

The impact of cyclonic activity during 1981-1985 and 2004-2009 on taxonomic diversity of mollusks in the Gulf of Batabanó, Cuba

Actividad ciclónica en los periodos de 1981-1985 y 2004-2009 y su impacto sobre la diversidad taxonómica de los moluscos del Golfo de Batabanó, Cuba

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ABSTRACT

The cyclonic activity within the Gulf of Batabanó has been historically documented and, in the past two decades, it has been possible to observe signals of environmental degradation in its physical and biological state. Yet a study aimed at evaluating the effects of cyclonic activity on the taxonomic diversity of mollusks has not been made. The objective of this study was to evaluate the effects of cyclonic activity during 1981-1985 and 2004-2009 on the taxonomic diversity of soft-bottom mollusks of this region. To measure the cyclonic activity, the Power of Dissipation Index for hurricanes (PDI) was used. The average taxonomic distinctness index (Δ^+) and the variation in the taxonomic distinctness (Λ^+) of the inventory of the mollusks species for both periods were used as a measure of taxonomic diversity. We detected high cyclonic activity (HCA) during 2004-2009 and low cyclonic activity (LCA) during 1981-1985. The taxonomic composition during both periods was made up of 3 classes, 20 orders, 68 families, 155 genus, and 208 species. Significant differences in the taxonomic composition between the two periods were detected, due principally to the loss of genus and species. The taxonomic distinctness index reveals significant changes of the taxonomic structure of mollusks during 2004-2009, which is related to a rise in cyclonic activity. These results suggest that the taxonomic diversity of mollusks was less complex during 2004-2009 than during 1981-1985.

Key words: Gulf of Batabanó, hurricanes, mollusks, soft bottoms, taxonomic distinctness.

RESUMEN

La actividad ciclónica en el golfo de Batabanó ha sido históricamente documentada y en las últimas dos décadas ha permitido observar señales de deterioro ambiental en su medio físico y biológico. Sin embargo un estudio dirigido a evaluar los efectos de dicha actividad sobre las comunidades de moluscos de fondos blandos no se ha realizado. El objetivo de este trabajo fue evaluar los efectos de la actividad ciclónica registrada en los periodos de 1981-1985 y 2004-2009 sobre la diversidad taxonómica de la malacofauna de fondos blandos de esta región. Para medir la actividad ciclónica se utilizó el Índice de Disipación de Energía de los Huracanes (PDI). Los índices de distintividad taxonómica promedio (Δ^+) y la variación en la distintividad taxonómica (Λ^+) de los inventarios de especies de moluscos de ambos periodos fueron utilizados como medida de diversidad taxonómica. Se detectó una actividad ciclónica alta (AaC) para el periodo de 2004-2009 y baja (BaC) para el de 1981-1985. La composición taxonómica entre ambos periodos se conformó de tres clases, 20 órdenes, 68 familias, 155 géneros y 208 especies. Se detectaron diferencias significativas en la composición taxonómica entre ambos periodos, debido fundamentalmente a la pérdida de géneros y especies. Los índices de distintividad taxonómica revelaron cambios significativos en la estructura taxonómica de los moluscos en el periodo 2004-2009 la que se relacionó con el aumento de la actividad ciclónica. Estos resultados indican que la diversidad taxonómica de los moluscos fue menos compleja en el periodo 2004-2009 que la del periodo 1981-1985.

Palabras claves: Distintividad taxonómica, fondos blandos, huracanes, Golfo de Batabanó, moluscos.

INTRODUCTION

Hurricanes are natural phenomena that induce mortality, displacement, changes in the community structure of species (Boesch *et al.*, 1976; Dauer, 1984; Knott & Martore, 1971; Álvarez-Filip *et al.*, 2009; Rodriguez & Claro, 2009), and severe changes in the physical and chemical conditions of ecosystems (Lowery, 1992; Tilmant *et al.*, 1994; Valiela *et al.*, 1996; Hua *et al.*, 2010).

Three hurricanes hit the Gulf of Batabanó during the first decade of this century. Hurricane Charley hit the region in August 2004, while Hurricanes Gustav and Ike struck in August and September of 2008, respectively. When they blew over the region, the strength of these three events measured 3, 4, and 2, respectively, on the Saffir Simpson hurricane scale.

Historically the Gulf of Batabanó has been affected by hurricanes, and researchers have begun to see signs of environmental degradation in several areas (Guerra *et al.*, 2005; Cerdeira-Estrada *et al.*, 2008). However, to date no study has determined the effects that these events have on mollusks of this region.

The Margalef and Shannon-Wiener species diversity indices and the Pielou evenness index (Shannon & Weaver, 1949; Margalef, 1951; Pielou, 1966) have been the most utilized biological indicators for monitoring purposes and/or for detecting ecosystem changes (Magurran, 2004; Hong *et al.*, 2010). This is because a reduction of species diversity to temporal or spatial scale is one of the main signs of a loss of biodiversity and habitats (Gaston & Spicer, 2004). However, their usefulness as a good environmental indicator is greatly limited when sampling is not adequately controlled because these indices are highly dependent on effort and sample size as well as on the inherent characteristics of the habitat.

To eliminate this disadvantage, the Average Taxonomic Distinctness index (AVTD) (Warwick & Clarke, 1995) and the Variation on the Taxonomic Distinctness index (VTD) (Clarke & Warwick, 2001) were created. The AVTD is the average taxonomic distance between branches of the taxonomic tree to which all pairs of species recorded in a sample are connected. The AVTD can be interpreted as the average taxonomic width for the sample, while the VTD is the variance of taxonomic distances between each pair of species and is a reflection of how equitable the taxonomic tree of a community is. Both indices surpass traditional measures because they are independent of effort, sampling size, and habitat characteristics, and thus they can be used for comparisons between historical data of species communities with different sampling efforts and in different localities or regions (Clarke & Warwick, 1998; Leonard *et al.*, 2006).

Historically, the Gulf of Batabanó is subject to severe meteorological events and, given the evidence of environmental degradation in the area, our objective in this study was to evaluate the effects of cyclonic activity recorded during 1981-1985 and 2004-2009 on taxonomic diversity of the soft-bottom mollusks from this region, by using the AVTD and VTD indices.

