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ARTICLE

Relationship between zooplankton biomass and continental water discharges in the southern Gulf of Mexico (1984-2001)

Relación entre la biomasa zooplanctónica y las descargas de aguas continentales, en el sur del Golfo de México (1984-2001)

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Resumen.- La biomasa zooplanctónica es reconocida como un importante indicador de la producción secundaria; su variación espacio-temporal en zonas neríticas es afectada particularmente por las descargas de los ríos, por lo que se analiza el efecto espacio temporal de las descargas de aguas continentales en la distribución de la biomasa zooplanctónica en el sur del Golfo de México, en 5 áreas frente a las costas de Veracruz, Tabasco y Campeche. El material analizado proviene de 534 muestras recolectadas en diferentes estaciones climáticas entre 1984 y 2001. Los volúmenes de descargas de 5 regiones hidrológicas se obtuvieron de la base de datos gubernamentales. Los resultados muestran que las variaciones de la biomasa durante las estaciones del año en las diferentes áreas son muy similares al patrón de las descargas. Los mayores valores de biomasa ocurren enfrente de las costas de Tabasco y los menores frente a Veracruz, donde se tienen las mayores y menores descargas de aguas continentales respectivamente. La variación de la biomasa depende de las descargas, no sólo en términos de un ciclo anual, sino también directamente relacionada con el tamaño del volumen vertido al océano. El análisis de árbol permitió concluir que en el sur del Golfo de México sobre la parte externa de la plataforma y zona oceánica, la biomasa siempre es baja, independiente de la estación del año o del área de que se trate. La mayor biomasa ocurre sobre la plataforma en profundidades bajas, pero su magnitud varía dependiendo del área y de la época. La biomasa frente a Campeche no depende de las descargas de aguas continentales sino se genera sobre la plataforma de Yucatán.

Palabras clave: Biomasa zooplancton, Golfo de México, agua de descargas continentales, técnica CART

Abstract.- Zooplankton biomass is recognized as an important indicator of secondary production, its spatial and temporal variation in neritic zones is particularly affected by discharges of the rivers, and the spatial-temporal effect of continental water discharges on the distribution of zooplankton biomass in the southern Gulf of Mexico was analyzed for 5 areas off the coasts of Veracruz, Tabasco and Campeche. The analyzed material was obtained from 534 samples collected during different climatic seasons from 1984 to 2001. The discharge volumes of 5 hydrological regions were obtained from the government's data base. The results obtained indicated that biomass variation throughout the seasons in the different areas was very similar to the pattern of discharges. The greater biomass values were recorded off Tabasco and the lower values off Veracruz, where the greater and lower continental water discharges were recorded respectively. Biomass variation depended on the discharges, not only in terms of an annual cycle, but was also directly related to the volumes discharged into the ocean. A Tree analysis made it possible to conclude that biomass is always low on the outer shelf and oceanic region of the southern Gulf of Mexico, independently of the season of the year or of a particular area. A greater biomass was recorded on the shallow shelf, with a magnitude that varied in relation to the area and season. The biomass off Campeche did not depend on the continental water discharges, but was generated on the Yucatán shelf.

Key words: Zooplankton biomass, Gulf of Mexico, continental water discharges, CART technique

INTRODUCTION

Zooplankton biomass has been widely recognized as an important indicator of secondary production (Boltovskoy 1981, Clark *et al*. 2001), apart from being a key factor in moving energy from primary production to higher trophic levels in pelagic food chains (Kane 1993, Fernández de Puelles *et al*. 1996, Clark *et al*. 2001, Steinberg *et al*. 2008). Its variation in space and time thus determines the dynamics of the system.

The patterns of distribution and abundance of zooplankton are affected by factors of a trophic nature (Reaugh *et al*. 2007, Steinberg *et al*. 2008), as well as hydrodynamic factors such as currents, gyres, mixing and stratification of the water column, distance from the coast (Salas de León *et al*. 1998, Espinosa-Fuentes *et al*. 2009) and continental water discharges (Grimes & Finucane 1991).

Water circulation in the Gulf of Mexico is strongly influenced by the Loop Current (Nowlin 1972). Coastal currents in particular have a marked seasonal cycle, and move to the south from October to March over the Veracruz and Tabasco shelves to the point where they meet an opposite current that originates as a branch of the Yucatán current. The coastal currents then move to the north throughout the year (Zavala-Hidalgo *et al*. 2003).

The coupling between the distribution of planktonic organisms and the hydrodynamics in the Bay de Campeche in the southern Gulf of Mexico has been analyzed for different climatic seasons by Flores-Coto *et al*. (1988, 1993), Salas de León *et al*. (1998) and Espinosa-Fuentes *et al*. (2009). These authors stated that the general distribution of zooplankton is strongly affected by river discharges and the meso-scale cyclonic gyre, and observed a marked gradient in zooplankton biomass from the coast offshore.

