



Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Epibenthic megacrustaceans from the continental margin, slope and abyssal plain of the Southwestern Gulf of Mexico: Factors responsible for variability in species composition and diversity

Elva G. Escobar-Briones^{a,*}, Adriana Gaytán-Caballero^b, Pierre Legendre^c

^a Universidad Nacional Autónoma de México (UNAM), Instituto de Ciencias del Mar y Limnología, Unidad Académica Ecología Marina, A.P. 70-305 Ciudad Universitaria, 04510 México, D.F., Mexico

^b Universidad Nacional Autónoma de México, Posgrado en Ciencias del Mar y Limnología, Ciudad Universitaria, 04510 México, D.F., Mexico

^c Département de sciences biologiques, Université de Montréal, C.P. 6128, succursale Centre-ville, Montréal, Québec, Canada H3C 3J7

ARTICLE INFO

Article history:

Accepted 14 July 2008

Available online 6 September 2008

Keywords:

Soft sediment assemblages

Diversity

Density

Trawling

ABSTRACT

The community structure of megacrustaceans (orders Lophogastrida, Isopoda, and Decapoda) collected in trawls on the continental margin, upper slope and abyssal plain of the southern Gulf of Mexico was studied to determine to what extent broad-scale variation in community composition and diversity was influenced by geographic regions environmental variability and depth. Trawls were collected in the Mexican Ridges, the Campeche Bank, and the Sigsbee abyssal plain. There was variability in species composition, density and diversity among geographic regions and along the depth gradient. A total of 106 species were identified and grouped in three orders; five infraorders, 40 families, and 70 genera. This study extends the known geographic ranges of the species *Homolodromia monstrosa* and *Ephyrina benedicti*. The largest number of species was recorded in the Mexican Ridges and on the upper continental shelf; lower values were found on the continental margin and in the abyssal plain. The largest densities were recorded on the continental margin in the Mexican Ridges. Megacrustaceans show in general low frequencies and low abundances in trawls, characterizing them as rare components of benthic assemblages. Contrary to an accepted paradigm about deep-sea biodiversity, the highest *H'* diversity values were recorded in the Sigsbee abyssal plain, followed by values from the upper continental slope; diversity values were correlated with evenness. Canonical Redundancy analysis results showed a significant affinity to regions for 18 crustacean species; 33 species showed a significant affinity to both regions and depth zones within regions.

© 2008 Elsevier Ltd. All rights reserved.

1. Introduction

A diminishing trend in the number of species in the crustaceans with increasing depth has been recorded by Zarenkov (1969), Pequegnat et al. (1971) and Wenner and Boesch (1979), who attributed this pattern, to the strategies of capture, on the one hand, and to the limited knowledge of the distribution of the different species on the other (Hessler and Wilson, 1983). Decapod crustaceans, which are of most diversified nature in shallow tropical environments, are common components of deep benthic assemblages (Crosnier and Forest, 1973; Roberts and Pequegnat, 1970; Pequegnat, 1970a). An example of this can be observed in the flatback lobster, the family Glyphocrangonidae, which attains large abundances in deep-sea trawls because it is protected from predators (Gage and Tyler, 1999) by a highly calcified and spiny exoskeleton (Rice, 1981). Shrimps from the family Polychelidae are

abundant in the deep sea (Firth and Pequegnat, 1971; Wenner, 1978). The genus *Willemoesia* has been frequently recorded in large abundance at 3000 m depth (Gordon, 1955), in contrast with fossil records from the Triassic and Jurassic periods where the genus occurs in shallow environments.

Lobsters of the family Nephropidae are distributed along the continental margin. The diversity hotspots for this group occur on the slope (Holthuis, 1974). The anomurans (family Galatheididae) are among the most diversified crustaceans in the deep sea, attaining over 100 species. Over 50 species have been recorded for the genus *Munidopsis* at depths below 3000 m (Gordon, 1955; Wolf, 1961; Birstein and Zarenkov, 1970; Baba and Poore, 2002; MacPherson and Segonzac, 2005; Jones and Macpherson, 2006). Although hermit crabs of the families Parapaguridae and Paguridae are confined to the upper continental slope, the genera *Parapagurus* and *Tylapsis* have broader ranges of distribution with records exceeding 3000 m depth (Wolf, 1961; Menzies et al., 1973). The brachyuran crabs have radiated with 125 endemic species to the deep-sea floor, occurring at depths to 3500 m (Wolf, 1961; Pequegnat, 1970b; Griffin and Brown, 1975; Griffin and Tranter,

* Corresponding author. Tel.: +52 55 5622 5841; fax: +52 55 5616 0748.

E-mail address: escobri@mar.icmyl.unam.mx (E.G. Escobar-Briones).

1986). The genus *Chaceon* (*Geryon*) of the family Geryonidae is a well-known component from the upper continental slope in the Atlantic Ocean. *Chaceon quinquedens* digs tunnels of almost 0.75 m depth being a dominant feature in the deep-sea floor (Malahoff et al., 1982). These geryonids are probably the only crustaceans of larger size that can be commercially exploited (Steimle et al., 2001; Gage and Tyler, 1999), in contrast to other dominant species occurring at similar depth, e.g. *Ethusina*, that are smaller and less robust than *Chaceon* (Gage and Tyler, 1999).

Our knowledge on lophogastrids is centered on the widespread species *Neognathophausia ingens* due to its importance as food source for marine mammals (Casanova, 1997; Cardona-Maldonado and Mignucci-Giannoni, 1999). Other studies deal with the physiology of the species by trying to understand its growth rate, distribution, population structure and survival along the minimum oxygen zone (Childress, 1968; Belman and Childress, 1976; Mickel and Childress, 1978; Childress and Price, 1978, 1983; Sanders and Childress, 1990; Moeller and Case, 1994). The studies on the bathyal isopod *Bathynomus giganteus* in the Gulf of Mexico have recorded that the reproductive peak is seasonally triggered and is not a strict scavenger. Its diet is based on a large variety of items (Briones-Fourzán and Lozano-Álvarez, 1991; Barradas-Ortiz et al., 2003) that the species detects with help of chemoreceptors on the sediment and benthic boundary layer (Chamberlain et al., 1986).

The megacrustaceans belong to the higher trophic levels and are, therefore, vulnerable to perturbations such as the disposal of mud from the industry (Charmasson et al., 1998), the extraction of energy resources from the sea floor (Steimle et al., 2001), or deep-sea trawling (Escobar-Briones, 2004). Caridean and penaeid shrimps of the genera *Acanthephyra* and *Plesiopenaeus* are opportunist scavengers as recorded on images from baited traps from the Arctic and North Atlantic oceans (Bowman and Manning, 1972; Desbruyères et al., 1985; Rowe et al., 1986). Carrion to different preys has been recorded as the main dietary components of deep-sea decapod crustaceans. DNA-based methods of gut contents and feces are expanding the range and diversity of dietary items and foraging strategies (Blankenship and Yayanos, 2005).

1.1. Background studies

The study of deep-sea fauna in the Gulf of Mexico is related to the geographic exploration of the basin (Marshall, 1979). Deep-sea crustaceans have been collected since the 19 century during different expeditions and contributed to the knowledge of the Gulf of Mexico through the description of new species, composition of the crustaceans in the region. A review of records compiled from published literature and from the crustacean catalog of the marine invertebrate collection of Texas A&M University (TAMU) from the continental slopes and abyssal plain in the Gulf of Mexico was published by Wicksten and Packard (2005). Information of this nature has been useful to implement the conservation strategies and management of resources in deeper-water ecosystems (Andrew and Mapstone, 1987; Holthuis, 1991; Steimle et al., 2001; Underwood et al., 2000).

The current study contributes by describing the crustacean assemblages collected by bottom-trawl gear and analyze their variability in three depth zones (continental margin, upper continental slope, and abyssal plain) in three regions of the Gulf of Mexico. The hypothesis underlying this study is based in the homogeneity and stability of the deep-sea ecosystem that, limited in biogenic carbon export, imposes to extreme conditions on the tropical and adjacent warm-temperate deep-sea species richness and densities. This differs notably from the highly variable shallower habitats (Tyler, 1988). Predictions from this hypothesis

are that the continental slope and abyssal plain should have low densities and species diversity, without much differentiation among regions. We will test these predictions by comparing the species diversity and taxonomic composition of crustaceans among regions and depth zones.

2. Materials and methods

2.1. Study area

The trawls were collected from 21 locations during four cruises (DGoMB-JSSD, SIGSBEE.5, 6, and 7) in the SW Gulf of Mexico, an ancient geological basin with a maximum depth of 3700 m. The Gulf of Mexico is located between 18° and 30° latitude N and between 82° and 98° longitude W. It covers an area of 1.5×10^6 km² and encompasses a volume of 2.3×10^6 km³. The distribution of sediments in the basin is variable (Balsam and Beeson, 2003). This study included trawls from three depth zones and three regions, namely the continental shelf and margin (50–200 m) and the upper continental slope (250–750 m), of the Mexican Ridges, located in the Western Gulf of Mexico, and from the Campeche Bank, located in the SW Gulf of Mexico and the abyssal plain (3000–3800 m) named the Sigsbee Abyssal Plain (Fig. 1).

The Mexican Ridges region is characterized by a narrow continental margin and a steep slope with hills parallel to the coast line (Antoine et al., 1974). This area is of high economic value to Mexico due to the presence of oil and gas (Aguayo and Trápaga, 1984). The Campeche Bank region is located in the Carbonate province in the SW extension of the Yucatan Peninsula (Roberts et al., 1999). Calcium carbonate exceeds 75% of the sediment mineralogical composition (Balsam and Beeson, 2003) in this region. The Sigsbee Abyssal Plain, located in the center of the basin, between 22° and 26°N and 90° and 95°W, extends over an area of 98,752 km² and has an average depth of 3000 m. Its calcium carbonate content is on average 25% and is of a hemipelagic origin. In the northern portion, mud from the Mississippi River affects sediment composition (Balsam and Beeson, 2003).

Among the three depth zones sampled in this study, the continental slope is a particularly complex topographic feature. It includes canyons, submarine channels, escarpments, salt domes and foldings that extend from the shelf break to the upper limit of the continental rise at depths of 2800 m in the north and west and to 3600 m off the Campeche Escarpment (Ewig and Antoine, 1966). A minimum oxygen zone occurs on the slope. Below that point, oxygen concentrations have similar values as those recorded in the surface water masses (Roberts et al., 1999).

