HOW DOES DIET INFLUENCE THE REPRODUCTIVE SEASONALITY OF TROPICAL FRESHWATER FISH? THE CASE STUDY OF A CHARACIN AT A TROPICAL MOUNTAIN RIVER

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A mi familia,

A mis amigos,

a Wilmer Pardo

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Resumen

TITULO. HOW DOES DIET INFLUENCE THE REPRODUCTIVE SEASONALITY OF TROPICAL FRESHWATER FISH? THE CASE STUDY OF A CHARACIN AL A TROPICAL MOUNTAIN RIVER*

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Palabras claves: Ecología trófica, variación estacional, fenología, trópico, *Creagrutus guanes*

Una explicación propuesta sobre la estacionalidad reproductiva de los peces tropicales de agua dulce es que la reproducción puede estar sincronizada con períodos de alto consumo de alimento. Nosotros exploramos esta hipótesis estudiando la relación entre la dieta y la actividad reproductiva de *Creagrutus guanes* (Teleostei, Characidae; un carácido de río de montaña), y la posibilidad de que el ciclo hidrológico influencia la estacionalidad reproductiva a través de su dieta, analizando la influencia de la ecología trófica en la estacionalidad reproductiva. Nuestros resultados muestran que *C. guanes* presentó una dieta generalista y omnívora dominada por insectos acuáticos (principalmente larvas de Diptera, material Autóctono) y semillas (material alóctono). *Creagrutus guanes* no presentó variación intersexual u ontogenética en la dieta. Para *C. guanes*, las semillas y larvas de Diptera presentaron patrones estacionales en su ingesta, posiblemente producto de su disponibilidad en el río. *C. guanes* presentó uso diferencial de los recursos, aprovechando la variación temporal del material alóctono (mayor durante los meses lluviosos) y del material autóctono (mayor durante meses secos). Picos de la actividad alimenticia durante los meses lluviosos no estuvieron sincronizados con la reproducción en los meses secos. Nuestros resultados y reportes publicados no soportan la hipótesis que la estación reproductiva esta sincronizada con el alto consumo de alimento. Reservas de grasa fueron intermediarios importantes entre la alimentación y la reproducción, además pueden ser un factor importante en la desincronización de los picos de alimentación y reproducción. Hipótesis alternativas que explican la estacionalidad reproductiva son discutidas.

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Abstract

TITULO. HOW DOES DIET INFLUENCE THE REPRODUCTIVE SEASONALITY OF TROPICAL FRESHWATER FISH? THE CASE STUDY OF A CHARACIN AL A TROPICAL MOUNTAIN RIVER*

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Keywords: Feeding ecology, seasonal variation, phenology, tropics, *Creagrutus guanes*

One proposed explanation for the seasonal breeding of tropical freshwater fish is that breeding may be synchronized with periods of high food consumption. We explored this hypothesis by studying the relationship between diet and reproductive activity of *Creagrutus guanes* (Teleostei, Characidae; a characin at a tropical mountain river), and the possibility that the hydrological cycle influences the reproductive seasonality through its diet by analyzing the influence of the feeding ecology on the reproductive seasonality. Our results showed that *C. guanes* had a generalist and omnivorous diet dominated by aquatic insects (mainly Diptera larvae, Autochthonous matter) and seeds (Allochthonous matter). *Creagrutus guanes* did not show intersexual or ontogenetic variation in diet. For *C. guanes*, the seeds and Diptera larvae showed seasonal patters of consumption, likely as a product of their availability into the river. *C. guanes* presented differential usage of resources, taking advantage of the temporal variation of allochthonous (higher during rainy months) and autochthonous matter (higher during dry months). Peaks of feeding activity during rainy months were not synchronized with breeding in dry months. Our results and published reports do not support the hypothesis that the reproductive season has to be synchronized with high food consumption. Fat reserves were important intermediaries between feeding and breeding. Besides, fat reserves may be an important factor for the desynchronization of peaks of feeding and reproduction. Alternative hypotheses for the explanation of seasonal breeding of the species are discussed.

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1. INTRODUCTION

Whereas reproductive seasonality of temperate fish is determined mostly by temperature, tropical freshwater fish are conditioned by hydrological cycle (Wooton, 1998). Most tropical freshwater fish breed during rainy season, and few others breed during dry season, or throughout the year. Several factors have been proposed to explain that variation, such as the availability of nursery areas (Rinne & Wanjala, 1983), adult or juvenile food availability (Lake, 1967; Kramer, 1978), competition for breeding sites, and phylogenetic inertia (Kramer, 1978). In this study we explored the possibility that the hydrological cycle influences the reproductive seasonality of tropical fish through their diet by analyzing the influence of the feeding ecology on the reproductive seasonality of a characin at a tropical mountain river, and assessed the Kramer´s hypothesis that the reproductive season is synchronized with high food consumption.

