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Research Article

Feeding habits of the Pacific sharpnose shark *Rhizoprionodon longurio* in La Paz Bay, Baja California Sur, Mexico

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ABSTRACT. The Pacific sharpnose shark, *Rhizoprionodon longurio*, is a small coastal carcharhinid widely distributed in the eastern Pacific and an important component of artisanal fisheries in Mexico. This study analyzed the feeding habits of *R. longurio* in La Paz Bay, Baja California Sur. Forty-two individuals were examined, with total length, sex, and capture site recorded. Stomach contents were extracted, and prey were identified to the lowest possible taxonomic level. Ecological and statistical analyses were applied to characterize the diet. Of the total individuals, 26 were males and 16 females. Twenty-one prey taxa were identified, with teleost fishes representing the dominant prey group based on frequency and numerical contribution. *Calamus brachysomus* (relative importance index, %RII = 18.87) and members of the family Hemiramphidae (%RII = 9.54) were the most representative prey. Females consumed mainly *C. brachysomus* (%RII = 54.47), whereas males showed higher consumption of *Diodon hystrix* (%RII = 18.62) and *D. holocanthus* (%RII = 18.20). The species exhibited a generalist trophic strategy (Bi = 0.83). Analysis of similarity indicated high dietary overlap between sexes (R = 0.084) and maturity stages (R = 0.021). This study documents, for the first time, the consumption of Hemiramphidae and Diodontidae by *R. longurio* in the Gulf of California, highlighting its dietary plasticity and ecological role as a coastal predator.

Keywords: stomach content; diet; trophic spectrum; prey; coastal shark; trophic ecology

INTRODUCTION

Coastal sharks play essential roles in marine ecosystems as mesopredators that regulate prey populations, connect habitats, and influence community structure (Gruber 1977, Gruber & Myrberg 1977). Despite their ecological importance and increasing concern over global population declines, knowledge of shark trophic ecology remains limited in many regions, particularly in the eastern Pacific (Heithaus et al. 2008).

The Pacific sharpnose shark *Rhizoprionodon longurio* (Jordan & Gilbert, 1882) is a small carcharhinid widely distributed along the eastern Pacific coast, especially in shallow coastal environments. The species is characterized by long labial folds and a second dorsal fin originating posterior to the anal fin (Fischer et al.

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1995). Although *R. longurio* is an important component of artisanal fisheries in Mexico, its trophic ecology remains insufficiently documented in several areas of the Gulf of California.

Stomach content analysis provides direct evidence of prey consumption and is one of the most widely used methods to infer trophic interactions and feeding strategies in elasmobranchs (Polo-Silva et al. 2007). Previous studies on *R. longurio* have been geographically restricted or taxonomically limited. For example, Hernández-Aparicio (2020) identified 61 prey species on the western coast of the Gulf of California, with bony fishes being the dominant group. However, regional differences in prey availability, habitat structure, and environmental conditions may generate spatial variation in feeding patterns.

Given this context, we evaluated whether sex and ontogenetic stage were associated with potential variation in the diet composition of *R. longurio* in La Paz Bay. To address this objective, we analyzed diet composition using stomach content analysis, ecological indices, and multivariate approaches to characterize the species' trophic ecology and assess patterns of dietary overlap among groups.

MATERIALS AND METHODS

Study area

La Paz Bay is a large body of water located in the southwestern region of the Gulf of California, between coordinates 24°07'-24°21'N, 110°17'-110°40'W (González-Acosta et al. 2018). La Paz Bay is characterized by shallow coastal habitats, heterogeneous benthic substrates, and seasonal oceanographic variability that may influence prey availability and shark foraging dynamics (González-Acosta et al. 2005). Sediments are predominantly sandy in central areas, while intertidal margins include silty and muddy substrates (Contreras 2010).

Two sites representing contrasting habitat conditions were considered: Pichilingue, a shallow coastal area functioning as juvenile habitat, and Tarabillas, a relatively deeper coastal zone where adult individuals were predominantly captured. These contrasting environmental conditions may influence prey availability and provide ecological context for evaluating dietary composition. The map of the study area is shown in Figure 1.

Sample collection and stomach content analysis

Forty-two specimens of *R. longurio* were collected using artisanal gillnets (mesh size of 3.5 inches). Total length was measured using an ichthyometer (± 0.1 cm), sex was recorded, and maturity stage was assigned based on published size-at-maturity criteria.

