Tidal, diel and seasonal effects on intertidal mangrove fish in a high-rainfall area of the Tropical Eastern Pacific

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ABSTRACT: Mangroves are recognized as nursery areas for a large number of marine organisms. Yet many properties of this nursery function and its equivalence between geographical areas remain poorly understood, especially in macrotidal estuarine systems. In this study, we investigated the influence of tides, diel and seasonal variation on intertidal mangrove fish assemblages in a high-rainfall area of the Tropical Eastern Pacific region. Over one year, block net sampling was undertaken during spring and neap tides during both night and day. Four sites along the length of a subtidal channel were sampled to account for salinity gradients. Clupeidae dominated catch abundances of a 50 species-rich assemblage. Catch weights, however, were dominated by Lutjanidae, Tetraodontidae and Ariidae. Fish biomass was low, likely as a result of a poor benthic in- and epi-faunal biomass in a mangrove system of low nutrient status and extremely rainy conditions. Higher salinity creeks yielded significantly greater catches and higher number of species than low salinity creeks. A depauperate freshwater fish fauna in this beogeographical region, unable to compensate for the lack of marine-estuarine species in a low salinity environment, may explain this pattern. A notable increase in rainfall at the end of the year correlated to a decrease in mangrove fish biomass. Partially in agreement with studies from other macrotidal areas, specific combinations of tidal magnitude and diel cycle explained recurring changes in fish assemblage structures, clearly observed at the species level, but not in the number of species or biomass. These results indicate not only how important tidal and diel cycles can be for fish habitat use in macrotidal mangroves, but also highlight how regional (biogeography) and local (geomorphology, precipitation) factors should be incorporated into further investigations of mangrove ecosystem equivalence over large geographical scales.

KEY WORDS: Intertidal mangrove creeks · Fish community · Block nets · Macrotides · Tropical Eastern Pacific · Panama Bight mangroves · Colombia · Bahía Málaga

INTRODUCTION

Mangroves are among the most threatened ecosystems in the world, with an estimated rate of loss of 1 to 2 % per year (Valiela et al. 2001, Polidoro et al. 2010). Carbon storage, sediment trapping, protection against storm surge and increased fisheries yields in adjacent waters are some of the ecosystem and economic benefits provided by mangroves (Alongi 2002, Donato et al. 2011). Approx. 30 % of the world's commercial fish species are considered mangrove-dependent (Naylor et al. 2000). Nevertheless, the

role of mangroves as a fish habitat and nursery continues to be little understood (Beck et al. 2001) and has proven to be variable across geographic areas (Sheaves 2005).

Many of the studies highlighting the nursery function of mangroves thus far have been carried out in the Caribbean biogeographic realm where mangrove forests are comparatively small, microtidal systems (Krumme 2009, Nagelkerken 2009, but see Blaber 2000 for a review of studies in the Indo-Pacific and African regions). However, mangroves elsewhere may be subject to medium or large tidal amplitudes and present a different habitat configuration from the mangrove-seagrass-coral reef continuum most often described in the literature. In meso- and macro-tidal regimes (range 2 to >6 m), fish accessibility to mangroves is limited to periods of intertidal inundation. Therefore, the dynamics of fish assemblages and value of the mangrove as a nursery habitat in these regions may be distinctly different compared to those in microtidal systems.

Fish assemblages on macrotidal coasts exploit temporarily accessible habitats via tidal movements that are an important part of their home ranges (Gibson 2003). The importance of tidal movements for fish, however, varies according to habitat. On the rocky shores of the Colombian Pacific these movements are not related to spring-neap tide cycles (Castellanos-Galindo et al. 2010) whereas in the mangroves, complex interactions in the organization of intertidal fish assemblages have been found following changes in spring, neap, diel and lunar cycles (Davis 1988, Krumme et al. 2004, Krumme 2009). These short to medium temporal scales are seldom considered in the study of fish community structure dynamics (Wilson & Sheaves 2001), although crucial to understanding the dynamics of these assemblages.

The influence of abiotic factors in shaping fish communities (salinity, turbidity) has been relatively well studied in different ecosystems throughout the world (Blaber 1997). Although most estuarine fish species can be considered euryhaline, in estuarine mangrove systems a strong relationship between salinity and fish community composition has been found (Sheaves 1998). Changes in salinity are ultimately a consequence of the precipitation regime, seasonality of the rainfall and size of the drainage system at each study site. Most investigations examining the relationship between salinity and fish assemblage structures have been carried out by sampling in the main channels of estuaries (Barletta et al. 2005, Simier et al. 2006). Only few studies have examined how intertidal mangrove creek fish assem-

blages (and fish tidal migrations) are affected by salinity change and/or precipitation (but see Lorenz & Serafy 2006, Giarrizzo & Krumme 2007, Rehage & Loftus 2007).

Mangrove forests on the Pacific coast of the Americas cover ca. 1.21 million ha (Lacerda et al. 2002). Important artisanal fisheries throughout the region depend either directly or indirectly on mangroves as they are considered essential habitats for the juveniles of commercial species (Aburto-Oropeza et al. 2008). The majority of these mangroves are located in the Panama Bight ecoregion (covering the Pacific coasts of Panama and Colombia and the coast of Ecuador), 1 of 8 major mangrove areas identified as a global conservation priority (Olson & Dinerstein 2002). Despite being relatively undisturbed, these mangroves are subject to environmental (i.e. ENSO events) and human-driven (deforestation and pollution) stressors that pose serious threats to local human populations and could drive major changes in coastal food webs (Valiela et al. 2012, Restrepo 2012).

This study examines, for the first time, the small and mid-term spatial and temporal patterns of mangrove creek fish assemblage structure in a macrotidal mangrove area of the Tropical Eastern Pacific Ocean (Colombian Pacific coast), filling a gap in the understanding of mangrove fish assemblage dynamics in this area (Faunce & Serafy 2006, Sheaves 2012, Blaber in press). For this purpose, 3 questions were investigated: (1) What is the taxonomic and functional composition of the intertidal mangrove fish assemblage in a high-rainfall area of this region? (2) How does the variability introduced by changes in the tidal magnitude (spring-neap tide cycle) and its interaction with the diel cycle affect the structure of the intertidal mangrove fish assemblage? and (3) How does an extremely high precipitation-low salinity period affect the structure of this mangrove fish assemblage?

MATERIALS AND METHODS

Study area

Bahía Málaga is located in the central region of the Colombian Pacific coast (3° 56′ to 4°05′ N and 77° 19′ to 77° 21′ W) in the Tropical Eastern Pacific (TEP) region (Fig. 1) and is an estuarine embayment (sensu Pritchard 1967) formed during a tectonic event which occurred in the Miocene-Holocene Epoch. It is believed that the bay was a narrow channel of an old (Pleistocene) tributary system of the San Juan River
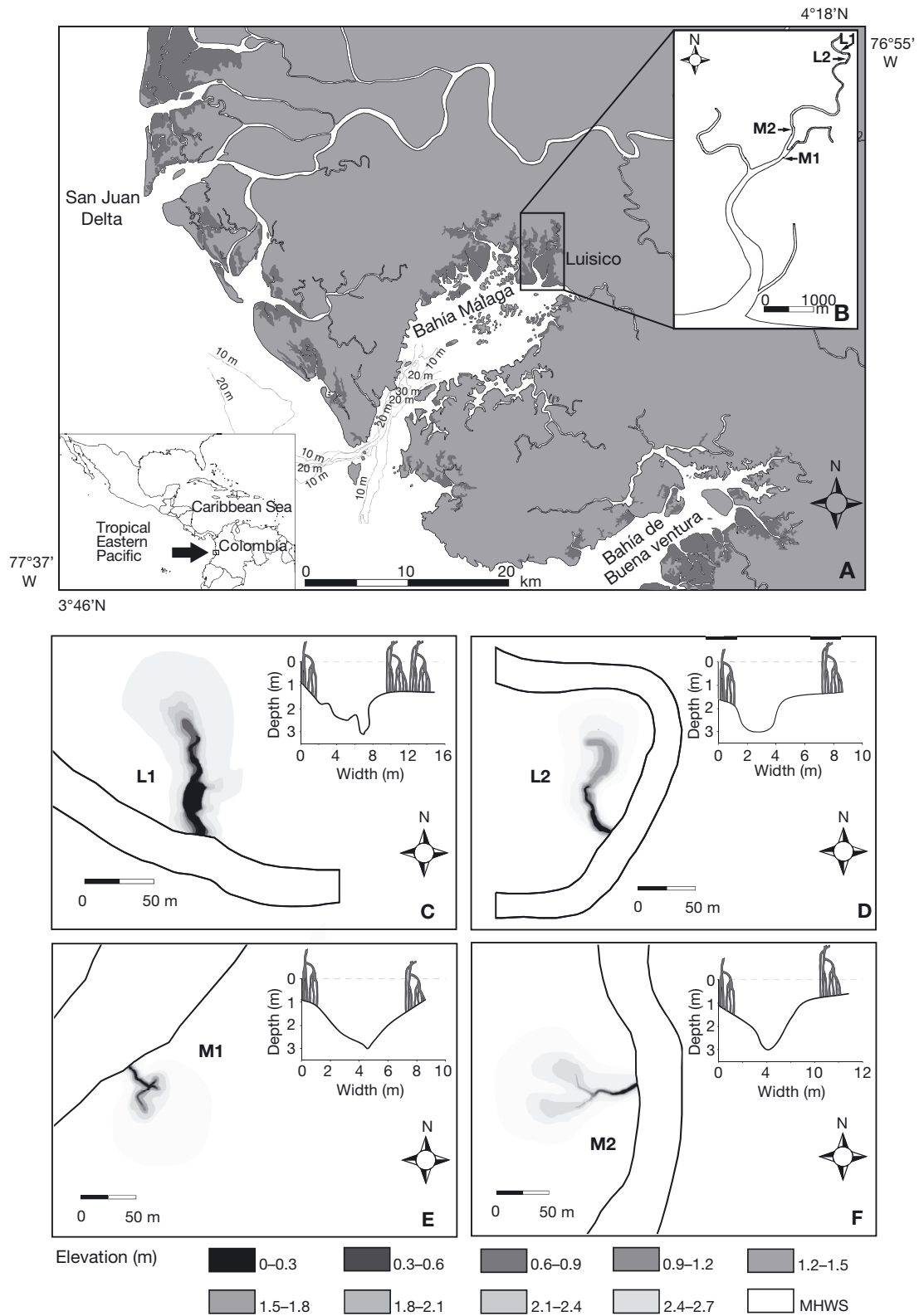
Fig. 1. (A) Coast of the Tropical Eastern Pacific region, and (B) location of the 4 intertidal mangrove creeks in the Luisico tributary of Bahía Málaga. Bathymetric maps of (C,D) the 2 low-salinity creeks (L1 and L2) and (E,F) the 2 medium salinity creeks (M1 and M2). Subfigures in C–F show a cross-sectional profile from the creek entrance, sampled from December 2009 to November 2010. MHWS = mean high water at spring tide

