Foraging patterns of four sympatric species of silversides (Atheriniformes: Atherinopsidae) in Lago de Pátzcuaro, Central Mexico

Francisco J. García-De-León[1,2], Juan P. Ramírez-Herrejón[1], Rafael García-Ortega[3] & Dean A. Hendrickson[4]

1. Laboratorio de Genética para la Conservación, Centro de Investigaciones Biológicas del Noroeste, Instituto Politécnico Nacional 195, Col. Playa Palo de Santa Rita Sur, La Paz, 23096, Baja California Sur, Mexico; fgarciadl@cibnor.mx, ramirezherrejon@gmail.com
2. Fundación Centro de Estudios del Cuaternario de Fuego-Patagonia y Antártica (CEQUA) 21 de Mayo, Punta Arenas, Magallanes, Chile
3. Laboratorio de Biología Acuática, Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán 58080, Mexico; rafael_garcia_ortega@hotmail.com
4. University of Texas, Texas Natural History Collection, R4000 / PRC 176, 10100 Burnet Rd., Austin, TX 78758-4445, U.S.A.; deanhend@austin.utexas.edu

ABSTRACT

Since Barbour proposed sympatric speciation to explain evolution of silversides in the Lerma-Santiago basin, relatively little subsequent study has been done. We assessed foraging patterns of four sympatric silversides species (*Chirostoma estor*, *Chirostoma grandocule*, *Chirostoma attenuatum* and *Chirostoma patzcuaro*) in Lago de Pátzcuaro to understand resource partitioning and their sympatric coexistence. We assessed the abundance of invertebrate prey in three feeding habitats and measured physical and chemical habitat parameters at two study sites. Fish were collected during the wet (September 1987) and dry (March 1988) seasons; a total of 242 gut contents were analyzed. We evaluated the trophic guild of each species using the index of relative importance (IRI), prey selectivity with the Ivlev Electivity Index (E), dietary diversity using Shannon and Wiener diversity index (H'), and diet overlap using Morisita index. All silverside species were determined to be predaceous carnivores that feed mainly on nekton and periphyton. Dietary diversity and prey selectivity patterns were similar among species and diet overlap was >70%. Our data do not support the proposition that coexistence of these four fish species is maintained by dietary specialization. We hypothesize that sympatric coexistence of atherinopsids in Lago de Pátzcuaro is explained by food resource availability and ontogenetic variation in their diets. This study highlights the importance of analyzing ecological patterns and mechanisms as basic elements for designing conservation strategies of species flocks, especially under habitat loss and introduction of exotic species. Conservation efforts are urgent to preserve the rare evolutionary process of sympatric speciation (habitat segregation) that is occurring in other lakes in central Mexico, and probably already lost in the Lago de Pátzcuaro, as a result of poor management and inadequate conservation strategies.

KEY WORDS: Atherinopsidae, feeding interactions, species flocks, evolutionary process, conservation.

RESUMEN

Desde que Barbour propuso la especiación simpátrica para explicar la evolución de pescados blancos y charles en la cuenca Lerma-Santiago, poco estudios posteriores se ha hecho. Los patrones de forrajeo de cuatro especies simpátricas del género *Chirostoma* (*Chirostoma estor*, *Chirostoma grandocule*, *Chirostoma attenuatum* y *Chirostoma patzcuaro*) fueron evaluadas en el Lago de Pátzcuaro, para entender la repartición de recursos alimenticios y su coexistencia simpátrica. La abundancia de invertebrados presa fue estimada en distintos hábitat alimenticios y se midieron parámetros físicos y químicos del hábitat en dos sitios de estudio. Los peces fueron recolectados durante las temporadas de lluvias (Septiembre 1987) y estiaje (Marzo 1988); 242 tractos digestivos fueron analizados. Se revaluó el gremio trófico, la selectividad de las presas, la diversidad y el traslape de dieta. Las cuatro especies fueron determinadas como carnívoros depredadores que se alimentan principalmente de necton y perifiton. La diversidad de la dieta y los patrones de selectividad de presas fueron similares entre los atherinopsidos y el traslape de dieta fue >70%. Los resultados no apoyan la propuesta de que la coexistencia de estas cuatro especies se mantiene por medio de la especialización de su dieta. Se hipotetizó que la coexistencia simpátrica de los atherinopsidos del Lago de Pátzcuaro se explica por la alta disponibilidad de recursos alimenticios y la variación ontogénica de su dieta. Este estudio resalta la importancia de analizar los patrones y mecanismos ecológicos como elementos básicos para el diseño de estrategias de conservación en especies en enjambre, bajo efectos antropogénicos como la pérdida del hábitat y la introducción de especies exóticas. Los esfuerzos de conservación son urgentes para preservar el raro proceso evolutivo de la especiación simpátrica (segregación del hábitat) que ocurre en otros lagos del centro de México, y que posiblemente se ha perdido en el Lago de Pátzcuaro, como resultado del manejo deficiente y estrategias de conservación inadecuadas.

PALABRAS CLAVE: Atherinopsidae, interacciones alimenticias, especies en enjambre, procesos evolutivos, conservación.

The silversides [Atherinopsidae – New World Silversides (Page et al., 2013)] of the genus *Chirostoma* are nearly endemic to the lakes of central Mexico (Miller, Minckley & Norris, 2005), such as Lago de Chapala, Lago de Pátzcuaro, and Lago de Zirahuén (Barbour, 1973a; Ross, Martínez-Palacios, Aguilar-Valdez, Beveridge & Chavéz-Sánchez, 2006). The origin and distribution of *Chirostoma* species flocks in this region have been examined using morphological, osteological, and genetic data (Barbour, 1973b; Echelle & Echelle, 1984). Although those studies revealed evolutionary patterns, morphological plasticity and low genetic diversity (Barriga-Sosa, Ibañez-Aguirre & Arredondo-Figueroa, 2002; Barriga-Sosa, Eguiarte & Arredondo-Figueroa, 2004; Bloom, Piller, Lyons, Mercado-Silva & Medina-Nava, 2009), potential hybridization among silversides (Soria-Barreto & Paulo-Maya, 2005), makes interpretation of the evolutionary process difficult (Herder et al., 2006).

The ichthyofauna of Lago de Pátzcuaro includes several sympatric and endemic species of both Goodeidae and Atherinopsidae and several studies focused on analyses to help understand the processes and mechanisms of speciation operating there (De Buen, 1945; Alvarez del Villar, 1972; Barbour, 1973a; Echelle & Echelle, 1984). However, since about 1970, Lago de Pátzcuaro has been subjected to ecological disruptions, including: (1) uncontrolled exploitation of forests at higher elevations; (2) increased siltation and nutrient input that favor proliferation of aquatic weeds (eutrophication); (3) introduction of exotic species; (4) urban pollution; (5) increased commercial harvesting of silversides; and (6) irrational management of fisheries resources (De Buen, 1944a,b; Solórzano, 1955; González, 1977; Rosas, 1983; Chacón-Torres, Ross & Beveridge, 1989; Chacón-Torres, 1993). The lake faces deterioration and imminent extinction of its endemic species. The Mexican government has tried to solve some of these problems with rehabilitation of the watershed's landscape, repopulating the most important commercial species, Pike silverside (*Chirostoma estor*), and introducing another large silverside, the shortfin silverside (*Chirostoma humboldtianum*) (Jimenez-Badillo & Gracia, 1995). These practices may have contributed to increased hybridization between atherinopsids (Oseguera-Figueroa & García de León, 1991; Ledesma-Ayala & García de León, 1991).

