

# TROPHIC INTERRELATIONS BETWEEN INTRODUCED COMMON CARP, *CYPRINUS CARPIO* (ACTINOPTERYGII: CYPRINIFORMES: CYPRINIDAE), AND FISH COMMUNITY IN A EUTROPHIC SHALLOW LAKE

Juan P. RAMÍREZ-HERREJÓN<sup>1</sup>, Rodrigo MONCAYO-ESTRADA<sup>2</sup>, Eduardo F. BALART<sup>1</sup>, Luis A. GARCÍA CAMACHO<sup>3</sup>, Berenice VITAL RODRÍGUEZ<sup>3</sup>, Reyna ALVARADO VILLANUEVA<sup>3</sup>, Rosario ORTEGA MURILLO<sup>3</sup>, and Javier CARAVEO-PATÍÑO<sup>1\*</sup>

<sup>1</sup> Centro de Investigaciones Biológicas del Noroeste (CIBNOR), Instituto Politécnico Nacional, Playa Palo de Santa Rita Sur, La Paz, B.C.S., México

<sup>2</sup> Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Instituto Politécnico Nacional, Unidad Michoacán (CIIDIR-Michoacán), COFAA, Jiquilpan, Michoacán, México

<sup>3</sup> Laboratorio de Biología Acuática, Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo (UMSNH), Morelia, Michoacán, México

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**Background.** Introduction of the common carp, *Cyprinus carpio* Linnaeus, 1758, may cause a cascade of alterations in trophic webs, among other negative effects, indirectly due to its feeding behaviour. A simplified model site, convenient for studying such interrelations is Lago de Pátzcuaro, México, a shallow lake where carp was first introduced in 1974. The aim of our study was to characterize diet composition, diet breadth and trophic position of *C. carpio* and local fish fauna, and to assess diet overlap between fish fauna from sites with different habitat characteristics during the wet and the dry seasons.

**Materials and methods.** We assessed the diet of *C. carpio* and local fish fauna in six sites during the wet and the dry seasons. Stomach content analysis was carried out separately for each length class. The importance of each item was estimated by the index of relative importance (IRI) and the omnivory index was used to assess the feeding behaviour. The trophic guild and trophic position were determined using the TrophLab software and stable isotope analysis. Diet breadth was calculated by Levin's Index and diet overlap by the Horn's Index. Fish dorsal muscle and water hyacinth tissues were obtained from nitrogen isotope signature analysis.

**Results.** We found that *C. carpio* is an omnivorous fish that feeds in shallow areas with water hyacinth cover and rooted macrophytes, consuming mainly detritus and plant debris (>60%). However,  $\delta^{15}\text{N}$  values indicate that *C. carpio* is also a secondary consumer because it also ingests invertebrates associated with plant debris. The carp diet overlaps with native blackfin, *Goodea atripinnis* Jordan, 1880, at most sites. Small carp (<120 mm SL) overlapped with the *Chirostoma* spp. diet, as well as the introduced *Oreochromis* spp. at shallower sites with surface water hyacinth and with plant detritus at the bottom.

**Conclusion.** Lago de Pátzcuaro is facing trophic food web reduction that seems to be a more serious problem than feeding competition between the common carp and other fish species.

**Keywords:** Lentic systems, habitat characteristics, native species, trophic ecology, feeding interactions, gut content analysis, stable isotope analysis

## INTRODUCTION

The common carp, *Cyprinus carpio* Linnaeus, 1758, is a fish species that has been widely introduced for farming and commercial fishing purposes. It was probably one of

the first species to be dispersed by humans (Billard 1999, Vilizzi 2012) because its capability to establish itself readily in freshwater ecosystems in subtropical and temperate regions (Zambrano et al. 2006). In Mexico, common carp

\* Correspondence: Dr Javier Caraveo-Patíño, Centro de Investigaciones Biológicas del Noroeste (CIBNOR), Instituto Politécnico Nacional 195, Col. Playa Palo de Santa Rita Sur, La Paz, B.C.S. 23096, México, phone +52 612-123-8484, fax: +52-612-125-3625, e-mail: (JCP) jcaraveo04@cibnor.mx, (JPRH) ramirezherrejon@gmail.com, (RME) rmoncayo@hotmail.com, (EFB) ebalart04@cibnor.mx, (LAGC) w\_icho\_beto@hotmail.com, (BVR) gueko\_rana@hotmail.com, (RAV) alvareyna@yahoo.com, (ROM) rosaormu@yahoo.com.mx.

was introduced and cultivated for human consumption as one of the solutions to increase animal-protein intake in rural human communities by national programs during the 1930s (Zambrano and Macías-García 2000). The common carp currently inhabits most freshwater systems of Mexico (>80%) and is established in the larger lakes of central Mexico such as Lago de Chapala, Lago de Cuitzeo, Lago de Pátzcuaro, Lago de Yuriria, and Lago de Xochimilco (Anonymous 2010). *Cyprinus carpio* was released accidentally into Lago de Pátzcuaro in 1974 from aquaculture pens (Rosas 1976) and currently it is found throughout the lake with spatial segregation, with increased abundance in the southern zone (Ramírez Herrejón unpublished\*).

The feeding behaviour of the common carp can cause increased sediment re-suspension and can directly affect fish habitat and destroy aquatic vegetation cover, and increasing water turbidity in shallow lakes (Zambrano et al. 2001, Leung et al. 2002, Scheffer et al. 2003, Özbay 2008). This kind of changes in habitat characteristics can indirectly cause a cascade of alterations on trophic webs (Khan 2003).

*Cyprinus carpio* is an omnivorous fish well adapted for bottom feeding; depending on the availability it can consume a wide range of small items like worms, molluscs, zooplankton, aquatic vegetation, plant debris, detritus, and insects (Summerfelt et al. 1971, Eder and Carlson 1977, Crivelli 1981, Powles et al. 1983, Chapman and Fernando 1994, Elías-Fernández and Navarrete-Salgado 1998, Colautti and Remes Lenicov 2001). The diversity of its diet makes this species resistant to food web change and capable of inhabiting a wide variety of habitats (Koehn 2004, Wolfe et al. 2009, Weber and Brown 2011). However, despite knowing the common carp feeding habits, understanding is limited regarding the trophic interrelations with the local fish biota co-inhabiting the lakes.

Lago de Pátzcuaro harbours native and introduced fish with different trophic specialization types such as, herbivores, carnivores (zooplanktivorous, insectivorous, and piscivorous) and omnivores (Rosas 1976, Berlanga-Robles et al. 2002). The physical and chemical water properties of this lake are well described (Alcocer and Bernal-Brooks 2002) and their habitat too (Ramírez-Herrejón et al. 2013). For these reasons, we postulated that Lago de Pátzcuaro probably would be a good model for assessing trophic interrelations between common carp and the lake fish fauna as well as the associations of habitat characteristics with trophic interrelations. This study hypothesizes that *C. carpio* is a omnivorous generalist fish with a diet that overlaps with all fish taxa at all sites regardless of habitat characteristics. To test this hypothesis, we characterized diet composition, diet breadth, trophic position and diet overlap between fish fauna from sites with different habitat characteristics during the wet and the dry seasons.

## MATERIALS AND METHODS

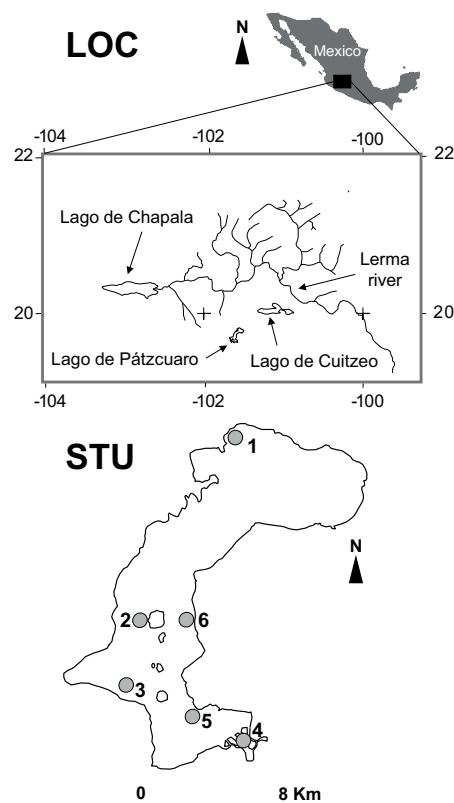
**Study area.** Lago de Pátzcuaro is located in the north-

central part of the state of Michoacán, Mexico (19°27'N, 101°26'W and 19°44'N, 101°53'W) 2038 m above sea level (Fig. 1). The lake belongs to the hydrologic region of the Lerma-Chapala, as part of the Mexican Volcanic Belt. The lake surface has a maximum area of 116 km<sup>2</sup> and a maximum depth of 12.2 m (Gomez-Tagle Chavez et al. 2002). The average depth is 4.9 m, and watershed covers of 9340 km<sup>2</sup> (Bravo-Espinosa et al. 2006). During September and November 2009 (wet season) and February and June 2010 (dry season), we sampled six sites the water properties (total dissolved solids, transparency, and turbidity) and habitat characteristics (depth, floating vegetation cover, and bottom type) as described by Ramírez-Herrejón et al. (2013):

- San Jerónimo (SAJ) (19°40'40.4"N, 101°36'16.9"W);
- Ucazanastacua (UCA) (19°35'51.1"N, 101°37'58.5"W);
- Napízaro (NAP) (19°35'20.8"N, 101°40'12.7"W);
- Ihuatzio (IHU) (19°35'35.1"N, 101°40'45.2"W) and;
- Embarcadero (EMB) (19°33'0.6"N, 101°37'30.7"W)

(Fig. 1).

