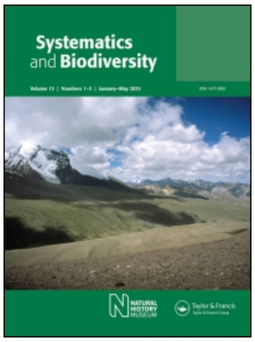

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Research Article

Biodiversity and biogeographic affinity of benthic amphipods from the Yucatan Shelf: an analysis across the warm Northwest Atlantic ecoregions

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The biodiversity and biogeographic affinity of benthic amphipods from the Yucatan continental shelf with the warm Northwest Atlantic ecoregions were analysed using species occurrence data from benthic marine habitats of the continental shelf (< 200 m). A comprehensive collection of distributional data (presence-only) was obtained from different sources and newly-sampled material and sorted according to 12 ecoregions from the Northwest Atlantic. Distribution of species richness, taxonomic distinctness, endemism, and spatial replacement was analysed across ecoregions. The faunal relationships among ecoregions were explored using a clustering analysis based on the Sørensen dissimilarity index, and a cladistic analysis of distributions and endemism based on parsimony. Results from the Yucatan shelf showed a representative species pool from the highly diverse Northwest Atlantic amphipod fauna (202 spp.), with intermediate levels of endemism and taxonomic distinctness. Results from dissimilarity and parsimony showed two groups of amphipod assemblages consistent with two of the main biogeographic provinces in the Northwest Atlantic: Carolinian and Caribbean. The incorporation of the Yucatan shelf species assemblage, as an ecoregion into the used classification scheme, had implications on the amphipods biogeographic affinity identification. The Yucatan ecoregion led to a latitudinal spatial replacement of amphipod species across ecoregions and provinces, revealing that the Yucatan ecoregion has a higher biogeographic affinity with tropical ecoregions of the Caribbean province. The spatial replacement of amphipods suggests that the Southern Gulf of Mexico ecoregion has a higher affinity with warm-temperate ecoregions of the Carolinian province and is proposed as a transitional zone between the identified provinces.

Key words: Amphipoda, Caribbean Sea, endemism, macroinfauna, province, tropic

Introduction

Knowledge of species distributions constitutes the basis for establishing marine ecoregions (Spalding et al., 2007; Costello et al., 2017), providing information to establish the geographic extension of species for conservation (Briggs & Bowen, 2012; Robertson & Cramer, 2014), and contributing to understanding the potential drivers on bioregionalisation, such as environmental filters or historical events (Carrillo-Briceño et al., 2018; Williams et al., 2015).

The community assemblages from the warm Northwest Atlantic (wNWA) have been divided into small geographic units (ecoregions) (Spalding et al., 2007) that spatially form two broadly known biogeographic provinces: Carolinian and Caribbean. The latitudinal gradient in temperature through these provinces causes a warm-temperate condition on the Carolinian province and a tropical condition on the Caribbean province (Belanger et al., 2012; Neigel, 2009), that converges in the Gulf of Mexico (GoM) and influences the distribution pattern of marine species assemblages (Macpherson, 2002; Reuscher & Shirley, 2014). Preliminary findings on amphipod

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distribution from the GoM suggest that the species composition from the northern GoM shows affinity with the Carolinian ecoregion, and species composition from the southern GoM with Caribbean ecoregions (Paz-Ríos et al., 2014; Paz-Ríos & Ardisson, 2013; Raz-Guzmán & Soto, 2017; Winfield et al., 2007). A close analysis of the geographic distribution trends of amphipods from the Caribbean Sea has shown a significant similarity in species composition among ecoregions, even in those geographically distant, such as the Western Caribbean and Southern Caribbean ecoregions (Martín et al., 2013; Miloslavich et al., 2010). This high resemblance suggests a homogeneous species composition, with species widely distributed throughout the Caribbean province. The known distribution of amphipods in the wNWA shows evidence regarding the faunal affinity among ecoregions, and the similarity in species composition suggests a concordance with the biogeographic provinces. However, aspects such as scarce species inventories, information mostly generated on shallow coastal habitats, and the limited representation of some ecoregions do not allow for establishing a clear biogeographic regionalisation.

The first insight on the biogeographic affinity of the benthic amphipods from the Yucatan continental shelf (YCS) with tropical areas from the wNWA suggests affinities with both the Carolinian and Caribbean provinces (Paz-Ríos & Ardisson, 2013). The biological and ecological characteristics of amphipods (e.g., direct development, relatively high fecundity rates, local recruitment, limited capacity for dispersal, and extended parental care) suggest they are a feasible biological model to analyze biogeographic regionalization; furthermore, they have been used as potential ‘markers’ of Earth’s historical events (Arfianti & Costello, 2020; Copilaş-Ciocianu et al., 2020).

The delimitation of species assemblages by biogeographic provinces in the wNWA has been broadly described based on epibenthic taxa distributions (e.g., corals, decapods, echinoderms, fish, and molluscs) with a wide-range dispersal mode by pelagic larvae (Boschi, 2000; Petuch, 2013; Robertson & Cramer, 2014; Spivey, 1981; Veron et al., 2015). In contrast, for organisms from the benthic macroinfauna, mostly without pelagic larvae and with restricted dispersal (e.g., peracarid crustaceans), their regional-scale distribution in the wNWA has only been partially described in the geographic space. Main findings suggest the eastern US and northern GoM species composition have a higher affinity for the Carolinian province (Engle & Summers, 1999, 2000), and the southern GoM and western central Atlantic to the Caribbean province (Escobar-Briones & Soto, 1991; Kensley & Schotte, 1989; Sieg, 1986).

The YCS is a heterogeneous and dynamic marine region located at the eastern border of the Southern Gulf of Mexico ecoregion (see Spalding et al., 2007), in a transitional area mostly dominated by carbonated karst substrates, and the western border by terrigenous clastic substrates. These carbonated karst substrates represent a particular sedimentary feature that provide a diversity of bottom habitats and would contribute to highlight a higher biotic resemblance with the Caribbean’s ecoregions, as observed in the Florida and northwestern Cuba carbonated karst substrates that have similar karstic environmental characteristics and geological history (Cobiella-Reguera et al., 2015; Iturralde-Vinent, 2006). Here we examine the biodiversity and distribution of benthic amphipods from continental shelves across tropical and warm-temperate ecoregions to determine the biogeographic affinity of the YCS amphipod assemblage within a wNWA province.

Materials and methods

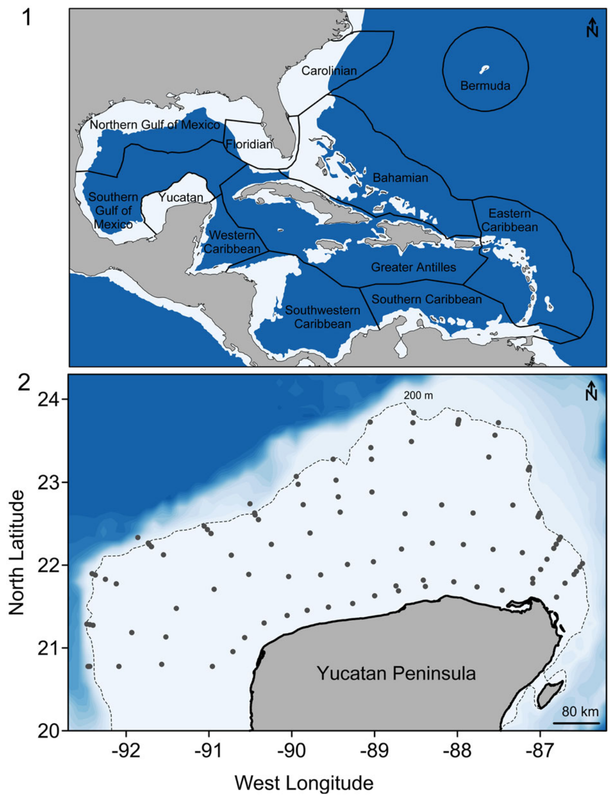
Study area

Eleven marine ecoregions defined by Spalding et al. (2007) were used (Fig. 1) as a basis to compare the affinities of the benthic amphipods from the YCS with the wNWA provinces. These ecoregions form part of the Warm Temperate Northwest Atlantic (Carolinian and Northern Gulf of Mexico) and Tropical Northwestern Atlantic (Bermuda, Bahamian, Eastern Caribbean, Greater Antilles, Southern Caribbean, Southwestern Caribbean, Western Caribbean, Southern Gulf of Mexico, and Floridian) provinces.

