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# Feeding habits of the spotted rose snapper, *Lutjanus guttatus*, (Actinopterygii, Perciformes, Lutjanidae), in the central Gulf of California, BCS, Mexico

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## Abstract

The spotted rose snapper, *Lutjanus guttatus* (Steindachner, 1869), is an important resource for the coastal fisheries of the Gulf of California, mainly due to its high commercial value. Despite this, there are no management measures for this species, owing in part to a lack of information on its basic biology and its trophic ecology in the area. In this context, the presently reported study had as objective to describe the feeding habits of *L. guttatus* through stomach content analyses, as well as to describe possible changes linked to sex, size, and season. Specimens were caught monthly from June 2016 to September 2017 with gillnets in Santa Rosalía, BCS, Mexico. The abundance, weight, and frequency of occurrence of each prey were assessed, and these parameters were integrated into the index of relative importance (%IRI) to determine the importance of each prey item in the *L. guttatus* diet. The Levin's index was used to assess the trophic niche width of the species, the feeding strategy was evaluated using Costello's graphic method and the trophic level was calculated. Finally, to establish whether there were significant differences in the diet by sex, size, or season a PERMANOVA test was used with a 95% confidence level. A total of 202 *L. guttatus* stomachs were analyzed, 191 of which contained food. A total of 26 prey items were identified. According to the %IRI, the most important prey were the teleost fishes *Harengula thrissina* (Jordan et Gilbert, 1882) (45.7%) and *Sardinops sagax* (Jenyns, 1842) (34.8%), the euphausiid *Nyctiphanes simplex* (13.4%), and the crustacean *Penaeus* spp. (5.6%). The PERMANOVA analysis resulted in significant differences between the analyzed categories; however, there were no significant differences in the interactions among the categories. According to Levin's index, *L. guttatus* had a narrow trophic width, with changes in the main prey consumed by the different categories. According to our results, *L. guttatus* can be considered a benthopelagic opportunistic carnivorous predator with a narrow trophic niche, presenting mostly quantitative variations in its diet according to sex, size, and season. Its trophic plasticity allows it to take advantage of the most available and abundant food resources.

## Keywords

Lutjanidae, diet, sardines, euphausiids, Gulf of California.

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# Introduction

Studies on the food habits of fish are fundamental to understand the structure and functioning of marine ecosystems (Díaz-Ruiz et al. 2004; Freitas et al. 2015), as they allow us to understand ecological aspects of species such as trophic interactions, their role in the food chain, and the energy flow through ecosystems (Brown et al. 2012). They are also extremely important when establishing management plans for species that are exploited due to their economic importance (Rojas-Herrera et al. 2004; Moreno-Sánchez et al. 2016). Within the family Lutjanidae, commonly known as snappers, the genus *Lutjanus* is the most diverse, as it includes 73 of the 113 species recorded in the family; among these, nine species are distributed in the eastern Pacific (Froese and Pauly 2019).

Snappers are commercially important components of artisanal fisheries worldwide. They are appreciated as a high-quality food resource, they are in high demand by the population, and their commercial value is higher than that of other fish species (Rojas 1997; Rojas-Herrera and Chiappa-Carrara 2002). This is reflected in the global catch numbers; according to the FAO (2020) over the past two decades, an average of 217 000 tons of snapper was caught annually.

Within this family, the spotted rose snapper, *Lutjanus guttatus* (Steindachner, 1869), is distributed from the Gulf of California, through Mexican Pacific coasts, to Peru. This is a demersal species that inhabits coastal reefs to a maximum depth of 30 m. Sexes are separate and those fish reach the size at first sexual maturity at 30 cm (Sarabia-Méndez et al. 2010).

*Lutjanus guttatus* is an important resource for fisheries in the coastal area of the Gulf of California, where one of the main economic activities is coastal fishing. Approximately 136 tons are captured annually in the area, representing an economic value of 4 million MXN (~ 207 590 USD) (CONAPESCA 2014).

Various studies have reported on the feeding habits of this species, although the majority of studies have been performed in the southernmost portion of its distribution, corresponding to tropical regions. These studies have reported that *L. guttatus* is a benthic carnivorous predator that feeds mainly on fish and small crustaceans (Rojas-Herrera and Chiappa-Carrara 2002; Rojas-Herrera et al. 2004; Tripp-Valdez and Arreguín-Sánchez 2009).

Previous studies have also shown latitudinal variations in the feeding habits of *L. guttatus*. The primary and secondary food items were, respectively, crustaceans and fishes at El Salvador (Rojas-Herrera et al. 2004), whereas they were, respectively, small-sized fish (Engraulidae and Clupeidae) and crustaceans, off the Guerrero coast, Mexico (Rojas-Herrera and Chiappa-Carrara 2002). Moreover, both crustaceans (Xanthidae) and fishes (Engraulidae) were the main prey items in the southern Gulf of California, Mexico (Tripp-Valdez and Arreguín-Sánchez 2009).

These data have led scientists to infer that the composition of the diet in *L. guttatus* depends mainly on variations in food availability, more than on resource selection by the predator (Rojas-Herrera and Chiappa-Carrara 2002). Moreover, the previously mentioned studies showed that there were changes in the diet of *L. guttatus* according to intraspecific variations such as size, and that sex and season did not lead to significant differences in diet (Rojas-Herrera and Chiappa-Carrara 2002). It should be noted that *L. guttatus* plays a role as predator and as prey and that this species is considered important in recirculation and energy transfers from the epifauna and infauna to upper trophic levels (Rojas 2006; Navia et al. 2016).

Despite its economic and ecological importance, there are no studies on the feeding habits of *L. guttatus* in the subtropical portion of its distribution area. The objective of the presently reported study was to evaluate the trophic spectrum of *L. guttatus* in the central Gulf of California, analyzing variations in the diet by sex, size, and season, to generate information on its diet in the higher latitudes of its distribution and identify possible variations compared with lower latitudes.

