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Fish communities of a disturbed mangrove wetland and an adjacent tidal river in Palmar, Ecuador

V.R. Shervette [a,*], W.E. Aguirre [b], E. Blacio [c], Rodrigo Cevallos [d], Marcelo Gonzalez [d], Francisco Pozo [d], F. Gelwick [a]

[a] *Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258, USA*
[b] *Department of Ecology and Evolution, State University of New York at Stony Brook, New York, NY 11794-5245, USA*
[c] *Centro Nacional de Acuicultura e Investigaciones Marinas, Guayaquil, Ecuador*
[d] *Facultad de Biología Marina, Universidad Estatal Peninsula de Santa Elena, Guayas Province, Ecuador*

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Abstract

Coastal Ecuador has lost 20–30% of mangrove wetlands over the past 30 years. Such habitat loss can impair the ecological functions of wetlands. A paucity of information exists concerning mangrove fish communities of Ecuador. In this study we identify the fish community of the remaining mangrove wetland in Palmar, Ecuador. Fish were sampled in the dry season of 2003 and the wet season of 2004 by seining in mangrove creeks and Main channel of Rio Palmar. For comparison, an adjacent tidal river without mangroves, Rio Javita, was also sampled. We collected a total of 12,231 individuals comprising 36 species in 16 families from Rios Palmar and Javita. Gobiidae (7 species) was the most diverse family for mangrove sites followed by Gerreidae (5 species) and Engraulidae (4 species). A total of 34 species were collected in the mangrove wetland, 21 of which were exclusive to the mangroves including three species of juvenile snook (Centropomidae), indicating that the mangrove habitat of Palmar may provide nursery habitat for these economically valued species. In Rio Javita, Carangidae (3 species) was the most diverse family followed by Engraulidae and Gerreidae (2 species each). A total of 14 species were collected in the tidal river, only two of which were exclusive to the river. Multivariate analyses of fish community data indicated significant differences in community composition between the mangrove creeks and the tidal river and between seasons in both. Juvenile white mullet, *Mugil curema*, were collected in high relative abundance in both Rios Palmar and Javita, as was the tropical silverside *Atherinella serrivomer* an ecologically important species. Although Rios Palmar and Javita are characterized by relatively low fish species richness compared to other tropical estuarine systems, they appear to provide an important habitat for several economically and ecologically valued species.

Keywords: community; mangroves; nursery; estuarine habitat; trophic structure; Tropics; Ecuador

1. Introduction

Mangroves are the dominant intertidal vegetation in subtropical and tropical estuarine systems (Chapman, 1976; Duke, 1992). Mangrove-dominated estuaries support essential ecological functions. Much like most estuarine ecosystems, mangrove wetlands intercept land-derived nutrients, pollutants, and suspended matter and act as a filtering system (Marshall, 1994; Rivera-Monroy and Twilley, 1996; Tam and Wong, 1999; Valiela et al., 2001). Mangrove systems also export materials supporting near-shore food webs (Twilley, 1988; Sasekumar et al., 1992; Twilley et al., 1997). Moreover, mangroves provide a direct benefit to humans through the provision of various extraction-based resources such as wood, lumber, honey, tannins, salt, and artisanal fisheries for mussels, crabs, and fish (Kathiresan and Bingham, 2001; Alongi, 2002).

Many studies have reported the important role mangroves play in the life history of countless fish and invertebrate

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* Corresponding author.
E-mail address: shervette@gmail.com (V.R. Shervette).

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species (Chong et al., 1990; Robertson and Duke, 1990; Yáñez-Arancibia et al., 1993; Ikejima et al., 2003; Hindell and Jenkins, 2004). Mangrove wetlands provide estuarine residents and marine and freshwater transient species with essential food and shelter resources (Blaber, 1986; Sheaves and Molony, 2000; Laegdsgaard and Johnson, 2001). However, unlike Florida, the Caribbean, Mexico, and Australia where mangroves are often coupled with seagrasses and nekton assemblages are well documented (e.g., Yáñez-Arancibia et al., 1993; Laegdsgaard and Johnson, 1995; Nagelkerken et al., 2001; Poulakis et al., 2003), in South America, little information exists concerning the importance of mangroves to fishes and invertebrates. Basic information detailing fish community structure and species utilization of estuarine habitat in general, and mangrove habitat in particular, is virtually non-existent for the tropical Pacific coast of South America.

In the past 30 years, coastal Ecuador has lost approximately 20−30% of mangrove wetlands (Parks and Bonifaz, 1994). Much of the loss of mangrove habitat in this region is primarily due to shrimp aquaculture (Olsen and Arriaga, 1989; Twilley et al., 1993, 1997). Such landscape modifications can impair the integrity of these wetlands and reduce their capacity to function as centers of biological diversity. Because subsistence fishing is a widespread method of provisioning families and fish production is likely mangrove-dependent, loss of these wetlands and their associated habitat also risks loss of a major source of livelihood and cultural tradition for people inhabiting coastal areas.

In order to assess environmental and ecological changes within a wetland, many studies have utilized fish community data (Whitfield and Elliott, 2002). A suite of environmental variables drive the conditions available for fish (Blaber, 1997; Lorenz, 1999). Ecosystem level alterations of a mangrove wetland, including habitat loss and alteration, directly and indirectly affect biodiversity, including that of fish (Twilley et al., 1996). Characteristics of the fish communities within an estuarine ecosystem, such as a mangrove wetland, including measures of diversity and richness, relative abundance, and trophic integrity can be useful in evaluating the relative health of an estuarine system (Whitfield and Elliott, 2002; Harrison and Whitfield, 2004). Eighty-nine percent of the total area of shrimp ponds constructed in intertidal zones in Ecuador resides in the southern coastal region (Parks and Bonifaz, 1994). Identifying the fish communities of mangrove wetlands in Ecuador is an important aspect in furthering the understanding of the ecological significance of mangrove habitat loss.

In Palmar, located in Guayas province, Ecuador, a small stand of mangroves remains amid a mosaic of shrimp aquaculture ponds. Our goal in this study was to document the remaining fish community of the heavily impacted mangrove wetland. Specifically we describe the fish assemblage across the two main seasons of coastal Ecuador (winter and summer) in the mangrove creeks of Palmar and compare our findings to those of the adjacent tidal river, Rio Javita, lacking mangroves. Less than 2 km separate the mouths of these two estuarine habitats.

2. Materials and methods

2.1. Study area

Palmar, 95 km northwest of Guayaquil, Ecuador, is a small coastal town with approximately 4300 inhabitants, a large proportion of whom are dedicated to fishing (Solís-Coello and Mendívez, 1999; Fig. 1A). Annual temperature averages 23 °C and the annual rainfall average is 250−300 mm (E. Blacio, unpublished data). Coastal Ecuador has two seasons, a dry season from December to May and a wet season from June to November. The mangrove wetland of Palmar (2°01′ S and 80°44′ W) is approximately 30 ha in size and comprised mainly of red mangrove *Rhizophora mangle* (Fig. 1B,C). This wetland supports several subsistence fisheries including a mullet *Mugil* spp. fishery and two crab fisheries, a *Callinectes* sp. (Portunidae) and the red crab *Ucides occidentalis* (Ocypodidae). The small patch of mangroves near the mouth of Rio Palmar (Fig. 1B,C,D) was much larger historically, and as recently as 25 years ago, may have been larger by an order of magnitude. Most of the original mangroves within the wetland were cleared for the construction of shrimp ponds (Fig. 1C). The Palmar mangrove wetland is an isolated stand. Ecuador's primary mangrove area in the south is in the Gulf of Guayaquil and is the closest estuary with mangroves to Palmar. Rio Palmar consists of two small creeks upstream that meet and form Main channel which empties directly into the Pacific Ocean (Fig. 1B,C). Rio Javita, a small coastal river lacking mangroves, is located approximately 2 km from the Palmar mangrove wetland (Fig. 1A). Rio Javita is a shallow, turbid river under strong tidal influence, with a sandy bottom. Shrimp ponds surround both Rio Palmar and Javita.