Most studies on the diet of tropical freshwater fish have focused on the comparison between feeding and hydrological cycle (Prejs & Prejs, 1987; Esteves & Pinto Lobo, 2001; de Alvarenga *et al.,* 2006), but there are few analyses focused on the interaction between feeding and reproductive seasonality. It has been shown that many fish totally or partially shift their diets across seasons (Prejs & Prejs, 1987; Mazzoni & Rezende, 2003), and the highest feeding activity usually occurs during the rainy seasons when the availability of preys is relatively higher (Prejs & Prejs, 1987). The scattered information shows that most tropical freshwater fish reproduce during or after peak food availability and consumption (Rinne & Wanjala, 1983; Esteves & Pinto-Lobo, 2001; de Alvarenga *et al.,* 2006), whereas other tropical freshwater fish can diminish or even cease food ingestion during reproductive season (Ikomi, 1996; Santamaría-Miranda *et al.,* 2005). Besides quantity of food, the type of food consumed may be related to reproduction. The high nutrient content from some food types may have a role on gonadal maturation trough their contribution in the store of fat reserves. More studies are necessary to understand the role of the diet in the reproductive seasonality of tropical fish, and the influence of hydrological cycle on both of them.

We analyzed the interaction between diet and reproduction of *Creagrutus guanes*, a tropical freshwater fish with a known reproductive seasonality (Torres-Mejía & Ramírez-Pinilla, 2008). Our main objectives were to analyze the trophic ecology of *C. guanes* throughout an annual cycle and to assess the relationship between the diet and the reproductive activity of this species. Our results were compared with the patterns reported in the literature for other tropical freshwater fish.

2. MATERIALS AND METHODS

2.1 SPECIES AND SITE STUDY

Creagrutus guanes is a small fish (maximum SL= 77 mm) that inhabits small embayments along river banks where water flow is reduced (Torres-Mejía & Ramírez-Pinilla, 2008). *Creagrutus guanes* is distributed in mountain rivers of the Río Magdalena basin, Colombia (Torres-Mejía & Vari, 2005). It breeds seasonally during dry months, and stores fat in response to rainfalls, presumably to invest it later in reproduction during dry periods (Torres-Mejía & Ramírez-Pinilla, 2008).

Specimens were collected at Río Fonce and 500 m upstream from the mouth of one of its tributaries, the Río Mogoticos (6°25’-31’ N, and 73°7’-9’ W, between 1100 and 1350 m altitude), between the towns of San Gil and Charalá, Santander, Colombia. Río Fonce is part of the Río Magdalena system and drains a region of the west side of the Andean Cordillera Oriental of Colombia. Rainfall follows a bimodal seasonal pattern that is characterized by a first rainy season from April to May, a rainfall decrease from June to August, a second rainy season from September to November, and a dry season from December to March (shadow on background of Fig. 3). Since the pattern of flow was similar to the rainfall pattern

(Torres-Mejía & Ramírez-Pinilla, 2008), we used the rain pattern as an indicator of the hydrological cycle.

2.2 FIELD AND LABORATORY PROCEDURES

Twenty to 30 fishes longer than 20 mm SL were collected monthly in field campaigns of two days by the middle of each month, from 11/2003 to 11/2004. The capture methods implemented depending on water conditions were cast nets, dip nets, seines, and hooks with worms as bait. Specimens were fixed in buffered formalin (10%), transferred to ethanol (70%) 15 to 30 days later and deposited at the ichthyological collection of Universidad Industrial de Santander, Colombia.

Specimens were dissected under a stereo microscope and digestive tracts were extracted. Stomach and intestine weights (± 0.001 g) and intestine length (± 0.02 mm) were recorded for each specimen. Analysis of diet was based on stomach contents. Total prey volume was measured in sized graduated cylinders by water displacement (Winemiller, 1990). Prey items were separated, counted, and identified to the lowest possible taxonomic category. The volume of each prey category was calculated visually as a percentage from the total (100%) prey volume. The digestive contents were differentiated in allochthonous (terrestrial) and autochthonous (aquatic) items.