Specimens were processed immediately after capture to minimize post-capture digestion effects. The gastrointestinal tract was removed from the esophagus to the spiral valve.

Because highly digested prey remains frequently extended beyond the stomach, gastrointestinal contents were examined to maximize prey identification under advanced digestion conditions, while acknowledging potential differential digestion biases. The same digestion-state criteria were applied consistently to all prey remains recovered from the gastrointestinal tract following Olson & Galván-Magaña (2002): 1) complete prey; 2) full body, without skin or eyes; 3) skeleton without muscle or only the exoskeleton in the case of crustaceans; and 4) unidentified organic material (UOM). To study the fish prey species found, external morphology and the axial or appendicular skeleton were used. To identify the fish remains, the work of Clothier (1950) and Miller & Jorgensen (1973) was used for counting vertebrae. Likewise, the identification keys of Miller & Lea (1972), Thomson et al. (1979), and Fischer et al. (1995) were used. Crustaceans were identified by exoskeletons using guides such as those by Brusca (1980) and Fischer et al. (1995). In addition, the percentage of stomach filling was recorded in the five categories established by Galván-Magaña (1989): 0 = empty; 1 = 1-25%; 2 = 26-50%; 3 = 51-75%; and 4 = 76-100%.

Representativeness of the stomachs

Cumulative curves of prey species were developed to evaluate whether the number of stomachs analyzed was representative of the diet of *R. longurio*. Diversity was estimated using the Shannon-Wiener index using the EstimateS 9.1.0 program. In addition, the coefficient of variation (CV) was calculated, considering values less than 0.05 as an indicator of homogeneity (Colwell 2006).

Trophic spectrum

To determine the importance of prey within the diet, the following indices were calculated: the numerical method (%N), the frequency of occurrence method (%FO), and the gravimetric method (%G). The relative importance index (%RII = (%G + %N) × %FO) was used as a complementary descriptor and interpreted jointly with frequency-based metrics and multivariate analyses, facilitating comparison with previous elasmobranch trophic studies.

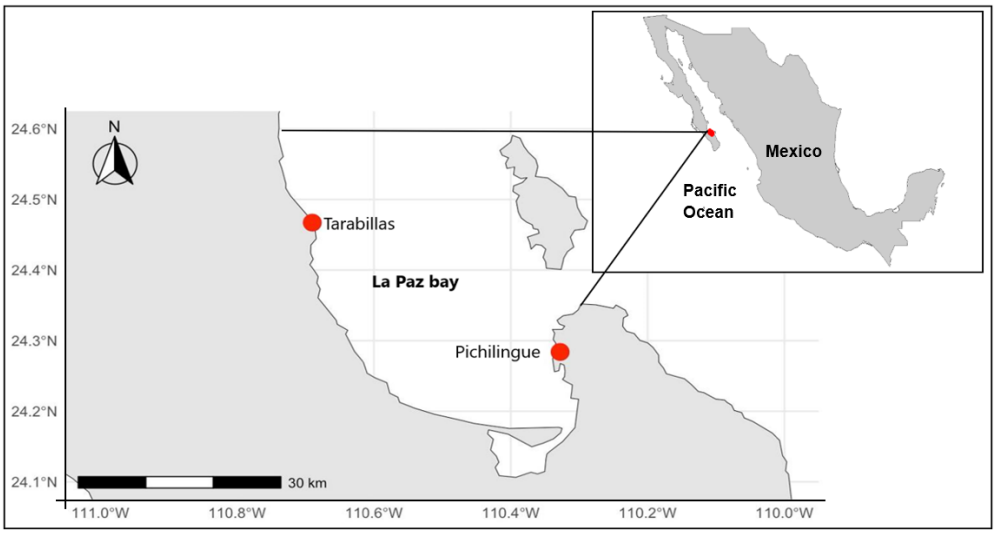

Figure 1. Areas where sampling of Pacific sharpnose sharks (*R. longurio*) was conducted (red dots) in Baja California Sur (Mexico). The inset shows the location of the sampling area in Mexico.

Ecological indexes

The diversity of prey consumed was estimated with the Shannon-Weaver index, $H' = -\sum_i^n (p_i \text{ Ln } p_i)$ where p_i is the proportion of individuals in the *i*-th species. Trophic amplitude was calculated using the Levin index, $B_i = \frac{1}{n-1}\left(\frac{1}{\sum p_{ij}^2}\right) - 1$ from the number of prey species obtained. This index, unlike others, assumes values from 0 to 1. When the values are less than or equal to 0.6, the shark will be considered a specialist (Polo-Silva et al. 2007). If the value is greater than 0.6, it is considered a generalist predator; that is, it exploits a broad spectrum of available prey resources.

