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Comparative analysis of diet composition and its relation to morphological characteristics in juvenile fish of three lutjanid species in a Mexican Pacific coastal lagoon

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The main goal of this research was to investigate the differences in diet composition among three species of the genus *Lutjanus* inhabiting a coastal lagoon as juveniles. The working hypothesis was that these species feed on a common base of food resources and therefore, some niche overlap is present in terms of general diet composition. However, changes in the trophic niche with size and differences in some morphological traits among species explain observed differences in diet. Fish were collected during 42 sampling trips conducted regularly from February 2011 to January 2012 using several types of fishing gear. Total number of analyzed stomachs was 288 for *Lutjanus argentiventris* from 2.3 to 19.9 cm total length (TL); 178 for *Lutjanus colorado* ranging from 2.4 to 30.1 cm TL; and 183 for *Lutjanus novemfasciatus* with 1.2 to 20.0 cm TL. Results indicate that juveniles of all three lutjanid species share a general diet based on decapods and fishes. However, *L. novemfasciatus* has a more piscivorous habit, which can be explained by a more slender body shape and larger teeth, characteristics, which increase fish catching performance. Larger fish of all three species eat larger prey, which is consistent with the optimum foraging theory.

Keywords: Estuarine habitat, Feeding, Lutjanidae, Ontogenic changes, Trophic morphology.

Se investigaron las diferencias en la composición de la dieta de juveniles de tres especies del género *Lutjanus* que habitan una laguna costera. La hipótesis de trabajo fue que estas especies se alimentan de una base común de recursos alimentarios y, por tanto, alguna superposición del nicho está presente en términos de la composición general de la dieta. Sin embargo, los cambios en el nicho trófico con la talla y diferencias entre especies en algunas características morfológicas, explican las diferencias observadas en la dieta. Los peces fueron colectados durante 42 viajes de muestreo realizados de febrero del 2011 a enero del 2012 usando varios tipos de artes de pesca. Se analizaron 288 estómagos de *Lutjanus argentiventris* de 2.3 a 19.9 cm de largo total (LT); 178 de *Lutjanus colorado* entre 2.4 y 30.1 cm LT; y 183 de *Lutjanus novemfasciatus* de 1.2 a 20.0 cm LT. Los resultados indican que los juveniles de las tres especies de lutjánidos comparten una dieta general basada en decápodos y peces. Sin embargo, *Lutjanus novemfasciatus* tiene un hábito piscívoro mayor, el cual puede ser explicado por la forma del cuerpo más delgada y dientes mayores, características que incrementan la eficiencia para capturar peces. Los peces mayores de las tres especies comieron presas mayores y este cambio ontogénico es consistente con la teoría del forrajeo óptimo.

Palabras clave: Alimentación, Cambios ontogénicos, Hábitat estuarino, Lutjanidae, Morfología trófica.

Introduction

Species of the family Lutjanidae (snappers) are important components of artisanal fisheries in tropical regions. These fish are popular to eat, and are frequently sold in markets at an elevated price (Pimentel, Joyeux, 2010). More important from an ecological point of view, several species of lutjanids are ontogenetic habitat shifters (*sensu* Adams *et al*., 2006) and use coastal lagoons as nursery areas (Cocheret de la Moriniere *et al*., 2003; Aburto-Oropeza *et al*., 2009). The yellow snapper *Lutjanus argentiventris* (Peters, 1869), the Pacific dog snapper *L. novemfasciatus* Gill, 1862 and with

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less frequency the colorado snapper *L. colorado* Jordan & Gilbert, 1882, have been repeatedly reported as characteristic species of fish assemblages in Mexican Pacific coastal lagoons and estuaries (*e.g.* Yañez-Arancibia, 1978; Flores-Verdugo *et al*., 1990; Tapia-Garcia *et al*., 1998; Castro-Aguirre *et al.*, 1999; Cabral-Solís, Espino-Barr, 2004; Díaz-Ruiz *et al*., 2006; Mendoza *et al*., 2009). Recent studies in Barra de Navidad lagoon have reported these three species as regular components of the icthyofauna, appearing always as juveniles (González-Sansón *et al*., 2014a, 2014b, 2016).

The coexistence of three lutjanid species which have much the same body shapes (Fischer *et al*., 1995) and similar diets which are expected to be dominated by decapods and fishes (Rojas, 1997; Santamaría-Miranda *et al*., 2005; Ruiz-Nieto, 2005; Flores-Ortega *et al*., 2010, 2014) poses an important research question related to trophic niche overlap and the role played by morphological differences among these species. A well established ecological paradigm says that coexisting species must differ in their ecological requirements by at least some minimal amount to avoid competitive exclusion (Pianka, 1974). Two main explanations can be invoked for understanding how similar species can share the same habitat avoiding competitive exclusion. Firstly, the extent to which dietary overlap occurs within and between species will most likely vary with body size due to size-specific changes in foraging ability (Pessanha, Araujo, 2014). Secondly, when biotic interactions are strong, species coexistence may be facilitated by functional trait complementarity that gives rise to some resource partitioning (Montaña *et al*., 2014). Therefore, subtle differences in morphology and dentition should be expected in otherwise very similar species, as is the case of the three species included in this study. The relationship between morphology and feeding characteristics in fishes has been investigated by numerous authors (Clifton, Motta, 1998; Hugueny, Pouilly, 1999; Pouilly *et al*., 2003; Ward-Campbell *et al*., 2005; Wesneat, 2006; Wittenrich *et al*., 2009; Pessanha *et al*., 2015; Novakowski *et al*., 2016). Based on results obtained from previous studies, Nanami, Shimose (2013) stated that body shape variations of fishes and the variety of their dentition affect feeding performance. These authors also remarked that clarifying the interspecific difference in prey items of fishes in relation to body shape variations is a fundamental aspect to understand the feeding ecology of fishes.

Main goals of this study were a) to perform comparative analyses of the diets of three sympatric species of the genus *Lutjanus* with emphasis in trophic niche breadth and overlap; b) to investigate the existence of ontogenic changes in feeding habits during their juvenile stages and c) to compare the species on the basis of some morphometric and teeth characteristics. The working hypothesis was that the species involved in this study feed on a common base of food resources formed by invertebrates and small benthic-pelagic fishes and therefore, some niche overlap is present in terms of general diet composition. However, changes in the feeding niche with size and differences in some morphological traits among species explain observed differences in diet composition and contribute to facilitate their coexistence in the same estuarine system.

