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Toward an Integrative Overview of Stygobiotic Crustaceans for Aquifer Delimitation in the Yucatan Peninsula, Mexico

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Abstract: The Yucatan Peninsula (YP) presents heterogeneous environments in a karstic landscape that has been formed from permeable sedimentary rocks dating from the Cretaceous period. Its aquifers now face significant pressure from tourism, agriculture, soil use changes and population growth. Aquifer delimitation typically relies on environmental and socioeconomic criteria, overlooking the subterranean fauna. Stygobiotic crustaceans are highly diverse in the YP's subterranean karstic systems, expressing adaptations to extreme environments while often also displaying the primitive morphology of evolutionary relics. With distributions restricted to specific environments, they are potential markers of water reserves. A literature review recovered records of 75 species of crustaceans from 132 subterranean systems in the YP, together with geomorphological, hydrological, hydrogeochemical and historical precipitation data. Fourteen UPGMA clusters were informative for mapping species composition, whereby the "Ring of Cenotes", "Caribbean Cave" and "Cozumel Island" regions were delineated as consolidated aquifers. These aquifers are distinguished by abiotic factors as well: freshwater species dominate the Ring of Cenotes, while marine-affinity species characterize the Caribbean Cave and Cozumel Island aquifers. Stygobiotic crustaceans, being linked to geologically ancient water reserves and having a restricted distribution, offer a complementary tool for aquifer delimitation. Their presence suggests long-term and stable water availability. The use of these unique organisms for integrative aquifer delimitation can provide a way to improve the monitoring networks of regional aquifers.

Keywords: aquifers; Yucatan Peninsula; stygobiotic crustaceans; subterranean systems

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1. Introduction

Biodiversity in groundwater environments is comprised of fauna incidentally associated with subterranean water systems (stygoxenes), fauna normally inhabiting both epicontinental and subterranean water systems (stygophiles), and fauna exclusively inhabiting subterranean water environments (stygobionts) [1]. This last group live in extreme, generally hypoxic environments with a total absence of sunlight [1,2] and require specific adaptations such as loss of pigmentation, reduction or loss of eyes, enhanced setation and reduced metabolism, among other unusual features [3]. In general, crustaceans are among the most diverse groups dwelling in subterranean environments, representing approximately 60% of the subterranean species richness worldwide [4,5]. Stygobiotic crustaceans tend to display primitive tagmosis with fused thorax and pleon (or abdomen) and multi-segmented appendages. They also tend to have restricted distributions, with strictly endemic forms being common [1].

In the Yucatan Peninsula (YP), more than 71 stygobiotic species have been recorded in 10 phyla: Porifera, Cnidaria, Gastrotricha, Tardigrada, Nematoda, Annelida, Arthropoda, Mollusca, Echinodermata, and Chordata. Studies by Angyal et al. (2020) [3], Álvarez et al. (2023) [4], Calderón-Gutiérrez et al. (2017) [5], Durán & Álvarez (2021) [6] and Iliffe (1992, 2002) [7,8] have contributed the understanding of the stygobiotic faunal diversity in the region for over the last 30 years. In particular, different researchers have inventoried 29 [7], 47 [5] and 55 [4] species of stygobiotic crustaceans there. The resulting taxonomic catalogs have revealed general distributional patterns, including a notable increase in locally endemic species. The YP, with the world's largest karstic aquifers, is considered one of the most aquatically biodiverse regions of Mexico [9]; nevertheless, an integrated understanding of these aquifers has yet to be achieved.

In this paper, the term "aquifer" is conceptualized in an ecological and socioeconomic context based on the systemic approach, as a porous rock mass that can store, discharge and transfer a significant amount of water, thereby satisfying consumers' needs [10–12]. Until now, few studies of aquifers have attempted to integrate their abiotic components with biotic ones, such as the stygobionts, to establish criteria for delimiting aquifer boundaries and designing monitoring networks for them [6]. In the YP, for example, CONAGUA (2021) [13]—the Spanish acronym for the National Water Commission—has delimited four aquifers based on studies related only to geology [14], edaphology (including geopedomorphology) [15–17], hydrology [18,19] and hydrogeochemistry [20,21], but not the region's stygofauna.

Although there are more than 2000 confirmed sources of natural groundwater in the YP, including those used for different anthropogenic activities, less than 5% of them have been biologically inventoried [3]. Consequently, from the point of view of conservation and sustainable management, only a fragmented and generalized understanding of the local water resources exists. Combined with the standardized and not always locally appropriate environmental legislation that is in force over all the Mexican territory, this could lead to misconceived management practices and water resource use in this region.

The present study is an attempt to integrate information on certain biological aspects of the YP's subterranean waters (presence/absence and specific composition of stygobiotic crustaceans) and various abiotic components including geomorphology, geology, edaphology, hydrology along with historical patterns of precipitation, including the general socioeconomic water uses. Inasmuch as the highly endemic distributional patterns of such crustaceans [1] are per se indicative of differences in water conditions [22]. Inclusion of biotic data may potentially lead to new proposals for delimiting aquifer boundaries. Such an integrated approach could improve the management of water resources in areas with high socioeconomic activity [18,23] and resultant anthropogenic pressure on the aquifers primarily related to tourism, agriculture, changes in landscape use and population growth [15,24,25].

