

THE EFFECTS OF IMPOUNDMENT AND NON-NATIVE SPECIES ON A RIVER FOOD WEB IN MEXICO'S CENTRAL PLATEAU

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ABSTRACT

Habitat modifications, non-native species and other anthropogenic impacts have restructured fish communities in lotic ecosystems of central Mexico. Conservation of native fishes requires understanding of food web changes resulting from the introduction of non-native species, flow alteration and other human impacts. Using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of fishes and invertebrates we investigated the effects of non-native species, and reservoirs on food webs of the Laja river ecosystem (Guanajuato, central Mexico). We estimated trophic position (TP), relative trophic niche and food web dispersion at 11 reservoir, river and tailwater sites. Reservoirs and non-native fishes modified food webs in the Laja. Food web dispersion was greater in reservoir than in tailwater and river sites. Reservoir food webs had the greatest range of $\delta^{13}\text{C}$ values, indicating a more diverse resource base compared to rivers. $\delta^{13}\text{C}$ values increased with distance downstream from reservoirs, suggesting declining subsidies of river food webs by reservoir productivity. Stable isotopes revealed potential effects of non-native fishes on native fishes via predation or competition. Non-native *Micropterus salmoides* were top predators in the system. Non-natives *Cyprinus carpio*, *Oreochromis mossambicus* and *Carassius auratus* exhibited lowest TP in the Laja but overlapped significantly with most native species, indicating potential for resource competition. Native *Chirostoma jordani* was the only species with a significantly different trophic niche from all other fish. Many rivers in central Mexico share similar anthropogenic impacts and similar biotas, such that food web patterns described here are likely indicative of other river systems in central Mexico. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS: invasive fishes; Lerma river; stable isotopes; habitat alteration; dam impacts; Mexico; exotic fishes

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INTRODUCTION

Food webs are used to depict and understand predator–prey relationships within ecosystems. Food webs can be used to help understand how an ecosystem responds to perturbation and to guide conservation of vulnerable species (Wootton *et al.*, 1996; Vander Zanden *et al.*, 2003). Two of the major drivers of ecosystem change in riverine ecosystems are altered flow regimes (Wootton *et al.*, 1996; Osmundson *et al.*, 2002) and introduction of non-native species (Vander Zanden *et al.*, 1999), but few studies have taken a food web approach to estimate their combined effects on native species.

Stable isotope analysis has become an important tool in the study of aquatic food webs because it helps identify the dominant pathways of nutrient transfers, and can be used to estimate assimilation of food resources over time (Minagawa and Wada, 1984; Peterson and Fry, 1987). Although coarse in taxonomic resolution, isotope data can reveal important feeding links among consumers and can overcome some of the difficulties associated with more traditional methods such as stomach content analysis (Jepsen and Winemiller, 2002). Stable isotope data can trace and measure energy flow pathway alterations arising from human induced ecosystem changes and guide ecosystem management efforts to conserve or restore ecosystems (Vander Zanden *et al.*, 1999, 2003).

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In freshwater ecosystems of Mexico's central plateau reservoir construction and rampant introduction of non-native species have caused native fish extirpations and population declines (Lyons *et al.*, 1998; Mercado-Silva *et al.*, 2006; Domínguez-Domínguez *et al.*, 2008). The effect of these changes on food web structure remains unknown. The Lerma river, which drains most of central Mexico, is considered one of the most degraded river basins in the country (Lyons *et al.*, 1998; Soto Galera *et al.*, 1998). Only a few isolated branches of this large system maintain environmental conditions required for the survival of a relatively intact fish fauna. The Laja River (Guanajuato, Mexico), although far from being considered pristine, is one such tributary (Soto Galera *et al.*, 1998) and has been proposed as representative of the general trends occurring in fish communities in central Mexico (Mercado-Silva *et al.*, 2006). The study of its food webs could help understand how modification of flow regimes and the introduction of non-native species could affect other river systems in the region. Further, this information could help ongoing conservation and restoration efforts in the river.

Our objective is to use stable isotopes to characterize effects of non-native species and reservoirs on food webs of the Laja River ecosystem. Knowledge of this food web is needed to integrate sound watershed management strategies that include conservation of biological communities as a central objective.

METHODS

Study area

The Laja watershed ($21^{\circ}33' - 20^{\circ}58'N$; $101^{\circ}28' - 100^{\circ}30'W$) covers 3476 km² of the semiarid State of Guanajuato in Central Mexico (Figure 1). Much of the basin has been impacted by agriculture, but the natural vegetation types include oak forests, chaparral and xeric vegetation with narrow and disperse patches of riparian vegetation along river banks. In many stretches along the river, riparian vegetation has been removed completely. Several

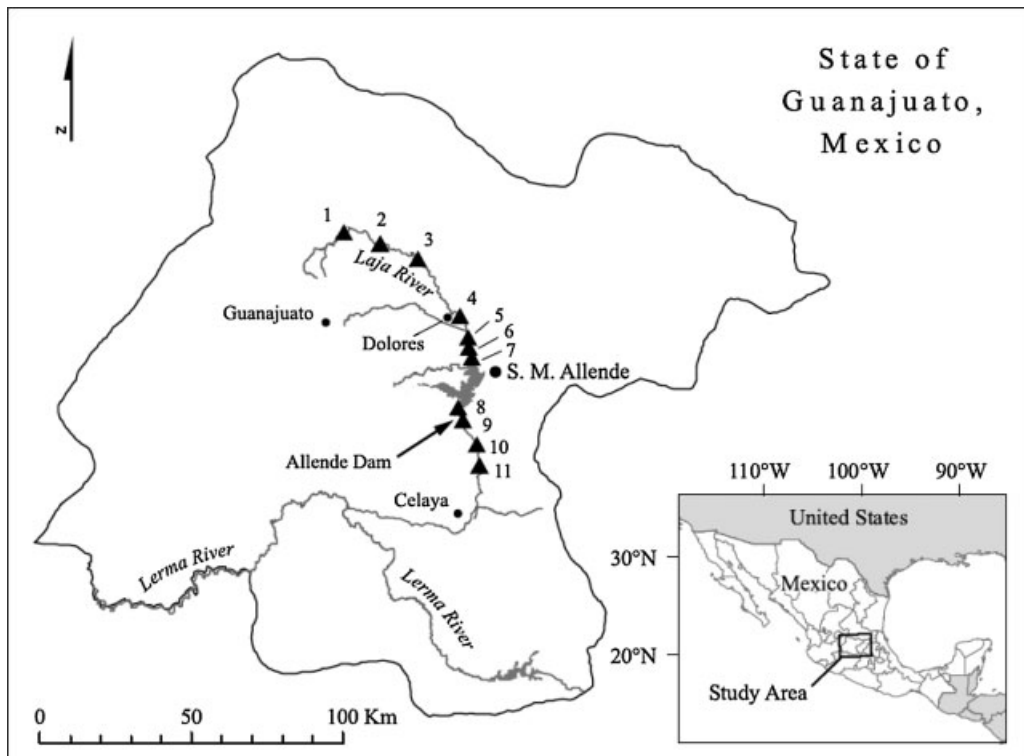


Figure 1. Sites sampled in the Laja River (Guanajuato, Mexico). Site 1, Jesús María (site type reservoir); site 2, Jesús María tailwater (tailwater); site 3, La Quemada (river); site 4, La Laja (river); site 5, Adjuntas del Río (river); site 6, Atotonilco (river); site 7, Cieneguilla (reservoir); site 8, Ignacio Allende (reservoir); site 9, I. Allende tailwater (tailwater); site 10, Rinconcillo de los Remedios (river); site 11, Empalme Escobedo (river)

point and non-point pollution sources occur along the river. Substrates in the main river channel are typically sand/silt-dominated with interspersed rocky segments. Two major reservoirs exist in the Laja River, but at least 12 more are located on tributaries (CNA, 2002). The Ignacio Allende and Jesús María reservoirs were built in 1968 and 1982, respectively, to provide water for irrigation, animal and human consumption. The main stem of the Laja is 154 km in length, of which 124 km are located upstream from the Ignacio Allende Dam and ~15 km are located above Jesús María (Hernández-Javalera, 2002). Dry land and irrigated agriculture dictate water use in the watershed and its headwaters are considered as a priority area for watershed conservation by CONABIO (2000). Except for the headwaters and a few canyons, the Laja has generally low to moderate gradient and presents seasonal and dam regulated flows. Water is stored in reservoirs during the rainy season, thus altering natural flow regimes. Especially during the later part of the rainy season when dams release water, flow fluctuates widely from isolated pools separated by dry river bed to fast runs exceeding 3 m in depth. Water surface width throughout the river varies from approximately 2–20 m depending on flow release from reservoirs and season, and the geomorphology of the surrounding landscape.