The hydrodynamics of the Gulf of Mexico is defined by mesoscale structures. Its dynamics is related to the Loop Current (Vidal Lorandi et al., 1999) with boundary currents and cross-shelf transport that reach speeds of 32–85 cm s⁻¹ (Vidal Lorandi et al., 1999; Elliot, 1982). The Gulf Common Water occurs at 150–250 m with salinity of 37.75 and oxygen concentration of 3.4 mg L⁻¹. Antarctic Intermediate Water is found at 750 m (34.86 ups, 6.2 °C), lying over the North Atlantic Deep Water at 1500 m with salinity of 34.98 ups and temperature of 4.02 °C (Nowlin and McLellan, 1967).

2.2. Field work

Crustaceans were collected with bottom-trawling gear (OTSB otter trawl) with the following specifications: 12 m long, 9 m wide, 6-cm mesh size and cod-end, and each trawl lasted 25 min of bottom contact, at speeds that varied from 1.3 to 3.5 knots covering distances from 1.85 to 7.49 km. The trawls collected on the

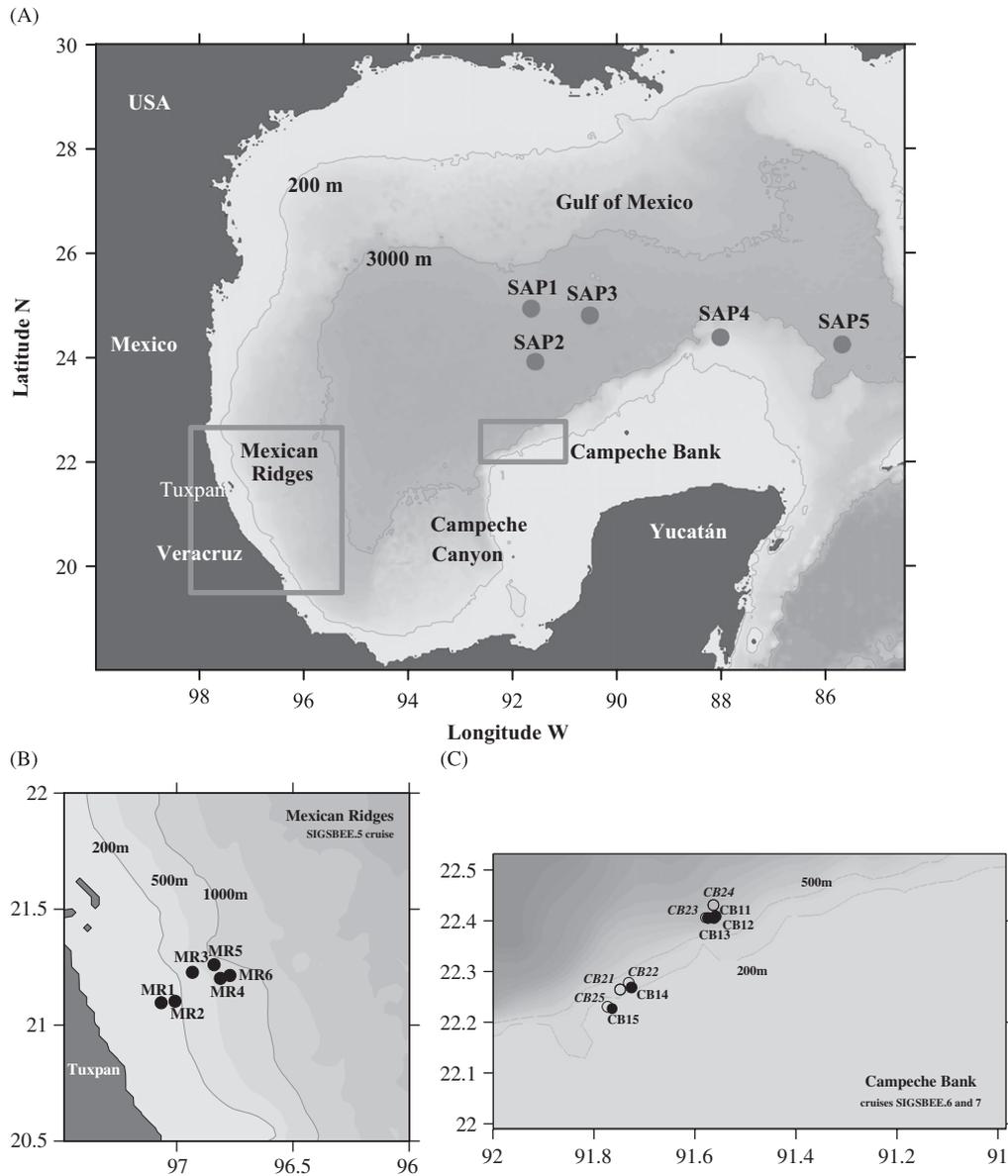


Fig. 1. The Area of study and the location of the samples collected in (A) the Central Gulf of Mexico DGoMB-JSSD (●), (B) the Mexican Ridges SIGSBEE.5 (●), and (C) the Campeche Bank SIGSBEE.6 (● and letters in bold) and SIGSBEE.7 (○ and letters in italics).

continental margin and upper continental slope of the Mexican Ridges (MR) and the Campeche Bank (CB) regions were collected onboard UNAM's R/V *Justo Sierra* in cruises SIGSBEE.5 (six stations, June 2002), SIGSBEE.6 (five stations, July 2003) and SIGSBEE.7 (five stations, June 2004). These cruises were carried out as part of the project *Factores que definen la variabilidad de la diversidad biológica y biomasa béntica en el mar profundo del golfo de México*. The trawls from the Sigsbee abyssal plain (AP) (five stations, August 2002) were collected onboard the R/V *Gyre* (Table 1) during the DGoMB-JSSD cruise as part of the Deep Gulf of Mexico Benthos Study.

After sorting on deck, the animals collected at the 21 stations were fixed in absolute ethanol at 4 °C, identified to species level where possible, counted, photographed, and preserved in glass jars with 70% ethanol solution for later study.

2.3. Laboratory work and data analyses

The specimens were identified in the lab with support of the specialized references for the group and classified to family level

according to Martin and Davis (2001). All specimens were deposited in the national crustacean collection at UNAM where records were included in the collection's database along with identification catalog numbers that are available upon request to the curator. The information for each specimen documented included the region, depth zone, and total number of specimens (*T*), specimens were cataloged by sex: males (M), females (F), ovigerous females (ovig), juveniles (juv), and undetermined specimens (ND). This information sheet provided the basic information of this study.

2.3.1. Species richness

Species richness (*s*) is the number of species identified at each sampling site (stations of each cruise). The species richness information was graphed; the trends observed were analyzed by region and depth zone using one-way ANOVA.

2.3.2. Density

Density was determined by transforming the abundance values (number of individuals per trawl) divided by the area of

Table 1
Geographic reference, depth and trawling information for stations where crustacean specimens were collected at cruises SIGSBEE.5, SIGSBEE.6, SIGSBEE.7 and DGoMB-JSSD

Cruise	# Station	Latitude N	Longitude W	Depth (m)	Distance (km)	Trawl date (dd/mm/yyyy)	Depth zone	Region
SIGSBEE.5	MR1	21°06.2'	97°04.28'	48	1.85	03/07/2002	CM	MR
	MR2	21°06.58'	97°0.43'	67	1.85	03/07/2002	CM	MR
	MR3	21°14.00'	96°55.95'	330	1.85	03/07/2002	UCS	MR
	MR4	21°12.05'	96°48.73'	610	2.78	09/07/2002	UCS	MR
	MR5	21°16.00'	96°50.36'	600	2.22	09/07/2002	UCS	MR
	MR6	21°13.25'	96°46.28'	450	1.85	09/07/2002	UCS	MR
SIGSBEE.6	CB1	22°24.15'	91°35.00'	548	3.78	27/06/2003	UCS	CB
	CB2	22°24.34'	91°34.86'	539	1.85	27/06/2003	UCS	CB
	CB3	22°24.12'	91°35.75'	548	2.96	27/06/2003	UCS	CB
	CB4	22°15.88'	91°44.88'	253	2.78	27/06/2003	UCS	CB
	CB5	22°13.43'	91°47.12'	154	2.22	27/06/2003	CM	CB
SIGSBEE.7	CB11	22°13.83'	91°46.37'	156	1.42	15/06/2004	CM	CB
	CB21	22°15.87'	91°44.89'	251	1.88	15/06/2004	UCS	CB
	CB31	22°16.66'	91°43.87'	252	2.01	15/06/2004	UCS	CB
	CB41	22°24.37'	91°34.74'	538	2.33	15/06/2004	UCS	CB
	CB51	22°25.85'	91°33.81'	705	2.24	15/06/2004	UCS	CB
DGoMB-JSSD	SAP1	24°56.44'	91°38.43'	3545	2.86	04/08/2002	AP	SAP
	SAP2	23°55.32'	91°33.58'	3725	5.05	05/08/2002	AP	SAP
	SAP3	24°48.49'	90°31.13'	3665	7.49	07/08/2002	AP	SAP
	SAP4	24°23.30'	88°01.33'	3350	4.62	09/08/2002	AP	SAP
	SAP5	24°15.19'	85°41.06'	3395	4.99	08/08/2002	AP	SAP

CM: continental margin, UCS: upper continental slope, AP: abyssal plain. MR: Mexican Ridges, CB: Campeche Bank, SAP: Sigsbee abyssal plain.

each trawling event and expressed as ind km^{-2} . The distribution patterns were described by region, depth zones, and sampling sites; the differences among regions and depth zones were analyzed by one-way ANOVA.

2.3.3. Frequency of occurrence

The frequency of occurrence of each species across the 21 stations was calculated. Together with the abundance, it was used to characterize each crustacean species as dominant or rare per region and depth zone. The Olmsted–Tukey test (Sokal and Rohlf, 1995) was used to graph the species along the frequency (x) and abundance (y) axes.

2.3.4. Diversity

The Shannon–Wiener index (Shannon and Weaver, 1963) was used to describe the diversity (H') by region, depth zone, and sampling site. Diversity (H') and evenness (J' ; Lloyd and Ghelardi, 1964) were computed using the Biodiversity—Pro.5 software; logarithms base 2 were used by this software to compute H' . The diversity (H') values were correlated with species richness (s) and evenness (J'). The distribution patterns of diversity were described by region, depth zone, and sampling site; the differences among regions and depth zones were analyzed by one-way ANOVA.