2.2. Sampling design

We sampled the fish communities of the Palmar mangrove wetland and Rio Javita at the end of the coastal dry season in Oct/Nov 2003 and during the coastal wet season Mar/Apr 2004. A 7 m wide by 2 m high bag seine with 3 mm mesh was used to sample the fish community of Rio Palmar Main channel, mangrove creeks, and Rio Javita during mid-tide. We refer to Rio Palmar Main channel, mangrove Creek 1, mangrove Creek 2, and Rio Javita as our four sampling areas. We sampled at three sites along each of the two mangrove creeks and along Main channel of Rio Palmar (Fig. 1). In Rio Javita, we sampled three sites along the river (Fig. 1). We collected two samples for each of the six Creek sites on different dates each season. Rio Palmar Main channel and Rio Javita sites were sampled one time each season. A total of 36 samples were collected [2 seasons × (6 creek sites × 2 sampling periods + 3 Main channel sites + 3 Javita sites)]. Within each sampling time period, we calculated means for the data across the total area sampled for each sampling area unless otherwise indicated. Sites are considered replicates within the four sampling areas.

For each sample, two people standing 6 m apart towed the bag seine for a series of measured distances in order to

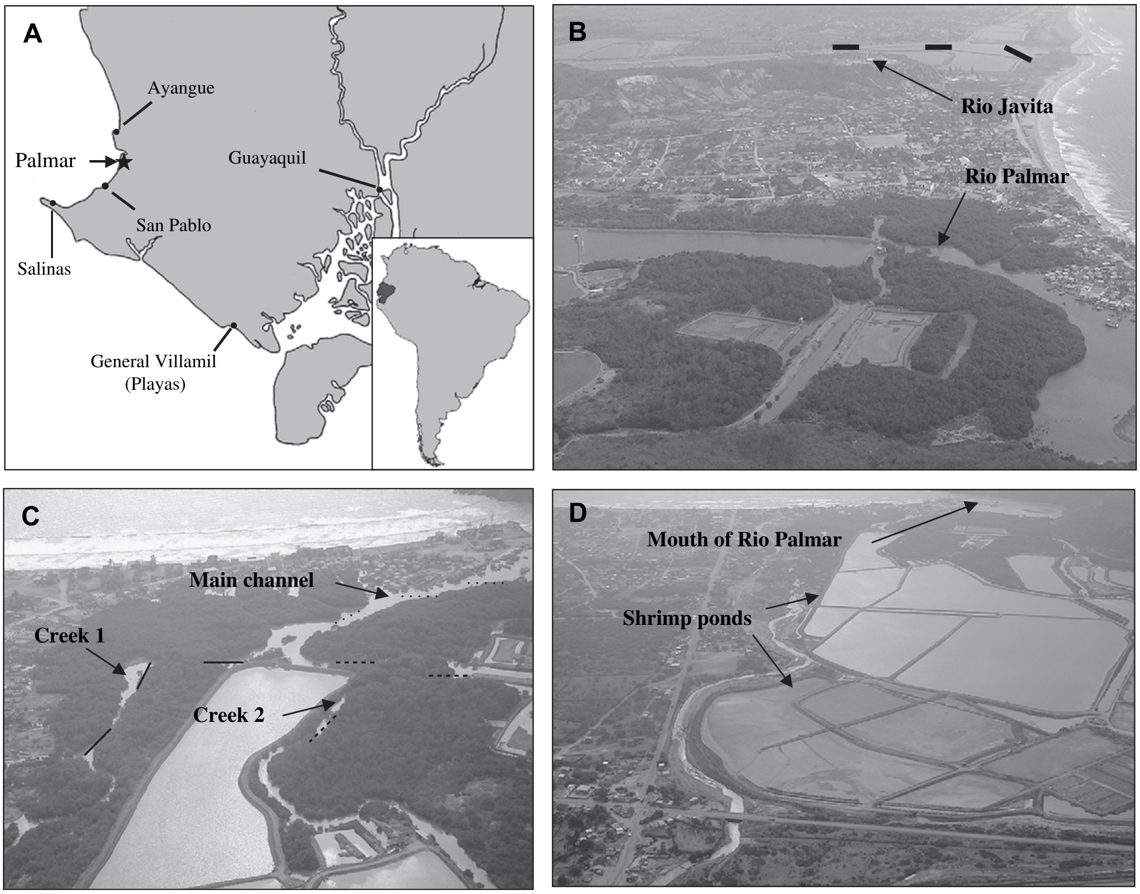

Fig. 1. (A) Location of Palmar on the coast of Ecuador. (B) Rio Palmar relative to Rio Javita. Solid lines are general representation of three sites sampled along Rio Javita. (C) The mangrove wetland of Palmar characterized by Main channel and Creeks 1 and 2. Dotted lines are a general representation of three sites sampled along Main channel; solid lines are general representation of three sites sampled along Creek 1; dashed lines are general representation of three sites sampled along Creek 2. (D) Picture illustrating some of the aquaculture ponds around and near Palmar mangrove wetland.

determine the catch per unit area. We determined the unit area sampled by assuming each seine tow covered a rectangular area and multiplied 6 m × total distance pulled (m). In order to determine the average depth of the creek or river site, we measured creek/river width at the beginning point, middle point, and end point of a seine tow then along each width, we measured depth at five equidistant points and calculated a mean depth from those measurements. We used a YSI-85 to measure salinity (PSU), dissolved oxygen (mg/l), and temperature (°C) for each sample. Additionally, we recorded percent mangrove cover as determined by the proportion of linear shoreline, on both sides directly parallel to seine path, occupied by mangrove structure for each sample.

All fish collected were immediately preserved in 10% buffered formalin for 48 h, soaked and rinsed with water, sorted, and then stored in 70% ethanol or isopropanol. Fish were transported to Texas A&M University and identified to the lowest taxonomic order (usually species) primarily according to Fischer et al. (1995) then measured (SL to 0.1 mm).

2.3. Statistical analyses

We calculated Shannon's Index of Diversity (H^1), Jaccard's Index of Evenness (J), and species richness (number of species collected) for each of the four sampling areas, for the mangrove sites combined, and for each of the two sampling seasons. We used the following formula for diversity: $H^1 = -\sum(p_i/Q) \times \ln(p_i/Q)$, where p_i is the proportion of the density comprised by the ith taxon and Q is the total density of individuals collected. We used the following formula to calculate evenness: $J = H^1/\ln S$ where S is the total number of species collected.

For each sampling area, we calculated species densities and species relative abundances (density of one species/total density of all individuals collected for sample × 100). Aggregated fish density data did not meet the assumption of normality. So, we tested for significant differences in aggregated fish densities across sampling areas and between sampling seasons using a non-parametric Friedman test. Our null hypothesis was that no significant difference in median values of overall density existed among the four sampling areas and between the two sampling seasons. Four species of economic and/or ecological importance were selected for further analysis. Differences in size distributions of *Mugil curema*, *Ctenogobius sagittula*, *Lile stolifera*, and *Atherinella serrivomer* were tested using the Mann–Whitney U-test where individuals from Rio Palmar (mangroves present) and Rio Javita (no mangroves present) were aggregated across seasons for each species group. For each species we tested the following null hypothesis: no significant difference in size existed between Rio Palmar and Rio Javita.

Correspondence analysis (CA) of the species-by-replicate matrix was used to examine variation in species relative abundance among sampling area and season. Density data were $\log(x+1)$ transformed. Multi-response permutation procedures (MRPP) were used to test the null hypothesis of no difference in species relative abundance between the two seasons within and among the four sampling areas. MRPP is a nonparametric technique used to test the significance of a priori sample groupings when the data violate the assumptions of parametric procedures such as multivariate analysis of variance. When significant sample groupings were detected, pairwise comparisons were made using a Bonferroni corrected α value.

Canonical correspondence analysis (CCA) was used to identify environmental gradients correlated with species' relative abundances. CCA is a weighted averaging method which directly relates community data to environmental variables by constraining species ordination patterns that correlate maximally with the environmental variables. Inter-set correlations between environmental variables (salinity, temperature, depth, and percent mangrove cover) were used to determine each variable's contribution. Monte Carlo permutation analysis simulation and forward selection were used to test the significance ($p < 0.05$) of the contribution of each variable to the CCA axes. All environmental variables were included in the CCA except DO because we did not have values for two sites in Rio Javita in the Mar/Apr samples due to equipment malfunction. Only significant, non-redundant variables were retained for interpretation. Both CA and CCA were performed using CANOCO (Version 4, Microcomputer Power) and MRPP was performed using PC-ORD version 4 (McCune and Mefford, 1999).