2. Materials and Methods

2.1. Study Area

The YP is composed mainly of heterogeneous karstic landforms formed by the erosion and dissolution of different strata of permeable sedimentary rocks that were laid down during the Cretaceous period (60 ma), late Pliocene and Pleistocene epochs (5.6 to 3.5 ma) and the Holocene period (1.8 ka) [15,24]. The region features many subterranean (or groundwater) habitats such as underground rivers, dry and submerged caves, and water-filled sinkholes, locally called "Cenote" from the Mayan word "Dzonot", meaning "holes with water". Chemical reactions between rainwater or saltwater and carbon dioxide result in the formation of carbonic acid and the dissolution of calcareous rock, a process referred to as karstification. Depending on the nature of the water source, these habitats can be classified as freshwater (rainwater only), marine (intrusive saltwater only) or anchialine (a combination of both) [26].

Because of the karst's permeable rocks, the YP has no important surface rivers [18,20]. The biggest surface water system is the Rio Hondo in the south of Quintana Roo state, where it serves as the border between Mexico and Belize [21]. Consequently, the hydrology of the YP depends mainly on subterranean water systems divided between four aquifers according to CONAGUA [13]: Yucatan Peninsula, Hills and Valleys, Xpujil, and Cozumel Island, which provide several ecosystemic and socioeconomic services for the more than 4,500,000 people who live-in the region [18,23]. These involve water resources for agriculture, industry, households and tourism-related activities in the three states that compose the YP: Quintana Roo, Yucatan and Campeche (Figure 1).

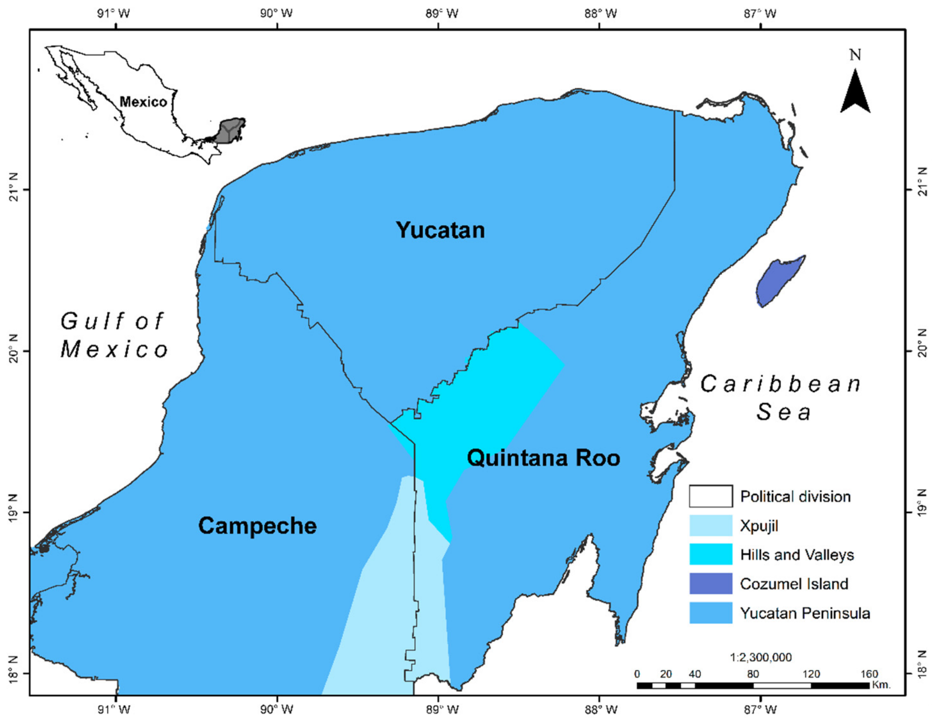

Figure 1. Study area showing the aquifers delimited by CONAGUA and the political divisions of the Yucatan Peninsula, composed of the states of Yucatan, Campeche and Quintana Roo.

2.2. Data Analysis

Based on a literature search for available records of stygobiotic crustaceans in the YP, related to data from relatively well-studied habitats, a database was created. Published literature compiled by Álvarez et al. (2023) [4], Angyal et al. (2020 a, b) [3,27] and Calderón-Gutiérrez et al. (2017) [5] was consulted, as well as specialized books, book chapters and journal articles listed in various online sources, including Web of Science, Google Scholar, Scopus, the World Register of marine Cave Species (WoRCS, https://www.marinespecies.org/worcs/ accessed on 27 November 2024) and the World Register of Marine Species (WoRMS, https://www.marinespecies.org/ accessed on 27 November 2024). New stygobiotic crustaceans recorded after 2022 from anchialine environments in the YP were also included. The finished database (Tables S1 and S3) includes taxonomic information for crustaceans of every rank from class to species as well as the name of each sampling site with its geopositional data and information as to the presence of fresh or salt water there [28]. Additionally, physicochemical variables of the water were recorded when available.

