

Diversity, seasonal and diel distribution of snappers (Lutjanidae: Perciformes) in a tropical coastal inlet in the southwestern Gulf of Mexico



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Snappers are marine fishes, but juveniles of many species migrate to estuaries, using these systems as nursery areas. The purpose of this study was to know the environmental factors mainly related to the migration patterns of lutjanids in La Mancha lagoon inlet. During 19 months, 24-hour cycles were performed monthly, taking samples every two hours (442 samples). Environmental variables recorded *in situ* and with regional records such as rainfall, atmospheric temperature and day length were considered. Genetic barcoding (COI) was used to validate species identity. Significant differences were evaluated by PERMANOVA and a Canonical Correspondence Analysis was used to determine the importance of environmental variables. Six species were recorded and the most abundant showed significant differences among months, with migration patterns during the warm-rainy season. Day length, salinity and rainfall (two of them with regional incidence) were the variables significantly associated with the distribution of the species. The abundance of *Lutjanus analis*, *L. jocu*, and *L. cyanopterus* was inversely associated with the length of daylight and directly related to rainfall, while *L. synagris* and *L. griseus* showed segregation along a salinity gradient. Thus, migration patterns were mainly correlated with factors of regional coverage and greater seasonal influence.

Keywords: Atmospheric Temperature, Competition, Photoperiod, Water Level, Zooplankton.

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Los pargos son peces marinos, pero los juveniles de muchas especies migran a los estuarios, utilizándolos como áreas de crianza. El propósito del estudio fue conocer los factores ambientales principalmente relacionados con los patrones de migración de lutjánidos en la boca de la laguna La Mancha. Durante 19 meses se realizaron ciclos de 24 horas, tomando muestras cada dos horas (442 muestras). Se consideraron variables ambientales registradas *in situ* y con registros regionales tales como lluvias, temperatura atmosférica y duración del día. Se utilizó código de barras genético (COI) para validar la identidad de las especies. Diferencias significativas fueron evaluadas por PERMANOVA y un Análisis de Correspondencia Canónica permitió determinar la importancia de las variables ambientales. Se registraron seis especies y las más abundantes mostraron diferencias significativas entre meses, con patrones de migración durante la época cálida-lluviosa. La duración del día, la salinidad y la precipitación (dos con incidencia regional) fueron las variables asociadas significativamente a la distribución de las especies. La abundancia de *Lutjanus analis*, *L. jocu* y *L. cyanopterus* estuvo inversamente asociada con la duración del día y directamente con las lluvias, mientras que *L. synagris* y *L. griseus* mostraron segregación a lo largo de un gradiente de salinidad. Así, los patrones de migración se correlacionaron principalmente con factores de cobertura regional y de mayor influencia estacional.

Palabras clave: Competencia, Efecto de Marea, Fotoperiodo, Temperatura Atmosférica, Zooplancton.

INTRODUCTION

Snappers (Lutjanidae) are marine fishes that occur in tropical and subtropical oceans, mostly bottom-associated, occurring from shallow inshore areas to depths of about 550 m, mainly over reefs or rocky outcrops. However, juvenile stages of some species enter estuaries and the lower reaches of rivers. They are mostly carnivores with nocturnal activity and spawning is also apparently at night (Anderson, 2002; McEachran, Fechhelm, 2005; Castillo-Rivera *et al.*, 2020).

The Lutjanidae family includes about 110 species (Nelson *et al.*, 2016), of which 16 species in six genera occur in the Gulf of Mexico (Anderson, 2002; McEachran, Fechhelm, 2005). Twelve of these species have been recorded on the continental shelf of Veracruz State in Mexico, although only seven of them have been recorded in estuarine systems (Lara-Domínguez *et al.*, 2011).

In this sense, for a better evaluation of the diversity and temporal distribution patterns of fishes in an area, a greater sampling effort is necessary, increasing the number of months sampled, as well as sampling throughout the 24-h cycle. Indeed, in many studies of estuarine communities it has been observed that during the twilight or at night, a greater number of fish species is caught due to their foraging activity (Ley, Halliday, 2007; Castillo-Rivera *et al.*, 2017). For this reason, surveys that also considered night and twilight samples can provide a better understanding of fish richness and abundance

(Hagan, Able, 2008; Castillo-Rivera *et al.*, 2017).

Seasonal and diel changes in the relative abundance of fish species may be influenced by constant fluctuations in environmental factors. Traditionally, environmental variables that are recorded *in situ*, such as water temperature and salinity, and dissolved oxygen levels, have been considered. However, environmental variables with regional rather than local coverage can also play an important role, as has been observed for currents (Sanvicente-Añorve *et al.*, 2011; Castillo-Rivera *et al.*, 2020), wind effects (Bruno *et al.*, 2013, 2015; Souza *et al.*, 2018), photoperiod (Capossela *et al.*, 2013; Garcia, Pessanha, 2018), and rainfall (Bruno *et al.*, 2013; Castillo-Rivera *et al.*, 2017; Souza *et al.*, 2018). Indeed, species abundance patterns at the local scale are likely to be influenced by environmental processes that operate at both the local and regional scales (Alonso Aller *et al.*, 2014; Valesini *et al.*, 2014; Hayduk *et al.*, 2019).

