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## Diel variation of the epibenthic community associated with seagrasses in a subtropical biosphere reserve

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### ABSTRACT

We evaluated the diel variability of abundance and species diversity of the epibenthic community associated with seagrasses in Los Petenes Biosphere Reserve (LPBR) in the southwestern Gulf of Mexico. For this purpose, four collection campaigns were conducted (rainy season: October 2011 and June 2016, dry season: March 2012 and 2016) in a diel cycle with a periodicity of 3 h. Our results showed significant differences in diversity, richness, and abundance as a function of the diel cycle ( $p < 0.05$ ), and in the community structure as a function of the diel cycle and the climatic sampling periods. Two different benthic assemblages, one for the day and the other for the night period were identified. Each assemblage varies on its species composition according to the climatic periods but maintains the general day-night pattern at all the sampled years. The abundance of diurnal species was significantly ( $p < 0.01$ ) associated with the temperature, salinity, oxygen, and depth values. Our results suggest that the epibenthic community associated with seagrass habitats shows significant diurnal and nocturnal changes in community composition and abundance due to changes in light intensity that favors the appearance of characteristic species in each period. Understanding such community changes will allow us to establish the baseline parameters for assessing the environmental health of the benthic habitats of the LPBR with greater accuracy.

### 1. Introduction

The description of macrobenthic community structure includes the comprehension of its complex organization at different spatiotemporal scales where different processes and phenomena occur that determine the observed patterns (Pech et al., 2007a). At the diel scale, variations in temperature, oxygen, solar radiation, precipitation, and tides are known to be the key environmental factors in shaping community structure, as well as species behavior, food webs, and predation dynamics (Rocha-Ramírez et al., 2016; Mendoza et al., 2018; Haro et al., 2019). These variations are poorly understood and incorporated into the descriptions of community dynamics (Ribeiro et al., 2006; Kwik et al., 2010; Park et al., 2020). In coral reefs, it has been shown that the major changes in species richness and abundance occur at diel scales with higher values during the night (Sogard and Able, 1994; Mattila et al., 1999; Unsworth et al., 2007). In the coastal habitats of the Gulf of Mexico (GoM) diverse evidence show that the structure and composition

of ichthyofauna (Löök et al., 2008; Ayala et al., 2014; Toro-Ramírez et al., 2017) and abundance of decapods (Briones-Fourzán et al., 2020) show diel changes associated to the short scale environmental variability occurring at the study sites.

At larger time scales (e.g., decadal variations, El Niño, La Niña), the spatial and temporal variations in temperature, salinity, hydrodynamics, organic matter, sediment characteristics, and primary productivity can modify the distribution, abundance, and structure of benthic macrofaunal assemblages (Paz-Ríos et al., 2020; Hall et al., 2021). For example, evidence from subtropical seagrass meadows shows changes in the abundance and richness of benthic invertebrates related to the weather seasonal variations in the study area (Park et al., 2020). In the coastal habitats of the southeastern GoM, it has been observed that the variability of the benthic community structure is associated with variations in the seasonal environmental conditions of dry, rainy, and frontal winter storms (Nortes) (Hernández-Guevara et al., 2008) during an annual cycle.

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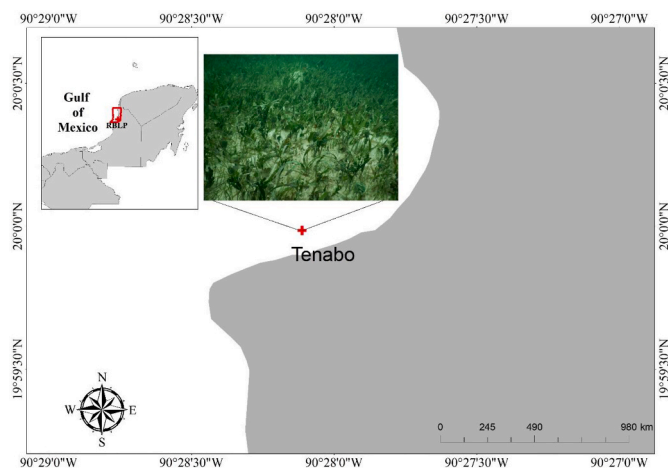
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**Fig. 1.** Geographic location of the sampling site. The red polygon represents Los Petenes Biosphere Reserve area. The red cross shows the sampling point within the coastal zone showing the seagrass coverage. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

This paper examines the diel variability of the epibenthic community structure associated with seagrasses in a subtropical karst environment located in Los Petenes Biosphere Reserve (LPBR) in the southeastern GoM. The main purpose was to evaluate the diel (day/night) changes in species composition and abundance of the epibenthic community associated with seagrasses under the hypothesis that benthic community characteristics will vary throughout the diel cycle in response to the small scale changes in the water and sediment values. Previous studies have shown that small scale changes in sediment and water salinity suffice to trigger significant changes in benthic community attributes at seasonal scales (Pech et al., 2007b) without modifying the general community patterns observed at years scale (Hernández-Avila et al., 2020). So diel variability of the benthic community attributes is expected to occur independently of sampling month and year.