High densities of zooplankton biomass recorded in coastal areas (Flores-Coto *et al*. 1988, Gasca *et al*. 1994, Salas de León *et al*. 1998, Espinosa-Fuentes *et al*. 2009) indicate an association between zooplankton and high primary production systems, generated by continental water discharges and forming coastal fronts rich in nutrients, which in turn constitute areas that favour the feeding and growth of planktonic organisms (Biggs & Sánchez 1997, Chen *et al*. 1997, Chen *et al*. 2002, Vera-Mendoza & Salas de León 2014).

This emphasize the importance of coupling between physical and biological processes in production processes. Thus, the purpose of this study was to analyze the spatial-temporal effect of continental water discharges on the distribution of zooplankton biomass on the continental shelf and oceanic region of the southern Gulf of Mexico during different climatic seasons, based on data recorded over more than fifteen years (1984-2001).

MATERIALS AND METHODS

The study area is located in the southern Gulf of Mexico between 18° and 21°30'N and 91° and 97°W, along the coasts of the states of Veracruz, Tabasco and Campeche (Fig. 1). The southern Gulf of Mexico is a highly dynamic coastal system that receives considerable volumes of water from the rivers and coastal lagoons of the states of Veracruz, Tabasco and Campeche, as well as from the Yucatán Canal currents. All this water carries great amounts of organic and inorganic materials and makes this one of the most important fishery areas of the country (Gracia *et al*. 1997). The main rivers that provide runoff to the Campeche Bay and Campeche Sound are the Grijalva-Usumacinta, Papaloapan, Coatzacoalcos, Tecolutla, Tuxpan, Antigua, Nautla, Candelaria and Cazones (Comisión Nacional del Agua 2009)[1].

These continental water discharges are collected in 5 hydrological regions, 3 located in the state of Veracruz (Veracruz Norte, Papaloapan and Coatzacoalcos), one in Tabasco (Grijalva-Usumacinta) and one in Campeche (Yucatán Oeste). Of these, the one with the greatest catchment area is the Grijalva-Usumacinta with 102,465 km^2, whereas the Yucatán Oeste has only 25,443 km^2 (Comisión Nacional del Agua 2009)[1].

Continental water discharges favour the formation of coastal fronts in neritic areas. The presence and the ecological role of coastal fronts in the study area have been recorded by several authors (Czitrom *et al*. 1986, Alatorre *et al*. 1989, Monreal-Gómez *et al*. 1992, Espinosa-Fuentes & Flores-Coto 2004). Since organisms tend to gather near fronts, the distribution of waste and pollutants may be affected by their presence (Klemas 1980, Salas de León *et al*. 1998).

The study area is characterized by the presence of cold fronts, mainly from October to April (Tapánes & González-Coya 1980). The presence of a cold front in the Gulf produces northerly winds, locally known as 'northers' that reach 30 m s^{-1}; these meteorological characteristics over the Gulf of Mexico affect the coastal zone through freshwater discharges, modify the position of the thermocline making it deeper, and generally affect circulation (Shirazago 1991).

Material was obtained from 534 samples collected in the southern Gulf of Mexico during 14 oceanographic cruises carried out on the R/V Justo Sierra during different seasons of the year from 1984 to 2001 (Table 1). Three cruises took place during winter, 4 in spring, 3 in summer and 4 in autumn.

Each of the 5 hydrological regions were considered as study area: areas 1- Norte de Veracruz, 2- Papaloapan and 3-Coatzacoalcos, in the state of Veracruz, area 4 to the hydrological region Grijalva-Usumacinta in Tabasco and area 5 to the hydrological region Yucatán Oeste in Campeche (Fig. 1).

[1]Comisión Nacional del Agua. 2009. Atlas del Agua en México, México. <www.conagua.gob.mx>

