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Understanding *Cassiopea andromeda* (Scyphozoa) Invasiveness in Different Habitats: A Multiple Biomarker Comparison

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Abstract: A dual nutrition mode (i.e., mixotrophy) can be advantageous for alien species in a new environment. In Cearà (Brazil), the symbiotic jellyfish *Cassiopea andromeda* is rapidly spreading under diverse environmental conditions across natural and human-altered coastal habitats, such as mangroves and shrimp farms. Here we report on the trophic ecology of the alien upside-down jellyfish sampled in these two contrasting coastal habitats during the dry (July–October) and rainy (January–April) seasons, investigated by means of organic biomarkers (lipids, carbohydrates) and bulk tissue stable isotope ($\delta^{15}N$ and $\delta^{13}C$) analyses. Total lipid content of jellyfish gonads was generally higher in shrimp farms, whereas no significant difference in carbohydrate concentration was found in jellyfish tissues from the two different habitats. Similarly, there were no significant differences in the $\delta^{15}N$ values of jellyfish tissues from the two contrasting habitats, whereas the $\delta^{13}C$ values were higher in jellyfish from shrimp farms. Overall, the higher carbon-enriched value in aquaculture ponds supports the hypothesis of differences of available food sources compared to the natural mangrove habitats, where food availability exhibits a stronger seasonality. In fact, aquaculture ponds are characterized by human-driven regular food supply, leading to more stable trophic conditions and to enhanced growth, lipid production, and gonadal output of *C. andromeda* jellyfish. This investigation may contribute to predicting how *Cassiopea* mixotrophy may contribute to explaining its differential success in different habitats.

Keywords: biochemical tracers; lipids; carbohydrates; stable isotopes; non-indigenous species

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1. Introduction

Anthropogenic pressures, such as overfishing, eutrophication, aquaculture, alien species introduction, and urbanization as well as climate change, have been proposed as multiple interacting drivers of increasing jellyfish populations worldwide [1]. Jellyfish outbreaks gain even more attention when considering invasive species and their ecological and socioeconomic impacts [2]. Invasiveness is the sum of synergic traits such as environmental tolerance, trophic plasticity, and life history strategies, and has been considered one of the most relevant aspects of ecosystem transformation during the last decades [2,3]. Understanding the trophic ecology of invasive organisms is thus essential to understanding their potential impact on the coastal ecosystems and, hence, having quantitative information for actions for their control or exploitation. The upside-down jellyfish *Cassiopea andromeda* [4] is commonly found in shallow-water ecosystems, such as mangroves, coral reefs, and seagrass beds as well as in aquaculture facilities, and displays frequent population outbreaks [5–7]. In addition, it has been increasingly recorded as a non-indigenous, outbreak-forming species across different countries [8–11]. *C. andromeda* has a relatively sessile behavior (epibenthic jellyfish), resting upside-down on the benthos to expose its endosymbionts to the light in calm waters. It is characterized by a mutualistic association with dinoflagellate microalgae (Symbiodiniaceae), which are able to adapt to different light conditions and provide the jellyfish with carbohydrates and lipids of photosynthetic origin, in return for a sheltered area with a regular supply of inorganic molecules [12–14]. The possibility of relying on different energy inputs (i.e., photosynthates from symbionts and heterotrophic input) allows *C. andromeda* to adapt to different environmental conditions with cascading consequences on primary productivity, nutrient cycling, and local food webs as observed in other symbiotic jellyfish species [15]. The study of animal diet (heterotrophic input) has been widely applied to understand the metazoan trophic interactions in food webs [16–20]. Many studies investigating the trophic position of several jellyfish species rely on direct approaches such as gut content [21]. However, this methodology delivers inaccurate or incomplete information, and discerning between autotrophic and heterotrophic energy inputs outside controlled experimental conditions (i.e., aquaria) is certainly a major issue [22–27]. Indirect combined approaches, such as stable isotopes, C:N ratios, lipid, carbohydrate, and fatty acid analyses, may help to disentangle the puzzle of direct diet and food capture rate observations, as these tools may integrate seasonal energy inputs as well as differences between different habitats or ecozones [28], and may also be used to discern the dominance of autotrophic or heterotrophic inputs in mixotrophic species [18,29]. This may be the case with *C. andromeda*. A combination of biomarkers (δ^{13}C and δ^{15}N, fatty acids, and lipid–carbohydrate storage) has been already used to understand the trophic position and the nutritional condition of both Semaeostomeae and Rhizostomeae jellyfish species such as *Aurelia aurita*, *Stomolophus meleagris*, and *Cyanea nozakii* [30]; *Chrysaora melanaster* [31]; *Catostylus mosaicus* [27]; *Pelagia noctiluca* [19,32,33]; and *Mastigias papua* [15]. It has thus been demonstrated to be a reliable and robust approach, especially in the understanding of jellyfish invasiveness potential under contrasting coastal habitats or environmental conditions. As elsewhere in the world, Brazilian mangroves are increasingly impacted by construction of harbors, city expansion, or multiple economic activities such as shrimp farms, causing a deep impact on biodiversity and the population dynamics of wild organisms [34–36]. The shrimp farm expansion on the Brazilian coast has oversimplified the functioning of the ecosystem, mainly impacting mangroves which have been eradicated to build up controlled ponds for shrimp aquaculture [35]. These ponds are deeply transformed, with much higher nutrient and particulate organic matter concentration compared to the mangrove areas [34]. Recently, *C. andromeda* was found to possess different invasiveness and physiological potentials in natural (mangrove) and artificial (aquaculture shrimp facility) habitats [7,10]. A greater number of jellyfish was found in the mangroves during the dry season (July: $n = 546$; October: $n = 158$) compared to the shrimp farms (July: $n = 207$; October: $n = 119$). However, while the abundance of *C. andromeda* was nearly stable in shrimp farms in both seasons, jellyfish in the mangroves disappeared during the rainy season. Moreover, *C. andromeda* in shrimp farms were three times larger (24.7 ± 5.8 cm) than those found in mangrove habitats (8.2 ± 3.4 cm) [37]. In the present study, we investigated the trophic ecology of *C. andromeda* in the two contrasting habitats (mangroves and shrimp farms), using a combination of analyses of macromolecules (lipids, carbohydrates, and total fatty acids) and stable isotopes (δ^{15}N and δ^{13}C), with the final aim of understanding how its nutritional condition is linked to its differing invasion success and population stability in the two environments.

