

Research Article

Seasonal variability of near-surface zooplankton community structure in the southern Gulf of Mexico

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ABSTRACT. The zooplankton taxonomic group composition was analyzed in a known spawning area for snooks of the family Centropomidae during March 2011-February 2012 near the González River's mouth, a tributary of the Grijalva-Usumacinta River system, discharging into the southern Gulf of Mexico. Zooplankton was collected near the surface using three distinct zooplankton nets (20, 64, and 120 μm). Sixteen zooplankton taxonomic groups were collected between the three nets. Copepoda (76.9%), Trematoda (6.7%), Bivalvia (4.6%), and Chaetognatha (Sagittoidea 4.3%) numerically dominated zooplankton community structure. The 120 and 64 μm nets collected the highest diversity of zooplankton (15 taxa). Zooplankton was more abundant during June-October (summer storm season). They associated with lower salinities (due to the increase in the discharge volume of the Grijalva-Usumacinta River system) and higher regional primary productivity than observed during the rest of the year (March-May, dry season, and November-February, winter storm season). The highest peak of zooplankton abundance was found in November during the beginning of winter storms. Nine taxonomic groups were observed frequently and abundantly during the summer storm season, while only five taxonomic groups were abundant during the dry season.

Keywords: zooplankton; taxonomic groups; abundance; distribution; seasonal variability; Gulf of Mexico

INTRODUCTION

Planktonic organisms constitute the base for most trophic connections in marine ecosystems. Space-time availability of zooplankton is essential for the survival of fish larvae that prey on them during the critical period of early development after depleting their yolk sac and when exogenous food must be ingested before reach the period-of-no-return (Yúfera & Darias, 2007). Zooplankton productivity and biomass strongly influence fish population recruitment and frequently delimit the reproductive periods and species reproductive behavior, including species targeted for regional fishery activities (Conde-Porcuna *et al.*, 2004; Álvarez-Fernández *et al.*, 2015; Jackson & Lenz, 2016). Several fish species tend to synchronize their reproductive spawning events with periods with high zooplankton abundance because fish larvae prey on dino-

flagellates, invertebrate eggs, and copepods (Phelps *et al.*, 2005; Álvarez-Fernández *et al.*, 2015) promoting high survival of fish larvae (Alvaríño, 1980; Sherman *et al.*, 1984). Fish larvae of several marine species prefer to prey on small zooplankton because of their small mouth size and limited swimming capabilities (Purcell & Grover, 1990; Støttrup, 2006; Puello-Cruz *et al.*, 2008).

The Mississippi and the Grijalva-Usumacinta rivers are the main freshwater discharges on the Gulf of Mexico. Other minor contributions are San Pedro, San Pablo, and Coatzacoalcos rivers. All these rivers significantly influence the ecological dynamics of the coastal habitats (Monreal-Gomez & Salas-de León, 2004). The river plumes promote higher primary production that contributes to the sustainment of cost-effective fisheries within the region (Botello *et al.*, 2005). Significant river plume nutrient-inputs in the

Gulf of Mexico occur during the rainy season (June-October) increasing, with some lag, zooplankton abundance (Contreras-Espinoza, 2016). This seasonal nourishment process coincides with the vast abundance of fish larvae along the littoral zone of the Gulf of Mexico (Hopkins, 1982; Ortnier *et al.*, 1989; Flores-Coto *et al.*, 2009).

In the southern Gulf of Mexico sub-region, the Usumacinta-Grijalva River system has water discharges between 3000 and 4400 m³ s⁻¹ (Yáñez-Arancibia & Day, 2004). This freshwater discharge provides a large load of sediments and nutrients to the southern region of the Gulf of Mexico, particularly during the discharge peaks (September-October) (West *et al.*, 1985). The high nutrient availability could promote massive planktonic blooms that represent available prey for fish larvae and juveniles. However, the taxonomic group composition and seasonal patterns of the zooplanktonic community in the southern Gulf of Mexico have not been studied yet. We investigated the fluctuations of the major zooplankton taxonomic groups collected near the González River mouth -a tributary of the Grijalva-Usumacinta River system-that is an area considered by the local anglers as a snook spawning ground. We investigate the surface sea layer because regionally, food particles exist in high concentrations, making it the most productive stratum in the epipelagic ecosystem, where most of the trophic interactions (Espinosa-Fuentes *et al.*, 2009).

MATERIALS AND METHODS

Monthly zooplankton samplings were collected from March 2011 to February 2012 near the influence of the González River, as part of the Grijalva-Usumacinta River system. Zooplankton was collected near the surface (2-3 m depth) from three sites in a spawning ground identified by local anglers and reported for two snook species: *Centropomus undecimalis* and *Centropomus parallelus* (Hernández-Vidal *et al.*, 2014). These three sampling sites were located at: site A, 18°26'4.10"N, 92°59'47.60"W (7-8 m depth); site B, 18°26'59.16"N, 92°59'59.51"W (7.5-9 m depth); and site C, 18°27'30.71"N, 93°00'5.94"W (8-10 m depth) (Fig. 1). Further statistical analysis showed no significant differences in zooplankton abundance and taxonomic group composition among sampling sites; therefore, each sampling station was considered as replicate for the entire sampled area.

