


# Feeding strategies and diet variation in livebearing fishes of the genus *Limia* (Cyprinodontiformes: Poeciliidae) in the Greater Antilles

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## Abstract

Feeding specialisations are known to play an important role in the ecology and evolution of many organisms. In this study, we performed a comparative analysis based on the data of the gut content of eight species of the genus *Limia* (family Poeciliidae) to explore the potential role of feeding ecology in the radiation of this genus in the Caribbean. We analysed the feeding strategies using the modified Costello's graphical method. In addition, we estimated the contribution of each food item to the diet by calculating the alimentary index of six different functional categories that summarised the variation in main type of consumed items. We also compared the niche breadth for all analysed species and the niche breadth variation between wet and dry seasons in four species we were able to sample in both periods of the year. Most of the analysed species showed preference for detritus and algae. Species that exhibited a more omnivorous diet such as *L. versicolor* and *L. perugiae* revealed moderate levels of consumption of terrestrial and aquatic invertebrates. Nonetheless, some species such as *L. yaguajali* and *L. nigrofasciata* showed specialisations towards detritus as the dominant food item found in the gut content analysis. In general, niche breadth values were higher in the wet season than in the dry period. Our study showed that the majority of species analysed tend to be feeding generalists, but some degree of specialisation occurs in some species from Hispaniola where the diversity of the genus *Limia* is remarkably higher compared to the rest of the Greater Antilles.

## KEYWORDS

ecology, feeding strategies, Greater Antilles, *Limia*, niche breadth, omnivorous

## 1 | INTRODUCTION

Feeding is relevant to every aspect of animal life and is tightly linked to the ecological niche a species occupies. In concordance with the enormous diversity found in teleost fishes, feeding specialisations are also abundant in this group. One example for this is the

order Cyprinodontiformes. This is the most diverse and speciose order of freshwater fishes within the Atherinomorphae. More than 1350 species are known in this order, which are distributed in temperate and tropical regions of the world usually inhabiting shallow freshwater environments or coastal brackish waters (Malabarba & Malabarba, 2020). The Cyprinodontiformes contain approximately

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twice the number of species of the sister groups Beloniformes and Atheriniformes combined (Hernandez et al., 2009), and they are especially diverse in Central America representing 13% of the neotropical ichthyofauna (Malabarba & Malabarba, 2020). Despite this extraordinary diversity, the whole group has traditionally been considered as having generalised feeding habits characterised by a broad diet range, high plasticity and usually preying on benthic and planktonic organisms (Hunt, 1953; Mansfield & Macardle, 1998; Motta et al., 1995; Weisberg, 1986). This seems to contradict the notion that often feeding adaptations contribute to speciation, as for example found in cichlids. Furthermore, this general classification does not correspond with the diverse feeding behaviours and specialisations that can be seen in some groups of cyprinodontiformes (Hernandez et al., 2009).

In this study, we provide comparative data on gut content in *Limia*, a genus of livebearing fishes (family Poeciliidae), which allows us to take a more fine-grained look at the potential role of feeding ecology in the radiation this genus found in the Caribbean. We are especially interested in discovering if the species of this genus may show cryptic differences in their feeding adaptations.

A group of freshwater fishes that is exceptionally well understood in this context is cichlids. Although not as notable as the examples of cichlid fishes (Cichlidae) from the East African Great Lakes where trophic specialisations in both diet and mouth morphology have contributed to an extraordinary adaptive radiation (Kornfield & Smith, 2000; Meier et al., 2019; Takahashi & Koblmüller, 2011), there are nonetheless a few examples of species showing feeding specialisations (species with narrow scope in diet) in Cyprinodontiformes that deserve more attention. For instance, it has been shown that three species of *Cyprinodon* (Cyprinodontidae) that coexist sympatrically in hypersaline lagoons within the San Salvador Island, Bahamas have trophic partitioning (Martin & Wainwright, 2013) with one species (*C. variegatus*) having a broad geographic distribution and detritivorous feeding habits and the other two species being diet specialists: *C. brontotheroides* specialises in consuming hard prey (i.e. ostracods, gastropods) and *C. desquamator* a specialised scale eater (Martin & Wainwright, 2013). Another example of extreme feeding specialisation in Cyprinodontiformes is the case of the pike killifish (*Belonesox belizanus*) a poeciliid mostly distributed in Central America (Rosen & Bailey, 1963). This species exclusively feeds on fish that are captured by moveable elongate jaws and large and pointed unicuspid teeth (Greven & Brenner, 2008).

Furthermore, although not as specialised as previously mentioned, a well-studied case within the Cyprinodontiformes is the predatory species of the genus *Gambusia* (mainly the invasive *G. affinis* and *G. holbrooki*), which have been shown to be primarily zooplanktivorous (Blanco et al., 2004; Mansfield & Macardle, 1998; Singh & Gupta, 2010; Specziár, 2004). Against this backdrop, there is a surprising lack of studies that characterise the diet, annual shifts in dietary composition and the morphology of the feeding apparatus for the majority of cyprinodontiformes. Particularly in livebearing fishes (family Poeciliidae), which are a dominant group in southern North America and Central America including the Caribbean islands,

there are only few analyses of the diet in individual species. For instance, Zandonà et al. (2015) studied some differences in the diet of the Trinidadian guppy (*Poecilia reticulata*) in relation to habitats with varying predation levels showing differences in dietary composition between high and low predation pressure environments. Furthermore, Sanchez and Trexler (2018) analysed the adaptive evolution of herbivory in the sailfin molly (*Poecilia latipinna*) using enclosure cages in the Everglades in Florida revealing that this species fed selectively on epiphyton to compensate deficiencies in the available food. Scharnweber et al. (2011) explored the differences in feeding behaviour and feeding efficiency between sexual (*Poecilia mexicana*) and asexual (*Poecilia formosa*) mollies concluding that competition for food plays a minor role in mediating coexistence in natural habitats in these two species. While these studies provide useful information to understanding the ecology of the analysed species, they do not offer a comparative perspective that allows inferring patterns of use of food resources, and interpretations of species relationships or interactions are limited.

