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The effect of the 1997-1998 ENSO on the benthic macrofaunal biomass in the southwestern Gulf of Mexico

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RESUMEN

Se llevaron a cabo mediciones de biomasa macrofaunal, desde 1987, con el objeto de evaluar el efecto episódico de incorporación de carbono biogénico durante el evento de ENOS en el bentos de la plataforma continental y talud del suroeste del Golfo de México. Este estudio se basó en la hipótesis que la mezcla generada en la superficie del mar por el viento en periodos prolongados promueve una productividad primaria mayor en el Golfo de México que es exportada a profundidad y sostiene tróficamente la comunidad béntica, incrementando la biomasa de macrofauna. El contenido de nitrógeno orgánico en sedimento se empleó para expresar el enriquecimiento orgánico del sedimento. Los cambios geográficos y estacionales se han registrado con anterioridad en la región reconociendo que el máximo de biomasa macrofaunal ocurre durante la presencia de una condición de mezcla de la columna de agua y disminuye con el inicio del período de estratificación. La biomasa macrofaunal registrada en 1998 fue mayor que los valores de biomasa registrados en años anteriores (plataforma 0.93±0.22 gC.m^{-2}, talud 0.55±0.23 gC.m^{-2}), pero siguiendo una tendencia similar estacional (plataforma 0.57±0.11gC.m^{-2}, talud 0.18±0.09 gC.m^{-2}). La biomasa macrofaunal sobre la plataforma mostró una variabilidad amplia durante el período de estudio en contraste con los valores registrados sobre el talud. Como característica común del seguimiento de los registros a largo plazo se reconoció que las medidas de aportes estacionales de fitodetritos conllevan a un enriquecimiento del sedimento y se correlacionan con cambios de biomasa macrofaunal (plataforma r= 0.77; talud r= 0.85). El evento de teleconección ENOS promueve, a partir del forzamiento por viento, pulsos estocásticos de detrito de origen fotoautotrófico que enriquecen el sedimento y permiten un incremento significativo de la biomasa macrofaunal.

PALABRAS CLAVE: Carbono biogénico, exportación, infauna, plataforma, talud.

ABSTRACT

Long term macrofaunal biomass measurements made since 1987 were used to evaluate the effect of episodic inputs of biogenic carbon during ENSO on the shelf and slope benthos in the southwestern Gulf of Mexico. This study was based on the hypothesis that wind- induced mixing over long periods on the sea surface of the Gulf of Mexico increases primary productivity exported to depth, that trophically sustains the benthic community by enhancing the macrofaunal biomass. The content of organic nitrogen in sediment was used to estimate sediment organic enrichment. Geographical and seasonal changes recorded previously in the region showed that macrofaunal biomass maxima occur during mixing in the water column and decrease with the onset of stratification. Macrofaunal biomass recorded during 1998 was larger than in previous years: shelf 0.93±0.22 gC.m^{-2}, slope 0.55±0.23 gC.m^{-2}, as compared to shelf 0.57±0.11gC.m^{-2}, slope 0.18±0.09 gC.m^{-2}. The shelf macrofaunal biomass showed a large variability in contrast to the values recorded on the slope. Seasonal inputs of phytodetritus produce sediment enrichment and correlate with macrofaunal biomass changes (shelf r= 0.77; slope r= 0.85). ENSO promotes stochastic pulses of phytodetrital material induced by wind forcing that enrich the sediment and lead to a significant increase in the macrofaunal biomass.

KEY WORDS: Biogenic carbon, export, infauna, shelf, slope.