2. Materials and Methods

2.1. Study Area

The study was carried out on the coast of Ceará state (Figure 1), Southwestern Atlantic (Brazil). In this area, the estuarine surface temperature is high, with a low interannual variability (27 to 34 °C) [37]. It is known as a semi-arid tropical region, where rainfall is scarce (500–1000 mm/per year) [38], with two distinct and well-defined periods: a rainy season (first half of the year, January–June) in which 90% of the precipitation occurs, while only 10% of the annual precipitation comes during the dry season (second half of the year, July-December) [39]. In the dry period—due to a combination of low rainfall, high insolation, high water residence time, and higher evaporation rates of low-latitude, shallow-water estuaries—the hypersaline condition (salinity higher than the sea) (e.g., >37 ppt) is an extreme and seasonal environmental feature [40]. The sampling was carried out in two localities 20 km apart from each other (Figure 1). In the first study area (Acaraú—2°49′59.12″ S/40°7′17.07″ W), the jellyfish *C. andromeda* were sampled inside the water canals of a shrimp farm (Sf) (Figure 1C). In the second area (Itarema—2°53′2.92″ S/39°54′41.95″ W), the jellyfish were sampled in a semi-enclosed, shallow-water estuary about 0.5–1 m depth, characterized by mangrove forests (M) and with no influence of shrimp farm activities (Figure 1D). Environmental parameters (temperature, salinity, and pH) as well as total nitrogen (TN) and phosphorous (TP) were measured for the two habitats [37] and are reported in Table 1. Sampling was carried out in July and October 2018 (dry period) and in January and April 2019 (rainy period).

