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Trophic Ecology of Endemic Andean killifish (Orestias Species Complexes): A Review

Carlos López [1,2,*], Patricio De los Ríos-Escalante [3,4], Juan Francisco Rivadeneira [5], Rodrigo Moncayo [6] and Guillermo Figueroa-Muñoz [1,7]

1 Centro del Agua y Desarrollo Sustentable. Escuela Superior Politécnica del Litoral (ESPOL). Campus Gustavo Galindo. Guayaquil. Ecuador. Email: cllopez@espol.edu.ec
2 Departamento de Biología. Facultad Experimental de Ciencias. Universidad del Zulia. Maracaibo 4005-A. Venezuela.
3 Departamento de Ciencias Biológicas y Químicas, Facultad de Recursos Naturales, Universidad Católica de Temuco, Casilla 15-D, Temuco, Chile. Email: prios@uct.cl
4 Núcleo de Estudios Ambientales UC Temuco.
5 Grupo de Estudios de Ecosistemas Acuáticos. Facultad de Ciencias Biológicas. Universidad Central de Ecuador. Quito. Ecuador. Email: jfrivadeneira@uce.edu.ec
6 Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, COFAA, La Paz, Baja California Sur, México. Email: rmoncayo@hotmail.com
7 Department of Wildlife, Fisheries, and Conservation Biology, University of Maine, Orono, ME, USA (current address). Email: guillermo.figueroa@maine.edu
* Correspondence: cllopez@espol.edu.ec (CL); prios@uct.cl (PDE)

Abstract: (1) Background: Understanding the trophic ecology of threatened freshwater fishes is relevant to managing their conservation. The genus *Orestias* is endemic to the Andes region and shows great biogeographical interest in the Neotropics due to its adaptation to the high-altitude systems of the Andes as well as because several species are considered threatened. (2) Methods: Here, we synthesize the documented trophic interaction of *Orestias* spp. in freshwater ecosystems of the Andes region available in the literature and use available data to explore the trophic interaction of *Orestias* species via null models. (3) Results: Our findings showed that *Orestias* spp. consume a wide range of prey (i.e., mainly aquatic insects, crustaceans, and mollusks) that varied according to their habitats and feeding morphology. The null model revealed that species associations in diet were random because of the presence of many repeated species. Our results would reveal that some *Orestias* spp. may show an opportunistic feeding strategy that concurs with previous reports. Additionally, we highlight major information gaps associated with the trophic ecology of *Orestias* spp. and propose some direction for future studies. (4): Our study provides valuable information on *Orestias* spp. trophic ecology, which may be useful for developing conservation strategies for native fish in the Neotropical region.

Keywords: feeding strategies; food webs; native species; trophic niche

1. Introduction

The Trophic ecology of understudied native and threatened fishes provides crucial information to manage their conservation. Trophic ecology of a species is thoroughly related to its population dynamics and contributes to the understanding of interesting subjects as resource partitioning, habitat preferences, prey selection, predation, evolution, competition, and energy transfer within and between ecosystems [1]. In freshwater fishes, the study of their trophic ecology has been mostly development through the diet analysis (i.e., stomach contents and dietary tracers as stable isotopes and fatty acids), which provide information about the type, quantity and origin of prey [2,3]. Here we leverage available information of the diet of freshwater species of the genus *Orestias* to improve our understanding of their trophic ecology.

The genus *Orestias* (Teleostei: Cyprinodontidae) is a group of fish of great biogeographical interest in the Neotropics due to its endemism and adaptation to the high-altitude systems of the Andes [4–7]. Currently there are 46 species of *Orestias* distributed from Lake Lacsha in northern Perú

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to the Salar de Ascotán in northern Chile, of which six are threatened [8–12]. In the Lake Titicaca, the largest lake of South America, there is 15 species of *Orestias* that form an important trophic network within it [4,13–15]. These systems are located 4000 meter after sea level (hereafter, masl), they are endorheic, with extreme differences of daily temperature, isolate (CITE). They are characterized by the development of a belt of macrophytes and associated fauna similar [16]. However, the biogeographical importance of genus *Orestias*, which is the unique representing of Family Cyprinodontidae of South America, the knowledge of many aspects related to their biology and particularly to food and feeding ecology are still very limited [17–19].