MATERIAL AND METHODS

Study zone and databases. The Gulf of Batabanó (GB) is on the southwestern continental shell of Cuba (N 21° 25' y 22° 41' and W 80° 52' y 84° 00'), covering 21,305 square kilometers (km²) with an

average depth of 6 m (Cerdeira-Estrada *et al.* 2008). On the north and west coasts of the Isle of Youth and in the hundreds of cays that exists in the area, there are stretches of mangrove forests. The south portion is limited by cays, banks, and a continual reef crest interrupted by various inflow channels, which at times have good communication with the open sea (Fig. 1).

We use mollusk information available from records of several varieties of benthonic soft bottoms habitats from GB. This study covered two environmental periods with different cyclonic activity: 1981-1985 and 2004-2009. For the 1981-1985 period, information was obtained from literature (Alcolado, 1990), comprising a species list with presence/absence data obtained at 20 sampling sites distributed throughout the GB (Fig. 1). The 2004-2009 period covers five years: 2004, 2005, 2007, 2008, and 2009. This data refer to a species list and the number of individuals recorded in each year. That information was obtained in 44 sampling sites distributed throughout the gulf.

In 2008, Hurricanes Gustav and Ike hit the gulf. Mollusk samples were taken 15 days before the passage of Hurricane Gustav (August 2008) and 25 days before the arrival of Hurricane Ike (September 2008). After the passage of these two hurricanes, we took samples at 36 days (October 2008), seven months (April 2009), and one year (August 2009).

We obtained this information from the databases of Cuba's Institute of Oceanology and Fisheries Research Center. The periods analyzed cover a total of 29 years.

The scientific names of the recorded species in each period were standardized according to current taxonomic nomenclature, using nomenclature checklists (Espinosa y Ortea, 1998, 2001, 2003, 2010; Ortea & Espinosa, 2001; Mikkelsen & Bieler, 2008; Rosenberg *et al.*, 2009; Turgeon *et al.*, 2009). The taxonomic ordination was also updated (Bouchet *et al.* (2005) and Espinosa *et al.* (2005)).

Taxonomic diversity measure and cyclonic activity. We calculated the average taxonomic distinctness index and the variation in the taxonomic distinctness of the samples by using equations proposed by Warwick & Clarke (1995) and Clarke & Warwick (1998, 2001).

1. Average Taxonomic Distinctness Index (Delta⁺)

$$\Delta^+ = [\sum_{i<j} w_{ij}] / [S(S-1)/2]$$

2. Variation in the taxonomic distinctness (Lambda⁺)

$$\Delta^+ = [\sum_{i<j} (w_{ij} - \Delta^+)^2] / [S(S-1)/2],$$

where w_{ij} is the distinctness weight given to the path length linking species i and j in the hierarchical taxonomic tree and S is the number of species (Clarke & Warwick, 1998).

Cyclonic Activity. The annual cyclonic activity that affected the GB in the two study periods was estimated by the Power Dissipation Index (PDI) using the equation $PDI = \sum V^3$ (Emanuel, 2005), where V is the maximum sustained wind speed, measured every 6 hours while the hurricanes were in the area ([http:// weather.unisys.com/hurricane/atlantic/index.php](http://weather.unisys.com/hurricane/atlantic/index.php)).

Taxonomic composition. We analyzed the observed taxonomic composition of each period of study to the levels of class, order, family, genus, and species, using a variance analysis (ANOVA), by comparing the species lists to detect the existence of differences between the two periods.

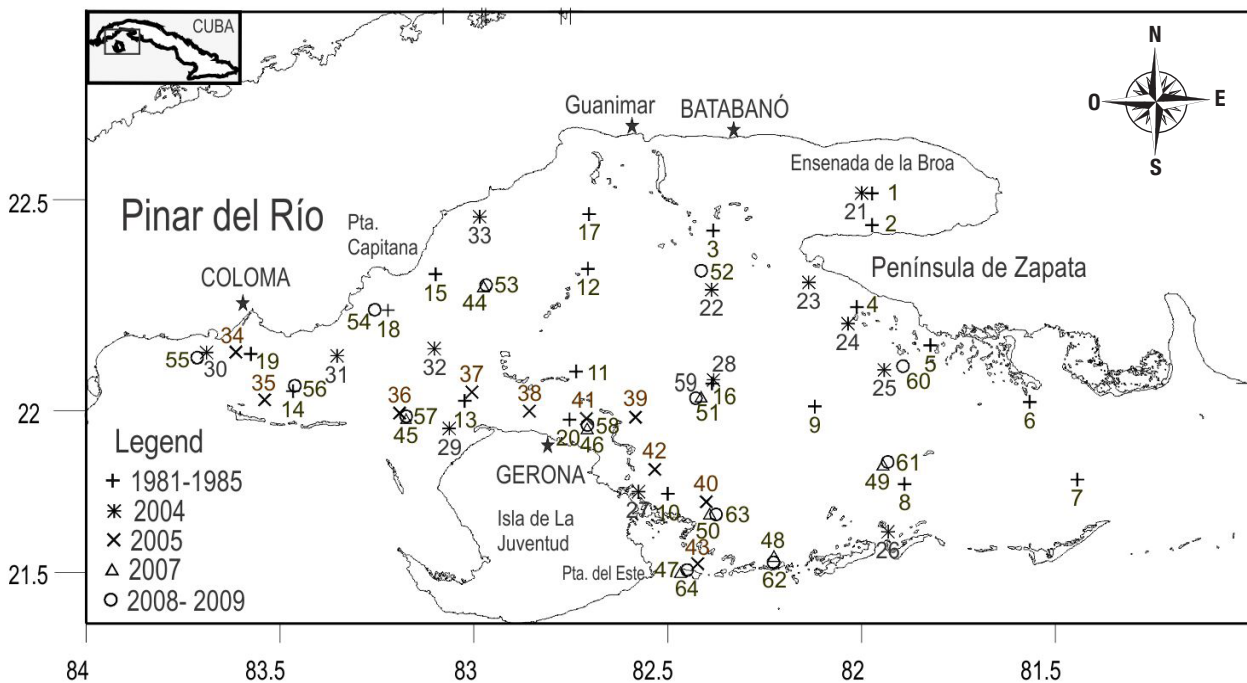


Figure 1. Sampling sites of the soft-bottom mollusks of the Gulf of Batabanó for two periods of cyclonic activity: 1981-1985 (Low cyclonic activity: LCA) and 2004-2009 (High cyclonic activity: HCA).