Livebearing fishes from the West Indies are definitely a group of freshwater vertebrates that is worth to analyse in terms of dietary adaptations since it has experienced the largest radiation in aquatic environments of the West Indies (Rodriguez-Silva & Schlupp, 2021a). Particularly in the genus *Limia*, the speciation process has resulted in the largest radiation of poeciliids in the Caribbean islands. There are 22 species of this genus that have been described so far from Cuba, Hispaniola, Jamaica and Grand Cayman. These species show a remarkably diverse ecology and are widespread in different types of habitats in the Greater Antilles from freshwater springs in the mountains to hypersaline coastal lagoons (Haney & Walsh, 2003; Rodriguez-Silva & Schlupp, 2021b; Weaver, Tello, et al., 2016). The centre of radiation of *Limia* is found on Hispaniola with 19 species, while only one endemic species from Cuba, Jamaica and Grand Cayman each are currently known (Burgess & Franz, 1989; Hamilton, 2001; Rodriguez-Silva et al., 2020; Rodriguez-Silva & Weaver, 2020; Weaver et al., 2016). The divergent species composition, mainly in the cases of Cuba and Hispaniola, is not predicted by the theory of island biogeography as the number of available ecological niches and island size are likely the same in both islands (Rodriguez-Silva & Schlupp, 2021a).

Niche specialisations, particularly foraging behaviour, coupled with resource partitioning and competition are thought to be essential factors in disruptive selection based on resource specialisation (Ackermann & Doebeli, 2004; Bürger et al., 2006). This is because specialisation in feeding habits and adaptations in trophic morphologies can be important diversifying forces leading to speciation (Bolnick et al., 2003; Knudsen et al., 2010; Skúlason & Smith, 1995). The speciation process based on food resource-based divergence, and ecological speciation in general, is thought to imply initial stages of resource polymorphism in which the ancestral lineage exploits multiple niches (Nyman et al., 2010; Smith & Skúlason, 1996). Consequently, the ability by which individuals can utilise different resources lead to disruptive selection and, if successful use of the new resources is established, to lineage splitting (Nosil et al., 2009).

In fact, selection acting on traits related to resource acquisition is considered to be critical in niche differentiation and even drive several cases of adaptive radiation (Schluter, 2000).

In this study, we characterise the diet of eight species of *Limia* collected in different habitats from Cuba, Jamaica and Hispaniola with the study of dietary changes between the wet and dry seasons for some of them. We also analyse niche specialisations and discuss the potential contribution of these specialisations to the radiation process of this genus. In addition, we analyse the variation of diet composition between species by comparison of the interspecific niche breadth. We hypothesise that even if the majority of *Limia* species could be categorised as feeding generalists like most other Cyprinodontiformes, there may be some level of diet specialisation for some species especially on Hispaniola where the genus shows the highest species diversity.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area, species and fieldwork methodology

The use of experimental animals complied with the University of Oklahoma animal welfare laws; guidelines and policies as approved by Animal Welfare Assurance on file with the Office of Laboratory Animal Welfare under the assurance number A3240-01. Fishes were collected and euthanized in the field following the approved IACUC protocol R18-005.

We collected eight species of *Limia* between May 2018 and January 2019 in different localities on Cuba, Jamaica and Hispaniola (Figure 1). Fishes were sampled using a 7.0-m long, 1.5-m height and 3.0-mm mesh size seine. We used a sampling effort of three seine hauls per collecting site. Collected fishes were euthanized in the field by immersion in a concentrated solution of MS 222 (tricaine methanesulfonate) and then preserved in 95% ethanol for further confirmation of species identity in the laboratory based on original descriptions and subsequent analysis of the gut content. All fishes were collected with the authorisation of the corresponding authorities in each country.

We sampled a variable number of specimens of the following species: *Limia vittata*, *L. melanogaster*, *L. perugiae*, *L. zonata*, *L. versicolor*, *L. yaguajali*, *L. nigrofasciata* and *L. islai*. The habitats where we collected these species showed notable variability ranging from a spring to hypersaline lagoon (Table S1). The species *L. melanogaster*, *L. perugiae*, *L. zonata*, *L. versicolor* and *L. yaguajali* were collected in freshwater springs or small creeks located in medium to low elevations, while *L. nigrofasciata* and *L. islai* were sampled in a lentic freshwater system (Lake Miragoane) from southwestern Hispaniola. Moreover, *L. vittata* specimens were collected in a hypersaline coastal habitat in southwestern Cuba (Figure 1). Sampling was carried out once in each period of the year: May–June (wet season) and also during December–January (dry season). For some species, we were able to do collections in both the wet and dry seasons from the same site to obtain a more complete picture of variation in the annual diet. However, in other species we were only able to collect specimens during the wet period, specifically in the months of May or June (Table 1).

### 2.2 | Diet analysis

Gut content of a total of 181 individuals of eight *Limia* species were analysed in order to characterise the diet of each species (Table 1). We only included adult specimens in this study to avoid effects of ontogenetic changes in diet. We measured the standard length of each individual and the length of the corresponding digestive tract. For this, individual guts were placed in a Petri dish and cut into three equal parts since the intestines can be very convoluted. Then we measured every part to obtain the total length of each gut.

To obtain dietary data, we analysed the contents found in the first third of the gut since the contents in this part of the digestive tract is not fully digested which allows identification and quantification of food items. Gut contents were examined individually in the laboratory under an Olympus SZX7 stereomicroscope with direct and transmitted light and 50X magnification, and items were identified to the lowest possible taxonomic level using specific literature sources for algae (Bellinger & Sigeo, 2010) and invertebrates

**FIGURE 1** Collecting sites of the *Limia* species analysed in the study. 1. Río Básima (*Limia versicolor*), 2. Río Verde (*Limia zonata*), 3. Río Jamao al Norte (*Limia yaguajali*), 4. Canal Los Tumbaos (*Limia perugiae*), 5. Caymana Springs (*Limia melanogaster*), 6. Lake Miragoane (*Limia islai*), 7. Lake Miragoane (*Limia nigrofasciata*), 8. Las Salinas de Brito (*Limia vittata*) (Map credit: OpenStreetMap contributors)

