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Fish underground

The amazing seasonal fish that can spend most of their lives buried. Jewels of Nature.



By Felipe Alonso^{1,2}Pablo A. Calviño², Wilson Sebastián Serra^{2, 3} and Ignacio García^{2,4}

Probably the last place one would expect to find a fish is out of the water, and much less buried underground. However, there are some fish that live in rain ponds that dry completely for long periods and survive because they have eggs that resist desiccation buried at the bottom of the puddle. With the arrivals of the rains these ponds accumulate water and are filled with small colorful fish that hatch from eggs that layed "asleep" underground waiting for the rains. Therefore, people often assume that these fish fall from the sky with rain.

"Annual" or "seasonal" killifish belong to the group of **aplocheiloid** fish (Cyprinodontiformes order, suborder Aplocheiloidei) that comprises 3 families and more than 600 species, both seasonal and from permanent waters.

¹Institute of Bio and Geosciences of North Western Argentina (IBIGEO), National Scientific and Technical Research Council (CONICET)-National University of Salta (UNSa), Rosario de Lerma, Salta, Argentina
felipealonso@gmail.com

²Killis Research and Conservation Group (GICK)

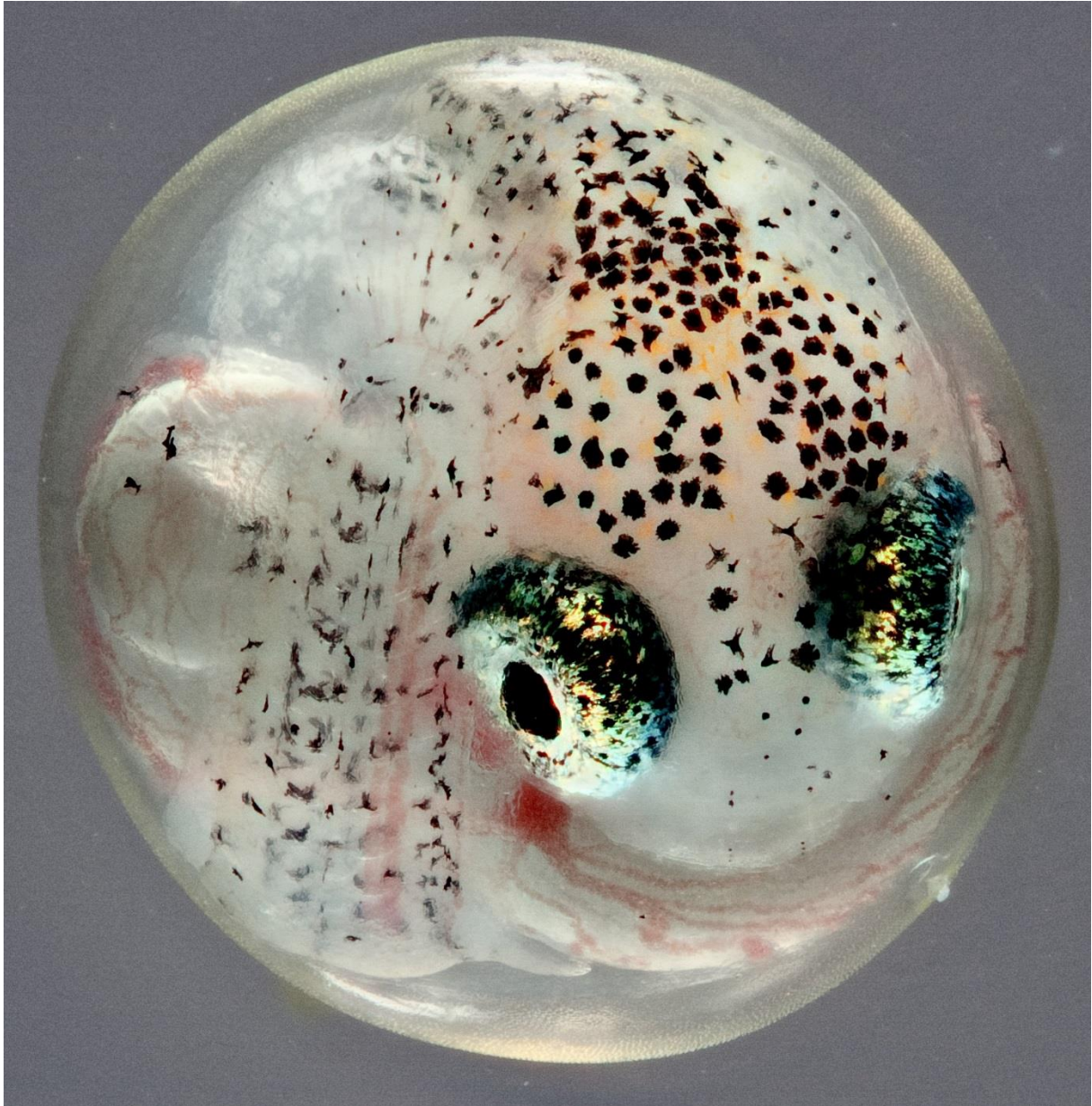
³ Ichthyology Section, Department of Zoology, National Museum of Natural History, Montevideo, Uruguay

