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Chapter

The Habitat Types of Freshwater Prawns (Palaemonidae: *Macrobrachium*) with Abbreviated Larval Development in Mesoamerica (Mexico, Guatemala and Belize)

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Abstract

The freshwater prawns of genus *Macrobrachium* with abbreviated larval development have been reported from a diversity of freshwater habitats (caves, springs and primary streams from so-long basins). Here we analysed 360 sites around the Mesoamerican region (Mexico, Guatemala and Belize). At each site, we measured temperature, salinity oxygen dissolved, pH, altitude and water flow velocity values. We documented the riparian vegetation and occurrence and abundance of *Macrobrachium* populations. All these values were analysed by multi-dimensional scaling and principal components analysis in order to identify key features of the environmental data that determine the habitat types and habitat diversity. The results show that there are *Macrobrachium* populations in 70 sites inhabiting two main habitats: Lotic and Lentic; and each one have fours subhabitat types. All are defined by altitude range and water velocity that involve the temperature and oxygen variables. In some specific areas, the karstic values on salinity and pH defined some groups. Within the lentic habitats, we identified the following subhabitats: (1) temperate streams, (2) neutral streams, (3) high dissolved oxygen, (4) multifactorial; and for lotic habitats, we identified: (5) water high carbonate, (6) moderate dissolved oxygen, (7) low dissolved oxygen, and (8) high altitude streams. All these subhabitats are located on the drainage basin to the Atlantic Sea, including places from 50 to 850 meters above sea levels and have specifically ranges from temperature, water velocity, pH and salinity for some cases. Also, the geological analysis from the basins where the *Macrobrachium* inhabit is located showed that the geological faults align with these habitat subdivisions. In this chapter, we discuss the environmental heterogeneity, morphological plasticity and their relationship to physiographic regions across the species ranges.

Keywords: *Macrobrachium*, abbreviated larval development, Mesoamerica, habitat

1. Introduction

The freshwater prawns of the genus *Macrobrachium* are characterized by living in the circumtropical region around the world, since these decapods have been reported from the five continents [1]. There are two main groups of freshwater prawns: (a) those that migrate at some point in their life looking for brackish water (amphidromy) and (b) those that are completely hololimnetic and that live restricted to the river springs or caves or grottoes [2–6]. In this chapter, we will cover the different habitat types from the freshwater shrimp that do not reach large sizes (abbreviated larval development) but are of great importance for local or indigenous cultures of the regions where they are found [7]. These organisms represent a great diversity of habitats (caves, primary rivers, creeks, and springs) as well as species (**Figure 1**). In 1999 *Macrobrachium tuxtlaense*, the first epigeous species, was reported from Mexico, and since then seven species have been recorded from Mexico (*M. vicconi*, *M. totonacum*, *M. sbordonii*, *M. cosoloapaensis*, *M. jacatepecensis*, *M. mazatecum*, *M. oaxensis*). In 2015, the first one was reported from Guatemala (*M. cemai*), which led to the study that is now being presented, including Belize.

Figure 1.
Diversity of freshwater prawns in Mesoamerica.

In general, these organisms had been reported between 100 and 500 meters from rivers, streams, and caves in the tropics and only on the Atlantic slope [1, 8–11]. A cave species with this type of development has been known (*Macrobrachium villalobosi* [12]) since 1973, and the last described species of this type of habitat was in 2008 (*M. sbordonii* [13]). Now several environmental data from caves in Mexico, Guatemala, and Belize are available for analysis. Our study shows with more specific detail how the habitats from these freshwater prawns are characterized by diverse environmental conditions that drive high plasticity in their morphological features.