For this investigation, we sampled 11 sites in the main stem of the Laja River during January, August and November 2003 (three reservoir, two tailwater and six river sites) (Figure 1). Site 1 was in the Jesús María reservoir. Site 7 was in the inlet of the I. Allende reservoir and site 8 was in the reservoir close to the dam. Sites 2 and 9 were tailwaters located within 100 m of the two dams. Sites 3–6 were located in a high plateau where the river is surrounded by slight hills. Site 10 was located downstream from an 11 km gorge starting at site 9. Site 11 was located in an urban valley area at the downstream end of our sampling area. Sites were chosen according to their accessibility and the location of major hydrological features in the channel (i.e. reservoirs).

Fish communities of the Laja

Mexico's Central Plateau, where the Laja River is located, hosts around 100 native freshwater fish species. Of these, 70% are considered endemic (Miller, 2005). Many species in the region face serious conservation problems (Domínguez-Domínguez *et al.*, 2008). Twenty-three fish species have been recorded from the Laja, of which 14 are native and 9 are introduced (Table I). Of these, only 15 persist today. The present-day fish community is dominated by species that are tolerant and omnivorous, and with a high proportion of non-native species. Species sensitive to habitat deterioration and poor water quality as well as native benthivores have been extirpated, and only a few representatives of these groups remain in isolated reaches of the Laja (Mercado-Silva *et al.*, 2006). Non-native fishes have been introduced to the Laja as food resources in reservoirs or as accidental aquarium releases. Most non-native species are common, and *Micropterus salmoides* and *Lepomis macrochirus* are dominant in upper reaches of the Laja. Throughout the rest of the watershed, non-native livebearers, cichlids, carp and goldfishes are common, but native livebearers and silversides still comprise an important component of the community (López-López and Díaz-Pardo, 1991; Mercado-Silva *et al.*, 2006).

Stable isotope samples

Fish, benthic invertebrate and zooplankton samples were obtained for stable isotope analysis during dry and wet seasons. Seines, DC backpack electroshockers and gillnets, as required, were used to obtain representative samples of the fish community in all habitats at each sampling site. Approximately 1 g of dorsal muscle tissue was obtained from 1 to 5 fish of each species (per size-class and site), and frozen for isotope analysis. Invertebrates were sampled with D-nets, Ekman grab samplers and zooplankton (80 μ m mesh) nets. Benthic invertebrates were identified to order or family, and classified as primary or secondary consumers using classification criteria in Merritt and Cummins (1996) and Thorp and Covich (2001). Zooplankton samples were processed in bulk. We followed Vander Zanden *et al.* (1999) and (2003) for sample processing. Stable isotope analysis was performed at the University of California—Davis Stable Isotope Facility. Two per cent of samples were analysed in duplicate (Mean standard error < 0.1‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$).

We estimated food web structure at each of our 11 sites using carbon and nitrogen stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). Stable isotope ratios are expressed in delta (δ) notation, which is defined as the parts per thousand (‰) deviation from standard material; $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = ([R_{\text{sample}}/R_{\text{standard}}] - 1) 1000$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or

Table I. Fishes of the Laja River (modified from Mercado-Silva *et al.*, 2006)

Family and species	Acronym	Status
Cyprinidae		
<i>Algansea tincella</i>		N
<i>Carassius auratus</i>	CA	I
<i>Cyprinus carpio</i>	CC	I
<i>Notropis calientis</i>		N
<i>Notropis sallaei</i>		EX
<i>Yuriria alta</i>	Y	N
<i>Ctenopharyngodon idella</i>		I
Catostomidae		
<i>Scartomyzon austrinus</i>		EX
Ictaluridae		
<i>Ictalurus dugesi</i>		EX
Atherinopsidae		
<i>Chirostoma jordani</i>	CJ	N
<i>Chirostoma arge</i>	CR	N
<i>Chirostoma humboldtianum</i>		EX
Poeciliidae		
<i>Poecilia sphenops</i>		I
<i>Poeciliopsis infans</i>	P	N
<i>Xiphophorus variatus</i>	XI	I
Goodeidae		
<i>Goodea atripinnis</i>	G	N
<i>Xenotoca variata</i>	XE	N
<i>Allophorus robustus</i>		EX
<i>Skiffia lermæ</i>		EX
Centrarchidae		
<i>Lepomis macrochirus</i>	L	I
<i>Lepomis cyanellus</i>		I (EX)
<i>Micropterus salmoides</i>	M	I
Cichlidae		
<i>Oreochromis sp.</i>	O	I

Acronym is used as a reference for all figures. Stable isotope data was available for species with acronyms only. Origin and conservation status of the species is indicated: Native (N), Non-native (I), Extirpated (EX—not found in 2003 samples).

$^{15}\text{N}/^{14}\text{N}$. $\delta^{13}\text{C}$ is conserved from prey to predator, and is used to trace energy sources for a food web (Hecky and Hesslein, 1995; Vander Zanden *et al.*, 1999). Since there is a 3–4‰ increase in $\delta^{15}\text{N}$ from prey to predator, $\delta^{15}\text{N}$ from fish samples can be converted to a continuous measure of trophic position (TP hereafter) which standardizes for among-site variation in $\delta^{15}\text{N}$ at the base of the food web. Organisms at the base of the food web can have wide variations in $\delta^{15}\text{N}$ (1–13‰ [Cabana and Rasmussen, 1996]) among sites. To allow among-site comparisons, standardization is essential. Standardization procedures followed Vander Zanden and Rasmussen (1999): $\text{TP}_{\text{consumer}} = (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}})/3.4 + 2$, where 3.4 is the assumed per-trophic-level enrichment in $\delta^{15}\text{N}$. $\delta^{15}\text{N}_{\text{baseline}}$ was established through a primary consumer $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ linear regression relationship which provided an adequate fit for these data (Vander Zanden *et al.*, 2003). The procedure for the determination of $\delta^{15}\text{N}_{\text{baseline}}$ for the Laja is detailed in Appendix A.

No differences in $\delta^{15}\text{N}$ values were found among fish samples collected from different months for individual sites (*t*-tests, all $p > 0.05$). Thus, the $\delta^{15}\text{N}$ values for all individuals of a species from a given site were averaged for analysis, regardless of season. Food web analyses described below are based on isotopic analysis of 384 fish specimens from 12 species of the 15 currently present in the Laja (Appendix B). Of these, six are non-native and six are native. Stable isotope samples were not obtained for one non-native (*Ctenopharyngodon idella*), and two native species (*Notropis calientis* and *Algansea tincella*) that can still be found in the river. We found no correlation between body length and TP or $\delta^{13}\text{C}$ for a species at a given site. One hundred and seven invertebrate samples were used in building the food web of the Laja (Appendix C).

Food webs

We first constructed niche space diagrams for each site by plotting the mean TP and $\delta^{13}\text{C}$ (± 1 SE) of each species sampled at each site. Second, we created composite food web diagrams for each habitat type (reservoir, tailwater and river). Finally, we focused on how three food web metrics: mean TP, mean $\delta^{13}\text{C}$ and food web dispersion (sensu Layman *et al.*, 2007; Schmidt *et al.*, 2007), vary with the degree to which a site is affected by impoundment. Food web dispersion is the average Euclidian distance of all species at a site relative to the site centroid (i.e. the mean TP and $\delta^{13}\text{C}$ for all species at a site) (Layman *et al.*, 2007).

We used general linear models (GLM) to fit the values of our three metrics for each site to each site's distance from impoundment (km). Other explanatory variables were site species richness (i.e. the number of fish species included in the food web) and site type; with the best fitting models chosen with step-wise selection (lowest AIC). The standard errors of each food web measure were used as weights in the models. Likelihood-ratio tests (LR) were used to assess the significance of the explanatory variables of the best fitting models. All three reservoir sites and the two tailwater sites were considered zero downstream distance, while the distance that all other sites were from their respective closest upstream dam was measured (km) using Google Earth[®] distance-measuring tool. All analyses were performed in the statistics program R, with model selection performed with the *step* function and summary statistics of the best fitting models performed with the *Anova* function of the *car* library.

