34

www.cerf-jcr.org

# Structural Complexity and Biomass of Arid Zone Mangroves in the Southwestern Gulf of California: Key Factors That Influence Fish Assemblages

Jonathan G. Ochoa-Gómez<sup>†</sup>, Elisa Serviere-Zaragoza<sup>†</sup>, Daniel B. Lluch-Cota<sup>†</sup>, Victor H. Rivera-Monroy<sup>‡</sup>, Walter Oechel<sup>§††</sup>, Enrique Troyo-Diéguez<sup>†</sup>, and Salvador E. Lluch-Cota<sup>†</sup>\*

<sup>†</sup>Centro de Investigaciones Biológicas del Noroeste La Paz, B.C.S. 23096, México

ABSTRACT

<sup>§</sup>Global Change Research Group San Diego State University San Diego, CA 92182, U.S.A. <sup>‡</sup>Department of Oceanography and Coastal Sciences College of the Coast and Environment Louisiana State University Baton Rouge, LA 70803, U.S.A.

<sup>††</sup>College of Life and Environmental Sciences University of Exeter Exeter EX4, England, U.K.



www.JCRonline.org

Ochoa-Gómez, J.G.; Serviere-Zaragoza, E.; Lluch-Cota, D.B.; Rivera-Monroy, V.H.; Oechel, W.; Troyo-Diéguez, E., and Lluch-Cota, S.E., 2018. Structural complexity and biomass of arid zone mangroves in the southwestern Gulf of California: Key factors that influence fish assemblages. *Journal of Coastal Research*, 34(4), 979–986. Coconut Creek (Florida), ISSN 0749-0208.

Arid zone mangroves of the southwestern Gulf of California provide ecosystem services because of their habitat heterogeneity, structure, and functions, which are important for the formation of fish assemblages. Structure, litterfall production, and leaf decomposition in three mangrove communities located at La Paz Bay, Mexico, were analyzed. Litterfall production was found to be within the range reported for the region. Leaf decomposition rate was similar between communities and species. The structural complexity and biomass of mangroves were inversely correlated with fish size, suggesting that they are key features, providing shelter and nursery for fish assemblages. *Laguncularia racemosa* appears to play an important role in providing greater habitat heterogeneity within mangroves, favoring fish species richness. *Avicennia germinans* is the most important mangrove species in the region, having the highest leaf decomposition rate, thus providing an important input of carbon to food webs and potentially stimulating fish biomass. Thus, mangroves with lower structural complexity and higher dominance of *A. germinans* likely have a higher potential for artisanal fisheries in the southwestern Gulf of California.

ADDITIONAL INDEX WORDS: Laguncularia racemosa, Avicennia germinans, habitat heterogeneity, fish assemblages, artisanal fisheries.

# **INTRODUCTION**

Heterogeneity (type of vegetation, cover, physiography, and microhabitats) and quality of mangrove communities are linked to the complex structure and functioning of the ecosystems they inhabit (Bazzaz, 1975). This complexity is frequently estimated through measurable attributes, such as number of tree species and their density, dominance, and height (Holdridge *et al.*, 1971), and is closely related to coastal landforms (Latrubesse, Stevaux, and Young, 2013; Woodroffe, 1992).

Mangrove structural complexity plays an important role in the way fish use their habitat. Juvenile and small adult fish use mangrove areas as a shelter and nursery because of their canopy shaded zones, mudflats, and creeks (Laegdsgaard and Johnson, 2001; Wang *et al.*, 2009). Mangroves are also suitable fish habitats because of their litterfall production, a feature that sustains the surrounding benthic and pelagic food webs (Odum and Heald, 1972). Mangroves in arid zones are

©Coastal Education and Research Foundation, Inc. 2018

especially important because of their relatively high contribution to primary productivity (López-Medellín and Ezcurra, 2012). Therefore, proper planning of human activities occurring near mangroves requires an understanding of the ecosystem status and processes that could result in significant mangrove changes.

In the Gulf of California, fringe mangroves dominated by Rhizophora mangle provide a nursery for various juvenile fishes (Aburto-Oropeza et al., 2015). Lopez-Rasgado et al. (2012) compared the structure and functioning of the fish communities of three mangrove systems, Balandra, Enfermería, and Zacatecas, with different degrees of human effects between 1981 and 2010, before and after the major effects occurred. They found that the fish assemblage's structure is related to the degree of anthropogenic impact and changes occurring in the mangrove's coverage. Balandra is the mangrove community least affected by human activity and has the greatest diversity of fish species, whereas Enfermería is the mangrove with the most anthropogenic effect and has the lowest diversity, with the largest biomass, of fish species (López-Rasgado et al., 2012). Despite this report, which clearly demonstrates differences in fish communities from human activities, the mechanistic linkage to the mangrove forest

DOI: 10.2112/JCOASTRES-D-16-00220.1 received 2 December 2016; accepted in revision 2 July 2017; corrected proofs received 16 August 2017; published pre-print online 23 February 2018. \*Corresponding author: slluch@cibnor.mx

structure or function was not addressed. The aim of this study is thus to report the different properties of the three mangrove systems studied by López-Rasgado *et al.* (2012) and relate them to the previously reported differences in fish communities.

