# Feeding Habits of the Non-Native Mayan Cichlid, *Mayaheros urophthalmus*, in Estuarine Tributaries of Southwest Florida

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# GULF AND CARIBBEAN

## R E S E A R C H

# FEEDING HABITS OF THE NON—NATIVE MAYAN CICHLID, *MAYAHEROS UROPHTHALMUS*, IN ESTUARINE TRIBUTARIES OF SOUTHWEST FLORIDA

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**ABSTRACT:** Foraging habits of the non—native Mayan Cichlid (*Mayaheros urophthalmus*) were investigated in the tidal tributaries to the Estero Bay and Wiggins Pass estuaries in southwest Florida (USA) during 2011–2013. Dietary analysis was conducted by identifying contents in the digestive tracts of 747 fish and volumetrically measuring the food items. Detritus was the predominant food item by frequency (97–100%), volume (34–48%), and alimentary importance index (47–64%). Bivalves, gastropods, decapod and cirriped crustaceans, coleopterans, serpulid polychaetes, and fish scales frequently (>50%) occurred in samples but volume and importance differed among tributaries. Results indicate that the Mayan Cichlid in southwest Florida tidal tributaries is an opportunistic predator of hard—shelled invertebrates. Although there was considerable overlap in dietary composition, percent volume of food items was significantly different among tributaries during dry seasons. In each tributary, detritus was consumed in greater percentage during the dry season and benthic invertebrates were consumed in greater percentages during the wet season. Consumption of detritus, algae, and plant material may be incidental to predation on benthic invertebrates but more information is needed on digestion and assimilation of food items. Variability in diet among the tributaries in the current study and among other studies was presumably a function of habitat characteristics and the corresponding availability of prey types.

**KEY WORDS:** Estero Bay, generalist, importance index, molluscivore, seasonal diet

## INTRODUCTION

A number of introduced fish species have become established in south Florida. Anthropogenic habitats such as canals and other stormwater conveyances may provide refuge for non—native fish during the dry season and facilitate dispersal during the wet season (Adams and Wolfe 2007, Kline et al. 2013). On the one hand, there appears to be limited evidence of impacts of non—native fish species on native communities (Courtenay 1997). However, quantitative analyses of community compositions have indicated an inverse relationship between the abundant Mayan Cichlid (*Mayaheros urophthalmus*; see Říčan et al. 2016) and native fish species inhabiting estuarine mangrove habitats (Trexler et al. 2000, Harrison et al. 2013). Furthermore, Mayan Cichlids were observed competing for spawning sites and foraging on nests of native centrarchid fishes (bass and sunfish; Trexler et al. 2000).

The Mayan Cichlid is native to the Gulf of Mexico and Caribbean coast drainages of Central America from southeast Mexico to Nicaragua (Miller 1966). The species was first documented in the United States in 1983 within the Taylor Slough drainage of Everglades National Park (Loftus 1987) and has since expanded its range to most freshwater and estuarine systems in south Florida (Faunce and Lorenz 2000, Paperno et al. 2008, Idelberger et al. 2011). A number of factors have contributed to the Mayan Cichlid's rapid range expansion including a generalist and opportunistic feeding strategy (Bergmann and Motta 2005), aggressive behavior, and tolerance to a variety of environmental conditions (Schofield et al. 2009). The species' broad salinity tolerance combined with extensive anthropogenic habitat alteration has likely facilitated its establishment in estuarine habitats throughout southwest Florida (Adams and Wolfe 2007).

Trophic interactions between Mayan Cichlids and native species need to be investigated to better understand the ecological role and potential effects of this introduced species in Florida (Bergmann and Motta 2005, Paperno et al. 2008). Comprehensive descriptions of Mayan Cichlid diet are available in native brackish coastal lagoons (Caso—Chávez et al. 1986, Martínez—Palacios and Ross 1988, Chávez—López et al. 2005, Guevara et al. 2007); however, detailed information is lacking on food items consumed in estuarine habitats within the introduced range of the species. The purpose of the current study was to fill this knowledge gap by characterizing the feeding habits of Mayan Cichlids inhabiting tidal tributaries of southwest Florida estuaries.

