

# Food web overlap among native axolotl (*Ambystoma mexicanum*) and two exotic fishes: carp (*Cyprinus carpio*) and tilapia (*Oreochromis niloticus*) in Xochimilco, Mexico City

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**Abstract** Two exotic fishes, common carp (*Cyprinus carpio*) and tilapia (*Oreochromis niloticus*), were introduced more than 20 years ago into Xochimilco for aquaculture, and now dominate the system in terms of biomass and numbers. Over this same period, wild populations of the microendemic axolotl salamander (*Ambystoma mexicanum*) have been dramatically reduced, and it currently persists in isolated areas of this aquatic system, which is situated at the edge of Mexico City. In this study, we examine potential trophic interactions and niche overlap among two exotic fishes: carp and tilapia, and the native axolotl. Axolotl had more diverse diets and a higher trophic position compared to the exotics. Stable isotope analysis revealed substantial trophic niche overlap among axolotl and the exotics. The two exotics occupied a larger niche area than the axolotl, suggesting higher levels of omnivory and diet specialization. Current exotic fish removal efforts

will further our understanding of interactions between the axolotl and exotic species, and are expected to benefit axolotl recovery efforts.

**Keywords** Isotopes · Gut contents · Urban lake · Salamander · Food web niche

## Introduction

Food web studies are useful for understanding changes in freshwater ecosystems caused by exotic species. Networks of predator–prey interactions play a central role in influencing population dynamics and community structure in diverse ecosystems (Paine 1966; Lynch 1979; Pringle and Hamazaki 1998; Hargrave et al. 2006; Vander Zanden et al. 2006a). Once established, exotic species can have major impacts on aquatic biodiversity (Li et al. 1999), as well as the ecosystem services humans derive from aquatic ecosystems. The introduction of exotic species is increasingly common in freshwater systems (Minns and Cooley 1999), though few studies have used a food web approach to help inform and guide efforts to manage and restore invaded aquatic ecosystems (Vander Zanden et al. 2003).

Information obtained from food web studies can be particularly useful in highly perturbed aquatic systems such as Xochimilco, the last remnant of a vast wetland

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that once covered the basin now occupied by Mexico City (Alcocer-Durand and Escobar-Briones 1992). As the city has grown, Xochimilco has been dramatically impacted by human activities, which has been detrimental to native species such as the axolotl (*Ambystoma mexicanum*), a neotenic salamander endemic to this system. This amphibian is listed as 'Critically Endangered' on the IUCN Red List because its population density has been dramatically reduced in recent years (Zambrano et al. 2007). In addition to axolotl, Xochimilco hosts 140 species of migratory birds (Stephan-Otto 2005) and two other organisms endemic to Central Mexico, the Goodeid fish *Gyrardinichthys viviparus* and the crayfish *Cambarellus montezumae*, which occur in low numbers in Xochimilco (Alvarez and Rangel 2007).

The dramatic decline of the axolotl could be related to the presence of two exotics: common carp (*Cyprinus carpio*) and tilapia (*Oreochromis niloticus* and very few *O. aureus*), which were introduced to Xochimilco ~20 years ago as part of an aquaculture program. Their high reproductive rates and the lack of an established fishery resulted in a sharp population increase over the last 10 years (Zambrano and Valiente 2008). Currently, these species make up more than 98% of the vertebrate biomass of the system (Valiente 2006). Recently, 20 fishermen were hired to remove carp and tilapia from this system. Approximately 7.5 tons per week were harvested over a period of several months between 2006 and 2008 (Zambrano and Valiente 2008).

The ecological effects of carp and tilapia introductions have been documented since the beginning of the last century (Cahn 1929). Carp increase water turbidity by sediment resuspension, changing the dynamics of shallow lakes (Zambrano et al. 2001). Similarly, tilapia reduce water quality (Figueredo and Giani 2005) as well as the abundance of native species (Canonico et al. 2005). The feeding habits of both carp and tilapia have been intensively studied because both are important aquaculture species. Carp are mainly benthivorous, whereas tilapia are omnivorous, eating mostly detritus and primary producers. There are no studies of axolotl diets in the wild, though in captivity, axolotl feeds mainly on zooplankton, insects and small fish (Brothers 1977). In addition to altering trophic pathways, there could be diet overlap between exotic and native species, resulting in diet and habitat shifts (Persson and

Greenberg 1990; Werner and Hall 1977) with potentially negative consequences for native species (Chase et al. 2002; Petern and Case 1996).

