CIENCIA 15(2), 193 - 204, 2007
Maracaibo, Venezuela

Temporal and spatial environmental structure of the Humacao Natural Reserve lagoon system, Puerto Rico

***Orlando J. Ferrer M.*[1]*, *Eric D. Dibble*[2], *Donald C. Jackson*[2] *and Kirk R. Rundle*[3]**

[1]*Departamento de Biología, Facultad Experimental de Ciencias, Universidad del Zulia, Apartado postal 10076, Maracaibo, Estado Zulia, Venezuela.* [2] *Department of Wildlife and Fisheries, Mississippi State Universiy, P.O. Box 9690 Mississippi State, MS 39762, USA.* [3]*North Carolina Wildlife Resources Commission, Division of Inland Fisheries, 1640 Barbara Estelle Rd. Deep Run, NC 28252, USA*

Recibido: 01-12-04 Ac eptado: 30-05-07

Abstract

In this paper we examined the temporal and spatial environmental structure of the lagoon system at Humacao Natural Reserve (HNR), Puerto Rico under a restricted, imposed water-flow regime to determine if: 1) the lagoon system maintained its estuarine conditions, 2) there were defined environmental gradients along the longitudinal distribution of the lagoons, and 3) there were hypo- or hyperhaline conditions in the lagoon system. We collected environmental data as part of a broad project effort to evaluate the fisheries of the HNR. Data were analyzed with analysis of variance using mixed linear models and principal components analysis. Two sub-systems environmentally different were identified in the HNR lagoon system: Mandri System (Mandri 1, 2, and 3 lagoons), and Santa Teresa System (Santa Teresa 1 and 2 lagoons). The lagoon system at HNR kept its estuarine conditions under low levels of precipitation and long-term isolation from the sea. There was a salinity gradient; salinity decreased as we moved along the linear series of lagoons from Mandri 1 to Santa Teresa 2. The environmental structure of the lagoons changed as a consequence of the interplaying effect of precipitation and evaporation; either hypo- or hyperhaline conditions that could eventually limit fish and invertebrate communities were not directly measured in the HNR lagoon system. Dissolved oxygen was sufficiently high to support even those species most sensitive to hypoxia; we never recorded hypoxia (<2 mg/L of dissolved oxygen). Under the prevailing exceptional environmental conditions, the HNR lagoon system offered sufficient spatiotemporal structure to fish and invertebrate populations to develop.

Key words: Caribbean Sea; Coastal lagoon; environmental structure, PCA; physicochemical gradient, Puerto Rico.

Estructura espacio-temporal del sistema lagunar de la Reserva Natural de Humacao, Puerto Rico

Resumen

Examinamos la estructura temporal y espacial del sistema lagunar de la Reserva Natural de Humacao (RNH), Puerto Rico bajo un régimen de flujo de agua restringido e impuesto para determinar si: 1) el sistema lagunar mantenía sus condiciones estuarinas, 2) habían gradientes

---

* Autor para la correspondencia. E-mail: carichuano@hotmail.com

ambientales definidos a lo largo de la distribución longitudinal de las lagunas, y 3) había condiciones hipo- o hipersalinas en el sistema lagunar. Colectamos datos ambientales como parte de un proyecto para evaluar las pesquerías de la RNH. Los datos fueron analizados con análisis de varianza usando modelos lineales mezclados y análisis de componentes principales. Se identificaron dos subsistemas ambientalmente diferentes: el subsistema Mandri (lagunas Mandri 1, 2, y 3) y el subsistema Santa Teresa (lagunas Santa Teresa 1 y 2). El sistema lagunar de la RNH mantuvo sus condiciones estuarinas bajo niveles de precipitación reducida y largo aislamiento del mar. Se identificó un gradiente de salinidad; la salinidad decrecía a medida que nos movíamos a lo largo de la serie lineal de lagunas desde Mandri 1 hasta Santa Teresa 2. La estructura ambiental de las lagunas cambió como consecuencia de la interrelación de la precipitación y la evaporación; no se reportaron condiciones hipo- o hipersalinas que pudieran limitar las comunidades de peces e invertebrados. El oxígeno disuelto fue suficientemente alto como para soportar aún aquellas especies más sensibles a hipoxia; nunca detectamos hipoxia (<2 mg/L de oxígeno disuelto). Bajo las condiciones ambientales excepcionales prevalecientes, el sistema lagunar de la RNH ofreció suficiente estructura espacio-temporal para el desarrollo de poblaciones de peces e invertebrados.

Palabras clave: Estructura ambiental; gradiente fisicoquímico; laguna costera; PCA; Puerto Rico; Mar Caribe.

Introduction

A significant body of literature exists on the importance of hydrology for wetland development and function (1-6). Hydrology is responsible for most physical and chemical features of wetlands, including tidal inundation patterns, water depth, and current speed (6). Hydrology determines vegetation composition and affects primary productivity, accumulation of organic material, decomposition, nutrient cycling and nutrient availability, among other ecosystem functions (5). These habitat features affect the degree of use by fish and invertebrates, including patterns of distribution (3), potential for colonization and growth, support of food chains, refuges from predation, reproduction, and nursery functions (6).