# Materials and methods

## Sample collection, processing, and data analysis

Monthly sampling was undertaken from June 2016 to September 2017 in the mining town of Santa Rosalía, Baja California Sur, in the central Gulf of California (Fig. 1). Specimens were obtained from the coastal fishery, which employs 300-m long gillnets with 102 mm mesh size; nets are left approximately 10 h in the water, from sunset to sunrise. Specimens were frozen and transported to the Ecology Laboratory of the Interdisciplinary Centre of Marine Sciences of the National Polytechnic Institute (Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional, CICIMAR-IPN). The total length ($L_t$, cm) and weight ($W$, g) of each organism were recorded. Sex was identified through the direct observation of the gonads and

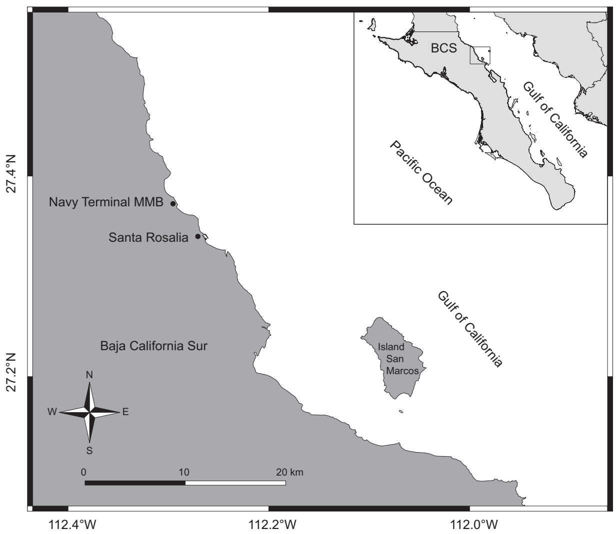


**Figure 1.** Map of the study area, Santa Rosalía, BCS, central Gulf of California.

confirmed through histological analyses following methods proposed by Arellano-Martínez et al. (2001). Because captured individuals were at or above the size at first maturity (i.e., 30 cm) (Sarabia-Méndez et al. 2010), the specimens were categorized into three groups following Sturges' rule (Daniel 1997) (group 1 = 28–38 cm, group 2 = 39–48 cm, and group 3 = 49–58 cm).

To identify the seasonal variation in sea surface temperature, the monthly and annual mean values of sea surface temperature were calculated based on MODIS-AQUA satellite images with 1.1 km resolution. Temperature data were obtained from the ERDDAP portal of the National Oceanic and Atmospheric Administration (NOAA). The general mean value of the time series was calculated and was used to define the seasons: cold-season months were below the surface temperature mean value (November–May) and warm-season months were above the surface temperature mean value (June–October) (Fig. 2).

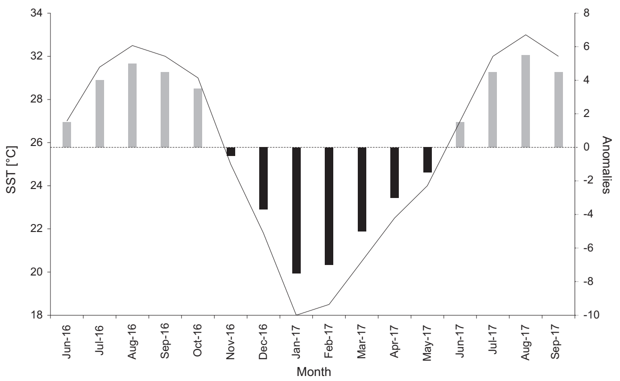


**Figure 2.** Monthly surface sea temperature (SST) records (black line) in the central Gulf of California during the sampling period. The dotted line indicates the general mean value of the time series. The gray bars indicate the warm months (months with SST above the mean value) and the black bars indicate the cold months (months with SST below the mean value). The primary *y* axis shows surface sea temperature values in degrees Celsius and the secondary *y* axis shows anomalies with respect to the general mean value of the time series during the sampled period.

Prey items were identified to the lowest possible taxonomic level using specialized identification keys. For fish, the keys by Whitehead (1985), Fischer et al. (1995), and Lowry (2011) were used. For crustaceans, the key by Morris et al. (1980) was used, and for other invertebrates, the keys by Iverson and Pinkas (1971), Brusca (1980), and Keen (2012) were used. For the trophic analysis of *L. guttatus*, specimens were categorized according to sex (male or female), size (group 1 = 28–38 cm, group 2 = 39–48 cm, and group 3 = 49–58 cm), and season (cold or warm).

## Feeding habits

A species accumulation curve was graphed to assess whether the number of stomachs containing food was adequate to represent the diet of *L. guttatus*. The curve was created using the program EstimateS Swins820 (Colwell 2009), using the numerical abundance of each prey item and Shannon–Wiener's diversity index ($H'$) for each stomach. The coefficient of variation (CV) was calculated to assess the number of stomachs necessary to adequately represent the diet in general and by category (sex, size, and season). If the CV took on values equal to or below 5% (0.05), the number of stomachs was deemed sufficient to adequately represent the diet (Jiménez-Valverde and Hortal 2003; Moreno-Sánchez et al. 2019).

The quantitative importance of each prey item in the *L. guttatus* diet was described using the numerical (%$N$), gravimetric (%$W$), and frequency of occurrence (%FO) indices (Hyslop 1980). These indices were then integrated into the index of relative importance (IRI) proposed by Pinkas et al. (1971):

$$\mathrm{IRI} = (\%N + \%W) \cdot \%\mathrm{FO}$$

To contrast the results of the presently reported study with those found in previous studies, results are presented as a percentage (Cortés 1997):

$$\%\,\mathrm{IRI}_i = \frac{100\,\mathrm{IRI}_i}{\sum_{i-1}^{n} IRI_I}$$

Levin's standardized index ($B_i$) was used (Krebs 1989) to assess the trophic width of *L. guttatus*. Values close to zero indicate that the species present a specialist feeding strategy, whereas values close to one indicate that the species has a generalist strategy (Labropoulou and Eleftheriou 1997):

$$B_i = \frac{1}{n-1}\left(\frac{1}{\sum_j P_{ij}^2} - 1\right)$$

Where $B_i$ is the niche width, $\sum_j P_{ij}^2$ is the proportion of the $j^{th}$ item in the diet of the $i^{th}$ predator, and $n$ is the total number of prey items.