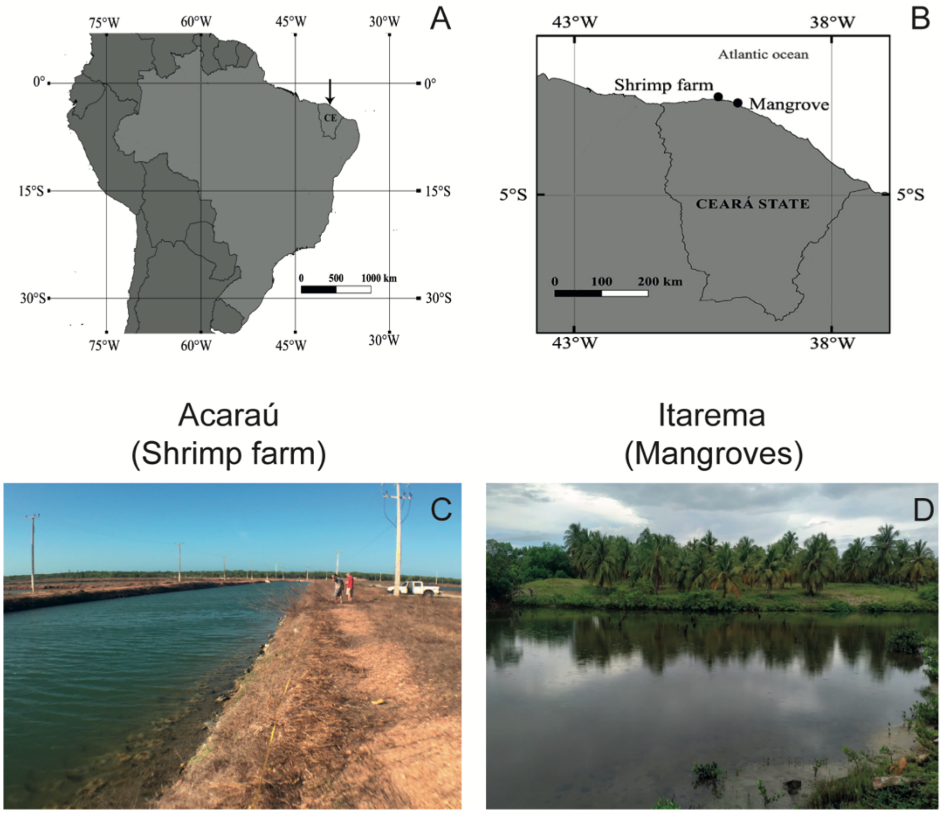

Figure 1. Study area in the Cearà State (northeastern Brazil, SW Atlantic) (**A**) with highlights indicating sampling stations (**B**) in a shrimp farm (Acaraù) (**C**) and a mangrove-estuarine ecosystem (Itarema) (**D**).

Table 1. Environmental parameters adapted from [37].

	Temperature °C	**pH**	**Salinity**	**TN (µM)**	**TP (µM)**
Shrimp farm	27.8–31.5	7.9–8.4	31.6–46.2	13–42	0.3–1.8
Mangroves	30.4–34	7.9–8.3	24.4–46.9	42–64	1.8–2.8

2.2. Sample Collection and Preservation

Five *C. andromeda* specimens were collected for each survey (July 2018; October 2018; January 2019; April 2019) from the shrimp farm. In mangrove stations, the jellyfish population is subject to seasonality and thus specimens were found only in the dry period (*n* = 5 per survey). Measurements of the umbrella diameter were made using a caliper before body parts were separated to be used for biochemical analyses. The *C. andromeda* specimens used for this study ranged between 8 and 20 cm in diameter in both locations and during the different sampling times. All sampled specimens were then separated into oral arms, umbrella, and gonads for the study of biomarkers (carbohydrates, lipids, organic matter, FA) and for stable isotope (SI) analysis (Table 2). Immediately after excision, all body parts were frozen (−20 °C). After the freezing process, samples were lyophilized and ground into a fine powder using an agate mortar and pestle (ideal for smashing frozen samples) for biomarker analysis.

Table 2. Summary of analysis performed on the upside-down jellyfish *C. andromeda* in contrasting coastal environments (shrimp farm and mangroves). N = number of samples; J = July; O = October; Ja = January; A = April; SF = shrimp farm; M = mangroves; U = umbrella; OA = oral arms; G = gonad. * For the last sampling date in the Sf we used only three samples for the gonads.

Analysis	Total N	N Replicates/Treatment	Month and Area	Body Part
Stable isotopes	18	3	J (SF, M); O (SF, M); Ja (SF); A (SF)	U
Organic matter	88	5 *	J (SF, M); O (SF, M); Ja (SF); A (SF)	U, OA, G
Carbohydrates	60	5	J (SF, M); O (SF, M); Ja (SF); A (SF)	U, OA
Lipids	88	5 *	J (SF, M); O (SF, M); Ja (SF); A (SF)	U, OA, G
Fatty acids	10	5	O (SF, M)	G

2.3. Biomarker Analysis

2.3.1. Organic Matter

Approximately ~7 mg of each sample (a total of 30 specimens considering the 3 different body parts; for the last sampling date in the Sf we used 3 samples for the gonads: *n* = 88) was weighed as DW (after drying for 48 h at 60 °C) and was burned in a muffle furnace for 5 h at 450 °C. Organic matter content (AFDW, i.e., ash-free dry weight) was then calculated as the difference between the DW and the ash weight [41]. AFDW was quantified for all the different body parts of all the specimens of the whole sampling period (*n* = 88, Table 2). AFDW was used to normalize lipid and carbohydrate data [18].