The native ichthyofauna of the lake (Rosas 1976, Berlanga-Robles et al. 2002) includes: the carnivore bull-



**Fig. 1.** Location of Lago de Pátzcuaro, Mexico (LOC) and study sites (STU): 1 = San Jerónimo (SAJ), 2 = Ucazanastacua (UCA), 3 = Napízaro (NAP), 4 = Ihuatzio (IHU), 5 = Embarcadero (EMB); Gray circles are the collection areas (~500 m × ~100 m); This map was taken and modified from Ramírez-Herrejón et al. 2013 and we thank for the reproduction permission given by the Revista de Biología Tropical

\* Ramírez Herrejón J.P. 2013. Ecología trófica de *Cyprinus carpio* y su relación con la estructura comunitaria de peces del Lago de Pátzcuaro, Michoacán. Doctorate thesis. Centro de Investigaciones Biológicas del Noroeste. La Paz, B.C.S., México

dog goodeid, *Allophorus robustus* (Bean, 1892) (insectivorous, piscivorous), the pike silverside, *Chirostoma estor* Jordan, 1880 (zooplanktivorous, insectivorous, piscivorous), the bigeye silverside, *Chirostoma grandocule* (Steindachner, 1894), the slender silverside, *Chirostoma attenuatum* Meek, 1902, the Patzcuaro silverside, *Chirostoma patzcuaro* Meek, 1902 (zooplanktivore), the Patzcuaro allotoca, *Allotoca diazi* (Meek, 1902) (zooplanktivorous, insectivore), the opal allotoca, *Allotoca dugesii* (Bean, 1887) (insectivore); the herbivore blackfin goodea, *Goodea atripinnis* Jordan, 1880, the olive skiffia, *Skiffia lermæ* Meek, 1902, the omnivore Patzcuaro chub, *Algansea lacustris* Steindachner, 1895, and the lerma livebearer, *Poeciliopsis infans* (Woolman, 1894). Other introduced fish also inhabit the lake, such as the carnivore largemouth bass, *Micropterus salmoides* (Lacepède 1802) (zooplanktivorous, insectivorous, piscivorous) and the omnivore *Oreochromis* spp.

**Fish sampling and trophic analysis.** Fish were captured during the day (0800–1300 h) with two seines net, one (75 m long, 5 m wide, 10 mm mesh) to capture small sized fish (<100 mm of standard length [SL]) and the other (150 m long, 9 m wide, 40 mm mesh) to capture large fish (>100 mm SL). Specimens were labelled and transported in ice to minimise enzymatic digestion (Cailliet et al. 1986). Standard length [mm], weight [g], and gastric repletion for each individual were measured. Fish were identified by species except individuals in the genera *Oreochromis* and *Chirostoma*. At least two species of *Oreochromis* were introduced to Lago de Patzcuaro: blue tilapia, *O. aureus* (Steindachner, 1864) and Nile tilapia *O. niloticus* (Linnaeus, 1758) (see Gaspar Dillanes et al. 2000, Berlanga-Robles et al. 2002) but much hybridization has occurred, making positive identification at the species level difficult. Among *Chirostoma*, taxonomic differences between four native species and their taxonomic status are currently in dispute: *C. grandocule*, *C. patzcuaro*, *C. attenuatum*, and *C. estor* and one introduced species, the shortfin silverside, *Chirostoma humboldtianum* (Valenciennes, 1835). (Barriga-Sosa et al. 2002, Bloom et al. 2009), thereby making presently specific determination not possible. Accumulated prey diversity was measured, using Simpson's index for a finite population to determine the minimum number of guts to characterize the feeding habits of each fish taxa (Magurran 2004). We chose the Simpson's Index because it is a Type II index, or sensitive to changes in the more abundant taxa, and we want to emphasize the most representative food items than the rare or incidental prey. The curve became asymptotic at 12 individuals for *Cyprinus carpio*, 19 for *Oreochromis* spp., 15 for *Chirostoma* spp., 22 for *Goodea atripinnis*, and 8 for *Allophorus robustus*. Fewer individuals by taxa at each site were not included in trophic analysis. We analyzed a total of 1744 specimens including all species, 938 guts during the wet season, and 806 during the dry season. A modified version of the quadrant method (Hynes 1950) for gut content analysis was used. Prey items were identified to equivalent taxa level

(Edmondson 1959, Pennak 1978). We only found remains of insects and it was not possible the identification of insects at a lower taxonomical level. A modified version of the index of relative importance (IRI) of Pinkas et al. (1971) proposed by Yáñez-Arancibia et al. (1976) was used:

$$IRI = FA \cdot 100^{-1}$$

where:  $F$  is the frequency of occurrence, and  $A$  is the area, following Ramírez-Herrejón et al. (2013). This method is used when the gut content is constituted by small feeding components (diatoms, copepods, ostracods, rotifers, cladocerans) or when its quantification is not possible (detritus, plant debris) (Vega Cendejas 1990, Canto-Maza and Vega-Cendejas 2008). The graphical method using the  $A$  [%] and  $F$  [%] proposed by Costello (1990) and IRI expressed as percentages (Cortés 1997) were used to describe and compare easily the importance of prey. Individuals of small sized (<100 mm SL; *Goodea atripinnis*, *Allophorus robustus*, *Chirostoma* spp.) were categorized in 5 mm intervals while large fish (>100 mm SL; *Cyprinus carpio*, *Oreochromis* spp.) were categorized in 10 mm intervals to determine a probable diet change with fish growth. The standardized Levins' Index ( $B_A$ ) was used to calculate diet breadth (values from 0 to 1). Values of  $B_A < 0.60$  consider the fish to be specialists and a value of  $B_A > 0.60$  denotes a generalist fish (Krebs 1989). Feeding behaviour was described by the Omnivory Index (OI); it was calculated as the variance of the trophic levels of a consumer's preys (Christensen and Pauly 1992). The trophic level of each fish taxa was estimated using the TrophLab Program (Pauly et al. 2000). It includes the number of groups in the diet, the prey fraction of the diet (IRI%), and the trophic level of the prey. The diet overlap between fish taxa was assessed with the index of Horn (Krebs 1989). Horn's index varies from 0 when there is no common use of feeding resources to 1.0 when there is complete resource overlap; it is considered as significant overlap when the value exceeds 0.60 (Wallace 1981). Some studies have argued that gut content analysis is biased because it considers ingested but not assimilated food (Bearhop et al. 2004). It is known that  $\delta^{15}\text{N}$  is an accurate indicator of fish trophic position because it reflects assimilated food and shows progressive enrichment (3‰ to 5‰) from feeding components (Jardine et al. 2003). For this reason, the trophic position of each fish taxa was corroborated with nitrogen isotope analyses. Approximately 1 g of dorsal muscle tissue was obtained from fish (>30 mm SL) and frozen for later isotope analysis. Phytoplankton were obtained using a 64 µm mesh net during dry and wet seasons, but these samples had important quantities of young zooplankton. Separation between phytoplankton and zooplankton was not accurate, for that reason 1 g of water hyacinth (*Eichornia crassipes*) root tissue was used to represent the primary productivity of lake. Stable isotope analysis was performed at the University of California-Davis Stable Isotope Facility. Nitrogen stable isotope ratios ( $\delta^{15}\text{N}$ ) are expressed in delta ( $\delta$ ) notation as parts per thousand (‰). Mean standard error was < 0.1 ‰ for  $\delta^{15}\text{N}$ . We estimated the fish

trophic position (TP) using  $\delta^{15}\text{N}$  following Vander Zanden and Rasmussen (1999) equation:

$$\text{TP} = (\delta^{15}\text{N}_S - \delta^{15}\text{N}_{\text{PP}} \cdot \Delta_{\text{TP}}) + 1$$

where;  $\delta^{15}\text{N}_S$  is the value of the fish tissue, and  $\delta^{15}\text{N}_{\text{PP}}$  is the value of primary productivity. We used 3.4‰ as trophic level enrichment ( $\Delta_{\text{TP}}$ ), as reported by Vander Zanden et al. (2003). The information of *Poeciliopsis infans* about trophic guild, niche breadth, trophic position and stable isotope analysis were taken from Ramírez-Herrejón et al. (2013).