Another key factor in maintaining biodiversity and nursery function of estuaries in coastal systems is regular contact with the marine environment (7). This connectivity allows successful recruitment of marine organisms into the system and the inflow of saline water necessary for maintaining a salinity gradient and estuarine conditions (8). As pointed out by Whitfield and Bruton (9), the continued proper functioning of estuaries also relies on the maintenance of the natural dynamism and the oscillating phases imposed on such systems by freshwater and marine influences. When this pattern is disturbed, naturally or anthropogenically, changes can occur in the estuarine environment often adversely affecting the estuarine community. Fluctuations in salinity, for example, are regarded as a major factor governing the diversity and abundance of fish in estuaries (10).

Humacao Natural Reserve (HNR), Puerto Rico, has a brackish water lagoon system that was created by Hurricane David and Tropical Storm Frederick in 1979. Important fisheries have developed in the HNR lagoon system, most of them supported by marine species using the lagoons as nursery areas. Previous to our study, connections between the lagoon system and the Caribbean Sea (i.e., Boca Prieta and Frontera canals) were intermittent, with periods of closing and opening following natural rhythms of meteorological and hydrological events. These rhythms allowed the HNR lagoon system to keep a pulsing water-flow regime in two inlets connections at HNR. In early 2000, the U. S. Army Corps of Engineers (USACE) initiated a flood control project, permanently closed the main connection (Boca Prieta Canal) of the HNR lagoon system with the sea while constructing a new connection. The other small inlet (Frontera Canal) was blocked by natural levees created by the accumulation of sand from long-shore currents. This flood control project initiated by the USACE and its effects on the lagoon in HNR represents a major landscape manipulation because of its potential effect on fisheries and available wetland habitat due to alteration of hydrology and connections of the HNR lagoon system to the sea.

A permanent connection with the sea at HNR may affect organisms adapted to the water pulse (e.g., by increasing salinity), and reduce water-flow energy necessary to maintain the lagoon system productivity (11), and from an ecological perspective it is important to assess the current ecological functionality of the lagoon system relative to environmental conditions (12). Understanding the current ecological status of the HNR lagoon system is essential to advance knowledge of community and ecosystem ecology for future application in the management of the HNR lagoon system.

In this paper we examine the temporal and spatial environmental stability of the HNR lagoon system. Because of the natural and temporal dynamics in water level and habitat conditions in coastal lagoons, the role of connectivity among habitats should be understood (13). Temporal and spatial patterns determine how a given habitat feature influences biota. For example, greater amplitude and duration of water-level fluctuation in a marsh lead to extended periods of emersed vegetation production, followed by periods of hypoxia associated with plant decay during reflooding (13). Three interrelated specific questions were addressed in our study: 1) did the HNR lagoon system maintain its estuarine conditions under the restricted, imposed water-flow regime, 2) were there defined environmental gradients along the longitudinal distribution of the lagoons under the restricted, imposed water-flow regime, and 3) were there hypo- or hyperhaline conditions in the lagoon system under the restricted, imposed water-flow regime?

Materials and Methods

Humacao Natural Reserve is located in eastern Puerto Rico (Figure 1), within a historic coastal plain estuary formed by three interconnected valleys and drainages, the Blanco and Antón Ruiz rivers and Frontera Creek [United States Department of Commerce (USDC) and Puerto Rico Department of Natural and Environmental Resources [(DNER); 14]. Six lagoons, encompassing 249 ha, compose the system: Mandri 1, 2, and 3; Santa Teresa 1 and 2; and Palmas. The lagoons are arranged in a series that connects to the Caribbean Sea during periods of substantial precipitation. Salinity throughout the lagoon system is influenced by freshwater runoff, saltwater intrusion, and tides, and it is particularly variable during periods of substantial precipitation when the rivers connect the entire system with the sea. Tides typically do not affect the hydrology of the lagoons because the connections usually are closed to the sea.

Environmental data were collected as part of a project effort to evaluate the fisheries of the HNR, which included several strategies and sampling gears (e.g., light traps, pop nets, seining). However, only environmental data collected at each light trap site were analyzed in this paper. Light traps were set monthly at specific microhabitats identified in each lagoon in the afternoon (~3-h before sunset) and retrieved the next morning (~1-h after sunrise) from May 2000 through April 2001. Seven microhabitats were identified using dominant vegetation in the lagoon system: mangrove (red mangrove, Rhizophora mangle and white mangrove, Laguncularia racemosa), cattail (Typha dominguensis), najas (Najas sp.), chara (Chara