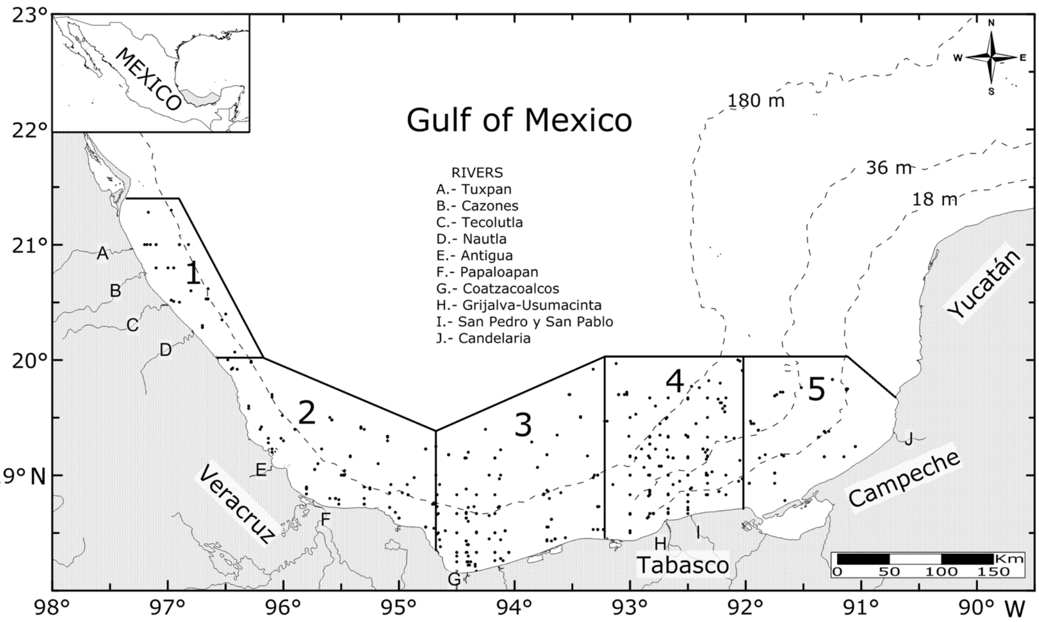

Figure 1. Study area, location of sampling stations and hydrological areas (1-5) / Área de estudio, ubicación de las estaciones de recolecta de zooplancton y áreas hidrológicas (1-5)

Table 1. Used oceanographic cruises for the analysis of zooplankton biomass. Year, season, number of samples and study area / Cruceros oceanográficos empleados para el análisis de la biomasa de zooplancton. Año, estaciones climáticas, número de muestras y área de estudio

Cruises	Year	Season	Samples	Study area	
				Latitude min-max	Longitude min-max
PROGMEX I	1983	Spring	40	18.22 to 20.53°N	91.13 to 96.95°W
IMECO	1984	Winter	20	18.25 to 21.00°N	91.28 to 97.15°W
PROGMEX II	1984	Spring	30	18.22 to 20.53°N	91.13 to 96.97°W
PROGMEX III	1984	Summer	46	18.22 to 20.53°N	91.12 to 96.97°W
OGMEX I	1987	Winter	42	18.33 to 21.00°N	91.05 to 96.90°W
OGMEX II	1987	Summer	58	18.25 to 21.00°N	91.05 to 97.18°W
OGMEX III	1987	Autumm	42	18.25 to 19.91°N	91.05 to 95.80°W
OGMEX V	1988	Summer	67	18.25 to 21.30°N	91.32 to 97.17°W
OGMEX VI	1988	Autumm	26	18.30 to 21.00°N	94.04 to 97.20°W
OGMEX VII	1989	Winter	42	18.25 to 19.50°N	92.80 to 95.80°W
PROMEBIO II	1999	Autumm	34	18.23 to 19.34°N	92.33 to 94.67°W
PROMEBIO III	2000	Spring	33	18.21 to 19.34°N	92.33 to 94.67°W
PROMEBIO IV	2001	Spring	20	18.50 to 19.67°N	92.33 to 93.01°W
PROMEBIO V	2001	Autumm	34	18.17 to 19.67°N	92.17 to 94.67°W

The information in the data base of the Banco Nacional de Datos de Aguas Superficiales BANDAS (IMTA 2000), recorded for 27 hydrometric stations over a period of 50 years, was consulted in order to obtain the volume of the average monthly discharges of the 5 hydrological regions.

A Bongo net with mesh sizes of 333 and 505 µm was used to collect the zooplanktonic material. Trawling was double oblique for 5 to 20 min at maximum depth of 200 m, as bathymetry allowed. The volume of filtered water was calculated using flowmeters (General Oceanics, model 2030R) placed at the mouth of the net.

The zooplankton samples were preserved in 4% formalin, neutralized with sodium borate and later transferred to 70% alcohol. Zooplankton biomass was analyzed only for the samples collected with the 333 µm mesh size net. Biomass was recorded as wet weight after eliminating the large and gelatinous organisms with a suction filtering system (Zavala-García & Flores-Coto 1989). The samples were weighed on an analytical scale and the data were standardized to g 100 m^{-3}.

The biomass and volume discharge values, previously transformed to Ln(x+1) and 1/√x respectively to normalize the variance, were analyzed considering the 5 areas into which the study area was divided, the 4 climatic seasons of the year, the distance from the coast and the depth of the stations. For each case, the obtained values represent the average biomass of an area, a season, or an area during a season.

The relationship of the average biomass values and the discharge for the whole study area was evaluated through a Pearson's correlation. In order to establish if there are significances differences of biomass between the 5 study areas and the climatic seasons, an analysis of variance was carry out (multifactorial ANOVA), as well as a Student-Newman-Keuls multiple comparisons test to determine which means were significantly different.

Spearman's rank correlation coefficient was applied to determine the distribution of the biomass in relation to the distance from the coast. The data were placed in 10 km-groups from the coast up to a distance of 100 km. Those recorded beyond 100 km formed one single group (>100). Thus, each value represents the average of the biomass in each 10 km-group within each area.

The Classification and Regression Trees (CART) technique proposed by Breiman *et al.* (1984) was applied to determine the relationship between the distribution of the zooplankton biomass (534 samples) on the continental shelf and adjacent oceanic region, and in the different areas, with respect to the climatic seasons of the year, the distance from the coast and the depth of the sampling stations.