**Data analysis.** Non-parametric Kruskal–Wallis rank sums-test was used to detect differences of area of food items ( $\text{mm}^2$ ),  $\delta^{15}\text{N}$  values, and trophic position among sites. Analyses were done for wet and dry seasons. The sum of the ranks was calculated for each group. Then the test statistic  $H$  was calculated to represent the variance of the ranks among groups. But, if the null hypothesis is true, the  $P$  value corresponding to  $\chi^2$  equal to  $H$  (McDonald 2009). For this reason, we use  $\chi^2$  in the results. If significant differences were found, multiple post-hoc test comparisons were made using the Tukey–Kramer HSD—honestly significant difference— (Zar 1999). Both analyses were performed with JMP 3.1.6.2 software (SAS Institute).

**Ethical issues.** The presently reported study has been carried out in accordance with the Mexico's government regulations on experiments on animals.

## RESULTS

We found 12 food items and about 90% of the guts were at least 50% full, ensuring a good description of the diet.

A total of 384 individuals of *Cyprinus carpio* from 30 to 450 mm SL were analyzed; 237 during the wet season and 147 during the dry season. We found nine food items. Individuals of *C. carpio* were grouped into three size classes (Table 1): Cc1 (< 120 mm SL), Cc2 (120–230 mm SL), Cc3 (>230 mm SL). The three size groups were mainly distributed in the southern zone of the lake at Embarcadero (EMB) and Ihuatzio (IHU) during the wet and the dry season (Fig. 2).

*Cyprinus carpio* (Cc1) fed mainly on detritus (Table 2, Fig. 3). Zooplankton (copepods and cladocerans) were secondary items found during the wet season at all sites where it was present. Detritus and zooplankton were the preferred

food at EMB and IHU during the dry season. Maximum amount ( $137.6 \pm 98.5 \text{ mm}^2$ , 64%) of detritus was found at EMB during the wet season and ( $47.1 \pm 29.3 \text{ mm}^2$ , 66%) for zooplankton at IHU during the dry season. The smallest common carp showed intake variations by site on incidental items; they fed more plant debris in UCA ( $31.4 \pm 26.1 \text{ mm}^2$ , 16%) than NAP ( $0.4 \pm 1.8 \text{ mm}^2$ , 0.4%) during the wet season ( $\chi^2 = 13.25$ , degrees of freedom (DF) = 1,  $P < 0.01$ ) and more chironomids in NAP ( $16 \pm 13.3 \text{ mm}^2$ , 14%) than in UCA ( $2.2 \pm 4.5 \text{ mm}^2$ , 1%) during the wet season ( $\chi^2 = 5.97$ , DF = 1,  $P < 0.02$ ). At this size the common carp was classified as omnivorous according to the IRI, Costello graph and OI (Table 2 and 3, Fig. 3).

*Cyprinus carpio* (Cc2) fed mainly on detritus and plant debris and secondary on zooplankton at EMB, IHU, NAP, and UCA during the wet and dry seasons, but filamentous algae and cladocerans were principally food items at SAJ where detritus and rotifers had secondary importance (Table 2, Fig. 3). The detritus recorded its maximum value ( $142.4 \pm 81.7 \text{ mm}^2$ , 71%) at EMB ( $\chi^2 = 101.37$ , DF = 4,  $P < 0.01$ ) and ( $12.6 \pm 9.1 \text{ mm}^2$ , 23%) for zooplankton at SAJ ( $\chi^2 = 67.19$ , DF = 4,  $P < 0.01$ ); during the wet season. Medium sized *Cyprinus carpio* fed principally on rotifers ( $14.4 \pm 14 \text{ mm}^2$ , 14%), fish scales ( $15.2 \pm 21.2 \text{ mm}^2$ , 15%), and detritus ( $18.4 \pm 26.1 \text{ mm}^2$ , 18%) in SAJ during the wet season ( $\chi^2 = 25.73$ , DF = 4,  $P < 0.01$ ). This size fish also fed more filamentous algae ( $32 \pm 11.6 \text{ mm}^2$ , 31%) and less insects ( $19.3 \pm 4.6 \text{ mm}^2$ , 5%) and plant debris ( $19.3 \pm 4.6 \text{ mm}^2$ , 11%) at SAJ during both seasons ( $\chi^2 = 52.65$ , DF = 4,  $P < 0.01$ , wet season;  $\chi^2 = 145.42$ , DF = 3,  $P < 0.01$ , dry season). Chironomids consumption ( $26.3 \pm 15.9 \text{ mm}^2$ ) was higher at NAP during the wet season ( $\chi^2 = 41.04$ , DF = 4,  $P < 0.01$ ). At this size the common carp was classified as omnivorous according to the IRI, Costello graph and the OI (Table 2 and 3, Fig. 3).

*Cyprinus carpio* (Cc3) fed mainly on detritus and secondary on plant debris, zooplankton; chironomids were incidental items at all sites during wet and dry season (Table 2). The detritus recorded its maximum value ( $217 \pm 108.9 \text{ mm}^2$ , 81%) at EMB during the wet season. The quantity of feeding resources consumed by the biggest sized carp was similar between sites in both seasons. At this size the common

**Table 1**  
Abundance of each food items by size of *Cyprinus carpio* in Lago de Pátzcuaro, Mexico

Food item	Total surface [mm <sup>2</sup> ]	$\chi^2$	DF	$P$	Standard length class [mm]					
					<120		120–230		>230	
					mm <sup>2</sup>	%	mm <sup>2</sup>	%	mm <sup>2</sup>	%
Copepods	9 506	41.24	2	< 0.001	$34.7 \pm 28.7^a$	64.50	$14.7 \pm 19.7^b$	27.32	$4.4 \pm 8.8^c$	8.18
Cladocerans	9 978	30.95	2	< 0.001	$32.9 \pm 29.9^a$	60.37	$15.7 \pm 19.6^b$	28.81	$5.9 \pm 10.4^c$	10.83
Plant debris	16 592	10.94	2	< 0.001	$23.46 \pm 38.1^a$	15.64	$45.07 \pm 49.57^a$	30.06	$81.39 \pm 50.53^b$	54.28
Detritus	49 816	26.33	2	< 0.001	$52.6 \pm 46.7^a$	19.61	$80.7 \pm 67.8^b$	30.09	$134.9 \pm 92.7^c$	50.30

*Cyprinus carpio*  $N = 301$ ;  $\chi^2$  = chi-squared test, DF = degrees of freedom; Abundance was estimated as  $\text{mm}^2$  in the quadrant method; Total surface = total surface represented by a food item; Abundance values are mean  $\pm$  standard deviation; Superscripts *a*, *b*, *c* refer to differences in data variation between sites (Tukey–Kramer honestly significant difference [HSD] post hoc test,  $P < 0.05$ ).

