Environ Biol Fish (2019) 102:985–996
https://doi.org/10.1007/s10641-019-00884-5

Trophic ecomorphology of cichlid fishes of Selva Lacandona, Usumacinta, Mexico

Miriam Soria-Barreto · **Rocío Rodiles-Hernández** ·
Kirk O. Winemiller

Received: 1 October 2018 / Accepted: 14 May 2019 / Published online: 23 May 2019

Abstract Neotropical cichlids exhibit great diversity of morphological traits associated with feeding, locomotion, and habitat use. We examined the relationship between functional traits and diet by analyzing a dataset for 14 cichlid species from rivers in the Selva Lacandona region, Usumacinta Basin, Chiapas, Mexico. Volumetric proportions of ingested food items were used to calculate diet breath and interspecific dietary overlap. Morphometric analysis was performed using 24 traits associated with feeding. Associations between morphological and dietary components were assessed using canonical correspondence analysis. The most common feeding guilds were omnivore, herbivore and carnivore (the latter consuming invertebrates and/or fish), with detritivores represented by relatively few species and strict piscivore by one species. Dietary overlap was highest among carnivores (*P. friedrichsthalii* and *T. salvini*), herbivores (*C. intermedium* and *C. pearsei*) and detritivore-herbivores (*V. melanura* and *K. ufermanni*). Dietary components were strongly correlated with several morphological traits, confirming patterns observed in other cichlids. For example, jaw protrusion and mandible length were positively correlated with consumption of fish and terrestrial invertebrates. A longer gut and a wider tooth plate on the lower pharyngeal jaw were correlated with ingestion of vegetation, algae and detritus. Findings confirmed a high degree of trophic specialization in certain species as well as interspecific divergence of functional traits associated with feeding among cichlids of the Usumacinta Basin, which is consistent with the idea that Middle American cichlids represent an adaptive radiation.

Keywords Cichlidae · Diet breadth · Diet overlap · Functional ecology · Morphometrics · Neotropics

Introduction

Ecomorphology has been used to test hypotheses in community ecology based on the assumption that morphological traits that influence organism performance can reveal ecological patterns and insights into ecological processes. Ecomorphology has been used to infer factors influencing adaptive divergence of lineages

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Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10641-019-00884-5) contains supplementary material, which is available to authorized users.

M. Soria-Barreto (✉)
Departamento de Conservación de la Biodiversidad, CONACYT-El Colegio de la Frontera Sur (ECOSUR), Carretera Panamericana y Periférico Sur s/n, Barrio María Auxiliadora, San Cristóbal de Las Casas, Chiapas, Mexico
e-mail: mmsoriab@gmail.com

R. Rodiles-Hernández
Departamento de Conservación de la Biodiversidad, El Colegio de la Frontera Sur (ECOSUR), Carretera Panamericana y Periférico Sur s/n, Barrio María Auxiliadora, San Cristóbal de Las Casas, Chiapas, Mexico

K. O. Winemiller
Department of Wildlife and Fisheries Sciences and Program in Ecology and Evolutionary Biology, Texas A&M University, College Station, TX, USA

(Streelman et al. 2002; Price et al. 2011; Arbour and López-Fernández 2013), community assembly from local to regional scales (Ricklefs and Miles 1994; Poff 1997; Micheli and Halpern 2005), and community response to environmental change (Villéger et al. 2010). Research on freshwater fish communities has established strong correlations between traits and function, principally with regard to habitat use and feeding (Gatz 1979; Watson and Balon 1984; Hugueny and Pouilly 1999), including biomechanical and experimental studies of performance (Wainwright and Bellwood 2002; Hulsey et al. 2005; Wainwright et al. 2007). Separation of species within functional trait space has been interpreted as evidence of niche segregation in response to environmental filtering and present or past competition (Wikramanayake 1990; Winemiller 1991; Montaña et al. 2014). Morphological diversification among closely related taxa is often cited as evidence for competition and other kinds of species interactions as agents influencing adaptive evolution and patterns of species coexistence (Winemiller et al. 1995; Arbour and López-Fernández 2013).

Cichlids are freshwater fishes distributed in Africa, Central and South America, the West Indies, Madagascar, Israel, Syria, India and Sri Lanka. Globally and regionally, cichlids reveal impressive morphological, behavioral and ecological diversity (Nelson et al. 2016), and this diversity often has been described as an adaptive radiation (Burress 2015). Cichlids are particularly diverse in Mesoamerica where they are dominant components of most local fish assemblages (Hulsey et al. 2004; Matamoros et al. 2015). Studies of cichlids from different regions of Mesoamerica have exhibited similar patterns of morphological diversity based on sets of traits associated with feeding and habitat use (Winemiller et al. 1995; Soria-Barreto and Rodiles-Hernández 2008; Cochran-Biederman and Winemiller 2010; Montaña and Winemiller 2013; Rican et al. 2016; Pease et al. 2018).

