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Population Structure and Seasonal Variability of two Luciferid Species (Decapoda: Sergestoidea) in the Western Gulf of Mexico

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Abstract: The population ecology of luciferids has been scarcely studied. This study examined the distribution and population parameters of *Belzebub faxoni* and *Lucifer typus* in the western Gulf of Mexico. Samples were collected using a Bongo net at 82 sampling stations during three periods (July, January, and October–November). Abundance data of species were subjected to a regression tree analysis to determine the main factors affecting their distribution. In addition, total length data of individuals were fitted to a logistic equation to estimate the size at first maturity. Food availability was the key factor affecting the distribution of *B. faxoni*, which exhibited its highest abundance over the inner shelf. In contrast, *L. typus* avoided low salinity waters (<35.9 psu), and its highest densities were found over the slope and oceanic areas. The sex ratio in *B. faxoni* was always biased towards females, but *L. typus* showed variable sex proportions. Several hypotheses attempting to explain these disparities are discussed. Size structure in *B. faxoni* favored small individuals in summer, the reproduction peak. In contrast, the *L. typus* population was always dominated by large individuals, probably transported by currents from the main hatching sites. Size at first maturity was higher in *L. typus* (females: 8.16 mm; males: 8.63 mm) than in *B. faxoni* (females: 6.53 mm; males: 6.74 mm). Information here provided may help to better understand the population dynamics of these species.

Keywords: *Belzebub*; *Lucifer*; sex ratio; size structure; size at first maturity; population ecology

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1. Introduction

Species of the family Luciferidae (Decapoda) are typical components—sometimes dominant—of plankton communities, commonly found in tropical and subtropical epipelagic waters from all oceans [1]. Luciferids are small shrimps of about 9 to 13 mm total length in the adult stage [2]. They spend their entire life cycle as plankton and have developed several morphological adaptations to remain in the pelagic environment. These animals are characterized by an extremely compressed body, a reduction of mouthparts and first and second pereopods [3,4]. The numerous setae on the thoracic and abdominal appendages and flabellate uropods enable luciferids to increase frictional resistance to sinking and remain afloat in the water.

Luciferids play a vital role in marine and estuarine food webs. They consume not only zooplankton prey of moderate size and even their own eggs [5,6], but also phytoplankton, as revealed by laboratory experiments [7]. In turn, they constitute significant food items for commercially or ecologically important fishes, shrimps, and even whale sharks [8–11]. Furthermore, luciferids and other related shrimps are used in the food manufacturing industry in the production of fermented pastes and sauces in some countries of Southeast Asia [12].

All luciferid species exhibit sexual dimorphism, evident in mature developmental stages of growth. Adult males are characterized by a sex organ called the petasma, located on the first pair of pleopods, two ventral processes on the sixth abdominal somite, and a prominent process on the telson [2–4,13]. In females, the sex organ, the thelycum, is located at the base of the third pair of pereopods. Uniquely among dendrobranchiate shrimps, luciferid females hold their eggs at the base of the third pair of pereopods and remain attached until eclosion, thus reducing offspring mortality. After eclosion, individuals have several developmental stages until maturity: nauplius, protozoea, zoea, mysis, and postlarva (juvenile) [5,13].

Luciferidae was considered a monotypic family in the superfamily Sergestoidea [14] until the phylogenetic analysis of Vereshchaka et al. [4], who recognized a second genus named *Belzebub* Vereshchaka, Olesen & Lunina, 2016, in addition to the former described genus *Lucifer* Thompson, 1829. From the seven currently accepted species [15], only *B. faxoni* (Borradaile, 1915) and *L. typus* Milne-Edwards, 1937 coexist in the western Atlantic including the Gulf of Mexico [4,16]. General distribution of *L. typus* comprises oceanic waters of tropical and temperate zones around the world, but it is not common to find the near the coast [17,18]. By contrast, *B. faxoni* is only found in the Atlantic Ocean with a more restricted distribution than *L. typus*, and it is especially abundant in the neritic and coastal areas of eastern America and western Africa [4,17].

The Gulf of Mexico is a semi-closed basin that provides goods and services for the social and economic development of Mexico, Cuba, and the United States. The gulf includes a great variety of ecosystems, harbors high biological diversity, supports important fisheries, and is a region of obligatory transit between the ports of the gulf facing the Atlantic. Despite their ecological relevance, studies targeting luciferids in the Gulf of Mexico are very scarce. Some works refer to the distribution of species [16] and others to the population characteristics of *B. faxoni* [5,19]. This study jointly addresses the population ecology of *B. faxoni* and *L. typus* through the analysis of the factors affecting their distribution and the main population parameters in the neritic and oceanic waters of the Mexican western Gulf of Mexico.

2. Materials and Methods

2.1. Study Area

The study area encompassed neritic and oceanic waters of the western Gulf of Mexico and was bounded by the 95° meridian to the east and the coastline of the Mexican state of Tamaulipas to the west (Figure 1).

Upper circulation in the Gulf of Mexico is dominated by the Loop Current, a warm ocean current that enters the gulf through the Yucatan Channel and flows out through the Florida Straits. The Loop Current sheds large anticyclonic eddies (200 to 400 km) that move westward into the western gulf and eventually dissipate near the Mexican slope [19]. The time interval between eddy detachments from the Loop Current is highly variable, ranging from 3 to 17 months, but physical causes of the shedding process are not well understood [20,21].

Over the shelves, surface circulation is affected by seasonal variations of wind stress and continental water discharges. Currents over the western shelf are mainly driven by the wind and run toward the southeast from September to March and toward the northwest from May to August [22]. The marine coastal zone in the western gulf is influenced by the runoff of the Bravo, San Fernando, Soto la Marina, and Pánuco Rivers as well as the Madre and Tamiahua coastal lagoons.