# Study Area

Three mangrove communities, Balandra, Enfermería, and Zacatecas, located in La Paz Bay, southwestern Gulf of California, were studied (Figure 1). These mangroves have different degrees of human impact. In these sites, mangrove species present a zonation from the lowest to the highest intertidal areas as follows: red mangrove *R. mangle*, white mangrove *Laguncularia racemosa*, and black mangrove *Avicennia germinans* (Figure 2).

In Balandra, the mangrove cover extends over 24.2 ha, of which 66% is forested mudflat with an average elevation of 3.0  $\pm$  2.6 cm. *Rhizophora*, *Laguncularia*, and *Avicennia* are the predominant species in this site. Its lagoon has a surface of 30 ha, an average water residence time of 1.5 days, and an inlet width of 180 m (Mendoza-Salgado *et al.*, 2011). Balandra is the mangrove affected the least by anthropogenic activity among all the studied areas (López-Rasgado *et al.*, 2016) and has not shown any mangrove cover loss since 1978 (CONABIO, 2010).

Enfermería has a mangrove cover of 1.9 ha, with A. germinans and R. mangle as predominant species. The forested mudflat represents 14% of its cover with an average elevation of 2.9  $\pm$  2.8 cm. In this site, the mangrove hydrology was affected by the construction of a highway that formed an artificial lagoon with a surface of 5 ha, an inlet width of 6 m, and an average water residence time of 20–26 days (Mendoza-Salgado *et al.*, 2011). It shows the highest degree of anthropogenic modification among the studied mangrove sites. This community has lost at least 50% of its cover area since 1978 (CONABIO, 2010).

Zacatecas is a tidal channel with 18 ha of mangrove cover, of which 77% is a forested mudflat with an average elevation of  $1.4 \pm 1.3$  cm. The two predominant species are *A. germinans* and *R. mangle*. The basin has an inlet width of 36 m, water surface of 6 ha, and an average water residence time of 1–6 days (Mendoza-Salgado *et al.*, 2011). This mangrove shows little anthropogenic modification (López-Rasgado *et al.*, 2016) and has not lost cover since 1978 (CONABIO, 2010).

## **METHODS**

Mangrove forest structural and functional properties of the three sites, Balandra, Enfermería, and Zacatecas, were assessed to determine their relationships with the fish assemblage attributes previously reported from the same sites by López-Rasgado *et al.* (2012).

## **Mangrove Structure**

At each site, three sampling areas were considered, bearing in mind the distance to the adjacent waterbody (La Paz Bay): (1) the nearest, (2) an intermediate distance, and (3) the farthest (Figure 1). In each sampling area, two or three  $28.2 \text{-m}^2$ circular plots were located, as per the mangroves species zonation: *R. mangle, L. racemosa*, and *A. germinans* (Kauffman and Donato, 2012). A total of 23 plots were sampled: nine in Balandra, seven in Zacatecas, and seven in Enfermería. In each plot, the individual height and diameter of stems were measured using a metric rod and vernier, respectively. In the case of *A. germinans* and *L. racemosa*, the diameter of stems was measured at breast height, at 1.3 m when stems reached breast height, and at 0.3 m above the ground in all individuals. For *R. mangle* individuals, measurements were only taken 0.3 m above the last main root (Dahdouh-Guebas and Koedam, 2006), counting stems per individual.

In every A. germinans and L. racemosa plot, three quadrants of  $25 \times 25$  cm were randomly placed to count and measure pneumatophore height. Main prop roots were counted for each R. mangle individual. In each plot, interstitial salinity was measured in the first 10–15 cm of soil depth with the use of a field refractometer.

For each mangrove community, the average density, basal area, height, and biomass were estimated. The complexity index (CI) was obtained considering two species in 0.1 ha for all sites (Holdridge et al., 1971). This index represents a quantitative description of structural complexity and allows comparisons with mangroves at other latitudes. The biomass was estimated for each stem by generic allometric equations for total above- and belowground biomass (Komiyama, Poungparn, and Katom, 2005), which are known to be adequate estimates (Ishihara et al., 2015; Rojas-García et al., 2015), and wood densities reported for each species, A. germinans  $(0.67 \text{ g cm}^{-3})$ , L. racemosa (0.60 g cm<sup>-3</sup>), and R. mangle (0.84 g cm<sup>-3</sup>) (Chave et al., 2009). For each species in each site, the average density, basal area, relative dominance (basal area of each species per total basal area), and height were estimated. The importance value index (IVI) was estimated for all mangrove species as per Curtis and McIntosh (1951). The IVI index estimates the importance of each species within the community through its relative density, frequency, and dominance.

## **Litterfall Production**

In each plot, two  $0.25 \text{-m}^2$  litterfall traps made of 1.0-mm screen mesh were placed above the highest water level. A total of 46 traps were placed in the three sites: Balandra (18), Zacatecas (14), and Enfermería (14). Litterfall was collected monthly from April 2015 to May 2016. Litterfall samples were dried in paper bags at 70°C for 48 hours, classified to the appropriate mangrove species, and weighed (±0.001 g). The litterfall production (g m<sup>-2</sup> d<sup>-1</sup>) was estimated as an annual average in each mangrove community and by species within the community.

# Leaf Decomposition

In each plot, 18 litter bags of  $25 \times 15$  cm made of 1.0-mm screen mesh, with  $10.0 \pm 1.0$  g dry weight of dominant species leaves, were placed on the ground in May 2015: Balandra (162), Zacatecas (126), and Enfermería (126). Three litterbags were collected per plot each month from June to November 2015. In the laboratory, litterbags were cleaned, removing the mud from the leaves, and leaves were dried in paper bags at 70°C for 48 hours and weighed ( $\pm 0.001$  g). Finally, the monthly rate of mass loss per day for each species and the average for the whole community were calculated.