Gut contents and stable isotopes of nitrogen and carbon are increasingly used to describe food web structure for aquatic ecosystems (Peterson and Fry 1987; Hecky and Hesslein 1995; Vander Zanden et al. 2006a). With both techniques it is possible to characterize the food web structure and the trophic linkages among native and exotic species (Vander Zanden et al. 1999). It is possible that the feeding habits of both carp and tilapia could reduce the resources available to axolotl. Trophic niche overlap may reduce the viability of the axolotl population and partially explain their dramatic decline. The information obtained by this food web characterization can be used to generate a better understanding of the linkages between exotic and native species within food webs, which has potential implications for ongoing restoration efforts aimed at supporting native species such as the endemic axolotl.

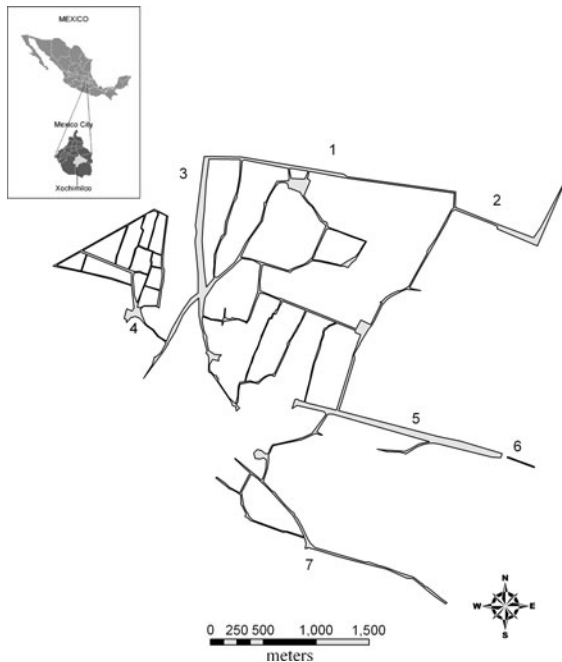
## Methods

### Study site

Xochimilco is a high altitude water body situated at 2,220 m above sea level. Its current state is a product of centuries of land use management, resulting in 207 km of canals, eight small lakes and two seasonal wetlands (Fig. 1). Before the 1950s, the system was fed by springs, but now Xochimilco is mainly recharged by treated and untreated wastewater as well as precipitation, which occurs in the rainy season from June to October (Jiménez et al. 1995). These hydrological alterations were the result of groundwater pumping, canal dredging, wastewater inputs and urbanization (Crossley 2004). At present, a slow current (<4 m/h) moves through the system from south (where sewage treatment plant outputs and natural springs are located) to north, which is the site of the biggest sewage outflow in Mexico (Gran Canal, Zambrano et al. 2009).

### Sampling

Organisms were sampled in Xochimilco from September of 2002 to October 2008 (Fig. 1). Fish and



**Fig. 1** Map of Xochimilco canals and lakes. 1 Bordo, 2 Japon, 3 Cuemanco, 4 El Toro, 5 Apatlaco, 6 Urrutia, 7 Nativitas

axolotl were collected using cast nets. Each cast net throw was counted to estimate catch per unit effort (CPUE). To obtain biomass density we extrapolated the area sampled by the cast net to the total area of the canals (Zambrano et al. 2007). Organisms were sampled in at least 20 canals each year, and there were at least 300 throws per year. Stomach contents were collected from September of 2002 to October of 2003, for axolotl (number of organisms sampled ( $n$ ) = 11; size average = 18.6 cm; size SD = 4), carp ( $n$  = 65; size average = 20.64 cm; size SD = 5.76) and tilapia ( $n$  = 79; size average = 19.9; size SD = 4.37). Isotopes samples were collected in April–May of 2003, June of 2004 and October 2005.

