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Assessment of fish and invertebrate assemblages, and availability of food supporting fishery resources at Humacao Natural Reserve lagoon system, Puerto Rico

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Abstract

The Humacao Natural Reserve (HNR) lagoon system, Puerto Rico has become an important fish source for eastern Puerto Rico. Principal fishes targeted are tarpon (*Megalops atlanticus*), common snook (*Centropomus undecimalis*), swordspine snook (*C. ensiferus*), Mozambique tilapia (*Orecochromis mossambicus*) and redbreast tilapia (*Tilapia rendalli*). We asked whether the HNR lagoon system had a sufficient functional structure to support sustainable principal fish fisheries. To answer this question, we collected fish and invertebrates with light traps (N = 129), pop nets (N = 224), seines (N = 208), gill nets (N = 228), and trap nets (N = 123) and determined the physicochemical and habitat structure of the lagoon system between March 2000 and May 2001. Canonical correspondence analysis (CCA) indicated that there was a strong association between salinity and the fish assemblage along the linear series of lagoons from the Mandri through the Santa Teresa systems. The CCA also indicated that each principal fish species was associated with a different set of environmental variables; tarpon was associated with low salinity, dissolved oxygen, and temperature; snook were associated with high salinity, whereas tilapia were associated with high dissolved oxygen and temperature. All our analyses indicated that the HNR lagoon system was a fully functional system supporting sustainable fisheries.

Key words: Assemblage; Caribbean Sea; coastal lagoon; Puerto Rico; snook; tarpon; tilapia.

Evaluación de los ensamblajes de peces e invertebrados y la disponibilidad de alimentos que soportan los recursos pesqueros de la Reserva Natural de Humacao, Puerto Rico

Resumen

La Reserva Natural de Humacao (RNH), Puerto Rico se ha convertido en una importante fuente de peces para la zona oriental de la isla. Los peces más buscados son el sábalo (*Megalops atlanticus*), el róbalo común (*Centropomus undecimalis*), el róbalo espina de espada (*C. ensife-*

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rus), la tilapia Mozambique (*Orecochromis mossambicus*) y la tilapia pecho rojo (*Tilapia rendalli*). Nos preguntamos si el sistema de lagunas de la RNH tenía una estructura funcional suficiente para soportar pesquerías sostenibles. Para responder esta pregunta, colectamos peces e invertebrados con trampas de luz (N = 129), redes emergentes (N = 224), redes de barrido (N = 208), redes de ahorque (N = 228) y redes trampa (N = 123) y determinamos la estructura fisicoquímica y de hábitat del sistema de lagunas entre marzo de 2000 y mayo de 2001. Un análisis de correspondencia canónica (ACC) indicó que había una fuerte asociación entre la salinidad y los ensamblajes de peces a lo largo de la serie de lagunas desde el sistema Mandri hasta el sistema Santa Teresa. El ACC también indicó que cada especie de pez sometido a pesca estaba asociado con un juego diferente de variables ambientales; el sábalo estuvo asociado con bajas salinidades, oxígeno disuelto y temperatura; los róbalos estuvieron asociados con alta salinidad, mientras que las tilapias estuvieron asociadas con altas concentraciones de oxígeno disuelto y temperatura. Todos nuestros análisis indicaron que el sistema de lagunas de la RNH era un sistema completamente funcional para soportar pesquerías sostenibles.

Palabras claves: Ensamblaje; laguna costera; Mar Caribe; Puerto Rico; róbalo; sábalo; tilapia,

Introduction

Coastal lagoons are used by many fishes for reproduction, feeding and shelter (1-4). The link between habitat suitability and fish and invertebrate assemblage structures in these ecosystems in particular, and in wetlands in general, has been studied intensively (4, 5-10). Fish abundance, species diversity, and habitat use have been evaluated to determine whether particular wetlands provide adequate functional value (11). The spatial distribution of food and habitat differences may be important in determining fish habitat use (12).

The functional value of a coastal lagoon is even more important to determine when the system support fisheries. Important fisheries have developed in the brackish water lagoon system at Humacao Natural Reserve (HNR), Puerto Rico. The reserve's marsh is a matrix of habitats (13), characterized by various plant species and communities that likely provides habitat structure important to fishes (14). Fishes principally targeted are tarpon (*Megalops atlanticus*), common snook (*Centropomus undecimalis*), swordspine snook (*C. ensiferus*), Mozambique tilapia (*Oreochromis mossambicus*) and redbreast tilapia (*Tilapia rendalli*). There are other estuarine fish species (e.g., gerrids, gobiids) and invertebrates (e.g., shrimps, crabs), in the HNR lagoon system that interrelate with each other and constitute assemblages, the dynamics of which remains unknown. The Puerto Rico Department of Natural and Environmental Resources (DNER) was interested in evaluating the fishery potential of the lagoons, and in implementing an appropriate strategy for their management. Understanding the spatial distribution of the fish resources in the lagoons and identifying factors shaping this distribution are necessary to future enhancing fish populations in the HNR lagoon system.

The primary objective of our study was to evaluate abundance of principal fishes in the HNR lagoon system and their relationships with habitat for reproduction, recruitment, and survival; and identify availability and distribution of forage items (invertebrates and early life stages of fishes). We addressed the specific hypothesis that lagoon-specific differences in habitat structure and salinity gradient mediated differences in fish communities and forage items across lagoons.

