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Macrofaunistic Diversity in
Vallisneria americana Michx. in a
Tropical Wetland, Southern Gulf of Mexico

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1. Introduction

The variety of macrofauna in limnetic and estuarine ecosystems is related to the spatial arrangement of habitats with different quantitative and qualitative complexities (Heck & Crowder, 1991; Taniguchi et al., 2003; Genkai-Kato, 2007; Gullström et al., 2008). Among these habitats, submerged aquatic vegetation (SAV), harbour a high diversity of molluscs, macrocrustaceans and fish, by favouring a greater survival and growth of the associated populations (Minello & Zimmerman, 1991; Pelicice & Agostinho, 2006; Rozas & Minello, 2006; Cetra & Petrere, 2007; Genkai-Kato, 2007; Hansen et al., 2011). In structured habitats, as SAV, the faunistic diversity tends to be greater and mortality rate have a tendency to be lower than in non-structured habitats (Taniguchi et al., 2003; Gullström et al., 2008), although with exceptions (Bogut et al., 2007; Florido & Sánchez, 2010; Schultz & Kruschel, 2010). In particular, SAV in coastal ecosystems provides structured habitats that shelter a greater abundance and diversity of invertebrates and fish, where species use the habitat to obtain protection against predators, and as feeding and reproduction areas (Minello & Zimmerman, 1991; Rozas & Minello, 2006; Genkai-Kato, 2007; Florido &Sánchez, 2010; Hansen et al., 2011).

SAV has been considered a key component in maintaining the functions of shallow aquatic ecosystems with bottom-up type trophic dynamics, as it affects the physical, chemical and biological processes of coastal ecosystems worldwide. At present, its vulnerability in face of the eutrophication of coastal aquatic ecosystems and the declination or disappearance of populations with the resulting loss of biodiversity are a matter of concern (Wigand et al., 2000; Ni, 2001; Bayley et al., 2007; Duarte et al., 2008; Orth et al., 2010). SAV populations, including those of the American Wildcelery *Vallisneria americana* Michx., have however decreased drastically or disappeared in coastal ecosystems throughout the world (Short et al., 2006; Best et al., 2008).

The American Wildcelery populations in the Biosphere Reserve of Pantanos de Centla (BRPC) have recorded wide fluctuations in space and time with respect to density, biomass, patch size and distribution (Sánchez et al., 2007). The high variability of this grass and other macrophytes has been associated both with an increase in total suspended solids (TSS), nutrients and physical disturbances caused by human activities (Touchette & Burkholder, 2000; Ni, 2001; Best et al., 2008), and with the low persistence (below 50%) of the patches on a local scale (Capers, 2003). In the BRPC, the marked variations in the *V. americana* patches have been analysed only with respect to the enrichment in N, with no symptoms of lethal stress or direct toxicity recorded experimentally in young plants as a result of enrichment in N by NH_4, NO_3 and NO_3:NH_4 up to 2000 µg L^{-1}, though variations in growth at the sublethal level were recorded (Ruiz-Carrera & Sánchez, 2012).

Aquatic macrofauna, that present distribution patterns associated with particular habitats, is more vulnerable in face of anthropogenic threats. This is reflected in the high number of species that are considered at risk and in the conservation status of the macrofauna itself (Revenga et al., 2005; Dudgeon et al., 2006). The high diversity values that have been recorded for aquatic invertebrates and fish in structured habitats are threatened by the drastic reduction in the surface area of limnetic ecosystems, as has been documented for several areas of the USA (Revenga et al., 2005; Dudgeon et al., 2006). The records of species that are threatened or in danger of extinction should thus be complemented in the short term with an analysis of their distribution patterns in habitats with a high biodiversity such SAV (for examples; Rozas & Minello, 2006; Genkai-Kato, 2007; Hansen et al., 2011), as these are drastically decreasing or disappearing in the wetlands of southeastern Mexico and, in general, on a global scale (Sheridan et al., 2003; Sánchez et al., 2007; Schloesser & Manny, 2007; Best et al., 2008). Considering the above, it has become necessary to carry out short term studies focused on understanding the dynamics, reproduction and production of macrophytes (Ruiz-Carrera & Sánchez, 2008; Liu et al., 2009), and to prepare inventories of species associated with SAV, together with their distribution, particularly in ecosystems and regions where information is still limited (Lévêque et al., 2005) and social and economic situations prevent conservation programmes from being successful (Fisher & Christopher, 2007; Kiwango & Wolanski, 2008). This is the case of tropical fluvial wetlands located in Mesoamerica.

Freshwater ecosystems are rich in species diversity and endemisms, but only a small proportion of species have been assessed in freshwater ecosystems of tropical areas (Lévêque et al., 2005; Dudgeon et al., 2006), including Mesoamerica. This lack of biodiversity data for tropical areas becomes critical considering the high rates of extinction that have been recorded (Revenga et al., 2005). The BRPC is a freshwater Protected Area that, together with the freshwater ecosystem of Pom-Atasta and the estuarine ecosystem of Laguna de Términos in Campeche, forms one the most extensive tropical wetlands in Mesoamerica. In spite of the increase in records of freshwater fauna for the BRPC over the last years, it is believed it is still underestimated (Reséndez & Salvadores 2000; Mendoza-Carranza et al., 2010; Montalvo-Urgel et al., 2010; Maccosay et al., 2011; Sánchez et al., 2012).

Vallisneria americana shelters a high diversity of macrofauna in the BRPC and other ecosystems (Rozas & Minello, 2006; Sánchez et al., 2012). The spatial and temporal variations of the fauna associated with *V. americana* may be explained by quantitative changes in habitat complexity (Rozas & Minello, 2006) and by the effects of flood pulses on the

physicochemical properties of the water column (Thomaz et al., 2007; Souza-Filho, 2009). However, the reasons behind the drastic decrease or disappearance of *V. americana* patches in the BRPC have not been well documented, in spite of the SAV patches occupying less than 1% of the total area of the aquatic substrate (Sánchez et al., 2007). For this reason, *in vitro* micropropagation of *V. americana* has been carried out (Ruiz-Carrera & Sánchez, 2008) considering the possibility of: 1) testing hypotheses through experimental designs focused on phytodiagnosis, and 2) generating a germoplasm bank for future repopulation programmes (Ruiz-Carrera & Sánchez, 2012).

Notwithstanding that the BRPC and most American tropical wetlands with *V. americana* shelter a high faunal diversity, these ecosystems still present a scarcity of information regarding the associated fauna and the spatial-temporal variations in the ecological condition. This lays emphasis on the need to update data bases, as well as ecological scenarios for freshwater ecosystems with few studies that, at the same time, receive anthropological pressures from agriculture, cattle ranching and oil industry activities, together with the construction of dams and hydrological structures to control floods and produce electricity. Moreover, the BRPC is located in the ichthyofaunistic Usumacinta Province where the greatest diversity has been recorded for Mexico (Miller et al., 2005), and in the only hydrological area with a high availability of water resources in the country (Sánchez et al., 2008). This chapter includes a 10 year checklist of macrofauna species associated with *V. americana*, together with an analysis of whether lagoons with a great number of species and high density (org/m^2) of fauna, maximum values of quantitative habitat complexity of SAV and a minimum degree of perturbation, present the most favourable ecological condition in the BRPC. This point is considered in three steps through the analysis of the spatial and temporal variations of 1) the environmental quality of the water column, 2) the quantitative habitat complexity of *V. americana*, and 3) the abundance and diversity of molluscs, crustaceans and fish.

