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Research Article

Feeding habits variability of *Lutjanus synagris* and *Lutjanus griseus* in the littoral of Campeche, Mexico: an approach of food web trophic interactions between two snapper species

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ABSTRACT. The study of the feeding habits variability (spatial and temporal scales) allows us to evaluate the trophic interactions between species, thus, the short and long-term effects of the removal of different species by the presence of different phenomena. In this study, we carried out stable isotope (δ^{13}C and δ^{15}N) and stomach content analyses to infer the trophic linkages between two snapper species (*Lutjanus synagris* and *Lutjanus griseus*) captured in the littoral of Campeche, Mexico. In total, 781 specimens were collected (528 *L. synagris* and 253 *L. griseus*) and based on relative importance index [%PSIRI] both snapper species consumed based on the prey-specific index of relative importance (PSIRI), Penaeidae family (PSIRI = 23.41%) was the most important species in the diet of *Lutjanus synagris*, while *Callinectes sapidus* (PSIRI = 21.45%) was the primary prey of *Lutjanus griseus*. The isotopic analyses indicated that both snapper species feed in the coastal-marine (δ^{15}N: 10.6 to 12.1‰ and δ^{13}C: -15.7 to -12.7‰); however, according to PERMANOVA, low diet similarity was found between snapper species (R = 0.07, $P < 0.01$), also, significant differences was detected in the δ^{15}N and δ^{13}C values between *L. synagris*, and *L. griseus*. Therefore, despite both snapper species presents similar trophic positions (*L. synagris*: 4.2 ± 0.2; *L. griseus*: 3.9 ± 0.1) and feeding behavior (according to SIBER = opportunistic predators), a low trophic overlap was observed, probably associated with the differential use of habitat in the coastal zone; where *L. synagris* is ecologically fed in areas of seagrass, while *L. griseus* is probably intermittent between pasture and mangrove areas, therefore, the role of each species is crucial in the dynamics of coastal-marine ecosystems as predators and potential structuring of the populations of their prey.

Keywords: *Lutjanus synagris*; *L. griseus*; stable isotope; small-scale fisheries; mixing model; coastal-marine; Gulf of Mexico

INTRODUCTION

The lutjanids fishes comprise 17 genera with 43 species of primarily reef-dwelling marine perciform fishes occurring in tropical and subtropical waters of the eastern Pacific, Indo-west Pacific, and eastern and western Atlantic oceans (Bester *et al*., 2015). The largest genus in the family, *Lutjanus*, has 68 valid species (Froese & Pauly, 2010), of which two snapper species (*Lutjanus synagris* and *L. griseus*) are the most representative in the Gulf of Mexico with high commercial value due to their high market demand. In the Gulf of Mexico, snapper landings accounted for close to 26 t yr^{-1}, with a commercial value of around USD 35,000 yr^{-1}, highlighting the economic importance of these species (CONAPESCA, 2019).

The littoral of Campeche constitutes suitable habitat for *L. synagris* and *L. griseus*, reporting high catch rates. In recent years, commercial snapper landings in the Gulf of Mexico reached maximum levels of 35 to

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40 t between 2016 and 2017. In this sense, the volume of landings increased by over 46% in the last decade (CONAPESCA, 2019). Therefore, one research effort has focused on the study of biodiversity and feeding habits variability in the trophic networks (Pimm, 2002; De Ruiter *et al.*, 2005). These studies on trophic interaction among species provide guidelines for identifying potential consequences of natural perturbations and management decisions on a coastal fishery system and the conservation of ecosystems.

The analyses of the feeding habits variability between two or more predators generate information to understand the interspecific relationships among different species in the community and the impact of the overexploitation of a resource or the presence of natural phenomena the ecosystems (Kareiva & Levin, 2003). For example, in other regions, lutjanids fishes are reported as species that capture, store, and transfer energy in the food-web complexity (Garrido *et al.*, 2008; Vaslet *et al.*, 2012). The importance of the lutjanids in the food web lies in the high number of interactions than they maintain with their prey. Specific studies related a diet of lutjanids inhabiting in the Gulf of Mexico have evidenced that *L. synagris* and *L. griseus* are nocturnal generalist predators (Rivera-Arriaga, 1993; Sámano-Zapata *et al*., 1998; Guevara *et al*., 2007), with differences in their trophic interactions relate to the ontogenetic condition (Sierra, 1996; Guevara *et al*., 2007; Bester *et al*., 2015). However, few studies have been carried out on the feeding habits variability of *L. synagris* and *L. griseus* in the Yucatan Peninsula. Therefore, the interactions of both snapper species in their natural habitat and the potential ecological impacts by overfishing that may decrease populations of these fishes remain unknown.

The combined use of stomach contents and stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) analyses have provided a taxonomic resolution of prey consumed by predators and habitat use, respectively (Maruyama *et al*., 2001; McIntyre & Flecker, 2006). $\delta^{13}C$ has been useful in providing information on autotrophic sources and $\delta^{15}N$ as an indicator of trophic position within a local or regional food web. Additionally, standard deviation evidence that the variety of food resources used by an organism over a long period (Post, 2002; Bearhop *et al*., 2004). Therefore, these techniques provide knowledge about niche width, trophic overlap, and trophic position at a spatial and temporal level.

The objective of the present study was to establish the feeding habits variability of *L. synagris* and *L. griseus* based on stomach contents and stable isotope ($\delta^{15}N$ and $\delta^{13}C$) analyses to describe possible variations among sex and fishing locations. This information could help describe the trophic interactions of two snapper species that are more relevant to ecosystem processes in the southern Gulf of Mexico for developing futures stages and adaptation options, which is considered key to the management of fisheries at the ecosystem level.

MATERIALS AND METHODS

Sample collection

Sampling was carried out at three different locations of Campeche, Mexico (Fig. 1). The first location is Champoton, which is characterized by sandy beaches and limos rich in organic matter product of the trawling of the nearby rivers; the second location in San Francisco de Campeche and is characterized by a transition of terrigenous materials and calcareous sediments; and the third location is Seybaplaya, which is characterized by rocky beaches and sands being a transition zone between Champoton and San Francisco de Campeche (Rivera-Arriaga *et al*., 2012).

In the three fishing locations, snapper species were sampled monthly during three climatic seasons in 2015 (12 months): dry (D) from February to May; rainy season (R) from June to September and wind/winter season (W) from October to January (Yáñez-Arancibia & Day, 1982). Samples were collected from the small-scale fishery (fishing boats were 7 m long with 75 hp outboard motors), which operates year-round. The fishing maneuvers are carried out by two or more fishermen by boat, with two sets for four hours each at night. The fishing gear consists of 200 m long monofilament gillnets of nylon, 75 meshes deep, and 7.5-8.8 cm mesh size. Once snappers were identified, 30 individuals were collected in each fishing location (781 ind) and kept frozen (-20ºC) until analysis in the Trophic Ecology Laboratory at the Instituto de Ecología, Pesquerías y Oceanografía del Golfo de México (EPOMEX) in Campeche, Mexico.

In the laboratory, fork length (FL) in cm and weight (g) of each specimen were recorded. We collected stomachs and dorsal white muscle tissue (5 g) to obtain information on recently consumed food (stomach contents = days) and assimilated food (white muscle tissue = months). The muscle tissue of the main prey items and stomach contents analysis was also collected in the same area and time as the snapper samples.