2.3.2. Total Carbohydrate Content

Total carbohydrate content was determined in the oral arms and umbrellas, where symbionts are mostly found. Oral arms and umbrellas (*n* = 5) were sampled for the shrimp farm (4 sampling dates) and the mangroves (2 sampling dates) (*n* = 60, Table 2). Approximately 6–7 mg of each sample DW was homogenized in 3 mL of distilled water following [42], adapted for cnidarians by [43]. (D)-Glucose was used as a standard and a calibration line was made prior to the sample's analysis. Carbohydrate concentrations were expressed in µg carbohydrates/mg AFDW.

2.3.3. Total Lipid Content

The total lipid content was quantified in five samples of gonads, oral arms and umbrellas in two locations and on four sampling dates (*n* = 88, Table 2). For the last sampling date in the Sf we used only three samples for the gonads. Total lipid content was quantified following [18] for jellyfish. Approximately 20 mg of umbrellas, ~10 mg of oral arms and 5 mg of gonads DW were weighed with a precision balance. The tissue was ground and the powder was resuspended in 3 mL of chloroform:methanol (2:1) following [44] (colorimetry) transformed by [45]. A calibration line was made using cholesterol as a standard and the final reaction was performed using vanillin. Measurements were analyzed with a spectrophotometer (UV mini1240, Shimadzu, Kyoto, Japan). The lipid content was expressed in µg lipid/mg AFDW. The total fatty acids (FA) of jellyfish from the two habitats were analyzed only in the last sampling time (October) in which both populations were present due to a lack of DW from the July sampling; thus, the methodology and results are reported in the Supplementary Materials.

2.3.4. C:N Ratios, δ^{15}N and δ^{13}C Composition

Both stable isotope (δ^{15}N and δ^{13}C) composition and the carbon/nitrogen (C:N) mass ratio were assessed in three umbrella samples [46] collected at the shrimp farm and the mangrove estuarine ecosystem on each sampling date ($n = 18$, Table 2). Approximately 1.8–2 mg of DW was introduced in tin capsules to run each sample separately, and analyses were performed using the Elementar IsoPrime 100 isotope ratio–mass spectrometry (IR–MS) instrument (IsoPrime Ltd., Cheadle Hulme, UK) coupled to an N–C–S elemental analyzer (Elementar Vario Pyro Cube EA CNS; Elementar Analysensysteme GmbH, Hanau, Germany). The elemental analyzer combustion tube was at 1020 °C and the reduction tube was at 850 °C. Helium (He) was at 230 mL/min and O_2 was at 35 mL/min. The CO_2 sample gas stream was diluted with additional helium and the CO_2 and N_2 reference gases at 8 and 4 bars, respectively. The reference materials were Sulfanilamide for determination of elemental composition, Glucose (BCR-657) and Polyethylene (IAEA-CH-7) for determination of the stable carbon isotopic values (δ^{13}C), and Potassium Nitrate (USGS32) and Ammonium Sulfate (USGS25) for determination of the stable nitrogen isotopic values (δ^{15}N).

The δ^{13}C and δ^{15}N values were calculated relative to Peedee Belemnite (PDB) and Vienna Pee Dee Belemnite (VPDB) for carbon and atmospheric N_2 (air), respectively, and expressed in the δ notation as parts per mille (‰).

2.3.5. Statistical Analysis

Data were tested for normal distribution by the Shapiro–Wilks test using Statistica 7.0 software. The whole dataset did not follow a normal distribution so stable isotopes, total carbohydrates and total lipids were analyzed using the nonparametric Mann–Whitney U test and Kruskal–Wallis test (Statistica 7.0 software) and also Dunn's post hoc test (Past 4.03). Plots were generated using the "ggplot2" package.

3. Results

3.1. Organic Matter

The gonads showed the highest AFDW content (>60%) in all the sampling dates compared to the oral arms and umbrellas (Table 3). The AFDW from the gonads of *C. andromeda* jellyfish were significantly different between the shrimp farm and the mangroves (Kruskal–Wallis test: H = 14.46, $p < 0.05$). Dunn's post hoc test (Supplementary Materials, Table S1) showed that the differences between the two places occurred in July and October (2018).

Table 3. Organic matter content (%) in specimens from the shrimp farm (Sf) and mangroves (M) in different body compartments (umbrella, oral arms and gonads) during the sampling periods. Data represent mean ± SD.