(one of the largest deltas along the west coast of South America) that was flooded after a tectonic uplift of the northwestern region of Bahía de Buenaventura (Martínez & López-Ramos 2011, Fig. 1).

The study area is located in one of the wettest regions of the American continent (Poveda & Mesa 2000). The average annual rainfall (±1 standard deviation) in Bahía Málaga from 1969 to 2010 was 7399 mm yr^{-1} ±1623, with a wet period from January to April ($\bar{x}$ = 422 mm mo^{-1}) and a very wet period from May to December ($\bar{x}$ = 746 mm mo^{-1}). (Weather data from IDEAM meteorological station No. 5407003 at Malaguita, ca. 10 km north of Luisico sampling points, see Fig. 10)

The bay has a surface area of ca. 130 km^2 and a mean water depth of 15 m. The coast is bordered by rocky cliffs composed of tertiary sediments, such as sandstones and mudstones, strongly modified by erosion and covered by well-developed riverine and fringe-type mangroves (ca. 4400 ha) and mudflats in depositional zones (Correa & Morton 2010). Several small rocky islands (as close as ca. 4 km to mangroves) are scattered within the bay. Some of these rocks can be completely submerged at high tide. Mangroves in Bahía Málaga are predominantly concentrated in the inner areas and are dominated by 2 species of *Rhizophora* (*R. racemosa* and *R. mangle*) with trees up to 40 m high (Cantera et al. 1999). Other less abundant mangrove species are *Avicennia germinans*, *Pelliciera rhizophorae* and *Mora oleifera*. The mangrove forests are drained by large dendritic subtidal channels ('esteros'). These are mostly composed of a soft bottom (mud and sand), but rocks and gravel banks can also be intermittently found in the range of 100 m away from mangroves. The catchment areas upstream of the mangroves are small, with no larger rivers draining into the bay. These mangroves are probably exposed to some of the wettest conditions on earth, in an erosional rather than accretional environment. This is indicated by the low sediment accumulation around the base of the mangroves (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m494p249_supp.pdf), resulting in a low elevation of the forest in relation to mean sea level. For this reason, the floor of most mangrove areas is already largely inundated at neap tides. Tides on the Pacific coast of Colombia are semidiurnal. In the inner part of Bahía Málaga, the mean tidal amplitude is 3 to >4.5 m at spring tides and 2 to 3 m at neap tides. Mean air temperature is 25°C, and sea surface temperatures range between 26 and 29°C throughout the year. Human population density on the Pacific coast of Colombia has been his-

torically very low; currently it is between 5 and 17 persons km^{-2} (Etter et al. 2006). Approximately 4000 people, distributed in small villages, live in Bahía Málaga.

Sampling design

From December 2009 to November 2010, an equal number of sampling campaigns were completed at spring and neap tide periods (6 times each; Table S1 in the Supplement). On a monthly basis, 4 intertidal mangrove creeks (Fig. 1a–d) dominated by *Rhizophora* spp. trees, possessing similar topographic characteristics, and de-watering directly into the Estero Luisico, were blocked at the mouth at slack high tides using block nets (20 × 4 m, 12 mm mesh size). Creeks occurred over a ca. 5 km gradient that captured the salinity variability observed in the bay (0 to 23). Block nets are a common method for artisanal fishers in several parts of the world including the Colombian Pacific. The method is regarded as highly efficient in capturing fish that enter intertidal vegetated creeks, and thereby accurately represent the composition of fishes using intertidal mangrove resources (Bozeman & Dean 1980, Thayer et al. 1987, Vance et al. 1996). At each creek, a block net was deployed at the creek mouth at low tide. The lead line of the net was pushed into the mud with hands and feet from one side to the other, the entire net enrolled and fixed with small wooden sticks at intervals on top of the mud to prevent lifting of the net during flood tide. A wooden pole (ca. 5 m above ground) was put vertically in the middle of the creek. The net was lifted the following high slack water with the headline moored to the top of the wooden pole (i.e. above the water level), thus completely blocking the creek mouth. The pole also retains the block net during strong ebb tide periods. At late ebb tide, all fish entangled in and concentrated in the already drained intertidal creek upstream of the net were intensively searched and collected by hand. Due to the time delay of the tidal cycle with respect to the diel cycle, slack low waters (LW) during spring and neap tides occurred at different times. Slack low water at spring tides occurred approximately at midday and midnight (12:00 and 24:00 h), whereas slack low tide at neap tides usually occurred around sunrise and sunset (6:00 and 18:00 h). Therefore, a factor 'tide-time of day' with 4 levels was established corresponding to the samples when fishes could enter the intertidal mangrove creeks: (1) until the early morning (approximately 06:00 h), spring tide – day (SD);

(2) after dusk (approx. 18:00 to 19:00 h), spring tide – night (SN); (3) until midday, neap tide – day (ND); and (4) until midnight, neap tide – night (NN). Two of the selected intertidal creeks were located in a low salinity zone (salinity at high tide: $\bar{x}$ (±1 standard deviation) = 12.3 ± 5.7, low tide: $\bar{x}$ = 1.9 ± 1.8) and 2 were located in a medium salinity zone (salinity at high tide: $\bar{x}$ = 16.5 ± 4.2, low tide: $\bar{x}$ = 7.8 ± 4.3; Fig. 2). Creeks were on average 10 m wide and 3 m high at the mouth and 80 to 100 m long. Samples were taken during both day and night LWs. For each sampling trip, the maximum water level at slack high water in the entrance of each creek and the surface salinity were measured. Salinities at low water were also measured in the main channel approximately at the creek mouths. Sampling of the 4 creeks was completed in 2 consecutive days of the corresponding spring or neap tide period (i.e. Day 1: lower salinity creeks; and Day 2: medium salinity creeks).

The topography of each creek was surveyed using GPS, a compass and a tape measure. Maps of the creeks were produced and a relationship between flooding height and inundated area (m²) and volume

(m^3) was established using a 3-dimensional model in GIS (see Table S2 in the Supplement). This information was used to standardize the catch abundance and weights to density (number of fishes m^{-2} or m^{-3}) and biomass (g m^{-2} or m^{-3}), respectively.

All sampled fishes were preserved in 10% formalin and later transferred to 70% ethanol in the laboratory. They were subsequently identified using taxonomic keys for the area (Fischer et al. 1995, Robertson & Allen 2008), measured (total length, TL) and wet weighed (g ± 0.1). Each fish species was then assigned to one spatial and trophic guild group according to this present study's stomach content analyses or information derived from Elliott et al. (2007) and Froese & Pauly (2012).

Data analyses

Individual-based rarefaction curves were constructed for each creek to evaluate the representativeness of the number of samples taken using EstimateS software (Colwell 2009). The non-parametric Chao1 species richness estimator was used to estimate the asymptotic species richness for each creek. Species abundance distribution models (SADs) were used to obtain a general description of the mangrove fish assemblages (lognumerical abundance versus rank plots; McGill et al. 2007).