3. Results

3.1. Environmental data

Temperature was higher in the Mar/Apr (30.6 °C) sampling period than the Oct/Nov sampling period (27. 0 °C; Table 1). Throughout both sampling periods, temperature, on average, was slightly lower at Rio Javita sites than at Rio Palmar sites (Table 1). Salinity appeared relatively stable across the two sampling periods (Table 1). Main channel appeared to have a lower salinity, on average, than the other sampling areas. Dissolved oxygen was relatively high during both sampling periods and at all sampling areas, although it was slightly lower during the Mar/Apr sampling period and in the Creeks 1 and 2 sampling areas. Depth was consistently shallow throughout sampling and at all sampling areas (Table 1). Percent mangrove cover was higher in Creeks 1 and 2 than in Main channel. No mangroves were present at Rio Javita (Table 1).

3.2. Species relative abundance and diversity

We collected a total of 12,231 individuals comprising 36 species (16 families) from Rio Palmar and Rio Javita. In terms of number of species per family, Gobiidae (7 species) was the most diverse for the mangrove sites followed by Gerreidae (5 species) and Engraulidae (4 species). For the tidal river sites, Carangidae (3 species) was the most diverse followed by Engraulidae and Gerreidae (2 species each). A total of 34 species were collected in the mangrove wetland, 21 of which were exclusive to Rio Palmar. A total of 14 species were collected in the tidal river, only two of which were exclusive to the river. Seven species contributed 95% of the total density collected from Rio Palmar. These species included *Evorthodus minutus* (Gobiidae) with a relative abundance of 28.0%, *Ctenogobius sagittula* (Gobiidae) 24.4%, *Atherinella serrivomer* (Atherinidae) 21%, *Mugil curema* (Mugilidae) 18.2%, *Anchoa lucida* (Engraulidae) 1.4%, *Sphoeroides annulatus* (Tetraodontidae) 1.2%, and *Anchoa walkeri* (Engraulidae) 1.2% (Table 2). In contrast, Rio Javita had four species contributing 95% of the total density. These species included *M. curema* with a relative abundance of 48.7%, *A. serrivomer* 36.2%, *Lile stolifera* (Clupeidae) 6.9%, and *S. annulatus* 3.5% (Table 2).

Gobies dominated in samples collected from the mangrove sites in Oct/Nov. *Evorthodus minutus* comprised 34.1% of density collected from Rio Palmar and *Ctenogobius sagittula* comprised 28.6%. *Atherinella serrivomer* was the third most abundant species in the Palmar Oct/Nov samples with a relative abundance of 27.5% followed by *Anchoa lucida* and *Anchoa walkeri* with relative abundances of 2.0 and 1.7%, respectively (Table 2; Fig. 2). Rio Javita Nov/Oct samples were dominated by *A. serrivomer* (77.7% relative abundance) and *Lile stolifera* (13.0% relative abundance). *Mugil curema* was the third most abundant species in Rio Javita Oct/Nov samples followed by *C. sagittula* and *Sphoeroides annulatus* with relative abundances of 3.0%, 2.8%, and 2.3%, respectively (Table 2). Creek 1 deviated from the other three sampling areas in Oct/Nov in that *E. minutus* had the highest relative abundance and *C. sagittula* had the second highest. *Atherinella serrivomer* ranked highest in abundance for the other three sampling areas (Fig. 2).

Table 1
Environmental variables collected for each sample. Mean values (standard error) for the two sampling periods and the four sampling areas are given

Variable	Oct/Nov	Mar/Apr	Creek 1	Creek 2	Main	Javita
Temperature (°C)	27.0 (0.77)	30.6 (0.42)	28.3 (0.60)	29.7 (0.94)	29.1 (1.89)	25.4 (0.74)
Salinity (ppt)	41.7 (1.08)	42.8 (2.11)	42.2 (1.89)	45.7 (1.71)	36.0 (1.84)	42.4 (0.54)
DO (mg/l)	6.2 (0.39)	5.6 (0.37)	5.7 (0.69)	5.8 (0.36)	6.0 (0.43)	6.9 (0.35)
Depth (cm)	35 (3.4)	37 (3.6)	36 (5.8)	38 (3.9)	38 (3.2)	26 (3.0)
% mangrove	63 (7.7)	61 (7.6)	78 (3.7)	83 (1.4)	50 (7.3)	0 (0)

Table 2
Species collected from Rios Palmar and Javita. The Resident/diet column lists the known resident status for each species: ED is species that are estuarine dependent and utilize estuarine habitat as juveniles; MA is species that are marine species ‘‘accidentally’’ occurring in the estuary; ER is species that are estuarine residents. The diet status of each species is indicated as follows: GP is general predator; BC is benthic carnivore; O is omnivore; Z is zooplanktivore; P is planktivore; D is detritivore; and U indicates that diet for the species is unknown. Relative abundance (%) and density (number collected/100 m^2) in parentheses is listed for each fish species collected from Rio Palmar and Rio Javita between the two sampling seasons. Density data are combined for sites. CODE is the abbreviation for each species used in the CA and CCA. Overall relative abundance is combined for sites and seasons