2. Materials and methods

2.1 Study area and habitat

The BRPC is a tropical fluvial wetland that covers an area of 302,000 ha, with approximately 110 lentic ecosystems and 2,934.1 km^2 of areas prone to flooding, where the volume of water increases by about 50% during the flood seasons (Sánchez et al., 2007). It is located in the low basin of the rivers Grijalva and Usumacinta (17°57'53"-18°39'03" N, 92°06'39"-92°45'58" W) and receives discharges from these two rivers and another four, all of which define the water changes in volume by flooding cycles (Salcedo et al., 2012). The volume of water discharged from the rivers Grijalva and Usumacinta is the third in importance in the Gulf of Mexico after those of the Mississippi and Atchafalaya (Velázquez-Villegas, 1994; Collier & Halliday, 2000).

The American Wildcelery, *V. americana*, is the dominant submerged aquatic vegetation species in the BRPC (Sanchez et al., 2007). It is widely distributed from Nova Scotia to La Libertad, Petén and Lago Petén, Itza in Guatemala (Korschgen & Green, 1988). It was selected for this study as it is the habitat with the greatest diversity of associated fauna in comparison with two other structured habitats present in the BRPC (Sánchez et al., 2012). A situation similar to this has been recorded in other wetlands (Pelicice & Agostinho, 2006; Rozas & Minello, 2006; Cetra & Petrere, 2007; Genkai-Kato, 2007).

2.2 Sampling and laboratory analyses and procedures

2.2.1 Macrofauna

Faunal specimens were collected from 1999 to 2010 in six lagoons and Polo Bank, a low-energy shallow area along the Usumacinta river. Sites with *V. americana* patches were selected for sampling. Sampling varied among the seasons and the years following the distribution and persistence of the patches. For example, Polo Bank and Tronconada lagoon present a spatially and temporally low persistence and were thus sampled only in 2005 (Table 1). Sampling took place during daylight hours in the minimum (April to March) and maximum (October to November) flood seasons.

Aquatic invertebrates and fish associated with submerged aquatic vegetation were collected with a drop net and a Renfro beam net. The drop net covers an area of 0.36 m², five random repetitions were carried out, and the macrofauna caught in the net was collected with a small dip net. The Renfro beam net has a 1.8 m mouth and a 0.8 mm mesh size. Two 25 m long transects were sampled at each site, each covering an area of 45 m².

2.2.2 Ecological condition

The spatial and temporal variations in the ecological condition were analysed considering the fauna associated with *V. americana*, the quantitative habitat complexity of *V. americana*, the degree of perturbation and the trophic state, in six lagoons and a low-energy shallow bank (Table 1) during two flood seasons (minimum and maximum) in the year 2005. The physicochemical and biological variables of the water column, the quantitative habitat complexity of *V. americana*, and the faunal samples were recorded simultaneously.

Sampling sites	UTM	1999 - 2010	2005 [2]
Laguna El Viento	536096 – 2015690	X	X
Laguna San Pedrito	542550 – 2030632	X	X
Laguna Chichicastle	559375 – 2014741	X	X
Polo Bank [1]	536869 - 2046013		X
Laguna El Guanal	558711 – 2022995	X	X
Laguna El Sauzo	567364 – 2013952	X	X
Laguna Tronconada	539661 - 2011309		X

Table 1. Sampling sites in six lagoons and a low-energy shallow bank along the Usumacinta river [1]. Geographical positions are Universal Transverse Mercator (UTM) units. [2] = sampling sites for the ecological condition analysis.

Sixteen physicochemical and biological variables were recorded at each sampling site. Five variables were quantified *in situ*: water temperature with a conventional thermometer (0-50°C), visibility with a Secchi disc (VSD), depth with a dead weight, pH with a pH meter with an accuracy of ± 0.05 (Hanna model HI98128), and electric conductivity (EC) with a conductivity meter (Yellow Springs Instruments [YSI] model 30). Water was collected with a van Dorn bottle at mid depth and stored at less than 4 °C. The 12 variables analysed in the laboratory were dissolved oxygen saturation (DOS), total suspended solids (TSS), ammonium (NH_4), nitrites (NO_2), total phosphorus (TP), orthophosphates (PO_4), biochemical oxygen demand (BOD_5), chemical oxygen demand

(COD), fats and oils (FO), chlorophyll a (chl *a*) and fecal coliforms (FC). All samples were preserved and analysed following the techniques established by Scientific Committee on Oceanic Research-United Nations Educational, Scientific and Cultural Organisation [SCOR-UNESCO] (1966), Wedepohl et al., (1990) and American Public Health Association [APHA] (1998).

Vallisneria americana stems were collected with a 0.0625 m² quadrant. Three replicas were taken per sampling site and the leaves and roots were frozen to measure leaf area (cm²), plant density (stems/m²) and biomass as ash free dry weight (g$_{AFDW}$/m²), as metrics of quantitative habitat complexity. The animal specimens obtained for this analysis were collected with a drop net as indicated in section 2.3.1. Faunal metrics were species richness (S´) and density (org/m²).

2.2.3 Species identification and determination of trophic groups

Mollusc species were identified mainly based on the taxonomic characters proposed by García-Cubas (1981), Hershler & Thompson (1992) and Taylor (2003) for gastropods and bivalves. Macrocrustaceans were identified following the taxonomic characters published by Bousfield (1973), Lincoln (1979), Villalobos-Figueroa (1983), Williams (1984), Nates & Villalobos-Hiriart (1990), and Pérez-Farfante & Kensley (1997). Fish species were identified considering the criteria established by Castro-Aguirre et al., (1999), Smith & Thacker (2000), Miller et al., (2005) and Marceniuk & Bentacur (2008). The trophic groups of all the species associated with *V. americana* were defined based on the information published by Hershler & Thompson (1992), Schmitter-Soto (1998), Miller et al., (2005), Rocha-Ramírez et al., (2007) and Froese & Pauly (2011).

2.3 Data analyses

2.3.1 Estimation of the Perturbation Degree Index (PDI) and Trophic State Index (TSI)

The variations in the 16 physicochemical and biological parameters quantified in the water column made it possible to select those that explain the variability through the estimation of the PDI, and to group the lagoons into perturbation categories for each flood season (Salcedo et al., 2012). A first selection of the physicochemical and biological metrics was based on their chemical and statistical effects on the temporal and spatial variations in the sampling sites. This selection eliminated eight parameters. A second selection was carried out with a principal components analysis (PCA) using the JMP vs 9.0 programme (Statistical Analysis System Institute [SAS Institute], 2010), with metrics values previously transformed into natural and standardised logarithms (Legendre & Legendre, 1998). The metrics were selected with values above 40 for the more important weights (Weilhoefer et al., 2008), and considered the correlations among the metrics with the greater weights (Liou et al., 2004). The five metrics selected were EC, DOS, TSS, NH$_4$ and PO$_4$.

