



ELSEVIER

Available online at www.sciencedirect.com

SCIENCE @ DIRECT®

Deep-Sea Research I 52 (2005) 1745–1765

DEEP-SEA RESEARCH
PART I

www.elsevier.com/locate/dsr

A qualitative zoogeographic analysis of decapod crustaceans of the continental slopes and abyssal plain of the Gulf of Mexico[☆]

Mary K. Wicksten^{a,*}, Jane M. Packard^b

^aDepartment of Biology, Texas A&M University, College Station, TX 77843-3258, USA

^bDepartment of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258, USA

Received 8 November 2004; received in revised form 25 April 2005; accepted 25 April 2005

Available online 19 July 2005

Abstract

Occurrence of 130 species of decapod crustaceans was compared between the continental slope (200–2500 m) and the abyssal plain (2500–3840 m) of the Gulf of Mexico. We compiled records of these species from published literature and from the crustacean catalogue of the Marine Invertebrate Collection of Texas A&M University. Each species was scored as present or absent in each of 10 polygons that were defined by physiographic features of the sea floor. Using cluster analysis, we identified inherent patterns of species richness. A distinct faunal assemblage occurred in the Sigsbee Abyssal Plain. This deep plain was a potential “coldspot” in terms of the number of species in the basin, compared to a “hotspot” in the vicinity of De Soto Canyon. Polygons of the eastern upper slopes (i.e. calcareous substrate of western Florida) contained the most species that were not found elsewhere in the Gulf of Mexico. Using an inductive approach, we identified the following hypotheses: (1) most crustacean species of the deep Sigsbee Abyssal Plain occur in oceans world-wide, (2) overall, almost a quarter of the deep sea species in the Gulf of Mexico range from the western Atlantic (south of Cape Hatteras) to the Caribbean, and (3) the Gulf of Mexico is particularly rich in species of *Munidopsis* (25 species).

© 2005 Elsevier Ltd. All rights reserved.

Keywords: Benthic macrofauna; Biodiversity; Crustaceans; Biogeography; Gulf of Mexico

[☆] Abbreviations: CAR = Caribbean, EATL = eastern Atlantic, EPAC = eastern Pacific, GoM = Gulf of Mexico, IN = Indian Ocean, IWP = Indo-Pacific, NATL = northern Atlantic, NPAC = northern Pacific, NWPAC = northwestern Pacific, SoF = Straits of Florida, SWPAC = southwestern Pacific, WATL = western Atlantic.

*Corresponding author. Fax: +1 979 862 1977.

E-mail address: wicksten@mail.bio.tamu.edu (M.K. Wicksten).

1. Introduction

Although biodiversity hotspots (areas with greater species richness than average) have been identified for shallow marine systems (Roberts et al., 2002), relatively little is known about deep sea patterns of beta diversity in tropical macrobenthic

fauna, i.e. comparison of species assemblages across habitats (Moritz, 2002). Biodiversity in warm deep seas may be sensitive to anomalous climatic (or oceanic current) events as well as global climate change (Danovaro et al., 2004). However, before patterns of global change in biodiversity can be evaluated quantitatively, several factors need to be addressed: (a) the completeness of taxonomic studies (Adrianov, 2003; Seifried, 2004), (b) the use of specific taxonomic groups (Cartes and Carrasson, 2004), (c) community structure of feeding guilds (Maynou and Cartes, 2000; Cartes et al., 2002), and (d) consistency across taxonomic levels (Doerries and Van Dover, 2003).

Decapod crustaceans (crabs, shrimp and lobsters) are large and conspicuous invertebrates, readily visible in bottom (in situ) photographs and often collected during ecological surveys. At least 130 species inhabit the bathyal regions at depths of 200–3840 m in the Gulf of Mexico. Being a well-defined, confined ocean basin, the Gulf of Mexico provides a good area in which to study geographic distribution of species.

A synthesis of information collected during the last half a century is now possible based on museum collections and published records. Studies on decapods of the Gulf of Mexico date back to the cruises of the U.S. Coast Survey Steamer *Blake*, under the direction of Alexander Agassiz, in 1877–78 (Milne-Edwards, 1880). More recent publications include reports of ecological or fisheries studies sponsored by various governmental agencies. Bullis and Thompson (1965) prepared lists of species taken at stations in 1956–1960 on the continental shelf and upper slope in the Gulf of Mexico. Thompson (1963) incorporated some of these records into his work on shrimp of the southwestern Atlantic, as well as including keys, illustrations and comments on nomenclature. Pequegnat and Chace (1970) and Pequegnat (1983) prepared detailed reports on locations and depths of collection for many species, and gave historical overviews of collecting. Pequegnat et al. (1990) provided a summary of geographic distribution, zonation by depth, and relative abundance of invertebrate groups in the Gulf of Mexico, with emphasis on the northern Gulf.

Soto et al. (1999) described decapod faunal assemblages by depth and related them to food sources on the upper continental slope in the southwestern Gulf of Mexico. Since 1970, new species have been described by Pequegnat and Pequegnat (1971), Dardeau and Heard (1983), Manning and Holthuis (1984), Lemaitre (1986), Williams (1988), Pequegnat and Williams (1995), and Felder and Kensley (2004).

The present inductive study synthesizes information on occurrence of decapod crustacean species in deep waters throughout the Gulf of Mexico (Appendix), using all records available in the published literature, ecological surveys and museum collections. Patterns of distribution are related to depth, bottom topography, patterns of currents, and sediments, to identify hypotheses that could be tested in future deductive analyses. The purpose is to identify which clusters of areas are most similar and which are most distinctive in terms of occurrences of species. For future studies, this exploratory analysis provides insights into the diversification of the deep Gulf decapod fauna in addition to providing an initial basis for other researchers to identify appropriate conservation units for ecosystem planning.

2. Methods

We define the Gulf of Mexico (Fig. 1) as that body of water lying within the northernmost part

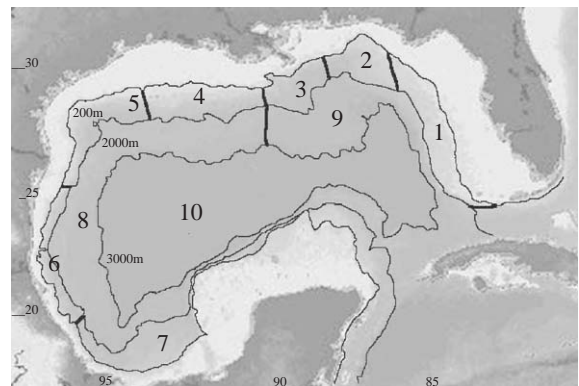


Fig. 1. Map of the Gulf of Mexico showing numbering system for polygons.

of the Yucatan Peninsula (approximately 21°30'N, 87° 00'), the mainland of northeastern Mexico and the southeastern USA and the Florida Peninsula southward to approximately 25° 00'N, 83° 00'W (north of the Florida Keys and Dry Tortugas). The Straits of Florida, Yucatan Channel and areas north and west of Cuba are excluded, although these areas were included in the work by Pequegnat and Chace (1970) as part of the southeastern Gulf of Mexico. We found that at least 10 species reported from the “Southeast Gulf” were taken only in the area between the Florida Keys and Cuba. Following Soto (1985), we consider this area as part of the Straits of Florida and exclude its fauna from this study.

Our primary source of information on records of decapods from the Gulf of Mexico was the Marine Invertebrate Collection, Texas Cooperative Wildlife Collection (TCWC), housed at Texas A&M University. The collection (formerly held by the Department of Oceanography) contains over 8000 lots of decapods, most of them taken at approximately 200 stations during cruises of the R/V *Alaminos* from 1963 to 1973. (See Pequegnat and Pequegnat, 1970a,b, for a map of stations through year 1969). Also present in the collections are specimens taken by the R/V *Oregon* and *Oregon II* in 1955–1974, the *Citation* and *Gyre* in 1984–85 as part of the Northern Gulf of Mexico Benthos Project (NGoMB), the fishing vessel *Success* in 1989–90, and specimens taken by other collectors or donated as vouchers from ecological surveys. We included new records from specimens collected by the R/V *Gyre* in 2000–2002 during the Deep Gulf of Mexico Benthos Project (DGoMB). These specimens are housed at the United States National Museum of Natural History (Smithsonian Institution (USNM)). Records are included of specimens taken by trawl or baited trap during 2003 as part of the JSSD-DGOMB joint cruise, with the Universidad Nacional Autónoma de México (UNAM). These specimens are housed at UNAM. We included all records of specimens taken at or between 200 and 3840 m (*Alaminos* station 68A3-5B, the deepest station). We followed the nomenclature given by Pérez-Farfante and Kensley (1997) for penaeoid shrimps, and Galil and

Crosnier (2000) for polychelid lobsters. Other records and information on world-wide species distributions came from the works of Rathbun (1918,1925,1937), Chace (1942), Bullis and Thompson (1965), Pequegnat and Chace (1970), Firth and Pequegnat (1971), Holthuis(1971), Manning and Chace (1971), Crosnier and Forest (1973), Perez-Farfante and Bullis (1973), Mayo (1974), Powers (1977), Chace and Holthuis (1978), Wenner (1979), Dardeau and Heard (1983), Takeda and Okutani (1983), Manning and Holthuis (1984), Gore (1985), Griffin and Tranter (1986), Williams and Turner (1986), Kensley and Tobias (1985), Williams (1988), Abele and Martin (1989), de Saint Laurent and Macpherson (1990a,b), Chan and Yu (1991), Lemaitre (1999,2004) and Soto et al. (1999). The earliest collection was *Albatross* station 2377, 11 February 1885; the latest was R/V *Ronald H. Brown* Northern Gulf Deep Sea Habitats Dive 36, 23 September 2003. In all, the specimens came from 407 sampling sites, including sampling stations of research vessels as well as locations of crustaceans taken during commercial fishing.

