

Diet composition of two sympatric snappers *Lutjanus synagris* and *Ocyurus chrysurus* from the north continental shelf of Yucatan, Mexico

by

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Abstract. – Snappers are opportunistic carnivores with a leading role in energy flows between trophic interactions within tropical ecosystems. In the southern Gulf of Mexico, the few reported trophic-structure models are based on snapper stomach content data from other geographic regions (*e.g.* Atlantic coast of United States, northern Gulf of Mexico, Caribbean Sea and Brazil). To optimise the reliability of these models, we present new information on the diet composition of two commercially important species: lane snapper *Lutjanus synagris* and yellowtail snapper *Ocyurus chrysurus*. From January 2008 to 2009, the stomach contents of 1,074 *L. synagris* and 1,516 *O. chrysurus* were collected from three fishing sites off the northern coast of Yucatan, Mexico. Contents were analysed using frequency, number and weight of the identified prey species. A three-level, nested PERMANOVA analysis was used to assess differences between the potential prey and their biomass using the factors of snapper species, fishing site and climate season. Multidimensional scale (MDS) and SIMPER analyses were run to establish dissimilarity within the discriminating factors. The main food items found in the *L. synagris* diet were Brachyura, Penaeoidea and unidentified shrimps. Penaeoidea were the most abundant items in the *O. chrysurus* diet. Prey biomass analysis revealed a dissimilarity in diet composition between the two snapper species, as well as between fishing sites and climate seasons. The principal discriminatory prey categories were Brachyura, Penaeoidea, Osteichthyes, with Caridea and unidentified shrimps accounting for slightly smaller proportions. The results confirm the trophic position of these two sympatric snappers, showing that each plays a different trophic role in the ecosystem of the northern coast of the Yucatan Peninsula.

Résumé. – Régime alimentaire de deux vivaneaux sympatriques *Lutjanus synagris* et *Ocyurus chrysurus* de la plateforme continentale nord du Yucatan, Mexique.

Les vivaneaux (Lutjanidae) sont des carnivores opportunistes qui assument un rôle prépondérant dans les flux d'énergie entre les maillons trophiques de la chaîne alimentaire des écosystèmes tropicaux. Au sud du golfe du Mexique la modélisation de la structure trophique de l'écosystème de la plateforme continentale nord du Yucatan a été basée sur des informations de contenus stomacaux de vivaneaux issues d'autres régions géographiques (côte atlantique des États-Unis, marge nord du golfe du Mexique, mer des Caraïbes et Brésil). Afin d'optimiser la fiabilité des résultats générés par ces modèles, le but de ce travail a été d'analyser la composition du régime alimentaire de deux espèces de vivaneau d'importance commerciale du Yucatan : le vivaneau gazou *Lutjanus synagris* et le vivaneau queue jaune *Ocyurus chrysurus*. Les contenus stomacaux de 1074 *L. synagris* et de 1516 *O. chrysurus*, collectés entre janvier 2008 et 2009 dans trois sites du littoral du Yucatan, ont été analysés au travers de l'utilisation d'une méthode mixte qui prend en considération la fréquence, le nombre et le poids des proies identifiées. Un test d'échelle multidimensionnelle (MDS), une analyse multivariée permutative de la variance (PERMANOVA), un test par paires et une analyse du pourcentage de similarité (SIMPER) ont été appliqués pour évaluer le degré de dissimilitude interspécifique, spatiale et temporelle dans la composition du régime alimentaire des deux vivaneaux. Les proies préférentielles de *L. synagris* furent les Brachyura, les Penaeoidea et des crevettes diverses et celles de *O. chrysurus* furent les Penaeoidea. Une dissimilitude entre espèces, sites et saisons, de la composition du régime alimentaire des deux vivaneaux a été mise en évidence. Les principaux groupes de proies discriminants ont été les Brachyura, les Penaeoidea, les Osteichthyes et, dans une moindre mesure, les Caridea et les crevettes diverses. Les résultats obtenus confirment la position trophique de ces deux vivaneaux sympatriques et indiquent qu'ils jouent vraisemblablement un rôle trophique distinct l'un de l'autre dans l'écosystème de la côte nord de la péninsule du Yucatan.

INTRODUCTION

Fish survival, growth and reproduction depend on the energy and nutrients obtained from feeding activity (Wootton, 1999). Understanding fish feeding habits is essential to

the study of population dynamics and to characterize certain aspects of trophic ecology such as habitat of predilection, prey selection, competition, interspecies resource sharing and energy transfers within and between ecosystems. Data on the feeding habits of commercially exploited fish

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also constitute inputs for trophic-level-based models aimed to analyse marine ecosystem functioning in the contexts of both ecology and fisheries (Gascuel, 2005; Fernández *et al.*, 2011). Researching fish trophic ecology is therefore vital for developing conservation strategies in fish populations which are fundamental to the protection of species and their ecosystems (Gerking, 1994; Braga *et al.*, 2012).

Snappers (Lutjanidae) are one of the principal active predators in tropical and subtropical benthic ecosystems (Allen, 1985; Parrish, 1987), and play a dominant role in top-down control mechanisms of energy flux (Parrish, 1987). In the southern Gulf of Mexico, on the northern continental shelf of the Yucatan Peninsula (Campeche Bank), snappers and groupers (Epinephelidae) are the most valuable fishery resources for the artisanal Mexican fleet. Between 2001 and 2015, the grouper (mean capture = 3,700 tonnes per year) and snapper (mean capture = 2,189 tonnes per year) complex represented between 50% and 80% of finfish landings for this fleet (Monroy-García *et al.*, 2019). Beginning in the 1990's, capture volume for red grouper *Epinephelus morio* (Valenciennes, 1828), the main species exploited in the region, began to fluctuate, driving fishers to redirect fishing effort towards snapper species (Monroy-García *et al.*, 2019). Neither commercial fishing regulations nor specific management plans exist for snappers in the region, representing a potential threat to the ecological stability of ecosystems shared by groupers and snappers (Arreguín-Sánchez and Manickchand-Heileman, 1998).