⁴Institute of Limnology "Dr. Raúl A. Ringuelet" (ILPLA-CONICET), La Plata, Buenos Aires, Argentina



An egg from a seasonal fish in remains of organic matter that form the bottom of the puddle.

The seasonal species are found in the plains of Africa (family Nothobranchiidae) and South America (family Rivulidae). Evolution has endowed these particular fish with a series of notable adaptations that have allowed them to conquer environments unattainable for most fish, which explains their evolutionary success in terms of their large number of species. Possibly its most notable feature lies in its eggs. When these are buried, embryonic development is stopped in a what is known as "diapause", which is divided into 3 stages. These are states of very low metabolic, cellular and developmental activity that are mediated by environmental factors that trigger the start and end of each stage. These diapauses are of varying duration and may or may not occur. Sometimes embryos can avoid all diapauses, called "escape embryos". As the duration of diapauses is variable, not all eggs are in the same state of development and therefore when a puddle is filled with water, not all eggs present hatch, and many remain in diapause. This reproductive strategy ensures that, if the puddle dries very soon and the fish did not reproduce, a set of "reserve" eggs will hatch in the next flood event preventing the fish from dying in that environment. This type of reproductive strategy is known in Biology as a bet-hedging strategy what can be translated as "don't put all your eggs in one basket" or, in this case, in the same rain. This is an adaptation to stressful and unpredictable environmental conditions. On the other hand, the eggs have the outer part (chorion) remarkably thickened, which prevents their drying and allows them to tolerate mechanical friction when buried, so they can be handled quietly with the fingertips without breaking them.



An embryo of *Austrofundulus limnaeus* Schultz 1949, a seasonal species of Venezuela. Photo: Jason Podrabsky

When the rains arrive the chorion, the outside of the eggs, softens, and in only a few hours the embryos come out of the egg and emerge from the mud, making their way through the substrate retrogradely with their tails.



Austrolebias larvae of just a few millimeters that hatched with the rain of the previous day, in late summer in the Pampasic region.

Something remarkable is that “seasonality”, and particularly the ability to have eggs that enter diapause state, does not respond to a single evolutionary event within this group of fish, but has evolved independently, that is, convergently, at least six times during the evolution of the Cyprinodontiformes, particularly within the suborder Aplocheiloidei. However, this characteristic does not appear only once in the evolution of vertebrates outside this group, although it is within other animal groups such as insects and crustaceans. This convergent evolution in seasonal fish involves some kind of preadaptation or set of characteristics that evolutionarily facilitated the appearance multiple times in the evolution of these particular characteristics in this group of fish.