## 2. Materials and methods

Samples of the epibenthic community associated with seagrasses were collected at four different times: October 2011, March 2012, and March and June 2016, at a reference site located in the coastal zone of LPBR (90°28'916" W and 20°00'588" N) in the southeastern GoM (Fig. 1). In the study area, three climatic seasons are distinguished whose temporal limits are not always clearly defined: 1) dry (March to May) characterized by mean precipitation of 164.8 mm/month and weak southeast winds 2) rainy (June to October) characterized by mean precipitation of 976.6 mm/month, and frequent and strong southeast winds; and 3) winter frontal storms regionally known as Nortes (November to February) characterized by mean precipitation of 345.6 mm/month and frequent strong north winds (Álvarez-Góngora and Herrera-Silveira, 2006; Pech et al., 2007b; Ayala et al., 2014). Near the sampling site (300 m from the coastline) the water column was between 1.20 and 2.40 m depth. The study site, like all the Yucatan Peninsula, is also characterized by a gentle slope, barely noted in the sampling site, and a short tidal range which can vary from 20 to 30 cm through the year. The sunset, sunrise, and day length time also have a short range of variability between 30 and 45 min in a year cycle. Submarine groundwater discharges are common in the study site due to the highly permeable and porous carbonate karst geology of the region (Aranda-Cirerol et al., 2006).

The samples collected in March corresponded to the dry season and those taken in June and October to the rainy season. The submerged aquatic vegetation is characterized by three species of seagrasses

(*Thalassia testudinum*, *Halodule Wrightii*, and *Siringodium filiforme*) and rhizophytic macroalgae (*Caulerpa* sp., *Halimeda* sp., *Peniculus* sp., and *Udotea* sp.) that colonize a karst substrate, with groundwater discharges through coastal springs.

The epibenthic macrofauna was collected every 3 h during a diel cycle (24 h), during a post-larval shrimp sampling campaign. The samples were obtained using a 1.8 m long by 0.7 m wide Renfro bar net with a 0.8 mm mesh size (Gracia et al., 1994). The trawls were carried out in triplicate over a 25 m long transect, oriented perpendicular to the coastline and against the wave direction and covering an area of approximately 112 m<sup>2</sup>. The collected samples were prefixed with a 10% magnesium chloride solution for 10 min and then fixed with 5% formaldehyde. Once in the laboratory, the samples were sieved through different mesh size sieves (i.e. 850, 700, 500, 150 μm) to obtain the different shrimp larval stages. The epibenthic macrofaunal organisms retained on the 500 μm mesh sieve were determined to the lowest possible taxonomic level, and their abundance was registered and used in the present study. Temperature, salinity, and dissolved oxygen were recorded at each trawl time using a YSI-6000 multiparameter probe. The depth was obtained using a graduated wooden marker (cm). The depth data was then used as a proxy for the tidal changes.

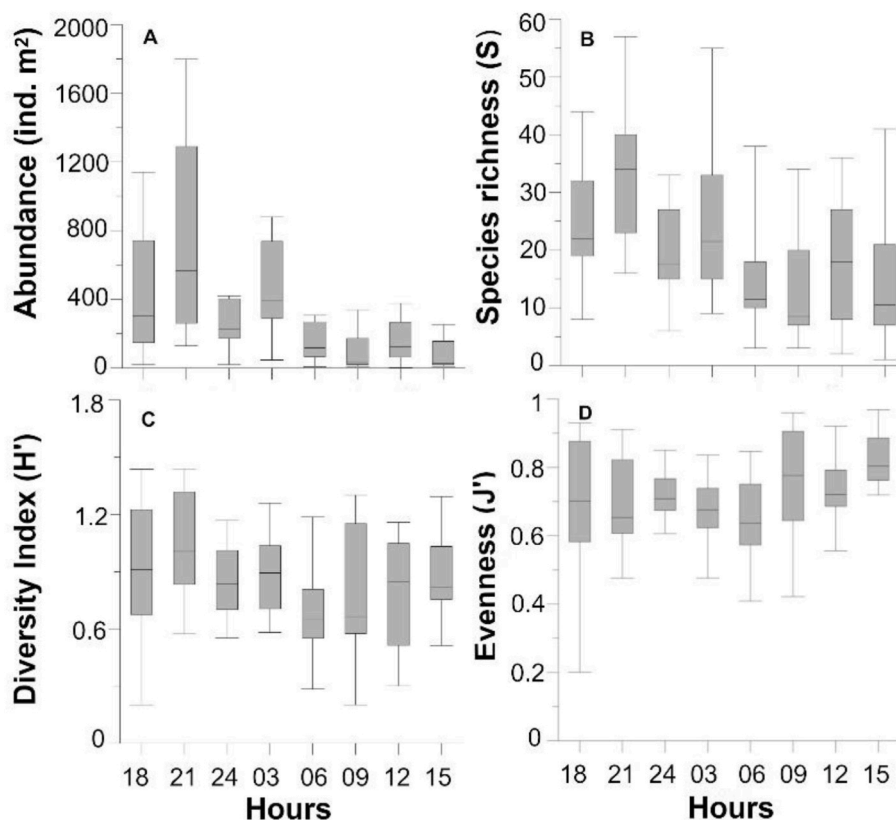
## 3. Data analysis

Abundance (No. Ind/m<sup>2</sup>), species richness (Number of species), species diversity ( $H'$ ), evenness ( $J'$ ), and species dominance were the characteristics used to evaluate the diel variability of the epibenthic community. The dominance index was estimated as the percentage of individuals of one species in the total collected (%RA) and the frequency index as the proportion of the samples in which each species is present (%F) (Rueda et al., 2008).