## Data analysis

To interpret the feeding strategy of *L. guttatus* in the study area, we created a dispersion diagram based on Costello´s graphic method (1990), modified by Amundsen et al. (1996). According to the authors, four strategies can be distinguished: 1) specialized on different trophic resources, (2) more generalist with little individual variation in trophic width, (3) specialist with one prey type, but occasional consumption of other species, and (4) mixed strategy where there are individuals with a specialized diet and other individuals with a more generalist diet. This technique was used complementarily to corroborate the trophic width niche of *L. guttatus*.

A permutational multivariate analysis of variance (PERMANOVA) with 1000 permutations was undertaken to evaluate possible differences in the *L. guttatus* diet with respect to sex (male or female), size (group 1 = 28–38 cm, group 2 = 39–48 cm, and group 3 = 49–58 cm), or season (warm or cold), and possible interactions between categories. For this analysis, a numerical matrix was constructed where columns were the prey species and rows were the analyzed stomachs. A Bray–Curtis dissimilarity matrix was used as a similarity measure for the PERMANOVA. This analysis was performed using the Adonis function in the Vegan 2.2-1 library (Oksanen et al. 2015) in the R platform version 3.0.1 (R Core Team 2016), with a 95% confidence interval.

The *L. guttatus* trophic level was calculated using the formula proposed by Cortés (1999). This equation took into account the type of prey found in stomach contents:

$$\mathrm{TL} = 1 + \left( \sum_{j=1}^{n} P_j \cdot \mathrm{TL}_j \right)$$

Where TL = trophic level of *L. guttatus*, $\mathrm{TL}_j$ = trophic level of each prey category consumed, $P_j$ = proportion of each prey category in the diet of the predator, and $n$ = number of prey items.

The trophic levels of prey were obtained from FishBase (Froese and Pauly 2019) and the Sea Around Us Project DataBase (Pauly et al. 2020).

## Results

A total of 202 *L. guttatus* specimens were caught, ranging in size from 28 to 55 cm $L_t$ and weighing from 290 to 1675 g. A total of 191 specimens (94.5%) had stomachs containing food and 11 (5.5%) were empty. The prey species accumulation curve reached an asymptote at 109 stomachs, which indicated that the number of analyzed stomachs was sufficient to characterize the diet (CV ≤0.05). The minimum sample size was also achieved for the categories of sex, size, and season (Table 1).

**Table 1.** Minimum sample size for *Lutjanus guttatus* for all samples, by sex, size, and season.

| Category | $N_s$ | $N_{sm}$ | CV |
|---|---|---|---|
| General | 191 | 109 | 0.05 |
| Female | 125 | 82 | 0.05 |
| Male | 66 | 61 | 0.05 |
| Group 1 | 94 | 79 | 0.05 |
| Group 2 | 79 | 54 | 0.05 |
| Group 3 | 18 | 16 | 0.05 |
| Cold season | 141 | 110 | 0.05 |
| Warm season | 50 | 43 | 0.05 |

$N_s$ = number of analyzed stomachs, $N_{sm}$ = minimum number of stomachs, CV = coefficient of variation for the respective sample size.

## General diet

The trophic spectrum of *L. guttatus* comprised 26 categories of prey items; it included 15 fish species, 11 invertebrate species, and fish remains. A total of 502 prey items were counted; the most abundant were invertebrates (65%, *n* = 327), mainly the euphausiid *Nyctiphanes simplex* (43.6%, *n* = 219) and the shrimp *Penaeus* spp. (16.9%, *n* = 85), as well as fish (35%, *n* = 175), mainly the sardines *Sardinops sagax* (Jenyns, 1842) (16.3%, *n* = 82) and *Harengula thrissina* (Jordan et Gilbert, 1882) (15.1%, *n* = 76).

The total biomass of stomach contents was 978 g, most of which corresponded to fishes (94.2%, 921.3 g), mainly *H. thrissina* (49.7%, 486.8 g) and *S. sagax* (29.8%, 291.5 g), and invertebrates (5.8%, 56.7 g), mainly *Penaeus* spp. (2.8%, 27.7 g) and *N. simplex* (1.8%, 18 g).

The most frequent prey items were the fishes *S. sagax* (38.7%, *n* = 82) and *H. thrissina* (36.1%, *n* = 76), the euphausiid *N. simplex* (15.1%, *n* = 219), and the crustacean *Penaeus* spp. (14.6%, *n* = 85). According to the %IRI the most important prey species were the fishes *H. thrissina* (45.7%) and *S. sagax* (34.8%), the euphausiid *N. simplex* (13.4%), and the shrimp *Penaeus* spp. (5.6%) (Table 2, Fig. 3).

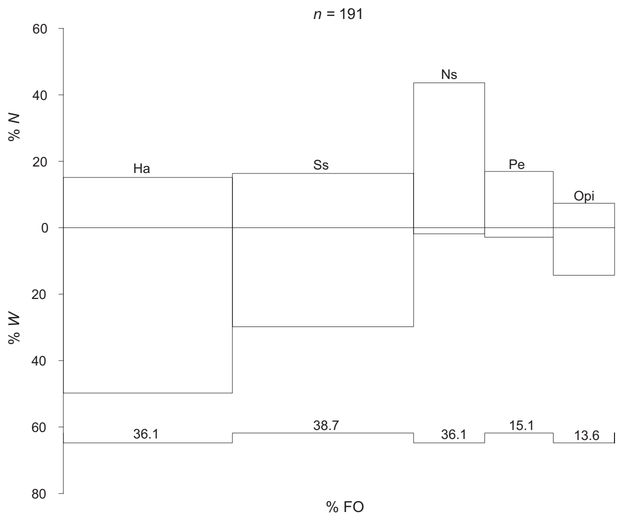


**Figure 3.** General trophic spectrum of *Lutjanus guttatus* in the central Gulf of California, measured with the index of relative importance (%IRI). %*W* = Prey-specific weight, %*N* = Prey-specific abundance, %FO = frequency of occurrence, Ss = *Sardinops sagax*, Ha = *Harengula thrissina*, Ns = *Nyctiphanes simplex*, Pe = *Penaeus*, Opi = Other prey items.