INTRODUCTION

Disturbances are characterised by several dimensions, the most important being the identity of the event within the type of disturbance that acts in the system (Pickett *et al.*, 1989). The model of disturbance suggested for the tropical shelf and slope benthos in the southwestern Gulf of Mexico is based on the seasonal food input that occurs in the form of pulses of phytodetrital material. The flux of phytodetritus correlates with blooms in surface water productivity, which are promoted by climate-ocean forcing of the tropical ocean (Legendre and Rassoulzadegan, 1996). Particles of biogenic carbon reaching the sediment can represent a more or less important fraction of surface production depending on their formation rate, quality and sinking conditions (Smith, 1989). In tropical basins organic carbon fluxes decrease from the surface to the sediments by a factor of 500 to 10000, with the largest changes in the upper ocean and at the sediment-water interface (Lee *et al.,* 1998). The benthic fauna responds to these episodic phytodetrital inputs, affecting the benthic community structure direct or indirectly (Smith, 1992).

The relationship in the variability of large-scale features of the atmospheric circulation related to ENSO has been named teleconnections (Trentberth and Hoar, 1996), a term that dates back to Angstroem (1935). The Pacific North American (PNA) teleconnection was considered among the 13 patterns described so far related to tropical anomalies (Bell and Halpert, 1995). The PNA pattern is one of the most prominent of all teleconnection patterns in the winter half-year, it arches from the tropical Pacific across North America and regionally stands out above other anomaly structures on inter annual timescales (Kushnir and Wallace, 1989). The PNA pattern acts over the Gulf of Mexico and has previously shown a positive response to El Niño during the northern Spring in 1992 and 1993 (Trenberth *et al.,* 1998). The effect of this teleconnection pattern has been classified within the category of fluctuations with timescales longer than a month (Schubert, 1986), that exhibit a geographical dependence organized about a north-south oriented dipole that prevails over the ocean near the jet exit regions. Anomalous forcing is strongest in the northern winter, coinciding with the mature stage of El Niño events (Karoly, 1989). Storms and storm track variability have been documented with teleconnection patterns and cyclone waves have been suggested to be particularly active at maritime sites (Trenberth, 1991).

The strong and regularly alternating forcing imposed by winter wind drives all processes of the ocean production. Several studies have shown a link between interannual variability and El Niño/Southern Oscilation (Luther 1991) events. Teleconnections between the atmospheric circulation of the tropics and mid-latitudes are implicated in the upwelling (Yasunari, 1991). How these fluctuations vary between ENSO and non-ENSO events, the export of carbon, the particle flux and macrofaunal biomass variability in the regional seas is unknown.

The disturbance, once recognised, is characterised by its intensity or severity (Picket *et al.,* 1989). By comparing different intensities of disturbances, as measured by energy expended by the event, results may lead to understand the nature of the macrofaunal biomass distribution, as the template, and its subsequent organisation in the benthic system. The duration of phytodetritus flux is the scale of intensity in the disturbance model and varies according to ENSO and non-ENSO climate-ocean forcing.

Long term measurements are important for determining interannual and seasonal variation (Chelton *et al.,* 1982; Mysak 1989). This study represents a semi-continuous long-term survey in the southwestern Gulf of Mexico. The objective tries to answer specific questions on the changes on macrofaunal biomass within the overriding hypothesis: Does the wind forcing create conditions in which the response of the region in terms of carbon fixing and transfer is immediate and massive and predictable as a time-varying signal of large amplitude? How closely coupled are productivity in the upper layer and the benthic biomass, both in time and space? Does the large seasonally forced input or organic material to the seabed result in a large benthic biomass that acts as an indicator of interannual variability and of the presence of El Niño?

This study will examine the response of the benthic macrofaunal biomass on the shelf and slope as a result of episodic inputs of phytodetritus pulsed by wind forcing, both seasonally and by teleconnection of the 1997-1998 El Niño event in the southwestern Gulf of Mexico. It is the aim of this study to describe and discuss the changes in macrofaunal biomass in order to provide a hindsight of the response to sediment enrichment promoted by the export of biogenic carbon during an anomalous year of wind forcing (more extended) in the southwestern Gulf of Mexico. It is herein assumed that limited wind forcing at non-ENSO years will have a moderate effect in sediment enrichment and limited increase in benthic biomass.

