SHALLOW LAKES

Stable isotope variation of a highly heterogeneous shallow freshwater system

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Abstract Food web structure is well known to vary widely among ecosystems. Recent research indicates that there can be a high degree of spatial heterogeneity within ecosystems as well. Xochimilco is a small heterogeneous freshwater system that has been transformed into a network of canals, small lakes, and wetlands. Located within Mexico City, this ecosystem has been intensively managed and highly impacted for more than 50 years. This system receives urban and agricultural runoff, with resulting impacts on water quality. The aquatic community is dominated by exotics such as carp (*Cyprinus carpio*) and tilapia (*Oreocrhomis niloticus*), though the system still supports endemic species such as the aquatic salamander, axolotl (*Ambystoma mexicanum*), and crayfish (*Cambarellus montezumae*), which are both endangered. In this study, we used carbon and nitrogen stable isotopes for the whole food web and gut content analysis from the exotic fishes to describe food web structure in different canals within Xochimilco. There were significant isotopic differences among canals. These differences may result from isotopic baseline differences as well as differences in actual food web structure: both are related to local spatial variation in water quality driven by nutrient inputs and exotic fishes. Within-ecosystem variability is likely to be seen in other perturbed shallow systems as well, and should be explicitly considered in future food web studies.

Keywords Exotic fish · Carp · Isotopes · Tilapia · Urban lake · Xochimilco

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Introduction

Environmental heterogeneity affects species distribution in freshwater systems by generating patchy environmental conditions and resource availability (Questad & Foster, 2008). This has been well described at the among-system scale, in which site attributes such as depth, nutrient status, and turbidity are related to fish community composition and trophic structure (Tonn & Magnuson, 1982; Magnuson et al., 1998; Jackson et al., 2001; Zambrano et al., 2006). In recent studies, spatial heterogeneity has been found to

affect ecological processes at finer scales (Vanbergen et al., 2007). Environmental conditions can differ widely within a system (Zambrano et al., 2009), and as a result, the distribution of organisms is often limited to just a small portion of the ecosystems they inhabit (Contreras et al., 2009).

Studies of aquatic food webs have generally attempted to characterize overall food web structure of a system, without regard to finer scale spatial heterogeneity. In fact, spatial heterogeneity of environmental conditions also influences food web structure within a system at larger scales (Moore, 2004; Thompson & Townsend, 2005). For example, large rivers, lakes, and wetlands that are characterized by strong environmental gradients (depth, shoreline, water current, or climate) exhibit corresponding variation in food web structure (Cifuentes et al., 1996; Fry et al., 1999; March & Pringle, 2003; Bucci et al., 2007; Abrantes & Sheaves, 2008). The relationship between environmental drivers and food web structure at finer scales (within-lake in small areas) is not well understood, but has important bearing on our understanding of trophic structure, and our ability to characterize it.

Xochimilco can be a useful system for evaluating food web variability deriving from environmental heterogeneity and contrasting land uses in a finer scale. This water body used to be part of a system of five shallow lakes that covered the whole Mexican Valley (more than 470,000 ha). The aquatic system has been reduced to approximately 3,000 ha, and now is the last remnant of the former lake system. The ecosystem has been transformed into a network of canals, small lakes, and wetlands, the product of centuries of land use management. It is located on the southern edge of Mexico City, which has more than 18 million inhabitants. During the last century, this system has undergone major hydrological alterations resulting from groundwater pumping, canal dredging, and wastewater inputs from green houses and from urbanization (Crossley, 2004). Water quality has declined in the last three decades, mainly as a result of the shift toward intensive greenhouse agricultural production (López et al., 2006; Méndez, 2006). This diversity of local land uses and anthropogenic impacts produces a high degree of spatial variability in abiotic conditions (Zambrano et al., 2009).