## Diet by sex

Of 191 analyzed stomachs containing food, 66 were from males and 125 were from females. There were 10 prey items in male stomachs (5 fishes and 5 invertebrates), and the most important prey according to the %IRI were the fishes *S. sagax* (64.6%) and *H. thrissina* (15.4%), and the crustaceans *N. simplex* (15.2%) and *Penaeus* spp. (3.7%). There were 19 prey items in

**Table 2.** General diet of *Lutjanus guttatus* in the central Gulf of California, Mexico.

| Tx | Prey | *N* | *W* | FO | %*N* | %*W* | %FO | IRI | %IRI | TL |
|---|---|---|---|---|---|---|---|---|---|---|
| Mo | *Chione* spp. | 1 | 0.5 | 1 | 0.20 | 0.05 | 0.52 | 0.13 | 0.003 | 2.00 |
| | *Loligo* spp. | 1 | 0.5 | 1 | 0.20 | 0.05 | 0.52 | 0.13 | 0.003 | 3.05 |
| | *Parvanachis* spp. | 1 | 0.5 | 1 | 0.20 | 0.05 | 0.52 | 0.13 | 0.003 | 2.10 |
| Cr | Poecilostomatoida | 4 | 1 | 2 | 0.80 | 0.10 | 1.05 | 0.94 | 0.018 | 2.00 |
| | *Penaeus* spp. | 85 | 27.7 | 28 | 16.93 | 2.83 | 14.66 | 289.74 | 5.651 | 2.70 |
| | *Callinectes* spp. | 10 | 2.5 | 2 | 1.99 | 0.26 | 1.05 | 2.35 | 0.046 | 3.70 |
| | *Sicyonia disedwardsi* | 1 | 0.5 | 1 | 0.20 | 0.05 | 0.52 | 0.13 | 0.003 | 2.40 |
| | *Nyctiphanes simplex* | 219 | 18 | 29 | 43.63 | 1.84 | 15.18 | 690.32 | 13.464 | 2.25 |
| | *Cymothoa exigua* | 1 | 0.5 | 1 | 0.20 | 0.05 | 0.52 | 0.13 | 0.003 | 3.18 |
| | *Squilla* spp. | 2 | 4.5 | 2 | 0.40 | 0.46 | 1.05 | 0.90 | 0.018 | 2.40 |
| Tu | Salpidae | 2 | 0.5 | 1 | 0.40 | 0.05 | 0.52 | 0.24 | 0.005 | 3.00 |
| Ac | *Acanthurus* spp. | 1 | 0.5 | 1 | 0.20 | 0.05 | 0.52 | 0.13 | 0.003 | 2.00 |
| | *Achirus* spp. | 1 | 38 | 1 | 0.20 | 3.89 | 0.52 | 2.14 | 0.042 | 3.00 |
| | *Ophioblennius steindachneri* | 1 | 9 | 1 | 0.20 | 0.92 | 0.52 | 0.59 | 0.011 | 2.50 |
| | *Harengula thrissina* | 76 | 486.8 | 69 | 15.14 | 49.78 | 36.13 | 2345.08 | 45.737 | 3.10 |
| | *Opisthonema libertate* | 1 | 19 | 1 | 0.20 | 1.94 | 0.52 | 1.12 | 0.022 | 2.89 |
| | *Sardinops sagax* | 82 | 291.5 | 74 | 16.33 | 29.81 | 38.74 | 1787.64 | 34.865 | 2.84 |
| | *Engraulis mordax* | 1 | 12 | 1 | 0.20 | 1.23 | 0.52 | 0.75 | 0.015 | 2.96 |
| | *Mugil curema* | 1 | 12 | 1 | 0.20 | 1.23 | 0.52 | 0.75 | 0.015 | 2.01 |
| | *Benthosema panamense* | 1 | 0.5 | 1 | 0.20 | 0.05 | 0.52 | 0.13 | 0.003 | 3.00 |
| | *Diaphus* spp. | 1 | 3 | 1 | 0.20 | 0.31 | 0.52 | 0.26 | 0.005 | 3.30 |
| | *Triphoturus* spp. | 1 | 0.5 | 1 | 0.20 | 0.05 | 0.52 | 0.13 | 0.003 | 3.00 |
| | *Ophichthus* spp. | 1 | 0.5 | 1 | 0.20 | 0.05 | 0.52 | 0.13 | 0.003 | 3.40 |
| | *Sebastes* spp. | 2 | 0.5 | 1 | 0.40 | 0.05 | 0.52 | 0.24 | 0.005 | 3.50 |
| | *Scomber japonicus* | 1 | 33 | 1 | 0.20 | 3.37 | 0.52 | 1.87 | 0.036 | 3.38 |
| | *Scorpaenodes* spp. | 1 | 0.5 | 1 | 0.20 | 0.05 | 0.52 | 0.13 | 0.003 | 3.87 |
| | Fish remains | 3 | 14 | 1 | 0.60 | 1.43 | 0.52 | 1.06 | 0.021 | |
| | Total | 502 | 978 | 191 | 100 | 100 | | 5127.29 | 100 | |

IRI = index of relative importance, %IRI = percent index of relative importance, Tx = highest taxon, Mo = Mollusca, Cr = Crustacea, Tu = Tunicata, Ac = Actinopterygii, *N* = number of individuals for each prey, *W* = total weight of the prey, FO = frequency of occurrence of each prey, %*N* = percent abundance of each prey, %*W* = percent weight of each prey, %FO = percent frequency of occurrence of each prey, TL = trophic level.

female stomachs (12 fishes and 7 invertebrates); the most important prey items were *H. thrissina* (56.8%), *S. sagax* (24.7%), *N. simplex* (11.7%), and *Penaeus* spp. (6.1%) (Fig. 4). The PERMANOVA showed significant differences in the diet between the two sexes ($F = 2.472$, $P < 0.05$) (Table 3).