The two most important commercial snapper species on Campeche Bank are lane snapper *Lutjanus synagris* (Linnaeus, 1758) and yellowtail snapper *Ocyurus chrysurus* (Bloch, 1790) (Monroy-García *et al.*, 2019); both provide annual yields between 1,400 to 3,400 tons (2011-2020 period; SAGARPA, 2020). They share the same geographical distribution area in the western Atlantic, inhabiting coral reefs and seagrass beds, from the coast to 70 m depth (Allen, 1985). Their trophic biology has been studied mainly for populations of diverse insular regions in the Caribbean Sea, such as Cuba (Rodríguez-Pino, 1962; Claro and Lapin, 1971; Valdés-Muñoz and Silva-Lee, 1977; Claro, 1981, 1983; González and Rodríguez, 1985; Carrillo de Albornoz and Ramiro, 1988; Aguilar-Betancourt *et al.*, 1992; Delgado *et al.*, 1996; Sierra, 1997; Sierra *et al.*, 2001), the Virgin Islands (Randall, 1967), Haiti (Beebe and Tee-Van, 1928) and Curacao (Cocheret de la Morinière *et al.*, 2003). Trophic studies of continental populations have been done in the northern Gulf of Mexico in Florida (Starck, 1971) and Mississippi coastal waters (Franks and VanderKooy, 2000), as well as in Panama (Heck and Weinstein, 1989), Colombia (Duarte and García, 1999; Doncel and Paramo, 2010) and Brazil (Rodrigues, 1974; Rosa *et al.*, 2015; Fernandes *et al.*, 2020). A recent study analysed variability in the feeding habits of *L. synagris* from the western coast of the Yuca-

tan Peninsula (State of Campeche) (Juárez-Camargo *et al.*, 2020). An analysis of community trophic structure on the Yucatan Peninsula was done using the ECOPATH II model (Arreguín-Sánchez *et al.*, 1993; Arreguín-Sánchez and Manickchand-Heileman, 1998), with stomach content data from fish populations from the Atlantic coast of the United States, the northern Gulf of Mexico, the Caribbean Sea and Brazil (Claro, 1981, 1983; Parrish, 1987). The relevance of results from this model to a specific region is directly linked to the data collected from the ecosystem of interest (Bayle-Sempere *et al.*, 2013); increasing data accuracy optimises model reliability. The present study objective was to characterize the feeding regime of *L. synagris* and *O. chrysurus* and to analyse the trophic relationships prevailing between these two sympatric snappers from the northern continental shelf of the Yucatan Peninsula.

MATERIAL AND METHODS

Sampling

The organisms were collected monthly from January 2008 to January 2009, near the three most important fishing ports of the artisanal fleet on the coast of the state of Yucatan, Mexico: Celestún (20°52'N, 88°45'W), Dzilam de Bravo (21°30'N, 88°45'W) and Río Lagartos (21°40'N, 88°10'W) (Fig. 1). Samples were collected during daylight (07:00-16:00) in small fishing vessels operated by fishers using hook-and-line at depths between 3 and 40 m. Fish were stored on ice until the return to port at day's end. Immediately after landing, all individuals (n = 1,074 *L. synagris* and 1,516 *O. chrysurus*) were measured (fork length [FL, cm]), weighed (whole weight [WW, g]) and their stomachs extracted and preserved in 10% formalin. After transport to the laboratory, the stomachs were rinsed in successive water baths to eliminate the formalin and preserved in 70% ethanol. The specimens were mainly adult since the Campeche Bank *L. synagris* and *O. chrysurus* populations reach sexual maturity onset at 15 cm FL and 14 cm FL, respectively (Trejo-Martínez *et al.*, 2011, 2021). Based on annual fluctuations in sea surface temperature (SST) in the Gulf of Mexico (Rivas, 1970; Piñeiro *et al.*, 2001) and rainfall variation on the northern coast of the Yucatan Peninsula (Espejel, 1987), two climate seasons (cold/dry: November-April and warm/rainy: May-October) were defined during the sampling period.

Stomach content analysis

Stomach content analysis was done following published procedures for quantitative assessment of food habits in fish (Hureau, 1970; Hyslop, 1980; Chipps and Garvey, 2007). Prey species were identified to the most specific taxonomic level possible given the degree of digestion. All prey items



Figure 1. – Location of fishing sites of *Lutjanus synagris* and *Ocyurus chrysurus* from the north continental shelf of the Yucatan Peninsula.

were counted (except for vegetal material and unidentified organic matter), and volume weighed with an analytic scale (0.001 g) after removal of excess ethanol. All loose prey fragments identified as belonging to the same individual were considered as a single prey item, unless two (or more) fragments clearly came from two (or more) individuals. Loose fragments that could not be assigned to a species were classified as unidentified. Stomach contents (items) were analysed by calculating the following indices: frequency of occurrence (%F), percentage by number (%Cn) and percentage by weight (%Cp) (Hureau, 1970; Hyslop, 1980). Hureau's coefficient (1970): $Q = \%Cn \times \%Cp$ was also calculated. For %F and Q, the main prey categories for each individual fish were classified as preferential or occasional. The vacuity index (VI) was calculated as the percentage of empty stomachs (n_e) to the total number of examined stomachs (n_t) $VI\% = n_e/n_t \times 100$ (Hureau, 1970).