## **Fish Assemblages**

In the three sites, Balandra, Enfermería, and Zacatecas, the average richness, density, biomass, and size of dominant



Figure 1. Study site locations showing delimitation of forested mudflat in each mangrove community. The numbers indicate the sampling areas, and the symbols indicate the dominant species in the plot.

juvenile fish species were taken from previously reported data of surveys done during 2009–2010 (López-Rasgado *et al.*, 2012) (Table 1). The species considered were *Diapterus brevirostris*, *Eucinostomus dowii*, *Eucinostomus currani*, and *Gerres simillimus* of the Family Gerreidae and *Mugil curema* of the Family Mugilidae. Trends in richness and dominance of fish assemblages reported by López-Rasgado *et al.* (2012) in Zacatecas and Balandra are similar to those found by an independent study conducted by Payan-Alcacio (2015).

In La Paz Bay, the average seawater temperatures registered during 2009–2010 were 25°C (±2.9), and 25.8°C (±3.1) in 2015–2016 as obtained from the Physical Oceanography Distributed Active Archive Center (PODAAC) database. Datasets were extracted with software (Pacheco-Ayub and Bautista-Romero, 2003) and used to obtain a monthly average water temperature. The average seawater temperature was not significantly different between periods (F = 0.7, p = 0.4). These seawater temperatures were within the ranges reported for the distribution of fishes of the Family Gerreidae, from 21.3°C to 31.4°C (Araújo and Alcántara, 1999), and for *M. curema*, from 19°C to 36°C (Collins, 1985). Both fish families are known to

tolerate a broad spectrum of environmental conditions (Nagelkerken *et al.*, 2001, 2008). Additionally, species of the genus *Mugil* and *Eucinostomus* are even tolerant to the high temperatures of El Niño events (Mora and Ospína, 2001). Because of the above, it is feasible to compare fish assemblages and link them with mangrove features, despite the data surveys having been done in different periods.

## Analysis

Before each statistical analysis was run, Kolmogorov-Smirnov and Levene tests were performed to test dataset normality and homoscedasticity, respectively. Parametric variables (mangrove height, litterfall production, and leaf decomposition) were analyzed using ANOVA tests (F). Conversely, nonparametric variables (density, basal area, and biomass) were analyzed using Kruskal-Wallis tests (H). Significant differences between nonparametric variables were analyzed using a Steel-Dwass-Critchlow-Fligner paired test (Wij). For regressions and correlations between mangroves and fishes, the determination coefficient and p value were estimated. All analyses were performed at 95% confidence using the statistical software Statistica version 8.0 and XLSTAT version 18.06. Fish data were correlated through linear regressions with mangrove structural (e.g., density, biomass, dominance, complexity) and functional (e.g., litterfall production) properties of each study site.

# RESULTS

The forest structural and functional properties of each of the mangrove communities were described and related to the fish assemblages that lived within the mangrove communities.

#### Mangrove Structure

In mangrove vegetation communities, the highest values of individual density (12,924), basal areas (BA<sub>1.3m</sub> = 13.7 m<sup>2</sup> ha<sup>-1</sup>; BA<sub>0.3m</sub> = 26.6 m<sup>2</sup> ha<sup>-1</sup>), height (3.3 m), and total biomass (113.5 Mg ha<sup>-1</sup>) were estimated in Balandra, followed by Zacatecas and Enfermería (Table 2). Nevertheless, there were no significant differences (p > 0.05) among the studied mangrove vegetation communities (Table 3). Individual density, basal area, and average height of mangrove vegetation gave rise to the greater structural complexity in Balandra, with an CI value of 11.7, followed by Zacatecas and Enfermería (Table 2).

Avicennia was the species with the highest density of individuals and stems in the three study sites, followed by *Laguncularia* (except in Enfermería) and *Rhizophora* (Table 4).

Avicennia germinans was the most important species in all the studied sites, with the highest IVI of 190.8 in Enfermería. *Rhizophora mangle*, compared with *L. racemosa*, had a higher IVI in Zacatecas (102.7) and Enfermería (95.3), but not in Balandra (Table 4).

The highest density of aerial roots was estimated for Zacatecas, followed by Balandra and Enfermería. For R. *mangle*, the highest prop root density was estimated in Zacatecas (Table 4).

# **Mangrove Litterfall Production**

Balandra had the highest litterfall production (2.4 g m<sup>-2</sup> day<sup>-1</sup>) (Table 2). Litterfall production was significantly differ-



Figure 2. Photographs from Balandra (left), Zacatecas (center), and Enfermería (right) showing the landscape (top), images from inside the mangrove (middle), and representative fauna (bottom).

ent (p < 0.05) between sites (Table 3). No significant differences between Balandra and Enfermería were found (F = 1.41, p = 0.24). Zacatecas had significant differences compared with Balandra and Enfermería (F = 10.26, p = 0.00 and F = 4.62, p = 0.04, respectively).

Laguncularia racemosa had the greatest average litterfall production of the three species in Balandra (1.3 g m<sup>-2</sup> d<sup>-1</sup>), but not in the other sites. In Enfermería and Zacatecas, the species with the highest average litterfall production was *R. mangle*, with 1.1 and 0.6 g m<sup>-2</sup> d<sup>-1</sup>, respectively (Table 5).