Trophic morphology appears to have been key to adaptive radiation for many groups like Darwin's finches, *Anolis* lizards (Streelman and Danley 2003) and teleosts such as reef fish (Wainwright and Bellwood 2002) and African rift-lake cichlids (Streelman and Danley 2003; Kocher 2004). In Mesoamerican cichlids, for example, feeding performance is strongly influenced by jaw protrusion that allows predators to capture evasive prey, such as fish and shrimp (Waltzek and Wainwright 2003; Hulsey and García de León 2005). Modifications of oral and pharyngeal jaws, as well as cranial configuration and musculature, are associated with dietary preference and feeding modes (Burress 2015, 2016; Rican et al. 2016). Although most cichlid diets are diverse, species have been grouped into trophic guilds, including piscivores that possess relatively specialized morphological traits for capture and ingestion of fish, and omnivores with more variable or intermediate traits and generalized diets (Barel 1983; Liem 1991; Burress 2016). Description of the relationship between morphology and diet is an essential step for understanding factors shaping cichlid diversification, community assembly and species coexistence.

Here we investigate the trophic ecomorphology of the cichlid assemblage in the Tzendales River within the Selva Lacandona region of the upper Usumacinta Basin, the largest in Mesoamerica (De la Maza and Carabias 2011). Fifteen native cichlid species inhabit the region's rivers and streams (Rodiles-Hernández et al. 1999; Lozano-Vilano et al. 2007; Soria-Barreto and Rodiles-Hernández 2008) and support important artisanal fisheries (Carabias et al. 2015). Based on findings from studies of other cichlid faunas, we hypothesized strong correspondence between function traits and diets as well as ecomorphological differentiation among species consistent with niche partitioning and adaptive radiation.

Methods

Study area

Selva Lacandona is a region of approximately 1,300,000 ha within the Usumacinta Basin in Chiapas, Mexico. The region's annual mean temperature ranges from 19 to 26 °C and annual precipitation varies between 1890 and 4300 mm. The region contains several protected areas, the most important and largest of which are the Montes Azules and Lacantun biosphere reserves. These areas contain rainforest and rivers that support some of the highest biodiversity in Mesoamerica (De la Maza and Carabias 2011; Carabias et al. 2015).

Cichlids were collected from diverse habitats of the Tzendales River within the Montes Azules Reserve (16° 16′ 08″ to 16° 19′ 08" N; 90° 53′ 06″ to 90° 59′ 44" W) using seines, gill nets, cast nets and baited hooks. Fish were collected during dry season from February to May 2006. Specimens were fixed in 10% formalin for five days and then rinsed in water and stored in 70%

ethanol. Formalin preservation can cause shrinkage of fish specimens (Parker 1963), but here we assume that distortion from preservation was minor and, given that all specimens were treated in the same way, interspecific comparisons of morphology should be largely unbiased. Fourteen cichlid species were captured (Online Resource 1); only adult size classes were included in the analysis to avoid allometric effects associated with ontogeny. We chose specimens larger than minimum size of first maturity reported by Chávez-Lomelí et al. (1988); Konings (1989); and Miller et al. (2005). Specimens were deposited in the Fish Collection of El Colegio de la Frontera Sur, Chiapas, Mexico.

Dietary analysis

Dietary analysis was performed based on examination of stomachs of 30 specimens per species, except to *P. friedrichsthalli* for which 28 specimens were available (Table 1). The ingested items were analyzed using the volumetric method described by Hyslop (1980) and Winemiller (1990). Estimates of the volume of recovered food items were obtained by water displacement in a graduate cylinder or, for very small items, by visual comparison with a water droplet of determined volume. Food items were removed from the anterior portion of gut and were identified using the keys in Merritt and Cummins (1996) and Springer et al. (2010). Some stomachs were empty or with high level of digestion, and these were not considered in our sample sizes. To verify that sample sizes were sufficient to describe dietary variation, accumulation curves for trophic diversity were plotted for each species using the EstimateS software (Colwell 2013; Online Resources 2). To facilitate interspecific comparisons, food items were grouped according to seven broad categories: detritus, aquatic insect larvae (AIL) (Coleoptera, Diptera, Hemiptera, Lepidoptera, Tricoptera, Odonata), terrestrial invertebrates (Coleoptera, Hemiptera, Formicidae, arachnids), algae, mollusks (Bivalvia and Gastropoda), fish (complete, fragments and scales) and vegetation material (VM) (including seeds). These categories describe basic trophic niches and better facilitate exploration of relationships between morphology and diet by reducing the frequency of zeros in the data matrix. For each diet item for each species, data were recorded as the percentage of the total volume summed for all diet items. Proportional volumetric diet data were used to compute niche breadth based on the standardized Levin's index, $BA = [(1 / \Sigma\, p_{jj}{}^{2}) - 1)] / (n-1)$, where p_{jj} is the proportion of items i in the diet for species j, and n is total number of items considered (Krebs 1998). Trophic niche overlap was computed for every possible species pairing using Pianka's index, $O_{ik} = \Sigma\, (p_{ij} * p_{ik}) / (\surd\, \Sigma\, p_{ij}{}^{2} * p_{ik}{}^{2})$ for species j and k and diet categories $i = 1$ to n (Krebs 1998). To assess the statistical significance of overlap, we performed a null model test with 1000 iterations using the RA3 algorithm in the EcosimR package (Gotelli et al. 2015).