## MATERIALS AND METHODS

### Study Area

The study area included small rivers and creeks that contribute freshwater to the Estero Bay and Wiggins Pass estuarine systems on the southwest coast of Florida (Figure 1). The primary tributaries to Estero Bay include Hendry Creek, Mullock Creek, and Estero River in the northern region, Spring Creek in the south—central region, and Imperial River in the extreme southern region. The Cocohatchee River flows into a series of small embayments identified as the Wiggins Pass Estuarine Area, which connect with the Imperial River and Estero Bay to the north. Shoreline vegetation along undeveloped portions of the tributaries consisted mainly of red mangroves (*Rhizophora mangle*), occasionally interspersed with black mangroves (*Avicennia germinans*). Developed shoreline includes residential areas with channelized waterways, docks, seawalls, riprap, trimmed mangrove, and other vegetation such as non—native Brazilian pepper (*Schinus terebinthifolius*),
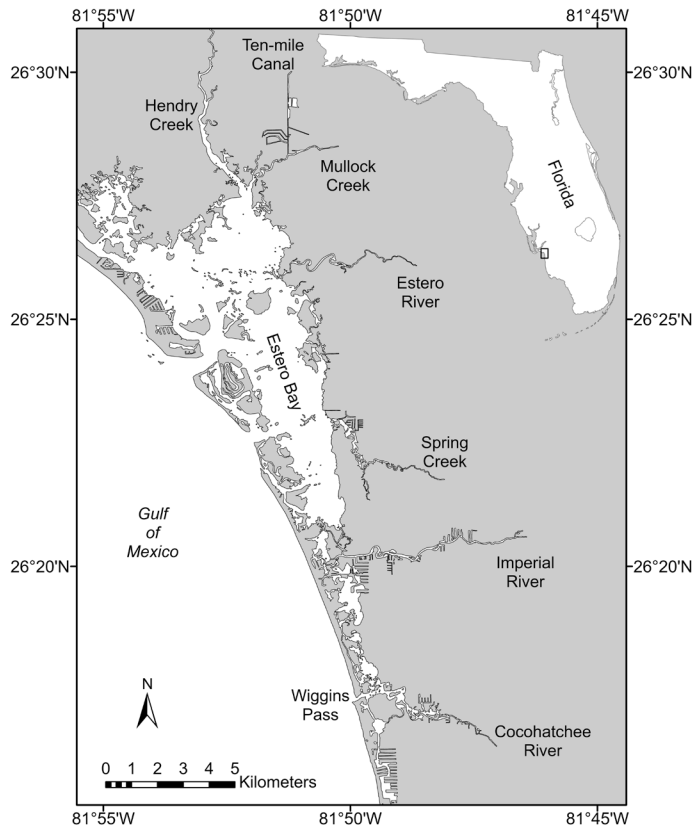
**FIGURE 1.** Map of southwest Florida showing the study tributaries to the Estero Bay and Wiggins Pass estuarine systems.

and native pines (*Pinus* spp.) and oaks (*Querqus* spp.).

Rainfall patterns in southern Florida vary seasonally, as do the subsequent salinity conditions in the estuaries, and were categorized as dry season (December through May) and wet season (June through November; Shirley et al. 2004). Urban areas surrounding the estuarine systems rely on drainage canals for flood control during the wet season with varying amounts of stormwater flowing into the tributaries. The Ten–Mile Canal, Kehl Canal, and Cocohatchee Canal systems are major conveyances of stormwater into Mullock Creek, Imperial River, and Cocohatchee River, respectively. The lower reaches of Estero Bay tributaries have been characterized as high freshwater inflow and/or lower salinities (Hendry and Mullock Creeks and Imperial River) or lower freshwater inflow and higher salinities (Estero River and Spring Creek; Tolley et al. 2006).

### Data collection

Sampling was performed in the tidal reaches of the estuarine tributaries. The majority of sampling was conducted during dry seasons with Mayan Cichlids collected March and April 2011 (n = 32 fish), January through April 2012 (n = 264 fish), and December 2012 through May 2013 (n = 320 fish). Wet season samples were collected in August 2012 (n = 8 fish) and July through September 2013 (n = 123 fish). Salinity was recorded at collection sites in 2012–13 using a handheld YSI Model 85 meter (Yellow Springs, OH). Fish were captured by

angling with small artificial lures in mangrove prop–root habitat as well as submerged woody debris (snags) and dock pilings in developed areas. This sample method favored the collection of larger fish, and individuals >102 mm standard length (SL) were considered adult (Martinez–Palacios and Ross 1992, Bergmann and Motta 2005). Captured fish were immediately placed on ice and later transported to shore for processing. Sex of each individual was identified by visual inspection of the gonads. Digestive tracts were placed in 10% buffered formalin for 1–2 weeks, soaked for 24 hours in freshwater, and transferred to 80% ethanol for storage. Tract contents were examined with a dissecting microscope and identified to the lowest possible taxon; however, food items were aggregated to the level of order for diet analyses. Fish scales were grouped separate from other fish remains. Sorted food items were placed in a graduated cylinder and the settled volume was measured to the nearest 0.1 ml. Trace amounts of food items were assigned a volume of 0.001 ml for analyses.

### Data Analyses

The exact binomial test (McDonald 2014, α = 0.05) was used to compare the sex ratio of Mayan Cichlids collected from each tributary with a 1:1 ratio. Given unequal sample sizes, unequal variances, and/or non–normality, the fish length data for each tributary were rank transformed and the ranks were compared by sex with the unequal variances t–test (Ruxton 2006, α = 0.05).