2.3.5. Affinity of the species to region and depth zone

The affinity of species was analyzed by geographical regions (SAP, MR, and CB) and by regions and depth zones using a Canonical Redundancy Analysis (RDA) described in textbooks such as Legendre and Legendre (1998). In both cases the species abundances were Hellinger-transformed, following Legendre and Gallagher (2001). The Hellinger transformation consists in two steps. First, the abundances are transformed to relative abundances per site, then; these relative abundances are subjected to a square-root transformation. When community composition data tables transformed in that way are subjected to methods that implicitly or explicitly use the Euclidean distance (this is the case for RDA), it is the Hellinger distance which is calculated. That

distance is recommended for community composition data because it eliminates double absences from the comparisons of sites, and the square-rooting reduces the influence of the most abundant species. This form of transformation was chosen instead of the chord transformation, also commonly used, because of the advantages of square-rooting and the characteristics of the crustacean assemblage. With the chord transformation, the rare species, which are the largest number in the crustacean assemblage, would have played too small a role in the analyses.

The canonical analyses were computed using the 'vegan' library of the R statistical language (R Development Core Team, 2004). Only the species whose variability was explained at 20% (for regions) or 25% (for regions and depth zones) or more by the explanatory variables were represented in the biplots presenting the results of the canonical analyses.

In the biplots, the lengths of the species arrows depend on two things: (1) how much variance they have in the data set and (2) how well-explained they are by the explanatory variables, in other words, how well-fitted they are in the canonical space. A species may have a big variance in the data set, yet have a small arrow because it is not well-explained by the explanatory variables. On the other hand, a species may be well-explained by the explanatory variables, yet have a small arrow because its variance in the data set is small. All tests of significance were permutation tests involving 9999 permutations of the residuals under the reduced model.

3. Results

A total of 995 specimens of the subphylum Crustacea were collected at the 21 sampling sites during the four cruises (Table 2).

3.1. Taxonomic composition

The specimens belonged to 106 species representing one class (Malacostraca), three orders (Lophogastrida, Isopoda, and Decapoda), five infraorders (Caridea, Astacidea, Palinura,

Table 2

Crustacean specimens classified by Martin and Davis (2001) and ordered by depth zone and geographical region

Infraorder	Family	Genus	Species	ID	M	F	ovig	juv	ND	T	Depth zone	Region
Subphylum Crustacea												
Class Malacostraca												
Order Lophogastrida												
x	Lophogastridae	<i>Neognathophausia</i>	<i>Neognathophausia ingens</i>	1					1	1	AP	SAP
x		<i>Gnathophausia</i>	<i>Gnathophausia zoea</i>	2					2	2	AP	SAP
x	Eucopiidae	<i>Eucopia</i>	<i>Eucopia</i> sp. 1	3					1	1	UCS	MR
x			<i>Eucopia</i> sp. 2	4					1	1	AP	SAP
Subphylum Crustacea												
Class Malacostraca												
Order Isopoda												
x	Cirolanidae	<i>Bathynomus</i>	<i>Bathynomus giganteus</i>	5	4	2		11	26	44	UCS, LCS	MR, CB
Subphylum Crustacea												
Class Malacostraca												
Order Decapoda												
x	x	x	Decapoda sp. 1	6				3		3	AP	SAP
x	x	x	Decapoda sp. 2	7				3		3	AP	SAP
x	Aristeidae	<i>Aristeus</i>	<i>Aristeus antillensis</i>	8	1					1	UCS	MR
x		<i>Aristaeomorpha</i>	<i>Aristaeomorpha foliacea</i>	9	4	15		12		31	UCS	MR, CB
x		<i>Aristaeopsis</i>	<i>Aristaeopsis edwardsiana</i>	10	10	13				23	UCS	MR, CB
x	Benthescymidae	<i>Benthescymus</i>	<i>Benthescymus bartletti</i>	11	2	2			16	20	UCS	CB
x			<i>Benthescymus</i> sp.	12		1				1	AP	SAP
x		<i>Gennadas</i>	<i>Gennadas valens</i>	13	1	1				2	AP	SAP
x			<i>Gennadas</i> sp. 1	14	1					1	AP	SAP
x			<i>Gennadas</i> sp. 2	15						1	AP	SAP
x	Penaeidae	<i>Funchalia</i>	<i>Funchalia villosa</i>	16		1			1	1	AP	SAP
x	Sicyoniidae	<i>Sicyonia</i>	<i>Sicyonia brevirostris</i>	17	1					1	CM	MR
x			<i>Sicyonia burkenroadi</i>	18		1				1	CM	MR
x	Solenoceridae	<i>Pleoticus</i>	<i>Pleoticus robustus</i>	19	4	17			63	88	UCS	MR, CB
x		<i>Solenocera</i>	<i>Solenocera vioscai</i>	20		1				1	CM	MR
x	SF Sergestoidea	x	Sergestoidea sp. 1	21					1	1	AP	SAP
x	Sergestidae	<i>Sergestes</i>	<i>Sergestes paraseminudus</i>	22	1					1	AP	SAP
x			<i>Sergestes</i> sp. 1	23	1					1	AP	SAP
x			<i>Sergestes</i> sp. 2	24					1	1	AP	SAP
x			<i>Sergestes</i> sp. 3	25					1	1	UCS	MR
x			<i>Sergestes</i> sp. 4	26					1	1	UCS	MR
x		<i>Sergia</i>	<i>Sergia robusta</i>	27	4	2				6	AP	SAP
x			<i>Sergia</i> sp.1	28	1	1				2	AP	SAP
Caridea												
	Pasiphaeidae	<i>Parapasiphae</i>	<i>Parapasiphae sulcatifrons</i>	29		1				1	AP	SAP
		<i>Pasiphaea</i>	<i>Pasiphaea merriami</i> ?	30		1				1	AP	SAP
	Oplophoridae	<i>Acanthephyra</i>	<i>Acanthephyra acutifrons</i>	31	1					1	AP	SAP
			<i>A. armata</i>	32		7		1		8	UCS	CB
			<i>A. eximia</i>	33			1			1	UCS	CB
			<i>A. purpurea</i>	34	1					1	AP	SAP
		<i>Ephyrina</i>	<i>Ephyrina benedicti</i>	35		1				1	AP	SAP
		<i>Heterogenys</i>	<i>H. microphthalma</i>	36	1	1			1	3	AP	SAP
		<i>Notostomus</i>	<i>Notostomus gibbosus</i>	37	1					1	AP	SAP
			<i>Notostomus</i> sp.1	38		1				1	AP	SAP
		<i>Oplophorus</i>	<i>Oplophorus gracilirostris</i>	39			2		6	8	AP, UCS	SAP, CB
			<i>Oplophorus</i> sp. 1	40				1		1	AP	SAP
		<i>Systellaspis</i>	<i>Systellaspis debilis</i>	41		2	2			4	AP	SAP
	Nematocarcinidae	<i>Nematocarcinus</i>	<i>Nematocarcinus rotundus</i>	42	2		5		32	39	UCS	CB
	Psalidopodidae	<i>Psalidopus</i>	<i>Psalidopus barbouri</i>	43	1		4			5	UCS	CB
	Pandalidae	x	Pandalidae sp.1	44		1				1	UCS	CB
		x	Pandalidae sp. 2	45			1			1	UCS	CB
		<i>Parapandalus</i>	<i>Parapandalus richardi</i>	46		1	1			2	AP	SAP
		<i>Plesionika</i>	<i>Plesionika holthuisi</i> ?	47		1				1	UCS	CB
			<i>P. longipes</i> ?	48	1					1	UCS	CB
	Glyphocrangonidae	<i>Glyphocrangon</i>	<i>Glyphocrangon longleyi</i>	49	45	3	26	1		75	UCS	CB

Table 2 (continued)