Material and Methods

Barra de Navidad lagoon is located on the Pacific coast of Mexico (19°11′25″N 104°39′53″W). It has a total surface of 3.76 km^3 and was categorized as III-A(III-B) by Lankford (1976), which means waves and coastal currents dominate its formation. The lagoon has a permanent inlet communicating with the sea. The freshwater input is strongly seasonal, due to a rainy season from June to October and a dry season with almost no rainfall from November to May. The lagoon is primarily euhaline (salinity 30-40), although it can be mixopolyhaline (salinity 18-30) during short periods during the rainy season (González-Sansón *et al*., 2014a).

Fish were collected during 42 regular sampling trips from February 2011 to January 2012. Sampling sites were chosen at random each month in an effort to cover the entire lagoon and to obtain a total sample representative of the water body. All sampling sites were characterized by a muddy substrate and relatively shallow depths (1-2 m). Monthly numbers of fish collected varied depending on natural abundance of the species, with 23 to 67 fish caught per month. Several supplementary samples were taken sporadically from 2013 to 2014. Fish were caught from late afternoon (4-5 pm) to midnight. Sampling gear included a beach purse seine (10 m long, 1 cm mesh size), a cast net (3 m, 2.5 cm mesh size) and four gill nets (60 m each) of different mesh sizes (7.0, 7.6, 8.9 and 10.2 cm). Sampled fish were taken to the laboratory where they were identified and their total lengths (TL) were measured. Stomachs were removed and contents preserved in 70% ethanol for later identification.

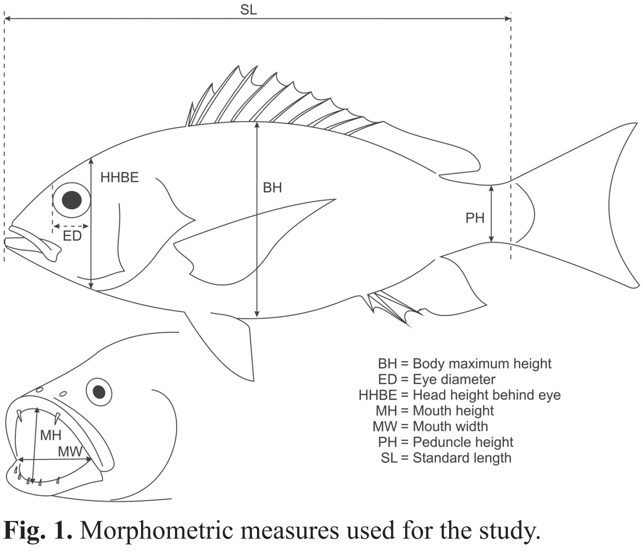
Stomach contents were examined under a dissecting DV4 Zeiss microscope and each food item was identified to the lowest possible taxonomic level, or recorded as unidentifiable. When possible, each item was measured to the nearest 0.1 mm. For shrimp and fish the total length was used, while for crabs the carapace width (Cw) was measured. Each food item was weighed using an Ohaus balance. The correlation of food item size with total fish length was analyzed using STATISTICA 7.1. To assess whether the number of sampled stomachs was sufficient to describe the diet, cumulative curves of trophic diversity were computed with EstimateS software (Colwell, 2013) based on 100 randomizations without replacement to ensure that the curves really reached an asymptotic value. The value of the Shannon index (H', Magurran, 2004) was plotted against the cumulative number of stomachs examined (Figueiredo *et al*., 2005). Each diversity curve was considered asymptotic if at least two previous values to the total sample trophic diversity (H'_{tot}) were in the range $H'_{tot} \pm 0.05H'_{tot}$ (Alonso *et al*., 2002). For further analyses, food items were pooled into food categories, using the family as the reference level. The relative importance of each food category in the diet was expressed after Hyslop (1980) as percentage of numerical abundance (N%), frequency of occurrence of food items in stomachs (F%), and weight (W%). The prey-specific index of relative importance (PSIRI) was calculated to get a better grasp of the importance of food items for each species, using the following equation (Brown *et al*., 2012):

$$\%PSIRI_i = [\%FO_i \text{ x } (\%PN_i + \%PW_i)]/2$$

where $\%PSIRI_i$ = PSIRI for prey i, expressed as percentage, $\%FO_i$ = Frecuency of ocurrency for prey i, expressed as percentage, $\%PN_i$ = Prey-specific numerical abundance for prey i, expressed as percentage, $\%PW_i$ = Prey-specific weight abundance for prey i, expressed as percentage.

To analyze ontogenetic changes, fish were classified into three groups based on their total length as follows: group 1, TL less than or equal to 7 cm; group 2, TL higher than 7 cm and less than or equal to 21 cm; and group 3, TL higher than 21 cm.

For morphological analyses standard length (SL), maximum body height (BH), head height behind eye (HHBE) peduncle height (PH), eye diameter (ED), mouth width (MW) and mouth height (MH) were measured to the nearest millimeter in a subsample of the individuals analyzed for stomach contents. Gape area (GA) was calculated assuming an elliptical form using the formula g=(3.1416 * MW * MH)/2 (Fig. 1). Dentaries and premaxillas of ten specimens of each species were obtained by boiling the fish heads, extracting the bones and cleaning them with a sodium hypochlorite solution. Cleaned bones were then photographed (Figs. 2-3) and teeth lengths were measured to the nearest tenth of millimeter using the free software ImageJ 1.42q (Schneider *et al*., 2012). Teeth were classified into three groups (Allen, 1985): (i) those in the dentary (DT), (ii) frontal large canine in the premaxilla (LCP) and (iii) smaller conical teeth in the premaxilla (SCP). All measures were expressed as ratios with respect to SL. Ratios were multiplied by convenient factors to avoid decimal zeros.



BH = Body maximum height
ED = Eye diameter
HHBE = Head height behind eye
MH = Mouth height
MW = Mouth width
PH = Peduncle height
SL = Standard length

Fig. 1. Morphometric measures used for the study.