Multivariate analysis

To preserve individual-level dietary information and avoid overreliance on pooled descriptors, multivariate analyses based on individual prey occurrence matrices were prioritized.

To determine the trophic overlap between sexes and stages of maturity, the non-parametric statistical test Analysis of Similarity (ANOSIM) was used using the PRIMER 7, V7, 0.24 Program (Clarke & Gorley 2006). The values obtained (R) in this analysis ranged between -1 and 1; values close to 1 indicate a clear differentiation between factors, while values close to zero do not show any difference between sites and negative values demonstrate greater similarity (Osuna-Peralta et al. 2014). Statistical significance was assessed using 999 permutations. To complement these results, the percentage similarity analysis of prey species (SIMPER) (Clarke 1993) was applied to identify the prey taxa contributing most to the observed compositional variation among groups. Non-metric multidimensional scaling (nMDS) was used to visualize dietary overlap among groups based on Bray-Curtis similarity matrices.

Trophic position

The trophic position (TP) was obtained using the equation proposed by Christensen & Pauly (1992), using the trophic level of the prey species, $TP = 1 + \left(\sum_{j=1}^{n} CDij\right)(TPj)$ where CDij is the proportion of prey in the predator's diet and TP_{ij} is the trophic position assigned to each prey.

RESULTS

General data and sample sizes

Forty-two *R. longurio* individuals were analyzed, including 26 males and 16 females. Juveniles (n = 24) ranged from 408 to 580 mm TL and were primarily captured in Pichilingue, whereas adults (n = 18) ranged from 820 to 1,100 mm TL and were mostly collected in Tarabillas. These size ranges match previously reported values for the species.

Filling percentage and digestion states

Of the 42 individuals analyzed, 18 (42.85%) contained food remains, whereas 24 (57.15%) had empty stomachs. Although the relatively high frequency of

empty stomachs reduced the number of samples available for prey-specific comparisons, the number of stomachs containing food was sufficient to characterize broad trophic patterns, as supported by prey accumulation analyses.

Most prey remains were recorded in advanced digestion states (categories 3-4), suggesting substantial prey processing before capture and partially explaining the occurrence of UOM.

Representativeness of the stomachs

The general cumulative curve of the prey species indicates that the number of stomachs analyzed was sufficient to describe the trophic spectrum, because from stomach number 15 a CV of less than 0.05 (CV = 0.041) was reached (Fig. 2).

While cumulative prey curves supported general sample representativeness, comparisons among sex and maturity stages should be interpreted cautiously due to lower subgroup sample sizes.

General trophic spectrum

Based on frequency and numerical contribution, supported by complementary dietary indices, teleost fishes constituted the dominant prey group representing 88.8% of its diet, while crustaceans contributed 11.2%. The prey with the highest importance value was the remains of bony fish, with a %RII = 96.21, highlighting the species *Calamus brachysomus* with a %RII = 18.87, followed by the family Hemiramphidae with a %RII = 9.54. In contrast, crustaceans presented a low value of relative importance, with a %RII = 3.79 (Table 1). UOM associated with advanced digestion, was treated cautiously as highly digested remains rather than interpreted as a biologically meaningful prey category.

Trophic spectrum by sex

In female *R. longurio*, bony fish were the dominant prey (%RII = 71.4), while crustaceans contributed 28.6%. The prey with the highest value of relative importance were the remains of fish of the species *C. brachysomus* with a %RII = 54.47 and *Lophiodes spilurus* with a %RII = 11.77. On the other hand, crustaceans of the species belonging to the family Squillidae and the superfamily Penaeoidea obtained a %RII = 5.60.

In reference to males, it was determined that bony fish constitute the main component of the diet, as in females; however, in this case, a value of %RII = 100 was recorded. Within this group, the species *Diodon hystrix* (%RII = 18.62) and *D. holocanthus* (%RII = 18.2) stood out in the diet of males.

Although some prey differences were observed descriptively between sexes, these patterns should be interpreted cautiously given sample size limitations and substantial dietary overlap detected in multivariate analyses.