To test the biogeographic affinity of the YCS amphipod assemblage with the wNWA provinces, we included the Inner and Outer Neritic zone of the Campeche/Yucatanean coast from Cabo Catoche to the northern Terminos Lagoon (see Wilkinson et al., 2009), as an additional ecoregion representing the particular environmental and ecological characteristics of the YCS. The YCS is characterised by its seafloor geology (Iturralde-Vinent, 2006), based on carbonated karst sediments (Balsam & Beeson, 2003) and well-developed reef systems (Tunnell et al., 2007), dominant westward advective transport (Ruiz-Castillo et al., 2016), upwelling pulses (Jouanno et al., 2018), and the confluence of different oceanic water masses (Enriquez et al., 2013).

Data acquisition

The data used here include records of benthic amphipods from marine/coastal bottom habitats from the continental shelf (< 200 m). Three sources of information



Figs. 1–2. Study area in the Northwest Atlantic. (1) Ecoregions adapted from Spalding et al. (2007) and Wilkinson et al. (2009); and (2) sampling stations from three oceanographic campaigns (GOMEX 2010–2012) to the Yucatan continental shelf.

were used to compile information on benthic amphipods: i) published articles including faunal inventories, taxonomic, systematics, and biogeographic studies; ii) open-access records available at online repositories for biodiversity data, such as the Ocean Biogeographic Information System (OBIS), Smithsonian Invertebrate Zoology Collection of the National Museum of Natural History (NMNH), Invertebrate Collection of the Gulf Coast Research Laboratory Museum (GCRL), and National Information System on Biodiversity of Mexico (CONABIO-SNIB); and iii) information from newly collected material in three oceanographic campaigns on the YCS from 2010–2012 (Fig. 2).

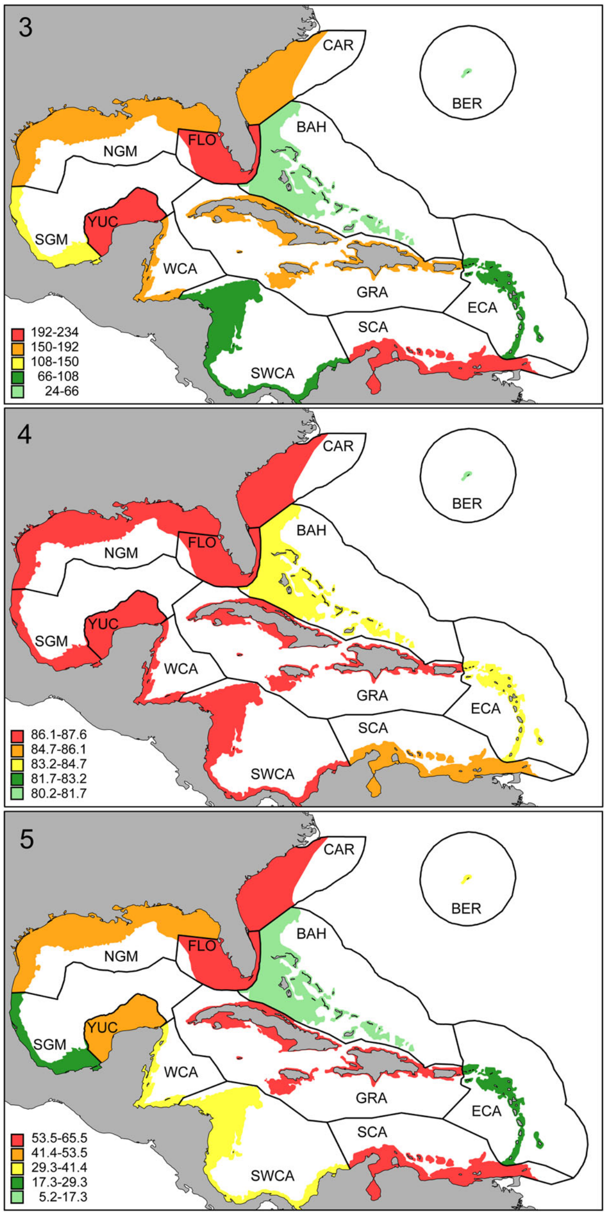
The species records from the different information sources were arranged into a presence/absence data matrix, as a function of the geographic distribution of each taxon by ecoregion. Each species information was revised to exclude any doubtful records from atypical habitats and distribution ranges. The most updated phylogeny proposed by Lowry and Myers (2017) was used for the systematic classification. The species names were verified and updated with the Taxon Match tool from the World Register of Marine Species (WoRMS, 2020), excluding synonymies and outdated taxonomic categories.

Data analysis

Species richness for each ecoregion was calculated from the total number of species recorded in each one. The average taxonomic distinctness index (AvTD) was calculated for each ecoregion using four categories of the systematics classification: species, genus, family, and suborder. The AvTD is the mean path length through the different taxonomic categories into a systematics classification that connects every pair of species in a faunal inventory, which allows for detecting species assemblages with highly variable categories (Clarke & Warwick, 2001). Endemicity for each ecoregion was obtained by calculating the weighted endemism index (Crisp et al., 2001), a measure that assigns a higher score to species with restricted distribution ranges.

A presence/absence data matrix was used to explore the relationship of species assemblages across ecoregions. The complete-link hierarchical clustering method, based on the Sørensen index, was used to determine the dissimilarity of species composition among ecoregions. This method enables the identification of different species assemblages within a biogeographic context (Vavrek, 2016), examining the distinctness in the composition among ecoregions. The differentiation in species composition of the generated cluster groups was examined using an analysis of similarity (ANOSIM) with 9999 permutations (Clarke, 1993). The relative contribution of the species turnover (β_{SIM}) and nestedness (β_{NES}) of the Sørensen dissimilarity index was analysed using the package betapart in R (Baselga, 2010; Baselga & Orme, 2012). The AvTD index and ANOSIM test were calculated using the PRIMER V7 software (Clarke & Gorley, 2006).

A cladistic analysis of distributions and endemism (CADE; Porzecanski & Cracraft, 2005), based on the parsimony criterion, was performed to identify the synapomorphies of the species composition and supraspecific taxonomic categories among ecoregions. The synapomorphies in the CADE represent geographic distributions consistently similar among taxa (i.e., shared exclusivity of taxa) that serve to recognize a spatial homology of the biota with a common biogeographic history (Morrone, 2014). The CADE includes species occurrence records and cladistic information of supraspecific taxonomic categories of the systematics classification of the amphipod assemblages, represented here by the genera, families, and suborders. A branch-and-bound search for parsimony analysis was performed in the PAUP software (Swofford, 1998). Before analysis,



Figs. 3–5. Geographic distribution of diversity descriptors in amphipod assemblages by ecoregion. (3) Species richness; (4) taxonomic distinctness; and (5) weighted endemism. Ecoregion: (BAH) Bahamian; (BER) Bermuda; (CAR) Carolinian; (ECA) Eastern Caribbean; (FLO) Floridian; (GRA) Greater Antilles; (NGM) Northern Gulf of Mexico; (SCA) Southern Caribbean; (SWCA) Southwestern Caribbean; (SGM) Southern Gulf of Mexico; (WCA) Western Caribbean; and (YUC) Yucatan.

one hypothetical area with absence of taxa (0) was incorporated in the data matrix for rooting the cladogram tree, and equal weight to characters (species) was assigned. The resultant cladogram was analysed using the MacClade software (Maddison & Maddison, 2001) to visualize the changes in taxa distribution (character optimisation) that define the tree topology.