Table 1. Richness, density, biomass, and length of fish assemblages of three arid mangroves (López-Rasgado et al., 2012).

Mangrove Community	Richness	$\begin{array}{c} Density \\ (ind \ m^{-2}) \end{array}$	$\begin{array}{c} Biomass \\ (g \ m^{-2}) \end{array}$	Length (mm)
Balandra	15.5	3	5.1	30.8
Enfermería	6.7	5.7	20.7	37.2
Zacatecas	7.0	1.4	4.5	35

ind = individuals

Enfermería's mangrove had the greatest litterfall production of *A. germinans* and *R. mangle* under high interstitial salinity conditions (Table 5).

# Leaf Decomposition

In each community, leaf decomposition varied between an average of 1.5% and 1.7% mass loss per day (Table 2). Leaf decomposition was not significantly different (p > 0.05) between study sites (Table 3) and species (Table 5).

Avicennia germinans had the highest leaf decomposition of the three sites studied, with average values between 1.8% and 2.0% mass loss per day (Table 5). Laguncularia racemosa and *R. mangle* had an average value between 1.3% and 1.5% mass loss per day (Table 5).

# Mangrove Properties Linked to Fish Assemblages

Each of the variables for fish assemblages were correlated with the structural and functional characteristics of mangroves, and only the following characteristics were identified.

:	Structural					Functional	
Mangrove Community	Density of Ind [Stems] (ha <sup>-1</sup> )	$\begin{array}{c} BA_{1.3m} \left[ BA_{0.3m} \right] \\ (m^2 \ ha^{-1}) \end{array}$	Height (m)	Biomass (Mg ha <sup>-1</sup> )	Complexity Index	$\begin{tabular}{c} Litterfall \\ Production \\ (g \ m^{-2} \ d^{-1})^* \end{tabular}$	Leaf Decomposition (% mass loss d <sup>-1</sup> )
Balandra Enfermería Zacatecas	$\begin{array}{c} 12,924 \pm 18,055 \left[22,734 \pm 30,010\right] \\ 5,775 \pm 2,901 \left[10,587 \pm 6,106\right] \\ 11,094 \pm 11,833 \left[26,747 \pm 23,314\right] \end{array}$	$\begin{array}{c} 13.7 \pm 7.3 \ [26.6 \pm 16.7] \\ 6.8 \pm 3.8 \ [15.2 \pm 12.9] \\ 9.7 \pm 7.9 \ [19.6 \pm 3.9] \end{array}$	$\begin{array}{c} 3.3 \pm 2.5 \ 2.4 \pm 0.7 \ 2.1 \pm 0.5 \end{array}$	$\begin{array}{c} 113.5\pm67.4\\ 65.2\pm44.3\\ 81.7\pm79.2\end{array}$	$11.7 \\ 1.9 \\ 4.5$	$2.4 \pm 0.9^{ m b} \ 2.0 \pm 0.7^{ m b} \ 1.3 \pm 0.5^{ m a}$	$\begin{array}{c} 1.6 \pm 0.7 \\ 1.5 \pm 0.9 \\ 1.7 \pm 0.8 \end{array}$

Table 2. Mangrove structural and functional variables of three arid mangroves ( $\bar{x} \pm SD$ ).

Ind = individuals; BA = basal area

\*Lowercase letters indicate significant differences by one-way ANOVA (p < 0.05).

Fish size was highly and inversely correlated with mangrove biomass and structural complexity. Balandra had the highest mangrove biomass and structural complexity, as well as the smallest fish. In contrast, Enfermería had the biggest fish, followed by Zacatecas (Table 1). *Avicennia germinans* had a positive correlation with fish biomass, and *L. racemosa* had a positive correlation with fish richness, although it was not significant (p = 0.08 and p = 0.07, respectively).

### DISCUSSION

Structural and functional properties measured in this study included heterogeneity, basal area, average stem density, density of trees, and litterfall production. These records are compared to previous studies for the region, and are considered in explaining differences in fish biomass and richness between locations (Balandra, Zacatecas, and Enfermería). The discussion is further extended to the fish-related ecosystem services provided by mangroves.

# **Mangrove Forest Structural and Functional Properties**

Mangroves of the southwestern Gulf of California, as in other mangrove ecosystems along the Gulf of California, are dominated by *A. germinans*, *R. mangle*, and *L. racemosa*. Black mangroves (*A. germinans*) are the most important mangrove species because of their plasticity and adaptive capacity to arid zone climatic conditions, similar to species like *Avicennia marina* in other parts of the world (Dahdouh-Guebas *et al.*, 2007; Duke, 1990). In Balandra, a higher relative dominance of *L. racemosa* occurs because of the groundwater input in the area (Urquidi-Gaume, Santos, and Lechuga-Deveze, 2015).

In La Paz Bay, mangroves cover small areas but have high heterogeneity (both within and between systems), with different average values in density and basal area, which explains why they are not statistically different. Height and basal area values are within the reported ranges for the region. However, average stem density and density of trees are higher

Table 3. Results of ANOVA or Kruskal-Wallis tests on structural and functional variables among three arid mangroves.