The STATGRAPHICS Centurion XV, V. 15.2.06 and S-PLUS, V. 8.0 software were used for all the statistics and classification tests.

Results

Continental water discharges

The analysis of 10,697 data of 27 hydrometric stations recorded from 1944 to 1999 provided the volumes of the monthly and seasonal discharges of the 5 hydrological regions. The information points to a general pattern of continental water discharges throughout an annual cycle. The lower discharge values were recorded during the first 5 months of the year, the values increased to a maximum from June to September and October, and they decreased towards the last 2 months of the year. Seasonally, this means that the greater discharges occurred in summer and autumn and the lower ones in winter and spring (Fig. 2a).

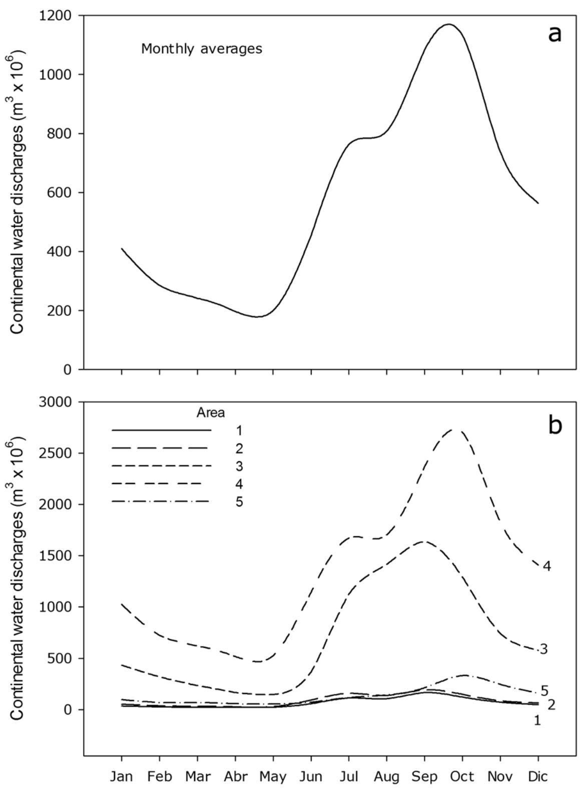

Figure 2.- Monthly averages of continental water discharges, for the whole study area and for each hydrological area (1-5) / Promedios mensuales de las descargas de aguas continentales, para toda la zona de estudio y para cada una de las áreas hidrológicas (1-5)

The greater continental water discharges occurred in area 4 in Tabasco, the lower discharges were recorded in areas 1 and 2 in Veracruz and area 5 in Campeche, and area 3 recorded intermediate values (Fig. 2b). The maximum discharges throughout the hydrological cycle occurred in September in areas 1, 2 and 3 and in October in areas 4 and 5.

Abundance and distribution of zooplankton biomass

The average biomass values expressed as g 100 m^{-3} varied among the different areas and seasons from 5.0 in area 1 in autumn to 31.4 in area 4 in summer. Areas 1, 2 and 3 registered the lower general average biomass values (<15 g 100 m^{-3}), while areas 4 and 5 had values nearer 20 g 100 m^{-3} (Table 2).

These data suggests a close relationship between biomass density and the volume of continental water discharges in the different areas. Thus, areas 1 and 2, where the lower values of zooplankton biomass were recorded, also recorded the lower values of continental water discharge, while greater values of these parameters were recorded for areas 3 and 4. Area 5 however broke this relationship, with a high biomass but low discharges similar to those of areas 1 and 2 in Veracruz (Fig. 3).

Seasonally, the general pattern of biomass density was similar to that of the discharges, with low values during winter and spring that increased in summer and decreased in autumn. However, this relationship changed from one area to another (Fig. 4).

The Shapiro-Wilk test for normality was applied to the transformed values of average biomass and the water discharge volumes, the results showed a normal distribution with values of W= 0.939, *P*= 0.197 and W= 0.937, *P*= 0.223 respectively and the Pearson's correlation coefficient for biomass and discharges were r= 0.689 ($F_{1,11}$= 16.297, N= 20, *P* < 0.05).

The multifactorial ANOVA results show a statistically significant relationship between biomass and the 5 study areas ($F_{4,11}$ = 5.24, *P* = 0.0152), and the seasons ($F_{3,11}$ = 13.56, *P* = 0.0002) (Table 3).

Considering the biomass values in the different areas, the Student-Newman-Keuls multiple comparisons test formed 2 homogeneous groups: the first with areas 1 and 2 that corresponded to 2 hydrological regions in Veracruz, and the second with areas 3, 4 and 5 that coincided with the areas of greater biomass production in Tabasco, Campeche and the region of Coatzacoalcos. A comparison of the biomass recorded for the different seasons of the year formed 2 homogeneous groups: the first with winter, spring and autumn, and the second with summer. It was during this season of the year that the greater biomass values were recorded in general in all the areas (Tables 4 and 5).