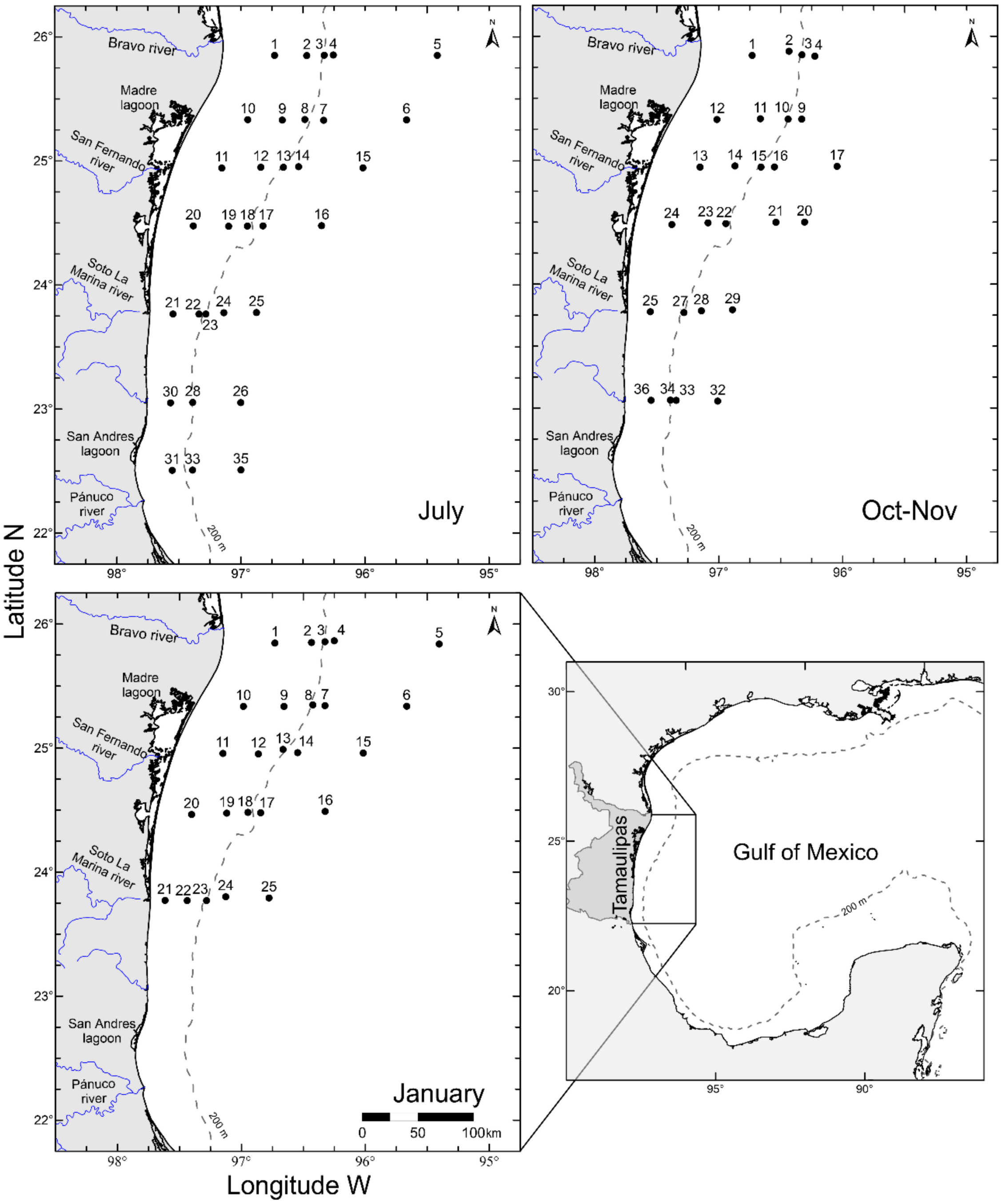

Figure 1. Study area and location of sampling stations during the three sampling periods.

2.2. Sampling and Laboratory Analysis

Samples analyzed in this study were collected within the framework of the monitoring program called "Environmental Framework of the Oceanographic Conditions in Mexico's Northwestern Exclusive Economic Zone in the Gulf of Mexico (MARZEE)". Zooplankton sampling was carried out during three oceanographic cruises named MARZEE 1 (2 to 7 July 2010), MARZEE 2 (27 to 31 January 2011), and MARZEE 3 (26 October to 2 November 2012). A total of 82 oceanographic stations located in both neritic and oceanic zones were sampled using a Bongo net (333 and 505 µm mesh) equipped with two flowmeters to estimate the volume of filtered water. Zooplankton samples were collected by oblique tows, and sampling depth varied between 15 and 200 m according to bottom depth. Samples were fixed with 4% formalin neutralized with sodium borate. At each oceanographic station, records of temperature and salinity were taken using a SBE 9Plus CTD profiler, and measurements of the chlorophyll concentration were also taken with a Wet Labs FLRTD sensor adapted to the profiler. These measurements were taken from the surface up to 1500 m depth, depending on the bottom depth.

Zooplankton biomass was estimated as wet weight (g 100 m^{-3}), using the samples obtained with the 333 µm mesh size after vacuum filtration to remove interstitial water within organisms [23]. All zooplankters were included in the measurements because samples did not contain large gelatinous organisms. Afterward, those samples were divided using a Folsom splitter, and all luciferids were sorted from the aliquots. Individuals were identified and sexed, when possible, based on previously published descriptions [3,4,18]. Each individual was measured from the base of the eye-stalk to the end of the sixth abdominal somite [24] (hereafter L). Processed individuals were quantified and standardized to 100 m^3 of filtered water (ind 100 m^{-3}).

2.3. Data Analysis

The influence of environmental variables on the distribution of species throughout the sampling period was evaluated using regression tree analysis (RTA). It is a powerful analytical method that helps identify the most important explanatory variables explaining the variability of a response variable. A tree is built by repeatedly splitting the response variable based on a single best explanatory variable, i.e., the one that minimizes the variance in the response variable. The process begins allocating data of the response variable into two mutually exclusive groups, each of them being as homogeneous as possible. Next, each of the groups is subjected to the same splitting procedure; the process continues until reaching a user-specified criterion. The result is a tree showing the mean values of the response variable at the terminal nodes [25–27]. In this study, the response variable was the abundance value of each species in each of the 82 sampling stations, and the explanatory variables were the temperature, salinity, chlorophyll concentration, bottom depth, distance to the shore, and the zooplankton biomass (as a measure of food availability). Examining the zooplankton samples, we thought that small copepods, ostracods, naked mollusks, and decapods as well as other crustacean larvae could be important prey for luciferids in the study area. These animals represented approximately 30% of the zooplankton biomass; thus, only this fraction was considered for the analysis. For salinity, temperature, and chlorophyll concentration, we took the mean integrated values in the upper 50 m, a layer in which the zooplankton were more abundant [28,29].

For each sampling season, the number of females (F) and males (M) of each species were counted, and the deviation from the 1:1 sex ratio (F:M) was evaluated using a χ^2 test at a significance level of $\alpha = 0.05$.

The non-parametric 'analysis of similarities' (ANOSIM) test was used to assess if there were differences between small and large individuals of each species among the seasons. The *Ro* statistic issued from this analysis was compared against a set of *R* random values that resulted from recomputing the statistic *n* times (9999 in this case) after randomly shuffling the sample labels [30]. A significance value of $\alpha = 0.05$ was used in this analysis

For each species and sex, we estimated the size at first maturity ($L_{0.5}$) by fitting the *L* to a logistic equation:

$$P_i = \frac{1}{1 + Ae^{BL_i}} \tag{1}$$

where, P_i is the cumulative frequency in percentage at the L_i value (in other words, the probability of finding a mature individual at size L_i), and *A* and *B* are parameters of the model. Particularly, the *L* value at which *P* is 0.5 represents the size at first maturity, conceived as the average size at which 50% of the individuals are mature [31].

3. Results

3.1. Environmental Conditions

High temperature values were recorded in July and October–November; the highest values (around 27 °C) were registered in neritic waters of the northern study area in July. The lowest temperatures (18 to 23 °C) were registered in January with a clear coastal–ocean gradient (Figure 2). Homogeneous salinity values (36.3 to 36.7 psu) were recorded in October–November in the entire study area; January registered the highest variability, with the lowest values (33 to 35 psu) over the inner shelf (Figure 3).

