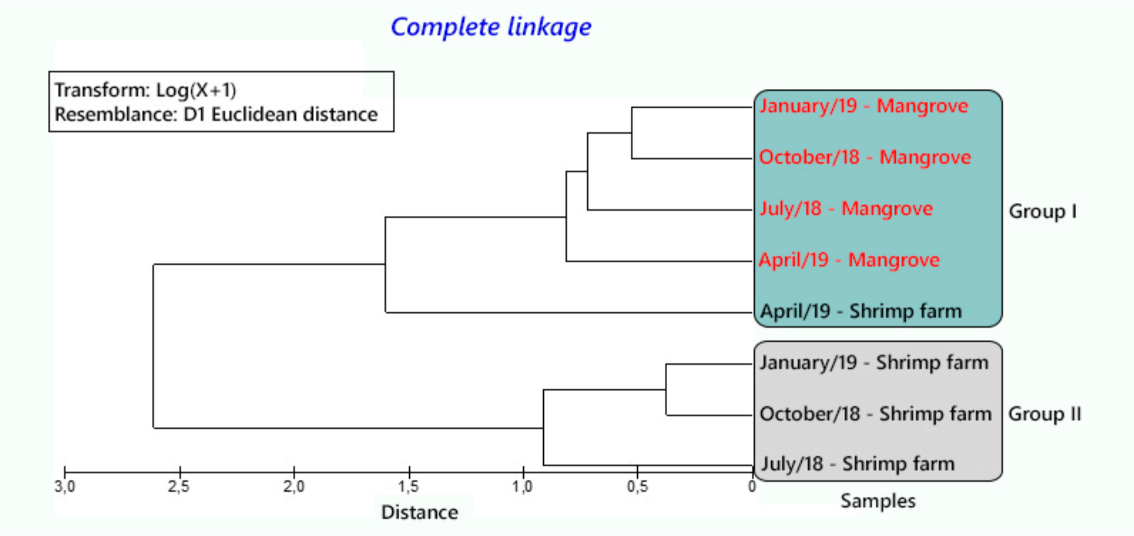


Figure 5. Cluster analysis performed on six environmental parameters (temperature, salinity, pH, total nitrogen, total phosphorus and chlorophyll-*a*) measured at a shrimp farm and adjacent semiarid mangroves containing invasive *Cassiopea andromeda* populations. Both sites were located on the tropical Brazilian coast in the Western Atlantic Ocean.

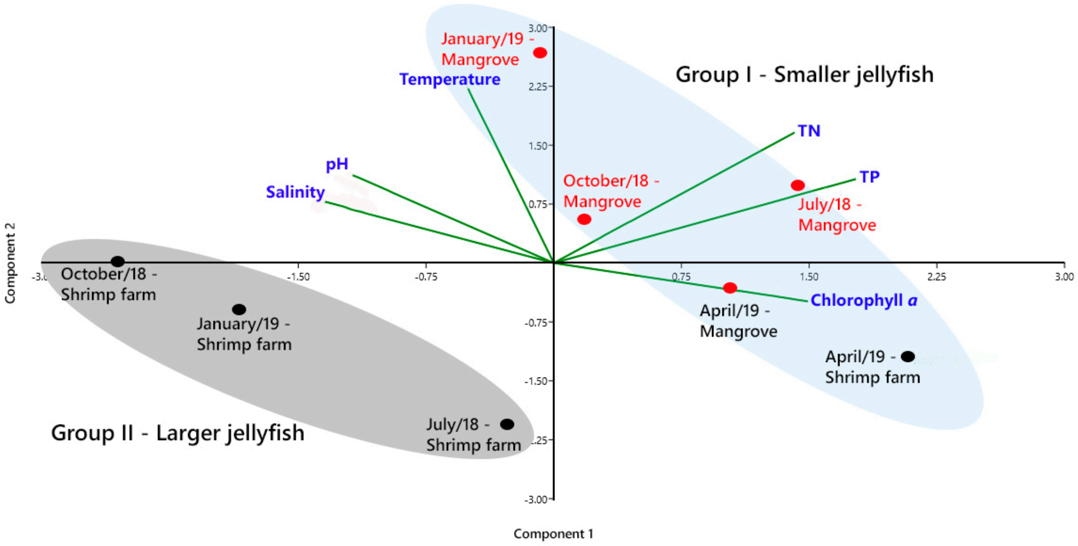


Figure 6. Principal component analysis (PCA) analysis of spatial and temporal variation in environmental parameters (temperature, salinity, pH, total nitrogen-TN, total phosphorus-TP and chlorophyll-*a*), and the umbrella size of the invasive jellyfish *Cassiopea andromeda* in a shrimp farm and semiarid mangroves located on the tropical Brazilian coast (Western Atlantic Ocean).

4. DISCUSSION

This work investigated if the invasive jellyfish *C. andromeda* is more adapted to the artificial shrimp farm environment than their typical mangrove habitat by assessing if they present more stable populations and grow to larger umbrella sizes. Our findings show that *C. andromeda* populations are similarly abundant throughout rainy and dry seasons in the shrimp farm. For the mangroves, however, while populations are larger during dry season, they become absent during rainy season. Therefore, shrimp farm populations are relatively stable, while mangrove populations are seasonal and dominated by smaller jellyfish. As for size, shrimp farm jellyfish grew three times larger than those in the Brazilian semiarid mangroves, regardless of season.