Materials and Methods

Study site description

The lagoon system of HNR is located in eastern Puerto Rico (Figure 1), within a historic coastal plain estuary formed by three interconnected valleys and drainages (i.e., Blanco and Antón Ruiz rivers, Frontera Creek) (15). Six lagoons, stretching 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 only connects to the Caribbean Sea during periods of substantial precipitation. The lagoon system contains many different habitats but can be broadly divided longitudinally into (1) the Mandri system (Mandri 1, 2, and 3); which is intermittently influenced by tides and contains no submersed vegetation, and (2) the Santa Teresa system (Santa Teresa 1 and 2), which has very little or no tidal influence and contains submersed vegetation. 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. The emersed vegetation of the reserve is characterized by erect, rooted, herbaceous hydrophytes (e.g., sedges, *Cyperus* sp.; grass, *Panicum* sp.and *Spartina* sp.; cattail, *Typha dominguensis*); the forested vegetation is characterized by red mangrove (*Rhizophora mangle*), and white mangrove (*Laguncularia racemosa*); the submersed vegetation (typically in the Santa Teresa system) is characterized by najas (*Najas* sp.) and chara (*Chara* sp.) (14, 16).

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 inlet connections at HNR. The connection and variation in hydrology is a key com-

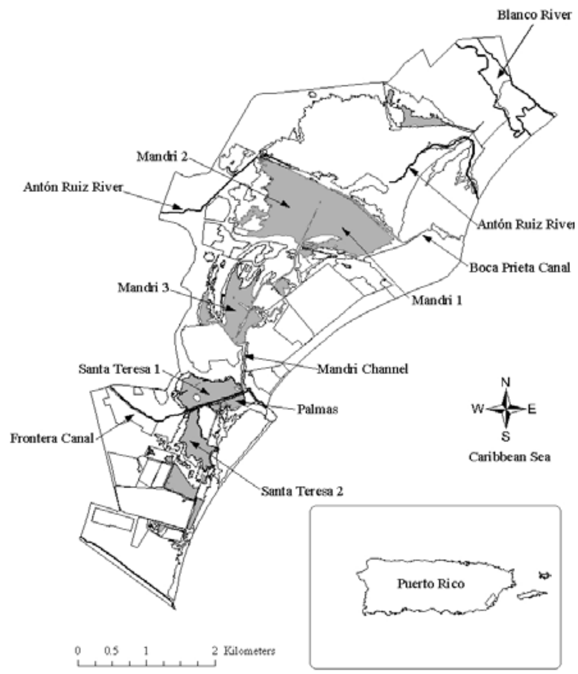

Figure 1. Map of Humacao Natural Reserve (Puerto Rico), showing major hydrographic features. Figure courtesy of Marisel López and José Burgos, Department of Wildlife and Fisheries, Mississippi State University.

ponent of wetland function and structure (17). 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 through the Antón Ruiz River. The other small inlet (Frontera Canal) was blocked by natural levees, created by the accumulation of sand from longshore 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 connection 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 (17). From an ecological perspective it is important to assess the current ecological functionality of the lagoon system relative to environmental conditions (18).

Snook, tarpon, and tilapia population assessment

For population assessment sampling purposes, all lagoons were considered as distinct units and sampled on an individual basis. Each lagoon was divided into six sections that served as experimental units. These experimental units covered the entire sampling area and did not overlap, and were small enough to all fishes present at a given sample date could be assessed. Each section was marked with global positioning system (GPS) coordinates and assigned a number from one to six. During each sampling period, gill nets and trap nets were deployed within one of these areas selected at random.

There were 228 gill nets fished during March, June, July, October 2000 and January-April 2001. Nets were 30-m long × 2-m deep and consisted of four 7.5-m panels of 1.3-, 2.5-, 3.8 and 5.1-cm bar-mesh monofilament nylon setting. Two to 15 gill nets per month were set early to mid-morning for an average of 1.02-h in each lagoon. In addition, 123 trap nets were set during the same period. Nets were 1.3-cm bar-mesh nylon with two 1.8-m × 0.9-m frames, four 0.8-m diameter hoops, and a 14-m × 0.8-m lead. One to nine trap nets were set per month in each lagoon. All trap nets were set in mid-morning and retrieved the following morning soon after sunrise. Fishes collected were measured (total length, TL) to the nearest millimeter, weighed to the nearest gram, and returned to the water.

Diet of principal fishes

A subsample of 32 snook, 13 tarpon and 50 tilapia was retained to determine stomach contents. All fishes were measured (TL) to the nearest millimeter and weighed to the nearest gram. Guts were removed and preserved in 5% formalin, and in the laboratory whole guts and gut contents were individually weighed (wet weight), and contents examined with a dissecting microscope. Gut contents were sorted by prey item and each individual item weighed to the nearest 0.001 g. All items were identified to the lowest possible taxon.

Evaluation of forage items

For assessment of invertebrates and early life stages of fishes, each lagoon was divided into four sections that served as experimental units. Each of these sections covered most representative microhabitats identified in the HNR lagoon system. Seven lagoon microhabitats, based on predominant vegetation, were identified in HNR: mangrove, cattail, najas, chara, water hyacinth (*Eichornia crassipes*), grasses, and fern (*Acrosticum* sp.). Each section was marked with GPS coordinates and assigned a number from one to four. During each sampling period, one of the four sections in the respective lagoon was chosen at random, and light traps and pop nets were set in representative microhabitats. Supplemental sampling by seining was conducted at all available seining beaches.

There were 129 light traps set from May 2000 through April 2001. Light traps used were modified from Floyd *et al.* (19), and consisted of a slotted trapping apparatus with four, 150-mm long, 5-mm wide entrance slots that allowed larval, juvenile and small fishes, and invertebrates to enter the trap's inner chamber. Four to six light traps per lagoon were set for one night/month from approximately 3-h before sunset to 1-h after sunrise. A 12-h Cyalume chemical stick illuminated each trap.