Environmental variables and zooplankton sampling

Seawater was collected between 1-2 m depth using a Vann Dorn bottle (WildCo, USA) at each sampling site

to measure sea surface temperature (°C), salinity, and dissolved oxygen concentration (mg O₂ L⁻¹). Temperature and DO were measured using a calibrated multisensor (YSI 55TM, Yellow Springs, OH, USA). Salinity (± 1.0) was measured with a Bio-Marine Inc. AquafaunaTM refractometer (Hawthorne, CA, USA). Sea surface chlorophyll-*a* (mg Chl-*a* m⁻³) was obtained from MODIS-Aqua NASA satellite images (five-day averages), sea surface temperature (SST, °C) data were obtained from MODIS-Terra-MODIS-Aqua satellite website (<https://podaac.jpl.nasa.gov/dataaccess>). Monthly rainfall (mm month⁻¹) was obtained from the Comisión Nacional del Agua (México) (CONAGUA) (<https://sih.conagua.gob.mx/>) station N°27034 located 22 km southwest from the present area of study (18°23'44.00"N, 93°12'43.99"W). The southern subregion of the Gulf of Mexico has three climatic seasons: dry, summer storms, and winter storms (Yáñez-Arancibia & Day, 2004). During the dry season (DS: March-May), SE winds prevail, with a mean air temperature of 28.1°C and mean rainfall of 164.8 mm month⁻¹. During the summer storm season (SSS: June-October), SE winds still prevail, and there is a similar mean air temperature of 28.3°C, but mean rainfall increases almost five times (976.7 mm month⁻¹). During the winter storm season (WSS: November-February), north winds frequently occur (regionally known as "nortes" in Spanish) with an average air temperature of 24.4°C and mean precipitation of 345.6 mm month⁻¹ (Ayala-Pérez *et al.*, 2012). The analysis of the last five years (2015-2019) Chl-*a* data obtained by the MODIS-Aqua NASA satellite indicate that the highest mean values correspond to the WSS (3.52) with a very distinctive peak during November (4.00) compared to mean values from the DS (2.56) and the SSS (2.73) coinciding with information reported at the nearby Terminos Lagoon by Yáñez-Arancibia & Day (2004), and Herrera-Silveira *et al.* (2019).

Zooplankton was collected during daytime every month using three simple, conical plankton nets, each one with a diameter of 30 cm and a length of 60 cm, but distinct mesh sizes: 20, 64, and 120 μ m. Nets were towed near the surface for 5 min while the boat was underway at 2.5 km h⁻¹. Plankton samples were preserved in 4% buffered formalin. A total of 108 zooplankton samples were collected from March 2011 to February 2012. Zooplankton abundance was standardized to the number of individuals per 100 m³ (ind 100 m⁻³). The identification of each zooplankton species in a diverse zooplankton community is complicated and time-consuming. Therefore, zooplankton was here identified to taxonomic levels, higher than suborder to evaluate zooplankton seasonal changes through an annual cycle using four zooplankton taxonomic keys (Smith, 1977; Boltovskoy, 1981; Báez, 1997;

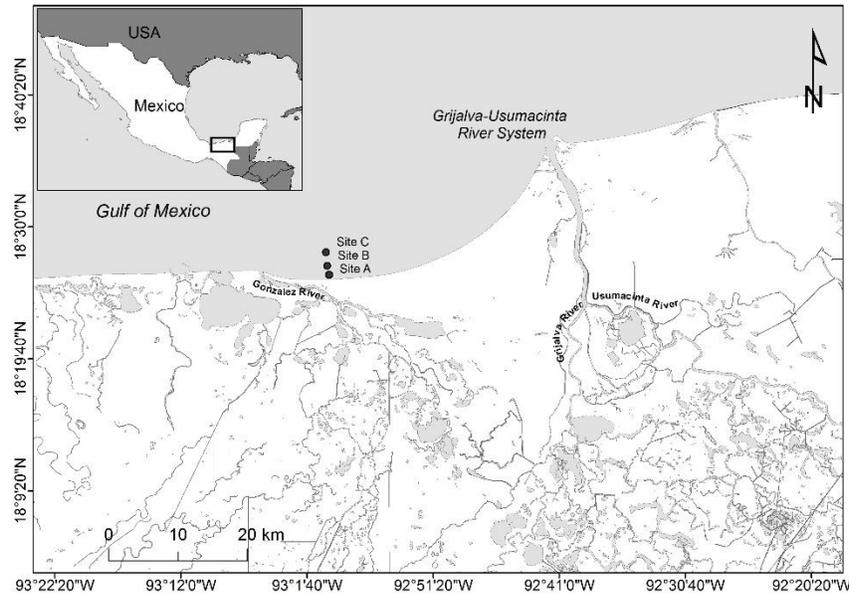


Figure 1. Study area showing the location of the three sampling sites, known by local anglers as snook spawning sites over the continental shelf of Tabasco, Mexico.

Perry, 2003). The names utilized for these taxa follow the World Register of Marine Species (WoRMS, 2019) database (<http://www.marinespecies.org/>). Three different groups were identified based on their frequency of the capture of each zooplankton taxonomic group: high (>9 months), moderate (5-8 months), and low (<4 months) frequency of appearance.

Data analysis

The statistical significance of differences between the community taxonomic composition and abundance of zooplankton among the three climatic seasons and the three mesh sizes was evaluated using Multi-Response Permutation Procedure (MRPP). The MRPP is a nonparametric multivariate procedure for testing the hypothesis that there are no differences between *a priori* classified group (McCune & Mefford, 2011). The Sorensen (Bray-Curtis) distance measure was chosen in the MRPP analyses because it retains sensitivity in heterogeneous data sets and gives less weight to outlier abundance values.

A canonical correspondence analysis (CCA) was conducted to infer how the zooplankton community structure was associated with the multi-dimensional gradients of the five environmental variables: sea surface temperature, salinity, satellite sea surface chlorophyll-*a* concentration, dissolved oxygen concentration, and monthly rainfall. Zooplankton abundance was $\log(x+1)$ transformed to linearize the species matrix, and data of the five environmental variables were transformed to generalized relativization per

column to give the five variables comparable weight (Ter Braak & Verdonschot, 1995; McCune & Mefford, 2011). Data matrices were organized using the Excel software, and statistical data analyses were performed using PC-ORD Multivariate Analysis of Ecological Data v.6.0 software (MjM Software design) (McCune & Mefford, 2011). Graphic representation of the data was done using the software SigmaPlot® v14.