We include all species known to the senior author from the Gulf, including five unidentified species. A complete list of these species with information on their occurrence in the Gulf and elsewhere in the world's oceans is given in Appendix. We provide synonyms for species whose names have been changed since the publication of the authoritative work edited by Pequegnat and Chace (1970). The records contain species either that are strictly benthic or that commonly are collected in bottom trawls despite some capability to swim. Species of the midwater families Oplophoridae, Pasiphaeidae and other shrimp that may be taken in benthic trawls, but usually occur in the water column, are not included.

Species ranges outside of the Gulf of Mexico are given according to the literature and the TAMU collections. Species whose published ranges are given as “Lesser Antilles” or any of the islands comprising the arc on the eastern side of the Caribbean are listed as occurring in the Caribbean, regardless of whether they actually came from the western Atlantic side of the islands or the

Caribbean in the strict sense. We specify that species came from the Straits of Florida only for those species that are not known to occur farther north in the western Atlantic.

We include only species for which the majority of records came from 200 m or deeper. This depth designation corresponds to the seaward limit of the continental shelf.

We report each species by presence or absence. We do not use abundance data in the analyses because the procedures and sampling gear varied so greatly across samples. Most specimens were taken by trawl, but three different types of trawls were operated for different lengths of time on the bottom. We cannot be certain that the trawl actually was on the sea floor during the entire time reported. Some cruises sampled stations along transects going shallow to deep, others went north to south, east to west, or in and out of canyons. Specimens also were taken in dredges, baited traps, skimmers and near-bottom plankton nets. We believe that the number of individuals per species per sample would not be meaningful.

Pequegnat and Pequegnat (1970a,b, Fig. 1-1) used a system assigning all stations to one of four subdivisions in the Gulf: northeast, northwest, southeast and southwest. We believe that this system (which includes part of the Straits of Florida in the “Southeast Gulf”) does not give adequate resolution to the distribution of the species. Instead, we defined areas (polygons) corresponding to depth and bottom topography (Fig. 1). We consider the upper slope to consist of those areas between 200 and 1500 m; the lower slope to be between 1500 and 2500 m, and the lowermost slopes and Sigsbee Abyssal Plain to be below 2500 m. These distinctions approximately follow those given by Pequegnat et al. (1990). We combine their lower Shelf/Slope Transition Zone, Archibenthal Zone and part of their Upper Abyssal Zone into the upper slope, and part of the Upper Abyssal Zone with part of the Upper Abyssal Zone into the lower slope. For decapods, our system seems to give a better resolution of distribution by depth and provides at least 15 species per polygon for our analyses.

Polygons were assigned according to bottom topography. (See “Seafloor Relief of Northern

Gulf of Mexico Deep Water”, Texas Sea Grant map TAMU-SG-00-404, for a detailed map). On the upper slope, Polygon 1 includes the Florida Escarpment. Only 15 collection sites were reported from this polygon. Polygon 2 includes the DeSoto Canyon and had the most collection sites (102). Polygon 3 includes the Mississippi Canyon and had 20 collection sites. Polygon 4 includes a rugged area of basins and ridges and contained 63 collection sites. Polygon 5 includes the Alaminos Canyon and vicinity and contained 64 collection sites. Polygon 6 is a narrow strip including one canyon and contained 34 collection sites. Polygon 7 includes the southern bend of the Gulf of Mexico and incorporates some of the area studied previously by Soto et al. (1999). This polygon contained 28 collection sites. This system is similar to that used by Gallaway et al. (2001) except that we subdivide their “Mexican Ridge System” into two areas separated by a submarine canyon. We do not include an area off the northern coast of Yucatan because we have no data from this steep escarpment. We divide the lower slope into only two polygons separated by an arbitrary line extending south from the head of the Mississippi Canyon. Polygon 8, west of the line, contained 30 collection sites; Polygon 9, to the east, had 17 collection sites. We have insufficient data for a more refined analysis of the lower slopes. There were 32 collection sites from the lower slope and abyssal plain. Except for species taken during the NGoMB and DGoMB studies, there are no data on temperature or type of substrate at collection sites. This information, although potentially highly useful, is not included in the present analyses.

We compare faunal composition among areas using hierarchical cluster analysis, constructing phenograms based on the Jaccard coefficient of similarity (Fig. 2) and the squared Euclidean distance (Fig. 3). The Jaccard coefficient is appropriate for questions of beta diversity in faunal assemblages (Omori and Ikeda, 1984; Izsak and Price, 2001; McNally et al., 2004). The Jaccard coefficient was used to explore the zoogeographic pattern by the unweighted pair-group procedure, based on an arithmetic average (UPGMA). This is

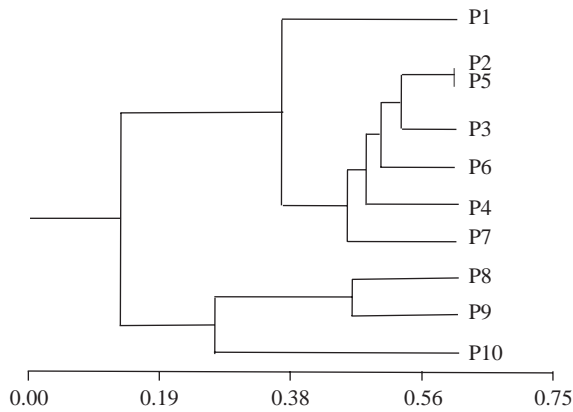


Fig. 2. Cluster diagram of area polygons by species, using the Jaccard Coefficient. P = Polygon.

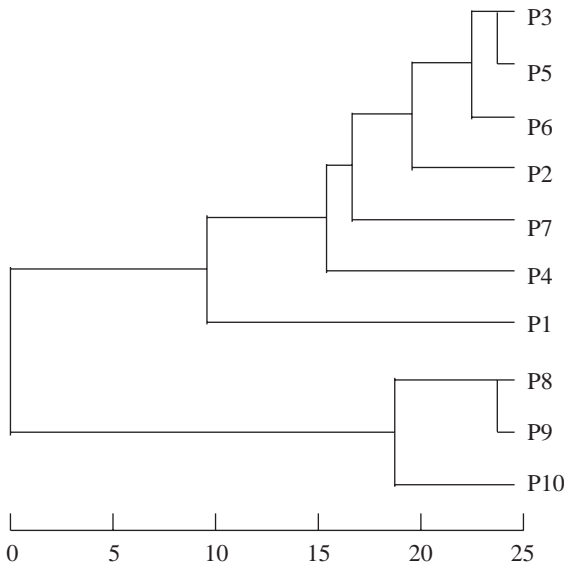


Fig. 3. Cluster diagram of area polygons by species, using the Euclidean Distance. P = Polygon.

a conservative and realistic approach to meta-analysis of presence/absence data resulting from multiple collections by several research teams. To examine robustness of the clusters, we repeated the analysis using the squared Euclidean distance (Statistical Package for the Social Sciences), a more widely used measure of similarity than the Jaccard.

3. Results

One hundred thirty species of decapod crustaceans have been reported from the continental slopes and abyssal plain of the Gulf of Mexico. Decapod faunal assemblages of the Sigsbee Abyssal Plain (2500–3840 m) and deeper slope (1500–2500 m) were more similar to each other than to those of the upper slopes (200–1500 m). Considering areas categorized as lower slopes, differences between the western and eastern Gulf were more evident based on the Jaccard Coefficient (Fig. 2) than the Euclidean distance (Fig. 3). On the upper slopes, the fauna of the western side of Florida (Polygon 1) was most distinct (in both phenograms) compared to assemblages in the extreme southern Gulf of Mexico (Polygon 7 in Fig. 2), and part of the Mississippi Fan (Polygon 4 in Fig. 2).

The resulting clusters of Polygons suggested characteristic suites of decapod species found at discrete depths throughout the Gulf, consistent with the findings of Pequegnat (1983) and Pequegnat et al. (1990). For example, the lobster *Nephropsis aculeata* and the crab *Acanthocarpus alexandri* were widespread at 200–500 m (the Shelf-Slope Transition Zone), the crab *Bathyplox typhla* and the craylet *Munida valida* at 500–775 m (the Archibenthal Zone), and the shrimps *Nematocarcinus rotundus*, *Glyphocrangon aculeata* and the flatback lobster *Polycheles sculptus* at 1000–2275 m (the Upper Abyssal Zone of Pequegnat et al., 1990).

There were more species reported from Polygons 1–3 than elsewhere. The maximum species richness occurred near the DeSoto Canyon (Polygon 2), where 63 species have been found. The shrimp *Prionocrangon echinata* and the golden crab *Chaceon fenneri* were documented in the Gulf only from Polygons 1 and 2 (eastern and northeastern areas). Some distributions were disjunct, e.g. the penaeoid shrimp *Aristeus antillensis* and the pandalid shrimp *Heterocarpus laevis* were reported from the northern as well as in the southwestern Gulf (Polygons 1–4 and 6–7; and 4 and 7, respectively). Five species were located only in the upper Florida slope (Polygon 1).

Four faunal assemblages were identified based on their distribution in the world's oceans (Appendix). The most common pattern of distribution (34 species, 27%) was in the Gulf of Mexico and south into the Caribbean. The second most common pattern of distribution of decapod species (30 species, 24% of the total species) included the western Atlantic, the Gulf of Mexico and the Caribbean. Of these, the majority ranged from south of Cape Hatteras, North Carolina, into the Gulf of Mexico and the Caribbean. Fifteen species (12%) ranged from the Gulf of Mexico north into the western Atlantic, but not into the Caribbean; and 19 species (15%) ranged from the Gulf of Mexico into the eastern Atlantic. Sixteen species (13%) ranged from the Gulf of Mexico into the Indian or Pacific Oceans. Eleven species have been reported only from the Gulf of Mexico. These patterns reflect the interchange of waters between the Caribbean, the western Atlantic and the Gulf.