PAST 4.03 software was used to compute similarities in species composition between sites for cluster analysis (useful for identifying groups containing species with distributions limited to a specific area) with the unweighted pair-group method using the arithmetic averages (UPGMA) method and the Dice-Sørensen coefficient (DS). This coefficient, which takes the double occurrence of species in the matrix into account, is generated with the following equation [29–31]:

$$DS = 2a/2a + b + c$$

where a represents the number of species in the first pair-group, b represents the number of species in the second pair-group and c represents the number of shared species present in both groups.

The similarity percentages test (SIMPER) was used to infer which species were present in various groups, versus being restricted to a single group or being an isolated entity. The complete results of this test are shown in Table S2.

Group delimitation was performed using the similarity profile test (SIMPROF) in PRIMER v6 [31], based on an average of 1000 permutations with a significance level of $\alpha = 0.05$. For a better understanding of crustacean-specific group composition, the stygobiotic crustacean groups inferred on the basis of the SIMPROF test were mapped using QGIS version 3.40.1 on the geomorphological model of the YP proposed by Bautista (2023), with the following concepts used in this study [15].

Karst controlled by buried morphostructure is related to the buried crater structures resulting from the Chicxulub impact that was later filled with relatively young rock formations in the Middle Miocene; incipient karst: karstic formations dating from the Pleistocene (1.8 ka) [24]; juvenile karst: karstic formations dating from the Pliocene (3.5 ma); karst with good drainage is related to karts covered mainly with thick shapes of vertisols and luvisols soils; karst with poor drainage is related to karst covered only with leptosols; paludal karst: karstic formations in waterlogged formations; and tectono-karst: kastic formations surrounded by tectonic faults.

2.3. General Characterization of Aquifers

Published information on the abiotic, biotic and anthropogenic components, which in combination constitute the systemic aquifer concept, was consulted. For the abiotic components, features related to geology, geomorphology, edaphology and hydrology were defined according to Bauer-Gottwein et al. (2011) [24], Bautista (2023) [15], Fragoso-Servón et al. (2016) [32], Hernández-Flores et al. (2021) [23], López-Ramos (1975) [14], Perry et al. (2002) [20], Ríos-Ponce et al. (2020) [18] and Sánchez-Sánchez (2015) [21]. For the biotic components, the endemic species inhabiting the area were listed according to the SIMPER test when specialized literature provided corroboration of endemism. The anthropogenic components considered here were the main socioeconomic activities, with water extraction sites and volumes consumed being obtained from Arroyo-Arcos et al. (2021) [33], Bautista (2023) [15], Estrada-Medina (2019) [17], Haro-Zea et al. (2021) [34] and CONAGUA (2021) [13]. Finally, historical precipitation data (averages from 1902–2011) from Ríos-Ponce et al. (2021) [18] were considered, along with the average annual rates of water extraction and use for Cozumel Island from Hernández-Flores et al. (2021) [23].

3. Results

The database created from published literature lists a total of 75 stygobiotic crustacean species—representing five classes, 15 orders, 34 families, and 49 genera—from 132 subterranean aquatic sites in the YP. Most of them have been recorded in the northern part of the peninsula, which is characterized by incipient and young rocks (1.8 ka) as well as older karstic formations (3.5 ma), and in particular from the Ring of Cenotes area of Yucatan state, where the karst is controlled by buried morphostructure. In contrast, the north coast of Quintana Roo and Cozumel Island is characterized by paludal karst. In those places there are records of stygobiotic crustaceans inhabiting karstic environments with good drainage that date from over 5.6 ma.

Cluster analysis of the crustacean fauna of 132 subterranean aquatic sites revealed a total of 14 groups (Figure 2), each of which is internally similar according to the SIMPROF test (Pi = 0.925, $p = 0.01$). In addition, some sites characterized by few species records and no species overlap with other subterranean systems represent isolated entities. SIMPER analysis identified species commonly shared among various groups in the YP (species names marked in bold in Table S2). They include the isopod *Creaseriella anops*, with 7.9% similarity. The amphipod *Tuluweckelia cernua* contributed 5.0%, and the decapods *Creaseria morleyi* and *Typhlatya mitchelli* 5.30% and 4.58%, respectively. The mysids *Antromysis cenotensis* (5.18%) and *Stygiomysis cokei* (3.37%) were also well distributed. Finally, the thermosbaenacean *Tulumella unidens* had a similarity value of 3.37%. Conversely, some species infrequently or never occurred outside a single locality (Tables S2 and S3). Among these are the copepod *Stephos fernandoi* (0.22%) and the remipedes *Xibalbanus cozumelensis* (0.24%) and *X. fuchscockburni* (0.47%).