A permuted multivariate analysis of variance (PERMANOVA) was used to detect significant differences in community characteristics (abundance, richness,  $H'$ ,  $J'$ ) and species composition as a function of the year, climatic season, and diel cycle. A three-factor nested hierarchical design was used for the analysis: I) years using three levels (2011, 2012, and 2016), II) climatic season using two levels (dry and rainy), and diel cycle with two levels: night (18:00, 21:00, 24:00, 3:00) and day (6:00, 9:00, 12:00, 15:00) as orthogonal fixed factors. The PERMANOVA univariate mode, using a matrix of Euclidean distances was used to detect differences in community characteristics. The standard mode of PERMANOVA was used to detect differences in species composition using a Bray-Curtis index similarity matrix adjusted to zero generated from the root-transformed species relative abundance and composition matrix. The significance of both models was tested using 9999 permutations of residuals and a sum of squares type I.

To determine the group of species that contribute most to the diel variation of the community assemblages, a similarity percentage analysis (SIMPER) was carried out using a matrix with species that contributed with 75% of the cumulative abundance of the community. To obtain a graphical representation of the diel distribution of the epibenthic community as a function of the hours, season, and year sampling periods, a principal coordinate analysis (PCA) based on the Bray Curtis index similarity matrix was performed using the Primer v.6.0 software.

Finally, a canonical redundancy analysis (RDA) was used to determine the potential association between epibenthic community assemblages with environmental variability. Epifauna abundance and environmental matrices were standardized by using a fourth root. A stepwise analysis was also performed to select the significant variables for the model. The potential association of the matrices was analyzed using a Monte-Carlo analysis with 9999 unrestricted permutations under a reduced model. The analysis was performed in CANOCO V4.5 software (ter Braak and Smilauer, 2002).



**Fig. 2.** Diel variation of benthic epifauna during a diel cycle (24 h) of abundance (A), species richness (B), diversity (C), and evenness (J). Boxes represent the interquartile range. Whiskers represent the range of data dispersion in relation to quartiles.

**Table 1**

Permutational multivariate analysis (PERMANOVA) for the differences in community attributes of benthic species using an orthogonal three-factor mixed model: years, season, and hours (diel cycle). Bold fonts represent significant values ( $p < 0.05$ ).

Source	df	MS	Pseudo-F	p(perm)
<b>Richness</b>				
Year	2	2339.7	0.33	0.83
Season x Year	1	3468	19.66	<b>0.01</b>
Hours x Season x Year	28	4937.7	2.72	<b>0.01</b>
<b>Abundance</b>				
Year	2	5.44E+05	17.21	0.40
Season x Year	1	31621	0.08	0.78
Diel x Season x Year	28	3.92E+05	3.18	<b>0.01</b>
<b>Diversity</b>				
Year	2	1.29	0.69	0.84
Season x Year	1	1.8703	26.59	<b>0.01</b>
Diel x Season x Year	28	7.037E-2	2.16	<b>0.01</b>
<b>Evenness</b>				
Year	2	0.11	1.48	0.67
Season x Year	1	7.037E-2	2.16	<b>0.01</b>
Diel x Season x Year	28	1.72E-2	2.19	<b>0.01</b>

**4. Results**

A total of 31,524 organisms grouped into 256 species, 177 genera, 12 classes, and 102 families were obtained from the sampling surveys. A total of 145 species (6835 organisms) were collected during the day and 225 (24,649 organisms) during the night.

The organisms belonging to the class Malacostraca were the most abundant (29,291 organisms), with the highest occurrence in all sampling periods (92.91%), followed by the classes Gasteropoda (513 organisms) and Polychaeta (134 organisms). The order Decapoda was the most abundant in all the sampling periods (19,906 organisms), and with

higher abundances during the night (13,114 organisms), followed by the order Mysidacea (2579 organisms) Amphipoda (4093 organisms) and Isopoda (1954 organisms). All these orders presented higher relative abundances during the night.

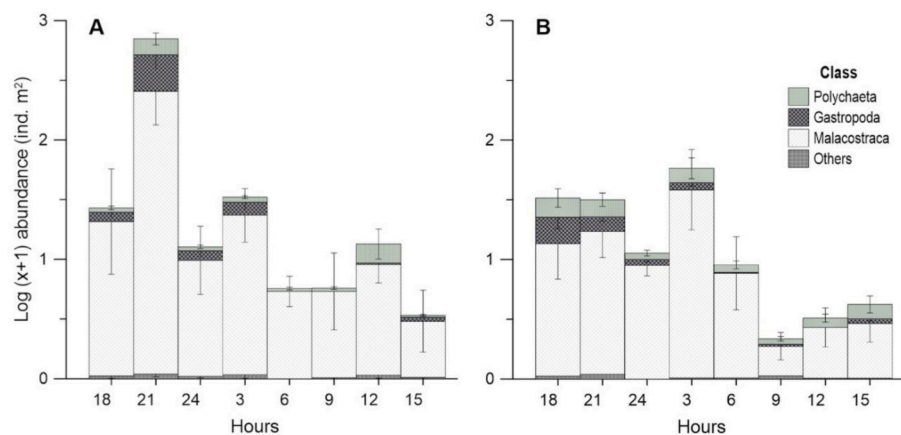
The univariate mode of PERMANOVA showed significant differences in diversity indices from day to night ( $p < 0.05$ ) evidencing an increment of species during the transition from day to night hours (sunset), occurring between 18 and 19 h along the year cycle, and the occurrence of a turnover from diurnal to nocturnal species. The general pattern of the community descriptors shows that the highest average values and variability of abundance (Fig. 2A), richness (Fig. 2B), and diversity (Fig. 2C) occurred between 18 and 21 h. The abundance values decrease and remain with minimal variability during the rest of the diel cycle. The average values for richness and diversity also decreased, but the large variability remained throughout the diel cycle. The highest evenness values and variability were observed at 18:00 h (Fig. 2D). *Hyppolite zostericola* was the most dominant during the day and *Thor dobkini* at night (Table 2). The PERMANOVA also showed significant differences in the abundance and species richness as a function of the climatic seasons (Table 1). The highest abundances were recorded during the rainy season ( $x = 406 \pm 251$ ), and the highest richness was during the dry season ( $x = 39 \pm 21$ ).