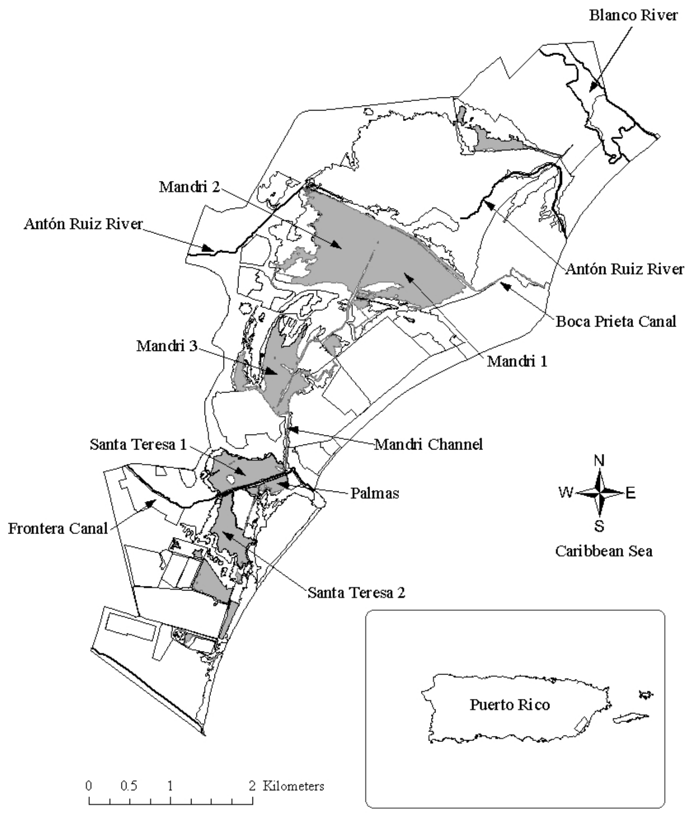

Figure 1. Map of Humacao Natural Reserve, Puerto Rico showing major hydrographic features. Figure courtesy of Marisel López and José Burgos, Department of Wildlife and Fisheries, Mississippi State University.

sp.), water hyacinth (Eichornia crassipes), cordgrass (Spartina sp.), and fern (Acrosticum sp.). Variables measured within microhabitats were: depth (m), Secchi transparency (m), water temperature (°C), dissolved oxygen (mg/L), specific conductance (μS/cm), salinity (ppt), total dissolved solids (g/L), turbidity (NTU), pH, and dissolved oxygen percent saturation. Depth was measured with a stadia rod, and the remaining variables with a Hydrolab (Hydrolab Corporation, Austin, Texas). Depth and Secchi transparency were taken only in the morning, whereas the rest of variables were taken in the morning and in the afternoon. Records of lagoon system water levels were taken weekly from a depth gauge at the canal in front of HNR headquarters. Daily precipitation data were obtained from the DNER records at HNR. The precipitation data encompassed the period 1988 through 2001, and were used to calculate monthly average precipitation for the 12 years (1988-1999) preceding my study, as well as for my study period.

Data analyses

Data were analyzed with analysis of variance (ANOVA) and principal components analysis (PCA). All ANOVAs were done with Statistical Analysis System (SAS), Version 8.02 (SAS Institute, Inc.; 15). Significance for all analyses was declared at α= 0.05. All environmental variables were compared with two-way mixed-model ANOVAs (PROC MIXED). Mixed models with repeated and random statements, and mixed models with only random statements were applied to each variable, and models with the lower Akaike's Information Criterion were selected. All ANOVAs underlying assumptions were tested; variables were transformed (e.g., $\log_e$- and/or square root-transformation, whichever was more appropriate) if treatment exhibited non-normality and/or heterogeneity of variances. When means differed significantly, a least square means (LSMEANS) approach was used to determine which means differed.

Data were split into rainy season (May 2000 and January-April 2001) and dry season (June-December 2000) to investigate seasonal effects. Each environmental variable was tested for differences between seasons with a paired-samples Student's t-test (PROC MEANS).

Principal components analysis has proven to be a valuable tool in identifying and assessing inter-correlations among the variables of interest (16). Principal components analysis combines a large number of correlated variables to generate axes representing types or groups of variables. Each axis accounts for more of the total variance in the data set than does any one of the individual variables. An indication of how strongly a variable contributes to its axis is reflected by a correlation value. Variables with either high positive or high negative correlations strongly contribute to the axis in question. The PCA on the environmental variables was conducted in PC-ORD V.4.20 (17) from the correlation matrix with scores standardized to unit variance. A 129 x 18 matrix (129 sites, 18 environmental variables; environmental variables taken in the morning and in the afternoon were introduced in the correlation matrix as individual variables) was created for this analysis. Inter-correlation between environmental variables was tested with PROC CORR; the broken-stick model (18) was used to evaluate the relative interpretability of the ordination results.

Results

Over 59% (93 out of 156 cm) of all precipitation during the study occurred between May and September 2000. The wettest months were May, August, and September 2000, when total precipitation was 53% higher than the 12-yr average (24.3 vs. 15.9 cm). The driest month was December 2000, when total precipitation was 45% lower than the 12-yr average (7.3 vs. 13.2 cm). Overall, 2000 was a drier year with a 26-cm (16%) precipitation deficit relative to 1988-1999.