An initial assessment of the effect of consecutive sampling in the same creeks revealed no significant correlations between the catch mass and the consecutive sampling events in any of the 4 creeks (see Fig. S2 in the Supplement). In contrast to other studies that have found reduced catches when consecutive sampling in the same area were completed (Vance et al. 1996, Rönnbäck et al. 1999, Huxham et al. 2004), in our study an interval of ca. 1 mo between sampling intervals was sufficient for the fish assemblage to recover from any disturbance.

Species richness, abundance and catch mass differences between the factors salinity zone, tide-time of day and month (repeated measure) were analyzed with 1-way parametric ANOVAs and/or non-parametric Kruskal-Wallis tests (for each factor), depending on the
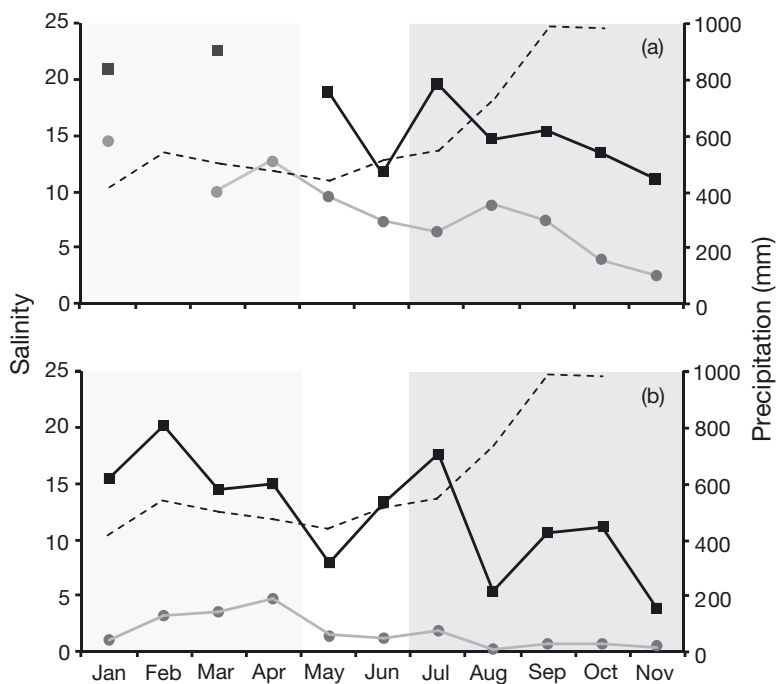

Fig. 2. Salinity variation at high (black lines and squares) and low tide (grey lines and circles) during the sampling period (January to November 2010) at (a) the medium salinity zone and (b) the low salinity zone. No data for December 2009 was recorded. Total monthly rainfall from the nearest meteorological station is shown by the dashed line. El Niño conditions: light grey box; La Niña conditions: dark grey box (weather data taken from the monthly Oceanic El Niño Index at www.cpc.ncep.noaa.gov/products/ analysis_monitoring/ensostuff/ensoyears.shtml)

violation of any of the assumptions of parametric statistics. When significant differences were observed pairwise comparisons were carried out (Tukey's HSD and Nemenyi-Damico-Wolfe-Dunn tests). Moreover, differences in fish density (ind. m^{-3}) and biomass (g m^{-3}) between salinity zones were tested using the non-parametric 2-sample Wilcoxon test (equivalent to a Mann-Whitney test).

Additionally, multivariate statistic techniques were employed to analyze data related to fish assemblage organization. A PERMANOVA test (permutational multivariate analysis of variance, Anderson 2001) was used to evaluate differences in fish assemblages between salinity zones (fixed factor with 2 levels: low and medium) and tide-time of day combination (fixed factor with 4 levels: SD, SN, ND, NN). Since there is no repeated measures module in PERMANOVA, we accounted for repeated measures by including factor month as fixed in the model. The routine PERMDISP was used to identify if differences obtained with the PERMANOVA test were an artifact of differences in dispersions among groups (Anderson 2006, Anderson et al. 2008). To visualize multivariate patterns revealed by PERMANOVA, unconstrained (principal coordinates analysis, PCO, a parametric analogue of multidimensional scaling) and constrained (canonical analysis of principal coordinates, CAP) ordination techniques were used (Anderson & Willis 2003). Based on the strength of the correlation (>0.4) of individual species with the canonical discriminant axes (CAP1 or CAP2), fish species with a frequency of occurrence of more than 0.2 were identified as responsible for differences in the observed patterns. All multivariate analyses were based on Bray-Curtis distances calculated from square-root transformed data and conducted using the Vegan package of the R statistical environment (Oksanen et al. 2010) and PERMANOVA+ for PRIMER software (Anderson et al. 2008).

RESULTS

Taxonomic, trophic and estuarine use composition

A total of 2993 fish from 50 species and 26 families were recorded during the entire sampling period. The most speciose families were Lutjanidae (6 species), Carangidae (5 species) and Gobiidae, Engraulidae, Centropomidae, Gerreidae and Eleotridae (3 species each family). *Lile stolifera* (Clupeidae) was the most abundant species representing one-third of all individuals collected. *Centropomus arma-*

tus (Centropomidae), *Lutjanus argentiventris* (Lutjanidae) *Diapterus peruvianus* (Gerreidae) and *Ariopsis seemanni* (Ariidae) accounted for 12, 8, 7 and 5% of the total abundance, respectively. In terms of catch weight, 3 species accounted for ca. 60% of the total catch weight: *L. argentiventris*, *Sphoeroides rosenblatti* (Tetraodontidae) and *A. seemanni*. The family Lutjanidae (snappers) represented 28% of the total catch weight in this mangrove fish assemblage, followed by Tetraodontidae (20%) and Ariidae (19%) (Table 1).

The fish assemblage was dominated by zoobenthivores and to a minor extent by zooplanktivores. The former trophic guild accounted for 66% of the total number of species and represented 47% and 84% of the total abundance and catch weight, respectively (e.g. Lutjanidae, Centropomidae, Tetraodontidae, Ariidae). Zooplanktivores were very abundant (36% of the total number of individuals) but were only represented by 4 species that contributed 6% of the total catch weight (Clupeidae, Atherinopsidae). Piscivores were almost as important as zooplanktivores in catch weight percentages (5%), and were mainly composed of jacks (Carangidae) and needlefishes (Belonidae). Most fish species in Bahía Málaga were marine estuarine opportunistic (42%), whereas estuarine species accounted for only 28% (14 species). Marine estuarine opportunistic species were also dominant in number of individuals (49%), followed by estuarine residents (27%) and marine estuarine dependent species (19%). Catch weights, however, were dominated by estuarine resident species (49%) with marine estuarine dependent and marine estuarine opportunistic species representing almost all the remaining catch weights (30% and 18%, respectively) (Table 1).

The individual-based rarefaction curves indicated that the observed number of species (S_{obs}) for the creeks with low salinity (26 and 27 for L1 and L2, respectively) was lower than the observed number of species in the creeks with medium salinity (35 and 37 for M1 and M2, respectively; Fig. 3). The Chao1 species richness estimator (S_{Chao1}) stabilized for 3 of the 4 creeks (M1 at 39 spp., L1 and L2 at 27 spp.) well before all the individuals were collected in these creeks. Only creek M2 did not show an asymptote as the S_{Chao1} continued to increase until the final number of individuals was collected, resulting in a final mean number of 53 species and the largest number of singleton species (11 spp. represented by a single individual). The overlapping number of species for all creeks at the lower number of individuals collected at creek L1 (277 individuals) indicates a con-