Statistical analyses

The multivariate approach applied here (PERMANOVA) is routinely used to test the simultaneous response of one or more variables (database of potential prey x biomass) to one or more factors (species, site and season) based on a triangular matrix using any resemblance measure and permutation methods (Anderson, 2001). The database of potential prey for each studied snapper species was transformed to fourth root, down-weighted (Clarke *et al.*, 2006). The main function of the fourth-root transformation was to reduce the high variability and weigh the contributions of prey with greater and lesser biomass from one sample unit (*i.e.* stomach) to

another. With the transformed data, a triangular matrix was calculated using the Hellinger distance index (Rao, 1995). The Hellinger distance offers better linearity and resolution than the chi-square metric and the chi-square distance (Legendre and Legendre, 1998). The distance matrix was then ordinated in a multidimensional scale (MDS) analysis related to the factors of snapper species, fishing site, and climate season. The MDS graphically represents the distance matrix in a metric space. The different factors were then compared using the average bootstrap and 95% confidence region bootstrap techniques. The minimum dimension value of the MDS metric was a 0.99 Pearson correlation using the original dissimilarity matrix. The three-level nested PERMANOVA analysis (Anderson, 2001), and pairwise tests were used to measure variation in the dissimilarity in relation to the three discriminant factors: snapper species (principal factor), fishing site and climate season (nested levels). Finally, the SIMPER (similarity percentage breakdowns) analysis (Clarke, 1993) was applied to calculate the average contributions to dissimilarity (using Bray-Curtis index; Bray and Curtis, 1957) of potential prey for each discriminant factor. All statistical analyses were run using an $\alpha = 0.05$.

RESULTS

General overview

Based on the VI%, 20% ($n = 220$) of *L. synagris* (VI = 80%) and 33% ($n = 505$) *O. chrysurus* (VI = 67%) had stomach contents. Of those specimens with stomach con-

Table I. - Food items recorded in stomach contents of *Lutjanus synagris* and *Ocyurus chrysurus* specimens from the north continental shelf of the Yucatan Peninsula. C: Celestún, DB: Dzilam de Bravo, RL: Río Lagartos, +: presence, -: absence.

Prey categories	<i>Lutjanus synagris</i>					<i>Ocyurus chrysurus</i>				
	Site			Season		Site			Season	
	C	DB	RL	Cold	Warm	C	DB	RL	Cold	Warm
Plant material	-	-	-	-	-	+	+	+	+	+
Annelida										
Polychaeta	-	-	-	-	+	+	+	+	+	+
Sipuncula	-	+	+	-	+	-	-	-	-	-
Crustacea										
Ostracoda	-	-	-	-	-	+	-	-	+	-
Malacostraca										
Stomatopoda	+	-	-	+	-	+	-	+	+	+
Mysida	-	-	-	-	-	+	+	+	+	+
Amphipoda	-	-	-	-	-	+	+	+	+	+
Isopoda	+	+	-	+	+	+	+	+	+	+
Decapoda										
Penaeoidea	+	+	+	+	+	+	+	+	+	+
Caridea	+	+	+	+	+	+	+	+	+	+
Unidentified shrimps	+	+	+	+	+	-	-	-	-	-
Palinura	+	-	-	+	-	-	-	-	-	-
Anomura	+	-	+	+	+	+	+	+	+	+
Brachyura	+	+	+	+	+	+	+	+	+	+
Unidentified decapods	-	-	-	-	-	+	+	+	+	+
Mollusca										
Gastropoda	+	-	-	+	-	+	-	+	+	+
Bivalvia	-	-	+	-	+	+	-	+	+	+
Cephalopoda	-	-	+	+	-	+	+	+	+	+
Chordata										
Osteichthyes	+	+	+	+	+	+	+	+	+	+
Unidentified remains	+	+	+	+	+	+	+	+	+	+

tents, size range was 18.0-39.3 cm FL for *L. synagris* and 16.3-40.0 cm FL for *O. chrysurus*.

A total of 44 unique prey items (20 identified to species) were identified in the stomach contents of *L. synagris*, and 74 items (45 identified to species) in *O. chrysurus*. Apparently, *O. chrysurus* has a more diverse feeding strategy than *L. synagris*. Annelids, crustaceans, molluscs and fishes constituted most of the diet items (Tab. I). Decapods represented the highest diversity of consumed prey (between 26 to 44 species). Caridea shrimp diversity (24 species) was higher in the *O. chrysurus* diet than in the *L. synagris* diet (3 species). In contrast, Brachyura crab diversity was higher in the *L. synagris* diet (15 species) than in the *O. chrysurus* diet (8 species). Bony fishes were more diverse in the *O. chrysurus* diet (17 species) than in *L. synagris* (5 species). Remains of tiny Mysida crustaceans, vegetal material and sea urchins were also identified in the *O. chrysurus* diet. Sipunculid worm remains were found only in the *L. synagris* stomach contents (Tab. I).

Dominance and Relative Importance

For *L. synagris*, the preferential prey were Brachyura crabs (Q = 548, %F = 36), Penaeoidea shrimps (Q = 558, %F = 21) and unidentified shrimps (Q = 357, %F = 34); for *O. chrysurus*, only Penaeoidea shrimps (Q = 1319, %F = 42) were preferential (Fig. 2). All the remaining prey in the stomach contents for both species was considered occasional; in *O. chrysurus*, Osteichthyes (Q = 56, %F = 29) and Caridea shrimps (Q = 14, %F = 37) predominated among the occasional prey (Fig. 2).