Patterns of richness at higher taxonomic levels (genera and families) were similar to the patterns described above for the species level. There was a positive correlation between the number of species, families and genera (i.e. the more species, the more families and genera). Richness at all three taxonomic levels declined with depth: 26 families and 37 genera on the upper slope (Polygons 1–7), 17–18 families and 23 genera on the deep slope (Polygons 8 and 9), and only 10 families and 13 genera on the abyssal plain (Polygon 10). If one were to examine all invertebrates surrounding gas hydrate seeps (equivalent to hydrothermal vent communities), one would see a relative increase in genera and families there, but there are only three decapod species, two of them species of *Alvinocaris*, found exclusively at the seeps in the Gulf of Mexico.

4. Discussion

The following hypotheses emerged from our interpretation of results: (1) most decapod inhabitants of the deep Sigsbee Abyssal Plain are cosmopolitan in global distribution, possibly remnants of ancient seas, (2) overall, almost a

quarter of the deep-water macrobenthic species in the Gulf of Mexico range from the western Atlantic (south of Cape Hatteras) to the Caribbean, possibly related to historic and present current flow patterns and (3) globally, the Gulf of Mexico is relatively rich in species of *Munidopsis*, possibly related to topographic relief and distinct slopes of calcareous substrate in the eastern basin in contrast to muddy slopes to the west. To explain the basis for this informal model, we discuss below the limitations of the sampling techniques, factors influencing species distribution within the Gulf of Mexico and then, finally, how the patterns of decapod distribution in the Gulf of Mexico compare with global distributions.

4.1. Factors influencing records of faunal distribution

Prior to our analysis, there were no previous studies that had compared the distributions of the deeper decapods relative to topographical features of the sea floor in the Gulf basin. Although previous studies had examined distributions by depth (Pequegnat et al., 1990), there had been no synthesis of diverse data sets to examine inherent patterns in faunal distributions below 200 m. One of the difficulties associated with the synthesis of multiple data sets is consideration of sampling bias.

Decapods usually are collected in trawls, dredges, traps and skimmers, which yield information on presence/absence rather than quantitative data about relative abundance. Often, there is no reliable measurement of the distance covered by the sampler while on the bottom. Because of uneven bottom topography, the linear distance covered by the sampling gear may not be the actual distance. Fast-moving or deep-burrowing species may escape from the sampler. Animals inhabiting steep vertical walls usually cannot be taken by trawls or dredges.

Among decapods, individual spacing varies with the taxonomic group. For example, nephropsid lobsters may have a clustered distribution, as has been seen in *Nephrops norvegicus* (Dybern and Höisaeter, 1965). Clustered distributions also are characteristic of species living in particular

habitats or in association with colonial invertebrates. For example, shrimp of the genus *Alvinocaris* are characteristic of hydrothermal vents and seeps (Williams, 1988). Other species of hermit crabs, brachyuran crabs and shrimp tend to wander across the bottom but may congregate at patches of food. Even when an attempt is made to trawl at exactly the same location, different species may be taken because the trawl missed an aggregation or favored substrate by less than one meter. Trying to determine an average number of animals of a particular species per unit of area appears unrealistic.

Temporal aspects hamper efforts to quantify decapod sampling. Trawls at depths of 3000 m may require up to 12 h, limiting the number of samples per cruise. Collecting efforts in the same general area have occurred at intervals of months, years or even decades. Without a regular sampling program, seasonal or long-range variation in deep-sea decapod assemblages is difficult to assess.

The completeness of species lists may have been influenced by variation in sampling effort. As with many deep-sea taxa, numerous decapod species in the Gulf of Mexico are known from fewer than five specimens. It may be difficult to determine if a species is absent from an area, or present but not collected, even if sampling by trawl is accompanied by photography. The entire Florida Escarpment has been poorly studied because it is difficult to use available sampling equipment on its steeply sloping to vertical terrain. There has been less study of the southern Gulf of Mexico than the north. There were more than 100 collection sites in Polygon 2 alone, in large part due to the extensive collections made by the *Oregon* and *Oregon II*. There has been more study of the upper slopes than the deeper bathyal areas or the Sigsbee Abyssal Plain. Despite these sampling difficulties, we found the broad patterns of species distribution were amenable to zoogeographic analysis.

4.2. Comparison of areas within the Gulf of Mexico

The major pattern of species occurrence was related to depth. The decapod faunas of the lower slope (Areas 8 and 9) and abyssal plain (Area 10) differed markedly from that of the upper slope.

Such a decline in species richness, correlated with depth, was in accord with the results of previous studies (Pequegnat et al., 1972, 1990). The relative paucity of species on the abyssal plain may be interpreted as a regional “cold spot”.

The greatest decapod faunal richness is on the slopes in the northeastern Gulf of Mexico, including the De Soto Canyon. This “hotspot” contains topographic diversity, including canyons, knolls, and alluvial fans. An area of ironstone occurs at the region of the 3250 m isobath and 86°05.3'W longitude (Pequegnat, 1983). It is likely that some of the carideans and galatheid crabs prefer hard substrates or coarser sediments. Soto (1985) collected *Rochinia hystrix* on “hard and rugged bottoms”. Underwater photographs taken during studies in 2000 show muddy areas, rocks ranging from boulders to isolated chunks, burrows, and occasional sponges and gorgonians. Because of the mixed relief of the area, some of the species diversity may be elevated or attributable to the edge effect—the overlap of faunas in adjacent but different habitats. Located near the mouth of the Mississippi and other smaller rivers, there is an enhanced supply of debris and detritus from production in shallow waters or washed down from the coast.

The analysis of the similarity between areas of the upper slope did not show any marked horizontal zoogeographic patterns except for a difference in faunal composition between the Florida slope (Polygon 1) and elsewhere. This difference may be due to the presence of species unique to this area in the Gulf and also of species confined to the eastern and northern Gulf. The Florida slope is composed of calcareous substrates instead of mud, and has a high degree of topographic relief. The northwestern Gulf (Polygon 4) and extreme southern Gulf (Polygon 7) showed some distinction from the rest of the upper slope. Both areas contained species reported only in each area respectively and not elsewhere in the Gulf of Mexico.

For the lower slope, we are more cautious in interpreting results as indicating that species richness is higher in the western than the eastern Gulf, due to inconsistencies related to the measure of similarity (Jaccard coefficient vs. Euclidean

distance). Although the majority of species were found in both areas, at least nine species occurred in one area but not the other. Gallaway et al. (2001) considered the deep slope to consist of a continental rise in the western Gulf and included part of the Mississippi Fan in the eastern Gulf. They did not separate out the lowermost slope and Sigsbee Abyssal Plain. Considering the lower slope as only two areas may give an inaccurate picture of zoogeographic distinctions. There may be regional differences detectable at a smaller scale than we used in our analyses.

West of the Mississippi Trough, the bottom topography of the northwestern Gulf is complex. There are numerous basins, some of them deeply concave, others partly filled with sediments. Six larger, named submarine canyons and smaller ones slope down to the Sigsbee Abyssal Plain. There are beds of the coral *Lophelia pertusa* west of the mouth of the Mississippi River, and also a zone of gas hydrate seeps. The slope narrows and steepens to the south, where calcareous sediments replace mud and silt (Roberts et al., 1999). Soto et al. (1999) found that organic material from smaller rivers and estuaries served as a food source for deep benthic animals to 500 m in the southern Gulf.

Observed differences between eastern and western species assemblages may be in part due to chance. At least 20 decapod species are known in the Gulf of Mexico from less than 10 specimens. Rare species inhabiting nearly vertical surfaces, recesses or isolated habitats may be difficult to catch and often cannot be identified to species from photographs.

Many widespread species of decapods occur throughout the Gulf on suitable substrates, especially silt or mud. Species typical of such substrates (e.g. *Glyphocrangon aculeata* and *Lyr-eidus bairdii*) are commonly collected on the upper slopes (the Shelf/Slope Transition Zone of Pequegnat et al., 1990). Species taken at 1000–2500 m throughout the Gulf include *Nematocarcinus rotundus* and *Polycheles sculpus*. At more than 2500 m (the Mesoabyssal and Lower Abyssal Zones of Pequegnat et al., 1990), species commonly taken include *Plesiopenaeus armatus* (a large red shrimp also photographed in situ),

Parapagurus nudus, *Willemoesia forceps* and *Munidopsis bermudezi*.

In addition to diversity of substrate, differences between eastern and western areas are likely influenced by the Loop Current, which enters the Gulf of Mexico through the Yucatan Channel and exits the Florida Straits (Wiseman and Sturges, 1999). In the eastern Gulf of Mexico, the anticyclonic Loop Current is the dominant pattern. The Loop Current can spawn cyclonic eddies that move into the western Gulf. The only area in which waters from the global ocean enter the Gulf of Mexico is through the Yucatan Channel, which connects to the Yucatan Basin of the Caribbean Sea.

4.3. Species ranges outside the Gulf Basin

We hypothesize that the deep water decapod fauna of the Gulf of Mexico may be divided into (1) a Carolinian component, including species or sibling species that occur in the northern Gulf and the northwestern Atlantic, (2) a Caribbean component, consisting of species that range from the Gulf of Mexico and southern Florida southward into the Caribbean Sea, and (3) a cosmopolitan component characteristic of deep sea plains throughout the globe. Furthermore, we interpret the species richness of deep sea crustaceans in the Gulf of Mexico to be relatively higher than other similar basins across the globe. This may indicate the Sigsbee Abyssal Plain is a regional “coldspot” within a global “hotspot”, in terms of species richness, as discussed by Price (2002).