RESULTS

Environmental conditions

Sea surface temperature varied from 24.4°C in March to 28.7°C in September with the highest mean value obtained during the SSS ($27.75 \pm 1.01^\circ\text{C}$). The lowest mean values were recorded during the DS. Salinity varied from 30.22 in September to 34.45 in July with the highest mean during the SSS (32.63 ± 2.35). Dissolved oxygen concentration was higher during the WSS with a mean value of $8.01 \pm 1.27 \text{ mg O}_2 \text{ L}^{-1}$, with a range of $4.75 \text{ mg O}_2 \text{ L}^{-1}$ in July and $8.68 \text{ mg O}_2 \text{ L}^{-1}$ in February (Table 1). Monthly cumulative rainfall was zero in April, and the highest rainfall was 468.20 mm month⁻¹ in October. Mean cumulative rainfall was five-fold higher during the summer storms season ($206.30 \pm 146.20 \text{ mm month}^{-1}$) than during the other two seasons. Satellite sea surface Chl-*a* concentration ranged from $0.75 \text{ mg Chl-}a \text{ m}^{-3}$ in February to $5.17 \text{ mg Chl-}a \text{ m}^{-3}$ in September being slightly higher during WSS ($3.24 \pm 2.26 \text{ mg Chl-}a \text{ m}^{-3}$) than during the other two seasons.

Table 1. Mean \pm standard deviation of environmental variables recorded *in situ* at the time of sampling in the three sampling sites (DO: dissolved oxygen, SST: sea surface temperature and salinity; n = 3), monthly average values of and satellite chlorophyll-*a* concentration (n = 29-31 d) and monthly cumulative rainfall recorded during March 2011-February 2012 at the continental shelf of Tabasco, Mexico. DS: dry season; SSS: summer storm season, WSS: winter storm season.

Season	Month	SST (°C)	Salinity	DO (mg O ₂ L ⁻¹)	Rainfall (mm month ⁻¹)	Chlorophyll- <i>a</i> (mg Chl- <i>a</i> L ⁻¹)
DS	Mar	24.43 \pm 0.30	32.22 \pm 1.30	8.30 \pm 0.82	60.43 \pm 0.00	3.00 \pm 0.31
	Apr	26.24 \pm 1.08	32.00 \pm 1.73	6.52 \pm 0.80	0.00 \pm 0.00	3.30 \pm 0.20
	May	26.48 \pm 0.79	31.66 \pm 1.32	7.32 \pm 0.43	34.02 \pm 0.00	2.62 \pm 0.74
SSS	Jun	27.95 \pm 0.49	33.44 \pm 1.94	6.09 \pm 0.07	70.68 \pm 0.00	2.57 \pm 0.57
	Jul	27.62 \pm 1.02	34.44 \pm 1.67	4.75 \pm 0.93	188.21 \pm 0.00	2.00 \pm 0.70
	Aug	26.77 \pm 1.12	33.29 \pm 2.50	7.56 \pm 0.55	62.03 \pm 0.00	2.14 \pm 0.07
	Sep	28.72 \pm 0.35	30.22 \pm 1.86	6.42 \pm 1.00	316.84 \pm 0.00	5.17 \pm 4.42
WSS	Oct	27.67 \pm 0.78	31.78 \pm 1.45	5.57 \pm 1.01	468.23 \pm 3.80	4.17 \pm 1.78
	Nov	27.18 \pm 0.70	32.33 \pm 1.00	6.93 \pm 0.98	131.88 \pm 0.00	5.03 \pm 2.76
	Dec	25.94 \pm 1.42	34.11 \pm 1.62	8.10 \pm 1.70	67.85 \pm 0.00	3.99 \pm 1.10
	Jan	25.12 \pm 1.12	32.44 \pm 0.88	8.31 \pm 1.07	127.89 \pm 0.07	3.18 \pm 0.29
	Feb	25.30 \pm 0.30	31.31 \pm 0.96	8.68 \pm 0.33	192.57 \pm 1.13	0.75 \pm 1.49
Annual mean	Range	24.43 - 28.72	30.22 - 34.44	4.75 - 8.68	00.00 - 468.20	0.75 - 5.17
	Mean	26.83 \pm 1.28	32.35 \pm 1.17	6.93 \pm 1.22	143.38 \pm 133.96	3.13 \pm 1.28
Seasonal mean	DS	25.71 \pm 1.20	31.96 \pm 1.43	7.38 \pm 1.02	31.47 \pm 25.19	2.97 \pm 0.54
	SSS	27.75 \pm 1.01	32.63 \pm 2.35	6.08 \pm 1.21	206.30 \pm 146.20	3.21 \pm 2.42
	WSS	25.89 \pm 1.24	32.55 \pm 1.49	8.01 \pm 1.27	39.41 \pm 20.46	3.24 \pm 2.26

Higher rainfall occurred from September to November, coinciding with high concentrations of sea surface Chl-*a* and high values of SST (Table 1).

Identified zooplankton taxonomic groups

Sixteen zooplankton taxonomic groups were identified from the 108 zooplankton samples collected between March 2011 and February 2012 (Table 2). Zooplankton included nine classes (Actinopterygii, Appendicularia, Bivalvia, Echinodermata, Euphausiacea, Hydrozoa, Insecta, Sagittoidea, and Trematoda) one subclass (Copepoda), four orders (Amphipoda, Decapoda, Gastropoda, and Stomatopoda), and two suborders (Cladocera and Polychaeta) with clearly distinct morphological and life strategy zooplankton taxonomic groups. Fish eggs and larvae abundance were combined as ichthyoplankton (Class Actinopterygii) for statistical analyses.

Annual relative abundance for all three types of mesh size

Out of the 16 zooplankton taxonomic groups, 15 were collected with the 120 μ m, and 64 μ m plankton mesh size nets and only 13 taxa with the 20 μ m mesh size net; this difference is caused by the absence of Stomatopoda, Hydrozoa, and Amphipoda in the latter. Ichthyoplankton was absent from the 64 μ m net and Amphipoda from the 120 μ m net. Copepods dominated

the relative monthly abundance in all the zooplankton sampling nets (73.7-79.8%) (Table 2, Fig. 2). The taxonomic groups that followed copepods in abundance for all nets were Trematoda (4.2-9.1%), Bivalvia (2.5-6.2%), Sagittoidea (3.8-5.14%); however, their relative abundances were much smaller than copepods. Ichthyoplankton was captured with the 120 and 20 μ m nets (Table 2). The rest of the taxonomic groups collected typically summed <2% in each net (Table 2, Fig. 2).