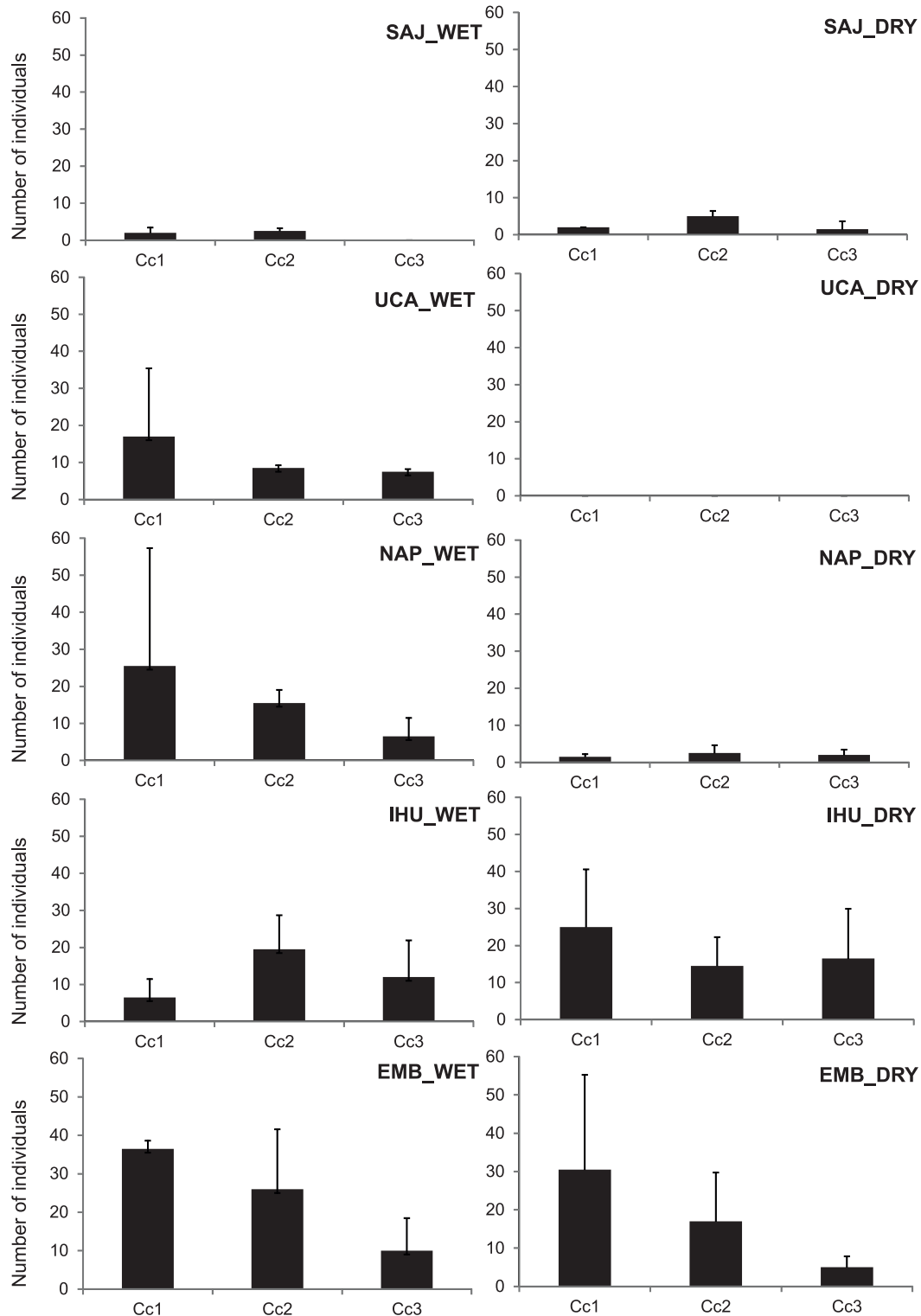


carp was classified as omnivorous according to the IRI, Costello graph and the OI (Tables 2 and 3, Fig. 3).

*Allophorus robustus* ingested mainly insects ( $89.6 \pm 54.1 \text{ mm}^2$ , 92%) where 12% ( $20 \pm 14.2 \text{ mm}^2$ ) were chironomids (Table 2). This species was included in the present analysis only

at SAJ during the wet season; it was determined to be carnivorous, according to the IRI and Costello graph (Table 2, Fig. 3).

We analyzed 133 individuals of *Oreochromis* spp. from 20 to 160 mm SL, 62 during the wet season and 71 during the dry season. *Oreochromis* spp. fed mainly on



**Fig. 2.** Size frequency of the three size groups of *Cyprinus carpio* in five study sites in Lago de Pátzcuaro, Mexico, during wet (WET) and dry season (DRY); Cc1 = *Cyprinus carpio* (< 120 mm SL), Cc2 = *Cyprinus carpio* (120–230 mm SL), Cc3 = *Cyprinus carpio* (> 230 mm SL), SAJ = San Jerónimo, UCA = Ucazanastacua, NAP = Napízaro, IHU = Ihuatzio, EMB = Embarcadero; Columns show the mean  $\pm$  SD of number of individuals

detritus, secondary on filamentous algae, and zooplankton were incidental items during wet and dry season (Table 2). The detritus recorded its maximum value ( $57.7 \pm 21.5 \text{ mm}^2$ , 96%) at NAP during the dry season. This species was determined to be omnivorous according to the IRI, Costello graph and the OI (Table 2 and 3, Fig. 3).

A total of 468 gut content of *Chirostoma* spp. from 35 mm to 70 mm SL was analyzed; 225 during the wet season and 243 during the dry season. Silverside fishes fed generally on copepods, cladocerans, scales, arachnids, and insects (Table 2, Fig. 3). The maximum value ( $25.2 \pm 33 \text{ mm}^2$ , 89%) of zooplankton was found at EMB during the dry season and fish scales ( $703.1 \pm 96.4 \text{ mm}^2$ , 37%) at SAJ during the dry season. *Chirostoma* spp. consumed more cladocerans ( $44.8 \pm 54.5 \text{ mm}^2$ , 36%) at IHU ( $\chi^2 = 85.19$ ,  $DF = 4$ ,  $P < 0.01$ ) and more scales at NAP ( $145.1 \pm 157.2 \text{ mm}^2$ , 89%) during the dry season ( $\chi^2 = 86.67$ ,  $DF = 4$ ,  $P < 0.01$ ). Silversides fed more chironomids at SAJ ( $7 \pm 14.8 \text{ mm}^2$ , 5%), UCA ( $5.7 \pm 12.5 \text{ mm}^2$ , 4%), NAP ( $7.5 \pm 36.5 \text{ mm}^2$ , 5%) also during the wet season ( $\chi^2 = 81.56$ ,  $DF = 4$ ,  $P < 0.01$ ). *Chirostoma* spp. was determined to be carnivorous according to the IRI and Costello graph (Table 2, Fig. 3).

We analyzed 85 specimens of *Goodea atripinnis* from 30 mm to 120 mm SL, 35 during the wet season and 50 during the dry season. *G. atripinnis* fed generally on fila-

mentous algae, detritus, zooplankton, and insects (Table 2, Fig. 3). The filamentous algae recorded its maximum value ( $28.2 \pm 40.9 \text{ mm}^2$ , 77%) at IHU during the wet season, detritus ( $29.6 \pm 11.8 \text{ mm}^2$ , 67%) at SAJ during the wet season, zooplankton (36%) at SAJ during the dry season and insects (12%) at SAJ during the dry season. During the dry season *G. atripinnis* fed more on detritus ( $37.3 \pm 18.4 \text{ mm}^2$ , 18%) at EMB ( $\chi^2 = 31.3$ ,  $DF = 5$ ,  $P < 0.01$ ), and more insects at SAJ ( $7.3 \pm 4.6 \text{ mm}^2$ , 12%) and IHU ( $2.6 \pm 4.8 \text{ mm}^2$ , 6%) ( $\chi^2 = 21.92$ ,  $DF = 5$ ,  $P < 0.01$ ). Filamentous algae was important ( $52 \pm 18.5 \text{ mm}^2$ , 46%) in the diet at UCA and less ( $5.2 \pm 8.4 \text{ mm}^2$ , 20%) at EMB ( $\chi^2 = 19.53$ ,  $DF = 5$ ,  $P < 0.006$ ) during we season. *G. atripinnis* was determined to be omnivorous according to the IRI, Costello graph and the OI (Tables 2 and 3, Fig. 3).

*Cyprinus carpio* was categorized as a specialist according Levins' niche breadth when combining all sites and both seasons ( $0.35 \pm 0.1$ ) as well for any fish size ( $Cc1 = 0.46 \pm 0.1$ ;  $Cc2 = 0.33 \pm 0.1$ ;  $Cc3 = 0.26 \pm 0.1$ ). *Oreochromis* spp. and *A. robustus* were determined to be a specialist. *Chirostoma* spp. was a specialist during the wet season and a generalist only at SAJ and IHU during the dry season. *G. atripinnis* behaved as a generalist only at UCA during the wet season and at SAJ and NAP during the dry season (Table 4).

