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Linking Ontogenetic, Seasonal, and Spatial Variability in the Trophic Biology of *Citharichthys spilopterus* to Environmental Conditions in a Tropical Estuary

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Abstract

The flatfish *Citharichthys spilopterus* is a common predatory species in the estuaries of the southwestern Gulf of Mexico. In general, factors controlling the foraging behavior of fish can be extrinsic (environmental conditions) or intrinsic (size-related differences). The main objective of this study was to analyze spatiotemporal and body size-related variations in the diet of this species and their coupling with main environmental conditions. Every two months, 24 h sampling cycles were conducted in two habitats, one with submerged vegetation and the other without vegetation. Fish were collected every 2 h during each cycle. Canonical correspondence analysis revealed that submerged vegetation and body size were the main factors influencing diet composition, while diurnal variation was not significant. Decapod larvae and copepods were consumed more frequently in the unvegetated habitat during the dry season and by smaller fish, while peracarids, shrimp, and fish were consumed more frequently in the vegetated habitat during the rainy season and by larger fish. PERMANOVA analysis detected significant differences in diet between size groups, habitats, and months. Similarly, the fullness index showed significant differences between size groups and months. These spatiotemporal and ontogenetic trophic changes reflect the adaptation processes of the species to the seasonal and spatial environmental variability of the system.

Keywords: spatiotemporal variation; ontogenetic changes; constrained ordination; environmental coupling

Key Contribution: The spatiotemporal and ontogenetic variations in the diet of *Citharichthys spilopterus* represents an adaptive response to the environmental variations in the system.

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1. Introduction

Cyclopsettidae is a family of flatfish primarily native to the coastlines of America, with a few species found off the western coast of Africa. Members of the family are benthic and typically predatory [1,2]. *Citharichthys spilopterus* Günter 1862 is a marine species distributed from New Jersey, USA, to Río Grande do Sul, Brazil [1,3,4], but it regularly enters brackish waters and is the most common flatfish in Mexico, occurring in all estuarine systems of the southwest Gulf of Mexico [5]. Its maximum length is 21.0 cm TL, but in

estuaries the common length is less than 15.0 cm TL, settling in the size range of 10 to 15 mm with a growth rate of around 0.5 mm TL/day [6–9]. In the southwestern Gulf of Mexico, this species shows a nocturnal habit and a spawning season from January to April and from September to November [4].

Citharichthys spilopterus is a visually oriented ambush predator and although it is a benthic species, its diet includes copepods and other planktonic prey, mainly when individuals are small [1,10,11]. Its potential importance as a predator [12] has also been observed in the Pueblo Viejo Lagoon, state of Veracruz, Mexico [13,14].

Factors influencing the foraging behavior of fish can be classified as either extrinsic or intrinsic. Extrinsic factors are external drivers that require a biological response from organisms but are generally beyond their control. These factors include abiotic variables (e.g., spatial and temporal variation in environmental conditions such as temperature and salinity) as well as anthropogenic disturbances (e.g., the opening or closure of an estuary mouth). In contrast, intrinsic factors are related to the biological attributes of fish, including body size, ontogenetic development, and digestive tract morphology [15].

Feeding behavior of fish in a specific area can be influenced by spatial and temporal variability of trophic resources. Diel and seasonal changes in the diet can be further affected by the changes in environmental conditions (salinity and temperature) [15,16]. At a diel scale, the sunrise and sunset cycle can affect the ability of fish to detect different types of prey [17–19]. Foraging behavior of species is also highly influenced by the ontogenetic changes in feeding habits and the body size [17,20,21], because fish are able to capture larger prey as they grow in size. Thus, in an ecological context, the analysis of the effects of spatiotemporal variation in environmental factors and body size on fish foraging behavior provides insights into energy transfer processes and their consequences for individual growth and survival, as well as for the trophic structure of the community.

Spatial, seasonal, and ontogenetic variations in the food habits of the *C. spilopterus* have been analyzed, in both warm temperate [11,22] and tropical environments [10,16,23,24]. However, information on dietary variability between vegetated and unvegetated habitats, across different periods of the day, and on feeding intensity (fullness index) has been poorly explored. Furthermore, there is a knowledge gap regarding the combined effects of body size, submerged vegetation, seasonal variation, and diel patterns on the diet of this species.