Delta⁺ and Lambda⁺ calculation. To simulate Delta⁺ and Lambda⁺, a hierarchical Linnaean classification of five taxonomic levels (class, order, family, genus, and species), was used as a proxy for cladograms representing the relatedness among species and a presence/absence data matrix was made.

For this study, the taxonomic weights used were those proposed by Clarke & Warwick (1998) in the context of mollusk classes: $w=1$ (species in the same genus), 2 (different genus in one family), 3 (different families in one order), and 4 (different orders in one class). The distinctness of two species linked to the higher level was fixed at a value of 100 (Clarke & Warwick, 1998; Warwick & Clarke, 2001). We obtained the values of Delta⁺ y Lambda⁺ by using the DIVERSE routine of the PRIMER-E v6 software (Clarke & Gorley, 2006).

Delta⁺ and Lambda⁺ simulation test. Using a randomized method without replacement, we derived the expected values of Delta⁺ and Lambda⁺ from the master species list. Once the number of species is plotted, the list gives a tunnel-shaped distribution in which the confidence intervals are at 95% (Clarke & Warwick, 1998). With this method, we made a bivariate representation of the values of Delta⁺ and Lambda⁺ from the expected values of both indices, whose distributions were represented in the shape of ellipses with confidence levels of 95% for a range of sub-lists of species of different sizes (Warwick & Clarke, 2001). Through these two simulated distributions, it is possible to measure the magnitude of the deviations between the observed and the expected values for both indices. We made these analyses using the TAXTES routine of PRIMER-E (Clarke & Gorley, 2006).

Impact of cyclonic activity on taxonomic diversity. This analysis was performed in two ways: 1- graphically comparing the standardized anomalies of taxonomic indices (Delta⁺ and Lambda⁺) with cyclonic

activity (PDI) in each year and/or period; and 2- comparing the observed variation in the values of taxonomic indexes before and after the passage of hurricanes in the gulf. The latter was performed using a comparative table.

Community structure. The temporal variation of the mollusk community structure at GB was analyzed using a multivariate ordination test (MDS), and the Sorensen index to compute the similarity matrix. The ANOSIM test checked for the existence of significant differences between groups formed by the ordination. The two analyses were run using the PRIMER-E software (Clarke & Gorley, 2006).

RESULTS

Cyclonic activity. Cyclonic activity during 1981-1985 was lower (LCA) than during 2004-2009 (HCA). In the latter period, 2004 and 2008 experienced the most cyclonic activity, given that hurricane Charley in 2004 and hurricanes Gustav and Ike in 2008 directly hit the GB. There was no cyclonic activity in 2005, 2007, and 2009 (Fig. 2).

Taxonomic Composition. The taxonomic composition of the soft-bottom mollusks of the GB was 208 species in 155 genus, 68 families, 20 orders, and 3 classes.

The most remarkable differences found in these categories were at the families, genus, and species levels, being most significant ($F=24.36$, $p=0.041$) for the LCA period with respect to the HCA (Fig. 3).

Temporal and spatial variation of the taxonomic distinctness indices. The expected results from delta⁺ and lambda⁺ indices for the 29 years of this study were 87.20 and 240 respectively. In Table 1 the observed values of the delta⁺ and lambda⁺ indices are shown for each period.

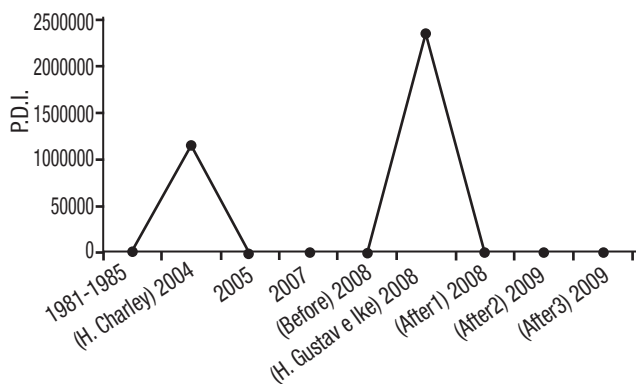


Figure 2. Annual variation of the Power Dissipation Index (PDI) of the hurricanes that affected the Golfo de Batabanó in the 1985-1981 and 2004-2009 periods.

The lowest value of Δ^+ (81.60) and the higher value of λ^+ (346.20) corresponded to 2008 of the HCA period, while for the remaining years of this period the Δ^+ values varied between 86.21–86.88 and the λ^+ values between the 255.95 - 279.93. The average values for Δ^+ and λ^+ for this period were 85.46 and 285.67 respectively (Table 1).

Figure 4 represents the probabilistic funnels for the simulated values of Δ^+ and λ^+ with its probabilistic contours at 95%. In this figure, we observe an evident separation of the LCA with respect to the HCA. In this last period, the values of Δ^+ (81.60) and λ^+ (346.20) for 2008 and λ^+ (290.54) for 2009 were located out of the probabilistic contour of their respective funnels (Fig. 4a and b respectively). The values of both indices for the remaining years (2004, 2005, and 2007) of the HCA and LCA periods fell inside the probabilistic contours. For 2009, Δ^+ fell within the contours of the probabilistic funnel.

The spatial analysis of taxonomic diversity patterns of mollusks assemblages at GB showed that all sampling sites during the LCA period (1981-1985) were located within the limits of probabilistic funnels for both indices (Fig. 4c and d). However, 37% of the sampling sites in the HCA period (2004-2009) were outliers, either below or above the limits of probabilistic funnels for both indices (Fig.4c and d). Most sampling sites that fell outside the contours of probabilistic funnels of Δ^+ and λ^+ belonged to 2004, 2008, and 2009.

The lowest values of Δ^+ were recorded at sites 24, 27, and 33 (2004) and 54, and 55 for 2008. Hurricanes were reported in both years. Regarding λ^+ sites, 33 and 24 had the lowest values, while site 54 had the highest value (Fig. 5a and b).

For 2005, sampling site 34 fell outside the lower limit of the probability funnel for Δ^+ (Fig. 5a). For 2007, site 48 was located outside and above the limit of the probability funnel for λ^+ (Fig. 5b).