For these reasons, studies of the natural history of the endemic *Chirostoma* species are urgent to understand the level of perturbation and deviation from the pristine conditions in which these species evolved and help guide more informed conservation management strategies. Many studies have hypothesized that trophic segregation of *Chirostoma* species in Lago de Pátzcuaro is a function of osteological and morphological differentiation of jaws (Soria-Barreto & Paulo-Maya, 2005), but studies of food habits of silversides in the lake are contradictory (Solórzano, 1961, 1963; Rosas, 1976; García de León, 1985) and comparisons of foraging patterns in the silversides species flock in nature have not been published. It remains unknown how differing foraging strategies of native silversides might relate to coexistence of, and niche segregation among the species and the morphological differences in pharyngeal and mouth structures among them.

Though recently disputed (Barriga-Sosa et al., 2002; Bloom et al., 2009) many studies argue that relatively recent hybridization among *Chirostoma* species has occurred in Lago de Pátzcuaro, making species identification difficult and obscuring taxonomic differences among the four native and one introduced species to the point that recent ecological studies could identify silversides only to genus (Vital-Rodríguez, 2011; Mar-Silva, 2011). Our data, taken more than 25 years ago (1987–1988), when *Chirostoma* species still maintained enough morphological characteristics to allow positive identifications, uniquely allow us to assess trophic guild, dietary diversity, prey selectivity, and overlap of diet among these fish.

METHODOLOGY

Study site

Lago de Pátzcuaro (~19°34'N - 101°36'W) is located on the Mexican Plateau, about 260km west of Mexico City (Fig. 1) in a hydrologically closed basin surrounded by mountains of volcanic origin (De Buen, 1941, 1944 a,b). The water level varies between 2 035 and 2 041m above sea level and the lake has a maximum surface area of 116km^2 and average depth of 4,9m (maximum 12,2m) at maximum capacity (Bernal-Brooks, Gómez, Alcocer, 2002).

Environmental parameters

We sampled two lake sites, one at the northeast, near Tzocurio, and the other in the southwest, near Santiago (Fig. 1). Both sites were visited in the wet summer (September 1987) and dry winter (March 1988), when water temperature, depth, transparency, pH, dissolved oxygen, alkalinity, and total hardness were measured at three-hour intervals for 24h, using standard methods (Wetzel & Likens, 1979). Additionally, sediment samples were collected to analyze texture, using the hydrometer
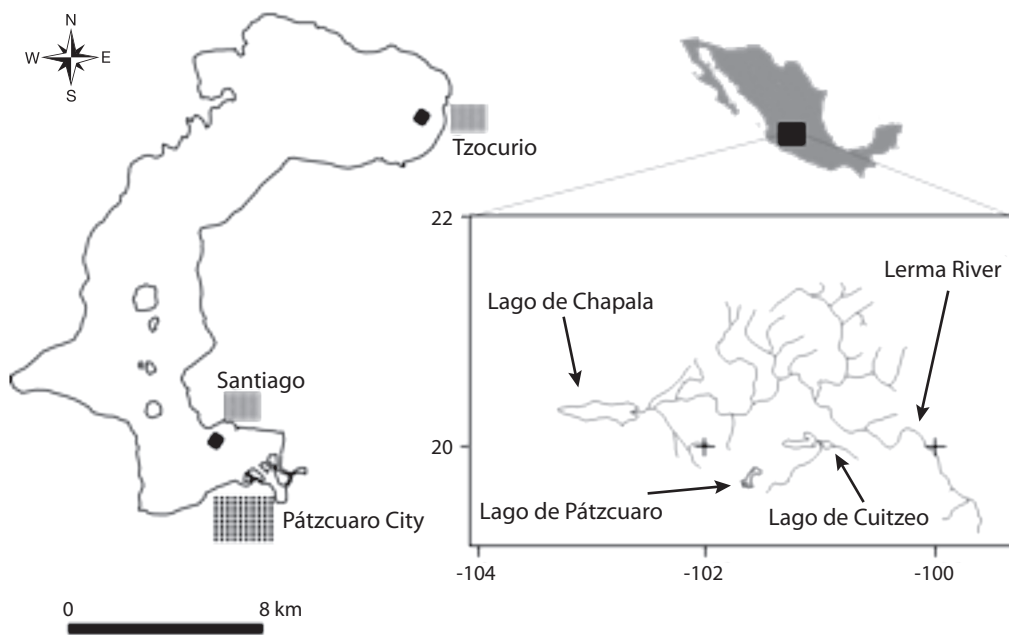
Fig. 1. Location of Lago de Pátzcuaro and study sites (black squares).

method (Bouyoucos, 1936), and organic matter content measured by loss on ignition (Dean, 1974).

Once per season we also collected samples of invertebrate communities to assess the potential food in each major habitat (nekton, periphyton, and benthos). Nektonic invertebrates were sampled from a boat with outboard motor by horizontal tows of a plankton net (0,3m diameter, 153μm mesh) at 0,3m depth at 5km per hour for 5min, thus sampling approximately 29 400L. Periphyton invertebrates were sampled by randomly placing a quadrant frame of 0,2m per side (0,04m^2) at each site and collecting all invertebrates from the square. Benthic invertebrates were captured with a Peterson dredge, collecting a single 0,09m^2 sample from each site in each season. The dredged sediment was washed through the USA standard sieve series (10, 18, 35, and 40µm mesh). Each sieve subsample was air-dried and weighed. All nekton, periphyton, and benthos organisms were preserved in formalin in the field (Ward & Whipple, 1945; Usinger, 1956; Edmonson, 1959; Merrit & Cummins, 1978; Pennak, 1978).

Fish sampling

At each site, during both wet and dry seasons, we collected fishes between 0700 and 0900h, using a 50m seine (1,5m high, 3,25mm mesh). Immediately after capture

specimens were identified using diagnostic characteristics of gill rakers, predorsal scales, scales in the lateral midline, and length of lower jaw (Barbour, 1973b).

Approximately equal numbers of specimens of each species were then selected, dissected and guts preserved in 10% formalin and carcasses discarded.

Contents of the anterior half of the gut of 242 specimens between 10 and 110mm standard length were analyzed in the lab (Table 1). The mean bulk index (MBI) was used for quantitative diet analysis (Saiki, 1976) and frequency of occurrence (FO) (Hyslop, 1980) was determined. The index of relative importance (IRI) (Pinkas, Oliphant & Iverson, 1971), as modified by Yañez, Curiel & Yañez (1976), was calculated and converted to percentage for easier interpretation (Cortés, 1997). Using the IRI, we calculated the Morisita index (Smith & Zaret, 1982) to measure diet overlap between species, as well as the Shannon and Wiener diversity index to estimate dietary diversity.