From June 2000 through May 2001, 224 pop nets were set. Pop nets used were modified from Larson *et al.* (20) and Killgore *et al.* (21). The pop net consisted of two 1-m^2 frames, with a 1.5-m deep woven mesh net. Nets were set for ten minutes four to eight times each month in each lagoon. Samples were retrieved by carefully inserting a 0.5-mm mesh net mounted in an aluminum frame below the pop net, then lifting it slowly to the surface.

There were 208 seine hauls conducted during August-October and December 2000, and January-April 2001. Seining was restricted to locations where seines could be deployed and pursed along moderately sloping bottoms. Seining was standardized following the methodology of Swingle (22) with a 4.7-m long × 1.6-m deep, 1.24-cm bar mesh net deployed perpendicular from the shoreline, retrieved through a stretched arc back to the shoreline and pursed there. Fishes and invertebrates collected were preserved in 5% formalin, counted and identified to the lowest possible taxon in the laboratory.

Environmental variables

Environmental variables were measured at each sampling site to characterize habitats and their relationships to the fish and invertebrate assemblage dynamics. Variables measured 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). For light traps, depth and Secchi transparency measurements were recorded at time of retrieving (morning), whereas the remaining variables were recorded at both time of setting (afternoon) and retrieving.

Data analyses

Relative abundance (catch-per-unit-effort, CPUE) of fishes (fish/gear-set) and invertebrates (individual/gear-set), and fish species richness (number of species) were determined independently for each sampling gear and habitat type. For light traps and pop nets, a set was defined as the number of gear pieces set at each habitat type per lagoon and sampling period. For seining, a set was defined as the number of hauls per lagoon. For gill nets a set was defined as the number of nets deployed during the average soak time (1.02-h). Trap nets were set overnight, also referred to as one net-set.

We examined temporal (month) and spatial (lagoon, microhabitat) dynamics of fish and invertebrate species CPUE with two-way mixed model ANOVA (PROC MIXED, 23). Significance for all analyses was declared at $\alpha = 0.05$. All ANOVA underlying assumptions were tested. A Kruskal-Wallis test (PROC NPAR1WAY, 23) was used if the assumption of the ANOVA were not confirmed. Where mean treatments differed, the least square means (LSMEANS) test was used to determine which means differed.

To assess possible seasonal effect on fish species richness and CPUE, we grouped data sets in rainy and dry season (rainy season: June-December, dry season: January-May). Data for all months were combined and CPUE for each sampling gear (N = 5) were tested for differences between seasons with a paired-samples Student's t-test (PROC MEANS, 23). Fish species richness for all sampling gears and months were combined and differences between seasons were also tested with a paired-samples Student's t-test.

We used ANOVA to examine the temporal and spatial environmental dynamics of the lagoon system. All ANOVA were conducted using the same approach used for analyzing fish and invertebrate species richness and CPUE. Data were grouped into rainy and dry season to investigate seasonal effects. Each environmental variable was tested for differences between seasons with a paired-samples Student's t-test following same protocol and criteria applied for fish species richness and CPUE.

We used canonical correspondence analysis (CCA) to identify relationships between environmental variables and fish assemblage structure. For this analysis we created data matrices combining environmental data and fish abundance for all sampling gears; the main matrix consisted of 282 sampling sites and 11 fish taxa, and the secondary matrix consisted of 282 sampling sites and 10 environmental variables

The CCA was done in PC-ORD V.4.02 (24), with variables of the second matrix standardized to a mean of zero and standard deviation of one. For testing significance of the axes, a Monte Carlo test with 1,000 randomizations was run. The relative contribution of the different variables to the CCA ordination axes was assessed from their canonical coefficients and intra-set correlations.

Results

To better quantify the role of the lagoon system for fishes, each species collected was assigned to one of three ecological categories on size and behavior, and to one of three residency categories on fish habitat use (25-26) (Table 1). Nomenclature of fishes followed references from Martin and Patus (27), the American Fisheries Society (28) and Froese and Pauly (29).

Overall data

There were 10,147 fishes, representing 12 families and 22 species, collected with all sampling gears (Table 2). Four fish taxa, crested goby (*Lophogobius cyprinoides*, N = 2,710), the two species of tilapia (N = 2,612), and hechudo (*Anchovia clupeoides*, N = 2,465), represented 76.7% of the total sample. Snook and tarpon represented 2.1% of the total sample. Benthic forage fishes dominated the ecological categories (59.1%), and estuarine transient fishes dominated the residency categories.

Collectively, the three lagoons forming the Mandri system yielded the largest number of principal fishes (i.e., snook, tarpon, and tilapia). Over 97% of the total catch of tarpon was collected in the Santa Teresa system, whereas over 56% of the snook and over 67% of the tilapia captured were collected from the Mandri system.

All fishes collected by light traps, pop nets, and seines were either larvae, juveniles of large species or small-bodied fishes. There was no evidence of spawning or recruitment within the lagoon system for tarpon and snook.

There were 37,696 invertebrates collected with pop nets and light traps. Shrimp in the family Palaemonidae dominated the collection of invertebrates and were the only shrimp collected. Other invertebrates collected were crabs (*Callinectes* sp. and *Gecarcinus* sp.) and a few individuals of the orders Odonata, Annelida, and Diptera.

Relative abundance of forage fishes

For fishes collected with light traps, there were no significant differences in crested goby CPUE among lagoons (P = 0.675) and months (P = 0.681), whereas there was a significant difference in tilapia CPUE among months (P < 0.001) but not among lagoons (P = 0.059). A Kruskal-Wallis test indicated that there were significant differences among lagoons (X^2 = 12.1; df = 4; P = 0.017) and months (X^2 = 26.9; df = 11; P = 0.003) for CPUE of mosquitofish (*Gambusia affinis*).