Species belonging to the class Malacostraca (M) were found to be dominant throughout the diel cycle in both the rainy (Fig. 3A) and the Dry (Fig. 3B) season. The dominant assemblage in terms of dominance (%RA) consisted of *Taphromysis bowmani*, *Urocaris longicaudara*, *Paracerceis caudata*, *Thor manningi*, *Thor floridanus*, *T. dobkini*, and *H. zostericola*. The species *T. dobkini* (24.23% RD) and *T. bowmani* (9.68% RD) were found in both periods, but their dominance was higher at night. While *H. zostericola* (21.11% RA), *U. longicaudara* (8.44% RD), *T. floridanus* (8.19% RD), *Thor carolinense* (5.15% RD) and *Grandidierella bonnieroides* (4.32% RD) were also present in both periods but were

**Table 2**

The 25 species with the highest relative dominance (%RD) and frequency (%F) in the overall epifaunal assemblage (day + night) and diel cycle (day + night) in seagrass beds of Los Petenes Biosphere Reserve. M = Malacostraca, G = Gastropoda, and P = Polychaeta.

General				Night				Day			
Species	N	%AR	%F	Species	N	%AR	%F	Species	N	%AR	%F
<i>Thor dobkini</i> (M)	6942	22.021	75	<i>Thor dobkini</i> (M)	5853	24.23	91.67	<i>Hippolyte zostericola</i> (M)	1451	21.11	81.25
<i>Hippolyte zostericola</i> (M)	4010	12.720	83.33	<i>Hippolyte zostericola</i> (M)	2386	10.38	85.42	<i>Thor dobkini</i> (M)	969	14.09	58.33
<i>Taphromysis bowmani</i> (M)	2575	8.168	50	<i>Taphromysis bowmani</i> (M)	2365	9.68	66.67	<i>Urocaris longicaudata</i> (M)	580	8.44	45.83
<i>Urocaris longicaudata</i> (M)	1967	6.240	55.21	<i>Thor manningi</i> (M)	1582	6.43	43.45	<i>Thor floridanus</i> (M)	563	8.19	45.83
<i>Thor manningi</i> (M)	1929	6.119	44.79	<i>Paracerceis caudata</i> (M)	1569	6.37	85.5	<i>Tozeuma carolinense</i> (M)	354	5.15	22.92
<i>Paracerceis caudata</i> (M)	1670	5.298	68.75	<i>Urocaris longicaudata</i> (M)	1291	5.63	64.58	<i>Hippolyte pleuracantha</i> (M)	343	4.99	33.33
<i>Thor floridanus</i> (M)	1667	5.288	48.96	<i>Cymadusa filosa</i> (M)	1249	5.07	39.58	<i>Thor manningi</i> (M)	343	4.99	45.83
<i>Hippolyte pleuracantha</i> (M)	1481	4.698	38.54	<i>Hippolyte pleuracantha</i> (M)	1102	4.62	43.75	<i>Grandidierella bonnieroides</i> (M)	297	4.32	27.08
<i>Cymadusa filosa</i> (M)	1259	3.994	25	<i>Thor floridanus</i> (M)	1039	4.48	52.08	<i>Taphromysis bowmani</i> (M)	189	2.75	33.33
<i>Periclimenes iridescens</i> (M)	700	2.221	25	<i>Periclimenes iridescens</i> (M)	513	2.15	25	<i>Periclimenes iridescens</i> (M)	170	2.47	25
<i>Tozeuma carolinense</i> (M)	621	1.970	27.08	<i>Ampithoe</i> sp. 1 (M)	470	2.08	20.83	<i>Chondrochelia dubia</i> (M)	136	1.98	4.17
<i>Ampithoe</i> sp. 1 (M)	513	1.627	10.42	<i>Cymusa ledoyeri</i> (M)	328	1.33	27.08	<i>Paracerceis caudata</i> (M)	100	1.45	50.00
<i>Grandidierella bonnieroides</i> (M)	446	1.415	27.08	<i>Penaeus duorarum</i> (M)	294	1.27	50	<i>Penaeus duorarum</i> (M)	85	1.24	35.42
<i>Penaeus duorarum</i> (M)	397	1.259	42.71	<i>Tozeuma carolinense</i> (M)	254	1.08	31.25	Nematoda (N)	71	1.03	22.92
<i>Cymusa ledoyeri</i> (M)	365	1.158	26.04	<i>Cerapus benthophilus</i> (M)	237	0.98	12.5	<i>Ceratonereis</i> (Compositia) versipedata (P)	67	0.97	18.75
<i>Cerapus benthophilus</i> (M)	242	0.768	7.29	<i>Dulichella appendiculata</i> (M)	212	0.86	43.75	<i>Pagurotanais largoensis</i> (M)	67	0.97	22.92
<i>Dulichella appendiculata</i> (M)	222	0.704	30.21	<i>Bemlos unicornis</i> (M)	149	0.72	12.5	<i>Laticorophium baconi</i> (M)	59	0.86	22.92
<i>Bemlos unicornis</i> (M)	216	0.685	12.5	<i>Grandidierella bonnieroides</i> (M)	137	0.60	27.08	<i>Syllis</i> sp. B (P)	55	0.80	6.25
<i>Chondrochelia dubia</i> (M)	168	0.533	5.21	<i>Modulus modulus</i> (G)	133	0.58	31.25	<i>Parapseudes</i> sp. A (M)	47	0.68	20.83
<i>Leptochelia forresti</i> (M)	158	0.501	35.42	<i>Leptochelia forresti</i> (M)	118	0.48	45.83	<i>Leptochelia forresti</i> (M)	40	0.58	25.00
<i>Modulus modulus</i> (G)	148	0.469	19.79	<i>Cerithium atratum</i> (G)	111	0.45	20.83	<i>Bemlos unicornis</i> (M)	39	0.57	12.50
Nematoda (N)	148	0.469	27.08	<i>Carpias algicola</i> (M)	110	0.45	29.17	<i>Cymusa ledoyeri</i> (M)	37	0.54	25.00
<i>Laticorophium baconi</i> (M)	142	0.450	26.04	<i>Grandidierella elongata</i> (M)	93	0.39	27.08	<i>Hoploplemius propinquus</i> (M)	32	0.47	25.00
<i>Ceratonereis</i> (Compositia) versipedata (P)	141	0.447	17.71	<i>Elasmopus</i> sp. A (M)	91	0.37	31.25	<i>Exogone dispar</i> (P)	31	0.45	33.33
<i>Carpias algicola</i> (M)	119	0.377	20.83	<i>Rocinela signata</i> (M)	90	0.37	64.58	<i>Rocinela signata</i> (M)	28	0.41	27.08