## Diet by size

A total of 94 stomachs belonging to group 1 (28–38 cm Lt) were analyzed; 14 prey items were found in these stomachs (8 fishes and 6 invertebrates). According to the %IRI, the most important prey in this group were the fishes *S. sagax* (42.7%) and *H. thrissina* (29.5%),

**Table 3.** Results of the PERMANOVA (Permutational multivariate analysis of variance) analysis of the *Lutjanus guttatus* diet between sexes (male and female), sizes (G1, G2, and G3), and seasons (warm and cold) in the central Gulf of California, Mexico.

| Factor | *F* | *r* | *P*(>*F*) | Significance |
|---|---|---|---|---|
| Sex | 2.472 | 0.005 | 0.022 | Yes |
| Size | 45.440 | 0.101 | 0.002 | Yes |
| Season | 5.054 | 0.011 | 0.002 | Yes |
| Sex:Size | 1.223 | 0.003 | 0.248 | No |
| Sex:Season | 0.628 | 0.001 | 0.767 | No |
| Size:Season | 1.585 | 0.004 | 0.120 | No |
| Sex:Size:Season | 0.605 | 0.001 | 0.799 | No |

*F* = Fisher's *F* statistic, *r* = similarity among groups, *P* = probability values.

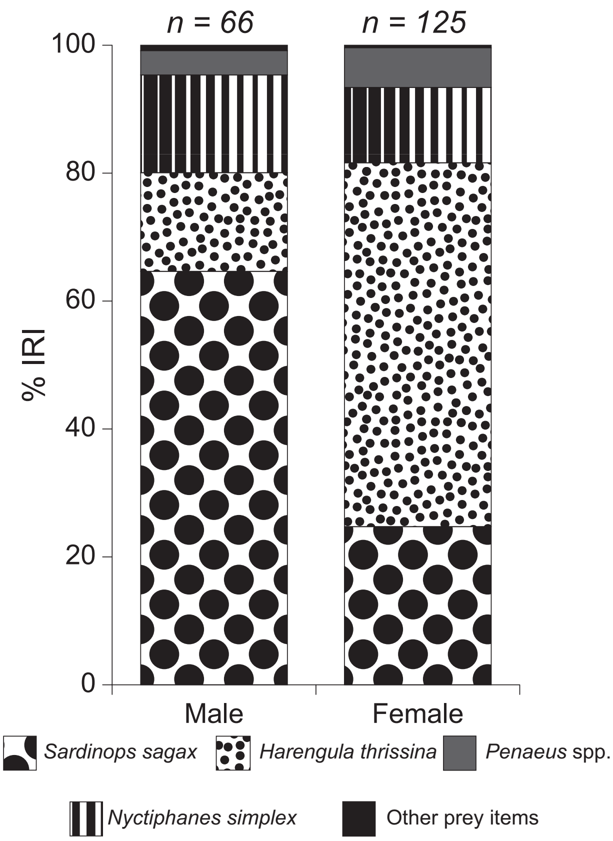


**Figure 4.** Inter-sexual variation (male or female) in prey items consumed by *Lutjanus guttatus* in the central Gulf of California, measured with the index of relative importance (%IRI).

the euphausiid *N. simplex* (23.4%), and the shrimp *Penaeus* spp. (3.9%). A total of 79 stomachs belonging to group 2 (39–48 cm $L_t$) were analyzed; 15 prey items were found in these stomachs (8 fishes and 7 invertebrates). The most important prey were *H. thrissina* (65.3%), *S. sagax* (21.7%), *Penaeus* spp. (7.9%), and *N. simplex* (4.2%). A total of 18 stomachs belonging to group 3 (49–58 cm $L_t$) were analyzed; 7 prey items were found in these stomachs (5 fishes and 2 invertebrates). The most important prey items were the fishes *S. sagax* (46.8%) and *H. thrissina* (44.4%), and the shrimp *Penaeus* spp. (3.2%) (Fig. 5). The PERMANOVA test showed significant differences in the diet between the three size groups ($F$ = 45.4, $P$ < 0.05) (Table 3).

## Diet by season

A total of 141 stomachs from the cold season and 50 stomachs from the warm season were analyzed. During the cold season, the diet included 16 prey items (7 fishes and 9 invertebrates). According to the %IRI, the most important prey were *H. thrissina* (46.4%), *S. sagax* (29.4%), *N. simplex* (21.1%), and *Penaeus* spp. (2.6%). During the warm season, the diet included 14 prey items (11 fishes and 3 invertebrates). According to the %IRI, the most important prey were *S. sagax* (43.1%), *H. thrissina* (34.1%), and *Penaeus* spp. (21.3%) (Fig. 6). The PERMANOVA test showed that there were significant differences in the diet between the two seasons ($F$ = 5, $P$ < 0.05) (Table 3).

According to the PERMANOVA test, there were no significant differences in the interaction between sex and size ($F$ = 1.2, $P$ = 0.24), between sex and season ($F$ = 0.62, $P$ = 0.76), between size and season ($F$ = 1.5, $P$ = 0.12), or between sex, size and season ($F$ = 0.6, $P$ = 0.79) (Table 3).

## Trophic niche width and feeding strategy

According to Levin's standardized index ($B_i$), *L. guttatus* can be considered a specialist predator ($B_i$ = 0.13). $B_i$ values were consistent across the studied categories: by sex (males: $B_i$ = 0.12; females: $B_i$ = 0.12), size (G1: $B_i$ = 0.12; G2: $B_i$ = 0.13; G3: $B_i$ = 0.11), and season (cold: $B_i$ = 0.11; warm: $B_i$ = 0.15). The feeding strategy confirmed that *L. guttatus* is a benthopelagic predator with a narrow trophic niche; it feeds on a reduced number of prey items that are abundant and frequent (*S. sagax*, *H. thrissina*, and *Penaeus* spp.). However, according to Costello's graph, the dominance of the main prey varies according to sex, size, and season (Fig. 7).