Morphometric analysis

Morphometric data were obtained from 20 specimens of each species (Table 1), including the same specimens used for diet analysis. Twenty-four traits associated with feeding were measured using calipers with precision to 0.1 mm (Table 2). The lower pharyngeal jaw was extracted and stained with alizarin solution before taking linear measurements. We measured the gut length of each specimen after extracting and uncurling the entire gastrointestinal tract.

All morphological measurements were log transformed to increase normality. Size correction was performed by linear regression of each measure against standard length. Principal components analysis (PCA) based on the correlation matrix was performed to ordinate species according to dominant gradients of morphological variation. Morphological traits with highest loadings were selected for use as variables to perform canonical correspondence analysis (CCA). Spearman correlation was performed with these morphological traits; large significant correlations were indicative of functional redundancy, and redundant traits were eliminated prior to performing CCA. Canonical correspondence analysis was performed to evaluate associations between dietary and morphological variables, with statistical significance of ordination axes assessed based on 999 random permutations. Multivariate analyses were performed with the vegan package (Oksanen et al. 2009) in R version 3.3.1 (R Core Team 2016).

Results

The first two PCA axes explained 54.9% of total morphological variation among cichlids (Table 3). Large positive loadings on PC1 were associated with

Table 1 Number of specimens examined and standard length ranges (SL in mm) for cichlid species from the Tzendales River, Selva Lacandona, Chiapas, Mexico

Species	Abbreviation	Morphometrics	Diet analysis
Chuco intermedium	Ci	20 (200.9–103.9)	30 (200.9–91.4)
Cincelichthys pearsei	Cp	20 (236.7–111.3)	30 (236.7–111.3)
Kihnichthys ufermanni	Ku	20 (208–107.2)	30 (208–82.8)
Maskaheros argenteus	Ma	20 (224.9–92.2)	30 (209.5–83.3)
Parachromis friedrichsthalii	Pf	20 (193.8–104.7)	28 (193.8–104.7)
Petenia splendida	Ps	20 (232.5–109.4)	30 (247.2–116.3)
Rheoheros lentiginosus	Rl	20 (138.3–91.3)	30 (138.3–52.2)
Theraps irregularis	Ti	20 (179.4–112.9)	30 (190–94.8)
Thorichthys helleri	Th	20 (106.7–71.7)	30 (106.7–63.7)
Thorichthys meeki	Tm	20 (102.7–44.7)	30 (102.7–44.7)
Trichromis salvini	Ts	20 (118.5–72)	30 (109.4–64.5)
Vieja bifasciata	Vb	20 (192.9–87.3)	30 (198.3–77)
Vieja melanura	Vm	20 (182–142.5)	30 (182–95.2)
Wajpamheros nourissati	Wn	20 (202–136.6)	30 (202–103.1)

subterminal mouths, large guts and an obtuse snout angle; negative loadings were associated with long first ceratobranchial and epibranchial arches and large heads. PC2 separated fish with longer mandibles, longer upper jaws, and greater jaw protrusibility (positive loadings) from those with a wider tooth plate on the lower pharyngeal jaw, wider lower pharyngeal jaw and an obtuse snout angle (negative loadings) (Fig. 1, Table 3). Two rheophilic species, *Theraps irregularis* and *Rheoheros lentiginosus*, were distinguished by having subterminal mouths, long guts and snouts with an obtuse angle. *Petenia splendida* had the longest upper jaw and mandible, longest head, greatest jaw protrusion, and a superiorly positioned mouth. *Parachromis friedrichsthalii, Trichromis salvini* and *Wajpamheros nourissati* were similar to *P. splendida* in many respects, and also have long first ceratobranchial and epibranchial arches. *Chuco intermedium*, *Cincelichthys pearsei, Kihnichthys ufermanni, Maskaheros argenteus, Vieja bifasciata* and *V. melanura* have a broad tooth plate on the lower pharyngeal jaw, a wide lower pharyngeal jaw, obtuse snout angle, long gut and subterminal mouth. *Thorichthys meeki* and *Thorichthys helleri* were similar to species in this group in many traits.

Dietary analysis indicated that *P. splendida* consumed fish almost exclusively, *T. salvini* and *P. friedrichsthalii* consumed mostly aquatic insects and fish, *T. irregularis* fed on aquatic insects and algae, and *R. lentiginosus* consumed a combination of mollusks and aquatic insects. Vegetation material dominated the diets of *C. pearsei* and *C. intermedium*, *K. ufermanni* and *V. melanura* consumed a combination of vegetation material and detritus, and *V. bifasciata* consumed vegetation material, detritus and algae. *W. nourissati* and *M. argenteus* fed on plant material and aquatic invertebrates. *Thorichthys helleri* and *T. meeki* both consumed aquatic invertebrates, with the former having a greater dietary fraction of mollusks. These benthivorous fishes also consumed large fractions of detritus, which likely was ingested incidentally during winnowing of sediment and food within the orobranchial chamber (López-Fernández et al. 2014). Diet breadth was highest for omnivorous *M. argenteus* (0.41) and *T. helleri* (0.37) and herbivorous *V. bifasciata* (0.37); in contrast, the piscivore *P. splendida* had lowest diet breadth (0.03) (Table 4).