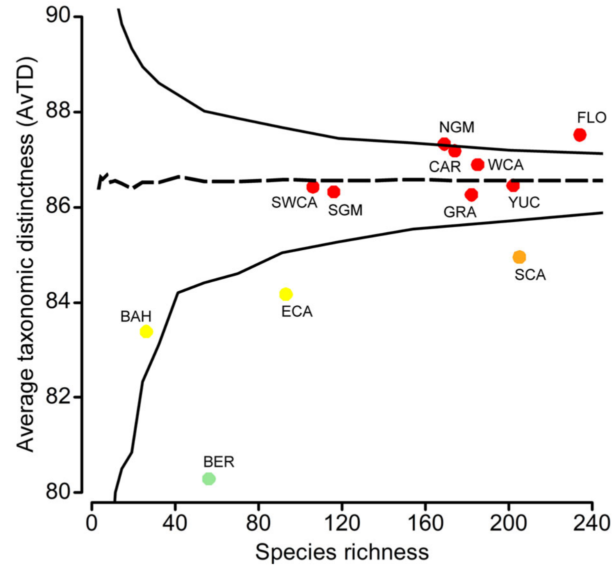
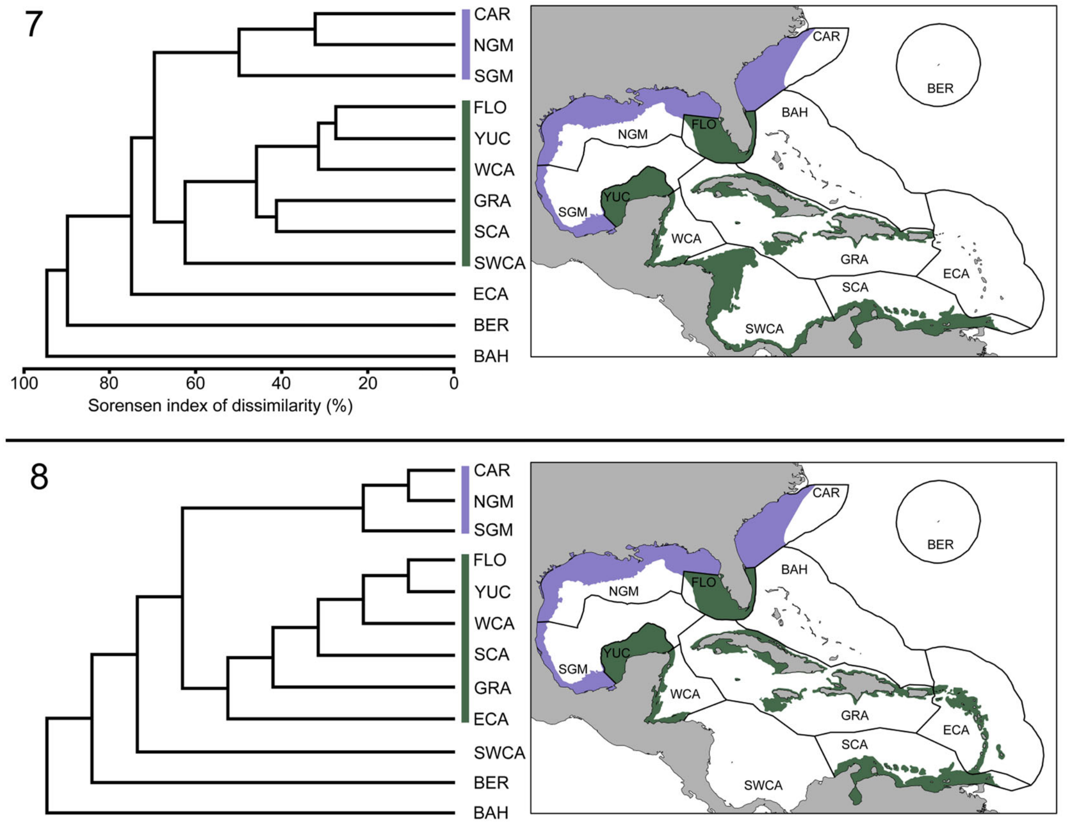


Fig. 6. Average taxonomic distinctness index versus species richness in amphipod assemblages by ecoregion. The dashed line represents the mean, and the continuous lines represent the 95% confidence intervals. Abbreviated names of ecoregions as in Figs. 3–5.

Results

A total of 491 benthic amphipod species was recorded from all ecoregions, belonging to 197 genera, 61 families, and three suborders. From this total, only 14 species were observed in more than 80% of ecoregions: *Americhelidium americanum* (Bousfield, 1973), *Ampelisca schellenbergi* Shoemaker, 1933, *Batea carinata* (Shoemaker, 1926), *Deutella incerta* (Mayer, 1903), *Elasmopus pocillimanus* (Bate, 1862), *Elasmopus rapax* Costa, 1853, *Ericthonius brasiliensis* (Dana, 1853), *Grandidierella bonnieroides* Stephensen, 1948, *Hemiaegina minuta* Mayer, 1890, *Hourstonius laguna* (McKinney, 1978), *Leucothoe spinicarpa* (Abildgaard, 1789) complex, *Paracaprella pusilla* Mayer, 1890, *Parhyale hawaiensis* (Dana, 1853), and *Shoemakerella cubensis* (Stebbing, 1897).

The highest species richness ($\geq$ 192 spp.) was observed in the Floridian, Yucatan, and Southern Caribbean ecoregions, and the lowest richness ($\leq$ 66 spp.) in the Bermuda and Bahamian ecoregions (Fig. 3). The Floridian and Northern Gulf of Mexico ecoregions presented the most diverse taxonomic categories, with higher taxonomic distinctness values. In contrast, the Southern Caribbean, Eastern Caribbean, and Bermuda ecoregions showed significantly lower taxonomic distinctness values (Figs. 4 and 6), indicating species assemblages formed by closely related taxonomic categories. The highest values of the weighted endemism



Figs. 7–8. Faunal relationship of amphipod assemblages across ecoregions in the Northwest Atlantic. (7) Dendrogram from a complete-link hierarchical cluster analysis based on dissimilarity; and (8) Cladogram from a cladistic analysis of distributions and endemism (CADE) based on parsimony, with the root omitted. Abbreviated names of ecoregions as in Figs. 3–5.

index were observed in the Southern Caribbean, Greater Antilles, Floridian, and Carolinian ecoregions, followed by the Yucatan and Northern Gulf of Mexico ecoregions (Fig. 5), showing species assemblages that are constituted by organisms with narrow geographic ranges. The Southern Gulf of Mexico, Bahamian, and Eastern Caribbean ecoregions showed lower weighted endemism values.

The hierarchical clustering analysis, at 63% dissimilarity, shows two cluster groups of related ecoregions, corresponding to two assemblages with different amphipod species composition (Fig. 7). The first cluster grouped the Carolinian, Northern Gulf of Mexico, and Southern Gulf of Mexico ecoregions, and the second one the Floridian, Yucatan, Western Caribbean, Greater Antilles, Southern Caribbean, and Southwestern Caribbean ecoregions. Bermuda, Bahamian, and Eastern Caribbean ecoregions were not grouped in any cluster. The ANOSIM test indicated significant differences ($R = 0.432$, $P = 0.048$) in the species composition of the cluster groups observed. The beta diversity analysis, using the Sørensen dissimilarity, revealed a higher contribution of the spatial replacement (β_{SIM}: 39–55%) in the two cluster groups, suggesting a marked species turnover between ecoregions.