In the present study, we hypothesized that the species' different feeding strategies—particularly those related to the types of prey consumed—would correspond to changes in individual size and to spatiotemporal variations in environmental factors, mainly temperature and salinity. Therefore, the objective was to analyze how diet and feeding intensity (fullness index) are coupled with extrinsic factors (such as the spatial, diel, and seasonal variability of environmental conditions) and intrinsic factors (such as size differences) in a predatory species from a tropical coastal lagoon.

2. Materials and Methods

2.1. Study Area and Sampling Design

The Pueblo Viejo Lagoon is located in the state of Veracruz, Mexico (22°05′–22°13′ N, 97°50′–98°00′ W). It is a shallow system and has an approximate surface area of 89 km^2. There are two estuarine subsystems: a habitat with submerged vegetation (VH), dominated by the widgeon grass *Ruppia maritima* (L) and a habitat with soft bare substrates (BH; Figure 1) [13,14]. In both habitats, samples were collected every two hours in 24 h cycles (12 samples per 24 h cycle), every two months for a year. The area has a rainy season (June to October) and a dry season (November to May).

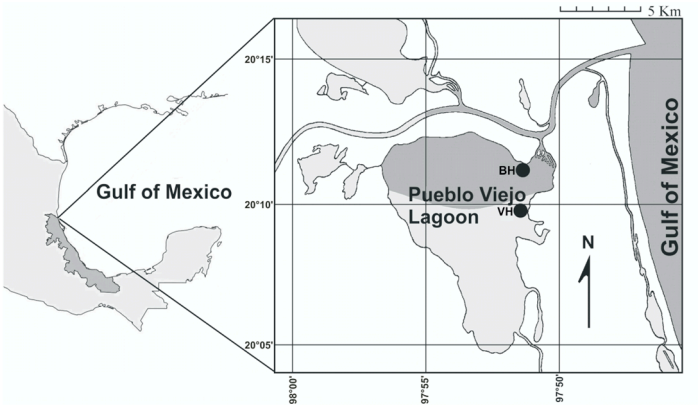

Figure 1. Geographical location of the Pueblo Viejo Lagoon, Veracruz, Mexico. The two types of habitat and sampling sites are shown: bare substrate (dark shading, BH) and with submerged vegetation (light shading, VH).

A total of 138 samples were collected using a beach seine net with a bag (30 m long, 1 m deep, and 1 cm mesh). During each sampling event, temperature, salinity, dissolved oxygen, and time of day were measured simultaneously. Additionally, the monthly averages (corresponding to 60 years) of rainfall in the area were considered [25]. In the field, specimens were anesthetized (clove oil solution) and immediately slit along the abdomen and placed in a 10% formalin solution, in accordance with the Institutional Ethics Approval Statement (CECBS23-24). Subsequently, fish were deposited in the Ichthyological Collection of the Fish Laboratory at the Universidad Autónoma Metropolitana, Iztapalapa, Mexico City.

2.2. Stomach Content Analysis

The standard length of the fish (mm SL) was measured and the stomach contents were analyzed as per the volumetric method for small stomach [26]. Stomach contents were examined with a stereoscopic microscope (40×) and identified to the lowest possible taxon. The relative importance of each food item was expressed as a percentage according to Hyslop [26].

We used a cumulative prey curve to determine whether our size sample was large enough to accurately describe the diet. Therefore, the presence of an asymptote indicates that an adequate number of samples was analyzed. To determine whether the species was more successful at capturing prey in any habitat, month, diel period, or size class, we calculated the stomach fullness index [26] as an indicator of feeding intensity, according to the following formula: Fullness index = 100 × (total weight of stomach contents/total weight of the fish).

2.3. Statistical Analyses

Canonical correspondence analysis (CCA) was applied to the overall prey data matrix (diet set) and the factors data matrix (explanatory set) to evaluate the influence of size and extrinsic factors (submerged vegetation presence, temperature, salinity, rainfall, dissolved oxygen, and diel effect) on the consumption of different prey categories. The resulting ordination plot illustrates the associations between prey categories and environmental conditions, highlighting the relative importance of each explanatory variable in shaping diet composition. In this and subsequent analyses, submerged vegetation was categorized as 1 (presence) and 0 (absence), while the time of day was classified into diel periods, considering a light–dark gradient on an ordinal scale, with values of 0 for night (20:00 to 4:00 h), 1 for twilight (06:00 and 18:00 h), and 2 for daytime (08:00 to 16:00 h). When used with diet data, CCA can explain the extent to which each of the factors drives diet variation [15,27]. The

significance of each of these factors was determined using 499 unrestricted Monte Carlo permutations. In addition, a biplot of prey items and explanatory factors was constructed to assess any dietary patterns associated with these factors. All of these analyses were performed using the package CANOCO ver. 4.5 [28].