The main reason for the population stability in the Brazilian shrimp farm is the stability of the physico-chemical environment. Mangroves are relatively unstable ecosystems (Hogarth, 2015), while shrimp farms are usually kept under controlled and stable conditions in order to optimize shrimp production (Yu et al., 2006). The semiarid mangroves were associated with a higher fluctuation in salinity, and reached a low value of 24.4 during the rainy season, which is much lower than the optimum range of 35–45 for *Cassiopea* jellyfish (Kristensen and Ypma, 1971; Klein et al., 2016b). This coincided with the disappearance of the jellyfishes in the mangrove, and with the high volume of rainfall (546 mm month-^{1}), which was the highest for the area in the past decade (FUNCEME, 2019). The rain could have transported the jellyfish in the mangrove downstream, but the study area is a bar-built and closed estuarine ecosystem with no connection to rivers. Therefore, transport of jellyfish was prevented and this very likely caused relevant mortality associated with low salinity. However, *Cassiopea* polyps are more resistant and likely to survive, which could explain repopulation of medusae in the dry season.

The hypersaline condition (32-47) in the mangroves during dry season and in the shrimp farm during both seasons was likely favorable for population maintenance. Temperature also plays a major part, as our results show that it was lower in the shrimp farm, not exceeding 32 °C, and usually stable with low intra-annual variation (28.6 to 31.5 ºC). This temperature range is considered ideal for the growth and development of *Cassiopea* spp. (Fitt and Costley, 1998; Klein et al., 2016; Newkirk et al., 2018; Aljbour et al., 2019). However, during the rainy season in the mangrove, temperature reached values higher than 34°C which is the threshold for bleaching and thermal stress in the jellyfish (McGill and Pomory, 2008). Higher temperatures such as these have been found to increase jellyfish mortality rates (Fitt and Costley, 1998; Klein et al., 2016b; Newkirk et al., 2018; Aljbour et al., 2019).

The populations of *C. andromeda* in the shrimp farm and semiarid mangroves are composed only of females (Thé et al., in press). This suggests that they have a low genetic variability (Morandini et al. 2017) that is associated with a higher susceptibility to negative impacts provoked by environmental instability (Le Roux and Wieczorek, 2008). A similar case was reported for *C. andromeda* in Cabo Frio (subtropical Brazil), which had a population composed only of males that disappeared after changes in temperature and salinity (Morandini et al., 2017). Therefore, the mangrove physico-chemical instability associated with the synergistic effects of salinity reduction and temperature increase during rainy season may have contributed to the disappearance of jellyfish. The aggregated distribution and low mobility of *C. andromeda* emphasizes the importance of abiotic parameters, which are often key drivers for this type of disappearance, and spatial distribution pattern (Legendre and Fortin 1989).

Our findings also show that *C. andromeda* grows to larger sizes in the shrimp farm throughout all seasons. This can be attributed to environmental stability and organic matter input. Nutrient and chl-a concentration were, unexpectedly, higher in the mangrove than at the shrimp farm. A possible explanation for higher growth in less eutrophic conditions is that nutrient concentrations in the semiarid mangroves may have been excessive. Total phosphorus (TP) in the shrimp farm and mangroves ranged from 0.3–1.8 and 1.8–2.8 µM, respectively. Stoner et al. (2011) suggested that the highest density of *Cassiopea* spp. is found when TP is lower than 1.5 µM, and there is evidence that nutrient intake is reduced when TP exceeds 2.0 µM (Todd et al., 2006).

It is likely that organic matter availability is likely a much stronger predictor for jellyfish fitness and growth than nutrients because *Cassiopea* spp. are efficient osmotrophs (McGill and Pomory, 2008; Welsh et al., 2009). Brazilian shrimp farms are notoriously intense producers of dissolved and particulate organic matter (Sousa et al., 2006; Venekey and Melo, 2016), which would promote a constant, aseasonal, and intense heterotrophic behavior in *Cassiopea* spp. The importance of heterotrophy (predation and/or osmotrophy) has been widely shown for several cnidarians, including reef-building corals (Grottoli et al., 2006; Houlbrèque and Ferrier-Pagès, 2009; Mies et al., 2018), pelagic jellyfish (McCloskey et al., 1994; Purcell et al., 2007; 2012), and also *Cassiopea* spp. (Pierce et al., 2005; McGill and Pomory, 2008; Banha et al., submitted). While the photoautotrophy performed by the symbionts may provide the host with a significant amount of carbon (Muscatine and Porter, 1977), photosynthetic products present a typically low nitrogen and phosphorus content, which are essential for protein synthesis (Battey and Patton, 1986; Ferrier-Pagès et al., 2003). Therefore, besides physicochemical stability, heterotrophic feeding may explain why the *C. andromeda* in the shrimp farm are among the largest ever recorded at 49 cm (of umbrella), unlike their typical size of less than 15 cm worldwide (Niggl and Wild, 2010; Stoner et al., 2011, 2014a,b; Zarnoch et al., 2020). However, a more robust experimental approach, possibly using stable isotopes or fatty acid markers, is required for confirming the relevance of heterotrophic input.

Research on upside-down jellyfish (*Cassiopea* spp.) has increased in recent years because it is considered a model organism for invasion, symbiosis, and climate change investigations (Odhera et al., 2018; Djeghri et al., 2019). Within these contexts, the major contribution from our findings is showing that nearshore aquaculture facilities provide stable conditions that stimulate *Cassiopea* growth at population and individual levels, thus aiding the invasion process. In addition, we present baseline information on the seasonal dynamics of *Cassiopea* populations, and also highlight that *Cassiopea* may also serve as a relevant model organism for trophic investigations. Nonetheless, given the inherent variability in jellyfish populations, more intensive and long-term ecological research programs are required to understand the spatial and temporal dynamics of the invasion processes.

5. ACKNOWLEDGEMENTS

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