The CADE analysis showed a single cladogram of 1463 steps, with a consistency index of 0.51 and a retention index of 0.53. The cladogram describes a monophyletic tree with two clades (Fig. 8), defined by a common node with distinctive taxonomic composition at the species category (*Ampelisca bicarinata* Goeke & Heard, 1983, *Bemlos unicornis* [Bynum & Fox, 1977], *Hartmanodes nyei* [Shoemaker, 1933], *Idunella carinata* [McKinney, 1978], *Lysianopsis alba* Holmes, 1903, *Monocorophium acherusicum* [Costa, 1853], *Photis pugnator* Shoemaker, 1945, *Phtisica marina* Slabber, 1769, *Protohyale macrodactyla* (Stebbing, 1899), and *Rudilemboides naglei* Bousfield, 1973), genus (*Globosolembos* Myers, 1985, *Hartmanodes* Bousfield & Chevrier, 1996, *Lysianopsis* Holmes, 1903, *Monocorophium* Bousfield & Hoover, 1997, *Netamelita* Barnard, 1962, *Phtisica* Slabber, 1769, *Protohyale* Bousfield & Hendrycks, 2002, and *Rudilemboides* Barnard & Reish, 1959), and family (Corophiidae). The two clades identify different areas of endemism. The first clade was composed of the Carolinian, Northern

Table 1. Shared taxa defining two clades in the cladogram, inferred by cladistics analysis of distributions and endemism (CADE). * = Homoplastic traits.

Clade	Taxa
I	**Species.** *Ampelisca abdita**, *Apocorophium louisianum**, *Apocorophium simile**, *Apolochus casahoya**, *Caprella equilibra**, *Cerapus benthophilus**, *Cerapus tubularis**, *Gammarus mucronatus**, *Jassa marmorata**, *Jerbarnia americana**, *Monocorophium tuberculatum**, *Nototropis urocarinatus**, *Photis longicaudata**, *Uhlorchestia uhleri**, *Unciola irrorata*, *Unciola serrata**. **Genus.** *Americorophium**, *Gammarus**, *Haustorius**, *Jassa**, *Jerbania**, *Parahaustorius**, *Parametopella**, *Pseudaeginella**, *Uhlorchestia**, *Unciola**. **Family.** Gammaridae*, Haustoriidae*.
II	**Species.** *Apohyale perieri*, *Audulla chelifera**, *Bemlos brunneomaculatus**, *Bemlos unifasciatus*, *Caribboecetes pterycornis*, *Chevalia mexicana**, *Colomastix gibbosa**, *Dulzura schoenerae**, *Elasmopus spinidactylus*, *Netamelita brocha**, *Photis tropherus**, *Pseudaeginella biscaynensis**, *Quadrimaera inaequipes*, *Stephonyx biscayensis*, *Tethorchestia antillensis*. **Genus.** *Audulla**, *Dulzura**, *Garosyrrhoe**, *Parhyalella**, *Stephonyx*, *Tethorchestia*. Family. Dogielinotidae*, Hadziidae*.

Gulf of Mexico, and Southern Gulf of Mexico ecoregions, and the second clade of the Floridian, Yucatan, Western Caribbean, Southern Caribbean, Greater Antilles, and Eastern Caribbean ecoregions. The species composition from the Bermuda, Bahamian, and Southwestern Caribbean ecoregions did not show genealogical relationships with any amphipod assemblage. Nodes of identified clades were defined by one or more synapomorphies (i.e., shared taxa) (Table 1), whereas each terminal branch (ecoregions) was defined by five or more autapomorphies (i.e., endemic taxa) (Table 2).

Discussion

The main result showed a YCS amphipod assemblage characterised by an elevated number of species and highly diverse faunal composition in terms of taxonomic categories, with a relatively high index of endemism, and a higher biogeographic affinity with the amphipod fauna from the Caribbean province. Also, the inclusion of the YCS amphipod assemblage as an ecoregion in the analyses of dissimilarity and parsimony contributed to identifying a spatial distribution pattern among ecoregions concordant with the tropical and warm-temperate biogeographic provinces from the wNWA.

Biogeographic provinces

The latitudinal temperature gradient across wNWA marine ecoregions causes a warm-temperate condition in the Carolinian province and a tropical condition in the Caribbean province (Briggs & Bowen, 2013; Robertson & Cramer, 2014). The faunal affinity analysis among ecoregions covering areas latitudinally arranged in space, such as those studied here, can contribute to understanding the potential environmental drivers structuring the marine taxa distribution that shape bioregions. The results of the present study suggest that the observed distribution on amphipod assemblages is determined by adaptive responses of species to different climate regimes related to biogeographic provinces (Belanger et al., 2012; Neigel, 2009), as has been described for the macroinfauna in general (Engle & Summers, 1999, 2000) and for amphipods (Raz-Guzmán & Soto, 2017). Results from the hierarchical analyses revealed a provincial amphipods distribution, similar to that observed in other benthic assemblages (e.g. decapods, molluscs, corals, and demersal fish) from the wNWA (Boschi, 2000; Dawson, 2002; Hedgpeth, 1953; Petuch, 2013). The amphipod composition from the Carolinian, Northern Gulf of Mexico, and Southern Gulf of Mexico ecoregions showed a higher affinity with the Carolinian province. In contrast, the Floridian, Yucatan, Western Caribbean, Southwestern Caribbean, Greater Antilles, Southern Caribbean, and Western Caribbean ecoregions showed a higher affinity with the Caribbean province.

The hierarchical analyses showed that amphipod species assemblages are geographically structured by province, represented on the dendrogram as two cluster groups of related fauna and the cladogram as two areas of endemism. The variation in amphipod assemblages between provinces due to the species turnover has probably been enhanced by the biological aspects associated with the species life-history traits (e.g., trade-off condition, density-dependent regulation, and limited dispersion capability), and the ecological particularities of each ecoregion. The direct development of the amphipods and its life cycle, entirely occurring in the bottom habitats, and their local recruitment (Desiderato et al., 2019; Myers, 1997; Sainte-Marie, 1991) would contribute to high species richness and weighted endemism heterogeneously distributed among ecoregions, and a species composition discreetly structured into homogeneous amphipod assemblages according to their biogeographic affinity. The lower species richness, taxonomic distinctness, and weighted endemism in species assemblages from the Bahamian and Bermuda ecoregions probably were related to the low sampling effort rather than a lack of suitable habitats (Miloslavich et al., 2010;

Table 2. Exclusive taxa defining related ecoregions of the two clades in the cladogram, inferred by cladistics analysis of distributions and endemism (CADE).