2.3 DIET ANALYSIS

We used the Index of Relative Importance (IRI) to indicate the importance of each prey category (Pinkas *et al*., 1971). IRI was calculated as $IRI_j = \%F_j (\%N_j + \%V_j)$, where *j* is each prey category, $\%F_j$ is the occurrence proportion (i.e., the proportion of guts containing each *j* item), $\%N_j$ is the proportion of the number of *j* items in all guts, and $\%V_j$ is the proportion of the volume of *j* items in all guts (Pinkas *et al*., 1971). To compare IRI values we used a relative value of IRI ($\%IRI_j = 100 (IRI_j/\Sigma IRI_n)$, where *n* is the number of total prey categories). We additionally explored the ontogenetic variations of diet, arranging specimens in size-age categories every 10 mm, from the smallest individual collected (20 mm SL) to the largest (71 mm SL). We also compared the correlation of trophic level and gut length to that reported for other species (Kramer & Bryant, 1995b). We compared the qualitative observations of diet with the gut size of *C. guanes* by measuring the Relative Gut Length (intestine length/ standard length) and Zihler´s Index (intestine length divided by 10*body mass$^{1/3}$; Kramer & Bryant, 1995).

We tested for ontogenetic differences in prey consumption using several methods. First, we used non-metric multi-dimensional scaling ordination (NMDS) and One-way Analyses of similarities (ANOSIM) to examine ontogenetic changes of the prey categories with respect to sex, based on a Bray-Curtis similarity matrix and IRI values of each prey category (Clarke, 1993; Clarke & Warwick, 1994). Multivariate analyses were conducted in PAST. exe, ver 1.85. The relationships between fish size (independent variable) vs. total prey volume or vs. total prey number were evaluated with simple regressions. Second, we quantified the overlap of diet between all pairs of size-age categories with Schoener´s Coefficient [$S= 1 – 0.5 (\sum P_{xi} - P_{yi})$], where P_{xi} and P_{yi} are the proportions of occurrence of each prey category *i,* in each pair of size-age category (*x*, *y*) (Schoener, 1970). The degree of overlap was categorized as low (< 33.3%), moderate (33.3-66.6%), or high (> 66.6%) (Schoener, 1970). The third method used was to analyze the ontogenetic variation in the spectrum of prey species consumed by calculating the Trophic niche breadth index (B_A) for each size-age category using Levins standardized formula: $B_A= ((1/\sum pi^2)-1)/ (n-1)$, where p_i is the proportion of occurrence of each prey category and *n* is the number of preys consumed in the fish diet (Hurlbert, 1978). B_A ranges from 0 to 1, with values near zero indicating that only one or few categories were consumed in high proportion or many prey categories were used in low proportions, and values near one indicating that all preys were consumed in equal proportion. *G*-tests were made to examine the differences in niche breadth.

Several aspects of annual variation in diet were analyzed. Since our results showed that there were not ontogenetic variations in diet, the following analyses include all individuals. First, we tested for variation of prey items consumed trough time. Monthly changes in diet for each sex were examined using Non-Metric Multi-Dimensional Scaling Ordination (NMDS). One way Analyses of Similarity (ANOSIM) were employed to determine the dietary similarity among seasons with respect to sex. Following the ANOSIM global test, we investigated differences between months with respect to sex by pair-wise comparisons. Prey categories most responsible for significant differences between months were determined using Similarity Percentages (SIMPER) (Clarke & Warwick, 1994). The analyses were made based on a Bray-Curtis similarity matrix and IRI values of each prey category. ANOVA was used to examine the effect of season in (log-transformed) total prey volume. Second, we described the diet overlap and breadth for this species. Diet overlap between seasons was calculated with Schoener´s Coefficient, and the seasonal variation in the spectrum of prey species consumed was quantified with the Trophic Niche Breadth index (B_A), and *G*-tests were made to test the significance of the seasonal differences. Third, it was checked if observed changes in diet through time were related to rainfall, using Pearson correlations of rainfall vs. total prey volume, and vs. volume of most consumed prey items. Assumptions of normality, linearity, and homogeneity of variance were fulfilled after log transforming the data.