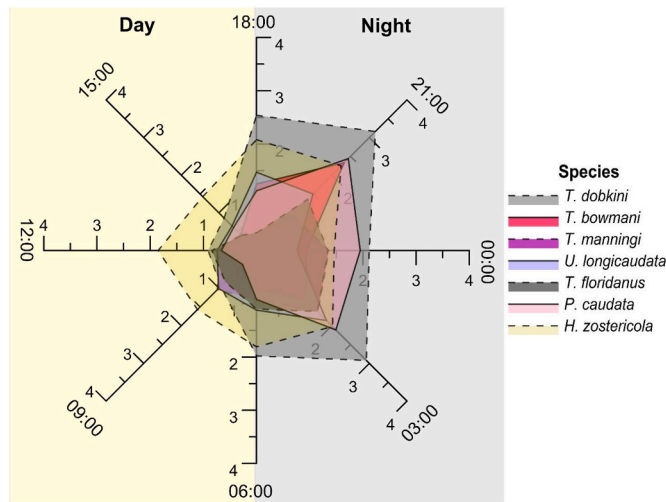


**Fig. 3.** Diel variability of the mean abundance of the major taxonomic classes in each sampling hour in the rainy (A) and dry (B) seasons. The mean abundance of others in the rainy season comprises Asteroidea, Holothuroidea, and Sipunculidea and in the dry season comprises Nemertea, Ostracoda, Holothuroidea, Sipunculidea, Hexanauplia, Asteroidea. Error bars indicate s.e.

dominated during the daytime. During the night, the dominant species were *Cymadusa filosa* (5.07% RD), *Ampithoe* sp. (2.08% RD), *Cerapus benthophilus* (0.98% RD), *Dulichella appendiculata* (0.86% RD), *Modulus modulus* (0.58% RD), *Cerithium atratum* (0.45% RD), *Carpias algicola* (0.45% RD), *G. elongata* (0.39% RD), and *Elasmopus* sp (0.37% RD) (Table 2).

The SIMPER analysis allowed for the identification of the species that contribute 75% of the variability along the diel cycle. It also revealed the identification of high dissimilarity (78.60%) of the species contribution

to the composition of the day and night assemblage. The major contribution (21%) to the assemblage conformation in terms of abundance was made by the Malacostracans as *T. dobkini* (4.94%), *P. caudata* (3.67%), *T. manningi* (3.27%), *T. bowmani* (3.26%) *H. zostericola* (3.17%), *U. longicaudata* (3.15%), and *T. floridanus* (2.92%). *T. dobkini* was the species with the highest average abundance during the night and *H. zostericola* during the day (Fig. 4). In general, it was observed that the relative abundance of the assemblage increased more than 50% during the night.



**Fig. 4.** Results from the SIMPER analysis showing changes in the average abundance of the species with the greatest contribution to the assemblage during the diel cycle.

**Table 3**

Permutational multivariate analysis (PERMANOVA) to test for differences in benthic community structure using an orthogonal three-factor mixed model: years, season, and hours (diel cycle). Bold fonts represent significant values ( $p < 0.05$ ).

Source	df	MS	Pseudo-F	p(perm)
Year	2	28562	1.0071	0.5045
Season (Year)	1	28361	8.0509	<b>0.01</b>
Hours(Season(Year))	28	3522.6	2.1226	<b>0.01</b>

The PERMANOVA standard mode showed significant differences in species composition among the seasons for the different years analyzed (Table 3). At this scale, the PCA results showed the formation of four groups, each one associated with a sampling period. The groups associated with the 2012 dry season and the 2016 rainy season are shown close to each other and separate from the clusters associated with the 2011 rainy season and the 2016 dry season (Fig. 5A). The PCA analysis of the diel cycle evidenced a spatial arrangement of species composition well differentiated between day and night, suggesting that the community structure is different in both periods regardless of the analyzed sampling years (Fig. 5B).