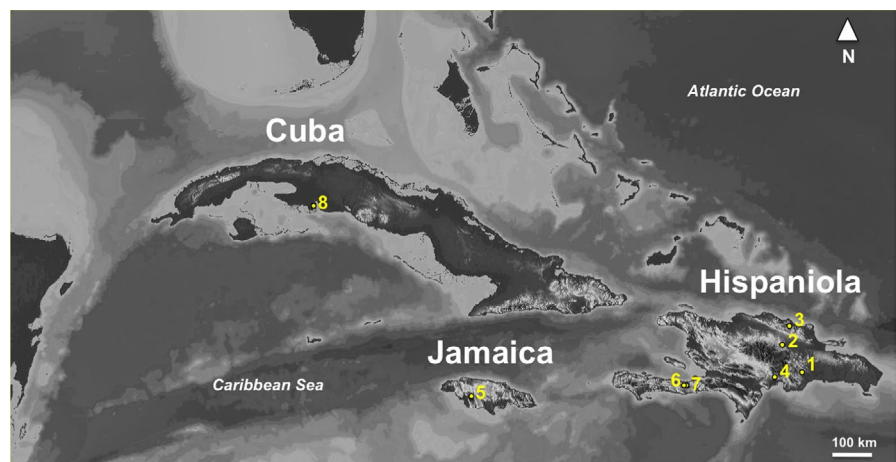


TABLE 1 Number of individuals analysed per species in each season of the year with information on the collecting sites, size ranges and gut lengths for each species

Species	GPS coordinates	N (wet season)	N (dry season)	SL range (mm)	GL (mean ± SD) (mm)
<i>Limia versicolor</i>	18°42'5.61" N 70°11'50.39" W	15	15	23–45	41.47 ± 15.60
<i>Limia zonata</i>	19°18'44.64" N 70°31'27.23" W	17	15	27–42	64.03 ± 23.16
<i>Limia yaguajali</i>	19°37'49.87" N 70°26'58.06" W	15	14	31–41	57.72 ± 13.72
<i>Limia perugiae</i>	18°14' 20.76" N 70°26'41.82" W	10	15	30–53	80.16 ± 27.20
<i>Limia nigrofasciata</i>	18°25'33.2" N 73°02'56.9" W	15	–	37–43	119.00 ± 19.48
<i>Limia melanogaster</i>	18°02'31.30" N 76°54'36.87" W	15	–	24–47	44.67 ± 16.33
<i>Limia islai</i>	18°25'59.4" N 73°03'33.5" W	13	–	28–31	43.46 ± 3.76
<i>Limia vittata</i>	22°10'40.76" N 81°15'13.18" W	22	–	22–36	44.32 ± 12.32

Abbreviations: GL, gut total length; N, sample size; SL, standard length.

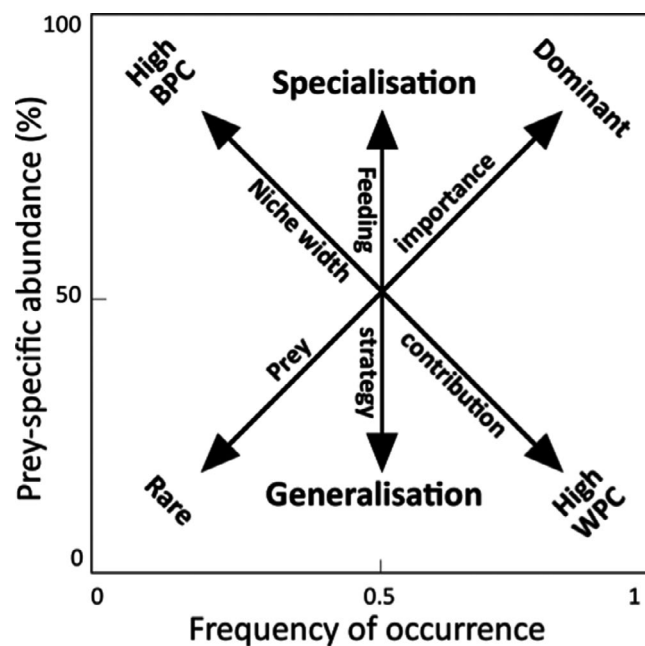


FIGURE 2 Explanatory diagram for interpretation of feeding strategy, niche width contribution and prey importance according to Amundsen et al. (1996). BPC: between-phenotype component; WPC: within-phenotype component. Figure modified from Amundsen et al., 1996

(Merritt & Cummins, 1996). The proportions of each component of the diet were quantified according to the volumetric method established by Hynes (1950). Data on the volume of each particular food item were obtained through eye estimation in which the gut contents were identified, separated and then squashed on a plate to a

uniform depth (1 mm) and the area of the squash is measured. This method has been shown to be useful and reliable when measuring small stomach volumes (Gelwick & Matthews, 2006; Hyslop, 1980), which is the case in livebearing fishes.

### 2.3 | Graphical representation of feeding strategies

We used the modification of the graphical method (Costello, 1990) made by Amundsen et al. (1996) that incorporates the prey-specific abundance into the graphical representation of dietary composition (Figure 2). In this graphical representation, the prey-specific abundance is plotted against frequency of occurrence expressed in fraction. The final plot is used to assess three important elements of the fish diet: (1) prey importance (dominant vs. rare), (2) feeding strategy (specialised vs. generalised) and (3) niche width. Hence, this method augments the ecological insight that may be derived from gut contents data (Amundsen et al., 1996).

### 2.4 | Data analysis

We calculated the diet breadth for each species analysed in this study using consumed food items according to the Levins' (1968) formula  $B = 1 / \sum p_i^2$ , where  $p_i$  is the proportion of the diet contributed by the food item  $i$ . This index tends to weight in favour of more abundant food types and is also an indicator of diet diversity for each species (Krebs, 1989; Terraube et al., 2011). To standardise the trophic niche measure (ranging from 0 to 1), we applied Hurlbert's (1978) formula  $B_i = 1 / (1 - n) \left[ \left( 1 / \sum_j p_{ij}^2 \right) - 1 \right]$  where  $B_i$  is the standardised index of niche breadth,  $p_{ij}$  is the proportion of diet of

predator  $i$  on prey  $j$  and  $n$  is the total number of resources.  $B_i$  values vary from 0 (species consuming a single item) to 1 (species consuming available items in equal proportion). Values of  $B_i$  are considered high when higher than 0.6, moderate when between 0.4 and 0.6 and low when below 0.4 (Novakowski et al., 2008).