Clade	Ecoregion	Taxa
I	**Carolinian.**	***Species.*** *Acanthohaustorius similis*, *Americorchestia longicornis*, *Americorchestia megalophthalma*, *Ampelisca macrocephala*, *Amphiporeia virginiana*, *Gammaropsis maculata*, *Gammarus daiberi*, *Gammarus jenneri*, *Gracilipleustes gracilis*, *Hippomedon serratus*, *Jassa falcata*, *Lembos hypacanthus*, *Lepidactylus dytiscus*, *Leptocheirus pinguis*, *Leptocheirus plumulosus*, *Microdeutopus gryllotalpa*, *Neohaustorius biarticulatus*, *Neohaustorius schmitzi*, *Orchomene pinguis*, *Parahaustorius attenuatus*, *Parametopella inquilina*, *Proboloides holmesi*, *Uhlorchestia spartinophila*, *Unciola dissimilis*, *Unciola spicata*. ***Genus.*** *Amphiporeia*, *Gracilipleustes*, *Neohaustorius*, *Orchomene*, *Proboloides*. **Northern Gulf of Mexico.** ***Species.*** *Americorchestia barbarae*, *Americorchestia heardi*, *Americorchestia salomani*, *Bemlos setosus*, *Idunella bahía*, *Maera lucinae*, *Melita intermedia*, *Microjassa floridensis*, *Parahaustorius obliquus*. ***Genus.*** *Maera*. **Southern Gulf of Mexico.** ***Species.*** *Colomastix escobarae*, *Colomastix sarae*, *Ensayara lozanoi*, *Leucothoe hortapugai*, *Leucothoe ortizi*, *Lysianopsis adelae*, *Paracaprella guerragarciai*, *Seba alvarezi*.
II	**Floridian.**	***Species.*** *Bemlos minimus*, *Bemlos tempus*, *Bemlos tigrinus*, *Boca elvae*, *Boca megachela*. **Yucatan.** ***Species.*** *Caribboecetes progreso*, *Curidia nunoi*, *Dulichiella celestun*, *Elasmopus yucalpeten*, *Gammaropsis elvirae*, *Sisalia carricarti*. ***Genus.*** *Sisalia*. **Western Caribbean.** ***Species.*** *Batea aldebaranae*, *Ensayara jumane*, *Eurythenes obesus*, *Nepanamixis dianthus*, *Nuuanu copillius*, *Nuuanu jaumei*, *Orchestia costaricana*, *Resupinus spinicaudatus*. ***Genus.*** *Eurythenes*, *Nepanamixis*, *Resupinus*. ***Family.*** Eurytheneidae. **Southern Caribbean.** ***Species.*** *Alania calypsonis*, *Americorophium rioplatense*, *Ampelisca paria*, *Amphideutopus dolichocephalus*, *Amphilochus ascidicola*, *Anelasmopus kraui*, *Bonassa bonairensis*, *Confodiopisa caesicola*, *Deutella margaritae*, *Eriopisa mochimae*, *Eusiroides monoculoides*, *Idunella andresi*, *Lysianopsis hummelincki*, *Melita leiotelson*, *Melita persona*, *Neomegamphopus heardi*, *Nuuanu curvata*, *Paracaprella digitimanus*, *Photis sarae*, *Psammogammarus scopulorum*, *Psammomelita uncinata*, *Pseudomegamphopus excavatus*, *Quadrivisio lutzi*, *Stygogidiella perla*, *Talorchestia marcuzzi*, *Talorchestia margaritae*, *Tiburonella moroccoyensis*, *Thalassostygius exiguus*. ***Genus.*** *Alania*, *Amphideutopus*, *Anelasmopus*, *Bonassa*, *Confodiopisa*, *Psammomelita*, *Pseudomegamphopus*, *Quadrivisio*, *Thalassostygius*. ***Family.*** Kamakidae, Stegocephalidae. **Greater Antilles.** ***Species.*** *Aristias bicornuta*, *Bahadzia yagerae*, *Bemlos macromanus*, *Bemlos rolani*, *Boca normae*, *Byblis cubensis*, *Coboldus chazaroi*, *Crassicorophium bonellii*, *Cubadeutella cavernícola*, *Curidia monicae*, *Cyphocaris anonyx*, *Cyphocaris johnsoni*, *Elasmopus lemaitrei*, *Guernea reduncans*, *Leucothoe luquei*, *Mallacoota carausui*, *Neoischyrocerus vidali*, *Rhachotropis wimvaderi*, *Spathiopus cojimarensis*, *Tantena zlatarskii*, *Tiron biocellata*, *Victoriopisa guanarocana*. ***Genus.*** *Bahadzia*, *Byblis*, *Coboldus*, *Crassicorophium*, *Cubadeutella*, *Cyphocaris*, *Guernea*, *Mallacoota*, *Neoischyrocerus*, *Rhachotropis*, *Tantena*, *Victoriopisa*. ***Family.*** Cyphocarididae, Eusiridae. **Eastern Caribbean.** ***Species.*** *Actogidiella cultrifera*, *Marigidiella crassipes*, *Podocerus jareckii*, *Pseudaeginella antiquae*, *Quadrimaera pieteri*, *Stygogidiella virginalis*, *Synopia scheeleana*, *Syrrhoe papyracea*, *Tethorchestia karukarae*. ***Genus.*** *Actogidiella*, *Marigidiella*, *Syrrhoe*.

Wildish et al., 2016). However, the low species richness and endemism at the Bermuda ecoregion has been related to its distance from the northernmost warm waters (Locke et al., 2013). At the Bahamian ecoregion, the geographic isolation could result in species loss due to the estimated relative contribution (54–58%) in the nestedness component (β_{NES}). These factors probably affected the relationship observed on the dendrogram and cladogram analysis, as none of those two ecoregions showed any faunal relationship with the rest of the ecoregions.

Diverse studies suggest that historical climatic (e.g., temperature range shifts) and geographic (e.g., plate tectonics) events were important driving forces for the differentiation or convergence in amphipod assemblages (Hancock et al., 2019; Myers & Lowry, 2009; Winfield et al., 2006) that possibly have contributed to determining the observed biogeographic distribution trend on marine benthic amphipods. The southward latitudinal spatial displacement of the Maya block in the Cretaceous (Iturralde-Vinent, 2006), could explain the close relationship of species assemblages in the Caribbean province among the Floridian, Yucatan, and the Western Caribbean ecoregions. Meanwhile, the opening of the Suwannee strait (southeastern United States) until the Miocene that enabled a seaway for the ancestral Gulf Stream (Neigel, 2009) could explain the close relationship of species assemblages in the Carolinian province between the Carolinian and the Northern Gulf of Mexico ecoregions. The marine transgressions and regressions caused by glacial cycles in the Pleistocene (Ludt & Rocha, 2015), could explain the distant relationship of species assemblages in the North Atlantic between ecoregions of the Carolinian and the Caribbean provinces.

Yucatan biogeographic affinity

The incorporation of the YCS species assemblage, as an ecoregion into the classification scheme of Spalding et al. (2007), had implications for identifying the biogeographic affinity of the YCS amphipods. The hierarchical analyses of dissimilarity and parsimony showed that the amphipod assemblage from the Yucatan ecoregion presented a major affinity with the Caribbean province, whose limits were established from Cabo Catoche to the northern Terminos Lagoon. The assemblage from the Southern Gulf of Mexico ecoregion showed a major affinity with the Carolinian province, whose limit was established at the southern of the Madre Lagoon. This regionalisation suggests the species composition in the Yucatan ecoregion could be constituted as a distinct amphipod assemblage into the GoM and as part of the northern border from the Caribbean province.

The Caribbean affinity of the amphipod assemblage in the Yucatan ecoregion is supported by the observed close faunal relationships with the Floridian, Western Caribbean, and Greater Antilles ecoregions. This biogeographic affinity also includes the Southern Caribbean ecoregion, whose continental shelves share similar environmental characteristics (e.g., carbonated sediments, tropical climatic regime, and upwelling pulses) and a common geological history with the Floridian, Western Caribbean, and Greater Antilles ecoregions (Cobiella-Reguera et al., 2015; Iturralde-Vinent, 2006). These results suggest the YCS is different from the Southern Gulf of Mexico ecoregion.

The proposed Yucatan ecoregion is characterised by a highly diverse amphipod assemblage (i.e., high species richness and taxonomic distinctness) that is narrowly distributed (i.e., high weighted endemism), which suggests an area of confluence of species from different ecoregions, but with similar biogeographic affinity to the Caribbean province. The high diversity and endemicity in benthic amphipods could be explained by the environmental heterogeneity represented in widely variable biogenic bottom habitats, such as coral reefs and seagrasses (Arfianti & Costello, 2020; Miloslavich et al., 2010). The structural complexity of benthic habitats could be a key factor to understanding the observed provincial distribution pattern, as heterogeneous biogenic habitats assume a large coexistence of species driven by ecological divergences (Best & Stachowicz, 2013; Bousfield, 1970; Paz-Ríos et al., 2019). This might imply resource partitioning in amphipods driven by life-history and functional traits, that could influence their patterns of biodiversity (Hernandez-Avila et al., 2020).

The inclusion of the Yucatan ecoregion, as part of the northern border of the Caribbean province, allows us to identify a latitudinal spatial replacement of amphipod species across ecoregions and provinces, and to show that the Southern Gulf of Mexico ecoregion is a biogeographic transition zone between the Carolinian and Caribbean province. This ecoregion, from the northern Terminos Lagoon to the southern of Madre Lagoon, is characterised by low species richness and low endemism, and was previously suggested as a transition zone for benthic amphipods (Paz-Ríos & Ardisson, 2013; Raz-Guzmán & Soto, 2017). The environmental variability in this biogeographic transition zone suggest that the western border of the Yucatan ecoregion is spatially overlapped by two major transitional physiographic traits, the geological suture between the Maya block and northern Central America (Iturralde-Vinent, 2006), and the sedimentary shelf environment between the carbonated and terrigenous substrates (Hernández-Arana et al., 2005). In addition, changes in temperature from a tropical to warm-temperate regime (Raz-Guzmán & Soto, 2017), productivity shift from mesotrophic to eutrophic waters (Manzano-Sarabia & Salinas-Zavala, 2008), and hydrodynamic circulation from highly connected to a relatively confined pattern (Miron et al., 2017), could act as environmental filters or barriers (see Ferro & Morrone, 2014) that might set apart the amphipod assemblages of the Yucatan ecoregion.