Infraorder	Family	Genus	Species	ID	M	F	ovig	juv	ND	T	Depth zone	Region	
Astacidea	Crangonidae	Parapontocaris	<i>Parapontocaris levigata?</i>	50			1			1	UCS	MR, CB	
	Nephropidae	<i>Acanthacaris</i>	<i>Acanthacaris caeca</i>	51	1	4			1	6	UCS	MR, CB	
		<i>Nephropsis</i>	<i>Nephropsis aculeata</i>	52	1	3				4	UCS	MR, CB	
			<i>N. rosea</i>	53	12	17	1			30	UCS	MR, CB	
Palinura	Polychelidae	<i>Polycheles</i>	<i>Polycheles typhlops</i>	54	1		1			2	UCS	CB	
		<i>Polycheles</i>	<i>Polycheles sculptus</i>	55	7	4				11	UCS	MR, CB	
		<i>Willemoesia</i>	<i>Willemoesia forceps</i>	56	1					1	AP	SAP	
	Scyllaridae	<i>Scyllarus</i>	<i>Scyllarus depressus</i>	57		2				2	CM	MR	
Anomura	Chirostylidae	<i>Uroptychus</i>	<i>Uroptychus nitidus</i>	58	12	6	1	1		20	UCS	MR, CB	
	Galatheididae	<i>Munida</i>	<i>Munida affinis</i>	59		1				1	UCS	CB	
			<i>M. constricta?</i>	60	1	1				2	UCS	CB	
			<i>M. forceps</i>	61	1	1				2	UCS	CB	
			<i>M. iris</i>	62		1	1			2	UCS	MR	
			<i>Agononida</i>	<i>A. longipes</i>	63	10	18	3		1	32	UCS	MR
				<i>M. valida</i>	64	11	10		1		22	UCS	MR, CB
			<i>Munidopsis</i>	<i>Munidopsis bermudezi</i>	65	1					1	AP	SAP
				<i>M. polita</i>	66		1				1	UCS	CB
			<i>M. robusta</i>	67	1					1	UCS	MR	
	Diogenidae	<i>Galacantha</i>	<i>G. spinosa</i>	68		1				1	UCS	CB	
		<i>Dardanus</i>	<i>Dardanus insignis</i>	69	1	1				2	UCS	CB	
		<i>Paguristes</i>	<i>Paguristes moorei</i>	70				1		1	CM	CB	
	Paguridae		<i>Paguristes lymani</i>	71	2	1				3	UCS	CB	
		x	Paguridae sp. 1	72	1					1	UCS	CB	
		x	Paguridae sp. 2	73	1					1	UCS	CB	
		<i>Anisopagurus</i>	<i>Anisopagurus bartletti</i>	74		4				4	UCS	CB	
	Parapaguridae	<i>Pagurus</i>	<i>Pagurus</i> sp. 1	75		1				1	UCS	CB	
		<i>Pylopagurus</i>	<i>Pylopagurus discoidalis</i>	80	1					1	UCS	CB	
<i>Parapagurus</i>		<i>Parapagurus alaminos</i>	76	1					1	AP	SAP		
		<i>P. nudus</i>	77	1	1				2	AP	SAP		
		<i>P. pilimanus</i>	78	42	4	20			66	UCS	CB		
		<i>P. pilosimanus</i>	79	2					2	UCS	MR		
Brachyura	Homolodromiidae	<i>Homolodromia</i>	<i>Homolodromia monstrosa</i>	81	1	1				2	UCS	CB	
	Dromiidae	<i>Cryptodromiopsis</i>	<i>Cryptodromiopsis antillensis</i>	82		1				1	CM	MR	
	Raninidae	<i>Lyseridus</i>	<i>Lyseridus bairdii</i>	83	17	25	3			45	UCS	MR	
		<i>Raninoides</i>	<i>Raninoides lamarcki</i>	84	13	6				19	CM	MR	
			<i>R. louisianensis</i>	85	2	3	3			8	CM, UCS	MR	
	Dorippidae	<i>Ethusa</i>	<i>Ethusa microphthalma</i>	86	7	1				8	UCS	CB	
	Calappidae	<i>Acanthocarpus</i>	<i>Acanthocarpus alexandri</i>	87	4	13		1		18	UCS	MR, CB	
		<i>Calappa</i>	<i>Calappa sulcata</i>	88	5	3				8	CM	MR, CB	
	Leucosiidae	<i>Iliacantha</i>	<i>Iliacantha liodactylus</i>	89	4		2			6	CM	MR, CB	
			<i>I. subglobosa</i>	90		1				1	UCS	CB	
		<i>Myropsis</i>	<i>Myropsis quinquespinosa</i>	91	2	2				4	UCS	MR	
	Inachidae	<i>Stenorhynchus</i>	<i>Stenorhynchus seticornis</i>	95	2					2	CM	MR	
	Inachoididae	<i>Pyromaia</i>	<i>Pyromaia cuspidata</i>	92	3	3	1			7	UCS	MR	
		<i>Anasimus</i>	<i>Anasimus latus</i>	93	4	4	4			12	CM, UCS	MR	
	Pisidae	<i>Rochinia</i>	<i>Rochinia crassa</i>	94	4	6				10	UCS	MR	
	Parthenopidae	<i>Leiolambrus</i>	<i>Leiolambrus nitidus</i>	96	4					4	CM	MR	
		<i>Parthenope</i>	<i>Parthenope agona</i>	97	2					2	UCS	CB	
	Ateleycyclidae	<i>Trichopeltarion</i>	<i>Trichopeltarion nobile</i>	98	6	6				12	UCS	MR, CB	
	Geryonidae	<i>Chaceon</i>	<i>Chaceon quinquedens</i>	99		1	1			2	UCS	CB	
	Portunidae	<i>Raymannius</i>	<i>Raymannius schmitti</i>	100	9	12				21	UCS	MR	
		<i>Portunus</i>	<i>Portunus spinicarpus</i>	101	58	27	6			91	CM	MR	
	Goneplacidae	<i>Bathyplax</i>	<i>Bathyplax typhlus</i>	102	39	31	4			74	UCS	MR, CB	
		<i>Thalassoplax</i>	<i>Thalassoplax angusta</i>	103	1					1	UCS	CB	
Goneplacidae													
Xanthidae	<i>Garthiope</i>	<i>Garthiope spinipes</i>	104	4	2				6	UCS	CB		
	<i>Tetrxanthus</i>	<i>Tetrxanthus rathbunae</i>	105	8	2	2			12	UCS	CB		
	x	<i>Speocarcinus</i>	<i>Speocarcinus carolinensis</i>	106		1			1	CM	MR		

Abbreviations: x: data absent in the category, ?: identity doubt. SF: superfamily, ID: identification number, T: total abundance. AP: abyssal plain, UCS: upper continental slope, LCS: lower continental slope, CM: continental margin, SAP: Sigsbee abyssal plain, MR: Mexican Ridges, CB: Campeche Bank.

Anomura, and Brachyura), 40 families, and 70 genera (Table 2). Four species were identified belonging to the order Lophogastrida; one species to the order Isopoda, and 101 species to the order Decapoda.

3.1.1. Species richness

The largest number of species was recorded from the Mexican Ridges (MR) with 8–14 species ($n = 6, 9.8 \pm 2.5$). A lower number of species was recorded in the Campeche Bank (CB), with 2–15 species ($n = 10, 9.2 \pm 4.5$), and the lowest species richness in the Sigsbee abyssal plain (SAP) with 5–12 species ($n = 5, 7.8 \pm 3.4$) (Fig. 2, Table 3). Several species were common to two or three regions, i.e. *Bathynomus giganteus* common to MR and CB, *Oplophorus gracilirostris* common to SAP and CB, and the species *Glyphocrangon longleyi*, *Aristaemorpha foliacea*, *Aristaeopsis edwardsiana*, *Pleoticus robustus*, *Acanthacaris caeca*, *Nephropsis aculeata* and *N. rosea*, *Munida valida*, *Polycheles sculptus*, *Ilicantha liodactylus*, *Trichopeltarion nobile*, and *Bathyplox typhlus* common to MR and CB (Table 2).

The largest number of species by depth zone was recorded in the upper continental slope of CB, 6–15 species ($n = 8, 10.8 \pm 3.4$). These values were similar to those recorded for a similar depth interval in MR ($n = 4, 10.0 \pm 2.9$) (Table 3, Fig. 1). The lowest species richness was recorded along the continental margin in CB,

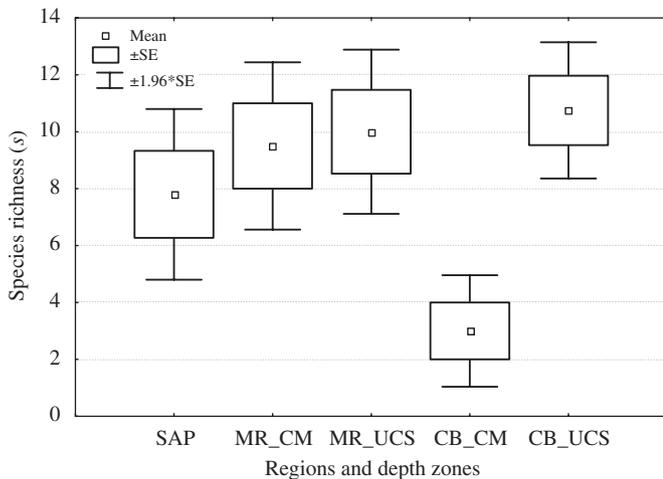


Fig. 2. Species richness (s) variability by region and depth zone: AP: abyssal plain, CM_MR: continental margin_Mexican Ridges, UCS_MR: upper continental slope_Mexican Ridges, CM_CB: continental margin_Campeche Bank, UCS_CB: upper continental slope_Campeche Bank.

Table 3

Species richness (s), density (ind km⁻²), Shannon–Wiener diversity (H') computed in log base 2, and evenness (J') in the three depth zones (AP: abyssal plain, CM: continental margin, UCS: upper continental slope) and three regions (MR: Mexican Ridges, CB: Campeche Bank, SAP: Sigsbee Abyssal Plain)

Depth zone	n	s			Density (ind km ⁻²)			H'			J'		
		Min–max	x̄	s _x	Min–max	x̄	s _x	Min–max	x̄	s _x	Min–max	x̄	s _x
AP	5	5–12	7.8	3.4	1.0–6.6	2.6	2.3	2.11–3.42	2.7	0.6	0.93–1.0	0.96	0.04
MR, CM	2	8–11	9.5	2.1	34.6–47.6	42.1	9.1	0.62–2.94	1.8	1.6	0.21–0.85	0.53	0.45
MR, UCS	4	7–14	10.0	2.9	7.2–62.7	29.6	23.6	2.32–3.11	2.7	0.4	0.71–0.95	0.83	0.10
CB, CM	2	2–4	3.0	1.4	1.4–1.8	1.6	0.27	1–2	1.5	0.7	1.0	1.0	0
CB, UCS	8	6–15	10.8	3.4	3.5–67.4	28.6	27.9	2.17–3.12	2.7	0.3	0.56–0.98	0.82	0.14
Region													
SAP	5	5–12	7.8	3.4	1.0–6.6	2.6	2.3	2.11–3.42	2.7	0.6	0.93–1.0	0.96	0.04
MR	6	8–14	9.8	2.5	7.2–62.7	33.4	19.6	0.62–3.11	2.4	0.9	0.21–0.95	0.73	0.26
BC	10	2–15	9.2	4.5	1.4–67.4	23.2	26.5	1.0–3.12	2.5	0.6	0.56–1.0	0.86	0.15

Abbreviations: n = number of sampling sites, x̄: mean, s_x: standard deviation.

2–4 species ($n = 2, 3.0 \pm 1.4$); these values were notably lower than those recorded for a similar depth interval in MR ($n = 2, 9.5 \pm 2.1$).

The most diversified and abundant crustacean group on the upper continental slope was the infraorder Caridea, with 12 species and 142 organisms. Mesopelagic species such as *Oplophorus gracilirostris* co-occur in the abyssal plain and the upper continental slope. Species that co-occur on the upper continental slope and the continental margin are *Raninoides louisianensis* and *Anasimus latus*. This study extends the known geographic ranges of *Homolodromia monstrosa* and *Ephyrina benedicti* to within the Gulf of Mexico. *Homolodromia monstrosa* was recorded from the continental margin in the Campeche Bank, the first record of this crab from the Gulf of Mexico. We also collected the pelagic shrimp *Ephyrina benedicti* in a trawl from the Sigsbee Abyssal Plain, also a first record in the Gulf of Mexico.