Diet overlap was high between the carnivores *T. salvini* and *P. friedrichsthalii*. High overlap also was observed between the herbivores *C. intermedium* and *C. pearsei*, the detritivore-herbivores *V. melanura* and *K. ufermanni*, and among certain pairs of herbivorous, detritivores-herbivorous and omnnivorous cichlids (*V. melanura* and *C. intermedium; V. melanura* and *V. bifasciata; M. argenteus* and *W. nourissati*; *K. ufermanni* and *V. bifasciata*) (Table 5). Overlap values were significantly higher than expected based on randomized simulations ($p = 0.001$), the average

Table 2 Morphological traits measured in cichlids from Selva Lacandona

Measurements	Description
Standard length	Measured from the tip of upper lip to the origin of the caudal fin (Barel et al. 1977).
Head length	Measured from the tip of the upper lip with the mouth completely closed to the caudal edge of the operculum (Gatz 1979; Winemiller 1991).
Head height	Vertical distance measured through the center of the eye, between the dorsal and ventral edges of the head (Gatz 1979; Winemiller 1991).
Head width	Measured from the left to right preorbital bone (Barel et al. 1977)
Eye diameter	Horizontal distance between the anterior and posterior edges of the eye (Gatz 1979; Winemiller 1991).
Snout length	Distance from the anterior edge of the orbit to the center the upper lip (Winemiller 1991).
Upper jaw length	Measured from the tip of the snout to posterior corner of maxilla.
Mandible length	Distance measured from the lower tip of mandible to caudal tip of retroarticular process (Barel et al. 1977).
Gape width	Distance horizontal internal between the tips of the premaxilla with the mouth fully open and protruded (Gatz 1979).
Cheek depth	Distance vertical from ventral margin of preopercule to margin ventral of eye (Barel et al. 1977).
Eye position	Vertical distance between the center of the eye and the ventral edge of the head (Gatz 1979; Winemiller 1991).
Jaw protrusion	Distance from the anterior edge of the orbit to the center the upper lip, when the mouth fully protruded (Gatz 1979).
Snout angle	In lateral view, the angle between the dorsal outline of premaxillary and line along the ventral border of the lower jaw (Barel et al. 1977).
Mouth position	Estimate by drawing a horizontal line that passes from the corner of the mouth to the middle of the insertion of caudal rays in the caudal peduncle. Other line is traced from anterior-most point of the orbit, and another corresponding to the tip of the upper lip. The angle between the two lines is measured with a protractor (Gatz 1979; Winemiller 1991).
Length of first ceratobranchial arch	Distance between join of ceratobranchial with basibranchial to the join to ceratobranchial with epibranchial (Cochran-Biederman and Winemiller 2010).
Length of epibranchial arch	Distance between of the epibranchial in the first arch.
Distance between gillrakers	Average distance between gillrakers of first ceratobranchial arch (Cochran-Biederman and Winemiller 2010).
Gillraker width	With of gillrakers in the first ceratobranchial arch (Cochran-Biederman and Winemiller 2010).
Gillraker height	Average distance from the base to the tip of gillrakers in the first ceratobranchial arch (Cochran-Biederman and Winemiller 2010).
Lower pharyngeal jaw width	Distance measured between the tips of the horns (Barel et al. 1977; Trapani 2003).
Length of lower pharyngeal jaw	Distance of the symphysis measured from the anterior tip to posterior center of the plate (Barel et al. 1977; Trapani 2003).
Width of the tooth plate on the lower pharyngeal jaw	Distance between the lateral margins of the tooth plate, of the most lateral left and right (Barel et al. 1977; Trapani 2003).
Length of the tooth plate on the lower pharyngeal jaw	Distance of tooth plate at symphysis, measured from the rostral to caudal margin (Barel et al. 1977; Trapani 2003).
Gut length	Length of entire digestive tract from esophagus to anus (Gatz 1979; Winemiller 1991).

observed index was 0.45 and average index calculated by null model was 0.38.

CCA revealed a statistically significant relationship between morphology and diet ($p = 0.001$). The first axis explained 40.5% of variance and the second axis explained 21.7%. The first axis was strongly influenced by an association between mandible length, jaw protrusion, length of first ceratobranchial arch and head length and the consumption of fish and terrestrial invertebrates (high loadings for carnivorous *P. splendida, P. friedrichsthalii* and *T. salvini*) and an association between an obtuse snout angle and subterminal mouth

Table 3 Factor loadings (eigenvalues) for the first two dimensions from principal components analysis of morphometrics of cichlids from Selva Lacandona. Abbreviations are in parenthesis. Morphological traits used in subsequent correlation analysis are in bold