Conclusion

The amphipod assemblage of the Yucatan ecoregion has a higher biogeographic affinity with the Caribbean province, whereas the amphipod assemblage of the Southern Gulf of Mexico ecoregion has a higher biogeographic affinity for the Carolinian province, suggesting the formation of a transition zone between those provinces. The YCS amphipods showed a spatially structured biotic affinity at the ecoregional-scale as a divergent species assemblage, which suggests that environmental conditions (e.g., temperature regime shifts) and historical events (e.g., latitudinal displacement of the Maya block) could contribute to shaping the observed distribution pattern in benthic amphipods of the Yucatan ecoregion. The spatial distribution pattern observed on the benthic amphipod composition of the wNWA indicates that the species assemblage in the Yucatan ecoregion is highly diverse (202 spp.), with intermediate levels of endemism and taxonomic distinctness that suggest this assemblage is a representative pool from the regional fauna and served to identify marine biogeographic provinces based on the turnover and endemicity of species.

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References

Abildgaard, P. C. (1789). *Zoologia Danica seu animalium Daniae et Norvegiae rariorum ac minus notorum Descriptiones et Historia*. Havniae, N. Möller et filius.

Arfianti, T., & Costello, M. J. (2020). Global biogeography of marine amphipod crustaceans: Latitude, regionalization, and beta diversity. *Marine Ecology Progress Series*, *638*, 83–94. https://doi.org/10.3354/meps13272

Balsam, W. L., & Beeson, J. P. (2003). Sea-floor sediment distribution in the Gulf of Mexico. *Deep Sea Research Part I: Oceanographic Research Papers*, *50*, 1421–1444. https://doi.org/10.1016/j.dsr.2003.06.001

Barnard, J. L., & Reish, D. J. (1959). *Ecology of Amphipoda and Polychaeta of Newport Bay*. Allan Hancock Foundation Publications, Occasional Paper 1–102.

Barnard, J. L. (1962). Benthic marine Amphipoda of southern California: Families Tironidae to Gammaridae. *Pacific Naturalist*, *3*, 73–115.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*, 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga, A., & Orme, C. D. L. (2012). betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, *3*, 808–812. https://doi.org/10.1111/j.2041-210X.2012.00224.x

Bate, C. S. (1862). Catalogue of the specimens of amphipodous Crustacea in the collections of the British Museum, London. *British Museum of Natural History*, *4*, 1–399.

Belanger, C. L., Jablonski, D., Roy, K., Berke, S. K., Krug, A. Z., & Valentine, J. W. (2012). Global environmental predictors of benthic marine biogeographic structure. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 14046–14051. https://doi.org/10.1073/pnas.1212381109

Best, R. J., & Stachowicz, J. J. (2013). Phylogeny as a proxy for ecology in seagrass amphipods: Which traits are most conserved? *Public Library of Science One*, *8*, e57550. https://doi.org/10.1371/journal.pone.0057550

Boschi, E. (2000). Species of decapod crustaceans and their distribution in the American marine zoogeographic provinces. *Revista de Investigación y Desarrollo Pesquero*, *13*, 7–136. http://hdl.handle.net/1834/2606

Bousfield, E. L. (1970). Adaptive radiation in sand-burrowing amphipod crustaceans. *Chesapeake Science*, *11*, 143–154. https://doi.org/10.2307/1351237

Bousfield, E. L. (1973). *Shallow-water Gammaridean Amphipoda of New England*. Cornell University Press.

Bousfield, E. L., & Chevrier, A. (1996). The Amphipod Family Oedicerotidae on the Pacific Coast of North America. 1. The *Monoculodes* & *Synchelidium* generic complexes: Systematics and distributional ecology. *Amphipacifica*, *2*, 75–148.

Bousfield, E. L., & Hoover, P. M. (1997). The amphipod superfamily Corophioidea on the Pacific coast of North America. Part V. Family Corophiidae: Corophiinae, new subfamily. Systematics and distributional ecology. *Amphipacifica*, *2*, 67–139.

Bousfield, E. L., & Hendrycks, E. A. (2002). The Talitroidean amphipod family Hyalidae revised, with emphasis on the North Pacific fauna: Systematics and distributional ecology. *Amphipacifica*, *3*, 17–134.

Briggs, J. C., & Bowen, B. W. (2012). A realignment of marine biogeographic provinces with particular reference to fish distributions. *Journal of Biogeography*, *39*, 12–30. https://doi.org/10.1111/j.1365-2699.2011.02613.x

Briggs, J. C., & Bowen, B. W. (2013). Marine shelf habitat: Biogeography and evolution. *Journal of Biogeography*, *40*, 1023–1035. https://doi.org/10.1111/jbi.12082

Bynum, K. H., & Fox, R. S. (1977). New and noteworthy amphipod crustaceans from North Carolina, U.S.A.

Chesapeake Science, *18*(1), 1–33. https://doi.org/10.2307/1350362

Carrillo-Briceño, J. D., Carrillo, J. D., Aguilera, O. A., & Sanchez-Villagra, M. R. (2018). Shark and ray diversity in the Tropical America (Neotropics)-an examination of environmental and historical factors affecting diversity. *PeerJ*, *6*, e5313. https://doi.org/10.7717/peerj.5313

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Austral Ecology*, *18*, 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Clarke, K. R., & Gorley, R. N. (2006). *PRIMER v6: User manual/tutorial*. PRIMER-E.

Clarke, K. R., & Warwick, R. M. (2001). A further biodiversity index applicable to species lists: Variation in taxonomic distinctness. *Marine Ecology Progress Series*, *216*, 265–278. https://doi.org/10.3354/meps216265

Cobiella-Reguera, J. L., Cruz-Gámez, E. M., Blanco-Bustamante, S., Pérez-Estrada, L., Gil-González, S., & Pedraza-Rozón, Y. (2015). Cretaceous-Paleogene boundary deposits and paleogeography in western and central Cuba. *Revista Mexicana de Ciencias Geológicas*, *32*, 156–176.

Copilaş-Ciocianu, D., & Borko, Š., & Fišer, C. (2020). The late blooming amphipods: Global change promoted post-Jurassic ecological radiation despite Palaeozoic origin. Molecular Phylogenetics and Evolution, *143*, 106664. https://doi.org/10.1016/j.ympev.2019.106664

Costa, A. (1853). Relazione sulla memoria del Dottor Achille Costa, di ricerche su' crostacei amfipodi del regno di Napoli. *Rendiconto della Societa Reale Borbonica, Accademia delle Scienze, new series*, *2*, 167–178.

Costello, M. J., Tsai, P., Wong, P. S., Cheung, A. K. L., Basher, Z., & Chaudhary, C. (2017). Marine biogeographic realms and species endemicity. *Nature Communication*, *8*, 1057. http://doi.org/10.1038/s41467-017-01121-2

Crisp, M. D., Laffan, S., Linde, H. P., & Monro, A. (2001). Endemism in the Australian flora. *Journal of Biogeography*, *28*, 183–198. https://doi.org/10.1046/j.1365-2699.2001.00524.x

Dana, J. D. (1853). Crustacea. Part II. *United States Exploring Expedition*, *14*, 689–1618.