Despite these impacts, this system is still of tremendous ecological value. Xochimilco hosts 140 species of migratory birds (Stephan-Otto, 2005);

Cambarellus montezumae, an endemic crayfish species from the High Plateau; and the last remaining population of an aquatic salamander species, the axolotl *Ambystoma mexicanum* (Zambrano et al., 2007). Exotic species such as carp (*Cyprinus carpio*) and tilapia (*Oreochromis niloticus*) were introduced more than 20 years ago and are now the most abundant fishes, comprising more than 95% of the vertebrate biomass of the system (Valiente, 2006). Consequently, axolotl abundance has declined sixfold over a 5-year period (Zambrano et al., 2007) surviving only in isolated areas (Contreras et al., 2009). Native crayfish, once widespread, can now only be found in a small number of locations (Alvarez & Rangel, 2007). These locations have higher transparency and lower nutrient concentrations (Contreras et al., 2009). Recent samples suggest that these isolated areas have a higher macrophytes coverage and lower exotic fish abundance.

Gut content studies are the traditional method for characterizing trophic relationships among organisms in shallow lakes. More recently, stable isotopes of nitrogen and carbon have been used to describe food web structure for aquatic ecosystems (Peterson & Fry, 1987; Hecky & Hesslein, 1995; Vander Zanden et al., 2006a). This approach allows the major pathways of energy flow through food webs to be elucidated, and has been used to characterize food web changes related to anthropogenic impacts such as invasive species (Vander Zanden et al., 1999) and habitat fragmentation (Layman et al., 2007). Use of the two approaches in conjunction provides a powerful means of characterizing food webs (Layman & Post, 2008). Gaining a better understanding of food web relationships provides a basis for guiding restoration of aquatic ecosystems (Vander Zanden et al., 2006b).

The goal of this research is to evaluate spatial differences in food web structure in Xochimilco, a highly heterogeneous shallow aquatic system. The information can be used to better understand the linkages between land use, exotic species, and water quality within a food web context.

Methods

Study site

Xochimilco is a high-altitude shallow (=1 m, mean depth) water body composed of canals connecting

small lakes and wetlands. Xochimilco includes 185 km of canals, 8 small lakes, and 2 seasonal wetlands. The system was historically fed by springs, but is now mainly recharged by treated and untreated sewage, as well as by rainwater from May to October (Jiménez et al., 1995). A small current (less than 4 m per hour, Zambrano et al., 2009) moves through the system from the south, where wastewater treatment plant outputs are located, to the north, where the biggest sewage outflow in Mexico is located. We sampled 10 canals within Xochimilco, selected to include the diversity of land uses such as urban areas, greenhouse agriculture, traditional agricultural, Olympic rowing canal, and ecological parks (Fig. 1).

Sampling abiotic variables and isotope analysis

Abiotic variables (conductivity, pH, turbidity, and dissolved oxygen) were measured monthly from 2002 to 2009 with a portable water quality meter (YSI Model 6600). Nutrient concentrations were determined immediately after collecting the water samples with a Lamothe SMART colorimeter. Nitrates were analyzed by zinc reduction, ammonia was obtained by Nesslerization, and phosphates following the ascorbic acid reduction method (APHA, 1998). Values presented are the mean of all measurements taken across years, since there were no significant differences among years (Zambrano et al., 2009).

Organisms were sampled from November 2002 to October 2005. Vertebrates (fish and amphibians) were collected using a cast net. Each throw from the cast net was counted, allowing us to estimate catch per unit effort (CPUE) for the two most important species (carp and tilapia), expressed as biomass per cast net throw. A pole net was used to collect aquatic invertebrates close to the shore where macrophytes were present.

A total of 269 organisms were sampled for stable isotope analysis from 4 plant groups and 11 animal groups. Plants were represented by phytoplankton (algae) $n = 5$; free-floating macrophytes (*Lemna* sp.) $n = 6$; rooted macrophytes (*Typha* sp.) $n = 5$; and terrestrial plants $n = 12$. Invertebrates were represented by zooplankton (Cladocera and Caecidotea) $n = 4$; *Hyallela* sp. $n = 17$; crayfish (*Cambarellus montez*umae) $n = 11$; insects (Hemiptera, Odonata, Coleoptera larvae, Corixidae larvae, Tipulidae larvae) $n = 48$; and chironomids $n = 11$, which were

considered separately because of their importance to higher consumers in the food web. Vertebrates were represented by the native aquatic salamander, axolotl (*Ambystoma mexicanum*) $n = 21$; silversides (*Menidia humboldtiana*) $n = 21$; and the exotic fishes *Goodea atripinnis* $n = 31$, carp *Cyprinus carpio* $n = 30$, and tilapia *Oreochromis niloticus* $n = 47$. We tested seasonal variation for the isotope signature of carp, tilapia, axolotl, crayfish, and odonata.