	PCA axis 1	PCA axis 2
Eigenvalue	7.599	5.033
Variance explained	33.0%	21.9%
Morphological variable		
Head length	−1.520	0.492
Head height	−0.394	−1.234
Head width	−0.263	−1.151
Eye diameter	−0.653	−0.163
Snout length	0.032	−0.227
Upper jaw length	−1.453	1.003
Mandible length	−1.464	0.939
Gape width	−1.486	0.033
Cheek depth	−0.784	−0.409
Eye position	−0.576	−1.080
Jaw protrusion	−0.593	0.757
Snout angle	0.743	−1.353
Mouth position	1.214	−0.869
Length of first ceratobranquial arch (LCA)	−1.658	0.254
Length of epibranchial arch (LEA)	−1.509	−0.335
Distance between gillrakers	−0.770	−0.753
Gillraker width	−1.417	0.112
Gillraker height	−1.125	0.182
Width of lower pharyngeal jaw (WLPJ)	−0.925	−1.310
Length of lower pharyngeal jaw (LLPJ)	−1.179	−1.069
Width of tooth plate on lower pharyngeal jaw (WTLPJ)	−0.705	−1.477
Length of the tooth plate on the lower pharyngeal plate (LTLPJ)	−1.201	−1.074
Gut length (Gut L)	0.798	−0.998

and consumption of vegetation, algae and detritus with detritivorous and herbivorous cichlids. The second CCA axis was strongly influenced by an association between gut length and wide tooth plate on the lower jaw with consumption of vegetation, algae and detritus. Herbivores (*C. pearsei, C. intermedium, V. bifasciata*) and detritivore-herbivores (*K. ufermanni*, *V. melanura*) had longest guts, and species that consumed mostly invertebrates (aquatic and/or terrestrial) had shorter guts (*R. lentiginosus, T. helleri, M. argenteus, W. nourissati, P. friedrichsthalli, T. salvini* and *T. irregularis*) (Fig. 2).

Discussion

Cichlids of Selva Lacandona exhibited extensive interspecific differences in morphological traits known to influence foraging and processing of ingested foods. Assemblage trophic diversity and patterns of trait-diet association were very consistent with those reported from ecomorphological studies of other Neotropical cichlid faunas (e.g., Cochran-Biederman and Winemiller 2010; López-Fernández et al. 2013; Montaña and Winemiller 2013; Rican et al. 2016; Pease et al. 2018).

Jaw protrusion and the length of the head mandible, and first ceratobranchial arch were correlated with consumption of fish and terrestrial invertebrates. In carnivorous fishes, head length and mouth gape tend to be correlated prey size (Gatz 1979; Watson and Balon 1984; Hugueny and Pouilly 1999; López-Fernández et al. 2013). Longer mandibles and first ceratobranchial arches can enhance suction feeding by piscivores and zooplanktivores (Barel 1983). Jaw protrusion is correlated with piscivory in other Neotropical cichlids (Cochran-Biederman and Winemiller 2010; Montaña and Winemiller 2013; Pease et al. 2018). Functional morphology research has shown that that jaw protrusion paired with a large oro-branchial chamber volume increases efficiency of suction feeding in teleosts (Barel 1983; Liem 1991). In cichlids, as in other teleost fishes, the premaxilla and maxilla undergo rotational movements that enhances jaw protrusion and suction (Westneat 2005). Our result confirmed that *Petenia splendida* has extremely protrusible jaws and long mandibles that should facilitate both suction feeding on elusive prey, mainly fish (Barel 1983; Waltzek and Wainwright 2003; Hulsey and García de León 2005). Similar functional traits and feeding habits are observed in *P. friedrichsthalii* and *T. salvini.*

A strong association was found between longer guts, wider tooth plates on the pharyngeal jaws and an obtuse snout angle and consumption of vegetation, algae and detritus by herbivores (*C. pearsei*, *C. intermedium* and *V. bifasciata*) and detritivore-herbivores (*K. ufermanni*, *V. melanura*). Long gastrointestinal tracts in detritivores and herbivores and shortest guts in carnivores apparently is a robust relationship among freshwater fishes (Gatz 1979; Winemiller et al. 1995; Hugueny and Pouilly 1999; Pease et al. 2018). A longer intestine facilitates digestion and absorption of plant material, which tends to be less nutritious and more recalcitrant than animal