Location	Month	Umbrella (%)	Oral Arms (%)	Gonads (%)
Sf	Jul	39 ± 2	40 ± 3	78 ± 7
M	Jul	39 ± 4	48 ± 2	63 ± 6
Sf	Oct	46 ± 13	42 ± 7	77 ± 1
M	Oct	52 ± 15	37 ± 7	79 ± 4
Sf	Jan	28 ± 2	28 ± 5	79 ± 3
M	Jan	absent	absent	absent
Sf	Apr	41 ± 4	44 ± 7	69 ± 1
M	Apr	absent	absent	absent

3.2. Total Carbohydrate Content

Overall, the Kruskal–Wallis test (H = 31.46, $p < 0.05$) and Dunn's post hoc test showed some significant differences (Figure 2, Table S2). Considering each month independently, in July, oral arm carbohydrate content was significantly different between the mangroves and the shrimp farm (Figure 2; $p < 0.05$; Table S2). Carbohydrate concentrations in oral arms did not differ significantly in the shrimp farm over the sampling period (Figure 2). In October, tissue differences were observed in both the shrimp farm and the mangroves, while in July this was true only in the mangroves. The jellyfish carbohydrate content of umbrella tissue and oral arms in the mangroves exhibited significant differences between July and October (Figure S1).

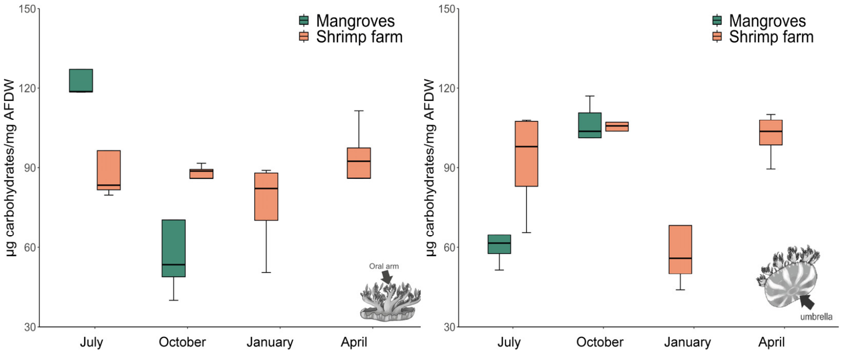

Figure 2. Carbohydrate content (μg carbohydrates/mg AFDW) of *C. andromeda* ($n = 60$) in oral arm tissues and umbrellas from shrimp farm (Sf) and mangroves (M) in Ceará State (Brazil, SW Atlantic).

3.3. Total Lipid Content

Throughout the surveys, there were significant differences in the lipid content of the gonad and umbrella tissues between the shrimp farm and the mangroves (Kruskal–Wallis test: $H_{gonads} = 14.73$ and $H_{umbrella} = 11.82$, $p < 0.05$). The results of Dunn's post hoc test are reported in Tables S3 and S4. The total lipid content of the gonads was higher in the shrimp farm during all the monitored period (Figure 3). In the umbrella tissues, the total lipid content was higher in the shrimp farm only in July (Figure 3). No significant differences were found in oral arm tissue throughout the sampling period.

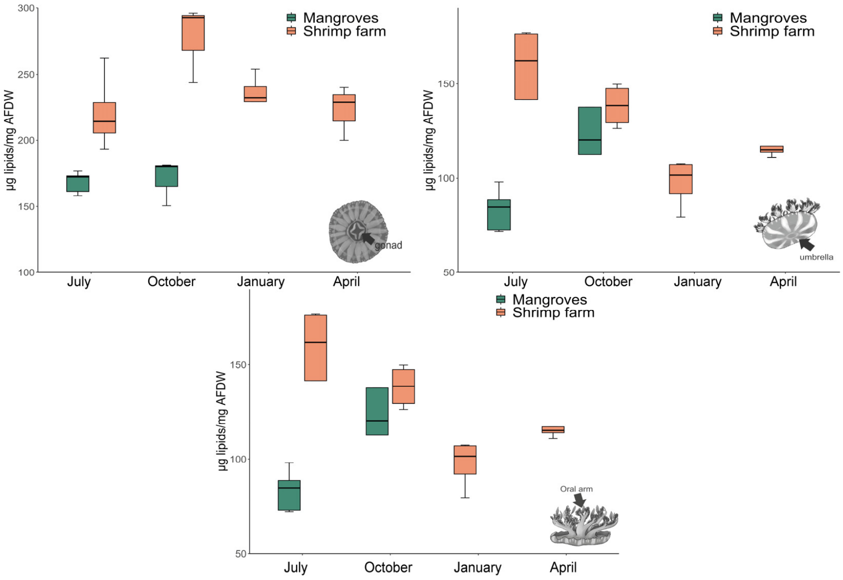

Figure 3. Total lipid contents (μg lipid/mg AFDW) of *Cassiopea andromeda* in gonad, umbrella and oral arm tissues ($n = 88$) from shrimp farm and mangroves in Ceará State (Brazil, SW Atlantic).