Muscle tissue was used in vertebrate samples, which has a low turnover and integrates over an extended time period (Hesslein et al., 1993; MacAvoy et al., 2001). For big invertebrates (big insects and crayfish), chitin was eliminated and internal tissues were used, whereas for small invertebrates, whole organisms were analyzed and samples were not acidified. The average of C:N for all vertebrates was 3.2 (Standard deviation = 0.2); therefore, mathematical corrections were not necessary (Kiljunen et al., 2006). All samples were dried and ground into a fine powder with a mortar and pestle, packed in tin capsules, and analyzed for nitrogen and carbon stable isotope ratios using continuous flow isotope ratio mass spectrometry (20-20 mass spectrometer: Europa Scientific, Sandbach, UK at the University of California-Davis). Isotopic ratios were expressed in standard delta "δ" notation. The mean standard error for sample duplicates was <5% in both C and N.

Gut content analysis

We used gut contents of carp ($n = 76$) and tilapia ($n = 85$) as a direct means of inferring food web differences among canals, since gut contents provide direct and high taxonomic resolution trophic information. Gut content samples were collected in all seasons during 2003; those canals for which we lacked fish samples from a season were eliminated from the analysis, and consequently, we only used six canals. Gut contents were obtained by dissecting the complete digestive system. 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 overcounting (Amundsen et al., 1996). Items were classified into the following categories: (a) particulate organic matter (POM), such as detritus and unidentified matter; (b) roots, seeds, and leaves from aquatic

Fig. 1 Map of Xochimilco showing the study area. Canal names: A = *Toro*, B = *Urrutia*, C = *Apatlaco*, D = *Nativitas*, E = *Costetexpan*, F = *Santa Cruz*, G = *Ampampilco*, H = *Bordo*, I = *Huetzali*, J = *P.Canotaje*
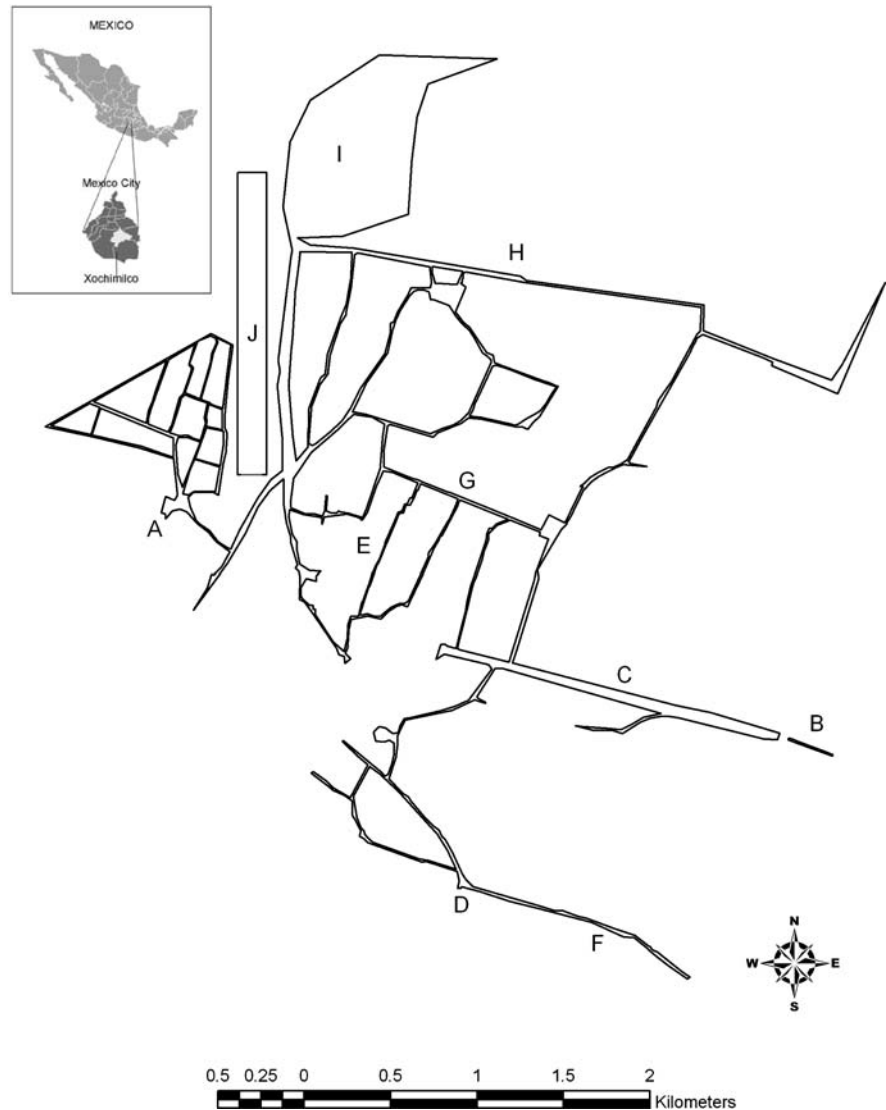
plants (macrophytes); (c) filamentous algae (algae); (d) zooplankton, including daphnia and rotifers; (e) insects; and (f) fish scales, bones, and other invertebrates such as snails.