Fishes	CODE	Resident/diet[a]	Oct/Nov		Mar/Apr		Overall RA	
			Palmar	Javita	Palmar	Javita	Palmar	Javita
Elopidae								
Elops affinis	Elo aff	ED/GP	0 (0)	0 (0)	0.07 (0.05)	0 (0)	0.02	0
Albulidae								
Albula vulpes	Alb vul	ED/O	0 (0)	0.14 (0.04)	0 (0)	0 (0)	0	0.06
Clupeidae								
Lile stolifera	Lile sto	ED/Z	0.42 (0.68)	13.00 (3.97)	0 (0)	1.9 (0.72)	0.30	6.9
Engraulidae								
Anchoa exigua	Anc exi	MA/U-GP[b]	0.01 (0.02)	0 (0)	0 (0)	0 (0)	0.01	0
Anchoa lucida	Anc luc	ED/ U-GP[b]	1.99 (3.19)	0.42 (0.13)	0 (0)	0 (0)	1.40	0.19
Anchoa walkeri	Anc wal	ED/ U-GP[b]	1.70 (2.72)	0 (0)	0.09 (0.06)	0.41 (0.15)	1.22	0.23
Anchovia macrolepidota	Anc mac	ED/ P	0.01 (0.02)	0 (0)	0 (0)	0 (0)	0.01	0
Batrachoididae								
Daector dowi	Dae dow	ER/U-BC	0.98 (1.57)	0 (0)	0.28 (0.19)	0 (0)	0.77	0
Poeciliidae								
Poeciliopsis sp.	Poe sp	ER/U-D[c]	0.44 (0.71)	0 (0)	2.60 (1.75)	0 (0)	1.08	0
Atherinidae								
Atherinella serrivomer	Ath ser	ER/O[d]	27.48 (43.97)	77.73 (23.71)	4.10 (2.76)	2.21 (0.82)	20.56	36.18
Centropomidae								
Centropomus armatus	Cen arm	ED/U-O[e]	0.92 (1.47)	0 (0)	0.39 (0.26)	0 (0)	0.76	0
Centropomus robalito	Cen rob	ED/GP	0.01 (0.02)	0 (0)	0 (0)	0 (0)	0.01	0
Centropomus unionensis	Cen uni	ED/U-O[e]	0.09 (0.14)	0 (0)	0 (0)	0 (0)	0.06	0
Carangidae								
Caranx caninus	Car can	ED/U-GP[f]	0 (0)	0 (0)	0.21 (0.14)	0.14 (0.05)	0.06	0.08
Oligoplites sp.	Oli sp	ED/U-GP[f]	0.06 (0.09)	0 (0)	1.88 (1.26)	0.55 (0.21)	0.60	0.30
Selene brevoortii	Sel bre	ED/GP	0.02 (0.03)	0.14 (0.04)	0 (0)	0 (0)	0.01	0.06
Gerreidae								
Diapterus peruvianus	Dia per	ED/GP	0.28 (0.44)	0 (0)	0.45 (0.31)	0 (0)	0.33	0
Eucinostomus argenteus	Euc arg	ED/O	0.37 (0.59)	0 (0)	0 (0)	0 (0)	0.26	0
Eucinostomus currani	Euc cur	ED/O	0.02 (0.04)	0.14 (0.04)	0 (0)	0 (0)	0.02	0.06
Gerreid sp.	Ger sp	ED/U-O[g]	0.20 (0.32)	0 (0)	0.17 (0.11)	0 (0)	0.19	0
Gerres cinereus	Ger cin	ED/O	0.05 (0.08)	0 (0)	0.05 (0.04)	0 (0)	0.05	0
Mugilidae								
Mugil cephalus	Mug cep	ED/D	0 (0)	0 (0)	0.06 (0.04)	0 (0)	0.02	0
Mugil curema	Mug cur	ED/D	1.35 (2.16)	2.97 (0.91)	58.23 (39.25)	86.30 (32.10)	18.22	48.68
Eleotridae								
Erotelis sp.	Ero sp	ER/U-O[h]	0.01 (0.02)	0 (0)	0.03 (0.02)	0 (0)	0.02	0
Gobiomorus sp.	Gob sp	ER/ U-O[h]	0.04 (0.06)	0 (0)	0 (0)	0 (0)	0.03	0
Gobiidae								
Bathygobius lineatus	Bat lin	ER/GP	0 (0)	0 (0)	0.02 (0.01)	0 (0)	0.01	0
Ctenogobius sagittula	Cte sag	ER/U-O[i]	28.62 (45.79)	2.83 (0.86)	14.26 (9.61)	4.00 (1.49)	24.37	3.47
Ctenogobius sp.	Cte sp	ER/U-O[i]	0.15 (0.24)	0 (0)	0 (0)	0 (0)	0.11	0
Evorthodus minutus	Evo min	ER/ U-O[i]	34.13 (54.60)	0 (0)	13.52 (9.12)	0 (0)	28.03	0
Gobionellus liolepis	Gob lio	ER/ U-O[i]	0.02 (0.04)	0 (0)	0.02 (0.01)	0 (0)	0.02	0
Gobionellus microdon	Gob mic	ER/ U-O[i]	0.04 (0.07)	0.14 (0.04)	0.14 (0.09)	0 (0)	0.07	0.06
Microgobius tabogensis	Mic tab	ER/ U-O[i]	0.01 (0.02)	0 (0)	0 (0)	0 (0)	0.01	0
Achiridae								
Achirus mazatlanus	Ach maz	ER/O	0 (0)	0 (0)	0 (0)	0.14 (0.05)	0	0.08
Paralichthyidae								
Citharichthys gilberti	Cit gil	ED/GP	0.06 (0.09)	0.28 (0.09)	0 (0)	0 (0)	0.04	0.13

(*continued on next page*)

Table 2 (*continued*)

Fishes	CODE	Resident/diet[a]	Oct/Nov		Mar/Apr		Overall RA	
			Palmar	Javita	Palmar	Javita	Palmar	Javita
Tetraodontidae								
Sphoeroides annulatus	Sph ann	ED/GP	0.34 (0.55)	2.26 (0.69)	3.36 (2.26)	4.55 (1.69)	1.24	3.51
Sphoeroides rosenblatti	Sph ros	ED/GP	0.13 (0.21)	0 (0)	0 (0)	0 (0)	0.09	0

[a] Diet information was obtained from the following sources: Odum and Heald, 1972; Díaz González and Soto, 1988; Whitehead et al., 1988; Allen and Robertson, 1994; Bussing, 1995; Fischer et al., 1995; Smith-Vaniz, 1995; Whitehead and Rodriguez-Sánchez, 1995; Teixeira and Helmer, 1997; Bussing, 1998; Crabtree et al., 1998; López-Peralta and Arcila, 2002; Sánchez Rueda, 2002.

[b] Speculative diets from Odum and Heald (1972): *A. mitchilli*.

[c] Speculative diet from Gerking and Plantz (1980): *P. occidentalis*.

[d] Shervette and Aguirre, unpublished data.

[e] Speculative diets from McMichael et al. (1989): *C. undecimalis*; Díaz González and Soto (1988): *C. nigrescens*, *C. robalito*.

[f] Speculative diets from Odum and Heald (1972): *O. saurus*; Blaber and Cyrus (1983): three species of *Caranx*.

[g] Speculative diet from Bussing (1995): *G. cinereus*.

[h] Speculative diets from Nordlie (1981): *G. dormitor*, *E. amblyopsis*, and *E. pisonis*.

[i] Speculative diets from Wyanski and Targett (1985): *E. lyricus*; Toepfer and Fleeger (1995): *C. boleosoma*.

Mugil curema increased in abundance in the Mar/Apr samples for all Palmar sampling areas (58.23%) and the Javita sampling area (86.30%; Table 2, Fig. 2). Gobies continued to occur in high abundance in mangrove samples during Mar/Apr. *Ctenogobius sagittula* and *Evorthodus minutus* comprised 14.26 and 13.52% of fishes collected in mangroves (Table 2). *Atherinella serrivomer* abundance declined in Mar/Apr mangrove and Rio Javita samples (Fig. 2).

Overall, diversity (H^1) was relatively low for all sampling areas and for both seasons (Table 3). More species were collected from the two creeks than Main channel or Rio Javita and species diversity followed the same trend (Table 3). Mangroves sites (Rio Palmar) had higher richness and diversity values compared to sites without mangroves (Rio Javita). More species were collected in the Oct/Nov sampling period than Mar/Apr and diversity was higher in Oct/Nov. Four and six species comprised 90% of the density from creeks 1 and 2, respectively. Evenness (J) was slightly lower in Creek 1 than Creek 2. Main channel and Rio Javita had four and five species, respectively, comprising 90% of the fish density collected in those sampling areas. Rio Palmar had four species comprising 90% of individuals and an evenness of 0.5, which was a little higher than Rio Palmar's evenness of 0.4. In both sampling periods, four species comprised 90% of the density of fishes collected and evenness was slightly greater in Oct/Nov than Mar/Apr because of overall differences in richness.

3.3. Fish density and size

Aggregated fish density did not differ significantly among the four sampling areas (Friedman test: $\chi^2 = 5.4$, d.f. $= 3$, $p = 0.145$), but did differ between sampling seasons (Friedman test: $\chi^2 = 4.0$, d.f. $= 1$, $p = 0.046$; Fig. 3). The *Ctenogobius sagittula* collected from Rio Palmar were significantly smaller than those collected from Rio Javita (Mann–Whitney U-test: $p < 0.001$; Fig. 4A). *Lile stolifera* collected from mangrove sites were also significantly smaller than those collected from Rio Javita (Mann–Whitney U-test: $p = 0.003$; Fig. 4B). The size of *Mugil curema* did not vary significantly between Rio Palmar and Rio Javita (Mann–Whitney U-test: $p = 0.260$; Fig. 4C). The *Atherinella serrivomer* collected from mangrove sites were significantly smaller than those collected from sites without mangroves (Mann–Whitney U-test: $p < 0.001$; Fig. 4D).

3.4. Fish communities

Differences in fish communities among sampling areas were significant both between and within seasons (Fig. 5; Table 4). The CA produced two axes that explained 63.2% of the variation in species relative abundance. The CA indicated significant differences in fish community structure within and between seasons for the mangrove creeks relative to Main channel and Rio Javita (Fig. 5; Table 4). Main channel and Rio Javita did not have significantly different communities overall or in either of the two sampling seasons (Fig. 5; Table 4). Samples from the mangrove creeks generally had lower scores on Axis 2 associated with more *Evorthodus minutus*, *Daector dowi*, *Centropomus* spp., and *Anchoa lucida* relative to Main channel and Rio Javita (Fig. 5). Main channel and Rio Javita had high scores on Axis 2 associated with *Lile stolifera*, *Mugil curema*, and *Sphoeroides annulatus* (Fig. 5). In Oct/Nov samples, all sites had higher scores on Axis 1 associated with more *Atherinella serrivomer*, *L. stolifera*, and *Sphoeroides rosenblatti*. Mar/Apr samples had lower scores on Axis 1 associated with more *Achirus mazatlanus* (in Rio Javita), *Elops affinis*, *Mugil* spp., and *Poeciliopsis* sp. (in mangrove creeks). The percent mangroves and mean depth were the only habitat variables significantly correlated with species relative abundances in CCA. Species that were strongly correlated with presence of mangroves on axis 1 and 2, such as *E. minutus*, *Poeciliopsis* sp., *Centropomus* spp., and *D. dowi*, were also associated with mangrove creeks in the CA ordination (Figs. 5 and 6). *Albula vulpes* was strongly correlated with depth on Axis 1, but was only collected once (in Rio Javita Oct/Nov; Table 2; Fig. 6). The species–environment relationship in our samples on Axis 1 and 2 of the CCA was relatively weak (eigenvalues of 0.165 and 0.150, respectively).