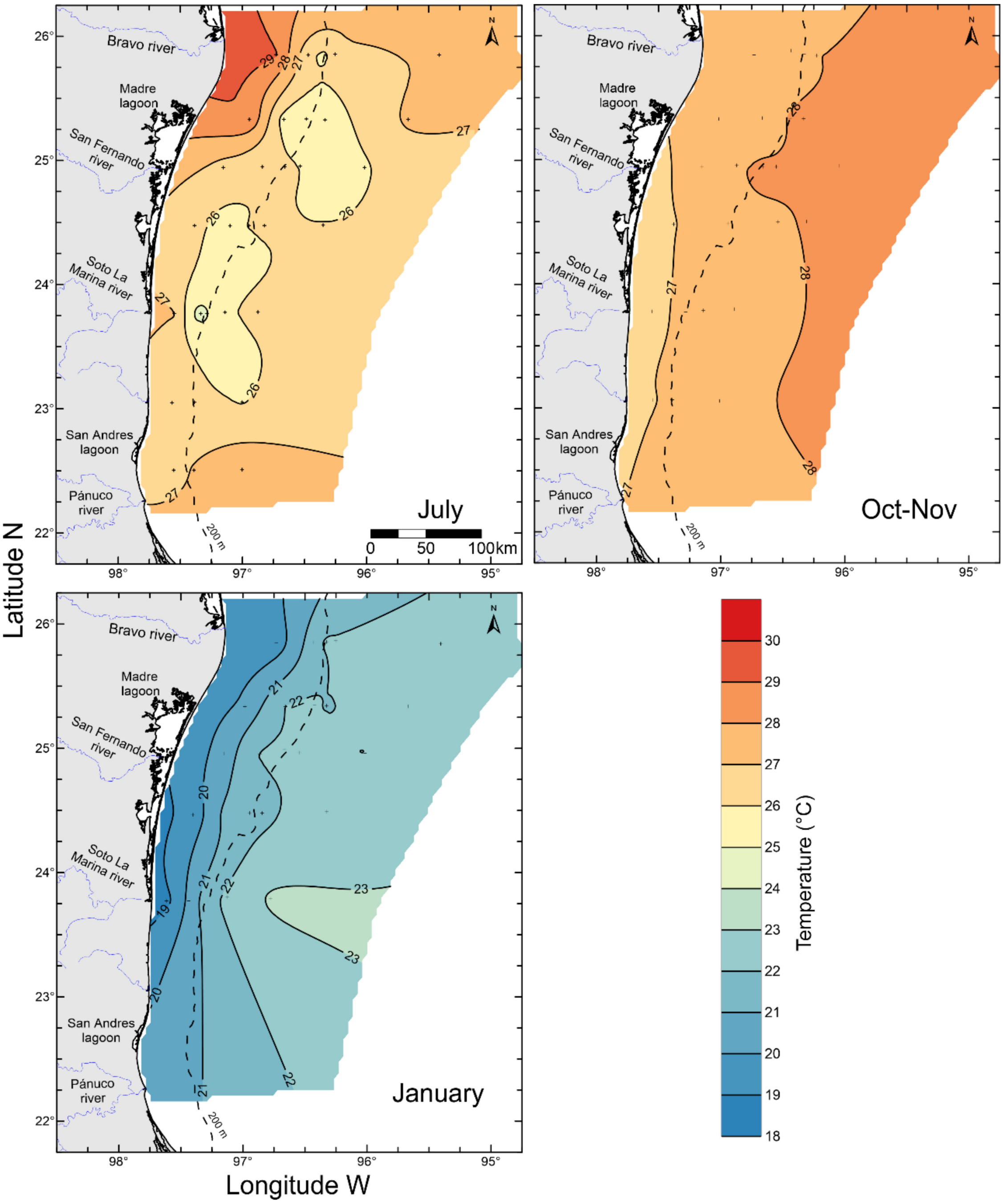

Figure 2. Mean integrated temperature (°C) in the upper 50 m layer in the western Gulf of Mexico.

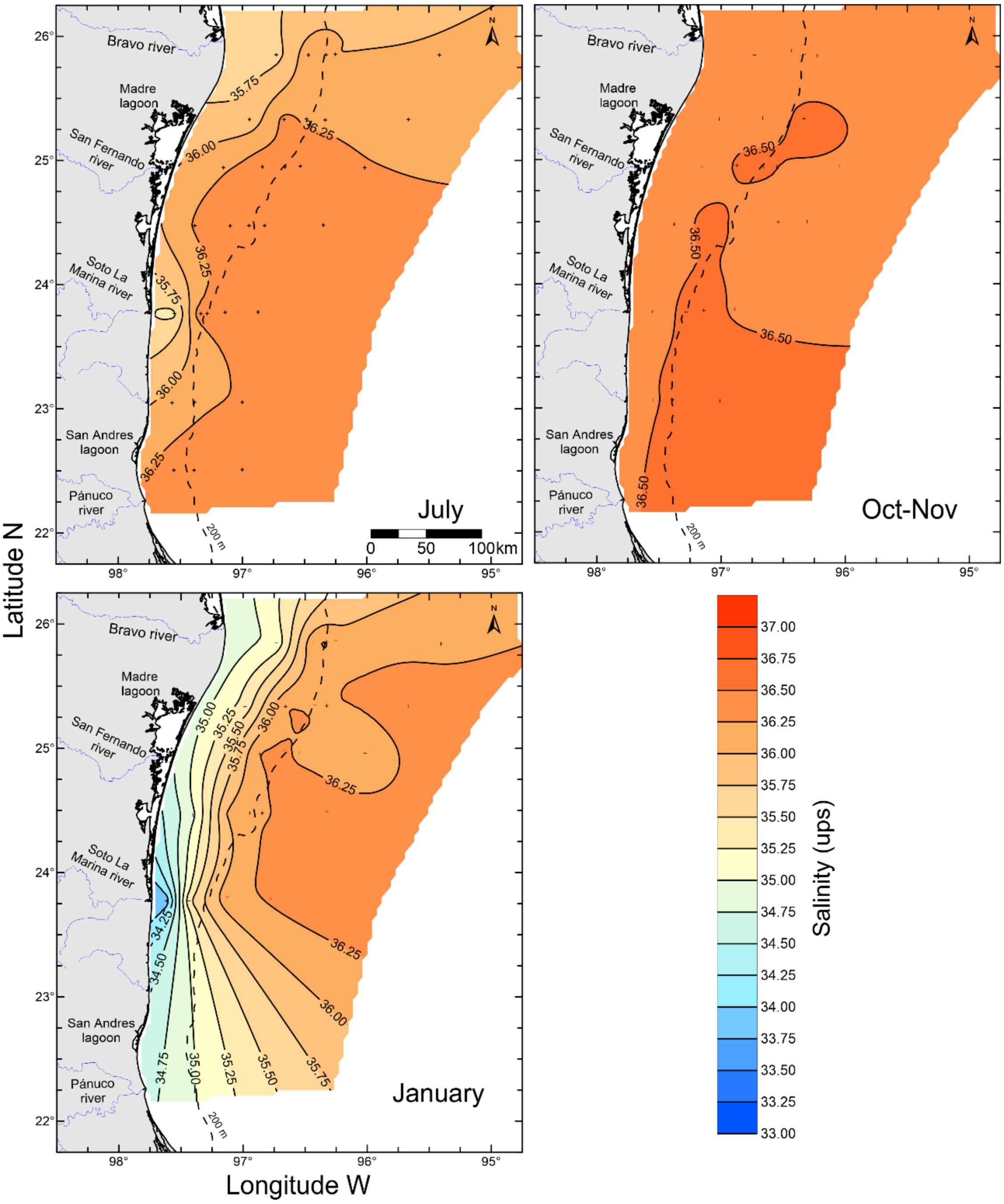

Figure 3. Mean integrated salinity (psu) in the upper 50 m layer in the western Gulf of Mexico.

Chlorophyll concentration was low (<1.5 mg m^{-3}) in all the studied seasons. The highest values were registered on the inner shelf in July and January (Figure 4). In addition, mean zooplankton biomass in the neritic zone was higher in July (9.7 ± 4.5 g 100 m^{-3}) and January (8.3 ± 4.9 g 100 m^{-3}) than in October–November (4.5 ± 3.5 g 100 m^{-3}). The highest biomass values were found at the stations close to the coast in July and January. In October–November, values were low both in the neritic zone and in the oceanic zone, with a maximum value close to the mouth of the Soto la Marina River (Figure 5).