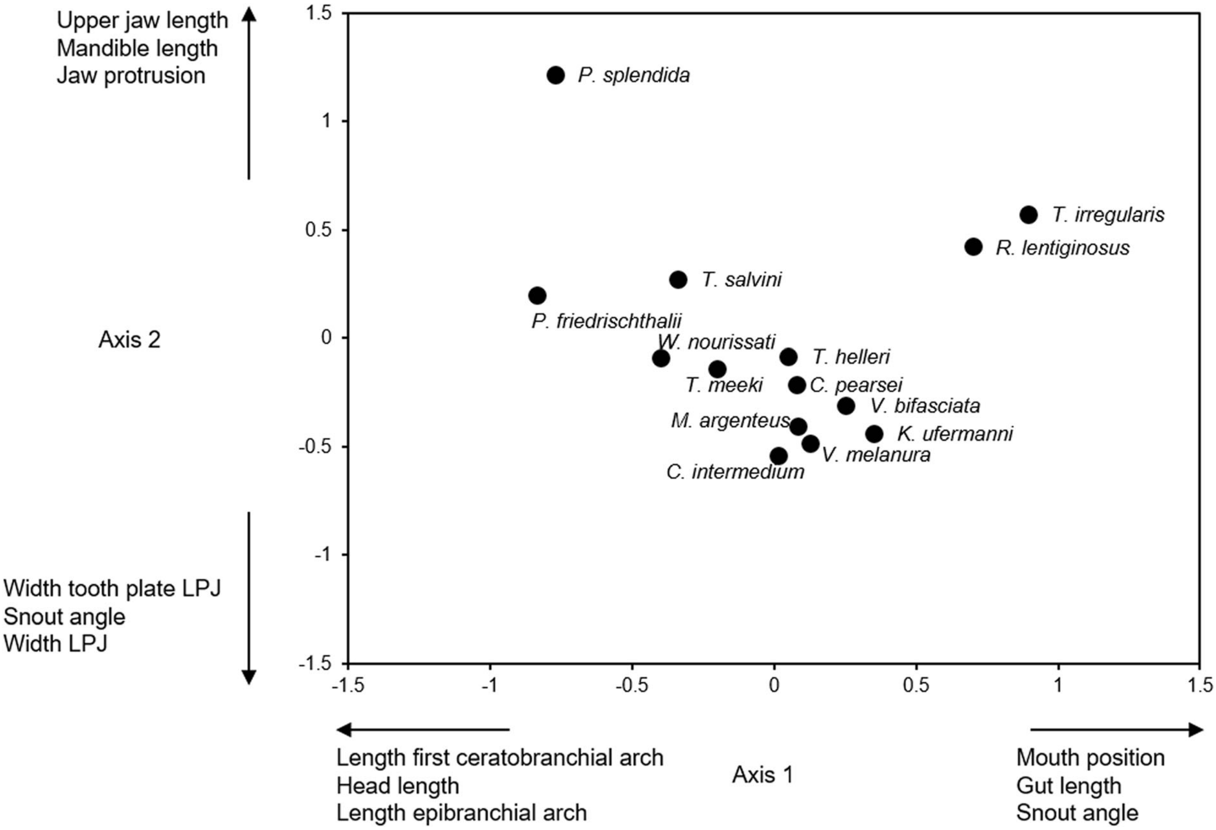

Fig. 1 PCA ordination of Selva Lacandona cichlids based on morphological traits associated with feeding. Circles represent means for species and abbreviations are in Table 1

Table 4 Proportional dietary composition of food items and diet breadth (standardized Levin's index) for cichlids from Selva Lacandona

Species	n	Vegetation material	Algae	Mollusks	Aquatic insect larvae	Terrestrial invertebrates	Fish	Detritus	Diet breadth
Chuco intermedium	30	0.66			0.04		0.01	0.29	0.15
Cincelichthys pearsei	30	0.80			0.00		0.02	0.19	0.08
Kihnichthys ufermanni	30	0.43	0.02				0.02	0.53	0.19
Maskaheros argenteus	27	0.41		0.25	0.19		0.02	0.12	0.41
Parachromis friedrichsthalii	25	0.06		0.05	0.56	0.04	0.27	0.03	0.26
Petenia splendida	28				0.07		0.93		0.03
Rheoheros lentiginosus	30	0.02		0.39	0.39	0.01		0.18	0.32
Theraps irregularis	17	0.08	0.22		0.68	0.02			0.15
Thorichthys helleri	28	0.05	0.03	0.23	0.21			0.47	0.35
Thorichthys meeki	30	0.01	0.21	0.03	0.16		0.02	0.57	0.25
Trichromis salvini	23	0.01			0.70		0.28		0.12
Vieja bifasciata	29	0.36	0.25		0.05		0.01	0.34	0.37
Vieja melanura	30	0.45	0.05	0.03	0.00		0.03	0.42	0.26
Wajpamheros nourissati	30	0.39		0.12	0.37	0.05		0.07	0.37

Table 5 Interspecific dietary overlap among cichlids from Selva Lacandona

	Ci	Cp	Ku	Ma	Pf	Ps	Rl	Ti	Th	Tm	Ts	Vb	Vm	Wn
Ci	–	0.98	0.88	0.82	0.16	0.01	0.20	0.16	0.44	0.39	0.08	0.85	0.94	0.73
Cp		–	0.78	0.80	0.11	0.02	0.11	0.11	0.28	0.22	0.03	0.77	0.86	0.71
Ku			–	0.66	0.10	0.03	0.27	0.08	0.70	0.73	0.02	0.90	0.99	0.53
Ma				–	0.46	0.04	0.65	0.42	0.58	0.32	0.36	0.67	0.74	0.91
Pf					–	0.43	0.68	0.86	0.41	0.28	0.99	0.16	0.13	0.69
Ps						–	0.00	0.00	0.00	0.03	0.37	0.01	0.05	0.01
Rl							–	0.64	0.79	0.49	0.63	0.27	0.28	0.66
Ti								–	0.38	0.34	0.88	0.28	0.11	0.71
Th									–	0.88	0.35	0.62	0.66	0.50
Tm										–	0.24	0.73	0.66	0.30
Ts											–	0.09	0.04	0.63
Vb												–	0.93	0.59
Vm													–	0.61

tissue (Kramer and Bryant 1995). The correlation between snout angle and herbivory and detritivory likely reflects feeding behavior, because these fishes either scrape or bite and tear tufts epilithic algae from substrates. Compact jaws (i.e., small mouth gape, short upper jaw and mandibles, less jaw protrusion, obtuse snout angle) facilitate strong biting force (Liem 1991). Molluscivores also had relatively short heads and blunt