Relation of Δ^+ y λ^+ indices with cyclonic activity. Δ^+ showed positive anomalies associated with negative anomalies for λ^+ in 1981-1985 and in 2004, 2005, and 2007 (Fig. 6). Except for 2004, during 1981-1985 and the remaining years (2005 and 2007), there was no cyclonic activity. In 2008, however, this pattern was reversed. Δ^+ and λ^+ showed positive anomalies before the impact of Hurricanes Gustav and Ike (2008B), and once they affected the region

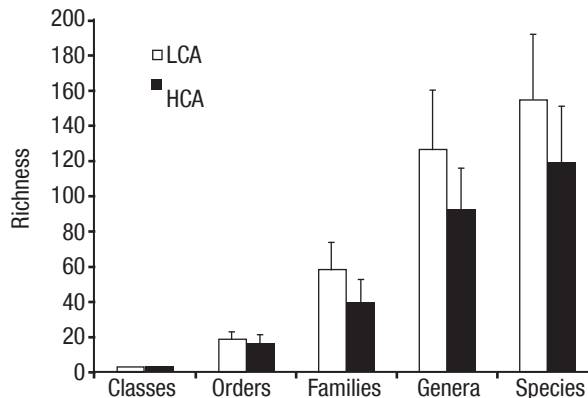


Figure 3. Number of classes, orders, families, genera, and species of the soft bottoms mollusks of the Gulf of Batabanó, for each period under study.

Table 1. Δ^+ and λ^+ index values of the soft bottom mollusks of the Gulf of Batabanó in the periods of low cyclonic activity (LCA) and high cyclonic activity (HCA).

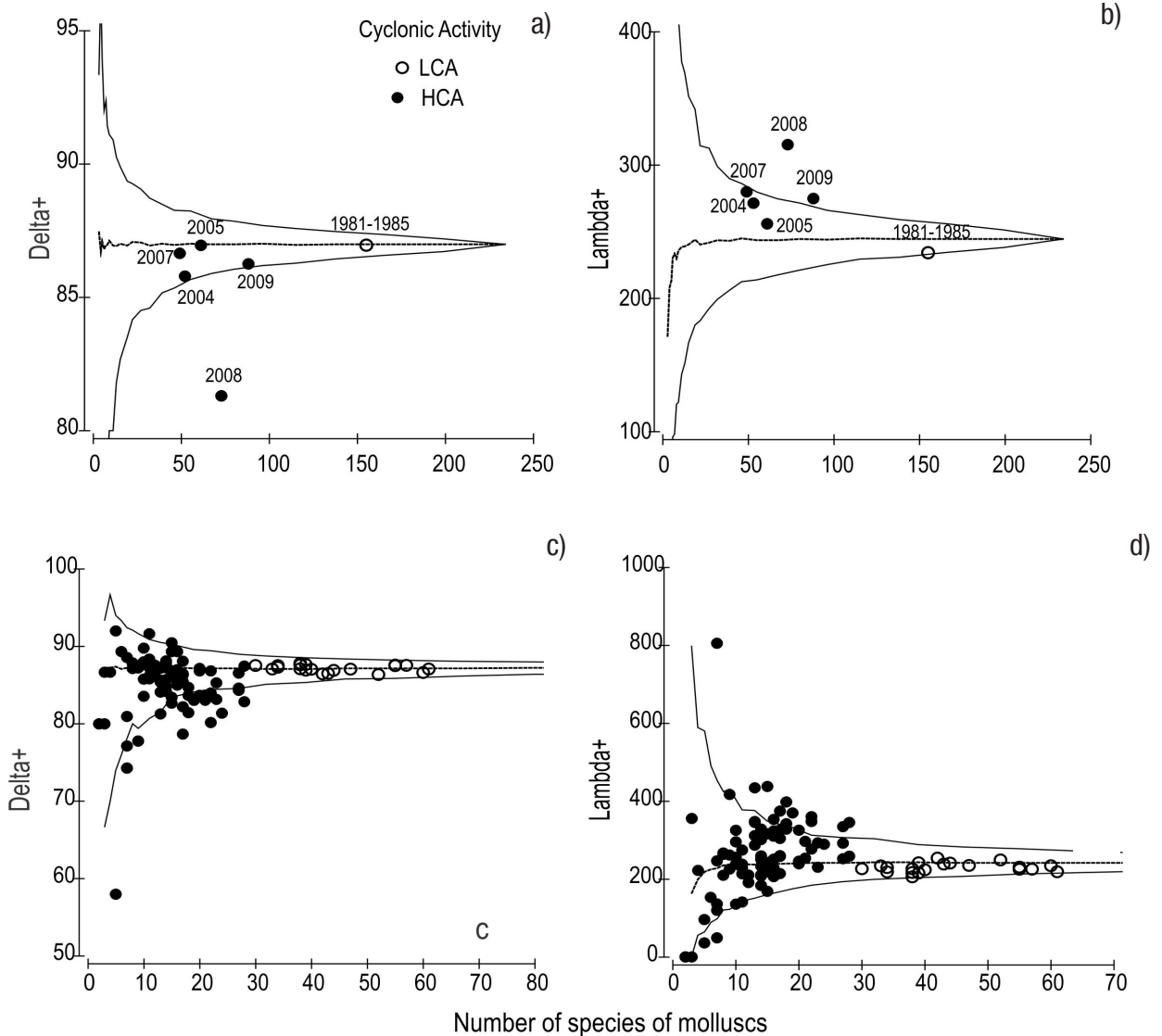
Cyclonic activity	Period/Years	Δ^+	λ^+
LCA	1981-1985	86.96	234.24
HCA	2004	86.21	271.42
	2005	86.88	255.95
	2007	86.40	279.93
	2008	81.60	346.20
	2009	86.25	274.89
	Mn	85.4ea6	285.67

(33 days of hurricane passage (2008A1), Δ^+ posted the lowest negative anomaly (- 2.4) and λ^+ the highest positive anomaly (+ 1.91) for the entire period (Fig. 6).

In 2009, a change was observed in the response pattern of these indices to cyclonic activity. Positive anomalies occurred in Δ^+ and λ^+ seven months after the hurricanes had passed, reestablishing the original pattern (positive anomalies of Δ^+ and negative anomalies λ^+), a year after the hurricanes passed. (Fig. 6).

A Pearson correlation analysis of the PDI, Δ^+ , and λ^+ indices reveals a very high correlation between the two indices and cyclonic activity (Δ^+ : $r = -0.72$, $p = 0.042$ y λ^+ : $r = 0.83$, $p = 0.031$). This correlation showed that the lowest Δ^+ and highest λ^+ values were due to high cyclonic activity. (Fig. 6)

Δ^+ and λ^+ showed significant changes in their values between, before, and after the passage of hurricanes (Table 2). The value of Δ^+ decreased in October 2008 (36 days after the passage of hurricanes), increased in April 2009 (seven months after the passage of hurricanes), and August 2009 (one year after the hurricanes). λ^+ increased its value in October 2008, decreasing in April and August 2009 (Table 2).