For fishes collected with pop nets, a Kruskal-Wallis test indicated that there were significant differences in CPUE among lagoons for crested goby (X^2 = 42.7; df = 4; P < 0.001) and tilapia (X^2 = 22.0; df = 4; P = 0.002), but not for mosquitofish (X^2 = 3.1; df = 4; P = 0.545); there were significant differences in CPUE among months for crested goby (X^2 = 29.9; df = 11; P = 0.002) but not for tilapia (X^2 = 17.1; df = 11; P = 0.105) and mosquitofish (X^2 = 19.6; df = 11; P = 0.06).

There were no significant differences in CPUE among microhabitats for any species (e.g., pop nets: crested goby P = 0.131, ti-

Table 1
Classification, according to ecological and residency categories (Day *et al.* 1989 and Ley *et al.* 1999), of fish taxa collected at Humacao Natural Reserve (Puerto Rico, March 2000-May 2001).

Family/species	Categories	
	Ecological Category	Residency Life History
Gobiidae		
Crested goby (*Lophogobius cyprinoides*)	B	R
Sirajo (*Sicydium plumieri*)	B	R
Bigmouth sleeper (*Gobiomorus dormitor*)	B	R
Darter goby (*Ctenogobius boleosoma*)	B	R
Psilotris sp.	B	
Cichlidae		
Mozambique tilapia (*Oreochromis mossambicus*)	B	FE
Redbreast tilapia (*Tilapia rendalli*)	B	FE
Poecilidae		
Mosquitofish (*Gambusia affinis*)	B	FE
Gerridae		
Yellowfin mojarra (*Gerres cinereus*)	B	T
Flagfin mojarra (*Eucinostomus melanopterus*)	B	R
Striped mojarra (*Eugerres plumieri*)	B	T
Engraulidae		
Hechudo (*Anchovia clupeoides*)	W	R
Sciaenidae		
Ground drummer (*Bairdiella ronchus*)	L	T
Carangidae		
Horse-eye jack (*Caranx latus*)	L	T
Elopidae		
Tarpon (*Megalops atlanticus*)	L	T
Ladyfish (*Elops saurus*)	L	T
Centropomidae		
Common snook (*Centropomus undecimalis*)	L	T
Swordspine snook (*C. ensiferus*)	L	T
Soleidae	B	R
Mugilidae		
White mullet (*Mugil curema*)	L	T
Mugil sp.	L	T
Plecostomidae	B	R

Categories: Ecological: B = benthic forage fish. W = water column forage fish. L = large roving fish.
Residency life history grouping: R = estuarine resident. FE = freshwater exotic. T = estuarine transient.

Table 2
Total collection of fishes by sampling gear from Humacao Natural Reserve
(Puerto Rico, March 2000-May 2001)

Family/species	Total	Gill Net	Trap Net	Light Trap	Pop Net	Seine
Engraulidae						
Anchovia clupeoides	2,465	616	1,828		2	19
Carangidae						
Caranx latus	435	414	3			18
Sciaenidae						
Bairdiella ronchus	1			1		
Gerridae						
Eugerres plumieri	625	231	382		2	10
Eucinostomus melanopterus	14					14
Gerres cinereus	9					9
Poecilidae						
Gambusia affinis	242			183	38	21
Gobiidae						
Ctenogobius boleosoma	1		7	285	1	457
Gobiomorus dormitor	2		224		2	1
Lophogobius cyprinoides	2,710				1,961	1
Sicydium plumieri	265				40	
Psilotris sp.	1					
Elopidae						
Megalops atlanticus	136	128	8			1
Elops saurus	490	486	3			
Mugilidae						
Mugil sp.	48	46	2			
Centropomidae						
Centropomus sp.	82	71	11			
Cichlidae						
Tilapia	2,612	661	221	1,280	190	260
Soleidae	8	8				
Plecostomidae	1	1				
Total	10,147	2,662	2,689	1,749	2,236	811

lapia $P = 0.183$, mosquitofish $P = 0.971$; light traps: crested goby $P = 0.245$, tilapia $P = 0.462$, mosquitofish $P = 0.143$). Only CPUE for crested goby collected with pop nets differed significantly among months ($P < 0.001$). Due to insufficient sample sizes, statistical analyses comparing lagoons and months were not performed for fishes collected with seines.

Relative abundance of invertebrates

Because shrimp dominated the collection of invertebrates, we only analyzed their relative abundance here. For light traps there was significant difference in shrimp CPUE among months (P < 0.001), but not among lagoons (P = 0.312). For pop nets, there were significant differences in shrimp CPUE among lagoons (P = 0.004) and months (P = 0.013). There were no significant differences among microhabitats for pop nets (P = 0.217) and light traps (P = 0.571). There was a significant difference among months for shrimp collected with light traps (P < 0.001), but not for shrimp collected with pop nets (P = 0.476).

Relative abundance of principal fishes

Catch-per-unit-effort of snook, tarpon, and tilapia collected with gill nets and trap nets were highly variable among months and lagoons. For gill nets, there were significant differences in CPUE of tilapia and tarpon among months (P ≤ 0.001) and lagoons (P ≤ 0.001). Snook CPUE differed significantly among months (P = 0.029), but not among lagoons (P = 0.131). For trap nets, only tilapia were sufficiently well represented in all months and/or lagoons to evaluate their spatial and temporal distribution. A Kruskal-Wallis test indicated that there were significant differences among lagoons (X^2 = 13.7; df = 4; P = 0.008) and months (X^2 = 27.9; df = 7; P = 0.002). There were significant differences between seasons in CPUE of principal fishes (except snook) and forage fishes for each sampling gear (gill nets: t = 3.01; df = 227; P < 0.01; trap nets: t = 2.90; df = 122; P < 0.04). However, there was no significant difference (t = 1.21; df = 911; P > 0.07) between seasons in fish species richness.