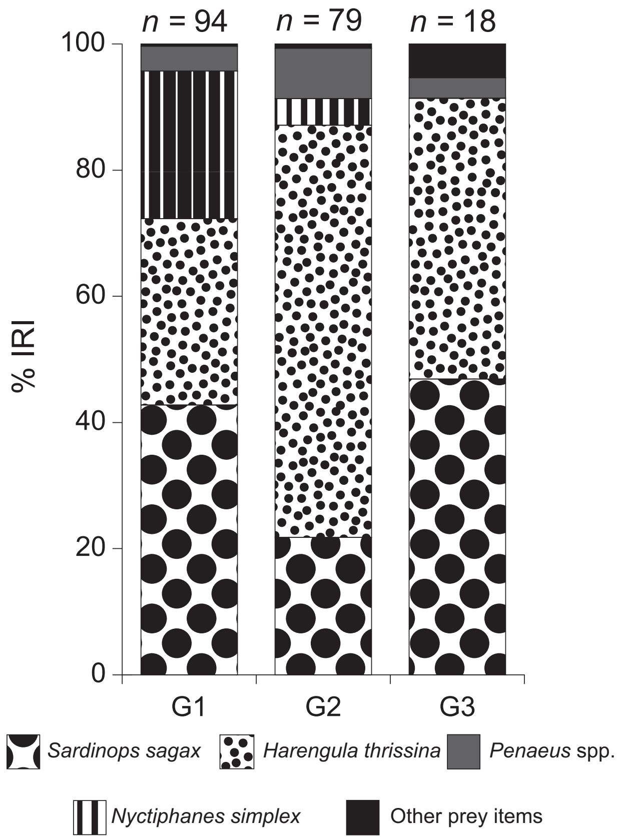


**Figure 5.** Size variation (G1, G2, or G3) in prey items consumed by *Lutjanus guttatus* in the central Gulf of California, measured with the index of relative importance (%IRI).

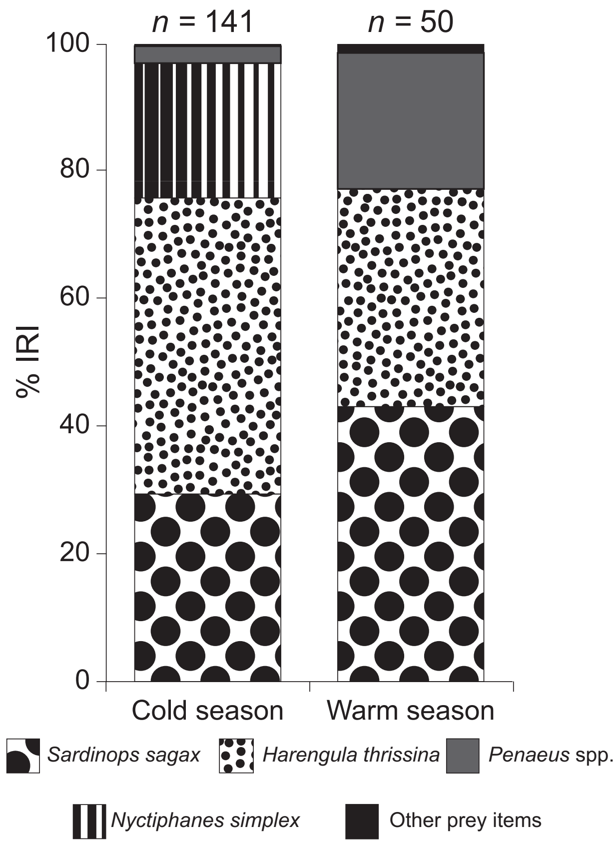


**Figure 6.** Seasonal variation (cold or warm) in prey items of *Lutjanus guttatus* in the central Gulf of California measured with the index of relative importance (%IRI).

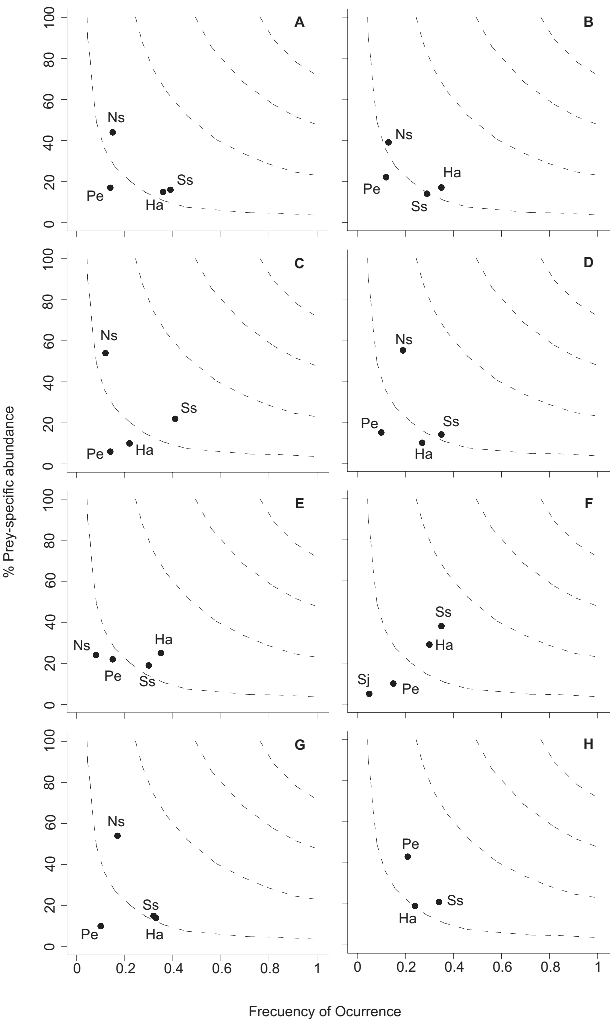


**Figure 7.** Costello graph. Prey-specific abundance (%*N*) vs. frequency of occurrence (%FO) in the general diet of *Lutjanus guttatus* in the central Gulf of California. (**A**) General, (**B**) female, (**C**) male, (**D**) size group 1, (**E**) size group 2, (**F**) size group 3, (**G**) cold season, (**H**) warm season. Ss = *Sardinops sagax*, Ha = *Harengula thrissina*, Ns = *Nyctiphanes simplex*, Pe = *Penaeus* spp., Sj = *Scomber japonicus*.

## Trophic level

The trophic level calculated for *L. guttatus* was 3.9. The trophic levels for males and females were 3.8 and 3.9, respectively; for size group 1, 2, and 3 trophic levels were 3.8, 4.0, and 4.0, respectively; for cold and warm seasons trophic levels were 3.8 and 3.9, respectively.