For stomach content analyses, we determined the percentage of stomach-filling based on Stillwell & Kohler (1982) and thawed the stomach contents and categorized the digestive state of the prey species according to the digestive levels described by Galván-Magaña (1988). The identification of fishes was based on descriptions given by Castro-Aguirre (1999), Fischer

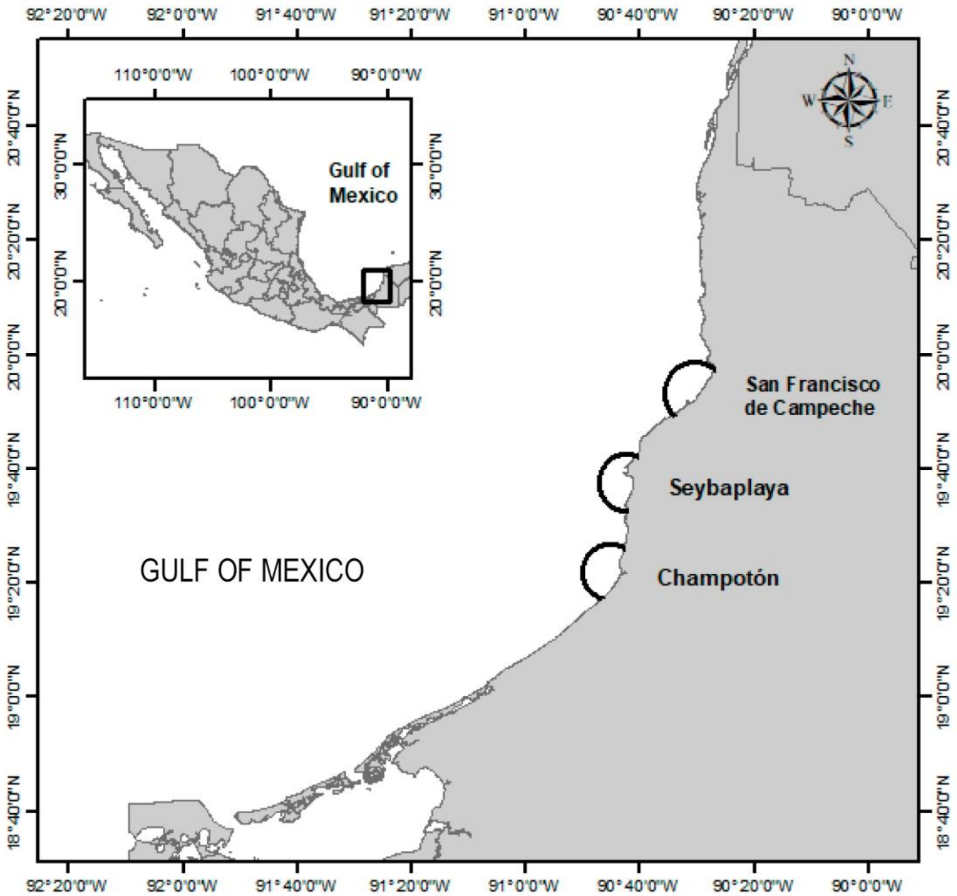

Figure 1. Map showing the study area. The semicircles indicate the extent of the fishing area of the artisanal Mexican fleet for each location.

(1978), Reséndez (1981a,b), and Christensen *et al*., (1992). Crustaceans were identified based on Fisher (1978), and Pérez & Kensley (1997). Once the prey items were identified, we collected the dorsal white muscle of those prey species digestion states 1 for the isotopic mixing model analysis.

For isotopic analyses ($\delta^{13}C$ & $\delta^{15}N$) snapper species and prey, tissues were placed in vials fitted and: 1) dried for 48 h in a Thermo Scientific forced convection oven (OMS 60) at 55°C to eliminate moisture, then 2) dry samples were ground in an agate mortar, and sub-sample (1 mg) were weighed and stored in tin capsules (8×5 mm) in a Radwag analytical microbalance. The $\delta^{13}C$ and $\delta^{15}N$ compositions were determined at the Mass Spectrometry Laboratory (LESMA) of the Centro Interdisciplinario de Ciencias Marinas (CICIMAR) at Instituto Politécnico Nacional (IPN), Mexico, using an Isotope Ratio Mass Spectrometer (Thermo Scientific Delta V Plus) with a precision of 0.1‰.

Stable isotope values (δ) were calculated using the formula proposed by Park & Epstein (1961):

$$\delta^{15}\mathrm{N} \text{ or } \delta^{13}\mathrm{C}\ (‰) = \left[\left(\frac{Rsample}{Rstandard}\right) - 1\right] \times 1000$$

where, *Rsample* is the isotopic ratio of the heaviest stable isotope relative to the lightest ($\delta^{13}C/\delta^{12}C$ or $\delta^{15}N/\delta^{14}N$ respectively) in the sample and *Rstandard* is the value of the isotopic ratio for a known standard: Vienna Pee Dee Belemnite (VPDB) for carbon and atmospheric N^2 for nitrogen.

Data analysis

Cumulative curves (CV's) and C:N ratio

For stomach contents analysis, cumulative prey curves (Ferry & Cailliet, 1996) were generated in the Estimates program (Colwell, 2006) based on Hoffman (1979) to determine whether the number of stomachs analyzed was adequate to represent the trophic spectrum. Also, the coefficient of variation was calculated as an indicator of diet variability, with a CV < 0.05 whether the number of stomachs analyzed was adequate to represent the trophic spectrum of *Lutjanus synagris* and *L. griseus* (Steel & Torrie, 1992). For stable isotopes analysis, the C:N ratios were used to determine whether samples had a low lipid content, assuming that values between 2.5 and 3.5 indicate less than 5% of lipid concentration in the tissue, which does not alter the isotopic signal (Post *et al*., 2007) significantly.

Estimates of feeding habits variability

To detect intraspecific diet variation, we sorted *L. synagris and L. griseus* data by sex, location (San Francisco de Campeche, Seybaplaya, and Champotón), climatic seasons (dry, rainy, and wind/winter) and months. For stable isotopes, we sorted by sex, location, and climatic season. For stomach content analysis, the prey-specific index of relative importance (%PSIRI) was calculated with the formula: %PSIRI = (%PNi + PWi) × %FO, where %FO is the percent frequency of occurrence (the number of stomachs containing prey i divided by the total number of stomachs, n), and %PNi and %PWi are the prey-specific abundances by number or weight, respectively (Brown *et al*., 2012).

For stable isotopes analysis, we estimated the contribution of each prey type to the diet by using the Bayesian mixing model (MixSiar v.1.0.4), which takes into account isotopic errors by using as inputs all $\delta^{13}C$ and $\delta^{15}N$ values of predators and the mean ± standard deviation (SD) of $\delta^{13}C$ and $\delta^{15}N$ values of the prey types. For this analysis, we followed the criteria established by Phillip *et al.* (2003), where isotopic values of at less six main prey species (which contributed >90% of the diet) were used to make the Bayesian mixing model. This analysis's results were reported as the distribution of percentages ranging from 0 to 99%, where the minimum and maximum values are used to determine the importance of food sources or prey types to the diet (Madigan *et al*., 2012).

Estimates of niche widths and trophic overlap

Based on stomach contents, the trophic niche width was evaluated using Levin’s standardized index, ‘‘Bi’’ (Krebs, 1999), which ranges from 0 to 1, with low values (<0.6) indicating the diet was dominated by few prey items (specialist predator), and high values (>0.6) indicating a generalist predator (Labropoulou & Eleftheriou, 1997). The feeding strategy was also evaluated using the graphs of Costello (1990) modified by Amundsen *et al.* (1996), containing the prey specific abundance (%PNi) and frequency of occurrence (%FO) plotted with points for prey categories (Brown *et al*., 2012). According to Amundsen *et al.* (1996), four feeding strategies were described: 1) specialize in individual prey types, 2) more generalized diet and higher within-individual variation in diet breadth, 3) specialization on a single prey type while occasionally consuming other prey, and 4) mixed feeding strategy in which some individuals have a specialized diet and other fish have a more generalized feeding strategy.

For the intraspecific trophic overlap (sex, location, climatic season, and months) and between *L. synagris* and *L. griseus* (interspecific comparison), a non-parametric multivariate analysis of variance permutation (PERMANOVA) was carried out. This analysis was applied with the Adonis function of the vegan package (Oksanen *et al*., 2015) in R (R Core Team, 2014). Subsequently, with the PRIMER v.6. software, a similarity percentage analysis (SIMPER) was applied to determine the trophic items responsible for the differences in the diets for each category analyzed. This analysis calculates the average of the differences between species and records each category's contribution to this inequality (Clarke & Warwick, 1994). Monthly average sea surface temperature (SST) data from 2015 was used to analyze the possible variations of *L. griseus* and *L. synagris* diets associated with changes in SST. This data was obtained by the NOAA and the NCDC (National Climatic Data Center-https://www.ncdc.noaa.gov/data-access).