MATERIALS AND METHODS

Study area. The Bay of Campeche in the southwestern Gulf of Mexico (Figure 1) was chosen as the study area to examine the changes on macrofaunal biomass for the extended period in which the continuous collections were carried out. This area is characterised by seasonal variations in the surface water chlorophyll concentration and the time lag response in macrobenthic biomass change (Soto and Escobar, 1995). The ENOS .1 and .2 cruises (March and June 1998) selected six stations on the shelf and slope in which samples of macrofauna were collected. Stations were sampled with five replicates each both on the shelf and slope.

Field collection and laboratory analyses. The macrofauna samples were obtained from undisturbed sediment with a 0.25 m^2 US-NEL box corer; the replicate nature of the samples allowed to determine the variability of macrofauna and statistically intercompare with biomass values from previous cruises in the area of study. Sub-sampling of the sediment included organic matter, hand collected from box core samples with sub-cores that were placed in plastic bags and frozen to -10°C to process ashore. Percent of organic matter content was used to assess sediment enrichment by exported biogenic carbon. Macrofauna restricted to the upper 10 cm of sediment was sorted onboard by replicates, sediment retained in 1000, 500 and 250 μm screens was preserved in absolute ethanol with Rose Bengal dye.

The sediment samples collected for the evaluation of the organic matter content were thawed at room temperature and portions weighed into tarred beakers and dried at 90°C overnight. Acid (1 N HCl) was added to remove $CaCO_3$. The sediments were combusted in a Perkin-Elmer 240B CHN Elemental Analyser to yield percent dry weight of organic nitrogen as a way to evaluate the organic matter content.