Reference values for these five metrics were obtained through the analysis of their spatial and temporal variations in the seven sampling sites, and their averages and standard errors (average ± standard error), using a data matrix where the seven sampling sites were placed on files and the five metrics in columns. The calculation of the averages and standard errors was based on 70 data (5 metrics x 7 sampling sites x 2 flood seasons). The reference values

were calculated with the average plus the standard error in the case of the parameters of which the maximum values represented conditions of environmental alteration (EC, TSS, NH_4 and PO_4). In contrast, the reference value was estimated with the average minus the standard error in the case of the metric (DOS) of which the minimum value defined conditions of environmental alteration.

The value of each metric per sampling site (5 metrics x 7 sites x 2 seasons = 70) was compared with its reference value to establish its effect. The negative effect of DOS was determined when its value was below or equal to the reference value. In contrast, the negative effect of EC, TSS, NH_4 and PO_4 was defined when its value was greater or equal to the reference value. Thus, positive effects were established in an opposite way for both groups of metrics. The effects of each metric were substituted by a value of cero when positive and a value of one when negative. The resulting binary matrix (n = 70) was divided into two independent matrices per season (5 metrics x 7 sites = 35). The independent evaluation of each flood season was carried out considering that the water changes in volume affect the temporal and spatial variations of the physicochemical parameters of the water, and the biota, in BRPC (Salcedo et al., 2012). Each binary or pondered values matrix included 35 data (5 metrics x 7 sites) with sites on files and metrics in columns.

The pondered value of each of the five metrics was averaged per sampling site (5 metrics x 7 sites = 35), for each of the two binary matrices. The seven averages of the pondered values were analysed through percentiles, and each sampling site was placed in a category of degree of perturbation. The perturbation categories were minimum (< 25%), medium-low (≥ 25 – < 50%), medium-high (≥ 50 – < 75%) and maximum (> 75%). In this study, the PDI was calculated only per sampling site.

The sum of the pondered values of each site was calculated for each metric (∑ 7 sites and 5 metrics = 5 sums). The sum per metric was divided by the number of sampling sites (7) to estimate the persistence as a percentage. The persistence reflects the negative effect of the metrics, as the positive effect was substituted by cero and the negative effect by one in the binary matrix with pondered metrics.

TSI is a parametric index with multimetric applications (Carlson, 1977), and is not referential. It defines trophic states with four trophic categories in a scale of 0 to 100 as: oligotrophic, mesotrophic, eutrophic and hypereutrophic (Carlson, 1977). Only the TSI for phosphorus (TSI$_{TP}$) was calculated in this study for each season, as its interpretation is comparative and complementary to the PDI (Salcedo et al., 2012).

2.3.2 Estimation of quantitative habitat complexity and faunal metrics

The physical complexity of the habitat has been determined qualitatively and quantitatively, and it has been related to increases in survival and growth of its associated populations (Stoner & Lewis, 1985; Heck & Crowder, 1991; Minello & Zimmerman, 1991; Rozas & Minello, 2006; Genkai-Kato, 2007). This study determined the quantitative habitat complexity through the SAV density (stems/m²), SAV leaf area (cm²) and SAV biomass (g_{AFDW}/m²), per sampling site for the two flood seasons (minimum and maximum), and excluded the architecture or qualitative complexity (Stoner & Lewis, 1985). These three habitat complexity variables were transformed into logarithms (Debels et al., 2005) and

analysed with a PCA. The metrics were selected as is mentioned in section 2.3.1, and the same programme was used. The SAV leaf area and biomass were selected in this process.

Density (org/m²), species richness (S´) and the invasive/native species rate were the metrics quantified for the macrofauna. The invasive/native rate was determined based on the density values (org/m²) of the macrofauna collected. The invasive species were those recorded by the Global Invasive Species Database (Invasive Species Specialist Group [ISSG], 2011). All biological metrics were estimated per sampling site for the two flood seasons.

2.3.3 Estimation of ecological condition

The ecological condition was estimated for each of the seven sampling sites, and each of the flood seasons, following the "Marco de Evaluación de Sistemas de Manejo de Recursos Naturales" (MESMIS) procedure (López-Ridaura et al., 2002). The MESMIS procedure was applied considering the PDI, the TSI_{TP}, two habitat complexity indices and the three faunal metrics mentioned in the previous section. The maximum reference value for each of the seven metrics was calculated based on 1) the value defined by the scale of each metric, as in the case of the PDI, the TSI_{TP} and the invasive/native rate, or 2) the value recorded in the study area for macrofauna density (org/m²) and species richness (S´), and SAV leaf area (cm²) and biomass (g_{AFDW}/m²). From these maximum reference values per metric, the indicator values of the MESMIS were calculated and expressed on a scale of averages (0-100%), with 100% corresponding to the greatest reference value per metric. The ecological condition was obtained 1) per sampling site by averaging the seven indicator values of the MESMIS, and 2) per season through the pondered average of the seven sampling sites. The inter-seasonal variation of each of the seven metrics included in the MESMIS, and of the estimated values for the ecological condition, was analysed independently with Kruskal-Wallis tests using the JMP vs 9.0 programme (SAS Institute, 2010), as the data did not satisfy the conditions of homocedasticity and normality (Underwood, 1997). The spatial distribution of the environmental condition of the seven sampling sites was grouped using average-linkage hierarchical clustering (Legendre & Legendre, 1998) and the JMP vs 9.0 programme (SAS Institute, 2010).

3. Results

3.1 Checklist

A total of 53 species of molluscs, macrocrustaceans and fish were collected. Fish dominated with 30 species, followed by macrocrustaceans with 14 species and lastly molluscs with 9 species. Two invasive species were recorded, the gastropod red rimmed Melania *Thiara tuberculata* and the amazon sailfin catfish *Pterygoplichthys pardalis*. Of the 53 species distributed in the SAV, the omnivores represented 36% and included 10 species of fish and nine of crustaceans. The carnivores included 13 fish and one crustacean species, representing 28% of the total. The detritivores made up 15% with two mollusk, three crustacean, and two fish species, including the two invasive species, *T. tuberculata* and *P. pardalis*. The herbivores represented 15% with eight species, and the planctivores and benthic filter feeders represented 4% each (Table 2).