Table 1. Fish species composition in 4 mangrove creeks of Bahía Málaga collected from December 2009 to November 2010, fish species sorted decreasing by abundance. Common fish names are given in Table S3 in the Supplement (www.int-res.com/articles/suppl/m494 p249_supp.pdf). Total number of individuals (n), spatial guilds (SG), trophic guilds (TG), catch weight for total as well as spring-day (SD), spring-night (SN), neap-day (ND), neap-night (NN) combinations, mean and range total length (TL) for each species, and maximum total lengths reported in the literature (Max-TL) (Robertson & Allen 2008). Spatial guilds (SG): pelagic (P), benthopelagic (BP), demersal (D), reef associated (RA) and freshwater (F) according to Froese & Pauly (2012). Trophic guilds (TG): zooplanktivore (ZP), detritivore (DV), herbivore-phytoplankton (HVP), piscivore (PV), zoobenthivore (ZB), and omnivore (OV). Estuarine use functional groups (in superscript) according to the present study's stomach content inspections and Elliott et al. (2007). Numbers in **bold** show the 2 highest catch weights in any of the tide-time of day combination levels (SD, SN, ND, NN) for the top 15 species

| Species | n | SG | TG | Catch weight (g) | | | | | TL (cm) | Max TL |
				Total	SD	SN	ND	NN	(range)	(cm)
Lile stolifera (Clupeidae)[a]	1015	P	ZP	5765.3	**2491**	**2814.9**	410.5	48.9	9.2 (6.8–11.2)	15.0
Centropomus armatus (Centropomidae)[c]	356	D	ZB	5650.2	704.3	**2043.7**	497.2	**2405**	10.7 (5.6–23.6)	37.0
Lutjanus argentiventris (Lutjanidae)[b]	237	RA	ZB	21472.6	3207.4	**9699.5**	2302.2	**6263.6**	15.4 (38.8–5.6)	71.0
Diapterus peruvianus (Gerreidae)[b]	206	D	ZB, DV	1359.4	**412.7**	**460.8**	222	263.9	7.8 (3.0–15.6)	38.0
Ariopsis seemanni (Ariidae)[c,‡]	143	D	ZB	19980.1	2971.6	**5134.2**	2984.7	**8889.6**	24.4 (15.6–34.0)	35.0
Sphoeroides rosenblatti (Tetraodontidae)[c]	109	D	ZB	20665.1	**9871.2**	1877.1	**6796.9**	2356.5	19.5 (14.0–35.0)	30.0
Centropomus medius (Centropomidae)[c]	89	D	ZB	3133.8	425.8	**1582.4**	119	**1006.6**	13.9 (8.0–34.5)	65.0
Poeciliopsis turrubarensis (Poeciliidae)[d]	62	BP	DV	82.9	11.6	**28.5**	0.6	**42.2**	5.0 (3.4–6.0)	9.0
Caranx caninus (Carangidae)[a]	55	P	PV	1254.8	**643.3**	136.3	**472.3**	2.9	12.2 (6.4–20.0)	101.0
Oligoplites altus (Carangidae)[a]	54	BP	ZB	997.4	**429.2**	88	**461.9**	18.3	12.7 (6.2–27.1)	56.0
Caranx sexfasciatus (Carangidae)[a]	53	RA	PV	1729.2	**1171.4**	18.4	**539.4**	–	13.4 (7.2–23.0)	120.0
Gobiomorus maculatus (Eleotridae)[d]	51	D	ZB	578.7	**94.9**	46.4	**419.7**	17.7	11.1 (7.4–18.3)	35.0
Lutjanus jordani (Lutjanidae)[b]	51	RA	ZB	4531.3	580.1	**1472.7**	523.8	**1954.7**	14.9 (5.6–29.4)	61.0
Strongylura scapularis (Belonidae)[b]	51	P	PV	2169.2	461.2	**693.6**	218.1	**796.2**	31.3 (7.8–41.0)	40.0
Lutjanus guttatus (Lutjanidae)[a]	48	RA	ZB	844.9	**297.4**	**463.5**	73.4	10.6	10.0 (6.1–18.7)	80.0
Bathygobius andrei (Gobiidae)[c]	47	RA	ZB	759.8	12.1	193.4	187.3	367	11.2 (3.6–21.7)	15.0
Citharichthys gilberti (Paralichthyidae)[a]	45	D	ZB	377.9	135.2	47.7	135.8	59.2	9.9 (6.1–16.6)	30.0
Atherinella serrivomer (Atherinopsidae)[a]	42	P	ZP	243.1	141.5	63.9	21.4	16.3	10.0 (9.4–12.4)	17.0
Brycon meeki (Characidae)[d]	34	BP, F	OV	983.5	259.8	58.5	574.1	91.1	14.5 (7.6–28.0)	
Opisthonema medirastre (Clupeidae)[a]	30	P	HVP	1564.1	–	–	1564.1	–	19.6 (17.7–21.3)	30.0
Daector dowi (Batrachoididae)[c]	29	D	ZB	203.8	47.2	87.2	21.9	47.5	8.7 (6.4–13.8)	16.0
Bairdiella ensifera (Sciaenidae)[a]	26	BP	ZB	265.8	11.3	–	183.3	71.2	10.2 (8.4–15.9)	35.0
Eucinostomus currani (Gerreidae)[a]	22	D	ZB	324.3	70.7	231.9	–	21.7	10.8 (6.1–13.8)	21.0
Mugil cephalus (Mugilidae)[b]	22	BP	DV	1387.6	246.3	448.8	15.5	677	16.7 (8.6–32.0)	135.0
Pomadasys macracanthus (Haemulidae)[a]	20	BP	ZB	3864.2	474.3	1124.1	1396.6	869.2	19.2 (5.5–33.1)	37.0
Lutjanus colorado (Lutjanidae)[e]	12	RA	ZB	1257.6	473.7	268.9	319.3	195.7	17.4 (8.1–34.9)	107.0
Centropomus unionensis (Centropomidae)[a]	10	D	ZB	124.6	–	94	20.1	10.5	9.3 (6.9–21.1)	46.0
Chloroscombrus orqueta (Carangidae)[a]	9	BP	ZP	168.1	–	12.2	155.9	–	13.6 (12.2–15.1)	31.0
Halichoeres aestuaricola (Labridae)[c]	7	D	ZB	297.5	209.5	–	77.4	10.6	13.7 (9.4–19.1)	30.0
Lutjanus novemfasciatus (Lutjanidae)[a]	6	RA	ZB	1024.1	302.5	–	721.6	–	21.5 (7.2–30.0)	170.0
Rypticus nigripinnis (Serranidae)[a]	6	RA	PV	275.3	21.4	182.4	–	71.5	14.3 (11.8–16.9)	35.0
Cathorops steindachneri (Ariidae)[c]	5	D	ZB	271.0	–	–	271.0	–	21.0 (15.2–25.0)	36.0
Eleotris picta (Eleotridae)[d]	5	D	ZB	45.3	–	3.5	5.4	36.4	10.7 (8.2–13.5)	53.0
Hyporhamphus snyderi (Hemiramphidae)[a]	5	P	ZP	72.1	25.4	29.5	17.2	–	19.5 (19.0–19.9)	19.0
Eugerres brevimanus (Gerreidae)[a]	4	BP	ZB	16.7	11.6	–	3.2	1.9	7.1 (5.8–9.6)	32.0
Selene brevoortii (Carangidae)[a]	4	BP	ZB	52.6	–	2.1	50.5	–	14.0 (5.4–17.2)	42.0
Achirus mazatlanus (Achiridae)[a]	3	D	ZB	9.4	–	–	2.3	7.1	6.2 (5.5–6.8)	20.0
Epinephelus quinquefasciatus (Serranidae)[b]	3	RA	ZB	1252.4	–	–	354.2	898.2	28.6 (21.4–39.3)	250.0
Synodus scituliceps (Synodontidae)[a]	3	D	ZB	53.1	–	28.7	24.4	–	–	55.0
Cynoscion phoxocephalus (Sciaenidae)[b]	2	D	ZB	9.3	–	–	5.7	3.6	8.3 (7.7–8.9)	66.0
Lophogobius sp. (Gobiidae)[c]	2	D	ZB	7.1	1.7	5.4	–	–	6.5 (5.2–7.8)	11.0
Ophidion fulvum (Ophidiidae)[c]	2	D	ZB	31.4	21.1	–	–	10.3	14.7 (13.6–15.8)	18.0
Anchoa exigua (Engraulidae)[e]	1	P	ZP, HVP	0.7	–	–	–	0.7	5.9	7.5
Anchoa sp. (Engraulidae)[e]	1	P	ZP, HVP	1.6	–	1.6	–	–	6.8	–
Anchoa spinifer (Engraulidae)[e]	1	P	ZP, HVP	5.6	5.6	–	–	–	10.2	26.0
Batrachoides pacifici (Batrachoididae)[c]	1	D	ZB	402.9	–	–	–	402.9	30.2	43.0
Ctenogobius sagittula (Gobiidae)[c]	1	D	DV	0.5	–	–	0.5	–	5.2	20.0
Guavina micropus (Eleotridae)[c]	1	D	ZB	22.7	–	–	–	22.7	12.6	11.5
Lutjanus aratus (Lutjanidae)[a]	1	RA	ZB	238.8	–	238.8	–	–	24.7	100.0
Pisodonophis daspilotus (Ophichthidae)[c]	1	D	ZB	87.8	87.8	–	–	–	47.0	68.0
Total	2993			106153.7	26331.8	29682.6	22170.4	27968.9		