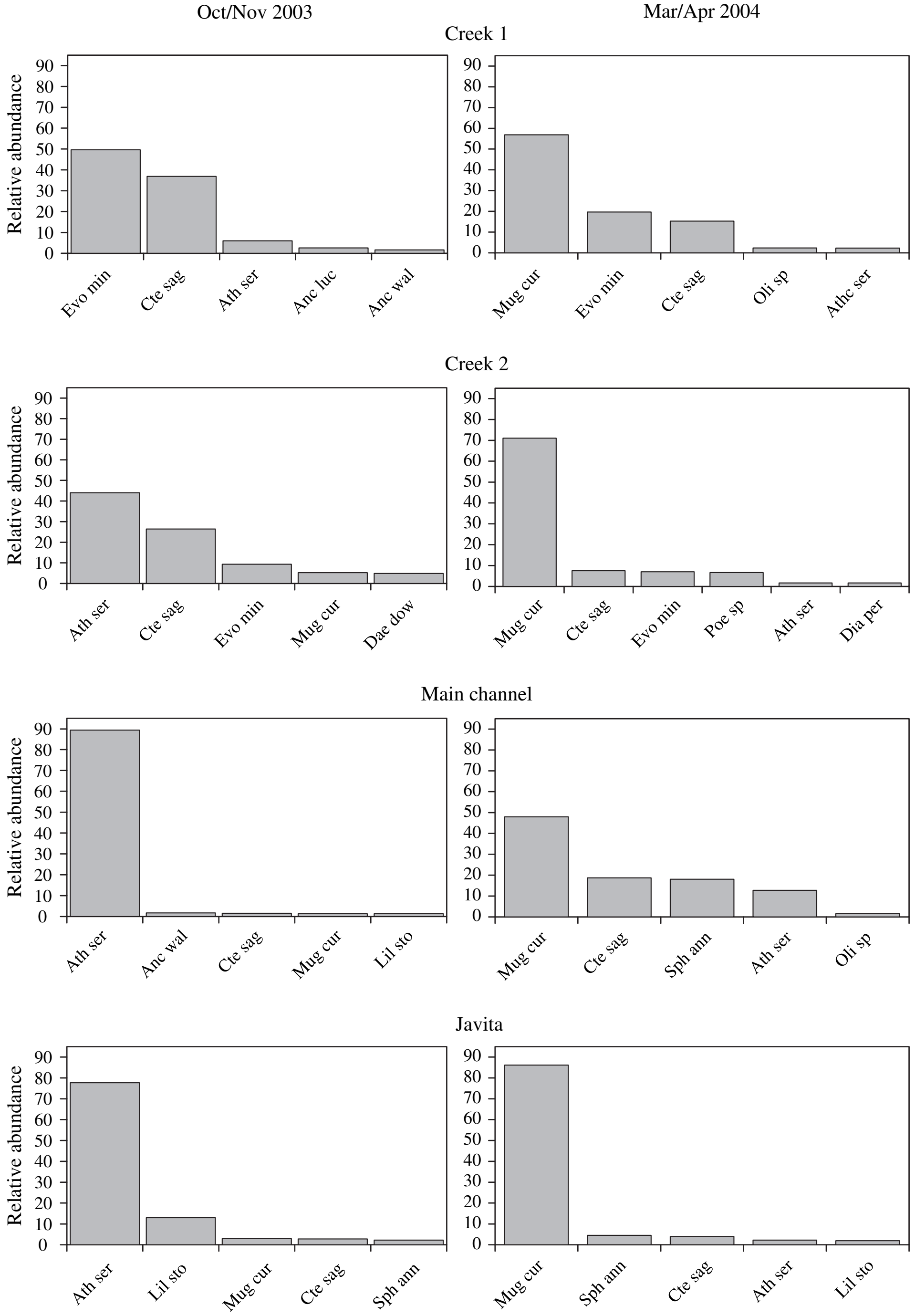

Fig. 2. Overall relative abundance of the five most abundant species for each sampling area during the two sampling seasons. Species codes are indicated in Table 2. In Mar/Apr 2004 Creek 2 samples, *Atherinella serrivomer* (*Ath ser*) and *Diapterus peruvianus* (*Dia per*) tied for the fifth highest relative abundance.

4. Discussion

Mangrove ecosystems support essential ecological functions acting as filters of land-derived materials, stabilizing shorelines, and providing nutrients to nearshore food webs (Sasekumar et al., 1992; Twilley et al., 1996; Twilley, 1998). A significant loss of habitat within a mangrove wetland may potentially have important ecological consequences reflected in the fish community (Valiela et al., 2001; Whitfield and Elliott, 2002). The goals of this study were to describe the fish community of the remaining mangrove wetland in Palmar, Ecuador, and to evaluate, to the extent possible, the relative ecological health of the fish community. Quantitatively assessing the relative ecological health of an estuarine system can be a difficult process, especially when no reference data exist. Harrison and Whitfield (2004) recognized four broad fish community attributes as key to assessing system health. These attributes include species diversity and composition, species relative abundance as it related to dominance by a few species, habitat nursery function as indicated by the occurrence of

Table 3
Shannon diversity index (H^1), Pielou's evenness index (J), and species richness (number of species) by sampling area, rivers, and sampling seasons. Data for sampling areas are pooled across sampling season. Data for Rio Palmar are pooled across the four sampling areas within Rio Palmar. Data for sampling seasons are pooled across sampling areas

	Creek 1	Creek 2	Main channel	Rio Palmar	Rio Javita	Oct/Nov 2003	Mar/Apr 2004
H^1	1.5	1.8	1.2	1.8	1.2	1.6	1.3
J	0.46	0.56	0.40	0.50	0.44	0.46	0.42
Number of species	26	26	20	34	16	31	23

juveniles of estuarine-dependent marine species, and fish community trophic integrity. Mainly, species diversity tends to decline in communities exposed to biotic stress (Odum, 1983) and stress may cause a shift in the relative abundance of a few species (Fausch et al., 1990). One measure of dominance by a few species under stressed conditions is the number of species comprising 90% of individuals collected (Harrison and Whitfield, 2004). Environmental stress on an estuarine system may also alter its ability to provide the function of nursery for juveniles of marine species (Harrison and Whitfield, 2004). Lastly, the trophic structure of a fish community can be altered under stress from environmental changes (Lorenz, 1999; Khalaf and Kochzius, 2002; Whitfield and Elliott, 2002). In order to address the potential health of the fish community of Palmar, we discuss each of these issues.