Trophic spectrum by stage of maturity

In juvenile *R. longurio*, bony fish were the main prey, with a %RII of 99.10, highlighting individuals of the species *C. brachysomus* (%RII = 31.51) and *Harengula thrissina* (%RII = 17.61). On the other hand, crustaceans had a %RII = 0.90.

In adult sharks, bony fish constituted the main component of the diet, with a %RII of 99.49. In this group, the fish of the species *D. holocanthus* (%RII = 27.58) and *D. hystrix* stood out with a %RII = 27.01 (Fig. 3), followed by the representatives of the family Hemiramphidae, with a %RII of 14.73.

Shannon-Weaver and Levin index

The Shannon-Weaver index showed that the diet of *R. longurio* from La Paz Bay is diverse (H′ = 2.39). Lower dietary diversity was observed in females, juveniles, and at the Pichilingue site (H′ = 1.7). At the same time, males, adults, and individuals captured in Tarabillas presented higher values of diversity (H′ values greater than 2.00).

The Levin index showed that the breadth of the trophic niche of *R. longurio* indicates a generalist tendency (Bi = 0.83), so it is considered a predator with a broad trophic niche characteristic of a generalist feeding strategy. By sex, females registered a value of Bi = 0.87, which indicates a more generalist diet than that of males (Bi = 0.79), although both remain within the generalist range. Regarding the stages of maturity, juveniles reached a value of Bi = 0.80, showing a lower amplitude compared to adults, who obtained Bi = 0.88 and reflected a broader diet.

ANOSIM, SIMPER and nMDS

The nMDS showed a high degree of overlap between sexes and stage of maturity, suggesting a strong similarity in diet composition between both groups (Fig. 4). This pattern was consistent with the ANOSIM results that showed R values close to zero for sex (R = 0.084) (Fig. 5) and maturity stage (R = 0.021) (Fig. 6). No statistically significant differences were detected, indicating high trophic overlap among groups.

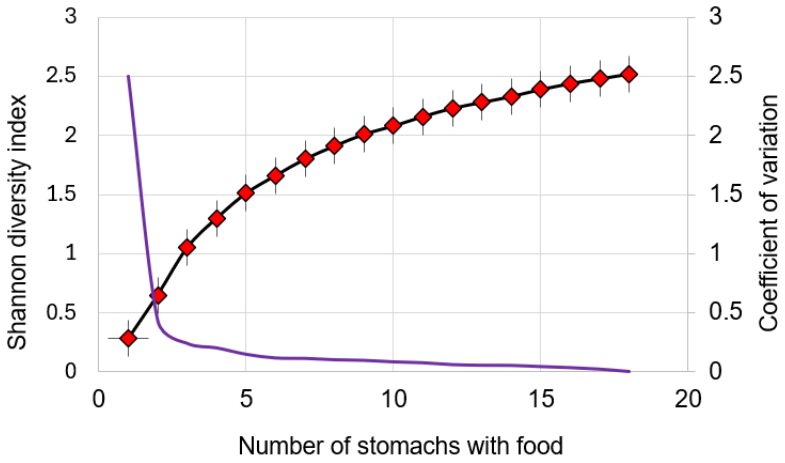

Figure 2. Cumulative curve of the prey species of *R. longurio*. The diamonds represent the Shannon diversity index with its standard deviation, while the purple line without marks indicates the coefficient of variation.

Table 1. General trophic spectrum of *Rhizoprionodon longurio* from La Paz Bay, with the absolute values and percentages of the statistical methods: N-%N: numerical method, FO-%FO: frequency of occurrence, G-%G: gravimetric method and RII-%RII: relative importance index. UOM: unidentified organic material.