Data analysis

Differences among canals in abiotic variables and fish densities were examined using ANOVA. Mean δ^{13}C and δ^{15}N values for each set of taxa was used to build bi-plots for each canal. To assess differences in isotope signatures among canals and species, we used all individuals in a MANOVA test. Taxa with only a single organism from a canal were excluded from

the analysis. Community niche analysis variables (Layman et al., 2007) such as distance to centroid (CD, the average distance of each set of taxa to the "center" of the food web) and total niche area (TA, the total area in food web space occupied by the set of taxa) were used to quantitatively compare food web structure among canals. Primary producers were excluded from community niche analysis because they were not thoroughly sampled from each canal.

We related these niche variables to water quality indicators, using a physicochemical index (PHQI), which is based on pH, DO, conductivity, and turbidity values, and a nutrient index (NQI), which is based on NO_3–N, NH_4–N, and PO_4–P concentrations. These

indices give numerical information by ranking values of each variable into three categories: (1) suitable conditions, (2) nonsuitable conditions, and (3) poor conditions, depending on the effect of each variable on aquatic organisms. Variables were added to form both indexes, and lower values of the indexes indicate higher water quality. These indexes were developed based on intensive water quality sampling of the area, and interpolated to generate water quality maps of the canals (see Zambrano et al., 2009).

Results

Individual canals had unique physicochemical conditions and differences were significant for most of the variables measured (Table 1). Abundances of carp and tilapia were also highly variable among canals and there was a significant canal effect (Table 1).

Sample sizes for stable isotope analysis of primary producers were generally small. $\delta^{15}N$ values for primary producers were below 14‰, though they spanned a wide range of $\delta^{13}C$ values, and were generally more enriched for floating producers. Invertebrate $\delta^{15}N$ values ranged from 14.5 to 16‰, with $\delta^{13}C$ values again occupying a broad range. Vertebrate $\delta^{15}N$ values were >15.8‰, with tilapia having the lowest values among the vertebrates. Surprisingly, crayfish $\delta^{15}N$ was higher than most of the vertebrates, and just below axolotl. A top native fish predator *Menidia humboldtiana* has the highest $\delta^{15}N$ of any taxa.

There were no significant differences among years in carbon or nitrogen for odonata, crayfish, carp, tilapia, and axolotl. There were no seasonal differences in $\delta^{13}C$ except for crayfish (average dry season = −23.65‰, average rainy season = −17.39‰; $t = 2.67$, df = 7, $P = 0.03$). Also, most taxa did not show seasonal differences in $\delta^{15}N$, except for axolotl, which were higher in the rainy season (average dry = 18.12‰, average rainy = 20.08‰, $t = 2.18$, df = 12, $P = 0.049$), and Odonata, which were higher in the dry season (average dry = 19.3‰, average rainy = 15.5‰, $t = 2.89$, df = 5, $P = 0.039$).