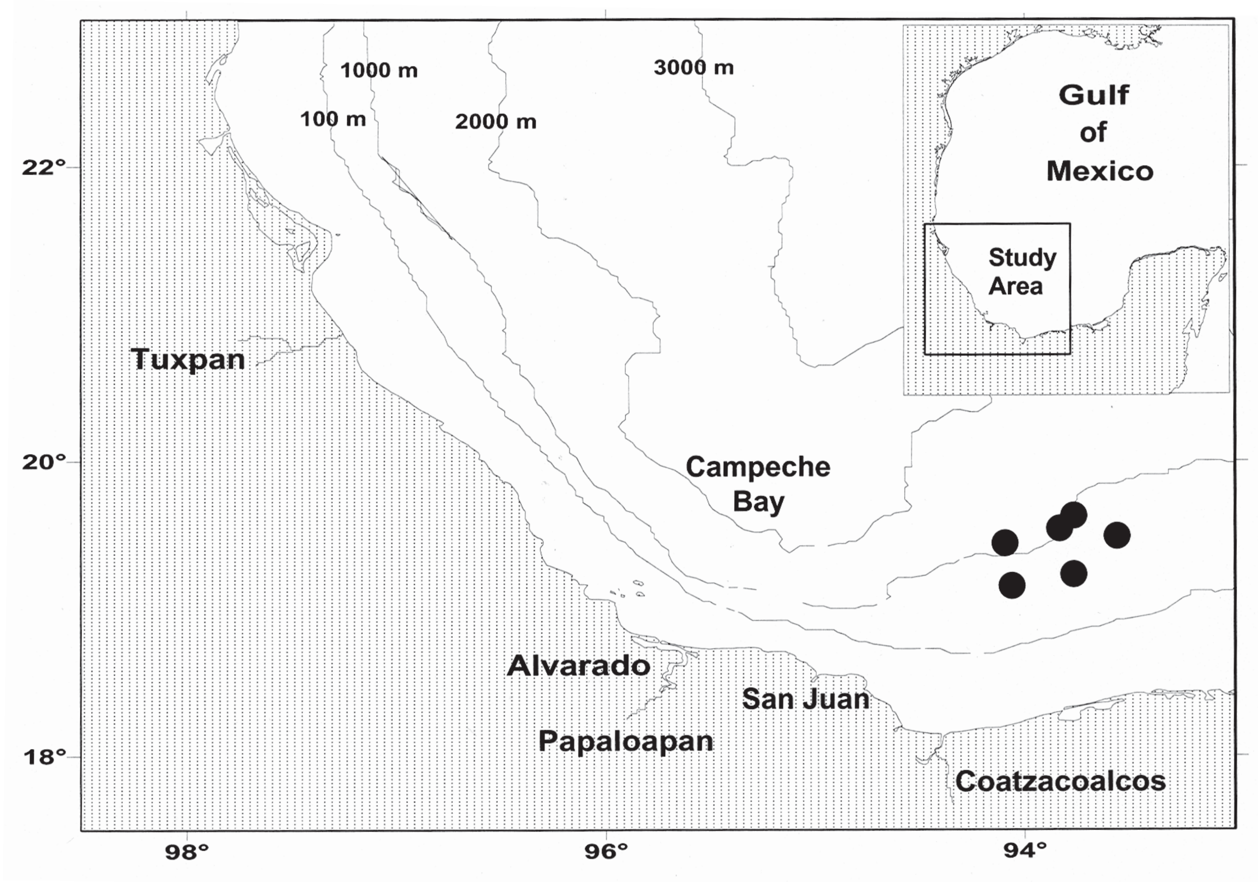

Fig. 1. Location of sampling sites and study area in the southwestern Gulf of Mexico.

The macrofauna was weighed in the laboratory, quantified per unit surface area of the bottom and wet weight biomass values were converted to mg C per m^2. Biomass data from cruises conducted in previous years have yielded information on the nature of the distribution of the macrofauna, as reported by Soto and Escobar (1995) and Escobar and Soto (1997). Biomass values obtained from the ENSO.1 and .2 cruises and those from previous cruises were grouped into two consecutive seasonal periods. One period represented the water column mixed condition beginning in November (when particle flux and export typically begins) and ending in May (when the water column stratifies with the warming of the surface and the detritus aggregates are being consumed in the seafloor). The second period represented the thermal and saline stratified condition (Table 1). These two periods were herein named as "mixed " and "stratified" conditions. The samples were also grouped into the two depth zones, namely continental shelf (less than 200 m depth) and continental slope (depth range of 200 and 1000 m). The results from the ENOS.1 and ENOS.2 cruises were compared with results from cruises from previous years; the data were analysed using the non-parametric Newman-Keuls two-way analysis of variance test between years and water column conditions to determine the interannual variability to a significance of $p<0.05$. The macroinfaunal biomass considered pre-existing seasonal variability in the region (Soto and Escobar, 1995).

RESULTS

Macrofaunal biomass variability. The polychaete annelids were the dominant components of the macrobenthic infaunal community that occurred in similar proportions (43-75%) in the two depth zones. Other taxa, such as bivalves, echinoderms, crustaceans and sipunculids, occurred in lesser abundance at all times. The general pattern of the mean biomass showed higher values on the shelf than on the slope. In this eight-year period significant differences occurred from 1995 to 1998 (Type III SS 1,2 df 1,128 $p<0.05$), but no differences were observed in 1993 and 1994. The biomass values were significantly larger (Newman-Keuls $p<0.05$) during the stratified condition in 1987 and 1988 on the shelf. In contrast, larger biomass was recorded during the mixed water column condition in 1997 and 1998 (Figures 2 and 3),

Table 1

Seasonal and spatial sampling effort (n) of the macrobenthic biomass in the southwestern Gulf of Mexico. ENSO teleconection sampling in bold

Depth zone	Year	Water column condition	n
Continental Shelf			
	1987	mixed	9
		stratified	9
	1988	mixed	9
		stratified	9
	1993	stratified	9
	1994	stratified	9
	1995	stratified	9
	1996	mixed	9
	1997	mixed	9
		stratified	9
	1998	mixed	15
		stratified	15
Continental Slope			
	1993	stratified	9
	1994	stratified	9
	1995	stratified	9
	1996	mixed	9
	1997	mixed	10
		stratified	9
	1998	mixed	15
		stratified	15

both on the shelf and slope. This large biomass showed significant differences on the shelf in both years and on the slope in 1998 only (Newman-Keuls $p<0.05$ shelf and slope).