Some aspects of the interaction between diet and reproduction were analyzed. First, we assessed the degree of association between total prey volume of females vs. rainfall, and vs. gonad weight, and fat weight vs. total prey volume, vs. diptera volume, and vs. seed volume. Second we explored the possibility that there was a lag in the correlation among variables (e.g., total prey volume could be more correlated with the fat weight of one month before than with fat weight of same month). In both analyses Pearson correlations were used, calculating the correlation between total prey volume, gonad weight, and fat weight in month *x* with a second variable at the same month (*x*), at one months before(*x*-1), at two months before (*x* -2), at one month later (*x*+1), and at two months later (*x*+2). A degree of freedom (i.e., the unmatched observations at the tail of each series) was lost every time a month was lagged (Torres-Mejía & Ramírez-Pinilla, 2008). A false discovery rate control (Verhoeven *et al.,* 2005) was implemented to correct for the repeated use of same data for several correlations (Type I error rate). ANOVA was used to examine the effect of the reproductive stage in (log-transformed) total prey volume.

3. RESULTS

We analyzed 215 digestive tracts of adults and juveniles of *C. guanes* (34 males, 126 females, and 55 juveniles). Only four tracts were empty. In total 989 preys from 11 categories were found in digestive tracts (Table 1). The diet of *Creagrutus guanes* can be classified as omnivorous, being dominated by aquatic insects (%IRI: 57.71%) and seeds (%IRI: 37.86%) (Table 1). Diptera was the most common insect order (%IRI: 29.53%), represented mostly by the family Chironomidae. The importance of the other aquatic orders (Ephemeroptera, Trichoptera, Coleoptera, Odonata and Hemiptera) was minimal (%IRI < 0.80%). Terrestrial insects were rare (Formicidae %IRI: 3.55%). Dietary niche breadth of *C. guanes* was small (B_A = 0.07), suggesting that even though the species was omnivorous, it consumed few types of prey items. The average Relative Gut Length (0.7632) and Zihler's (3.42) indices were in the range of omnivorous fishes (Kramer & Bryant, 1995), giving support to the conclusion obtained from the stomach content analysis.

The diet of *C. guanes* varied little between sexes and among ontogenetic categories. NMDS did not show considerable variation in diet across size age categories (Fig 1). There were not significant differences among size categories in prey items consumed (ANOSIM, global $R = -0.08$, $P = 0.65$), nor niche breadth ($G_{0.05,\,1} = 0.40$, $P > 0.05$). The overlap of diet between all pairs of size-age categories was always high. The only ontogenetic change observed in diet were that the average prey volume increased with fish body size ($r^2 = 0.43$, $P < 0.05$, $N = 160$). There was not a negative relationship between number of prey and fish body size

(r^2 = 0.04, $P < 0.01$, N = 160). *C. guanes* consumed the same types of prey along its ontogeny, but the size of preys increased with body size.

There was variation in consumption of prey among seasons and among months. The ordination of the contributions of the different dietary categories showed two groups: males and females samples of rainy month samples were distributed across the right half of the plot, whereas samples of females from dry months occupied the left half of the plot (Fig. 2). The moderate stress coefficient of 0.1 indicated that the resulting ordination plot is reliable (Clarke & Gorley, 2001). There were significant differences among rainy and dry months (global R = 0.25, P = 0.02). Pair-wise comparisons showed significant dissimilarities between several months (females of April vs. females of January, females of May vs. females of February, and males of April vs. females of January). An analysis of similarity percentage (SIMPER) indicated that seeds and diptera larvae were respectively the first and second main contributing preys to the overall observed differences (Table 2). Specifically, the consumption of seeds, Diptera larvae, and in less extent Formicidae changed over time. The highest ingestion of seeds was during April, September, and November (rainy months), moderate from May to August (all dry months except May), and the lowest ingestion from December to March (dry months). The highest consumption of Diptera larvae was during March, August and October (dry months except October), moderate from April to July (dry months except April), and the lowest consumption during September and November (rainy months) (Fig. 3).

The annual differences in diet of *C. guanes* were mainly quantitative, all prey categories were always consumed but quantity of food consumed varied among the seasons. Total prey volume was slightly (but non significantly) higher during rainy months ($F_{0.05\ (1)\ 1,\ 200}$ = 3.87, P = 0.05). The overlap of diet between rainy and dry season was high (S = 85.25%), indicating that the fishes ate similar preys among seasons. Dietary niche breadth was similar between seasons (rainy season B_A = 0.04, dry season B_A = 0.11; $G_{0.05,\ 1}$= 0.04, $P > 0.05$). Reproduction was not synchronized with the highest consumption of food (Table 3). Fat weight was not correlated with total prey volume, diptera or seed volume (Table 3). Rainfall was correlated with consumption of seeds (r^2 = 0.46, *P* = 0.015, *N* = 12), but not with consumption of Diptera larvae, or ants, or with total prey consumption. Lagging did not produce any significant correlation (Table 3).