Based on the assortment of dietary composition, we created six functional categories that summarised the variation in main type of consumed items (Delariva & Neves, 2020). These categories were: algae (mainly filamentous algae), aquatic invertebrates (larvae and pupae of Odonata, Hemiptera, Coleoptera and Diptera and also Crustacea, Arachnida and Nematoda), terrestrial insects (Coleoptera and Hymenoptera), vegetal material (plant remains), fishes (fish remains) and detritus (sand grains and other sediment). Then, we calculated the alimentary index ( $IA_i$ ) for each functional category of the diet (Kawakami and Vazzoler, 1980). This index is also known in the literature as the index of preponderance (Natarajan & Jhingran, 1961), and it provides a summary representation of the frequency of occurrence as well as the volume of different food items. The  $IA_i$  offers a distinct and measurable foundation for grading the level of consumption of specific food elements and it is calculated through the formula  $IA_i = FO_i V_i / \sum FO_i V_i \times 100$ , where  $FO_i$  and  $V_i$  are the frequency of occurrence percentage and volume percentage, respectively, the of food item  $i$  with  $i = 1, 2, 3, \dots, n$  food items.

Diet breadth indexes were compared by a Student's  $t$  test to verify differences between the wet and dry seasons (for the species analysed in both periods) after confirming that the assumptions for normality and homogeneity of variance were met using the Shapiro-Wilk and Levene's tests respectively. Another Student's  $t$  test was used to determine significant differences in the alimentary index values for detritus and algae across all analysed species as these were the only two food items found in all of them. We tried to run an ANOVA test to compare the mean of the gut length among all the species analysed, but the data did not meet the assumption of normality and equal variances even after trying data transformations. Therefore, we ran a Quade's rank analysis of covariance (Quade, 1967) using gut length as dependent variable, species as independent variable and standard length of each individual as covariate. Then, we ran a Scheffe post hoc test to compare contrasts between means because we had different number of observations (gut samples) per treatment (species). These statistical tests were performed in SPSS version 26. Finally, we investigated the relationship between the proportion of invertebrates in the diet and the relative gut length in all species analysed with the corresponding correction for phylogenetic independence. For this analysis, we used a phylogenetic generalised least squares (PGLS) model based on a recent phylogeny of the genus *Limia* (Spikes et al., 2020). We ran this analysis in R (R

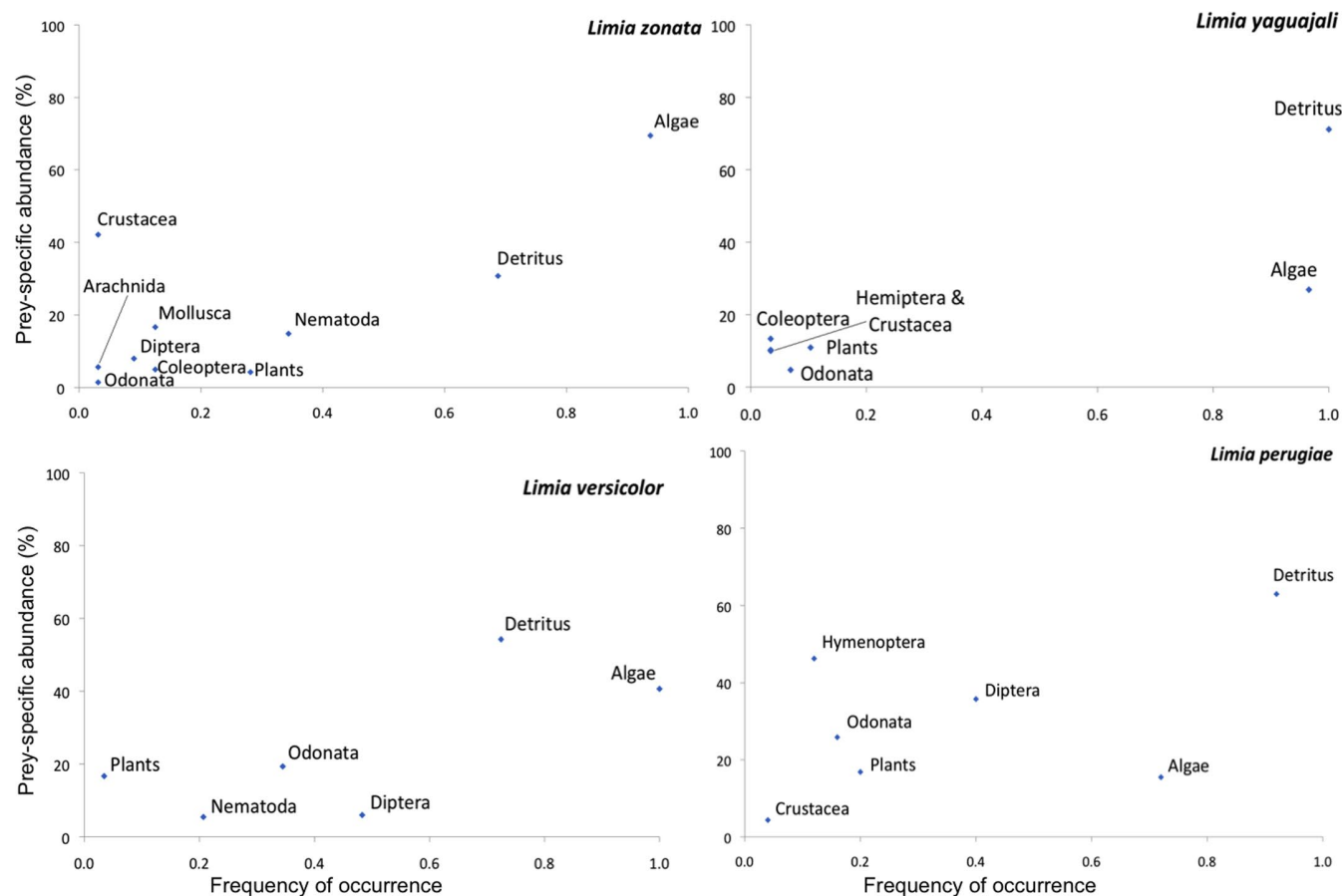


FIGURE 3 Graphic representation according to Amundsen et al. (1996) of the feeding strategies of four *Limia* species from Hispaniola (*Limia zonata*, *Limia yaguajali*, *Limia versicolor* and *Limia perugiae*) analysed during the wet and dry seasons

Core Development Team, 2014) using the R package Caper (Orme et al., 2018).