The PERMANOVA analysis showed that all the environmental variables showed significant differences in function of the season (Table 4). The significant change in-depth (Fig. 6a), oxygen (6b), and temperature (6d) values occurred during the 2016 dry season. The salinity (Fig. 6c) showed significant changes in the 2011 rainy season. Only the temperature also showed significant differences in function of

the diel cycle.

The RDA (Fig. 7) showed the potential associations between species abundance and environmental variables, in which the first two axes explained 91.2% of the total observed variance. The relative abundance of diurnal species was significantly associated ( $p < 0.05$ ) with temperature, salinity, oxygen, and depth values. The dominant species associated with the 2016 dry season were positively related to the environmental gradient formed by depth and salinity, and negatively related to oxygen values. The second group of species related to the 2011 rainy season showed a positive association with the gradient formed by the depth and oxygen and a negative association with the salinity values. Only the species *T. manningi*, one of the dominant species in the whole diel cycle, was positively associated with the gradient formed by salinity and temperature. In general, the abundance of the diurnal species showed a significant relationship with the values of temperature, salinity, and oxygen concentrations in the water column. The abundance of the nocturnal species did not show any potential association with the environmental variables considered in this study.

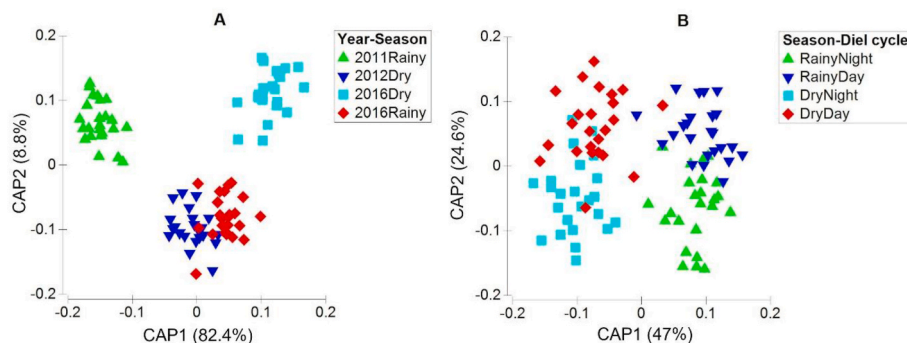
### 5. Discussion

This study evidenced the existence of a diel variation of the epibenthic community associated with the LPBR seagrasses. The overall results evidenced a marked turnover of species during the evening hours occurring all along the year in a range from 18 to 20 h, with maximum peaks of abundance, richness, and diversity during nighttime. This species turnover has also been observed in previous studies conducted in tropical environments where the highest macroinvertebrate diversity

**Table 4**

Permutational multivariate analysis (PERMANOVA) to test for differences in the environmental variables using an orthogonal three-factor mixed model: years, season, and diel cycle. species using an orthogonal three-factor mixed model: years, season, and hours (diel cycle). Bold fonts represent significant values ( $p < 0.05$ ).

Source	df	MS	Pseudo-F	p(perm)
Depth (m)				
Year	2	4.7774	1.1918	0.669
Season x Year	1	4.006	10.278	<b>0.04</b>
Hours x Season x Year	4	0.3897	0.5888	0.683
Dissolved Oxygen (mg/l)				
Year	2	2.5674	0.2053	0.833
Season x Year	1	12.05	79.972	<b>0.01</b>
Hours x Season x Year	4	0.1563	0.2944	0.899
Salinity (%)				
Year	2	12.295	4.6168	0.501
Season x Year	1	2.663	10.989	<b>0.02</b>
Hours x Season x Year	4	0.2423	2.0934	0.110
Temperature (°C)				
Year	2	2.0673	8.8788	0.153
Season x Year	1	23.284	39.513	<b>0.01</b>
Hours x Season x Year	4	0.5928	11.552	<b>0.01</b>



**Fig. 5.** Spatial distribution of the composition and abundance of benthic epifauna associated with seagrasses in A) the climatic seasons and B) the diel cycle.