To examine if there are significant differences in diet between habitats, as well as among months, diel periods, and size groups, one-way and factorial multivariate PERMANOVA were used to evaluate these effects and their interactions. This method is robust because it uses multiple random permutations to obtain *p*-values, thus normality and homogeneity of variances are directly implied by the permutation procedure [29]. In addition, statistical power was estimated for each hypothesis test to assess the robustness of analyses conducted with relatively small sample sizes. Similarly, one-way and factorial univariate PERMANOVA were used to evaluate changes in environmental variables and fullness index. For these analyses, to evaluate the effect of size, three classes were defined, smaller fish (<39 mm), medium size (40 to 79 mm) and larger fish (>80 mm), according to Castillo-Rivera et al. [23]. These analyses were performed using the software PRIMER v7. For diet analyses, square-root-transformed data were used to reduce the influence of highly abundant prey categories relative to less abundant ones and to improve data symmetry and suitability for multivariate statistical analyses, following the recommendations of Anderson, Gorley, and Clarke [29].

3. Results

3.1. Environmental and Size Variability

Temperature (overall mean ± SD = 25.07 ± 5.02) and salinity (overall mean ± SD = 14.11 ± 7.32) showed significant spatial differences (Pseudo-F = 5.886, d.f. = 1/103, $p = 0.017$; Pseudo-F = 17.074, d.f. = 1/103, $p = 0.001$, respectively), with higher temperatures in the vegetated habitat and higher salinity values in the bare-substrate habitat. Similarly, both variables differed significantly among months (Pseudo-F = 139.81, d.f. = 5/103, $p = 0.001$; Pseudo-F = 605.44, d.f. = 5/103, $p = 0.001$, respectively), with higher temperatures and lower salinities during the rainy season, and lower temperatures and higher salinities during the dry season. At the diel scale, temperature and salinity also showed significant differences (Pseudo-F = 21.715, d.f. = 2/103, $p = 0.001$; Pseudo-F = 5.378, d.f. = 2/103, $p = 0.006$, respectively), with the highest values recorded at twilight and the lowest at night.

In relation to the size of the individuals, individual size did not show significant differences among diel periods (Pseudo-F = 0.888, d.f. = 2/80, $p = 0.417$). However, individual size was different among months (Pseudo-F = 6.903, d.f. = 5/80, $p = 0.001$), with the smallest individuals observed in November–January. Although no significant differences in size were found between habitats (Pseudo-F = 0.199, d.f. = 1/80, $p = 0.628$), the mean size of individuals in the bare-substrate habitat during the dry season ($\bar{x} = 50.5$) was significantly smaller (Pseudo-F = 31.431, d.f. = 1/80, $p = 0.001$) than that of individuals in the vegetated habitat during the rainy season ($\bar{x} = 75.5$).

3.2. Foraging Behavior

A total of 107 *C. spilopterus* were analyzed (from 20.2 to 96.5 mm SL), of which 21 showed empty stomachs. The overall diet (Table 1) consisted mainly of decapod larvae (megalopa and mysis) (24.60%) and copepods (mainly the calanoids *Acartia* (*Acanthacartia*) *tonsa* and *Pseudodiaptomus pelagicus*) (21.70%). Fish (principally Gobiidae and Eleotridae families), caridean and penaeid shrimp, peracarids, and detritus were also important prey. The cumulative number of ingested prey categories approached an asymptote at 50% of the examined stomach contents (Figure 2).

Table 1. Overall and ontogenetic variation in the diet (percentage of relative importance) of *Citharychthys spilopterus* in the Pueblo Viejo Lagoon, Mexico. Size Class I (n = 21, $\bar{x}$ = 30.94, SD = 6.52), Size Class II (n = 52, $\bar{x}$ = 60.47, SD = 10.03) and Size Class III (n = 13, $\bar{x}$ = 86.36, SD = 5.98).