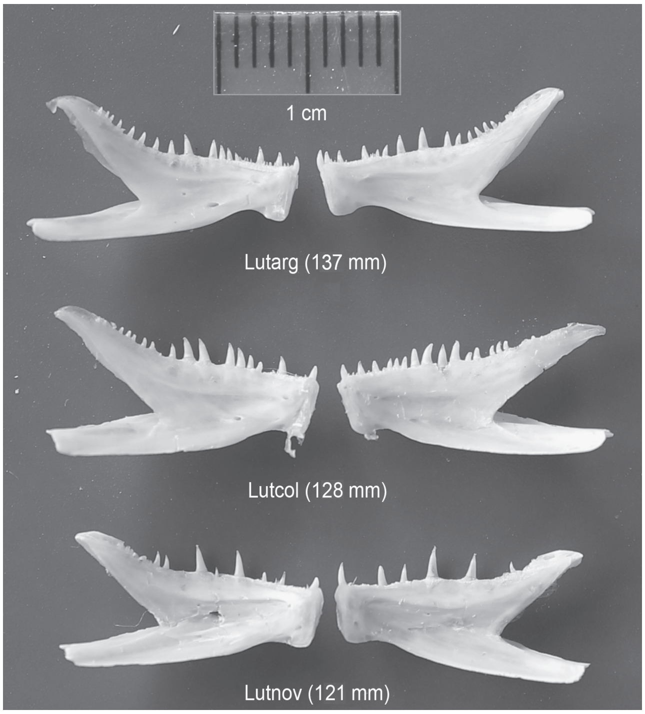


Fig. 2. Dentaries of three species of snappers. In brackets, standard lengths of fish. Lutarg: *Lutjanus argentiventris*; Lutcol: *Lutjanus colorado*; Lutnov: *Lutjanus novemfasciatus*

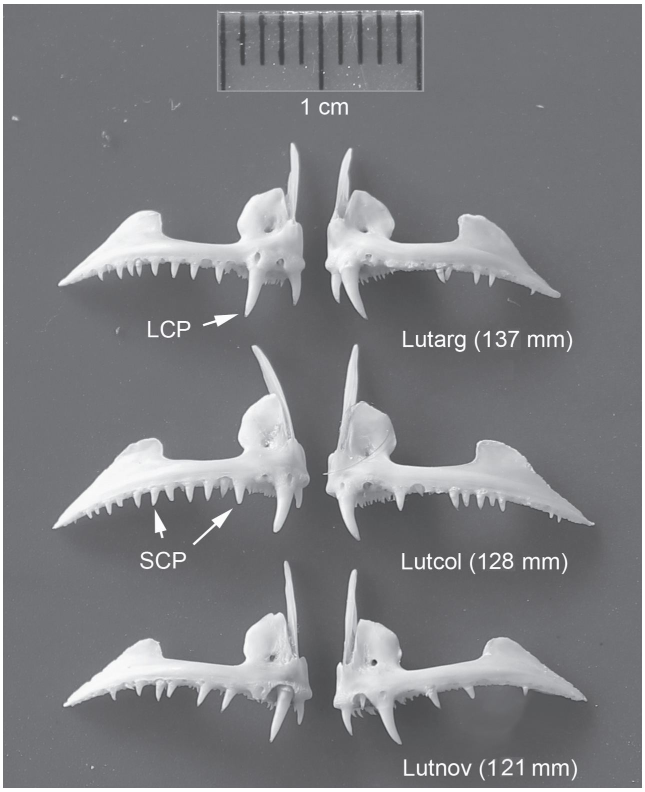


Fig. 3. Premaxillas of three species of snappers. In brackets, standard lengths of fish. LCP=Large canines in premaxillas; SCT=Smaller conical teeth in premaxillas. Lutarg: *Lutjanus argentiventris*; Lutcol: *Lutjanus colorado*; Lutnov: *Lutjanus novemfasciatus*.

All numerical analyses related to niche breadth and overlap were performed on W% values because we are primarily interested in future assessment of energy flow in the food web of the lagoon (Hansson, 1998). Statistical significance of differences among diet compositions of all pairs of species-size classes groups was assessed using numerical classification based on the Bray-Curtis index of similarity and UPGMA cluster algorithm. Similarity values were calculated on fourth-root transformed data of percentage weight diet composition to compensate the effect of dominant prey items in the comparisons. A SIMPROF test (Clarke *et al*., 2008) was used to assess the significance of the groups in the dendrogram. To further explore diet relationships, a Principal Coordinate Analysis (PCO) was performed on the same similarity matrix used for classification and a vector overlay was superimposed on the scatterplot of the two first PCO-axes including only food categories with 0.5 or higher values of Spearman correlations with the axes. The relative size and position of the vector overlay on the graph is arbitrary with respect to the underlying plot (Anderson *et al*., 2008).

Trophic niche breadth was measured using Smith´s index (FT), using the following equation (Krebs, 1998): $FT = \Sigma (\sqrt{p_j a_j})$, where p_j = proportion of diet item j, a_j = proportion of diet item j of total food items available (assumed equal for all items).

This measure was selected because its theoretical distribution is known and confidence intervals can be calculated (Krebs, 1998). Diet overlap was calculated using Pianka´s index (Gotelli, Graves, 1996). The null hypothesis of no niche overlap was tested using the methodology based in null models as described in Gotelli, Graves (1996). The program ECOSIM v. 7.72 (Gotelli, Entsminger, 2004) was used for simulations with 1000 iterations, using resampling algorithm R3 (*i.e.* retention of niche breadth with zero states reshuffling) and defining resource states as equiprobable.

The significance of differences in morphological variables among species was tested using one-way fixed effects ANOVAs followed by the Student-Newman-Keuls multiple comparisons test when F ratios were significant. Prior to ANOVAs the assumptions of normality and homoscedasticity were checked following the criteria of Underwood (1997). Analyses were made with packages STATISTICA 7.1 (StatSoft, 2006), PRIMER 6.0 (Clarke, Gorley, 2006) and PERMANOVA+ for PRIMER (Anderson *et al*., 2008). Significance level for all tests was $\alpha = 0.05$.