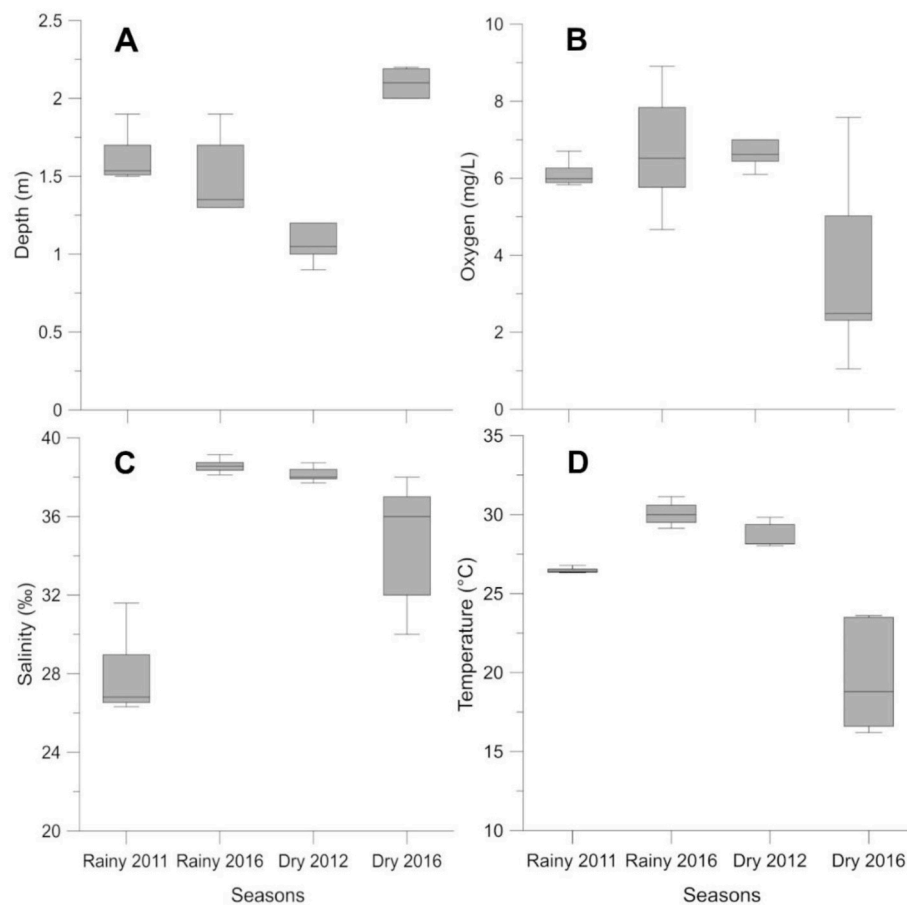


Fig. 6. -Box plots of (A) depth, (B) oxygen, (C) salinity, and (D) temperature showing the variability at the seasonal scale. Lines inside the box represent the median and error bars represent 10th and 90th percentile.

(Mendoza et al., 2018), biomass, and density increment (Brito et al., 2016) was observed in the evening (between 18 and 20 h). These changes were related to the activities and species behavior such as breeding, feeding, dispersal, and predator evasion (Oliveira-Neto et al., 2008; Toro-Ramírez et al., 2017; Mendoza et al., 2018), as is probably occurring in our study site.

The dominant species, during all the diel cycles, identified in this study belonged to the decapod group, which has also been previously reported as dominant in the lagoon and coastal ecosystems of the Yucatan Peninsula (Román-Contreras and Martínez-Mayén, 2009; Macías, 2012; Martínez-Mayén et al., 2020). The decapods have been considered the most prevalent group in the seagrasses, as well as keystone and engineering species that could have a major impact on the structure and functioning of the seagrass ecosystem (Valentine and Duffy, 2006). The observed pattern of variability suggests a stable ecological state of the benthic seagrass habitat. Recent evidence has shown the occurrence of a diel variability of the decapod community associated with *Thalassia testudinum* in coastal environments of the Mexican Caribbean with higher abundance and richness values during the night (Briones-Fourzán et al., 2020).

The observed decapods were mainly foraging herbivores that feed on epiphytes and macroalgae associated with seagrasses. The LPBR coastal environmental conditions are favorable for high biomass production, density, plant growth, and seagrass productivity (Pérez Espinoza et al., 2019). This characteristic, together with the presence of groundwater discharges that may generate euryhaline conditions, could be providing a diversity of suitable habitats for observed decapods. During the night, the decapod *T. dobkini* was the most dominant, and during the day *H. zostericola* was dominant. Both species have previously been reported

as being abundant and dominant in the benthic communities from the Gulf of Mexico and the Caribbean Sea, tolerant to salinity changes, and able to colonize euryhaline environments (Barba et al., 2005).

According to our results from the diel scale, a significant species turnover with an increment of species richness occurred during the sunset hours in all the sampling periods. This suggests that a marked change in light intensity during the sunset can be an important factor determining the epibenthic diel patterning. It has been recognized that changes in light intensity influence vertical and horizontal migrations and the activity of predators and prey in benthic environments (Sánchez-Jerez et al., 1999; Rocha-Ramírez et al., 2016). Some evidence suggests that groups such as crustaceans and polychaetes usually hide in the sediment or the seagrass rhizosphere during the day and, in the evening, migrate to the leaf structures of *T. testudinum* to obtain food (van Tussenbroek et al., 2016; Briones-Fourzán et al., 2020). The Sunset period in the study sites, as in all southeastern GoM, has a very short range of duration occurring in a range of approximately 30 min duration between 18.30 and 20 h all year round. It is probably that over this short period, the decline and later absence of daylight will trigger some ecological mechanisms, related to predation, or vertical migration that cause an increment in the species richness. The PERMANOVA results reveal that only the species richness and diversity may be influenced by the environmental seasonal changes. At this scale, the highest abundances of malacostracans and gastropods were observed in the rainy season, while a significant increment in polychaetes abundance was observed in the dry season. These shifts have also been reported for some benthic groups such as polychaetes, mollusks, and decapods from subtropical coastal lagoons (Pech et al., 2007b; Mateo-Ramírez et al., 2016). The environmental condition such as the increment of freshwater