### 3 | RESULTS

#### 3.1 | Feeding strategies

Overall, the analysis of feeding strategies provided evidence that most of the *Limia* species exhibited preferences for detritus and algae in the two groups of species analysed: the ones studied in the wet and dry seasons (Figure 3, both seasons represented together) and the species analysed only in the wet period (Figure 4). However, certain species showed slightly more mixed, generalised feeding habits such as the cases of *L. versicolor* and *L. perugiae* with moderate preference for invertebrates in the diet too (Figure 3).

In a more fine-grained analysis, it can be noticed that in the first group the species *L. yaguajali* showed a population specialisation towards detritus with most individuals feeding on this dominant food item. In this case, there is also a small portion of other prey items, but they were included only occasionally in the diet of a few individuals and there were neither high within- nor between-phenotype

contributions to the niche width (see Figures 2 and 3 for interpretation of the results). A similar trend towards specialisation in consumption of detritus and algae was observed in *L. nigrofasciata* with these two being the only food items found in the gut of all analysed individuals (Figure 4).

Surprisingly, the diet analysis in the *L. vittata* population demonstrated a situation in which there was a high between-phenotype contribution to the niche width, with most of the food items situated towards the upper left corner of the graph. In this case, individuals were specialised on fishes, crustaceans and detritus (in decreasing order), but each food category was consumed by only a limited fraction of them (see Figures 2 and 4 for interpretation of the results).

#### 3.2 | Niche breadth (B) and alimentary index (IA<sub>i</sub>)

All species but *L. nigrofasciata* showed low trophic standardised niche breadth values (B<sub>i</sub>), mainly in the dry season, which indicates that most species consume relatively few food items. In the case of *L. nigrofasciata*, the niche breadth value was moderate indicating that this species consumes available items in similar proportions (Table 2). There were significant differences in the niche breadth

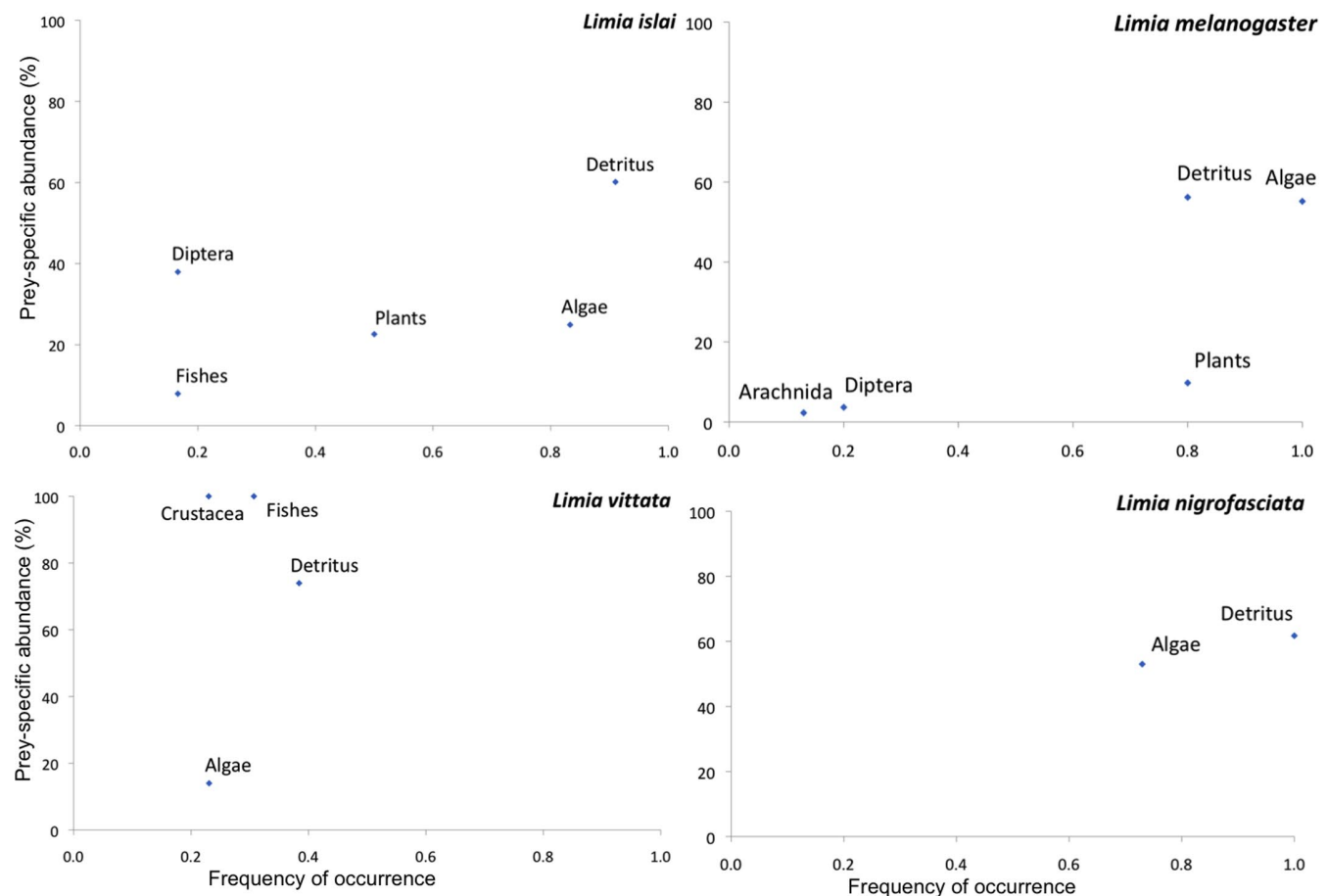


FIGURE 4 Graphic representation according to Amundsen et al. (1996) of the feeding strategies of two *Limia* species from Hispaniola (*Limia islai*, *Limia nigrofasciata*), the single endemic species from Jamaica (*Limia melanogaster*) and Cuba (*Limia vittata*). Specimens analysed were collected only in the wet season

indexes (B) between the wet and dry seasons for the species analysed in both periods ( $t(3) = 3.00899$ ,  $p = .012$ ). Niche breadth values were higher in the wet season (mean  $\pm$  SD:  $1.82 \pm 0.18$ ) than in the dry season (mean  $\pm$  SD:  $1.31 \pm 0.29$ ) for all species except *L. yaguajali*, which had niche breadth values slightly higher in the dry season compared to the wet period (Figure 5).