species	species
molluscs	*Astyanax aeneus* [a, b, 2] (Günther, 1860)
Neritina reclivata [a, b, 3] (Say, 1822)	*Hyphessobrycon compressus* [a, 5] (Meek, 1904)
Cochliopina francesae [a, b, 4] (Goodrich & Van der Schalie 1937)	*Pterygoplichthys pardalis* [a, c, 3] (Castelnau, 1855)
Pyrgophorus coronatus [a, 4] (Pfeiffer, 1840)	*Rhamdia quelen* [1] (Quoy & Gaimard, 1824)
Aroapyrgus clenchi [a, b, 4] (Goodrich & Van der Schalie 1937)	*Opsanus beta* [1] (Goode & Bean, 1880)
Pomacea flagellata [a, 4] (Say, 1827)	*Atherinella alvarezi* [1] (Díaz-Pardo, 1972)
Thiara tuberculata [a, b, c, 3] (Müller, 1774)	*Carlhubbsia kidderi* [a, 1] (Hubbs, 1936)
Mexinauta impluviatus [a, 4] (Morelet, 1849)	*Gambusia yucatana* [2] Regan, 1914
Rangia cuneata [a, 6] (Sowerby I, 1831)	*Gambusia sexradiata* [a, 1] Hubbs, 1936
Cyrtonaias tampicoensis [a, 6] (Lea, 1838)	*Heterophallus (aff) rachovii* [1]
Crustaceans	*Poecilia mexicana* [3] Steindachner, 1863
Discapseudes sp. [a, b, 3]	*Ophisternon aenigmaticum* [1] Rosen & Greenwood, 1976
Hyalella azteca [a, b, 2] Saussure, 1857	*Amphilophus robertsoni* [a, 2] (Regan, 1905)
Litopenaeus setiferus [2] (Linnaeus, 1767)	*Rocio octofasciata* [a, 2] (Regan, 1903)
Potimirim mexicana [3] (Saussure, 1857)	*Cichlasoma pearsei* [a, 4] (Hubbs, 1936)
Macrobrachium acanthurus [a, b, 2] (Wiegmann, 1836)	*"Cichlasoma" salvini* [a, 2] (Günther, 1862)
Macrobrachium hobbsi [a, 2] Nates and Villalobos, 1990	*"Cichlasoma" urophthalmum* [a, 1] (Günther, 1862)
Macrobrachium olfersii [2] (Wiegmann, 1836)	*Parachromis friedrichsthalii* [a, 1] (Heckel, 1840)
Procambarus (Austrocambarus) llamasi [4] Villalobos, 1954	*Paraneetroplus synspilus* [a, 4] (Hubbs, 1935)
Callinectes sapidus [a, 2] Rathbun, 1896	*Petenia splendida* [1] Günther, 1862
Callinectes rathbunae [a, 2] Contreras, 1930	*Theraps heterospilus* [a, 2] (Hubbs, 1936)
Rhithropanopeus harrisii [a, 1] (Gould, 1841)	*Thorichthys helleri* [a, 1] (Steindachner, 1864)
Platychirograpsus spectabilis [a, 3] de Man, 1896	*Thorichthys meeki* [a, 2] Brind, 1918
Armases cinereum [2] (Bosc, 1802)	*Thorichthys pasionis* [a, 1] (Rivas, 1962)
Goniopsis cruentata [2] (Latreille, 1802)	*Dormitator maculatus* [a, 2] (Bloch, 1792)
Fish	*Eleotris amblyopsis* [a, 2] (Cope, 1871)
Anchoa parva [5] (Meek & Hildebrand, 1923)	*Gobionellus oceanicus* [1] (Pallas, 1770)
Dorosoma petenense [2] (Günther, 1867)	*Microdesmus longipinnis* [a, d, 3] (Weymouth, 1910)

Table 2. Species list of macrofauna associated with *Vallisneria americana* in Pantanos de Centla. [a] = species included in the ecological condition analysis (2005); [b] = dominant species; [c] = invasive species; [d] = first record in the study area; [1] = carnivores; [2] = omnivores; [3] = detritivores; [4] = herbivores; [5] = planctivores; [6] = benthic filter feeders.

3.2 Ecological condition

3.2.1 Water quality

In general, the seven sampling sites were placed in the category of minimum perturbation during the minimum flood season, whereas during the maximum flood season the

perturbation was medium-low. However, the spatial distribution of the perturbation categories was more homogeneous during minimum flooding, when only Polo Bank recorded a medium perturbation and the six lagoons presented a minimum perturbation. In contrast, during maximum flooding two lagoons and Polo Bank were recorded with minimum perturbation, three lagoons with medium-low perturbation and one lagoon with medium-high perturbation (Table 3). The variations in the season of minimum floods were mainly due to the effect of the EC and the TSS, whereas during maximum flooding the metrics that increased and explained the variability were DOS, NH_4 and PO_4.

Prevailing conditions were eutrophic (four lagoons) in the minimum flood season and hypereutrophic (five sites) in the maximum flood season. This difference was observed in the TSI_{TP} values which were lower in the minimum (55 to 73) than in the maximum (65 to 73) flood season, and in the tendency of TP to increase in most lagoons to hypereutrophic or to remain in this category (Table 3). The increase in TP was notable in Polo Bank and was reflected in a 20-unit increase in the TSI_{TP} (Table 3).

The PDI and TSI_{TP} values increased with a directly proportional tendency in the two flood seasons. During minimum flooding, four lagoons with a minimum perturbation coincided with a eutrophic state, and Polo Bank with a medium-low perturbation presented a hypereutrophic state. During maximum flooding, two lagoons with a minimum perturbation were eutrophic, and two lagoons and Polo Bank with a medium-high perturbation were hypereutrophic.

3.2.2 Habitat complexity and macrofauna

The greatest values of habitat complexity were recorded for San Pedrito lagoon and Polo Bank in the two seasons. However, during the minimum flood season the San Pedrito values of plant density (stems/m²) and leaf area occupied second place after Polo Bank and the lagoon Tronconada, respectively (Table 3). Polo Bank also occupied second place in biomass during minimum flooding, and in stem density during maximum flooding (Table 3). El Guanal lagoon stood out for its lack of SAV during minimum flooding and for its minimum values of structural complexity during maximum flooding (Table 3).

Species richness was greater in the minimum (S´ = 28) than in the maximum (S´ = 23) flood seasons. The greatest number of species in the minimum flood season was recorded for San Pedrito (11 species), followed by three lagoons with 10 species. No species were collected in El Guanal as there was no SAV. In contrast, the greatest number of species in the maximum flood season was recorded for El Guanal and the lowest number for Chichicastle (Table 3). The species collected with the greatest frequencies differed between the seasons. These were *Macrobrachium acanthurus*, *Dormitator maculatus*, *Hyalella azteca* and *Neritina reclivata* in the minimum flood season, and *N. reclivata*, *Astyanax aeneus* and *"Cichlasoma" salvini* in the maximum flood season.

With respect to macrofauna density, four molluscs, three crustaceans and one fish species were dominant (Table 2). On a spatial scale, the greatest value was recorded for El Sauzo in the two flood seasons (Table 3). The molluscs *Thiara tuberculata* and *Aroapyrgus clenchi* and the fish *Astyanax aeneus* and *Carlhubbsia kidderi* represented 87 and 11% of the density in the minimum flood season, whereas the gastropods *T. tuberculata*, *Cochliopina francesae* and *A. clenchi* contributed 87% of the density in the maximum flood season. In this locality, El

Sauzo, crustaceans were totally absent during the maximum flood season, and only *Macrbrachuim acanthurus* was collected during the minimum flood season.