Diet of principal fishes

Total length ranges of fish used for stomach content analyses were 192 to 562 mm TL for snook (N = 32), 380 to 552 mm TL for tarpon (N = 13), and 224 to 321 mm TL for tilapia (N = 50). Only 11 snook (34%; eight from Santa Teresa 1, three from Santa Teresa 2) and six tarpon (46%; two from Santa Teresa 1, four from Santa Teresa 2) stomachs contained prey items. Many tilapia stomachs contained undefined material, presumably mud and vegetal matter, although most stomachs were empty. Consequently, we were not able to discern specific prey for tilapia. Vegetal matter, followed by shrimp, fishes, crabs, and snails dominated stomach contents of snook. Fishes and shrimp dominated tarpon stomachs. Due to small sample size, temporal patterns in principal fish prey preferences were not discerned.

Environmental characteristics

As indicated above, connections between the lagoon system and the Caribbean Sea typically were closed during our study. In August 2000, Hurricane Debby caused an increase in water level throughout the lagoon system (Figure 2), but did not open the connections. Between late March and early April 2001, the USACE finished the construction of the new canal and opened the connection for a few days. This caused water levels in the lagoons to fall. Therefore, the HNR lagoon system was isolated from the sea, and fluctuations in lagoon water levels were independent of tides from the Caribbean Sea.

Although environmental variables were measured at all sampling sites, we only present data for light traps because they represented a better description of the general characteristics of the lagoon system. There were significant differences among months (P < 0.03) for all variables, and among lagoons (P < 0.04) for all variables except dissolved oxygen and dissolved oxygen percentage saturation in the morning. Depth, dissolved oxygen in the morning and in the afternoon, turbidity in the morning and in the afternoon, and dissolved oxygen percentage saturation in the morning and in the afternoon did not differ significantly (t ≤ 2.08; df = 128; P ≥ 0.06) between seasons.

All analyses revealed environmental gradients among the lagoons, and differentiated the Mandri system from the Santa

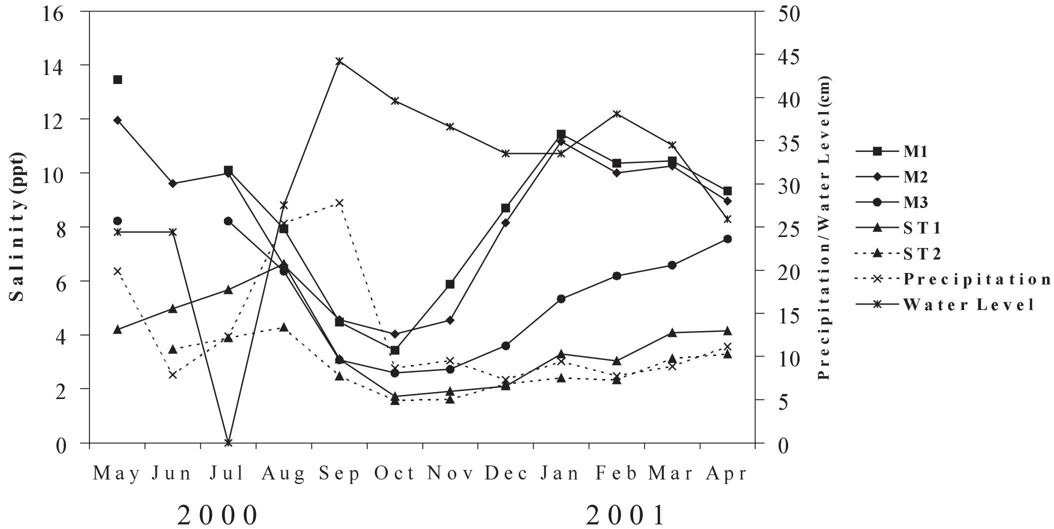

Figure 2. Mean monthly water level and salinity, and monthly precipitation values for each lagoon at Humacao Natural Reserve (Puerto Rico). M1 = Mandri 1, M2 = Mandri 2, M3 = Mandri 3, ST1 = Santa Teresa 1, ST2 = Santa Teresa 2.

Teresa system. Relative to the Mandri system, the Santa Teresa system had greater depth and lesser pH, dissolved oxygen in the afternoon, salinity, and turbidity. Gradients in salinity and turbidity were observed. Salinity and turbidity decreased along the linear series of lagoons from the Mandri through the Santa Teresa systems.

Salinity and water level were associated with precipitation (Figure 2). Average salinity decreased and water level increased in all lagoons with increased precipitation during August-October, and then both variables reversed as precipitation decreased. Overall, HNR had a 26-cm (16%) precipitation deficit during our study period relative to 1988-1999.

Canonical correspondence analysis

The positions of fish species on the first two axes extracted by CCA are shown in Figure 3. Environmental variables that made a major contribution to the fit of the species data (i.e., variables with highly significant correlation coefficients) are represented by arrows pointing in the direction of maximum variation, with their length proportional to the rate of change. The first two CCA axes accounted for 24.1% of the variance in species composition, but the eigenvalues (first axis = 0.501, second axis = 0.382) showed that the extracted gradients were large (30), indicating that the probability of occurrence of the fish species along the gradients actually sampled followed the required unimodal distribution (31), and Monte Carlo testing revealed that these axes were significant ($P < 0.01$) (Table 3).