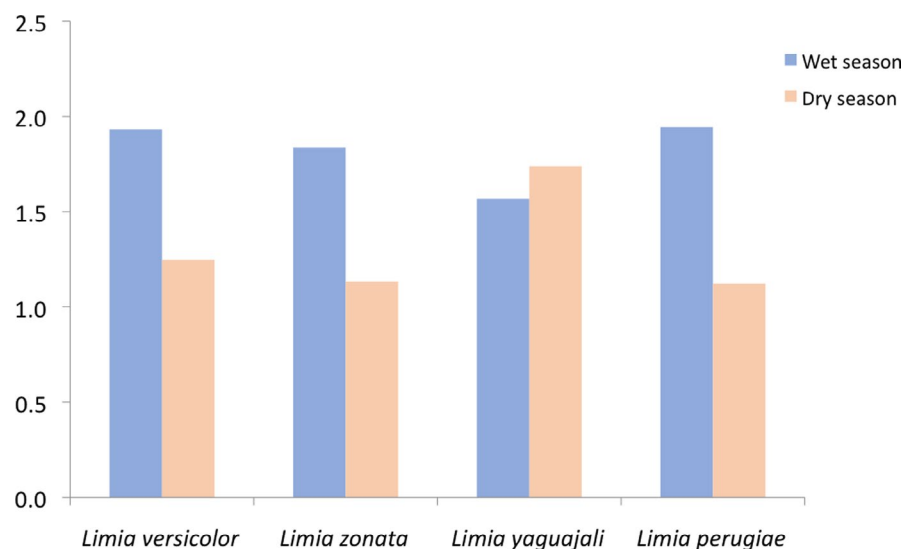
The analysis of the importance of the functional food categories that summarised the variation in main type of consumed items was calculated in terms of frequency of occurrence, volume and alimentary index of each food category (Table 3). Overall, detritus and algae represent the two most important components of the diet for the analysed species. We detected no significant differences in the alimentary index values for detritus and algae, which were the only two food items common to all species ( $t(7) = -1.42167$ ,  $p = .089$ ) revealing the importance of both items in the diet of *Limia*.

*Limia nigrofasciata* had the largest relative gut length of the eight species (Figure 6), and it fed only on detritus and algae without animal food items. The results of the analysis of covariance revealed significant differences between species in the gut length when controlling for size of each specimen ( $F(7) = 13.36$ ,  $p < .001$ ). Results of the post hoc test showed *L. versicolor* as the species that differed the most in gut length with the rest of analysed species (Table 4).

TABLE 2 Standardised niche breadth values ( $B_i$ ) of *Limia* species analysed in different periods of the year (wet and dry seasons)

Species	Wet season	Dry season
<i>Limia versicolor</i>	0.19	0.08
<i>Limia zonata</i>	0.14	0.02
<i>Limia yaguajali</i>	0.11	0.25
<i>Limia perugiae</i>	0.20	0.02
<i>Limia melanogaster</i>	0.15	
<i>Limia nigrofasciata</i>	0.51	
<i>Limia islai</i>	0.15	
<i>Limia vittata</i>	0.20	

FIGURE 5 Seasonal variations in dietary niche breadth of the four *Limia* species analysed in the wet and dry seasons. Values in the vertical axis are the niche breadth (Levins' index) for each period



We found a nonsignificant relationship between the proportion of invertebrates in the diet and the relative gut length in all species analysed using a PLGS analysis ( $r^2 = 0.01$ ,  $p = .808$ ). However, most of the species showed to some extent a negative association between the proportion of invertebrates in the diet and relative length of the gut (Figure 6).

## 4 | DISCUSSION

Our analysis of the gut contents shows that some degree of specialisation occurs in *Limia* species mainly from Hispaniola where the diversity of the genus is remarkably higher compared to the rest of the Greater Antilles. Studies of the ecology, especially the diet of the genus *Limia* are scarce. There are only a few published works that analyse the diet of species in this genus, mostly in the Cuban *Limia* (*L. vittata*) (Barus et al., 1980; Poey, 1854; Ponce de León & Rodríguez, 2008). None of them, however, provide a thorough examination of the diet, analyse multiple species from a comparative perspective or study potential feeding specialisations in the genus.

Our analysis of the feeding strategies showed a preference for detritus and algae independent of season for seven of the eight *Limia* species included in the study. This result was confirmed by the analysis of the importance of the functional food categories where detritus and algae represented the two most important components of the diet for the analysed species. This finding sheds light on the importance and potential impact of the fishes of this genus, which is the dominant group of freshwater vertebrates on Hispaniola, on sediment reduction, organic matter decomposition and their influence on the carbon flow in tropical streams (Taylor et al., 2006). By reducing sediment resources these fish species may indirectly affect populations of other grazers consuming the same food item. This has been experimentally tested in a tropical river in Venezuela where the temporary exclusion of the dominant detritivorous fish, *Prochilodus mariae*, from the order Characiformes, caused a significant increase

**TABLE 3** Percentage values of frequency of occurrence (FO), volume (V) and alimentary index (IA) for the six functional categories that summarised the variation in main type of food items in the eight *Limia* species analysed