Although snapper adults inhabit the marine environment, larvae and juveniles of many species migrate to estuaries, where they may spend their first life stages, using these systems as nursery areas (Anderson, 2002; Serrano *et al.*, 2011; Lustosa-Costa *et al.*, 2020). In this sense, the contribution of the current study is to know what are the main environmental factors related to the migration patterns of lutjanids in an estuary.

In this way, it was hypothesized that snapper migration patterns to estuarine systems may be more related to seasonal variations in environmental factors than to diel variations in these factors. Our main objective was, through a high-frequency temporal sampling, to determine the diversity of lutjanids, and to evaluate the relationship of environmental factors with the seasonal and diel distribution patterns of these species at the inlet of La Mancha lagoon.

MATERIAL AND METHODS

Study area. La Mancha lagoon is located in Veracruz State, Mexico (19°33'55" –19°35'44"N and 96°22'41" – 96°23'39"W), in the southwestern Gulf of Mexico. It is a small system, with an area of ~1.6 km² and bordered by mangrove forest. At its northeastern end, the system opens to the ocean via an inlet that discharges through a sand barrier, showing a seasonal pattern of open/close, which is regulated by the tides and freshwater discharge (Lara-Domínguez *et al.*, 2006).

The region has a warm sub-humid climate (Köppen climate classification: Aw2), with mean monthly rainfall between 12.8 mm in February and 265.8 mm in August, including a warm-rainy season (mean values > 100 mm from June to October) and a dry season (mean values < 60 mm from November to May). In La Mancha lagoon, the abundance of zooplankton and chlorophyll *a* show two peaks: one during August–October and another in February–March (Contreras-Espinosa *et al.*, 2005; Mecalco-Hernández *et al.*, 2018).

Data collection. In a sandy habitat within the lagoon, for 19 months, 24-hour cycles of collection activities were carried out, taking samples every two hours, simultaneously, and monthly, at two sites, one at 325 m and the other at 225 m from the inlet system (a total of 442 samples) (Fig. 1). The samples were taken with a beach seine net (37 m long, 1.2 m deep and 1 cm mesh size). The net was pulled 50 m parallel to the shore

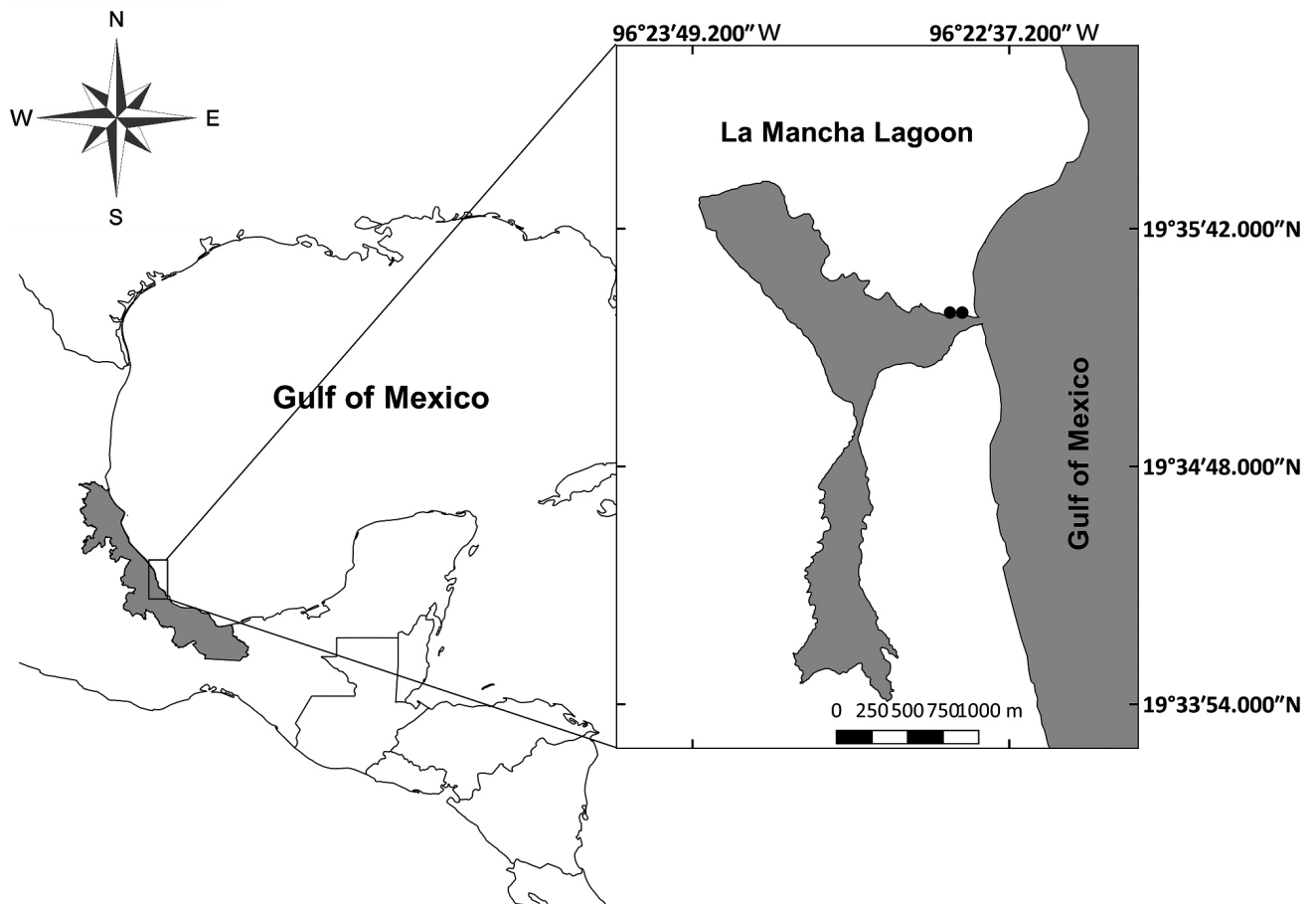


FIGURE 1 | Geographical location of La Mancha lagoon and sampling points (black circles).