Niche comparison of native and non-native species

We examined Euclidian distance among all pairs of species in the river (i.e. 12 species, thus 66 comparisons) in order to ask if there are differences in niche overlap between native and non-native species. We first calculated the residuals of a GLM regression for all sampled individuals of all species of $\delta^{13}\text{C}$ on site identity and the residuals of a regression of TP on site identity. These residuals give the $\delta^{13}\text{C}$ and TP values for each individual fish after taking into account the effects of site on stable isotope values. We then calculated the pairwise Euclidean distance among all species centroids in residual $\delta^{13}\text{C}$ and TP space (i.e. the 66 comparisons). To test if pairs of species were significantly different, we used a null model approach (Gotelli and Graves, 1996) where we randomized the residual $\delta^{13}\text{C}$ and TP data between each species pair maintaining the observed association between each $\delta^{13}\text{C}$ and TP data point and calculated a null-residual-centroidal pairwise distance. We did this 10 000 times for each species pair and compared the distribution of 10 000 null distances to the observed distance at $\alpha = 0.05$. This randomization test maintained the total niche space encompassed by each species pair, and required fewer statistical assumptions of the data than other methods (e.g. MANOVA) (Gotelli and Ellison, 2004). All analyses were performed in the statistics program R, and code used to perform these analyses is available from the authors.

Reservoir–non-native species interactions

To test the hypothesis that non-native species are associated with impoundments (Havel *et al.*, 2005), we regressed $\delta^{13}\text{C}$ on distance from dam outlet for each species (native and non-native). A regression was not possible with *Chirostoma arge* because it was found at only one site. The slope of each regression represents the shift from pelagic/reservoir carbon to in-stream carbon reliance as one moves downstream from an impoundment. Species with high slopes utilize reservoir exports more than species with slopes closer to zero. Similarly, a low intercept also indicates reliance on reservoir-derived carbon, thus we examined whether non-native fishes had significantly lower intercepts than native species. We examined whether non-native fishes had higher slopes and lower intercepts than native fishes with weighted t-tests, where each species was weighted by the estimated standard error of each slope or intercept. Note, there was no evidence for phylogenetic signal in either the slope or the intercept data (i.e. more closely related species were not more likely to have similar values of either coefficient); therefore, the assumption that each species is an independent data point in the t tests we performed and in the site level regressions we described above was not violated (Helmus *et al.*, 2007).

RESULTS

Food webs of streams, reservoirs and tailwaters

Food web plots for the three site types in the Laja River are depicted in Figure 2. Plots for individual sites are presented in Appendix D. Reservoirs had well separated benthic and pelagic (for $\delta^{13}\text{C} < -23\text{‰}$) components (Figure 2a). The dominant pelagic zooplanktivore (*Chirostoma jordani*) separated from all other species. At the top of the food web were *M. salmoides*, *Xenotoca vatiata* and *Yuriria alta* relying on a combination of benthic and zooplankton resources. Of these three, *M. salmoides* was the most enriched in $\delta^{13}\text{C}$. Non-native *L. macrochirus* also

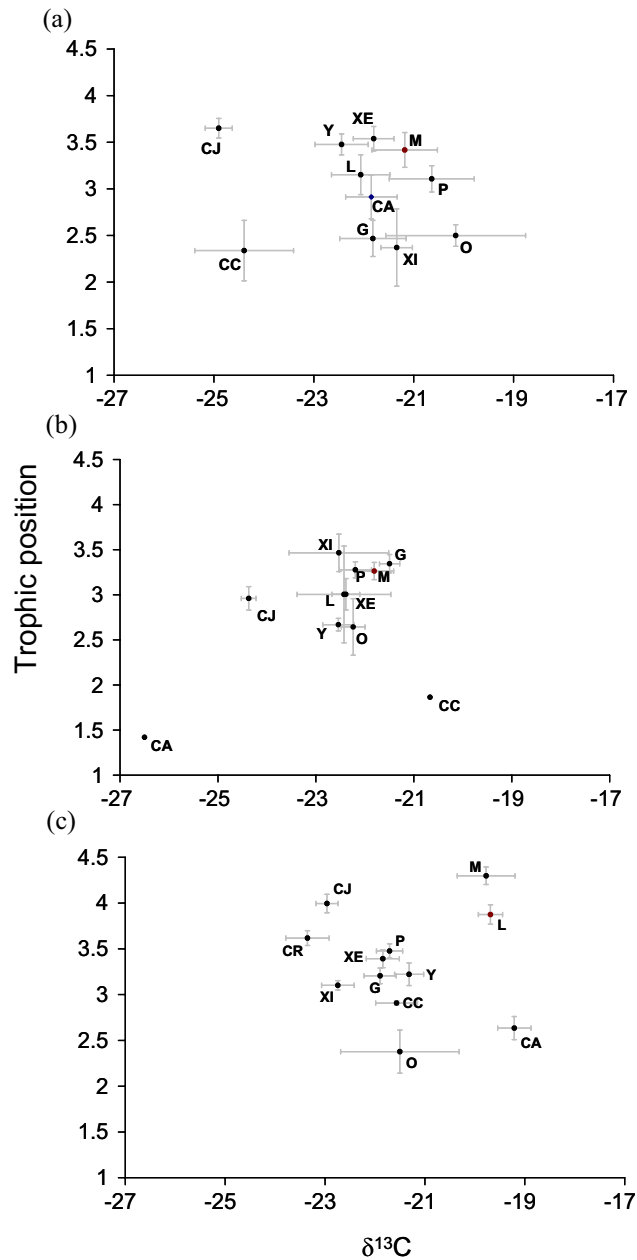


Figure 2. Food web diagrams of three different habitat types in the Laja river (Guanajuato, Mexico). (a) Reservoirs, (b) tailwater and (c) river sites. Acronyms correspond to species in Table I. Values are mean TP and $\delta^{13}\text{C} \pm 1$ SE (see text)

had a relatively high TP. *Poeciliopsis infans* and *Oreochromis* sp. were also highly enriched in $\delta^{13}\text{C}$. One native, *Goodea atripinnis* and three non-natives (*Oreochromis* sp., *Carassius auratus* and *Xiphophorus variatus*) had low TP and depended on both benthic and pelagic resources. *Cyprinus carpio* had lowest TP in the food web and a $\delta^{13}\text{C}$ depleted signature.

Tailwater food webs were relatively more compact than those of reservoirs (Figure 2b). *C. jordani* dominated the pelagic component of the food web, but had similar TP to most other fishes. *C. carpio* and *C. auratus* differed in $\delta^{13}\text{C}$ compared to reservoir sites, and were at the bottom of the food web, but the rest of the fish community had generally higher TP than in reservoir sites. Compared to reservoirs, fish from tailwaters relied on more pelagic-derived resources.

M. salmoides and *C. jordani* also had the highest TP in river sites (Figure 2c). TP of *M. salmoides* at river sites was higher than any other species at any of the site types. *M. salmoides*, *L. macrochirus* and *C. auratus* had enriched $\delta^{13}\text{C}$ relative to other fishes. Compared to the rest of the species, *C. jordani* and its congener *C. arge* were the most $\delta^{13}\text{C}$ depleted. *Y. alta*, *P. infans*, *X. variata* and *G. atripinnis* formed a cluster of species similar to tailwater sites. *Oreochromis* sp. was at the bottom of the riverine site food web, and had similar TP to that in reservoirs and similar $\delta^{13}\text{C}$ to that in tailwaters. In general, food web structure of riverine sites was similar to both reservoir and tailwater sites, but riverine fishes had less depleted $\delta^{13}\text{C}$ values compared to other site types.

Niche comparison of native and non-native species

Our analysis identified the trophic niches occupied by native and non-native species in the Laja. The native zooplanktivore *C. jordani* had a unique trophic niche compared to other species (2.28 mean pairwise Euclidian distance from all other species ± 0.16 SE), and did not significantly overlap with any of the other 11 species. All other species had statistically indistinguishable trophic niches (Tukey test, $p > 0.05$ for all pairwise comparisons). Twenty-seven out of the 66 comparisons were significant according to our permutation, with most of the significant comparisons caused by *C. jordani*. The next most distant species was the non-native *M. salmoides* (1.40 ± 0.24 SE)—it was significantly divergent from seven other species. All other species significantly overlapped with at least five other species. Thus, as anticipated from the above results, natives and non-natives had similar trophic niches (native mean pairwise distance: 1.15 SE = 0.1, non-native mean: 1.16 SE = 0.08). We also classified distances into three groups: non-native/non-native, native/native and non-native/native and found no significant difference in pairwise distances among the three groups ($F = 0.03$, $p > 0.05$). This suggests that niche overlap is pervasive among non-natives and natives and across most species, an assertion that can be inferred in Figure 3 which gives the niche space estimates of all 11 species.