These fish have an extraordinarily fast growth associated with very high metabolic rates and consequently reach very quickly sexual maturity, being, in fact, an African killi (*Nothobranchius furzeri*) the fastest vertebrate reaching it in just 14 days after the hatching of the egg. But this frenetic life has its costs and is that these fish also age very fast, and individuals in just a few months present typical signs of aging such as loss of muscle mass, curvature of the skeleton, and appearance of tumors. For this reason these fish have become an organism model to study aging in vertebrates, since they are easy to breed in laboratory, require little space and in a short time you can have elderly specimens for study.



The life of these little fish can be measured in months. They do everything quickly: hatch, mature, reproduce and even age. In the photo an old specimen of *Nothobranchius furzeri*, an African genus that reaches sexual maturity in just 2 weeks, being the fastest vertebrate to do so and that in only a couple of months are already elderly, they lose muscular mass, their spine is curved, develop cataracts in their eyes and often have tumors.

They are one of the most promising models of aging studies. (Photo by Radim Blazek).

Another noteworthy feature of these species is that, in general, they have a marked sexual dimorphism, in which generally males have very striking coloration patterns and a larger size than females. This is related to competition among males, who perform displays with their fins extended when fighting each other and when they court females, who choose more colorful males or with certain coloring patterns. Females have a faint coloration, in the color gamut of browns and greys, with different patterns of lines and/or darker spots depending on each species. In contrast and usually, males have a much more conspicuous coloration and in the case of some genera such as *Austrolebias*, the length of the base of the dorsal and anal fin is much larger than that of females. This pronounced dimorphism suggests that sexual selection could play a key role in the differentiation, speciation and evolution of this diversified group of fish.



Cross-section of the bottom of a pool of seasonal fish. Eggs are buried below the driest part of it in an area that retains some moisture.

Due to this set of unique biological characteristics related to life in extreme aquatic environments, these fish have become highly interesting biological models for various disciplines and increasingly attract the attention of various research groups in fields as diverse as embryology, molecular biology, physiology, behavior, population genetics, ecology, senescence and evolution.

Seasonal fish from Argentina and its environments

In the Neotropics, seasonal fish are represented within the family Rivulidae, although not all members of this family are seasonal as we mentioned. In Argentina there are present 6 genera of the family Rivulidae, 5 of which are seasonal (*Austrolebias*, *Pterolebias*, *Neofundulus*, *Papiliolebias* and *Trigonectes*) with 16 valid species, and a single species of permanent waters, *Melanorivulus punctatus* (Boulenger, 1895) that does not possess drought resistant eggs.



Melanorivulus punctatus, the only non-seasonal species of the family Rivulidae present in Argentina, male at the top and a female at the bottom.

Biogeographical regions and ecological characteristics of seasonal fish in Argentina

Within Argentina seasonal fish are located within the Chacoan-Pampasic plain, below 350 m above sea level. This South American plain, one of the largest in the world, part of Argentina, Bolivia, Brazil, Uruguay and Paraguay, has a relief of flat shapes, without outstanding formations and a gentle decline from the northwest to the southeast. Within this plain, we can distinguish two large regions where seasonal fish live, the Pampasic region and the Chacoan region. Each of these regions has endemic species and in some cases, some shared seasonal fish species.



Approximate distribution of the geographical regions mentioned here.

Chacoan Region

This region is in the north of the Pampasic region and is drier than the latter. It is characterized by the presence of forests, grasslands and wetlands. It corresponds to a basin which was filled by sediments from the erosion of the neighboring massifs. Rainfall decreases from east to west in this region. It can be subdivided into 2 regions:

Western Chacoan (or semi-arid)

It is in the western portion of the Chacoan region, encompassing the east of Salta province, north of Santiago del Estero and western Formosa and Chacoan provinces of Argentina. The precipitation is concentrated almost exclusively in summer, between December and March approximately and hover around 300 to 500 mm per year. This determines that the cycle of seasonal ponds in this area starts with the filling between December and January and they usually dry out between March and April. In this area most of the year (9 months from April to December) the puddles will be dry. It is the longest period of drought among annual fish. The species present here are *Austrolebias vandenbergi*, *A. monstrosus*, *A. wichi*, *Trigonectes aplocheiloides*, *Neofundulus paraguayensis* and *Papiliolebias bitteri*.