Prey species in general								
Species	N	%N	FO	%FO	G	%G	RII	%RII
Bony fish								
Family Clupeidae								
Sardinops caeruleus	1	4.76	1	4.76	2.09	0.44	24.75	1.85
Harengula thrissina	2	9.52	1	4.76	22.79	4.89	68.59	5.13
Family Ariidae								
Occidentarius platypogon	1	4.76	1	4.76	20.46	4.39	43.59	3.26
Family Sparidae								
Calamus brachysomus	2	9.52	2	9.52	78.95	16.95	252.14	18.87
Family Cynoglossidae								
Symphurus chabanaudi	2	9.52	1	4.76	8.96	1.92	54.51	4.14
Family Diodontidae								
Diodon holocanthus	1	4.76	1	4.76	91.64	19.67	116.28	8.70
Diodon hystrix	1	4.76	1	4.76	95.35	20.47	120.09	8.98
Family Hemiramphidae	2	9.52	2	9.52	18.07	3.87	127.65	9.54
Family Scombridae								
Scomber japonicus	1	4.76	1	4.76	13.15	2.82	36.12	2.70
Family Haemulidae	1	4.76	1	4.76	20.80	4.46	43.94	3.28
Family Lophiidae								
Lophiodes spilurus	1	4.76	1	4.76	56.74	12.18	80.68	6.03
Fish remains	1	4.76	1	4.76	2.98	0.64	25.72	1.92
UOM	3	14.29	4	14.29	28.50	6.12	291.50	21.81
Crustaceans								
Family Squillidae	1	4.76	1	4.76	3.22	0.69	25.96	1.94
Superfamily Penaeoidea	1	4.76	1	4.76	2.04	0.43	24.76	1.85

The SIMPER analysis by sex showed an average dissimilarity between females and males. Seven species accounted for 72.69% of this variation, highlighting *C. brachysomus*, the Squillidae family, and UOM, which together accounted for 40.85% of the total diet.

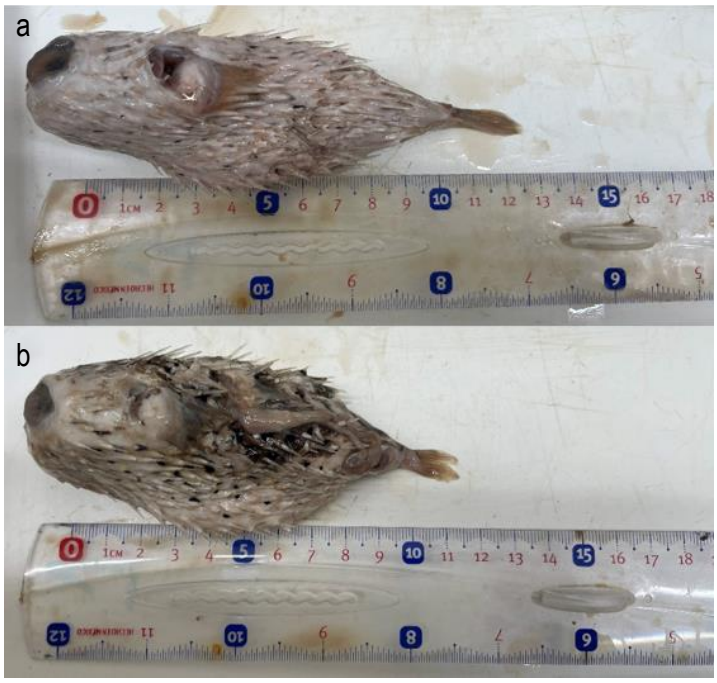

Figure 3. First documented record of a) *Diodon hystrix* and b) *D. holocanthus* in *R. longurio* from La Paz Bay.