2. Material and methods

The study area focused on the Southeast of Mexico with Veracruz, Oaxaca, Tabasco, and Chiapas States, as well as the Alta Verapaz, Peten, and Lake Izabal regions in Guatemala and the region mountain range that drains into the Atlantic Ocean in Belize (**Figure 2**). This study was carried out from 2006 to 2018. Throughout this period, sites were visited one time where we searched for freshwater prawns and recorded environmental data. We sampled from all of these regions (rivers, streams, springs, and caves) that had the following characteristics: (1) between 800 and 100 meters above sea level (masl), (2) a tropical origin, and (3) predominantly freshwater. We sampled 360 sites measuring the following ecological features with an Oximeter Oakton: dissolved oxygen (±0.01 mg/l), pH (±001 pH), salinity (±0.01%), and temperature of the water (±0.01°C). The altitude and the GPS values were recorded with a Garmin GPS, and the speed of the surface current was recorded taking the speed at which a floating object takes to travel a known distance. After the environmental data were recorded, the prawns were collected

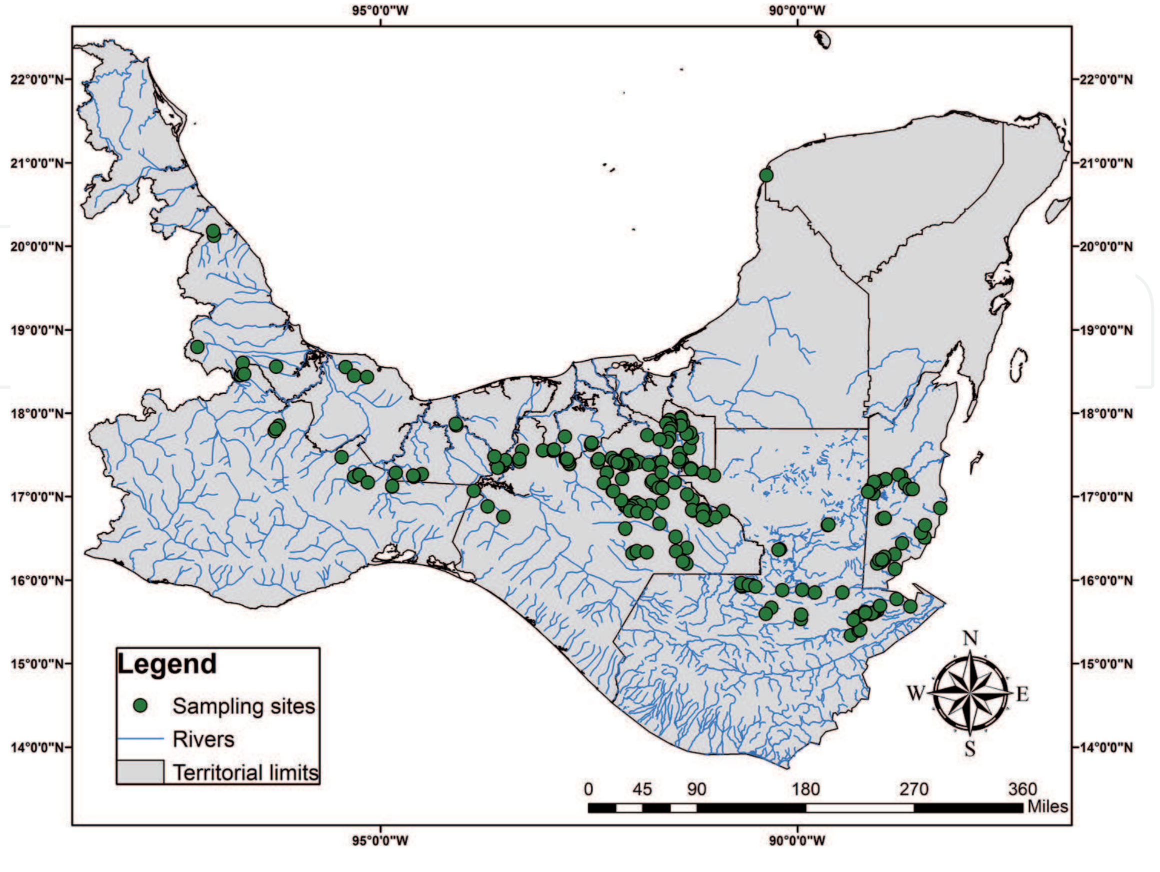

Figure 2.
Sampling sites around Mesoamerica.

with a target number of at less 30 animals, including larger animals with few eggs as indicators of abbreviated larval development. Animals were collected using a net or manually according to the conditions of the site; for example, in the ponds with lentic features, the manually sampled was used, while in the lotic features, the net was the better method. The animals were identified according to genus using the taxonomic keys described previously [11]. The first step was a basin analysis using the geographic information system (GIS) procedure to identify the stream morphometric traits in the different basins where these animals occur (tectonic faults and hypsometric slopes) [14].