Intraset correlations (Table 3) indicated that of the ten environmental variables included in the CCA, salinity was the most significant predictor, followed by temperature and dissolved oxygen. No other variables added significantly to the amount of variation explained. The first axis mainly corresponded to salinity, and most fish species were associated with this gradient. For example, tarpon and crested goby were associated with lower salinity sites (Santa Teresa system), whereas snook, ladyfish, and mojarra were associated with higher salinity sites (Mandri system). The first axis largely separated typical marine fish transients (e.g., ladyfish, snook, mullet) from

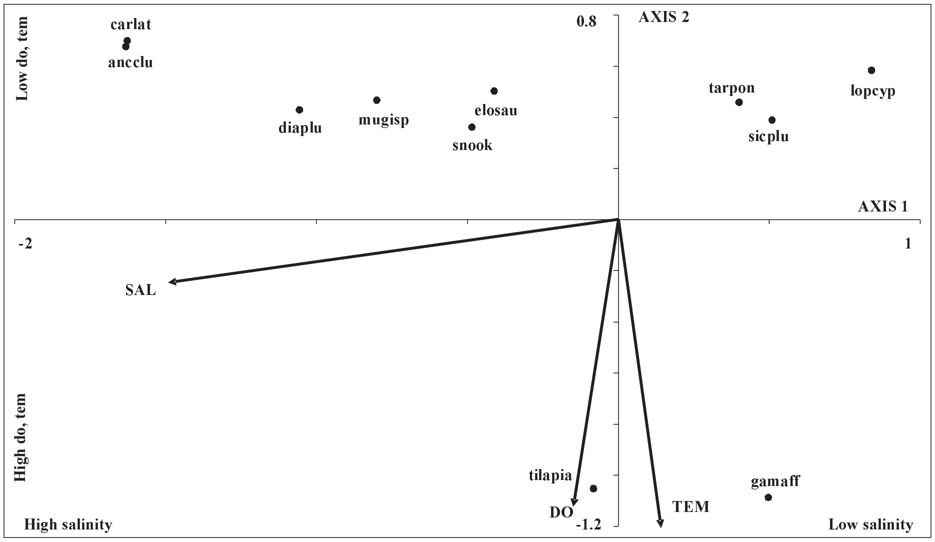

Figure 3. Plot of final scores of fish species and biplot scores of environmental variables on the first two canonical axes (Axis 1, Axis 2) for the canonical correspondence analysis on samples collected with all sampling gears at Humacao Natural Reserve (Puerto Rico; March 2000-May 2001). Arrows indicate direction of increasing value for environmental variables. More acute angles between arrow and axis indicate stronger correlation of variables with the axis; e.g., salinity (SAL) is highly correlated with Axis 1, whereas dissolved oxygen (DO) and temperature (TEM) are highly correlated with Axis 2. For clarity only environmental variables highly correlated with axes are shown. Fish taxa (filled circles): ancclu = hechudo, *Anchovia clupeoides*; carlat = horse-eye jack, *Caranx latus*; diaplu = striped mojarra, *Eugerres plumieri*; mugisp = mullet, *Mugil* sp.; elosau = ladyfish, *Elops saurus*; snook = common snook, *Centropomus undecimalis* and swordspine snook, *C. ensiferus*; tarpon = *Megalops atlanticus*; sicplu = sirajo, *Sicydium plumieri*; lopcyp = crested goby, *Lophogobius cyprinoides*; gamaff = Mosquitofish, *Gambusia affinis*; tilapia = Mozambique tilapia, *Oreochromis mossambicus*, redbreast tilapia, *Tilapia rendalli*.

resident fishes (e.g., crested goby). Although tarpon is a transient fish, it was almost exclusively captured in the Santa Teresa system; this explained its position on the ordination graph. The second axis corresponded mainly to temperature and dissolved oxygen. Mosquitofish were associated with sites with high dissolved oxygen and temperature, and low salinity, whereas tilapia were associated with sites with high dissolved oxygen and temperature, but higher salinity.

Discussion

Fishes and invertebrates are integral components of functioning wetland ecosystems (32), and are primary attributes reflecting habitat value for wetlands (33). Invertebrates provide food-web support for consumers such as birds and fishes (34), and fishes function as vehicles for nutrient cycling and energy transfer across habitats at a number of trophic levels in the estuarine food-web (35). In turn, wetlands provide these animals with areas for refuge, reproduction, feeding, and other essential functions (32).

The results of our study indicated that in a short period of time (~25 years) the HNR lagoon system has evolved adequate estuarine habitat conditions to support sustainable populations of fish and invertebrate species. The HNR lagoon system fish assem-

Table 3
Intraset correlations, eigenvalues, and variance explained for the first two axes of canonical correspondence analysis for fish abundance and environmental variables for all gears and dates sampled at Humacao Natural Reserve (Puerto Rico, March 2000-May 2001)

Variable	Axis 1	Axis 2
Depth	0.293	0.033
Temperature	0.085	–0.740
Dissolved oxygen	–0.079	–0.564
Specific conductance	–0.766	–0.126
Salinity	–0.771	–0.124
Total dissolved solids	–0.766	–0.125
Turbidity	–0.350	–0.415
pH	–0.254	–0.336
Dissolved oxygen percent saturation	–0.080	–0.601
Secchi transparency	0.317	0.078
Eigenvalue	0.501	0.382
Percentage of variance explained	13.7	10.4
Correlation fish-environmental variables	0.768	0.719
	Monte Carlo test*	
Axis	Correlation	P
1	0.768	0.01
2	0.719	0.01

*The correlations between fishes and studied variables, and P values for a Monte Carlo test are also shown for the significance of axes.

blage, like most coastal lagoons (36-38) represented a mixture of ecological groupings that contained species adapted to brackish environments, plus others more typical of either marine or freshwater systems. In addition, the HNR lagoon system was an important habitat for grass shrimp (*Palaemonetes* spp.), which is regarded as a good indicator of wetland habitat values (33, 39). This evolution has occurred without any directed attempts to modify the physical habitat and the biota within the habitat (16). These findings are not just based on the paradigm that fish presence reflects habitat functional value, but a confirmation that the HNR lagoon system can provide spawning habitat and refuge to fishes and invertebrates that in turn serve as food for principal fish species.

