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Diet and morphology through ontogeny of the nonindigenous Mayan cichlid '*Cichlasoma* (*Nandopsis*)' *urophthalmus* (Günther 1862) in southern Florida

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Synopsis

We evaluated diet and morphology through ontogeny for a freshwater population of the Mayan cichlid '*Cichlasoma* (*Nandopsis*)' *urophthalmus* (Günther 1862) in Florida's Big Cypress National Preserve. This species is a generalist predator throughout ontogeny. Fish remained the primary prey item throughout ontogeny, but there was a shift from detritus and ostracods among juveniles to algae, gastropods (snails), decapods, Hymenoptera, and adult Diptera among adults. All morphological variables grew isometrically except total molariform tooth area and pharyngeal jaw mass, which exhibited positive allometry. Despite a moderately robust adult pharyngeal jaw apparatus, this species does not specialize on hard prey at this south Florida site. Compared to its native range in Mexico, fish in Florida have undergone a pronounced niche shift with the diet being dominated by fish and snails, probably due to greater availability. The invasive success of *C. urophthalmus* does not appear to be related to ontogenetic morphological shifts or dietary specialization. Rather, its successful and rapid colonization of southern Florida might in part be related to its generalized and opportunistic feeding habits and morphology.

Introduction

Many studies have examined the ecology and environmental impact of nonindigenous fishes, and some have attributed the decline of native communities to them (Taylor et al. 1984, Chapman et al. 1996, Courtenay 1997). The majority of exotic fishes in Florida are in the Cichlidae; a family with no species indigenous to the state but with 13 established (Courtenay et al. 1974, Courtenay 1993, 1997, Shafland 1996). The Mayan cichlid '*Cichlasoma* (*Nandopsis*)' *urophthalmus* (Günther 1862),[1] hereafter referred to as *Cichlasoma urophthalmus*, is native to the Atlantic slope of tropical Central America and was first recorded in Florida from Everglades National Park in 1983 (Miller 1966, Loftus 1987). This species has proven to be an effective invader, spreading westward and northward to occupy most of southern Florida by 1999, a period of 16 years or about three generations (Faunce & Lorenz 2000, Faunce et al. 2002). In much of this range, *C. urophthalmus* is common (Trexler et al. 2001). Being a relatively recent introduction, little is known about how its trophic ecology or morphology in Florida compare to its native range, or how it has managed to become a successful invader in such a short time.

All fish species undergo ontogenetic dietary shifts, and many teleost fishes experience several of

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[1] The genus is placed between quotation marks here in accord with the convention for taxonomically undetermined cichlids (Stiassny 1991).

them (Galis & de Jong 1988, Noakes 1991, Wainwright & Richard 1995). Fishes may also undergo a corresponding ontogenetic shift in cranial and post-cranial morphology (Ehlinger & Wilson 1988, Ehlinger 1990). Some fishes develop the ability to consume harder prey as adults because they are larger, and have stronger, more robust oral and pharyngeal jaws (Osenberg et al. 1994, Hernandez & Motta 1997, Cutwa & Turingan 2000, Durie & Turingan 2001), which can result in a reduction in diet breadth through ontogeny as they exploit novel food resources (hard prey), to the exclusion of soft prey (Wainwright 1988, Osenberg et al. 1992, 1994, Hernandez & Motta 1997). The invasive success of *Cichlasoma urophthalmus* may in part be due to ontogenetic changes in trophic morphology with a corresponding ability to exploit novel resources, particularly by means of its pharyngeal jaw apparatus. This kind of advantage is apparent in the evolution of the large species flocks of the East African Great Lakes cichlids (Liem 1973, Galis 1998). The invasive success of *C. urophthalmus* may also be related to generalized and opportunistic feeding habits (Arthington & Mitchell 1986, Galis 1998). This study evaluates the diet and morphology of a freshwater population of *C. urophthalmus* through ontogeny. The goal of this study was to determine whether freshwater *C. urophthalmus* in southern Florida experience a post-larval ontogenetic dietary shift with a concomitant shift in dietary breadth and morphology. By understanding the trophic ecology and morphology of this species, we hope to elucidate one potential aspect of its invasive success.