4. DISCUSSION

Our observations indicate that for *C. guanes* the reproduction was not synchronized with food consumption. In fact, the food item most consumed by *C. guanes*, seeds, was more frequently found in specimens collected during rainy season, whereas these fishes breed during the dry season. This evidence does not support the Kramer´s hypothesis (Kramer, 1978) that the reproductive season is synchronized with high food consumption. In the next paragraphs we discuss this result and other hypotheses for the seasonal reproductive patters of tropical freshwater fish.

The diet of *C. guanes* is not unusual among tropical freshwater fish. *Creagrutus guanes* is an omnivore and generalist species that consumed high proportion of benthic fauna (mostly Diptera larvae), and allochtonous matter (mostly seeds). The diet of *C. guanes* is similar to the diet of other members of the genus *Creagrutus* (Ortaz, 1992, 2001; Román-Valencia, 1998), and other members of the order Characiforms, even from different habitats such as floodplain rivers (Ortaz, 1992; Esteves & Galetti, 1995; Ortaz, 2001; Vilella *et al.,* 2002; Barreto & Aranha, 2006). We conclude that the diet of *C. guanes* is not a rare case, but instead may represent the diet composition of many tropical freshwater fish.

The absence of variation in the type of prey along the ontogeny was an unusual aspect of the diet of *C. guanes*. Many tropical fish present ontogenetic diet shift of the type of prey (Mérigoux & Ponton, 1998) associated mainly with change of habit use (Barros, 2004; Santamaría-Miranda *et al.,* 2005) or related to morphological changes that lead to shifts in prey selection and capture (Araújo *et al.,* 2005). It is unknown whether *C._guanes* presents morphological and habitat use variations. We speculate that *C. guanes* has a diet shift, but it occurred at a body size smaller that our range of sampling. Another interesting result was that in *C. guanes* food consumption was not dependent on sex. Probably, males and females did not show spatial or seasonal habitat segregation, and adult males continued feeding in the same areas occupied by females, even during the breeding season.

For *C. guanes*, the most consumed items showed seasonal patters of consumption, likely as a product of their availability into the river. It has been proposed that the seasonal changes in diet composition partly reflect the seasonal changes of food resources (Xie *et al.,* 2000). Many species show seasonality in food uptake related to hydrological cycle (Esteves & Galleti, 1995; González & Oyarzún, 2003; Balcome *et al.,* 2005), what may also be the case of two of the types of food items most consumed by *C. guanes*. During the rainy seasons seeds are more abundant and available into the stream (Ponce-Calderón, 2002; Lemus-Jiménez & Ramírez, 2002), and coincidentally the rainy season was the period when *C. guanes* had the highest ingestion of seed. The highest abundance of some species of Diptera (Velásquez de Ríos *et al.,* 2004) occurs at intersection period between rainy-dry season, also the period of greatest ingestion of Diptera larvae by *C. guanes*. In the habitats of many temperate and tropical fishes the timing of the allochthonous food input coincides with a period of reduced availability of aquatic preys (Garman, 1991). That also seems to be the case for *C. guanes*, whose diet showed that the ingestion of seeds was concomitant with a decline in ingestion of Diptera larvae. In general, it seems that *C. guanes* presented differential usage of resources, taking advantage of the temporal variation of allochthonous (higher during rainy months) and autochthonous matter (higher during dry months).

Despite the dramatic difference in flooding pattern between upland and lowland rivers (Chapman & Kramer, 1991), flooding after rainfalls may increase allochtonous materials in both types of systems. In many floodplain rivers the rainfall increases the river discharge and brings allochthonous matter into the river (Castillo-Rivera *et al.,* 1994), increasing the spectrum of available preys. A similar trend may occur in mountain rivers, where floods commonly drive terrestrial organisms to the water, some use floods for dispersal (Friedman & Auble, 2000), and others are catastrophically dragged (animals: Garman, 1991; plants: Castillo-Rivera *et al.,* 1994; Swanson *et al.,* 1998). Contrary to the considerable attention that the relationship of floods in lowland rivers and allochthonous food availability for fishes (e.g. Goulding, 1980), such relationship has been rarely investigated for upland rivers (see Winemiller, 1990 for an exception).