Dawson, J. P. (2002). Biogeography of azooxanthellate corals in the Caribbean and surrounding areas. *Coral Reefs*, *21*, 27–40. https://doi.org/10.1007/s00338-001-0207-4

Desiderato, A., Costa, F. O., Serejo, C. S., Abbiati, M., Queiroga, H., & Vieira, P. E. (2019). Macaronesian islands as promoters of diversification in amphipods: The remarkable case of the family Hyalidae (Crustacea, Amphipoda). *Zoologica Scripta*, *48*, 359–375. https://doi.org/10.1111/zsc.12339

Engle, V. D., & Summers, J. K. (1999). Latitudinal gradients in benthic community composition in Western Atlantic estuaries. *Journal of Biogeography*, *26*, 1007–1023. https://doi.org/10.1046/j.1365-2699.1999.00341.x

Engle, V. D., & Summers, J. K. (2000). Biogeography of the benthic macroinvertebrates in estuaries along the Gulf of Mexico and western Atlantic coasts. *Hydrobiologia*, *436*(1/3), 17–33. https://doi.org/10.1023/A:1026572601578

Enriquez, C., Mariño-Tapia, I., Jeronimo, G., & Capurro-Filograsso, L. (2013). Thermohaline processes in a tropical coastal zone. *Continental Shelf Research*, *69*, 101–109. https://doi.org/10.1016/j.csr.2013.08.018

Escobar-Briones, E., & Soto, L. A. (1991). Biogeografía de los Misidaceos (Crustacea: Peracarida) del Golfo de Mexico. *Caribbean Journal of Science*, *27*, 80–89.

Ferro, I., & Morrone, J. J. (2014). Biogeographical transition zones: A search for conceptual synthesis. *Biological Journal of the Linnean Society*, *113*, 1–12. https://doi.org/10.1111/bij.12333

Goeke, G. D., & Heard, R. W. (1983). Amphipods of the family Ampeliscidae (Gammaridea). I. *Ampelisca bicarinata*, a new species of amphipod from the Gulf of Mexico. *Gulf Research Reports*, *7*, 217–223.

Hancock, Z. B., Hardin, F. O., & Light, J. E. (2019). Phylogeography of sand-burrowing amphipods (Haustoriidae) supports an ancient suture zone in the Gulf of Mexico. *Journal of Biogeography*, *46*(11), 2532–2547. https://doi.org/10.1111/jbi.13686

Hedgpeth, J. W. (1953). An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. *Publications of the Institute of Marine Science*, *3*, 107–224.

Hernández-Arana, H. A., Attrill, M. J., Hartley, R., & Gold-Bouchot, G. (2005). Transitional carbonate-terrigenous shelf sub-environments inferred from textural characteristics of surficial sediments in the Southern Gulf of Mexico. *Continental Shelf Research*, *25*(15), 1836–1852. https://doi.org/10.1016/j.csr.2005.06.007

Hernandez-Avila, I., Ocaña, F. A., & Pech, D. (2020). Testing marine regional-scale hypotheses along the Yucatan Continental Shelf using soft-bottom macrofauna. *PeerJ*, *8*, e8227. https://doi.org/10.7717/peerj.8227

Holmes, S. J. (1903). Synopses of North American invertebrates 28: The Amphipoda. *The American Naturalist*, *37*(436), 267–292. https://doi.org/10.1086/278286

Iturralde-Vinent, M. A. (2006). Meso-Cenozoic Caribbean paleogeography: Implications for the historical biogeography of the region. *International Geology Review*, *48*, 791–827. https://doi.org/10.2747/0020-6814.48.9.791

Jouanno, J., Pallàs-Sanz, E., & Sheinbaum, J. (2018). Variability and dynamics of the Yucatan Upwelling: High-resolution simulations. *Journal of Geophysical Research: Oceans*, *123*, 1251–1262. https://doi.org/10.1002/2017JC013535

Kensley, B., & Schotte, M. (1989). *Guide to the marine isopod crustaceans of the Caribbean*. Smithsonian Institution Press.

Locke, J. M., Coates, K. A., Bilewitch, J. P., Holland, L. P., Pitt, J. M., Smith, S. R., & Trapido-Rosenthal, H. G. (2013). Biogeography, biodiversity and connectivity of Bermuda's coral reefs. In C. R. C. Sheppard (Ed.), *Coral reefs of the United Kingdom overseas territories* (pp. 153–172). Springer.

Lowry, J. K., & Myers, A. A. (2017). A phylogeny and classification of the Amphipoda with the establishment of the new order Ingolfiellida (Crustacea: Peracarida). *Zootaxa*, *4265*, 1–89. https://doi.org/10.11646/zootaxa.4265.1.1

Ludt, W. B., & Rocha, L. A. (2015). Shifting seas: The impacts of Pleistocene sea-level fluctuations on the evolution of tropical marine taxa. *Journal of Biogeography*, *42*, 25–38. https://doi.org/10.1111/jbi.12416

Macpherson, E. (2002). Large-scale species-richness gradients in the Atlantic Ocean. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *269*(1501), 1715–1720. https://doi.org/10.1098/rspb.2002.2091

Maddison, D. R., & Maddison, W. P. (2001). *MacClade 4: Analysis of phylogeny and character evolution. Version 4.03. (Computer program and manual)*. Sinauer Associates.