The mean biomass values on the shelf ranged from 0.93±0.22 gC.m^{-2} during the mixed condition to 0.57±0.11gC.m^{-2} during the stratified condition. The mean biomass during the mixed condition showed significant differences over the study period (Kruskal-Wallis analysis of variance test, $p<0.05$; Figure 2) and only in few cases during the stratified condition. The shelf mean biomass values determined in 1998 during the mixed period were in most cases twice the biomass values recorded from 1987 to 1997 in the same season. The mean biomass values during the stratified period were highly variable in the shelf environment. These values were twice those recorded from 1993 to 1997 but were similar to the mean biomass values observed during the years 1987 and 1988 (Figure 2).

The mean biomass values in the slope environment, in contrast to the shelf, varied significantly when compared with biomass values from cruises from previous years (Kruskal-Wallis analysis of variance test, $p<0.05$; Figure 3). The mean values on the slope ranged from 0.55±0.23 gC.m^{-2} during the mixed condition to 0.18±0.09 gC.m^{-2} during the stratified condition. The biomass recorded during the mixed condition in the slope in 1998 exceeded six times the values in 1996 and in 1997. The mean values during the stratified period were three times higher than values from 1993 to 1997 (Figure 3).

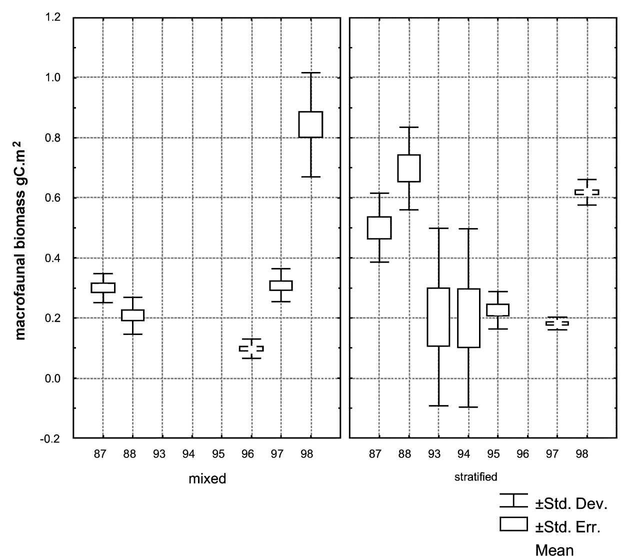

Fig. 2. Continental shelf macrofaunal biomass variability from 1987 to 1998 in the southwestern Gulf of Mexico.

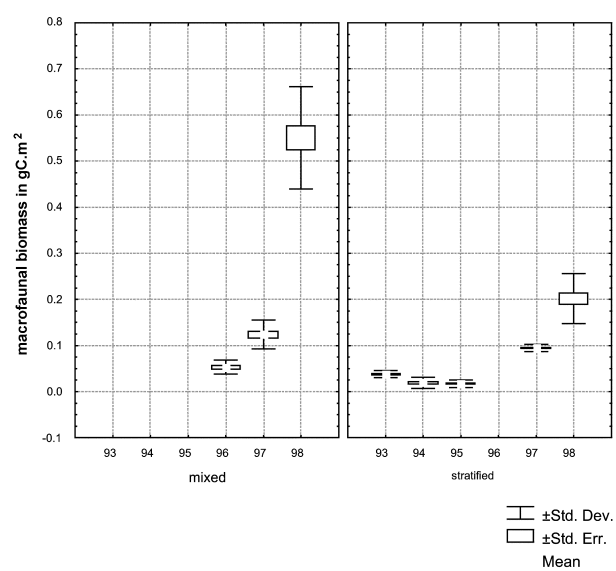

Fig. 3. Continental slope macrofaunal biomass variability from 1993 to 1998 in the southwestern Gulf of Mexico.