Based on stable isotopes analysis, the SIBER method (Euclidean distance) was used for calculating the ellipse-based metrics of trophic overlap and isotopic niche widths for *L. synagris* and *L. griseus* (Jackson, 2011) available in R (R Core Team, 2014). For isotopic niche width (NW), values <1 reflect a broad trophic niche; for trophic overlap, values >1 indicate considerable overlap between species (Bearhop *et al*., 2004). Also, our stable isotope data failed the assumptions of normality (Shapiro-Wilk test) and homogeneity of variance (Levene's test); therefore, a Mann-Whitney test was used to detect intraspecific variation between sex and Kruskal-Wallis test was used to detect interspecific variation (location and season). Statistical analyses were performed in Statistica v.8.0, with the significance level set to $P < 0.05$.

Estimates of trophic level and position

The trophic level (TL) based on stomach content was calculated using the equation proposed by Christensen & Pauly (1992);

$$\mathrm{TL} = 1 + (\Sigma_{j=1}^{n} \mathrm{DC}_{ji})(\mathrm{TL}_{j})$$

where, DC_{ji}: diet composition in weight, in terms of the prey proportion (j) in the predator’s diet (i); TL_j: trophic position of prey species j; and n is the number of prey groups in the diet. In this equation, trophic position values for fish species were obtained from FishBase (Froese & Pauly, 2010), and those for cephalopods, crustaceans’ species were obtained from Cortés (1999).

We calculated the trophic position (TP) for *L. synagris* and *L. griseus* using isotope values with the equation proposed by Post (2002). We select prey species which, according to Post (2002), should be present in the area and in the diet of the predator; its TP value should preferably be higher than 2.

Therefore, the $\delta^{15}N_{base}$ (2.9‰) used for the trophic position at the base of the food web was the pink shrimp (*Farfantepenaeus duorarum*), a crustacean captured in the littoral of Campeche and present in the diet of *L. synagris* and *L. griseus*.

For *F. duorarum* was assigned a trophic position of 2.8 (calculated in the present study), and for all trophic estimations, enrichment (Δ) in $\delta^{15}N$ was assumed to be 3.0‰ (Rooker *et al*., 2006) per trophic level:

$$TP = \lambda + \left[\frac{\delta^{15}N_{predator} - \delta^{15}N_{Base}}{\Delta_n}\right]$$

where, λ: trophic position for the base (2.8 for *F. duorarum*), Δ: theoretical value for ^{15}N-enrichment per trophic level (3.0; according to Rooker *et al*., 2006), $\delta^{15}N_{Predator}$: $\delta^{15}N$ value of each *L. synagris* and *L. griseus*, $\delta^{15}N_{Base}$: $\delta^{15}N$ value for *F. duorarum.*

RESULTS

A total of 781 specimens (528 *Lutjanus synagris* and 253 *L. griseus*) were sampled, ranging from 20.0 to 40.0 cm FL with a mean size of 29.5 ± 4.1 cm for both snapper species. No significant difference was found in size classes between *L. synagris* and *L. griseus* (U = 10.00, $P > 0.05$); thus, all specimens were considered adults, and no comparison was made between size classes.

A total of 491 individuals (Table 1) contained food (359 for *L. synagris* and 124 for *L. griseus*), where Champoton was the location with more stomachs collected (40.6%), followed by Seybaplaya (34.3%) and San Francisco de Campeche (25.0%). *L. synagris* present a higher number of stomachs with content in D ($n = 102$) and N season ($n = 198$) than *L. griseus* (n =12 and 15, respectively); however, in R season both species present a similar number of stomachs with content (n = 75 and 60, respectively). For the isotopic composition, 59 muscle samples of *L. synagris* and 49 muscle samples of *L. griseus* were analyzed.

Cumulative curves (CV's), C:N ratio, digestive state of prey species and percentage of filling

The prey species (items) accumulation curve showed that the number of stomachs analyzed was enough to characterize the diet of *L. synagris* and *L. griseus* (Fig. 2), with CV's less than 0.05 for all categories (*i.e.*, sexes, size-classes, location and season). The C:N ratio for muscle presented an average value of 3.2 (Table 1), which corresponds to low lipid concen-trations in the tissue (Post *et al*., 2007). Thus, the effect of lipid content on the $\delta^{13}C$ values in this study was considered negligible, and the chemical extraction of lipids before isotopic analysis or an arithmetic correction was not required. The prey's state of digestion was mostly in state 2 (40%) and 3 (30%) for both snapper species, whereas the percentage of filling was mostly in states 1 and 2 (Table 2).

Trophic spectrum and isotopic composition

The trophic spectrum of *L. synagris* comprised one bivalve, one gastropod, one cephalopod, 34 crustaceans, and 22 fish species (Table 3). $\delta^{15}N$ values ranged from 10.6 to 12.1‰ with an average of 11.5 ± 0.5‰, while $\delta^{13}C$ values ranged from -15.7 to -12.7‰ with an average of -14.7 ± 0.9‰ (Table 4). According to %PSIRI (Fig. 3), the most important prey items were *Penaeus* spp. (23.4%), fish (23%) and *Callinectes sapidus* (13.4 %).

The trophic spectrum of *L. griseus* comprised one gastropod, one cephalopod, 14 crustacean, and 16 fish species (Table 3). $\delta^{15}N$ values ranged from 9.8 to 12.9‰, with an average of 10.9 ± 1.0‰. $\delta^{13}C$ values ranged from -13.8 to -11.4‰, with an average of -12.9 ± 0.8‰ (Table 4). According to %PSIRI (Fig. 3), the most important prey items were *Callinectes sapidus* (21.5%), fish (20.5%), *Penaeus* spp. (15%), and *Farfantepenaeus duorarum* (6.1%) present in most months.

Intraspecific variation for *L. synagris* and *L. griseus*

For *L. synagris*, PERMANOVA indicated high similarity in diets between sex ($P > 0.05$), but low similarity between fishing locations ($P < 0.05$) and climatic seasons ($P < 0.05$). According to SIMPER, the trophic group that contributed to the dissimilarity among fishing locations (specifically between San Francisco de Campeche *vs.* Seybaplaya and Champoton) was the Penaeidae family (relative contribution = 14.7 and 15.5%, respectively); whereas, among climatic seasons (specifically between N *vs.* R and D) was the Penaeidae family (relative contribution = 20.3 and 20.6%, respectively) and *Callinectes* spp. (relative contribution = 17.2 and 15.8%, respectively). Based on stable isotopes, no significant differences were found between sex for $\delta^{15}N$ (U = 22.00, $P > 0.05$, and $\delta^{13}C$ (U = 4.50, $P > 0.05$), and among climatic seasons for $\delta^{13}C$ (H = 2.94, $P > 0.05$), but significant differences were found for $\delta^{15}N$ (H = 8.68, $P < 0.05$). Also, significant differences were found among locations for $\delta^{13}C$ (H = 12.68, $P < 0.05$) and $\delta^{15}N$ (H = 9.12, $P < 0.05$).

Table 1. *Lutjanus synagris* and *L. griseus* analyzed stomachs in different locations and climatic seasons. W: wind/winter season; D: dry, R: rainy season, TS: total stomachs, ES: empty stomach, SC: stomach with content and C:N = C:N ratio.