The two sampling sites with the greatest quantitative habitat complexity, San Pedrito and Polo Bank, recorded high densities during both seasons, although with lower values than those of El Sauzo (Table 3). The gastropod *Neritina reclivata* was dominant in density in these two localities, and was followed by the crustaceans *Discapseudes* sp, *Hyalella azteca* and *Macrobrachium acanthurus* in the minimum flood season. However, in the maximum flood season, the densities of *Discapseudes* sp and *H. azteca* were greater than that of *Neritina reclivata* in San Pedrito and Polo Bank.

Sample site	PDI	TSI_{TP}	SAV biomass	SAV leaf area	S´	org/m²	inv/nat
Minimum flood season							
San Pedrito	20	75	174.2	32.3	11	24.9	0
Polo Bank	40	73.8	158.7	39.7	6	25.4	0
El Guanal	0	55	0	0	0	0	0
Chichicastle	20	65	56.6	27.2	10	12.7	0
El Sauzo	20	58	117.3	24.9	8	55.3	77
Tronconada	0	73	129.4	40.0	10	10.6	2
El Viento	20	68	133.2	28.3	10	8.4	0
Maximum flood season							
San Pedrito	60	83	217.7	54.6	8	17.5	0
Polo Bank	40	93	151.5	39.2	7	11.7	0
El Guanal	20	73	57.9	37.6	11	11.9	63
Chichicastle	40	71	130.1	40.1	3	8.3	0
El Sauzo	20	65	100	44.6	7	20.6	40
Tronconada	20	65	130.3	37.4	9	8.1	4
El Viento	40	84	181.3	49.3	7	4.7	8

Table 3. Values of water quality indices (PDI, TSI_{TP}), quantitative habitat complexity of *Vallisneria americana* as SAV biomass (g_{AFDW}/m²) and SAV leaf area (cm²), macrofauna species richness (S´) and density (org/m²), and invasive/native species rate (inv/nat), in the Biosphere Reserve of Pantanos de Centla.

The lagoon of El Guanal had no SAV and no fauna during the minimum flood season, however it recorded 11.9 org/m², and occupied third place in density during the maximum flood season (Table 3). The invasive snail *Thiara tuberculata* represented 61% of the total density in this sampling site, where the invasive fish *Pterygoplichthys pardalis* was also collected. The fish presented high densities (13 - 13.8 org/m²), whereas the crustaceans were scantily (2.7 - 4.6 org/m²).

With respect to the invasive species, the gastropod *Thiara tuberculata* was collected in El Sauzo during both seasons, in Tronconada during minimum flooding and in El Guanal during maximum flooding. The amazon sailfin catfish, *Pterygoplichthys pardalis*, was collected only during maximum flooding in these same three sites, El Sauzo, Tronconada and El Guanal. The greatest value of the invasive/native rate was calculated for El Sauzo for the minimum flood season (Table 3), in response to the high density of this mollusc (77% of the total density) in this sampling site in this season. The second greatest value of the invasive/native rate was calculated for El Guanal (Table 3), as the two invasive species represented 63% of the total density in this site in this season.

3.2.3 Spatial and temporal variation of the ecological condition

The PDI and the invasive/native species rate acted positively on the ecological condition with values above 60% in both seasons, although the PDI increased 17% during the minimum flood season. In contrast, the TSI_{TP}, S´ and macrofauna density values were below 35%. The percentages calculated for SAV leaf area and SAV biomass were intermediate (38 – 60%) and, inversely to the PDI and TSI_{TP}, decreased by 22 and 11% during the minimum flood season (Figure 1). The SAV decrease was mainly associated with the effect of the absence of SAV in El Guanal. Notwithstanding the temporal variation of the seven metrics described in this paragraph, only the SAV leaf area and PDI values were significantly different in the two seasons (Kruskal-Wallis; p = 0.0181 and p = 0.0527, respectively), as the other five metrics were statistically similar.
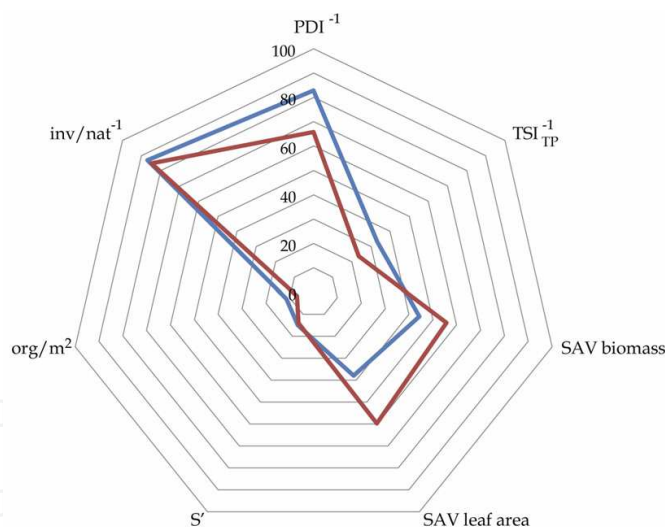

Fig. 1. Temporal variation of the ecological condition for macrofauna associated with *Vallisneria americana* in the Biosphere Reserve Pantanos de Centla (minimum flood season = blue line; maximum flood season = red line) (PDI-1 = Perturbation Degree Index; TSI_{TP}-1 = Trophic State Index for total phosphorus; S´ = species richness of macrofauna; inv/ nat-1 = Invasive/native species rate; org/m2 = macrofauna density; SAV leaf area = *Vallisneria americana* leaf area; SAV biomass = *Vallisneria americana* biomass).

The ecological condition estimated for the minimum (45%) and the maximum (44%) flood seasons was statistically similar (Kruskal-Wallis; p = 0.9491). This similarity is explained by the fact that the effect of the temporal variation of the two environmental indices of the

water (PDI and TSI_{TP}) was neutralised by similar opposite values recorded for the two habitat complexity metrics, SAV leaf area and SAV biomass (Figure 1).

The increase in the quantitative complexity of the habitat during the maximum flood season is reflected in the increase in the number of species and density of the associated macrofauna on a local scale, as occurred in El Guanal lagoon (11 species). However, this was not the case in general, as the S´ (23 species) was lower during this season than during the minimum flood season (28 species) (Figure 1). In contrast, the decrease in the environmental condition of the water (PDI and TSI_{TP}) was associated with the decrease in the macrofauna collected during maximum flooding, particularly in San Pedrito lagoon and Polo Bank where the only medium-high perturbation (PDI) and the highest value of hypereutrophia (TSI_{TP}), respectively, were recorded (Table 3).

This temporal variability in the metrics explained the spatial distribution of the lagoons and Polo Bank in three different groups for the two seasons. During minimum flooding (Figure 2), a group with the greatest ecological condition values (> 45%) was formed by three lagoons and Polo Bank, characterised by the greatest values of habitat complexity. A second group with intermediate values was formed by El Sauzo with high habitat complexity values and the greatest density of the invasive mollusc *Thiara tuberculata*, and Chichicastle with low values of habitat complexity. Lastly, the lagoon of El Guanal remained separated due to the disappearance of its SAV patch and the resulting absence of macrofauna (Table 3).