Several aspects of biogeographic history may have influenced these patterns of macrobenthic diversity. Wiseman and Sturges (1999) provided a good summary of the physical oceanography of the Gulf of Mexico. Mooers and Maul (1998) described circulation in a broader context of the Intra-American Sea. Both the entrance to, and exit of, water from the Gulf is across straits with relatively shallow sills. The Yucatan Strait is 1850 m and the Straits of Florida is 800 m, making the Gulf a partially enclosed basin. Until perhaps 20 million years ago, there was free interchange of waters between the western Atlantic and the Gulf

of Mexico across what is now the northern Florida Peninsula (Worrall and Snelson, 1989).

It is possible that some of the species in the Gulf recruit from reproducing populations in the Caribbean, so that the Gulf acts as a “sink” for larvae. Possible examples include the shrimps *Heterocarpus laevis*, *Eugonatonotus crassus* and *Parapenaeus americanus*, which occur in the eastern Gulf and near the tip of the Yucatan peninsula, and are widespread in the Caribbean.

Recruitment through the Straits of Florida may be infrequent. Lee et al. (1994) found that, in the presence of a strong Loop Current, a gyre may form off the Dry Tortugas, entraining larvae within it. In the absence of a strong Loop Current, flow from the Yucatan Channel turns eastward into the Straits of Florida and gyre formation does not occur. Further studies are needed at greater depths to determine the relevance of larval recruitment in the Straits of Florida.

Soto (1985) described distributional patterns of brachyuran crabs in the Straits of Florida. Of species living on the continental slope, the greatest degree of overlap in species composition with the Gulf of Mexico is in the deep slope. Other species in common fall into Soto's Continental and Cross-Strait Second Subpattern. These species include *Bathyplox typhla*, *Rochinia crassa*, and *Acanthocarpus alexandri*, which are associated with muddy bottoms. None of the species reported to follow the Insular Pattern, including the northern coast of Cuba, have been reported in the Gulf of Mexico.

The 10 °C isotherm seems to be important in limiting vertical and horizontal distribution of many crabs. The depth at which this isotherm occurs varies across the Straits of Florida according to the pattern of currents and bottom topography. Stenothermal crabs, such as species of *Cancer*, may be unable to colonize the Gulf of Mexico if the 10 °C isotherm lies below the sill depth.

Geologic evidence suggests that the Gulf of Mexico first opened to the rest of the world ocean in the Jurassic (Worrall and Snelson, 1989). Decapod fossils date back to the Devonian (Schram, 1986), so there were species available to colonize the Gulf at that time. Of living groups found today on the slopes, the Polychelidae are

represented among Triassic fossils and might have been present in the area during the Jurassic.

Although the Gulf of Mexico has been a distinct ocean basin since the Jurassic, we detected no reason to hypothesize that extant endemic decapod families or genera indicate speciation events. Eleven rare decapod species are thought to be endemic to the slopes of the Gulf of Mexico. Of these, only the crabs *Euphosynoplax clausa* and *Collodes leptocheles* are known from more than 10 specimens. The others may inhabit scattered or inaccessible substrates under-represented in the samples we examined. Taxonomic revision may shorten the list of endemic species. Chace (1997) speculated that the shrimp *Bathypalaemonella texana* might be a juvenile stage of *B. serratipalma*. The craylet *Munidopsis geyeri* Pequegnat and Pequegnat, 1970a,b was synonymized with the cosmopolitan species *M. subsquamosa* by Ambler (1980).

Our analysis shows a difference in species composition and richness between the north-eastern and northwestern Gulf of Mexico. However, there is no sharp break in faunal distributions off Alabama or Mississippi. No species pairs of decapods are known to occur on the slopes of the eastern and western Gulf, suggesting that there has been no effective geographic barrier historically separating the two areas long enough for divergence in phenotypic characteristics. In contrast, a vicariant zone has been recognized for fish species around Mobile Bay in the northeastern Gulf of Mexico (McClure and McEachran, 1992). However, finer grain analysis of genetic diversity (Moritz, 2002) and feeding guilds (Cartes and Carrasson, 2004) may reveal patterns we could not detect using a “coarse grain” approach.

Some shallow-water crustacean species have diverged into closely related species pairs, such as *Menippe mercenaria* in the western Atlantic and *Menippe adina* in the Gulf (Williams and Felder, 1986). However, closure of the northern Florida seaway did not seem to have affected the deep-water decapod fauna of the slopes. Probably, the waterway between the Atlantic and Gulf was shallow. Adult deep-sea decapods would not have crossed the waterway. Only larvae that reached

epipelagic zones could have been interchanged. Probably, the modern pattern of currents hinders the interchange of larvae between the Gulf of Mexico and the western Atlantic.

A unique feature of the Gulf of Mexico is the unusual abundance of species of *Munidopsis* (lobster-like anomurans), for which 25 species have been reported. In comparison, 39 species of *Munidopsis* are known so far from the entire eastern Pacific Ocean (Wicksten, 1989; Hendrickx and Harvey, 1999; Hendrickx, 2003). Pequegnat (1983) noted that some of these species inhabit characteristic depths. Their geographic ranges vary. *Munidopsis glabra* is endemic to the Gulf of Mexico (Pequegnat and Williams, 1995). In contrast, *Munidopsis subsquamosa* is considered to be a world-wide inhabitant of the lower continental slope and abyssal plains (Ambler, 1980). *Munidopsis tridens* is reported in the Gulf of Mexico, the eastern and western Atlantic and the Indian Ocean. The other 22 species range from the Gulf of Mexico into the western Atlantic or the Caribbean (Pequegnat and Pequegnat, 1970a,b; Pequegnat, 1983; Rice and Miller, 1991; Pequegnat and Williams, 1995). Because most specimens were collected with trawls or skimmers, the exact habitat of the species usually is not known. It is likely that the species occupy distinct habitats according to bottom topography, food sources and local currents.

Wenner and Boesch (1979) wrote of the distributional patterns of decapods along the shelf-slope coenocline of the Middle Atlantic Bight (between 37°9.0'N and 36°32.4'N). Of their list of 48 benthic species taken at similar depths to those on the slope of the Gulf of Mexico, 36 species were in common. The fauna of the Middle Atlantic Bight included the shrimps *Pandalus propinquus* and *Spirontocaris lilljeborgii*, the crabs *Cancer borealis* and *Cancer irroratus*, and the lobster *Homarus americanus*, which rarely range south of Cape Hatteras and never have been reported in the Gulf of Mexico. Species of the burrowing lobster *Nephropsis*, which are common in the Gulf of Mexico, were not reported from the Bight, nor were spider crabs of the genus *Rochinia*. In the Atlantic, *Acanthocarpus alexandri* and the shrimp

Plesionika edwardsi were reported as shallow as 95–118 m. These species generally occur at more than 200 m in the Gulf of Mexico. These two species and others may follow gradients of temperature, and submerge at lower latitudes. Gueguen (2000) also found the decapod crustacean assemblage on the upper continental slope of French Guiana was similar to the northwestern Atlantic.

Takeda and Okutani (1983) reported on decapods and other invertebrates trawled off Suriname and French Guiana in the southern Caribbean. Of the 41 species taken from deep slopes, 33 were in common with those of the Gulf of Mexico. In contrast, the hermit crab *Paragiopagurus pilimanus* has a peculiar distribution, occurring in the western Atlantic off Florida and in the Caribbean but not entering the Gulf of Mexico. The craylet *Munida iris* also is common in the western Atlantic, Caribbean, and the Straits of Florida, but has been reported only once in the southernmost Gulf of Mexico (Soto et al., 1999).

Several species of shrimp have been collected on the continental slopes of the Caribbean but not in the Gulf of Mexico. These include the shrimps *Glyphocrangon aurantiaca*, *G. neglecta*, *Stylodactylus rectirostris* and *S. serratus* (Holthuis, 1971; Chace, 1984; TAMU unpubl. records). In the Gulf of Mexico, the shrimps *Eugonatonotus crassus*, *Heterocarpus laevis*, *Metacrangon agassizii*, *Parapontocaris caribbaea*, and *Plesionika longipes* are reported from less than 10 specimens taken mostly in Polygons 1–4. Based on the records in the TAMU collections, these species are much more common in the Caribbean.

Sixteen species (13%) of the decapods range from the Gulf of Mexico into waters other than the Atlantic. Three species are known also from the Indian Ocean and the rest are considered to be cosmopolitan, ranging world-wide. Three species, *Parapagurus pilosimanus*, *Polycheles sculptus* and *Pontophilus gracilis*, once were considered to be cosmopolitan but now have been divided into separate Pacific and Atlantic species or subspecies (Chace, 1984; Firth and Pequegnat, 1971; Lemaitre, 1999; Galil and Crosnier, 2000). It is noteworthy that all of the cosmopolitan and

wide-ranging species are inhabitants of either the lowermost slopes or abyssal plains (the Abyssal Zones of Pequegnat et al., 1990).

In comparing the distributional patterns of the decapods in the Gulf of Mexico, the most likely explanation for patterns on a wider scale is that the fauna now and in the past has shared species with the Caribbean. Most of the species ranged from the southeastern United States and the Caribbean into the Gulf, or ranged widely across the Atlantic or entire world's oceans. Unlike the shallow coastal fauna of the Gulf of Mexico, the fauna of the deep slopes did not consist of stenothermal species in the northern Gulf and more tropical species to the south, nor were there sibling species pairs. Further genetic and phylogenetic studies will be necessary to determine the degree of isolation of the species in the deeper parts of the Gulf from their counterparts in the western Atlantic and Caribbean. Ethanol-preserved or frozen deep sea specimens may be suitable for genetic analyses (Boyle et al., 2004).