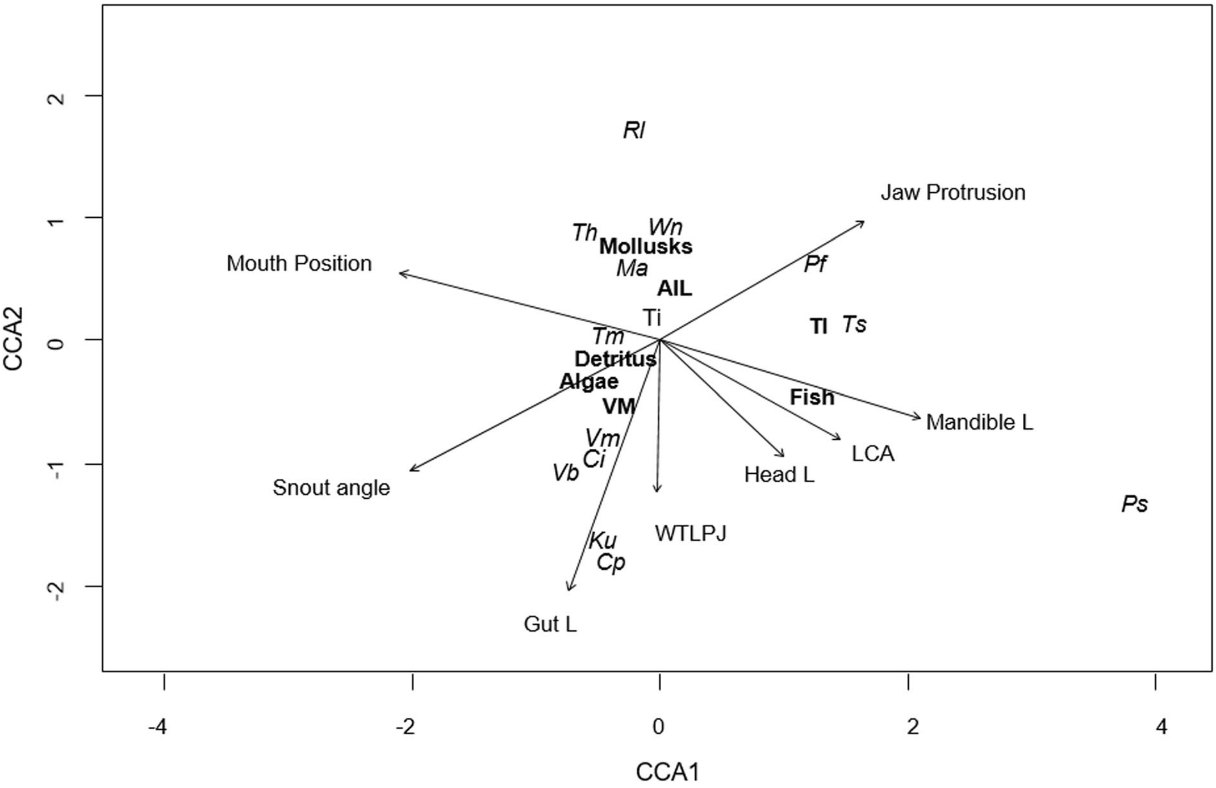

Fig. 2 CCA ordination of cichlid species from Selva Lacandona based on morphology and diet; abbreviations are explained in Tables 1 and 3 and methods section. Vectors portray correlations of morphological variables with axis 1 and 2

snouts, traits likely associated with muscle attachment and mechanics for crushing shells within the pharyngeal jaws (Barel 1983; Wainwright 1987; Hulsey et al. 2005; Burress 2016).

Mouth orientation tends to be associated with both diet and the position within the water column where feeding takes place (Keast and Webb 1966; Gatz 1979; Wikramanayake 1990). For example, *Petenia splendida* has a superior positioned mouth that should facilitate feeding on prey positioned higher in the water column, *P. friedrichsthalii* and *T. salvini* have terminal mouths that should facilitate capture of prey at the same vertical position, and *R. lentiginosus* and *T. irregularis* have subterminal mouths that permit them to forage on substrates while maintaining position in flowing water. A wide pharyngeal tooth plate was associated with herbivory and detritivory. Although not analyzed here, interspecific differences in dentition of pharyngeal jaws were noted. In cichlids, the shape and dentition of pharyngeal jaws have shown to be plastic in response to diet (Huysseune 1995; Trapani 2003; Muschick et al. 2011) and genetic effects (Fruciano et al. 2016). The plasticity of pharyngeal jaws is considered an adaptation that facilitates exploitation of diverse food resources and a significant contributor to the trophic diversification of cichlids in Africa (Meyer 1987) and the Neotropics (Trapani 2003; Burress 2015, 2016; Rican et al. 2016).