Although consideration of mean isotopic values (i.e., cross sites) provide a general picture of food web structure (Fig. 2), all taxa showed high variability, particularly for $\delta^{13}C$. MANOVA using both isotopes revealed significant effects of "canal" and

"taxa,", but no significant interaction (Table 2). Considering $\delta^{15}N$ alone, there was a significant effect of both canal and taxa. For $\delta^{13}C$, only the canal effect was statistically significant (Table 2).

Individual canals exhibited strong isotopic differences (Fig. 3). *P.Canotaje*, *Huetzali*, and *Bordo* canals had elevated $\delta^{13}C$ values, while the rest of the canals exhibited substantial overlap and lower $\delta^{13}C$ signatures. Niche areas were highly variable among canals; for example, one canal (*Huetzali*) had TA values five times smaller than that of the *Bordo* canal. However, CD values were more similar among canals (Table 1).

There was an inverse relationship between niche area and the nutrient-based water quality index (TA = −17.12 NQI + 205.87; $r^2 = 0.62$, $F = 8.24$, df = 6, $P = 0.035$). There was also a negative trend between niche area and tilapia abundance, though the relationship was not significant (TA = −6.8 CPUEgr + 401; $r^2 = 0.68$, $F = 6.41$, df = 4, $P = 0.08$). On the contrary, there was no relationship between food web niche variables and the other water quality index or values (PHQIvsTA: $r^2 = 0.24$, $F = 1.94$, df = 7, P = ns; NQIvsCD: $r^2 = 0.07$, $F = 0.39$, df = 6, P = ns; PHQIvsCD: $r^2 = 0.27$, $F = 2.3$, df = 7, P = ns).

Carp diet differed substantially among canals (Fig. 4). In some canals, carp feed largely on animals (i.e., *Urrutia*), while in other canals, diet was dominated by primary producers (i.e., *Bordo* and *Japon*). Sediments and macrophytes dominated tilapia diets at all canals. The importance of algae was high for both exotics in canals such as *Huetzali*, which is the most turbid canal (Table 1).

Discussion

Our results reveal clear differences in food sources and isotopic signatures among canals of Xochimilco. This ecosystem has the same type of sediment throughout, similar depth (close to 1 m), and a high degree of connectivity among canals and lakes. These characteristics would tend to result in lower spatial variation in $\delta^{15}N$ and $\delta^{13}C$ values, as observed in tropical complex lagoon–wetland–river systems (Roach et al., 2009). This is not the case in Xochimilco, where we see high spatial heterogeneity in nutrient concentrations (Solis et al., 2006; Mazari-Hiriart et al., 2008) as

Table 1 Physicochemical data and vertebrate abundances from the three areas of Xochimilco

Canal	Cond (mS cm^{-1})	DO (mg l^{-1})	pH	Turb NTU	NH$_4$ (ppm)	NO$_3$ (ppm)	PO$_4$ (ppm)	PHQI	NQI	Exotic fish CPUE	Food web niche TA	CD
Apampilco	1.38	5.41	8.40	nd	7.77	1.67	5.43	5.74	8.24	nd	60.91	2.95
Apatlaco	1.43	6.75	8.84	49.00	0.92	1.82	7.33	5.90	8.14	nd	67.75	2.65
Bordo	1.19	5.02	8.82	72.83	0.22	2.32	5.70	5.73	3.70	1.75	145.18	3.62
Costetexpan	0.88	3.77	7.64	29.05	1.86	13.04	10.17	5.10	9.00	7.48	52.16	3.36
Huetzali	1.40	14.20	8.91	120.54	nd	0.01	nd	nd	nd	4.92	33.21	3.33
Japón	1.97	5.57	8.58	42.25	4.08	4.78	4.86	nd	nd	4.26	nd	nd
Nativitas	0.66	3.13	7.40	42.53	1.59	30.38	7.57	5.51	8.17	nd	38.39	2.51
P.Canotaje	1.03	8.37	8.42	105.33	0.77	0.65	8.67	nd	nd	nd	75.15	2.54
Santa Cruz	1.33	6.55	8.66	nd	0.68	16.38	8.33	6.00	nd	nd	12.56	2.11
Toro	1.74	7.60	8.47	53.32	0.50	0.25	12.60	6.00	5.13	3.40	94.48	2.93
Urrutia	1.20	2.26	7.76	16.41	1.32	9.75	3.33	7.00	7.00	0.28	137.60	4.69
ANOVA *F* test	12.67	34.98	11.74	21.65	2.01	5.7	1.99	–	–	2.61	–	–
DF	12.00	10	10	7.00	8.00	9	8.00	–	–	6	–	–
P	<0.001	<0.001	<0.001	<0.001	0.07	<0.001	0.07	–	–	0.05	–	–