In conclusion, museum collections, such as the one used in this study, provide highly valuable information for ongoing efforts to prioritize protection of terrestrial and marine biodiversity on global scales (Pimm et al., 2001). We agree with Funk and Richardson (2002) that the knowledge of systematists, who curate such collections, needs to be integrated with the perspectives of ecological and evolutionary biologists to better understand evolutionarily significant units for conservation (Moritz, 2002; Mace, 2004). Although our synthesis was relatively coarse grain, we hope it will stimulate other researchers to determine the

manner in which seascapes influence isolation of macrobenthic populations, analogous to the application of landscape genetics (Manel et al., 2003) in support of regional conservation planning (Ferrier, 2002; Noss, 2004).

Acknowledgements

We are grateful to Linda Pequegnat of La Jolla, California, for her years of work on decapods from the Gulf of Mexico. Rafael Lemaitre, National Museum of Natural History, Smithsonian Institution; and Alain Crosnier, Muséum d'Histoire Naturelle, Paris, identified some of the specimens. Richard Haedrich, Memorial University, St. John's, Newfoundland, performed the analysis using the Jaccard coefficient. We are grateful to Robert Avent, U.S. Department of the Interior Minerals Management Service, and Michael Rex, University of Massachusetts Boston, for their painstaking reviews of earlier drafts of the manuscript and their constructive suggestions. We appreciate the efforts of undergraduate honors students in Marine Biology, Department of Biology, Texas A&M University, in preparing lists of species from hand-written catalogs and unsorted and unidentified specimens. The original map used in the preparation of Fig. 1 came from the website of the Gulf of Mexico Foundation (<http://gulfmex.org>). The DGoMB study and JSSD-DGoMB were sponsored by the U.S. Department of the Interior Minerals Management Service, contract number 1435-01-99-RP-30991 with Texas A&M University.

Appendix. List of Deep Benthic Decapods in the Gulf of Mexico

Order Decapoda
 Suborder Dendrobranchiata
 Infraorder Penaeoidea

Family Aristeidae

Aristaeopsis edwardsiana (Johnson, 1867) (formerly *Plesiopenaeus edwardsianus*): Polygons 3, 4, 5, 6, 7; WATL, GoM, CAR, EATL, IWP.
Aristeus antillensis A. Milne Edwards and Bouvier, 1909: Polygons 1, 2, 3, 4, 6, 7; WATL, GoM, CAR.
Hemipenaeus carpenteri Wood-Mason and Alcock, 1891: Polygons 8, 9, 10; WATL, GoM, CAR, IWP, EPAC.
Hepomadus tener Smith, 1883: Polygons 8, 9, 10; WATL, GoM, EATL, IWP.
Plesiopenaeus armatus (Bate, 1881): Polygons 8, 9, 10; WATL, GoM, CAR, EATL, IWP, NPAC.
Plesiopenaeus coruscans (Wood Mason, 1891): Polygons 8, 9; WATL, GoM, IN.

Family Benthescymidae

Benthescymus bartletti Smith, 1882: Polygons 2, 3, 4, 5, 6, 7, 8, 9, 10; WATL, GoM, CAR, EATL, IWP, NPAC.
Benthescymus carinatus Smith, 1884: Polygon 8, GoM, CAR, IN, NPAC.
Benthescymus cereus Burkenroad, 1888: Polygons 6, 8, 10; WATL, GoM, SWPAC.
Benthescymus iridescens Bate, 1881: Polygon 10, WATL, GoM, EATL, IWP, NPAC.

Family Penaeidae

Parapenaeus americanus Rathbun, 1901: Polygon 1; WATL, GoM, CAR.
Parapenaeus politus (Smith, 1881) (formerly as *P. longirostris* [Lucas, 1849], a Mediterranean species): Polygons 1, 2, 3, 4, 5, 6, 7; WATL, GoM, CAR.
Penaeopsis serrata Bate, 1881: Polygons 1, 2, 3, 4, 5, 6, 7; WATL, GoM, CAR, EATL.

Family Solenoceridae

Hymenopenaeus aphoticus Burkenroad, 1936: Polygons 7, 8; WATL, GoM, CAR, EATL.
Hymenopenaeus debilis Smith, 1885: Polygons 1, 2, 3, 5, 6; WATL, GoM, CAR, EATL.

Mesopenaeus tropicalis (Bouvier, 1905): (formerly *Hymenopenaeus tropicalis*): Polygon 1; WATL, GoM.

Pleoticus robustus (Smith, 1885): Polygons 1, 2, 3, 4, 5, 6, 7; WATL, GoM, CAR.

Solenocera necopina Burkenroad, 1936: Polygons 2, 5, 10; WATL, GoM, CAR.

Infraorder Stenopodidea

Family Stenopodidae

Richardina spinicineta A. Milne-Edwards, 1881: Polygons 1, 4, 5; NEATL, GoM.

Infraorder Caridea

Family Bresiliidae

Alvinocaris muricola Williams, 1988: Polygon 10, GoM.

Alvinocaris stactophila Williams, 1988: Polygon 4, GoM.

Family Campylonotidae

Bathypalaemonella serratipalma Pequegnat, 1970: Polygons 2, 5, 8, 9; GoM, EATL.

Bathypalaemonella texana Pequegnat, 1970: Polygon 8, GoM.

Family Crangonidae

Parapontocaris caribbaea (Boone, 1927): Polygon 5; WATL, GoM, CAR.

Pontocaris vicina Dardeau and Heard, 1983: Polygon 3, WATL, GoM, CAR.

Pontophilus gracilis talismani Crosnier and Forest, 1973: Polygons 1, 2, 3, 4, 5, 6, 8, 9; GoM, EATL.

Prionocrangon pectinata Faxon, 1896: Polygons 1, 2, 4, 8; GoM, CAR.

Sabinea hystrix (A. Milne Edwards, 1881): Polygon 9, WATL, GoM, CAR.

Sabinea tridentata Pequegnat, 1970: Polygon 1, GoM.

Family Eugonatonotidae

Eugonatonotus crassus (A. Milne-Edwards, 1881): Polygon 1, WATL, GoM, CAR. (Records from the Pacific refer to *E. chacei* Chan and Yu, 1991).

Family Glyphocrangonidae

Glyphocrangon aculeata A. Milne-Edwards, 1881: Polygons 2, 4, 5, 6, 7, 8, 9; WATL, GoM, CAR.

Glyphocrangon alispina Chace, 1939: Polygons 1, 2, 3, 4, 5, 6; GoM, CAR.

Glyphocrangon longirostris (Smith, 1882): Polygons 8, 9, 10; WATL, GoM, CAR, EATL.

Glyphocrangon longleyi Schmitt, 1931: Polygons 1, 2, 3, 4, 5, 6, 7; WATL, GoM, CAR.

Glyphocrangon nobilis A. Milne-Edwards, 1881: Polygons 2, 3, 4, 5, 6, 7, 8, 9; WATL, GoM, CAR.

Glyphocrangon sculpta (Smith, 1882): Polygons 8, 9; WATL, GoM, EATL.

Glyphocrangon spinicauda A. Milne-Edwards, 1881: Polygons 1, 2, 4, 5, 7; WATL, GoM, CAR.

Family Hippolytidae

Bythocaris nana Smith, 1885: Polygon 1, WATL, GoM.

Family Nematocarcinidae

Nematocarcinus acanthitelsonis Pequegnat, 1970: Polygons 9, 10; GoM, CAR.

Nematocarcinus cursor A. Milne-Edwards, 1881: Polygon 2; WATL, GoM, CAR.

Nematocarcinus ensifer (Smith, 1882): Polygons 3, 5, 8, 9, 10; NATL, WATL, GoM, EPAC.

Nematocarcinus rotundus Crosnier and Forest, 1978: Polygons 1, 2, 3, 4, 5, 6, 7, 8, 9; WATL, GoM, CAR.

Family Pandalidae

Heterocarpus ensifer A. Milne-Edwards, 1881: Polygons 1, 3, 5, 7, 8; WATL, GoM, CAR.

Heterocarpus laevis A. Milne-Edwards, 1881: Polygons 4, 7; GoM, CAR.

Heterocarpus oryx A. Milne-Edwards, 1881: Polygons 2, 3, 4, 5, 6, 7, 8, 9; GoM, CAR, WATL.

Plesionika acanthonotus (Smith, 1882): Polygons 1, 2, 3, 5; WATL, GoM, CAR, EATL.

Plesionika edwardsii (Brandt, 1851): Polygon 7, WATL, GoM, CAR, EATL.

Plesionika holthuisi Crosnier and Forest, 1967: Polygons 2, 3, 4, 5, 6, 7; WATL, GoM, CAR, EATL.

Plesionika longipes (A. Milne-Edwards, 1881): Polygon 1, WATL, GoM, CAR.

Plesionika polyacanthomerus Pequegnat, 1970: Polygons 2, 3, 5, 7; GoM.

Plesionika tenuipes (Smith, 1881): Polygons 1, 2, 3, 4, 5, 7, 9; WATL, GoM.

Plesionika willisi (Pequegnat, 1970) (formerly *Parapandalus willisi*): Polygons 1, 2, 3, 4, 5; GoM, CAR.