Table 2

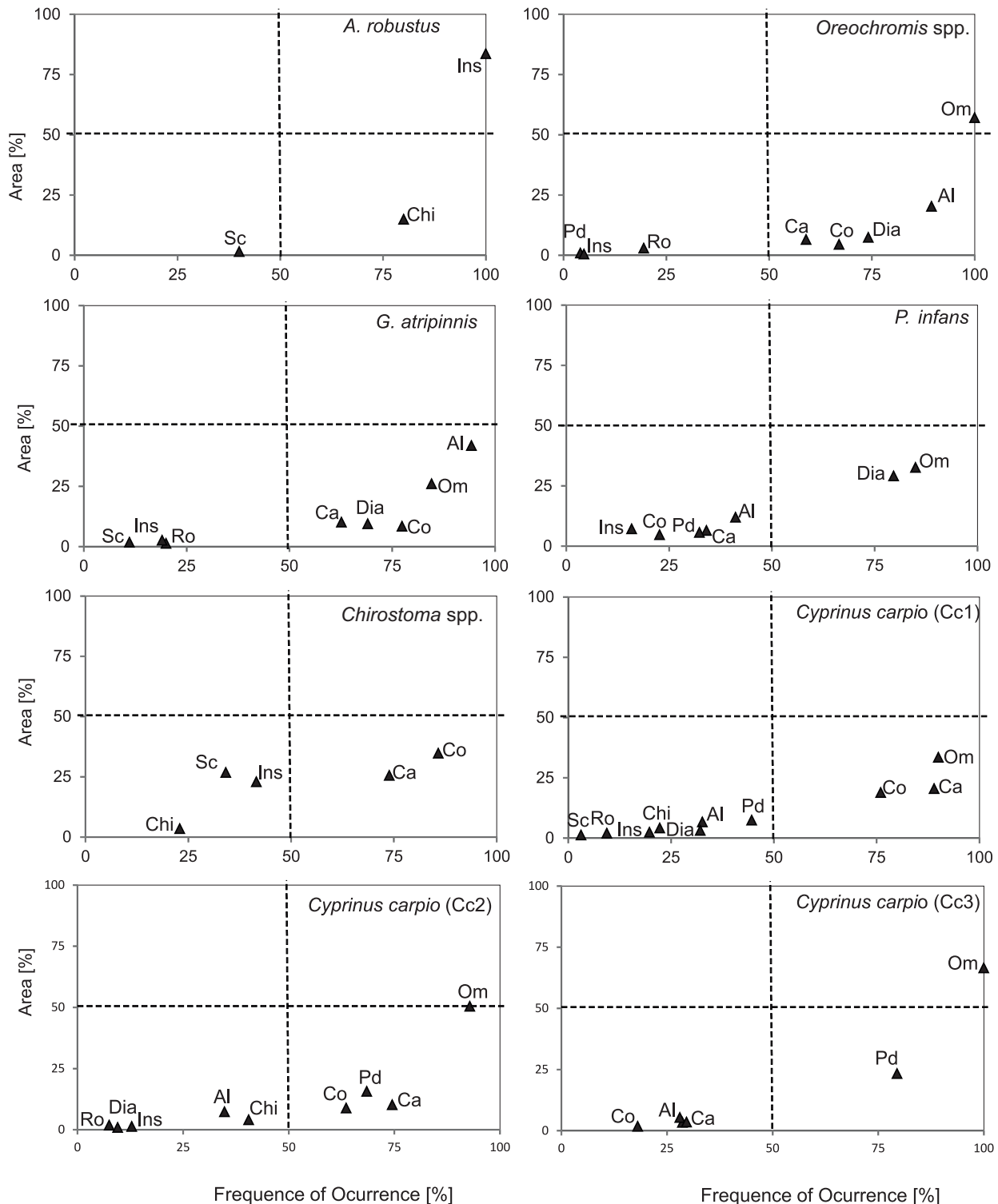
Index of relative importance (IRI) [%] for each food item per fish species by site during wet and dry seasons in Lago de Pátzcuaro

		Copepods	Cladocerans	Rotifers	Ostracods	Fish scales	Insects	Chironomids	Diatoms	Filamentous algae	Plant detritus	Organic matter
San Jerónimo	Cc2	1.33 [10.71]	21.06 [8.82]	11.97	—	8.43	2.66 [2.36]	—	[4.83]	44.35	[9.03]	10.20 [64.25]
	Cx	59.44 [29.51]	28.36 [27.44]	—	[5.71]	10.01 [37.34]	—	2.19	—	—	—	—
	Ga	0.91 [23.11]	18.52 [12.92]	—	—	—	[11.55]	—	2.72 [5.15]	11.15 [26.26]	—	67.70 [21.01]
	Ar	—	—	—	—	0.6	84.21	12.03	—	—	—	3
Ucapanastacua	Cc1	15.7	14.45	—	—	—	—	—	1.74	—	13.7	54.41
	Cc2	8.22	8.49	—	—	—	—	3.11	—	—	18.19	61.99
	Cc3	—	1.95	—	—	—	—	—	—	2.54	20.1	75.41
	Cx	59.76 [37.49]	35.88 [36.62]	—	[2.04]	3.03 [17.93]	[5.92]	1.35	—	—	—	—
	Ga	10.64	11.35	—	—	—	—	—	20.57	46.1	—	11.35
Nápipazaro	Cc1	20.78	12.54	—	—	—	—	11.91	2.59	—	—	52.19
	Cc2	8.23	9.49	—	—	—	—	11.38	—	8.38	6.91	55.62
	Cc3	—	—	—	—	—	—	6.03	—	—	15.07	78.9
	Ox	2.92 [1.41]	4.29 [2.28]	—	—	—	—	—	8.81	19.06 [1.34]	—	64.92 [94.96]
	Cx	89.21 [28.02]	9.41 [25.42]	—	[2.01]	[41.44]	[3.11]	1.38	—	—	—	—
	Ga	1.28[15.69]	2.40 [11.36]	—	—	—	—	9.77 [2.93]	59.58 [41.90]	—	—	26.97 [28.12]
Ihuatzio	Cc1	21.87 [31.65]	22.71 [33.77]	—	—	—	—	1.96	2.15 [4.73]	—	4.09 [6.35]	47.03 [23.50]
	Cc2	8.49 [8.03]	7.78 [9.71]	—	—	—	—	1.72 [5.07]	—	—	23.34 [19.08]	58.67 [58.11]
	Cc3	[3.51]	1.45 [4.38]	—	—	—	—	2.20 [5.67]	—	1.02	19.53 [20.17]	75.80 [66.28]
	Ox	6.41 [14.03]	7.59 [3.04]	[13.09]	—	—	[1.75]	—	7.25 [6.72]	23.62 [23.38]	—	55.13 [37.99]
	Cx	14.46 [8.73]	15.37 [31.62]	—	—	2.77 [11.64]	67.39 [48]	—	—	—	—	—
	Ga	8.08 [8.82]	3.42 [8.98]	[2.95]	—	[1.60]	[2.57]	—	3.59 [3.53]	77.21 [58.71]	—	7.70 [12.83]
Embarcadero	Cc1	8.55 [26.81]	11.85 [24.24]	—	—	—	—	2.56 [1.53]	[2.22]	4.14 [6.91]	8.17 [7.91]	64.73 [30.38]
	Cc2	3.18 [6.39]	2.94 [8.36]	—	—	—	—	1.85 [4.28]	—	1.37 [2.40]	19.19 [25.62]	71.46 [52.95]
	Cc3	[1.38]	—	—	—	—	—	1.31	—	—	17.65 [33.63]	81.05 [64.99]
	Ox	1.72 [4.02]	2.60 [3.17]	1.44	—	—	—	—	8.83 [9.47]	17.01 [22.73]	—	68.40 [60.61]
	Cx	49.24 [28.18]	46.63 [61.11]	—	—	4.13 [7.55]	—	[3.16]	—	—	—	—
	Ga	[12.18]	3.01 [13.16]	2.45 [1.25]	—	[2.95]	—	—	7.34 [2.34]	22.09 [55.87]	—	65.11 [12.25]

Data from dry season are shown in square brackets; Cc1 = *Cyprinus carpio* (<120 mm SL), Cc2 = *Cyprinus carpio* (120–230 mm SL), Cc3 = *Cyprinus carpio* (>230 mm SL), Ox = *Oreochromis* spp., Cx = *Chirostoma* spp., Ga = *Goodea atripinnis*, Ar = *Allophorus robustus*.