Here, we synthesize the documented trophic interaction of *Orestias* spp. in freshwater ecosystems of the Andes region available in the literature and use available data to explore the trophic interaction of *Orestias* species via null models. Our study provides valuable information on *Orestias* spp. trophic ecology, which may be useful for developing conservation strategies for native fish in the Neotropical region.

2. Materials and Methods

Literature search: We conducted a comprehensive literature revision including information from peer-reviewed journal articles, technical reports, and theses. Peer reviewed journal articles were obtained from the Web of Science, Google Scholar, and Scopus database. We used the keywords, *Orestias*, Chilean Altiplano, Bolivian Altiplano, Peruvian Altiplano. We selected relevant articles as papers explicitly considering *Orestias* spp. trophic information from any publication year to create our database used here (supplementary material). The last searches was conducted on October 2022

Analyses a species presence/absence matrix was constructed, with the species in rows and the sites in columns on the basis of data from different species of *Orestias* genus and different sites. First, we calculated a Checkerboard score (“C-score”), which is a quantitative index of occurrence that measures the extent to which species co-occur less frequently than expected by chance [20]. A community is structured by competition when the C-score is significantly larger than expected by chance [20–24]. It compared co-occurrence patterns with null expectations via simulation. [25] suggested the as statistical null models Fixed-Fixed: in this model, the row and column sums of the matrix are preserved. Thus, each random community contains the same number of species as the original community (fixed column), and each species occurs with the same frequency as in the original community (fixed row). The null model analyses were performed using the package EcosimR [25,26].

3. Results

This Composition, diversity and food selectivity: The results of null model analysis revealed that species associations are random, this mean that the species reported in the diet have not structured pattern (Mean index: 8.283; Observed index: 8.388; Variance of simulated index: 0.053; Standard Effect Size: 0.453; P = 0.294), due probably that the presence of many species repeated for studied sites. On this view point the fishes of *Orestias* genus would be an opportunistic predator, this mean that it would predate on species offer available on each ecosystem.

Copepods and cladocerans were about equally represented in the average diet of adult *O. ispi*, but larvae contained only copepods (Table 1). Four of the species (*O.ispi, O. pentlandi, O. mulleri* and *O. agassii*) fed heavily on zooplankton, *O. ispi* exclusively so, but with moderately high levels in the other three species also. Five species (especially *O. agassii* and *O. luteus*) fed heavily on hyalellid amphipods and aquatic insects (mainly chironomid larvae and pupae) (Table 1). Only one species, *O. olivaceus*, used hydrobiid snails (mainly *Littoridina* spp.) to a major extent, along with smaller amounts of sphaerid clams. Fish eggs in various stages of development and similar in size to those found in ripe orestiids were taken by both *O. pentlandi* and *O. luteus*, although they never contributed greatly to mean volumes (Table 1). Plant material (mainly filamentous algae along with occasional *Lemna* and *Chara* fragments) was only found in appreciable amounts in *O. agassii*, especially those fish from the littoral of inner Puno Bay. Oligochaetes and free-living nematodes were found rarely in *O. agassii* alimentary canals. Only for three species were enough individuals of differing size ranges available

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to examine the effects of intraspecific body size differences on food type selectivity (Table 1). For *O. pentlandi* there was a shift from heavy zooplanktivory in the smaller size group to more benthic type prey in the larger size group. Such a shift also occurred in *O. olivaceus*, with the larger size group concentrating on snails (*Littoridina* spp.). For *O. agassii* the two larger size groups fed much more on zooplankton than did the small size group, and also broadened their use of different food types.

Table 1. Results of preys reported for *Orestias* species in Bolivia, Peru and Chile.