Percent frequency of occurrence (% F) and percent volume (% V) of food types were determined by:

$$\% \, F = \frac{(\text{number of samples containing food type})}{(\text{total number of samples})} \times 100 \qquad \text{Equation 1}$$

$$\% \, V = \frac{(\text{volume of food type})}{(\text{total volume of all food types})} \times 100 \qquad \text{Equation 2}$$

Food types were not enumerated owing to difficulties with identifying masticated prey fragments, macrolagae, and detritus as discrete units (Hyslop 1980). An alimentary importance index (AII; Kawakami and Vazzoler 1980) was calculated for each food type *i* with the equation:

$$\% \, AII = \frac{100 \, (\%F_i \, \%V_i)}{\sum_{i=0}^{n} (\%F_i \, \%V_i)} \qquad \text{Equation 3}$$

Multivariate analyses were used to examine differences in diet compositions of Mayan Cichlids using PRIMER v6 software (Clark and Gorley 2006). The digestive tract of each fish was the sampling unit and the volume of food items for each fish was converted to percent composition using the total volume of the respective sample. Volume is one of the most representative measures of food bulk and therefore a more satisfactory method for quantitative analyses of gut contents (Hynes 1950, Hyslop 1980). Furthermore, calculating the percent composition for each sample standardizes for individual differences in volume of digestive tract contents (Hinojosa–Garro et al. 2013). A Bray–Curtis similarity matrix was generated for the untransformed food volume percentages. Food compositions were compared among tributaries with a one–way analysis of similarity (ANOSIM; 9999 permutations)

using data for the 2011–2013 dry seasons. Pairwise comparisons were made in the event of a significant difference among tributaries. The similarity percentages (SIMPER) routine was used to identify food items contributing to any significant differences in dry season diet compositions between tributaries. Wet and dry season food volume percentages were compared for each tributary with one—way ANOSIM using samples collected in December 2012 – September 2013. Food items contributing to any significant seasonal differences for a given tributary were identified with SIMPER.

## RESULTS

A total of 747 Mayan Cichlids were collected from the tributaries of the Estero Bay and Wiggins Pass estuarine systems in southwest Florida. Salinity at collection sites ranged from meso—polyhaline conditions with vertical

**TABLE 1.** *Mean seasonal salinities at Mayan Cichlid collection sites in the mangrove tidal creeks of southwest Florida from 2012-2013. Location of tributaries shown on Figure 1. Measurements expressed as mean ± sd.*

| Tributary and season | No. of readings | Salinity Surface | Bottom |
|---|---|---|---|
| **Cocohatchee River** | | | |
| Dry | 8 | 14.8 ± 4.8 | 20.5 ± 5.4 |
| Wet | 6 | 0.5 ± 0.3 | 0.8 ± 0.6 |
| **Estero River** | | | |
| Dry | 6 | 14.3 ± 7.9 | 23.1 ± 3.6 |
| Wet | 3 | 0.3 ± 0.1 | 0.3 ± 0.0 |
| **Imperial River** | | | |
| Dry | 43 | 9.2 ± 5.0 | 13.1 ± 6.1 |
| Wet | 12 | 0.7 ± 1.8 | 2.7 ± 4.3 |
| **Mullock Creek** | | | |
| Dry | 10 | 10.1 ± 8.3 | 24.3 ± 5.3 |
| Wet | 3 | 0.4 ± 0.1 | 0.5 ± 0.1 |
| **Spring Creek** | | | |
| Dry | 42 | 11.1 ± 5.4 | 19.7 ± 4.8 |
| Wet | 7 | 2.4 ± 3.1 | 5.7 ± 6.6 |

stratification during the dry season to oligohaline conditions during the wet season (Table 1). Diet samples were collected from adult—size fish with the exception of 3 immature fish 75-95 mm SL from the Imperial River. Males dominated the

catch in most tributaries with significant male bias in the sex ratios for Cocohatchee and Imperial Rivers (Table 2). Mean size of males was larger than females in all tributaries with significantly larger males in Estero River, Mullock Creek, and Spring Creek.

Mayan Cichlids consumed 41 food items during all sampling seasons combined and 13 of these items had an alimentary importance index (AII) >1% in at least one of the tributaries (Table 3). Detritus was the dominant item consumed in all tributaries, occurring in 97-100% of the samples, accounting for 34-48% of volume, and as 47-64% for the importance index. Gastropods and bivalves had relatively high frequency of occurrence (77-95% F) for the Cocohatchee, Estero, and Imperial Rivers but these items only contributed 4-16% to the total food volume with correspondingly low importance (4-20% AII). Bivalves were also a frequent food type in Mullock (87% F) and Spring (95% F) Creeks and had a relatively higher contribution to food volume (32–33% V) and higher importance (36–38% AII). Other comparatively frequent (>50% F) food types with low volume and importance included fish scales in all tributaries, isopods in Cocohatchee and Estero Rivers, decapods in Estero River, dipterans in Imperial River, gastropods in Mullock and Spring Creeks, and serpulid polychaetes in Mullock Creek (Table 3).