Likewise, we analyzed habitat types using the software Primer 6 [15]. All these values were standardized and analyzed by nonparametric multidimensional scaling (MDS) using the Kruskal-Wallis test and principal component analysis (PCA) procedures [16], in order to identify which environmental characteristics determine the sub-habitat types and how many types are possible to identify.

3. Results

3.1 Sites with freshwater prawns

Freshwater prawns with abbreviated larval development were found in 70 sites from 360, analyzed, and distributed mainly between 100 and 860 meters above sea level. In all cases the freshwater environments originated in tropical areas. The species found were just mentioned above together with three more cave species: *Macrobrachium villalobosi*, *M. acherontium*, and *M. catonium*. However, from the 70 populations, we believe there are at less 15 new species that are currently in the process description. All these populations show a pattern of distribution along the mountain range of the Sierra Madre Oriental and the Sierra Madre de Chiapas reaching the region of Alta Verapaz and Peten until ending at Lake Izabal through the Guatemalan territory and the Belizean mountain mass in the rivers that drain to the Caribbean and therefore to the Atlantic Ocean (**Figure 3**). In general, the sites can be characterized as freshwater environments (cave or epigeal) and springs or primary streams. Their distribution is restricted to the presence of large volumes of water and higher current flow, as well as the presence of migratory species of prawns (amphidroms) that are generally larger with a lot of eggs. In a basin analysis with the sites where *Macrobrachium* shrimp were found, our results show that most populations live in areas with tectonic faults, where one finds the majority of the springs and caves and only few populations live in areas where the deposition and erosion processes are dominant.

3.2 Cluster analysis

In the first grouping analysis with the most specific data, we found two higher-order habitat divisions, namely, lotic and lentic sites (**Figure 4**). But within each higher-order environment, there were four subtypes of habitat with the subterranean habitat not clearly partitioned between lotic and lentic but was more frequent in lentic environments: (1) temperate streams, (2) neutral streams, (3) high dissolved oxygen, and (4) multifactorial habitats. And for lotic habitats, we identified the following sub-habitats: (5) water high carbonate, (6) moderate dissolved oxygen, (7) low dissolved oxygen, and (8) high-altitude streams (see **Table 1**).

Some sub-habitats overlapped with each other, but others are well defined and are separated from others (**Figure 5**). These overlapping habitats occurred in 3, 4,