and covered an approximate sampling area of 1,500 m² (gear length x haul distance). Immediately after their capture, some fish individuals were processed and frozen for DNA analysis and the others were anesthetized (clove oil solution) and posteriorly fixed with 10% formalin and preserved with 70% ethanol. The individuals were identified according to Anderson (2002), counted, and measured (Total length – TL and Standard length – SL) in the laboratory. One specimen of each species was cataloged and deposited in the fish collection of the Department of Biology, Universidad Autónoma Metropolitana, Unidad Iztapalapa (UAMI-CI).

In each sampling, the time of day, water salinity (ATAGO S-10E Refractometer), water temperature, dissolved oxygen (YSI 550A DO Instrument), chlorophyll *a* (spectrophotometric method, SCOR, 1966), and zooplankton biomass (circular trawl with 150 µm mesh net and volumetric method) were recorded *in situ*. Additionally, the monthly averages of rainfall were considered, as well as the duration of daylight hours for each sampling day and the water level (tidal stage effect) for each sampling time, all recorded for the study period (regional data for the state from Veracruz). The monthly averages (corresponding to 60 years: 1951–2010) of the atmospheric temperature were also considered (SMN, 2020).

DNA analyses. Particularly for snappers, it should be noted that juveniles and young adults could be difficult to identify taxonomically, since most species share meristic and overlap in morphometrics. Therefore, the use of DNA barcodes has been suggested, especially when rare and common species coexist and share a similar appearance (Victor *et al.*, 2009). Therefore, 47 specimens (including at least one specimen per species) were used for DNA analysis to validate species identity using genetic barcoding (mtDNA, partial sequence of cytochrome oxidase subunit I – COI). For each of these individuals, tissue samples collected from caudal fins were preserved in molecular grade 95% ethanol. The extraction, amplification, and sequencing protocols were in accordance with Castillo-Rivera *et al.* (2020). The sequence electropherogram was edited in MEGA-X and was compared with the database of BOLD Systems. A sequence of each registered snapper species was submitted to GenBank database.

Statistical analyses. For the most abundant species (> 10% of relative abundance), two-way univariate PERMANOVA was used to assess significant differences in the number and size of fish, with months and diel periods (day, twilight, and night) as fixed factors, followed by *posteriori* pair-wise comparisons among factor levels. In the same way, the environmental variables recorded *in situ* were analyzed. PERMANOVA is a routine based on a resemblance measure, generally highly appropriate, because most ecological data (being counts of abundances of species) tend to be overdispersed, with a substantial proportion of zeros. This method is also robust because uses multiple random permutations to obtain P-values, thus normality and homogeneity of variances are directly implied by the permutation procedure (Anderson, 2001; Anderson *et al.*, 2008). These analyses were performed using Euclidean distance (on square root transformed data), and permuted residuals under a reduced model, Type III (maximum permutations = 999). The square-root transformation is used most frequently with count data, which often follows a Poisson distribution (Gotelli, Ellison, 2004), as in the present case. These analyses were performed using PRIMER v7 (Clarke, Gorley, 2015).

For ordination purposes, according to Lepš, Šmilauer (2003), a Detrended Correspondence Analysis (DCA) was first calculated, which showed that the gradient lengths for the first two axes were 3.121 and 3.340 respectively. These values suggested that the use of unimodal ordination methods is appropriate. Thus, a Canonical Correspondence Analysis (CCA) was applied to the abundance matrix of all species (dependent set) and to the environmental data matrix (independent set). Rare species were downweighted according to ter Braak, Šmilauer (2002). CCA is an appropriate ordination technique designed to describe and visualize differential habitat preferences of species via an ordination diagram. Thus, this method explores the correspondence between species distribution and environmental factors. The significance of these factors was determined using 499 unrestricted Monte Carlo permutations. Correlations between environmental variables and species-derived sample scores (inter-set correlations) were used to determine correspondence between these data sets (ter Braak, Šmilauer, 2002). These analyses were performed using the package CANOCO ver. 4.5.

RESULTS

Environmental variables that characterized the system are shown in Tab. 1. All of them showed differences between months and between diel periods (Tab. 2). Pair-wise comparisons showed that the significantly higher monthly values were for temperature during June–October, for salinity in November–December and July–August of the second year, and for dissolved oxygen during June–May and January–March of the second year. A significant pulse was reached for chlorophyll *a* in June–July and for zooplankton biomass in January (dominated by copepods) and August (dominated by decapod larvae). Diel variation shown that temperature, dissolved oxygen, and chlorophyll *a* presented significantly higher values during daylight hours, while salinity and zooplankton biomass shown the highest values at night and twilight. The inlet of the lagoon was closed during January–March and the tidal cycle was mainly diurnal with high tides at 04:00 h from March to August and at 16:00 h from September to February.