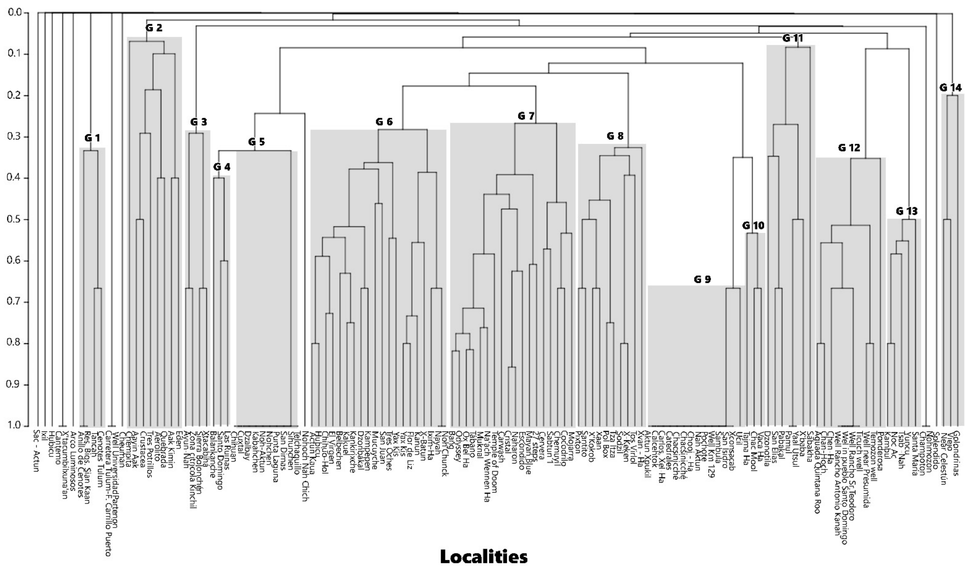

Figure 2. UPGMA clusters inferred with the Dice-Sørensen coefficient for 132 subterranean aquatic systems and 75 stygobiotic crustacean species from the Yucatan Peninsula. Similarity scales represent the similarity between groups, range from 0.0 (no similarity) to 1.0 (complete similarity). Groups were discriminated using the SIMPROF test. G = Group.

In the cluster analysis, Groups 1 and 10 consist of species that are restricted to the northeast coast of the YP, while the species in Group 2 occur only on Cozumel Island. Both regions are characterized by incipient and paludal karst formations and express the highest pluvial precipitation in the entire region (annual mean rainfall: 1200–1500 mm) (Figures 3 and 4). These three groups show marine affinities and include numerous decapods (n = 9) and amphipods (n = 7). Notable species include the shrimps *Agostocaris zabaletai* and *Triacanthoneus akumalensis*, alongside endemic species such as remipedes of the genus *Xibalbanus* (SIMPER values: 0.24–0.47%). The copepods *Stephos fernandoi* and *Exumella tsonot* also have low SIMPER values (0.01 and 0.03%, respectively). The amphipod *Bahadzia bozanici* stands out with a SIMPER value of 0.9% (Tables S2 and S3). The restricted distributions of species in these groups suggests isolation of the water reserves or aquifers in the northeast and Cozumel from those in the rest of the YP.