Species	Location	Season	(TS)	ES	SC	C:N
L. synagris	Champoton	W	(147)	115	32	2.7
		D	(68)	53	15	2.5
		R	(65)	35	30	2.8
	San Francisco de Campeche	W	(55)	32	23	2.9
		D	(47)	34	13	2.7
		R	(47)	28	19	2.8
	Seybaplaya	W	(63)	46	17	2.8
		D	(29)	22	7	2.7
		R	(44)	20	24	2.6
L. griseus	Champoton	W	(26)	12	14	2.8
		D	(77)	65	12	2.8
		R	(89)	36	53	2.7
	San Francisco de Campeche	W	(17)	7	10	2.8
		D	(31)	23	8	2.7
		R	(32)	14	18	2.8
	Seybaplaya	W	(15)	7	8	2.7
		D	(27)	21	6	2.6
		R	(33)	12	21	2.5

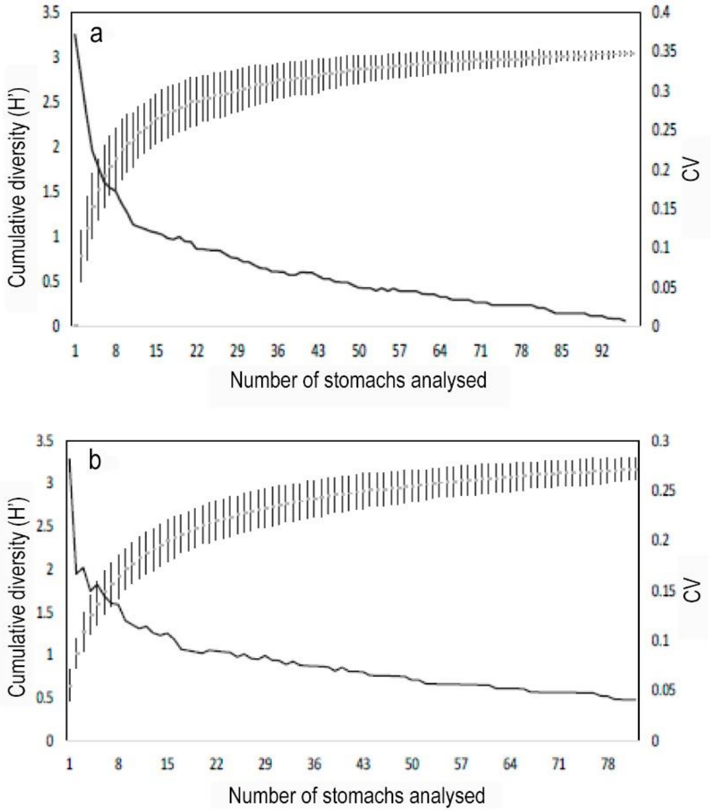

Figure 2. Diversity cumulative curve of prey species of a) *Lutjanus griseus* and b) *L. synagris* in the littorals of Campeche, Mexico.

For *L. griseus*, PERMANOVA indicated high similarity in diets between sex ($P > 0.05$), but between fishing locations ($P < 0.05$) and climatic seasons ($P < 0.05$) a similarity of means was determined. Based on stable isotopes, no significant differences were found between sex [$\delta^{15}N$ (U = 34.00, $P > 0.05$) and $\delta^{13}C$ (U =

Table 2. Number of prey groups recorded in the digestive stages ("DS" from 1 to 4) present in *Lutjnaus synagris* and *L. griseus* (separated by "/") in the different location and season. F: fish, Cr: crustaceans, Ot: others (algae, organic matter, echinoderms); W: wind/winter season; D: dry; A: rainy season.

Species	Location	Season	Prey species	Digestive state			
L. synagris / L. griseus				DS 1	DS 2	DS 3	DS 4
	Champoton	W	F	1/0	2/2	7/1	13/2
			Cr	4/0	36/2	50/4	19/0
			Ot	0/0	0/0	1/0	11/0
		D	F	1/0	4/1	5/0	8/0
			Cr	0/0	17/2	33/0	3/0
			Ot	0/0	0/1	1/1	0/2
		R	F	1/0	2/0	7/1	10/0
			Cr	1/0	9/2	16/2	6/1
			Ot	0/0	0/2	2/3	2/3
	San Francisco de Campeche	W	F	0/1	0/0	1/0	4/3
			Cr	0/0	2/4	5/1	1/0
			Ot	0/0	1/0	1/0	7/2
		D	F	0/1	7/5	5/5	7/0
			Cr	0/4	15/5	4/1	0/0
			Ot	0/0	1/0	3/0	0/0
		R	F	0/0	5/3	7/3	13/2
			Cr	0/0	7/0	11/2	1/0
			Ot	0/0	2/0	1/2	7/2
	Seybaplaya	W	F	0/0	4/2	2/1	8/1
			Cr	0/0	29/1	14/4	1/0
			Ot	0/0	0/0	0/0	0/0
		D	F	1/0	2/3	1/2	14/0
			Cr	3/1	21/4	38/0	7/0
			Ot	1/0	0/1	0/0	0/0
		R	F	0/0	0/2	1/1	7/3
			Cr	0/0	10/10	17/7	0/1
			Ot	0/0	0/0	3/0	0/0

18.00, $P > 0.05$)], climatic seasons [$\delta^{15}N$ (H = 0.58, $P > 0.05$) and $\delta^{13}C$ (H = 4.93, $P > 0.05$)], and location for $\delta^{13}C$ (H = 4.81, $P > 0.05$); however, significant diffe-rences were found for $\delta^{15}N$ (H = 14.22, $P < 0.05$).

The interspecific variation between *L. synagris* and *L. griseus* (niche width, trophic overlap, and trophic position)

For *L. synagris and L. griseus*, niche width (*Bi*) values were <0.6 for all categories (Table 5), while Costello's graphs show that both lutjanids species specialize on individual prey types (feeding strategies I; Fig. 4). According to SIBER, *L. synagris* in W present generalist behavior (NW > 1) while in D and R present specialist behavior NW < 1; (Fig. 5). For *L. griseus*, SIBER indicated a generalist behavior in San Francisco de Campeche (NW > 1), but a specialist behavior in Seybaplaya and Champoton (NW < 1; Fig. 6).

For the trophic overlap, PERMANOVA indicated low similarity between *L. synagris* and *L. griseus* in abundance ($P < 0.05$) among months. According to SIMPER, the trophic groups that contributed to the similarity in abundance were *Penaeidae* (15.7%), *Callinectes* spp. (13.7%), and *Portunus* spp. (8.7%). Based on isotopes stables, no significant differences were found between *L. synagris* and *L. griseus* for $\delta^{15}N$ (U = 34.00, $P > 0.05$) and $\delta^{13}C$ (U = 18.00, $P > 0.05$). SIBER analysis confirms a low trophic overlap in general (0.14; Fig. 7).

The trophic level for *L. synagris* obtained from stomach contents was 3.7 ± 0.3, and the trophic position based on stable isotopes was 4.2 ± 0.2, while for *L. griseus*, the trophic level obtained from stomach contents was 3.8 ± 0.1 and the trophic position based on stable isotopes was 3.9 ± 0.1 (Table 5).

Preys contribution for *L. synagris* and *L. griseus*

The prey's values ($\delta^{13}C$) in San Francisco de Campeche were recorded from -11.2 to -13.4 and $\delta^{15}N$ from 3.8 to