Percent food volumes of Mayan Cichlid was significantly different (Global R = 0.173, p = 0.0001) among the tributaries during 2011—13 dry seasons. The greatest pairwise differences in diet were between Spring Creek and the other tributaries (Figure 2) but the low R values (0.19–0.25) indicated minor differences with considerable overlap in the food volume compositions. Negligible R values (0.01–0.07) for comparisons between the other tributaries indicated no differences in food volume percentages. The SIMPER routine identified detritus as contributing the most to the dietary dissimilarities with Spring Creek; however, high variability in the consumption of this food item within each tributary may have confounded pairwise contrasts as indicated by the relatively small differences in mean volume percentages of detritus between tributaries (Figure 2). Bivalves appeared to be a more distinctive food item with greater mean percent volumes for Spring Creek samples during dry seasons than any other tributary. Diet samples from the other tributaries had higher mean percentages of items such as gastropods, decapods, isopods, and chlorophytes (Figure 2).

**TABLE 2.** *Analyses of sex ratio and mean standard length by sex for adult Mayan Cichlid collected from estuarine tributaries in southwest Florida from 2011-2013. Difference in length of females and males tested using unequal variance t-test on ranked values (t).*

| Tributary | No. of females | No. of males | Sex Ratio | p | Standard length (mm±sd) Female | Male | t | p |
|---|---|---|---|---|---|---|---|---|
| Cocohatchee River | 29 | 51 | 1.0F:1.8M | 0.02 | 178 ± 26 | 184 ± 28 | 1.46 | 0.15 |
| Estero River | 17 | 28 | 1.0F:1.7M | 0.14 | 186 ± 17 | 202 ± 31 | 2.80 | 0.01 |
| Imperial River | 72 | 130 | 1.0F:1.8M | < 0.001 | 167 ± 25 | 171 ± 30 | 1.09 | 0.28 |
| Mullock Creek | 48 | 67 | 1.0F:1.4M | 0.09 | 186 ± 33 | 203 ± 37 | 2.41 | 0.02 |
| Spring Creek | 141 | 145 | 1.0F:1.0M | 0.86 | 187 ± 25 | 199 ± 32 | 3.80 | < 0.001 |

**TABLE 3.** *Percent frequency of occurrence (% F), volume (% V), and alimentary importance index (% AII) for major food items of Mayan Cichlid collected from estuarine tributaries in southwest Florida during all seasons combined in 2011-2013. Food items ordered by AII > 1% for at least one of the tributaries.*

| | Cocohatchee River | | | Estero River | | | Imperial River | | | Mullock Creek | | | Spring Creek | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | %F | %V | %AII | %F | %V | %AII | %F | %V | %AII | %F | %V | %AII | %F | %V | %AII |
| Detritus | 98.8 | 43.3 | 64.0 | 100.0 | 38.5 | 59.7 | 97.1 | 33.8 | 51.7 | 96.6 | 35.8 | 46.6 | 99.3 | 48.1 | 56.7 |
| Bivalvia | 77.5 | 4.3 | 5.0 | 80.0 | 7.2 | 9.0 | 81.0 | 15.8 | 20.2 | 87.1 | 32.1 | 37.8 | 94.5 | 32.8 | 36.8 |
| Gastropoda | 95.0 | 8.3 | 11.8 | 80.0 | 4.4 | 5.5 | 80.5 | 6.9 | 8.7 | 55.2 | 1.5 | 1.1 | 52.9 | 1.3 | 0.8 |
| Decapoda | 23.8 | 3.8 | 1.3 | 52.7 | 10.6 | 8.7 | 42.4 | 13.9 | 9.3 | 45.7 | 4.0 | 2.4 | 35.4 | 8.6 | 3.6 |
| Plant material | 26.3 | 22.3 | 8.7 | 14.5 | 5.7 | 1.3 | 18.0 | 4.4 | 1.3 | 14.7 | 3.9 | 0.8 | 18.2 | 3.1 | 0.7 |
| Sabellida | 26.3 | 1.1 | 0.4 | 38.2 | 1.4 | 0.8 | 35.1 | 1.3 | 0.7 | 69.0 | 8.0 | 7.5 | 35.1 | 0.9 | 0.4 |
| Isopoda | 67.5 | 5.0 | 5.0 | 63.6 | 6.2 | 6.2 | 33.2 | 1.1 | 0.6 | 29.3 | 1.2 | 0.5 | 35.1 | 0.7 | 0.3 |
| Chlorophyta | 12.5 | 5.5 | 1.0 | 14.5 | 16.9 | 3.8 | 13.2 | 6.5 | 1.4 | 13.8 | 7.8 | 1.5 | 6.2 | 0.5 | < 0.1 |
| Coleoptera | 11.3 | 0.7 | 0.1 | 27.3 | 2.1 | 0.9 | 21.5 | 4.9 | 1.6 | 19.0 | 2.7 | 0.7 | 10.7 | 0.2 | < 0.1 |
| Sessilia | 2.5 | < 0.1 | < 0.1 | 43.6 | 1.8 | 1.2 | 29.8 | 3.2 | 1.5 | 32.8 | 1.2 | 0.5 | 24.7 | 0.5 | 0.2 |
| Fish scales | 66.3 | 1.4 | 1.4 | 65.5 | 0.9 | 0.9 | 54.1 | 0.6 | 0.5 | 54.3 | 0.6 | 0.4 | 55.3 | 0.6 | 0.4 |
| Diptera | 37.5 | 0.2 | 0.1 | 47.3 | 0.9 | 0.6 | 51.7 | 1.6 | 1.3 | 29.3 | < 0.1 | < 0.1 | 40.2 | 0.1 | < 0.1 |
| Amphipoda | 15.0 | 0.3 | 0.1 | 40.0 | 2.0 | 1.3 | 12.2 | 0.3 | 0.1 | 8.6 | 0.3 | < 0.1 | 19.6 | 0.1 | < 0.1 |