Seasonal variation in zooplankton taxonomic composition

The identification of zooplankton taxonomic groups, based on their frequency of appearance, indicated that Copepoda, Decapoda, Sagittoidea, and Trematoda were highly frequent. Bivalvia, Cladocera, and Polychaeta were moderately frequent, and Appendicularia, Amphipoda, Echinodermata, Euphausiacea, Gastropoda, Hydrozoa, Ichthyoplankton, Insecta, and Stomatopoda showed low frequency of appearance (Table 2).

Combining zooplankton abundance of the three sampling sites and the three mesh sizes showed zooplankton abundances had the maximum abundance during November (303.21 \pm 152.76 thousands of individuals per 100 m³; median \pm interquartile range). The lowest abundances were observed during February (53.70 \pm 116.95) and March (48.46 \pm 22.92) (Fig. 3).

Table 2. Annual mean \pm standard deviation of zooplankton abundance (thousands of individuals per 100 m⁻³), relative abundance (%), and frequency of appearance (shown between parentheses) for each zooplankton taxonomic group collected over the continental shelf of Tabasco (three sampling locations combined) collected between March 2011-February 2012 with three different zooplankton net mesh sizes (20, 64, and 120 μ m). Actinopterygii (includes fish eggs and larvae).

Taxonomic groups	Zooplankton net mesh size (μ m)			Relative abundance (frequency)		
	20	64	120	20	64	120
Copepoda	57.14 \pm 46.68	127.64 \pm 93.41	114.57 \pm 81.37	77.33 (12)	79.83 (12)	73.70 (12)
Trematoda	6.72 \pm 7.06	6.77 \pm 8.78	10.45 \pm 17.04	9.09 (9)	4.23 (8)	6.72 (9)
Bivalvia	1.85 \pm 1.74	8.01 \pm 16.2	9.63 \pm 11.52	2.50 (8)	5.01 (8)	6.20 (7)
Sagittoidea	3.80 \pm 6.36	5.99 \pm 7.62	6.01 \pm 5.74	5.14 (8)	3.75 (11)	3.87 (10)
Decapoda	0.53 \pm 0.76	4.64 \pm 9.20	5.87 \pm 15.10	0.72 (6)	2.90 (11)	3.77 (10)
Echinodermata	0.16 \pm 0.57	1.13 \pm 3.45	5.31 \pm 15.70	0.22 (1)	0.71 (3)	3.41 (3)
Polychaeta	1.01 \pm 1.68	1.27 \pm 3.94	2.10 \pm 3.43	1.36 (6)	0.80 (5)	1.35 (5)
Cladocera	2.18 \pm 5.67	2.87 \pm 6.88	0.73 \pm 1.86	2.95 (3)	1.80 (3)	0.47 (5)
Appendicularia	0.09 \pm 0.15	1.07 \pm 2.62	0.35 \pm 0.81	0.13 (4)	0.67 (4)	0.22 (3)
Stomatopoda	0.00 \pm 0.00	0.07 \pm 0.25	0.16 \pm 0.50	0.00 (0)	0.05 (1)	0.11 (2)
Hydrozoa	0.00 \pm 0.00	0.04 \pm 0.08	0.10 \pm 0.21	0.00 (0)	0.02 (2)	0.07 (3)
Euphausiacea	0.15 \pm 0.39	0.04 \pm 0.13	0.07 \pm 0.19	0.20 (2)	0.02 (1)	0.05 (2)
Actinopterygii	0.04 \pm 0.08	0.00 \pm 0.00	0.05 \pm 0.14	0.02 (2)	0.00 (0)	0.02 (2)
Insecta	0.01 \pm 0.03	0.02 \pm 0.06	0.04 \pm 0.13	0.01 (1)	0.01 (2)	0.02 (1)
Gastropoda	0.22 \pm 0.50	0.05 \pm 0.14	0.02 \pm 0.06	0.30 (3)	0.03 (2)	0.01 (1)
Amphipoda	0.00 \pm 0.00	0.27 \pm 0.88	0.00 \pm 0.00	0.00 (0)	0.17 (2)	0.00 (0)

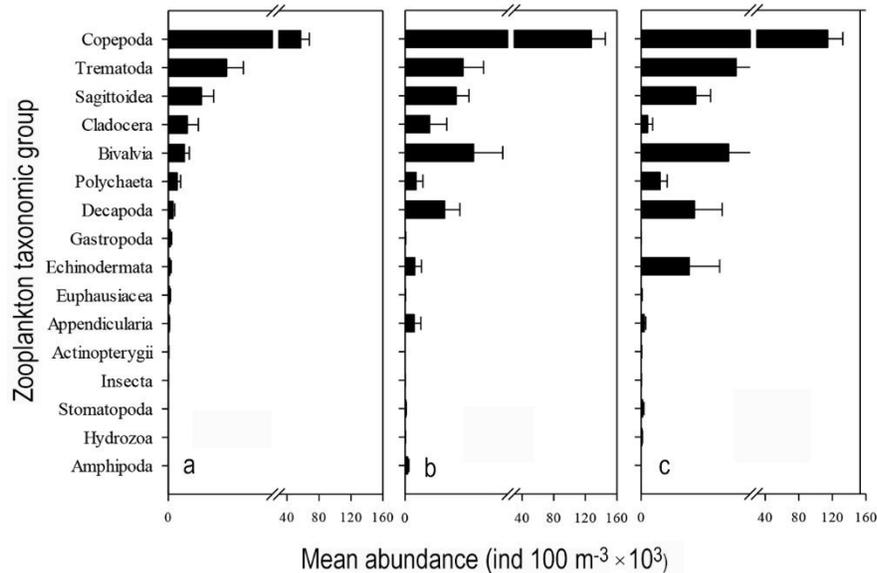


Figure 2. Average standardized (\pm SE, standard error) abundance expressed in thousands of individuals per 100 m³ for each zooplankton taxonomic group (n = 36) captured with each type of zooplankton net: a) 20, b) 64, and c) 120 μ m. Axis break in figures omits data between 12-30 ind 100 m⁻³.