3.4. Stable Isotopes Analysis and C:N Ratio

The isotopic δ^{13}C values from umbrellas of *C. andromeda* jellyfish were significantly different between the shrimp farm and the mangroves (Kruskal–Wallis test: H = 14.59, $p < 0.05$) and ranged between −18.90 and −15.92‰ in the shrimp farm and between −19.75 and −17.61‰ in the mangroves. The results of the Dunn's post hoc test (Table S5) showed differences between the two places in July and October (2018), with δ^{13}C values significantly higher in jellyfish from the shrimp farm than those from the mangroves (Figure 4). There were no significant differences (Kruskal–Wallis test: H = 9.1, $p > 0.05$) between jellyfish from the two study areas in the δ^{15}N proportions throughout the seasonal cycle with values ranging between 2.3 and 4.59‰ and between 2.41 and 4.55‰ in the shrimp farm and the mangroves, respectively (Figures 4 and 5). Samples from different periods of the year and different locations showed clear separation into clusters (Figure S1).

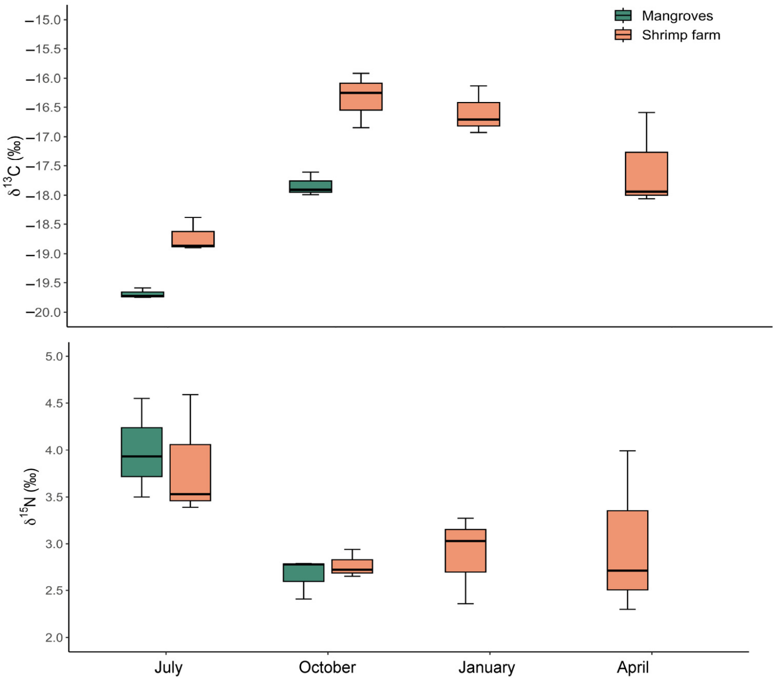

Figure 4. Boxplot representing δ^{13}C and δ^{15}N values of *C. andromeda* umbrella tissue from shrimp farm (Sf) and mangroves (M) in Ceará State (Brazil, SW Atlantic). Sample size (n = 18).

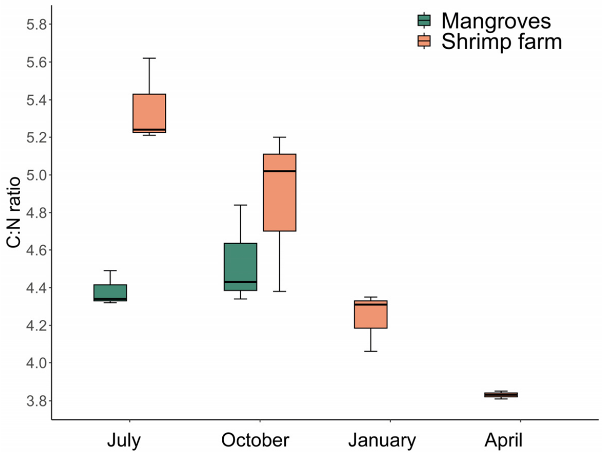

Figure 5. C:N mass ratio of *C. andromeda* umbrella tissue from shrimp farm (Sf) and mangroves (M) in Ceará State (Brazil, SW Atlantic). Sample size (n = 18). In January and April (2019), no *C. andromeda* jellyfish were found in the mangrove ecosystem.