All original data were transformed logarithmically and Repeated-Measures ANOVA (RMANOVA) was performed with Statistica 6.0 software (StatSoft, Tulsa, OK) to compare (1) physical and chemical water parameters and sediment characteristics between sites, (2) invertebrate abundance in each habitat (benthos, periphyton, and nekton) between sites, (3) abundance of invertebrates at each site, (4) prey eaten by each silverside species at each

TABLE 1
Number of individuals of four *Chirostoma* species used for gut content analysis during wet and dry seasons at two sites

	Santiago		Tzocurio		Total	% of total
	Wet	Dry	Wet	Dry		
C. patzcuaro	16	15	16	16	63	26
C. grandocule	16	8	16	16	56	23
C. estor	16	13	14	16	59	24
C. attenuatum	16	16	16	16	64	26

site, and (5) prey items of the four species at each site. For assessing food selectivity, the Friedman test (Zar, 1999) was used to rank IRI% and relative abundance (%) of each biological community per habitat. We used the percentage values to determine the Ivlev electivity index (Ivlev, 1961) at each site and season.

RESULTS

Environmental parameters

Water transparency, temperature, dissolved oxygen, pH, alkalinity, and total hardness did not differ between sites (RMANOVA, p>0,80 all variables), nor did benthic substrates: organic matter (RMANOVA, p=0,65), clay (RMANOVA, p=1), silt (RMANOVA, p=0,89), and sand (RMANOVA, p=0,49) (Table 2).

Total invertebrate abundance was similar between sites for benthos, periphyton, and nekton; the *P* values for all invertebrate taxa were>0,06 (Table 3). Gastropods, pelecypods, and ostracods were more abundant than dipteran larvae and amphipods in the benthos at Santiago (RMANOVA, p<0,01) and Tzocurio (RMANOVA, p<0,01). Amphipods, bryozoans, cladocerans, adult coleoptera, larval coleoptera, copepods, larval dipterans, and larval ephemeropterans were the most abundant taxa among invertebrates of the periphyton at Santiago (RMANOVA, p<0,01). At Tzocurio, abundance of all invertebrates of the periphyton was similar between seasons (RMANOVA, p=0,22). Nekton invertebrate abundance did not differ between seasons at either Tzocurio (RMANOVA, p=0,18) or Santiago (RMANOVA, p=0,61).

Diet composition

Of the 250 stomachs sampled, (226) 93% were at least 50% full, ensuring a good description of the diet. Cladocerans and copepods were the most common prey in all silverside species (Table 4). Slender silverside (*C.*

TABLE 2
Physical and chemical water parameters (mean±SD) and sediment components at two sites
during the wet and dry seasons at Lago de Pátzcuaro

	Santiago		Tzocurio	
	Wet	Dry	Wet	Dry
Physical and chemical water parameters				
Transparency (m)	0.4±0.02	0.5±0.03	0.3±0.04	0.4±0.01
Water temperature (°C)	21.3±3.7	24.7±4	20.7±2.2	22.7±0.8
Dissolved oxygen (ppm)	4.0±1.2	3.6±1	3.8±0.8	3.4±1.1
pH	7.4±0.4	7.7±0.3	7.5±0.8	7.4±0.2
Alkalinity (ppm)	25.7±5	27.2±2.8	25±4.7	26.2±4.9
Total hardness (mg/L)	16.8±1.9	17.5±0.8	17.7±0.5	17.7±1.2
Sediment components				
Organic matter (mg)	6.3	10.6	3.6	10.2
Clay (% of dry weight)	2	1	8	39
Silt (%)	41	27	17	52
Sand (%)	56	72	75	9

TABLE 3
Density of invertebrates by taxonomic group in different habitats at two sites during
the wet and dry seasons at Lago de Pátzcuaro

Taxonomic group		Santiago		Tzocurio	
		Wet	Dry	Wet	Dry
	Benthos (ind/0.09 m^2)				
Crustaceans	Ostracods	702.6	302.3	222.1	356.9
	Amphipods		4.8	2.7	
Insects	Dipteranlarvae		4.8	4.0	
Molluscs	Gastropods	223.8	731.9	603.1	583.9
	Pelecypods	184.7	67.1	277.9	170.3
	Periphyton (ind/0.04 m^2)				
Poriferans	Poriferans				102.3
Platyhelminthes	Turbellarians		13.3	4.0	136.3
Nematodes	Nematodes			4.5	
Bryozoans	Bryozoans	196.3	759.3	435.3	
Annelids	Oligochaetes	39.8	7.0	130.3	462.5
	Hirudineans	147.3	19.5	12.3	4.8
Crustaceans	Cladocerans	6.0		10.0	
	Copepods	98.3	6.3	896.5	77.8
	Ostracods	85.8	37.8	181.8	70.5
	Amphipods	1304	1262.5	489.3	740.0
Chelicerata	Hydracarids	6.0	2.0	1.8	53.5
Insects	Ephemeroptera larvae	92.0	19.5	48.3	
	Odonate larvae	478.5	8.3	76.3	29.3
	Hemiptera larvae		1.3		9.8
	Hemiptera		1.3	13.5	92.5
	Coleoptera	6.0	243.5	2.3	
	Coleoptera larvae		0.8		53.5
	Dipteranlarvae	39.8	20.3	194.0	355.5
	Dipteran				43.8
	Hymenoptera		2.0		14.5
Mollusks	Gastropods		6.3		9.8
	Nekton (ind/L)				
Rotifer	Rotifers	1.6	0.76	1.03	0.90
Crustaceans	Cladocerans	0.13		0.10	0.02
	Copepods	2.12		2.80	3.10
	Ostracods	0.02		0.03	
Chelicerata	Hydracarids	0.10		0.07	

attenuatum) at both sites had more ostracods, silverside embryos, and dipterans than copepods. Silverside embryos were a secondary diet item for *C. estor* at Santiago (Table 4). Relative importance of prey items of each silverside species between sites were similar (RMANOVA, p>0,09 for all prey items) and there were no significant differences between species at either Tzocurio (RMANOVA, p>0,3 for all prey items) or Santiago (RMANOVA, p>0,7 for all prey items).

Prey selection, dietary diversity, and diet overlap

The four silverside species showed the same patterns of prey selection. Amphipods and dipteran larvae were selected from the benthos at Santiago in the wet season and Tzocurio in the dry season (Table 5). Cladocerans (in the dry season), hemipteran, and dipteran adults (in the wet season) were selected from the periphyton at Santiago and cladocerans, copepods (during the wet and dry seasons), and dipterans adults (in the wet season) at

TABLE 4
Index of relative importance (IRI%) for each food item of *Chirostoma patzcuaro* (1*), *C. grandocule* (2*), *C.estor* (3*),
and *C. attenuatum* (4*) during the wet and dry seasons at two sites

| | Santiago | | | | | | | | Tzocurio | | | | | | | |
| | Wet | | | | Dry | | | | Wet | | | | Dry | | | |
	1*	2*	3*	4*	1*	2*	3*	4*	1*	2*	3*	4*	1*	2*	3*	4*
Poriferans								1								
Nematodes	2		1	5				1	2	2			2		1	1
Bryozoans		1														1
Oligochaetes			2						2			7				3
Hirudineans	4	4	1	2	4		2	1	2							2
Amphipods	2	1	2	3	1		4	1	1	1		2	1		8	1
Hemiptera larvae	1	1	2	2			1	1	2			2				3
Ephemeroptera larvae		1				1						2				
Odonate larvae	7	5	6	8	5	1	4	10	9	6	7	9	1	6	3	5
Hemiptera adults				1		6				1		1	2			3
Coleoptera adults												2				
Coleoptera larvae				1						1		1				
Dipteran larvae	4	10	7	8	1		2		5	6	6	8	4	1	1	2
Dipterans adults	1	1	5	5				11	4	2	5	2	2			6
Rotifers	3	5	6	2				4	1		1	1		2		
Cladocerans	49	41	40	23	53	49	46	32	29	29	23	15	29	39	47	17
Copepods	12	23	20	13	20	43	13	3	31	45	47	36	43	40	31	39
Ostracods	6	3	5	8	15		6	19	8	6	8	11	3		1	2
Hydracarids				1				5		1				7		
Silverside eggs	5			10	1				2					1	5	1
Silverside embryos		1					18	15								
UOM	4	4	4	6					2		3	1	12	7	1	14

* UOM Unidentified organic matter.