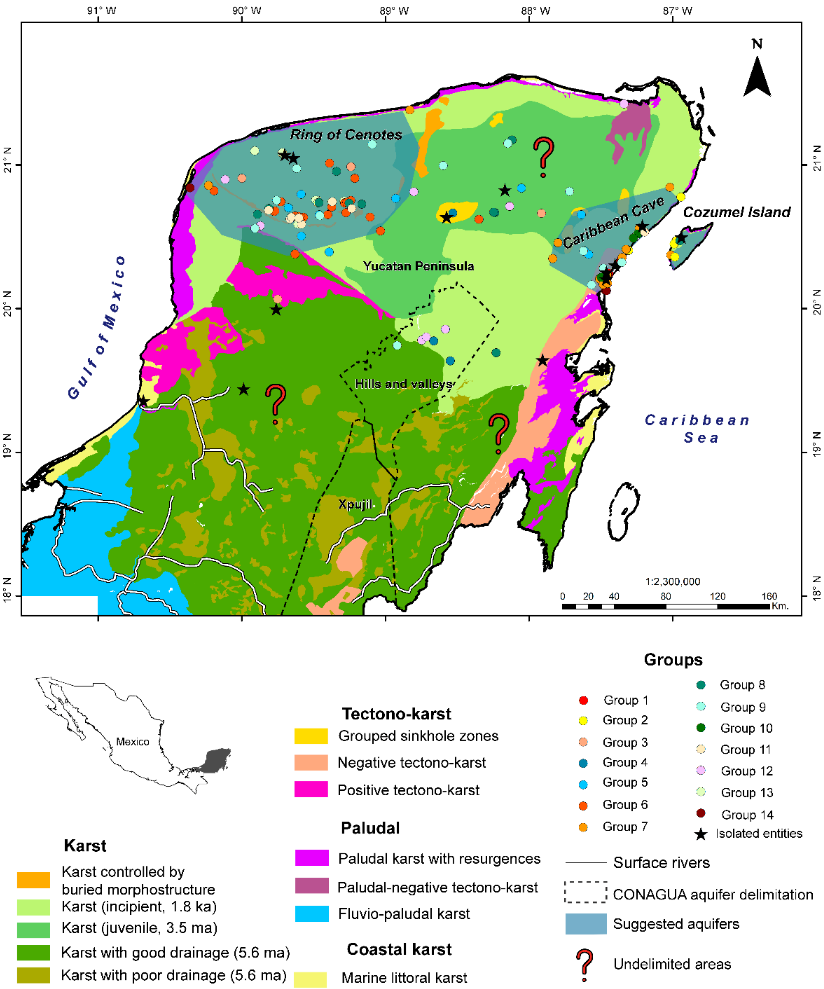

Figure 3. Species composition according to UPGMA cluster analysis using the Dice-Sørensen coefficient. The geomorphological representation is modified from Bautista (2023) [15], and the aquifer delimitation is based on CONAGUA (2021) [13].

Groups 7 and 14 are well differentiated and are distributed mainly alongon the coasts of the eastern region of the YP in the paludal karst (Figure 3), with few records from the western coast. These areas are characterized by the region's lowest pluvial precipitation (mean annual rainfall: 600–800 mm) (Figure 4). The ostracod *Spelaeoecia mayan* and the copepods *Mexicophria cenoticola* and *Urocorycaeus lautus*, which are associated with intrusive sea water, are restricted to these areas.

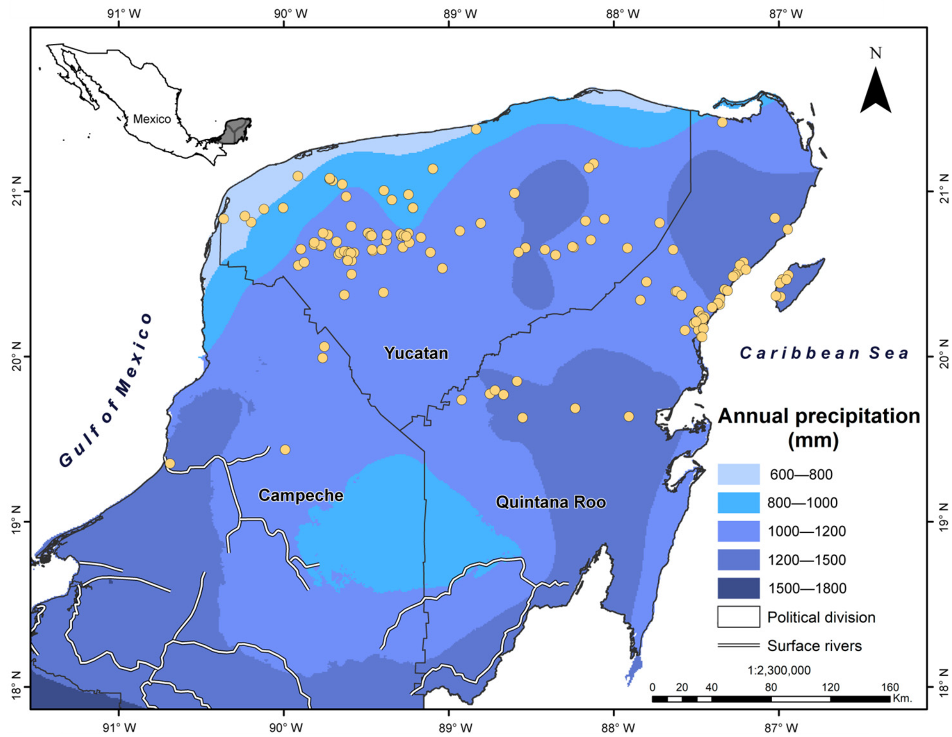

Figure 4. Catalogued subterranean aquatic systems where stygobiotic crustaceans have been recorded in the Yucatan Peninsula. Annual precipitation (mean from 1902–2011) data were modified from Ríos-Ponce et al. (2020) [18].

Groups 6, 11, and 13 are primarily composed of widespread species found across the YP, while some species are restricted to areas associated with karst formations influenced by buried morphostructure and incipient karst (Figure 3). Notable examples include the copepods *Diacyclops chakan*, *Halicyclops cenoticola*, *Mesocyclops chaci*, *Mesocyclops yutsil* and *Prehendocyclops* spp., as well as the isopod *Haptolana bowmani*. These all contribute to a distinct species composition at the relevant sites compared to the eastern regions of the YP.

The remaining Groups (3, 4, 5, 8, 9 and 12) show no clear geographic distribution within the study area, and most of the species comprising them are widely distributed in the YP. Nevertheless, sites from Groups 5 and 9 present the only localities of the isopods *Creaseria morleyi* and *Creaseriella anops*, respectively (Figure 2, Tables S1 and S3), and a few species in the remaining groups are known from either specific sites or single records, e.g., the cladoceran *Streblocerus pygmaeus* and the copepod *Parapseudoleptomesochra subterranea*.