C:N ratios (Figure 5 were significantly different between the shrimp farm (5.36 ± 0.2) and the mangroves (4.38 ± 0.09) in July. Over the sampling period they changed significantly in the shrimp farm from 5.36 ± 0.2 to 3.81 ± 0.05.

4. Discussion

In the present study, we used different trophic biomarkers to investigate the trophic ecology of the non-indigenous jellyfish *Cassiopea andromeda*, collected from an artificial aquaculture pond and a natural mangrove–estuarine habitat.

4.1. Nutritional Condition of Cassiopea andromeda

Within the different body compartments, gonads showed the highest amount of organic matter (AFDW) in both habitats and the difference between the two habitats was significant, with a higher lipid content in the shrimp farm. The environmental stability of the shrimp farm habitat, in terms of regular food supply for the white shrimp *Litopenaeus vannamei*, may be reflected by a nearly constant carbohydrate concentration in *C. andromeda* tissues over the year. In fact, despite the more remarkable fluctuations in salinity, nutrients, and temperature of the mangrove habitat [7,37], jellyfish tissues from mangroves revealed carbohydrate levels comparable to those from the shrimp farm medusae, except in July in the oral arms. This is the part of the jellyfish body with the highest density of microalgal symbionts [47], where higher quantities of photosynthates are produced and translocated to the host [24]. A higher level of translocation/production activity due to less turbid waters in the mangroves may explain the higher carbohydrate content in July. While carbohydrate content is nearly constant in all body compartments in the shrimp farm, in the mangroves it undergoes seasonal variations. In the oral arms it decreases from July to October, while in the umbrella we observe the opposite behavior; it increases from July to October, suggesting either a different rate of photosynthetic products in the two different tissues or a different allocation of resources that might be used for growth. The same behavior was observed for lipids in mangrove jellyfish, suggesting different energy allocation in different seasons. Compared to the specimens living in mangroves, a higher lipid content was detected throughout the whole study in the gonads of *C. andromeda* specimens from the shrimp farm. Individual jellyfish specimens of larger size were found throughout the year in the artificial structures (canals) of the shrimp farm, where the environmental conditions—forced by feed supply and aeration of the shrimp aquaculture farm—are more stable compared to the natural mangrove habitat ruled out by seasonal changes in environmental variables [37]. This is witnessed by the size of *C. andromeda* specimens, which is much larger in the shrimp farm (up to 49.2 cm of umbrella diameter) than in the mangroves (up to 26.7 cm in diameter) [37]. In shrimp farms, stable environmental conditions secure continuity of jellyfish growth throughout the year [7], paralleled by a high lipid storage in the gonads. The jellyfish disappeared just after the rainy season in the mangroves, whereas a stable jellyfish population with mature oocytes (as per [48]) was observed in the shrimp farm at the same time of the year [7]. Jellyfish growth could be promoted by increased nutrient availability [3,49] and the mixotrophic ability of *Cassiopea* spp. may modify benthic biogeochemical fluxes, acting as a sink of inorganic nutrients and affecting sediment microbial processes and oxygen consumption [50,51]. Surprisingly, [37] reported a higher amount of TN and TP in the mangrove estuarine system, where jellyfish specimens may achieve, on average, a smaller size. This may suggest that pulse inputs of high nutrient concentrations might not favorably sustain regular, i.e., vigorous jellyfish growth; conversely, a controlled and constant nutrient supply, such as on a shrimp farm, may be a better booster for jellyfish growth [49,52].