During May and September, high values were also observed (216.11 \pm 171.58 and 183.37 \pm 250.16, respectively).

The analysis of the zooplankton abundance showed higher SSS abundance during WSS storms season than during DS and WSS? (these two with similar magnitude of zooplankton abundance) (Fig. 4a).

Copepod abundance accounted for >70%, mostly driving monthly total zooplankton abundance patterns throughout the year (Fig. 4b). Nine taxonomic groups were observed frequently and abundantly during summer, while only five zooplankton taxonomic groups were abundant during DS. Bivalvia, Cladocera, Sagittoidea, and Trematoda abundance showed a similar seasonal

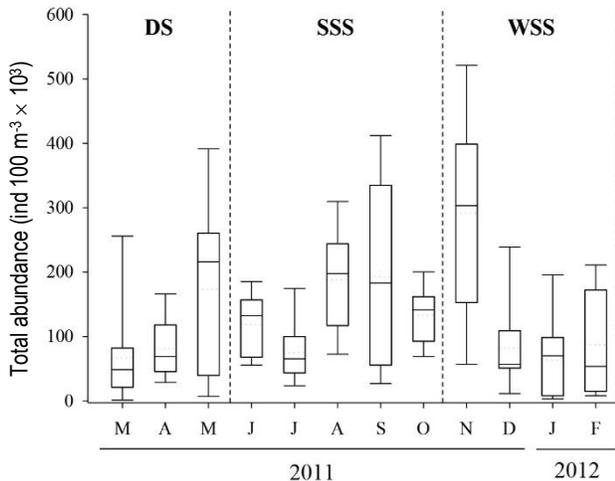


Figure 3. Whisker box plots of monthly standardized total zooplankton abundance (all groups combined) expressed in thousands of individuals per 100 m^3 . Each value in the boxes is the sum of all taxonomic groups captured in three sites with three net sizes ($n = 9$). Dotted lines inside the boxes show mean values, while solid lines represent the medians. Climatic seasons are separated by shaded lines. DS: dry season; SSS: summer storms season; WSS: winter storms season. The year of the sampling is stated underneath the sampled month.

trend throughout the year (Figs. 4c-f). In contrast, Decapoda and Polychaeta were more abundant during the DS than during the rest of the year (Figs. 4g-h). During summer and the beginning of WSS (July-November), the higher values for SST, salinity, and rainfall coincided with zooplankton abundance high values. The highest abundance of zooplankton that occurred during November was preceded by two months of high sea surface Chl-*a* concentrations, which progressively decreased in December.

Zooplankton community assemblage

Zooplankton abundance and community taxonomic structure showed statistically significant differences among the three climatic seasons (MRPP analysis, $A = 0.018$, $P < 0.05$). Zooplankton abundance was significantly higher during the SSS than during DS ($P = 0.04$) and WSS ($P = 0.001$). However, zooplankton abundance was not significantly different between DS and WSS (MRPP; $P = 0.50$). Zooplankton had significant differences in abundance among taxonomic groups from samples collected using different plankton mesh net sizes (MRPP; $A = 0.02$, $P = 0.04$). The smaller zooplankton (captured in the $20 \mu\text{m}$ mesh size) was significantly less abundant (by several orders of magnitude) and diverse than zooplankton samples collected with the other two plankton net mesh sizes ($64 \mu\text{m}$ $P < 0.001$ and $120 \mu\text{m}$ $P = 0.004$). Zooplankton

groups collected with the 64 and $120 \mu\text{m}$ mesh size nets were practically identical (MRPP, $P = 0.99$). Zooplankton community structure and abundance showed no significant statistical differences among the three sampling sites located close to each other over the continental shelf (MRPP; $A = 0.005$, $P > 0.2$).

The results from CCA ordination of zooplankton groups and environmental parameters indicated that the surveyed environmental parameters might play a minor role in the zooplankton assemblage, only explaining 6.0% of the total variance. The zooplanktonic abundance observed during the climatic seasons, indicated in the CCA biplot, shows that during the SSS, abundances have strong associations with rainfall and SST. Abundances during WSS and the DS were strongly correlated to high values of DO, and lower-than-average temperature and precipitation (Table 3, Fig. 5a). The seasonal effects of the variables incorporated in the second axis mainly consisted of a strong positive association with Chl-*a* (Table 3, Fig. 5). In terms of zooplanktonic groups, Appendicularia and Bivalvia mostly occur at higher than average rainfall values, while Echinodermata, Insecta, Ichthyoplankton, Decapoda, and Hydrozoa occur when DO values are higher. Polychaeta was associated with high Chl-*a* values. Copepoda, Sagittoidea, and Trematoda were zooplanktonic taxonomic groups located near the center of the ordination due to their high frequency of appearance and abundance, showing minimal correlation with environmental changes.