Results

The total number of analyzed stomachs was 288 (97 empty) for *Lutjanus argentiventris* from 2.3 to 19.9 cm TL; 178 (43 empty) for *Lutjanus colorado* ranging from 2.4 to 30.1 TL; and 183 (62 empty) for *Lutjanus novemfasciatus* from 1.2 to 20.0 cm TL. Diets of the three species were dominated by fish and decapods (Tab. 1).

The diet of *L. argentiventris* was composed mainly of decapods (62% PSIRI) with an important contribution of fish in weight (21% PSIRI) and much smaller contributions of stomatopods and other invertebrates (Tab. 1). Decapods pertained mostly to four families (in descending order of their contributions as % PSIRI): i) Penaeidae, which was represented by juveniles of *Penaeus californiensis* Holmes, 1900 (5.3-15 mm TL); ii) Portunidae, dominated by juvenile *Callinectes arcuatus* Ordway, 1863 (1.8-16.0 mm Cw); iii) Xanthidae, represented mainly by *Panopeus* sp. (4.5-16.0 Cw) with small quantities of *Lophoxanthus lamellipes* (Stimpson, 1860) (4.5-7.7 mm Cw), *Actea* sp., *Eurypanopeus* sp., and *Lophopanopeus* sp; and iv) Alpheidae, represented by four species dominated by *Alpheus mazatlanicus* Wicksten, 1983 (10.0-14.0 mm TL) and *A. pacificus* Dana, 1852 (7.7-16.0 mm TL), with small contributions by *A. floridanus* Kingsley, 1878 (one specimen of 5.4 mm TL) and *A. cylindricus* Kingsley, 1878 (not measured, partially digested). Identifiable fish remains were dominated by Gobiidae (not measured, partially digested) with a smaller representation of Congridae (one species of genus *Heteroconger* Bleeker, 1868, 42 mm TL), Lutjanidae (genus *Lutjanus* Bloch, 1790, 15.0-18.0 mm TL), Eleotridae (*Erotelis armiger* (Jordan & Richardson, 1895), 20 mm TL) and Paralichthydae (not measured, partially digested).

The main components in the diet of *L. colorado* were decapods (68% PSIRI) and in less proportion fish which contributed 28% of total PSIRI. Incidental contributions of stomatopods, mollusks and other invertebrates were found (Tab. 1). Decapods were dominated by five families (in descending order of their contributions as % PSIRI): i) Portunidae, represented by juveniles of *C. arcuatus* (1.7-37.0 mm Cw); ii) Upogebiidae, mainly *Upogebia dawsoni* Williams, 1986 (19.0-23.0 mm TL); iii) Alpheidae with only one species, *A. mazatlanicus* (8.0-29.0 mm Cw); iv) Penaeidae, represented by juveniles of *F. californiensis* (7.0-10.0 mm TL) and v) Grapsidae, represented by *Goniopsis pulchra* (Lockington, 1877) (7.2-21.0 mm Cw) and *Grapsus grapsus* (Linnaeus, 1758) (8.6 mm Cw). A high percentage of fish remains found in stomachs of this species were too digested for identification to any taxonomical level. Of those which were identifiable, the dominant family was Eleotridae, represented by *Erotelis armiger* (80.0-95.0 mm TL).

The diet of *L. novemfasciatus* was dominated almost equally by decapods (50% PSIRI) and fishes (44% PSIRI) with a small amount of other invertebrates (Tab. 1). Decapods were dominated by four families (in descending order of their contributions as % PSIRI): i) Palaemonidae, dominated by *Palaemon hiltoni* (Schmitt, 1921) (6.2-12.9 mm TL); ii) Penaeidae, represented by juveniles of *F. californiensis* (7.0-15.0 mm TL); iii) Portunidae, represented by juveniles of *C. arcuatus* (2.0-14.0 mm Cw) and iv) Upogebiidae, mainly *U. dawsoni* (14.0-22.0 mm TL). Although a high percentage of fish remains found in stomachs of this species were too digested, a portion was identifiable and revealed higher prey diversity (seven families) in this species compared to the other two species included in this research. Those fish which were less damaged by digestion and could be measured included: an unidentified specimen of Ariidae (possibly *Sciades guatemalensis* (Günther, 1864), 27.0 mm TL); *Centropomus robalito* Jordan & Gilbert, 1882 (22.0-24.0 mm TL); unidentified specimens of Gerreidae (14.0-16.0 mm TL); *Heteroconger* sp. (50.0-70.0 mm TL) and the genus *Anchoa* Jordan & Evermann, 1927 (22.0-54.0 mm TL).

Fish longer than 21 cm were not present in sampled individuals of the species *L. argentiventris* and *L. novemfasciatus*. Therefore, only seven groups resulted from the combination of species and length classes. In all groups the cumulative curves of trophic diversity reached an asymptote, indicating adequate sample sizes (Fig. 4).

Tab. 1. Diet composition of three species of snappers in Barra de Navidad lagoon. W%: percentage weight; N%: percentage number; F%: percentage frequency; P%: percentage of prey-specific index of relative importance (PSIRI). NI=Not identified.