Variable	Test Result	p Value
Density	H = 0.36,  df = 2	0.83
Stem Density	H = 3.29,  df = 2	0.19
Basal Area (0.3 m)	$H = 0.28,  \mathrm{df} = 2$	0.86
Basal Area (1.3 m)	H = 1.19,  df = 1	0.27
Height	F = 3.37	0.06
Biomass	$H = 0.34,  \mathrm{df} = 2$	0.84
Litter Production	F = 5.01	$0.01^{*}$
Leaf Decomposition	F = 2.97	0.06

\*Significantly different

in this study than those of previous reports from the Gulf of California (Arreola-Lizárraga, Flores-Verdugo and Ortega-Rubio, 2004; Félix-Pico *et al.*, 2006; Sánchez-Andrés *et al.*, 2010). Differences in density may be explained by the different field methods used. Previous studies were based on rapid appraisal of forest structure that measured the distance between individuals to estimate density (Cintrón *et al.*, 1978); however, because, in this case, the estimation of biomass was also considered important, all individuals in a defined area were included, as proposed by Kauffman and Donato (2012).

The average litterfall production ranged from 1.3 to 2.4 g m<sup>-2</sup> d<sup>-1</sup>, which falls within the reported values for the region (Félix-Pico *et al.*, 2006; López-Medellín and Ezcurra, 2012). The lowest litterfall production value was recorded in Zacatecas, the system which also has the lowest value in tree height.

This is the first study that reports leaf decomposition rates (percent mass loss per day) for the three species in the region (*i.e. A. germinans, R. mangle*, and *L. racemosa*). Reported values are not statistically different between the three systems. However, higher values were observed in Zacatecas, which may be explained by a tidal inundation and therefore higher decomposition of the organic matter on the soil (Twilley, Lugo, and Patterson-Zucca, 1986).

# Mangrove Properties Linked to Fish Assemblages

Results corroborate that mangrove structural complexity is positively related to fish community richness (Manson *et al.*, 2005), but it also indicates that it is inversely related to fish size. Surprisingly, no direct relationship was found between mangrove biomass and fish biomass.

Balandra is the site with the highest structural complexity and heterogeneity of habitat, as well as fish richness, partly because of a relatively extended forested mudflat and dominance of *L. racemosa*, which creates diverse microhabitats for the fish to use. The presence of *Laguncularia* in Balandra is very extensive, unlike the other two sites, thus providing this community with a more diverse array of conditions. Moreover, this species also generates the largest litterfall production when compared with the other mangrove species, contributing to the carbon and nutrient input of the lagoon. In Balandra, a factor that has been proposed to influence fish richness is the site's direct connection to the Gulf of California, which would explain the occurrence of pelagic species (*e.g.*, anchovy; López-Rasgado *et al.*, 2012) that are not found in the other study sites.

Balandra has the second highest fish biomass of the three systems, mostly composed of a very diverse community of earlystage fishes. High fish biomass has been previously linked to fringe mangrove areas dominated by *R. mangle* (Aburto-

		Density of			Relative			
Mangrove Community	Species (n)	Ind [Stems] (ha <sup>-1</sup> )	$\begin{array}{c} BA_{0.30m} \\ (m^2 \ ha^{-1}) \end{array}$	$\begin{array}{c} BA_{1.30m} \\ (m^2 \ ha^{-1}) \end{array}$	Dominance (%)	Height (m)	IVI	$\begin{array}{l} \mbox{Aerial Root Density} \\ (\mbox{roots } m^{-2}) \ [\mbox{Height (cm)}] \end{array}$
Balandra	A. germinans (180)	$12,765 \pm 16,387 \ [22,553 \pm 30,940]$	$17.4\pm6.4$	$6.4\pm3.7$	26	$2.1\pm0.8$	141.3	$453.3 \pm 153.7 \ [8.1 \pm 2.1]$
	L. racemosa (119)	$7,033 \pm 11,128 \ [11,524 \pm 17,309]$	$16.7 \pm 21.7$	$9.4~\pm~10.8$	45.5	$3.4~\pm~1.8$	113.7	$240\pm55.4[9.17\pm4.6]$
	R. mangle (28)	$1,418 \pm 1,356 \ [2,381 \pm 2,284]$	$5.0\pm6.0$	_	28.5	$3.0\pm2.0$	45	$7.0 \pm 4.7^{*}$
Enfermería	A. germinans (67)	$4,752\pm3,656[9,078\pm8,025]$	$17.0 \pm 14.6$	$6.3\pm5.0$	66	$2.6\pm0.8$	190.8	$325.3\pm69.3[14.3\pm6.1]$
	L. racemosa (8)	†	†	†	5.8	$2.4\pm0.2$	13.8	$115 \pm 48 \; [4.9 \pm 1.4]$
	R. mangle (39)	$2{,}571 \pm 2{,}660 \; [7{,}021 \pm 5{,}466]$	$3.4~{\pm}~1.9$	_	28.1	$2.1\pm1.1$	95.3	$7.2 \pm 3.3^{*}$
Zacatecas	A. germinans (157)	$13,918 \pm 9,730 \ [27,926 \pm 11,943]$	$14.9\pm6.2$	$3.0\pm2.0$	17.8	$1.5\pm0.5$	155.8	$768 \pm 144.9 \ [12.5 \pm 1.5]$
	L. racemosa (26)	$4{,}610 \pm 4{,}511 \ [17{,}908 \pm 22{,}316]$	$7.6~\pm~7.4$	$2.9\pm2.6$	11.5	$1.3\pm0.5$	41.5	$251\pm33.3[5.2\pm2.6]$
	R. mangle (30)	$2,128\pm1,525\;[8,688\pm6,277]$	$9.6\pm8.5$	—	70.7	$2.1\pm0.3$	102.7	$12.7 \pm 14.6^{*}$

Table 4. Species structural variables of three arid mangroves ( $\bar{x} \pm SD$ ).