Diet composition varied between fishing sites for *L. synagris*. The dominant items in individuals collected at Celestún and Dzilam de Bravo were Brachyura crabs (740 ≤ Q ≤ 884; 14 ≤ %F ≤ 17) and unidentified shrimps (328 ≤ Q ≤ 444; 12 ≤ %F ≤ 13), while in those collected at Río Lagartos it was Penaeoidea shrimps (Q = 1263, %F = 11) (Fig. 3). Penaeoidea shrimps (679 ≤ Q ≤ 2015; 28 ≤ %F ≤ 53) dominated diet composition in *O. chrysurus* regardless of fishing site (Fig. 4), although Caridea shrimps (Q = 146, %F = 53)

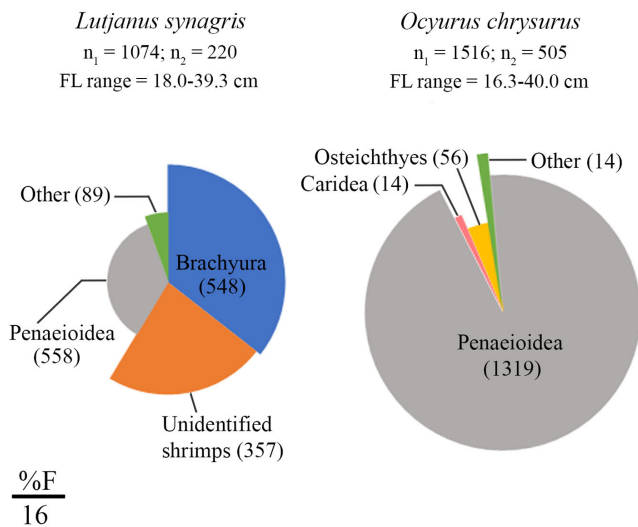


Figure 2. – Diet composition of *Lutjanus synagris* and *Ocyurus chrysurus* specimens from the north continental shelf of the Yucatan Peninsula. Angle of sector are proportional to Q (Hureau’s coefficient; Q value is given in parentheses), and radius is proportional to %F (frequency of occurrence). n_1 = total number of fish collected; n_2 = number of fish with stomach contents; FL = fork length of fish with stomach contents.

and Osteichthyes ($Q = 127$, $\%F = 45$) were also identified in individuals from Celestún and Dzilam de Bravo. The VI for *L. synagris* per fishing site was 80% at Celestún, 79% at Dzilam de Bravo and 80% at Río Lagartos, and for *O. chrysurus* it was 71% at Celestún, 65% at Dzilam de Bravo and 63% at Río Lagartos.

Brachyura crabs ($494 \leq Q \leq 550$; $12 \leq \%F \leq 24$), Penaeoidea shrimps ($250 \leq Q \leq 839$; $5 \leq \%F \leq 15$) and unidentified shrimps ($273 \leq Q \leq 419$; $10 \leq \%F \leq 24$) dominated *L. synagris* diet composition in both climate seasons (Fig. 5). Penaeoidea shrimps ($555 \leq Q \leq 1465$; $40 \leq \%F \leq 43$) dominated *O. chrysurus* diet composition in both climate seasons, although Caridea shrimps ($Q = 88$, $\%F = 47$) were present at significant levels during the cold/dry season (Fig. 5). Values for VI in *L. synagris* were 76% during the cold/dry season and 84% during the warm/rainy season, while for *O. chrysurus* they were 57% in the cold/dry and 77% in the warm/rainy.

The PERMANOVA analysis identified differences in prey biomass and composition between the snapper species (Fig. 6A), between climate seasons (Fig. 6B) and between