	Lutjanus argentiventris				*Lutjanus colorado*				*Lutjanus novemfasciatus*			
	W%	N%	F%	P%	W%	N%	F%	P%	W%	N%	F%	P%
Decapoda				**61.85**				**68.53**				**49.9**
Alpheidae	8.58	4.19	7.18	6.39	4.25	13.54	15.11	8.90	1.13	1.05	2.46	1.09
Callianassidae									0.01	0.26	0.82	0.14
Gecarcinidae	0.02	0.12	0.51	0.07	0.62	0.79	2.88	0.71				
Epialtidae	0.74	0.12	1.54	0.43								
Grapsidae	0.37	0.12	1.03	0.25	6.22	5.17	10.79	5.70	0.35	0.79	1.64	0.57
Ocypodidae					1.39	1.33	2.16	1.36				
Palaemonidae	0.29	1.23	3.08	0.76	0.47	3.98	5.76	2.23	11.82	8.92	11.47	10.37
Penaeidae	15.76	18.13	23.59	16.95	6.11	6.89	10.79	6.50	4.76	11.8	18.85	8.28
Pinnotheridae	0.17	0.25	1.03	0.21	0.04	0.27	2.16	0.16				
Porcellanidae	4.04	2.22	4.1	3.13	0.26	1.59	6.47	0.93	0.13	0.53	3.28	0.33
Portunidae	13.05	14.8	20.51	13.93	22.59	20.82	23.02	21.71	3	13.52	12.29	8.26
Processidae	0.19	0.25	1.03	0.22	0.01	0.53	2.16	0.27				
Sicyoniidae	0.04	0.12	0.51	0.08								
Upogebiidae	6.33	2.1	5.64	4.22	9.58	8.41	13.67	9.00	9	4.2	7.38	6.60
Xanthidae	14.16	3.94	8.2	9.05	1.89	3.98	5.75	2.94	0.48	0.53	4.1	0.51
Decapoda NI	1.9	10.42	15.9	6.16	1.43	14.8	12.23	8.12	2.21	25.29	22.13	13.75
Stomatopoda												
Squillidae	1.2	0.49	1.54	0.85	0.2	0.41	2.16	0.31				
Mollusca				**0.00**				**2.95**				**0.00**
Solecurtidae					0.98	0.53	2.16	0.76				
Bivalvia NI					0.32	0.27	1.44	0.30				
Molluska NI					0.14	0.53	2.16	0.34				
Other invertebrates	2.03	31.18	5.13	16.61	0.45	2.65	7.19	1.55	3.66	9.14	12.3	6.40
Fish				**20.73**				**28.30**				**43.73**
Ariidae									1.53	0.26	0.82	0.90
Centropomidae									0.81	0.79	2.46	0.80
Congridae	1.16	0.12	0.51	0.64					1.43	0.53	1.64	0.98
Eleotridae	0.71	1.14	3.08	0.93	10	3.36	5.75	6.68	0.68	0.14	2.46	0.41
Engraulidae									4.4	2.72	10.65	3.56
Gerreidae									3.32	0.79	2.46	2.06
Gobiidae	9.85	3.39	7.18	6.62					2.4	1.72	5.74	2.06
Lutjanidae	0.74	0.25	1.03	0.50								
Paralichthyiidae	0.07	0.12	0.51	0.10	0.38	0.27	0.72	0.33				
Fish NI	18.58	5.29	10.26	11.94	32.68	9.89	15.83	21.29	48.89	17.02	27.05	32.96

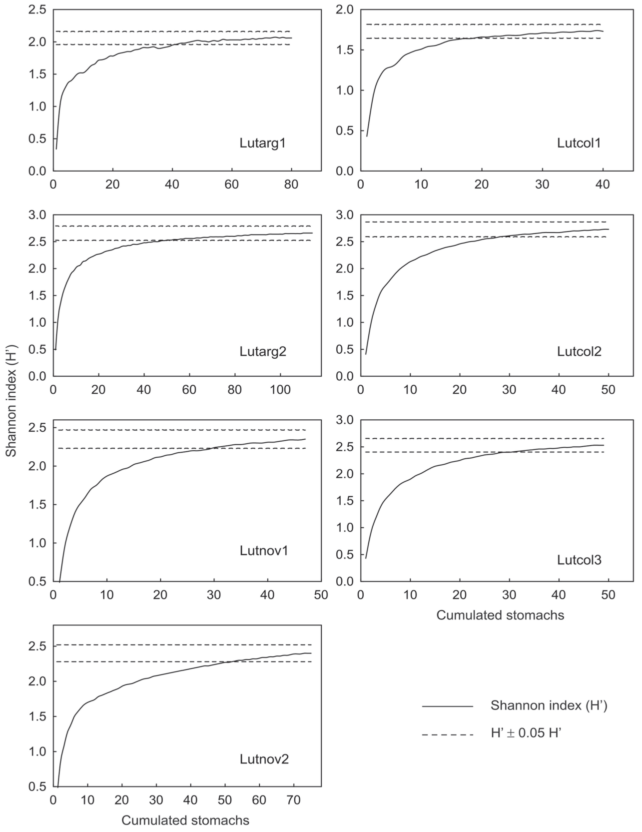


Fig. 4. Cumulative curves of food items. Lutarg: *Lutjanus argentiventris*; Lutcol: *Lutjanus colorado*; Lutnov: *Lutjanus novemfasciatus*. Numbers indicate size classes: 1 for LT < 7 cm; 2 for LT ≥ 7 cm and LT < 21 cm; 3 for LT ≥ 21 cm.

Numerical classification of the seven species-size groups yielded two significant clusters (Fig. 5a). The first cluster (I) included both size-classes of *Lutjanus novemfasciatus* joining at a similarity value of 86.7. The second cluster (II) was formed by all size-classes pertaining to *L. colorado* and *L. argentiventris* which join at a similarity level of 58.8%. The first axis of PCO explained 50.2% of total variation while the second axis explained 23.2%, resulting in an easily interpretable two dimensional diagram with a 73.4% of explained variation (Fig. 5b). Based on the vector overlay of prey categories it can be concluded that the main food items explaining the ordination of samples along the first axis are most fish categories and some invertebrate categories (*e.g.* Palaemonidae, Callianassidae) to the left side while Eleotridae, Paralichthyiidae and most decapod families (*e.g.* Solecurtidae, Alpheidae, Portunidae, Gecarcinidae, Ocypodidae, Grapsidae) dominated in the right side of this axis. This can be considered as a gradient of decreasing piscivory. Ordination of species-size groups along the first axis match well with numerical classification results separating *L. novemfasciatus* from the two other species. Projection on the second axis allows further separation of *L. argentiventris* from *L. colorado*, supporting the clustering observed in the numerical classification which was, however, a non-significant grouping after the SIMPROF test. Considering the percentage prey weight and the vector overlay, it is evident that the separation along this axis is due mainly to Eleotridae and Portunidae, which are dominant preys items in *L. colorado*, and Gobiidae, Panaeidae and Xanthidae, which are dominant in *L. argentiventris* diet (Tab. 1).