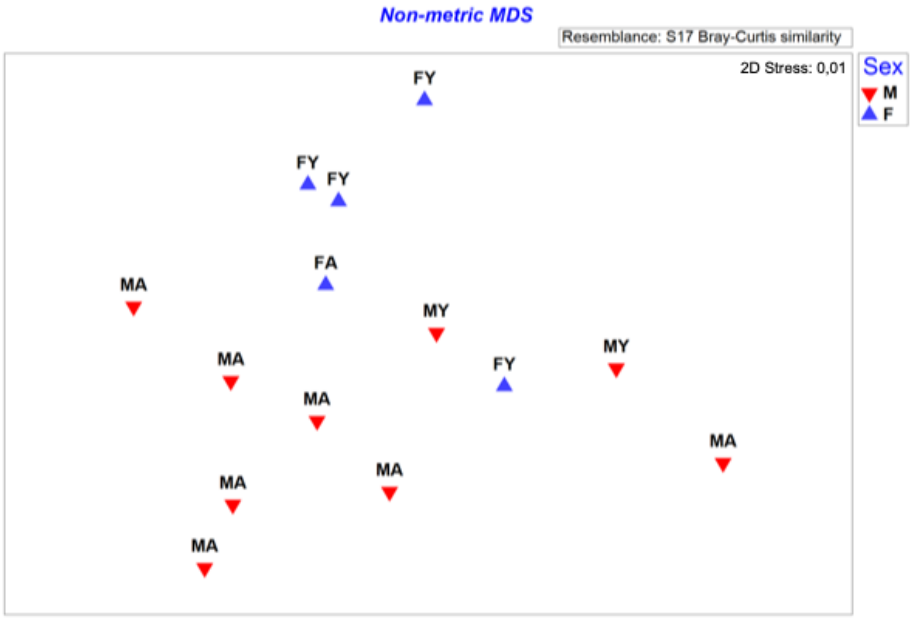

Figure 4. Non-metric multidimensional scaling (nMDS) ordination of diet composition of *R. longurio* in La Paz Bay based on Bray-Curtis similarity. Each point represents an individual shark, grouped by sex (M: male; F: female) and maturity stage (A = adult; Y = juvenile). The ordination shows substantial overlap among groups (stress = 0.01).

By maturity stages of *R. longurio*, the SIMPER analysis indicated an average dissimilarity of 99.18% between juveniles and adults. Nine species accounted for 75.21% of this difference, with UOM, the Hemiramphidae family, and *C. brachysomus* being the most abundant food components, which together accounted for 36.42% of the total diet.

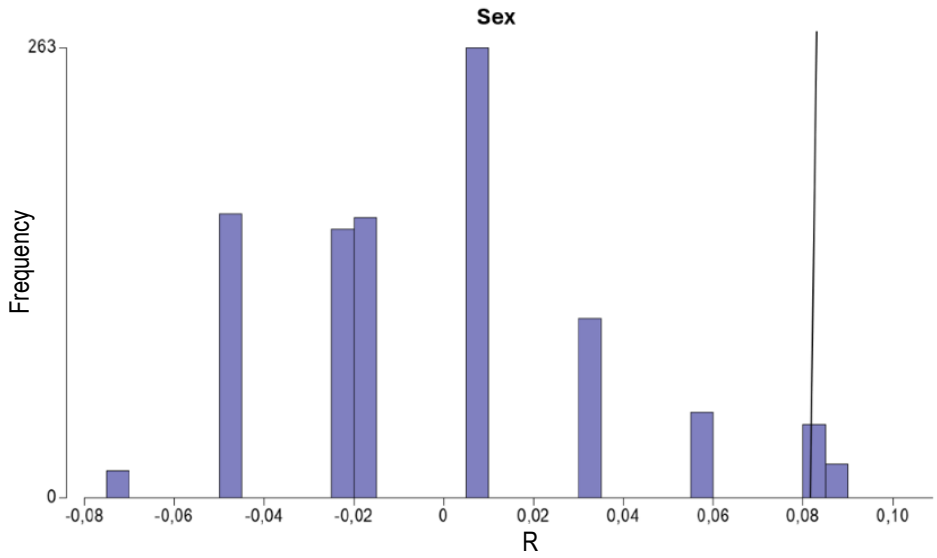

Figure 5. Analysis of Similarity (ANOSIM) of sexes of *R. longurio* from La Paz Bay. R: ANOSIM values that range from -1 to 1, in which values close to 1 indicate a clear dissimilarity between groups, while values close to zero show no dissimilarity between groups.

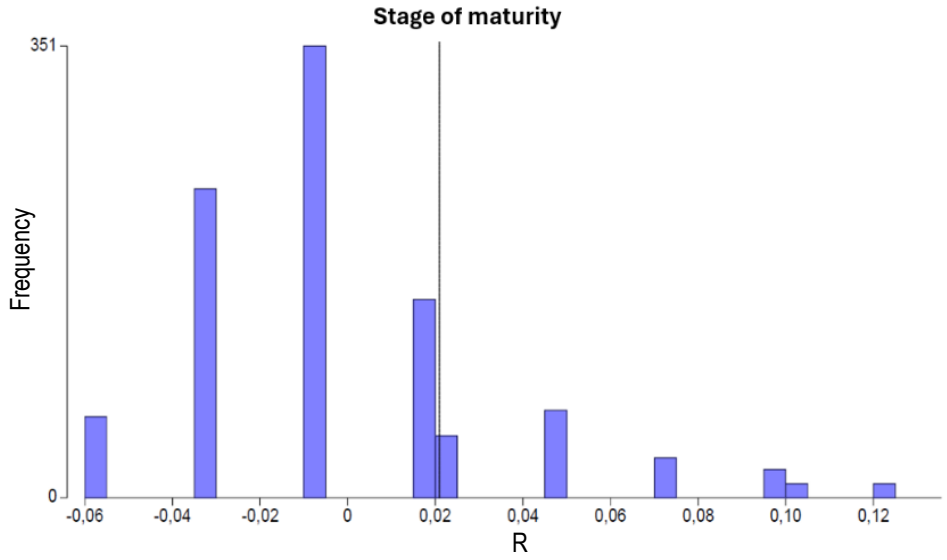

Figure 6. Analysis of Similarity (ANOSIM) of maturity stages of *R. longurio* from La Paz Bay. R: ANOSIM values that range from -1 to 1, in which values close to 1 indicate a clear dissimilarity between groups, while values close to zero show no dissimilarity between groups.