Table 2. Average biomass values (g 100 m^{-3}) per season and area in the states of Veracruz, Tabasco and Campeche / Valores promedio de biomasa (g 100 m^{-3}), estaciones climáticas del año y áreas en los estados de Veracruz, Tabasco y Campeche

Seasons	Veracruz			Tabasco	Campeche
	1	2	3	4	5
Winter	8.7	6.0	14.0	19.2	15.4
Spring	6.4	10.1	13.9	16.4	18.0
Summer	18.4	9.3	18.1	31.4	23.3
Autumn	5.0	6.5	13.3	15.9	20.0
Average	11.8	8.0	15.0	20.0	19.8

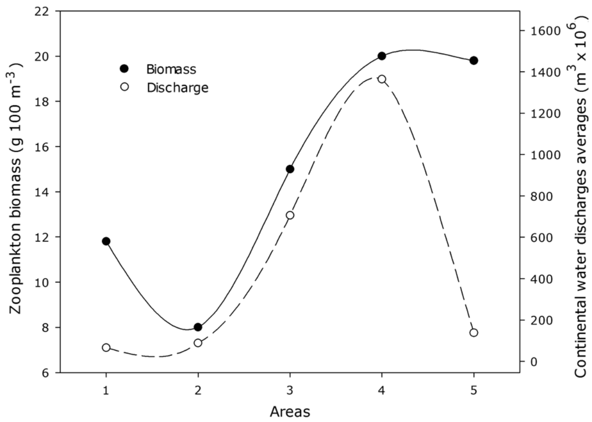

Figure 3. Zooplankton biomass and continental water discharge averages for each area / Promedios de la biomasa zooplanctónica y descargas de aguas continentales para cada una de las áreas

Table 3. Multifactorial variance analysis for biomass (g 100 m^{-3}) with respect to the seasons and 5 areas / Análisis de varianza multifactorial para la biomasa (g 100 m^{-3}) con respecto a las estaciones climáticas y las 5 áreas

Source	Sum of squares	Degrees of freedom	Mean square	*F*- test	*P*-value
Main effects					
Areas (1-5)	3.8442	4	0.9611	13.59	0.0002
Seasons	1.1129	3	0.3710	5.24	0.0152
Residuals	0.8488	11	0.0707		
Total (Corrected)	5.8059	19			