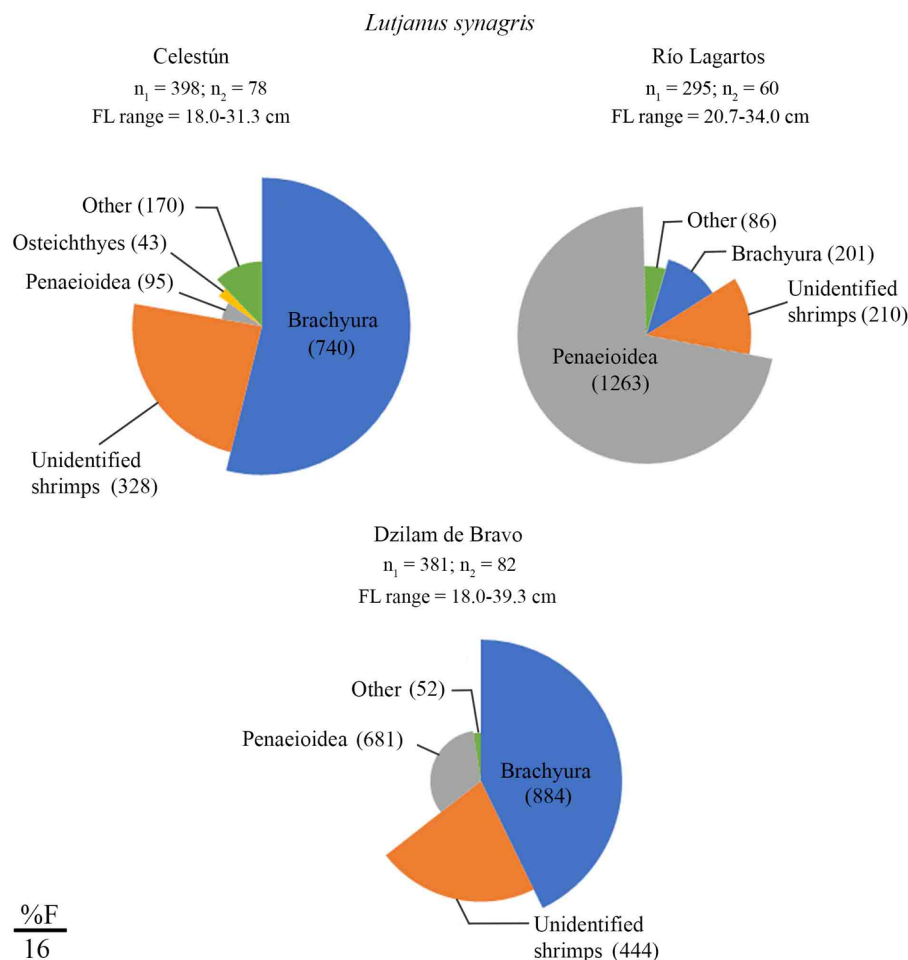


Figure 3. – Diet composition of *Lutjanus synagris* specimens from the north continental shelf of the Yucatan Peninsula according to fishing sites. Angle of sector are proportional to Q (Hureau’s coefficient; Q value is given in parentheses) and radius is proportional to %F (frequency of occurrence), n_1 = total number of fish collected; n_2 = number of fish with stomach contents; FL = fork length of fish with stomach contents.

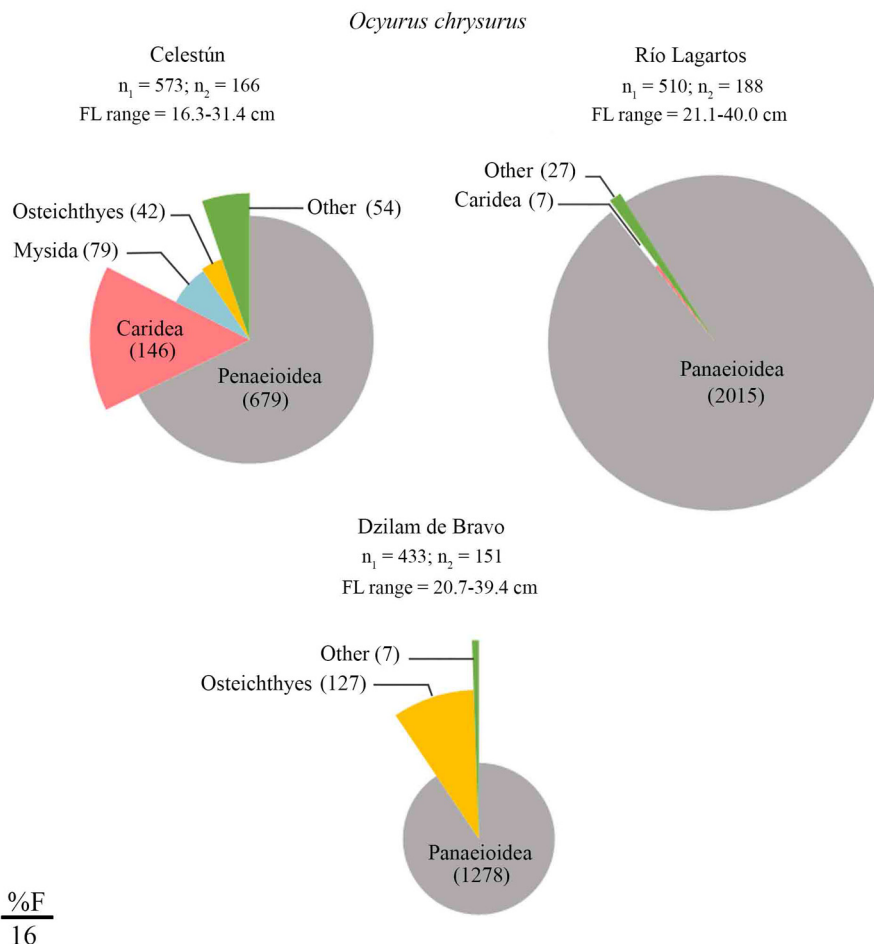


Figure 4. – Diet composition of *Ocyurus chrysurus* specimens from the north continental shelf of the Yucatan Peninsula according to fishing sites. Angle of sector are proportional to Q (Hureau’s coefficient; Q value is given in parentheses), and radius is proportional to %F (frequency of occurrence). n_1 = total number of fish collected; n_2 = number of fish with stomach contents; FL = fork length of fish with stomach contents.

fishing sites (Fig. 6C) (Tab. II). Average dissimilarity values calculated in the SIMPER analysis were 94% between species, 91-93% between fishing sites, and 92% between climate seasons (Tab. II). When the factors of snapper species, fishing site and climate season were considered, Penaeoidea shrimps, Brachyura crabs, and Osteichthyes were found to be the discriminant prey groups for all three factors. To a lesser degree, unidentified shrimps were identified as a discriminant prey group between snapper species and Caridea shrimps was a discriminant prey group between specimens from Celestún and Río Lagartos (Tab. II).