A total of 272 individuals of *Lutjanus griseus* (Linnaeus, 1758), 95 of *L. synagris* (Linnaeus, 1758), 64 of *L. analis* (Cuvier, 1828), 41 of *L. jocu* (Bloch & Schneider, 1801), seven of *L. cyanopterus* (Cuvier, 1828) and one of *Ocyurus chrysurus* (Bloch, 1791) were caught. The catalog numbers of each specimen deposited in the fish collection were: *L. griseus* (UAMI-CI 356), *L. synagris* (UAMI-CI 359), *L. analis* (UAMI-CI 352), *L. jocu* (UAMI-CI 357), *L. cyanopterus* (UAMI-CI 354) and *O. chrysurus* (UAMI-CI 361). The COI sequences of the 47 specimens selected for DNA analysis, which included at least one specimen per species (24 *L. griseus*, four *L. synagris*, 14 *L. analis*, three *L. jocu*, one *L. cyanopterus*, and one *O. chrysurus*), confirmed the identity of species. For these specimens, the overall genetic identities ranged from 99% to 100%. In addition, a DNA sequence of each species was submitted to the GenBank database under the following accession numbers: KU314762 for *L. griseus*, KU314765 for *L. synagris*, KU314763 for *L. analis*, KX119130 for *L. jocu*, KX119131 for *L. cyanopterus* and KU314764 for *O. chrysurus*.

TABLE 1 | Mean values, standard deviations (SD), and range of environmental parameters of La Mancha lagoon, recorded throughout the 19 months of sampling.

	Mean±SD	Range
Salinity	22.53±9.36	5–40
Water temperature (°C)	28.01±2.92	20.9–34.7
Dissolved oxygen (mg/L)	5.38±1.12	2.1–8.8
Chlorophyll <i>a</i> (mg/m ³)	12.88±29.30	0.05–299.4
Zooplankton (mL/m ³)	7.38±10.11	0.0–49.0
Water level (tidal effect, cm)	6.62±18.17	-23.06–61.42

TABLE 2 | Univariate two-way PERMANOVA to test the effects of months and diel period (daytime, twilight, and nighttime) on the *in situ* environmental variables studied. Significant P values are shown in bold.

Source of variance	df	MS	Pseudo-F	P (permuted)
Salinity				
Months	18	1392.00	88.03	0.001
Diel	2	69.18	4.375	0.023
Months x Diel	36	60.27	3.811	0.001
Residual	385	15.81		
Water temperature				
Months	18	126.49	56.30	0.001
Diel	2	18.66	8.306	0.001
Months x Diel	36	1.812	0.806	0.761
Residual	385	2.247		
Dissolved oxygen				
Months	18	14.301	29.455	0.001
Diel	2	2.184	4.498	0.013
Months x Diel	36	0.855	1.761	0.007
Residual	385	0.486		
Chlorophyll α				
Months	18	1765.6	3.171	0.018
Diel	2	4075.4	7.320	0.006
Months x Diel	36	1243.0	2.232	0.022
Residual	385	556.77		
Zooplankton				
Months	18	1055.4	30.798	0.001
Diel	2	151.38	4.417	0.014
Months x Diel	36	101.04	2.949	0.001
Residual	385	34.268		

The monthly variation of the relative abundances showed that the three most abundant snapper species enter the system during the warm-rainy season, which presents the longest periods of daylight (June–October) (Fig. 2). This variation showed differences among the monthly mean values (Tab. 3). According to a posteriori pair-wise comparisons, the significantly highest monthly mean values of abundance throughout the 19 months were in July of the first year and October of the second year for *L. griseus*, while for *L. synagris* these were during July and August of the second year. For *L. analis* the significantly higher monthly mean values were in September and October of the second year. In this way, a segregation pattern was observed, in which *L. griseus* occurs

mainly in June–August of the first year (when the mean salinity is less than 27) and *L. synagris* in June–August of the second year (when salinity mean is greater than 32). The main entry of *L. analis* was in September–October of the second year (mean salinity around 25) (Fig. 2A). For the three species, there was no interaction between the month and diel period factors, indicating independence of each factor. Day length was longer in June–July and rainfall peaked in August–September in both years, while during these periods mean salinity was higher in the second year (Fig. 2B).

At the diel level, only *L. griseus* showed differences in abundance among diel periods with a pulse from 16:00 to 18:00 h (Fig. 3). Pair-wise comparisons showed that the mean values during the day and twilight hours were higher than those at night. By contrast, *L. synagris* and *L. analis* did not show differences among diel periods (Tab. 3). Individuals of *L. cyanopterus* and *O. chrysurus* were captured only during twilight and night hours.