- Family Processidae *Processa profunda* Manning and Chace, 1971: Polygons 2, 4; GoM.
- Family Psalidopodidae
Psalidopus barbouri Chace, 1939: Polygons 2, 3, 4, 5, 6, 7; WATL, GoM, CAR.
- Infraorder Astacidea
- Family Nephropidae
Acanthacaris caeca (A. Milne-Edwards, 1881) (formerly *Neophoberus caeca*): Polygons 2, 3, 4, 6, 7; GoM, CAR.
Nephropsis aculeatus Smith, 1881: Polygons 1, 2, 3, 4, 5, 6, 7, 8; WATL, GoM, CAR.
Nephropsis agassizii A. Milne-Edwards, 1880: Polygon 2, 4, 5, 8; GoM, CAR.
Nephropsis rosea (Willemoes-Suhm, 1888): Polygons 1, 2, 3, 4, 5, 6; WATL, GoM, CAR.
Thaumastocheles zaleucus (Willemoes-Suhm, 1873): Polygon 2; GoM, CAR.
- Infraorder Palinura
- Family Polychelidae
Cardus crucifer (Willemoes-Suhm, 1873): Polygons 2, 8, 9; WATL, GoM, CAR, EATL.
Polycheles typhlops Heller, 1862: Polygons 1, 2, 3, 4, 5, 6, 7; WATL, GoM, CAR, EATL.
Polycheles validus (A. Milne-Edwards, 1880): Polygons 8, 9, 10; WATL, GoM, CAR, EATL.
Polycheles sculptus Smith, 1880: Polygons 1, 2, 3, 4, 5, 6, 7, 8, 9; NATL, WATL, GoM, CAR, EATL, IN.
Willemoesia forceps A. Milne-Edwards, 1880: Polygon 10, GoM, CAR.
- Infraorder Thalassinidea
- Family Axiidae
Axiopsis sp.: Polygon 9.
Calaxius carneyi Felder and Kensley, 2004: Polygon 4, GoM.
- Family Callianassidae (unidentified species): Polygon 2.
- Infraorder Anomura
- Family Chirostylidae
Eumunida picta Smith, 1883: Polygons 3, 4; GoM, WATL. (Records of this species from the southern Pacific are a misidentification. See de Saint Laurent and MacPherson, 1990).
Gastroptychus spinifer (A. Milne-Edwards, 1880): Polygon 8, GoM, SoF, CAR.

Uroptychus nitidus (A. Milne-Edwards, 1880): Polygons 1, 2, 5, 6, 8, 9; SoF, GoM, CAR.

Family Galatheididae

Munida constricta (A. Milne-Edwards, 1880): Polygon 1, 2.; GoM

Munida iris A. Milne-Edwards, 1880: Polygon 7, WATL, GoM, CAR.

Munida longipes A. Milne-Edwards, 1880: Polygons 1, 2, 3, 4, 5, 6, 7; WATL, GoM, CAR.

Munida media Benedict, 1902: Polygon 7, WATL, GoM.

Munida microphthalma A. Milne-Edwards, 1880: Polygons 2, 4, 9; NATL, WATL, GoM, CAR, EATL.

Munida valida Smith, 1883: Polygons 1, 2, 3, 4, 5, 6, 7; WATL, GoM, CAR.

Munidopsis abbreviata (A. Milne-Edwards, 1880): Polygon 5, SoF, GoM, CAR.

Munidopsis alaminos Pequegnat, 1970: Polygons 2, 5; GoM, CAR.

Munidopsis bahamensis Benedict, 1902: Polygon 4, WATL, GoM.

Munidopsis barbarae (Boone, 1927): Polygon 1, WATL, GoM.

Munidopsis bermudezi Chace, 1939: Polygon 10, SoF, GoM, CAR, EATL.

Munidopsis erinacea (A. Milne-Edwards, 1880): Polygons 1, 2, 5, 7; GoM, CAR.

Munidopsis glabra Pequegnat and Williams, 1995: Polygon 4, GoM.

Munidopsis gulfensis Pequegnat, 1970: Polygon 8, GoM, CAR.

Munidopsis livida (A. Milne-Edwards, 1886): Polygon 2, GoM, CAR.

Munidopsis longimanus (A. Milne-Edwards, 1880): Polygons 2, 3, 4, 5, 8; WATL, GoM.

Munidopsis nitida (A. Milne-Edwards, 1880): Polygon 8, GoM, CAR.

Munidopsis penescabra Pequegnat and Williams, 1995: Polygon 4, WATL, GoM.

Munidopsis polita (Smith, 1883): Polygons 4, 5, 7; WATL, GoM, CAR.

Munidopsis ramahtaylorae Pequegnat, 1970: Polygons 1, 2; GoM, CAR.

Munidopsis robusta (A. Milne-Edwards, 1880): Polygons 1, 2, 3, 4, 5, 7; GoM, CAR.

Munidopsis serratifrons (A. Milne-Edwards, 1880): Polygon 4, WATL, GoM, CAR.

Munidopsis sigsbei (A. Milne-Edwards, 1880): Polygons 2, 3, 4, 5, 6, 7, 8, 9; SoF, GoM, CAR.

Munidopsis simplex (A. Milne-Edwards, 1880): Polygons 2, 3, 5, 6, 7; SoF, GoM, CAR.

Munidopsis spinifer (A. Milne-Edwards, 1880): Polygon 7, WATL, GoM, CAR.

Munidopsis spinoculata (A. Milne-Edwards, 1880): Polygons 2, 6, 7; GoM, CAR.

Munidopsis spinosa (A. Milne-Edwards, 1880): Polygons 4, 7, 8, 10; SoF, GoM, CAR.

Munidopsis subspinoculata Pequegnat, 1971: Polygon 7, GoM, CAR.

Munidopsis subsquamosa Henderson, 1885: (including *M. geyeri*, a synonym):

Polygon 10, WATL, GoM, CAR, EATL, IN, NWPAC, EPAC.

Munidopsis tridentata (Esmark, 1857): Polygon 4, WATL, GoM, EATL, IN.

Munidopsis undescr. sp. (Mayo, in MS): Polygons 1, 2; SoF, GoM, CAR.

Family Lithodidae

Neolithodes agassizii (Smith, 1882): Polygons 3, 4, 5, 7, 9; WATL, GoM, CAR, EATL, IN.

Paralomis cubensis Chace, 1939: Polygon 4; SoF, GoM.

Family Paguridae

Catapaguroides microps A. Milne-Edwards and Bouvier, 1892: Polygons 5, 6; WATL, GoM, EATL, IN.

Family Parapaguridae

Parapagurus alaminos Lemaitre, 1986: Polygons 4, 5, 6, 7, 8, 9, 10; WATL, GoM, CAR, EATL.

Parapagurus nudus (A. Milne-Edwards, 1891): Polygons 8, 10; WATL, GoM, CAR, EATL.

Parapagurus pilosimanus Smith, 1879: Polygons 2, 3, 4, 5, 6, 8, 9; NATL, WATL, GoM, CAR, EATL.

Sympaguru spictus (Smith, 1883): Polygons 2, 3, 4, 5, 6, 7; WATL, GoM. *Tomopaguropsis* sp.: Polygon 7.

Infraorder Brachyura

Family Atelecyclidae

Trichopeltarion nobile A. Milne-Edwards, 1880: Polygons 2, 3, 4, 5, 6, 7; GoM, CAR.

Family Calappidae

Acanthocarpus alexandri Stimpson, 1871: Polygons 1, 2, 3, 4, 5, 6, 7; WATL, GoM, CAR.

Family Cymonomidae

Cymonomus sp. (Possibly undescribed): Polygons 1, 2, 4.

Family Dorippidae

Ethusa micropthalma Smith, 1881: Polygons 2, 3, 4, 5, 6, 7; WATL, GoM, CAR.

Ethusina abyssicola Smith, 1884: Polygons 8, 9, 10; WATL, GoM, EATL.

Family Geryonidae

Chaceon fenneri (Manning and Holthuis, 1984): Polygons 1, 2; WATL, GoM, CAR.

Chaceon quinquedens (Smith, 1879) (formerly *Geryon quinquedens*): Polygon 1, 2, 3, 4, 5, 8, 9; WATL, GoM, CAR.

Family Goneplacidae

Bathyplox typhla A. Milne-Edwards, 1880: Polygons 2, 4, 5, 6; WATL, GoM, CAR.

Euphrosynoplax clausa Guinot, 1969: Polygons 2, 4, 5, 7; GoM.

Robertsia mystica Guinot, 1969: Polygon 4, WATL, GoM.

Thalassoplax angusta Guinot, 1969: Polygon 2, 4, 6, 7; WATL, GoM.

Family Homolidae

Homologenus rostratus (A. Milne-Edwards, 1880): Polygons 6, 8; WATL, GoM, CAR, EATL.

Family Majidae

Collodes leptocheles Rathbun, 1894: Polygons 1, 2, 3, 4, 5, 6; GoM.

Dorhynchus thompsoni Norman, 1873: Polygons 1, 4; NATL, WATL, GoM, EATL, IN.

Pyromaia arachna Rathbun, 1924: Polygons 1, 3, 5, 7; WATL, GoM.

Rochinia crassa (A. Milne-Edwards, 1879): Polygons 1, 2, 3, 4, 5, 6, 7, 9; WATL, GoM.

Rochinia hystrix (Stimpson, 1871): Polygons 2, 3, 5; SoF, GoM, CAR.

Rochinia umbonata (Stimpson, 1871): Polygons 1, 2, 4; WATL, GoM, CAR.

Family Palicidae

Palicus gracilis (Smith, 1883): Polygons 5, 6; WATL, GoM, CAR.

Family Portunidae

Raymannius schmitti (Rathbun, 1931) (formerly *Benthochascon schmitti*): Polygons 1, 2, 4, 5, 6, 7; WATL, GoM.

Family Raninidae

Lyreidus bairdii Smith, 1881: Polygons 2, 3, 4, 5, 6, 7; WATL, GoM, CAR.