Trophic position (TP)

According to the analysis of stomach contents, *R. longurio* presented a general TP of 4.62. Regarding sex, females registered a TP = 4.65 and males a TP = 4.60. Regarding the stage of maturity, juveniles had a TP value = 4.45, while adults reached TP = 4.81.

DISCUSSION

General data and sample sizes

Of the 42 specimens collected, 61.90% were males and 38.10% were females, suggesting possible sexual segregation related to the use of gillnets, which tends to favor the capture of males. This result coincides with what was reported by Motta & Wilga (2001),

who pointed out that fishing gear influences the sex ratio in shark catches.

Filling percentage and digestion states

Regarding filling percentage, 57.15% of the stomachs analysed were empty, while 42.85% contained food, so category 0 registered the highest frequency with respect to the percentage of filling. The prey species identified had degradation levels 3 and 4, indicating an advanced digestion process. This result is consistent with what was reported by Cortés (1997). It is associated with the use of gillnets, which cause high levels of stress during capture and generate regurgitation of stomach contents, accelerating the degradation process (Torres-Rojas et al. 2009).

General trophic spectrum

Although composite indices such as %RII are widely used in elasmobranch dietary studies, their interpretation should be considered alongside frequency-based descriptors and multivariate approaches, as they may mask individual-level variability and be influenced by differential digestion. In this study, multivariate analyses were prioritized to assess dietary overlap, while %RII was retained to facilitate comparison with previous studies.

Twenty-one prey were identified, of which 88.8% corresponded to bony fish and 11.2% to crustaceans. Wetherbee & Cortés (2004) point out that teleost fishes are frequently important components of coastal shark diets, although composition varies widely among species and ontogenetic stages.

In trophic studies carried out in this species, the diet shows similarities with that reported in other groups. However, until now, no previous work had documented the consumption of fish from the family Hemiramphidae (%RII = 9.54) by *R. longurio*. On the other hand, *Galeocerdo cuvier* has also been recorded consuming similar prey items (Froese & Pauly 2025). This finding confirms that hemiramphids may be part of the diet of coastal sharks, as noted by Simpfendorfer et al. (2001).

Trophic spectrum by sex and maturity stages

The analysis by sex and maturity stage showed that females and juveniles of *R. longurio* caught in Pichilingue fed mainly on bony fish, highlighting *C. brachysomus* as the species of greatest relevance within the diet (%RII = 54.47). This finding coincides with what was found by Hernández-Aparicio et al. (2023), because *C. brachysomus* is a highly available prey in the study area.

In the males and adults captured in Tarabillas, the species *D. holocanthus* and *D. hystrix* were found with RII values above 18, being the most relevant prey. So far, no previous study has reported the consumption of fish from the family Diodontidae by *R. longurio*, which suggests that the consumption of these fish by sharks is infrequent and occurs occasionally, due to their natural defenses, such as spines, the ability to inflate, and the presence of tetrodotoxin in their internal organs, as presented by Shepherd et al. (2019). This novel record highlights previously unrecognized trophic plasticity in *R. longurio* and deserves ecological attention.

As for crustaceans, these were found only in females; however, no previous reports indicate that consumption is exclusive to this sex, since they have been found in both sexes, as indicated in the works of Márquez-Farías et al. (2005) and Osuna-Peralta et al. (2014). Therefore, this result may be due to limited samples rather than an actual difference in feeding habits.

Shannon-Weaver index

According to the Shannon index, a general value of H′ = 2.39 was obtained, which reflects that *R. longurio* has a diverse diet. This species has been considered a predator with diverse prey consumption by several authors, including Saucedo-Barrón (1982) and Castillo-Géniz et al. (1996).

In males and adults captured in Tarabillas, they showed greater dietary diversity than the juveniles and females captured in Pichilingue. These results are similar to those obtained by Alderete-Macal (2007), who points out that differences in prey diversity may be related to the different habitat structure and the availability of trophic resources between the two areas.