Food Items	Overall Diet	Diet by Size Classes		
		Size Class I <39 mm	Size Class II 40 to 79 mm	Size Class III >80 mm
Plant remains	1.89	0.00	0.71	11.88
Polychaetes	5.30	14.38	2.86	0.00
Copepods	21.70	39.05	19.10	0.63
Peracarids	5.73	4.06	2.81	24.36
Peracarid remains	2.88	1.25	3.81	1.25
Decapod larvae	24.60	24.38	26.51	15.00
Penaeids	5.18	0.00	8.14	0.00
Carideans	6.29	0.00	7.50	12.50
Crustacean remains	1.89	6.25	0.36	1.25
Other invertebrates	3.94	4.38	4.52	0.00
Fish	6.89	0.00	6.90	20.63
Fish remains	4.47	6.25	2.26	12.50
Detritus	9.24	0.00	14.52	0.00

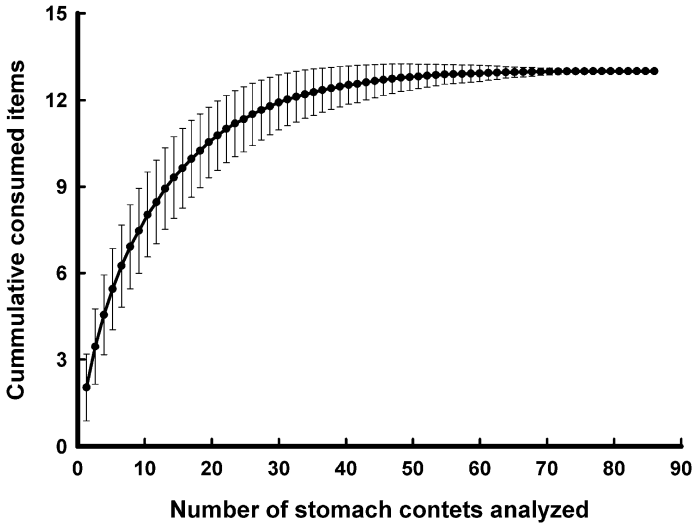

Figure 2. Cumulative number of prey categories (mean and standard deviation) consumed by *Citharichthys spilopterus* in the Pueblo Viejo Lagoon, Mexico, as a function of increasing sample size.

Regarding the CCA, all canonical axes were significant (p = 0.004), and the first two axes explained 61.8% of the total constrained variance, showing strong correlations (0.798 and 0.621, respectively) between diet composition and both intrinsic (body size) and extrinsic factors (presence of submerged vegetation, temperature, salinity, rainfall, dissolved oxygen and diel effect). In the biplot of this analysis (Figure 3), the length and direction of arrows indicate the relative importance and direction of change that each factor has on the diet composition. As submerged vegetation and diel period are categorical variables, the corresponding vector indicates, in the direction of the arrows, a trend in the presence of submerged vegetation and daylight hours, respectively.