‡Considered as *Sciades seemanni* by Marceniuk et al. (2012); [a]Marine estuarine–opportunist; [b]Marine estuarine–dependent; [c]Estuarine residents; [d]Freshwater migrants; [e]Marine stragglers
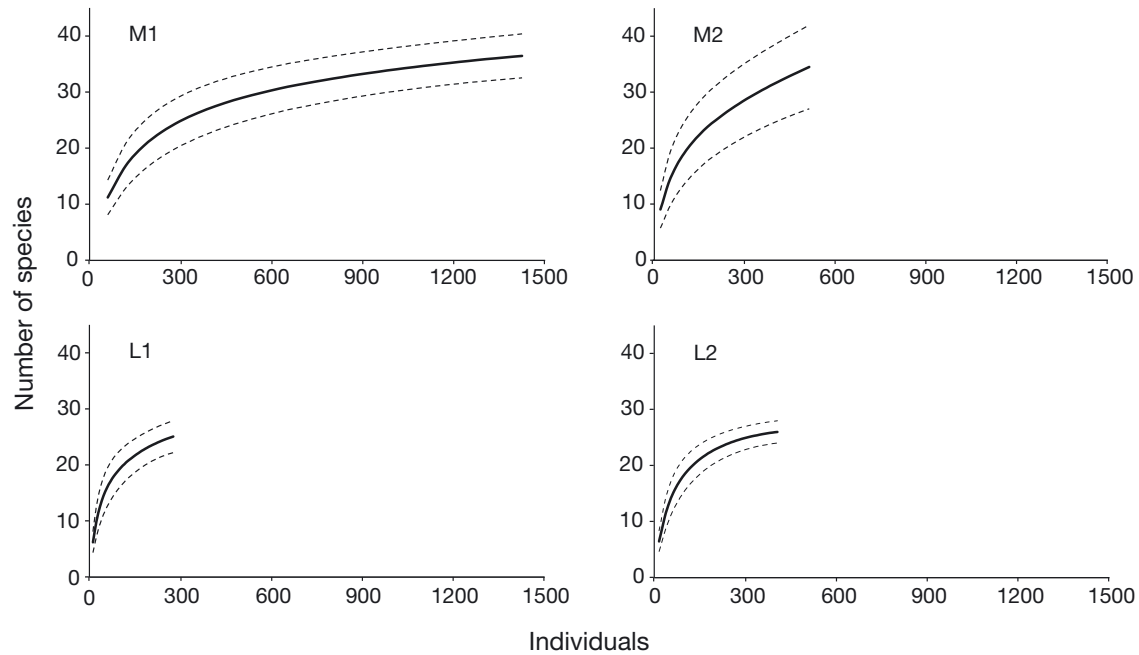
Fig. 3. Individual-based rarefaction curves of mangrove creek fish species from medium salinity creeks (M1 and M2) and low salinity creeks (L1 and L2) sampled from December 2009 to November 2010. Dashed lines indicate 95% confidence intervals

siderable density effect with creeks in the low salinity zone having fewer individuals than creeks in the medium salinity zone. Therefore, mangrove creeks with low salinities have lower species density, but not necessarily lower species richness than mangrove creeks with medium salinities (see Gotelli & Colwell 2001 for an explanation of this species density artifact). A relatively even fish assemblage was found in the intertidal mangrove creeks of Bahía Málaga. The shape of the SAD using individual abundance as a currency resembled that of a log-normal distribution (Fig. 4).

Tide-, diel- and salinity-related patterns

The temporal niche axis of the mangrove fish assemblage in Bahía Málaga was divided by a combination of the tidal magnitude and the diel cycle. Most zoobenthivores species had higher catch weights during the neap and spring tides occurring at night (i.e. *Centropomus armatus*, *Lutjanus argentiventris*, *Ariopsis seemanni*). Catch weights of the most abundant species in the intertidal mangrove creeks of Bahía Málaga, the zooplanktivore clupeid *Lile stolifera*, was highest only during spring tides, at both day and night. The zoobenthivore pufferfish *Sphoeroides rosenblatti* had higher catch weights during days at spring and neap tides. The catch

weights of the piscivore species of the family Carangidae (*Caranx caninus*, *C. sexfasciatus*, and *Oligoplites altus*) were especially high during days at both spring and neap tides (Table 1).

Species richness differed significantly between salinity zones ($t = -6.8697$, $p < 0.0001$), with medium salinity creeks (M1 and M2) having consistently more species than low salinity creeks (L1 and L2).
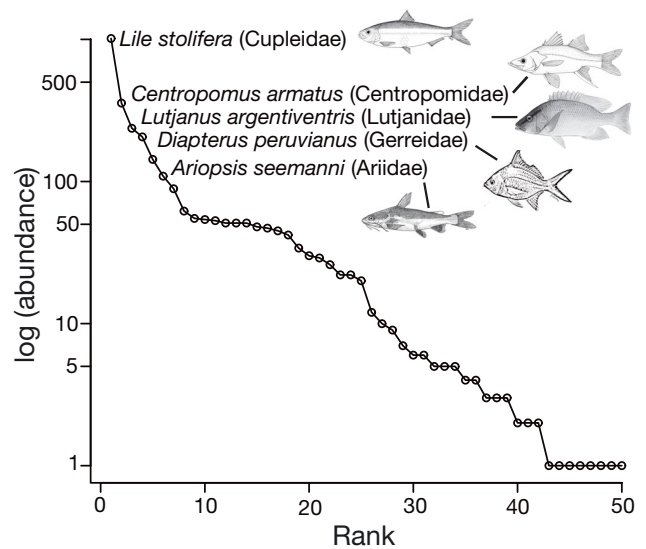

Fig. 4. Rank-abundance plot of intertidal mangrove fishes captured from all 4 creeks from December 2009 to November 2010

Mean species richness did not differ significantly between tide-time of day ($F_{3,88}$ = 1.5018, p = 0.2197; Fig. 5a) or between months (repeated measures ANOVA, $F_{11,68}$ = 0.926, p = 0.521). Mean fish abundance was significantly different between creeks (K = 40.6265, p < 0.0001; Fig. 5b); with the highest
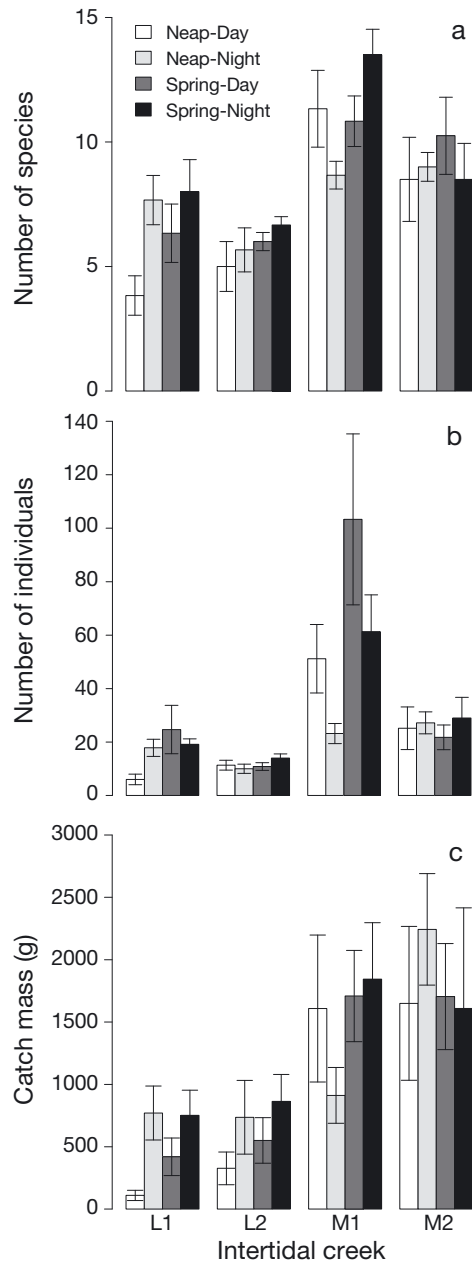

Fig. 5. (a) Mean number of species, (b) abundance (number of individuals) and (c) catch mass (±SE) per block net sample in 4 intertidal mangrove creeks during spring tide – day (SD), spring tide – night (SN), neap tide – day (ND) and neap tide – night (NN) from December 2009 to November 2010. Low salinity creeks, L1 and L2. Medium salinity creeks: M1 and M2

abundance values in medium salinity creeks and the lowest values in the 2 creeks with the lowest salinity. Mean catch weight also varied significantly between salinity zones, with higher values in medium salinity than in low salinity creeks (salinity factor, W = 390, p < 0.0001; Fig. 5c). Abundance and catch weight, however, were not significantly different between levels of the tide-time of day factor (K = 4.6392, p = 0.2002, for abundance; and K = 5.112, p = 0.1638 for catch weight; Fig. 5b,c) or between months (K = 12.4499, for abundance; and K = 15.8155, p = 0.1481, for catch weight).

Mean overall fish density (±1 standard deviation) was 0.013 ± 0.016 ind. m^{-2} (range: 0.0666–0.0007) or 0.021 ± 0.026 ind. m^{-3} (range: 0.106–0.001). Mean overall fish biomass (±1 standard deviation) was 0.515 ± 0.657 g m^{-2} (range: 2.852–0.008) or 0.851 ± 1.194 g m^{-3} (range: 5.925–0.001). Both fish density (W = 1894, p < 0.0001) and biomass (W = 1823, p < 0.001) were significantly higher in medium salinity than in low salinity zones (Fig. 6). Catch weights for each creek were always higher during the wet than during the very wet season. These differences, however, were not statistically significant (Fig. 7).