Levin index

Levin's index indicated that this species presents a generalist trophic behavior, with values close to 1 when considering sex and stage of maturity. Females and adults captured in Tarabillas presented higher values in this index, which suggests a greater trophic amplitude compared to males and juveniles captured in Pichilingue. These differences could be related to the availability of prey in each area, the dietary plasticity of the species, and the greater stomach capacity of adult individuals, which coincides with the work carried out by Osuna-Peralta et al. (2014).

ANOSIM, SIMPER and nMDS

The lack of significant differences in diet composition detected by ANOSIM is further supported by the

nMDS ordination, which showed no clear separation among individuals of different sex and maturity groups. In this case, the R value was close to zero; no significant dietary differentiation was detected among groups, indicating substantial trophic overlap (Clarke & Warwick 2001). The SIMPER analysis identified *C. brachysomus* as one of the relevant prey in all groups. This result does not coincide with what was reported by Alatorre-Ramirez et al. (2013), Osuna-Peralta et al. (2014) and Hernández-Aparicio (2020), who obtained other prey of greater relevance. Rather than indicating failure of the original hypothesis, these results support ecological trophic overlap under shared prey availability.

The substantial dietary overlap observed among sex and maturity groups suggests that *R. longurio* exploits broadly similar trophic resources within La Paz Bay, likely reflecting shared prey availability in this coastal environment. Similar patterns of trophic overlap and generalized feeding behavior have been documented in other coastal shark species, where prey use is strongly influenced by local prey availability and environmental variability rather than by strict trophic segregation (Kroetz et al. 2016, Gül & Demirel 2021). Generalist feeding strategies may provide ecological advantages under fluctuating environmental conditions by allowing predators to exploit a wider spectrum of prey resources and maintain trophic flexibility (Gerry 2008). In coastal ecosystems, such trophic plasticity has been associated with the ecological role of mesopredators in maintaining food web connectivity and ecosystem stability (Lipscombe et al. 2024).

Trophic position

According to Cortés (1999), *R. longurio* is classified as a tertiary consumer (TP > 4). In this study, TP values ranged from 4.4 to 4.8, in agreement with what was previously reported in the Gulf of California by Hernández-Aparicio et al. (2023). This result indicates that this species feeds mainly on secondary consumers, and to a lesser extent, on primary consumers. Finally, due to its high TP, *R. longurio* plays an important role in ecosystem balance by controlling secondary consumers. If this species were to become endangered, this could create an imbalance in the trophic web, which would also create a trophic cascade impacting the lower levels. Therefore, the TP of a commercially important species like *R. longurio* is a useful indicator, especially in fisheries, because it helps to implement management strategies to protect the species using an ecosystemic approach (Arreguín-Sánchez 2006, Roff et al. 2016, Hernández-Aparicio 2020).

CONCLUSION

The present study indicates that *R. longurio* in La Paz Bay exhibits a broad trophic niche dominated by teleost prey, substantial dietary overlap among examined groups, and notable trophic plasticity, including novel prey records for the species. Together, these findings support a generalist feeding strategy and provide baseline ecological information relevant to ecosystem-based fisheries management and the understanding of trophic interactions in the Gulf of California.

Author contributions

D.G. Bernal Espinoza: conceptualization; research; writing, original draft; methodology; J.M. López Vivas, M.B. Pérez Milicua, A.K. Romo Piñera, M. Lara Uc, J.A. Armenta Quintana, and J. Aguilar Parra: writing, review and editing; E. Barjau González: conceptualization; supervision; resources; writing, review and editing.

Conflict of interest

The authors declare no conflict of interest.

Use of artificial intelligence

Artificial intelligence (AI) tools were used exclusively for language editing and stylistic refinement during manuscript preparation. These tools did not generate, modify, or interpret scientific data, analyses, or conclusions. All scientific content derives from original research conducted by the authors, who remain fully responsible for the accuracy and integrity of the manuscript.

Declaration of originality

The authors declare that this manuscript is an original work that has not been published previously, in whole or in part, and is not under consideration for publication in any other journal.

Ethical statement

All sampling procedures complied with institutional and national guidelines for the ethical handling of aquatic organisms. Fieldwork was conducted under the authorization and institutional support of the Universidad Autónoma de Baja California Sur (UABCS). No endangered or protected species were harmed during this study.

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