Cond conductivity, *DO* dissolved oxygen, *Turb* turbidity, *CPUE* catch per unit of effort, *PHQI* physicochemical quality index, *NQI* nutrient quality index, *TA* total food web niche area, *CD* centroid distance in the food web, *nd* no data

Fig. 2 Bi-plot showing the mean and standard deviation of $\delta^{13}C$ and $\delta^{15}N$ values, averaged across all canals
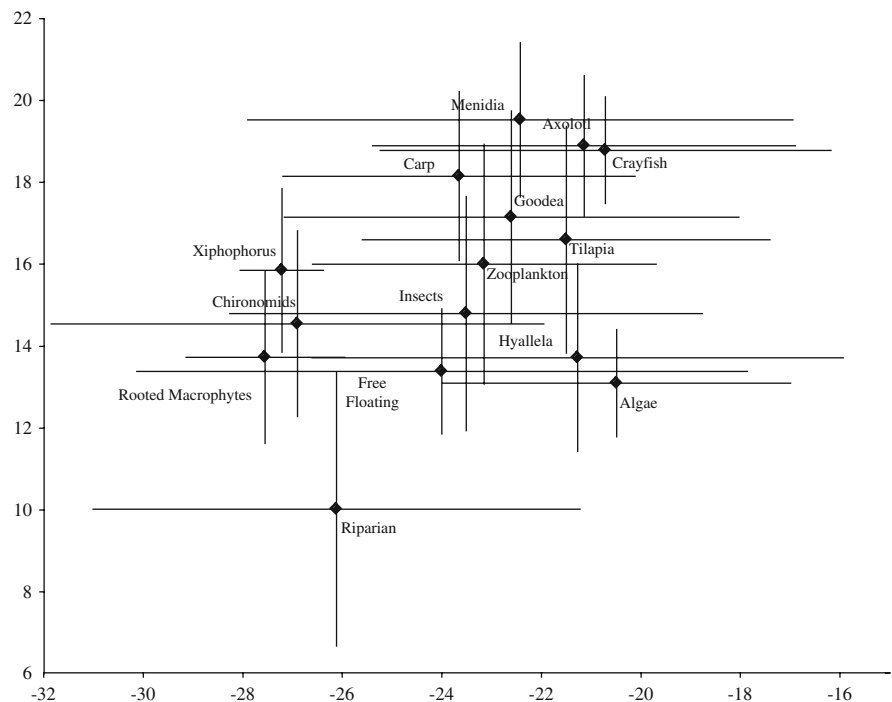
well as the distribution of exotic fishes. These variables can have major influences on aquatic community processes, and consequently, may drive variation in food web structure among canals.

Inorganic nitrogen concentrations in Xochimico's water column are high enough to be considered hypereutrophic (Zambrano et al., 2009). Correspondingly, average nitrogen isotopes values of organisms

Table 2 MANOVA and ANOVA analyses to test differences among species and canals using both isotopic signatures (δ^{15}N and δ^{13}C)