Species	Location	Type of Water Body	Prey									References
			1	2	3	4	5	6	7	8	9	
O. agassii	Lake Titicaca (Puno Bay: 15º50′ S, 71º01′W, Peru).	Great Lake	x	x	x	x				x	x	Northcote 2000
O. agassii	Lake Titicaca (Copacabana bay 16º09′ S; 69º05′W Bolivia; Puno Bay: 15º50′ S, 71º01′W, Peru).	Great lake	x	x			x			x	x	Maldonado et al. 2009
O. agassii	Salar del Huasco (20º15, S; 68º52′ W, Chile).	Pond	x	x	x	x	x			x	x	Guzmán & Sielfield 2009
O. agassii	Sud Lipez (22º19′S; 67º22, W Quetena grande, Bolivia; 22º13′S, 67º06′W Celeste, Bolivia; 22º11′S; 67º06′ W Chipapa, Bolivia; 22º07′ 67º15′W, Sol de Mañana, Bolivia).	Wetlands, one pond, one river	x		x	x			x	x	x	Flores 2013
O. agassii	Salar del Huasco (20º15, S; 68º52′ W, Chile).	Rivers	x		x	x					x	Riveros et al. 2013
O. agassii	Lake Titicaca (16º00′S; 18º85′W Toke Pocuro Bay, Bolivia).	Great Lake	x	x		x		x			x	Loayza 2019
O. albus	Lake Titicaca (Copacabana Bay 16º09′ S; 69º05′W Bolivia; Puno bay: 15º50′ S, 71º01′W, Peru).	Great Lake	x	x	x			x	x	x	x	Maldonado et al. 2009
O. ascotensis	Salar de Ascotán, (21º29′ S; 68º15′ W, Chile).	Wetlands	x	x		x						Sobarzo 2014
O. ascotensis	Salara de Ascotán, (21º29′ S; 68º15′ W, Chile).	Wetlands	x	x		x						Gonzalez, 2018
O. ispi	Lake Titicaca (Puno Bay: 15º50′ S, 71º01′W, Peru).	Great lake	x									Vaux et al. 1988
O. ispi	Lake Titicaca (Puno Bay: 15º50′ S, 71º01′W, Peru).	Great Lake	x									Nortcote 2000
O. ispi	Lake Titicaca (Mayor lake: 14º03′S; 66º21′W, Bolivia).	Great Lake	x									Gutierrez 2013
O. jussie	Lake Titicaca (Copacabana Bay 16º09′ S; 69º05′W Bolivia; Puno bay: 15º50′ S, 71º01′W, Peru).	Great Lake	x	x			x			x	x	Maldonado et al. 2009
O. luteus	Lake Titicaca (Puno Bay: 15º50′ S, 71º01′W, Peru).	Great Lake	x	x	x	x		x				Northcote 2000
O. luteus	Lake Titicaca (Mayor lake: 14º03′S; 66º21′W, Bolivia).	Great Lake										Puña 2004
O. luteus	Lake Titicaca (Copacabana Bay 16º09′ S; 69º05′W Bolivia; Puno bay: 15º50′ S, 71º01′W, Peru).	Great Lake	x	x	x			x		x		Maldonado et al. 2009

Note: 1. Zooplankton; 2. Amphipods (Hyalella sp); 3. Mollusks; 4. Aquatic Insects (larvae without identification); 5. Other arthropods; 6. Eggs fish; 7. Fish; 8. Algae +Vegetal material; 9. Other.

4. Discussion

Gut contents- Lakes Titicaca and other water bodies from Bolivia and Perú, the available literature [27–30] studied the gut crops in species of the genus Orestias in Lake Titicaca. These authors found that *O. mulleri* and *O. ispi* were feeding on zooplankton, but O. *mulleri* also included benthic crustaceans in its diet. Other study [10] carried on a most complete gut analysis considering more species in littoral zone, what is similar to the present results. The six orestiid species taken in the littoral zone of Puno Bay were using at least eight widely differing categories of food that is similar to the results of the present study