Food type	%FO	%V	%IA
<i>Limia versicolor</i>			
Algae	100	40.64	49.37
Aquatic invertebrates	65.50	10.79	8.59
Plants	3.45	0.35	0.01
Detritus	72.4	47.78	42.03
<i>Limia zonata</i>			
Algae	93.75	68.65	74.83
Aquatic invertebrates	59.38	6.25	4.32
Plants	28.13	1.44	0.47
Detritus	68.75	25.50	20.38
<i>Limia yaguajali</i>			
Algae	96.55	26.73	26.53
Aquatic invertebrates	17.24	0.96	0.17
Plants	10.34	1.14	0.12
Detritus	100	71.17	73.18
<i>Limia perugiae</i>			
Algae	72.00	11.52	10.71
Aquatic invertebrates	56.00	20.43	14.78
Terrestrial invertebrates	56.00	3.37	2.44
Plants	20.00	3.48	0.90
Detritus	92.00	59.89	71.17
<i>Limia nigrofasciata</i>			
Algae	73.33	38.26	31.24
Detritus	100	61.74	68.76
<i>Limia melanogaster</i>			
Algae	100	55.18	60.95
Aquatic invertebrates	26.67	0.94	0.28
Plants	80.00	8.85	7.82
Detritus	80.00	35.03	30.95
<i>Limia islai</i>			
Algae	83.33	22.59	23.60
Aquatic invertebrates	16.67	3.65	0.76
Fishes	16.67	2.33	0.49
Plants	50.00	13.29	8.33
Detritus	91.67	58.14	66.82
<i>Limia vittata</i>			
Algae	23.08	3.66	2.90
Aquatic invertebrates	23.08	4.19	3.32
Fishes	30.77	53.40	56.43
Detritus	38.46	28.27	37.34

Note: Total values that represent the wet and dry seasons together are presented for *L. versicolor*, *L. zonata*, *L. yaguajali* and *L. perugiae*, while values that represent only the wet season are presented for *L. nigrofasciata*, *L. melanogaster*, *L. islai* and *L. vittata*.

in the standing stock of benthic organic sediment and biomass of aquatic insects (Hall et al., 2011).

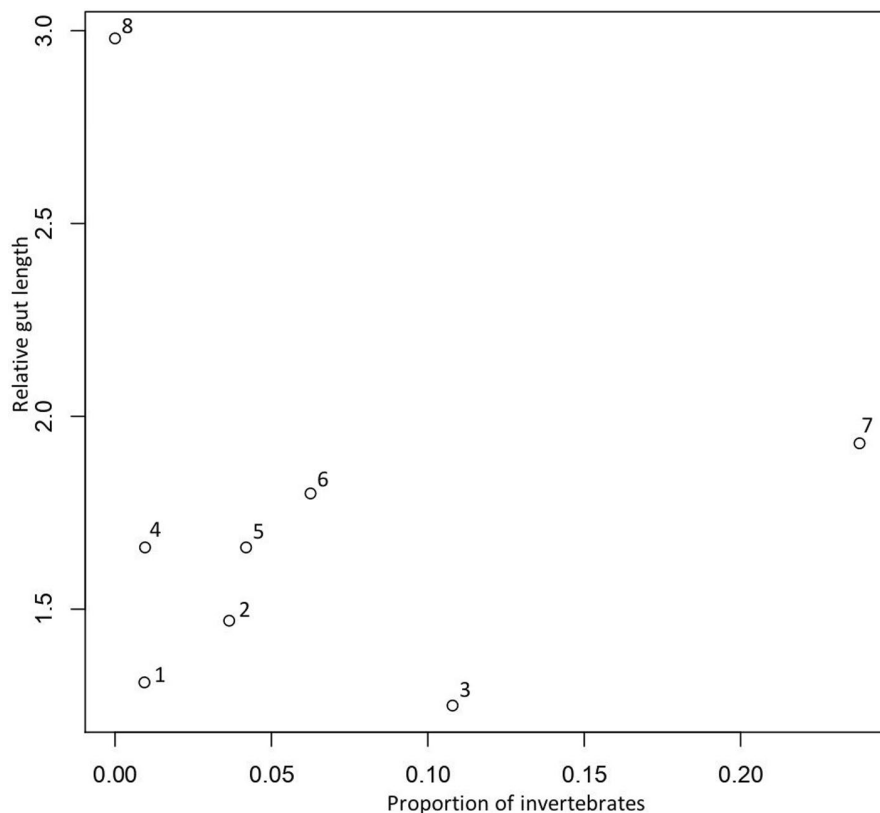
On the other hand, *L. vittata* from Cuba was the only species that showed a strong prey preference for fishes and crustaceans; food resources that were consumed by only a limited fraction of individuals (Figure 4). This is an unexpected result as this Cuban endemic has been reported as a primarily detritivorous species since its original description by Poey (1854) (Barus et al., 1980; Falcón-Hidalgo et al., 2011; Ponce de León & Rodríguez, 2008). It is important to note, however, that the few dietary analyses that have been published for this species have only included populations from freshwater environments and the individuals analysed here were collected in a hypersaline lagoon. This type of coastal habitats shows spatially highly variable physical and chemical features as their position at the boundaries of terrestrial and marine ecosystems creates a patchwork of environmental gradients (Namba et al., 2020; Prado et al., 2014). The environmental heterogeneity inherent to coastal ecosystems makes them distinctive settings in terms of the high levels of biodiversity that they contain (Palmer et al., 2011). Populations of *L. vittata* that live in coastal habitats can benefit from high productivity and different food availability, which may shift the diet towards a more predatory habit compared to freshwater environments (Barus et al., 1980).

There are studies showing diet shifts associated with habitat type in fishes. For instance, Andersen et al. (2005) confirmed considerable variation in the diet of juvenile flounder (*Platichthys flesus*) in habitats that differed in algae abundance. Specifically, they showed that in heavily vegetated sites this species fed on a varied diet of aquatic invertebrates including copepods, polychaetes and oligochaetes, while in the less vegetated sites the species fed primarily on amphipods. Yang et al. (2018) also documented significant changes in diet for the largemouth bronze gudgeon (*Coreius guichenoti*) under three different environmental conditions in the Yangtze River basin. Zandonà et al. (2015) also showed differences in the diet of the Trinidadian guppy (*P. reticulata*) related to different predation levels. Our results of the diet analysis in *L. vittata* draw attention to the importance of developing comparative analyses in populations of this species that live under different saline gradients to determine its dietary plasticity in relation to the habitat type. Recently, it has been discovered that salinity levels *L. vittata* may be linked to maintaining different colour morphs in natural populations (Rodríguez-Silva et al. in preparation).