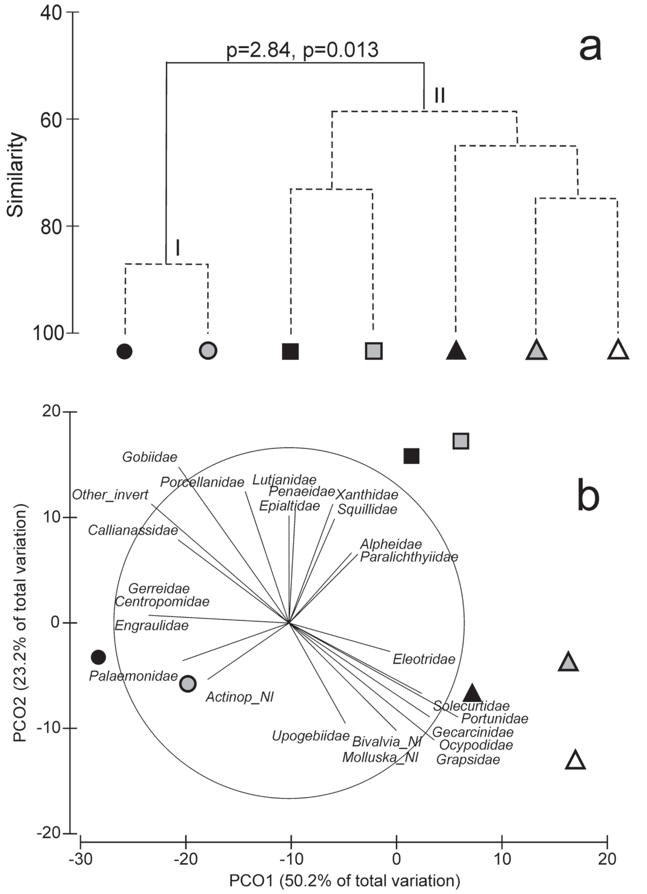


Fig. 5. a: Dendrogram showing the result of numerical classification of stomach contents. Results of SIMPROF test separating significant groups are given. **b:** Principal coordinate analysis plot. Vector overlay shows food categories with Spearman's correlation values of 0.5 or higher with ordination axes. Data pooled by species (circles: *Lutjanus novemfasciatus*; squares: *Lutjanus argentiventris*; triangles: *Lutjanus colorado*) and size classes (black: ≤ 7 mm TL; grey: > 7 y ≤ 21 mm TL; white: > 21 mm TL).

Estimates of Smith's index (niche breadth) varied from 0.732 to 0.890 with lower values associated to larger sizes and higher percentage of fish by weight in diet composition inside each species (Fig. 6). Estimates of Pianka's index (niche overlap) varied between 0.598 and 0.990 (Tab. 2). In all cases pairs of size-classes within each species showed higher values than pairs of size-classes between species. Mean observed overlap was 0.761 and was significantly higher (p=0.001) than mean expected overlap (0.193) yielded by simulation under the null model of no diet overlapping. Variance of overlap values was 0.011 and was not significantly different (p=0.058) with the mean of simulated variance values (0.023) obtained under the null model.

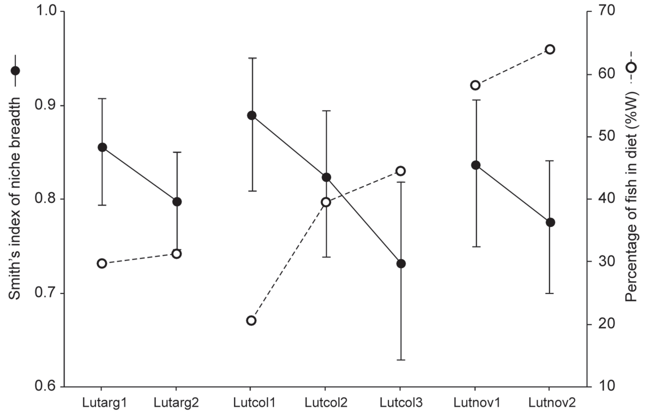


Fig. 6. Estimated values of Smith´s index of niche breadth (black circle, continuous line) and 95% confidence intervals (vertical lines). Also shown percentage weight of fish in diet (white circles, dashed lines). Data pooled by species (Lutarg: *Lutjanus argentiventris*; Lutcol: *Lutjanus colorado*; Lutnov: *Lutjanus novemfasciatus*) and size classes (1: ≤ 7 mm TL; 2: > 7 y ≤ 21 mm TL; 3: > 21 mm TL).

Tab. 2. Pianka's overlap indices among species size classes. Highlighted values correspond to pairs including size-classes of the same species. Lutarg: *Lutjanus argentiventris*; Lutcol: *Lutjanus colorado*; Lutnov: *Lutjanus novemfasciatus* ; 1: ≤ 7 mm TL; 2: > 7 y ≤ 21 mm TL; 3: > 21 mm TL.

	Lutarg1	Lutarg2	Lutcol1	Lutcol 2	Lutcol3	Lutnov1	Lutnov2
Lutarg1	-						
Lutarg2	0.906	-					
Lutcol1	0.826	0.774	-				
Lutcol2	0.798	0.715	0.820	-			
Lutcol3	0.799	0.707	0.846	0.898	-		
Lutnov1	0.696	0.620	0.711	0.619	0.801	-	
Lutnov2	0.693	0.598	0.692	0.641	0.832	0.990	-

A significant rank correlation between prey size and fish length was found for food items classified as decapods (Fig. 7) and fishes (Fig. 8) for pooled data. The analyses for decapod prey made for each species separately yielded significant correlations for *L. argentiventris* (r_s=0.43, p<0.001, n=113) and *L. colorado* (r_s=0.72, p<0.001, n=73) but no significant correlation for *L. novemfasciatus* (r_s=0.06, p=0.561, n=80). Fish prey showed significant correlations with predator size for *L. colorado* (r_s=0.92, p=0.003, n=7) and *L. novemfasciatus* (r_s=0.69, p=0.018, n=11) but not for *L. argentiventris* (r_s=0.74, p=0.153, n=5), where the sample size was too low.