Tzocurio. From nekton, cladocerans, copepods, and ostracods were selected by the four species in the same way at Santiago during the dry season, and ostracods were selected at Tzocurio during the dry season.

Dietary diversity was similar among the four silversides (Table 6) and diet overlap was generally >75% at both sites and both seasons; only big eye silverside (*C. grandocule*) and *C. attenuatum* showed lower diet overlap (56%) at Santiago during the dry season (Table 7).

DISCUSSION

This is the first study to attempt to explain trophic specialization of silversides in Lago de Pátzcuaro and it is noteworthy as the samples were collected 25 years ago before most of the perturbation of the lake. Our finding of similar trophic patterns and dietary diversity, with high dietary overlap and similar selectivity patterns across all species suggests that they all more or less equally shared the same food resources and thus counters the hypothesis that coexistence of these four fishes was maintained by dietary specialization.

Although the sample size was small, the study sites were strategically selected in anticipation that environmental differences might be found between these two distant locations. Both sites, however, were similar in physical and chemical water characteristics and bottom type, consistent with Rosas, Mazari, Saavedra & Báez (1985) who found, at about the same time, that water quality was similar throughout the lake, except for a small, highly polluted area near the town of Pátzcuaro (at the far south end of the lake).

Silversides at both sites were carnivorous, with the capability to feed in different habitats, but they fed mainly on resources from nekton (cladocerans and copepods),

TABLE 5
Electivity index of *Chirostoma patzcuaro* (1*), *C. grandocule* (2*), *C.estor* (3*) and *C. attenuatum* (4*)
during the wet and dry seasons at two sites

	Santiago								Tzocurio							
	Wet				Dry				Wet				Dry			
	1*	2*	3*	4*	1*	2*	3*	4*	1*	2*	3*	4*	1*	2*	3*	4*
Benthos																
Ostracods	-0,8	-0,9	-0,9	-0,8	-0,4	-1	-0,7	-0,2	-0,8	-0,7	-0,7	-0,6	-0,9	-1	-0,9	-0,9
Amphipods	1	1	1	1	-0,8	-1	-0,5	-0,9	-0,8	-0,8	-1	-0,7	1	-1	1	1
Dipteran larvae	1	1	1	1	-0,8	-1	-0,8	-1	-0,4	-0,3	-0,3	-0,3	1	1	1	1
Gastropods	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1
Pelecypods	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1
Periphyton																
Poriferans	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1
Turbellarians	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1
Nematodes	1	-1	-1	1	-1	-1	-1	1	-0,3	-0,4	-0,3	-0,4	1	-1	1	1
Bryozoans	-1	-0,7	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	1
Oligochaetes	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1
Hirudineans	-0,2	-0,4	-0,8	-0,5	-0,2	-1	-0,4	-0,8	-1	-1	-1	-1	-1	-1	-1	-0,6
Cladocerans	0,6	0,4	0,5	0,2	1	1	1	1	0,5	0,5	0,4	0,2	1	1	1	1
Copepods	-0,1	0,2	0,1	-0,1	0,5	0,7	0,4	-0,3	0,5	0,7	0,7	0,6	0,6	0,5	0,5	0,5
Ostracods	-0,4	-0,7	-0,5	-0,3	0,4	-1	0,05	0,5	-0,1	-0,2	-0,1	0,1	-0,3	-1	-0,6	-0,4
Amphipods	-0,6	-0,4	-0,6	-0,3	-0,8	-1	-0,4	-0,8	-0,7	-0,7	-1	-0,6	-0,8	-1	0,2	-0,7
Hydracarids	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1
Ephemeroptera larvae	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1
Odonate larvae	0,1	-0,3	-0,1	0,1	-0,2	-0,7	-0,2	0,3	0,3	0,1	0,2	0,3	-0,59	0,01	-0,28	-0,02
Hemiptera larvae	-1	-1	-1	-1	-1	-0,1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1
Hemiptera adults	1	1	1	1	-1	-1	-1	-1	-0,9	-1	-1	-0,3	-0,5	-1	-1	-0,3
Coleoptera adults	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1
Coleoptera larvae	-1	-1	-1	1	-1	-1	-1	-1	-1	1	-1	1	-1	-1	-1	-1
Dipteran larvae	-0,3	0,1	-0,01	0,03	-0,8	-1	-0,7	-1	-0,2	-0,2	-0,2	-0,1	-0,2	-0,8	-0,8	-0,5
Dipterans adults	1	1	1	1	-1	-1	-1	1	1	1	1	1	-0,5	-1	-1	0.1
Hymenoptera	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1
Gastropods	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1
Necton																
Rotifera	-0,8	-0,7	-0,6	-0,8		-1	-0,78	-1	-0,9	-1	-0,9	-0,9	-1	-1	-0,9	-1
Cladocerans	0,4	0,2	0,2	-0,02	1	1	1	1	0,1	0,2	0,1	-0,2	-0,1	0,1	0,1	-0,3
Copepods	-0,3	-0,1	-0,1	-0,3	1	1	1	1	0,1	0,4	0,4	0,2	0.1	0.1	-0,05	0,05
Ostracods	-0,5	-0,8	-0,7	-0,5	1	1	1	1	-0,5	-0,5	-0,4	-0,3	1	1	1	1
Hydracarids	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1	-1

periphyton (insect larvae and silverside embryos), and occasionally from benthos (ostracods). *Chirostoma attenuatum* showed a similar pattern at both study sites, feeding secondarily on invertebrates from periphyton and benthos, with a tendency to have a wider diet than the congeners.

Soria-Barreto & Paulo-Maya (2005) and Barbour (1973a) argue that the interspecific morphological differentiation of silversides in Lago de Pátzcuaro could be related to trophic divergence; however, our results indicate strong trophic similarities among the same species. Our findings are also consistent with recent studies at Lago de Pátzcuaro (Vital-Rodríguez, 2011) that found that individuals of *Chirostoma* spp. of different sizes range (38-51mm and 66-71mm) did not show trophic differences at four different study sites. Vital-Rodríguez

TABLE 6

Dietary diversity of four *Chirostoma* species expressed by Shannon-Wiener index (*H'*) of each silversides species at Santiago and Tzocurio in Lago de Pátzcuaro

	Santiago	Tzocurio
C. patzcuaro	1,9±0,2	2,0±0,4
C. grandocule	1,7±0,5	1,5±0,1
C. estor	2,0±0,3	1,6±0,0
C. attenuatum	2,4±0,3	2,2±0,1

(2011) determined silversides as generalist carnivore fishes and secondary consumers that fed generally on copepods, cladocerans, scales, arachnids, insect larvae and adult terrestrial insects. This author also argued that *Chirostoma* fish fed on different habitats (bottom, periphyton, surface and nekton) and on unlike trophic webs.