# Discussion

Several studies have reported on the feeding habits of lutjanid species at various locations. For example, studies on *Lutjanus analis* (Cuvier, 1828) (see Duarte and García 1999), *Lutjanus argentiventris* (Peters, 1869) (see Vázquez et al. 2008), *Lutjanus campechanus* (Poey, 1860) (see Wells et al. 2008), *Lutjanus decussatus* (Cuvier, 1828), *Lutjanus fulviflamma* (Forsskål, 1775), *Lutjanus fulvus* (Forster, 1801), *Lutjanus gibbus* (Forsskål, 1775) (see Kamukuru and Mgaya 2004; Nanami and Shimose 2013), *Lutjanus griseus* (Linnaeus, 1758) (see Guevara et al. 2007), *Lutjanus malabaricus* (Bloch et Schneider, 1801) (see Takahashi et al. 2020), *Lutjanus peru* (Nichols et Murphy, 1922) (see Moreno-Sánchez et al. 2016), *Lutjanus sanguineus* (Cuvier, 1828), and *Lutjanus sebae* (Cuvier, 1816) (see Senta and Peng 1977) have found that snappers are active, mainly carnivorous predators that feed on a wide variety of pelagic and benthic prey, mainly fishes and crustaceans, as well as on bivalves, gastropods, cephalopods, and planktonic organisms such as urochordates. Several authors have also reported that the species within the genus feed on different prey according to the study area, and they have therefore been considered opportunistic predators, which could reflect the high trophic plasticity that allows them to take advantage of the most abundant resources.

In the presently reported study, the trophic spectrum of *L. guttatus* included 26 categories of prey items. The most important prey items in the diet were fish from the family Clupeidae and crustaceans of the families Euphausiidae and Penaeidae. This is similar to what was reported by Rojas (1997) for this species off the Costa Rica coast, where it fed on 22 categories of prey items, mainly crustaceans from the family Penaeidae. Rojas et al. (2004) reported that off the coast of El Salvador the *L. guttatus* trophic spectrum comprised 15 categories of prey items, mainly crustaceans of the families Squillidae, Portunidae, and Penaeus. Tripp-Valdez and Arreguín-Sánchez (2009) reported that off Nayarit, Mexico, *L. guttatus* fed on 26 categories of prey items, the most important of which were crustaceans of the family Xanthidae and fish of the family Engraulidae. However, what was found in the presently reported study differs from what was found by Rojas-Herrera and Chiappa-Carrara (2002) off Guerrero, Mexico, mainly regarding the number of prey item categories; these authors found that at that location the trophic spectrum of the species comprised 88 prey item categories, mainly fish of the families Engraulidae, Clupeidae, and Bregmacerotidae.

Differences among trophic spectra at different locations could be associated with the characteristics of each habitat. At locations where the number of prey items consumed by the species was lower, the ecosystems presented more homogeneous conditions; for example, *L. guttatus* individuals in Costa Rica are surrounded by mangroves, whereas in Nayarit, Mexico, the area has sandy bottoms and rocky substrates (Tripp-Valdez and Arreguín-Sánchez 2009). However, off Guerrero, Mexico (Rojas-Herrera and Chiappa-Carrara 2002) where the number of prey items consumed by the species was greatest, the species richness could be due to the heterogeneity of the ecosystem, which includes rocky substrates, reef patches, soft bottoms, and a wide continental platform with variable oceanography dynamics (Palacios-Salgado et al. 2014), which allows the species to feed on a greater number of prey items. The study area in the presently reported investigation (Santa Rosalía, BCS) was characterized by sandy and rocky bottoms, where oceanographic processes such as the dominance of regional winds that favor upwelling led to large numbers of prey species such as *S. sagax*, with approximate abundances of 488 640 t (Martínez-Zavala et al. 2010), *Harengula thrissina*, with approximate abundances of 150.3 ind. 10 $m^{-2}$ (Franco-Gordo et al. 2008), and *N. simplex*, with approximate abundances of 889 ind. 1000 $m^{-3}$ (Gómez-Gutiérrez et al. 2010).

Significant inter-sexual differences in the proportion of prey items were found; the main prey consumed by the two sexes were the same, but there were differences in the proportions of each prey type consumed. Females consumed a greater proportion of *Sardinops sagax*, whereas males ate a greater proportion of *Harengula thrissina*. This same behavior has been reported for other species in the study area (e.g., *Mycteroperca rosacea*; see Moreno-Sánchez et al. 2019), and could be the result of an ecological strategy by the species to optimize prey consumption and reduce or avoid intraspecific competition (Werner 1979).

Moreover, the difference in diet between the sexes could reflect the energy needs of males and females. For other species in the genus, such as *L. campechanus*, it was reported that females presented greater energy reserves in muscle as well as liver compared with males; these energy reserves were later used for the formation and maturation of gonads (Schwartzkopf and Cowan 2016). In the case of prey species consumed by *L. guttatus*, sardines are known for their high energy value, as was reported by Abitia-Cárdenas et al. (1997) and Navarro-García (unpublished*) for the striped marlin, *Kajikia audax* (Philippi, 1887), and the leopard grouper *Mycteroperca rosacea*, with values oscillating around 3.19–4.97 kcal· $g^{-1}$ dry weight.

This suggests that the diet differences observed are not due to the energetic demands of females and their different metabolic requirements, but to both sexes having a marked preference for seasonally abundant prey, providing thus an excellent example of the optimal foraging theory. Individuals are selecting prey based on the prey's vulnerability to capture and time spent to find and handle prey, maximizing thus their energy gains to maximize meeting their requirements (Gerking 1994).

Regarding the difference in the number of prey item categories between sexes, we found a greater number of prey categories ($n = 19$) in females than in males ($n = 10$). This type of result has been reported by Doncel and Paramo (2010) for the species *Lutjanus synagris* (Linnaeus, 1758) in the Colombian Caribbean, where females fed on a greater number of prey categories ($n = 23$) than males ($n = 16$). These authors attributed this result to differences in size between the sexes; females were smaller and consumed more crustaceans and mollusks compared with males, which were larger and consumed large amounts of crustaceans and fish. In the presently reported study, the two sexes were of similar size (females = 38.4 ± 5 cm $L_t$; males = 38.1 ± 4.9 cm $L_t$), so differences in the diet could be due to other factors. Differences could be due to variations in the distribution and habitat of the two sexes. Santamaría-Miranda et al. (2003) reported that off Guerrero, Mexico, *L. peru* females were more abundant in areas close to the coast compared with males. This would agree with what was found in the presently reported study because the proportion of males to females was 1:1.9 (M:F), resulting from their capture relatively close to the coast. It has been observed that *H. thrissina* forms large schools near the coast (Hobson 1968). In this study it was found that *L. guttatus* females fed on large amounts of *H. thrissina* compared with males, which could reflect differences in distribution between the two sexes.