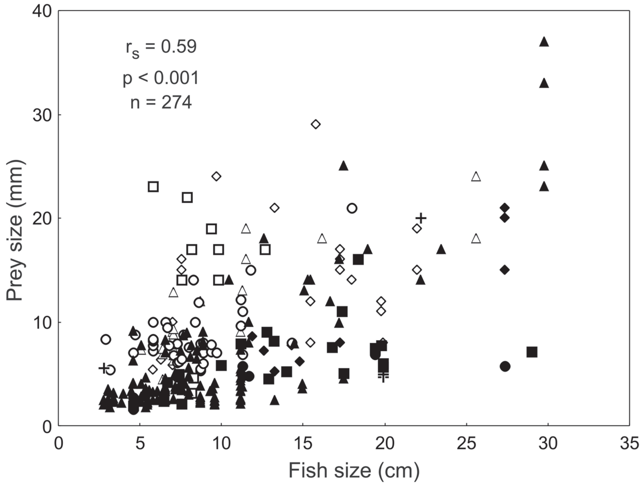


Fig. 7. Scatterplot of prey size *vs.* fish size for decapods found in the stomachs of three species of snappers. Main food categories identified by different symbols: White diamons = Alpheidae; white triangles = Palaemonidae; White circles = Penaeidae; White squares = Upogebiidae; black diamonds = Grapsidae; black triangles = Portunidae; black circles = Porcellanidae; black squares = Xanthidae; crosses = other items.

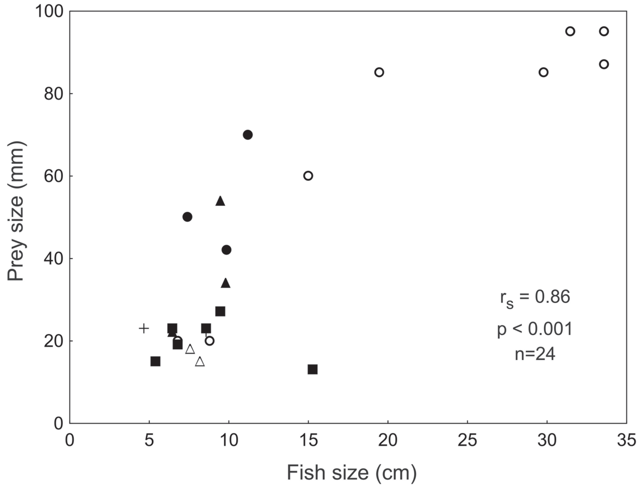


Fig. 8. Scatterplot of prey size *vs.* fish size for fishes found in the stomachs of three species of snappers (data pooled for all species). Main food categories identified by different symbols: White circles = Eleotridae; Black circles = Congridae; Triangles = Engraulidae; White triangles = Lutjanidae; Crosses = Centropomide; Black square = Other.

Most morphometric measures showed significant differences among species (Tab. 3). Relative body height and head height behind the eye were not different between *L. argentiventris* and *L. colorado*, but were significantly greater in those two species than *L. novemfasciatus*, which resulted to be the more slender species. Relative eye diameter was different among species, with *L. argentiventris* having the largest eye and *L. colorado* the smallest. Relative peduncle height and mouth width were significantly larger in *L. novemfasciatus* compared to the other species, which showed no statistical differences between them. Relative mouth gape was not different between *L. novemfasciatus* and *L. colorado*, but was significantly greater in these two species compared to *L. argentiventris.* In pooled data for all three species, a high correlation was found between length and mouth gape (Fig. 9). Relative length of dentary and conical premaxilla teeth were significantly higher in *L. novemfasciatus* compared to the other two species. In addition, the conical premaxilla teeth were relatively larger in *L. colorado* compared to *L. argentiventris*.

Tab. 3. Means, standard errors (SE) and ANOVAs results for the morphometric variables of *Lutjanus argentiventris* (Lutarg), *L. colorado* (Lutcol) and *L. novemfasciatus* (Lutnov) expressed as ratios on standard length. SL: standard length, BH: maximum body height, ED: eye diameter, HHBE: Head height behind eye, PH: peduncle height, MH: mouth height, MW: mouth width, GA: Gape area, DT: length of dentary's teeth, LCP: length of large canines in premaxilla, SCT: length of small conical teeth in premaxila. Different letters besides the means indicate significant differences after the SNK test.

Variable		Lutarg		Lutcol		Lutnov		F	df	p
BH*100/SL	Means	36.98	a	36.97	a	34.41	b	19.42	2,153	<0.001
	SE	0.22		0.51		0.24				
ED*100/SL	Means	11.01	a	8.96	c	9.90	b	29.72	2,153	<0.001
	SE	0.13		0.34		0.11				
HHBE*100/SL	Means	26.07	a	25.24	a	24.04	b	4.18	2,153	0.017
	SE	0.21		0.26		0.17				
PH*100/SL	Means	12.03	b	12.27	b	12.73	a	7.80	2,153	<0.001
	SE	0.10		0.18		0.10				
MH*100/SL	Means	10.74		10.35		10.76		0.73	2,153	0.482
	SE	0.16		0.30		0.25				
MW*100/SL	Means	7.78	b	8.13	b	9.05	a	10.11	2,153	<0.001
	SE	0.13		0.27		0.31				
log(GA)*10/log(SL)	Means	7.51	b	8.88	a	8.36	a	6.75	2,153	0.002
	SE	0.19		0.33		0.23				
DT*1000/SL	Means	30.26	b	34.19	b	57.95	a	97.81	2,221	<0.001
	SE	0.95		1.03		2.39				
LCP*1000/SL	Means	150.28		153.48		148.38		2.61	2,27	0.091
	SE	2.09		0.67		1.66				
SCT*1000/SL	Means	30.42	c	36.27	b	59.84	a	150.80	2,182	<0.001
	SE	0.84		1.01		1.44				

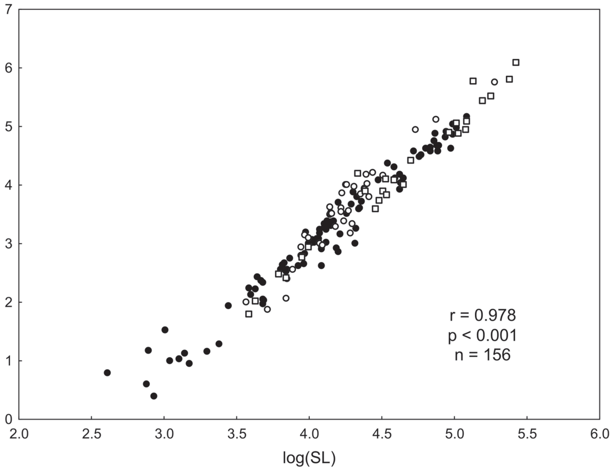


Fig. 9. Variation of gape size (log transformed) with standard length (SL, log transformed) for individuals of three species of *Lutjanus*. Filled circles: *L. argentiventris*; Open circles: *L. novemfasciatus*; Squares: *L. colorado*.