DISCUSSION

The present study is the first contribution to understand the dynamics of the zooplankton community in the influence of the González River, the well-known spawning ground of snooks by local anglers. The zooplankton community in the area of study was vastly dominated by copepods, showing seasonal variations with significant peaks during the SSS, which is also strongly influenced by the dynamics of the river discharge. The increases in the abundance of zooplankton during the SSS are associated with the increased nutrient inputs of the González River plume, particularly during August-October. Zooplankton abundance peaks appear a few weeks after rainfall and SST increases. Zavala-García *et al.* (2016) reported that south of Campeche Bay, the magnitude of the zooplankton biomass depended on the continental water discharges directly related to the volume discharged into the ocean. The nutrient load is reflected by an increase of sea surface Chl-*a* concentrations during September-November starting its descent in concentration during December. This seasonal pattern agrees

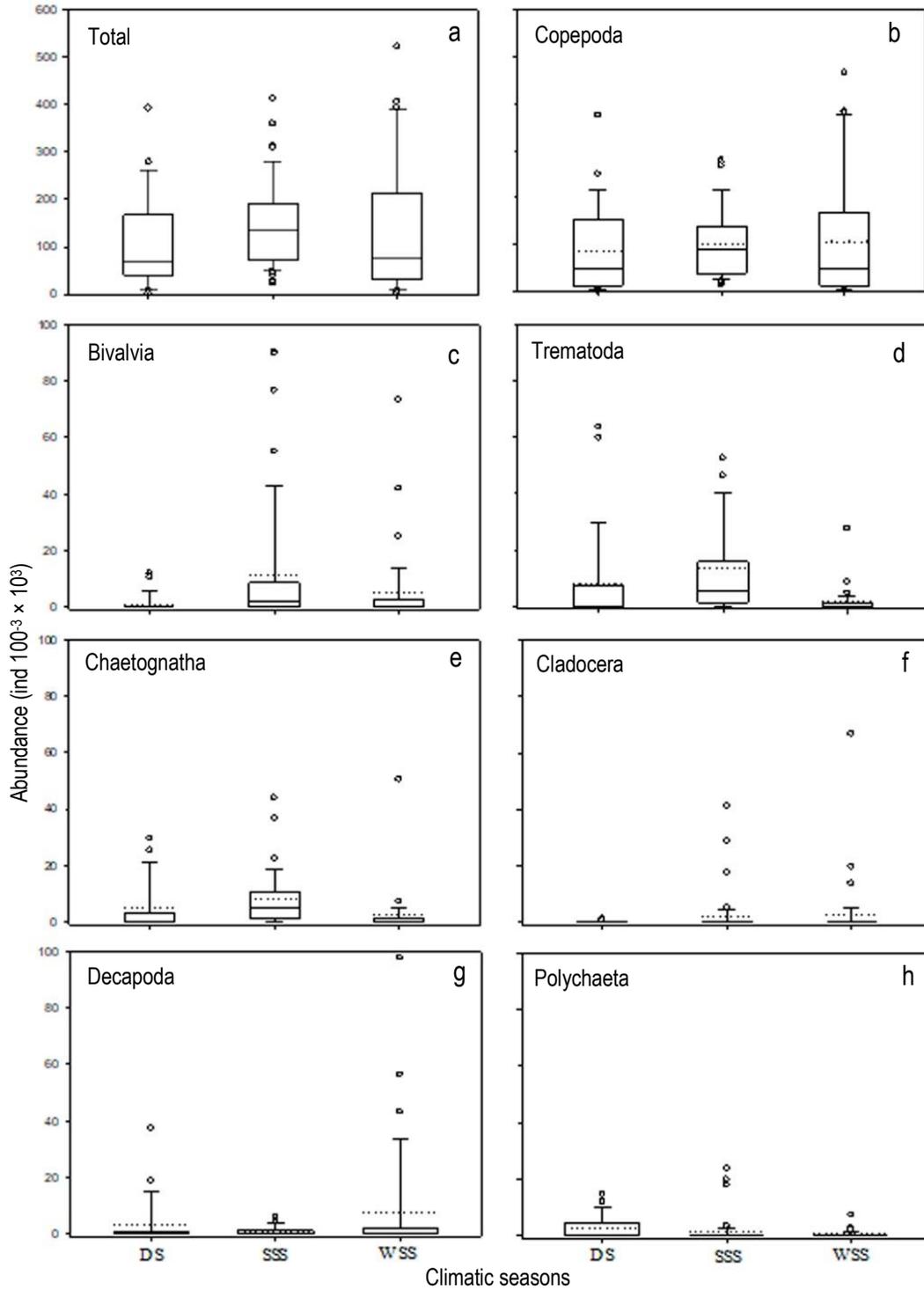


Figure 4. Seasonal average standardized abundance expressed in thousands of individuals per 100 m³. DS: dry season (n = 27); SSS: summer storm season (n = 45); and WSS: winter storm season (n = 36). Open dots indicate individual extreme cases.

with the increase of abundance and diversity of siphonophores in the southern Gulf of Mexico during October (Sanvicente-Añorve *et al.*, 2007).

Similarly, the density of benthic macroinfauna also considerably increases during SSS in the area of influence of the Grijalva-Usumacinta River system

Table 3. Pearson (r) and Kendall (τ) correlation values from the Canonical Correspondence Analysis showing the first three axes using correlation values for each environmental variable and abundance of zooplankton taxonomic groups collected at the three zooplankton sampling stations during 2011-2012 (combined abundance of the three zooplankton mesh sizes). The larger Pearson correlation values are shown in bold. SST: sea surface temperature; Sal: salinity; DO: dissolved oxygen concentration; Rain: cumulative rainfall; sea surface Chl- a : chlorophyll- a concentration. Actinopterygii (includes fish eggs and larvae).