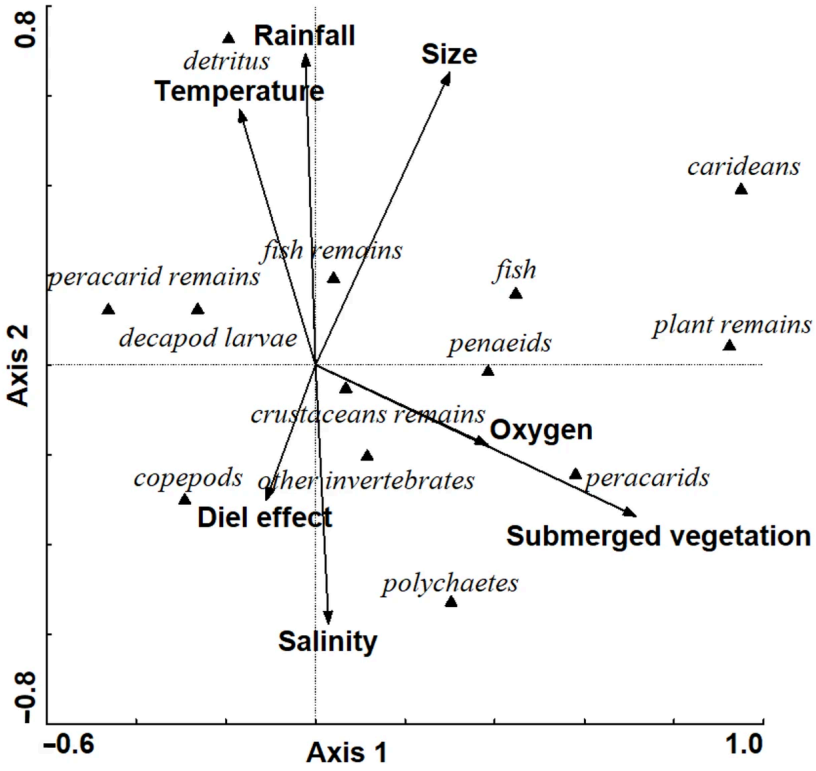

Figure 3. Canonical correspondence analysis biplot for the diet of *Citharichthys spilopterus* in the Pueblo Viejo Lagoon, Mexico. Data points represent individual prey (▲) and arrows represent explanatory variables.

According to significance tests, presence of submerged vegetation ($p = 0.002$) and body size ($p = 0.014$) were the most important variables affecting the diet of the species. Dissolved oxygen in the same submerged vegetation gradient was also significant ($p = 0.018$). Salinity ($p = 0.098$), temperature ($p = 0.124$), diel effect ($p = 0.518$), and rainfall ($p = 0.524$) were not significant.

Thus, ontogenetic changes in the diet were observed as fish increased in size, with copepods and decapod larvae as the main trophic resources for the smaller fish (39.05 and 24.38%, respectively), which were progressively replaced by peracarids (24.36%), fish (20.63%), carideans, and plant remains in larger fish (Table 1, Figure 3). Peracarids (24.38–12.5%), carideans (20.00–12.50%), polychaetes, penaeids, and plant remains were proportionally more consumed in the habitat with submerged vegetation, whereas decapod larvae (42.94–22.06%), copepods (9.12–34.00%), and detritus (24.12–6.06%) were more consumed in the habitat without submerged vegetation (Table 2, Figure 3).

The rainy season (with low salinities and high temperatures) was associated with greater consumption of decapod larvae (8.13–42.94%), detritus (0.00–24.12%), and fish (20.63–5.59%), whereas the dry season (with high salinities and low temperatures) was associated with the greater proportional consumption of copepods (6.88–34.00%), penaeids (16.25–6.42), and polychaetes (28.75–3.03%) (Table 2, Figure 3).

According to one-way multivariate PERMANOVA, there were significant differences in diet among size groups (pseudo-F = 2.185, df = 2/83, $p = 0.008$, power = 0.996). Similarly, there were also multivariate significant differences between vegetated and non-vegetated habitats, and among months, but not between diel periods (Table 3). All interactions among factors were not significant ($p > 0.1$), except the interaction habitat/month ($p = 0.001$) because some items such as copepods, peracarids, carideans, and fish were consumed more during the rainy season in the vegetated habitat, but they were also consumed more during the dry season in the non-vegetated habitat. Decapod larvae were consumed more during

the dry season in the vegetated habitat, but also consumed more during the rainy season in the non-vegetated habitat (Table 2).

Table 2. Spatial and seasonal variation in the diet (percentage of relative importance) of *Citharichthys spilopterus* in the Pueblo Viejo lagoon, Mexico, in areas both with submerged vegetation (*Ruppia maritima*) and without vegetation. Rainy season was from June to October and dry season from November to May.

Food Items	With Vegetation		Without Vegetation	
	Rainy n = 11	Dry n = 10	Rainy n = 22	Dry n = 43
Plant remains	11.88	3.75	0.00	0.00
Polychaetes	0.00	28.75	1.18	3.03
Copepods	12.50	6.88	9.12	34.00
Peracarids	24.38	12.50	0.29	2.36
Peracarid remains	0.00	0.00	8.82	1.21
Decapod larvae	8.13	12.50	42.94	22.06
Penaeids	0.00	16.25	0.00	6.42
Carideans	20.00	12.50	0.00	4.70
Crustacean remains	1.24	0.00	0.88	3.03
Other invertebrates	1.24	6.87	2.35	4.70
Fish	20.63	0.00	5.59	5.91
Fish remains	0.00	0.00	4.71	6.52
Detritus	0.00	0.00	24.12	6.06

Table 3. Results from multivariate factorial PERMANOVA to test effects of habitat (with and without vegetation), month, and diel (night, twilight and day) on the relative importance of all prey of the *Citharichthys spilopetrus*.