The PERMANOVA test showed significant effects for the factors salinity zone, tide-time of day and month; and for the interaction between salinity zone × time of day and salinity zone × month (Table 2). The PERMDISP routine, however, indicated that these results should be taken with caution due to artifacts introduced by multivariate dispersion in the case of the factor tide-time of day ($F_{3,88}$ = 8.62, p = 0.0002) and salinity ($F_{1,90}$ = 4.63, p = 0.0437). Individual pairwise tests and visual inspection of unconstrained ordinations (non-metric multidimensional scaling) showed that for the factor tide-time of day, only samples from the neap-day combination were particularly overdispersed (average Bray-Curtis distance-to-centroid = 57%). Unconstrained ordinations also indicated clear differences between samples from low salinities and medium salinities, despite distinctly different multivariate variances (according to the PERMDISP test). The PERMDISP routine for the factor month was non-significant ($F_{11,80}$ = 2.15, p = 0.0787), indicating that the differences shown in the PERMANOVA test were real. Most pairwise comparisons in the PERMANOVA test for the factor month, however, were non-significant, indicating that overall significant effects were only due to differences from a few samples from specific months (June and October).

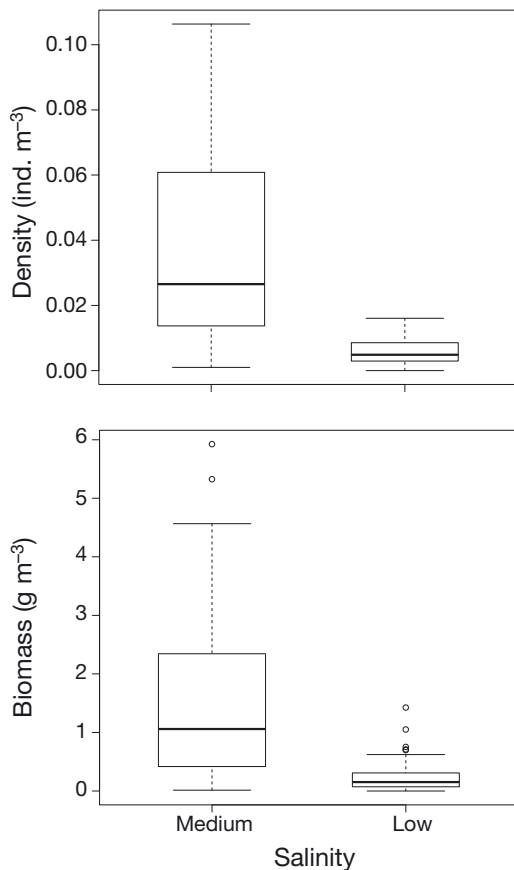A deeper examination of the factors in the PERM-ANOVA test, with the CAP and PCO routines,

Fig. 6. Boxplots showing differences in (a) density and (b) catch weight of intertidal mangrove creek fishes collected from a low and medium salinity zone. **Bold** lines indicate medians, hinges indicate the 25th and 75th percentiles, whiskers indicate the largest and smallest observation within a distance of 1.5 the box size and circles represent outliers
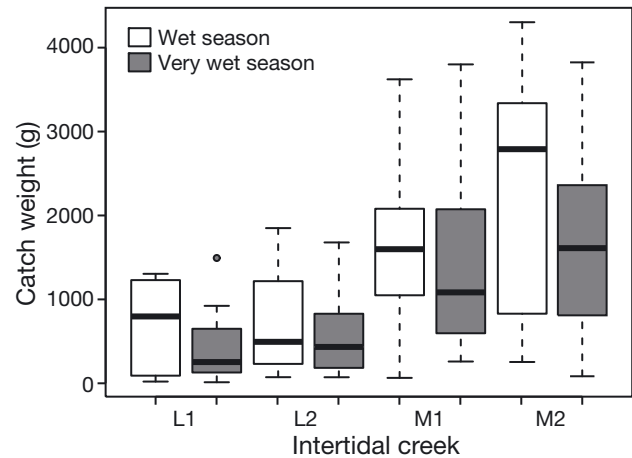

Fig. 7. Boxplots of catch weight of mangrove fish assemblages per block net sample from 4 intertidal creeks (L1, L2, M1, M2) during wet (January to April) and very wet period (May to December) in 2009 and 2010. **Bold** lines indicate medians, hinges indicate the 25th and 75th percentiles, and whiskers indicate the largest and smallest observation within a distance of 1.5 the box size and circles represent outliers

and one species (*Lile stolifera*) was correlated with spring tide samples (both at day and night; Figs. 8 & 9a).

Overall leave-one-out allocation success for the factor salinity was high (93.48%) with few misallocations between medium and low salinity samples (Table 3b). An unconstrained ordination (PCO, Fig. 10) showed that samples from low and medium salinities could be differentiated and that 2 species were especially correlated with low salinities (*Brycon meeki* and *Gobiomorus maculatus*) and at least 11 species were correlated with medium salinities (Figs. 9b & 10).

showed that the factors salinity and tide-time of day could be discriminated (Figs. 8 & 9), but not the factor month. Overall leave-one-out allocation success was 72.8% for the factor tide-time of day (Table 3a). Spring (day and night) were clearly separated from neap (day and night) tides along the CAP2 axis, whereas night samples were divided from day samples along the CAP1 axis, irrespective of the tidal magnitude (i.e. spring or neap; Fig. 8). Three species (*Ariopsis seemanni*, *Centropomus armatus* and *Strongylura scapularis*) were strongly correlated with neap-night samples

Table 2. Results of a 3-way model PERMANOVA testing the effects of salinity zone (medium versus low), tide-time of day combination (spring tide day – SD, spring tide night – SN, neap tide day – ND, neap tide night – NN) and month (12 levels, repeated measures component) on 4 mangrove creek fish assemblages

| Source	df	SS	MS	*F*	p
Salinity zone	1	27149	27149	13.046	0.0001
Tide-time of day	2	16213	8106.4	3.8956	0.0001
Month	10	34805	3480.5	1.6726	0.0002
(Salinity zone) × (tide-time of day)	2	9206.1	4603.1	2.212	0.0012
(Salinity zone) × (month)	10	26581	2658.1	1.2774	0.0286
(Tide-time of day) × (month)	10	25858	2585.8	1.2426	0.0519
(Salinity zone) × (tide-time of day) × (month)	10	15157	1515.7	0.72836	0.9837
Residual	44	91561	2080.9		
Total	91	272100			
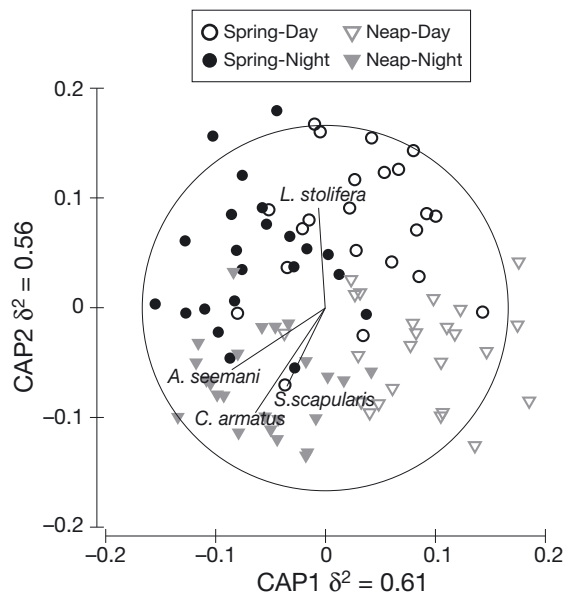
Fig. 8. Canonical analyses of principal coordinates (CAP) of intertidal mangrove creek fish assemblages taken at different tide-time of day combinations. Symbols represent individual block net catches and vectors represent correlation of individual species with CAP1 or CAP2 axes. See Table 1 for full species names

Fig. 9. Mean density (±SE) of fish species responsible for differences in (a) tide-time of day factor combinations, and (b) low and medium salinity zones. See Table 1 for full species names

Finally, the CAP analysis was not able to reliably allocate samples according to the factor month. Overall leave-one-out allocation success was 18.5% with most of the months having an allocation success of <30% (Table 3c). This indicates that despite having a significant difference in the PERMANOVA test for the factor month, samples were not easily distinguishable from each other.

Combined results from the PERMANOVA and CAP routines showed that the factors salinity and tide-time of day drive changes in the structure of the intertidal mangrove fish assemblage in Bahía Málaga. Examination of unconstrained plots for these 2 factors shows a clear separation between the samples, despite differences in multivariate dispersions between groups. Month, despite being significant for the overall PERMANOVA test, was not identified as a reliable factor that could separate samples based on *a posteriori* pairwise comparisons and the CAP ordination.