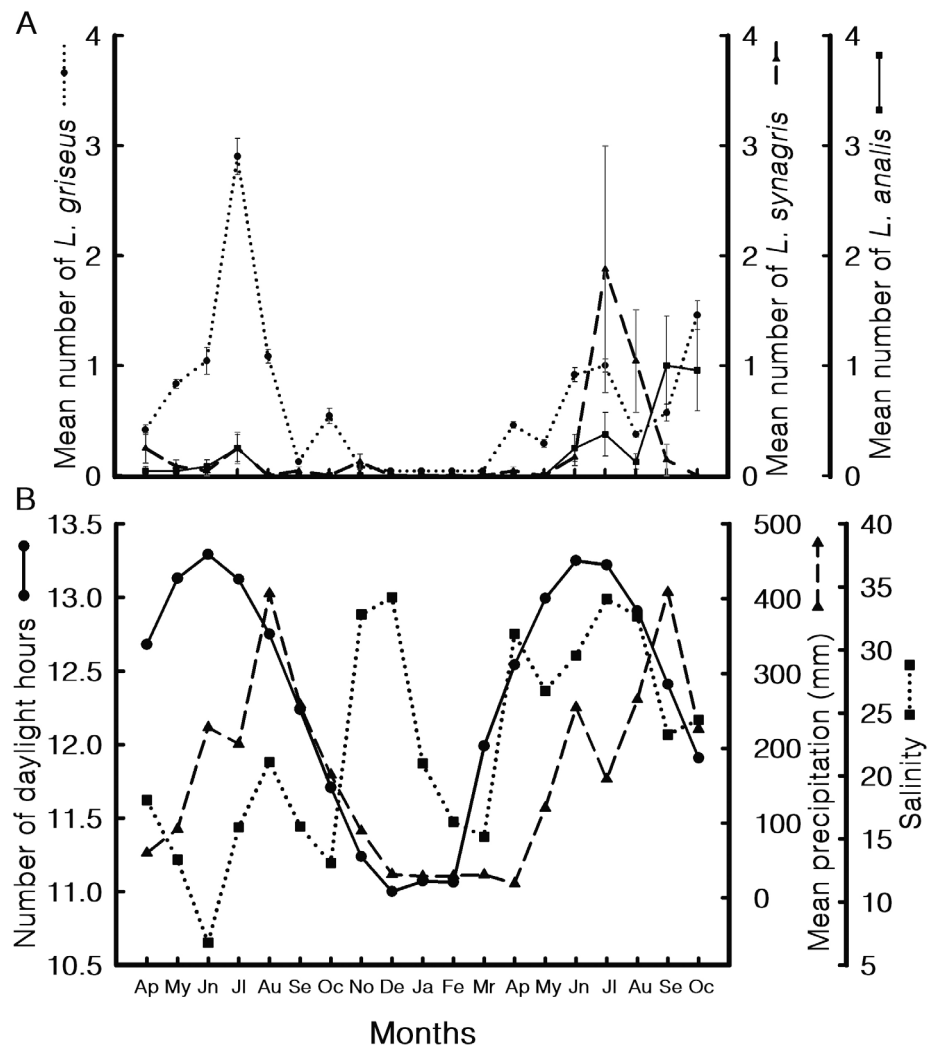


FIGURE 2 | Monthly variation of: **A.** Mean and standard error values of the three most abundant lutjanid species, and **B.** Values of the main environmental conditions studied in the study area.

TABLE 3 | Univariate two-way PERMANOVA to test the effects of months and diel period (daytime, twilight, and nighttime) on species abundance. Significant P values are shown in bold.

Source of variance	df	MS	Pseudo-F	P (permuted)
<i>Lutjanus griseus</i>				
Months	18	2.287	6.039	0.001
Diel	2	1.621	4.280	0.017
Months x Diel	36	0.512	1.352	0.132
Residual	385	0.379		
<i>Lutjanus synagris</i>				
Months	18	0.686	3.898	0.002
Diel	2	0.036	0.205	0.820
Months x Diel	36	0.221	1.255	0.210
Residual	385	0.176		
<i>Lutjanus analis</i>				
Months	18	0.376	3.159	0.004
Diel	2	0.013	0.109	0.919
Months x Diel	36	0.145	1.218	0.183
Residual	385	0.119		

The range and mean values of TL (mm) were: *L. griseus* (19–254, \bar{x} = 131.89), *L. synagris* (21–160, \bar{x} = 56.21), *L. analis* (21–172, \bar{x} = 64.85), *L. jocu* (19–254, \bar{x} = 131.89), *L. cyanopterus* (161–391, \bar{x} = 181.71), *O. chrysurus* (76.08). The three most abundant species showed significant differences in size among months (P 's = 0.001) and according to multiple comparison tests, the smaller individuals of *L. griseus* were recorded during October, while the smallest of *L. synagris* and *L. analis* were recorded in July and October. Regarding diel variation, only the length of *L. synagris* showed differences between diel periods (P = 0.001), with the larger individuals collected during the night and twilight hours.