Source of Variance	df	MS	Pseudo-F	*p* (Perm)	Power
Habitat	1	6819.7	2.347	0.043	0.817
Month	5	5197.3	1.789	0.013	1.000
Diel	2	3021.2	1.039	0.430	0.452
Habitat × Month	4	6384.2	2.198	0.001	1.000
Habitat × Diel	2	3001.5	1.033	0.427	0.478
Month × Diel	5	3989.1	1.373	0.114	0.933
Error	44	2905.2			

Although there were no significant differences between diel periods, some trends were evident. Thus, all food items were represented during the night and detritus (14.88%), as well as remains of fish (7.2%), crustaceans (3.05%) and plants (3.05%) were consumed only in this period (20:00 to 04:00 h). Copepods (37.20%) and carideans (16.20%) were consumed mainly during twilight (06:00 and 18:00 h), while the decapod larvae (42.00%) and fish (11.00%) were consumed more during the day (08:00 to 16:00 h).

In relation to the fullness index, there were significant differences among size groups (pseudo-F = 4.850, d.f = 2/100, p = 0.008, power = 0.786), with decreasing mean values from smallest fish (>39 mm, $\overline{x}$ = 1.406) to medium size (40 to 70 mm, $\overline{x}$ = 0.607) and larger fish (>80 mm, $\overline{x}$ = 0.329). The inverse relationship between the monthly mean values of the fullness index and body size is shown in Figure 4. The mean value of the index was significantly greater in dry season months ($\overline{x}$ = 1.088; particularly in January) than in rainy season months ($\overline{x}$ = 0.226, Figure 4), without significant interaction with habitat and diel factors (Table 4). In contrast, mean values of fullness index did not show differences between habitats and between diel periods.

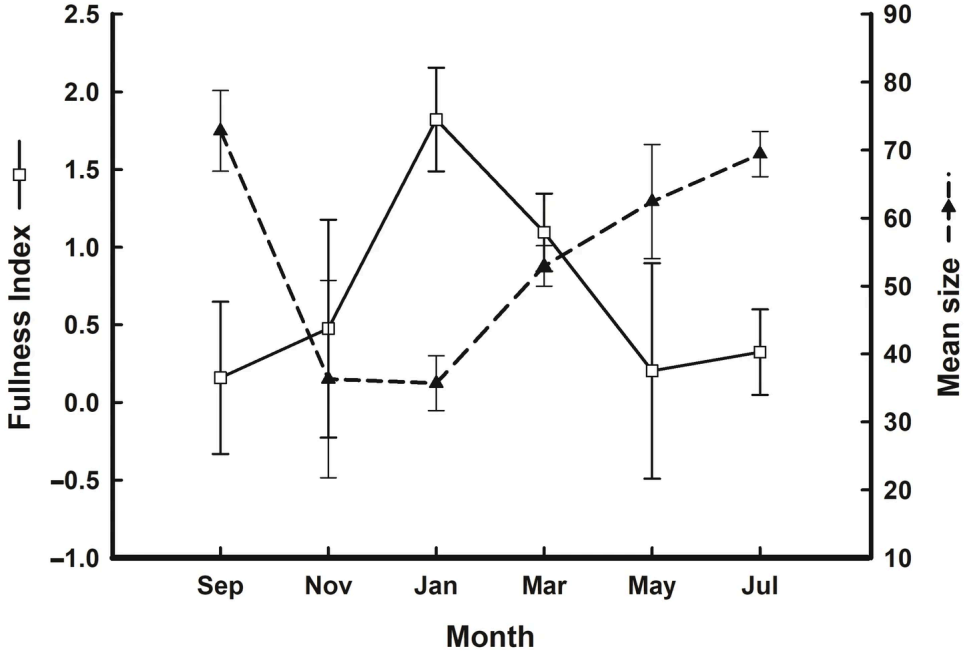

Figure 4. Monthly mean and standard error values of the fullness index and size (mm SL) for *Citharichthys spilopterus* in the Pueblo Viejo Lagoon, Mexico.

Table 4. Results from univariate factorial PERMANOVA to test effects of habitat (with and without vegetation), month, and diel (night, twilight and day) on the fullness index of *Citharichthys spilopetrus*.