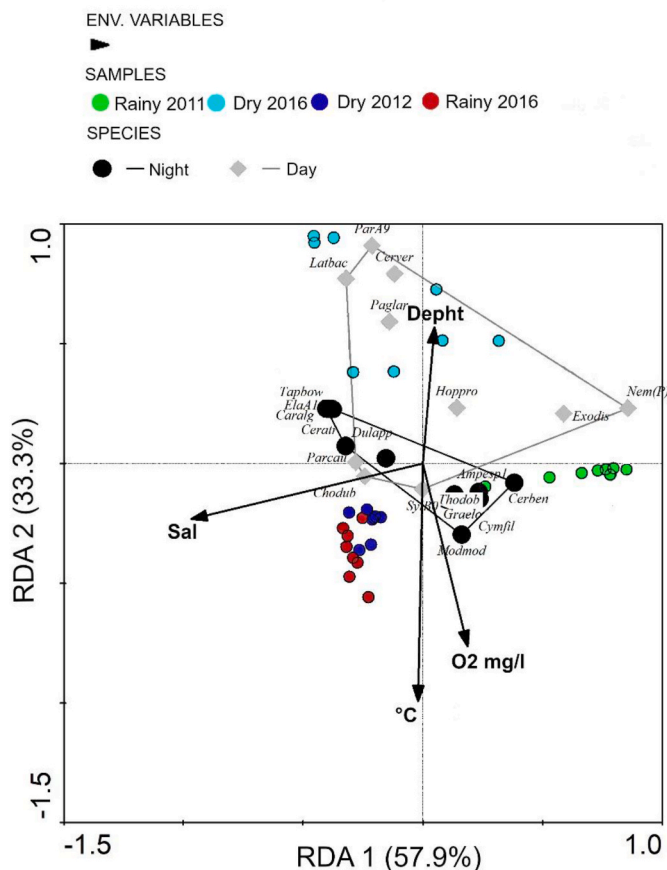


Fig. 7. Spatial arrangement of RDA results between the environmental variables and the dominant species. Envelopes delimit the position of species according to the day and night hours. The abbreviations of the species names are composed of the first three letters of the genus and the first three letters of the species (see Table 2). O<sub>2</sub> mg/l = dissolved oxygen, Sal = salinity, °C = temperature.

input during the rainy season or the marked water column stratification during the dry season (Hernández-Guevara et al., 2008) would cause significant changes in species richness and diversity but not abundance. This evidence suggests the system maintains benthic productivity even with significant changes in richness and diversity.

The RDA results showed two types of potential associations. The first one showed a set of species related to the 2016 dry environmental characteristics whose abundance was negatively related to both oxygen and temperature values. Previous studies have found a direct relationship between oxygen changes during a diel cycle and inducing changes in the community dynamics of benthic communities in tropical environments (Gacia et al., 2005; Clavier et al., 2008). Our results, even not conclusive, show the presence of epifaunal species that could change its abundance and presence in function of the dissolved oxygen (DO). The second type of potential association showed that the set of species characteristic of the 2011 rainy season was associated with low salinity values ( $27.65 \pm 1.82$ ) caused by groundwater discharges from the study site. The input of large volumes of freshwater from rainfall and submarine discharges during the rainy season led to a decrease in salinity values (Medina-Gomez and Herrera-Silveira, 2006) probably causing significant changes in species richness and diversity (see Table 1). This condition might be favoring the species of the genus Thor (e.g. *T. dobkini*, *T. manningi*), Hyppolite (e.g. *H. zostricola*) Urocaris (e.g. *U. longicaudata*) which can tolerate significant changes in the salinity and that according to our results (see Fig. 4), they had the greatest contribution to the assemblage during the entire diel cycle.

The unusually low precipitation values recorded for the 2016 rainy season could be associated with large-scale phenomena such as El Niño/La Niña Southern Oscillation (ENSO), which causes changes in rainfall patterns. 2016 was reported as a La Niña year (L'Heureux, 2017) and its influence was observed in the 2016 rainfall patterns characterized by low precipitation and evaporation, causing similar characteristics to the 2016 dry season (Kendrick et al., 2019; Moura et al., 2019). The La Niña effects could have caused changes in the biomass and cover of seagrass beds affecting the epibenthic community (van Tussenbroek et al., 2012; Abrogueña et al., 2021). It has been shown that environmental changes caused by the ENSO phenomena influence the productivity of coastal ecosystems that can modify the reproductive patterns of species, as well as the colonization and/or proliferation of macroalgae and the community structure of the infauna that inhabit these environments (Lin et al., 2018; Kendrick et al., 2019; McKenzie et al., 2021).

Finally, the dominant nocturnal species did not show any significant relationship with the recorded environmental variables. It is likely that the presence of species that only appear during the nocturnal period may be related to their nocturnal feeding behavior, dispersal mechanisms, and protection from predators (Oliveira-Neto et al., 2008; Toro-Ramírez et al., 2017) or to other habitat variables that were not considered in the study, such as nutrient concentration or light intensity.

## 6. Conclusions

Our results showed that the assemblage formed by the decapods *T. dobkini*, *P. caudata*, *T. manningi*, *T. bowmani*, *H. zostricola*, *U. longicaudata*, and *T. floridanus* was the dominant one in terms of abundance during the whole diel cycle, independent of the sampling period. The decapod *H. zostricola* was the most dominant and abundant during the daytime period, and *T. dobkini* during the night. The abundance, richness, and diversity values increased during the evening period, suggesting that species turnover between day and night occurs in this period.

Species abundance and richness also showed significant changes as a function of sampling periods, but the overall pattern of the dominant species assemblage did not change. The understanding of the temporal variability observed from the diel scale and larger intra-annual (seasons) and inter-annual (sampling years) scales suggests the ecological stability of the epibenthic community associated with seagrasses in the LPBR, regardless of the scale at which it is analyzed.

Our results demonstrate that the community dynamics of benthic epifauna are determined by the variability that occurs at the diel scale, which is manifested in the diurnal and nocturnal changes in community characteristics. The understanding of these community changes provides more certainty in the establishment of benchmarks for assessing the environmental health of benthic habitats in the LPBR.

## CRediT authorship contribution statement

**José Ángel García-Trasviña:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Conceptualization. **Daniel Pech:** Writing – review & editing, Writing – original draft, Supervision, Software, Resources, Project administration, Investigation, Funding acquisition, Conceptualization. **Mariana E. Callejas Jiménez:** Writing – review & editing, Writing – original draft. **Alberto De Jesus-Navarrete:** Writing – review & editing, Writing – original draft, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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