The first two canonical axes were significant (P = 0.002 and P = 0.018) and jointly explained 88.3% in “species–environment relation” of the total cumulative variance (Fig. 4). The species–environment correlation coefficients of these two axes were 0.567 and 0.454, respectively. In the tri-plot of this analysis, the length and direction of arrows indicate the relative importance and direction that each factor has on the species ordination. As inlet state and diel period (daytime, twilight, and nighttime) are

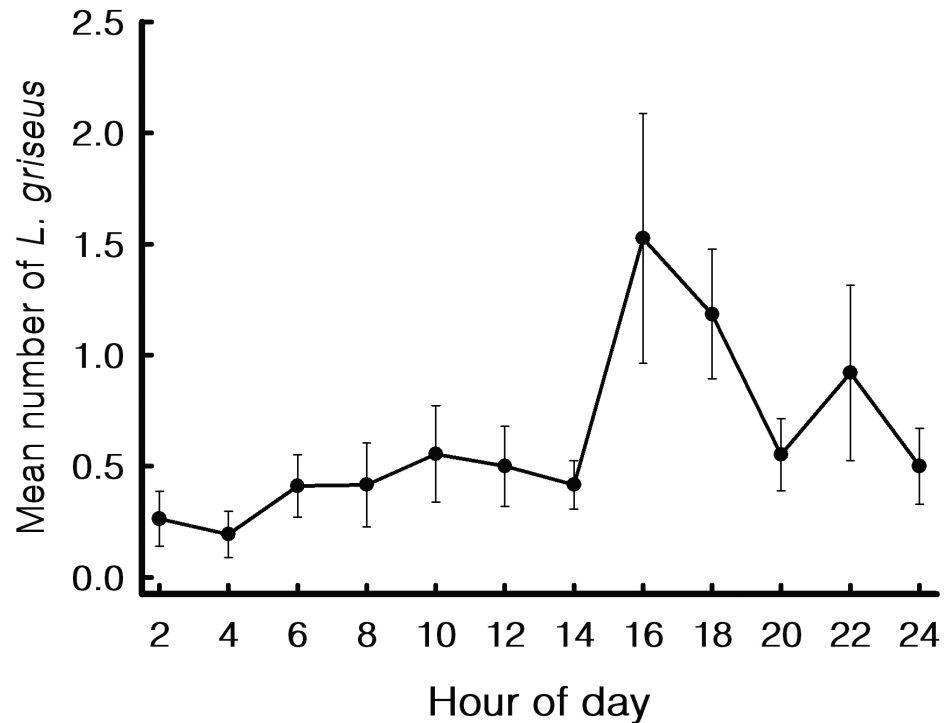


FIGURE 3 | Mean number and standard error of *Lutjanus griseus* abundance by hour of day at the inlet of La Mancha lagoon.

ordinal variables, the corresponding vector indicates, in the direction of the arrows, a preference for open inlet and day period, respectively. According to significance tests derived from CCA, only daylight hours of each diel cycle, water salinity and mean monthly rainfall were the environmental variables related to the species distribution (Tab. 4). These environmental factors also showed high values of inter-set correlations. According to ter Braak, Šmilauer (2002), the variance inflation factors (VIF) showed that the measurements are not strongly correlated.

Although zooplankton biomass, mean atmospheric temperature and water level show relatively high correlations with the first or second axis, these variables did not have a significant effect on species distribution. Furthermore, chlorophyll *a*, diel effect, water temperature and dissolved oxygen had a negligible importance on the species distribution (P 's > 0.50).

These results reveal a main ordination gradient related to daylight hours, and in the opposite direction to rainfall (Fig. 4). In this sense, the abundance of *L. analis*, *L. jocu* and *L. cyanopterus* was inversely associated with the duration of daylight and directly related to rainfall. High water levels also seem to be positively linked to the abundance of these species. Another major trend, nearly perpendicular to the first, was related to a salinity gradient, in which *L. synagris* was mainly related to higher salinities, while in the opposite way, *L. griseus* was mainly associated with relatively lower salinities (Fig. 5).

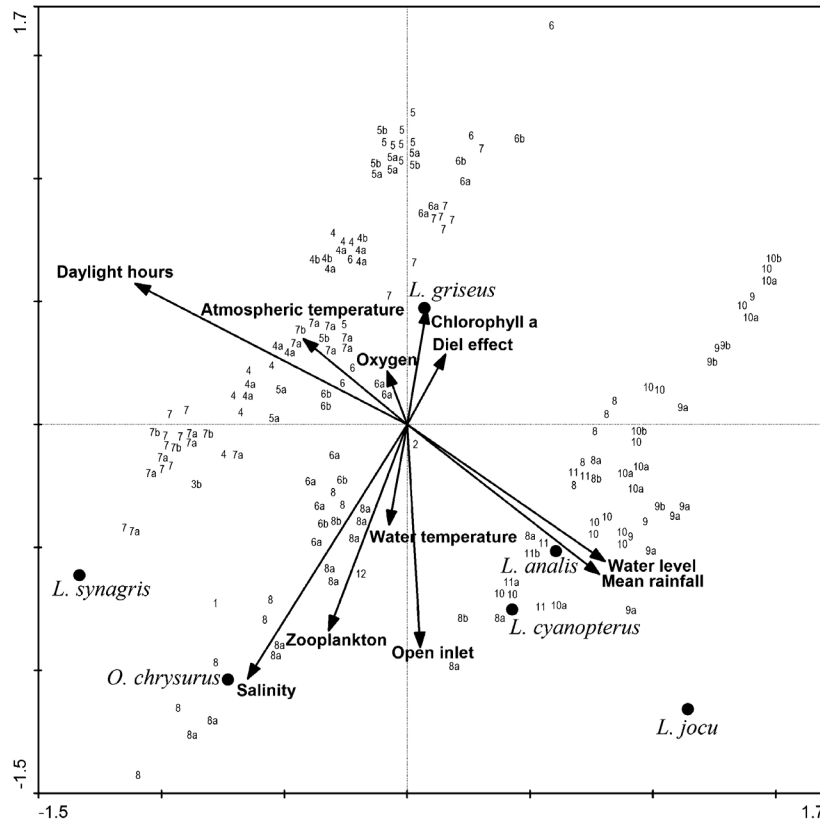


FIGURE 4 | Canonical Correspondence Analysis tri-plot of species, samples (months represented by numbers; letters “a” and “b” represent night and twilight samples, respectively, and the absence of letter represents daytime samples) and environmental variables (arrows). Diel periods were considered to be in a light-dark gradient in an ordinal scale with values of 2 (day), 1 (twilight), and 0 (night).