There were significant seasonal differences in food volume percentages for Mayan Cichlid collected in each tributary during December 2012–September 2013 (Figure 3). The low to intermediate R values (0.24–0.49) indicated moderate differences in seasonal diet compositions but with varying dietary overlap between wet and dry seasons. Higher mean percentages of detritus were consumed in all tributaries during the dry season. The wet season diet had lower mean volumes of detritus and included greater percentages of bivalves, decapods, gastropods, and/or coleopterans, but relative contributions by these food items varied among the tributaries.

## DISCUSSION

Adult–size Mayan Cichlid primarily consumed detritus in the tidal tributaries of southwest Florida. Most diet studies have documented a preponderance of detrital, algal, and plant material in their digestive tracts, leading some to consider this species omnivorous (Caso–Chávez et al. 1986, Nico et al. 2007, Pease et al. 2018, Tomojiri et al. 2019), detritivorous–omnivorous (Hinojosa–Garro et al. 2013, Flores–Ramos 2014), or herbivorous (Chávez–López et al. 2005, Guevera et al. 2007). An omnivorous trophic position has also been calculated using proportional food volumes (Loftus 2000) or stable isotope analyses (Vaslet et al. 2012). However, the latter study did not estimate the isotopic contributions of individual food items such as detritus or plant materials to the Mayan Cichlid diet. Consumption of these items does not necessarily entail they are digested and therefore provide nutritive value to the fish (Keenleyside 1979, Gerking 1994). Studies of Mayan Cichlid digestive physiology have focused on larvae and juveniles with regard to developing artificial foods used in aquaculture. Enzymatic processes during initial ontogeny were indicative of carnivorous feeding habits (López–Ramírez et al. 2011, Cuenca–Soria et al. 2014) but the corresponding physiology of free–ranging and adult–size fish have not been studied in natural environments. A combination of stable isotope and enzyme activity analyses could determine whether detritus, algae, and plant

materials are digested by the species and thus contribute to the assimilated nutrients in their tissues (Deegan et al. 1990, Leigh et al. 2018). Additionally, fatty acid trophic signatures could be combined with stable isotope and stomach content analyses to identify the relative contribution of the putative food items (Kuusipalo and Käkelä 2000, Abd El–Karim et al. 2016).

Alternatively, the consumption of detritus by Mayan Cichlid inhabiting southwest Florida tributaries may have occurred incidentally while feeding on invertebrate prey. Martínez–Palacios and Ross (1988) and Vaslet et al. (2012) suggested the ingestion of algal and plant materials was a result of predation on benthic crustaceans, although the relative volume and importance of vegetative materials were secondary to animal prey in these studies. Mayan Cichlid were observed picking at red mangrove prop roots and submerged tree snags during current sampling efforts, presumably feeding upon the epibiontic communities. Consumption of sessile invertebrates firmly adhered to these substrates (e.g., mussels, barnacles, and serpulid polychaetes) would facilitate incidental ingestion of bark, rootlets, and other woody fragments that were major components of the detritus category. Epiphytic filamentous macroalgae were also consumed, which provide habitat to a variety of motile invertebrate prey (Tunnell and Withers 2009, Heard et al. 2002). The anatomical characteristics of Mayan Cichlid include well–developed canine teeth, molariform pharyngeal teeth, relatively short intestine length, and other ecomorph features found in carnivores, piscivores, and specialized predators (Martínez–Palacios and Ross 1988, Bergmann 2002, Bergmann and Motta 2005, Říčan et al. 2016). The comparatively short intestine length would reduce the efficiency of digesting large amounts of detritus, algae, or plant materials (Zihler 1982, Martínez–Palacios and Ross 1988, German 2011). Based on these feeding structures, the Mayan Cichlid would be considered a carnivorous fish with omnivorous habits implied from conventional diet studies (Martínez–Palacios and Ross 1988, Vaslet et al. 2012).
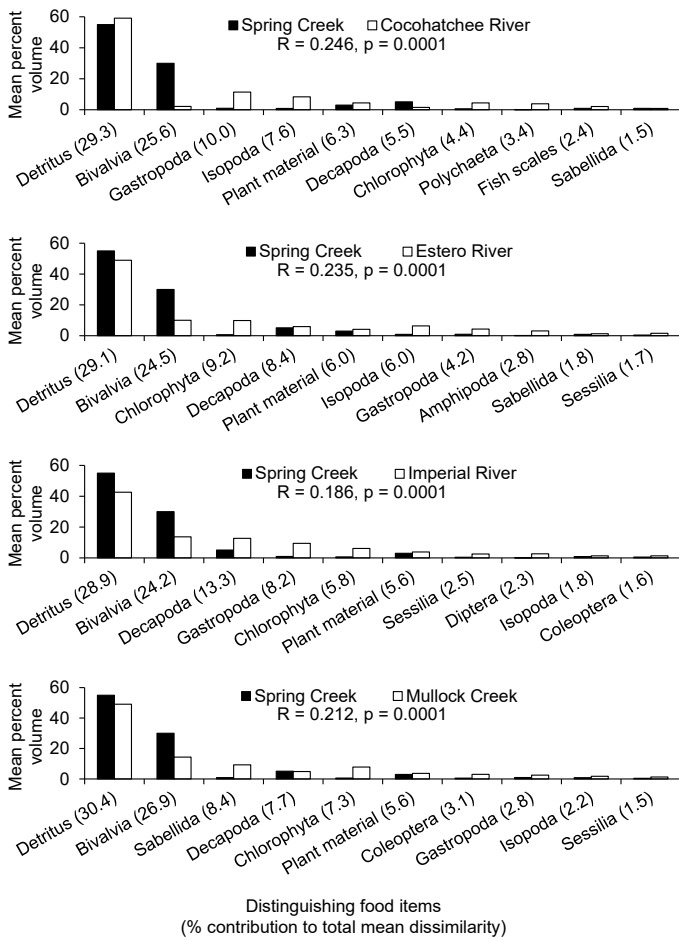
The pharyngeal jaw apparatus of the Mayan Cichlid is