As indicated above, during our study period connections of the lagoon system with the Caribbean Sea were typically closed. In August 2000, Hurricane Debby induced a substantial increase in the water level of the lagoon system (Figure 2A), although it did not force the entrance to open. Between late March and early April 2001, the USACE finalized the construction of the new canal connecting the lagoon system with the sea and mechanically opened the entrance for a few days, which resulted in a gradual declining of the water level (Figure 2A). Thus, until the end of our study, the HNR lagoon system was isolated from the sea and therefore fluctuations in the lagoon water levels were primarily associated with rainy and dry periods, and were independent of tides from the Caribbean Sea.

Mean values for all environmental variables are shown in Table 1. There were differences among months for all variables and among lagoons for all variables except for dissolved oxygen and dissolved oxygen percent saturation in the morning. Interaction for Secchi transparency, temperature in the morning, dissolved oxygen in the afternoon, turbidity in the afternoon, pH in the afternoon, and dissolved oxygen percent saturation in the morning were not significant. Seasonal data were significantly different

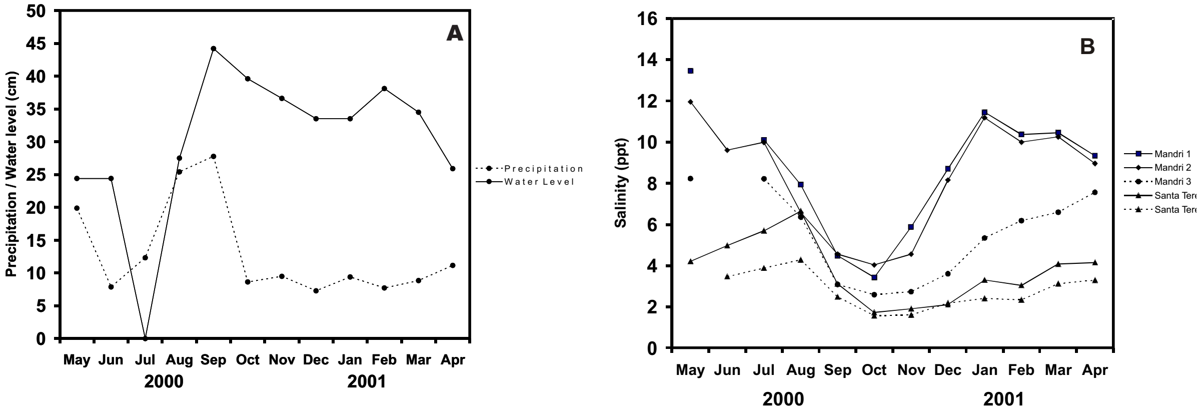

Figure 2. (A) Mean monthly water level and monthly precipitation values; and (B) mean monthly salinity values for each lagoon, Humacao Natural Reserve, Puerto Rico.

among lagoons ($P < 0.001$) although depth, dissolved oxygen in the morning and in the afternoon, turbidity in the morning and in the afternoon, and dissolved oxygen percent saturation in the morning and in the afternoon were not significantly different ($P \leq 0.23$) between seasons. Interaction terms for depth, dissolved oxygen in the morning and in the afternoon, turbidity in the morning and in the afternoon, and dissolved oxygen percent saturation in the morning and in the afternoon were not significant.

Most of the variables were significantly correlated (Table 2). The PCA produced three PCs with eigenvalues that exceeded those of the broken-stick model, and explained 77.5% of the standardized variation in the environmental /site data matrix (Table 3). Axis 1, explaining 51.9% of the variation, was a composite axis consisting of specific conductance, salinity, and total dissolved solids in the morning and in the afternoon. Axis 2, which explained 13.9% of the variation, was represented by dissolved oxygen and dissolved oxygen percent saturation in the morning and in the afternoon, and Axis 3, explaining an additional 11.7% of the variation, was represented by temperature in the morning and in the afternoon (Table 3).

Figure 3 shows the coordinate scores generated for PCA. Lagoons are ordered from right to the left according to a salinity (Axis 1) gradient, and from bottom to top according to a dissolved oxygen (Axis 2) gradient. Lagoons with low salinity (Santa Teresa System) are grouped in the right portion of the diagram, whereas lagoons with high salinity (Mandri System) are located in the left portion. The figure also shows that most sites in Mandri 3 (~67% of all sampling sites in that lagoon) are grouped in the middle lower portion of the diagram (mid salinity and low dissolved oxygen).

Thus, two environmentally different sub-systems can be defined in the HNR lagoon system: Mandri System (Mandri 1, 2, and 3 lagoons), and Santa Teresa System (Santa Teresa 1 and 2 lagoons). Relative to Mandri System, Santa Teresa System had greater depth and lower pH, dissolved oxygen in the afternoon, salinity, and turbidity (Table 1). Water level and salinity were associated with precipitation (Figure 2A-B). Average salinity decreased in all lagoons and water level increased with an increase in precipitation during August-October, and the opposite when precipitation decreased, indicating that the environmental fluctuations during the study in the entire lagoon system were a result of precipitation.

Table 1
Mean values (SE) of environmental variables measured at light trap sites (N = 129) in Humacao Natural Reserve, Puerto Rico, May 2000-April 2001.