During the season of maximum floods, three groups were formed (Figure 3) where, in contrast with the other season, Polo Bank moved to the group with intermediate values of ecological condition, in response to the increase in TP that was reflected in the extreme value of hypereutrophic condition detected by the TSI_{TP}. Although El Guanal recorded 11 species of macrofauna in SAV, this locality again remained separated, with the smallest value of ecological condition as a result of 1) the density of two invasive species, *T. tuberculata* and *Pterygoplichthys pardalis*, and 2) the change from an eutrophic to a hypereutrophic condition (Table 3).
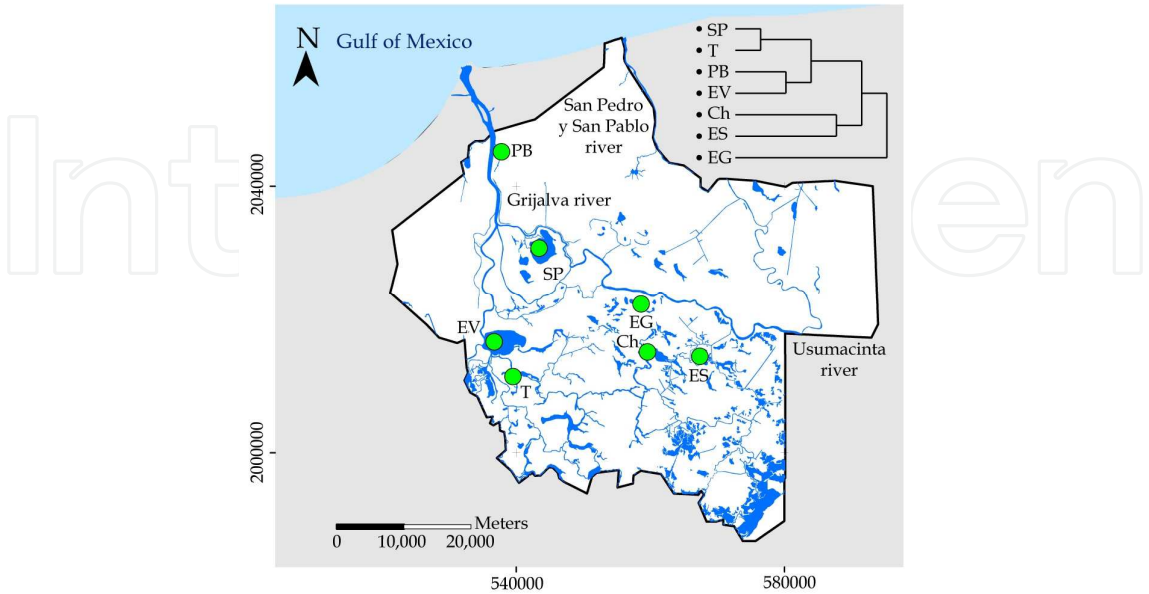

Fig. 2. Spatial variation of the ecological condition for macrofauna associated with *Vallisneria americana* in the minimum flood season in the Biosphere Reserve Pantanos de Centla.
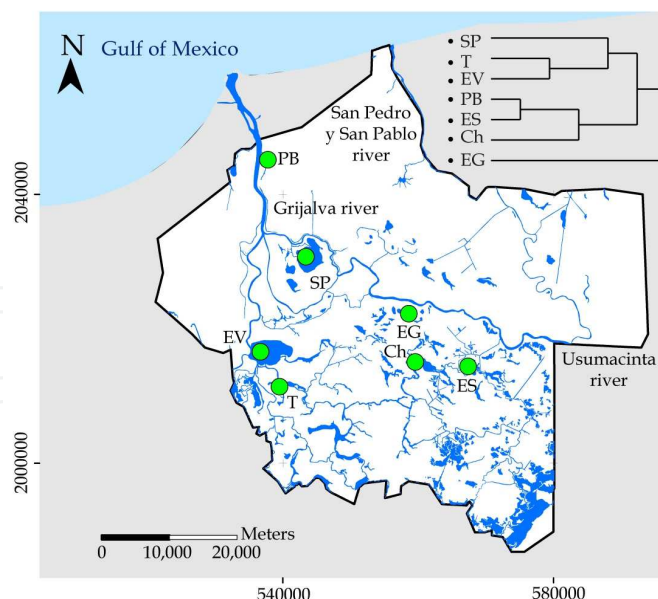
Fig. 3. Spatial variation of the ecological condition for macrofauna associated with *Vallisneria americana* in the maximum flood season in the Biosphere Reserve Pantanos de Centla.

4. Discussion

The water quality indicators (PDI and TSI$_{TP}$) had greater values in the minimum flood season than in the maximum flood season, although the degree of perturbation (PDI) in the SAV sampling sites was lower than that recorded for SBS in 2000-2001 (Salcedo et al., 2012). In contrast, the quantitative complexity of *V. americana* increased during maximum flooding, although this was not reflected in a significant increase in species richness and density of associated macrofauna. This is contrary to the general situation where an increase in habitat complexity, understood as a greater availability of microhabitats, favours a greater abundance and diversity of associated fauna (Heck & Wilson, 1987; York et al., 2006; Gullström et al., 2008). However, quantitative habitat complexity not always increase the relative habitat value of SAV (Seitz et al., 2006; Bogut et al., 2007; Florido & Sánchez et al., 2010; Schultz & Kruschel, 2010).

The greater abundance and diversity of fauna associated with SAV is explained considering the part the vegetation plays as feeding and nursery areas, and as physical refuges against predators (Moskness & Heck, 2006; Pelicice & Agostinho, 2006; Rozas & Minello, 2006; Genkai-Kato, 2007; Hansen et al., 2011). SAV is also a key component in maintaining ecosystem function, particularly in shallow systems with bottom-up trophic dynamics (Ni, 2001; Jaschinski & Sommer, 2008). The record of 53 species of macrofauna associated with SAV in this study was greater than those published for other similar ecosystems with structured habitats (Vega-Cendejas, 2004; Bogut et al., 2007; Quiroz et al., 2007). One species, the omnivorous fish *Microdesmus longipinnis*, was not recorded previously by Reséndez and Salvadores (2000), Mendoza-Carranza et al. (2010), Macossay et al. (2011) or Sánchez et al. (2012).

The high number of species associated with *V. americana* that was recorded in this study and other studies carried out in the BRPC (Mendoza-Carranza et al., 2010; Macossay et al., 2011;

Sánchez et al., 2012) emphasizes the importance of the *V. americana* patches, that occupy less than 1% of the substrate of the permanent aquatic ecosystems (Sánchez et al., 2007). Among the molluscs that were collected, most of the species of the Hydrobiidae family are recorded as herbivorous (Hershler & Thompson, 1992) and *Neritina reclivata* is a microphage with a distribution associated with SAV (as examples, García-Cubas et al., 1990; Lane, 1991). The invasive detritivorous snail *Thiara tuberculata* is widely distributed, numerically dominant and was collected both in SAV and SBS (Contreras-Arquieta et al., 1995; Sánchez et al., 2012).