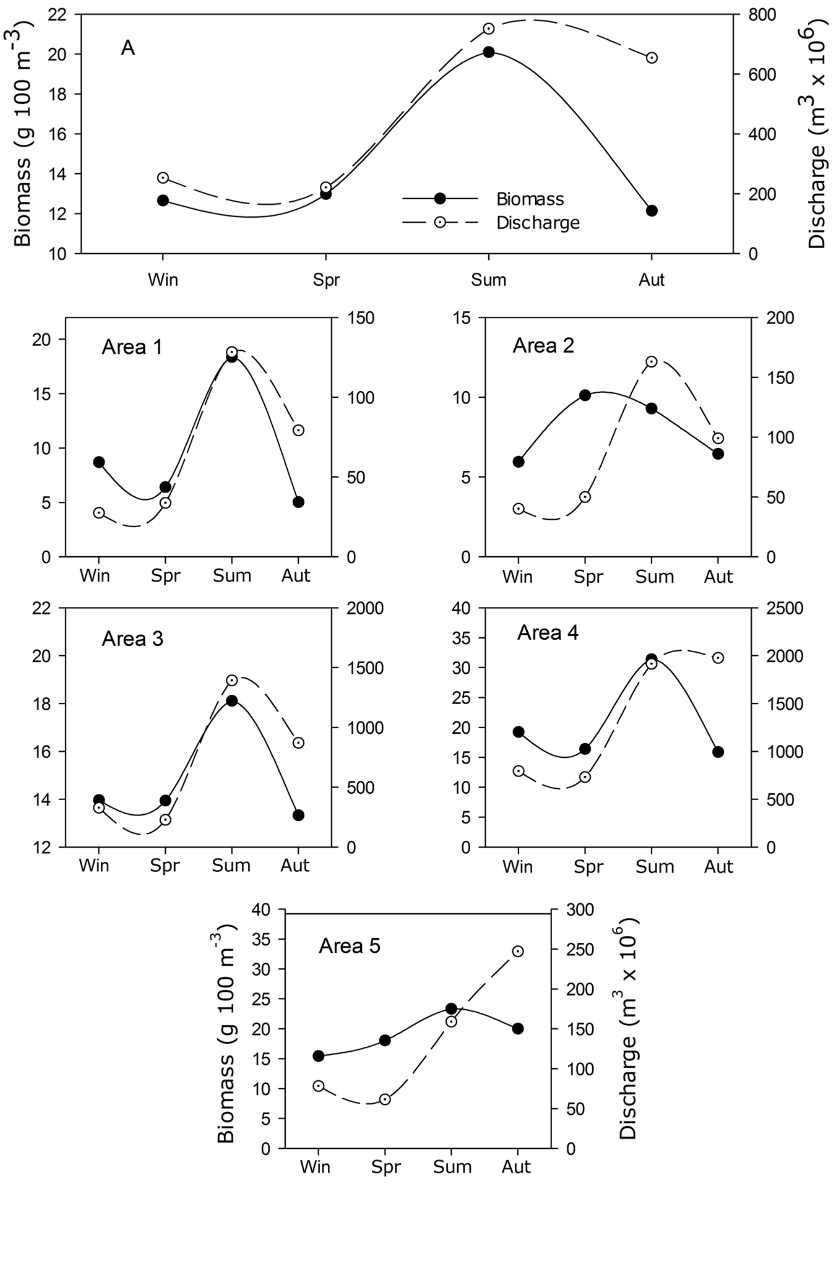

Figure 4. Seasonal averages of zooplankton biomass and continental water discharges for the whole study area (A) and for each area (1-5) / Promedios estacional de la biomasa zooplanctónica y descargas de aguas continentales, para toda la zona de estudio (A) y para cada una de las áreas (1-5)

Table 4. Student-Newman-Keuls multiple comparisons values for biomass (g 100 m^{-3}) per season and area, at a confidence level of 95% / Comparaciones múltiples de Student-Newman-Keuls de los valores de biomasa (g 100 m^{-3}) por estaciones climáticas y áreas, a un nivel de confianza del 95%

	N	Mean	Standard error	Homogeneous groups
Areas				
2	4	1.9058	0.13298	1
1	4	1.9952	0.13298	1
3	4	2.6185	0.13298	2
5	4	2.8895	0.13298	2
4	4	2.9382	0.13298	2
Season				
Winter	5	2.4698	0.11893	1
Spring	5	2.3560	0.11893	1
Summer	5	2.4058	0.11893	1
Autumn	5	2.8662	0.11893	2

Table 5. Multiple comparisons values between each pair of means for areas and seasons / Valores de la comparación múltiple entre cada par de medias por áreas y épocas

Areas	Significance	Seasons	Significance
1 - 2	0.0895	Win - Aut	0.106
1 - 3	* -0.6232	Win - Sum	-0.049
1 - 4	* -0.9430	Win - Spr	* -0.510
1 - 5	* -0.8942	Aut - Sum	-0.156
2 - 3	* -07127	Aut - Spr	* -0.616
2 - 4	* -1.0325	Sum - Spr	* -0.460
2 - 5	* -0.9837		
3 - 4	-0.3197		
3 - 5	-0.2710		
4 - 5	0.0487		

* indicates a significant difference

The distribution of the biomass with respect to the distance from the coast produced a negative Spearman's correlation coefficient and a marked coast-ocean gradient off Veracruz and Tabasco. In contrast, in Campeche the pattern was inverted and the correlation was positive. The dependence of these parameters was statistically significant at a confidence level of 95%, except for area 1 (Fig. 5).

The Tree analysis was applied to all the biomass samples (534). Its binary classification system showed that the distribution of the biomass was strongly conditioned by the depth of the stations. It formed 2 groups of stations, or branches, at the root of the tree. The first grouped the stations at depths >101 m (213 stations) with very low biomass values of 6.5 g 100 m^{-3} or less. This group had no more branches (Figs. 6a and b). The second grouped 321 stations with greater biomass values than those recorded for the first group. The next branching factor in this second group was the season, with one branch for summer and the other branch for winter, spring and autumn (Fig. 6a).

The branch for winter, spring and autumn generated 2 branches in which the areas were the main factor. The first branch grouped areas 1, 2 and 3 (106 stations) with an average biomass of 14.3 g 100 m^{-3}, and the second branch (115 stations) recorded an average biomass of 21.2 g 100 m^{-3} (Fig. 6c).

The branch for summer was divided by the depth into 2 new branches, one with the greater depths (> 33.5 m, 59 stations) and an average biomass of 20.8 g 100 m^{-3}, and another with the shallower depths (< 33.5 m, 41 stations) and an average biomass of 36.9 g 100 m^{-3} (Fig. 6d).

Discussion

The results obtained in this study indicate that the variation in zooplankton biomass throughout the year and throughout the study areas in the southern Gulf of Mexico is very similar to the pattern of continental water discharges.

The continental water discharges in the study area recorded lower values in winter and spring, a maximum in summer, and a decrease in autumn. The discharge volume of each hydrological region is determined by the surface area, as well as by the amount of rain that falls in each basin.

According to the Tree analysis for winter, spring and autumn, the main factor that determined differences in biomass distribution was the areas. Thus, areas 1, 2 and 3 off Veracruz presented the lower values, while areas 4 and 5 recorded the higher values. In the case of the summer, when the greater biomass values were recorded, it was the depth that conditioned the variations in the distribution.