Our results also agree with numerous investigations done 10 or 20 years before our study; multiple studies of *C. estor* (Solorzáno, 1963; Rosas, 1976; García de León, 1984), *C. attenuatum* (Solórzano, 1961; Morelos-López & García de León, 1987), *C. grandocule* (Rosas, 1976), and Patzcuaro silverside (*C. patzcuaro*) (Rauda-Ortega & García de León, 1987) concluded that these silversides are carnivores that feed mainly on micro-crustaceans (cladocerans, copepods, amphipods, and ostracods) and insects (dipteran and odonate larvae), and secondarily on rotifers, diatoms, and fish eggs. They also argue that silverside species change diet from nekton to periphyton with increasing fish size (though our study did not consider ontogenetic diet changes).

We found that silversides selected amphipods and dipteran larvae, the least abundant taxa from the benthos. Nematodes, cladocerans, copepods, hemipterans, and adult dipterans were principally selected from periphyton, but these were not the most abundant invertebrates. Cladocerans and ostracods were common in diets, even though copepods were the most abundant prey in the nekton. For this reason, these silversides are considered predators.

On the basis of morphology of oral jaws, Soria-Barreto & Paulo-Maya (2005) concluded that *C. grandocule* could feed on zooplankton from the water surface and that *C. estor*, *C. patzcuaro*, and *C. attenuatum* could feed on prey located anywhere in the water column and are capable of eating hard shell invertebrates. Our study indicated that all four silversides species fed from all available resources and habitats. In other lakes, such as Lago de Chapala, it may be that zooplanktivorous fishes might partition their habitat on depth, such as Moncayo-Estrada, Owen & Escalera-Gallardo (2010) reported, but we did not observe evidence of this in Lago de Pátzcuaro. In our study, diets of the four species overlapped by >70% and dietary diversity was similar across species, though *C. attenuatum* showed a slight increase in its unique inclusion of benthos and fish embryos in its diet.

MacArthur & Levins (1964), Hutchinson (1965) and Williams (1972) all theorized that sympatry of highly-related species could be maintained by ecological divergence or specialization that could produce morphologic differentiation. Some modifications of morphologic structures, such as body size, jaw length, and teeth or gill rakers are common in *Chirostoma* (Barbour1973a, b). Hence, previous authors invoked size differences, feeding specialization, and use of diverse available habitats to explain sympatric co-existence among atherinopsids in the Central Mexican Plateau (Barbour, 1973b; Berlanga-Robles, Madrid-Vera & Ruiz-Luna, 2002; Moncayo-Estrada et al., 2010; Moncayo-Estrada, Owen & Escalera-Gallardo, 2011).

Silversides in Lago de Pátzcuaro are a complex fish assemblage, from the largest species (*C. estor* 308mm SL) to the smallest (*C. attenuatum* 89mm SL), with two

TABLE 7

Morisita index for diet overlap between *Chirostoma patzcuaro*, *C. grandocule*, *C.estor*, and *C. attenuatum* at Santiago and Tzocurio during the wet* and dry** seasons in Lago de Pátzcuaro

Site		*C. patzcuaro*	*C. grandocule*	*C. estor*	*C. attenuatum*
Santiago	*C. patzcuaro*		0,90**	0,88**	0,77**
	C. grandocule	0,86*		0,78**	0,56**
	C. estor	0,92*	0,98*		0,80**
	C. attenuatum	0,76*	0,83*	0,86*	
Tzocurio	*C. patzcuaro*		0,95**	0,88**	0,95**
	C. grandocule	0,92*		0,95**	0,87**
	C. estor	0,89*	0,99*		0,76**
	C. attenuatum	0,92*	0,91*	0,91*	

medium-size species (*C. grandocule* 170mm SL and *C. patzcuaro* 104mm SL). The diversification process of these sympatric species is probably a product of geographic isolation and interspecific interactions (Barbour, 1973a), followed by sympatry. These species are diphyletic and belong to different lineages: the *jordani* species group (*C. estor*, *C. patzcuaro*, and *C. grandocule*) and the *arge* species group (*C. attenuatum*), with different evolutionary morphological characteristics (Barbour, 1973a). They may coexist by minimizing competition for prey selection by maintaining size differences. However, when analyzing diet of each species using specimens of comparable sizes (10 to 110 mm SL), we see little, if any, evidence for segregation based on feeding resources. Thus, if silversides species of Lago de Pátzcuaro show similar feeding habits, how do they continue to coexist? Here we can only hypothesize that one potential mechanism allowing coexistence could be that these species have specific foraging patterns in different habitats and that Lago de Pátzcuaro, when our data were obtained, harbored enough feeding habitats and food resource diversity to support the complex of *Chirostoma* species. This is similar to the hypothesis of Barluenga, Stölting, Salzburger, Muschick & Meyer (2006), that ecological speciation mechanisms through divergent habitat preferences caused sympatric speciation of two cichlid fish species, Arrow cichlid (*Amphilophus zaliosus*) and Midas cichlid (*Amphilophus citrinellus*) in Nicaragua's Lago Apoyo. Alternatively, the sample size in our study was small and could not detect differences in foraging patterns or that any difference in foraging patterns among species is very small, and was not detected with our sampling protocol. Also, our study based feeding analyses on invertebrate taxonomic groups, not species-level taxonomy; there may be prey species-specific trophic specializations among silverside species. For example, Moncayo-Estrada et al. (2010) reported subtle intra- and interspecific trophic partitioning between three silversides species in Lago de Chapala. The Ranch silverside (*C. consocium*) fed mainly on copepods, the charal (*C. jordani*) fed on small cladocerans (genus *Bosmina*), and the sharpnose silverside (*C. labarcae*) fed mainly on large cladocerans (*Ceriodaphnia* and *Daphnia*).

Despite high values of diet overlap (>70%), the silversides could vary feeding strategies during ontogeny from larva through juvenile to adult. For example, *C. estor* has a long jaw length (12–14% of SL) with vomerine fangs (Barbour, 1973b) and becomes a carnivorous specialist piscivore very early in its ontogeny (91mm SL) (Rosas, 1976; García de León, 1985). When smaller, this species feeds on periphyton and completes its diet with resources from nekton. *Chirostoma attenuatum* mainly forages on periphyton and benthos resources,

coinciding with the data obtained by Rosas (1976) and Morelos-López & García de León (1987). *Chirostoma patzcuaro* has less trophic specialization because it uses resources from periphyton or nekton, similar to what was observed by Rosas (1976) and Rauda-Ortega & García de León (1987). *Chirostoma grandocule* has trophic specialization, feeding on nekton zooplankton (Rosas, 1976). These feeding strategies may allow silversides to coexist in Lago de Pátzcuaro. In this study the diet of *Chirostoma* species broadly overlapped, but this does not necessarily imply competition among them. Differential foraging patterns in different habitats could be the primary coexistence mechanism. A study by Sánchez-Hernández, Vieira-Lanero, Servia & Cobo (2011) of feeding habits of four sympatric fishes, sea trout (*Salmo trutta*), gjëmbaçi (*Gasterosteus gymnurus*), panjorca (*Achondrostoma arcasii*), and boga (*Pseudochondrostoma duriense*) in the Iberian Peninsula, supports the hypothesis that segregation among microhabitats was a main factor reducing competition among them.