The distribution of macrocrustaceans in fringe wetlands (Brinson, 1993) has been frequently associated with macroalgae and aquatic angiosperms (Minello et al., 1990; Sheridan, 1992; Sánchez et al., 2012), although their dependence on SAV and their feeding habits vary according to the stage of ontogenetic development, behaviour, foraging strategies and predator-prey interactions, as is the case of the swimming crabs (Kuhlmann & Hines, 2005; Florido & Sánchez, 2010). Their use of the habitat also varies, as for example penaeid shrimp during the various phases of epibenthic postlarvae and juveniles in estuarine ecosystems (McTigue & Zimmerman, 1991; Sánchez, 1997; Pérez-Castañeda & Defeo, 2001; Beseres & Feller, 2007). The brachyurans *Platychirograpsus spectabilis*, *Armases cinereum* and *Goniopsis cruentata* collected in SAV were small in size, as the adults are semi-terrestrial (Schubart et al., 2002; Álvarez et al., 2005).

Most of the 12 cichlids collected in SAV in this study were not associated with any particular habitat (Miller et al., 2005; Macossay et al., 2011). This may be because only *Paraneetroplus synspilus* and *Cichlasoma pearsei* are herbivores, while the other species are carnivores or omnivores (Schmitter-Soto, 1998; Miller et al., 2005; Froese & Pauly, 2011). The smaller number of species of the family Poeciliidae collected in this study, in comparison with Macossay et al. (2011), is related to most of the species inhabiting MV (Sánchez et al., 2012) and feeding mainly on insect larvae (Schmitter-Soto, 1998; Miller et al., 2005), which is not the case of the omnivore *Poecilia mexicana*. The batracoid *Opsanus beta* was the only species associated exclusively with SAV in Pantanos de Centla (Sánchez et al., 2012) and seagrasses in other ecosystems (Schofield, 2003; Vega-Cendejas, 2004). The preference of the carnivore *O. beta* for epibenthic prey distributed in SAV and its stalking strategy are common in fish that are associated with this habitat (Schultz & Kruschel, 2010).

Electric conductivity (EC) and TSS increased markedly during the minimum flood season. The increase in EC was related to the effect of the tidal currents, as the water volume decreases by 40% (18,722 million m³) during this season (Salcedo et al., 2012). This increase in EC, during the smaller phase of the flood pulse, coincides with reports for other fringe wetlands that consider water chemistry and ecology at different scales (see Thomaz et al., 2007; Fernandes et al., 2009; Souza-Filho, 2009). The resuspension of TSS in response to the high energy in tidal-current dominated environments (Brinson, 1993) and the decrease in DOS (Varona-Cordero & Gutiérrez, 2003) have been related to an increase in EC.

Ecologically, the spatial and temporal variation of the estuarine condition has helped explain the distribution of species in SAV in coastal wetlands, the temporal immigration of marine fauna and the establishment of estuarine fauna (Pérez-Castañeda & Defeo, 2001; Barba et al., 2005; Sosa-López et al., 2007). In the case of the BRPC, the effect of sea water by the tidal currents influence is restricted during the high tide in the minimum flood season

with EC long term values (2001-2010) below 10,880 µScm[-1] (Salcedo, unpublish data). This restricted estuarine effect may be observed through the dominance of freshwater aquatic angiosperms and the minimum amount of estuarine fauna in the BRPC. For example, the presence of *V. americana* is indicative of frequent freshwater or oligohaline conditions, as it is common in 1.3 to 5 PSS and has been found in 12 PSS under natural conditions (Korschgen & Green, 1988; Boustany et al., 2010). Thus, the absence of estuarine molluscs and the occasional immigration of estuarine or marine crustaceans are to be noted, though expected, in this study, with only the blue crab *Callinectes sapidus* collected once in Polo Bank, in the minimum flood season, in 0.5 PSS. This euryhaline swimming crab is numerically dominant in many estuarine ecosystems of the Western Atlantic, and shows no preference for a particular type of structured or unstructured habitat (Kuhlmann & Hines, 2005; Florido & Sánchez, 2010). Only the cirripedian *Balanus improvisus* Darwin, 1854, a stenohaline macrocrustacean distributed in polyhaline and marine environments and was reported with a distribution restricted to the area with marine influence (Montalvo-Urgel et al., 2010), where Polo Bank is located. Moreover, there were no estuarine species and only two marine fish species (*Anchoa parva* and *Gobionellus oceanicus*) among the 30 collected in SAV in this study, as well as among the 12 estuarine and marine species previously recorded for the BRPC (Macossay et al., 2011). Also, the macrofauna collected from *V. americana* in the area that receives the effect of the tides differs markedly from that recorded for oligo-mesohaline environments in other coastal wetlands (Zimmerman et al., 1990; Domínguez et al., 2003).

The increase in TSS during minimum flooding is explained by the resuspension of sediments generated by the dominant northerly and southeasterly winds. Sediment resuspension by the wind has been reported for other ecosystems (Schallenberg & Burns, 2004; Thomaz et al., 2007). The resuspended TSS affect the presence, diffusion and assimilation of nutrients that, in turn, affect the transparency of the water and the primary production in shallow aquatic ecosystems (Ni, 2001; Schallenberg & Burns, 2004; Ahearn et al., 2006). The obstacle that the TSS present to light penetration has been considered one of the main hypotheses to explain the drastic decrease and disappearance of SAV in coastal wetlands (Boustany et al., 2010). However, *V. americana* has a competitive advantage over other aquatic angiosperms in conditions of limited growth caused by the availability of light, as its rate of photosynthesis is more efficient and it rapidly acclimatises to light variations (Barko et al., 1982; Catling et al., 1994; Harley & Findlay, 1994). Under experimental conditions of low light intensity, *V. americana* responds with a decrease in the below and above sediment biomass and in the length and width of the leaves (Kurtz et al., 2003). However, light in wetlands is irregular in intensity, and rooted macrophytes recuperate by the translocation of resources through interconnected rametes, that allows nutrient and metabolic products to move among the patches that receive light (Catling et al., 1994).

The increase in TSS deteriorates the ecological condition by favouring eutrophic-hypereutrophic conditions (Salcedo et al., 2012). The eutrophic state obtained with the TSI_{TP} may be related to the homogeneous distribution of the TSS, TP and PO_4 that was established by the flooding cycle (Salcedo et al., 2012). The deterioration of the ecological condition due to the increase in TSS, and the eutrophic state, have also been related to the loss of the indirect ecological services generated by the SAV, such as the control of the bottom-up dynamics in aquatic ecosystems (Ni, 2001; Bayley et al., 2007; Genkai-Kato, 2007; Heck & Valentine, 2007). In contrast, the perturbation categories (PDI) resulted lower than those

estimated in 2000-2001 for sampling sites with SBS in the BRPC (Salcedo et al., 2012). The local disappearance of the *V. americana* patch in El Guanal during the minimum flood season, as well as the marked variation in SAV biomass and SAV leaf area, negatively affected the value of the ecological condition estimated for the minimum flood season. This disappearance coincided with the low persistence on a local scale recorded in the freshwater wetland of Whalebone Cove, that is connected to Connecticut river in the USA (Capers, 2003). This point is relevant as the value of EC (8000 μScm^{-1}) quantified in SAV sites in the BRPC is not reported as critical for the growth and survival of *V. americana* (Boustany et al., 2010). In contrast, the maximum value of TSS (42 mg L^{-1}) is near the critical value for the survival of SAV (Catling et al., 1994).