The three species were sampled for gut content and stable isotope analyses. Gut contents from exotic fishes were obtained by dissecting the complete digestive system. For axolotl, gut contents were sampled using gastric lavage, allowing the animals to be released unharmed. Each gut sample was fixed with 70% alcohol and analyzed with a stereoscopic microscope in a Petri dish divided into 136 squares. The percentage of squares occupied by each item was measured, using the same volume to avoid over-counting (Amundsen et al. 1996). Items were

classified into different categories: (1) particulate organic matter (POM), such as detritus and unidentified matter, (2) roots, seeds, and leaves from plants, (3) filamentous algae, (4) zooplankton, including daphnia and rotifers, (5) small crustaceans, such as amphipods (i.e. *Hyallela*) and isopods (i.e. *Caesidotea*), (6) chironomids, (7) Hemiptera larvae, (8) unidentified insects, (9) other invertebrates, such as leeches and snails, (10) axolotl eggs, and (11) fish scales and bones.

Stable isotope analysis was performed on muscle tissue of the three vertebrate species. A total of 30 samples of primary consumers (zooplankton, *Hyallela* and chironomids) were collected throughout the whole system to serve as a baseline for estimating trophic position and benthic reliance. A total of 128 fish and invertebrate samples were dried and ground into fine powder with a mortar and pestle, packed in tin capsules and analyzed for nitrogen and carbon isotope signatures using continuous flow isotope ratio mass spectrometry (20-20 mass spectrometer: Europa Scientific. Sandbac. UK). Isotopic ratios were expressed in standard delta ' $\delta$ ' notation.

#### Data analysis

We estimated the trophic position and benthic reliance of the three focal species using both stable isotope and gut content methods. The  $\delta^{15}\text{N}$  baseline was defined as the mean  $\delta^{15}\text{N}$  value of the three main primary consumer taxa in the system: *Hyallela*, chironomids and zooplankton. Trophic position was estimated assuming a per-trophic level fractionation of 3.4‰, using the equation of Vander Zanden et al. (2006b). We classified gut content items into three trophic categories: primary producers such as algae, seeds and roots (trophic level 1), primary consumers such as zooplankton, small crustaceans, chironomids and *Hyallela* (trophic level 2), and secondary consumers such as fish scales, hemiptera insects and leeches (trophic level 3). A handful of prey items of unknown trophic position were left out of the analysis (<6% of the items). The trophic position of each individual was calculated as the average trophic level of the prey items contained in the stomach, weighted according to the contribution to total stomach volume. We compared trophic positions among the three species obtained using the two techniques using non-parametric Kruskal–Wallis tests.

Benthic reliance was estimated from  $\delta^{13}\text{C}$  data using a two end-member mixing model (Vander Zanden et al. 2006b). The benthic-end member was *Hyalella*, while the pelagic end-member was the mean value of chironomids (which feed on particulate-matter/detritus) and zooplankton. Gut contents were used to estimate benthic reliance by classifying prey into the following categories: pelagic (zooplankton, chironomids, and algae) and benthic (insects, *Hyalella*, terrestrial seeds, POM). Items that could not be classified as benthic or pelagic comprised a small fraction of overall gut volume and were left out of the analysis. We compared benthic reliance among species using ANOVA for isotope data and non-parametric Kruskal–Wallis tests for gut content data.

Community niche analysis using  $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$  bi-plots (Layman et al. 2007) was used to compare trophic niche partitioning among the three species. Originally, this technique evaluates the trophic niche area of a community using isotopic distances among species in a two-dimensional  $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$  space (Layman et al. 2007). We adapted the technique to evaluate the trophic niche of individual species instead of for communities. Thus, this approach measures a species' trophic niche based on values such as nitrogen range (NR), carbon range (CR) and total niche area (TA) of axolotl, and compares them to those of carp and tilapia, rather than comparing whole food webs from different sites. NR represents the difference between the highest and lowest  $\delta^{15}\text{N}$  of each species, indicating the capacity of the species to consume organisms occupying different trophic levels. CR is the distance between the highest and lowest  $\delta^{13}\text{C}$  of each species, indicating the variability of food sources consumed by the species. TA represents the trophic niche area for a species, estimated as the convex hull area in the bi-plot (Layman et al. 2007).