Methods

Study site

The study site is part of the canal system of southern Florida and is located within the Big Cypress National Preserve, Monroe County (N 25.75972°, W 81.00250°). This area is a freshwater cypress *Taxodium distichum* swamp. Sampling took place on a monthly basis from 24 June to 19 October 2000. The width of the canal varies from about 4 to 10 m and the depth to about 2 m. It is characterized by clear, slowly flowing water, and by a cement bed overlain with shells, sand, silt, and detritus. It consists mostly of a large mid-channel, open water region with minimal ledge along the banks. Many species of algae and plants, emergent and submergent, native and exotic, inhabit the canal along the bank and in both shallow and deep water.

We collected 204 fish, including 136 juveniles and 68 adults, from 12:00 to 18:00 hours using hook and line angling, minnow traps, and dip nets. The standard lengths of these fish ranged from 17 to 181 mm, and we considered all individuals greater than 102 mm SL adult (Caso Chávez et al. 1986, Martinez-Palacios & Ross 1992, Martinez-Palacios et al. 1993, Faunce & Lorenz 2000). Fish were euthanized by an overdose of tricaine methanesulfonate (MS-222), the abdominal cavity injected with 10% buffered formalin, and placed on ice. Upon return to the laboratory we removed the visceral mass, containing the digestive tract, placed it in a solution of 10% buffered formalin for a period of 2 weeks and then transferred it to a solution of 70% ethanol. The contents of the entire alimentary canal were examined under a dissecting microscope and prey organisms present in the stomach identified to the level of order whenever possible. We recorded prey abundance as percent frequency of occurrence. This measure shows how many fish contained a given prey type and is not cumulative, so the values are not additive (Caso Chávez et al. 1986).

Morphometrics

Dissection of the feeding apparatus involved excision of the lower pharyngeal jaw (LPJ) and upper pharyngeal jaw (UPJ), the maxilla and premaxilla, and the entire mandible. We cleaned the LPJ in a sonicator with 10% sodium hypochlorite solution and then allowed it to dry. The following 10 morphometric measurements were taken on each fish using calipers (Figure 1): standard length, maximum body depth, head length, snout length, mandibular length, maxillary length, premaxillary ascending and descending process lengths, pectoral fin length, and gape width (Hambright 1991, Huskey & Turingan 2001).

Lower pharyngeal jaw dry mass was weighed (Mettler balance). Mass was used as an index of robustness for the LPJ. Finally, we examined molariform teeth on the LPJ and dichotomized the teeth of *C. urophthalmus* as either papilliform

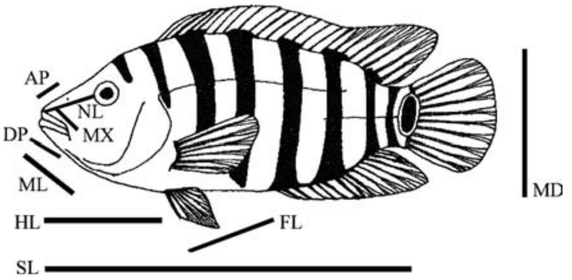

Figure 1. Diagram of Mayan cichlid,*Cichlasoma urophthalmus*, showing morphometric measurements taken. Gape width is not shown because it was measured anteriorly. SL = standard length, MD = maximum depth, HL = head length, NL = snout length, ML = mandibular length, MX = maxilla length, AP = length of ascending process of premaxilla, DP = length of descending process of premaxilla, and FL = pectoral fin length.

(small, slender, and cuspidate) or molariform (large, smooth, and rounded, with width at least as great as height). The papilliform teeth were located toward the periphery of the LPJ, whereas the molariform teeth were near the center. We observed some intermediate teeth at the interface between the center and periphery of the LPJ, and classified them as either papilliform or molariform. Using digitized images of the LPJ from a dissection microscope and a Sanyo CCD video camera (model VDC-2524), we recorded the number and area of LPJ molariform teeth using SigmaScan Pro 4.01 (SPSS Science).