Reservoir–non-native species interactions

Species $\delta^{13}\text{C}$ increased with downstream distance from dams and was the only explanatory variable in the best fitting GLM (downstream distance LR: 8.49, $p < 0.005$; $\delta^{13}\text{C}$ variation explained: 49%) (Figure 4a). Food web dispersion decreased in sites further downstream from reservoirs (LR: 23.60, $p < 0.001$; dispersion variation explained 54%) (Figure 4b), though sites with higher species richness had higher food web dispersion (LR: 7.70, $p < 0.01$; size variation explained: 18%). After accounting for the effects of downstream distance and species richness, tailwater sites were less dispersed than river and reservoir sites (LR: 6.31, $p < 0.05$; size variation explained: 15%). The best fitting GLM model explained 87% of the total variation in food web dispersion across sites. None of the explanatory variables explained significant variation in mean TP across sites.

Since the $\delta^{13}\text{C}$ of the pelagic food web components of reservoirs (e.g. zooplankton, phytoplankton) are isotopically depleted, fish species that rely on reservoir production should have isotopically depleted $\delta^{13}\text{C}$ values, which should increase as a function of downstream distance from the dam as reliance shifts from reservoir-derived to riverine resources. Three species showed significant increases in $\delta^{13}\text{C}$ with downstream distance: *C. auratus* ($r^2 = 0.51$, slope = 0.07, intercept = -23.12), *C. jordani* ($r^2 = 0.49$, slope = 0.04, intercept = -24.58) and *Y. alta*

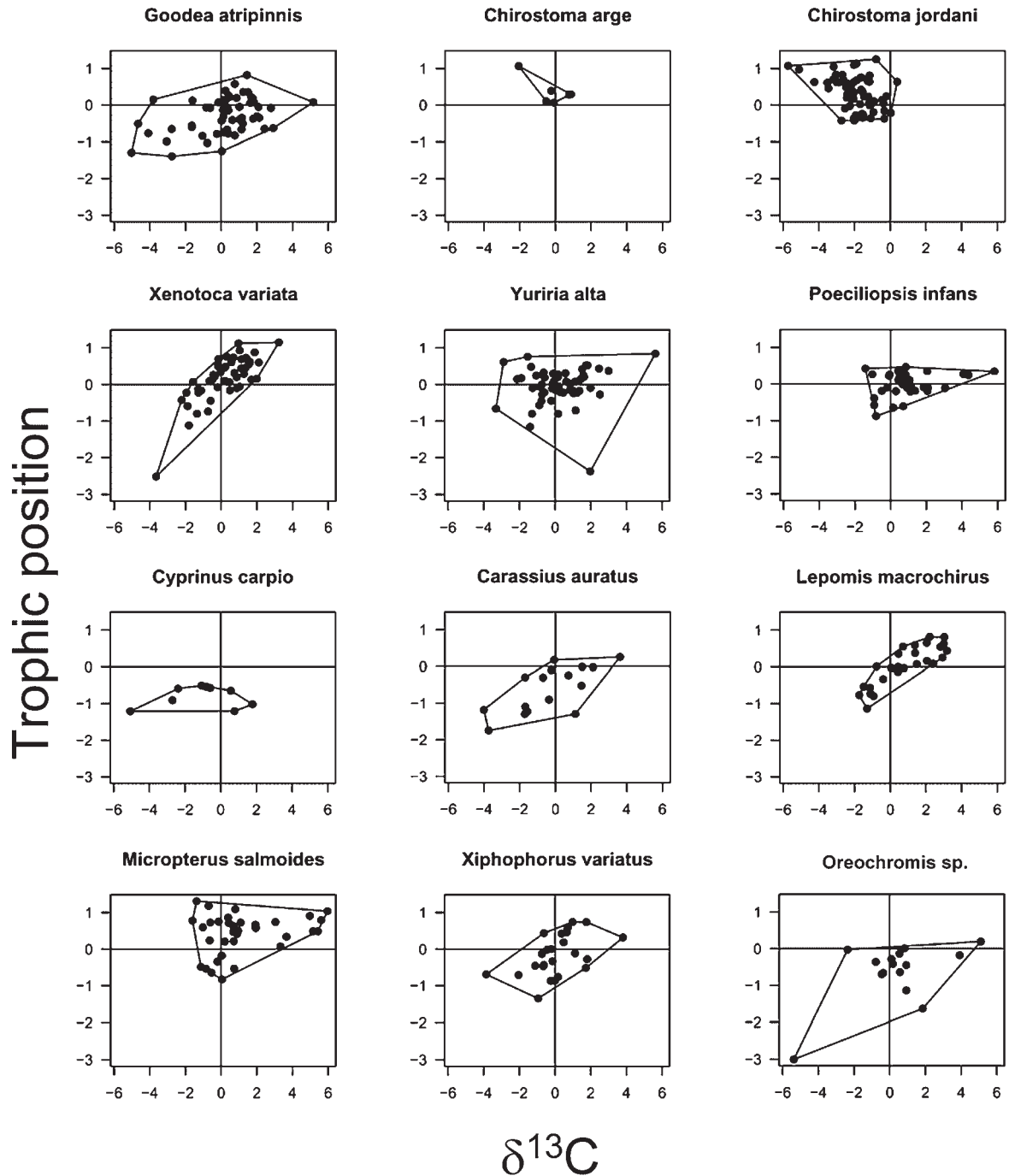


Figure 3. Trophic niche of fishes in the Laja River (Guanajuato, Mexico). Each point is an individual fish. See methods for centroid calculations

($r^2 = 0.22$, slope = 0.03, intercept = -22.51). All other species had lower slopes, higher intercepts and/or lower r^2 values. There were no significant differences between non-native and native species in either the slope ($t = 0.37$, $p > 0.05$) or the intercept ($t = 1.32$, $p > 0.05$) of the species-specific regressions, thus indicating that non-natives are not more likely to use reservoir-derived production.

EFFECTS OF IMPOUNDMENT AND NON-NATIVE SPECIES

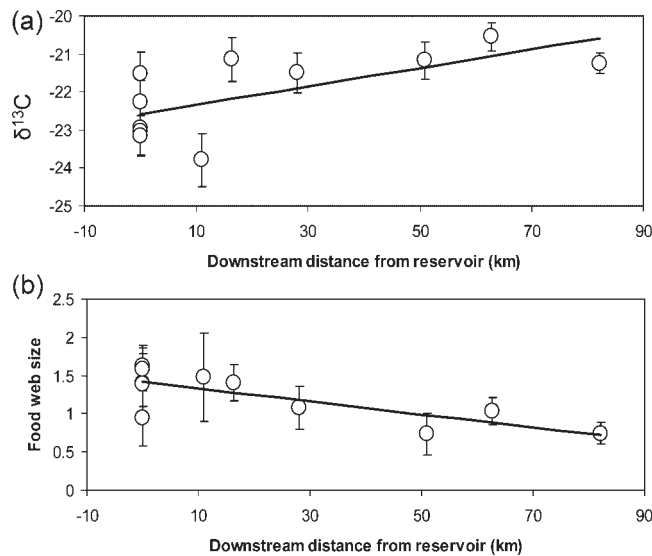


Figure 4. Relationship of mean fish $\delta^{13}\text{C}$ value (a) and food web dispersion (b) with site-specific distance from the reservoir in 11 sites of the Laja river (Guanajuato, Mexico) (see text)

DISCUSSION

Many of the environmental impacts that have occurred in Mexican freshwater ecosystems have resulted in large changes in the composition, structure and function of their fish communities (Lyons *et al.*, 1995, 1998; Soto Galera *et al.*, 1998; Mercado-Silva *et al.*, 2002, 2006; Contreras-Balderas *et al.*, 2005) but much less is known about how some of these impacts have altered ecological interactions in aquatic food webs. Reservoirs and non-native fishes have altered food webs in Mexican freshwater ecosystems.