The 12 "isolated entities" discussed above were found scattered around the YP, or with records restricted to a single site featuring species such as the atyid shrimp *Typhlatya campecheae*, catalogued only on areas with good drainage in Campeche state (Figure 3, Table S3).

Species with a restricted distributions within Groups, such as those from Groups 1 and 10 on the east coast of the YP (Caribbean Cave area), Groups 6, 11 and 13 in the Ring of Cenotes area, and Group 2 on Cozumel Island, may be informative for proposing a new and more precise delimitation of the boundaries of aquifers in the YP than CONAGUA's [13] statement (Figure 1). Each of the three proposed aquifers can be mapped (Figure 3: highlighted in light blue) and characterized in terms of its abiotic and biotic features (Table 1). One, named the "Ring of Cenotes", is located within the karstic area controlled by buried morphostructure. Another, named "Caribbean Cave," is located in the northeastern coastal area of the YP. The third one, named "Cozumel Island", underlies that island. These aquifers' names are based on the distributional areas of the stygobiotic fauna, which are coincident with those proposed previously by Álvarez et al. (2023) [4].

Table 1. General characteristics of the proposed aquifers.

Component	Feature	Ring of Cenotes *	Caribbean Cave *	Cozumel Island *
Abiotic	Geology	Formation corresponding to the Late Cretaceous Chicxulub crater [24,35]. Combination of Miocene-Pliocene, Oligocene and Eocene sedimentary rocks [14].	Miocene-Pliocene and patches of Quaternary sedimentary rocks [14].	Developed by block-faulting in the Late Mesozoic and Cenozoic [23]. Miocene-Pliocene sedimentary rocks [14].
	Geomorphology [15]	Incipient karst and karst controlled by morphostructure.	Negative tectono-karst, paludal karst with resurgences, incipient karst, and grouped sinkhole zones.	Paludal and incipient karst.
	Edaphology	Carbonate rocks ($CaCO_3$) from the early Tertiary period, with high permeability [20], mainly composed of leptosols [15].	Soils dominated by pure leptosols, with areas containing a combination of leptosols with luvisols and vertisols [32].	Limestone composed of leptosol with patches of gleysol and arenosol [23].
	Hydrology	Mean annual precipitation 600 to 1200 mm [18]. Water composed of $CaCO_3$ and $CaMg(CO_3)_2$ ions [20]. Halocline may be present in subterranean ecosystems with a depth of more than50 m [3,20].	Mean annual precipitation 1200 to 1800 mm [18]. Heterogeneity of $CaHCO_3$, mixed CaMgCl, $CaSO_4$ and NaCl, contributing to rapid erosion and the development of extensive anchialine environments along the fractures [21].	Mean annual precipitation 1400 to 1500 mm [23] Water composed of $Ca(HCO_3)_2$, characterized by heterogeneous environment with unconfined and highly permeable rocks [23].
Biotic	Endemic stygobiotic crustaceans	Freshwater species *Diacyclops chakan* [36]. *Halicyclops cenoticola* [37]. *Mesocyclops chaci* [36]. *M. yutsil* [36]. *Prehendocyclops abbreviatus* [38]. *P. boxshalli* [38]. *P. monchenkoi* [38]. *Haptolana bowmani* [39].	Mainly species with marine affinities *Bahadzia bozanici* [4]. *Hyalella azteca* [5]. *Exumella tsonot* [40]. *Triacanthoneus akumalensis* [41]. *Xibalbanus fuchscockburni* [42]. *X. tulumensis* [42].	Mainly species with marine affinities *Agostocaris zabaletai* [43]. *Anchialinocaris paulini* [43]. *Bahadzia bozanici* [44]. *Cirolana adriani* [45]. *Procaris mexicana* [46]. *Pseudopolycope helix*. *Speleophria germanyanezi* [47]. *Stenopus hispidus*. *Stephos fernandoi* [48]. *Xibalbanus cozumelensis* [49].

Table 1. *Cont.*

Component	Feature	Ring of Cenotes *	Caribbean Cave *	Cozumel Island *
Anthropogenic	Socioeconomic activities	Agriculture, pig farming, industrial use (beverage bottling), national projects (Tren Maya) [15,17].	Tourist activities (cenote snorkeling-diving), national projects (Tren Maya) [15,33].	Tourist activities (cruise ships, sun and beach, reef diving) [34].
	Water uses and average annual extraction	Mean total extraction: 859,919,519.57 m^3/year. Three main socioeconomic activities requiring high amounts of water extraction: agriculture, urban use, and industrial [13].	Mean total extraction: 907,712,597.72 m^3/year. Three main socioeconomic activities requiring high amounts of water extraction: services, urban use, and aquaculture [13].	Estimated mean extraction: 4,149,684 m^3/year. Three main socioeconomic activities requiring high amounts of water extraction: commercial, hotels and domestic [23].

* Aquifer names proposed by Álvarez et al. (2023) and adopted herein are based on the stygobiotic crustaceans.