Fish species richness and abundance

Despite using different gear types, the number of fish species collected was less than those found in similar ecosystems in Puerto Rico and other tropical lagoons, albeit with different species. For example, Stoner (40) reported 41 species of juvenile an adult fishes representing 18 families in Laguna Joyuda, Puerto Rico, Yáñez-Arancibia *et al.* (41) collected 121 species in Terminos Lagoon, southern Gulf of Mexico, Thayer *et al.* (42) collected 64 species in southern Florida, USA, and Sedberry and Carter (43) collected 87 species in Belize, Central America. We collected 22 species representing 12 families.

We expected that the HNR lagoon system would be an important habitat for adult and early life history stages of fishes in southeastern Puerto Rico because coastal lagoons provide protection from predators and ensure high food availability (1-2). We found two factors that could have constrained fish species richness in the HNR lagoon system: 1) freshwater input to the lagoons is via precipitation, runoff, and intermittent stream containing few or no resident fishes; we only collected three truly freshwater fish species (i.e., the two species of tilapia and mosquitofish), introduced species adapted to live in brackish water; and 2) although we could not test this premise, some evidence allowed us to hypothesize that the time of the year and duration of open connection to the sea may have controlled fish abundance and species composition within the HNR lagoon system.

Only two marginal connections with the sea occurred during the entire study period; one in August 2000, when heavy precipitation as a consequence of Hurricane Debby established a temporary connection with a marginal (0.30 m) rise in the water level within the lagoon system, and another in March-April 2001, when the USACE opened the connections for a few days. On both occasions the water level in the lagoon system rose and fell within a few hours, and likely no significant influx of fishes into the lagoon system occurred during that period.

Several studies (e.g., 10, 44-45) suggest that the longer an estuarine system is open to the sea, the greater the chance of marine fishes entering it. Thus, permeability of the lagoon-ocean boundary seems to be important in mediating the amount of fish movement from the ocean to the lagoons. Probably, no major connection to the sea has occurred in the lagoon system since Hurricane Georges traversed the region in September 1998, causing extensive flooding. At that time, abundance and richness of fishes likely increased as juveniles and adult specimens entered the lagoon system. Since then, fish abundance and fish species richness have probably declined following the lagoon system's natural rhythms and fishery harvest. However, the fish assemblage of HNR lagoons appeared qualitatively and quantitatively consistent with the hydrological characteristics of the system. Spatial differences in the composition and abundance of fishes in the lagoon system were evident, with greater numbers of fishes and overall species richness in the more saline system (Mandri system). Eighteen fish species (N = 6,448) were collected in the Mandri system and 13 fish species (N = 3,699) were collected in the Santa Teresa system. Although the whole HNR lagoon system is interconnected via a canal, and two connections with the sea exist, most fishes enter the lagoons through the Antón Ruiz River. Once fishes enter the Mandri system, they disperse throughout the three Mandri lagoons. Further dispersal into the Santa Teresa system is apparently limited to opportunistic diffusion from the Mandri lagoons.

Fish-invertebrate-habitat relationships

The HNR lagoon system had sufficient diversity and complexity of habitats, along the estuarine gradient, provided by plant communities to support potential food resources for fishes and invertebrates. Emersed shoreline macrophytes (e.g., cordgrass, cattail), submersed forms (i.e., najas, chara), and mangrove were common features in the waterscape of the HNR lagoon system.

However, some macrophytes recorded in the HNR lagoon system do not tolerate salinities > 15 ppt (e.g., cattail, najas, chara) (46). This is especially relevant to our study, because where submersed macrophytes were present (i.e., Santa Teresa system), abundances of small fishes (particularly early life history stages of tilapia) and grass shrimp were high. Fishes are attracted to aquatic plants because they reduce predation risk (47-51), and increase the invertebrate prey species that utilize macrophytes for substrates and food (52-55). Thus, if the salinity level in the lagoons increases, important supportive habitat for fishes will be lost.

Results of the CCA revealed that salinity was the dominant gradient and had the strongest association with the fish assemblage. The first CCA axis, represented by salinity, separated typical marine fishes (except for tarpon; see below) from resident fishes. The CCA also indicated that each principal fish species was associated with a different set of environmental variables: tarpon was mainly associated with low salinity, dissolved oxygen, and temperature; snook were mainly associated with high salinity; and tilapia were mainly associated with high dissolved oxygen and temperature. Nevertheless, the proportion of variation explained by the measured environmental variables was low. This is probably caused to a large extent by noise, and/or that other unmeasured gradients are important (56). Because there was only a few fish species per sampling site, there is much stochastic variation in terms of which species were present or absent. However, despite the stochastic variation, highly replicated sampling sites were sufficient to detect major gradients in species composition.

Principal fishes

There are spawning areas for snook and tarpon around Puerto Rico (57), which makes the HNR lagoons potentially important nursery and refuge habitats for these fishes. For example, evidence from Zerbi (57) indicated that during flood tides early life history stages of tarpon and snook extensively use the available food and habitats in Rincón Lagoon, a coastal lagoon in southwestern Puerto Rico.