During the maximum flood season, the decrease in DOS and the increase in NH_4 and PO_4 recorded for the six sampling sites with the lower degree of perturbation (PDI) occurred in response to the homogenisation generated by river transportation at the time of the maximum level of the flood pulse, as has been reported in this and other coastal wetlands (Contreras-Espinoza & Wagner, 2004; Debels et al., 2005; Thomaz et al., 2007; Salcedo et al., 2012). In the case of the decrease in DOS, this has been related to the greater dispersion of the algal community generated by the increase in the water volume of the rivers throughout the flood plain (Ahearn et al., 2006; Weilhoefer et al., 2008), as has occurred in other neotropical and tropical wetlands (Thomaz et al., 2007).

The decrease in DOS has also been related to the remineralisation of organic matter that was observed through the increase in NH_4 (Carvalho et al., 2003; Ahearn et al., 2006). The greater amounts of PO_4 during maximum flooding in comparison with minimum flooding have been related to fluvial and agricultural runoff, and input of waste water from villages along the river margins (Contreras-Espinoza & Wagner, 2004; Debels et al., 2005; Salcedo et al., 2012). This pattern of spatial distribution has been reported for other fringe wetlands (Contreras-Espinoza & Wagner, 2004; Debels et al., 2005). The increase in TP, detected through the dominance of the hypereutrophic condition of TSI_{TP} during maximum flooding, is related to the effect of the greatest flood pulse level. It has also been associated with the remineralisation of organic matter from macrophytes established in areas of temporal flooding, from where it is freed into the water column (Carvalho et al., 2003; Kansiime et al., 2007).

The ecological integrity of coastal rooted macrophytes is directly threatened on a worldwide scale by the decrease in DOS and the overload of N, a chronic stress situation that has recently been recognised (Burkholder et al., 2007; Waycott et al., 2009). In contrast, the impact of the deficiency of P has been more significant with respect to the growth and survival of SAV (Touchette & Burkholder, 2000; Leoni et al., 2008). American Wildcelery has been proposed as a bioindicator of eutrophication considering its $\delta^{15}N$ values (Benson et al., 2007). However, no symptoms of lethal stress or direct toxicity were experimentally recorded in the leaves and roots of young plants of the population established in the BRPC, as a result of the enrichment of N with NH_4, NO_3 and the $NO_3:NH_4$ ratio of 2000 μg L^{-1}, although variations in growth were detected at the sublethal level (Ruiz-Carrera & Sánchez, 2012). In the case of *Vallisneria spinulosa* Yan, the interaction between N and P produces differences in the stress response in a wide range of N concentrations that explain the absence of toxicity (Li et al., 2008), implying that the N/P synergism may be associated with the vitality of the plants. In this season, the increase in SAV quantitative habitat complexity

may be explained by the minimum values of DOS (18%) and maximum values of NH_4 (321 μgL^{-1}), TP (460 μgL^{-1}) and PO_4 (100 μgL^{-1}) that have not yet generated lethal effects for the *V. americana* in the BRPC, as well as by the resilience mechanism that is active in the aquatic ecosystems with *V. americana* populations that have been affected by increases in nutrient concentrations (Morris et al., 2003a; 2003b).

Also to be considered is that, at the start of the maximum flood season in the BRPC, *V. americana* presents a direct relationship between the growth in length of the leaves and the depth of the water column, which implies growth occurs in a short time, as depth increases from 0.2-0.4 to 2.5-5 m. The hypotheses to explain this growth of more than 1 m in a short time have not been solved, although it is believed that phototropism and gas accumulation in the system may play a part. The variation in the length of the grass leaves has been related to the increase in the abundance and diversity of the associated fauna (Bell & Westoby, 1986). This however has not been experimentally tested for the BRPC. The effect of the increase in quantitative habitat complexity provided by the greater on the density of the fauna is expected to be minimised and remain similar, especially in the case of fish, as mobile fauna colonises areas with emergent rooted vegetation that are prone to flooding, in coastal plain wetlands that are regulated by flood pulses (Fernandes et al., 2009; da Silva et al., 2010).

5. Conclusions

The ecological condition of the sampling sites with *V. americana* was favourable for the growth and survival of SAV and the associated macrofauna, in both flood seasons. In spite of the spatial differences in the ecological condition, as well as in the eutrophic and hypereutrophic conditions estimated in the SAV patches, the perturbation degree (PDI) was lower than that recorded for sites with SBS in the BRPC. Similarly, the macrofauna species number in the SAV sites was greater than in the SBS sites. The effect of two invasive species, the snail *Thiara tuberculata* and the fish *Pterygoplichthys pardalis*, requires a special analysis considering the high density of the snail. The similarity in the ecological condition estimated for both flood seasons is explained by the fact that the effect of the temporal variation of the two water environmental indices (PDI and TSI_{TP}) was neutralised by similar opposite values recorded for the two quantitative habitat complexity metrics (SAV leaf area and SAV biomass). This means that the water changes in volume by flooding cycles has a regulation effect on the physical structure of the SAV and an indirect effect on the faunal metrics, as the variations in the macrofauna are regulated by the physical structure of the SAV. The importance of the SAV patches and the flood pulses in the ecological regulation in the BRPC emphasize the necessity to review: 1) the programmes for the construction of flood control structures that alter the natural flood cycles, and 2) the hypotheses concerning the wide spatial and temporal variations and the local disappearance of the SAV patches that shelter the greatest biodiversity and occupy less than 1% of the substrate of the aquatic ecosystem in the tropical wetland of the BRPC.

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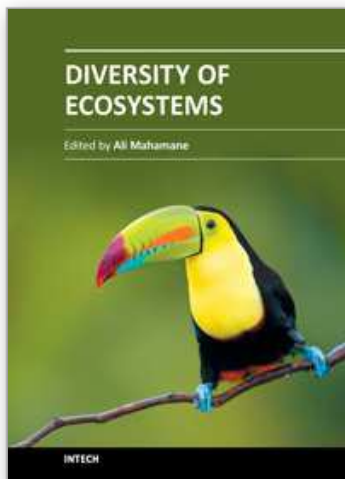
Diversity of Ecosystems

Edited by Prof. Mahamane Ali

The ecosystems present a great diversity worldwide and use various functionalities according to ecologic regions. In this new context of variability and climatic changes, these ecosystems undergo notable modifications amplified by domestic uses of which it was subjected to. Indeed the ecosystems render diverse services to humanity from their composition and structure but the tolerable levels are unknown. The preservation of these ecosystemic services needs a clear understanding of their complexity. The role of research is not only to characterise the ecosystems but also to clearly define the tolerable usage levels. Their characterisation proves to be important not only for the local populations that use it but also for the conservation of biodiversity. Hence, the measurement, management and protection of ecosystems need innovative and diverse methods. For all these reasons, the aim of this book is to bring out a general view on the function of ecosystems, modelling, sampling strategies, invading species, the response of organisms to modifications, the carbon dynamics, the mathematical models and theories that can be applied in diverse conditions.

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