Data analysis

We used the Jaccard Similarity Index to compute the percent dietary similarity between the juvenile and adult life stages, as well as between the first and last quartiles of fish by size (Ludwig & Reynolds 1988). We used the z-test to compare the percent frequency of occurrence for individual food items between juveniles and adults (Glantz 1997). We evaluated dietary richness and morphology through ontogeny by linear regression to determine whether these dependent variables followed an isometric or allometric growth pattern. We plotted the dependent variables of morphology and dietary richness against the independent variable of standard length (SL), which was used to represent ontogenetic growth. The one-dimensional dependent variables (length) were plotted directly against SL. However, we $\log_{10}$ transformed two-dimensional (area) and three-dimensional (mass) variables in order to plot them against $\log_{10}$ SL (Zar 1996, van Snik et al. 1997). A single-factor ANOVA tested the association between standard length and the dependent variables, and a *t*-test was used to test for significant departure from the expected slope (Montgomery et al. 2001). The statistical programs used were SigmaStat 2.03 and SYSTAT 10.0 (SPSS Science).

Results

Cichlasoma urophthalmus consumed a total of 33 prey types, 31 among juveniles, and 29 among adults. Only 26 prey types were common to both stages, and *z*-tests showed that only nine differed in frequency of occurrence (Table 1). The Jaccard Similarity Index indicated that dietary composition was 78.79% similar between adults and juveniles

Table 1. Results of *z*-tests comparing the frequency of occurrence between juvenile and adult *Cichlasoma urophthalmus* for all prey items.

Prey item	Juvenile (%)	Adult (%)	Statistic
Gastropoda	12.50	33.82	$z = 3.429, p < 0.001$
Hydracarina	17.65	4.41	$z = 2.411, p = 0.016$
Ostracoda	41.91	16.18	$z = 3.518, p < 0.001$
Decapoda	13.97	38.24	$z = 3.761, p < 0.001$
Hymenoptera	11.03	27.94	$z = 2.856, p = 0.004$
Caddisfly larva	21.32	7.35	$z = 2.325, p = 0.020$
Odonate naiad	10.29	29.41	$z = 3.255, p = 0.001$
Diptera adult	8.09	22.06	$z = 2.598, p = 0.009$
Beetle adult	5.88	19.12	$z = 2.688, p = 0.007$

Only items with significantly different frequencies are listed.

and 68.75% between the first and last quartiles of fish by size. Dietary richness was weakly associated with SL and showed no real change with fish length ($m = 0.0172$, $r^2 = 0.0781$, $p < 0.001$), the values ranging from 1 to 10 for juveniles and 0 to 15 for adults. Fish remained the dominant prey item by percent frequency of occurrence throughout ontogeny. Among adults (n = 68), fish was the most frequent prey (66.04%), followed by filamentous algae (44.12%), decapods (38.24%), and snails (33.82%). The snails consumed measured approximately 3 mm in length and included *Armiger*, *Cerithium*, *Melanoides*, *Physella*, and *Planorbella* species. For juveniles (n = 136), fish was also the most frequent prey (63.24%), followed by ostracods (41.92%), filamentous algae (40.44%), and detritus (30.15%). Juveniles more frequently consumed Hydracarina (mites), ostracods, and Trichoptera larvae. Adults more frequently consumed snails, decapods, Hymenoptera, odonate naiads, Diptera adults, and adult beetles. Thus, *Cichlasoma urophthalmus* appears to remain a generalized predator throughout ontogeny in this Florida freshwater habitat, consuming a variety of different animals, including gastropods (snails), crustaceans, insects, and fish, as well detritus and vegetation. Only two morphological variables did not exhibit isometric growth through ontogeny ($t_{0.025,202} = 1.960$, Table 2). Total molariform tooth area exhibited positively allometric growth: the observed slope ($m_{\text{observed}} = 3.200$) was significantly greater than the expected slope ($m_{\text{expected}} = 2$, $t_0 = 8.274$). Lower pharyngeal jaw mass also exhibited positive allometry, with an observed slope ($m_{\text{observed}} = 3.343$) that was significantly greater than that expected ($m_{\text{expected}} = 3$, $t_0 = 11.679$).