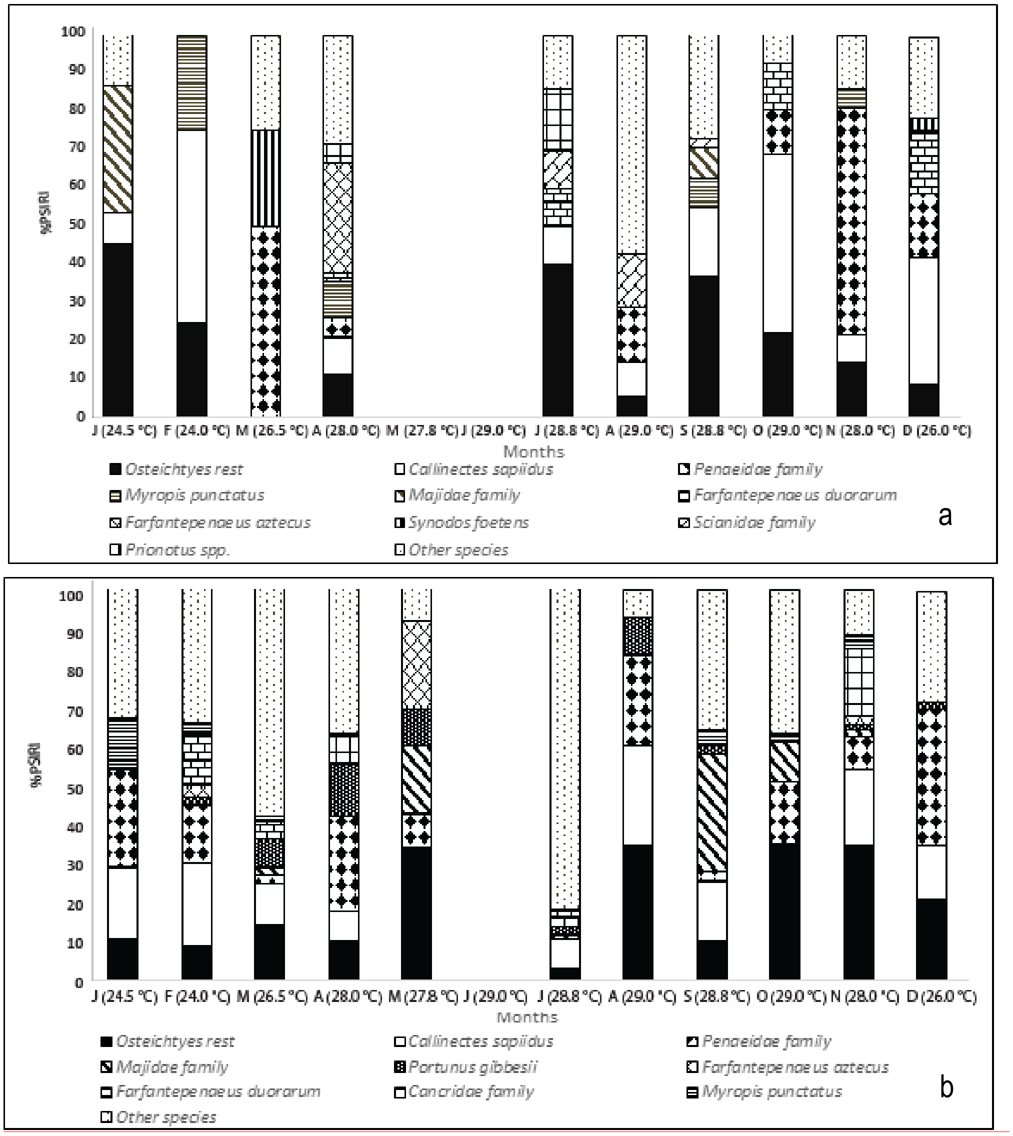

Figure 3. Diets contributions (%PSIRI) and sea surface temperature "SST" (National Climatic Data Center) by months for a) *Lutjanus griseus* and b) *L. synagris* in the littoral of Campeche, Mexico.

9.0. In Seybaplaya, δ^{13}C from -10.4 to -16.4 and δ^{15}N from 5.8 to 8.1, Champoton δ^{13}C from -11.8 to -16.7, and δ^{15}N from 4.8 to 10.1 (Table 6). The mixing models (MixSiar) indicated that the most important trophic groups of *L. synagris* were: *Farfantepenaeus duorarum* (10-63%), *Squilla empusa* (0-50%) and *Callinectes* spp. (0-40%), whereas, for *L. griseus* were *Farfantepenaeus duorarum* (0-63%), *Callinectes* spp. (0-55%) and *Squilla empusa* (0-60).

DISCUSSION

The individuals analyzed were considered adults due to the recorded sizes since snappers generally reach sexual maturity of approximately 23 cm (Brulé *et al.*, 2004). In both species, the filling percentage was low (30%) and with a medium degree of digestion, as has been reported for other species of the genus (*Lutjanus peru*; Santamaría-Miranda *et al.*, 2003). It was related due to the carnivorous fish have an evolved stomach that secretes acids to quickly digest bone, meat, and scales of ingested prey, it has a much shorter intestine than herbivores, causing digestion to be faster (Lagler *et al.*, 1984). The presence of a high number of stomachs with low content has made it difficult for years to study the diet in different species; however, in the present study, the analysis of stable isotope analysis helped understand the feeding habits variability of both snapper species.

Table 3. The trophic spectrum of *Lutjanus synagris* and *L. griseus*, expressed in percentages values of the prey-specific abundances by number (%PNi), prey-specific abundances by weight (%PWi), and frequency of occurrence (%FO) and prey-specific index of relative importance (%PSIRI); UOM: unidentified organic matter.

Phylum	Species	*L. synagris*				*L. griseus*			
		%PNi	%PWi	%FO	%PSIRI	%PNi	%PWi	%FO	%PSIRI
Antophyta	*Thalassia testudinum*	-	-	-	-	38.8	9	3	0.7
Mollusca	*Octopus maya*	56.6	62.4	0.8	0.5	100	100	1	1
Arthropoda	*Squilla empusa*	53.3	79.5	0.8	0.5	-	-	-	-
	Penaeus spp.	77.6	67.2	32.3	23.4	94.2	92.8	13.2	15
	Farfantepenaeus duorarum	71.1	72.9	3.9	2.8	95.8	89.1	6.1	6.4
	Farfantepenaeus aztecus	70	60.2	1.4	0.9	100	100	6.1	6.1
	Trachypenaeus constrictus	94.2	92	1.1	1	-	-	-	-
	Penaeus vannamei	75	57.1	0.3	0.1	-	-	-	-
	Litopenaeus setiferus	61.6	59.7	1.4	0.8	-	-	-	-
	Sicyonia typica	30.5	8.6	0.5	0.1	-	-	-	-
	Tethraxantus spp.	100	100	0.3	0.3	-	-	-	-
	Pagurus bernhardus	100	100	0.5	0.5	-	-	-	-
	Calappa ocellata	50	68.6	0.5	0.3	-	-	-	-
	Speocarcinus lobatus	9	4.1	0.3	0.1	-	-	-	-
	Menipe mercenaria	61.5	59.3	1.4	0.8	-	-	-	-
	Callinectes spp.	17.7	17.4	10.2	12	6.4	5.6	0.9	2.5
	Callinectes bocourti	60.1	60.5	4.2	2.5	-	-	-	-
	Callinectes sapidus	59.4	61.5	22.1	13.4	86	82.1	25.5	21.5
	Callinectes danae	4.6	32.6	0.5	0.1	33.3	5.5	1	0.2
	Callinectes similis	100	100	0.8	0.8	-	-	-	-
	Callinectes rathbunae	52.3	50.8	0.8	0.4	-	-	-	-
	Portunus spinnimanus	49.4	53.8	2.5	1.3	-	-	-	-
	Portunus gibbesii	52.8	53.2	7.8	4.1	83.3	84.6	3	3.5
	Pilumnus dasypodus	75	58	0.5	0.3	-	-	-	-
	Myropsis quinquespinosa	41.1	36.1	3	1.1	-	-	-	-
	Hepatus epheliticus	48.1	57.5	3	1.6	-	-	-	-
Chordata	*Ariopsis felis*	33.3	52.3	0.2	0.1	-	-	-	-
	Bagre marinus	50	56.1	0.5	0.3	-	-	-	-
	Achirus achirus	100	100	0.2	0.2	-	-	-	-
	Opsanus beta	100	100	0.5	0.5	75	82	2	2.5
	Harengula jaguana	50	84	0.2	0.1	66.6	52.8	2	1.2
	Symphurus plagiusa	25	30.7	0.2	0.1	-	-	-	-
	Anchoa spp.	0.6	0.4	0.5	0.1	-	-	-	-
	Eucinostomus gula	50	65.8	0.5	0.3	-	-	-	-
	Ocyurus chrysurus	25	9.3	0.2	0.1	-	-	-	-
	Citharichthys macrops	-	-	-	-	50	60	1	0.5
	Monacanthus ciliatus	100	100	0.5	0.5	50	68.4	1	1
	Myrophis punctatus	57.5	58.2	4.2	2.4	85	89	5.1	6
	Synodus foetens	-	-	-	-	75	67.9	2	2
	Hippocampus erectus	50	92.3	0.2	0.2	-	-	-	-
	Syngnathus louisianae	50	14.5	0.2	0.1	50	31.5	1	0.5
	Starksia spp.	50	8.9	0.2	0.1	-	-	-	-
	Diplectrum formosum	25	76	0.3	0.1	-	-	-	-
	Odontoscion dentex	50	77.4	0.3	0.2	100	100	1	1
	Menticirrhus saxatilis	-	-	-	-	100	100	2	2
	Lagodon rhomboides	-	-	-	-	100	100	1	1
	Archosargus rhomboidalis	-	-	-	-	100	100	1	1
	Scarus spp.	-	-	-	-	25	65	1	0.4
	Prionotus spp.	57.5	48.9	1.6	0.9	83.3	90.6	3	2.6
	Urobatis jamaicensis	50	98.1	0.2	0.2	-	-	-	-
Other groups	Bivalves	61.1	51.8	0.8	0.4	-	-	-	-
	Gastropods	100	100	0.2	0.2	100	100	1	1
	Fish	25	72.8	81.3	23	83.7	90.6	23.4	20.4
UOM	-	50	9	0.2	0.1	-	-	-	-

Despite the high number of stomachs with low content, the trophic groups reported in *Lutjanus synagris* (33 species of crustaceans, 22 fish and mollusks) and *L. griseus* (13 species of crustaceans, 16

Table 4. Isotopic composition (δ^{13}C and δ^{15}N presented in ‰) of *Lutjanus synagris* and *L. griseu*s. W: wind/winter season, D: dry, R: rainy season, SD: standard deviation.