Axis	1			2			3		
	r	R ²	tau	r	R ²	tau	r	R ²	tau
SST	-0.532	0.283	-0.394	-0.213	0.046	-0.220	0.548	0.301	0.408
Sal	-0.249	0.062	-0.273	0.281	0.071	-0.217	0.059	0.004	0.031
DO	0.770	0.593	0.597	-0.084	0.007	-0.046	-0.642	0.412	-0.510
Rain	-0.854	0.728	-0.625	-0.104	0.011	-0.167	-0.229	0.053	0.008
Chl- a	-0.290	0.084	-0.122	0.781	0.610	0.551	-0.099	0.010	-0.095
Copepoda	-0.303	0.092	-0.206	0.054	0.003	0.023	0.169	0.028	0.120
Polychaeta	0.015	0.000	0.041	0.332	0.111	0.259	0.064	0.004	0.056
Euphausiacea	-0.071	0.005	-0.034	-0.058	0.003	-0.025	-0.073	0.005	-0.047
Amphipoda	0.127	0.016	0.115	0.095	0.009	0.098	-0.122	0.015	-0.098
Gastropoda	0.014	0.000	-0.011	-0.209	0.044	-0.177	-0.039	0.001	0.003
Decapoda	0.140	0.020	0.103	-0.158	0.025	-0.119	0.082	0.007	0.063
Echinodermata	0.166	0.027	0.106	-0.174	0.030	-0.169	0.115	0.013	0.168
Appendicularia	-0.316	0.100	-0.223	-0.073	0.005	-0.043	0.267	0.072	0.184
Hydrozoa	0.167	0.028	0.130	0.037	0.001	0.049	-0.018	0.000	-0.016
Bivalvia	-0.463	0.211	-0.297	-0.071	0.005	-0.062	-0.198	0.039	-0.127
Stomatopoda	-0.097	0.009	-0.111	0.345	0.119	0.116	0.042	0.002	0.037
Sagittioidea	-0.308	0.098	-0.257	-0.183	0.033	-0.192	0.124	0.015	0.096
Cladocera	-0.078	0.006	-0.066	-0.128	0.016	-0.095	-0.153	0.023	-0.093
Trematoda	-0.310	0.096	-0.258	-0.076	0.006	-0.062	0.234	0.055	0.176
Insecta	0.065	0.004	0.042	-0.036	0.001	-0.042	0.146	0.021	0.127
Actinopterygii	0.075	0.006	0.046	-0.020	0.000	-0.002	0.051	0.003	0.051

(Hernández-Arana *et al.*, 2003). The increase of zooplankton abundance during the SSS is consistent with a pattern associated with high rainfall, an increase in sea surface temperature, and a decrease in salinity (Flores-Coto *et al.*, 2009), particularly during September and October. The first small zooplankton peak abundance observed in May, is probably related to the first rainfalls of the year, with a previous slight increase in sea surface Chl- a concentration. However, during the following months of early summer, when the temperature reaches the highest values, zooplankton richness and abundance decreased considerably. Estrada *et al.* (2009) showed that sea surface temperature varies seasonally (25-30°C) in the area of study, indicating that this situation is characteristic for the southern Gulf of Mexico. Espinosa-Fuentes *et al.* (2009) highlighted that zooplanktonic biomass and ichthyoplankton density were strongly influenced by temperature and the mixing processes present in the same region of the Gulf of Mexico. As mentioned above, planktonic blooms are related to the nutrient

load incoming from the river discharges during heavy rainfalls.

The study area is considered a highly productive region (Zavala-García *et al.*, 2016), presenting a close relationship between zooplankton biomass and the volume of continental water discharges. During 2011, the highest levels of rainfall occurred during September-October, considerably increasing the freshwater volume discharged by the Grijalva-Usumacinta River system. In this region, stable horizontal salinity and density gradients are induced by the inflow of the Grijalva-Usumacinta river plume (Monreal-Gómez *et al.*, 1992; Flores-Coto *et al.*, 2010a). The sediment load in the Grijalva-Usumacinta River system usually has the highest values in September and October, with the highest water discharges of these rivers (Muñoz-Salinas & Castillo, 2015). The phytoplankton community assimilates the input flow of nutrients on the continental shelf, causing higher concentrations of chlorophyll- a during rainfall season, promoting an increase of diversity and abundance of the herbivore

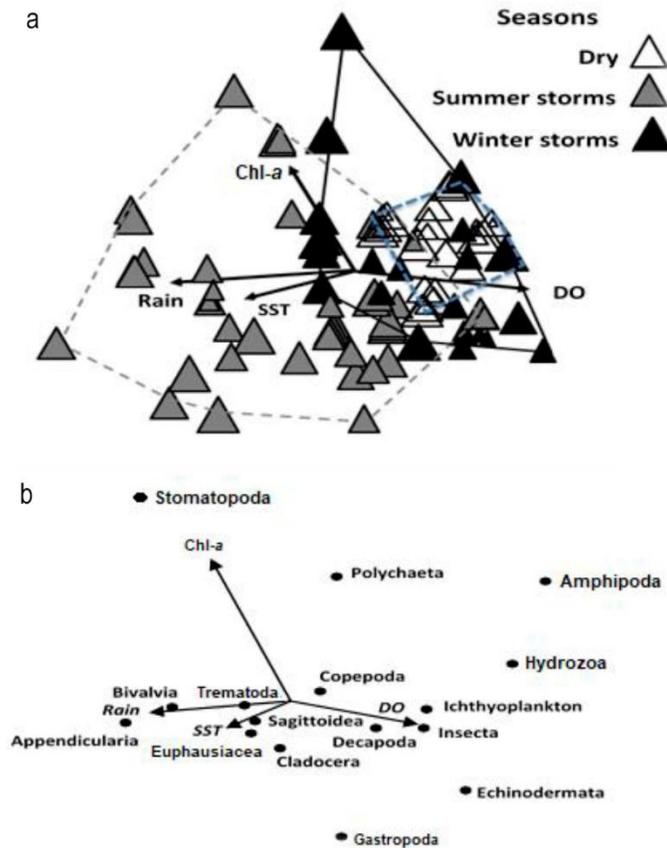


Figure 5. Biplot from the canonical correspondence analysis of zooplankton taxonomic groups collected from March 2011 to February 2012 at the southern Gulf of Mexico. a) Seasonal associations of zooplankton samples (classified per climatic seasons) as a function of the most influential environmental variables: cumulative rainfall (rain), dissolved oxygen concentration (DO), sea surface temperature (SST), and chlorophyll-*a* (Chl-*a*), b) same CCA showing seasonal association of the zooplankton identified per taxonomic group as a function of the same five environmental variables. Vector length indicates the magnitude of the explained variability by environmental variables. The origin (0,0) is the mean of each environmental variable, transects projecting on the side opposite to the arrow are inferred to exhibit a lower-than-average variable value.