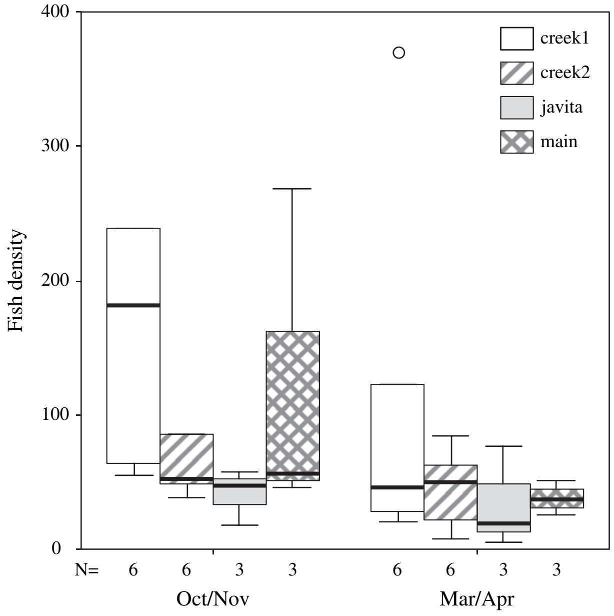

Fig. 3. Boxplot of total fish density (number of fish collected/100 m^2) across the four sampling areas and between the two sampling seasons. The rectangular boxes represent the interquartile range which contains the 50% of values. The whiskers are lines that extend from the box to the highest and lowest values, excluding outliers. A line across the box indicates the median. The circle represents an outlier which is a data point whose value is between 1.5 and 3 box lengths from the upper edge of the box. Creek 1 in Oct/Nov had one data point of fish density with a value of 1134 which has been excluded from this graph.

4.1. Species diversity and community composition

When we compared the Palmar fish community with that of the tidal river, Rio Javita, we found that Palmar supported both a more diverse and significantly different fish community than Javita. Out of the 34 species collected in Rio Palmar, 21 were exclusive to the mangrove creeks and Main channel and did not occur in Rio Javita, only 2 km away. Any differences observed between the two rivers cannot conclusively be ascribed to the presence or absence of mangroves. No studies could be found in the peer reviewed literature concerning fish communities of tropical estuarine habitats along the Pacific coast of South America for comparisons. An Ecuadorian government report documenting the biodiversity of the Gulf of Guayaquil (GOG), a mangrove dominated estuary, sampled a total of 90 stations over a period of 4 months (June–September 1998) and documented a total of 50 fish species and species complexes (Yoong and Reinoso, 1999). Of these, approximately 18 were also collected in our Rio Javita and Palmar samples. At least 19 of the species collected in Palmar and Javita were not documented in the Gulf of Guayaquil. One group of species collected frequently in GOG samples but absent from Palmar and Javita samples were members of the croaker/corvina family, Sciaenidae.

Upon initial examination, the fish communities of Palmar and Javita appeared lacking in species richness and diversity compared with other tropical and subtropical mangrove fish community studies that reported upwards of 80 species (Louis et al., 1995: 87 species; Chong et al., 1990: 119 species; Robertson and Duke, 1990: 128 species; Tongnunui et al., 2002: 135 species). However, direct comparisons are difficult to make due to differences in overall area of wetlands and estuaries, experimental design, sampling effort, inclusion/exclusion of larval fishes, and length and frequency of sampling period (Rozas and Minello, 1997). For our study, because we were targeting juvenile and small fishes of creek and tidal river habitats, we ultimately chose to use only one method for collecting fishes—seining, which we acknowledge as having a suite of disadvantages associated with it (see review in Rozas and Minello, 1997). Possibly, if we had used a different sampling method, sampled more frequently and over a longer period of time, or included more sampling areas in our design, we may have collected additional species. Several other studies of mangrove fish communities have also employed tow nets, such as seines and trawls, as their collection method (Table 5). In order to account for some of the compounding factors limiting comparisons of our study with others, we have confined most of our comparisons to those studies employing similar sampling techniques (see citations in Table 5).

Out of seven studies of fish communities in mangroves that employed seining or trawling, this study had the lowest species richness, although by a small margin (Table 5). Williamson et al. (1994) examined the fish community of a mangrove-lined mudflat in Raby Bay located in the subtropical Moreton Bay, Queensland, Australia. Their study documented a total of 36 species and had a species diversity index (1.4) and an evenness index (0.4) lower than the current study ($H^1 = 1.8$;

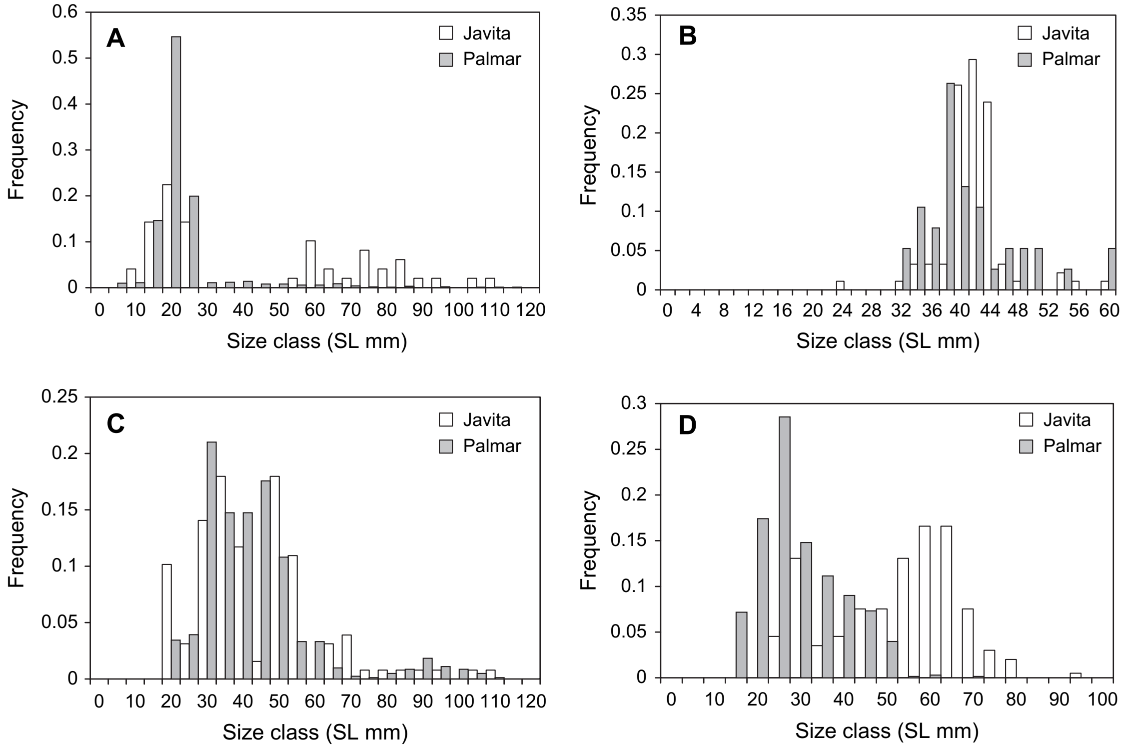

Fig. 4. Size frequency distributions of (A) *Ctenogobius sagittula*, (B) *Lile stolifera*, (C) *Mugil curema*, and (D) *Atherinella serrivomer* collected from mangrove sites (Rio Palmar) and sites without mangroves (Rio Javita). Mean sizes of *C. sagittula* and *L. stolifera* collected from mangrove sites were significantly smaller than those collected from sites without mangroves.

$J = 0.5$). Six species comprised 90% of individuals collected in Williamson et al. (1994) compared to the current study in which four species comprised 90% of individuals (Table 5). Pinto and Puchihewa (1996) collected a total of 56 species in their study of the fish community of a mangrove-lined shore in the tropical Negombo Estuary of Sri Lanka. They had a Shannon diversity index of 1.1 and a Pielou's evenness index of 0.3 (Table 5). Even though Pinto and Puchihewa (1996) documented 22 more species than the current study, their diversity and evenness values appeared much lower indicating that, similar to our study, only a few species dominated their samples (three species comprised 90% of individuals collected). In contrast, Ikejima et al. (2003) collected only two species more (total of 58 species of fish) from a mangrove

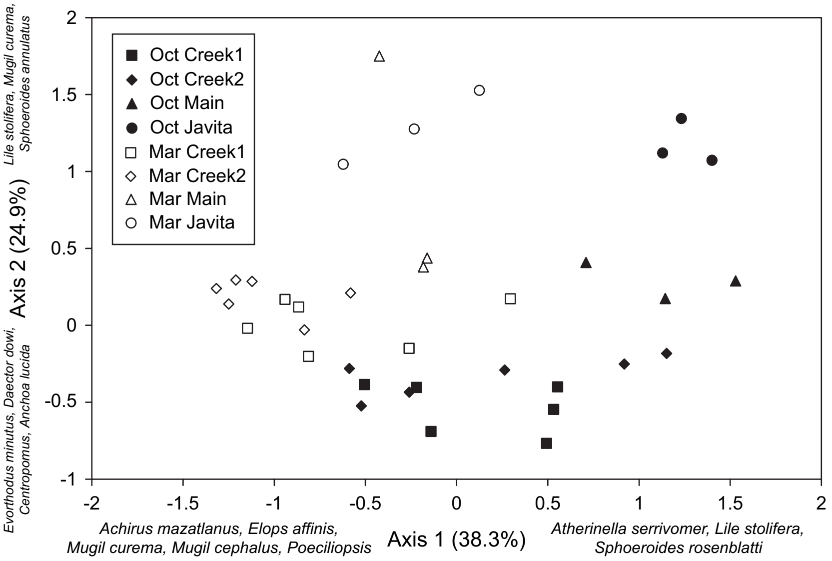

Fig. 5. Plot of site scores for correspondence analysis (CA). The species associated with extreme scores are listed on each axis end. Creeks 1 and 2 communities were significantly different from Rio Javita during both sampling seasons.