Figures 4a-d. Relation between values of the average taxonomic distinctness index (Δ^+) and variations of taxonomic distinctness (Λ^+) in mollusk species richness in the Gulf of Batabanó, calculated for the LCA and HCA periods. The mean (thick line) and the contour of confidence of 95% (thin line) were obtained by a randomized process (999 iterations) of the subsamples of the number of species of a master list throughout the period. a and b: temporal analysis and c and d: spatial analysis.

Mollusk community structure. The MDS test of temporal and spatial scale shows two clearly separated groups with significant differences ($\text{ANOSIM}_{\text{temporal}} R=1, p=0.01$ and $\text{ANOSIM}_{\text{spatial}} R=0.424, p=0.01$), which corresponded to each of the periods analyzed (Fig. 7a y b). In the group that belongs to the HCA, we observed a certain dispersion of the sampled years, with 2005 being the most isolated and 2008 and 2009 the

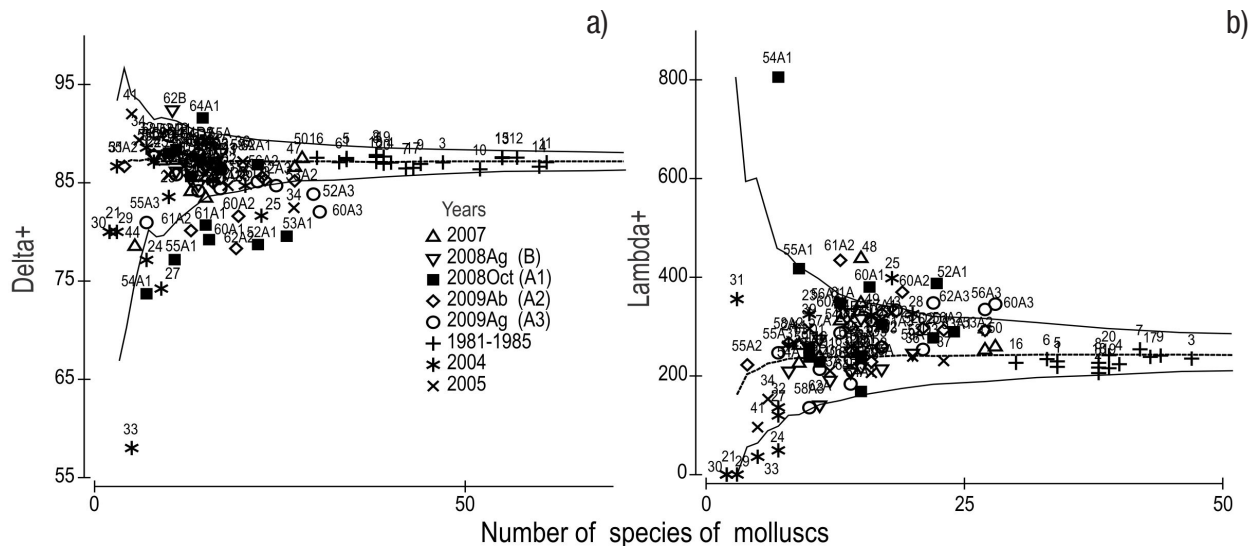
closest (Fig. 7a). This situation was similar to the spatial scale where sites sampled during the HCA period were observed with some dispersion with respect to the LAC (Fig. 7b).

The MDS test before and after the passage of hurricanes in 2008 showed a clear separation between sites sampled before (B) and 36

Table 2. Average values of Δ^+ and Λ^+ mollusks in the Gulf of Batabanó measured before and after the passage of Hurricanes Gustav and Ike in 2008.

Indices	2008B	2008A1	2009A2	2009A3	K-W	p
Δ^+	86.7±0.9	68.5±4.8	83.9±3.2	84.6±2.2	8.64	0.040
Λ^+	299.6±23.2	368.2±16.41	319.7±93.9	285.7±64.2	9.83	0.031

Note: 2008B: August 2008 (before p/h), 2008A1: October 2008 (36 days after p/h), 2009A2: April 2009 (seven months after p/h), 2009A3: August 2009 (one year after p/h), p/h: passage of hurricanes, K-W: Non parametric ANOVA Kruskal Wallis.



Figures 5a-b. Relation of the values of the average taxonomic distinctness index (a) and the variation of the taxonomic distinctness (b) with mollusk species richness in the Gulf of Batabanó before (B) and After (A1: 36 days, A2 (seven months) and A3 (one year) after of passage of hurricanes Gustav and Ike in 2008. The mean (thick line) and the contour of confidence of 95% (thin line) were obtained by a randomized process (999 iterations) of the subsamples of the number of species of a master list throughout the period.

days after the passage of hurricanes (A1). Seven months (A2) and one year (A3) after hurricanes had passed, a good separation of sampling sites was not observed (Fig 7c). Applying the ANOSIM test before and after the passage of hurricanes showed significant differences in mollusk community structure (Table 3).

DISCUSSION

The decrease in variety of orders, families, genus, and species in the HCA period (Fig. 3) is a result of the increase in cyclonic activity in the GB, characterized by the increase in the frequency and intensity of the hurricanes (Fig. 2). Puga *et al.* (2013) and Alzugaray (2015) have also documented this trend in the entire Caribbean region over the past 30 years (IPCC, 2007).

Cyclonic activity (PDI) is controlled by inter-annual variability, decadal, and multi-decadal processes (for example, ENSO events (Chu,

2004), and multi-decadal Atlantic Oscillation (AMO) (Vimont & Kossin, 2007)). The fact that cyclonic activity was observed in 2004 and 2008, but not in 2005, 2007, and 2009, can be justified by the dynamics of these processes.

Significant changes in mollusk taxonomic structure were detected through the delta+ and lambda+ indices and through probabilistic funnels before and after the passage of hurricanes (Fig. 5).