## Results

Tilapia comprised more than 77% of the vertebrate biomass sampled, followed by carp (21%) and axolotl (0.5%). These data were obtained from the axolotl sampling program between 2002 and 2004 (Valiente 2006). Tilapia catch increased dramatically during the early years of this study, followed by a rapid decline in abundance, which corresponds with the exotic fish reduction program (Fig. 2). Carp exhibited

little change in abundance, while axolotl exhibited a dramatic population decline over this period.

Gut content analysis revealed that axolotl had the highest frequency of empty stomachs (16.7%), followed by carp (6.6%) and tilapia (1.2%). Diets differed among species, with axolotl consuming a wider variety of items than either of the exotic fishes (Table 1). The most important preys in axolotl diets were insects and fish. Almost half of carp's diet was comprised of primary producers, but their diet also includes axolotl eggs. Particulate organic matter and primary producers dominated tilapia diet.

Benthic reliance estimated using gut contents shows that all three species are more reliant on benthic resources compared to pelagic resources (Fig. 3a). Axolotl and carp were significantly less reliant on benthos compared to tilapia (Table 2). Estimates of benthic reliance based on stable isotopes did not yield a significant difference among species.

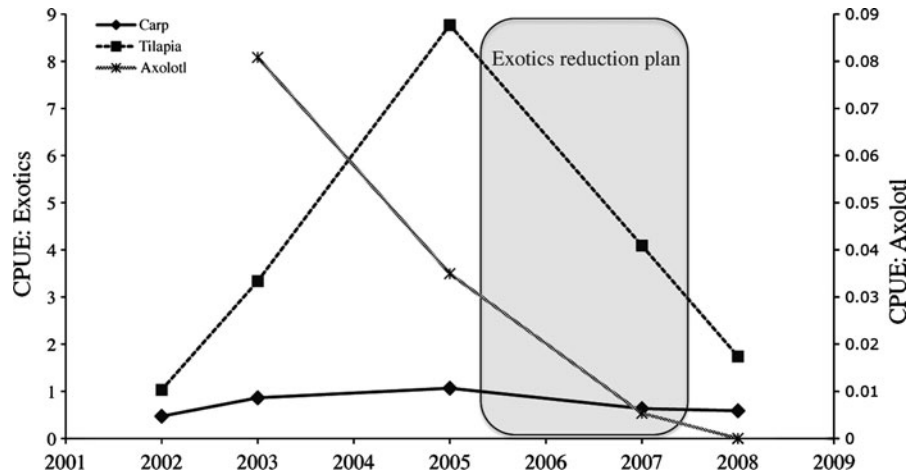
Gut contents and stable isotopes produced more consistent results for comparison of trophic position. Axolotl occupy the highest trophic position of the three species and were significantly different from tilapia based on isotope signatures and significantly different from both exotics based on gut contents (Table 2). Carp trophic position was slightly below that of axolotl, while tilapia were almost one trophic level below axolotl (Fig. 3b).

The bi-plot comparing trophic niche areas and food web metrics of the three species reveals substantial overlap in niche space (Fig. 4). The area occupied by axolotl coincides entirely with both exotic species. Carp exhibit higher  $\delta^{15}\text{N}$ , while tilapia tend to have more enriched  $\delta^{13}\text{C}$ . All three of the trophic niche measures (NR, CR and TA) were higher for tilapia compared to the other species, while the axolotl had the lowest values (Table 3).