Reservoirs are major modifications in river systems and have detrimental effects on native stream communities, fisheries and terrestrial riparian habitats (Bain *et al.*, 1988; Malmqvist and Rundle, 2002; Rahel, 2002; Havel *et al.*, 2005). Non-native species are major factors of global change, as they alter not only community composition but also the interactions and processes that occur within ecosystems (Vitousek *et al.*, 1997). Further, reservoirs facilitate and promote non-native establishment (Havel *et al.*, 2005; Vander Zanden, 2005).

In the Laja River, reservoirs play an important role in determining the trophic interactions among fishes. Reservoir food webs exhibited the highest range in $\delta^{13}\text{C}$ values indicating a greater range of basal carbon sources to the fish community. Consequentially, reservoir food webs also had the largest dispersion relative to tailwater and distant riverine sites. It was in reservoirs where *C. jordani*, a well-known zooplanktivore (Soto Galera, 1993), separated the most from the rest of the fish community. Zooplanktivory is not exclusive to *C. jordani*, but our data suggest that other species depended less on these pelagic resources. *M. salmoides* and *L. macrochirus* are known to feed on zooplankton during their early life stages (Becker, 1983) and all the native livebearers and *Y. alta* residing in the Laja are considered omnivores, feeding primarily on algal mats and benthic invertebrates, but also pelagic resources (Wischnath, 1993; Moncayo-Estrada, 1996). In reservoirs, the comparatively lower TP of omnivores such as *C. carpio*, *Oreochromis* sp., *G. atripinnis* and *C. auratus*, could suggest increased availability of detritus and algae, which are preferably consumed by these species. In other site types in the Laja, such as tailwaters, detrital resources and algae are not as abundant, which forces these fishes to consume food items with comparatively higher ^{15}N .

Since food web dispersion decreases with downstream distance from dams, and food webs at tailwaters are significantly more compact than reservoir and riverine food webs (i.e. once dam distance and species richness are taken into account); our data suggest that interspecific food web interactions could be much stronger in riverine habitats and somewhat stronger in tailwaters than in reservoirs, thus native fishes could be comparatively more affected by non-native species via predation or competition in these habitats. Data from river sites suggest that

sources of terrestrial carbon could be relatively more important here than in reservoirs and tailwater sites for largemouth bass, bluegill and goldfish. Still, *M. salmoides* and *L. macrochirus* could also affect natives via piscivory. As juveniles, these two species most likely compete with native livebearers and cyprinids, but as adults, they undoubtedly are predators of these groups and atherinopsids, complementing their diets with food items of terrestrial provenience. In reservoirs, although trophic niches of most species are similar, greater habitat availability could allow for decreased interactions between natives and non-natives. This may be especially so for atherinopsids who prefer pelagic areas of these ecosystems. Throughout the Laja, if native species have no other adaptations that allow for coexistence with non-natives, then competitive exclusion may eventually occur. Reservoirs are typically stocked with non-native species, thus the more disperse food webs in reservoirs could be a stepping stone for establishment and then eventual spread of non-natives to riverine sites where increased interactions could affect native riverine species (Havel *et al.*, 2005). However, non-native species were not more likely than native species to assimilate carbon produced by reservoirs.

Although trophic niches for most species overlap in the Laja, stable isotope data for some species suggested some tendencies on the origin of their resources. For example, *G. atripinnis* used food items with a variety of ^{13}C values including items of pelagic provenience while *P. infans* used more ^{13}C enriched items. The comparative size of these species could be responsible for this separation. While large individuals (>90 mm TL) of *G. atripinnis* were collected from deeper, pelagic areas of reservoirs and pools in river sites, *P. infans*, which attain a maximum size of ~50 mm TL, were only found along the banks of reservoirs and relatively protected (i.e. boulders, vegetation, etc.) habitats in river and tailwater sites.

Our results suggest that reservoir subsidies to the Laja food web decline with downstream distance from reservoirs, sites within reservoirs had more disperse food webs than tailwater and riverine sites, and TP was not affected by reservoirs. Reservoirs can subsidize food webs in downstream reaches of rivers (Petts, 1984), and although consumers may rely on production derived from local habitats, their $\delta^{13}\text{C}$ values suggest that they also depend on resources from adjacent areas (Finlay *et al.*, 2002). As water is released from reservoirs, zooplankton is exported and becomes part of riverine food webs. Zooplankton abundances are known to decline with distance from reservoirs (Ward, 1975) depending on their size and form as they are liable to mechanical destruction or predation. Average site $\delta^{13}\text{C}$ values increased strongly with increased downstream distance. Thus, we provide strong evidence that the two dams on the Laja are exporting pelagic derived production into the river that is being assimilated in downstream fishes.

In addition to food web alterations produced by habitat modifications and entrance of non-natives, Laja food webs have undoubtedly changed as a consequence of changes in community composition. Extirpation of native carnivores has been documented for the Laja (Mercado-Silva *et al.*, 2006) and the addition of a carnivorous non-native such as *M. salmoides* has most likely increased piscivory on native fishes in the Laja.

The considerable niche overlap that we found among the species of the Laja may become significant under conditions of very low to no flow in the channel. In the Laja extensive reaches of stream are often reduced to low flows with little or no connection between isolated pools. Under these circumstances, in addition to water temperature increases in these pools, competition and predation are likely to intensify. River management should contemplate water flow increases in the river that allow fishes to better partition their habitats and diversify their food resources. Recreation of natural flows could improve the condition of riparian buffers and benthic communities, which could in turn provide the fish community with additional and more diverse resources. Improving flows would not only benefit aquatic ecosystems, but also terrestrial communities that rely on aquatic resources (Nakano and Murakami, 2001; Sabo and Power, 2002).

Our study found high variability in $\delta^{13}\text{C}$ signatures in fish samples from the Laja and we have discussed these based on the difference in the availability of primary producers among our site types. It is also possible however, that differences in ^{13}C signatures among species could stem from micro habitat differences (i.e. riffles vs. pools), flow velocity (Finlay *et al.*, 1999; Finlay, 2001) or the influence of other allochthonous sources (i.e. sewage) of resources to our study sites (deBruyn *et al.*, 2003). We have used existing knowledge of the dietary biology of Laja fishes and the position of each species relative to the rest of the community in the food web to facilitate interpretation of our stable isotope results. Also, although we carried standardization procedures to account for baseline differences among sites, it is still possible that differences in $\delta^{15}\text{N}$ signatures among fishes could be influenced by anthropogenic activity differences in the Laja watershed. Baseline $\delta^{15}\text{N}$ is generally elevated by

anthropogenic nutrient inputs (Cabana and Rasmussen, 1996), and there are several towns and cities in the Laja watershed. Further, we defined trophic niches of Laja fishes using stable isotope data lumped from multiple sites (per site-type). This could have caused larger niche overlap among species than that which could occur at a given site. Further, we recognize that there could be limitations to our estimations of trophic niches using stable isotope data (Hoeninghaus and Zeug, 2008). Future studies could use complementary methods (i.e. diet analysis, population estimations), to aid understanding of ecological processes beyond what can be inferred from stable isotope information (Layman and Post, 2008).

Our study transcends the Laja River. Many freshwater systems in Mexico's central plateau and throughout the country share a common suite of non-native, functionally similar fish assemblages and similar environmental challenges. Our study offers insights into spatial variability in aquatic food web structure across a broad geographic region, and could aid in predicting the consequences of future habitat modifications or species introductions on not yet affected areas.