The probabilistic funnels of the two indices indicated a clear separation between the mollusk taxonomic patterns in both periods. These patterns were significant due to the observed variations in the HCA period. This period was affected by three hurricanes with different frequencies and intensities, causing the variations in the values of delta+ and lambda+ (Table 2) and in mollusk taxonomic patterns (Fig. 2). Mollusk taxonomic patterns in 2004, 2005, 2007, and 2009A3, were similar to those of the LCA period. In 2005, 2007, and 2009A3, this was

Table 3. ANOSIM test results between before and after the passage of Hurricanes Gustav and Ike in the Gulf of Batabanó. Analyses were based on the similarity coefficient of Bray -Curtis. (R (global) = 0.195, p = 0.1 %).

Groups	Statistic R	Significance Level (%)	Permutations		No. >= Observed
			Possible	Actual	
Before, After1	0.397	0.1	5200300	999	0
Before, After2	0.227	0.1	5200300	999	0
Before, After3	0.228	0.1	5200300	999	0
After1, After2	0.254	0.1	5200312	999	0
After1, After3	0.103	1.8	5600200	999	17
After2, After3	-0.001	44.3	5400210	999	442

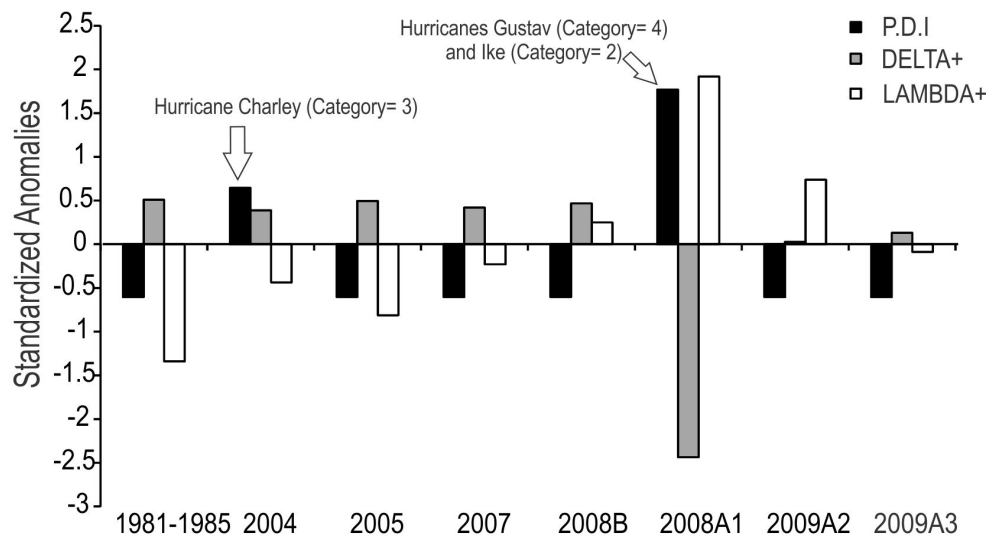


Figure 6. Standardized anomalies Delta⁺ and Lambda⁺ mollusks in the Gulf of Batabanó with cyclonic activity (PDI). Before (B) and after (A1: 36 days, A2: seven months and A3: one year) of passage of hurricanes Gustav and Ike.

due to the absence of cyclonic activity. In 2004, when Hurricane Charley struck, this result was due to the delay in sampling after the hurricane passed, some three months after the event. It is possible that by the time samples were taken, mollusk assemblages had recovered from the effects of the hurricane.

Taxonomic patterns for 2009A2 and 2008B (Table 2, Fig. 2) were due to environmental conditions that prevailed before and seven months after Hurricanes Gustav and Ike. These conditions might include the differences and/or similarities in temperature (2008B : 31.7°C vs 2009A2 : 27.4°C), salinity (2008B : 38.73‰ vs 2009A2 : 38.23‰), and turbidity (2008B : 1.23 FTU vs 2009A2 : 2.41 FTU) recorded before and seven months after the hurricanes (Capetillo *et al.*, 2011). These variables of turbidity had significant changes before and after the hurricanes, as well as the spatial scale, whose recovery occurred about one year after the hurricanes in some zones of GB (Capetillo *et al.*, 2011). This situation may have affected seagrass beds in the region.

In 2008A1, the taxonomic pattern was very different from those observed previously (Table 2, Fig. 2). This was due to two causes: 1- the sum of the effects caused by Hurricanes Gustav and Ike, spaced just 11 days apart; and 2- the samples taken just 36 days after their passage in GB. This gives tests to detect the effects caused by hurricanes influences, besides the intensity and frequency of these, time in sampling after the passage of these natural events.

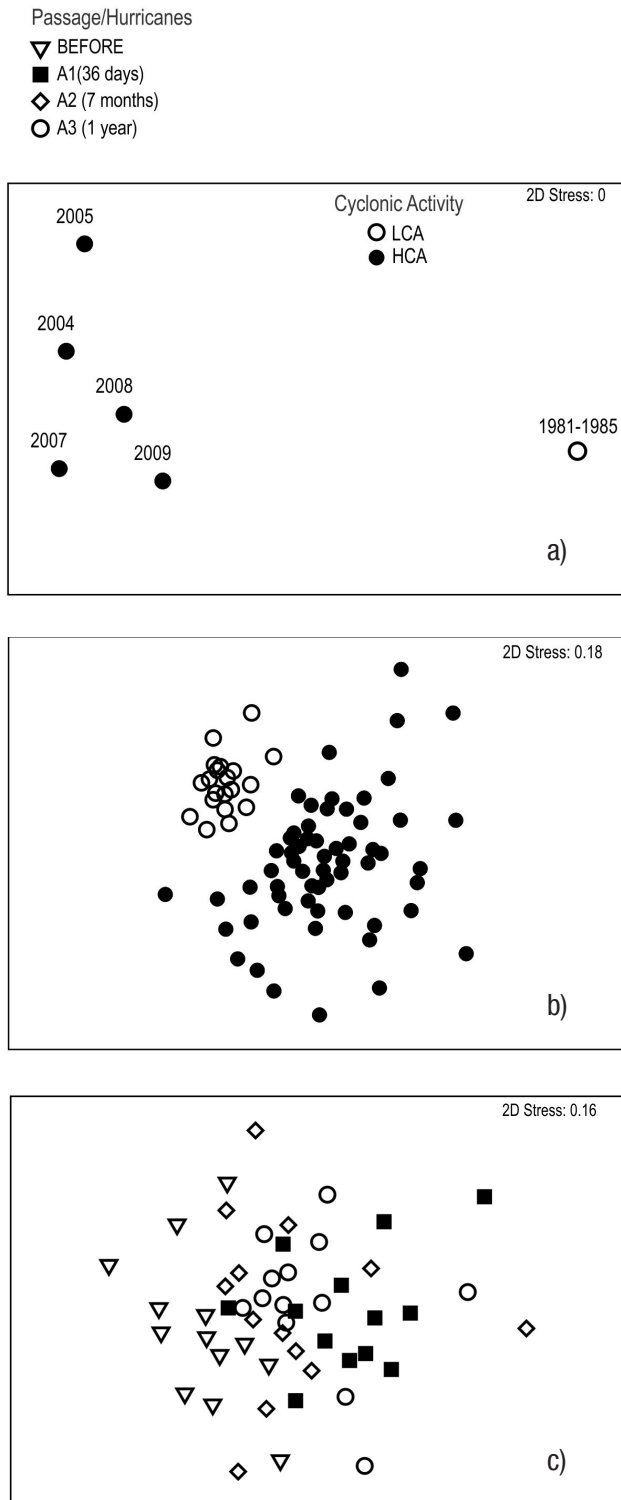
During the LCA period, the values from delta⁺ and lambda⁺ fell inside the contours of probabilistic funnels (Fig. 4a and b) showing that the mollusk taxonomic pattern in this period did not change over the 29 years covered by both periods. The closeness of the delta⁺ value (86.96) and lambda⁺ value (234.2) to their expected values, i.e., (87.20) and (240), respectively, demonstrates the high stability of the mollusk communities' taxonomic pattern during this period. This was due to the low cyclonic activity that prevailed in this period (Fig. 2), although we could not dismiss the incidence of other environmental variables. An-