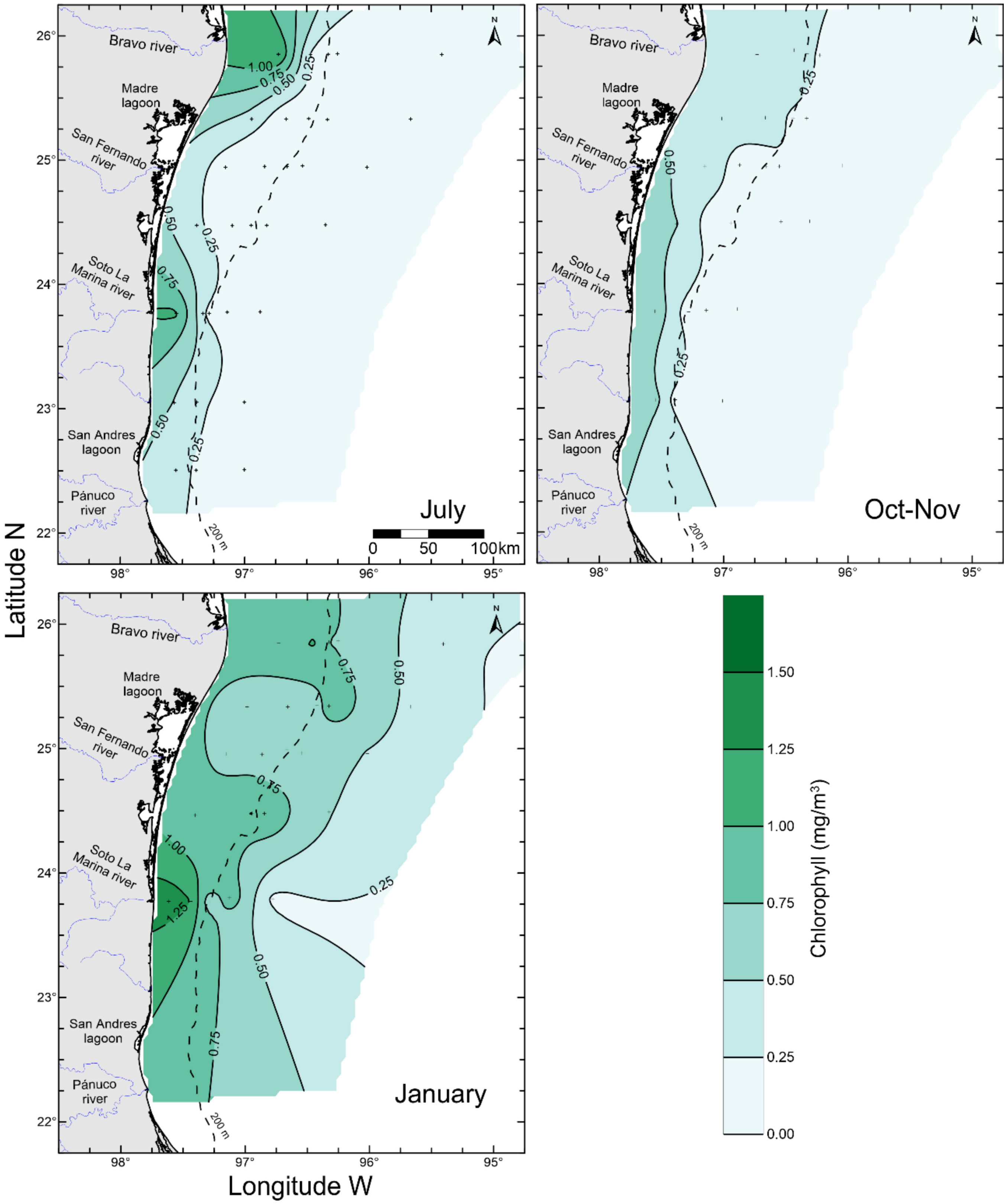

Figure 4. Mean integrated chlorophyll concentration (mg m^{-3}) in the upper 50 m layer in the western Gulf of Mexico.

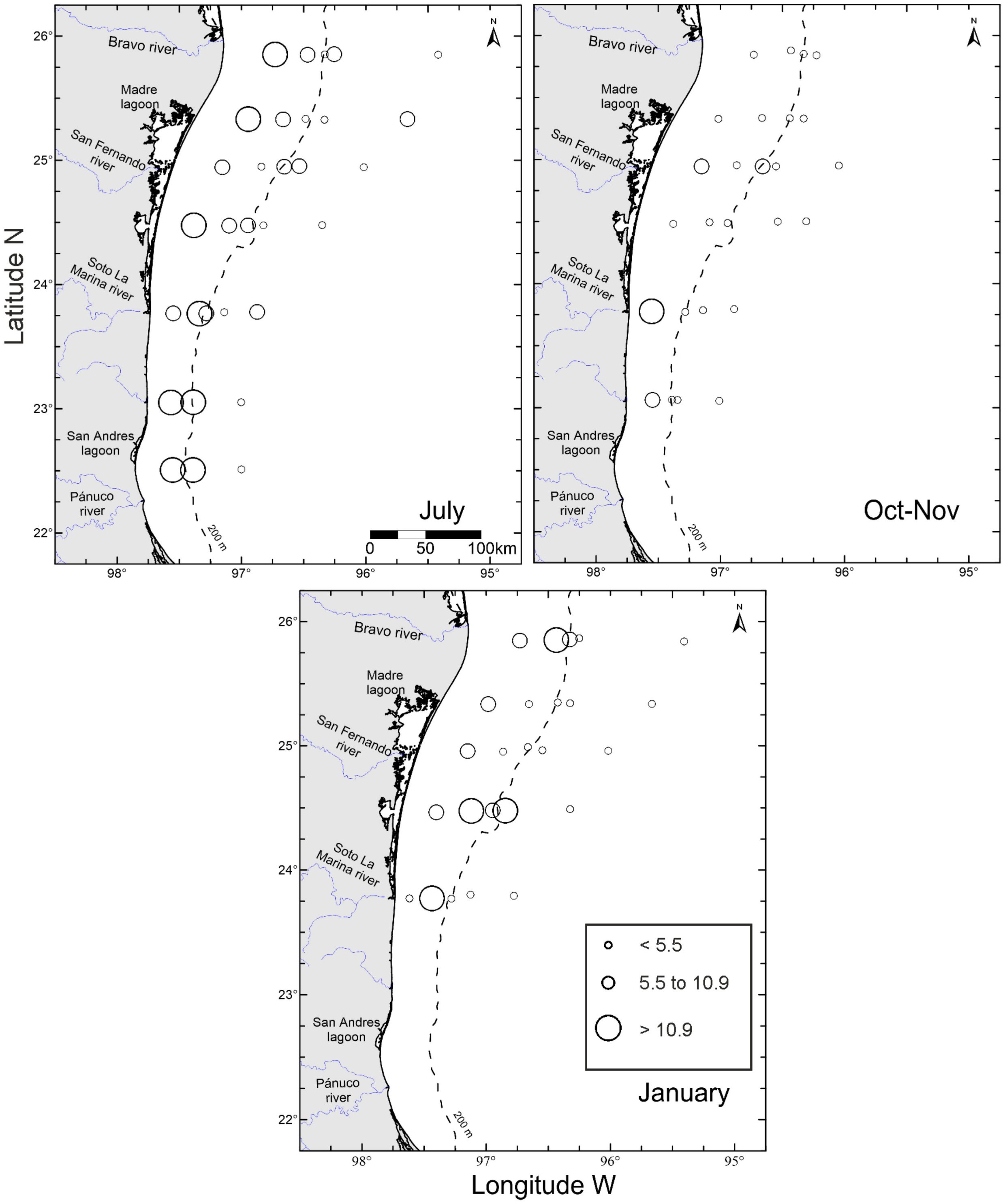

Figure 5. Distribution of zooplankton biomass (g 100 m^{-3}) values in the western Gulf of Mexico.