3.2. Density

The largest density values were recorded in MR with 7.2–62.7 ind km⁻² ($n = 6, 33.4 \pm 19.6$ ind km⁻²) followed by values from the Campeche Bank with 1.41–67.4 ind km⁻² ($n = 10, 23.2 \pm 26.5$ ind km⁻², Table 3). The lowest density values were recorded in the Sigsbee abyssal plain with 1.0–6.6 ind km⁻² ($n = 5, 2.6 \pm 2.3$ ind km⁻²). By depth zone, the largest density values were recorded along the continental margin of MR with 34.6–47.6 ind km⁻² ($n = 2, 42.1 \pm 9.1$ ind km⁻²), whilst the lowest values occurred in the Sigsbee abyssal plain.

The density values along the continental margin were significantly different between the MR and the CB regions (42.1 ± 9.1 and 1.6 ± 0.27 ind km⁻², respectively; ANOVA $F_{(5,15)} = 2.1086, p = 0.028$). The superfamily Penaeoidea qualified as the most abundant group with 162 specimens, followed by the infraorder Caridea with 142 individuals. The density values in the Campeche Bank recorded during the cruises SIGSBEE.6 (2003) and SIGSBEE.7 (2004) show between year differences in one region with the lowest density values in 2003 ($1.4–67.4$ ind km⁻², $n = 5; 29.5 \pm 36.6$ ind km⁻²). The number of species correlate with the density values in the equation $y = 0.1152x + 6.6033; R^2 = 0.5345; F = 21.81452; p = 0.000167; n = 21$.

3.3. Frequency of occurrence

The frequency of occurrence of the crustaceans was low. Most species (99) were limited to one location. In contrast, the species *Nephropsis rosea* and *Bathyplox typhlus* occurred at 33% of the sites

(seven locations) and the isopod *Bathynomus giganteus* occurred at six stations. The composition and number of the dominant crustaceans changed with region and with depth zone. In the Sigsbee abyssal plain, the dominant crustaceans collected were the mesopelagic species *Sergia robusta* and *Systellapsis debilis*. Considering their high regional frequencies and high abundances, the species *Portunus spinicarpus*, *Lysirude bairdii*, *Bathylax typhlus*, *Raymannius schmitti*, and *Raninoides lamarcki* were the dominant components in MR while the species *Pleoticus robustus*, *Glyphocrangon longleyi*, *Parapagurus pilimanus*, *Bathynomus giganteus*, *Bathylax typhlus*, and *Nephropsis rosea* were the dominant components in CB.

3.4. Shannon–Wiener diversity

The diversity values were $H' \leq 3.46$. The largest values were recorded in SAP with $H' = 2.1–3.46$ ($n = 5$, 2.7 ± 0.6) followed by values recorded in CB with $H' = 1.0–3.12$ ($n = 10$, 2.46 ± 0.6) and in MR with $H' = 0.62–3.11$ ($n = 6$, 2.4 ± 0.9). By depth zone, the lowest values were recorded along the continental margin in both MR with $H' = 0.6–2.93$ ($n = 2$, 1.78 ± 1.64) and CB with $H' = 1.0–2.0$ ($n = 2$, $H' = 1.5 \pm 0.7$; Table 3). The low diversity values recorded along the continental margin were related to the large abundance of *Portunus spinicarpus* in the trawl composition. Variations in the diversity values was more related to variation in the number of species $R^2 = 0.95$, $F_{(1,3)} = 60.57$, $p = 0.004$, $n = 5$ than to variation in evenness values ($R^2 = 0.61$, $F_{(1,2)} = 3.25$, $p = 0.2127$, $n = 4$).

3.5. Affinity of the crustacean species

3.5.1. Affinity to the geographical regions

The biplot of the canonical analysis (RDA) of the Hellinger-transformed community composition data by the regions (SAP, MR, and CB) is shown in Fig. 3. The relationship is very highly significant (bimultivariate redundancy statistic $R^2 = 0.15633$, adjusted $R^2 = 0.06259$, $p = 0.001$). The variability of 18 species

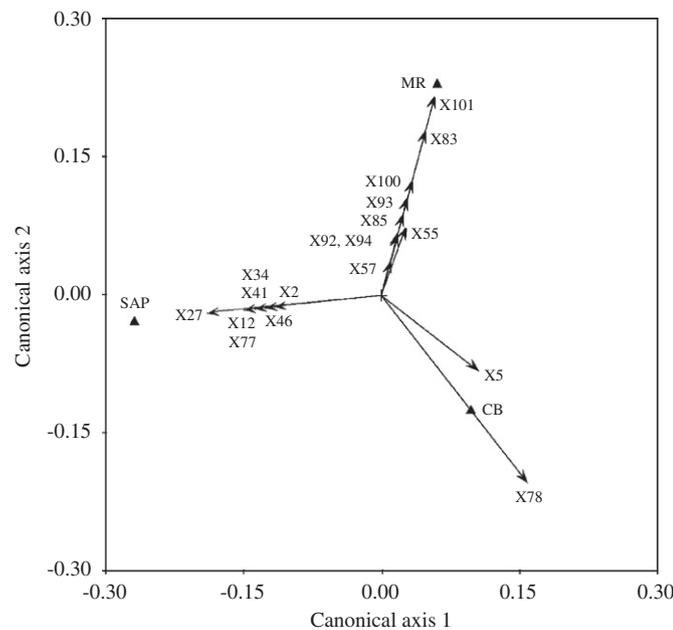


Fig. 3. RDA double projection graph of Hellinger-transformed species analyzed by regions (SAP, MR, and CB) and fitted at 20% or more by the canonical analysis. The triangular markers show the three regions. The species are represented by the number besides the X marker along the axis; the ID number next to the marker corresponds to the species list (Table 2).

was explained at 20% or more by the regions; these species are represented in the biplot.

Caridean, lophogastrid, benthescymid, and sergestid shrimp species were found in SAP. In general all species with affinity to SAP had low abundance (i.e. *Benthescymus* sp. (X12) with 1 and *Sergia robusta* (X27) with six individuals) and like *Gnathopausia zoea* (X2) may display vertical migration in the water column. The exception in this group was *Parapagurus nudus* (X77) an abyssal hermit crab. The species with affinity to CB and MR were abundant with a few exceptions (*Scyllarus depressus* (X57), *Raninoides louisianensis* (X85), *Pyromaia cuspidata* (X92) in MR with 2–8 individuals). A species of hermit crab (*Parapagurus pilimanus* (X78)) was found in CB. Only brachyuran and palinuran were found in CB. The species *Bathynomus giganteus* (X5) and *Polycheles sculptus* (X55) occurred in two regions, MR and CB.

3.5.2. Affinity to the regions and depth zones

The biplot of the canonical analysis (RDA) of the Hellinger-transformed community composition data by regions and depth zones is shown in Fig. 4. The relationship is very highly significant ($R^2 = 0.26046$, adjusted $R^2 = 0.12996$, $p = 0.001$). The variability of 33 species was explained at 25% or more by the regions and depth zones; these species are represented in the biplot.

The same caridean, lophogastrid, benthescymid, and sergestid shrimp species found in SAP (Fig. 3) were found in the AP/SAP (Fig. 4). A total of 15 species were recorded in the continental margin/shelf of which four (*Scyllarus depressus* (X57), *Raninoides louisianensis* (X85), *Anasimus latus* (X93), *Portunus spinicarpus* (X101)) had shown an affinity to the MR (Fig. 3). Of these four species, *Portunus spinicarpus* (X101) is an abundant shelf crab. In addition, 2 Anomura (*Dardanus insignis* (X69), *Paguristes moorei* (X70)), 7 Brachyura and 3 shrimp (*Sicyonia brevirostris* (X17), *S. burkenroadi* (X18), *Solenocera vioscai* (X20)) were found in the continental margin/shelf, all had low abundances (Fig. 4).

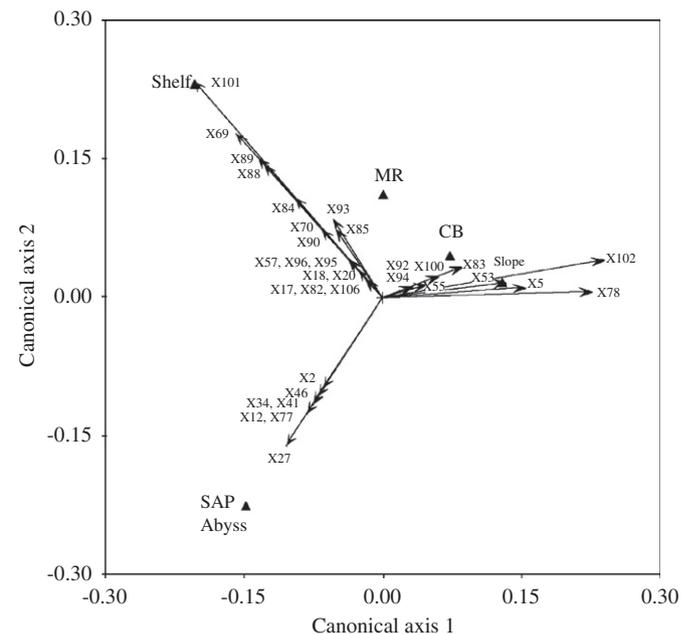


Fig. 4. RDA double projection graph of Hellinger-transformed species analyzed by regions (SAP, MR, and CB) and depth zones (Shelf = continental margin, Slope = upper continental slope, Abyss = abyssal plain) fitted at 25% or more by the canonical analysis. The triangular markers show both the three regions and the three depth zones. The species are represented by the number besides the X marker along the axis; the ID number next to the marker corresponds to the species list (Table 2).

The crabs *Anasimus latus* (X93) and *Raninoides louisianensis* (X85) were found at two depth zones in MR. Seven species found in CB (Fig. 3) were found in UCS in the CB (Fig. 4). In addition 5 Brachyura, 1 Polychelidae (*Polycheles sculptus* (X55)) and 1 Nephropidae (*Nephropsis rosea* (X53)) were only found in the UCS in CB (Fig. 4). All these species displayed abundances between 7 and 74 individuals.