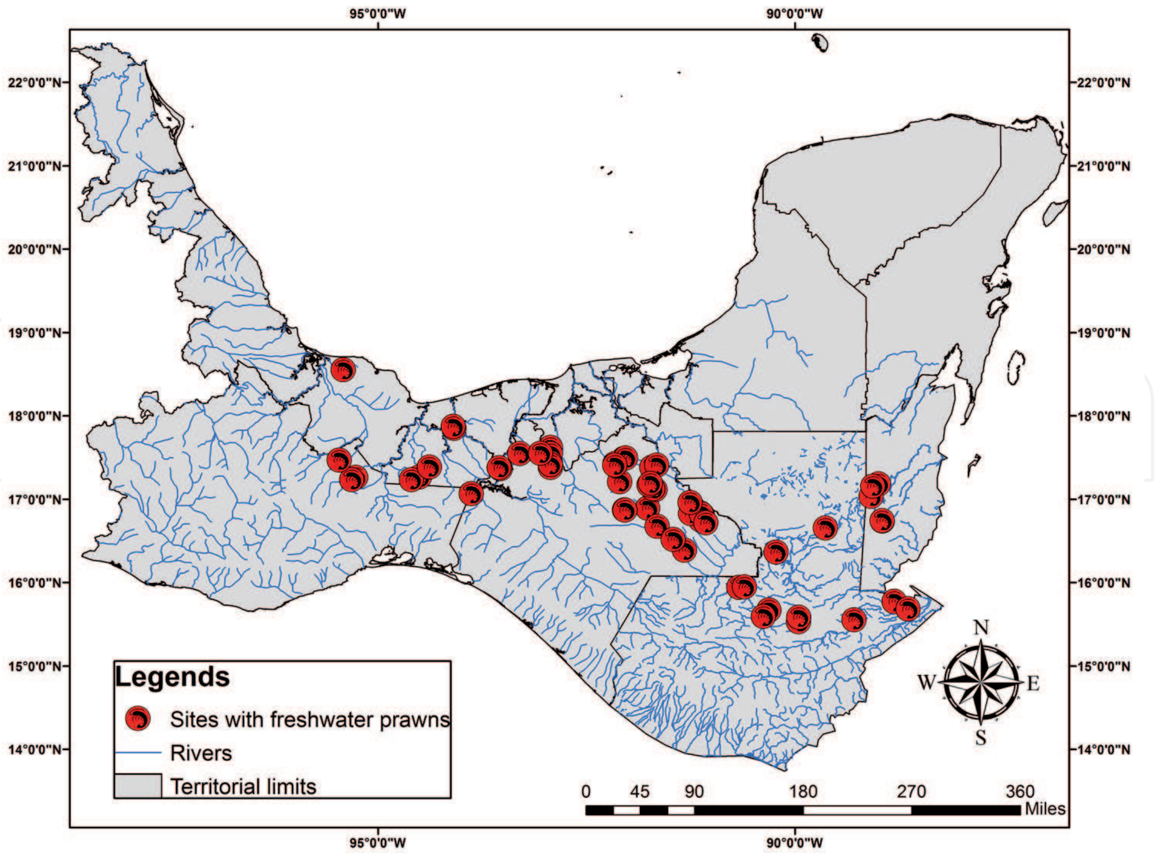

Figure 3.
Sites with freshwater prawns along Mesoamerica.

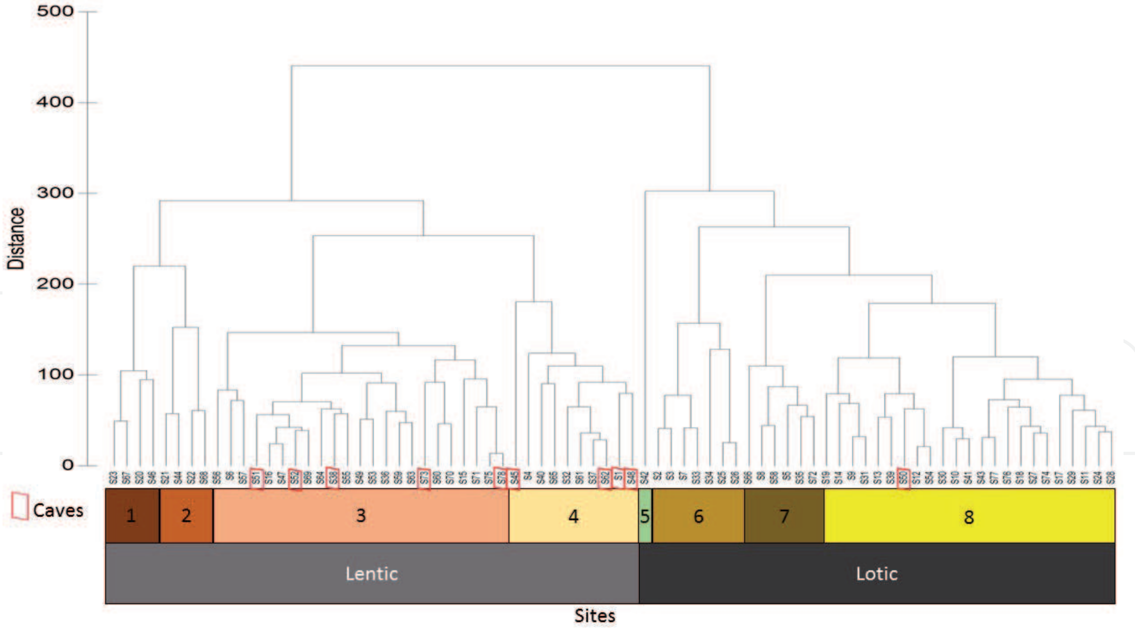

Figure 4.
Cluster analysis using the nearest neighbor method and Euclidean distance (normalized data). Within lentic habitats, the following sub-habitats were identified: (1) temperate streams, (2) neutral streams, (3) high oxygen dissolved, and (4) multifactorial habitats. And for lotic habitats, the following were identified: (5) water high carbonate, (6) moderate dissolved oxygen, (7) low dissolved oxygen, and (8) high-altitude streams.