## Discussion

Two exotic fishes, carp and tilapia, have been highly successful in Xochimilco. Carp generally invade temperate habitats, whereas tilapia invade tropical regions (Zambrano et al. 2006). Xochimilco is one of the few subtropical locations in which the two species co-exist (Mercado-Silva et al. 2008). The combination of these two exotic species has had a dramatic impact on this aquatic system. The effect of these

**Fig. 2** Catch-per-unit-effort (CPUE) for carp, tilapia, and axolotl. Note the different axes for the two exotic fishes and axolotl



**Table 1** Gut content analysis for axolotls ( $n = 12$ ), carp ( $n = 76$ ) and tilapia ( $n = 85$ )

Item	Axolotl		Carp		Tilapia	
	Area	%	Area	%	Area	%
POM	0.64	13.50	19.27	27.10	93.05	71.08
Plants	0.65	19.52	23.87	43.98	25.66	20.01
Filamentous algae	0.12	6.25	3.96	5.62	10.37	5.78
Zooplankton	0.08	4.28	5.58	5.64	0.36	0.72
Small Crustaceans	0.30	15.05	4.13	2.65	0.07	0.13
Chironomids	1.11	19.63	6.03	6.60	0.51	2.09
Hemiptera larvae	0.00	0.00	0.01	0.01	0.00	0.00
Unidentified insects	0.25	11.18	3.21	5.26	0.03	0.10
Other invertebrates	0.18	3.29	0.02	0.04	0.01	0.02
Axolotl eggs	0.00	0.00	0.21	1.24	0.00	0.00
Other fish	0.25	7.29	0.53	1.86	0.09	0.09
TOTAL	3.59	100.00	66.81	100.00	130.13	100.00

Area refers to the number of filled squares in the Petri dish (see “Methods”), and % refers to the percentage of the total gut contents’ area occupied by each item. Organisms with empty stomach are not included

POM particulate organic matter

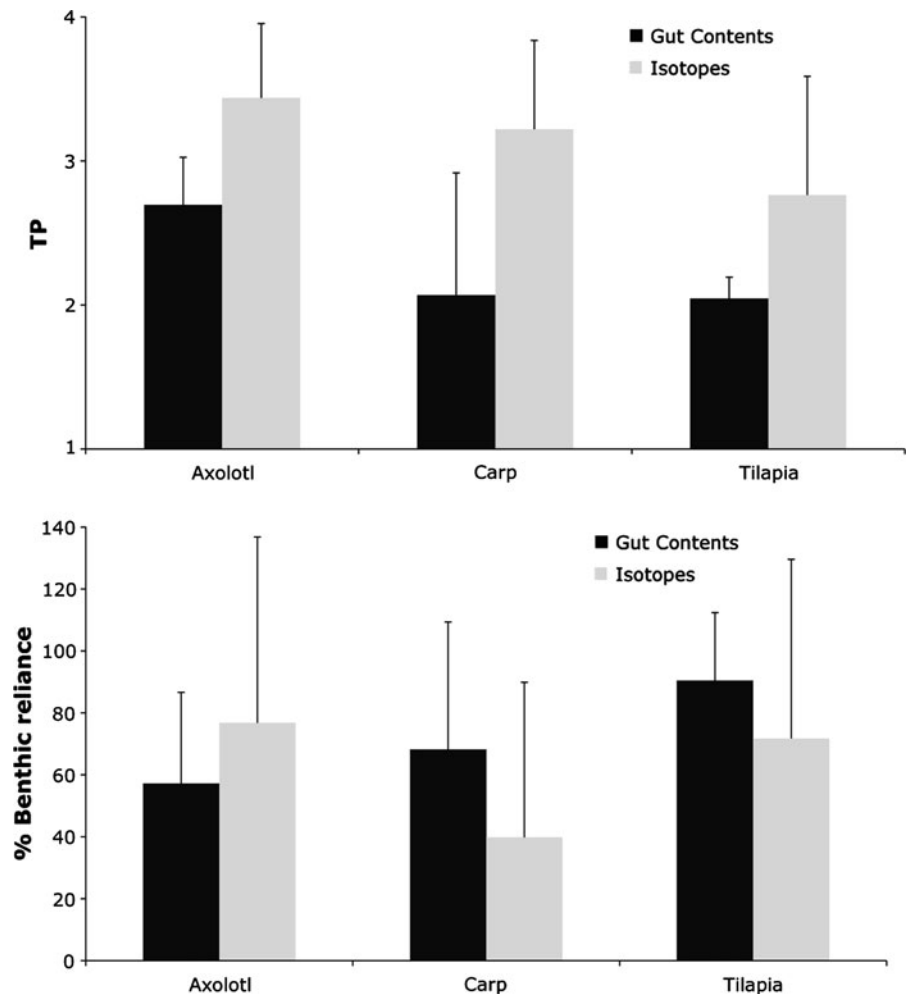
exotic fishes on Xochimilco appears to be focused at the base of the food web because tilapia have the lowest trophic position, followed by carp. The dramatic increase in their abundance in recent years has the potential to reduce the quality and quantity of food sources. Theoretical work indicates that food