However, opportunities for recruitment of tarpon and snook into the HNR lagoon system were limited because, as indicated above, the lagoon system was rarely connected to the sea. In addition, to allow recruitment of snook and tarpon into Santa Teresa 2, heavy precipitation is required to connect it with the other lagoons. Hurricane Georges (September 1998), was the last meteorological event that likely caused a substantial connection between the sea and all HNR lagoons (M. Corbet, DNER personal communication). Rundle (58) indicated that all snook and tarpon aged from Santa Teresa 2 were at least two years old, coinciding with the timing of Hurricane Georges. Although fishes of any age can move into Santa Teresa 2 once a connection is established, the finding of fishes no younger than the timing of the last major meteorological event is relevant in showing the importance of heavy precipitation on fish exchange with Santa Teresa 2.

Also, we found no evidence of spawning within the lagoon system for snook and tarpon. None of the snook and tarpon specimens we analyzed showed evidences of sexual maturity, and no early life history stages of these fishes were collected. However, some snook specimens we collected were larger (TL ranged from 125 to 529 mm) than the size of maturity reported in the literature, indicating the potential to reproduce. For example, Peters *et al.* (59) reported that female common snook in Florida mature at 500-522 mm fork length (FL) and males at 330-348 mm FL. The low salinity in the lagoons likely prevented snook from spawning. Studies in Florida demonstrated that snook spawn inshore near estuaries and seagrass beds at salinities > 27 ppt (59). Average salinity in HNR lagoons ranged from 2.83 to 9.49 ppt.

Low salinity probably also prevented tarpon from spawning in the HNR lagoons. There were no sexually mature tarpon collected from the HNR lagoons. Smith (60) reported that tarpon leptocephali larvae required stable high salinities, and were normally restricted to offshore waters.

Tarpon represented a notable exception to the graded distribution of fishes along the salinity gradient. Tarpon are typical marine fishes. However, they were almost exclusively recorded from the Santa Teresa lagoons, particularly Santa Teresa 2, which was the least saline lagoon.

Santa Teresa 2 has developed various attributes and functions enhancing habitat conditions for tarpon. Low salinity in Santa Teresa 2 favored submersed vegetation (i.e., najas and chara), which dampened wave action so that fine-grained mud, characteristic of the whole lagoon system bottom, accumulated in shallow water among the vegetation, rendering Santa Teresa 2 a clearer water system. Clearer water systems allow predatory fishes visual detection and discrimination and increasing feeding efficiency (61-64).

Tilapia deserve special consideration. Since their introduction in the late 1950's, tilapia have become an important component of many aquatic systems in Puerto Rico (65). Tilapia were the most recorded fishes (N = 107).

However, the most important role played by tilapia in the lagoon system is their serving as prey for snook and tarpon. Tilapia were found more in tarpon than in snook stomachs; 96% of the tarpon diet was composed of tilapia and 4% was grass shrimp, whereas only 11% of the snook diet was composed of tilapia and 23% was grass shrimp. Although tilapia were ubiquitous in the lagoon system and spawned successfully in all the lagoons several times a year, tilapia collected with all sampling gears were significantly more abundant in Santa Teresa 2 than in Santa Teresa 1. Thus, tarpon, which were more abundant in Santa Teresa 2, seem to take advantage of tilapia.

Management Implications

Our data suggested that a salinity-turbidity gradient played a significant role on the HNR fisheries, and should be monitored closely to determine the trend in the environmental characteristics and habitat that support fish populations in the lagoon system. These data are particularly important because they represent post-treatment information after the USACE completed work that permanently connected the lagoons with the Caribbean Sea. This connection may allow an increase in recruitment of marine fishes (particularly tarpon and snook) into the lagoon system along with an influx of marine waters. Current evidence suggests that the estuarine habitat in HNR may already be affected by this water exchange, and that lagoon salinity has increased where salinities have recently been recorded up to 26 ppt in the Santa Teresa system (M. Corbet, DNER personal communication).

Disturbance of the estuarine environment will be particularly relevant to the Santa Teresa system. This system offered better habitat conditions for visual feeders like snook and tarpon. These improved habitat conditions were created by submersed vegetation (i.e., chara and najas) that does not tolerate high salinity levels. Thus, significant increases in salinity will affect submersed plants that in turn can affect fish and invertebrate populations. Aquatic plants provided cover and a source of invertebrates and fish preys to predatory fishes (e.g., tarpon and snook).

In conclusion, data presented here suggest that the new permanent connection with the sea may influence environmental characteristics of the lagoon system, and represent pre-treatment condition in the lagoon system. Because these data were collected during the period when the lagoon system was not connected to the sea, they represent important information to investigate the influence of the flood control project initiated by the USACE on the lagoon system at HNR.

As pointed out by Whitfield and Bruton (66) and emphasized by Odum *et al.* (17), the continued proper functioning of estuaries relies on the maintenance of the natural dynamism and the oscillating phases imposed on such systems by freshwater and marine influences. If this pattern is disturbed, naturally or anthropogenically, changes can occur in the estuarine environment affecting the estuarine assemblage. Previous studies of wetland function of systems similar to the HNR lagoons have been conducted (e.g., 4, 67-72), however, they lack experimental manipulation. Because the HNR lagoon system was temporally disconnected from the sea by the USACE landscape manipulation, it offered a unique opportunity to gather data that allow for future investigation to determine its effect. This perturbation should be viewed as an experimental treatment and further post-treatment data should be gathered to monitor for system shifts in habitat and ecology.

Future research to advance both ecological and human baselines useful to fishery management strategies at HNR should include evaluation of synergistic relationships between environmental dynamics and habitat variability that influence spatiotemporal fish and invertebrate communities. 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 environmental variables identified in this study (e.g., salinity, turbidity), and habitat zones identified and characterized by species and their optima across gradients.

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