6, 7, and 8 groups. Likewise, each of these sub-habitats can be separated first by altitude as a predominant variable and then by dissolved oxygen and temperature as well as the current water flow that involves the first classification as lentic or lotic. In general, it is understandable the interrelation of the sub-habitats shares some

Sub-habitat	Characteristics
(1) Temperate streams	They are streams with high temperatures of 25.3–32.4°C; they are at an altitude of <353 masl, have a pH of 6.38–7, are mostly epigeous-type environments, and have an oxygen saturation <34.7% with the exception of a site that presented super saturation
(2) Neutral streams	They are streams with a pH close to neutrality; they exist at altitudes <280 masl, temperatures from 25.2–28.3°C, epigeous-type environments; and they have an oxygen saturation of 11.7–87%
(3) High-oxygen streams	They are streams that mostly have oxygen saturation >60% reaching over saturation in several places. They are found at altitudes of 9–599 masl, temperatures of 18.7–27.7°C, in most epigeal environments although we can find hypogeal representatives
(4) Multifactorial	Streams in which we can find both epigeal and hypogeal sites; lentic and predominantly lotic environments; at altitudes from 34 to 330 masl, temperatures of 22.5–28.2°C, oxygen saturation of 10.3–90.6%, and have a pH of 5–8.3
(5) Water high carbonate	Site with freshwater stream with a height of 371 masl; originating from a karstic cave with a dissolution of the rock higher than other caves, which allows the conductivity to increase and the site to be separated from the rest by values of salinities of 0.9%, with an alkaline pH, a temperature of 22.7°C in a lotic and epigeous environment, and a current speed of 6.6 cm/sec and oxygen saturation of 48.6%
(6) Moderate-oxygen streams	Streams with an oxygen saturation of 38.2–60.5%, having an average altitude of 301 masl and a temperature of 21–24.6°C. They are epigeous environments with an average current speed of 4.8 cm/sec
(7) Few oxygen dissolved	Streams with oxygen saturation of 29.4–46.8%; they have an average altitude of 25.6 masl and a temperature of 20.6–27.1°C and are epigeous environments with an average pH of 6.45
(8) High-altitude streams	Streams with an average altitude of 425.5 masl with a maximum of 844 masl. Oxygen saturation of 31.6–96.9% and a pH of 6.03 at 8.21

Table 1.
Sub-habitat types of Macrobrachium *populations in the Mesoamerican region.*