**FIGURE 2.** The top 10 Mayan Cichlid food items distinguishing diet comparisons between Spring Creek and the other southwest Florida tributaries during the dry seasons in 2011-2013. Groups were compared by untransformed volume percentages of food items and the contribution of each item to the total mean dissimilarity between tributaries is given in parentheses. Pairwise R indicates degree of separation in diet between Spring Creek and each tributary.



**FIGURE 3.** The top 10 Mayan Cichlid food items distinguishing seasonal diet comparisons for each southwest Florida tributary from December 2012–September 2013. Groups were compared by untransformed volume percentages of food items and the contribution of each item to the total mean dissimilarity between tributaries is given in parentheses. Global R indicates degree of separation in diet between wet and dry season.

adapted for crushing shelled invertebrates and more similar in arrangement to that of molluscivorous rather than piscivorous fishes (Martínez—Palacios and Ross 1988, Hulsey et al. 2008). For example, hard—shelled prey such as bivalves (primarily mussels), gastropods (hydrobiid snails), decapod (xanthid and sesarmid crabs) and cirriped crustaceans, coleopterans (adult scarabaeid beetles), and serpulid polychaetes were frequently consumed by Mayan Cichlid in the current study, although these items contributed less to sample volume and subsequent importance in the diet. Bivalve shells, barnacle plates, and worm tubes were fragmented in diet samples and the presence of soft body parts (viscera, cirri, radioles, etc.) indicated mastication of living organisms rather than benthic scavenging on shell hash. Hydrobiid snails were consumed whole or slightly crushed owing to their small size, whereas the shells of larger and less frequent thiarid (*Melanoides tuberculata*) and melampid (*Melampus coffeus*) snails were fragmented within the gastrointestinal tract. Feeding experiments demonstrated that Mayan Cichlid offered Seminole Ramshorn (*Planorbella*
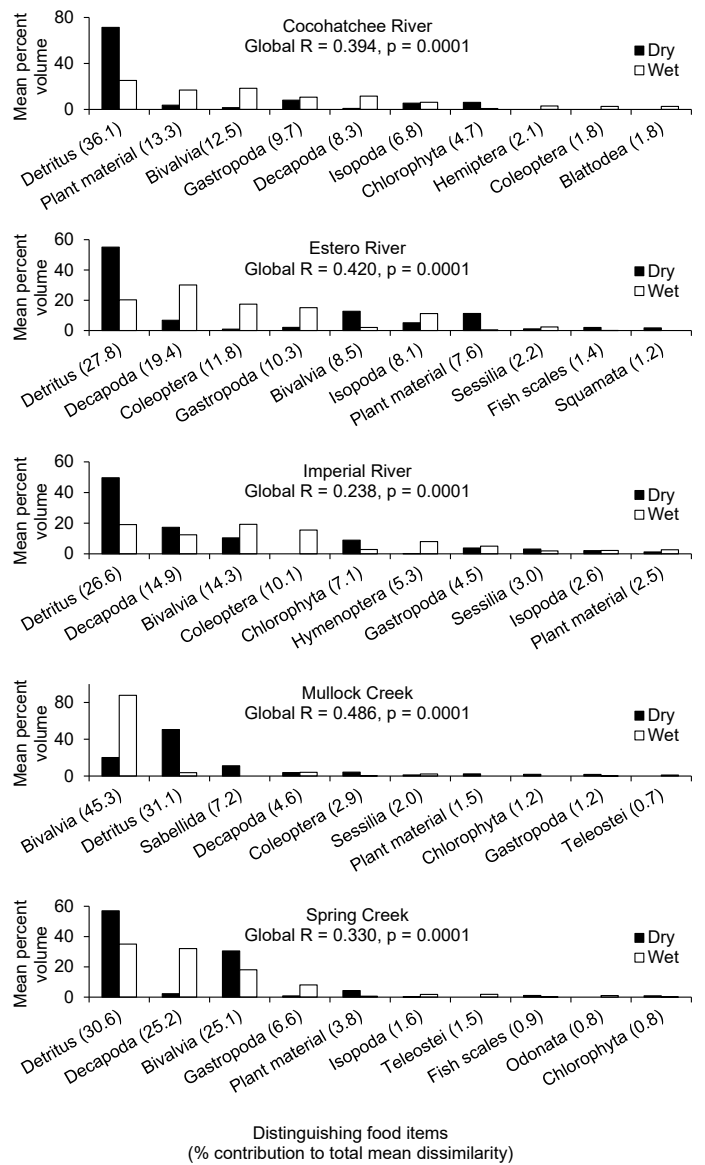
*duryi*) would crush the snail, swallow the tissue, and expel shell fragments from their mouth (Ruehl 2010). The dietary contribution of larger snails may be underestimated in gut content analyses if fish in the wild expel shell fragments as observed in the laboratory experiments.