Results of analysis of gut contents of *O. lutes* [31] denoted that the Punku's food preferences in volume are: Amphipods 22.17 fish eggs 19.04 ostracods 16.67gastr = flat pods 12.11 and gastropods long pods 9.47 complementing with insects in different states such as chironomids (larvae 5.71, naiads 1.66, adults 0.17) hemipterans 0.65odonates 0.09 There have been important findings, such as: that the eating habits of this species are conditioned by the characteristics of its environment. Likewise, this dependence is notorious as an effect of the size of the specimen. However, no significant changes are observed due to the effect of sex. Although it is a very rare event, it is worth mentioning that a fish has been found in the digestive tract of a studied specimen, this fact confirms the suspicions that the Punku is changing its eating habit to ichthyphage (Carabuco)

A study based on the gut crops of the largest species: *O. agassii*, *O. albus*, *O. jussiei* and *O. lutes*, denoted that Cladocerans and amphipods were the most common items found [4]. Except for *O. albus*, they occurred in the gut contents of >80% of the specimens analysed and represented 14–77% of ingested food. Likewise, algae, other arthropods and macrophytes were common in terms of their frequency of occurrence which ranged between 27 and 76% of the specimens of the species. The exception was *O. albus*, where arthropods were not recorded. The relative abundance of these items, however, was low ranging from 0_6 to 13%. Substratum and bryozoans were found only in *O. albus* and *O. agassii* but were more abundant in the latter. Fish eggs were found in all the species except *O. agassii*, but they represented only a small fraction of the ingested food even if they occurred in up to 40% of the specimens. Molluscs were observed in *O. albus* and *O. luteus* but were common in the latter only. Finally, fishes were found only in the gut contents of O. albus. The results of diet of *O. ispi* [32,33] examined the seasonal and depth variations in diet composition and dietary overlap of *O. luteus*, *O. agassii* and *O. mulleri* from a bay of Lake Titicaca during rainy and dry season that are similar with the present study. Finally, the analysis of the variations in the diet and food available in *O. cf. agassii* populations in two wetlands, a pond and a river in the Sud Lipez Region, Potosí, Bolivia [34].

Gut contents - Chilean waterbodies: The descriptions for diet of Chilean populations of *O. agassii* in ponds in streams studied the diet of *O. agassii* in water bodies associated with the Salar del Huasco in the highlands of Region I of Chile. [35,36]. The stomach contents presented; ostracods, amphipods, copepods, mollusks, coleopterans, mites and macrophytic algae. The Results allow us to affirm that *O. agassii* is a carnivorous predator, which consumes a wide variety of microcrustacean actively searching among vegetation. Whereas the results observed for *O. ascotanensis* a few locations of wetland Salar de Ascotán were similar with the present study [37,38]. Finally, the results of diet of five species of *Orestias* which inhabit eight different sites of the Arica and Parinacota Region, Lauca National Park, Chile. Show a pooled diet [39].

Morphology and feeding: the results based in littoral zone of Lake Titicaca shown that *Orestias* species span differentially a wide range in trophogastric morphology (gill raker number, spacing, length; pharyngeal dentition; alimentary canal length) which in part must relate to demonstrated differences in feeding: one species being exclusively zooplanktivorous, another using a broad coverage of food types and probably feeding processes including phytophagy, zooplanktivory and benthophagy, and still others being largely benthophagous [10]. All four of the mechanisms previously proposed to account for long-term coexistence of closely related species flocks - community/habitat instability, marked environmental patchiness, diel (or other forms of temporal) separation, and trophic/spatial partitioning - are shown to apply in the littoral zone of Puno Bay, and probably also in other parts of Lake Titicaca.

Current status and gaps perspectives: Nevertheless, the current trend we see in the literature is, that authors recognize that species interactions in inland water communities are complex systems that need more detailed studies [40–43]. In this scenario, existing literature reports would indicate that algivorous macroinvertebrates have a main role in the trophic webs that are operational in Andean rivers [44]. These results agree with the literature descriptions exposed in the present study about the role and functioning of benthic inland water crustaceans. Within this same context, the current literature mentioned the role of individual size and biomass [42]. Accordingly, it will be necessary to study the size and biomass structure of benthic crustaceans in rivers in order to improve our knowledge of benthic invertebrates in South American inland waters.

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