3.2. *Distribution and Population Structure of Belzebub faxoni*

The highest density values of *B. faxoni* were found in July, particularly in neritic waters, with a maximum of 4639.4 ind 100 m^{-3}. In October–November, the density of the species was less than 100 ind 100 m^{-3} except for the station close to San Andrés lagoon; in January, the species rebounded (Figure 6).

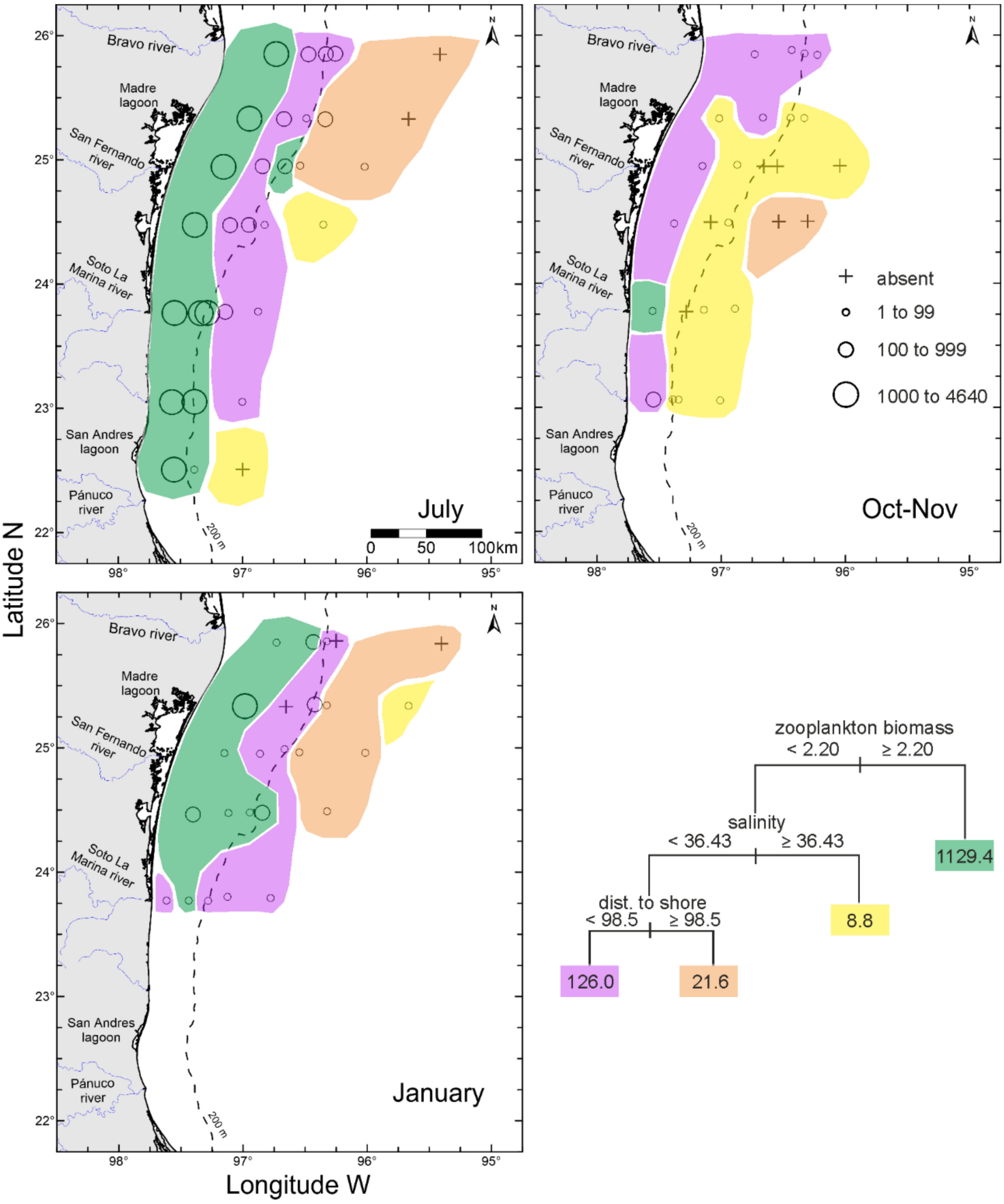

Figure 6. Abundance (ind 100 m^{-3}) of *Belzebub faxoni* in the western Gulf of Mexico and results of the regression tree analysis showing the mean abundance value of the response variable at the end of the branch.

Results of RTA indicated that the areas with the highest *B. faxoni* densities were associated with high zooplankton biomass (>2.20 g 100 m^{-3}). By contrast, low *B. faxoni* densities were registered in areas with available zooplankton biomass less than 2.20 g 100 m^{-3} and salinities higher than 36.43 psu (Figure 6).

Sex ratio (F:M) was significantly (χ^2, $p < 0.05$) skewed toward females in all the seasons: 1.8:1 in July, 1.7:1 in October–November, and 1.9:1 in January. These results showed that the number of females was almost twice the number of males in all the seasons.

Total length of *B. faxoni* individuals varied between 2.42 and 12.64 mm, and five size classes were considered to analyze the seasonal variation of the population structure (Figures 7 and 8). These classes were arbitrarily chosen in order to show a general trend in the size distribution. In July, size classes II and III registered the highest density values with a gradual decline toward classes IV and V. In the other seasons, size structure did not show a clear trend, and density values of all the size classes were low, especially in October–November. Comparing the abundance values of classes I and V among the seasons, the ANOSIM test indicated that July was different from the other months ($p < 0.05$), but January was not significantly different ($p > 0.05$) from October–November.