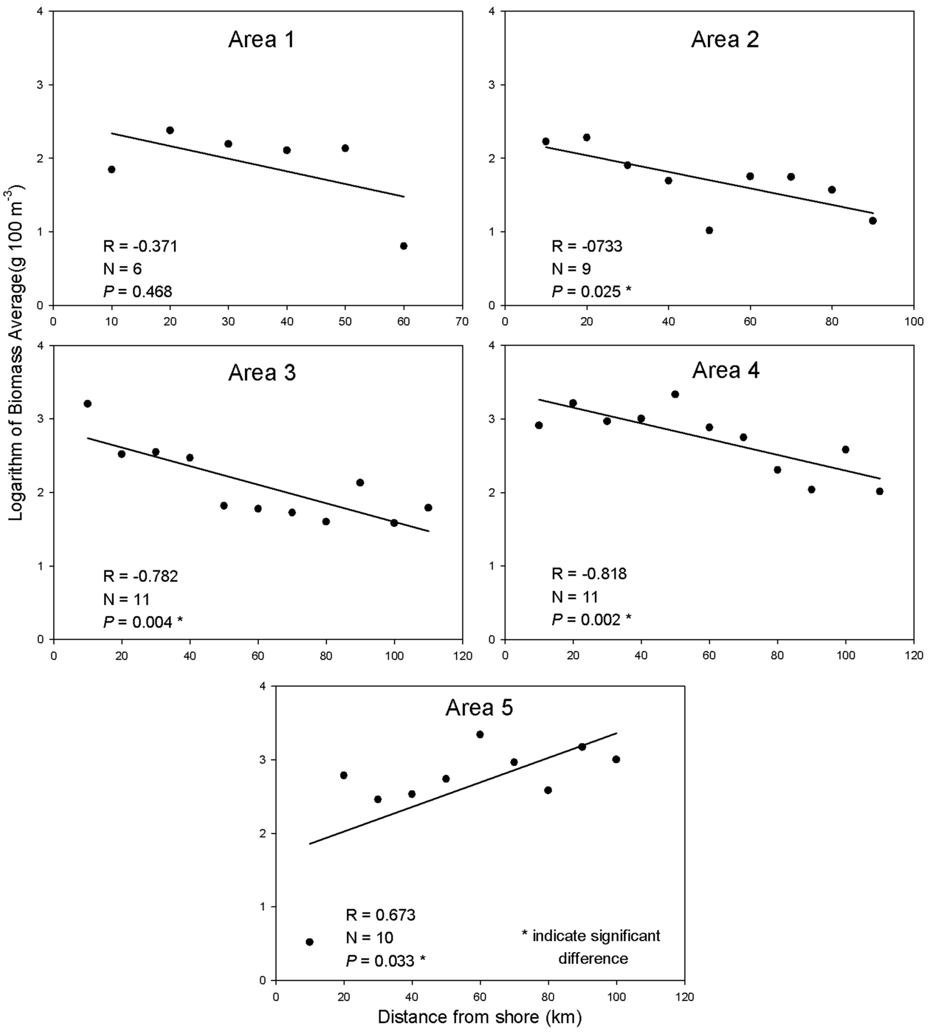

Figure 5. Zooplankton biomass distribution with respect to the distance from the coast in each area (1-5) / Distribución de la biomasa zooplanctónica respecto a la distancia a la costa, en cada una de las áreas (1-5)

Geographically, the greater biomass values were recorded in the southern of the Campeche Bay, off Tabasco and the lower values in the northwest of the bay, off Veracruz; areas were through the year the greater and lower continental water discharges occur, respectively. This indicates that magnitude of the biomass depend on the continental water discharges for their annual cycle, but also in direct relationship to the volume discharged into the ocean.

The Tree analysis made it possible to conclude that the biomass on the outer shelf (>101 m depth) and in the oceanic region of the southern Gulf of Mexico is always low, independently of the season of the year or of a particular area. A greater biomass was recorded on the shallow shelf, however its magnitude varied with respect to the area and the season.