DISCUSSION

Diet composition in *L. synagris* and *O. chrysurus* from the continental shelf of the Yucatan Peninsula is very similar to that reported for other populations of the same species. Both snappers displayed carnivorous and generalist-opportunist habits, consuming a wide range of benthic prey represented mainly by crustaceans and fishes. Regardless of geographical region, decapods, in particular, as well as

shrimps (Penaeoidea, Caridea) and crabs (Brachyura) predominated over fishes in the *L. synagris* diet (Beebe and Tee-Van, 1928; Randall, 1967; Starck, 1971; Rodrigues, 1974; Valdés-Muñoz and Silva-Lee, 1977; Claro, 1981; Heck and Weinstein, 1989; Duarte and García, 1999; Doncel and Paramo, 2010; Fernandes *et al.*, 2020). In the study area, *L. synagris* and *O. chrysurus* exhibited differences in diet largely in terms of prey biomass variations. This suggests that competition for prey between the two species is limited. For example, both species feed on shrimps, but any competition for this prey is eclipsed by the substantially higher intakes of crabs by *L. synagris* and fishes by *O. chrysurus*. The interspecies discrepancy in stomach contents prey biomass highlights the fact that both snapper species feed on the same prey groups but clearly consume different quantities of them. This difference between *L. synagris* and *O. chrysurus* diet composition may also have been influenced by species diversity in consumed prey, as indirectly inferred from consumed prey counts. For example, shrimp and fish species were more abundant in the *O. chrysurus* diet than in that of *L. synagris*, whereas crab species counts were higher in the latter. These differences in biomass composition and spe-

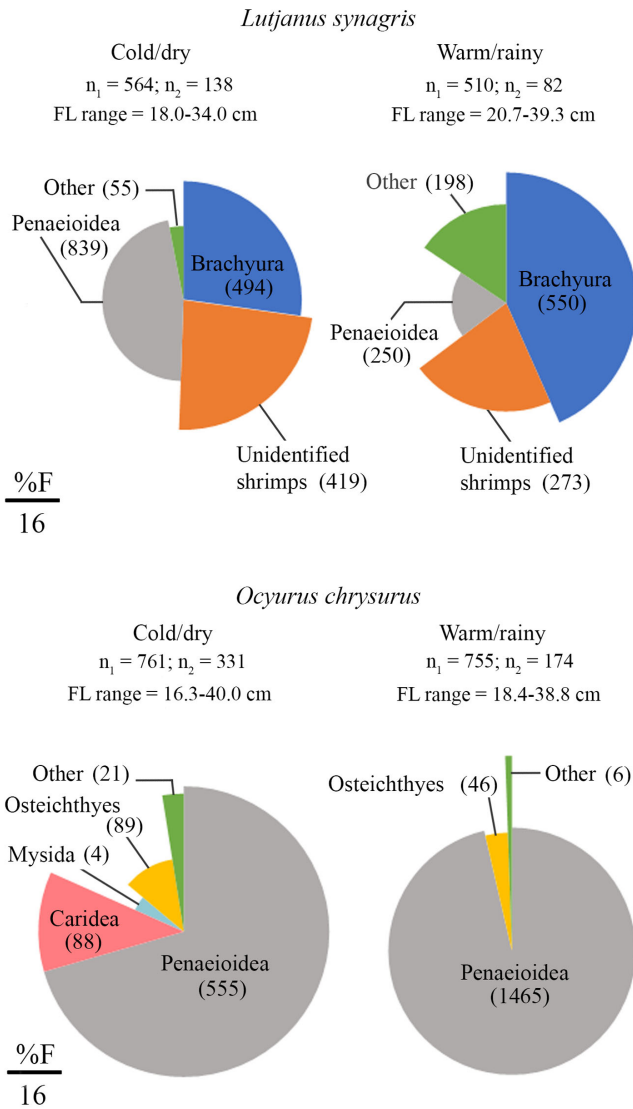


Figure 5. – Diet composition of *Lutjanus synagris* and *Ocyurus chrysurus* specimens from the north continental shelf of the Yucatan Peninsula according to climate seasons. Angle of sector are proportional to Q (Hureau's coefficient; Q value is given in parentheses), and radius is proportional to %F (frequency of occurrence). n_1 = total number of fish collected; n_2 = number of fish with stomach contents; FL = fork length of fish with stomach contents.

cies diversity may be explained by each snapper species' feeding behaviour. *Lutjanus synagris* is a zoobenthivore while *O. chrysurus* is a combination zooplanktivore/zoo-benthivore (Randall, 1967; Claro, 1983; Nagelkerken and Van der Velde, 2004). Therefore, *O. chrysurus* is considered a semi-pelagic species feeding near the bottom that also exploits prey resources in the water column up to the surface (Longley and Hildebrand, 1941; Claro, 1983; Thompson and Munro, 1983; Cocheret de la Morinière *et al.*, 2003). This finding generally coincides with a study of *L. synagris* and grey snapper *Lutjanus griseus* (Linnaeus, 1758) diets on the