web stability is reduced in the absence of basal resource diversity (Rooney et al. 2006). Empirical studies of food webs such as this help to bridge the gap between theoretical studies, and our understanding of the trophic pathways supporting higher trophic levels in natural aquatic ecosystems.

Axolotl were found to occupy the highest trophic position among the species studies. This is not surprising, as in captivity they only feed on moving organisms such as fish, insect larvae and oligochaetes (Valiente 2006). These same items accounted for a significant percentage of their diet in Xochimilco. Higher  $\delta^{15}\text{N}$  values confirm the elevated trophic position of axolotl. The uniformity of their diet in both captive and wild populations, even given the potentially reduced prey availability in Xochimilco, suggests that axolotl lack plasticity in their feeding habits. This lack of flexibility in feeding makes the salamander particularly vulnerable to ecosystem changes or the introduction of exotics with similar food preferences.

Our approach of comparing species’ trophic niches has potential to help elucidate interactions among native and exotics species. The highly omnivorous nature of these two exotic fishes (Huchette et al. 2000; Zhao et al. 2000) is evident from the trophic niche analysis. The high NR, CR, and TA values of exotic fishes indicate broad diets relative to axolotls. This is consistent with the role of axolotl as predators, which tend to have less variable diets than consumers at lower trophic positions (Hecky and Hesslein 1995). Gut content data may not fully capture the extent of omnivory, since they only provide a snapshot of

**Fig. 3** Trophic position (*TP*) and benthic reliance of axolotl, carp and tilapia. *Error bars* indicate 1 standard deviation. Comparisons are shown in Table 2



consumer diet, while the stable isotopes integrate over a longer time period. This highlights the complementary nature of these two approaches for elucidating food web relationships. Furthermore, a common diet item for carp and tilapia, particulate organic matter (POM), may be diverse in origin. Therefore the high proportion of POM in gut contents of tilapia and carp may also help explain the high TA values for these species, as POM may be comprised of material from diverse origins.

Based on a recent axolotl population viability analysis (PVA), a slight reduction in axolotl egg and larval survival rates increases extinction probabilities (Zambrano et al. 2007). Considering the observed carp abundances in Xochimilco, and that axolotl eggs were found in more than 10% of carp stomachs, it is possible that carp is causing a significant reduction in

the salamander population growth rate. The fact that axolotl population declines correspond with increases in carp abundance supports this possibility.

Exotics can also have indirect effects on aquatic systems by increasing water turbidity. Carp increase turbidity in shallow systems by re-suspending sediments in the water column (Avnimelech et al. 1999; Persson and Svensson 2006; Webster et al. 2001), while tilapia may increase turbidity through cascading effects on zooplankton and phytoplankton abundances (Okun et al. 2008). Another factor that could cause sediment resuspension is the traditional “poling”, in which a long pole is pushed into the sediment to move the boat. This activity may increase turbidity, but is concentrated in a small number of tourist areas. In most of the canals, boats are rare compared to carp and tilapia. An increase in turbidity not only