Specie	Location	Season	n	Length (mean ± SD)	δ^{13}C (‰) ± SD	δ^{15}N (‰) ± SD
L. synagris	General		59	29.6 ± 2.9	-14.7 ± 0.9	11.5 ± 0.5
	San Francisco de Campeche	W	5	31.9 ± 3.2	-12.7 ± 1.1	10.6 ± 0.5
		D	6	29.6 ± 3.0	-14.5 ± 1.0	11.3 ± 0.5
		R	7	30.0 ± 2.9	-14.3 ± 1.0	11.4 ± 0.6
	Seybaplaya	W	7	28.9 ± 2.1	-15.0 ± 1.1	11.2 ± 0.5
		D	7	25.4 ± 3. 1	-15.2 ± 1.0	12.1 ± 0.5
		R	5	28.9 ± 2.1	-14.6 ± 1.0	11.2 ± 1.2
	Champoton	W	8	30.2 ± 2.9	-15.7 ± 1.1	11.8 ± 0.6
		D	6	30.1 ± 2.9	-14.8 ± 1.0	11.6 ± 0.5
		R	7	30.2 ± 2.0	-14.5 ± 1.0	11.6 ± 0.5
L. griseus	General		49	30.5 ± 3.2	-12.9 ± 1.0	10.9 ± 0.8
	San Francisco de Campeche	W	4	32.5 ± 2.4	-12.4 ± 0.7	10.8 ± 0.8
		D	9	29.6 ± 3.2	-12.7 ± 0.9	9.8 ± 0.9
		R	9	32.3 ± 3.2	-13.6 ± 1.0	10.8 ± 0.8
	Seybaplaya	W	2	30.0 ± 3.4	-13.5 ± 1.0	11.5 ± 0.8
		D	4	25.4 ± 3.2	-13.8 ± 1.0	12.9 ± 0.9
		R	7	31.0 ± 3.2	-13.2 ± 0.9	11.3 ± 0.8
	Champoton	W	3	30.1 ± 3.5	-11.4 ± 1.1	10.2 ± 0.8
		D	4	29.2 ± 3.9	-13.4 ± 0.8	11.5 ± 0.7
		R	3	30.0	-13.0	11.2

Table 5. Niche width and trophic position of *Lutjanus synagris* and *Lutjanus griseus*. SC: stomach content, SI: stable isotopes: SD: standard deviation, W: wind/winter season, D: dry, R: rainy season.

Specie	Location	Season	n	Niche width		Trophic position	
			(SC-SI)	SC	SI	SC ± SD	SI ± SD
L. synagris	San Francisco de Campeche	WS	36-4	<0.01	1.1	3 ± 0.6	4 ± 0.7
		D	47-9	0.01	0.9	3.2 ± 0.5	3.8 ± 0.5
		R	61-9	0.02	1.2	3 ± 0.6	3.7 ± 0.4
	Seybaplaya	W	100-2	0.03	1.13	2.9 ± 0.6	3.2 ± 0.5
		D	76-4	0.2	0.7	2.8 ± 0.7	3.4 ± 0.9
		R	47-7	0.04	0.9	3 ± 0.4	4 ± 0.5
	Champoton	W	140-3	0.1	1	4 ± 0.4	4.1 ± 0.6
		D	53-4	<0.01	0.6	3.3 ± 0.5	4.2 ± 0.5
		R	64-3	0.03	0.9	3.5 ± 0.2	4 ± 0.1
L. griseus	San Francisco de Campeche	W	11-5	0.04	2.1	3.2 ± 0.6	3.9 ± 0.1
		D	14-6	0.1	2	3 ± 0.4	3.6 ± 0.3
		R	26-7	0.03	1.8	3.9 ± 0.2	3.7 ± 0.2
	Seybaplaya	W	14-7	0.02	1.1	3 ± 0.3	3.9 ± 0.3
		D	10-7	0.01	0.9	3.2 ± 0.4	3.7 ± 0.4
		R	25-5	0.03	0.9	3.8 ± 0.1	3.8 ± 0.2
	Champoton	W	9-8	<0.01	0.6	3.9 ± 0.2	3.5 ± 0.6
		D	11-6	0.02	0.8	3.7 ± 0.1	3.3 ± 0.6
		R	11-7	0.02	0.9	3.8 ± 0.4	3.9 ± 0.3

fish and mollusks), coincide with those reported by Duarte & Garcia (1999) for *L. synagris* in Colombia (106 prey species) and Pimentel & Joyeux (2010) in Brazil (24 prey species). The differences in the number of prey species are possibly due to differences in the diversity-related to sites. For example, the number of crustacean's species identified in the present study is reported in the high diversity of the littoral of Campeche (more than 200 species), which is a fundamental part of the food web for both snappers.

The trophic group with a high contribution (%PSIRI) in *L. synagris* and *L. griseus* were crustaceans, which

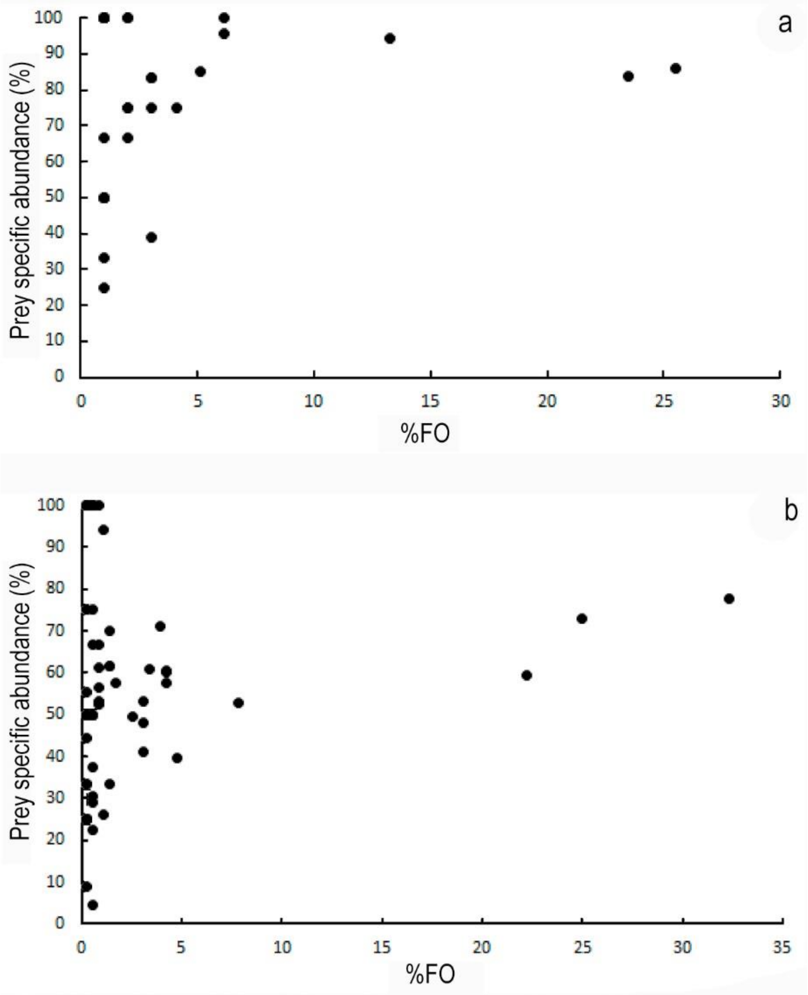

Figure 4. Costello's graph represents the general food strategy and categories of a) *Lutjanus griseus* and b) *L. synagris*.

coincides with MixSIAR, previously reported by other authors (Yáñez-Arancibia & Day, 1986; Harrigan *et al*., 1989; Hettler, 1989; Rivera-Arriaga, 1993; Guevara *et al*., 1994; Rooker, 1995; Sierra, 1996; Rojas-Herrera *et al*., 2004). For example, Guevara *et al*. (2007) and Juárez (2011) report that preys species *F. duorarum* and other crustaceans are the most important in the diet of these two snapper species. Therefore, the diet of *L. synagris* and *L. griseus* is mainly based on the consumption of crustaceans.