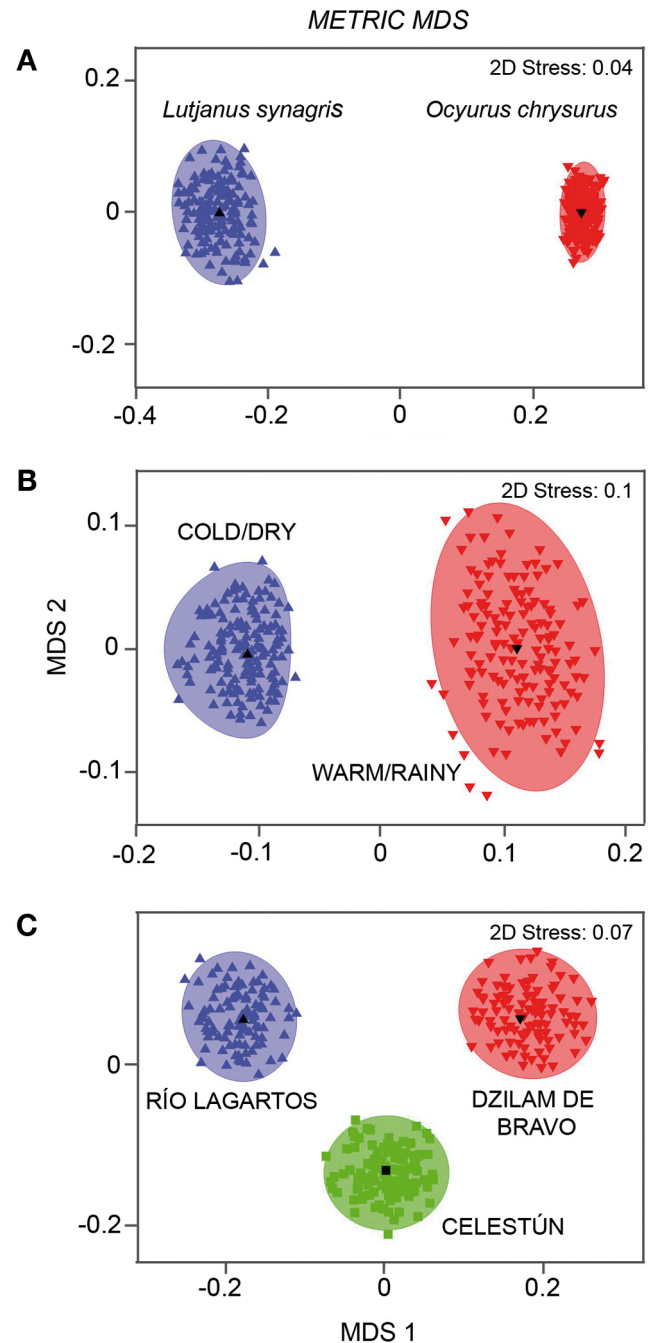


Figure 6. – Result of Multi-Dimensional Scale (MDS) analysis on diet composition of *Lutjanus synagris* and *Ocyurus chrysurus* specimens from the north continental shelf of the Yucatan Peninsula related to the factors: snapper species (A), climate seasons (B), and fishing sites (C).

west coast of the Yucatan Peninsula (Campeche state), in which stomach content analysis and stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analysis found minimal similarity between these species due to their differential use of habitat (Juárez-Camargo *et al.*, 2020).

Table II. – Interspecific, regional, and seasonal average abundance and average dissimilarity of main prey categories recorded in stomachs contents of *Lutjanus synagris* and *Ocyurus chrysurus* specimens from the northern coast of the Yucatan Peninsula. *: nested factors; **: pair wise test; SD: standard deviation.

Prey categories	Average abundance		Average dissimilarity	Dissimilarity/SD
Species (Sp)* (df = 1; 653; Pseudo-F = 7.537; P (perm) = 0.03)				
	<i>Lutjanus synagris</i>	<i>Ocyurus chrysurus</i>		
Penaeoidea	0.32	0.29	23.36	0.75
Brachyura	0.42	0.14	22.77	0.71
Osteichthyes	0.10	0.75	16.90	0.57
Unidentified shrimp	0.11	0.00	11.46	0.50
Average dissimilarity = 94.04				
Sites (Si (Sp))* (df = 4; 653; Pseudo-F = 2.498; P (perm) = 0.018)				
	Río Lagartos	Dzilam de Bravo		
Penaeoidea	0.40	0.41	25.61	0.82
Osteichthyes	0.18	1.49	26.72	0.72
Brachyura	0.20	0.33	15.89	0.55
Average dissimilarity = 91.64 t = 4.1905; P (perm) = 0.001**				
	Río Lagartos	Celestún		
Penaeoidea	0.40	0.11	28.63	0.89
Brachyura	0.20	0.15	16.30	0.58
Osteichthyes	0.18	0.09	11.46	0.48
Caridea	0.03	0.06	9.74	0.55
Average dissimilarity = 90.61 t = 3.1392; P (perm) = 0.001**				
	Dzilam de Bravo	Celestún		
Osteichthyes	1.49	0.09	28.84	0.76
Penaeoidea	0.41	0.11	19.35	0.64
Brachyura	0.33	0.15	18.14	0.60
Average dissimilarity = 92.96 t = 3.0806; P (perm) = 0.001**				
Seasons (Se (Si (Sp)))* (df = 6; 653; Pseudo-F = 2.083; P (perm) = 0.001)				
	Cold	Warm		
Penaeoidea	0.30	0.31	23.27	0.75
Osteichthyes	0.41	0.85	24.77	0.70
Brachyura	0.19	0.28	16.43	0.57
Average dissimilarity = 91.64				

Diet composition also differed by fishing site for both *L. synagris* and *O. chrysurus*. In both species, shrimps were an important prey item, although Penaeoidea gradually increased as a proportion of diet from west to east (Celestún/Dzilam de Bravo/Río Lagartos). In contrast, the proportion represented by crabs in the *L. synagris* diet decreased from Celestún to Río Lagartos. For both species, differences in diet between sites, such as variations in species diversity and prey biomass, may be due to the prevailing hydrodynamic conditions in the eastern and western portions of the coast of Yucatan state. Celestún, in the west, is influenced by the Gulf of Mexico’s hydrodynamics and that of a large adjacent

coastal lagoon. Río Lagartos, in the east, is affected by the hydrodynamics of the Caribbean Sea, which drive formation of the Loop Current in the Gulf of Mexico and Campeche Bank, and upwelling of cold nutrient-rich waters. Dzilam de Bravo, in the centre of Yucatan’s northern coast, experiences freshwater discharges from the underground aquifer system (Merino, 1997; ArandaCirerol *et al.*, 2006; Herrera-Silveira and Morales-Ojeda, 2009). These results coincide with previous reports of spatial variation in the diet composition of these two snapper species in response to habitat characteristics and/or hydrodynamic conditions (Claro, 1983; Doncel and Paramo, 2010; Juárez-Camargo *et al.*, 2020).