thropogenic activity in the region in those years was low. In this regard, several authors have suggested that the 1980s were characterized by low cyclonic activity, and anthropogenic effects did not cause any significant changes in ecosystem quality in the GB, due to low human activity in this period (Puga *et al.*, 2013).

The lowest significant value of delta⁺ (81.60; $p < 0.05$) and the highest significant value of lambda⁺ (346.20; $p < 0.05$) in 2008 indicate that the mollusk taxonomic tree (taxonomic structure) was the most separated (least complex) and least balanced (less equitable) of all trees compared in the remaining years (2005, 2007, 2009) of the HCA and the LCA. This situation was due to the loss of some taxonomic categories and to the existence of a very irregular distribution of species on the taxonomic tree that occurred after the hurricanes struck. A detailed analysis of mollusk taxonomic composition during both periods indicated that the Class Gasteropoda was the most affected during HCA, due to the loss of 20 genera (LCA 62 vs HCA 42) and 28 species (LCA:81 vs HCA:53) compared to the LCA period. However, since this period was characterized by an increase in human activity (Puga *et al.*, 2013), which was confined in areas located in or near the coast of the northern of GB (Pérgo *et al.*, 2005; Alonso-Hernández *et al.*, 2011), changes observed in gastropods cannot be attributed solely to hurricanes.

The effects caused by these natural events and by human activity (or the combination of these) can be identified by using these indices (Fig. 5a).

Except for site 27, the lower values of delta⁺ were located in the northern gulf coast (sites 24, 33, 54, 55), (Fig. 5a). In this region and neighboring areas, contamination by organic matter (sites 33 and 55) and heavy metals (site 54) have been recorded (Pérgo *et al.*, 2005; Alonso-Hernández *et al.*, 2011). At these sites researchers have observed muddy or sandy mud bottoms with little coverage or absence of seagrass (Arias-Schreiber *et al.*, 2008; Cerdeira-Estrada *et al.*, 2008). This situation could have intensified with the passage of hurricanes,



Figures 7a-c. Non metric Multi Dimensional scaling (MDS) of periods of LCA and HCA for the analysis of the community structure of molluscs soft bottom of the Golfo de Batanó. a) Temporal scale. b) Spatial scale. c) Before and after the passage of hurricanes Gustav and Ike in the year 2008. A1, A2 an A3, refer to the samples taken after the passage of the hurricanes.

given the increased land-to-gulf transport of sediment and pollutants. This demonstrates that the low values recorded in those sites could be due to the combined effect of hurricanes with anthropic activity.

The changes in the mollusk taxonomic structure in sites 24 and 33 were similar to the results reported by Arias-Schreiber *et al.* (2008) and Hidalgo & Areces (2009). They found significant differences in community structure, biomass, and densities in the macrozoobenthos when compared to the results obtained by Alcolado (1990) and Ibarzábal (1990).

Sites 52, 53, 60, 61, and 64, had higher Δ^+ values and were located in remote areas of the north gulf coast. At these sites, however, mollusk taxonomic structure was affected because the trajectories of Gustav and Ike passed directly or close to them (Fig 8b). This showed that only hurricanes had an impact.