Eastern Chacoan

It presents higher annual rainfall (between 850 and 1350 mm) than the western Chacoan and summer is relatively dry, with bimodal periods of rain whose peaks are in autumn and spring, while winter is relatively dry with moderate temperatures. This pattern of precipitation is the same to the south, in the Pampasic region, being the main difference that temperatures are lower and the amount of precipitation are increased towards the south. This determines that seasonal puddles in the Eastern Chacoan district tend to fill in autumn and spring and dry in winter and summer. In other words, in this area it is very common for there to be more than one filling and drying cycle per year. In this area the species present are *A. bellottii* and *A. nigripinnis*, (shared with the Pampasic region), *N. paraguayensis* (shared with the western Chacoan region) *Pterolebias longipinnis* (the most commonly distributed seasonal species in the world that reaches the Amazon) and *Austrolebias toba*, *A. patriciae* and *Trigonectes balzanii* (which are endemic to this area).

Pampasic Region

Similar to the Eastern Chacoan, in the flood zones in the Pampasic region, two annual filling cycles are observed, but associated with a greater precipitation and lower temperature which can bind the spring and autumn cycles in a single cycle with only partial drying in winter, depending on the year, or total drying in winter and summer. This determines a relative ecological continuum between the floodplain of the Paraguay and Paraná rivers with species such as *Austrolebias nigripinnis* and *A. bellottii* that inhabit almost this entire area, while other species such as *Pterolebias longipinnis* are found in the warmest portion of this continuum from the north of the province of Santa Fe approximately. Another species in this region is *Austrolebias alexandri*, endemic to the Uruguay River basin. In turn, *Austrolebias robustus* is endemic to the province of Buenos Aires and *Austrolebias elongatus* of the southern portion of the Pampasic region, it is the largest seasonal fish in the world, reaching 22 cm in

length. Also, it is one of the few seasonal species that feeds on other also seasonal fish with which it lives, as well as *Austrolebias monstrosus* of the western Chacoan.



Adult male of *Austrolebias elongatus*, the largest seasonal fish species in the world and one of the few strokes (Photo by Marcos Waldbillig).



Cycle of a seasonal pond in the Pamasic region. It is characterized by having two wet periods in autumn and spring where puddles fill with water. Depending on the year and the size of the puddle these go through a partial or total drying during the winter, so they usually dry during the summer to fill up again at the end of this or early autumn.

Species of Argentina

Below, we present the seasonal species of Argentina and some of its most noteworthy characteristics. The length is expressed as "standard length" which is the length of the body minus the caudal fin, from the tip of the snout to the origin of this fin.

Genus *Austrolebias*

The males in general are larger, colorful and have the base of the dorsal and anal fins longer than the females. It is the most abundant seasonal fish genus in Argentina.

Austrolebias bellottii (Steindachner, 1881)

It is distributed in the Pampasic region and the Eastern Chacoan (wet), from the south of the province of Buenos Aires to the north to the east center of the province of Formosa, on both sides of the rivers Paraná, Uruguay and Paraguay. In the province of Buenos Aires, it is often referred to as "pearl killifish", "azulejo", "palometa azulada" and "castañeta azul". It is characterized by the bluish green color and relatively tall laterally compressed body of males. The females are brownish in color and may have dark brown to almost black spots or bands. It has a medium size for the genus, reaching about 8 cm long (females smaller).