Ind = individuals; BA = basal area, IVI = importance value index

\*Root density per individual of R. mangle.

 $^{\dagger}T$ his data was not calculated given that L. racemosa was only present in one of the plots with very few individuals.

Oropeza *et al.*, 2008). Nonetheless, in this research, fish biomass (*i.e.* artisanal fisheries potential) is more related to the dominance of *A. germinans*, which may in turn be related to the high litterfall production and leaf decomposition of *A. germinans* (Barroso-Matos, Bernini, and Rezende, 2012; Fernando and Bandeira, 2009; Lima and Colpo, 2014) that then provides food for detritivorous fish. Additionally, in this study, lower complexity has been associated with a higher fish biomass (Carey *et al.*, 2010). In this sense, Enfermería's mangrove community has the lowest habitat complexity, yet the highest fish biomass.

Enfermería is a system affected by several human interventions (Mendoza-Salgado *et al.*, 2011; Santamaría-Gallegos, Danemann, and Ezcurra, 2011), with habitat fragmentation and coverage loss of over 50% between 1978 and 2005 (CONABIO, 2010). Habitat heterogeneity (*i.e.* forested mudflat and *L. racemosa*) and fish richness is therefore reduced. It is clearly important to adopt and maintain monitoring and management plans to prevent further degradation. However, it is interesting to note that in terms of promoting local fisheries (*i.e.* mojarras and mullets), Enfermería in its current condition provides a more efficient ecosystem service than the other two systems.

# CONCLUSIONS

Complexity and biomass are mangrove features considered important as fish breeding and shelter zones. In the southwestern Gulf of California region, mangrove communities showing high habitat heterogeneity are linked to high fish species richness, whereas low structural complexity systems are dominated by *A. germinans*, promoting higher biomass in species that are important for artisanal fisheries.

Analysis of the three contrasting sites suggests that, when considering fish-related ecosystem services provided by mangroves, the most desirable situation is having high-diversity mangrove systems; the most complex systems, with the highest habitat heterogeneity, promote higher fish diversity, and the simplest systems promote the highest biomass of fishes important for artisanal fisheries. This argument may be further extended when considering other ecosystem services, such as the ecological role of other aquatic and aerial groups, carbon sequestration, coastal protection, and aesthetic value.

## ACKNOWLEDGMENTS

We are grateful to Obdulia Gómez Domínguez and Horacio Bervera León for their technical assistance. México's Consejo Nacional de Ciencia y Tecnología (CONACYT) financially supported this research, and JGOG holds a doctoral scholarship grant (388919) from CONACYT. Centro de Investigaciones Biológicas del Noreste (CIBNOR) provided laboratory support. All fieldwork was carried under Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) scientific collecting permit SGPAIDGVSI 05102/15.

Table 5. Litter production, leaf decomposition, and interstitial salinity by species in three arid mangroves ( $\bar{x} \pm SD$ ).

Mangrove Community	Species	Litterfall Production $(g m^{-2} d^{-1})^*$	$\begin{array}{c} \text{Leaf Decomposition} \\ (\% \text{ mass loss } d^{-1}) \end{array}$	Interstitial Salinity at 10–15 cm (psu)
Balandra	A. germinans	$0.5\pm0.3^{ m b}$	$1.8\pm0.7$	$54.0 \pm 11.5$
	L. racemosa	$1.3\pm0.8^{ m a}$	$1.3\pm0.6$	$43.3\pm6.6$
	R. mangle	$0.6\pm0.4^{ m b}$	$1.5\pm0.7$	$37.4\pm1.6$
		p < 0.05		
Enfermería	A. germinans	$0.9\pm0.5^{ m b}$	$1.8 \pm 1.0$	$56.0 \pm 13.5$
	L. racemosa	$0.01\pm0.00^{ m a}$	$1.3\pm0.7$	$38.5\pm0.2$
	R. mangle	$1.1\pm0.5^{ m b}$	$1.3\pm0.6$	$39.6\pm0.9$
		p < 0.05		
Zacatecas	A. germinans	$0.3\pm0.2^{ m b}$	$2.0~\pm~1.0$	$50.2\pm5.2$
	L. racemosa	$0.4\pm0.3^{ m ab}$	$1.5\pm0.7$	$51.5 \pm 1.4$
	R. mangle	$0.6\pm0.3^{\mathrm{a}}$	$1.4\pm0.6$	$39.4\pm1.9$
		p < 0.05		

 $psu = practical \ salinity \ unit$ 

\*Lowercase letters indicate significant differences by one-way ANOVA.