Regional differences in molluscivory by Mayan Cichlid are likely due to the hydrologic characteristics of the estuarine systems, spatiotemporal aspects of where fish were collected in each estuary, and the corresponding availability of these food types. Estuarine mussels were prevalent in the diet of Mayan Cichlid collected from the mangrove—fringed tributaries to Estero Bay, especially Mullock and Spring Creeks. These bivalves are considered important to mangrove food webs and a major component in the diet of Sheepshead (*Archosargus*

*probatocephalus*) inhabiting central and south Florida estuaries (Odum and Heald 1972, Hernandez and Motta 1997, Cutwa and Turnigan 2000). Thus, there is potential for food competition where Mayan Cichlid and Sheepshead coexist but there is no information on possible interactions between these or any other molluscivorous species (e.g., blue crab, *Callinectes sapidus*). Nonetheless, mussels would not be considered a limited resource in Estero Bay tributaries as they were the most abundant and opportunistic (as indicated by their rapid colonizing ability; Sedberry 1987) macroinvertebrate in the mixohaline waters (Schmid et al. 2006). Although mussels were a prevalent root—fouling organism in the mangrove lagoon systems of Mexico, particularly those in the state of Veracruz (Tunnell and Withers 2009, Ruiz and López,—Portillo 2014, Lucas and De la Cruz—Francisco 2018), there is limited information on whether these bivalves contribute to the food items of Mayan Cichlid in their native range. For example, bivalves were a seasonal component in the diet of Mayan Cichlid inhabiting Alvarado Lagoon, Veracruz (Chávez—López et al. 2005) and were a relatively infrequent component for fish in Celestun Lagoon, Yucatan (Martínez—Palacios and Ross 1988) but mussels were not specifically identified in these studies. Molluscs in general contributed very little to the diet of Mayan Cichlid collected from Terminos Lagoon, Campeche (Caso—Chávez et al. 1986, Guevera et al. 2007). More information is needed on prey community structure in a given study area to determine if Mayan Cichlid feeds opportunistically on available prey and therefore exhibits a generalist feeding strategy (Bergmann and Motta 2005, Vaslet et al. 2012, Pease et al. 2018).

Gastropods, particularly the serrate crownsnail (*Pyrgophorus platyrachis*), were a relatively important invertebrate prey item for Mayan Cichlid in the Cocohatchee River but this may have been a function of the habitat characteristics of the sampling location. Although the lower reach of this tributary was lined with mangroves, most of the fish were collected from the tidal portion of the Cocohatchee Canal that has a developed shoreline (roadway on one side and residential area on the opposite side) and downstream from a water—control structure. Snails were also a common food item in other estuarine diet studies in western Florida that had similar riparian features; a brackish sampling site was located in a borrow canal system adjacent to a major roadway intersection (Bergmann 2002) and a channelized waterway surrounded by residential development with secondary sites in canals and highly urbanized tributaries (Tharpe 2020). The non—native red—rimmed melania snail (*Melanoides tuberculata*) was the dominant food item for Mayan Cichlid in the latter study. The serrate crownsnail and other estuarine hydrobiids have been collected from a variety of anthropogenic features such as ditches, canals, drainage pipes, culverts, and water—control structures (Heard et al. 2002), while the red—rimmed melania snail commonly occurs in canals and becomes concentrated where water discharges into estuaries (Roessler et al. 1977, Wingard et al. 2008). The consumption of these gastropods may reflect the generalist feeding strategy of Mayan Cichlid and likely enhances their ability to become established in Florida's stormwater conveyance structures.