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APPENDIX A

Procedure for the determination of $\delta^{15}\text{N}_{\text{baseline}}$ for the standardization of trophic position values for fishes in the Laja River

Primary producer $\delta^{15}\text{N}$ can vary from site to site in an ecosystem (Vander Zanden and Rasmussen, 1999). Food web studies that compare $\delta^{15}\text{N}$ values (and derived measures such as TP) among sites require a standardization process that accounts for basal $\delta^{15}\text{N}$ variations. In our study $\delta^{15}\text{N}$ from fish samples were converted to a continuous measure of TP which required standardization for among-site variation in $\delta^{15}\text{N}$ at the base of the food web. Our TP calculation followed Vander Zanden and Rasmussen (1999) where $\text{TP}_{\text{consumer}} = (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}}) / 3.4 + 2$. Primary consumers were identified from our invertebrate samples using classification criteria in Merritt and Cummins (1996) and Thorp and Covich (2001). Since primary consumer data were not available for all sites, to obtain $\delta^{15}\text{N}_{\text{baseline}}$ to calculate TP for each species at each site we regressed $\delta^{15}\text{N}$ on $\delta^{13}\text{C}$ for the primary consumers at eight sites (Sites 1–6, 9 and 11). There were no differences among baseline regressions from the three river sites (ANCOVA, $\alpha = 0.05$). Tailwater and reservoir site baseline regressions were also not significantly different. The coefficients for the river sites regression were significantly different from those of tailwater and reservoir sites. Thus, we developed a tailwater/reservoir $\delta^{15}\text{N}_{\text{baseline}}$ ($\delta^{15}\text{N} = -0.673 \delta^{13}\text{C}_{\text{consumer}} - 2.9535$) and a riverine $\delta^{15}\text{N}_{\text{baseline}}$ ($\delta^{15}\text{N} = -0.5813 \delta^{13}\text{C}_{\text{consumer}} - 4.9188$) (Figure A1). Using the regressions an estimated $\delta^{15}\text{N}_{\text{baseline}}$ value was calculated for each consumer using the consumer's $\delta^{13}\text{C}$ accounting for the average site-specific residuals from the specific $\delta^{15}\text{N}$ – $\delta^{13}\text{C}$ linear model. For three sites (7, 8 and 10) we used the mean of site-specific deviations to calculate $\delta^{15}\text{N}_{\text{baseline}}$ since their secondary invertebrate consumer curves were no different than those from sites where primary consumers were available. In two river sites with primary consumer data (Sites 5 and 6) there was no relationship between primary consumer $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Thus, TP for fishes in these sites was established by using the riverine TP formula above, but considering the average of all invertebrates to obtain $\delta^{15}\text{N}_{\text{baseline}}$.

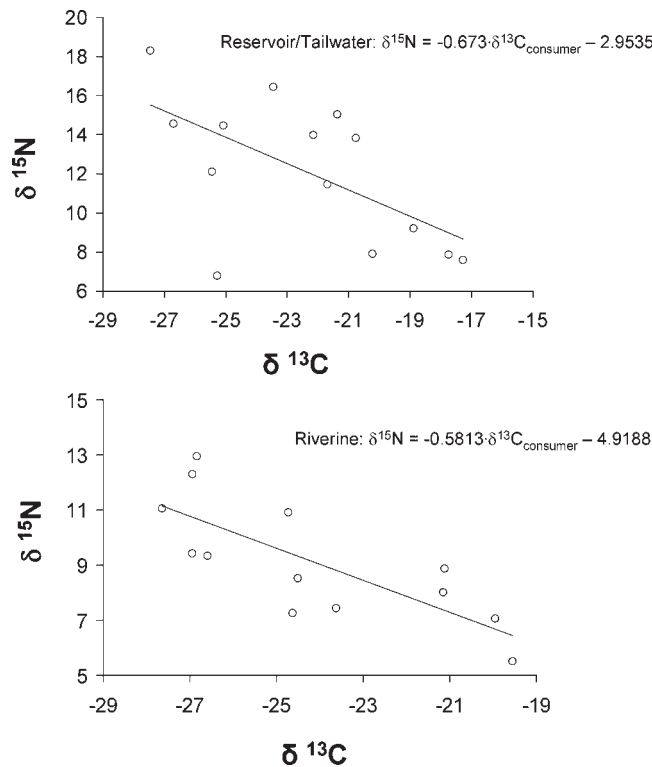


Figure A1. Baseline curves and equations used to determine the trophic position of fishes in the Laja river (Guanajuato, Mexico)

APPENDIX B

Stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and trophic position (mean \pm 1 SE) for fishes in 11 sites of the Laja River

Site no.	Taxa	<i>n</i>	$\delta^{15}\text{N}$	SE	TP	SE	$\delta^{13}\text{C}$	SE
Site 1	<i>C. auratus</i>	4	11.46	0.15	2.10	0.09	-24.01	0.33
	<i>C. jordani</i>	9	17.77	0.88	3.65	0.15	-25.55	0.60
	<i>G. atripinnis</i>	5	12.51	0.64	2.46	0.15	-23.74	1.37
	<i>L. macrochirus</i>	12	13.72	0.37	3.15	0.21	-22.06	0.58
	<i>M. salmoides</i>	13	14.05	0.52	3.42	0.20	-21.19	0.71
Site 2	<i>Y. alta</i>	6	15.01	0.75	3.72	0.08	-21.08	1.18
	<i>C. jordani</i>	6	16.21	0.17	2.56	0.06	-24.08	0.18
	<i>C. carpio</i>	1	11.54	—	1.86	—	-20.67	—
	<i>L. macrochirus</i>	3	16.02	0.38	2.84	0.05	-22.42	0.40
Site 3	<i>M. salmoides</i>	6	17.07	0.38	3.26	0.10	-21.81	0.39
	<i>Y. alta</i>	7	15.54	0.24	2.71	0.06	-22.33	0.27
	<i>C. jordani</i>	12	15.81	0.42	4.09	0.11	-23.40	0.16
	<i>C. carpio</i>	1	9.84	—	2.79	—	-20.74	—
	<i>G. atripinnis</i>	4	12.74	0.48	3.33	0.13	-22.52	0.40
	<i>L. macrochirus</i>	6	13.78	0.24	4.20	0.07	-19.22	0.30
	<i>M. salmoides</i>	7	15.20	1.02	4.55	0.15	-19.64	1.10
Site 4	<i>P. infans</i>	1	13.49	—	3.89	—	-20.58	—
	<i>Y. alta</i>	5	12.91	0.66	3.50	0.21	-21.87	0.42
	<i>C. auratus</i>	1	10.54	—	3.14	—	-20.00	—
	<i>G. atripinnis</i>	6	10.70	0.61	2.96	0.11	-21.28	0.48
	<i>Xenotoca variata</i>	6	11.83	0.28	3.11	0.06	-22.38	0.35
Site 5	<i>Y. alta</i>	5	12.11	0.29	3.42	0.07	-21.00	0.51
	<i>C. auratus</i>	3	9.53	1.10	2.47	0.32	-18.95	0.29
	<i>C. jordani</i>	8	14.33	0.68	3.88	0.20	-21.74	0.45
	<i>G. atripinnis</i>	7	12.13	0.75	3.23	0.22	-21.45	1.16
	<i>L. macrochirus</i>	4	12.48	0.52	3.34	0.15	-20.23	0.28
	<i>M. salmoides</i>	6	14.75	0.31	4.00	0.09	-19.93	0.17
	<i>Oreochromis mossambicus</i>	4	10.47	0.21	2.75	0.06	-20.53	0.24
	<i>P. infans</i>	1	12.17	—	3.24	—	-21.01	—
	<i>X. variata</i>	5	12.14	0.50	3.23	0.15	-19.84	0.53
	<i>X. variatus</i>	1	11.30	—	2.99	—	-22.56	—
Site 6	<i>Y. alta</i>	5	11.66	0.66	3.09	0.19	-19.24	0.38
	<i>C. jordani</i>	2	16.10	1.08	3.63	0.32	-22.08	0.83
	<i>C. carpio</i>	2	13.87	0.06	2.97	0.02	-21.98	0.11
	<i>G. atripinnis</i>	1	16.63	—	3.78	—	-20.87	—
	<i>Oreochromis mossambicus</i>	2	12.97	2.79	2.71	0.82	-19.94	0.51
	<i>P. infans</i>	6	16.80	0.11	3.83	0.03	-21.32	0.38
	<i>X. variata</i>	6	17.29	0.21	3.98	0.06	-21.34	0.10
	<i>Y. alta</i>	4	13.75	2.11	2.93	0.62	-21.17	0.81
Site 7	<i>C. auratus</i>	1	13.45	—	4.03	—	-19.74	—
	<i>C. jordani</i>	4	17.96	0.14	4.45	0.05	-25.01	0.30
	<i>C. carpio</i>	2	13.39	0.21	3.07	0.20	-25.25	0.81
	<i>G. atripinnis</i>	3	14.92	1.02	3.84	0.54	-23.40	1.51
	<i>P. infans</i>	6	12.76	0.21	3.36	0.13	-22.45	0.65
	<i>X. variata</i>	9	14.89	0.46	3.84	0.19	-23.30	0.43
	<i>X. variatus</i>	1	16.18	—	4.51	—	-21.60	—
	<i>Y. alta</i>	7	14.45	0.70	3.68	0.16	-23.49	0.75
Site 8	<i>C. auratus</i>	6	13.42	0.32	2.34	0.19	-22.52	0.69
	<i>C. jordani</i>	10	17.97	0.19	3.33	0.06	-24.28	0.17
	<i>C. carpio</i>	3	12.64	0.68	1.85	0.20	-23.82	1.62
	<i>G. atripinnis</i>	10	11.04	0.20	2.06	0.15	-20.38	0.65
	<i>M. salmoides</i>	1	15.99	—	3.38	—	-21.09	—
	<i>Oreochromis mossambicus</i>	5	12.38	0.86	2.50	0.12	-20.16	1.40