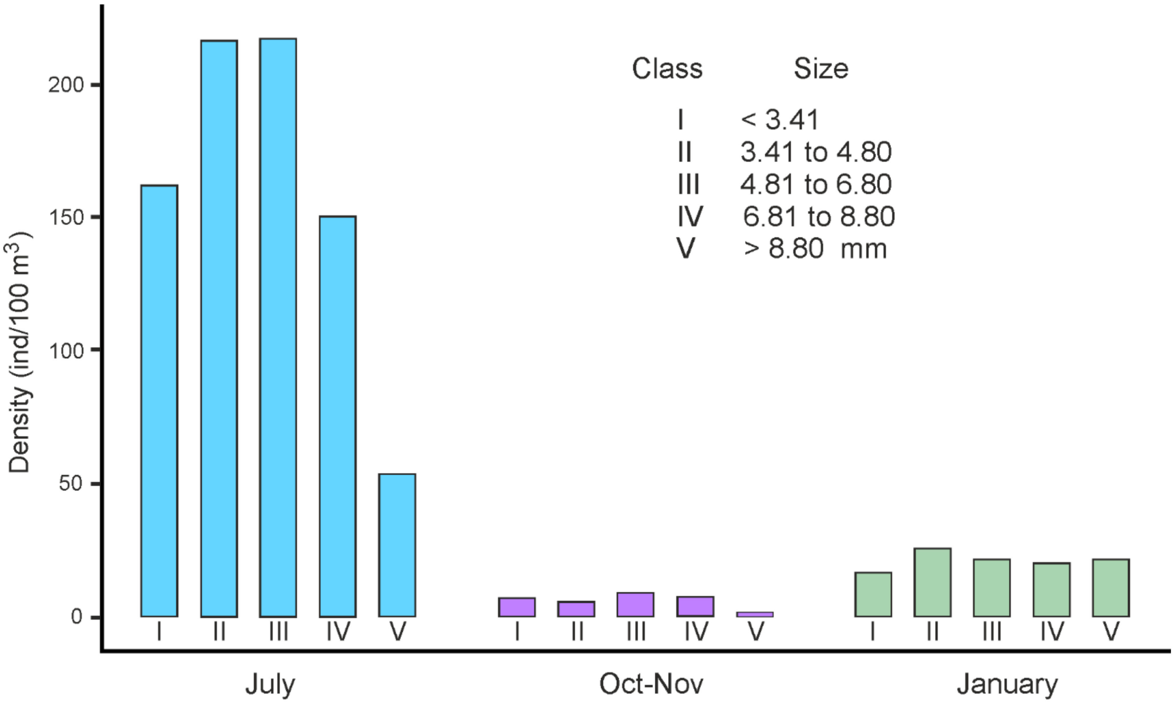

Figure 7. Size structure of the *Belzebub faxoni* population throughout three sampling seasons.

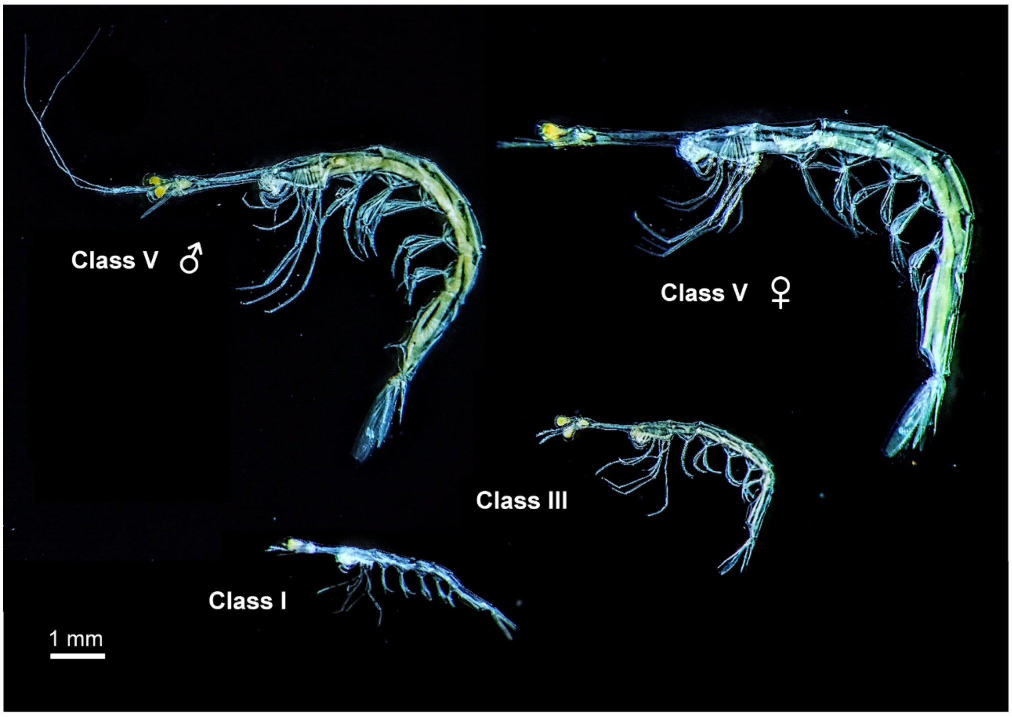

Figure 8. *Belzebub faxoni*. Habitus in lateral view from size classes I, III, and V.

Size at first maturity was 6.53 mm in females and 6.74 mm in males, as shown by fitting the L data to a logistic equation.

3.3. Distribution and Population Structure of Lucifer typus

July was the season with the highest abundance of *L. typus*, with a maximum value of 64.2 ind 100 m^{-3}; the highest densities were located in oceanic waters and over the shelf break (Figure 9). In October–November and January, the density decreased, with maximum values of 12.8 and 27.7 ind 100 m^{-3}, respectively.