DISCUSSION

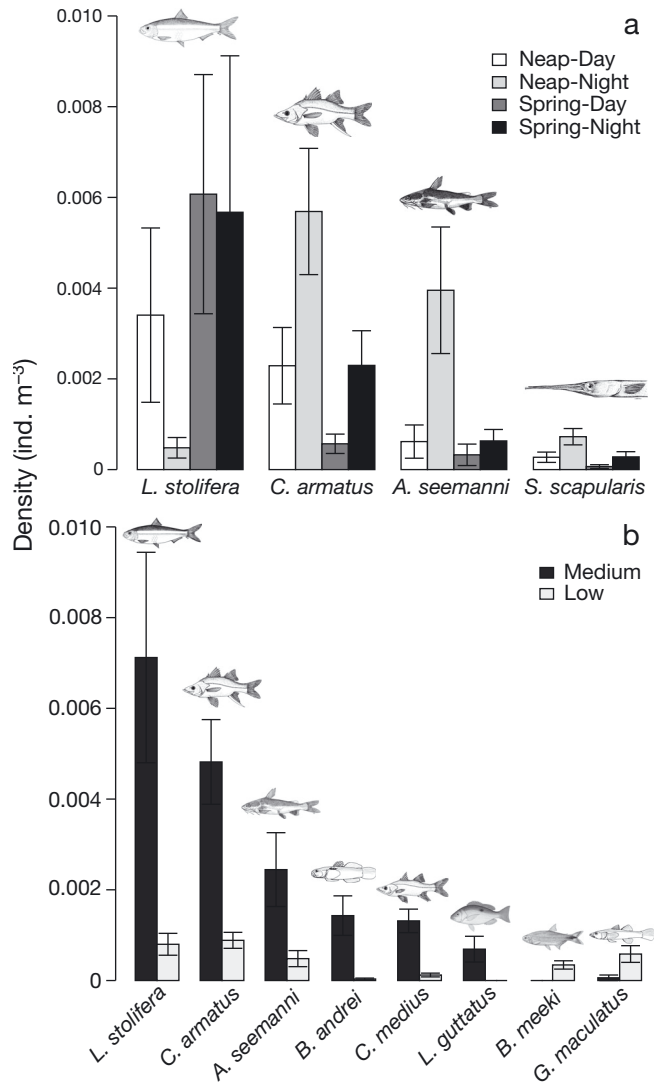The study provides strong evidence that fish inhabiting intertidal mangrove forests in macrotidal areas establish their niches along temporal scales subject to the interaction of tidal and diel cycles. The endogenous circadian rhythm of the fish (diel cycle) interacts with the spring-neap tide cycle, enabling coexistence of a set of species using the intertidal mangroves. The study also provides the first evidence of the influential role of salinity on fish assemblage structure in the wettest mangrove area of the Neotropics. Additionally, we suggest that the trend in fish biomass reduction in mangroves of Bahía Málaga during the rainiest months (August to November), although weak, could be related to the notable freshening of the system at the end of the year.

The composition of the fish faunas observed in this study is similar at the family level when compared to

Table 3. Canonical analysis of principal coordinates (CAP) testing the effect of (a) tide-time of day combination (spring tide day – SD, spring tide night – SN, neap tide day – ND, neap tide night – NN), (b) salinity zone (medium versus low), and (c) month (December 2009 to November 2010) on mangrove creek fish assemblages. %Var = percentage of the total variation explained by the first m principal coordinate axes; allocation success = percentage of points correctly allocated into each group; δ^2 = square canonical correlation. For (a), (b) and (c): p = 0.0001

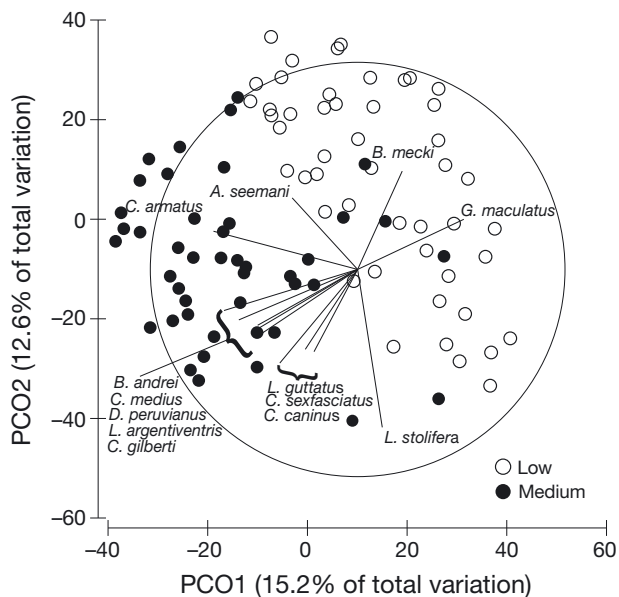| m	%Var	Allocation success (%)												Total	δ^2
(a) Tide-time of day		SD	SN	ND	NN										
7	63.63	63.6	63.6	83.3	79.2									72.8	0.605
(b) Salinity		Medium		Low											
17	98.24	88.64		97.92										93.48	0.755
(c) Month		Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov		
16	95.9	17	13	0	25	25	0	13	38	13	13	38	25	18.5	0.77

Fig. 10. Principal coordinate analysis ordination (PCO) of the intertidal mangrove creek fish assemblages, showing variation between low and medium salinity zones. Species in vectors have high correlation (>0.4) with axes. Symbols represent individual block net catches, and vectors represent correlation of individual species with CAP1 or CAP2 axes. See Table 1 for full species names

other studies in the TEP as well as similar macrotidal areas of the western central Atlantic (i.e. northern Brazil). Mangrove fish assemblages in the TEP are dominated by Gerreidae, Clupeidae, Engraulidae, Mugilidae and Centropomidae (Castellanos-Galindo et al. 2013). All these families were also abundant in the present study with the exception of Engraulidae and Mugilidae. Similarly, mangrove creek fish as-

semblages in the macrotidal areas of northern Brazil are dominated in catch weight by Ariidae and Tetraodontidae (Barletta et al. 2003, Krumme et al. 2004, Giarrizzo & Krumme 2008, Castellanos-Galindo & Krumme 2013). In our study area, both Ariidae and Tetraodontidae ranked among the first 3 families in terms of catch weight. Lutjanidae is the most important family in the intertidal mangroves of Bahía Málaga, an indication of the unique environmental configuration of this coastal area. From the earliest life stages of the Lutjanidae, the fish move between the mangroves and the rocky subtidal habitats in Bahía Málaga. The yellow snapper *Lutjanus argentiventris* is a particularly well-known example in the TEP which shifts its ontogenetic habitat between mangroves and rocky reefs (Aburto-Oropeza et al. 2009).

Effects of salinity on fish assemblage composition

Our results indicate that the fish biomass in intertidal mangroves can be substantially affected by salinity. Salinity has been demonstrated to be one of the major determinants of the dynamics of estuarine mangrove fish assemblages (Cyrus & Blaber 1992). Extremely high precipitation producing high runoff through the subtidal channels is the main driver of salinity changes in Bahía Málaga. Creeks located in low salinity zones had significantly lower number of species, fish densities and biomasses than creeks in medium salinity zones. This is partly explained by the lack of tolerance of most coastal-marine fish species to long-term low salinities in the upper reaches of the estuary (Sheaves 1998). These results could

also be explained by the lack of a regionally diverse and abundant freshwater fish fauna in a very small drainage system (that otherwise could compensate for the absence of estuarine and marine fishes in the upper estuary, e.g. North Andean Pacific slopes, Abell et al. 2008). In contrast, in the Caeté River (North Brazil), Barletta et al. (2005) found the highest number of species and greatest biomasses in the upper estuary (lower salinities). This pattern was explained by higher biomasses of a single estuarine species (Sciaenidae), but also by a significant contribution of freshwater-related catfishes (i.e. Aspredinidae, Auchenipteridae, Pimelodidae) in a region where the freshwater fish fauna is rich and abundant. Therefore, it seems likely that low numbers and biomass of fish species in the upper estuaries in different parts of the world (tropical Australia, Sheaves 1998; West Africa, Simier et al. 2006) can be explained by the lack in tolerance of most estuarine and marine fish species to long-term low salinity values, but also to the depauperate freshwater fish fauna of these regions.