The evidence that we collected in this analysis does not support Kramer´s hypothesis that the reproductive season is synchronized with food consumption (Kramer, 1978). *Creagrutus guanes* breeds later during dry months, but presented the highest feeding activity dominated by seeds during the rainy months. The peaks of availability of different sorts of foods were not synchronized with the breeding seasons. This asynchrony is not an unusual among tropical fish (Kramer, 1978; Esteves & Pinto Lobo, 2001; de Alvarenga *et al*., 2006), either from floodplain rivers (e.g. *Bryconamericus emperador* and *Brycon petrosus*, Kramer, 1978; *Salminus maxillosus*, Esteves & Pinto Lobo, 2001; *Curimatella lepidura*, de Alvarenga *et al*., 2006) or from mountain rivers (e.g. *Creagrutus brevipinnis*, Román-Valencia, 1998).

Fat reserves may have been the crucial factor in the desynchronization of feeding and reproductive peaks in *C. guanes*. During rainy months, the highest consumption of seeds coincided with the maximum fat weight of the females. The contradictory observation that fat weight was not significantly correlated with total prey volume nor seeds volume may be a result of the reduction in statistical power by the correction for multiple testing. Possibly, the nutrients from seeds were responsible of the highest proportion of fat reserves. The observation of females with the highest total prey volume during heavy rains, the increase of fat weight soon after heavy rains and subsequent increase of gonad weight on dry months indicated that resources are being stored during rainy months to be invested later in reproduction (Esteves & Pinto Lobo, 2001; Torres-Mejía & Ramírez-Pinilla, 2008). In some tropical fish, the capacity to build up fat reserves allows the time of spawning to be independent of the time of food abundance (Kramer, 1978; de Avarenga *et al*., 2006). There is a need of more studies that assess the role of fat reserves in the reproduction of tropical fish.

Other factors like evolutionary history, availability of nursery areas (Rinne & Wanjala, 1983), interspecific competition for food among juveniles, species social system (Kramer, 1978), and habitat stability (Humphries *et al.,* 1999) have been hypothesized to influence reproductive seasonality of tropical freshwater fish. For explaining the reproductive pattern of *C. guanes* we lean towards the hypothesis that a more stable habitat (no flash floods) during dry seasons (Humphries *et al.,* 1999) could favor survival of offspring and female recover. Indirectly, the absence of floods during dry season may favor fish larvae by allowing the growth of small aquatic organisms (zooplancton, macroinvertebrates) which usually are consumed by fish larvae. In mountain rivers the reproduction during dry months is a common pattern (Torres-Mejía & Ramírez-Pinilla, 2008). Possibly, the intensity and predictability of the flow regimes in mountain rivers may have lead to life history adaptations (Lytle & Poff, 2004), favoring breeding during the low-flow season.

Further analyses of the factors associated with the reproductive pattern of tropical fish are needed. Due to variations in the flow regimes and life history adaptations of fish, the analyses should involve floodplain, lowland and mountain rivers. More research is necessary to asses the synchrony of reproductive seasonality with food consumption and food availability, fat storage, and the influence of the hydrological cycle on them. For a greater understanding of the reproductive timing of tropical fish, additional studies of the importance of the fat reserves as intermediaries between feeding and breeding would be useful.

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Fig. 1. Non-Metric Multi-Dimensional Scaling Ordination (NMDS) of ontogenetic variations of the diet with respect to sex. Stress = 0.1632. ▲Mature female, ◆ Mature male, ▽ Inmature female, ○ Inmature male.