# LITERATURE CITED

- Aburto-Oropeza, O.; Cota-Nieto, J.; Domínguez-Guerrero, I.; Girón-Nava, A., and Costa, M., 2015. How distance between mangroves and reefs could affect snapper populations. DataMares InteractiveResource. doi:10.13022/M3Z303
- Aburto-Oropeza, O.; Ezcurra, E.; Danemann, G.; Valdez, V.; Murray, J., and Sala, E., 2008. Mangroves in the Gulf of California increase fishery yields. *Proceedings of the National Academy of Sciences of the U. S. A.*, 105(30), 10456–10459.
- Araújo, F.G. and Alcántara, A.C., 1999. Distribution and recruitment of mojarras (Perciformes: Gerreidae) in the continental margin of Sepetiba Bay, Brazil. Bulletin of Marine Sciences, 65(2), 431–439.
- Arreola-Lizárraga, J.A.; Flores-Verdugo, F.J., and Ortega-Rubio, A., 2004. Structure and litterfall of an arid mangrove stand on the Gulf of California, Mexico. *Aquatic Botany*, 79(2), 137–143.
- Barroso-Matos, T.; Bernini, E., and Rezende, C.E., 2012. Decomposition of mangrove leaves in the estuary of Paraiba do Sul River, Rio de Janeiro, Brazil. Latin American Journal of Aquatic Research, 40(2), 398.
- Bazzaz, F.A., 1975. Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology*, 56(2), 485–488.
- Carey, M.P.; Maloney, K.O.; Chipps, S.R., and Wahl, D.H., 2010. Effects of littoral habitat complexity and sunfish composition on fish production. *Ecology of Freshwater Fish*, 19(3), 466–476.
- Chave, J.; Coomes, D.A.; Jansen, S.; Lewis, S.L.; Swenson, N.G., and Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. *Ecology Letters*, 12(4), 351–366.
- Cintrón, G.; Lugo, A.E.; Pool, D.J., and Morris, G., 1978. Mangroves of arid environments in Puerto Rico and adjacent islands. *Biotropica*, 10(2), 110–121.
- Collins, M.R., 1985. Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (South Florida)—White Mullet. South Florida: U.S. Fish Wildlife Service. Biological Report 82(11.39), Vicksburg, Mississippi: U.S. Army Corps of Engineers, TR EL-82-4, 7p.
- CONABIO (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad), 2010. Mangrove Coverage in Baja California Sur in 1978, 2005, and 2010. http://speck.conabio.gob.mx/manglarfotos/ BCS/diacronico/index.html.
- Curtis, J.T. and McIntosh, R.P., 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology*, 32(3), 476– 496.
- Dahdouh-Guebas, F.; Kairo, J.G.; De Bondt, R., and Koedam, N., 2007. Pneumathopore height and density in relation to microtopography in the grey mangrove Avicennia marina. Belgium Journal of Botany, 140(2), 213-221.
- Dahdouh-Guebas, F. and Koedam, N., 2006. Empirical estimate of the reliability of the use of the point-centred quarter method (PCQM): Solutions to ambiguous field situations and description of the PCQM+ protocol. *Forest Ecology and Management*, 228(1), 1–18.
- Duke, N.C., 1990. Phenological trends with latitude in the mangrove tree Avicennia marina. The Journal of Ecology, 78(1), 113–133.
- Félix-Pico, E.F.; Holguín-Quiñones, O.E.; Hernández-Herrera, A., and Flores-Verdugo, F., 2006. Estero El Conchalito mangrove's primary production in La Paz Bay (Baja California Sur, México). *Ciencias Marinas*, 32(1A), 53–63.
- Fernando, S.M. and Bandeira, S.O., 2009. Litterfall and decomposition of mangrove species Avicennia marina and Rhizophora mucronata in Maputo Bay, Mozambique. Western Indian Ocean Journal of Marine Science, 8(2), 173–182.
- Holdridge, L.R.; Grenke, W.C.; Hathaway, W.H.; Liang, T., and Tosi, J.A., Jr., 1971. Forest Environments in Tropical Life Zones: A Pilot Study. New York: Pergamon Press, 747p.
- Ishihara, M.I.; Utsugi, H.; Tanouchi, H.; Aiba, M.; Kurokawa, H.; Onoda, Y.; Nagano, M.; Umehara, T.; Ando, M.; Miyata, R., and Hiura, T., 2015. Efficacy of generic allometric equations for estimating biomass: a test in Japanese natural forests. *Ecological Applications*, 25(5), 1433–1446.
- Kauffman, J.B. and Donato, D.C., 2012. Protocols for the Measurements, Monitoring and Reporting of Structure, Biomass and

Carbon Stocks in Mangrove Forests. Bogor, Indonesia: Center for International Forestry Research Working Paper No. 86, 50p.