TABLE 4 | Inter-set correlations between environmental factors and species scores, significance of these factors (unrestricted Monte Carlo permutations), and variance inflation factors (VIF), from Canonical Correspondence Analysis. Significant P values are shown in bold.

Environmental factors	Inter-set correlations			
	Axis 1	Axis 2	P(permuted)	VIF
Daylight hours	-0.386	0.184	0.002	8.416
Salinity	-0.227	-0.332	0.002	3.294
Mean rainfall	0.273	-0.196	0.002	3.570
Zooplankton	-0.111	-0.270	0.078	1.327
Atmospheric temperature	-0.148	0.112	0.112	7.682
Day/twilight/night effect	0.054	0.091	0.530	1.185
Dissolved oxygen	-0.029	0.070	0.612	3.486
Open inlet	0.019	-0.291	0.654	2.858
Water level	0.281	-0.179	0.718	2.431
Chlorophyll a	0.027	0.151	0.78	1.271
Water temperature	-0.026	-0.132	0.828	4.734

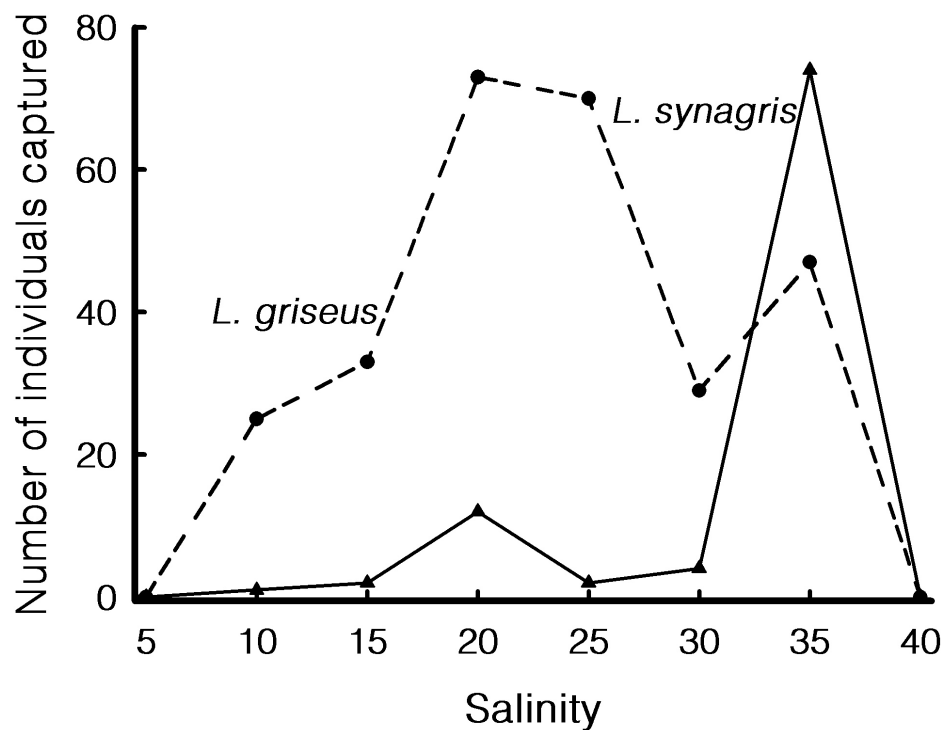


FIGURE 5 | Number of individuals captured of the two most abundant species, *Lutjanus griseus* and *L. synagris*, according to a salinity gradient.

DISCUSSION

Considering that the length at first maturity of these species varies from 225 to 520 mm (García-Cagide *et al.*, 1994), the individuals captured by us were mostly juveniles. Thus, although adults of most snapper species are associated with reefs, juvenile of several species of lutjanids are known to enter brackish waters (Anderson, 2002; Chen, 2017), as observed herein. In this way, six species of snapper were recorded, all confirmed by DNA barcoding (COI). In particular, the capture of *O. chrysurus* represents one of the few records of this species for estuarine systems in the southwestern Gulf of Mexico (Castillo-Rivera *et al.*, 2020). Thus, La Mancha lagoon is the system with the highest number of snapper species recorded in all estuarine environments of the southern Gulf of Mexico (Lara-Domínguez *et al.*, 2011), mainly due to intensive sampling used by us, both seasonal and diel.

Seasonal migration of snapper species to the lagoon occurred mainly during the summer and early autumn, when the smallest individuals of *L. griseus*, *L. synagris*, and *L. analis* were recorded (July and October). During this period, longer daytime, higher atmospheric temperature, and heavy rainfall characterized the study area. In this sense, CCA results showed that the variables with a higher seasonal incidence (daytime length, salinity, and rainfall) had a significant correlation with the abundance of the lutjanid species.