Discussion

The present study showed clear difference in diet composition among three lutjanid species. Both the numerical classification and simulation using null models support the idea of some niche overlap. At the same time, slight but significant differences in diet composition were present and significant among species. This result matches well with the fact that diet overlap among size classes inside each species is always higher than diet overlap among size classes of different species. Interspecific differences in diet composition found in this study result from variations in the proportion of decapod and fish prey, with an increase in the proportion of fish from *Lutjanus argentiventris* and *L. colorado* to *L. novemfasciatus*. These results indicate a more piscivorous habit in *L. novemfasciatus* compared to the other two species. A similar pattern emerges from the following summary of the results obtained for the same three species by several authors in other places of the Mexican Pacific. Flores-Ortega *et al*. (2010; 2014) found a diet based in crustaceans and fishes for *L. argentiventris* collected off Jalisco. Vazquez *et al*. (2008) investigated the diet of same species in La Paz bay (Gulf of California) and reported that main items in the diet of juvenile fish were non identified organic matter, the decapod *Upogebia pugettensis* and penaeid shrimps. Ruiz-Nieto (2005) reported the feeding habits of *L. argentiventris* in Sinaloa and found a diet dominated by shrimps and crabs for medium sized fishes (14-26 cm) while larger fish (27-58.8 cm) fed mainly on fishes. Santamaría-Miranda *et al*. (2005) analyzed stomach contents of *L. colorado* (14.4-40 cm LT) caught with long-line in coastal waters of the Gulf of California and found a diet based on invertebrates dominated by decapods and stomatopods with no fish reported in stomach contents. In contrast with the two former species, a diet dominated by fishes with a small proportion of crustaceans was reported for *L. novemfasciatus* by Yañez-Arancibia (1978) in several coastal lagoons from Guerrero, Ruiz-Nieto (2005) in estuarine habitats of Sinaloa, both.

Comparative analyses of morphometric characteristics help explain the interspecific differences in the diet of the three studied species. The significant lower relative body height (BH) and head height behind the eye (HHBE) found for *L. novemfasciatus* implies flatter body and head, a characteristic which Nanami, Shimose (2013) associated with a higher proportion of fishes in the diet of snapper species. These authors also found that fish were the major prey items for species of snappers with a shallower body depth and longer teeth, which match well with the findings for *L. novemfasciatus* reported here.

Prey sizes showed positive correlation with fish size, which in turn was strongly correlated with mouth gape. This result is explained by the ability of predators with larger gape for capturing and ingesting larger prey, and it is an important ontogenetic change that has also been identified for other fish species (Edgar, Shaw, 1995; Hyndes *et al*., 1997; Duarte, Garcia, 1999; Saucedo-Lozano *et al*., 1999; Scharf *et al*., 2000; Cocheret de la Moriniere *et al*., 2003; Pessanha, Araujo, 2014). The decrease in niche breadth for increasing size-classes inside each species found in our research, can be interpreted as a progressive specialization in feeding habits. This is consistent with the increase in the percentage of fish in the diet of larger size-classes inside each species. As snappers become larger, invertebrates play a lesser role in their diets and fish adopt a more piscivorous feeding behavior narrowing their food spectra. A similar result has been found for species of genus *Lutjanus* by other authors (Ruiz-Nieto, 2005; Vazquez *et al*., 2008; Wells *et al*., 2008; Pimentel, Joyeux, 2010). A transition from invertebrates to fishes in diet appears to be very general in ram-suction feeding fishes and is probably driven largely by the constraints of mouth size on prey capture ability (Wainwright, Richards, 1995). This is to be expected after the optimum foraging theory, which states that with an increase in size, predators tend to consume heavier prey, thus maximizing the energetic gain relative to capture effort (Duarte, Garcia, 1999). This result supports also our working hypothesis.

Numerical classification did not show differences in diet composition among size-classes for any species. This seems contradictory with the well supported ontogenic changes discussed above. A plausible explanation for this inconsistency is that the significance test used to define interpretable clusters (SIMPROF) is sensitive to the number of samples (in our case seven combinations of species by size-classes). More specifically, the power of the test to detect structure will tend to increase as the number of samples increases, so that the similarity profile displays a richer set of similarities (Clarke *et al*., 2008). In other words, the SIMPROF test was able to detect differences in diet composition among species (number of samples = 7) but was not powerful enough for detecting differences among size-classes inside each species (number of samples = 2 or 3).

After Gotelli, Graves (1996) a significantly large overlap might indicate shared resource utilization and a lack of competition. These authors argument that it is also possible that high overlap implies strong competition that has not yet led to divergence in resource use. In our case, additional data on resource availability and species interactions would be necessary for a definitive answer (Raborn *et al*., 2004). It should be emphasized, however, that fish included in our study are juvenile individuals which are part of the lagoon´s fish assemblage just for a short period (compared to their life spans). For this reason, any competition by food resources inside the lagoon (in case such resources were in shortage) will be transitory. In addition, ontogenetic changes towards larger preys as fishes grow have also played a fundamental role to reduce inter and intraspecific competition (Cocheret de la Moriniere *et al*., 2003; Pimentel, Joyeux, 2010; Pessanha, Araujo, 2014).

In summary, the results obtained indicate that juveniles of three lutjanid species cohabiting an estuarine lagoon share a general diet based on decapods and fishes. However, one of these species, *Lutjanus novemfasciatus*, has a significantly more piscivorous habit and this can be explained by a more slender body shape and larger teeth, characteristics which increase fish catching performance. Size-related changes in the proportion of food categories in the diet could not be demonstrated for any species but larger fish of all three species eat larger prey, and this ontogenetic change is consistent with the optimum foraging theory.

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