Climate season also affected *L. synagris* and *O. chrysurus* diet composition. During the warm/rainy season, both species consumed more crabs and shrimps. This agrees with a reported higher intake of shrimp by *L. synagris* during the rainy season (June to September) due to greater primary production in the form of zooplankton and benthic organisms (Juárez-Camargo *et al.*, 2020). Changes in the diet of juvenile *L. synagris* in Brazil are induced by prey availability, which is indirectly controlled by reproductive pulses in prey species, and by physiochemical variations in the aquatic environment (Rosa *et al.*, 2015). Another study in Brazil, on the coast of Amazon state, found seasonal changes in *L. synagris* diet composition to be related to temperature variations and rainfall intensity (Fernandes *et al.*, 2020). For *O. chrysurus*, seasonal changes in diet have only been reported for Cuba, where zooplankton consumption increased during the summer (July-August) (Claro, 1983).

All available stomach content analysis methods present some disadvantages (Amundsen and Sánchez-Hernández, 2019), but the %F (presence-absence method) applied in the present study generates some of the most robust data for diet composition description in fish (Amundsen and Sánchez-Hernández, 2019; Baker *et al.*, 2014). Some of the main factors potentially affecting the type, amount and bulk of items in fish stomach contents include diel and seasonal cycles, fish size and differential digestion rates (Bowen, 1992). In the present study, all analysed fish were sampled during daylight and stomach contents were processed and fixed after dead specimens were preserved on ice for several hours. *Lutjanus synagris* actively feeds at dawn (Claro and Lindeman, 2008), leading to probable overestimation of the relative importance of slowly digested prey (*i.e.* crustaceans) (Bowen, 1992; Amundsen and Sánchez-Hernández, 2019). For example, crabs take twice as long to digest than fish in *L. synagris* (Sierra *et al.*, 2001). Diet composition in *O. chrysurus* is probably less affected by sampling time since this snapper feeds both during the day and night (Longley and Hildebrand, 1941; Claro and Lindeman, 2008). Indeed, VI values in the present results were higher for *L. synagris* (76-84%) than for *O. chrysurus* (63-77%), regardless of fishing site and climate season. All individuals were captured during the day, suggesting that the probability of capturing individuals with empty stomachs would be higher for *L. synagris* than for *O. chrysurus*. Water temperature also strongly affects digestion rate in fish. Snappers such as dog snapper *Lutjanus jocu* (Bloch & Schneider, 1801), schoolmaster snapper *Lutjanus apodus* (Walbaum, 1792), *L. griseus*, and *L. synagris* exhibit longer digestion periods in winter (45-50 h) than in summer (22-26 h) (Sierra *et al.*, 2001). The high VI values observed in species studied here may also be due to continued digestion post-capture. Therefore, bias in results can be expected when analysing seasonal variation in feeding habits, especially when stomach contents

are not fixed soon after capture. Fishing gear may also have had some effect on the high proportion of empty stomachs in the present results. The baited hooks and lines used in this study could have encouraged capture of hungry individuals with empty stomachs. However, similar VI values have been reported for *L. synagris* individuals captured using unbaited gear (91% with traps and 77% with gill nets) (Claro, 1981). Unlike hook-and-line gear, gill nets and traps can hold fish underwater for longer, making prey identification more difficult due to post-capture digestion of stomach contents (Bowen, 1992; Baker *et al.*, 2014). Finally, collection at greater depths (up to -40 m) can contribute to regurgitation and loss of stomach contents in specimens caused by the sudden change in hydrostatic pressure at the time of capture. For example, when captured at depths greater than about 20 m, many reef fishes such as vermilion snapper *Rhomboplites aurorubens* (Cuvier, 1829) often experience anatomical traumas due to the decompression experienced during the rapid ascent associated with capture (Collins *et al.*, 1999). In physoclastic fishes such as snappers, the swim bladder can rupture with rapid change from two to one atmospheres of pressure (20-10 m) (Burns and Restrepo, 2002; Burns *et al.*, 2008). In red snapper *Lutjanus campechanus* (Poey, 1860), a protruding stomach was observed in 28% of individuals caught at 27 m mean depth (Dorf, 1999), while an everted gas bladder was reported in 1% of those caught at 21-24 m but in 56% of those caught at 27-40 m (Gitschlag and Renaud, 1994).

On the continental platform north of the Yucatan Peninsula, all snapper species tend to occur at a rather high level (> 3) in the trophic web (Arreguín-Sánchez and Manickchand-Heileman, 1998). The present results confirm the high trophic position of *L. synagris* and *O. chrysurus* in this region even though the observed interspecific dissimilarity in diet composition suggests they play differentiated trophic roles in the ecosystem. Both species are depredated by some sharks and other large carnivores such as barracudas and groupers (Claro and Lindeman, 2008). Overexploitation of these two valuable snapper species could have significant impacts in the trophic web and contribute to disturbances in the ecosystem. The IUCN Red List of Threatened Species currently lists *L. synagris* as *Near Threatened* and *O. chrysurus* as *Data Deficient* (Lindeman *et al.*, 2016a, b). The diet composition data provided here is a vital addition to the biology of these snapper species, but much more data is needed before an effective legal framework for fishery management and monitoring can be developed to promote their sustainable exploitation and maintain their ecosystems in equilibrium.

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