4.2. Trophic Strategy of Cassiopea andromeda

Cassiopea andromeda couples typical heterotrophic feeding based on zooplankton, POM (particulate organic matter), DOM (dissolved organic matter) and detritus, with an additional autotrophic energy supply from its endosymbiotic dinoflagellates [50,53,54]. In mixotrophic metazoans, stable isotope analysis and C:N ratios can contribute as nutritional indicators to unravel the predominant trophic strategy, as well as the nutrient exchanges between host and endosymbionts [15,55,56]. In our study, a significant difference was observed between the two environments, with δ^{13}C values lower in jellyfish tissues from mangroves (July: Sf −19; M −20; October: Sf −16; M −18). This may be reflected by the carbon local sources utilized. In fact, Brazilian mangroves are characterized by a high quantity of nutrients and POM is primarily produced by mangrove detritus, which represents the dominant carbon source [57]. The shrimp farm water is enriched with OM, nutrients, and detritus due to the constant amount of feed necessary for the shrimps' growth, which is eventually broken down along the food chain [58,59]. Jellyfish in the shrimp farm were more Carbon-enriched due to the different feed used for shrimp aquaculture in the study site [60–62]. Moreover, across the October, January, and April samplings, *C. andromeda* in the shrimp farm showed a general constancy in δ^{13}C and δ^{15}N values, underlying the maintenance of stable and controlled environmental conditions by the occurrence of the aquaculture facilities. However, regardless of the effort of the farm activities in buffering drastic seasonal changes, the prevalence of the trophic mode is still related to seasonal variations. As C:N ratios demonstrated, jellyfish in the shrimp farm seemed to move from an autotrophic–mixotrophic strategy (C:N 5.36 ± 0.23) to a more heterotrophic one at the end of the rainy season (C:N 3.81 ± 0.05). [15] reported a similar behavior in the symbiotic *M. papua*, where jellyfish populations showed instead different autotrophy/heterotrophy contributions based on the sampling location, in Palau [15].

The *C. andromeda* behavior may be due to a decrease in light intensity with the upcoming rainy season [39], but a constant presence of POM and nutrients is guaranteed in the shrimp farm. In specimens collected in mangroves, a shift in δ^{13}C, from July (δ13C: −20‰) to October (δ^{13}C: −18‰) was observed, together with a small increase in the C:N ratio and a significant decrease in δ^{15}N values, suggesting a possible predominancy of autotrophy. This might be explained by less turbid, i.e., more transparent waters, related to increased light irradiance and enhanced photosynthesis of symbiotic dinoflagellates, thus increasing the δ^{13}C value of the symbiotic association [63,64].

4.3. Why Did Cassiopea andromeda Disappear in the Mangroves?

Based on the measurements of carbohydrates and lipids conducted in this research, it appears that the steady availability of energy sources in various tissues enabled jellyfish in the shrimp farm to maintain a consistent energy supply for their growth and reproduction. We observed a higher proportion of saturated fatty acids in the shrimp farm jellyfish (SFAs = 46%) compared to the mangrove system jellyfish (SFAs = 35%) while a higher amount of polyunsaturated fatty acids (PUFAs) was found in the mangrove-related jellyfish. This may suggest a better quality in the origin of the food present in the estuary (C3 plants). However, due to the low number of samples, our data are not conclusive and additional studies are needed. As a result of *Cassiopea*'s nutritional condition, the jellyfish population is able to thrive and persist in this particular environment. On the contrary, jellyfish disappeared from the mangrove habitat at the end of the rainy season; the high turbidity of the water column during the concentrated rainfall of 2019 (546 mm/month, i.e., the largest monthly rainfall in 11 years) [37] reduced the amount of incoming light available for photosynthesis. Coupled with a drastic salinity decrease (24.4), high water turbidity may affect the autotrophic potential of *Cassiopea*, overshooting its adaptability to light conditions [14] and eventually leading to its seasonal disappearance from the natural mangrove habitat.

5. Conclusions

Disentangling the relative contribution of autotrophy and heterotrophy may be challenging in a symbiotic jellyfish such as *Cassiopea andromeda*. Here, we shed light on the differences in the nutrition mode in a natural vs. human-made environment. We show that *C. andromeda* seems strongly controlled by the seasonal variability of abiotic factors in the mangrove system, notwithstanding its ecophysiological plasticity and its mixotrophic potential. On the contrary, coastal systems modified for food production and subsidized by man-controlled inputs of energy and organic matter, such as shrimp aquaculture farms, may better support a stable jellyfish population. This suggests that human-controlled, modified coastal habitats may enforce the capability of *C. andromeda* to maintain populations in exotic areas, using artificial marinas and other coastal habitats as stepping stones for a worldwide bioinvasion.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/w15142599/s1, Figure S1: Plot of δ^{15}N versus δ^{13}C values of *Cassiopea andromeda* umbrella tissue; Table S1: Dunn's post hoc of AFDW; Table S2: Dunn's post hoc of total carbohydrates; Table S3: Dunn's post hoc of total lipids in gonads; Table S4: Dunn's post hoc of total lipid in umbrellas; Table S5: Dunn's post hoc of isotope values; Table S6: List of *C. andromeda* gonad fatty acids.

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