Although data were limited to a single year, Mayan Cichlid exhibited a pronounced seasonal pattern of higher volumetric percentages of detritus ingested during the south Florida dry season with a shift to lower detritus and higher invertebrate percentages in the wet season. Aquatic macroinvertebrates exhibited higher taxonomic richness in Estero Bay tributaries during the early wet season (Schmid et al. 2006), indicating a greater range of prey available for consumption. Mayan Cichlid inhabiting coastal lagoons and inland lakes in Mexico have also demonstrated greater diversity or importance of aquatic invertebrates in their diet during the wet season (Martínez—Palacios and Ross 1988, Chávez—López et al. 2005, Flores—Ramos 2014). Furthermore, a reduction in prey abundance, particularly aquatic insect and gastropod diversity, during the dry season was observed for coastal freshwater wetlands in Mexico (Hinojosa—Garro et al. 2013). Other neotropical cichlid species displayed higher consumption of detritus and plant matter in the dry season and higher diversity of insect prey during the wet season (Trujillo—Jimenéz 1998, Cavalcante et al. 2014). However, the question remains whether detritus, algae, and plant materials were consumed for their nutritive value or incidentally when invertebrate prey were harder to find. Seasonal variability in food availability and consumption has implications for the timing of diet sample collection and the majority of current efforts during dry seasons may have overestimated the contribution of detritus to the Mayan Cichlid diet while underestimating those of animal prey in the wet season.

Piscivory customarily applies to consumption of the entire fish or removal of flesh instead of certain parts of the body such as fins or scales (Gerking 1994, Peterson and Winemiller 1997). Fish scales were frequently consumed by adult Mayan Cichlids in southwest Florida tidal tributaries but contributions of other fish remains were negligible (<4.0% F, <1.0% V, and <0.1% AII among tidal tributaries). The scales were about 1 cm in size, arranged in a stacked fashion, and not accompanied by fish flesh or bones. The latter attribute is indicative of lepidophagy (i.e., scale eating; Peterson and Winemiller 1997). Scale consumption by Mayan Cichlids has been noted in both native (Martinez—Palacios and Ross 1988, Chávez—López et al. 2005) and introduced ranges (Howard 1995, Bergmann 2002, Tomojiri et al. 2019, Tharpe 2020), and appears prevalent in juvenile fish from non—native locales. In contrast, Mayan Cichlid collected in freshwater habitats of Florida exhibit a more piscivorous feeding mode. Small—bodied marsh fishes such as Eastern Mosquitofish (*Gambusia holbrooki*), Sailfin Mollies (*Poecilia latipinna*) and Bluefin Killifish (*Lucania goodei*), as well as smaller Mayan Cichlids, were the piscine prey identified from diet studies in the Everglades and Big Cypress regions (Howard 1995, Loftus 2000, Bergmann 2002). Mayan Cichlids across a range of size classes averaged 3–9 fish per diet sample, and a sample for a smaller (90–135 mm) individual contained 33 identifiable fish (Howard 1995). Fish were also prominent

prey in the few studies of freshwater habitats in Mexico (Hinojosa–Garro et al. 2013, Pease et al. 2018). Piscivory was suggested as a potential explanation for the negative relationships between Mayan Cichlid density and those of native fish species in estuarine mangrove habitat of southern Florida (Harrison et al. 2013) but this inference was based on diet from studies in freshwater habitats (Howard 1995, Loftus 2000; Bergmann and Motta 2005).

Our study supports the pattern that has emerged from available literature that Mayan Cichlid exhibit variable carnivorous feeding habits with durophagy (i.e., eating hard prey) common in estuarine habitats with piscivory more prevalent in freshwater habitats, particularly for the introduced range in Florida (Table S1). Given the generalist feeding strategy of the species, there is likely a continuum associated with habitat features and food availability along salinity gradients. Bergmann (2002) first noted that hard–shelled prey were more prevalent in Mayan Cichlid from brackish waters compared to those collected in freshwater. Molluscs were the predominant food items reported for the species in estuarine habitats within the introduced range (Loftus 1987, Lament 1999, Bergmann 2002, Tharpe 2020, current study) and crustaceans predominated in some native estuarine habitats (Martínez–Palacios and Ross 1988, Vaslet et al. 2012).

However, Bergmann (2002) also reported a relatively high frequency of fish consumption in brackish waters that could be related to the characteristics of that study site, a coastal stormwater conveyance in southwest Florida with aquatic vegetation (*Vallisneria americana*, *Hygrophila polysperma*, *Ludwigia repens*, and *Hydrochloa caroliniensis*) indicative of low salinity conditions during dry season sampling. An inland lake in Tabasco, Mexico also had beds of *V. americana* as benthic habitat and Mayan Cichlid inhabiting this oligohaline system ingested relatively high volumes of fish (Pease et al. 2018). Fish consumption was also reported for adult cichlids in coastal west–central Florida but samples were only collected during the wet season when the primary study site receives considerable urban runoff and there was no differentiation in diet among multiple sites with a range of salinity profiles (i.e., freshwater springs, oligo–mesohaline rivers, and polyhaline tidal tributaries; Tharp 2020). Future studies of Mayan Cichlid diet should consider the seasonality of sample collection and include well–defined salinity conditions and description of habitat characteristics at collection sites. Furthermore, concurrent collection of diet samples along a salinity gradient is needed to further elucidate the purported pattern of fish predation in freshwater habitats and benthic invertebrate predation in estuarine habitats.

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