- Komiyama, A.; Poungparn, S., and Katom, S., 2005. Common allometric equations for estimating the tree weight of mangroves. *Journal of Tropical Ecology*, 21(4), 471–477.
- Laegdsgaard, P. and Johnson, C.R., 2001. Why do juvenile fish utilize mangrove habitats? Journal Experimental Marine Biology and Ecology, 257(2), 229–253.
- Latrubesse, E.M.; Stevaux, J.C., and Young, K.R., 2013. Hydrogeomorphologic processes and Quaternary landforms controlling biotic components in South American wetlands: Introduction. *Journal of South American Earth Sciences*, 46, 110–112.
- Lima, R.G. and Colpo, K.D., 2014. Leaf-litter decomposition of the mangrove species Avicennia schaueriana, Laguncularia racemosa and Rhizophora mangle. Journal of the Marine Biological Association of the United Kingdom, 94(2), 233–239.
- López-Medellín, X. and Ezcurra, E., 2012. The productivity of mangroves in northwestern Mexico: A meta-analysis of current data. *Journal of Coastal Conservation*, 16(3), 399–403.
- López-Rasgado, F.J.; Herzka, S.Z.; Del-Monte-Luna, P.; Serviere-Zaragoza, E.; Balart, E.F., and Lluch-Cota, S., 2012. Fish assemblages in three arid mangrove systems of the Gulf of California: Comparing observations from 1980 and 2010. Bulletin of Marine Science, 88(4), 919–945.
- López-Rasgado, F.J.; Lluch-Cota, S.E.; Balart, E.F., and Herzka, S.Z., 2016. Variation in isotopic trophic structure and fish diversity in mangrove systems subject to different levels of habitat modification in the Gulf of California, México. *Bulletin of Marine Science*, 92(4), 399–422.
- Manson, F.J.; Loneragan, N.R.; Skilleter, G.A., and Phinn, S.R., 2005. An evaluation of the evidence for linkages between mangroves and fisheries: A synthesis of the literature and identification of research directions. Oceanography and Marine Biology, 43, 485–515.
- Mendoza-Salgado, R.A.; Lechuga-Deveze, C.H.; Amador, E., and Pedrín-Avilés, S., 2011. Environmental quality of the Baja California Sur mangroves. In: Félix-Pico, E.F.; Serviere-Zaragoza, E.; Riosmena-Rodríguez, R., and León de la Luz, J.L. (eds.), Mangroves of the Baja California Peninsula. La Paz, México: Centro de Investigación Biológica del Noreste-Centro Interdisciplinario de Ciencias Marinas-Universidad Autónoma de Baja California Sur. pp. 9-26.
- Mora, C. and Ospína, A.F., 2001. Tolerance to high temperatures and potential impact of sea warming on reef fishes of Gorgona Island (tropical eastern Pacific). *Marine Biology*, 139(4), 765–769.
- Nagelkerken, I.; Blaber, S.; Bouillon, S.; Green, P.; Haywood, M.; Kirton, L.G.; Meynecke, J.O.; Pawlik, J.; Penrose, H.M.; Sasekumar, A., and Somerfield, P.J., 2008. The habitat function of mangroves for terrestrial and marine fauna: A review. Aquatic Botany, 89(2), 155-185.
- Nagelkerken, I.; Kleijnen, S.; Klop, T.; van den Brand, R.; Cocheret de la Morinière, E., and van der Velde, G., 2001. Dependence of Caribbean reef fishes on mangroves and seagrass beds as nursery habitats: A comparison of fish faunas between bays with and without mangroves/seagrass beds. *Marine Ecology Progress Series*. 214, 225–235.
- Odum, W.E. and Heald, E.J., 1972. Trophic analyses of an estuarine mangrove community. *Bulletin of Marine Science*, 22(3), 671–738.
- Pacheco-Ayub, C.A. and Bautista-Romero, J.J., 2003. Optimal Interpolation Sea Surface Temperature. CD-ROM (Ver. 2.0). La Paz, México: Centro de Investigaciones Biológicas del Noroeste S.C.
- Payan-Alcacio, J.A., 2015. Functional diversity of fish communities in mangrove habitats in La Paz Bay, B.C.S. México. La Paz, México: Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional, Master's thesis, 107p.
- Rojas-García, F.; De Jong, B.H.; Martínez-Zurimendí, P., and Paz-Pellat, F., 2015. Database of 478 allometric equations to estimate biomass for Mexican trees and forests. *Annals of Forest Science*, 72(6), 835–864.
- Sánchez-Andrés, R.; Sánchez-Carrillo, S.; Alatorre, L.C.; Cirujano, S., and Álvarez-Cobelas, M., 2010. Litterfall dynamics and nutrient decomposition of arid mangroves in the Gulf of California: Their

role sustaining ecosystem heterotrophy. Estuarine, Coastal and Shelf Science, 89(3), 191–199.

- Santamaría-Gallegos, N.; Danemann, G., and Ezcurra, E., 2011. Conservation and management of mangroves in the Baja California Peninsula. In: Félix-Pico, E.F.; Serviere-Zaragoza, E.; Riosmena-Rodríguez, R., and León de la Luz, J.L. (eds.), Mangroves of the Baja California Peninsula. La Paz, México: Centro de Investigación Biológica del Noreste-Centro Interdisciplinario de Ciencias Marinas-Universidad Autónoma de Baja California Sur. pp. 274-292
- Twilley, R.; Lugo, A., and Patterson-Zucca, C., 1986. Litter production and turnover in basin mangrove forests in southwest Florida. *Ecology*, 67(3), 670–683.
- Urquidi-Gaume, M.; Santos, I.R., and Lechuga-Deveze, C., 2015. Submarine groundwater discharge as a source of dissolved nutrients to an arid coastal embayment (La Paz, Mexico). *Environmental Earth Sciences*, 75(2), 1-13.
- Wang, M.; Huang, Z.; Shi, F., and Wang, W., 2009. Are vegetated areas of mangroves attractive to juvenile and small fish? The case of Dongzhaigang Bay, Hainan Island, China. *Estuarine, Coastal* and Shelf Science, 85(2), 208–216.
- Woodroffe, C.D., 1992. Mangrove sediments and geomorphology. In: Robertson, A.I. and Alongi, D.M. (eds.), Tropical Mangrove Ecosystems. Washington, D.C.: American Geophysical Union, pp. 7–41.