An optimal foraging model generates estimations of how animals maximize their fitness while they forage. The model building process involves identifying the currency, constraints, and appropriate decision rule for the forager (Stephens & Krebs, 1986; Sinervo, 1997), and this model allow us to predict how a fish behaves when searching for food. In this sense, some authors indicate that lutjanids have generalist-opportunistic behavior (Duarte & García, 1999; Rojas-Herrera *et al*., 2004). However, results obtained in other species of lutjanids, show the low amplitude of the trophic niche (<0.50), denoting specialization in the diet (Saucedo-Lozano, 2000; Santamaría-Miranda *et al*., 2005; Guevara *et al*., 2007). In the present study, the preference for crustaceans and temporal and spatial changes in diet confirm that *L. synagris* and *L. griseus* have trophic plasticity (Costello's graphs). However, with specific selectivity (Levin's index) to abundant trophic groups in the different ecosystems present in the area (seagrasses and mangroves), also, the low isotopic variability (standard deviation) indicated specialization in a particular trophic group (crustaceans), which indicated an ecological strategy for the optimization in the use of trophic resources, to reduce or avoid the level of intraspecific competition (Schoener, 1974; Werner, 1979).

The isotopic composition of *L. synagris* and *L. griseus* indicated that both snapper species could be found in coastal zones with low migration to pelagic zones, being important predators in the coastal ecosys-

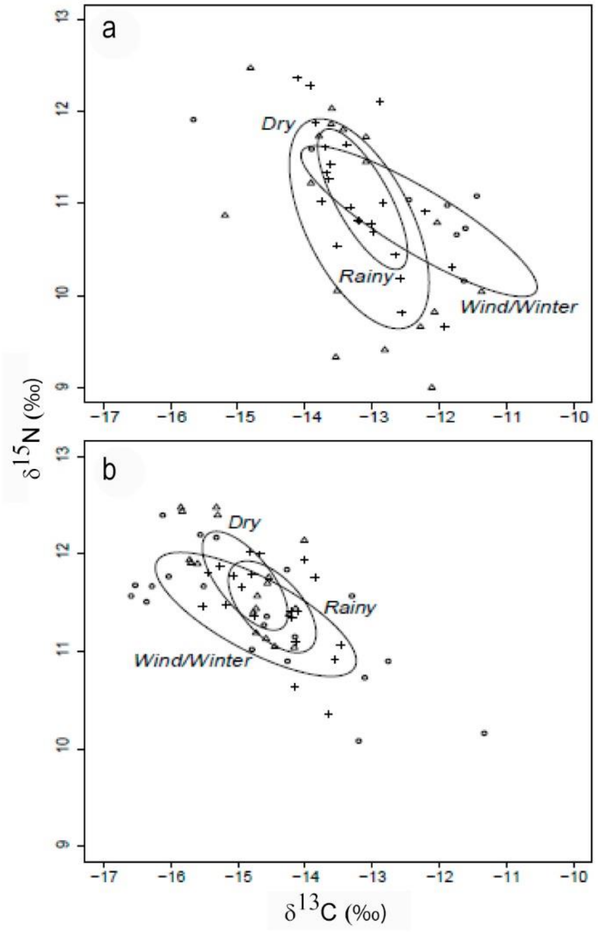

Figure 5. Standard ellipses for the muscle of a) *Lutjanus griseus* and b) *L. synagris* among climatic seasons in the littoral of Campeche, Mexico. In both figures, triangles: dry season, circles: wind/winter season, and crosses: rainy season.

tem. In Florida, the isotopic composition (δ^{15}N) of *L. synagris* and *L. griseus* caught in areas near to mangrove and seagrass were 9.2 ± 0.4 and 9.7 ± 0.8‰, respectively (Vaslet *et al.*, 2012). Romo-Ríos (2012) indicated that *L. synagris* its one of the predators with high δ^{15}N value (13‰). Registered in areas with seagrass contributions in Laguna de Terminos, Campeche, which like other species that are distributed in the coastal-marine zone, present values of δ^{13}C from -18 to -10‰, probably related to: 1) the consumption of preys with intermediate carbon values, and 2) to the ingestion of a combination of depleted and enriched food sources in δ^{13}C (Nagelkerken & Van Der Velde, 2004), related to the daily trophic migrations of fish between mangroves and seagrass beds (Hobson, 1999; Nagelkerken & Van Der Velde, 2004).

The location where more organisms were collected was Champoton, which is characterized by sandy beaches and limos rich in organic matter products of the trawling of the nearby rivers and with the presence of seagrass and mangroves. It has been confirmed that lutjanids are highly dependent on adjacent mangrove and seagrass ecosystems since they are breeding or feeding areas (Nagelkerken, 2007; Vaslet *et al.*, 2012), therefore, *L. synagris* is ecologically fed in areas of seagrass and *L. griseus* is probably intermittent between seagrass and mangrove areas. Since both snapper species occupy different habitats of the food web in the Campeche coast, like other lutjanids species (Garrido *et al.*, 2008; Vaslet *et al.*, 2012), the absence of these species probably can cause a top-down effect on the ecosystem. The existence of top-down control, which means the regulation of lower food-web components by one or several upper-level predators, as species mostly interact through predation, should be critical in the functioning of marine ecosystems (Cury *et al.*, 2003). Predation mortality is estimated to be a significant source of mortality for marine exploited species. An analysis of six marine ecosystems (Benguela

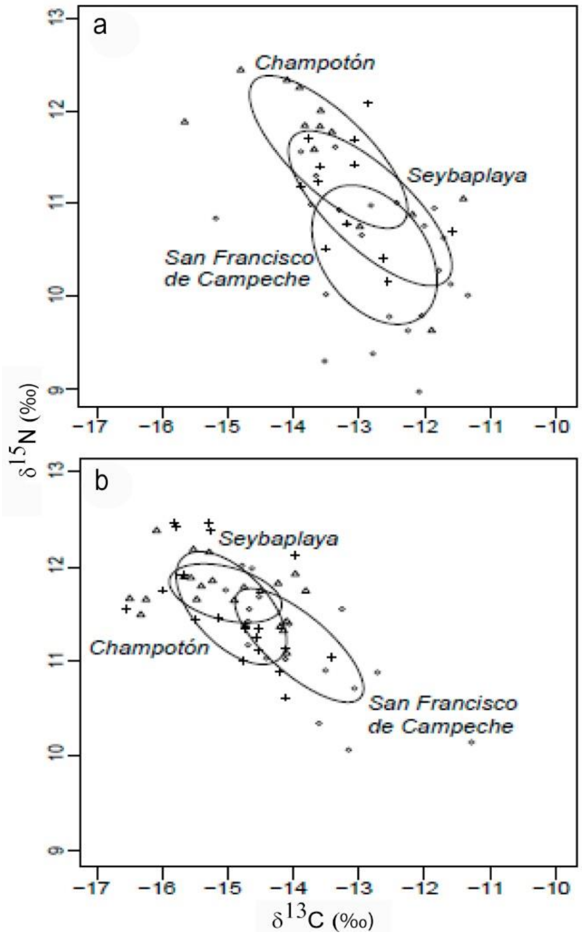

Figure 6. Standard ellipses for the muscle of a) *Lutjanus griseus* and b) *L. synagris* in the litoral of Campeche, Mexico. In both figures, triangles: Champotón, circles: San Francisco de Campeche and crosses: Seybaplaya.