4. Discussion

4.1. Species composition

The geographical span of *Homolodromia monstrosa* (Martin et al., 2001) and *Ephyrina benedicti* (Smith, 1885; Stephensen, 1935; Crosnier and Forest, 1973) have been expanded within the Gulf of Mexico. Many of the species recorded have an ample geographic distribution and have a biogeographic relationship with other assemblages of the Atlantic Ocean (*Raymannius schmitti*, *Thalassooplax angusta*, *Chaceon quinquedens*, and *Stenorhynchus seticornis*) and the Caribbean Sea (Pequegnat, 1983) and others being widespread (lophogastrids, several shrimp species and *Bathynomus*). Our results agree with the distribution patterns recorded by Crosnier and Forest (1973). Widespread distribution in crustaceans can be explained in some decapod crustacean as a dispersion strategy exemplified by larval stages (Yang, 1976) and to species whose distribution is related to specific deep water masses. However, it is important to mention that many deep-sea crustaceans produce few, yolk-packed eggs, rather than numerous eggs with planktonic larval stages.

4.2. Species richness

The number of crustacean species recorded in the present study (106: 4 lophogastrid, 1 isopod, 2 unidentified decapods, 13 peneids, 8 sergestids, 22 caridean, 3 astacids, 4 palinurids, 23 anomurids, and 26 brachyurans) is lower than recorded basin-wide in the Gulf of Mexico by other authors, both in the deep sea (165 species in Pequegnat, 1983; 130 species in Wicksten and Packard, 2005) and on the continental shelf and margin (243 species in Hernández-Aguilera et al., 1996). These values remain low when comparing records from the tropical Pacific, Indian and Atlantic Oceans (Crosnier and Forest, 1973). However the number of species recorded at 21 stations represents 65% of the species previously recorded by Pequegnat (1983) at 184 stations and 82% of the records compiled by Wicksten and Packard (2005) from 407 sampling sites from published literature and catalogs. From this, we conclude that rare species are added with sampling sites to attain the maximum number recorded in the Gulf of Mexico.

The caridean shrimp were the most diversified taxon in this study. This agrees with previous records from the Northern Gulf of Mexico (Pequegnat, 1983) and other tropical deep habitats (Crosnier and Forest, 1973). Our results disagree with the low species richness of megafaunal species found elsewhere in the deep sea (Gage and Tyler, 1999; Hessler and Sanders, 1967).

4.3. Density

The highest abundances were recorded in the MR, which may be explained by a larger food supply to the sea floor. This region has a large organic input from the rivers Grande, San Fernando, and Tuxpan (Escobar-Briones and Soto, 1997; Escobar et al., 1999; Escobar-Briones, 2000, 2004). Similar large densities have been

recorded on the continental slopes and abyssal plain off the Amazon River (Sibuet et al., 1984), on the Hudson canyon (Rowe et al., 1982), off the Mississippi Fan in the Northern Gulf of Mexico (Pequegnat, 1983), off the Coatzacoalcos River (Soto and Escobar, 1995), and along the Campeche canyon in the SW Gulf of Mexico (Estrada-Santillan, 2004).

The lowest density values were recorded for crustaceans from the Sigsbee Abyssal Plain. This may be due to reduced food input, as seen in other studies (Gage and Tyler, 1999). Brachyurans in the Gulf of Mexico have been recorded to diminish their density and biomass at depths of 600 m and more (Pequegnat, 1983). This diminishing trend with depth has been attributed to the high trophic position of the group and the energy limitation at depth.

The large densities of caridean shrimps on the slope have caught the attention of nations to use these as fishery resources (Navarrete del Proo and Gracia, 1996; Arreguín et al., 1997; Gómez-Ponce and Gracia, 2003). However, in spite of the large densities encountered, the slow growth rates and time required to mature, e.g. for *Chaceon quinquedens*, are limiting factors to sustainable use of deep-sea crustacean species (Hastie, 1995; Steimle et al., 2001).

4.4. Frequency of occurrence

Among the most frequent and abundant species recorded on the upper continental slope are *Nephropsis rosea*, *Bathylax typhlus*, and *Bathynomus giganteus*. Previous records in the Gulf of Mexico agree that *Bathylax typhlus* and *Nephropsis rosea* are frequent key components of the deep-sea Gulf crustacean assemblage together with *Benthesicymus* sp. and *Parapagurus nudus* (Pequegnat, 1983). The presence of a limited number of dominant components is common in the deep sea and is explained in response to perturbation (Thistle et al., 1985; Smith et al., 1986). Species with restricted distribution are easily impacted by human activities and are usually of primary concern for conservation (Ricketts et al., 2005). With small populations, long time spans, and low recruitment as is the case of many of the deep-sea crustaceans, and the extreme vulnerability to habitat destruction by extraction of resources and limited options for conservation as faced in the Gulf of Mexico region, crustacean species can face heavy impact in the absence of appropriate conservation action for deep-sea habitats.

4.5. Diversity

The diversity values recorded in this study are low considering that the maximum reachable value in communities is $H' = 5.3$ (Margalef, 2002) when using base log 2 the same used in this paper. The lack of records at depths of 1000–3000 m limits our interpretation of the diversity distribution patterns along the depth gradient. In other invertebrates (polychaetes, cumaceans, gastropods, and bivalves), the diversity pattern with depth has been recorded to be of parabolic shape with a maximum at depths of 2300–2800 m and diminishing again with depth (Rex, 1981, 1983). The maximum was recorded at depths of 700–2250 m in the Gulf of Mexico for megafaunal components (Pequegnat, 1983).

The increase of the diversity with depth and the occurrence of the maximum on the continental slope has been attributed by Rex (1973) to environmental stability and has been further explained in mollusk assemblages by the source-sink hypothesis and the effects of immigration, predation, and energetic restrictions on the reproductive viability (Rex et al., 2005). The values of diversity and their link to evenness agree with studies of other taxa in different regions (Rex, 1973; Haedrich et al., 1980).

4.6. Affinity of species

Studies with crustacean assemblages from the slope have recognized a change in the composition of species clearly defined by the end of the mudline, penaeid, and caridean shrimps of the Eastern Atlantic (Crosnier and Forest, 1973) brachyurans of the tropical Western Atlantic (Wenner and Boesch, 1979; Soto, 1997). Below 3000 m the physical and chemical conditions are stable and the vertical distribution and variation is attributed to current velocity, topography as well as to sediment type (Rowe and Headrich, 1979; Gardiner and Haedrich, 1978). In some locations differences are determined by the abrupt change in dissolved oxygen concentration (Levin, 2003). It is unlikely that the restricted crustacean distributions are a result of these changes. However, in the case of isopods the species distinctiveness suggested that the abyssal province can be divided into biogeographical and bathymetric zones (Menzius et al., 1973).

This study identified a zonation within the abyssal faunal province but in addition to pagurid crabs (*Parapagurus pilosimanus*) and barnacles (*Scalpellum regium*) other large epifaunal animals included seapens, echinoderms, porifera that was recorded as discontinuities by Vinogradova (1959). These studies concur that the shallower bathyal zone has larger abundances of large animals in comparison to the abyssal zone.

5. Conclusion

A total of 106 crustacean species were recorded in this study, of which 87 were identified to species level, three to order, one to superfamily, four to family, 11 to genus) a total of nine species require further study. We showed the following:

1. This study extends the known geographic ranges of the species *Homolodromia monstrosa* and *Ephyrina benedicti* into the Gulf of Mexico.
2. The largest number of species was recorded in the Mexican Ridges followed by the Campeche Bank, the lowest in the Sigsbee Abyssal Plain. In terms of depth zones, the largest number of species was recorded on the upper continental slope where density values and number of caridean species were large.
3. The lowest density values were recorded in the Sigsbee Abyssal Plain. Due to their low frequencies of occurrence and abundances, most crustaceans are rare components of the benthic assemblages.
4. Diversity values were low ($H' \leq 3.46$) and correlated with evenness values. Diversity was higher in the Sigsbee Abyssal Plain (where evenness was the highest in this study) and on the continental slopes of the other two regions than on the continental margin.
5. Crustacean species showed a strong, highly significant affinity to regions and depth zones: for example, *Portunus spinicarpus* characterizes the continental margin of the Mexican Ridges region, *Bathyplax typhlus* the upper continental slope of the Campeche Bank, and *Sergia robusta* the Sigsbee Abyssal Plain. This study identified variability of the crustacean assemblages, collected with trawls, that was significantly associated with both regions and depth zones.
6. Tyler's (1988) paradigm, which served as the starting point of this research, was that tropical deep-sea species richness and densities were low and homogeneous over large areas, due to limited biogenic carbon export from the productive areas on the ocean surface. A prediction from that paradigm is that the continental slope and abyssal plain should have low species

diversity, without much differentiation among regions. Our results contradict that part of Tyler's predictions.

7. The information generated by this study contributes to a baseline of species distribution in the southern Gulf of Mexico. Potential hotspots of biodiversity are identified and characterizes so that such areas can be adequately conserved.

Acknowledgments

Specimens were collected in the abyssal plain with support of the *Deep Gulf of Mexico Benthos Study (DGoMBS)–Joint US/Mexico Studies of the Sigsbee Deep (JSSD)* MMS, USGS Contract 1435-01-99-CT-30991 to TAMU. The specimens from the continental slope and margin were collected and processed with additional support from ICML (UNAM, CU) and projects CONACyT 40158 F; DGAPA UNAM IN224503, 204307 and CONABIO BE013 *Base de datos de fauna batial, abisopelágica y abisal de México*. The species identification was validated by M. Wicksten, TAMU and J.L. Villalobos-Hiriart IBUNAM. The crews of UNAM's R/V *Justo Sierra* and TAMU's R/V *Gyre* provided invaluable help onboard. To F. Álvarez, IB-UNAM for support at the Colección Nacional de Crustáceos.