(Continues)

EFFECTS OF IMPOUNDMENT AND NON-NATIVE SPECIES

Appendix B. (Continued)

Site no.	Taxa	<i>n</i>	$\delta^{15}\text{N}$	SE	TP	SE	$\delta^{13}\text{C}$	SE
Site 9	<i>P. infans</i>	5	12.26	0.67	2.80	0.20	-18.47	1.09
	<i>X. variata</i>	10	15.18	0.38	3.26	0.13	-20.46	0.24
	<i>X. variatus</i>	6	11.50	0.72	2.01	0.25	-21.30	0.37
	<i>Y. alta</i>	5	15.37	0.35	2.89	0.08	-22.61	0.29
	<i>C. auratus</i>	1	14.15	—	1.42	—	-26.50	—
	<i>C. jordani</i>	6	19.51	0.20	3.36	0.08	-24.66	0.18
	<i>G. atripinnis</i>	6	17.33	0.45	3.35	0.10	-21.50	0.21
	<i>L. macrochirus</i>	1	18.46	—	3.52	—	-22.30	—
	<i>Oreochromis mossambicus</i>	3	15.44	1.19	2.64	0.31	-22.24	0.24
Site 10	<i>P. infans</i>	6	17.56	0.25	3.28	0.09	-22.19	0.33
	<i>X. variata</i>	6	16.79	1.19	3.00	0.54	-22.43	0.96
	<i>X. variatus</i>	6	18.43	0.53	3.47	0.21	-22.53	1.02
	<i>Y. alta</i>	1	15.71	—	2.36	—	-24.05	—
	<i>C. arge</i>	6	14.14	0.71	3.62	0.15	-23.35	0.43
	<i>C. jordani</i>	4	15.61	1.16	3.94	0.29	-23.98	0.37
	<i>G. atripinnis</i>	9	12.86	0.34	3.30	0.08	-23.02	0.24
	<i>P. infans</i>	8	12.14	0.31	3.20	0.07	-22.37	0.35
	<i>X. variata</i>	7	12.83	0.37	3.25	0.15	-23.24	0.58
Site 11	<i>X. variatus</i>	7	12.15	0.33	3.06	0.09	-23.18	0.36
	<i>Y. alta</i>	7	12.19	0.24	3.17	0.10	-22.63	0.32
	<i>C. jordani</i>	3	16.44	0.29	4.25	0.03	-23.68	0.35
	<i>G. atripinnis</i>	4	10.63	0.40	3.05	0.19	-20.71	0.56
	<i>L. macrochirus</i>	1	13.84	—	4.06	—	-20.32	—
	<i>P. infans</i>	1	11.78	—	3.41	—	-20.56	—
	<i>X. variatus</i>	3	11.89	0.37	3.23	0.11	-21.79	0.61
	<i>Y. alta</i>	1	11.25	—	3.02	—	-21.91	—

APPENDIX C

Stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, mean \pm 1 SE) for invertebrates in 11 sites of the Laja River

Site no.	Taxa	<i>n</i>	$\delta^{15}\text{N}$	SE	$\delta^{13}\text{C}$	SE
Site 1	Amphipoda	1	7.87	—	-17.75	—
	Coenagrionidae	1	12.12	—	-20.79	—
	Corixidae	1	9.22	—	-18.89	—
	Diptera	1	7.95	—	-17.93	—
	Ephemeroptera	1	7.61	—	-17.28	—
	Hydrophilidae larv.	1	9.68	—	-18.80	—
	Naucoridae	1	10.48	—	-19.41	—
	Zooplankton	2	10.68	3.88	-25.99	0.71
Site 2	Chironomidae	1	14.99	—	-25.25	—
	Coleoptera	1	9.67	—	-13.91	—
	Diptera	1	9.62	—	-19.39	—
	Ephemeroptera	1	15.05	—	-21.37	—
	Hemiptera	1	10.62	—	-21.55	—
	Isopoda	1	7.92	—	-20.23	—
	Simuliidae	1	14.47	—	-25.08	—
Site 3	Trichoptera	1	18.30	—	-27.46	—
	Belostomatidae	2	10.78	2.17	-24.63	0.13
	Chironomidae	1	11.49	—	-27.74	—
	Corixidae	1	9.43	—	-26.95	—
	Diptera	3	10.59	0.58	-25.12	0.89
	Dytiscidae	1	11.71	—	-27.25	—

(Continues)

Appendix C. (Continued)

Site no.	Taxa	<i>n</i>	$\delta^{15}\text{N}$	SE	$\delta^{13}\text{C}$	SE
Site 4	Ephemeroptera	3	10.43	1.67	-26.37	0.90
	Gerridae	1	10.38	—	-23.26	—
	Hemiptera	1	9.33	—	-24.95	—
	Odonata	1	10.40	—	-26.47	—
	Trichoptera	1	10.92	—	-24.73	—
	Belostomatidae	2	9.06	0.51	-22.47	0.73
	Chironomidae	1	10.85	—	-26.18	—
	Coleoptera	1	5.73	—	-16.23	—
	Corixidae	1	8.53	—	-24.51	—
	Elmidae	1	9.34	—	-26.60	—
	Gyrinidae	1	6.88	—	-23.50	—
	Hemiptera	1	8.57	—	-23.89	—
Site 5	Simulidae	1	12.31	—	-26.94	—
	Tadpole	1	7.07	—	-19.96	—
	Belostomatidae	1	10.42	—	-20.96	—
	Dytiscidae	1	7.80	—	-29.26	—
	Dytiscidae larvae	1	8.89	—	-21.43	—
	Elmidae	1	9.51	—	-20.56	—
	Ephemeroptera	1	7.92	—	-22.80	—
	Hemiptera	1	9.81	—	-26.97	—
	Homopteran	1	1.95	—	-11.40	—
	Hydrophilidae larv.	1	8.27	—	-21.59	—
	Lepidoptera	1	4.40	—	-12.80	—
	Odonata	1	10.47	—	-25.30	—
Site 6	Belostomatidae	3	11.65	1.37	-23.43	0.56
	Chaoborinae	1	12.00	—	-23.73	—
	Corixidae	1	8.78	—	-25.99	—
	Dytiscidae	1	5.41	—	-25.50	—
	Ephemeroptera	1	5.97	—	-27.33	—
	Gerridae	1	10.34	—	-20.96	—
	Hydrometidae	1	10.17	—	-21.12	—
	Mesoveliidae	1	10.39	—	-27.04	—
	Notonectidae	1	6.57	—	-28.52	—
	Odonata	2	14.09	2.15	-22.89	0.18
	Coenagrionidae	1	13.33	—	-29.04	—
	Corixidae	1	9.20	—	-23.19	—
Site 7	Gastropoda	1	11.42	—	-22.92	—
	Hemiptera	1	10.03	—	-25.34	—
	Naucoridae	1	7.40	—	-14.55	—
	Hemiptera	1	14.23	—	-22.71	—
Site 8	Zooplankton	1	9.52	—	-24.45	—
	Belostomatidae	1	19.14	—	-21.73	—
Site 9	Diptera	1	12.32	—	-28.79	—
	Elmidae	1	11.46	—	-21.69	—
	Ephemeroptera	2	12.98	0.86	-23.11	2.34
	Gerridae	1	11.38	—	-21.72	—
	Nepidae	1	9.51	—	-21.76	—
	Notonectidae	1	9.73	—	-25.87	—
	Simulidae	1	16.45	—	-23.45	—
	Trichoptera	1	13.99	—	-22.15	—
	Belostomatidae	1	8.69	—	-24.89	—
	Chironomidae	1	7.07	—	-26.21	—
Site 10	Coleoptera	1	7.62	—	-25.11	—
	Gerridae	1	10.76	—	-24.95	—