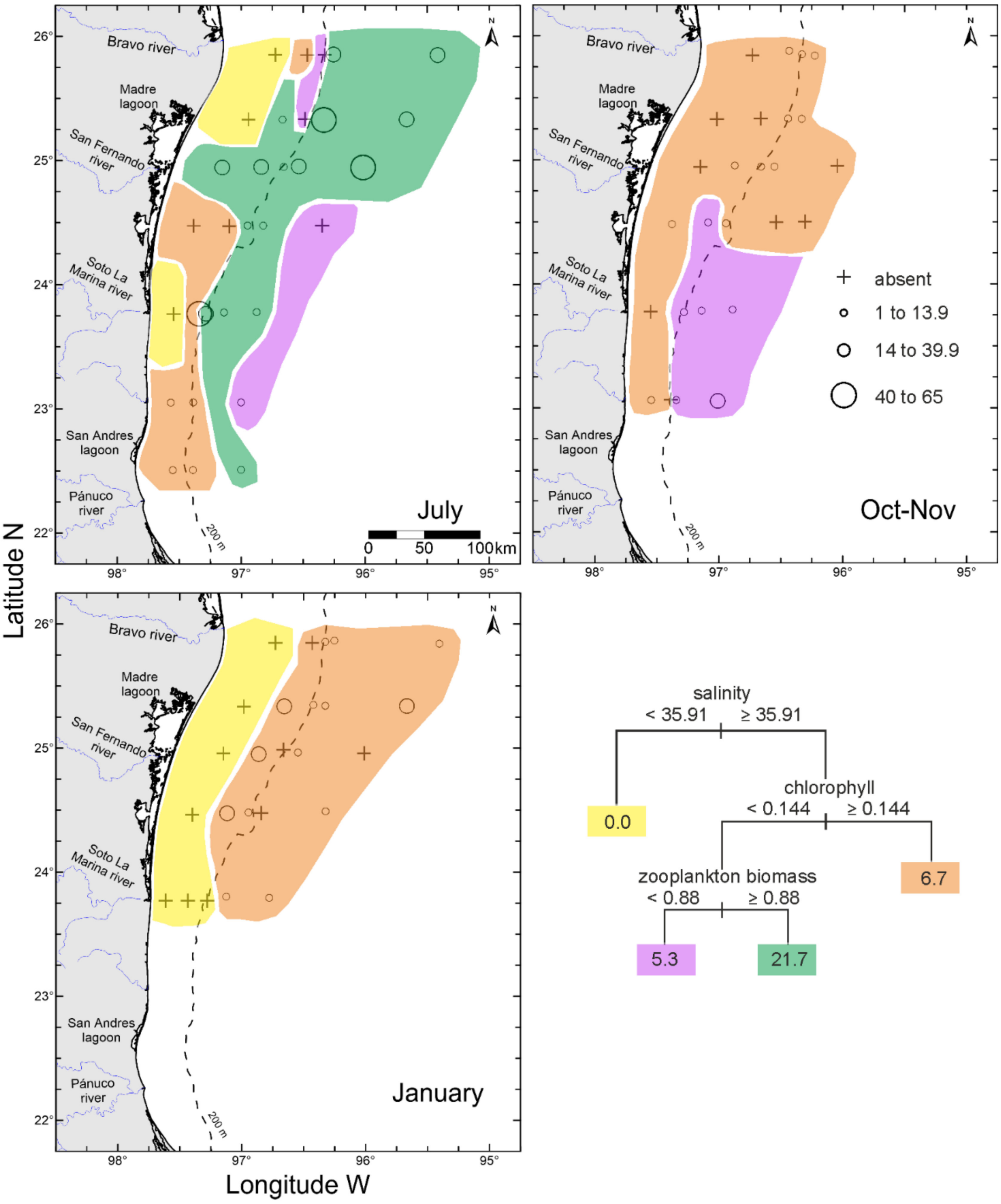

Figure 9. Abundance (ind 100 m^{-3}) of *Lucifer typus* in the western Gulf of Mexico and results of the regression tree analysis showing the mean abundance value of the response variable at the end of the branch.

Results of the RTA showed that the species was absent in areas where salinity was less than 35.91. The highest mean density value of this species was recorded in areas with salinity higher than 35.91 and available zooplankton biomass higher than 0.88 g 100 m^{-3} (Figure 9).

The sex proportion (F:M) was significantly (χ^2, $p < 0.05$) skewed towards the females (1.3:1) in July and toward the males (0.6:1) in January. In October–November, the proportion of both sexes was almost equal (0.9:1) (χ^2, $p > 0.05$).

The total lengths of individuals were between 2.33 and 11.18 mm. Size structure was similar in all the seasons, showing increasing abundance with size (Figures 10 and 11). However, the ANOSIM test indicated that there were no differences ($p > 0.05$) between densities of class I and V among the seasons.

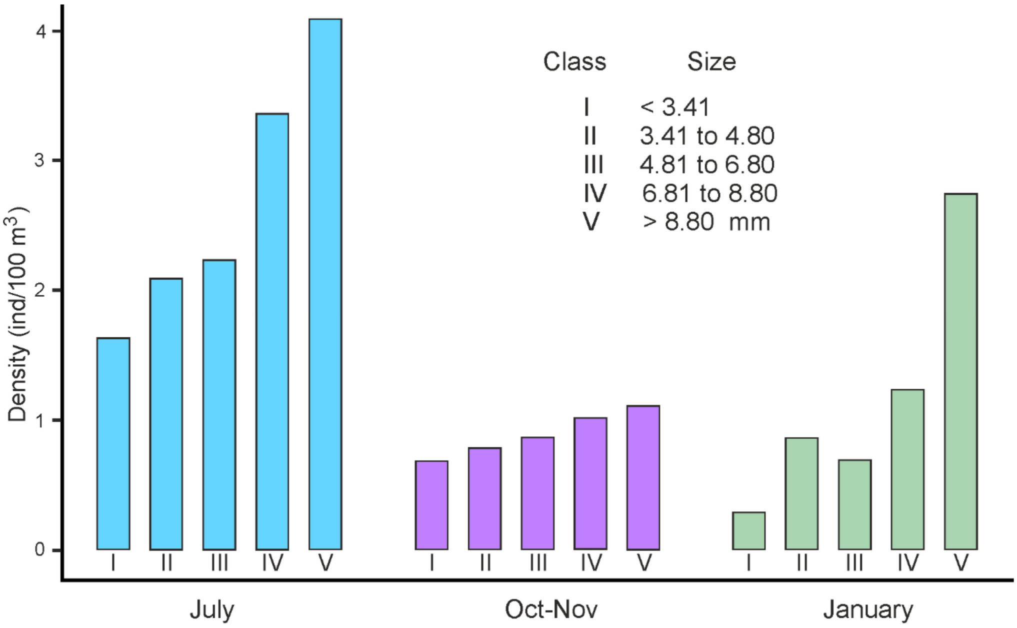

Figure 10. Size structure of the *Lucifer typus* population throughout three sampling seasons.

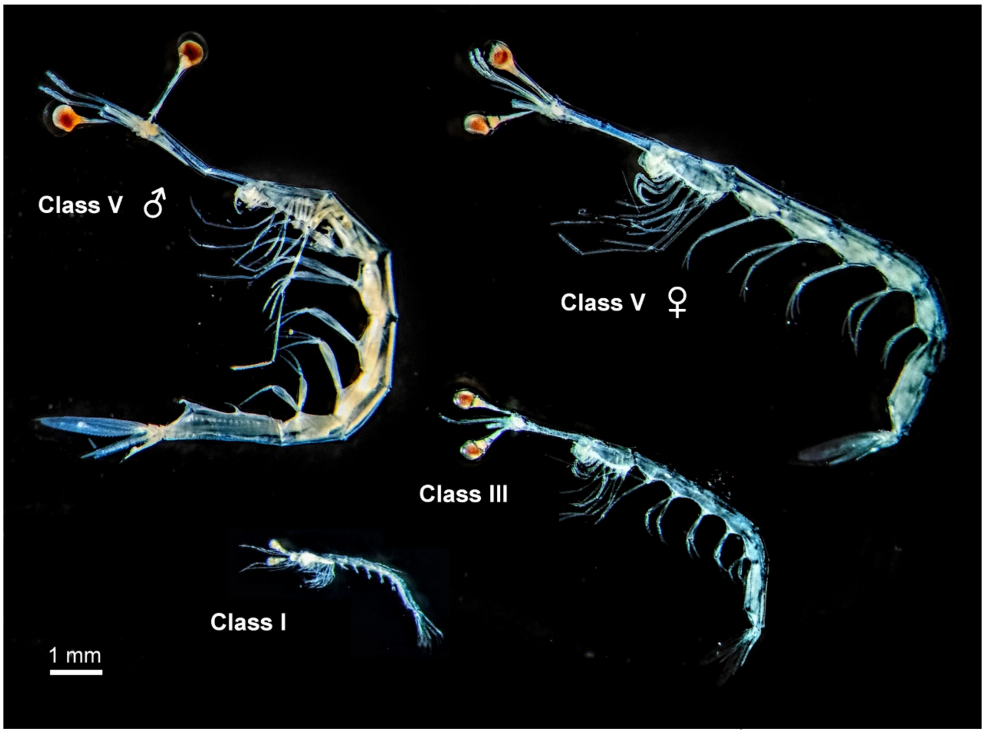

Figure 11. *Lucifer typus*. Habitus in lateral view from size classes I, III, and V.

Size at first maturity, estimated by fitting *L* data to a logistic equation, was 8.16 mm in females and 8.63 mm in males.

4. Discussion

In the western Gulf of Mexico, *Belzebub faxoni* was recorded in all the sampling periods and exhibited a marked variation in seasonal abundance with the peak in July. Similarly, in the northern Gulf, Harper [16] found that the species showed their maximum abundance in August–September and decreased in October–November. In southern Brazil, field observations indicated that the species had continuous reproductive activity throughout the year, greater during the spring–summer period [32,33]. On the other hand, *Lucifer typus* was also recorded in all the sampling periods. Density values were low throughout the year, with slightly higher abundance in July. Despite being related species, abundance values registered by *L. typus* were between two or three orders of magnitude lower than those recorded by *B. faxoni*. Along the western Atlantic, high abundance values for *B. faxoni* were also found in the coastal waters of Texas [16], the southern Gulf of Mexico [19], Venezuela [34], and northern and southern Brazil [24,35,36]. The success of *B. faxoni* in plankton communities could be attributable to a short adult lifespan associated with a rapid turnover of generations and the protection of eggs until eclosion [5].