Source of Variance	df	MS	Pseudo-F	*p* (Perm)	Power
Habitat	1	0.980	3.121	0.088	0.785
Month	5	1.000	3.186	0.012	0.914
Diel	2	0.603	1.922	0.160	0.113
Habitat × Month	4	0.655	2.087	0.093	0.417
Habitat × Diel	2	0.104	0.330	0.719	0.087
Month × Diel	5	0.205	0.654	0.371	0.273
Error	80	0.314			

4. Discussion

In Pueblo Viejo Lagoon, environmental factors and the local rainfall regime create a rainy season—characterized by low salinities and high temperatures—and a dry season with high salinities and lower temperatures. These seasonal shifts produce pulses in the abundance of different prey species throughout the year [13,30,31]. Because feeding resources are distributed differently depending on the presence or absence of submerged vegetation [32,33], prey availability and consumption are expected to vary spatiotemporally. Although spatial diet variability has been analyzed with respect to depth, salinity gradients, and human influences [10,16,24], and across different sounds [22], differences between vegetated and non-vegetated habitats have received little attention. At the diel scale, the light/dark cycle can influence fishes' ability to detect different prey types [18,30].

Although ontogenetic variability in fish diet has been extensively reviewed and documented [15], and ontogenetic effects have been examined alongside seasonal and spatial variation for *C. spilopterus* [10,16], the interaction between size-related dietary differences and spatiotemporal variation in prey consumption has not previously been addressed.

The potential importance of *C. spilopterus* as a predator in estuarine systems has been documented in the northern Gulf of Mexico [12]. However, since this species is not a commercial target, little is known about its habitat use [34]. Despite being a bottom dweller,

C. spilopterus efficiently uses the water column and feeds on plankton components. Thus, the overall diet of this species was based mainly on decapod larvae and copepods (both planktonic), but detritus, fish, penaeids and carideans (all primarily benthic) were also important. The consumption of detritus by *C. spilopterus* seems purposeful, because detritus in general is an important food source in estuarine systems, where the majority of fish biomass can be supported by this resource, in addition to being a very accessible prey for fish [15,32,35,36]. On the contrary, the consumption of plant remains seems incidental, due to its low relative importance and the fact that it is only consumed in the vegetated habitat and at night.

The well-defined asymptote reached by the cumulative prey curve indicates that the sample size was sufficient to describe adequately the diet of this species for the study area. This diet's composition is very similar to that reported for this species in other tropical estuarine systems from the Gulf of Mexico [23,37] and Brazil [10,16,24], also based on zooplankton, polychaetes, peracarid, shrimp and fish.

The CCA is a powerful multivariate technique that has been used successfully to determine the influence of fish size and extrinsic factors on variation in the diet of fish [27,38–40]. According to this analysis, the most important driving forces in the diet composition of the species was the presence of submerged vegetation associated with dissolved oxygen gradient, and body size. In this sense, factorial PERMANOVA supported the results of the CCA for both body size and spatial variability. In addition, these analyses show that diel variation has no effect on the diet. However, there was a tendency to consume copepods and decapod larvae (small zooplanktonic prey) at twilight and during the day, which is related to the fact that *C. spilopterus* is a visually oriented ambush predator [1], enabling it to capture small prey more efficiently during daylight hours. In this regard, this species consumes exclusively inert resources (detritus and remains of fish, crustaceans and plants) at night.

A gradient was observed in the composition of *C. spilopterus* diet, with smaller individuals consuming the largest proportions of copepods and decapod larvae (small prey < 3 mm), and larger individuals consuming more peracarids (medium-size prey ~ 7 mm), fish and carideans (large prey > 15 mm). This ontogenetic change has also been observed for this species in other studies [10,11,16,23,37]. In general, small marine fishes eat zooplankton, consuming primarily copepods during their young stages, and then shift to larger prey as they grow [15,16]. This is mainly because a small fish would be unable to capture larger prey, but when a fish grows, it can capture bigger prey, which is related mainly to changes in mouth size and gape [17]. According to optimal foraging theory, the feeding behavior of fish should allow them to take the highest-quality food with the least effort [19]. Thus, ontogenetic changes in feeding habits have the advantage to avoid intra and interspecific competition and enable the catching of larger and more energetic prey [10,16,17].