4. Discussion

Stygobiotic crustaceans with restricted distributions can be used as complementary evidence for an integrative aquifer delimitation. They have probably been associated with subterranean waters for long periods of geological time and inhabit areas with a long-term stable supply of water. Within the YP, hydrological conditions in different areas are not uniform due to the heterogeneity of environmental conditions. Tectonic faults, different types of sinkholes produced by karstification processes (depending on proximity to or distance from the coast) and diverse rock and soil types will be involved in the differentiated capture, absorption and infiltration of recharge water for the aquifers [20,21,24].

Stygobiotic crustaceans in the YP include both freshwater forms and species of marine origin. Although all stygobiotic crustaceans have been recorded in juvenile and incipient karstic environments (Figure 3), most of the purely freshwater forms are found in the northern area of the YP near the Ring of Cenotes, where the karst is controlled by buried morphostructure. Species with freswater and saltwater affinities are found in paludal karst with resurgences [15], which are areas with anchialine habitats, and a halocline generally found at 18 m depth in the water column [24].

Several hypotheses have been proposed to explain the distributional patterns of stygofauna across the world, frequently invoking Tethyan distributions, marine regressions, deep-sea origins and active and passive migration [50]. For the subterranean crustaceans of the YP, one of the most popular theories relies on marine regressions and transgressions during the Tertiary period [Paleocene (65 ma) to Pliocene (7 ma)], when different areas of the region were sometimes exposed to form barriers that prevented the dispersal of aquatic species [51]. Considering the freshwater crustaceans associated with the Ring of Cenotes, for example, this theory maintains that mysid species such as *Antromysis cenotensis* became confined there after a series of regressions and transgressions. According to this theory, amphipods such as *Mayaweckelia cenoticola*, *M. yucatanensis* and *Tuluweckelia cernua* entered the YP from the sea at the beginning of the Quaternary period and, similarly to the now widespread isopods *Metacirolana mayana* and *Creaseriella anops*, became more associated with freshwater habitats than marine environments [52].

The aquifer subdivisions proposed in this study are the result of integrally considering abiotic, biotic and anthropogenic components (Table 1). The species distributions (freshwater vs. marine affinities) are related to the ionic composition of the subterranean water at the respective sites, as reported by Suarez-Moo et al. (2022) [22]. The majority of inland sinkholes are exclusively freshwater whereas those close to the coast display a marked vertical stratification of surface freshwater and deeper saltwater. In consequence, compared to inland sinkholes, the ichthyofauna and invertebrate diversity of coastal sinkholes are more similar to those of marine environments, a situation that agrees with the present study's findings for crustaceans. It was found that inland aquatic systems in the northern part of the YP harbor stygobiotic crustaceans with freshwater affinities, whereas in near-coastal systems the stygobiotic crustaceans show a clear affiliation with coastal marine environments.

The Ring of Cenotes aquifer mainly contains dissolved $CaCO_3$ [21,23], which is typical of freshwater environments [20]. In contrast, the Caribbean Cave and Cozumel Island aquifers in paludal karst have a different ionic composition, a mixture of $CaHCO_3$, CaCl, MgCl, $CaSO_4$ and NaCl, due to their proximity to the coast [15].

Álvarez et al. (2023) [4] and CONAGUA [13] classified Cozumel as a zone and aquifer respectively independent from the continental part of the YP. Aside from the physical separation of the island, its rocks—calcarenites formed during the Quaternary period (2 ma to 1 ka) from cemented fragments of shells deposited on the shore [23]—are among the youngest in the YP—. Cozumel's insular character might explain why it has several endemic crustacean species of marine origin, including the remipede *Xibalbanus cozumelensis*, the copepods *Stephos fernandoi* and *Speleophria germanyanezi* and the decapods *Agostocaris zabaletai* and *Anchialinocaris paulini* [5]. Similarly, the Caribbean Cave aquifer is inhabited exclusively by the remipedes *Xibalbanus fuchscockburni* and *X. tulumensis*, the amphipods *Bahadzia bozanici* and *Hyalella azteca*, the copepod *Exumella tsonot* and the decapod *Triacanthoneus akumalensis*. Conversely, the Ring of Cenotes (approximately 200 km from the two former aquifers, as shown in Figure 3) species with freshwater affinities such as the copepods *Diacyclops chakan*, *Halicyclops cenoticola*, *Mesocyclops chaci*, *M. yutsil*, *Prehendocyclops abbreviatus*, *P. boxshalli*, and *P. monchenkoi*. All the latter species are only distributed at sites within the same aquifer, which means that they do not spread to other aquifers. This supports the assumption of a limited distribution of crustaceans due to geological isolation.

Although some studies in the YP have made physicochemical measurements of the water, in most cases there has been no standardization of the addressed parameters nor of sample depth. This makes it difficult to gain a general perspective of role of the water in defining the diversity and distribution of the YP's stygofauna. Future research should include a detailed descriptions of water sampling (incorporating as many variables as possible, along with site-specific data such as depth and geolocation) in an effort to standardize methodologies and foster an integrative approach to aquifer management.