References

- Aguayo, J.E., Trápaga, R., 1984. Geodinámica de México y minerales del mar. Colección La Ciencia para todos. Fondo de Cultura Económica, 185pp.
- Andrew, N.L., Mapstone, B.D., 1987. Sampling and the description of spatial pattern in marine ecology. *Oceanography and Marine Biology Annual Review* 25, 39–90.
- Antoine, J.W., Martin, R.G., Pyle, T.G., Bryant, W.R., 1974. Continental margins of the Gulf of Mexico. In: Burk, C.A., Drake, C.L. (Eds.), *The Geology of the Continental Margins*. Springer, New York, pp. 683–693.
- Arreguín, F., Schultz-Ruiz, L., Gracia, A., Sánchez-Chávez, J., Alarcón-Fuentes, T., 1997. Las Pesquerías de Camarón de alta mar: explotación, dinámica y evaluación. In: Flores-Hernández, D., Sánchez-Gil, P., Seijo, J.C., Arreguín-Sánchez, F. (Eds.), *Análisis y Diagnóstico de los Recursos Pesqueros Críticos del Golfo de México*, EPOMEX Serie científica, vol. 7, pp. 145–172.
- Baba, K., Poore, G.C.B., 2002. *Munidopsis* (Decapoda, Anomura) from south-eastern Australia. *Crustaceana* 75 (3–4), 231–252.
- Balsam, W.L., Beeson, J.P., 2003. Sea-floor sediment distribution in the Gulf of Mexico. *Deep-Sea Research I* 50, 1421–1444.
- Barradas-Ortiz, C., Briones-Fourzán, P., Lozano-Álvarez, E., 2003. Seasonal reproduction and feeding ecology of giant isopods, *Bathynomus giganteus*, from the continental slope of the Yucatán Peninsula. *Deep-Sea Research I* 50, 495–513.
- Belman, B.W., Childress, J.J., 1976. Circulatory adaptation to the oxygen minimum layer in the benthypelagic mysid *Gnathopausia ingens*. *Biology Bulletin* 150, 15–37.
- Birstein, Y.A., Zarenkov, N.A., 1970. On the bottom decapods (Crustacea, Decapoda) of the Kurile-Kamchatka region. *Trudy Institute Okeanologii, SSSR* 86, 420–426 (in Russian, translated by Israel Program for Scientific Translations, Jerusalem 1972).
- Blankenship, L.E., Yayanos, A.A., 2005. Universal primers and PCR of gut contents to study marine invertebrate diets. *Molecular Ecology* 14 (3), 891–899.
- Bowman, T.E., Manning, R.B., 1972. Two arctic bathyal crustaceans: the shrimp *Bythocaris cryonensis* new species, and the amphipod *Eurythenes gryllus*, with in situ photographs from the Ice Island T-3. *Crustaceana* 23, 187–201.
- Briones-Fourzán, P., Lozano-Álvarez, E., 1991. Aspects of the biology of the giant isopod *Bathynomus giganteus* A. Milne-Edwards, 1879 (Isopoda: Cirolanidae) off the Yucatan peninsula. *Journal of Crustacean Biology* 11 (3), 375–385.
- Cardona-Maldonado, M.A., Mignucci-Giannoni, A.A., 1999. Pygmy and Dwarf sperm whales in Puerto Rico and the Virgin Islands, with a review of *Kogia* in the Caribbean. *Caribbean Journal of Science* 35 (1–2), 29–37.
- Casanova, J.P., 1997. Les mysidacés Lophogastrida (Crustacea) du canal de Mozambique (côte de Madagascar). *Zoosystema* 19 (1), 91–109.
- Chamberlain, S.C., Mayer-Rochow, V.B., Dossert, W.P., 1986. Morphology of the compound eye of the giant deep-sea isopod *Bathynomus giganteus*. *Journal of Morphology* 189, 145–186.
- Charmasson, S., Germain, P., Leclerc, G., 1998. ^{210}Po as a tracer of variations of tropic input to deep-sea benthic ecosystems: a study of the deep-sea amphipod *Eurythenes gryllus* from the tropical Atlantic. *Radiation Protection Dosimetry* 75 (1–4), 131–137.
- Childress, J.J., 1968. Oxygen minimum layer: vertical distribution and respiration of the mysid *Gnathopausia ingens*. *Science* 106, 1242–1243.
- Childress, J.J., Price, M., 1978. The growth rate of a bathypelagic crustacean, *Gnathopausia ingens* (Mysidacea: Lophogastridae) I. Dimensional growth and population structure. *Marine Biology* 50, 47–62.

- Childress, J.J., Price, M., 1983. The growth rate of a bathypelagic crustacean, *Gnathophausia ingens* (Mysidacea: Lophogastridae) II. Grow in material and energy. *Marine Biology* 76, 165–177.
- Crosnier, A., Forest, J., 1973. Les crevettes profondes de l'Atlantique Oriental Tropical. *Faune Tropicale XIX ORSTOM Paris*, vol. 19, 409pp.
- Desbruyères, D., Deming, J., Dinot, A., Khripounoff, A., 1985. Réactions de l'écosystème benthique profond aux perturbations: nouveaux résultats expérimentaux. In: Laubier, L., Monniot, C. (Eds.), *Peuplements du Golfe de Gascogne*. Institut Français de Recherche pour l'Exploitation de la Mer, Brest, pp. 121–142.
- Elliott, B.A., 1982. Anticyclonic rings in the Gulf of Mexico. *Journal of Geophysical Oceanography* 12, 1292–1309.
- Escobar, E., Signoret, M., Hernández, D., 1999. Variation of the macrobenthic infaunal density in a bathymetric gradient: Western Gulf of Mexico. *Ciencias Marinas* 25 (2), 193–212.
- Escobar-Briones, E., 2000. La biodiversidad del mar profundo en México. *Biodiversitas* 6 (29), 2–6.
- Escobar-Briones, E., 2004. Estado del conocimiento de las comunidades bénticas en el Golfo de México. In: Caso, M., Pisanty, I., Ezcurra, E. (Compiladores), *Diagnóstico ambiental del golfo de México I*, pp. 201–246.
- Escobar-Briones, E., Soto, L.A., 1997. Continental shelf biomass in the western Gulf of Mexico. *Continental Shelf Research* 17 (6), 585–604.
- Estrada-Santillan, E.L., 2004. Macroinfauna béntica del cañón de Campeche, SW del Golfo de México. Tesis Licenciatura (Biólogo)-UNAM, Facultad de Estudios Superiores Iztacala, 73pp.
- EWIG, M., Antoine, J., 1966. New seismic data concerning sediments and diapiric structures in Sigsbee Deep and upper continental slope, Gulf of Mexico. *American Association Petroleum Geology Bulletin* 50 (3), 479–504.
- Firth Jr., W.R., Pequegnat, W.E., 1971. Deep-sea lobsters of the families Polychelidae and Nephropidae (Crustacea, Decapoda) in the Gulf of Mexico and Caribbean Sea. A&M Project 700-15. Reference 71-11T.
- Gage, J.D., Tyler, P.A., 1999. *Deep-sea Biology. A Natural History of Organisms at the Deep-sea Floor*. Cambridge, 504pp.
- Gardiner, F.P., Haedrich, R.L., 1978. Zonation in the deep benthic megafauna: application of a general test. *Oecologia* 31, 311–317.
- Gómez-Ponce, M.A., Gracia, A., 2003. Distribution and abundance of larvae and adults of *Solenocera* (Decapoda, Solenoceridae) in the southwestern Gulf of Mexico. *Crustaceana* 76 (6), 681–698.
- Gordon, I., 1955. Crustacea decapoda. Report of the Swedish Deep-Sea Expedition 2. *Zoology, Fasc 2* (19), 237–245.
- Griffin, D.J.G., Brown, D.E., 1975. Deepwater decapod crustacea from eastern Australia: brachyuran crabs. *Records of the Australian Museum* 30, 248–271.
- Griffin, D.J.G., Tranter, H.A., 1986. Some majid spider crabs from the deep Indo-west Pacific. *Records of the Australian Museum* 38, 351–371.
- Haedrich, R.L., Rowe, G.T., Polloni, P., 1980. The megabenthic fauna in the deep sea south of New England, USA. *Marine Biology* 57, 165–179.
- Hastie, L.C., 1995. Deep-water geryonid crabs: a continental slope resource. In: Ansell, A.D., Gibson, R.N., Barnes, M. (Eds.), *Oceanography Marine Biology Annual Review*, vol. 33, pp. 561–584.
- Hernández-Aguilera, J.L., Toral-Almazán, R.E., Ruiz-Nuño, J.A., 1996. Especies catalogadas de crustáceos estomatópodos y decápodos para el Golfo de México, Río Bravo, Tamaulipas a Progreso, Yucatán. Dirección General de Oceanografía Naval, Secretaría de Marina. Comisión Nacional para el conocimiento y uso de la biodiversidad (CONABIO), México, 132pp.
- Hessler, R.R., Sanders, H.L., 1967. Faunal diversity in the deep sea. *Deep-sea Research* 14, 65–78.
- Hessler, R.R., Wilson, G.D.F., 1983. The origin and biogeography of the malacostracan crustaceans in the deep sea. In: Sims, R.W., Price, J.H., Whalley, P.E.S. (Eds.), *Evolution, Time and Space: the Emergence of the Biosphere*. Academic Press, London, pp. 227–254.
- Holthuis, L.B., 1974. The lobsters of the superfamily Nephropsidea of the Atlantic Ocean. *Bulletin of Marine Science* 24, 67–76.
- Holthuis, L.B., 1991. *Marine Lobsters of the World: An Annotated and Illustrated Catalogue of Species of Interest to Fisheries Known to Date*. Food and Agriculture Organization of the United Nations, Rome, Italy, viii+292pp.
- Jones, W.J., Macpherson, E., 2006. Molecular phylogeny of the east Pacific squat lobsters of the genus *Munidopsis* (Decapoda: Galatheidae) with the descriptions of seven new species. *Journal of Crustacean Biology* 27 (3), 477–501.
- Legendre, P., Gallagher, E., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280.
- Legendre, P., Legendre, L., 1998. *Biological ecology*, second ed. (English edition). Elsevier Science, Amsterdam, 853pp.
- Levin, L., 2003. Oxygen minimum zone benthos: adaptation and community response to hypoxia. *Oceanography and Marine Biology: An Annual Review* 41, 1–45.
- Lloyd, M., Ghelardi, R., 1964. A table for calculating the "equitability" component of species diversity. *Journal of Animal Ecology* 33, 217–225.
- Macpherson, E., Segonzac, M., 2005. Species of the genus *Munidopsis* (Crustacea, Decapoda, Galatheidae) from the deep Atlantic Ocean, including cold-seep and hydrothermal vent areas. *Zootaxa* 1095, 1–60.
- Malahoff, A., Embley, R.W., Fornari, D.J., 1982. Geomorphology of Norfolk and Washington Canyons and the surrounding continental slope Washington Canyons and the surrounding continental slope and upper rise as observed from DSRV ALVIN. In: Scrutton, R.A., Talwani, M. (Eds.), *The Ocean Floor*, Bruce Heezen commemorative volume. Wiley, London, pp. 97–111.
- Margalef, R. (Ed.), 2002. *Teoría de los sistemas ecológicos*, second ed. Alfaomega Grupo Editor, 290pp.
- Marshall, N.B., 1979. *Deep-sea Biology, Developments and Perspectives*. Blandford, Londres, 566pp.
- Martin, J.W., Davis, G.E., 2001. An updated classification of the recent Crustacea. *Natural History Museum of Los Angeles, Science Series* 39, 124pp.
- Martin, J.W., Christiansen, J.C., Trautwein, S.E., 2001. *Homolodromia monstrosa*, new species, from the western Atlantic, with a redescription of the holotype of *H. paradoxa* A. Milne Edwards, 1880. *Bulletin of Marine Science* 68 (2), 313–326.
- Menzies, R.J., George, R.Y., Rowe, G.T., 1973. *Abyssal Environment and Ecology of the World Oceans*. Wiley-Interscience, New York, 488pp.
- Mickel, T., Childress, J.J., 1978. The effect of pH on respiration and activity in the bathypelagic mysid *Gnathophausia ingens*. *Biology Bulletin* 154, 138–147.
- Moeller, J.F., Case, J.F., 1994. Properties of visual interneurons in a deep-sea mysid, *Gnathophausia ingens*. *Marine Biology* 119 (2), 211–219.
- Navarrete del Proo, A., Gracia, A., 1996. La pesquería de camarón en Alta Mar. Golfo de México y Caribe Mexicano. In: Instituto Nacional de la Pesca, SEMARNAP. *Pesquerías relevantes de México, XXX Aniversario del INP. México, Tomo, vol. 1*, pp. 29–63.
- Nowlin Jr., W.D., McLellan, H.J., 1967. A characterization of the Gulf of Mexico waters in winter. *Journal of Marine Research* 25, 29–59.
- Pequegnat, L.H., 1970a. Deep-sea caridean shrimps with descriptions of six new species. In: Pequegnat, W.E., Chace, F.A. (Eds.), *Contributions on the Biology of the Gulf of Mexico. Texas A&M University Oceanographic Studies*, vol. 1. Gulf Publishing, Houston, pp. 125–170.
- Pequegnat, L.H., 1970b. Deep-water barchyuran crabs. In: Pequegnat, W.E., Chace, F.A. (Eds.), *Contributions on the Biology of the Gulf of Mexico. Texas A&M University Oceanographic Studies*, vol. 1. Gulf Publishing, Houston, pp. 125–170.
- Pequegnat, W.E., 1983. The ecological communities of the continental slope and adjacent regimes of the northern Gulf of Mexico. Report of Contract AA851-CTI-12. Mineral Management Service, 398pp.
- Pequegnat, W.E., Pequegnat, L.H., Firth, R.W., James, B.M., Roberts, T.W., 1971. Gulf of Mexico deep sea fauna. Decapoda and euphasiacea. In: Webster, W. (Ed.), *Serial Atlas of the Marine Environment*. American Geographical Society, New York, pp. 1–12.
- R Development Core Team, 2004. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rex, M.A., 1973. Deep-sea species diversity: decreased gastropod diversity at abyssal depths. *Science* 181, 1051–1053.
- Rex, M.A., 1981. Community structure in the deep-sea benthos. *Annual Review Ecology System* 12, 331–353.
- Rex, M.A., 1983. Geographic patterns of species diversity in deep-sea benthos. In: Rowe, G.T. (Ed.), *The Sea*, vol. 8. Wiley, New York, pp. 453–472.
- Rex, M.A., McClain, C.R., Johnson, N.A., Etter, R.J., Allen, J.A., Bouchet, P., Warén, A., 2005. A source-sink hypothesis for abyssal biodiversity. *The American Naturalist* 165 (2), 163–178.
- Rice, A.L., 1981. The abdominal locking mechanism in the deep-sea shrimp genus *Glyphocrangon* (Decapoda, Glyphocrangonidae). *Crustaceana* 40, 316–319.
- Ricketts, T.H., Dinerstein, E., Boucher, T., Brooks, T.M., Butchart, S.H.M., Hoffmann, M., Lamoreux, J.F., Morrison, J., Parr, M., Pilgrim, J.D., Rodrigues, A.S., Sechrest, W., Wallace, G.E., Berlin, K., Bielby, J., Burgess, N.D., Church, D.R., Cox, N., Knox, D., Loucks, C., Luck, G.W., Master, L.L., Moore, R., Naidoo, R., Ridgely, R., Schatz, G.E., Shire, G., Strand, H., Wettengel, W., Wikramanayake, E., 2005. Pinpointing and preventing imminent extinctions. *Proceedings National Academy of Sciences* 102 (51), 18497–18501.
- Roberts, T.W., Pequegnat, W.E., 1970. Deep-water decapod shrimps of the family Penaeidae. In: Pequegnat, W.E., Chace, F.A. (Eds.), *Contributions on the Biology of the Gulf of Mexico. Texas A&M University Oceanographic Studies*, vol. 1. Gulf Publishing, Houston, pp. 125–170.
- Roberts, H.H., McBride, R.A., Coleman, J.M., 1999. Outer shelf and slope geology of the Gulf of Mexico: an overview. In: Kumpf, H., Steidinge, D., Sherman, K. (Eds.), *The Gulf of Mexico Large Marine Ecosystem: Assessment, Sustainability, and Management*. Blackwell Science, Berlin, pp. 205–234.
- Rowe, G.T., Headrich, R.L., 1979. The biota and biological processes of the continental slope. In: Pilkey, O., Doyle, L. (Eds.), *Continental Slopes*. Society of Economic and Petroleum Mineralogist, Tulsa, pp. 49–59.
- Rowe, G.T., Polloni, P., Hardrich, R.L., 1982. The deep-sea macrobenthos on the continental margin of the northwest Atlantic Ocean. *Deep-sea Research* 29A, 257–278.
- Rowe, G.T., Sibuet, M., Vangriesheim, A., 1986. Domains of occupation of abyssal scavengers inferred from baited cameras and tramps on the Demerara Abyssal Plain. *Deep-sea Research* 33A, 501–522.
- Sanders, N.K., Childress, J.J., 1990. Adaptations to the deep-sea oxygen minimum layer: oxygen binding by the hemocyanin of the bathypelagic mysid, *Gnathophausia ingens* Dohrn. *Biological Bulletin* 178, 286–294.
- Shannon, C.E., Weaver, W., 1963. *The Mathematical Theory of Communication*. University Illinois Press, Urbana, 177pp.
- Sibuet, M., Monniot, C., Desbruyères, D., Dinot, A., Khripounoff, A., Rowe, G., Segonzac, M., 1984. Peuplements benthiques et caractéristiques trophiques du milieu dans la plaine abyssale Demerara dans l'océan Atlantique. *Océanologica Acta* 7, 345–358.
- Smith, S.I., 1885. On some new or little known Decapod Crustacea, from recent Fish Commission dredgings off the east coast of the United States. *Proceedings United States National Museum* 7, 493–511.