References

- Abele, L.G., Martin, J.L., 1989. American species of the deep-sea shrimp genus *Bythocaris* (Crustacea, Decapoda, Hippolytidae). *Bulletin of Marine Science* 45, 26–51.
- Adrianov, A.V., 2003. Marine biological diversity: patterns, processes and modern methodology. *Russian Journal of Nematology* 11, 119–126.
- Ambler, J.W., 1980. Species of *Munidopsis* (Crustacea, Galatheidae) occurring off Oregon and in adjacent waters. *U.S. Fisheries Bulletin* 78, 13–34.
- Boyle, E.E., Zardus, J.D., Chase, M.R., Etter, R.J., Rex, M.A., 2004. Strategies for molecular genetic studies of preserved deep-sea macrofauna. *Deep Sea Research I* 51, 1319–1336.
- Bullis, H.R., Thompson, J.R., 1965. Collections by the exploratory fishing vessels *Oregon*, *Silver Bay*, *Combat* and *Pelican* made during 1956–1960 in the southwestern North Atlantic. U.S. Department of Interior Fish and Wildlife Special Science Report-Fisheries 510, 1–130.
- Cartes, J.E., Carrasson, M., 2004. Influence of trophic variables on the depth-range distributions and zonation rates of deep-sea megafauna: the case of the western Mediterranean assemblages. *Deep-Sea Research I* 51, 263–279.
- Cartes, J.E., Abello, P., Lloris, D., Carbonell, A., Torres, P., Maynou, F., De Sola, L.G., 2002. Feeding guilds of western Mediterranean demersal fish and crustaceans: an analysis based on a spring survey. *Sciencias Marinas* 66 (Suppl. 2), 209–220.
- Chace Jr., F.A., 1942. Reports on the scientific results of the *Atlantis* expeditions to the West Indies, under the joint auspices of the University of Havana and Harvard University. The Anomuran Crustacea. I. Galatheidae. *Torreia* 11, 1–106.
- Chace Jr., F.A., 1984. The caridean shrimps (Crustacea: Decapoda) of the *Albatross* Philippine Expedition, 1907–1910, Part 2: Families Glyphocrangonidae and Crangonidae. *Smithsonian Contributions to Zoology* 397, 1–63.
- Chace Jr., F.A., 1997. The caridean shrimps (Crustacea: Decapoda) of the *Albatross* Philippine Expedition, 1907–1910, Part 7: Families Atyidae, Eugonatonotidae, Rhynchocinetidae, Bathypalaemonellidae, Processidae and Hippolytidae. *Smithsonian Contributions to Zoology* 587, 1–106.
- Chace Jr., F.A., Holthuis, L.B., 1978. *Psalidopus*: the scissor-footed shrimps (Crustacea: Decapoda: Caridea). *Smithsonian Contributions in Zoology* 277, 1–22.
- Chan, T., Yu, H., 1991. *Eugonatonotus chacei* sp. nov., second species of the genus (Crustacea, Decapoda, Eugonatonotidae). *Bulletin du Muséum National d'Histoire Naturelle*, Paris, 4th series, 13, section AA, nos. 1–2, pp. 143–152.
- Crosnier, A., Forest, J., 1973. Les crevettes profondes de l'Atlantique oriental tropical. *Faune Tropical (Cahiers de l'Office de la Recherche Scientifique et Technique Outre Mer)* 19, 1–409.
- Danovaro, R., Dell'Anno, A., Pusceddu, A., 2004. Biodiversity response to climate change in a warm deep sea. *Ecology Letters* 7, 821–828.
- Dardeau, M.R., Heard Jr., R.W., 1983. Crangonid shrimps (Crustacea: Caridea), with a description of a new species of *Pontocaris*. *Memoirs Hourglass Cruises VI (II)*, 1–39.
- Doerries, M.B., Van Dover, C.L., 2003. Higher-taxon richness as a surrogate for species richness in chemosynthetic communities. *Deep-Sea Research I* 50, 749–755.
- Dybern, B., Höisaeter, T., 1965. The burrows of *Nephrops norvegicus* (L.). *Sarsia* 21, 49–55.
- Felder, D.L., Kensley, B., 2004. A new species of axiid shrimp from chemosynthetic communities of the Louisiana continental slope, Gulf of Mexico (Crustacea: Decapoda: Thalassinidea). *Proceedings of the Biological Society of Washington* 117, 68–75.
- Ferrier, S., 2002. Mapping spatial pattern in biodiversity for regional conservation planning: Where to from here? *Systematic Biology* 51, 331–363.
- Firth, R.W., Jr., Pequegnat, W.E., 1971. Deep-sea lobsters of the families Polychelidae and Nephropodidae (Crustacea, Decapoda) in the Gulf of Mexico and Caribbean Sea. Texas A&M University Department of Oceanography A&M Project 700-15, Reference 71-1 IIT.
- Funk, V.A., Richardson, K.S., 2002. Systematic data in biodiversity studies: use it or lose it. *Systematic Biology* 51, 303–316.
- Galil, B., Crosnier, A., 2000. Crustacea Decapoda: Review of genera and species of the family Polychelidae Wood-Mason, 1874. *Resultats des campagnes MUSORSTOM. Memoires du Muséum National d'Histoire naturelle* 1993, 184, 285–387.
- Galloway, B.J., Cole, J., Martin, L.R., 2001. The deep sea Gulf of Mexico: an overview and guide. U.S. Department of Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans. OCS Study MMS-2001-065.
- Gore, R.H., 1985. Some rare species of abyssobenthic shrimp (families Crangonidae, Glyphocrangonidae and Nemato-carcinidae) from the Venezuela Basin, Caribbean Sea (Decapoda, Caridea). *Crustaceana* 48, 269–285.
- Griffin, D., Tranter, H., 1986. The Decapoda Brachyura of the Siboga Expedition. Part VIII. Majidae. *Siboga-Expeditie Monographie XXXIX C4*, 1–335.
- Guéguen, F., 2000. Distribution and abundance of decapod crustaceans of the continental slope (200–900 m) of French Guiana. *Crustaceana* 73, 685–703.
- Hendrickx, M.E., 2003. Geographic and bathymetric distributions of species of *Munidopsis* (Crustacea: Decapoda: Galatheidae) in the SE Gulf of California, Mexico. In: Hendrickx, M.E. (Ed.), *Contributions to the study of east Pacific Crustaceans*. Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, vol. 2, pp. 21–30.
- Hendrickx, M.E., Harvey, A.W., 1999. Checklist of anomuran crabs (Crustacea: Decapoda) from the Eastern Tropical Pacific. *Belgian Journal of Zoology* 129, 327–352.
- Holthuis, L.B., 1971. The Atlantic shrimps of the deep-sea genus *Glyphocrangon* A. Milne-Edwards, 1881. *Bulletin of Marine Sciences* 21, 267–373.

- Izsak, C., Price, A.R.G., 2001. Measuring beta-diversity using a taxonomic similarity index, and its relation to spatial scale. *Marine Ecological Progress Series* 215, 69–77.
- Kensley, B., Tobias, W., 1985. Redescription of *Heterocarpus laevis* A. Milne Edwards (Crustacea: Decapoda: Pandalidae). *Proceedings of the Biological Society of Washington* 98, 237–242.
- Lee, T.N., Clarke, M.E., Williams, E., Szmant, A., Berger, T., 1994. Evolution of the Tortugas Gyre and its influence on recruitment in the Florida Keys. *Bulletin of Marine Science* 54, 621–646.
- Lemaitre, R., 1986. Western Atlantic species of the *Parapagurus pilosimanus* complex (Anomura: Paguroidea: Parapaguridae): description of a new species and morphological variations. *Journal of Crustacean Biology* 6, 525–542.
- Lemaitre, R., 1999. Crustacea Decapoda: a review of the species of the genus *Parapagurus* Smith, 1879 (Parapaguridae) from the Pacific and Indian Oceans. *Résultats des Campagnes MUSORSTOM*, vol. 20, *Mémoires du Muséum National d'Histoire Naturelle* 180, 303–378.
- Lemaitre, R., 2004. A worldwide review of hermit crab species of the genus *Sympagurus* Smith, 1883 (Crustacea: Decapoda: Parapaguridae). In: Marshall, B., Richer de Forges, B. (Eds.), *Tropical Deep-Sea Benthos*, vol. 23. *Mémoires du Muséum National d'Histoire Naturelle* 191, 85–149.
- Mace, G.M., 2004. The role of taxonomy in species conservation. *Philosophical Transactions of the Royal Society of London B* 359, 711–719.
- Mac Nally, R., Fleishman, E., Bulluck, L.P., Betrus, C.J., 2004. Comparative influence of spatial scale on beta diversity within regional assemblages of birds and butterflies. *Journal of Biogeography* 31, 917–929.
- Manel, S., Schwartz, M.K., Luikart, G., Taberlet, P., 2003. Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology and Evolution* 18, 189–197.
- Manning, R.B., Chace Jr., F.A., 1971. Shrimps of the family Processidae from the northwestern Atlantic Ocean (Crustacea: Decapoda: Caridea). *Smithsonian Contributions in Zoology* 89, 1–41.
- Manning, R.B., Holthuis, L.B., 1984. *Geryon fenneri*, a new deep-water crab from Florida (Crustacea: Decapoda: Geryonidae). *Proceedings of the Biological Society of Washington* 97, 666–673.
- Maynou, E., Cartes, J.E., 2000. Community structure of bathyal decapod crustaceans off south-west Balearic Islands (western Mediterranean): seasonality and regional patterns in zonation. *Journal of the Marine Biology Association, U.K.* 80, 789–798.
- Mayo, B.S., 1974. The systematics and distribution of the deep-sea genus *Munidopsis* (Crustacea, Galatheidae) in the western Atlantic Ocean. Ph.D. dissertation, University of Miami.
- McClure, M.R., McEachran, J.D., 1992. Hybridization between *Prionotus alatus* and *P. paralatus* in the northern Gulf of Mexico (Pisces: Triglidae). *Copeia* 1992, 1039–1046.
- Milne-Edwards, A., 1880. Reports on the results of dredging under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78), in the Caribbean Sea (1878–79), and along the Atlantic coast of the United States (188), by the U.S. Coast Guard Survey Steamer “Blake”, Lieut.-Com. C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. VIII. *Études préliminaires sur les Crustacés. 1^e Partie. Bulletin of the Museum of Comparative Zoology, Harvard College* 8, 1–68.
- Mooers, C.N.L., Maul, G.A., 1998. Intra-American Sea Circulation. Coastal Segment (3,W). In: Robinson, A.R., Brink, K.H. (Eds.), *The Sea*, vol. 11. Wiley, New York, pp. 183–208.
- Moritz, C., 2002. Strategies to protect biological diversity and the evolutionary processes that sustain it. *Systematic Biology* 51, 238–254.
- Noss, R.F., 2004. Conservation targets and information needs for regional conservation planning. *Natural Areas Journal* 24, 223–231.
- Omori, M., Ikeda, T., 1984. *Methods in marine zooplankton ecology*. Wiley-Interscience, Wiley, New York.
- Pequegnat, L.H., 1970. Deep-sea caridean shrimps with descriptions of six new species. In: Pequegnat, W., Chace, Jr., F.A. (Eds.), *Contributions on the biology of the Gulf of Mexico*, vol. 1. Gulf Publishing Company, Houston, pp. 59–123.
- Pequegnat, W.E., 1983. The ecological communities of the continental slope and adjacent regimes of the northern Gulf of Mexico. Prepared by TerEco Corporation for the Minerals Management Service, U.S. Department of the Interior, Contract AAA851-CT1-12.
- Pequegnat, W.E., Chace Jr., F.A. (Eds.), 1970. *Contributions on the biology of the Gulf of Mexico*, vol. 1. Gulf Publishing Company, Houston.
- Pequegnat, W.E., Pequegnat, L.H., 1970a. Station list for benthic and midwater samples taken by R/V Alaminos 1964 to 1969. In: Pequegnat, W.E., Chace, Jr., F.A. (Eds.), *Contributions on the biology of the Gulf of Mexico*, vol. 1. Gulf Publishing Company, Houston, pp. 1–16.
- Pequegnat, L.H., Pequegnat, W.E., 1970b. Deep-sea anomurans of supefamily Galatheoidea with descriptions of three new species. In: Pequegnat, W., Chace, Jr., F.A. (Eds.), *Contributions on the biology of the Gulf of Mexico*, vol. 1. Gulf Publishing Company, Houston, pp. 125–170.
- Pequegnat, W.E., Pequegnat, L.H., 1971. Supplement to Volume 1, Texas A&M University Oceanographic Studies. New species and new records of *Munidopsis* (Decapoda: Galatheidae) from the Gulf of Mexico and Caribbean Sea. Gulf Publishing Company, Houston.
- Pequegnat, L.H., Williams, A.B., 1995. Two new species of *Munidopsis* (Decapoda: Anomura: Galatheidae) from the western Atlantic Ocean. *Journal of Crustacean Biology* 15, 786–792.
- Pequegnat, W.E., Bryant, W.R., Fredericks, A.D., McKee, T., Spaulding, R., 1972. Deep-sea ironstone deposits in the Gulf of Mexico. *Journal of Sedimentary Petrology* 42 (3), 700–710.