	Mandri 1	Mandri 2	Mandri 3	Santa Teresa 1	Santa Teresa 2
Variable	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)	Mean (SE)
Depth (m) (**)	0.40 bc (0.03)	0.35 c (0.02)	0.49 b (0.03)	0.68 a (0.04)	0.73 a (0.04)
Secchi transparency (m) (**)	0.27 c (0.02)	0.22 c (0.00)	0.28 c (0.01)	0.44 b (0.02)	0.65 a (0.05)
DO in the morning (mg/L) (NS)	3.05 (0.63)	2.78 (0.29)	2.91 (0.20)	2.87 (0.23)	3.06 (0.33)
DO in the afternoon (mg/L) (**)	9.49 a (0.77)	9.47 a (0.43)	7.08 bc (0.47)	6.39 c (0.29)	8.30 ab (0.56)
pH in the morning (**)	8.39 a (0.09)	8.46 a (0.06)	7.68 b (0.08)	7.55 b (0.07)	6.93 c (0.12)
pH in the afternoon (**)	8.66 a (0.09)	8.87 a (0.07)	7.91 c (0.09)	8.04 bc (0.09)	8.29 b (0.19)
SAL in the morning (ppt) (**)	9.48 a (0.39)	8.05 b (0.72)	6.01 b (0.34)	3.52 c (0.29)	2.83 c (0.33)
SAL in the afternoon (ppt) (**)	9.49 a (0.38)	8.05 b (0.71)	6.01 b (0.32)	3.52 c (0.29)	2.83 c (0.32)
DOS in the morning (%) (NS)	46.46 (9.08)	35.53 (3.64)	36.93 (2.78)	35.42 (2.79)	35.92 (3.80)
DOS in the afternoon (%) (**)	125.11 a (16.68)	134.28 a (7.68)	94.45 bc (5.75)	88.62 c (3.51)	116.53 ab (8.54)
SPC in the morning (S/cm) (**)	16206 a (622)	13798 ab (1190)	10566 b (574)	6328 c (491)	5136 c (577)
SPC in the afternoon (S/cm) (**)	16231 a (611)	13803 ab (1180)	10578 b (535)	6327 c (499)	5124 c (568)
TDS in the morning (g/L) (**)	10.37 a (0.39)	8.83 b (0.76)	6.76 b (0.37)	4.05 c (0.31)	3.29 c (0.37)
TDS in the afternoon (g/L) (**)	10.38 a (0.39)	8.83 b (0.76)	6.77 b (0.34)	4.05 c (0.32)	3.28 c (0.36)
TEM in the morning (C) (**)	29.59 a (0.39)	28.69 ab (0.20)	26.98 c (0.24)	28.23 b (0.33)	27.78 bc (0.47)
TEM in the afternoon (C) (**)	32.15 ab (0.37)	33.16 a (0.24)	29.61 d (0.29)	30.84 cd (0.39)	31.87 bc (0.70)
TUR in the morning (NTU) (**)	43.12 b (5.11)	77.49 a (9.33)	28.54 cb (1.88)	21.29 cd (1.84)	22.57 d (7.24)
TUR in the afternoon (NTU) (**)	53.06 b (4.59)	120.50 a (11.12)	36.12 c (3.56)	32.81 cd (4.53)	38.68 d (16.14)

DO= dissolved oxygen, SAL=salinity, DOS= dissolved oxygen percent saturation, SPC= specific conductance, TDS= total dissolved solids, TEM= temperature, TUR= turbidity. (**) *P* 0.05; (NS) *P* 0.05. Means followed by different letters were significantly different

Table 2

Correlation matrix for environmental variables measured at light trap sites (N= 129) in Humacao Natural Reserve, Puerto Rico, May 2000-April 2001, used in principal component analysis (PCA). Underlined correlation values were significant at P<0.05.

	DEP	SDD	DOm	DOa	pHm	pHa	SALm	SALa	DOSm	DOSa	SPCm	SPCa	TD Sm	TDSa	TE Mm	TE Ma	TU Rm
ST	0.7																
DOm	0.1	0.1															
DOa	-0.2	-0.2	0.3														
pHm	-0.5	-0.7	-0.2	0.3													
pHa	-0.4	-0.3	-0.3	0.4	0.6												
SALm	-0.7	-0.6	-0.3	0.3	0.7	0.5											
SALa	-0.7	-0.6	-0.3	0.3	0.7	0.5	0.9										
DOSm	-0.1	-0.1	0.9	0.3	-0.1	-0.2	-0.2	-0.2									
DOSa	-0.2	-0.1	0.3	0.9	0.3	0.5	0.2	0.2	0.2								
SPCm	-0.7	-0.6	-0.3	0.3	0.7	0.5	0.9	0.9	-0.2	0.2							
SPCa	-0.7	-0.6	-0.3	0.3	0.7	0.5	0.9	0.9	-0.2	0.2	0.9						
TDSm	-0.7	-0.6	-0.3	0.3	0.7	0.5	0.9	0.9	-0.2	0.2	0.9	0.9					
TDSa	-0.7	-0.6	-0.3	0.3	0.7	0.5	0.9	0.9	-0.2	0.2	0.9	0.9	0.9				
TEMm	-0.1	-0.3	-0.2	0.1	0.5	0.5	0.2	0.2	-0.1	0.1	0.2	0.2	0.2	0.2			
TEMa	-0.2	-0.2	-0.2	0.2	0.5	0.7	0.3	0.3	-0.2	0.2	0.3	0.3	0.3	0.3	0.7		
TURm	-0.5	-0.4	-0.1	0.2	0.5	0.4	0.6	0.6	-0.1	0.1	0.6	0.6	0.6	0.6	0.1	0.2	
TURa	-0.5	-0.4	-0.1	0.2	0.4	0.4	0.5	0.5	-0.1	0.1	0.5	0.5	0.5	0.5	0.1	0.3	0.7