*Cyprinus carpio* at any of the three sized-groups was determined to be a primary consumer according to the TROPH Program during wet and dry season at all sites (Table 5). However, based on  $\delta^{15}\text{N}$ , *C. carpio* (Cc1) was considered as a secondary consumer at IHU and EMB during the wet and dry seasons; at Cc2 it was found to be

a primary consumer only at SAJ in both seasons, and at Cc3 only at UCA during the wet season; in the other sites it behaved as a secondary consumer (Table 6). *Chirostoma* spp. was determined to be secondary consumer during the wet and dry seasons by TROPH Program and  $\delta^{15}\text{N}$  analysis. *Goodea atripinnis* fall as pri-



**Fig. 3.** The importance of food items for all fish taxa in Lago de Pátzcuaro, Mexico, as determined by the Costello analysis; Sc = fish scales, Chi = Chironomids, Ins = insects, Pd = plant detritus, Ro = rotifers, Ca = cladocerans, Co = copepods, Dia = Diatoms, Al = filamentous algae, Om = organic matter

mary consumer according to TROPH Program during the wet and dry seasons; based on  $\delta^{15}\text{N}$ , it behaved as a secondary consumer at IHU and EMB during the wet and dry seasons. The trophic position of *Allophorus robustus* and *Oreochromis* spp. were similar using both TROPH Program and  $\delta^{15}\text{N}$  (Table 5 and 6).

The  $\delta^{15}\text{N}$  mean of water hyacinth root tissue was  $8.2 \pm 0.3\text{‰}$ . The  $\delta^{15}\text{N}$  mean of each fish taxa by site and both seasons are shown in Table 7. The  $\delta^{15}\text{N}$  of muscle and trophic positions based on nitrogen isotopic signatures of *Oreochromis* spp. were higher at EMB during the dry season ( $\chi^2 = 11.29$ ,  $DF = 2$ ,  $P = 0.03$ , in both analyses) and was less at NAP during the wet season ( $\chi^2 = 8.26$ ,  $DF = 3$ ,  $P = 0.04$ ). For *Chirostoma* spp., the lowest value of  $\delta^{15}\text{N}$  of muscle ( $\chi^2 = 19.95$ ,  $DF = 5$ ,  $P < 0.01$ ) and trophic positions ( $\chi^2 = 19.87$ ,  $DF = 5$ ,  $P < 0.01$ ) were at EMB (Tables 7 and 8). *Goodea atripinnis* had the highest value of  $\delta^{15}\text{N}$  ( $\chi^2 = 11.88$ ,  $DF = 5$ ,  $P = 0.03$ ) and trophic position ( $P = 0.03$ ,  $DF = 5$ ,  $\chi^2 = 11.90$ ) at EMB and the lowest at NAP. At

SAJ, the lowest value of  $\delta^{15}\text{N}$  of muscle and trophic position were found during the wet season for *C. carpio* (Cc2) ( $\chi^2 = 12.82$ ,  $DF = 3$ ,  $P < 0.01$ , both analyses).

*Cyprinus carpio* (Cc2) diet overlapped with *Goodea atripinnis* at SAJ during both wet and dry season (Table 8). The three sizes of *C. carpio* overlapped its diet between themselves and with *Poeciliopsis infans* at UCA during the wet season. At NAP and IHU, the three sizes of *C. carpio* overlapped its diet between each other, *Oreochromis* spp. and *Poeciliopsis infans*. *Cyprinus carpio* (Cc2) overlapped its diet with *Goodea atripinnis* at NAP during the wet season and *C. carpio* (Cc1) at IHU during the dry season. At EMB, *C. carpio* (Cc1) overlapped its diet with all fish taxa during the dry season and *C. carpio* (Cc2 and Cc3) with *Oreochromis* spp., *Poeciliopsis infans* and *Goodea atripinnis* during the wet season (Table 8).

Table 3

Omnivory index for fish taxa by site during both seasons in Lago de Pátzcuaro, Mexico

	Site	Cc1	Cc2	Cc3	<i>Oreochromis</i> spp.	<i>Goodea atripinnis</i>
Wet season	San Jerónimo	—	0.31	—	—	0.39
	Ucazanastacua	0.36	0.39	0.44	—	0.38
	Napízaro	0.3	0.36	0.42	0.42	0.44
	Ihuatzio	0.31	0.39	0.44	0.4	0.41
	Embarcadero	0.37	0.42	0.44	0.43	0.43
Dry season	San Jerónimo	—	0.38	—	—	0.32
	Ucazanastacua	—	—	—	—	—
	Napízaro	—	—	—	0.44	0.36
	Ihuatzio	0.25	0.38	0.4	0.34	0.37
	Embarcadero	0.29	0.39	0.44	0.42	0.36

Cc1 = *Cyprinus carpio* (<120 mm SL), Cc2 = *Cyprinus carpio* (120–230 mm SL), Cc3 = *Cyprinus carpio* (>230 mm SL).

Table 4

Diet breadth for fish taxa by site during both seasons in Lago de Pátzcuaro, Mexico

		Cc1	Cc2	Cc3	<i>Oreochromis</i> spp.	<i>Chirostoma</i> spp	<i>Goodea atripinnis</i>	<i>Allophorus robustus</i>
Wet season	SAJ	—	0.44	—	—	0.41	0.24	0.12
	UCA	0.44	0.32	0.21	—	0.35	0.6	—
	NAP	0.47	0.37	0.27	0.28	0.12	0.32	—
	IHU	0.41	0.35	0.15	0.41	0.3	0.15	—
	EMB	0.24	0.16	0.22	0.19	0.58	0.27	0.24
Dry season	SAJ	—	0.25	—	—	0.75	0.8	—
	UCA	—	—	—	—	0.55	—	—
	NAP	—	—	—	0.03	0.54	0.6	—
	IHU	0.65	0.38	0.26	0.52	0.61	0.23	—
	EMB	0.54	0.35	0.43	0.33	0.39	0.29	0.54

Cc1 = *Cyprinus carpio* (<120 mm SL), Cc2 = *Cyprinus carpio* (120–230 mm SL), Cc3 = *Cyprinus carpio* (>230 mm SL); SAJ = San Jerónimo, UCA = Ucazanastacua, NAP = Napízaro, IHU = Ihuatzio, EMB = Embarcadero.



## DISCUSSION

*Cyprinus carpio* behaves as an omnivorous fish in Lago de Pátzcuaro. Its food items can be detritus, primary producers and primary consumers. However, this species was classified not as generalist. This peculiar trophic situation derives from the benthic feeding behaviour of common carp; the shallow lake bottom is mainly covered by detritus and plant debris, which are the principal elements available in this eutrophic ecosystem. The similarity in stomach contents and nitrogen isotopic composition between *C. carpio* and fish fauna reveal no clear patterns

of food resource partitioning that could be achieved through selective feeding. The common carp overlapped its diet in a significant way with all introduced fish taxa, with the native *Goodea atripinnis* at most sites, and with *Chirostoma* spp. at sizes below 120 mm SL. However, a trend was clear: diet overlapping was more evident at sites with high water turbidity ( $>200$  NTU), detritus ( $\approx 100\,000\text{ m}^3$  each year) and plant debris on the bottom, and water hyacinth on the surface ( $\approx 44$  plant individuals  $\cdot\text{ m}^{-2}$ ).

Gut content analysis revealed that smaller sizes of *C. carpio* fed on zooplankton (ca. 50%) and as it grows,

Table 5

Trophic position for fish taxa—based on index of relative importance—during wet and dry season by site in Lago de Pátzcuaro, Mexico