MANOVA δ^{15}N–δ^{13}C	DF	Pillai trace	F	Num DF	P
Canal	12	1.0319	15.4545	24	<0.001
Taxa	7	0.5558	9.5661	14	<0.001
Canal * Taxa	31	0.2785	0.908	62	0.671
Residuals	174				
ANOVA δ^{13}C	DF	Sum Sq	Mean Sq	F value	P
Canal	12	3047.78	253.98	26.0161	<0.001
Taxa	7	131.22	18.75	1.9202	0.06897
Canal * Taxa	31	212.63	6.86	0.7026	0.87696
Residuals	174	1698.67	9.76		
ANOVA δ^{15}N	DF	Sum Sq	Mean Sq	F value	P
Canal	12	496.33	41.36	9.3866	<0.001
Taxa	7	634.28	90.61	20.5635	<0.001
Canal * Taxa	31	160.28	5.17	1.1734	0.2569
Residuals	174				

The first section shows the MANOVA results, the second δ^{13}C ANOVA, and the third δ^{15}N ANOVA results
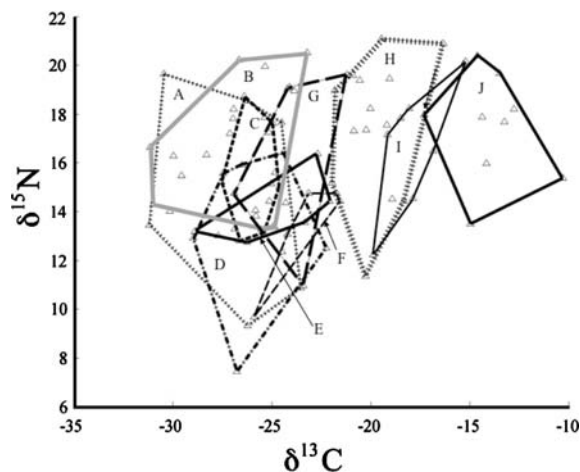


Fig. 3 Polygons encompassing the convex hull area for each sample canals in δ^{13}C–δ^{15}N niche space. Each triangle is the average value for a taxa collected from a canal. Primary producers were excluded from this analysis. Canal names: A = *Toro*, B = *Urrutia*, C = *Apatlaco*, D = *Nativitas*, E = *Costetexpan*, F = *Santa Cruz*, G = *Ampampilco*, H = *Bordo*, I = *Huetzali*, J = *P.Canotaje*

from Xochimilco are at least 10‰ higher than those sampled from less impacted systems in Central Mexico (Mercado-Silva et al., 2009). The highly elevated δ^{15}N of the biota in human-impacted Xochimilco is consistent with previous work linking elevated δ^{15}N with anthropogenic nutrient inputs to aquatic systems (Steffy & Kilham, 2004).

There were significant differences in biotic δ^{13}C among canals, though, notably there were no significant "taxa" effects in our analysis. If all organisms with the same feeding habits would obtain food from multiple base lines, they would have similar isotopic signatures, because this signature represents a mix of all items consumed. On the contrary, these organisms are consuming sources with different base lines, and they have different isotope signatures. Thus, canal-to-canal variation in δ^{13}C appears to reflect underlying biogeochemical differences among canals rather than food web differences. In other words, isotopic differences among canals may be partially attributed to baseline effects, which are independent of actual differences in food web structure among canals.