- Pequegnat, W.E., Gallaway, B.J., Pequegnat, L.H., 1990. Aspects of the ecology of the deep-water fauna of the Gulf of Mexico. *American Zoologist* 30, 45–64.
- Pérez-Farfante, I., Bullis Jr., H.R., 1973. Western Atlantic shrimps of the genus *Solenocera* with description of a new species (Crustacea: Decapoda: Penaeidae). *Smithsonian Contributions in Zoology* 153, 1–33.
- Pérez-Farfante, I., Kensley, B., 1997. Penaeoid and sergestoid shrimps and prawns of the world. *Mémoires du Muséum National d'Histoire Naturelle* 175, 1–233.
- Pimm, S.L., Ayres, M., Balmford, A., Branch, G., Brandon, K., Brooks, T., Bustamante, R., Costanza, R., Cowling, R., Curran, L.M., Dobson, A., Farber, S., da Fonseca, A.B., Gascon, C., Kitching, R., McNeely, J., Lovejoy, T., Mittermeier, R.A., Myers, N., Patz, J.A., Raffle, B., Rapport, D., Raven, P., Roberts, C., Rodriguez, J.P., Rylands, A.B., Tucker, C., Safina, C., Samper, C., Stiansny, M.L.J., Supriatna, J., Hall, D.H., Wilcove, D., 2001. Environment—Can we defy nature's end? *Science* 293, 2207–2208.
- Powers, L., 1977. Crabs (Brachyura) of the Gulf of Mexico. University of Texas Marine Science Institute Contributions in Marine Science. Supplement to vol. 20, 1–190.
- Price, A.R.G., 2002. Simultaneous 'hotspots' and 'coldspots' of marine biodiversity and implications for global conservation. *Marine Ecology-Progress Series* 241, 23–27.
- Rathbun, M.J., 1918. The grapsoid crabs of America. *U.S. National Museum Bulletin* 97, 1–461.
- Rathbun, M.J., 1925. The spider crabs of America. *U.S. National Museum Bulletin* 129, 1–613.
- Rathbun, M.J., 1937. The oxystomatous and allies crabs of America. *U.S. National Museum Bulletin* 166, 1–278.
- Rice, A.L., Miller, J.E., 1991. Chirostyliid and galatheid crustacean associates of coelenterates and echinoderms collected from the *Johnson-Sea-Link* submersible including a new species of *Gastroptychus*. *Proceedings of the Biological Society of Washington* 104, 299–308.
- Roberts, H., McBride, R., Coleman, J., 1999. Outer shelf and slope geology of the Gulf of Mexico: an overview. In: Kumf, H., Steidinger, K., Sherman, K. (Eds.), *The Gulf of Mexico large marine ecosystem*. Blackwell Science, Malden, Massachusetts, pp. 93–112.
- Roberts, C.M., McClean, C.J., Veron, J.E.N., Hawkins, J.P., Allen, G.R., McAllister, D.E., Mittermeier, C.G., Schueler, F.W., Spalding, M., Wells, F., Vynne, C., Werner, T.B., 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* 295, 1280–1284.
- de Saint Laurent, M., MacPherson, E., 1990a. Les espèces atlantiques du genre *Eumunida* Smith, 1883 (Crustacea: Decapoda: Chirostyliidae). *Journal of Natural History* 24, 647–666.
- de Saint Laurent, M., MacPherson, E., 1990b. Crustacea Decapoda: Le genre *Eumunida* Smith, 1883 (Chirostyliidae) dans les eaux néo-calédoniennes. In: Crosnier, A. (Ed.), *Résultats des Campagnes MUSORSTOM*, vol. 6. *Mémoires Muséum National d'Histoire Naturelle (A)* 145, 227–288.
- Schram, F.R., 1986. *Crustacea*. Oxford University Press, New York.
- Seifried, S., 2004. The importance of a phylogenetic system for the study of deep-sea harpacticoid diversity. *Zoological Studies* 43, 435–445.
- Soto, L.A., 1985. Distributional patterns of deep-water brachyuran crabs in the Straits of Florida. *Journal of Crustacean Biology* 5, 480–499.
- Soto, L.A., Manickhand-Heileman, S., Flores, E., Licea, S., 1999. Processes that promote decapod diversity and abundance on the upper continental slope of the southwestern Gulf of Mexico. In: von Vaupel Klein, J.C., Schram, F.R. (Eds.), *The Biodiversity Crisis and Crustacea*. Proceedings of the Fourth International Crustacean Congress, Amsterdam, The Netherlands, July 20–24, 1998, pp. 385–400.
- Takeda, M., Okutani, T., 1983. Crustaceans and mollusks trawled off Suriname and French Guiana. Japan Marine Fishery Resource Research Center, Tokyo.
- Thompson, J.R., 1963. The bathyalbenthic caridean shrimps of the southwestern North Atlantic. Ph.D. dissertation, Department of Zoology, Duke University.
- Wenner, E., 1979. Distribution and reproduction of nematocarinid shrimp (Decapoda: Caridea) from the northwestern North Atlantic. *Bulletin of Marine Science* 29, 380–393.
- Wenner, E., Boesch, D.F., 1979. Distributional patterns of epibenthic decapod Crustacea along the shelf-slope coenocline, Middle Atlantic Bight, U.S.A. *Bulletin of the Biological Society of Washington* 3, 106–133.
- Wicksten, M.K., 1989. Ranges of offshore decapod crustaceans in the eastern Pacific Ocean. *Transactions of the San Diego Society of Natural History* 21, 291–316.
- Williams, A.B., 1988. New marine decapod crustaceans from waters influenced by hydrothermal discharge, brine, and hydrocarbon seepage. *U.S. Fisheries Bulletin* 86, 263–287.
- Williams, A.B., Felder, D.L., 1986. Analysis of stone crabs: *Menippe mercenaria* (Say), restricted, and a previously unrecognized species described (Decapoda: Xanthidae). *Proceedings of the Biological Society of Washington* 99, 517–543.
- Williams, A.B., Turner, R., 1986. Squat lobsters (Galatheididae: *Munidopsis*) associated with mesh-enclosed wood panels submerged in the deep sea. *Journal of Crustacean Biology* 6, 617–624.
- Wiseman Jr., W.J., Sturges, W., 1999. Physical oceanography of the Gulf of Mexico: processes that regulate its biology. In: Kumf, H., Steidinger, K., Sherman, K. (Eds.), *The Gulf of Mexico large marine ecosystem*. Blackwell Science, Malden, Massachusetts, pp. 77–92.
- Worrall, D.M., Snelson, S., 1989. Evolution of the northern Gulf of Mexico, with emphasis on Cenozoic growth faulting and the role of salt. In: Bally, A.W., Palmer, A.R. (Eds.), *The geology of North America—An overview: Geological Society of America, the Geology of North America*, vol. A, Boulder, Colorado, pp. 97–138.