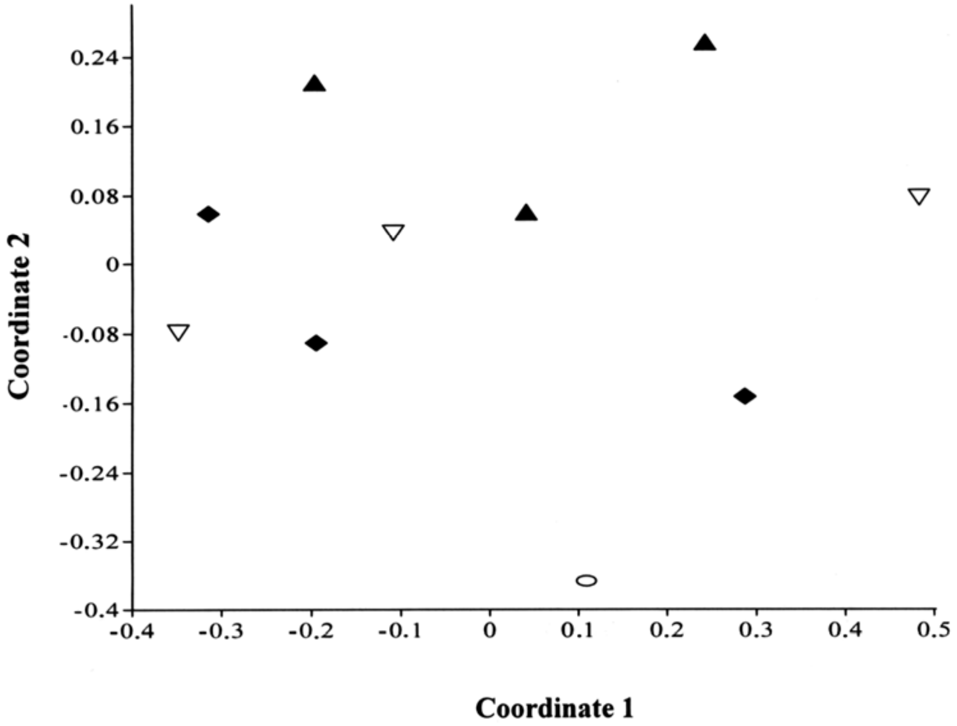

Fig. 2. Non-Metric Multi-Dimensional Scaling Ordination (NMDS) of monthly variations of the diet with respect to sex. Stress = 0.1. ▲ Rainy months-female, ▽ Rainy months-male, ○ Dry months-female, ■ Dry months-male.

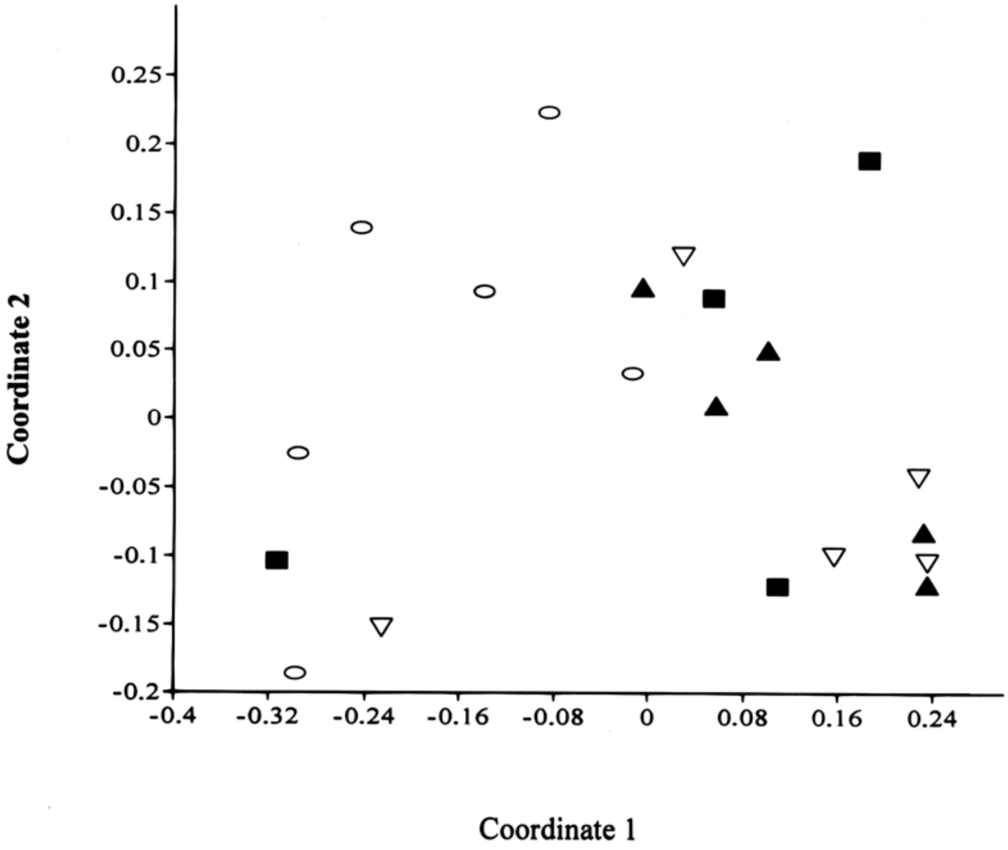

Fig. 3 . Monthly variation of prey categories-IRI values.