Tide-related patterns

Fish species-specific tide- and diel-related patterns were clearly observed and closely resemble those observed in other macrotidal mangrove systems in the neotropical area (i.e. North Brazil, Krumme et al. 2004). Similar patterns in intertidal use that were also consistent across taxonomic groups involve the families Ariidae and Tetraodontidae. Catch weights of Ariidae in Bahía Málaga and North Brazil were consistently higher at night. In northern Brazil, however, catch weights for this family were higher at spring tide. In Bahía Málaga, catch weights of Ariidae were higher at neap tide night compared to spring tide night. For Tetraodontidae, important species both in Brazil and Colombia (*Colomesus psittacus* and *Sphoeroides rosenblatti*, respectively) were more abundant during the day at both spring and neap tide. Regardless of taxonomic affinity, the zoobenthivorous trophic guild had higher catch weights at night in the Colombian and Brazilian mangroves. This may be the result of a higher level of activity of their potential prey (predominantly shrimp) at night (e.g. Vance 1992). Very abundant Centropomidae in Bahía Málaga had higher catch weights at night both during the spring and neap tides. Similarly, in estuarine systems of north-eastern Australia, *Lates calcalifer* (Latidae, closely related to Centropomidae) was found to be extremely abundant during the night in

the mangroves (Ley & Halliday 2007). Finally, piscivores belonging to Carangidae presented their highest catch weights in Bahía Málaga during the day at both spring and neap tides, very similar to Carangidae — as shown in Ley & Halliday (2007). Similarities in the diel and tidal patterns in taxonomically related species across mangroves in different areas indicate the existence of a phylogenetic signal related to foraging strategies. This phylogenetic signal, however, seems to be influenced by the ecological and environmental features specific to a particular mangrove system.

The total catch weight and species richness in our study area was not significantly influenced by tidal magnitude or the diel pulse interaction (SD, SN, ND, NN). These results do not agree with results obtained in a macrotidal mangrove system in northern Brazil (Krumme et al. 2004). In that system, Krumme et al. (2004) found that the number of species and catch weight of fish entering intertidal mangrove creeks were highest during spring tides (particularly at night), whereas at neap tide these numbers decreased considerably. In northern Brazil, mangrove progradation has occurred for the last 2000 yr (Cohen et al. 2005), causing mangrove forests to grow in even higher elevation zones in relation to mean sea level. Consequently, in northern Brazil mangrove forests are only flooded during spring tides, providing fish with greater accessibility to intertidal habitats and food sources. During neap tides the tidal creeks become flooded but the mangrove areas remain relatively dry at high tide; the reduced inundation of intertidal habitats means less foraging area for the fish.

At our study site in the TEP, *Rhizophora* trees feature impressive above-ground stilt root systems (often >5 m high) on a mangrove floor that is usually located below the mean high water level and which is extensively inundated during each tide (see Fig. S1 in the Supplement). As a consequence, mangroves are inundated at high tide during both spring and neap tides and fish have almost equal accessibility to food sources at high tide, irrespective of tidal magnitude. This difference in the interplay between geomorphological settings and the tidal pulse can possibly explain why tide-related patterns in the structure of intertidal mangrove fish assemblages can vary in strength. In regions where the mangrove floor is located above mean high water level, most of the mangrove area will be only available for foraging fish at spring tides (i.e. northern Brazil and other accretional mangroves). Therefore, foraging during spring tides would maximize prey availability for these fishes. In

contrast, in regions where the mangrove floor is located below mean high water level, an almost equal extent of mangrove area will be available for fish at spring and neap tides (i.e. Colombian Pacific and other erosional mangrove regions). In this case, foraging during spring tides will not represent a significant increase of foraging grounds, thus resulting in a weak signal in tidal-related patterns in fish distribution. This geomorphological influence on fish habitat use has been acknowledged before for intertidal marshes (Kneib 1997), but has never been thoroughly considered when analyzing intertidal mangrove habitat use by fishes (but see Lugendo et al. 2007).

Mangrove fish productivity

Mean fish biomass and density estimates at our study site were strikingly low in comparison to the estimates from other mangrove creek systems in the world (Table 4). For example, mean biomass (g m^{-3}) was threefold higher in the intertidal mangrove creeks of northern Brazil compared to the values obtained from the TEP region. Studies from the relatively undisturbed areas in Australia also showed considerably higher densities. Huxham et al. (2004) estimated lower fish density values in Gazi Bay (Kenya) than those obtained from our study. Low values were attributed to: problems with the efficiency

and location of the sampling method, overexploitation, intrinsic characteristics of the mangrove fish fauna of the region and differences in the predation refuge function of the mangrove system in Gazi Bay. For Bahía Málaga, overfishing as a cause for low biomasses in mangrove fishes is unlikely because of the low human population density and minimal fishing activity compared to other areas of the world. The sampling method used in the present study is regarded as highly efficient to estimate fish biomass in vegetated intertidal creeks (Bozeman & Dean 1980). Some degree of underestimation of fish abundance and catch masses might have occurred especially at slack high water, when small fishes could have escaped to the main channel by swimming away from the net. Further experiments to estimate this potential bias will be needed. However, we assumed these losses to be minor and unlikely in explaining the low catch weight values obtained in this area. It can be that the low intertidal fish biomass and density can be attributed to differences in the productivity of the mangrove systems between biogeographical regions. This explanation was also proposed by Huxham et al. (2004) but ruled out, due to the similarity of the fish diversity in Gazi Bay compared to other mangrove systems. Nevertheless, diversity does not necessarily translate into a productive system. The intertidal mangrove creeks of northern Brazil with a similarly diverse fish assemblage to

Table 4. Comparison of the number of species, mean fish density and biomass estimates from different intertidal mangrove creek studies where block nets and stake nets have been used; studies sorted according to marine biogeographical regions and descending by density

Study	Number of species	$\bar{x}$ Density ind. m^{-2}	$\bar{x}$ Biomass g m^{-2}	g m^{-3}
Tropical Indo-West Pacific region				
Indo-Polynesian province				
Luzon, Philippines (Rönnbäck et al. 1999)	37	5.1	10.4	–
Queensland, Australia (Robertson & Duke 1990)	92	3.5	–	10.9
Embley River, Australia (Vance et al. 1996)	55	0.83	3.9	–
Trang province, Thailand (K. Grinvalds & U. Krumme unpubl.)	45	0.02	0.2	–
Western Indian Ocean Province				
Gazi Bay, Kenya (Huxham et al.2004)	30	0.004	–	–
Western Atlantic region				
Caribbean province				
Rockery Bay, Florida, USA (Ellis & Bell 2013)	69	4.56	6.61	25.22
Brazilian province				
Curuçá estuary, Brazil (Giarrizzo & Krumme 2007)	65	0.3	6.0	–
Caeté estuary, Brazil (Barletta et al. 2003)	49	0.11	2.06	–
Caeté estuary, Brazil (Krumme et al. 2004)	40	0.1	1.4	2.6
Eastern Pacific region				
Panamic province				
Bahía Málaga, Colombia (present study)	50	0.013	0.515	0.851

that in Bahía Málaga (ca. 50 to 60 species) sustain a higher biomass of second and third order consumers that can rely on a rich epifaunal biomass and nutrients that are recycled in the system (Saint-Paul & Schneider 2010). In contrast, in the high-rainfall area Bahía Málaga, epifaunal biomass and diversity is relatively low (Cantera et al. 1999), probably reflecting low nutrient supply from relatively short rivers draining a small pristine catchment area. This is likely to result in a system with very low productivity where fish biomass is naturally low.

Effects of an extreme precipitation regime

Our sampling campaign took place during an ENSO event of 2009–2011 and included a first period of a warm phase (El Niño; December 2009 to April 2010) and a second period of a cold phase (La Niña; July to November 2010). Our results, however, cannot confirm any causal effects from ENSO on potential changes in mangrove fish assemblage structures because data is lacking on non-ENSO periods. Furthermore, the intra-annual variability in precipitation in this particular area is not significantly affected during ENSO years. In 2010, a wet period between January and July (400 to 550 mm mo^{-1}), followed by a very wet period from August to November (700 to 1000 mm mo^{-1}) was observed. This pattern, despite occurring during an ENSO period, lies within the normal historical inter-annual rainfall variability occurring in this area (see Fig. S3 in the Supplement and Fig. 2). Fish catch weights in intertidal mangroves during the very wet period were always lower (but non-significant) than those during the wet season. The extreme freshening of this mangrove system during the last 5 mo of the year may have had adverse consequences on marine organisms (including fish) of this region as was observed on the Pacific coast of Panama (Valiela et al. 2012).

Conclusions

This study illustrates the complexity that can be encountered in the organization of mangrove fish assemblages in (neotropical) macrotidal areas. Despite similarities, which can be found in the way mangrove fish assemblages segregate along the temporal axis (tide- and diel-related patterns) between macrotidal regions, it is clear that specific patterns can change according to local environmental characteristics. When referring to the megahumid area of the Tropi-

cal Eastern Pacific, the geomorphological setting seems to play an important role influencing how fish use the mangroves according to the tidal cycles. Of comparable importance are the local precipitation regimes and the diversity and abundance of regional freshwater fish faunas. These 2 factors can explain the distribution of fishes along salinity gradients in mangroves and also help understand differences in the productivity between geographical areas. The understanding of how fish use mangrove ecosystems, including how the mangrove nursery function varies across geographical areas, has increased over the last few years (e.g. Sheaves 2012, Blaber in press); such knowledge, however, needs to be carefully interpreted in the light of local characteristics when extrapolation and equivalence from one system to another is attempted.

LITERATURE CITED

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