The stygobiotic fauna remains unknown in some regions of the YP (question marks in Figure 3). One area is the northern part of Yucatan state, where there are many subterranean water systems [20], juvenile karst is predominant, including some patches of grouped sinkhole zones and the paludal-negative tectono-karst (Figure 3) [15], and water extraction for livestock is important [13]. Similar uncertainties exist in the southeastern and southwestern areas of the YP, with respect to karst with poor and good drainage, including areas classified as positive tectono-karst.

The deficit in studies of the stygobiotic fauna there is mostly due to difficulties in accessing the relevant sites [53]. As for the broader picture, Angyal et al. (2020) [3] stated that less than 5% of the known subterranean ecosystems in the YP have been biologically inventoried. Although this region is considered the most diverse in Mexico [9], with 15 orders containing 34 families of stygobiotic crustaceans, these records could be expanded with other groups that have not yet been recorded or catalogued in the region, such as the malacostracan order Bathynellacea, which commonly inhabit springs, wells, caves, and rivers in Australia and some regions of Europe [54]. However, future investigations will reveal whether they also occur in the Yucatan peninsula caves, as the closest records of the family Parabathynellidae are found in Texas, USA, in karst and non-karst landscapes [55].

The results of this study support the idea of routinely using additional collection techniques to survey stygobiotic microcrustaceans with a body length of less than 1 mm, such as copepods and ostracods, which are usually more species-rich than macrocrustaceans such as malacostracans, but usually go unnoticed [56]. Collecting only crustaceans that are over 2 cm in size, such as amphipods, isopods, mysids, decapods and thermosbaenaceans, is insufficient to provide a complete picture.

On the assumption that stygobiotic species with restricted distributions are likely to be associated with water bodies with ancient geological histories and a degree of stability, we propose that the sites of stygobiotic crustaceans revealed by comprehensive sampling can be used as a complementary criterion for delimiting aquifer boundaries. Adding such data to the environmental criteria that are currently in use will allow more informed management and conservation decisions in areas with high human impact. These impacts include: massive pig and poultry farms, water-intensive agriculture and the use of pesticides in the northern YP [15,17]; high tourist pressure, including cave diving, on cenotes and anchialine systems; and national infrastructure projects such as the completion of the peninsular railroad "Tren Maya", which will attract more visitors demanding water resources but at the same time affect vulnerable fragile environments such as karstic aquifers. It may also be used eventually to assign "isolated entities" to larger aquifers as the true ranges of current "local endemics" become clear in such locations and more species are recorded from there [44] (Figures 2 and 3; Supplementary Material Table S2).

5. Conclusions

This study represents a significant step toward an integrative vision for aquifer delimitation in the YP by considering biotic and abiotic components.

The presence of stygobiotic crustaceans with restricted distributions can be used as complementary evidence for aquifer delimitation, when considering species with restricted distributions, as they are likely to be associated with water from ancient geological periods, indicating areas that could be stable.

The three proposed aquifers (Ring of Cenotes, Caribbean Cave and Cozumel Island) demonstrate distinct biotic and abiotic characteristics that reflect unique hydrological, geological and anthropogenic contexts. The Ring of Cenotes is characterized by freshwater systems with endemic species linked to ancient water stability, nonetheless, disturbed by socioeconomic activities such as agriculture and industry. The Caribbean Cave aquifer hosts a mixure of freshwater and marine species influenced by its proximity to the coast and stratified waters. Cozumel Island is characterized by its marine affinities and a high degree of endemism. It was formed by geological isolation and a younger age of formation than the rest of the YP and is currently dominated by tourism.

The results highlight the heterogeneity of the YP's groundwater systems as revealed by the species composition of their stygobiotic crustaceans. This assessment makes it possible to contribute biotic data to the paradigms for aquifer delimitation. Namely, CONAGUA's current concept of four aquifers can be refined under a new systemic approach involving the diversity and restricted distributional patterns of the groundwater species. This in turn can lead to more informed decision-making regarding water use and management in different areas of the YP.

Many knowledge gaps remain concerning the distribution and composition of stygobiotic species, including crustaceans, in various regions of the YP. More collecting and a greater monitoring effort are essential and should be focused on unexplored areas such as the northern and central YP—characterized by juvenile karst—and zones of grouped sinkholes, along with other areas where future knowledge of the stygobiotic fauna may imply water reserves. Such sampling efforts should not only be limited to macrocrustaceans, but also to microcrustaceans such as copepods and ostracods, which are the most species-rich groups in these habitats.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d17020077/s1, Table S1: Database of stygobiotic crustacean records from the Yucatan Peninsula; Table S2: Similarity Percentage (SIMPER) test from stygobiotic crustacean species recorded in the Yucatan Peninsula, including values in each group inferred in the cluster analysis; Table S3: Known records of stygobiotic crustaceans in the Yucatan Peninsula, indicating the Similarity Percentage (SIMPER) of each species and their presence/absence in each group recognized by cluster analysis. FW = Freshwater, MW = Marine water, BW = Brackish water, IE = Isolated entities.

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