Chirostoma humboldtianum, the silverside introduced to Lago de Pátzcuaro (Jiménez-Badillo & Gracia, 1995), is thought to be an ancestral form that is morphologically similar to the four native Lago de Pátzcuaro species (Echelle & Echelle, 1984). Probably, the foraging patterns of *C. humboldtianum*, until now unknown, would increase competition among native atherinopsids using competitive exclusion in this ecosystem and imbalance in lake productivity. Further studies might clarify the function of this introduced species in the ecosystem.

Considerations for conservation

Echelle & Echelle (1984) established that lakes in the Central Plateau of Mexico allowed evolution of the Atherinopsid species flock by ecological specializations mainly driven the development of native fauna. However, Soria-Barreto & Paulo-Maya (2005) argue that anthropogenic and ecological changes have forced hybridization between silversides in Lago de Pátzcuaro by reducing spawning area and increasing the probability of interspecific ova and sperm mixtures. The current morphological similarities of silversides in Lago de Pátzcuaro make identification to species difficult (Miller et al., 2005) and the taxonomic differences between the four native species are currently in dispute (Barriga-Sosa et al., 2002; Bloom et al., 2009). It seems likely that genetic diversity has been lost, yet conservation efforts to preserve silversides in Lago de Pátzcuaro have focused on aquaculture and restocking of one species (*C. estor*). Meanwhile, the ecosystem is losing fish species (Berry, Lee, Walton,

Wilson & Bernal-Brooks, 2011) and ecological and evolutionary processes are changing.

The species flock of silversides in Lago de Pátzcuaro is a sympatric group of species endemic to a small area and with close phyletic relationships (Echelle & Kornfield, 1984). The key evolutionary processes (habitat segregation) for intra-lacustrine speciation are related to ecological specialization in localities where numerous niches become available for occupation and exploitation (Greenwood, 1984). For this reason, we argue that the abundance of resources and differences in diet in early stages can be related with the speciation process of silversides in Lago de Pátzcuaro. However, currently the surface area of the lake has lost more than 25 km^2 and water depth has declined ~ 6 m since 1960s (Bernal-Brooks et al., 2002). Therefore, it is imperative to warn that the uniqueness of this endemic lacustrine fauna is at risk of disappearing due to anthropogenic destruction of habitat and introduction of congeneric species. Habitat segregation is a rare evolutionary mechanism and biological models to study it are also scarce. Examples currently documented include cyprinids of Lake Lanao (Philipines), *Orestias* in Lake Titicaca, silversides in the Mexican Plateau, cichlids at Cuatro Cienegas, Mexico, Midas cichlids in the volcanic crater lakes of Nicaragua, cichlids of Lake Malawi and Lake Victoria in Africa (Echelle & Kornfield, 1984) and *Cyprinodon* species in Chichankanab, Mexico. The Lake Lanao cyprinid flock went extinct in less than 25 years as a result of overfishing, introduction of exotic predators or competitors, and human population growth and associated pollution. In Lago de Cuitzeo, Mexico, once inhabited by four *Chirostoma* species (least silverside *C. charari*), Pescado blanco (*C. compressum*), *C. humboldtianum*, and *C. jordani*, changes in water quality and decrease in depth caused the loss of three species, leaving only *C. jordani*. At Cuatro Ciénegas in Coahuila, Mexico, major channelization for irrigation has caused reduction of habitat of Minckley's cichlid (*Herichthys minckleyi*) and hybridization with a close relative, the Texas cichlid *Herichthys cyanoguttatum* from the Rio Grande basin (Hulsy & F.J.G.d.L., 2013), is also impacting the species. At three crater lakes in Nicaragua (Lake Apoyo, Lake Xiloá, and Lake Masaya), the Midas cichlid species flock (*Amphilophus citrinellus*, *A. labiatus*, *A. zaliosus*), in incipient stages of sympatric speciation (Barluenga & Meyer, 2004) is threatened by introduction of African cichlids (*Oreochromis niloticus* and *O. aureus*) for aquaculture, with related habitat destruction, competition for feeding and courtship sites, predation on juveniles, and proliferation of parasites (McCrary, van der Berghe, McKaye, & López, 2001). In Lake Malawi,

introduction of exotic clupeids caused the decline in diversity of endemics (Echelle & Kornfield, 1984). In Lake Victoria, where the extreme diversity of cichlids can be explained by sexual selection with body color playing an important role, eutrophication caused by deforestation and agriculture greatly reduced visibility and modified other ecological conditions to precipitate decreases in species diversity (Seehausen, van Alphen & Witte, 1997). Additionally, introduction of the Nile perch (*Lates niloticus*) also decreased native cichlid diversity there (Echelle & Kornfield, 1984). These events took place more than 25 years ago (Seehausen et al., 1997; Echelle & Kornfield, 1984) and the lack of appropriate management policies will surely lead to the disappearance of unique examples of processes of evolution and speciation in vertebrates.

These same anthropogenic impacts have occurred in Lago de Pátzcuaro starting over 40 years ago and the same poor management and inadequate conservation strategies are also decimating other endemic silverside communities elsewhere in México. Currently, only Lago de Zirahuén, harboring two silverside flock species, *C. estor* and *C. attenuatum* (Miller et al., 2005), has an ecosystem that, compared to many lakes in Mexico, is regarded as having pristine conditions (Davies et al., 2005). However, increasing sedimentation and inputs of untreated sewage clearly indicate a need for viable and effective watershed and lake conservation strategies (Chacón-Torres & Rosas-Monge, 1998). It is urgent to lead direct conservation efforts to prevent the loss of the rare evolutionary process of sympatric speciation, probably already lost in Lago de Pátzcuaro. Managers and policy makers should encourage long-term programs for protection and restoration of natural habitats and preservation of ecosystem processes to protect these species and their evolutionary processes.

ACKNOWLEDGEMENTS

REFERENCES

Alvarez del Villar, J. (1972). Ictiología Michoacana V. Origen y distribución de la ictiofauna dulceacuícola de Michoacán. *Anales de la Escuela Nacional de Ciencias Biológicas México, 19*, 155-161.

Barbour, C. D. (1973a). A biogeographical history of *Chirostoma* (Pisces: Atherinidae): A species flock from the Mexican Plateau. *Copeia, 3*, 533-566. Retrieved from http://www.jstor.org/stable/1443118

Barbour, C. D. (1973b). The systematics and evolution of the genus *Chirostoma* Swainson (Pisces, Atherinidae). *Tulane Studies in Zoology and Botany, 18*, 97-143.