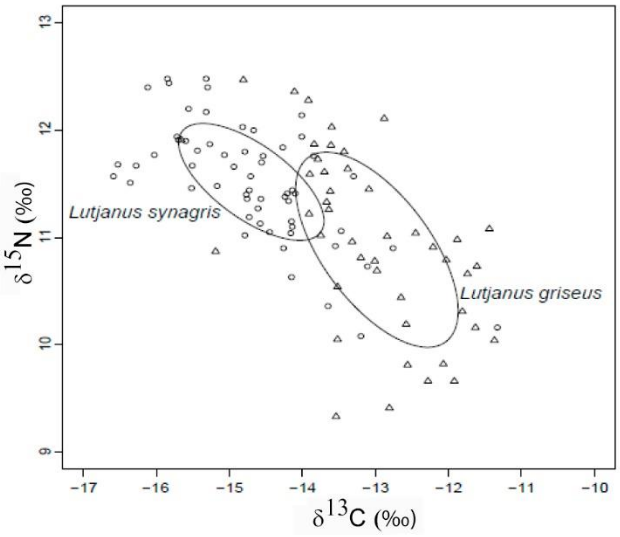

Figure 7. Biplot of $\delta^{13}C$ and $\delta^{15}N$ for *Lutjanus griseus* and *L. synagris* in the littoral of Campeche, Mexico.

Current, Georges Bank, Balsfjord, east Bering Sea, North Sea, Barents Sea) suggests that predation represents between 2-35 times fishing mortality (Bax, 1991; Cury *et al*., 2003). The top-down is closely linked to keystone species as well as trophic cascade, and these processes have been well demonstrated in several aquatic ecosystems by Paine (1966), Power *et al*. (1996), Oleson (1995), Estes *et al*. (1998) and most recently by Schneider & Brose (2012), Hall (2015) and Lynam *et al*. (2017).

The temporal trophic spectrum of *L. griseus* indicated that the diet was similar throughout the year. Several authors mention for *Lutjanus* genus not seasonal variations in the composition of the diet, for example, *Lutjanus colorado*, present no significant difference in food preferences during dry and rainfall season in the Gulf of Nicoya (Claro, 1981a,b, 1983a,b,c; Guevara *et al*., 1994, Sierra *et al*., 1994), and the difference in $\delta^{15}N$ among location can be related to change in the organic matter. The type of substrate being the determining factor of the sea, Rivera-Arriaga *et al*. (2012), indicated a transition zone between Champoton and San Francisco de Campeche with changes in sediments.

The location of San Francisco de Campeche presents slime-clays; while Seybaplaya and Champoton, sands (68.87%) and with high density of seagrasses, also, the vast supply of nutrients from the Champoton River in wind/winter season (W), coupled with the efficient use by the ichthyofauna of the energy in the leaves of *Thalassia testudinum*. Therefore, ichthyofauna tends to present an isotopic composition of locally available organic matter (Poppe *et al*., 2000; Romo-Ríos, 2012), where although *L. griseus* feed very similarly at the spatial level, the isotopic difference ($\delta^{15}N$) can be due to changes in the autotrophic source between localities.

In *L. synagris*, the significant difference at the spatial and temporal levels was found in stomach content and stable isotopes. In the winter/wind season, *L. synagris* consumed mainly shrimps (Penaeidae) and crabs (*Callinectes* spp.). In D season, swimming crabs and shrimps (*Portunus* spp. and Sycionidae), and R season crabs and swimming crabs (Majidae and *Portunus* spp.), coincident with Guevara *et al*. (1994) who reported for R season, that crustaceans represented the highest percentage of food consumed for three lutjanids species, since during this season there is an increase in primary productivity, increasing productivity in zooplankton and benthic organisms. However, the differences detected with stable isotopes suggested a differential pattern in the use of prey resources according to the temporality.

In Campeche throughout the year, crustaceans have a high abundance. However, there have been changes at the temporal/spatial level in this taxonomic group's abundances. For example, juveniles of the family Portunidae are usually found in the sediment in areas less than 20-30 m deep to spend the winter (months of northerly) (Williams *et al*., 1990), as well as the Penaeidae, have higher activity under very turbid conditions in the water column (Hughes, 1968), probably associated to changes in temperature or the influx of nutrients (especially in the rainy season) as well as other environmental factors. Therefore, in N season, *L. synagris* feed on benthos; whereas in dry and rainy seasons in the water column.

The trophic level of *L. synagris* and *L. griseus* (around 3.9) corresponds to that of tertiary consumers (Vander-Zanden *et al*., 1999). However, Sierra *et al*. (1994) have reported higher trophic levels for *L. synagris* and *L. griseus* (from 4.0 to 4.3). These differences can be attributed to the fact that the main prey in the diet of snappers in Cuba is mostly Osteichthyes (high TL). The trophic positions based on stable isotopes are slightly higher than trophic positions of lutjanids trophic in Florida, probably related to the type of habitat (Vaslet *et al*., 2012 - study = neritic areas). Therefore, the present study proves that lutjanids in their different distributions (mangroves, seagrass, neritic areas) have a unique and critical role in the dynamics of marine ecosystems as predators and potential structuring of their prey populations mainly of benthic organisms.

In summary, despite being sympatric species captured in the coastal area, with a preference for crustaceans, the isotopic composition allows us to detect that *L. synagris* and *L. griseus* occupy different

Table 6. Values of δ^{15}N, δ^{13}C, and C:N ratio of food sources (prey species) of lutjanids at the corresponding locations. n: number of individuals, SD: standard deviation.

Location	Prey items	n	δ^{13}C (‰) ± SD	δ^{15}N (‰) ± SD	C:N
San Francisco de Campeche					
	Lagodon rhomboidalis	2	-12.2 ± 0.2	9.0 ± 0.2	2.8
	Majidae	4	-12.5 ± 0.2	3.9 ± 0.3	3.1
	Fultodromia spp.	7	-12.3 ± 1.5	3.8 ± 1.2	2.7
	Epathus epheliticus	1	-11.2	6.7	3.2
	Ocyurus chysurus	2	-11.8 ± 0.7	6.1 ± 0.5	4.2
	Farfantepenaeus aztecus	2	-13.4 ± 0.1	5.3 ± 1.0	3.1
	Farfantepenaeus duorarum	2	-12.5 ± 0.1	7.3 ± 1.5	3.2
Seybaplaya					
	Portunus gibbesii	6	-14.7 ± 0.8	7.4 ± 0.9	3.8
	Trachypenaeus constrisctus	2	-15.5 ± 0.4	6.0 ± 0.6	3.3
	Farfantepenaeus duorarum	2	-12.8 ± 8.3	6.4 ± 8.2	3.4
	Archosargus rhomboidalis	2	-15.6 ± 0.3	8.0 ± 0.5	2.8
	Lutjanus synagris	2	-13.1 ± 1.0	8.1 ± 1.1	2.3
	Menipe mercenaria	1	-10.4	5.8	4.0
	Partenophe pourtalessi	3	-15.7 ± 1.0	6.0 ± 1.2	3.0
	Callinectes spinnimanus	2	-16.4 ± 0.9	7.6 ± 1.0	4.0
Champoton					
	Myrophis punctatus	2	-11.8 ± 0.2	8.7 ± 3.1	2.9
	Portunus gibbesii	2	-13.4 ± 0.9	6.1 ± 0.4	3.0
	Squilla empusa	2	-15.3 ± 0.3	7.7 ± 0.1	3.5
	Farfantepenaeus duorarum	2	-13.5 ± 1.4	5.9 ± 1.5	3.0
	Urobatus jamaicensis	2	-12.4 ± 0.1	10.1 ± 0.2	3.2
	Callinectes sapidus	3	-15.7 ± 0.1	6.0 ± 0.4	2.0
	Menipe mercenaria	3	-12.2 ± 0.7	4.8 ± 1.0	3.6
	Fultodromia spp.	7	-16.7 ± 1.7	5.0 ± 1.6	2.8

trophic roles in different habitats like mangrove and seagrass areas, confirming that these areas are potential areas for the breeding and growth of snappers in the coastal zone of the Campeche. There are few studies based on stable isotope for the Gulf of Mexico's coastal area, and this study proves that the application of this technique is crucial to understand the biology and behavioral characteristics of snappers in other regions. However, future studies need to determine the importance of the coastal zone's organic sources for ichthyofauna and this through intensive analyzes in the determination of δ^{13}C at different points of the coast, such as in seagrass, mangrove, coral areas, with the contribution of rivers or groundwater. All these aspects will allow us to contribute to the ecosystem management of one of the most valuable fisheries in the Gulf of Mexico.

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