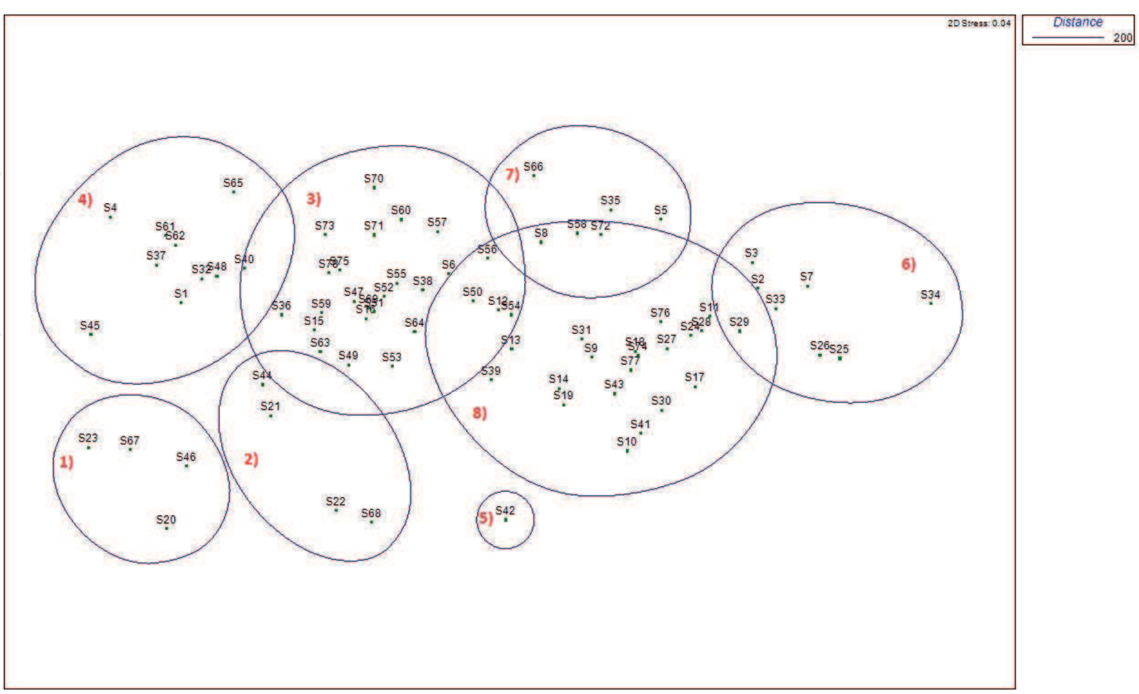

Figure 5.
Nonparametric multidimensional scaling (MDS) analysis using the Euclidean distance at 0.01% stress with standardized data, showing the sub-habitat types of Macrobrachium *populations in Mesoamerica. Within lentic habitats the following sub-habitats were identified: (1) temperate streams, (2) neutral streams, (3) high oxygen dissolved, and (4) multifactorial habitats. And for lotic habitats, the following were identified: (5) water high carbonate, (6) moderate dissolved oxygen, (7) low dissolved oxygen, and (8) high-altitude streams.*

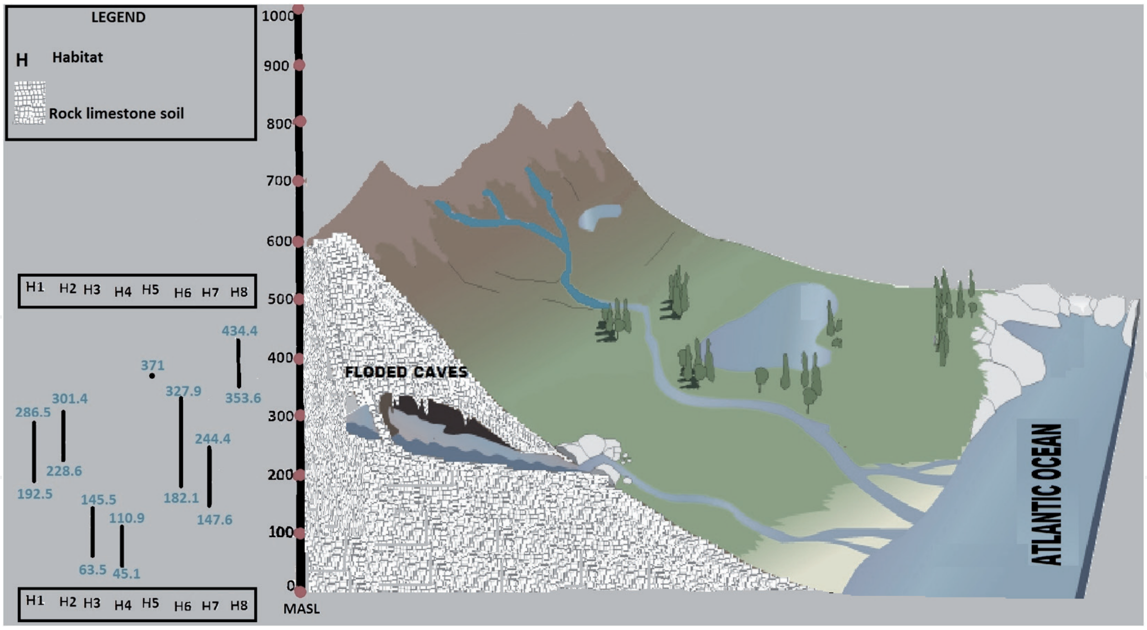

Figure 6.
Diagrammatic scheme of sub-habitat types of Macrobrachium *populations across the coastal slope of Mesoamerica.*

sites with similar characteristics because they are all in the same altitude range as well as the characteristics of tropical springs and rivers.