DEP= depth (m), ST= Secchi transparency (m), DOm= dissolved oxygen in the morning (mg/L), DOa= dissolved oxygen in the afternoon, pHm= pH in the morning, pHa= pH in the afternoon, SALm= salinity in the morning (ppt), SALa= salinity in the afternoon, DOSm= dissolved oxygen percent saturation in the morning (%), DOSa= dissolved oxygen percent saturation in the afternoon, SPCm= specific conductance in the morning (S/cm) , SPCa= specific conductance in the afternoon, TDSm= total dissolved solids in the morning (g/l), TDSa= total dissolved solids in the afternoon, TEMm= temperature in the morning (C), TEMa= temperature in the afternoon, TURm=turbidity in the morning (NTU), TURa= turbidity in the afternoon.

Table 3

Loadings of individual variables on axes 1, 2, and 3 for the principal component analysis (PCA) on environmental variables measured at light trap sites (N= 129) in Humacao Natural Reserve, Puerto Rico, May 2000-April 2001 (underlined values represent variables characterizing the axis).

Variable	PC1	PC2	PC3
Depth	0.254	0.073	0.138
Secchi transparency	0.239	0.056	0.041
Dissolved oxygen in the morning	0.125	-0.518	-0.055
Dissolved oxygen in the afternoon	-0.109	-0.496	0.157
pH in the morning	-0.261	-0.021	0.204
pH in the afternoon	-0.213	-0.019	0.405
Salinity in the morning	-0.313	0.032	-0.128
Salinity in the afternoon	-0.313	0.022	-0.129
Dissolved oxygen percent saturation in the morning	0.065	-0.496	-0.075
Dissolved oxygen percent saturation in the afternoon	-0.099	-0.436	0.227
Specific conductance in the morning	-0.314	0.030	-0.101
Specific conductance in the afternoon	-0.314	0.021	-0.104
Total dissolved solids in the morning	-0.313	0.032	-0.129
Total dissolved solids in the afternoon	-0.313	0.023	-0.130
Temperature in the morning	-0.099	0.132	0.544
Temperature in the afternoon	-0.147	0.074	0.525
Turbidity in the morning	-0.224	-0.107	-0.157
Turbidity in the afternoon	-0.228	-0.036	-0.071
Eigenvalue	9.36	2.50	2.09
Broken-stick eigenvalue	3.49	2.49	1.99
Explained variance (%)	51.9	13.9	11.7

Discussion

Our results demonstrated the lagoon system at HNR kept its estuarine conditions under extreme low levels of precipitation and long-term isolation from the sea. Under these conditions the lagoon system has undergone changes in its environmental structure due to the interplaying effect of precipitation and evaporation; either hypo-or hyperhaline conditions that could eventually limit fish and invertebrate communities were not directly measured in the HNR lagoon system during the study period.

Our data suggested a gradient in salinity existed among the HNR lagoons; salinity decreased as we moved along the linear series of lagoons from Mandri 1 to Santa Teresa 2, and the lagoon system can be considered a mesohaline-oligohaline system (0.5-18 ppt; 5). In contrast with this, however, earlier evidences suggested the lagoon