Table 4
Effect size (A) and probability values for pairwise comparisons of sampling area groupings for seasons combined, Oct/Nov sampling, Mar/Apr sampling, and between the two sampling seasons. Significance was assessed at $\alpha = 0.003$ (Bonferroni correction)

Comparison	A	p
Seasons combined		
Creek 1 × Creek 2	0.001	0.342
Creeks × Main	0.072	0.007
Creeks × Javita	0.185	< 0.001
Main × Javita	0.007	0.346
Oct/Nov sampling		
Creek 1 × Creek 2	0.039	0.199
Creeks × Main	0.148	0.008
Creeks × Javita	0.397	< 0.001
Main × Javita	0.206	0.025
Mar/Apr sampling		
Creek 1 × Creek 2	0.049	0.128
Creeks × Main	0.127	0.004
Creeks × Javita	0.248	< 0.001
Main × Javita	0.084	0.688
Between seasons (Oct/Nov × Mar/Apr)		
Creek 1	0.239	0.005
Creek 2	0.238	0.005
Main	0.199	0.024
Javita	0.437	0.022

creek in the tropical Trang Province of Thailand, but had a diversity index of 3.0, the highest of the nine studies. A total of 22 species comprised 90% of individuals collected indicating that a relatively more equal amount of individuals were collected for each species.

In a Florida estuary with mangroves and seagrasses, Poulakis et al. (2003) documented 81 fish species of which 10 comprised 90% of total abundance. Sedberry and Carter (1993), sampled mangroves creeks of coastal Belize, collecting 74 fish species. Twenty-one species comprised 90% of total abundance which helps to explain the relatively high fish diversity index of 2.7 from that study (Sedberry and Carter, 1993; Table 5). The one study that collected more than 100 species had one of the lowest diversity index values (1.1) with an equally low evenness value (0.2; Tzeng and Wang, 1992). Compared with these other studies, the fish community of Palmar appears to have a diverse fish community with lower species richness, overall.

Several global patterns in fish species richness exist (Alongi, 2002) that may help in explaining why the Palmar mangrove wetland had fewer species. One potential factor contributing to the low species richness of Palmar is that the mangrove wetland is relatively small. Larger estuarine systems typically have more fish species than smaller ones (Alongi, 2002; Blaber, 2002; Raz-Guzman and Huidobro, 2002). Additionally, habitat loss tends to result in lowering population densities and a loss of diversity and richness of most mangrove associated organisms (Alongi, 2002). The mangrove wetland of Palmar may have once supported a larger number of fish species, but due to the reduction in total area of wetland, currently supports a smaller number. Another global pattern is that mangrove fish communities of the Indo-western Pacific are more speciose compared to Atlantic estuaries (Alongi, 2002) and the same trend may apply to eastern Pacific estuaries. Moreover, connectivity between mangrove ecosystems and adjacent ecosystems such as coral reefs and seagrass beds may influence fish community composition (Robertson and Blaber, 1992) and the mangrove wetland in this study does not appear to be in close proximity to other species-rich systems.

Another potential factor contributing to the low species richness of Palmar is the consistently higher salinity of the Palmar creeks and Main channel compared to the other studies (Table 5). However, in a study on fish community structure in a coastal hypersaline lagoon lined with mangroves, Vega-Cendejas and Hernández de Santillana (2004) documented 81 species, most of which were collected in salinities greater than 38. Thirty-five of the 81 species were found in salinities greater than 60 (Vega-Cendejas and Hernández de Santillana, 2004). Rios

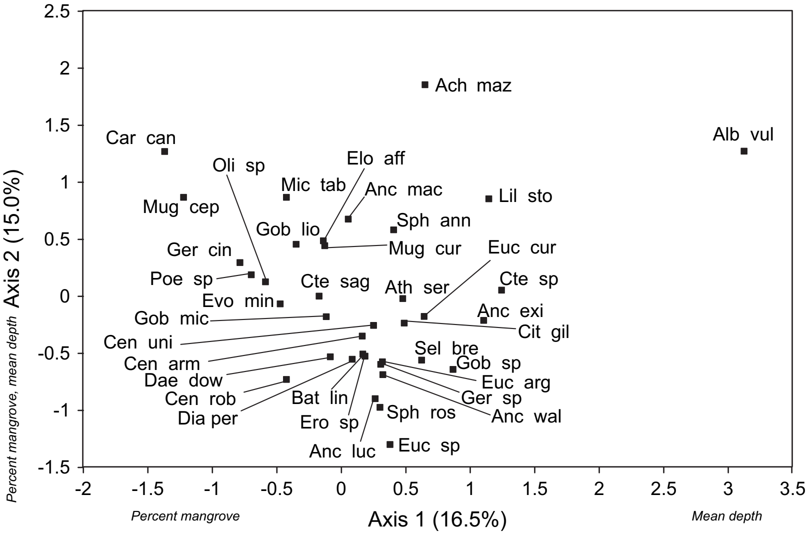

Fig. 6. Plot of species score with the significant environmental variables in the first and second CCA axes. Species codes are given in Table 2. Percent of variation explained by the two CCA axes are given in parentheses.

Table 5

Comparison of studies concerning fish communities of mangrove wetlands that utilized seining or trawling. Location and habitat indicates ocean connected to study wetland and main habitats sampled. Richness is the number of species collected. Shannon diversity index (H^1) and Pielou's evenness index (J) were determined by the authors of this study from information given in cited text. H^1 and J were calculated using the equation given in Section 2. Also, the number of species comprising 90% of individuals collect is listed for each study. The salinity range for each study is also listed. Data that were not available directly from the studies are listed as NA

Location and habitat	Sampling gear and regime	Richness (H^1; J)	Spp. 90%	Fish density	Sal. range	Reference
Pacific, Palmar, Ecuador; Mangrove creeks at midtide	Seine (3 mm mesh) 1× each season for two seasons	34 (1.8; 0.5)	4	1.3	28–55	This study
Indian, Negombo Estuary, Sri Lanka; Mangrove-lined shore	Drag and enclosure nets (9 mm mesh) monthly Sept 1986–Sept 1988 on new moon days high tide	56 (1.1; 0.3)	3	~0.05	1–33	Pinto and Punchihewa, 1996
Pacific, Trang Province, Thailand; Mangrove creek	Seine (3 mm mesh) 1× each season in Mar, Aug/Sept, Nov/Dec from Aug 1996–Mar 1999 at midtide	58 (3.0; 0.8)	22	NA	20–35	Ikejima et al., 2003
Gulf of Mexico, Florida; Mangrove-line shore	Seine (3.2 mm mesh) monthly 1996–2000	81 (2.4; 0.5)	10	3.7	5–39	Poulakis et al., 2003
Caribbean, east coast Belize; Mangrove creeks	Otter trawl (48.3 mm mesh in wings and 15.2 mm mesh in cod end) 10-min tows 2× each month Feb 1985–April 1986	74 (2.7; 0.6)	21	NA	27–35	Sedberry and Carter, 1993
Pacific, Australia; Mangrove-lined beach	Seine (12 mm mesh) monthly Jan 1990–Jan 1991	36 (1.4; 0.4)	6	NA	NA	Williamson et al., 1994
Pacific, Taiwan; Mangrove-lined river	Drift bagnets (1–110 mm mesh range) monthly Nov 1987–July 1990	105 (1.1; 0.2)	3	NA	4–33	Tzeng and Wang, 1992

Palmar and Javita experienced low flow from freshwater sources during the wet season of our study. In fact, in the Oct/Nov collections, at the end of the coastal dry season, diversity and richness measures were higher compared to the Mar/Apr collections, during the coastal wet season. This is contrary to the increase in fish diversity and richness with the wet season that many other fish community studies of mangroves have documented (Flores-Verdugo et al., 1990; Laroche et al., 1997; Barletta et al., 2003). Both Palmar and Javita lose freshwater upstream to shrimp farming and irrigation. Moreover, both rivers receive effluents from the shrimp ponds and shrimp hatcheries located along their path. In spite of what appears to be a large amount of environmental stress, the mangrove creeks and Main channel of Rio Palmar support a relatively diverse fish community especially for the overall small total area it covers.