(Continues)

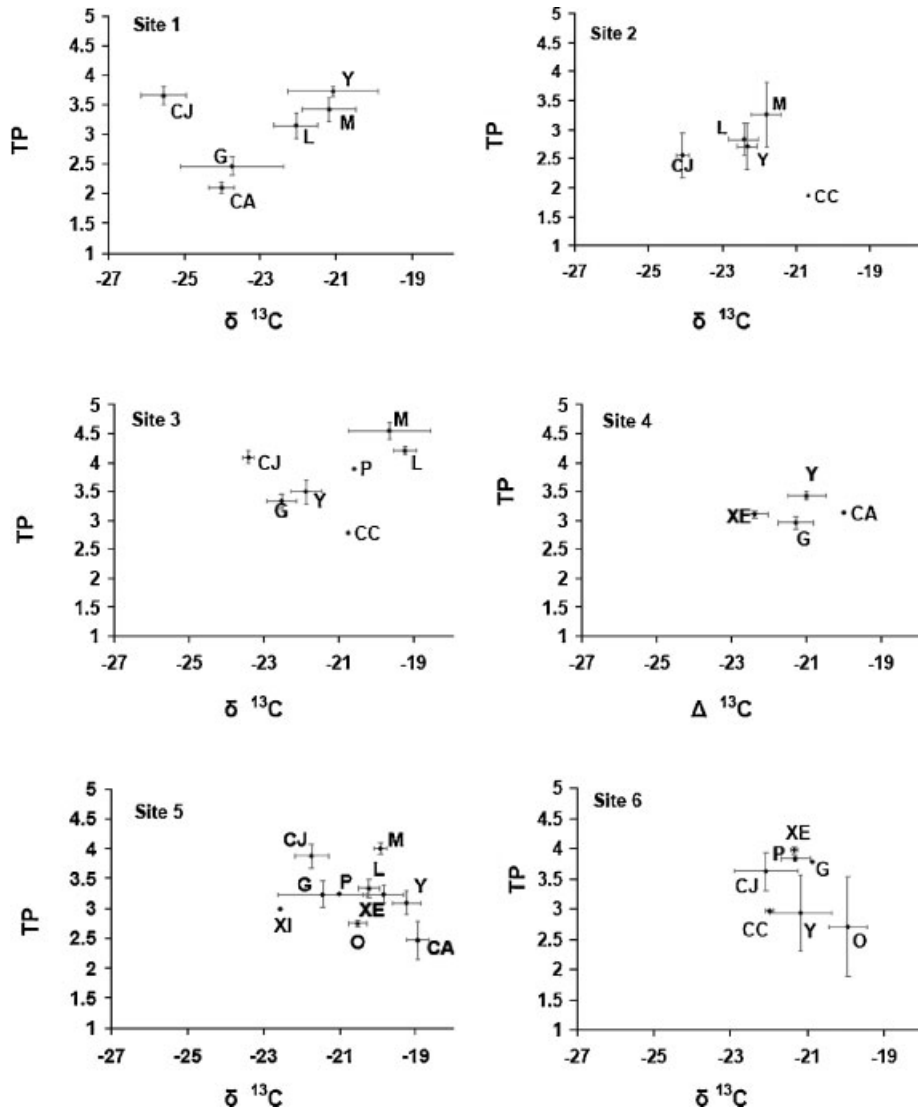
EFFECTS OF IMPOUNDMENT AND NON-NATIVE SPECIES

Appendix C. (Continued)

Site no.	Taxa	<i>n</i>	$\delta^{15}\text{N}$	SE	$\delta^{13}\text{C}$	SE
	Gomphidae	1	9.53	—	-21.18	—
	Isopoda	1	6.46	—	-26.65	—
	Odonata	2	11.46	0.52	-30.50	0.17
	Simulidae	1	12.57	—	-40.33	—
	Trichoptera	2	12.71	0.00	-36.46	1.30
Site 11	Chaoborinae	1	2.67	—	-24.63	—
	Chironomidae	1	7.42	—	-22.01	—
	Coenagrionidae	1	6.37	—	-23.06	—
	Coleoptera	1	4.99	—	-18.62	—
	Corixidae	1	8.02	—	-21.16	—
	Culicidae	1	8.88	—	-21.13	—
	Diptera	1	5.56	—	-22.09	—
	Dytiscidae	1	5.46	—	-22.08	—
	Ephemeroptera	1	7.44	—	-23.63	—
	Gastropoda	1	4.96	—	-20.83	—
	Notonectidae	2	9.10	3.41	-27.11	1.80
	Syrphidae	1	5.51	—	-19.56	—
	Zooplankton	1	6.18	—	-21.94	—

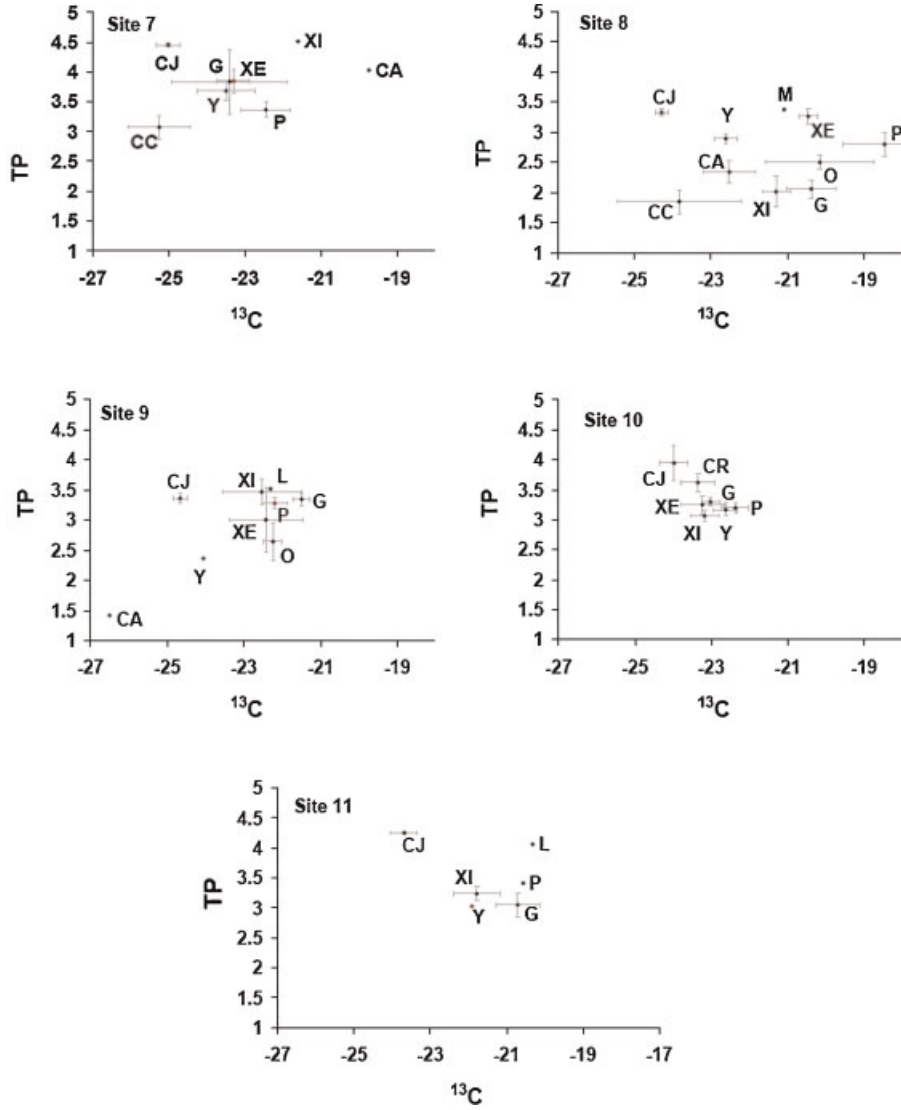
APPENDIX D

Food web plots (trophic position versus $\delta^{13}\text{C}$ for each species [mean \pm 1 SE]) for 11 sites of the Laja



(Continues)

EFFECTS OF IMPOUNDMENT AND NON-NATIVE SPECIES



Appendix D. (Continued)