Barluenga, M., & Meyer, A. (2004). The Midas cichlid species complex: incipient sympatric speciation in Nicaraguan cichlid fishes? *Molecular Ecology, 13*, 2061-2076. doi: 10.1111/j.1365-294X.2004.02211.x

Barluenga, M., Stölting, K. N., Salzburger, W., Muschick, M., & Meyer, A. (2006). Sympatric speciation in Nicaraguan crater lake cichlid fish. *Nature, 439*, 719-723. doi:10.1038/nature04325

Barriga-Sosa, I., Ibañez-Aguirre, A. L., & Arredondo-Figueroa, J. L. (2002). Morphological and genetic variation in seven species of the endangered *Chirostoma* "humboldtianum species group" (Atheriniformes: Atherinopsidae). *Revista de Biología Tropical, 50*, 199–216. Retrieved from http://biologiatropical.ucr.ac.cr/attachments/volumes/vol50-1/25-Barriga_Morpholog.pdf

Barriga-Sosa, I., Eguiarte, L. E., & Arredondo-Figueroa, J. L. (2004). Low but significant subdivision among populations of *Chirostoma grandocule* from Lake Patzcuaro, Mexico. *Biotropica, 36*, 85–98. doi: 10.1111/j.1744-7429.2004.tb00299.x

Berlanga-Robles, C. A., Madrid-Vera, J., & Ruiz-Luna, A. (2002). Fish abundance and trophic structure from the commercial catch in Lake Patzcuaro, Mexico. *Hydrobiologia, 467*, 117–122. doi: 10.1023/A:1014965504486

Bernal-Brooks, F. W., Gómez, T. R., & Alcocer, J. (2002). Lake Patzcuaro (Mexico): a controversy about the ecosystem water regimen approached by field references, climatic variables, and GIS. *Hydrobiologia, 467*, 187–197. doi: 10.1023/A:1014919032228

Berry, J., Lee, E., Walton, K., Wilson, A., & Bernal-Brooks, F. (2011). Microcystin production by a persistent cyanobacterial bloom in Lago de Pátzcuaro (Michoacán, México), and apparent bioaccumulation of the toxin in small commercial catches of fish. *Environmental Toxicology & Chemistry, 30*, 1621–1628. doi: 10.1002/etc.548

Bloom, D. D., Piller, K. R., Lyons J., Mercado-Silva, N., & Medina-Nava, M. (2009). Systematics and biogeography of the silverside tribe Menidiini (Teleostomi: Atherinopsidae) based on the mitochondrial ND2 gene. *Copeia, 2*, 408–417. doi: 10.1643/CI-07-151

Bouyoucos, G. J. (1936). Directions for making mechanical analysis of soils by the hydrometer method. *Soil Science, 42*, 225-230.

Chacón-Torres, A., Ross, L. G., & Beveridge, M. C. (1989). Lake Patzcuaro, Mexico: results of a new morphometric study and its implications for productivity assessments. *Hydrobiologia ,184*, 125-132. doi: 10.1007/BF00014307

Chacón-Torres, A. (1993). Lake Patzcuaro, Mexico: Watershed and water quality deterioration in a tropical high-altitude Latin American lake. *Lake Reservoir Management, 8*, 37–47. doi: 10.1080/07438149309354457

Chacón-Torres, A., & Rosas-Monge, C. (1998). Water quality characteristics of a high altitude oligotrophic Mexican lake. *Aquatic Ecosystem Health & Management, 1*, 237-243. doi: 10.1080/14634989808656920

Cortés, E. (1997). A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Science, 54*, 726-738. doi: 10.1139/f96-316

Davies, S. J., Metcalfe, S. E., Bernal-Brooks, F., Chacón-Torres, A., Farmer, J. G., MacKenzie, A. B., & Newton, A. J. (2005). Lake sediments record sensitivity of two hydrologically closed upland lakes in Mexico to human impact. *AMBIO: A Journal of the Human Environment, 34*, 470-475. doi: http://dx.doi.org/10.1579/0044-7447-34.6.470

Dean, W. E. (1974). Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. *Journal of Sedimentary Petrology, 44*, 242–248. doi: 10.1306/74D729D2-2B21-11D7-8648000102C1865D

De Buen, F. (1941). El Lago de Pátzcuaro. *Revista Geográfica del Instituto Panamericano e Historia, 1*, 1-44.

De Buen, F. (1944a). Limnobiología de Pátzcuaro. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México, 15*, 69-78.

De Buen, F. (1944b). Los lagos Michoacanos II: Pátzcuaro. *Revista de la Sociedad Mexicana de Historia Natural, 5*, 99-125.

De Buen, F. (1945). Investigaciones sobre ictiología mexicana. Atherinidae en aguas continentales de México. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México, 16*, 475-532.

Echelle, A. A., & Echelle, A. F. (1984). Evolutionary genetics of a "species flock": Atherinid fishes on the Mesa Central of Mexico. In A.A. Echelle & I. Kornfield (Ed.), *Evolution of Fish Species Flocks* (pp. 93–110). USA: University of Maine Press.

Echelle, A. A., & Kornfield, I. (1984). *Evolution of fish species flocks*. USA: University of Maine Press.

Edmonson, W. T. (Ed.). (1959). *Fresh-Water Biology*. New York: John Wiley & Sons.

García de León, F. J. (1985). Relaciones alimenticias y reproductivas entre *Chirostoma estor* y *Micropterus salmoides*

en el Lago de Pátzcuaro, Michoacán. *Memorias de VIII Congreso Nacional de Zoología. Sociedad Mexicana de Zoología* , *1*, 41-59.

González, M. L. (1977). La Muerte de un Lago. *Técnica Pesquera, 116*, 22-28.

Greenwood, P. H. (1984). What is a species flock? In A. A. Echelle & I. Kornfield (Ed.). *Evolution of Fish Species Flocks* (pp. 13-19). USA: University of Maine Press.

Herder, F., Nolte, A. W., Pfaender, J., Schwarzer, J., Hadiaty, R. K., & Schliewen, U. K. (2006). Adaptive radiation and hybridization in Wallace's Dreamponds: evidence from sailfin silversides in the Malili Lakes of Sulawesi. *Proceedings of the Royal Society, 273*, 2209–2217. doi:10.1098/rspb.2006.3558

Hulsey, C.D. & García-De-León F.J . (2013). Introgressive hybridization in a trophically polymorphic cichlid. Ecology and Evolution. 3 (13): 4536–4547. doi: 10.1002/ece3.841

Hutchinson, G. E. (1965). The niche: an abstractly inhabited hypervolume. In G. E. Hutchinson (Ed.). *The ecological theater and the evolutionary play* (pp. 26-78). New Haven, C.T.: Yale University Press.

Hyslop, E. J. (1980). Stomach contents analysis a review of methods and their application. *Journal of Fish Biology,17*, 411-429. doi: 10.1111/j.1095-8649.1980.tb02775.x

Ivlev, V.S. (1961). *Experimental Ecology of the Feeding of Fishes*. New Haven, C.T.: Yale University Press.

Jiménez-Badillo, M. L., & Gracia, A. G. (1995). Evaluación de la pesquería multiespecífica de charales (*Chirostoma* spp., Pisces, Atherinidae) del Lago de Pátzcuaro, Michoacán, México. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México, Serie Zoología, 66*, 205-231. Retrieved from http://revistas.unam.mx/index.php/zoo/article/view/7136

Ledesma-Ayala, P. C., & García de León, F. J. (1991). Analysis of primary ontogenetic phases and recognition of the hybrid obtained by artificial fertilization between *Chirostoma attenuatum* and *Chirostoma patzcuaro* (Pisces: Atherinidae) from Lake Patzcuaro, Michoacán, Mexico. *Abstracts from American Fisheries Society, 1*, 8-12.

MacArthur, R., & Levins, R. (1964). Competition, habitat selection and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences, 51*, 1207-1210. Retrieved from http://www.ncbi.nlm.nih.gov/pmc/articles/PMC300237/

Mar-Silva, V. (2011). *Variación espacio-temporal de la comunidad de peces en el lago de Pátzcuaro, Michoacán, México*. Thesis. Facultad de Biología. Universidad Michoacana de San Nicolás de Hidalgo. Morelia, Michoacán, Mexico.