Seasonal ecological effects caused by photoperiod and temperature are often considered minimal in tropical regions (Castillo-Rivera, 2013; Souza *et al.*, 2018; Whitfield, 2021). However, although the difference in daylight length throughout the year was only 2:18 h (13:18 h in June and 11:00 h in December), this seasonal variation of the photoperiod (*i.e.*, day length) in the study area was the factor with the highest correlation value with the abundance of lutjanid species. The importance of the length of day is that it can act as a stimulus (along with changes in water temperature), for migration, reproduction and feeding. For estuarine fish, photoperiod and temperature have been shown to affect larval growth and survival (Sirois, Dodson, 2000), sexual maturity (Wang *et al.*, 2001; Guèye *et al.*, 2013), migration and residence within the estuary (Capossela *et al.*, 2013; Garcia, Pessanha, 2018). Thus, as in many species, the photoperiod can act as a cue for seasonal migration. In this sense, the migration within the lagoon of *L. analis*, *L. jocu* and *L. cyanopterus* was linked to shorter days, and the migration of *L. griseus* and *L. synagris* was associated with longer periods of daylight.

Regarding salinity, a segregation of the two most abundant species was observed along a gradient, in which *L. griseus* was more abundant at lower salinities (< 27), while this species was slightly displaced by *L. synagris* at higher salinities (> 32). Salinity has important direct effects on the distribution of fish in estuarine areas (Barletta *et al.*, 2005; Whitfield, 2021), as well as indirectly through the modification of the result of biotic interactions, such as competition between species (Pessanha, Araújo, 2003; Castillo-Rivera, Kobelkowsky, 2000; Whitfield, 2021). In relation to interspecific competition for resources, it is relatively common for eurytopic species to be weaker competitors, while stenotopic species are stronger competitors. In general, *L. griseus* has been found to possess similar or higher osmoregulatory capabilities compared to many euryhaline species (especially compared with *Lutjanus* species), and thus should be considered an euryhaline species (Castro-Aguirre *et al.*, 1999; Serrano *et al.*, 2011). In contrast, in the current study, *L. synagris* was found more regularly under euhaline conditions. In this context, the observed segregation between these species may also be related to osmoregulatory capabilities and metabolic costs. Thus, in a low salinity range, metabolic costs are significantly lower for *L. griseus* (Wuenschel *et al.*, 2005), whereas *L. synagris* will require more energy simply to maintain itself, putting it at a serious competitive disadvantage with *L. griseus*. In a high salinity range, *L. griseus* requires more energy for daily maintenance and less is available for other biological functions (Wuenschel *et al.*, 2005), whereas metabolic costs may be lower for *L. synagris* and its abundance in number may be greater than that of *L. griseus*.

Rainfall and associated runoff constitute an important environmental drive of fish abundance in tropical estuarine communities (Castillo-Rivera, 2013; Andrade *et al.*, 2015; Castillo-Rivera *et al.*, 2017; Souza *et al.*, 2018). In general, higher rainfall in tropical latitudes increases river discharge and riverine freshwater runoff, and brings an increased amount of allochthonous organic matter and dissolved nutrients to systems, leading to higher primary productivity and food availability. Thus, an increase in food resources would favor juvenile individuals entering the estuarine system for food (Castillo-Rivera *et al.*, 2010; Garcia, Pessanha, 2018).

Although zooplankton biomass and water level did not have a significant effect, these variables tended to have some importance on migration patterns. Zooplankton biomass showed a significant pulse in August and the migration of *L. synagris* and *O. chrysurus*

may be favored when this resource is abundant. Indeed, planktonic crustaceans are dominant in the diet of juveniles of these species (e.g., Sierra, 1997; Lustosa-Costa *et al.*, 2020). Similarly, flood and high tide, when the inlet is open, can be primarily used by *L. analis*, *L. cyanopterus*, and *L. jocu* to enter the estuarine system.

CCA also revealed negligible importance of environmental variables recorded *in situ*, such as water temperature, dissolved oxygen, and chlorophyll *a*, even though these variables showed differences between months and between diel periods. In the same way, the diel variability also seems to be of little importance. Thus, although the less abundant species were recorded exclusively at twilight and night hours, only *L. griseus* showed differences among diel periods (with greater abundance in the late afternoon and dusk). This may be related to migrations at dusk from their daytime shelter sites to the lagoon at night to feed, as has been observed for lutjanid species in other coastal environments (Nagelkerken *et al.*, 2000; Ley, Halliday, 2007).

Thus, the migration patterns of lutjanid species into La Mancha lagoon were mainly correlated with variables of greater seasonal influence (i.e., day length, salinity and rainfall), present during the warm-rainy period (summer and early autumn). Two of these environmental variables (day length and rainfall) have regional rather than local coverage. In this sense, the variables with regional records had the same or more importance than the variables recorded *in situ*, so the environmental processes operating at local and regional scales may act synergistically on the distribution patterns at the local scale.

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Alejandra Serrato-D az: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Supervision, Validation, Writing-original draft, Writing-review and editing.

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The authors declare no competing interests.

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