Organic matter content in sediment. The organic nitrogen during the mixed condition ranged from 0.14 to 0.20% on the continental shelf and from 0.08 to 0.14% on the continental slope. The values remained constant on the shelf during the stratified condition, but on the slope the values decreased (shelf mean 0.17%; slope mean 0.07%). The shelf environment sediments had larger nitrogen content throughout the eight-year study period (range 0.03 to 0.19%) in contrast to the slope (range 0.02 to 0.1%). The content of organic nitrogen in the sediment was larger in 1997 and 1998 than in previous years, both on the shelf and slope. The macrofaunal biomass changed in accordance to the content of organic nitrogen in sediment and showed a significant positive correlation both in the shelf (r= 0.77) and the slope (r= 0.85).

DISCUSSION

The cycling of material in the deeper water column is intimately linked to the biogenic carbon produced in the euphotic zone (Legendre, 1990). The material sinks as particulate matter, undergoing various physical and biochemical transformations in the water column before reaching the seafloor (Smith, 1987; 1989). The fraction exported from the euphotic zone as particulate organic matter sinking into the deep-sea exhibits temporal variability, reflecting the changes in surface water hydrodynamics (Legendre and Rassoulzadegan, 1996).

The large spatial heterogeneity in the macrofaunal community recorded on the shelf suggests a large heterogeneity. Alongi (1987) and Smith (1992) have documented similar patterns. The dynamics of recurrent disturbance on the shelf (seasonal input of biogenic carbon, tidal, longshore and riverine resuspension, trawling, etc.), followed by colonisation creates an ever-changing patchwork of successional stages (Picket and White, 1985). If disturbances are frequent, gaps in the sediment will constantly reset to an early successional stage from which it can be concluded that some processes affecting macrofaunal spatial structure in the study area operate at scales smaller than the area enclosed by the boxcore. Features such as animal burrows and polychaete tubes have an affect at a small-scale in the sediment adding patchiness to the abundace patterns (Mann and Lazier, 1991). However, despite the spatial heterogeneity in the macrofaunal community, the temporal comparisons are justified in lieu of our large sample size. Patches are therefore constantly changing as a result of a succession that is affected by the fluctuations in environmental factors.

It is concluded that the macrofaunal biomass values show seasonal and larger scale variability that may derive indirectly from the inputs and the export of biogenic carbon to the seafloor. The exported biogenic carbon contributes to the large organic matter pool in the superficial sediments in the southwestern Gulf of Mexico shelf and slope and its origin, based on stable isotopic signatures, is based on neritic and pelagic production (Soto and Escobar, 1995). Similar seasonal pelagic-benthic coupling fuels the benthic food web in other regions (Walsh, 1981; Brown *et al.,* 1991).

The strong seasonal cycle in carbon fixation and transformation, alternating between high eutrophic and fairly oligotrophic conditions, is evident between seasons and among years due to contrasting physical forcing associated with the El Niño-Southern Oscillation (Surgi, 1991). The link between interannual variability and El Niño/Southern Oscillation events has been suggested by diverse studies in the world ocean (Luther, 1991). This interannual variability is not fully understood but teleconnections between the atmospheric circulation of the tropics and mid-latitudes are implicated suggesting that variability in upwelling is part of a global fluctuation in climate (Brock and McClain, 1992). The Gulf of Mexico can be used as an analogue to the Arabian Sea for studying possible trends and changes in other parts of the world's ocean. Among the studies are predictions on upwelling enhancement by winds in a warm ocean resulting in high primary productivity that leads to suboxic coastal conditions, peculiar food webs, increased carbon storage in the sediments and increased methane production.

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