McCrary, J., van der Berghe, E., McKaye, K. R., & López Pérez, L. (2001). El cultivo de tilapias: una amenaza a las especies ícticas nativas en Nicaragua. *Encuentro*, *58*, 9–19.

Merrit, R. W., & Cummins, K.W. (1978). *An Introduction to the Aquatic Insects*. Dubuque, IA, USA: Kendall Hunt Publishing.

Miller, R. R., Minckley, W. L. & Norris, S. M. (2005). *Freshwater fishes of Mexico*. Chicago, USA: The University of Chicago Press.

Moncayo-Estrada, R., Owen, T. L., & Escalera-Gallardo, C. (2010). Trophic partitioning of sympatric zooplanktivorous silverside in a tropical shallow lake: fish morphometry and diet composition. *Copeia,* 3,431-436. doi: 10.1643/CE-08-024

Moncayo-Estrada, R., Owen, T.L. & Escalera-Gallardo, C. (2011). Trophic interactions among sympatric zooplanktivorous fish species in volume change conditions in a large, shallow, tropical lake. *Neotropical Ichthyology* 9, 169-176. doi: http://dx.doi.org/10.1590/S1679-62252011005000003

Morelos-López, M. M., & García de León, F.J. (1987). Aspectos reproductivos del charal prieto, *Chirostoma attenuatum*, Meek 1902 (Pisces: Atherinidae) en el Lago de Pátzcuaro, Michoacán, Méx. *Memorias del IX Congreso Nacional de Zoología, Sociedad Mexicana de Zoología, 1*, 77-84.

Oseguera-Figueroa, L., & García de León, F.J. (1991). Morphology of larvae and juveniles of *Chirostoma grandocule* Steindachner (1896) and its hybrids with *Chirostoma attenuatum* Meek (1902) from Lake Patzcuaro, Michoacán, Mexico. *Abstracts from American Fisheries Society, 1*, 12-16.

Page, L. M., Espinosa-Pérez, H., Findley, L. T., Gilbert, C. R., Lea, R. N., Mandrak, N. E., Mayden, R. L., & Nelson, J. S. (2013). Common and scientific names of fishes from the United States, Canada, and Mexico. Bethesda, M.D.: American Fisheries Society.

Pennak, R. W. (1978). Freshwater Invertebrates of the United States. New York, USA: John Wiley & Sons.

Pinkas, L., Oliphant, M., & Iverson, I. (1971). Food habits of albacore, bluefin tuna, and bonito in California waters. *California Department of Fish and Game, 152*, 1-105.

Rauda-Ortega, J., & García de León, F. J. (1987). Análisis trófico de *Chirostoma patzcuaro* Meek 1902 (Pisces: Atherinidae) del Lago de Pátzcuaro, Mich., México.*Memorias del IX Congreso Nacional de Zoología, Sociedad Mexicana de Zoología, 1*, 85-94.

Rosas, I., Mazari, M., Saavedra, J., & Báez, P. (1985). Benthic organisms as indicators of water quality in Lake Pátzcuaro, México. *Water, Air, and SoilPollution, 25*, 401–414. doi: 10.1007/BF00283792

Rosas, M. M. (1976). Datos biológicos de la ictiofauna del Lago de Pátzcuaro, con especial énfasis en la alimentación de sus especies. *Memorias del Simposio de Pesquerías de Aguas Continentales. Instituto Nacional de la Pesca de México,11*, 299-366.

Rosas, C. V. (1983). El pescado blanco de Pátzcuaro (*Chirostoma estor* Jordan), presente pasado y futuro de una especie en peligro de extinción. *Ocelote, 1*, 12-15.

Ross, L. G., Martínez-Palacios, C., Aguilar-Valdez, M., Beveridge, M., & Chavez-Sánchez, M. (2006). Determination of feeding mode in fishes: the importance of using structural and functional feeding studies in conjunction with gut analysis in a selective zooplanktivore *Chirostoma estor estor* Jordan 1880. *Journal of Fish Biology, 68*, 1782–1794. doi: 10.1111/j.1095-8649.2006.01061.x

Sánchez-Hernández, J., Vieira-Lanero, R., Servia, M. J., & Cobo, F. (2011). Feeding habits of four sympatric fish species in the IberianPeninsula: keys to understanding coexistence using prey traits. *Hydrobiologia, 667*, 119–132. doi: 10.1007/s10750-011-0643-2

Saiki, M. (1976). Mean bulk index. Method of fish food analysis. *The Progressive Fish Culturist, 38*, 55-56. doi: 10.1577/1548-8659(1976)38[55:MBIMOF]2.0.CO;2

Seehausen, O., van Alphen, J. J. M., & Witte, F. (1997). Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science, 277*, 1808-1811. doi: 10.1126/science.277.5333.1808

Smith, E. P., & Zaret, T. M. (1982). Bias in estimating niche overlap. *Ecology, 63*, 1248-253. Retrieved from http://www.jstor.org/stable/1938851

Solórzano, P. A. (1955). *La pesca en el Lago de Pátzcuaro, Michoacán y su importancia económica regional*. México: Secretaría de Marina, Dirección General de Pesca.

Solórzano, P. A. (1961). *Contribución al conocimiento de la biología del charal prieto del Lago de Patzcuaro, Chirostoma bartoni Jordan y Everman, 1986*. México: Secretaría de Industria y Comercio. Dirección General de Pesca.

Solórzano, P. A. (1963). *Algunos aspectos biológicos del pescado blanco del Lago de Pátzcuaro, Mich*. México: Secretaría de Industria y Comercio. Dirección General de Pesca.

Soria-Barreto, M., & Paulo-Maya, J. (2005). Morfometría comparada del aparato mandibular en especies de *Chirostoma* (Atheriniformes: Atherinopsidae) del Lago de Pátzcuaro, Michoacán, Mexico. *Hidrobiológica, 15*, 161-168. Retrieved from http://investigacion.izt.uam.mx/rehb/publicaciones/index.htm

Usinger, L.R. (1956). *Aquatic Insects of California*. Berkeley, CA: University of California Press.

Vital-Rodríguez, B. (2011). *Hábitos alimentarios del género Chirostoma del lago de Pátzcuaro, Michoacán, México*. Master's Thesis. Universidad Michoacana de San Nicolás de Hidalgo. Morelia, Michoacán, Mexico.

Ward, H. P., & Whipple, G. (1945). *Fresh-Water Biology*. New York, USA: John Wiley & Sons.

Williams, E. E. (1972). The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. *Evolutionary Biology, 6*, 47-89. doi: 10.1007/978-1-4684-9063-3_3

Wetzel, R. G., & Likens, G. E. (2000). *Limnological Analyses*. New York, USA: Springer-Verlag.

Yañez, A. A., Curiel, G., &Yañez, V. L. (1976). Prospección biológica y ecológica del bagre marino *Galeichthys caerulescens* (Gunther) en el sistema lagunar costero de Guerrero, México (Pisces: Ariidae). *Anales del Centro de Ciencias del Mar y Limnología, Universidad NacionalAutónoma de México*, 3, 125-180.

Zar, J. H. (1999). *Biostatistical Analysis*. Upper Saddle River, NJ, USA: Prentice Hall.