The schematic representation in the coastal slope of the sub-habitats and their presence is defined by the altitude above sea level, as well as by the water flow and the higher presence of carbonate salts for a specific point such as the case of sub-habitat 5 (**Figure 6**). It is important to mention that most of the places where these organisms live are located in the tectonic faults of the different regions and few populations are found in the river areas where sedimentation and erosion are the main processes of formation of these basins. This makes sense when listing the six general characteristics of the habitats of these organisms: (1) tropical rivers, (2) altitude ranges from 50 to 850 meters above sea level, (3) mainly tectonic faults (springs, primary rivers, and caves), (4) preferably rich in oxygen, (5) with riparian arboreal vegetation, and (6) on the Atlantic slope with karstic origin.

4. Discussion

According to their distributional range, the freshwater prawns with abbreviated larval development inhabit areas from 50 to 600 masl; however, there are some extreme values in the lower range down to 9 masl and up to 840 masl. All species are located along the mountain systems of the Atlantic slope in Mexico, Guatemala, and Belize in contrast with those species of amphidromous prawns that need to migrate along the rivers to reach the brackish waters to complete their development such as *Macrobrachium carcinus*, *M. heterochirus*, *M. olfersii*, *M. americanum*, and *M. acanthurus* [1, 6, 22]. The genus *Macrobrachium* has their origins estimated to have occurred in the Cretaceous [17] and just is when these mountain systems arose, with the volcanic belt serving as a geographical barrier for this group. The *Macrobrachium* species colonized these freshwater habitats together with *Creaseria morleyi* before the emergence of the Yucatan Peninsula [18]. Because the diversification among the freshwater prawns with abbreviated larval development occurred from an ancestor previously adapted [19] to the freshwater habitats, the isolation of suitable freshwater conditions (cooler temperatures, etc.) worked as driving force in the diversification of these species. With the distributional pattern now established, resolving relationships among these species and populations will aid in testing hypotheses concerning the patterns and timing of diversification events across this group.

Here we distinguish eight sub-habitat types where the freshwater prawns with abbreviated larval development occur. Lentic habitats had the following characteristics: (1) temperate streams, (2) neutral streams, (3) high dissolved oxygen, and (4) multifactorial habitats. And the lotic habitats had the following characteristics: (5) water high carbonate, (6) moderate dissolved oxygen, and (7) low dissolved oxygen. Finally, the last sub-habitat was represented by (8) high-altitude streams independent of epigeal or subterranean populations. This classification is the most detailed analysis across a large region, allowing us to propose six general characteristics of the habitats of these organisms: (1) tropical rivers, (2) altitude ranges from 50 to 850 meters above sea level, (3) mainly tectonic faults (springs, primary rivers, and caves), (4) preferably rich in oxygen, (5) with riparian arboreal vegetation, and (6) on the Atlantic slope with karstic origin. As a result, few sites were recorded where these species coexisted with another *Macrobrachium* species (those with complete larval development species; specifically with *M. carcinus* and *M. olfersii*). In general, all sites are clean without records of pollutants both solids and dissolved. These freshwater shrimp with abbreviated larval development are preferentially distributed in areas where these amphidromous shrimps do not live because the amphidroms are predators of the abbreviated development shrimps. As a result, the abbreviated development shrimps have a microdistribution in each hydrological basin that is limited to the primary rivers and springs where species of amphidroms cannot migrate as it has been invariably reported in different species [10, 20–23]. Our analysis shows that even on a small scale, multiple environmental factors define not only the sub-habitats within lotic or lentic areas but even the differences within and among springs, primary streams, or caves. Consequently, we infer that *Macrobrachium* species are not only plasticity in the morphological traits as has been in another papers, but this plasticity extends to their habitat requirements with oxygen dissolved potentially being more important than even light or temperature. However, if the freshwater prawns of the genus *Macrobrachium* can be so specific to live in certain sub-habitats, this also makes them vulnerable to a such changing environment and so exposed to pollution due to the increase of wastewater or the disappearance of these tropical rivers, given the demand for drinking water by humans. Thus, monitoring of these habitats and especially dissolved oxygen levels is encouraged for the protection of these species.

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