Niche breadth comparisons between the wet and dry seasons for the species analysed in both periods revealed that *L. versicolor*, *L. zonata* and *L. perugiae* expanded their dietary niche breadth in the wet period, while *L. yaguajali* had similar values for this variable in both seasons, even though niche breadth was slightly higher in the dry period for *L. yaguajali* (Table 2). Seasonal variations in diet composition have been commonly reported in several fish species (Liu et al., 2019; Novakowski et al., 2008; Stefani & Rocha, 2005). Concurrently, the three species we observed that expanded their niche breadth during the wet season were the ones that showed a more diverse feeding strategy with trends towards an omnivore diet



**FIGURE 6** Relationship between the proportion of invertebrates in the diet and the relative gut length of *Limia* species. 1. *Limia melanogaster*, 2. *Limia islai*, 3. *Limia versicolor*, 4. *Limia yaguajali*, 5. *Limia vittata*, 6. *Limia zonata*, 7. *Limia perugiae*, 8. *Limia nigrofasciata*



**TABLE 4** Results of the Scheffe's post hoc analysis comparing mean of gut lengths among species

	<i>L. ver.</i>	<i>L. zon.</i>	<i>L. yag.</i>	<i>L. per.</i>	<i>L. nig.</i>	<i>L. mel.</i>	<i>L. isl.</i>	<i>L. vit.</i>
<i>L. ver.</i>		<b>0.000</b>	<b>0.028</b>	<b>0.001</b>	<b>0.000</b>	1.000	<b>0.039</b>	<b>0.000</b>
<i>L. zon.</i>	<b>0.000</b>		0.983	1.000	0.206	<b>0.025</b>	1.000	0.793
<i>L. yag.</i>	<b>0.028</b>	0.983		0.984	<b>0.025</b>	0.249	0.999	0.250
<i>L. per.</i>	<b>0.001</b>	1.000	0.984		0.281	<b>0.034</b>	1.000	0.858
<i>L. nig.</i>	<b>0.000</b>	0.206	<b>0.025</b>	0.281		<b>0.000</b>	0.371	0.974
<i>L. mel.</i>	1.000	<b>0.025</b>	0.249	<b>0.034</b>	<b>0.000</b>		0.189	<b>0.000</b>
<i>L. isl.</i>	<b>0.039</b>	1.000	0.999	1.000	0.371	0.189		0.879
<i>L. vit.</i>	<b>0.000</b>	0.793	0.250	0.858	0.974	<b>0.000</b>	0.879	

Note: Probability values are presented in the table for all possible comparisons. Values highlighted in bold represent significant differences with an alpha level of 0.05. *L. ver.*: *Limia versicolor*, *L. zon.*: *Limia zonata*, *L. yag.*: *Limia yaguajali*, *L. per.*: *Limia perugiae*, *L. nig.*: *Limia nigrofasciata*, *L. mel.*: *Limia melanogaster*, *L. isl.*: *Limia islai*, *L. vit.*: *Limia vittata*.

by incorporating aquatic invertebrates more frequently into the diet (Figure 2, Table 3), which may be due to the fact that these preys are more abundant in the wet season. Conversely, *L. yaguajali* showed a narrower niche breadth with evident specialisation in ingesting detritus. For this species in particular, this food category displayed the highest value of alimentary index (over 73%) among the eight species included in our study (Table 3).

Gut length is known to correspond with the feeding patterns in a way that absorption of nutrients could be more efficient (Karasov et al., 2011). In this sense, our analysis of the relative gut length in relation to the dietary composition revealed an overall pattern similar to previous studies in fish where species with shorter guts presented a more carnivorous diet (more invertebrates) and species with longer

guts corresponded to a more herbivorous dietary mode (more detritus and algae) (German & Horn, 2006; Kramer & Bryant, 1995). However, we also found one species, *L. perugiae*, which showed some deviation from the pattern seen in the rest of other species. Particularly, *L. perugiae* showed a large relative gut length combined with a high proportion of invertebrates in the diet. This result might indicate that this species, which is the most widespread *Limia* on Hispaniola, may have some dietary plasticity mirroring different types of environments with divergent food availability. Although gut length and the dietary composition did not show a significant association, we found that regardless of phylogenetic relatedness some species seemed to be more specialised as primary consumers of detritus and algae such as the case of *L. nigrofasciata* from

Lake Miragoane, and other species showed a more omnivore feeding habit that included more invertebrates in their diet (e.g. *L. versicolor*, *L. islai*, *L. zonata*) (Figure 6).

Our findings revealed common trends towards a limnivore diet in *Limia*. However, a more generalised feeding strategy may also occur in this genus, mainly in widespread species (e.g. *L. perugiae* and *L. zonata*). Particularly some species from Hispaniola, where the genus *Limia* shows a notable radiation, seemed to have narrower feeding strategies moving in the direction to detritivory (e.g. *L. nigrofasciata* from Lake Miragoane). The novel and comparative nature of our study provides a basis for deeper analyses of the trophic relationships in the genus *Limia* incorporating morphological examination of the trophic apparatus that has been hypothesised to play a role in speciation in *Limia* species from Lake Miragoane (Rodriguez-Silva et al., 2020). Although not conclusive on whether diet specialisations may drive speciation in the genus *Limia*, our findings support the idea that the degree of diet specialisation in the genus might be a factor to be considered when exploring the causes of diversification of this group of fishes in the Caribbean.

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#### AUTHOR CONTRIBUTIONS

RR-S and IS designed the study, performed analyses and drafted the manuscript, and all authors contributed to the data collection and revising the manuscript.

#### CONFLICT OF INTEREST

The authors have no competing interests.

#### DATA AVAILABILITY STATEMENT

Data of diet analysis (gut contents quantification) are available in the Dryad digital repository (<https://doi.org/10.5061/dryad.sn02v6x4s>).

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