There were changes in diet according to size with differences in the proportions of prey consumed, as well as in the variety of prey present in stomach contents. There was an increase in the proportion of fish in the diet compared with invertebrates with increasing *L. guttatus* size. This change in diet with predator ontogeny has been observed in other species of the genus such as *L. analis* (see Duarte and García 1999), *L. campechanus* (see Wells et al. 2008), and *L. peru* (see Moreno-Sánchez et al. 2016), and has also been observed in other locations where this species has been studied (e.g., Rojas-Herrera and Chiappa-Carrara 2002; Rojas-Herrera et al. 2004; Tripp-Valdez and Arreguín-Sánchez 2009). This has been attributed to morphological differences among the size groups. According to Allen (1985), prey selection in snappers is linked to mouth diameter, with smaller individuals having a smaller mouth aperture, which leads them to consume small-sized prey (e.g., crustaceans), compared with larger individuals with larger mouth apertures that can consume larger prey such as fish. Moreover, the ability to move, hunt, and capture prey could increase with increasing spotted rose snapper size (Rojas 1997; Moreno-Sanchez et. al. 2019).

Seasonal variations in prey items were also detected. For example, there was a notable increase in the consumption of the euphausiid *N. simplex* during the cold season. It has been reported that euphausiids *N. simplex* carry out daily vertical migrations in the water column; they are found at greater depths during the day and move to the surface at night. It has also been reported that they undertake their migrations closer to the surface in the cold season when the water column homogenizes, reaching temperatures ≤17°C, whereas in the warm season euphausiids migrate upwards to waters over 50 m deep, avoiding warm surface waters (Gómez-Gutiérrez et al. 2010).

This could explain the increase in the importance of *N. simplex* in the diet of *L. guttatus* in the cold season and its lower importance in the diet in the warm season. According to this and the optimal foraging theory, *L. guttatus* individuals could obtain greater energy benefits by

* Navarro-García RA (2018) Bioenergética de la cabrilla sardinera *Mycteroperca rosacea* (Streets, 1877) en Santa Rosalía, Baja California Sur, México. Tesis de Licenciatura. Universidad Autónoma de Sinaloa, Facultad de Ciencias del Mar (UAS-FACIMAR), 93 pp.

feeding on prey items that are abundant in winter, as they do not spend energy searching for less abundant organisms that are harder to catch (Gerking 1994). This could also be due to the reproductive season of the spotted rose snapper; there are two reproductive periods, one from March to April, which coincides with euphausiid consumption, and a longer period from August to November when *L. guttatus* consumed mainly sardines. These changes in the consumption of prey species could be due to the reproductive season having a high energetic cost for individuals (Arellano-Martínez et al. 2001).

In the presently reported study, according to Levin's standardized index values obtained, *L. guttatus* could be considered a predator with a narrow trophic width, as it used few trophic resources. Of 26 categories of prey items, only four (i.e., *Harengula* spp., *Sardinops sagax*, *Nyctiphanes simplex*, and *Penaeus* spp.) were found in great proportions in stomach contents, with high abundance and frequency of occurrence. However, it should be mentioned that according to Costello's graph, there was a change in the importance of the main prey according to sex, size, and season, which would allow us to classify this species as an opportunist predator that feeds on the most available and abundant prey in a given time and place (Gerking 1994).

This behavior has been observed in other species of the genus *Lutjanus* such as *L. argentiventris* (see Vázquez et al. 2008) and *L. synagris* (see Doncel and Paramo 2010). The strategy of reducing the trophic niche and alternating prey allows an efficient distribution of trophic resources and therefore a reduction in intra- and interspecific competition, as *L. guttatus* in the Gulf of California shares its habitat with similar predators (e.g., *L. peru*, *L. argentiventris*, *M. rosacea*, among others) (Gerking 1994; Moreno-Sánchez et al. 2016). It has been reported that differences in the diet with other sympatric predators can be a strategy to reduce interspecific competition. This could have an evolutionary component, with the shape of the body and head, the type of dentition, and the mandibular mechanism influencing the type of prey consumed (Rooker 1995; Rojas-Herrera et al. 2004; Nanami and Shimose 2013). Nanami and Shimose (2013) described differences in the type of prey consumed by four sympatric lutjanids based on the body type and dentition. *L. decussatus* and *L. fulviflamma* presented a compressed body, long teeth, and a mandibular mechanism that allowed them to open and close the mouth rapidly, and they tended to consume a large number of fish. *L. fulvus* and *L. gibbus* had a wider body, short conical teeth, a mandibular mechanism with greater strength in the bite, and consumed a larger number of crustaceans. The species *L. peru* fed mainly on invertebrates such as the shrimp *Penaeus californiensis*, the crab *Pleuroncodes planipes*, and the ostracods *Myodocopida* gen. spp. in the Gulf of California (Moreno-Sánchez et al. 2016), whereas in the presently reported study *L. guttatus* fed mainly on fish such as *S. sagax* and *Harengula thrissina*, as well as on euphausiids *N. simplex* and shrimp *Penaeus* spp. These differences in the type of prey consumed could be due to morphometric differences in the dental and premaxillary bones, as was mentioned by Rojas-Herrera et al. (2004).

The trophic level calculated for *L. guttatus* was 3.9, which classifies it as a tertiary consumer, coinciding with what has been reported for other species in the genus, such as *L. campechanus* (TL = 4.2) (Tarnecki and Paterson 2015), *Lutjanus purpureus* (Poey, 1866) (TL = 3.8), and *L. synagris* (TL = 3.5) (García and Contreras 2011) and for the same species in Colima, Mexico (TL = 3.7) (Tripp-Valdez and Arreguín-Sánchez 2009). This reflects its feeding habits as a carnivorous predator that feeds mainly on intermediate trophic levels.

According to the results obtained, we conclude that *L. guttatus* in the central Gulf of California is an opportunistic carnivorous benthopelagic predator, presenting a narrow trophic niche and also displaying changes in feeding strategy according to sex, size, and season, which allows it to minimize intra- and interspecific competition.

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