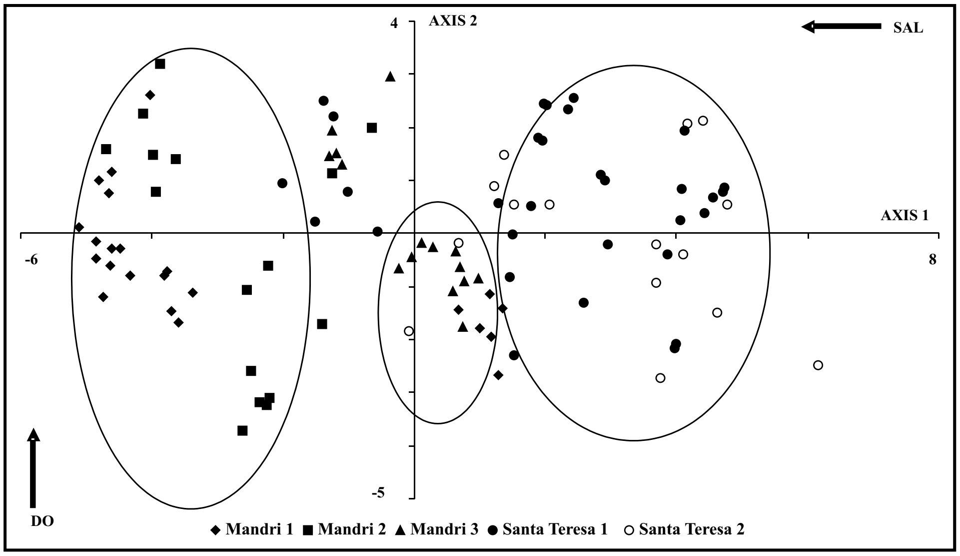

Figure 3. Ordination of the lagoon system according to the first two significant components of principal components analysis (PCA) for environmental variables recorded at light trap sites (N= 129), Humacao Natural Reserve, Puerto Rico, May 2000-April 2001. The SAL gradient increases from right to the left, and the DO gradient increases from bottom to the top. The biggest ellipse represents lagoon sites at Mandri System, and includes habitats with higher SAL and both low and high DO. The mid size ellipse represents lagoon sites at Santa Teresa System, and includes habitats with lower SAL and mid DO. Most sites in Mandri 3 are clustered in the smallest ellipse, and represent habitats with mid SAL and low DO. SAL= salinity (ppt), DO= dissolved oxygen (mg/L).

system was mixohalinic (0.5-30 ppt; 5). For example, Burger et al. (19) reported salinities 5-6 ppt in the Mandri System and 2-3 ppt in the Santa Teresa System, whereas the DNER (20) reported salinities up to 25 ppt in the Mandri System and as low as 0.5 ppt in the Santa Teresa System in 1994-1995, and Vilella and Gray (21) reported salinities ~20 ppt in the Mandri System and ~3 ppt in the Santa Teresa System.

During our study average salinity rarely dropped below 2.5 ppt in the Santa Teresa System, or rose above 10 ppt in the Mandri System. Any lower or higher salinity we recorded were probably a consequence of the predominant hydrologic regime. No inflow of seawater into the lagoon system occurred during our study period, and additionally likely no major inflows of seawater had occurred since September 1998, when Hurricane Georges caused extensive flooding. At that time seawater probably flowed into the lagoons, increasing salinity. Most of the freshwater flowing into the lagoons came from major storms, which occur on a regular basis.

Dissolved oxygen was sufficiently high to support even those species most sensitive to hypoxia. According to Diaz and Rosenberg (22) hypoxia is a condition characterized by water containing less than 2 mg/L of dissolved oxygen. Morning concentrations of dissolved oxygen ranged from 2.78 mg/L in the Mandri System to 3.06 mg/L in the Santa Teresa System, whereas in the afternoon dissolved oxygen ranged from 6.39 mg/L in the Santa Teresa System to 9.49 mg/L in the Mandri System.

Differences in dissolved oxygen concentrations between Santa Teresa and Mandri systems can be explained by the interplay of several biological and physical factors. Low dissolved oxygen concentrations in estuarine waters have been associated with the proliferation of submersed vegetation (23). Emersed shoreline vegetation (e.g., cordgrass, cattail) and submersed forms (i.e., najas and chara) occurred in the HNR lagoon system, although dominant plant species varied along the salinity gradient. Low salinities favored submersed vegetation in the Santa Teresa System, which in turn played an important role in explaining dissolved oxygen variability. Mandri lagoons had a bigger overall surface area than Santa Teresa lagoons, thus increasing the oxygenation action of the waves by diffusion, whereas Santa Teresa lagoons were smaller and protected from the wind by abundant flora along their perimeters, which diminished the wind action. However, the high abundance of submersed vegetation in the Santa Teresa System allowed these lagoons to reach mean dissolved oxygen of up to 8.30 mg/L in the afternoon. Thus, the entire lagoon system offered sufficient oxygen for animal communities to develop.

Although the Mandri System presented higher turbidity than the Santa Teresa System, elevated turbidities were only recorded in Mandri 2 in the afternoon when the wind action re-suspended fine-grained mud characteristic of the entire lagoon system bottom. The belt of submerged vegetation in the Santa Teresa System dampened wave action, rendering it a clearer water system.

Water level in the HNR lagoon system was seasonally fluctuating, with minima recorded at the end of the dry season. A seasonally fluctuating water level is the rule in most wetlands (5). The year 2000 was an exceptionally dry year in Puerto Rico, indicating that water levels were probably at or near their lower records. However, as noted above, we never recorded extreme hypoxia or anoxia, indicating that dissolved oxygen was not a limiting factor in the HNR lagoon system. However, extremely low water levels reduce habitat availability that in turn can affect fish community. Reduction of aquatic habitats that periodically concentrate fish can increase their competition for resources (24-25).