Manzano-Sarabia, M., & Salinas-Zavala, C. A. (2008). Variabilidad estacional e interanual de la concentración de clorofila *a* y temperatura superficial del mar en la región occidental del Golfo de México: 1996–2007. *Interciencia*, *33*, 628–634.
Martín, A., Díaz, Y., Miloslavich, P., Escobar-Briones, E., Guerra-García, J. M., Ortiz, M., Valencia, B., Giraldo, A., & Klein, E. (2013). Regional diversity of Amphipoda in the Caribbean Sea. *Revista de Biologia Tropical*, *61*, 1681–1720. https://doi.org/10.15517/rbt.v61i4.12816
McKinney, L. D., Kalke, R. D., & Holland, J. S. (1978). New species of amphipods from the western Gulf of Mexico. *Contributions in Marine Science*, *21*, 133–159.
Miloslavich, P., Díaz, J. M., Klein, E., Alvarado, J. J., Díaz, C., Gobin, J., Escobar-Briones, E., Cruz-Motta, J. J., Weil, E., Cortés, J., Bastidas, A. C., Robertson, R., Zapata, F., Martín, A., Castillo, J., Kazandjian, A., & Ortiz, M. (2010). Marine biodiversity in the Caribbean: Regional estimates and distribution patterns. *Public Library of Science One*, *5*, e11916. https://doi.org/10.1371/journal.pone.0011916
Miron, P., Beron-Vera, F. J., Olascoaga, M. J., Sheinbaum, J., Pérez-Brunius, P., & Froyland, G. (2017). Lagrangian dynamical geography of the Gulf of Mexico. *Scientific Reports*, *7*, 7021.https://doi.org/10.1038/s41598-017-07177-w
Morrone, J. J. (2014). Parsimony analysis of endemicity (PAE) revisited. *Journal of Biogeography*, *41*, 842–854. https://doi.org/10.1111/jbi.12251
Mayer, P. (1890). Die Caprelliden des Golfes von Neapel under angrenenden Meeres-Abschnitte. Nachtrag zur Monographie derselben. *Fauna und flora des golfes von Neapel*, *17*, 1–157.
Mayer, P. (1903). Die Caprellidae der Siboga-Expedition. *Siboga-expeditie*, *34*, 1–160.
Myers, A. A. (1985). Studies on the genus *Lembos* Bate. XI. *Globosolembos* sub-gen. nov., *L. (G.) francanni* Reid, *L. (G.) indicus* Ledoyer, *L. (G.) ovatus* sp. nov., *L. (G.) tiafaui* sp. nov., *L. (G.) excavatus* Myers. *Bolletino del Museo Civico di Storia Naturale di Verona*, *10*, 341–367.
Myers, A. A. (1997). Biogeographic barriers and the development of marine biodiversity. *Estuarine, Coastal and Shelf Science*, *44*, 241–248. https://doi.org/10.1006/ecss.1996.0216
Myers, A. A., & Lowry, J. K. (2009). The biogeography of Indo-West Pacific tropical amphipods with particular reference to Australia. *Zootaxa*, *2260*, 109–127. https://doi.org/10.11646/zootaxa.2260.1.4
Neigel, J. E. (2009). Population genetic and biogeography of the Gulf of Mexico. In D. L. Felder & D. K. Camp (Eds.), *Gulf of Mexico: Origins, waters and biota, volume 1, biodiversity* (pp. 1353–1369). A&M University Press.
Paz-Ríos, C. E., & Ardisson, P.-L. (2013). Benthic amphipods (Amphipoda: Gammaridea and Corophiidea) from the Mexican southeast sector of the Gulf of Mexico: Checklist, new records and zoogeographic comments. *Zootaxa*, *3635*, 137–173. https://doi.org/10.11646/zootaxa.3635.2.4
Paz-Ríos, C. E., Guerra-García, J. M., & Ardisson, P.-L. (2014). Caprellids (Crustacea: Amphipoda) from the Gulf of Mexico, with observations on *Deutella mayeri*, redescription of *Metaprotella hummelincki*, a taxonomic key and zoogeographical comments. *Journal of Natural History*, *48*, 2517–2578. https://doi.org/10.1080/00222933.2014.931481
Paz-Ríos, C. E., Simões, N., & Pech, D. (2019). Species richness and spatial distribution of benthic amphipods (Crustacea: Peracarida) in the Alacranes Reef National Park, Gulf of Mexico. *Marine Biodiversity*, *49*, 673–682. https://doi.org/10.1007/s12526-017-0843-8
Petuch, E. J. (2013). *Biogeography and biodiversity of western Atlantic molluscs*. CRC Press.
Porzecanski, A. L., & Cracraft, J. (2005). Cladistic analysis of distributions and endemism (CADE): Using raw distributions of birds to unravel the biogeography of the South American aridlands. *Journal of Biogeography*, *32*, 261–275. https://doi.org/10.1111/j.1365-2699.2004.01138.x
Raz-Guzmán, A., & Soto, L. A. (2017). Updated checklist and zoogeographic remarks of benthic amphipods (Crustacea: Peracarida: Amphipoda) of two coastal lagoons in the western Gulf of Mexico. *Revista Mexicana de Biodiversidad*, *88*, 715–734. https://doi.org/10.1016/j.rmb.2017.07.002
Reuscher, M. G., & Shirley, T. C. (2014). Diversity, distribution, and zoogeography of benthic polychaetes in the Gulf of Mexico. *Marine Biodiversity*, *44*, 519–532. https://doi.org/10.1007/s12526-014-0222-7
Robertson, D. R., & Cramer, K. L. (2014). Defining and dividing the Greater Caribbean: Insights from the biogeography of shorefishes. *Public Library of Science One*, *9*, e102918. https://doi.org/10.1371/journal.pone.0102918
Ruiz-Castillo, E., Gomez-Valdes, J., Sheinbaum, J., & Rioja-Nieto, R. (2016). Wind-driven coastal upwelling and westward circulation in the Yucatan Shelf. *Continental Shelf Research*, *118*, 63–76. https://doi.org/10.1016/j.csr.2016.02.010
Sainte-Marie, B. (1991). A review of the reproductive bionomics of aquatic gammaridean amphipods: Variations of life history traits with latitude, depth, salinity and superfamily. *Hydrobiologia*, *223*, 189–227. https://doi.org/10.1007/BF00047641
Shoemaker, C. R. (1933). Two new genera and six new species of Amphipoda from Tortugas. *Papers from the Tortugas Laboratory*, *28*, 247–256.
Shoemaker, C. R. (1926). Amphipods of the family Bateidae in the collection of the United States National Museum. *Proceedings of the United States National Museum*, *68*(2626), 1–26. https://doi.org/10.5479/si.00963801.68-2626.1
Shoemaker, C. R. (1945). The amphipod genus *Photis* on the east coast of North America. *Charleston Museum Leaflet*, *22*, 3–17.
Sieg, J. (1986). Distribution of the Tanaidacea: Synopsis of the known data and suggestions on possible distribution patterns. In R. H. Gore & K. L. Heck (Eds.), *Crustacean biogeography. Crustaceans issues* (Vol. 4, pp. 165–194). A.A. Balkema.
Slabber, M. (1769). *Natuurkundige verlustigingen: behelzende microscopise waarneemingen van in- en uitlandse water- en land-dieren*. J. Bosch, Te Haarlem.
Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., Halpern, B. S., Jorge, M. A., Lombana, A., Lourie, S. A., Martin, K. D., McManus, E., Molnar, J., Recchia, C. A., & Robertson, J. (2007). Marine ecoregions of the World: A bioregionalization of coast and shelf areas. *BioScience*, *57*, 573–583. https://doi.org/10.1641/B570707
Spivey, H. R. (1981). Origins, distribution, and zoogeographic affinities of the Cirripedia (Crustacea) of the Gulf of Mexico. *Journal of Biogeography*, *8*, 153–176. https://doi.org/10.2307/2844558

Stebbing, T. R. R. (1897). Amphipoda from the Copenhagen Museum and other sources. *Transactions of the Linnean Society of London. 2nd Series: Zoology*, *7*(2), 25–45. https://doi.org/10.1111/j.1096-3642.1897.tb00400.x

Stebbing, T. R. R. (1899). Amphipoda from the Copenhagen Museum and other sources. Part II. *Transactions of the Linnean Society of London. 2nd Series: Zoology*, *7*(8), 395–432. https://doi.org/10.1111/j.1096-3642.1899.tb00202.x

Stephensen, K. (1948). Amphipods from Curacao, Bonaire, Aruba and Margarita. *Studies on the Fauna of Curacao, Aruba, Bonaire and the Venezuelan Islands*, *3*, 1–20.

Swofford, D. L. (2002). *PAUP: Phylogenetic analysis using parsimony (* and other methods). Version 4. (Computer program)*. Sinauer Associates.

Tunnell, J. W., Jr., Chavez, E. A., & Withers, K. (2007). *Coral reefs of the southern Gulf of Mexico*. Texas A&M University Press.

Vavrek, M. J. (2016). A comparison of clustering methods for biogeography with fossil datasets. *PeerJ*, *4*, e1720. https://doi.org/10.7717/peerj.1720

Veron, J., Stafford-Smith, M., DeVantier, L., & Turak, E. (2015). Overview of distribution patterns of zooxanthellate Scleractinia. *Frontiers in Marine Science*, *1*, e81. https://doi.org/10.3389/fmars.2014.00081

Wildish, D. J., Smith, S. R., Loeza-Quintana, T., Radulovici, A. E., & Adamowicz, S. J. (2016). Diversity and dispersal history of the talitrids (Crustacea: Amphipoda: Talitridae) of Bermuda. *Journal of Natural History*, *50*, 1911–1933. https://doi.org/10.1080/00222933.2016.1180719

Wilkinson, T., Wiken, E., Bezaury-Creel, J., Hourigan, T., Agardy, T., Herrmann, H., Janishevski, L., Madden, C., Morgan, L., & Padilla, M. (2009). *Marine ecoregions of North America*. Commission for Environmental Cooperation.

Williams, S. M., Chollett, I., Roff, G., Cortés, J., Dryden, C. S., & Mumby, P. J. (2015). Hierarchical spatial patterns in Caribbean reef benthic assemblages. *Journal of Biogeography*, *42*, 1327–1335. https://doi.org/10.1111/jbi.12509

Winfield, I., Escobar-Briones, E., & Álvarez, F. (2007). *Clave para la identificación de los anfípodos bentónicos del Golfo de México y el sector norte del Mar Caribe*. Universidad Nacional Autónoma de México – Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.

Winfield, I., Escobar-Briones, E., & Morrone, J. J. (2006). Update checklist and identification of areas of endemism of benthic amphipods (Caprellidae and Gammaridea) from offshore habitats in the SW Gulf of Mexico. *Scientia Marina*, *70*, 99–108. https://doi.org/10.3989/scimar.2006.70n199

WoRMS. (2020). *World register of marine species*. http://www.marinespecies.org

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