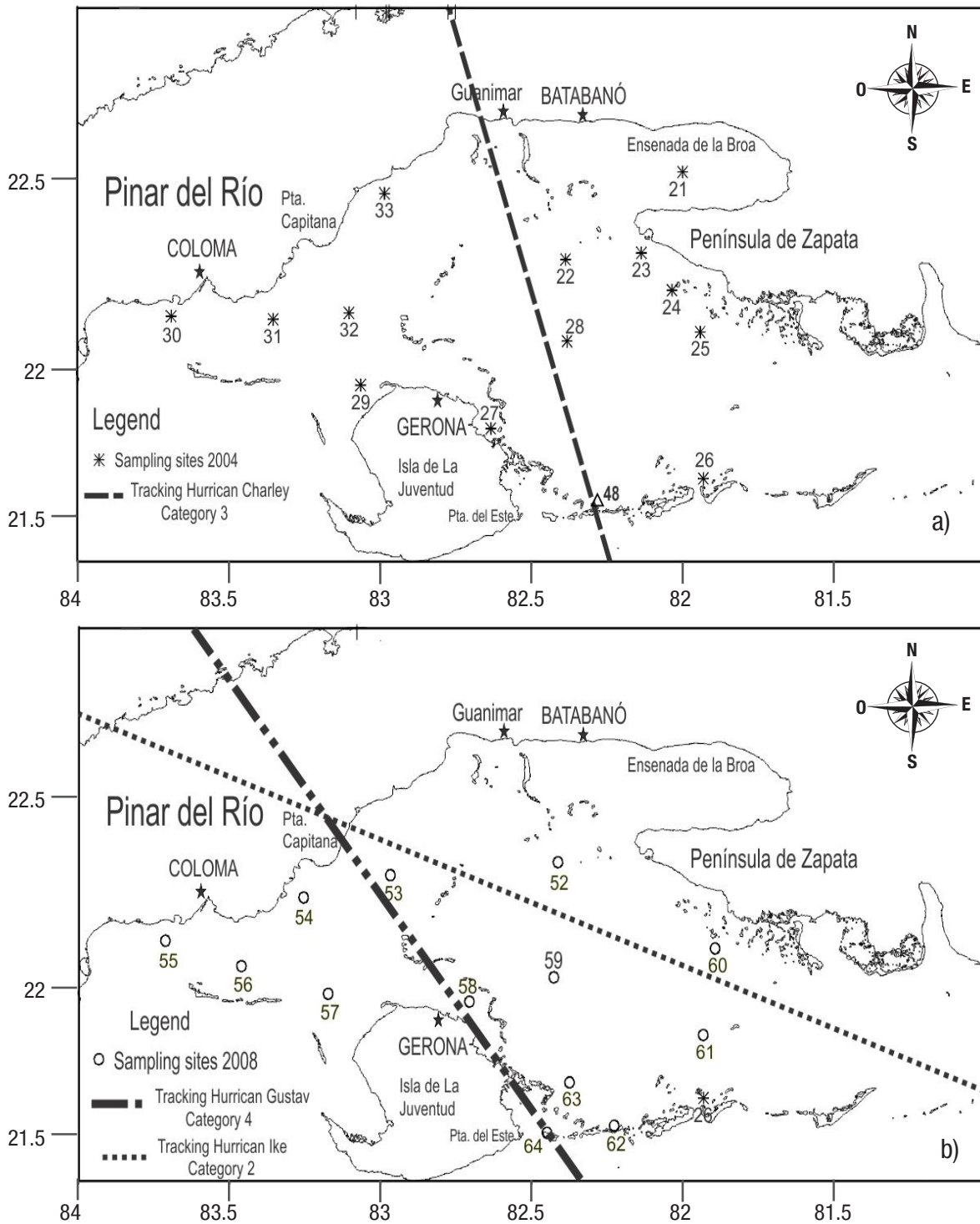
The low value of Δ^+ at site 34 (in 2005), the high value of λ^+ at site 48 (2007), and high value of Δ^+ at site 61B (2008B) can be explained by environmental conditions prevailing in those years. Further, high temperatures (27.7°C – 31.7°C) and salinities (38.2‰ – 38.7‰) were recorded in those years (Capetillo *et al.*, 2011). Hoskins (1964), Martinez - Estalella & Alcolado (1990), and Espinosa (1992) stated that salinity, presence of vegetation, among other factors, can control mollusk distribution.

Several authors, in addition to testing the usefulness of Δ^+ and λ^+ to measure human impact, proved that Δ^+ was an effective index to detect the impacts of natural disturbances, by recording changes in salinity at estuaries and coastal lagoons, and showed that λ^+ is a better indicator of eutrophication (Warwick & Clarke, 1995; Clarke & Warwick, 2001; Mouillot *et al.* (2005). This suggests that these indices are capable of detecting the effects induced by natural events, a point demonstrated with this study.

The high negative correlation of Δ^+ ($r = -0.72$) and positive correlation of λ^+ ($r = 0.83$), both of which are significant, with the PDI (Fig. 6a and b), as well as their sensitivity in detecting the effects of hurricanes (Table 2), demonstrate that both can detect the effects caused by hurricanes due to the clear trend in the temporal and spatial variation of the width (Δ^+) and balance (λ^+) of the soft-bottom mollusk taxonomic tree in the region. The taxonomic structure becomes narrower and less balanced in the 2004 and 2008, being both properties (width and balance) of the taxonomic tree that were significant in 2008 but not in 2004 (Fig. 4a and b). During 2009, the value of λ^+ was higher and more significant than 2004 (Fig. 4b), which showed low evenness in the distribution of species in the taxonomic tree.

However, the fact that no hurricane hit this region that year seems to indicate that the situation found in 2009 could be due to the effect caused by the hurricanes in 2008.

The MDS tests regarding the temporal and spatial scale of the mollusk community structure demonstrated the existence of two different structures in each of the scales analyzed. One of the structures was made up of the mollusks communities in the LCA period and the other in the HCA (Fig. 7a and b). The separation observed between the sampled years in the HCA period could be due to the different inter-annual environmental conditions, characterized by the hurricanes of 2004 and



Figures 8a-b. Map of the path of hurricanes Charley (a), Gustav and Ike (b) in the Gulf of Batabanó.

2008. This was not the case in 2005, 2007, and 2009. The spatial scale differences, however, may be due to: 1. the spatial difference in the effects of human activity in the gulf; and, 2- the severity of the hurricanes at each particular site, according to its trajectory.

The existence of significantly different mollusk community structures before and after the passage of hurricanes Gustav and Ike in 2008 (Fig. 7c) confirmed previous observations, as do the results obtained by Δ^+ and λ^+ .

A question we find interesting is why differences exist in the community structure and taxonomic patterns in the years when the effects of hurricanes were felt, when supposedly their effects on mollusk communities should have been the same. However, this result suggests the existence of a temporal variation in the community structure of these organisms, confirming the taxonomic patterns detected by the Δ and λ indices described in this study.

Hurricanes cause changes in reef biota, mangroves, sea grasses, and the sedimentary dynamics, while the frequency of occurrence, intensity, and duration of these events on a particular zone will determine if the affected ecosystems can recover (Salazar-Vallejo, 2002). From this statement, we can hypothesize that one of the elements that affect the difference of the effects in mollusk community and taxonomic structure during 2004 and 2008 was the frequency and intensity of the hurricanes during the HCA period. In order to confirm this statement, future studies should be made after hurricanes strike the GB with different intensities and duration.

In synthesis, the effect caused by cyclonic activity on the taxonomic diversity of the soft-bottom mollusks of GB was to reduce complexity and evenness of the taxonomic structure of these organisms. Given this condition, mollusks species were more closely related in the period of HCA, compared to the LCA. The loss of complexity in the taxonomic structure was due to: 1. the reduction of higher taxonomic categories; and 2. low evenness of species in these taxonomic categories.

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