	Fish species	San Jerónimo	Ucazanastacua	Napízaro	Ihuatzio	Embarcadero
Wet season	<i>C. carpio</i> (Cc1)	—	$2.32 \pm 0$	$2.47 \pm 0.13$	$2.43 \pm 0.08$	$2.25 \pm 0.07$
	<i>C. carpio</i> (Cc2)	$2.45 \pm 0.21$	$2.21 \pm 0.08$	$2.30 \pm 0.13$	$2.23 \pm 0.09$	$2.08 \pm 0.06$
	<i>C. carpio</i> (Cc3)	—	$2.02 \pm 0$	$2.07 \pm 0.10$	$2.04 \pm 0.06$	$2.01 \pm 0.04$
	<i>Chirostoma</i> spp.	$2.95 \pm 0.17$	$2.99 \pm 0.10$	$3 \pm 0.04$	$3.02 \pm 0.6$	$2.88 \pm 0.04$
	<i>G. atripinnis</i>	$2.06 \pm 0.02$	$2.22 \pm 0$	$2.03 \pm 0$	$2.06 \pm 0.01$	$2.05 \pm 0.06$
	<i>A. robustus</i>	$3.16 \pm 0.4$	—	—	—	—
	<i>Oreochromis</i> spp.	—	—	$2.07 \pm 0$	$2.09 \pm 0$	—
Dry season	<i>C. carpio</i> (Cc1)	—	—	—	$2.66 \pm 0$	$2.53 \pm 0.06$
	<i>C. carpio</i> (Cc2)	$2.21 \pm 0.08$	—	—	$2.24 \pm 0.09$	$2.19 \pm 0.08$
	<i>C. carpio</i> (Cc3)	—	—	—	$2.15 \pm 0.1$	$2.01 \pm 0$
	<i>Chirostoma</i> spp.	$2.85 \pm 0.31$	$2.93 \pm 0.24$	$2.80 \pm 0.34$	$3.03 \pm 0.32$	$2.97 \pm 0.16$
	<i>G. atripinnis</i>	$2.50 \pm 0.14$	—	$2.27 \pm 0$	$2.26 \pm 0.12$	$2.29 \pm 0.1$
	<i>Oreochromis</i> spp.	—	—	$2.04 \pm 0$	$2.35 \pm 0.16$	$2.06 \pm 0.04$

Values are mean  $\pm$  standard deviation; Cc1 = *Cyprinus carpio* ( $<120$  mm SL), Cc2 = *Cyprinus carpio* (120–230 mm SL), Cc3 = *Cyprinus carpio* ( $>230$  mm SL).

Table 6

Trophic position for fish taxa during wet and dry season by site in Lago de Pátzcuaro (based on  $\delta^{15}\text{N}$ )

	Fish species	San Jerónimo	Ucazanastacua	Napízaro	Ihuatzio	Embarcadero
Wet season	<i>C. carpio</i> (Cc1)	—	$2.2 \pm 0^a$	$2.7 \pm 0.5^a$	$3.2 \pm 0.6^a$	$3.1 \pm 0.1^a$
	<i>C. carpio</i> (Cc2)	$1.6 \pm 0.8^a$	$3.0 \pm 0.3^b$	$3.1 \pm 0.4^b$	$3.4 \pm 0.1^b$	$3.1 \pm 0.4^b$
	<i>C. carpio</i> (Cc3)	—	$2.0 \pm 0.4^a$	$2.8 \pm 0.0^a$	$3.5 \pm 0.3$	$3.3 \pm 0$
	<i>Chirostoma</i> spp.	$3.8 \pm 0.4^a$	$3.8 \pm 0.2^a$	$3.7 \pm 0.2^a$	$3.8 \pm 0.2^a$	$3.6 \pm 0.3^a$
	<i>G. atripinnis</i>	$2.5 \pm 0.5^{ab}$	$2.4 \pm 0.2^{ab}$	$2.5 \pm 0.5^b$	$2.8 \pm 0.2^{ab}$	$3.2 \pm 0.3^a$
	<i>A. robustus</i>	$2.9 \pm 0.4$	—	—	—	—
	<i>Oreochromis</i> spp.	—	—	$1.5 \pm 0.5^a$	$2.6 \pm 0.3^a$	$2.7 \pm 0.2^a$
Dry season	<i>C. carpio</i> (Cc1)	—	—	—	$3.1 \pm 0.2$	$3.2 \pm 0.1$
	<i>C. carpio</i> (Cc2)	$2.2 \pm 0.6$	—	—	$3.1 \pm 0.3$	$3.1 \pm 0.2$
	<i>C. carpio</i> (Cc3)	—	—	—	$3.5 \pm 0.3$	$3.2 \pm 0$
	<i>Chirostoma</i> spp.	$4.3 \pm 0.4^{ab}$	$4.1 \pm 0.4^{ab}$	$4.1 \pm 0.3^{ab}$	$3.8 \pm 0.4^{bc}$	$3.7 \pm 0.5^c$
	<i>G. atripinnis</i>	$2.7 \pm 0^a$	—	$2.7 \pm 0.2^a$	$3 \pm 0.4^a$	$2.6 \pm 0.7^a$
	<i>Oreochromis</i> spp.	—	—	$1.7 \pm 0.1^a$	$2.3 \pm 0.2^a$	$2.7 \pm 0.1^b$

Values are mean  $\pm$  standard deviation; Cc1 = *Cyprinus carpio* ( $<120$  mm SL), Cc2 = *Cyprinus carpio* (120–230 mm SL), Cc3 = *Cyprinus carpio* ( $>230$  mm SL); Superscripts *a*, *b* refer to differences in data variation between sites (Tukey–Kramer honestly significant difference [HSD] post hoc test,  $P < 0.05$ ).

preferred to feed on hyacinth roots and plant detritus (>60%). The nitrogen stable isotopes analysis showed that common carp can also ingested invertebrates associated to detritus and water hyacinth roots, a feeding practice recorded in “natural” lakes and rivers of different continents (Summerfelt et al. 1971, Eder and Carlson 1977, Crivelli 1981, Powles et al. 1983, Chapman and Fernando 1994, Elías-Fernández and Navarrete-Salgado 1998, Colautti and Remes Lenicov 2001) or highly modified systems as the Xochimilco canals in Mexico City (Zambrano et al. 2010).

Evidence of the preference of the common carp for water hyacinth and rooted macrophytes as a preferred feeding habitat is the frequency of sizes found along the six study sites. The three groups of sizes of *C. carpio* were present during the wet and dry seasons at sites with higher aquatic vegetation coverage (IHU, EMB) located in the southern zone of the lake. And few individuals of common carp were captured at habitat with rocks at bottom and <5% of floating aquatic vegetation cover (SAJ) located in the northern zone. In addition, at SAJ, plant debris was scarce in the gut of *C. carpio*. These findings agree with Britton et al. (2007) in the Lake Naivasha in Kenya, a shallow, warm and high productive lake. These authors argued that after carp initial establishment, the effects of benthic foraging by carp have not altered macrophytes regeneration, because the abundance of macrophytes is directly proportional to carp abundance.

*Cyprinus carpio*, *Oreochromis* spp., and *Goodea atripinnis* in Lago de Pátzcuaro are primary consumers that feed on the most abundant resources. The same occurs for *Poeciliopsis infans* (see Ramírez-Herrejón et al. 2013). Common carp fed mainly on the bottom (except for juvenile individuals < 100 mm SL), whereas *G. atripinnis*

and *Oreochromis* spp. on water column and bottom, and *P. infans* on bottom and periphyton. However, according to nitrogen stable isotopes *C. carpio* (Cc1, Cc2, Cc3) and *G. atripinnis* can be primary and secondary consumers since isotopic analysis show the assimilated food items, despite if these items were or not founded with gut content analysis (Jardine et al. 2003). This situation may be the common in degraded system. Conversely, Mercado-Silva et al. (2009) found in the Laja River system that in the reservoir itself, as well as the tail water exiting the reservoir, the common carp was located at the lowest trophic position, while in river ecosystems common carp where secondary consumers.

Fishes of the genus *Chirostoma* are known to be specialist that feed on invertebrates (Rosas 1976, García de León and Pérez-Velázquez 1996, Ross et al. 2006, Moncayo-Estrada et al. 2010). However, *Chirostoma* fishes in this study behaved as predacious with the capacity to behave as generalist during dry season, showing the aptitude to find its food items in different habitats (bottom, periphyton, surface and nekton) and in different trophic webs (nekton, periphyton and terrestrial). This multi-chain feeder behaviour has been described by Vadeboncoeur et al. (2005) for generalist predators that feed on different functional groups and has been found in other silversides (Contente et al. 2011, Strongin et al. 2011). In addition, such behaviour could be related to the analysis of all species together as *Chirostoma*. Omnivore fish as *Poeciliopsis infans* also show this type of behaviour in the Lago de Pátzcuaro (Ramírez-Herrejón et al. 2013). *Chirostoma* spp. and *Allophorus robustus* were secondary consumers, the first fed mainly on zooplankton and insects and the second fed principally on insects. Stable isotope analysis located *Chirostoma* spp. also within tertiary

**Table 7**

Isotopic signatures of  $\delta^{15}\text{N}$  for each fish taxa by site in Lago de Pátzcuaro during wet and dry season