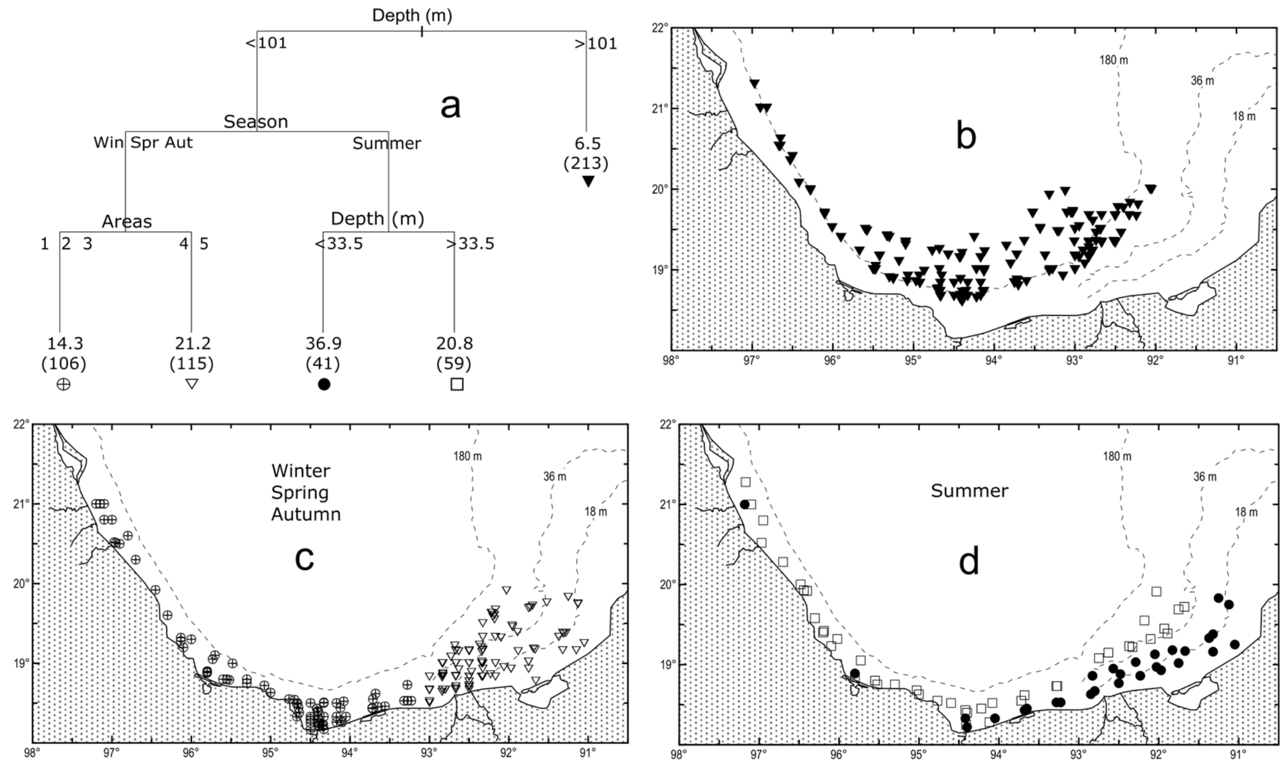

Figure 6. CART analyses applied to the biomass data recorded for the 5 areas. Classification and regression tree (a), stations located at > 101 m of depth (b), stations located at < 101 m of depth in winter, spring and autumn (c) and in summer (d) / Análisis CART aplicado al total de datos de biomasa recolectadas en las 5 áreas. Árbol de clasificación y regresión (a), estaciones ubicadas a más de 101 m de profundidad (b), estaciones ubicadas a menos de 101 m de profundidad en invierno, primavera y otoño (c) y verano (d)

Variations in biomass, which depend on the volume of continental water discharges, respond to the greater concentration of nutrients that is discharged, together with river water, to the continental shelf (Lohrenz *et al*. 1990, Dagg & Whitledge 1991, Chen *et al*. 2002), generating areas of high primary productivity that lead to a progressive increase in zooplankton biomass (Roman *et al*. 2005, Reaugh *et al*. 2007). High biomass densities have frequently been recorded y areas near the Grijalva-Usumacinta system (Flores-Coto *et al*. 1988, Monreal-Gómez *et al*. 2004, Loman-Ramos *et al*. 2007, Flores-Coto *et al*. 2010), for which reason this area is considered to be a highly productive region (CECODES 1981). The results of this study presented a very close relationship between these parameters, with a correlation coefficient of 0.689 and a statistical significance at a 95% confidence level.

The greater zooplankton biomass recorded near the coast, is an expected result of the production generated by the continental water discharges and their dispersion towards the sea, generated a coast-ocean gradient off Veracruz, and even more so off Tabasco due to the local currents (Zavala-Hidalgo *et al*. 2003). This dispersion process has been documented for this same area and other parts of the world for fish larvae, indicating that the penetration of freshwater onto the shelf takes place rapidly and carries with it whole associations of organisms as far as it spreads (Sabatés 1990, Reiss & McConaugha 1999, Espinosa-Fuentes *et al*. 2004).

The biomass distribution pattern in area 5, which corresponds to the Campeche shelf, was opposite to that in the other 4 areas. In this area, greater biomass values were recorded at the stations located furthest from the coast. This suggests that the biomass in this region is advected from the Banco de Campeche and does not depend on the continental water discharges, but is generated on the Yucatán shelf after nutrient enrichment due to upwelling off Cabo Catoche (López-Veneroni *et al*. 1986, Merino-Ibarra 1992, Pérez de los Reyes *et al*. 1996, Merino 1997) or by coastal upwelling in the Banco de Campeche (Zavala-Hidalgo & Fernández-Eguiarte 2006).

In conclusion the variation of the zooplankton biomass through the year in the southern Gulf of Mexico has a similar pattern to the continental water discharges, not only in terms of annual cycle, but in direct relation to the magnitude of the volume discharged into the ocean in each area, except in the Campeche-Yucatán shelf were the biomass has another origin.

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