Estuaries in general, and coastal lagoons in particular, are known never to reach a typical or stable state, but rather display numerous small successional changes directed by episodic events (9). The hydrology of these ecosystems creates the environmental conditions that make them unique (5). Although further research is needed to completely delineate the physicochemical structure of the HNR lagoon system, particularly after the USACE completed the new connection with the Caribbean Sea, this paper indicated that under the prevailing exceptional environmental conditions, the HNR lagoon system offered sufficient spatiotemporal structure to fish populations to develop. Synergism of environmental dynamism and habitat variability should, in turn, influence spatiotemporal fish and invertebrate assemblage patterns. Assemblage structure (e.g., species composition, abundance, life-history stages) and fish food resources availability should be evaluated across seasonal and spatial gradients of important physicochemical variables identified in this paper (e.g., salinity, dissolved oxygen), and habitat zones identified and characterized by species and their optima across gradients.

Acknowledgments

We thank Manuel Córbet and the Humacao Natural Reserve personnel for their support during the implementation of this project. Thanks are also due to Ramón Del Moral and Miguel Ortiz for helping us with much of the fieldwork. Federal Aid Project F-44.1 provided financial assistance.

References

1. FERREL D.J., BELL J.D. ***Mar Ecol Prog Ser*** 72:15-24, 1991.
2. FERREL D.J., McNEIL S.E., WORTHINGTON D.G., BELL J.D. ***Aust J Mar Freshwat Res*** 44: 881-899, 1993.
3. McIVOR C.C., ROZAS L.P. Direct nekton use of intertidal saltmarsh habitat and linkage with adjacent habitats: a review from the southeastern United States. In: K.F. Nordstrom and C. T. Roman (editors). Estuarine shores: evolution, environments and human alterations. John Wiley and Sons, Chichester (U.K.), pp. 311-334, 1996.
4. HANNAN J.C., WILLIAMS R.J. ***Estuaries*** 21: 29-51, 1998.
5. MITSCH W.J., GOSSELINK J.G. Wetlands. John Wiley and Sons, Inc., New York (USA), pp. 920, 2000.
6. WILLIAMS G.D., DESMOND J.S. Restoring assemblages of invertebrates and fishes. In: J. B. Zedler (editor). Handbook for restoring tidal wetlands. CRC Press, Boca Raton, Florida (USA), pp. 235-269, 2001.
7. WALLACE J.H., KOK H.M., BECKLEY L.E., BENNET B., BLABER S.J. M., WHITFIELD A. K. ***S Afri J Sci*** 80: 203-207, 1984.
8. VIVIER L., CYRUS D.P. ***Mar Freshwat Res*** 53: 457-464, 2002.
9. WHITFIELD A.K., BRUTON M.N. ***S Afr J Sci*** 85: 691-694, 1989.
10. KOK H.M., WHITFIELD A.K. ***S Afr J Zool*** 21: 309-315, 1986.
11. ODUM W.E., ODUM E.P., ODUM H.T. ***Estuaries*** 18: 547-555, 1995.
12. DIAMOND J. Overview: Laboratory experiments, field experiments, and natural experiments. In: J. Diamond and T. J. Case (editors). Community ecology. Harper and Row, New York (USA), pp. 3-22, 1986.
13. GELWICK F.P., AKIN S., ALBREY-ARRINGTON D., WINEMILLER K.O. ***Estuaries*** 24: 285-296, 2001.
14. PUERTO RICO DEPARTMENT OF NATURAL AND ENVIRONMENTAL RESOURCES. Documento de designación reserva natural pantano y bosque de Pterocarpus de Humacao. Estado Libre Asociado de Puerto Rico, San Juan (Puerto Rico), pp. 54, 1986.
15. SAS. SAS/STAT Version 8.02. SAS Institute, Inc., Cary, North Carolina (USA), 2001.
16. GAUCH H.G., Jr. Multivariate analyses in community ecology. Cambridge University Press, Cambridge, Massachusetts (USA), pp. 298, 1982.
17. MCCUNE B., MEFFORD M.J. PC-ORD for Windows - Multivariate analysis of ecological data. Version 4.20. MJM Software, Inc., Gleneden Beach, Oregon (USA), 1999.
18. JACKSON D.A. ***Ecology*** 74: 2204-2214, 1993.
19. BURGER J., COOPER K., GOCHFELD D.J., SILVA J.E., SAFINA C., LIPSKY D., GOCHFELD M. ***Estuaries*** 15: 239-245, 1992.
20. PUERTO RICO DEPARTMENT OF NATURAL AND ENVIRONMENTAL RESOURCES. Fishing access facilities for Humacao Wildlife Refuge. Project F-31-4. Annual Report. Humacao (Puerto Rico), pp. 27, 1995.
21. VILELLA F., GRAY M. Ecological assessment and management plan for the Humacao Wildlife Refuge. Final Report. Federal Aid Project FW-10. Puerto Rico Department of Natural and Environmental Resources, San Juan (Puerto Rico), pp. 315, 1997.
22. DIAZ R.J., ROSENBERG R. ***Oceanogr Mar Biol Annu Rev*** 33: 245-303, 1995.
23. VIVIER L., CYRUS D.P. ***Mar Freshwat Res*** 53: 457-464, 2002.
24. LOWE-MCCONNELL R. H. Ecological studies in tropical fish communities. Cambridge University Press, Cambridge (UK), pp. 390, 1987.
25. WINEMILLER K.O. ***Env Biol Fish*** 26: 177-199, 1989.