Although spatial variation in the diet of *C. spilopterus* has been analyzed [10,16,24], no changes in feeding habits have been documented between habitats with and without vegetation, nor between diel periods. In the Pueblo Viejo Lagoon, the variation in the diet of *C. spilopterus* between habitats is related to the availability of prey, with individuals consuming more organisms associated with plant beds (peracarids, carideans, polychaetes, and fish) in the vegetated habitat and more zooplankters (decapod larvae and copepods) and detritus in bare substrates. For many fish species, increased habitat structural complexity due to the presence of vegetation can provide a greater amount of food because of the large number and diversity of small epibenthic, infaunal, and epiphytic invertebrates that it shelters and on which juveniles and adults feed. In habitats where this associated fauna is less abundant, zooplanktonic food resources and detritus are important sources of food [33,41].

The temperature and salinity gradients correspond to follow seasonal changes, suggesting the seasonal trend in the diet of *C. spilopterus*. Hence, there was a greater consumption of decapod larvae, detritus, and fish during the rainy season (high temperatures and low salinities), and a higher proportional consumption of copepods, penaeid shrimps, and polychaetes during the dry season (low temperatures and high salinities).

In tropical coastal lagoons of the Gulf of Mexico, during the rainy season, decapod larvae show a first pulse in September–October (rainy season) [30]. In addition, there are significant inputs of organic matter (which is important for trophic chains) from August to October due to the constant supply of freshwater and water runoff that occur in this period [42,43]. Particularly in the Pueblo Viejo Lagoon, there are pulses in fish abundance (mainly small fish) in July–September [14].

During the dry season, also in the Pueblo Viejo Lagoon, as in other coastal lagoons of the Gulf of Mexico, there is a pulse in copepod abundance in February–March [30]. In this period, there are also pulses in the abundance of polychaetes [31] and juvenile penaeid shrimp when they are present in high numbers, immediately following a major recruitment event [12,44,45]. For *C. spilopterus* in the Pueblo Viejo Lagoon, the seasonal changes in food habits are strongly related to seasonal changes in the availability and vulnerability of prey, as observed in other studies of this species [16,23].

A significant interaction was observed between habitat and seasonal factors, mainly because decapod larvae, copepods, carideans, and peracarids were consumed in greater quantities in one habitat during the rainy season, whereas in the other habitat they were consumed in greater quantities during the dry season, allowing for an adequate distribution of food resources within the system.

There was a significant decrease in the fullness index as fish size increased, which may be related to the greater food requirements needed by small fish for their maturation and growth. In addition, larger individuals consumed larger and more energetic prey such as fish [17], reducing the intensity to which they must forage, as observed in the relationship between the fullness index and the mean size of the fish.

There were no significant differences between habitats and diel periods for the fullness index, indicating that *C. spilopterus* feed with the same intensity in vegetated and non-vegetated habitats and in diel periods. In contrast, the fullness index varied significantly among the different months, being higher in the dry season (mainly in January). In tropical lagoons of the Gulf of Mexico, this species shows a maximum reproductive pulse in the rainy season from September to November [4,37], so the maximum feeding intensity coincides with the recruitment of young individuals to the system. Thus, fish size drops from September to November, because the fish in September are the oldest fish and the fish in November are the recently settled. The latter could be related to the fact that during these stages of the life cycle, fish also need more food to mature, develop, and grow.

Overall, the statistical power of the hypothesis tests was close to or greater than 80% for comparisons across habitats, months, and size classes, for both dietary variation and fullness index analyses, indicating a high probability of correctly detecting significant effects despite the relatively small sample sizes. In contrast, analyses of diel variation were not significant and exhibited low statistical power.

5. Conclusions

This study confirms that the species' feeding habits are linked to its growth pattern and to the types of food available, which are modulated by spatiotemporal variations in environmental conditions. Small fish feed primarily on small prey such as copepods and decapod larvae, which dominate the open, bare substrate and are most abundant during the dry season. As individuals grow, they move into vegetated habitats during the rainy season

and feed mainly on relatively larger prey—fish, peracarids, and caridean shrimp—which have higher energy content than zooplankton. Ontogenetic changes in feeding throughout the life cycle thus appear adapted to the system's spatiotemporal variability, matching prey availability to energy requirements. Although diel variation was not statistically significant, some trends were evident and provide the first evidence of dietary changes over 24 h cycles. The main contribution of the study is documentation that spatiotemporal and ontogenetic variations in the diet of *Citharichthys spilopterus* represent an adaptive response to environmental change in the system.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author.

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