4.2. Nursery function

Estuaries provide an important habitat for larvae and juveniles of an assortment of marine organisms, many of which are economically valued. Several studies have documented that mangrove habitats provide unique resources for juvenile fish when compared with adjacent habitats such as seagrasses and mudflats (Robertson and Duke, 1987; Chong et al., 1990; Laegdsgaard and Johnson, 1995; Ikejima et al., 2003). Halliday and Young (1996) found that juveniles of economically important species contributed more than 76% of individuals collected from a subtropical mangrove forest in Tin Can Bay, Australia. Bell et al. (1984) documented that 38% of the fish density in a temperate tidal mangrove creek in Botany Bay, New South Wales, was represented by juveniles of commercially important species. Morton (1990) documented that 75% of the fish density in a subtropical mangrove area was comprised of economically important species. Little et al. (1988) also collected a high proportion of juvenile individuals (46%) in a mangrove creek on the coast of Kenya and noted a similar trend from other mangrove studies including Stoner (1986) with 55% of individuals collected being juveniles and Yáñez-Arancibia et al., 1980 documenting 46% of individuals collected as juveniles.

In the present study, 21 species of the 36 collected from both rivers occurred as juveniles only. Species from families we collected, including Engraulidae, Gerreidae, Mugilidae, Centropomidae, and Carangidae, many of which are economically valued, are known to use estuaries as juveniles (Robertson and Blaber, 1992; Halliday and Young, 1996; Blaber, 1997; Ikejima et al., 2003). Therefore, the mangroves of Palmar and the tidal river habitat of Rio Javita, may provide an important nursery area for multiple economically valued species. Moreover, the three centropomids, four of the five gerreid species, and two of the four engraulid species collected in the current study only occurred in the Palmar mangrove habitat, potentially indicating that even a mangrove system as environmentally altered as Palmar provides a unique habitat for juveniles of economically important species. In addition to the aforementioned families, we collected hundreds of leptocephalus larvae, belonging to the Albulidae and Elopidae families, in Rio Palmar and Rio Javita samples. This may indicate that both rivers provide habitat for larvae of these other two economically valued groups (V. Shervette and W. Aguirre, unpublished data).

4.3. Trophic integrity

Mangroves function both structurally and ecologically in sustaining nearshore marine habitats and providing food and refuge for a myriad of organisms at different trophic levels (Odum and Heald, 1972; Twilley, 1988; Twilley et al., 1996). The complexity of food sources documented from mangroves illustrates changes in food diversity and fish preferences through fish ontogeny (Thayer et al., 1987; Robertson and Duke, 1990; Twilley et al., 1996; Sheaves and Molony, 2000). Diets of single species are often composed of 20 or more different food categories. In fact, one characteristic of fish communities in mangrove wetlands is that the whole trophic structure is not comprised of definitive trophic levels, but rather, fish consume food resources from a diversity of sources (Twilley et al., 1996). The general characteristics of feeding relationships among fishes of mangrove habitats are characterized by five components (Twilley et al., 1996). First, feeding habitats are generally flexible in time and space in that fish consume what is available when it is available. Second, mangrove fishes share a common pool of the most abundant food resources. Third, most species take food from different levels of the food web. Fourth, fish diets tend to shift with growth, food diversity, and locality within a mangrove estuary. Fifth, most fish use both pelagic and benthic trophic pathways.

Although we did not conduct diet analyses on the fishes we collected, we found no evidence that the trophic structure of the small and juveniles fish communities of Palmar and Javita were negatively impacted or altered compared to other estuarine fish communities from tropical, subtropical, and temperate studies (Sheaves and Molony, 2000; Wilson and Sheaves, 2001; Zetina-Rejón et al., 2003; Carrió et al., 2004). However, our sampling method limited us to small individuals and we cannot comment on the occurrence and trophic role of larger piscivorous predators, such as adult centropomids and carangids that often feed on smaller estuarine fishes.

Of the 36 species we collected in Rios Palmar and Javita, at least 20 species (or closely related species of those for which no data have been collected concerning diet) are documented as consuming a combination of planktonic and benthic food sources (see Table 2 for trophic groups). No major trophic group appeared to be absent or represented in relatively low numbers (Table 2). We collected at least 13 species categorized as general predators or benthic carnivores and 17 species categorized as omnivores (Table 2).

The two species with the highest relative abundances in our study were juvenile mullet *Mugil curema* and tropical silverside *Atherinella serrivomer*. As juveniles and adults *M. curema* and *Mugil cephalus*, often characterized as detritivores, consume benthic diatoms, foraminifers, nematodes, copepods, ostracods, amphipods, gastropods, and invertebrate and fish eggs, basically eating whatever is available (Sánchez Rueda, 2002). Although the diet of *A. serrivomer* is undocumented, other tropical and temperate silverside species (both Atherinopsidae and Atherinidae) consume plankton during the day and can shift to benthic food sources during the night (Odum and Heald, 1972; Logothetis et al., 2001; Cassemiro et al., 2003). The same may be true for *A. serrivomer*.

One study in Australia examined the tropic fate of shrimp farm effluents in mangrove creeks (McKinnon et al., 2002). In their study they found that at least two fish species (both clupeids) fed directly on effluents suggesting the direct assimilation of particulates from the aquaculture ponds (McKinnon et al., 2002). Possibly, fish from Palmar and Javita utilize shrimp ponds effluents in a similar manner. Further dietary analysis of the fish communities in Rio Palmar and Javita would be useful in evaluating the trophic fate and impacts of shrimp pond effluents in those systems.

4.4. Conclusions

The mangrove wetland of Palmar appears to support a more diverse and species rich fish community than the nearby tidal river, Rio Javita, although these differences cannot conclusively be ascribed to the presence or absence of mangroves. Palmar has lost approximately 90% of its wetland to shrimp farming and this habitat loss may partially explain the relatively low fish species richness found in the mangrove creeks and Main channel compared to other mangrove fish communities. No other studies exist in the scientific peer-reviewed literature reporting the biodiversity of fishes in mangroves in the tropics along the eastern Pacific coast of South America which makes determining the potential level of the impact of habitat loss and alteration in Palmar difficult. However, other studies conducted in Central America and other tropical/subtropical mangrove systems have consistently documented fish communities with higher fish species richness. Other potential reasons for the lower fish species richness in Palmar include the small size of the wetland, lack of connectivity to other ecosystems, elevated salinity, reduced freshwater input, and the potential contamination or pollution from shrimp farms. Study design and sampling methods could have contributed to our findings of low species richness, as well. Regardless of the comparatively low richness, the mangrove habitat of Palmar contained juveniles of several economically important species in the snook family (Centropomidae), which were not present in Rio Javita, a less structurally complex area. Both areas contained relatively high densities of juvenile mullet (*Mugil* spp.), a popular food fish, as well as large populations of *Atherinella* species, commonly found in fish and wading bird diets and often utilized as fish meal. Both Javita and Palmar appear to provide important habitats for ecologically and economically important fishes. Although further analysis of trophic integrity is needed, the Palmar mangrove wetland appears to support a complex trophic structure and does not appear to deviate in an obvious manner from the general characteristics of feeding relationships among fishes of mangrove habitats.

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