- Smith, C.R., Jumars, P.A., DeMaster, D.J., 1986. *In situ* studies of mefaunal mounds indicate rapid sedimentation turnover and community response at deep-sea floor. *Nature*, London 323, 251–253.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry*, third ed. W.A. Freeman and Co., San Francisco, 776pp.
- Soto, L.A., 1997. Composition and zoogeographic relationships of the decapod crustacea shelf-fauna of the northeastern Gulf of Mexico. *Revista de la Sociedad Mexicana de Historia Natural* 47, 141–148.
- Soto, L.A., Escobar, E., 1995. Coupling mechanisms related to benthic production in the southwestern Gulf of Mexico. In: Eleftheriou, A., Ansell, A.D., Smith, C.J. (Eds.), *Biology and Ecology of Shallow Coastal Waters*, Olsen & Olsen International Symposium Series, pp. 233–242.
- Steimle, F.W., Zetlin, Ch.A., Chang, S., 2001. Essential fish habitat source document: red crab, *Chaceon* (*Geryon*) *quinquedens*, life history and habitat characteristics. NOAA Technical Memorandum NMFS-NE-163, 27pp.
- Stephensen, K., 1935. Crustacea Decapoda. The Godthaab expedition 1928. *Meddelelser om. Gronland* 80 (1), 1–94.
- Thistle, D., Yingst, J.Y., Fauchald, K., 1985. A deep-sea benthic community exposed to strong bottom currents on the Scotian Rise (Western Atlantic). *Marine Geology* 66, 91–112.
- Tyler, P.A., 1988. Seasonality in the deep-sea. *Oceanography and Marine Biology: An Annual Review* 18, 227–258.
- Underwood, A.J., Chapman, M.G., Conell, S.D., 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology* 250, 97–115.
- Vidal Lorandi, F.V., Vidal Lorandi, V.M., Rodríguez Espinosa, P.F., Zambrano Salgado, L., Portilla Castillas, J., Rendón Villalobos, J.R., Jaimes de la Cruz, B., 1999. Circulación del Golfo de México. *Revista de la Sociedad Mexicana de Historia Natural* 49, 1–15.
- Vinogradova, N.G., 1959. The zoogeographical distribution of the deep-water bottom fauna in the abyssal zone of the ocean. *Deep-sea Research* 5, 205–208.
- Wenner, E.L., 1978. Some aspects of the biology of deep-sea lobsters of the Family Polychelidae (Crustacea, Decapoda) from the western North Atlantic. *Fishery Bulletin* 77, 435–444.
- Wenner, E.L., Boesch, D.F., 1979. Distribution patterns of epibenthic decapod Crustacea along the shelf-slope coenocline, Middle Atlantic Bight, USA. *Bulletin of the Biological Society of Washington* 3, 106–133.
- Wicksten, M.K., Packard, J.M., 2005. A qualitative zoogeographic analysis of decapod crustaceans of the continental slopes and abyssal plain of the Gulf of Mexico. *Deep-Sea Research I* 52, 1745–1765.
- Wolf, T., 1961. Animal life from a single abyssal trawling. *Galathea Report* 5, 129–162.
- Yang, W.T., 1976. Studies on the western Atlantic arrow crab genus *Stenorhynchus* (Decapoda, Brachyura, Majidae) I. Larval characters of two species and comparison with other larvae of Inachinae. *Crustaceana* 31 (2), 157–177.
- Zarenkov, N.A., 1969. Decapoda. In: Zenkevitch, L.A. (Ed.), *Biology of the Pacific Ocean. Part II. The Deep-sea Bottom Fauna* (in Russian, translated by US Naval Oceanographic Office, Washington, DC).