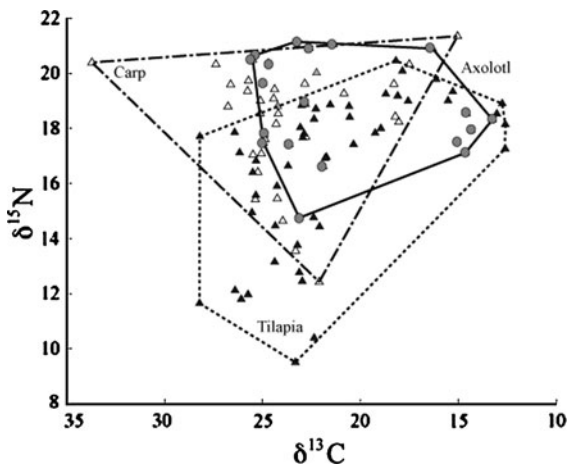


**Table 2** Trophic position and benthic reliance comparisons among axolotl, carp, and tilapia

	Kruskal–Wallis			Mult. comp. test	
	<i>H</i>	<i>df</i>	<i>P</i>	<i>Q</i>	<i>P</i>
Trophic position based on gut contents	18.9	2	<0.001		
Axolotl vs. Tilapia				4.21	<0.05
Axolotl vs. Carp				3.85	<0.05
Tilapia vs. Carp				0.738	NS
Trophic position based on isotopes	12.94	2	<0.01		
Axolotl vs. Tilapia				3.249	<0.05
Axolotl vs. Carp				0.881	NS
Tilapia vs. Carp				2.576	<0.05
% Of benthic reliance based on gut contents	26.19	2	<0.001		
Axolotl vs. Tilapia				3.54	<0.05
Axolotl vs. Carp				4.17	<0.05
Tilapia vs. Carp				1.54	NS
	<i>F</i>	<i>df</i>	<i>P</i>		
% Of benthic reliance based on isotopes	0.965	2	NS		

*Q* value refers to Dunn’s multiple comparison test

*NS* not significant



**Fig. 4** Trophic niches of axolotl, carp and tilapia (Layman et al. 2007). Each symbol (triangle or circle) is an individual from one of the three species. Enclosed areas represent the total trophic niche occupied by each species. The single line enclosing grey circles represents axolotl, the dashed line with dots enclosing white triangles represents carp and the dotted line enclosing dark triangles represents tilapia

decreases overall productivity, but also shifts the system from having multiple resource pathways (benthic and pelagic) to having only a few, in this case, dominated by a detritus-based benthic pathway. Recent theoretical work indicates that simplification

**Table 3** Trophic niche variables estimated for each species, based on Layman et al. (2007)

	Axolotl	Carp	Tilapia
NR	6.39	8.91	10.93
CR	12.24	18.67	15.61
TA	53.14	79.79	105.55

See “Methods”

*NR* nitrogen range, *CR* carbon range, *TA* total area

of the food web in this way may have important implications for food web dynamics and stability (McCann et al. 1998; Vadeboncoeur et al. 2005).

Food web studies can provide useful information regarding energy fluxes within an ecosystem. Theoretical research suggests that changes in food webs could lead to modifications in community structure in aquatic ecosystems, but there is little empirical understanding of the trophic pathways involved, or the impact of exotic species (Vander Zanden et al. 2006b). A critical aspect of this study was to assess the trophic niches of two successful exotics and one endangered native species in a highly perturbed system. This perspective allowed us to examine possible consequences for the trophic pathways in the system, and the consequences for axolotl populations.

The current restoration program for the axolotl includes a long-term exotic species removal program, with the goal of promoting favorable food web conditions for the axolotl by expanding trophic diversity at the base of the food web. To date, intensive carp and tilapia removal has not halted the decline of axolotl, and there may be time lags in ecosystem-level changes. In addition, other factors may be contributing to the decline of axolotl such as poor water quality (Contreras et al. 2009). Though exotic species removal is likely to be helpful, additional strategies are also needed and would likely include establishing exotic-free areas as axolotl refuges.

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