	Fish species	San Jerónimo	Ucazanastacua	Napízaro	Ihuatzio	Embarcadero
Wet season	<i>C. carpio</i> (Cc1)	—	12.4 ± 0 <sup>a</sup>	13.8 ± 1.8 <sup>a</sup>	15.7 ± 2.1 <sup>a</sup>	15.4 ± 0.1 <sup>a</sup>
	<i>C. carpio</i> (Cc2)	10.1 ± 2.8 <sup>a</sup>	15.1 ± 1 <sup>b</sup>	20 ± 1.4 <sup>b</sup>	16.4 ± 0.3 <sup>b</sup>	15.3 ± 0.4 <sup>b</sup>
	<i>C. carpio</i> (Cc3)	—	15.1 ± 1.4	14.3 ± 0	16.7 ± 1	15.9 ± 0
	<i>Chirostoma</i> spp.	16.9 ± 1.2 <sup>a</sup>	16.8 ± 0.7 <sup>a</sup>	16.5 ± 0.6 <sup>a</sup>	16.9 ± 0.8 <sup>a</sup>	16.4 ± 1.1 <sup>a</sup>
	<i>G. atripinnis</i>	12.4 ± 1.6 <sup>ab</sup>	12.2 ± 0.8 <sup>ab</sup>	12.2 ± 1.6 <sup>b</sup>	13.3 ± 0.6 <sup>ab</sup>	14.8 ± 1 <sup>a</sup>
	<i>A. robustus</i>	13.9 ± 1.4	—	—	—	—
	<i>Oreochromis</i> spp.	12.3 ± 2.2 <sup>ab</sup>	—	10 ± 1.5 <sup>b</sup>	13.8 ± 0.9 <sup>a</sup>	14.2 ± 0.2 <sup>a</sup>
Dry season	<i>C. carpio</i> (Cc1)	—	—	—	15.5 ± 0.7 <sup>a</sup>	15.6 ± 0.5 <sup>a</sup>
	<i>C. carpio</i> (Cc2)	12.4 ± 1.9 <sup>a</sup>	—	—	15.3 ± 1 <sup>a</sup>	15.5 ± 0.7 <sup>a</sup>
	<i>C. carpio</i> (Cc3)	—	—	—	16.5 ± 1.1 <sup>a</sup>	15.5 ± 0 <sup>a</sup>
	<i>Chirostoma</i> spp.	18.4 ± 1.1 <sup>ab</sup>	18 ± 1.5 <sup>ab</sup>	18 ± 1 <sup>ab</sup>	16.9 ± 1.5 <sup>bc</sup>	16.6 ± 1.6 <sup>c</sup>
	<i>G. atripinnis</i>	13 ± 0 <sup>a</sup>	—	13 ± 0.8 <sup>a</sup>	14 ± 1.4 <sup>a</sup>	13.6 ± 0.6 <sup>a</sup>
	<i>Oreochromis</i> spp.	—	—	10.5 ± 0.5 <sup>a</sup>	12.5 ± 0.5 <sup>a</sup>	14.1 ± 0.6 <sup>b</sup>

Values are mean ± standard deviation; Cc1 = *Cyprinus carpio* (<120 mm SL), Cc2 = *Cyprinus carpio* (120–230 mm SL), Cc3 = *Cyprinus carpio* (>230 mm SL); Superscripts *a*, *b* refer to differences in data variation between sites (Tukey–Kramer honestly significant difference [HSD] post hoc test,  $P < 0.05$ ).

**Table 8** Diet overlap between fish taxa by site during wet and dry (below the diagonal of the table) seasons in Lago de Pátzcuaro, Mexico

San Jerónimo						
	Cc2	Pi	Cx	Ga	Ar	
Cc2		0.6	0.4	0.6	0.2	
Pi	0.5		0.2	0.8	0.3	
Cx	0.3	0		0.3	0.1	
Ga	0.7	0.4	0.4		0.1	
Ar	—	—	—	—		

Ucasanastacua						
	Cc1	Cc2	Cc3	Cx	Pi	Ga
Cc1		1	0.8	0.5	0.7	0.5
Cc2	—		0.9	0.3	0.6	0.4
Cc3	—	—		0.1	0.6	0.4
Cx	—	—	—		0.2	0.4
Pi	—	—	—	0		0.55
Ga	—	—	—	—	—	

Napízaro							
	Cc1	Cc2	Cc3	Ox	Pi	Cx	Ga
Cc1		0.9	0.7	0.8	0.6	0.5	0.5
Cc2	—		0.8	0.8	0.6	0.3	0.6
Cc3	—	—		0.7	0.7	0.0	0.4
Ox	—	—	—		0.7	0.2	0.9
Pi	—	—	—	0.8		0.1	0.5
Cx	—	—	—	0.1	0.2		0.1
Ga	—	—	—	0.6	0.6	0.4	

Ihuatzio							
	Cc1	Cc2	Cc3	Ox	Pi	Cx	Ga
Cc1		0.9	0.7	0.8	—	0.4	0.5
Cc2	0.8		0.9	0.7	—	0.2	0.3
Cc3	0.7	1		0.7	—	0	0.2
Ox	0.7	0.6	0.6		—	0.2	0.7
Pi	0.7	0.7	0.7	0.8			0.2
Cx	0.5	0.3	0.1	0.2	0.3		0
Ga	0.6	0.4	0.3	0.8	0.6	0.4	

Embarcadero							
	Cc1	Cc2	Cc3	Ox	Pi	Cx	Ga
Cc1		0.9	0.8	0.8	0.7	0.4	0.8
Cc2	0.8		1	0.8	0.7	0.2	0.7
Cc3	0.6	0.9		0.7	0.7	0	0.7
Ox	0.7	0.7	0.6		0.9	0.1	1
Pi	0.6	0.5	0.5	0.8		0.1	0.8
Cx	0.7	0.3	0	0.2	0.1		0.1
Ga	0.7	0.5	0.3	0.7	0.5	0.5	

Cc1 = *Cyprinus carpio* (< 120 mm SL), Cc2 = *Cyprinus carpio* (120–230 mm SL), Cc3 = *Cyprinus carpio* (> 230 mm SL), Ox = *Oreochromis* spp., Pi = *Poeciliopsis infans*, Cx = *Chirostoma* spp., Ga = *Goodea atripinnis*, Ar = *Alloophorus robustus*.

consumers, coinciding with Moncayo-Estrada (2007) analysis of *Chirostoma lucius* Boulenger, 1900 from a natural and an artificial system.

Diet overlapped substantially between common carp and local fish fauna, an aspect that suggests competition (Lampert and Sommer 2007). However, the shared food-items are the most typically available in the lake. This result from the increasing eutrophication of the lake associated with the reduction of the water column and the increase of macrophytes where the water hyacinth is the predominant species (Huerto Delgadillo and Amador García 2011). This promotes the availability of feeding resources related to plant detritus in the southern zone of the lake. Water hyacinth cover has increased steadily in Lago de Pátzcuaro, from 9.8% in 1970, before the carp introduction, 22% in 1990, to 35% in 2000 (Calderón-García and Ángeles-López 1971, Chacón Torres 1993, Esteva and Reyes 2002). In other words, it seems the eutrophication process has lowered competition in the fish community by increasing the availability of a few food items associated to water hyacinth.

An important aspect to be taken into consideration is that, the native fishes in Lago de Pátzcuaro face not only impacts from introduced species, they are also threatened by human activities that has caused trophic and reproductive habitat destruction, a decrease in water quality, unprecedented plant detritus and sediment accumulation, depth loss and overfishing. All these facts also threaten the introduced species, and the decrease of the fisheries in this lake is a clear indicator. In Lago de Pátzcuaro fish capture volumes have declined from ~2500 t in 1988 to <30 t in 2007 (Anonymous 2010). *Cyprinus carpio* catches in Lago de Pátzcuaro have varied from > 600 t in the 1980s (Gaspar Dillanes et al. 2000) to <10 t in 2009 (Zambrano et al. 2011).

The analyses of trophic ecology of the fishes suggest trophic web reduction in Lago de Pátzcuaro. We suggest that this problem is more serious than feeding competition between the common carp and other species. This food web alteration is evidenced by the low energy food items used by all species, the quantities of detritus found in the gut of most fish taxa, and the decline of top predator population such as native *Chirostoma estor* (>170 mm SL) as well as the introduced largemouth bass, *M. salmoides*. In 1981 *C. estor* catches reached 136 t, but by 2000 catches dropped to only 4 t, and in 2006 catches represented only 1% of the total production of the lake (Rojas and Sasso 2006). The results suggest that all the fish, both native and introduced are trying to adapt and survive to the cumulative changes in the food web. However, presently with the data available it is still too difficult to separate the negative impacts of *C. carpio* on this ecosystem with affects caused directly or indirectly by anthropogenic activities.

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