and omnivore zooplankton groups (Contreras-Espinoza, 2016). The ecological influence that nutrient discharges of rivers have on phytoplankton and zooplankton has been documented worldwide (Flores-Coto *et al.*, 2000; Cotrim da Cunha *et al.*, 2007). The Mississippi River discharges have been well recorded to directly associate with zooplankton abundance and composition and the zooplankton's predators in the northern region of the Gulf of Mexico (Ortner *et al.*, 1989; Lohrenz *et al.*, 1990). High levels of zooplankton abundance have been associated with fluvial and lagoon systems in the southern part of the Gulf of Mexico while decreasing the abundance of zooplankton offshore (Ordóñez-López & Ornelas-Roa, 2003; Contreras-Espinoza, 2016; Rowe, 2017).

The abundance of copepods drives numbers of zooplankton seasonal variability in the area of study.

Their broad distribution patterns and high abundance are mainly due to their short life cycles and fast reproduction rates (adult females can release eggs daily) (Suárez-Morales, 2000; Suárez-Morales *et al.*, 2009; Morales-Serna & Gómez, 2012). Copepoda is the dominant taxonomic group (both in numbers and biomass) in most coastal and open-ocean habitats of the Gulf of Mexico (Rowe, 2017) and the National Park Sistema Arrecifal Veracruzano (Okolodkov *et al.*, 2011). Similarly, Espinosa-Fuentes *et al.* (2009) concluded that nauplii and copepodite stages dominated zooplanktonic biomass on the continental shelf of Campeche, Mexico.

Chaetognaths (Sagittoidea) and Bivalvia were other abundant zooplankton taxonomic groups. A direct association between Copepoda and Sagittoidea abundance has been observed because arrow worms

mostly prey on copepods (Sato *et al.*, 2011; Cota-Meza *et al.*, 2015). The Gulf of Mexico contains almost 20% of all known species of Sagittoidea (Hernández-Flores *et al.*, 2009) with distribution patterns primarily influenced by salinity and temperature, and they may be frequent predators of fish larvae (Mille-Pagaza & Carrillo-Laguna, 2003; Lozano-Cobo *et al.*, 2017). High abundances of Bivalvia larvae are likely related to the natural oyster production in the coastal lagoons near the region (Zamora & Aranda, 2000).

Appendicularia and Euphausiacea were mainly observed during the rainfall season. Euphausiacea species tend to form dense aggregations in temperate zones and cold upwelling waters, providing highly attractive biomass for plankton and nekton predators (Galtsoff, 1954; Fernández *et al.*, 2002). The ecology of Euphausiacea has been widely investigated in the Caribbean Sea and the Gulf of Mexico, showing considerably higher abundances and lower diversity along the coastal zones than in oceanic regions (Gasca *et al.*, 2001; Castellanos & Gasca, 2002; Castellanos *et al.*, 2009). In any case, their abundance estimated in the present study did not reach the highly-dense aggregations observed in temperate zones of the Gulf of Mexico (Gasca *et al.*, 2001; Castellanos & Gasca, 2002). Biggs *et al.* (1997) showed that high levels of reproductive activity of krill (evidenced by the high abundance of early larval stages) in the southern Gulf of Mexico occur during summer. The high abundance of Appendicularia has been reported near the continental shelf of Tabasco, influenced by continental water discharge, which decreases salinity and causes low temperatures. These conditions favor food availability during the rainfall season (Flores-Coto *et al.*, 2010a,b).

Fish eggs and larvae diversity and richness are considerably higher in coastal than in oceanic habitats (Monreal-Gómez & Salas de León, 2004; Flores-Coto *et al.*, 2009). Zooplankton community structure and abundance, as well as sea surface chlorophyll-*a* concentration recorded in the present study, were spatially homogenous due to the small area investigated over the continental shelf, but with significantly distinct seasonal variability. Centropomids have been reported spawning in the Grijalva-Usumacinta River system during periods with high zooplankton availability (Hernández-Vidal *et al.*, 2014). Copepods were noticeably dominant throughout the year in this coastal and shallow habitat, suggesting they are the most abundant and frequent prey available for fish larvae. Fish eggs and larvae collected during September and November 2011 confirmed the area of study is also an active spawning site. To understand the role that zooplankton play in the diets of fish larvae in this

region, future research must investigate their feeding habits using evidence of stomach content and meta genetic methods. The results of the present study help to delimit the periods in the year with a higher abundance of each of the zooplankton taxonomic groups, and knowing the feeding habitat of fish larvae may help to detect which species of the zooplankton can be reared to feed fish larvae under laboratory conditions.

Generalizations of the seasonal fluctuations of the zooplanktonic community observed in the present annual cycle (March 2011-February 2012) should be treated with caution since the association between the measured environmental variables and the taxonomic composition of the zooplanktonic community certainly change interannually. Rowe (2017) proposed the hypothesis that the low densities and biomass of zooplankton in the southern Gulf of Mexico is caused by the limited production of phytoplankton, which is limited by the lack of inorganic nutrients, principally nitrates. The author acknowledged that there are exceptions in areas near the river's mouth at the base of the Gulf of Campeche. The effect of type and concentration of nutrients, not included in this study, must be investigated in this region to infer the mechanisms that control phytoplankton and zooplankton species assemblages in the Grijalva-Usumacinta River system.

CONCLUSIONS

Zooplankton collected off the coast of Tabasco exhibited a higher relative abundance during the DS than during dry and WSS. This pattern is probably due to increased levels of nutrients provided by rivers of the Grijalva-Usumacinta River system. These rivers favor primary productivity and foster energy transference within the regional pelagic food web. Copepoda, Bivalvia, Trematoda, and Sagittoidea were the zooplankton taxonomic groups with the highest abundance throughout the year.

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