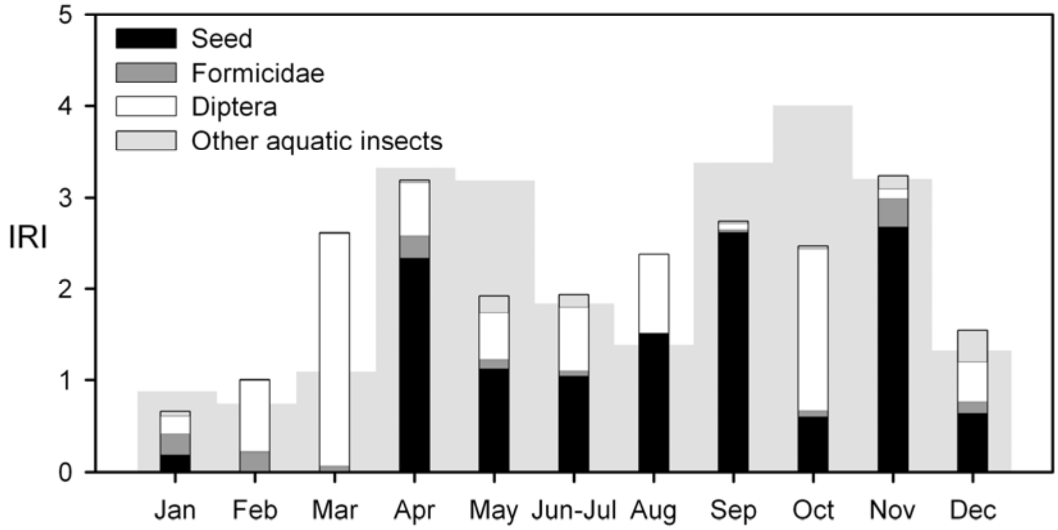

Table 1. Diet of *Creagrutus guanes*. N= number of each prey item, % N= Percentage of N. V= Volume of each prey item, % V = Percentage of V, F= Frequency of each prey item, % F= Percentage of F, IRI = Index of Relative Importance.

Prey type	N	%N	F	%F	V	%V	IRI
Seeds	485	49	101	46.97	1.93	35.21	3955.34
Filamentous algae			12	5.58			
Terrestrial arthropodos	103	10.41	55	25.58	0.41	7.62	461.20
Aranae	1	0.1	1	0.46	0.02	0.25	0.16
Terrestrial insects	97	9.8	55	25.58	0.35	6.47	416.18
Formicidae	92	9.3	54	25.11	0.30	5.47	370.87
Adult Diptera	3	0.3	2	0.9	0.01	0.127	0.38
Aquatic insecto	401	40.54	133	61.86	3.12	56.92	6028.87
Diptera	325	38.86	101	46.97	1.47	26.81	3084.51
Chironomidae	292	29.52	91	42.32	0.87	15.90	1922.17
Ephemeroptera	12	1.213	8	3.72	0.12	2.22	12.77
Trichoptera	19	1.921	13	6.04	0.187	3.42	32.26
Coleoptera	36	3.64	23	10.69	0.186	3.41	75.36
Hemiptera	3	0.3	3	1.39	0.02	0.31	0.85
Odonata	6	0.60	6	2.79	1.16	21.16	60.72

TOTAL	989	215	5.48	10445.41

Table 2. ANOSIM-Pairwise comparisons and dissimilarities between months with respect to sex.

Pairwise comparisons	*R*	*P*	Overall diss. (%)	Prey category	Contribution %	Cumulative %
April-Female vs. January-Female	0.45	0.007	62.39	Seed	52.44	52.44
				Diptera	32.74	85.18
April-Male vs. January-Female	0.37	0.03	63.8	Seed	54.26	54.26
				Diptera	33.64	87.90
May-Female vs.Feb-Female	0.54	0.02	67	Seed	57.99	57.99
				Diptera	34.81	92.8

Table 3. Correlation lagged between Gonad and Fat weight, total prey volume, Diptera volume, seeds volume and Rain, lagging One or Two Months, and without lagging. [a] *P* < 0.05 without adjustment nominal *P*-values for multiple testing. After the adjustment no one correlation was significant.

Fixed variable	Lagged variable	Month -2	Month -1	Same month	Month + 1	Month +2
Gonad	Total prey volume	0.66[a]	-0.40	-0.31	-0.42	0.47
Rainfall	Total prey volume	0.02	-0.12	0.27	-0.30	-0.25
Fat	Total prey volume	0.24	0.27	0.12	-0.24	-0.19
	Seeds volume	0.32	0.38	0.03	-0.40	-0.37
	Diptera volume	0.35	-0.62	-0.62	-0.39	-0.028