Results of the RTA suggested that zooplankton biomass (food availability) was the main factor influencing the distribution of *B. faxoni*, which registered its greatest density values on the inner shelf (Figure 6). As stated, we think that the main potential prey for luciferids in the study area includes small copepods, ostracods, naked mollusks, and decapods as well as other crustacean larvae. However, these animals share the habitat with potential predators for luciferids; thus, the inclusion of this parameter in the analysis may also represent the risk of luciferids being preyed upon. The examination of samples showed that chaetognaths, shrimp post larvae, gelatinous organisms (medusae and siphonophores), shelled mollusks, and polychaetes could be potential predators for luciferids. However, regarding the high numbers of the species, it seemed that *B. faxoni* found suitable conditions to grow and reproduce in the study area despite the detrimental consequences of predation and other environmental factors. In situ and laboratory studies indicated that adults of *B. faxoni* were mainly carnivorous, although their feeding appendages indicated the possibility of omnivory [5]. Main prey for adults are difficult to determine because the shrimp completely masticates the food, whereas larvae can consume microalgae and small rotifers, as revealed by laboratory experiments [5,7]. The food consumption rate of this species depends on prey density [5,6], a fact that could explain the major abundance of *B. faxoni* associated with higher food availability. Concerning *L. typus*, the RTA revealed that the species avoided coastal areas where salinity was less than 35.9 psu (Figure 9). Field observations of Xu [37] showed that *L. typus* was a eurythermal but stenohaline species. In addition, Bowman and McCain [17] considered *L. typus* as an indicator of oceanic waters. In this study, the major mean abundance of this species corresponded to areas over the slope and open waters, associated with available zooplankton biomass higher than 0.88 g 100 m^{-3} (Figure 9).

The sex ratio favored the females in the *B. faxoni* population in all the sampled seasons as observed in other localities of the northern and southern Gulf of Mexico [19,38], southern Brazil [36], and the South Atlantic Gyre [39]. By contrast, the *L. typus* population showed variable sex proportions that were only skewed towards females in July when the species exhibited its highest abundance values. If reproductive costs of producing male or female progeny are the same, an equal number of males and females are expected [40]. However, in crustaceans and other marine invertebrates, deviation of this 1:1 Fisherian proportion may occur due to several factors: (i) Mechanisms of sexual determination. Sex determination can result from genetic or environmental causes. In the former, sex is determined by the genotype, while in the second, sex is not given during fertilization but in response to certain environmental factors such as temperature [41]; (ii) Sex reversal. Also called sequential hermaphroditism, it occurs when at a certain size, individuals change sex [42,43].

Sex reversal is a phenomenon commonly observed in crustaceans [43,44]; however, no studies evidence sequential hermaphroditism in luciferids or close taxa; (iii) Differential sex longevity and/or mortality. If one of the sexes has a higher mortality rate and/or lower longevity, the proportion will favor the other [42,45]. This phenomenon may occur if one of the sexes exhibits foraging or mating behavior, which represent a greater risk of being predated [46,47]; (iv) Migration. Differential migratory behavior between sexes could be the cause of sex disparity in a sample. Concerning luciferids, Marafon-Almeida et al. [39] supported differential vertical migration between the sexes, but Álvarez [48] found no differences in the migration patterns of males and females. The causes of sex disparity observed in this study are not fully understood. As in many species of crustaceans, genetic factors must play a significant role in this difference along with environmental factors and ecological relationships.

Regarding the size structure of *B. faxoni* in July, it was noteworthy that the small size classes were the most abundant except for class I (Figure 7). However, if we considered that many of the small organisms of this species escaped from the plankton nets, class I may have been the most abundant. Significantly higher abundance of class I over class V ($p < 0.05$) may indicate that the species reproduces in the study area with a peak in July. The predominance of small individuals is generally indicative of growing populations [49,50]. Townsend et al. [51] stated that the coexistence of many young individuals and few adults occurs when the birth and mortality rates are high. This means that many individuals are born, but they do not have a high probability of survival. Perhaps summer environmental conditions such as high temperatures have a positive influence on the reproductive processes of the species as has been observed for other holoplanktonic organisms [52,53]. The size structure in *L. typus* showed a gradual ascent towards larger sizes in all the seasons (Figure 10). Molles [50] indicated that in the absence of young individuals, a population could not persist. As indicated above, *L. typus* preferentially occurred in the open ocean [17,54,55]; therefore, it was likely that the studied area did not represent the optimal site for population growth. Class V was more abundant than class I, but the ANOSIM test indicated that abundance values between these classes were not significantly different among seasons ($p > 0.05$). This result could indicate that the species reproduced outside the study area and that large individuals had more time to disperse in the ocean from the main hatching sites.

Sizes at first maturity ($L_{0.5}$), estimated here for B. faxoni (females: 6.53 mm, males: 6.74 mm), are similar to those found in Ubatuba, Brazil (females: 5.97 mm, males: 6.92 mm) [36]. In another locality of southern Brazil, López [32] calculated $L_{0.5}$ in terms of the pre-buccal somite length (females: 1.19 mm; males: 1.18 mm), which in this study, corresponded to 6.08 mm for females and 6.41 mm for males. Estimations of $L_{0.5}$ for L. typus (females: 8.16 mm; males: 8.63 mm) given in this study represented the first approach for the species. Differences in the estimated values of $L_{0.5}$ among studies could be due to the model employed to calculate the parameters, the size of the sample, the environmental conditions of populations, or the genetic heritage [31,56,57]. Knowledge of size at first maturity and other population parameters have significant importance in the planning and management of luciferid resources [58].

5. Conclusions

This study provides new and valuable information on the population ecology of the two luciferid species coexisting in the western Atlantic, *Belzebub faxoni* and *Lucifer typus*. In the study area, these species were found during the three examined seasons, indicating continuous reproduction throughout the year with a peak in the summer. *Belzebub faxoni* was more abundant in the waters of the inner shelf, associated with sites of high food availability. In contrast, *L. typus* was mainly found over the slope and open waters, avoiding inshore low-salinity areas. The global distribution pattern of both species, in which *B. faxoni* mostly inhabited the neritic province and *L. typus* the oceanic one, could be the result of a long competition process causing partial resource partitioning. Population density values of *B. faxoni* were two or three orders of magnitude greater than *L. typus*. Previous studies attributed the success of *B. faxoni* in plankton communities to its short adult lifespan, a rapid turnover of generations, and the protection of eggs. Sex ratio favored the females in the *B. faxoni* population in all the periods analyzed, whereas in the *L. typus* population, the sex ratio was biased toward females in only one season. The underlying causes of the skewed sex ratios in the luciferid populations are not fully understood. The size structure of *B. faxoni*, favorable to small size classes in July, may have been indicative of a growing population; in contrast, the *L. typus* population was dominated by large individuals in all seasons, which could be the result of a long transport of these individuals from the main hatching sites. Size at first maturity for both males and females in the *B. faxoni* population agreed with previous records; information regarding this parameter for the *L. typus* population provided here represents the first approximation for the species. As an important part of the zooplankton, knowledge of the distribution and population parameters of luciferids provides important elements to better understand the ecological relationships of pelagic communities and develop future management strategies of shrimps.

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