In addition to the baseline effects noted above, our analysis also detected food web differences among canals. Food web niche variables varied among canals. In particular, TA was negatively related to our nutrient index, thus suggesting a potential effect of anthropogenic nutrient inputs on food web structure itself. In this case, one can hypothesize that higher nutrient inputs reduce the diversity of the resource base, and as a result, reduce the area occupied by the food web in isotope niche space. Canals with reduced niche areas also tended to be more invaded by tilapia, suggesting a potential impact of this highly abundant and omnivorous fish
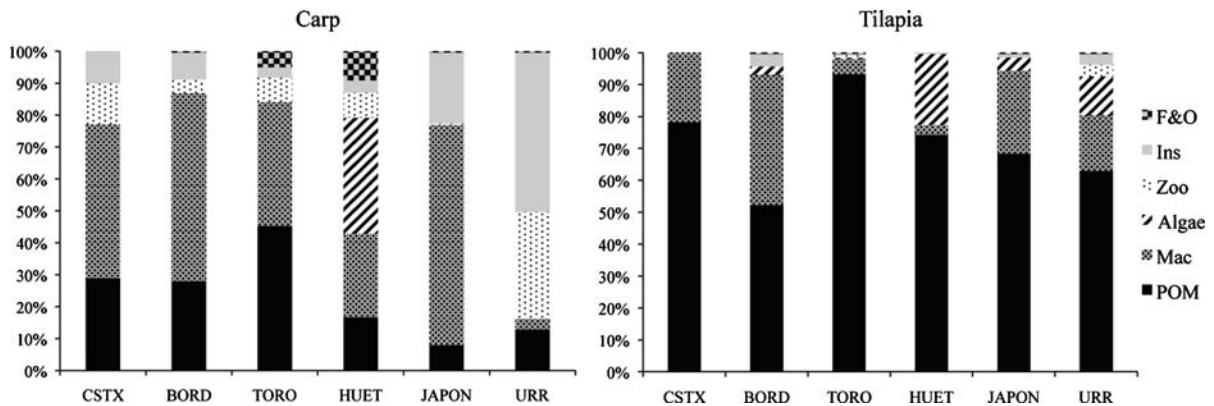
Fig. 4 Gut contents, expressed as percent of total food consumed, for the two most abundant exotic fishes in the system, carp and tilapia, from six different canals. CSTX = *Costetexpan*, BORD = *Bordo*, HUET = *Huetzali*, URR = *Urrutia*. F&O = Fish and other insects, Ins = Insects, Zoo = Zooplankton, Mac = Macrophytes, POM = Particulate organic matter

on food webs as have been seen in other tropical regions (Zaret & Paine, 1973; Ogutuohwayo & Hecky, 1991; Campbell et al., 2005). More research should be conducted to clarify which factors have higher influence on the niche space.

Seasonal environmental changes can affect isotopic signature (Douglas et al., 2005; Gu, 2009). But in systems under less variable conditions, seasonality may have a lower effect on isotope signatures. Temporal changes in Xochimilco freshwater system used to be related more to dry and wet seasons than any other variable. But modifications to its hydrology generated a constant depth in most of the canals and lakes, reducing a possible seasonal effect on organisms' isotope signatures. Significant seasonal changes were limited to just a few taxa and did not reflect major food web shifts. But they tend to affect native species, which seem to keep variations in their food habits throughout the year. Therefore, these variations must be considered in the future studies particularly for native species such as the axolotl and crayfish. Overall, spatial isotopic variability far outweighed temporal variability in this system.

Gut content analysis indicates differences in fish resource use among canals. Exotic fish at lower levels of the food web, such as tilapia, tend to exhibit higher isotopic variation compared to other species (Gu et al., 1997). In Xochimilco, all species exhibited highly variable isotopic signatures. In addition, canals with higher TA values such as *Bordo* and *Urrutia* had lower densities of exotic fishes. These canals also had more macrophytes, and our diet analysis indicated

that insects and zooplankton were more important in the fish diets. These areas are also some of the few places where native axolotl and crayfish can survive. Canals with smaller TA values had higher densities of exotics such as *Costetexpan*, and fish diets were dominated by POM.

Extreme nutrient loading, as a consequence of urban development and greenhouse agriculture (Zambrano et al., 2009), and elevated abundances of exotic fishes are likely drivers of within-system isotopic and food web variation in this system. These impacts appear to cause a reduction in the diversity of trophic pathways in the ecosystem. With the diversity of basal resources depleted, consumers' capacity to respond to changes in food quality or quantity is also reduced. This capacity is critical for maintaining the stability of a complex food web (Kondoh, 2003). Consistent with our previous findings (Zambrano et al., 2007; Zambrano et al., 2009; Zambrano et al., 2010), restoration measures should include the control or removal of exotic species coupled with nutrient and sediment reductions from urban and agricultural areas.

Stable isotope studies supported by gut content analysis can provide useful information about food web structure and energy fluxes within an ecosystem. In Xochimilco, local heterogeneity in environmental and food web properties was found to be quite high. This information can be used to highlight some of the biogeochemical and ecological differences among canals within the system, and relate them to anthropogenic impacts such as exotic fishes and the loss of water quality due to nutrient loading. This shallow

system represents an extreme case of within-system heterogeneity since it is located within one of the biggest cities in the world, though other human-impacted aquatic systems may also be characterized by this type of intrasystem heterogeneity.

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