Some cichlids from Selva Lacandona have morphology and diets that are convergent with cichlids from South America and other regions of Central America. *Petenia splendida* has are specialized piscivores (Chávez-Lomelí et al. 1988; Cochran-Biederman and Winemiller 2010; Pease et al. 2018) with traits similar to those described for piscivorous cichlids in the South American genera *Cichla, Crenicichla* (López-Fernández et al. 2012; Montaña and Winemiller 2013) and *Caquetaia* (Winemiller et al. 1995; Rican et al. 2016) and the Central American piscivore *Parachromis dovii* (Winemiller et al. 1995). *Thorichthys helleri* and *T. meeki* are benthic feeders that use winnowing to separate invertebrate prey from sediments in a manner convergent with behavioral patterns observed in the South American cichlid genera *Geophagus* and *Satanaperca* species (López-Fernández et al. 2012, 2014). The invertebrate feeders *R. lentiginosus* and *T. irregularis* that inhabit fast-flowing riffles (Soria-Barreto and Rodiles-Hernández 2008) are quite similar morphologically and ecologically to rheophilic *Hypsophrys* and *Tomocichla* species in southern Central America (Rican et al. 2016).

In contrast with cichlid assemblages in South American that tend to be dominated by the invertivore guild (López-Fernández et al. 2012; Montaña and Winemiller 2013), the Selva Lacandona cichlid assemblage has many omnivorous and herbivorous species. These cichlids would be considered trophic generalist (Montaña and Winemiller 2013), because they had broad diets consisting mostly of vegetation, algae and detritus but including aquatic insects. These cichlids had high dietary overlap, which suggests a potential for competition under conditions of food resource limitation and or ability to switch to alternative food resources as availabilities shift. Coexistence of species with similar food requirements can be achieved if species segregate niches on dimensions of time (Arrington and Winemiller 2003) or habitat (Ross 1986; Schoener 1986), or if they undergo temporal dietary shifts in response to variation in food resource availability (Ross 1986; Winemiller 1989). Additionally, coexistence of species with similar trophic niches also could be facilitated by differences in periods or habitats where reproduction occurs (Streelman and Danley 2003; Kocher 2004). In carnivorous cichlids *T. salvini* and *P. friedrichsthalii*, although they have similar diets, probably experience little food resource overlap because *T. salvini* often occurs along stream margins, and *P. friedrichsthalii* tends to be found in deeper areas with little or no current and high structural complexity (Soria-Barreto and Rodiles-Hernández 2008). Despite the broad food categories employed in our analysis, we nonetheless identified considerable food resource partitioning. Future analyses of cichlid trophic ecology at a finer level of resolution, combined with evaluation of foraging microhabitat, feeding periodicity ontogenetic patterns, would more fully elucidate mechanisms of species coexistence.

Omnivory is common in tropical freshwater fish assemblages (González-Bergonzoni et al. 2012), and it is particularly common among Mesoamerican cichlids (Winemiller et al. 1995; Cochran-Biederman and Winemiller 2010; Burress 2015; Pease et al. 2018). In contrast, most South American cichlids feed on aquatic invertebrates and fish (López-Fernández et al. 2012; Montaña and Winemiller 2013). These differences could be explained by historical zoogeography (González-Bergonzoni et al. 2012), with South American cichlids being a much older group that evolved as part of species-rich assemblages dominated by characiform and siluriform fishes. These latter groups contain diverse trophic niches that include algivory, herbivory, detritivory and omnivory, which could have limited opportunities for cichlid trophic evolution exclusion of cichlids (Winemiller et al. 1995). Middle American cichlids are a relatively young clade within the Neotropical clade, and one that extensively colonized and diversified within the region along with poeciliid fishes (Matamoros et al. 2015). Middle American cichlids and poeciliids would have evolved in habitats containing relatively few species and few other freshwater fish families. Great ecomorphological similarity among omnivorous species of the Lacandona cichlid assemblage appears to represent phylogenetic niche conservatism, i.e., related species have ecological traits more similar than would be expected at random (Losos 2008; Wiens et al. 2010). Recent phylogenies that included some of the Lacandona cichlids (López-Fernández et al. 2010; Rican et al. 2016) reveal a clade containing *C. intermedium, K. ufermanni* and *W. nourissati,* and another clade with *C. pearsei, M. argenteus¸ V. bifasciata* and *V. melanura*.

Cichlids of Selva Lacandona exhibit patterns of morphological and trophic variation generally consistent with those described for other Neotropical cichlid assemblages. Some species, including piscivores and invertebrate feeders, have specialized morphology and diets, whereas others, such as omnivores, are trophic generalists with similar morphology and broad diets. In future research, these ecomorphological and dietary data could be analyzed together with data from species from other regions along with phylogenetic information to model ecological diversification in Middle American cichlids.

Acknowledgements We thank Celedonio Chan Sala and Alfonso A. González Díaz for assistance with fieldwork; Yuriria Olvera for edit photographs and to the two anonymous reviewers to improve the manuscript. Samples were collected under Mexican scientific permit # PPF/DGOPA249/14 (SAGARPA-CONAPESCA). Miriam Soria-Barreto thanks to Fellowship of CONACYT.

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