Discussion

Morphological variables grew isometrically with the exception of total molariform tooth area and LPJ mass, both of which exhibited positively allometric growth (Table 2). This pattern is consistent with the general lack of dietary shift with age, although the increase in consumption of decapods and snails in adult fish may be related to the hypertrophy of the LPJ and crushing molariform tooth area. Environmental determinants of body and jaw form changes, including dentition, are widely reported for cichlid fishes (Meyer 1990, Wimberger 1991, 1992, Trapani 2003). C*ichlasoma urophthalmus* has a moderately robust pharyngeal jaw apparatus, but it does not specialize on hard prey at this southern Florida site, nor does its dietary richness change with age. Thus, its invasive success in south Florida does not appear to be

Table 2. Results of *t*-tests evaluating departure from isometric growth ($t_{0.025,\ 202} = 1.960$) for *Cichlasoma urophthalmus.*

Morphological variable	Actual slope	Expected slope	*t*-Value	Type
Maximum body depth	0.448	1.0	−32.881	Isometry
Mandibular length	0.155	1.0	−142.932	Isometry
Maxillary length	0.114	1.0	−203.699	Isometry
Descending process length	0.104	1.0	−224.897	Isometry
Ascending process length	0.158	1.0	−138.684	Isometry
Pectoral fin length	0.262	1.0	−72.827	Isometry
Head length	0.311	1.0	−57.138	Isometry
Snout length	0.159	1.0	−139.555	Isometry
Gape width	0.103	1.0	−228.349	Isometry
Molariform tooth number	0.170	1.0	−118.502	Isometry
Log_{10} mean tooth area	2.206	2.0	−119.348	Isometry
Log_{10} largest tooth area	2.397	2.0	−51.012	Isometry
Log_{10} total tooth area	3.200	2.0	8.274	Positive allometry
Log_{10} LPJ mass	3.343	3.0	11.679	Positive allometry

Thus, computed *t*-values greater than 1.960 indicate growth that is significantly different from expected. We computed slopes for simple linear regression for all of the morphological variables versus standard length through ontogeny. We $\log_{10}$ transformed LPJ mass and mean LPJ molariform tooth area and plotted them against $\log_{10}$ SL. Only the growth rates of total tooth area and LPJ mass differed significantly from isometry.

related to ontogenetic morphological shifts or dietary specialization. Rather, *C. urophthalmus* appears to be like most successful invasive species in that it is a dietary generalist (Arthington & Mitchell 1986, Fox & Fox 1986, Nix & Wapshere 1986, Swincer 1986).

At the taxonomic levels used in the present study, *C. urophthalmus* was found to prey heavily on fishes and filamentous algae throughout its life and to experience some ontogenetic dietary shift from ostracods to gastropods, decapods, Hymenoptera, and adult Diptera at Big Cypress National Preserve, Florida. Comparing its diet in Florida to that of its native Mexico reveals that this species appears consistently to prefer the same general suite of prey items despite its dietary flexibility. At Terminos Lagoon in Mexico, the most frequent prey items for juvenile *C. urophthalmus* ($n = 50$) are detritus (100%) and crustacean remains ($\sim$72%), and for adults ($n = 112$), detritus (100%), crustacean remains ($\sim$60%), and vegetation ($\sim$52%) (Caso Chávez et al. 1986). Such ecological consistency between the native and introduced range of a nonindigenous fish appears to be typical (Faunce & Paperno 1999, Weyl & Hecht 1999, Bøhn & Amundsen 2001). However, despite the general similarity between the two regions, the fish in Florida have undergone a pronounced niche shift from their native range. Whereas the most important item in Mexico is detritus, in Florida its diet is dominated by fish and includes snails, probably due to greater availability (Hickley et al. 1994, Nunes Godhino et al. 1997, Nordstrom 1998, García-Berthou & Moreno-Amich 2000). This dietary flexibility of *C. urophthalmus*, which permits it to capture and process prey ranging from fish to gastropods, may be one aspect of this species' ability to colonize new habitats. The successful and rapid colonization of *C. urophthalmus* in south Florida might in part be related to its generalized and opportunistic feeding habits and morphology.

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