Austrolebias vanderbergi (Huber, 1995)

Endemic species of Western Chacoan. Closely related to *A. bellottii*, similar in appearance to this one. It differs from this species by presenting a series of scales at the base of the anal fin, small bone spines on the same fin and a grayish to light green coloration of the body. Females similar to those of the anterior species, with elongated vertical light grey bars. It has a medium size for the genus about 9 cm long (females smaller).



Austrolebias robustus (Gonther, 1883)

This species is endemic to the Pampasic region and exclusive to the province of Buenos Aires. It is a not a colorful species, of greenish brown coloration. Females are brown with a marbled pattern and usually have some darker spots on the caudal peduncle.



Austrolebias elongatus (Steindachner, 1881)

It is the largest seasonal fish in the world, being able to reach 22 cm long and one of the few ichthyophage (which eats other fish) species within this group of fish. Its distribution ranges from Gualeguaychú, in Entre Ríos, present on both banks of the Uruguay River, and the area of Zárate in the Buenos Aires province to the south of Buenos Aires. Males are light grey, females greyish brown with irregular grey spots on the body.



Austrolebias monstrosus (Huber, 1995)

Endemic species of western Chacoan (= semi-arid Chacoan). Together with *A. elongatus* are the only two ichthyophages species from Argentina. Similar to that species but has a silvery grey background color with vertical dark grey bands on the body, both in males and females. Its maximum recorded size reaches 15 cm.



Austrolebias nigripinnis (Regan, 1912)

One of the most eye-catching species in the genus. Small size (4.5 cm). Males have a black background color with small iridescent celeste greenish spots that form vertical lines on the body. The distal edge of the dorsal has an iridescent band. It is characterized by presenting the orange pupil of the eye and the vertical dark band below it larger than the pupil. Females are brown with a darker brown spot pattern. It has a large distribution, from the area of La Plata to the south of Misiones and Formosa.



Austrolebias alexandri (Castello y López, 1974)

A colorful medium-sized species (9 cm). Males have a background color ranging from iridescent to greenish light blue, with a series of vertical gray bands characteristic of this species. Another distinctive feature is the presence of a black spot at the base of the first radius of the dorsal fin, both in males and females. Iris grey. Brown females with irregular grey spots on the body, may have some darker in the center. This species is found on both the banks of the Uruguay River basin, in Corrientes and Entre Ríos, on the Argentinean side.



Austrolebias patriciae (Huber, 1995)

Endemic (exclusive) species of the eastern (or wet) Chacoan, of medium size (4 cm). Males have a greenish coloration with characteristic violet reflections and the edge of the anal and serrated dorsal fins. Dorsal profile of the head convex. The origin of the dorsal fin posterior to the origin of the anal fin. Medium-sized iridescent white spots on the fins. Reddish iris. Females grayish brown with dark spots sometimes iridescent.



Austrolebias wichi Alonso, Terán, Calviño, García, Cardoso & García, 2018.

Endemic species of western Chacoan (or semi-arid), small size (5cm). Similar to *A. patriciae*, from which it differs by presenting a concave profile of the head, and the origin of the dorsal fin anterior to the origin of the anal fin. Unpair fins with small iridescent white dots. The males have a dark green coloration with characteristic violet reflections and the edge of the anal and dorsal fins is not serrated. Reddish iris. Females similar to that of the previous species.



Austrolebias toba Calviño, 2006

Endemic species of the eastern Chacoan (or wet), of medium size (4 cm). The males are greenish over a grey background. It has a longitudinal iridescent white band on the dorsal fin in its middle portion and the pectoral fins green. Females similar to those of *A. nigripinnis* and *A. alexandri*.



Other genus

Trigonectes balzanii (Perugia, 1891)

Endemic species of the eastern Chacoan (or wet), of medium to large size (16cm). Present a greenish-background coloration with 3 longitudinal brown lines in the posterior portion of the body and 5 in the anterior portion. The base of the dorsal fin is smaller than the base of the anal fin. Males have anal, dorsal and caudal fins with rounded and irregular brown spots while females have hyaline fins with some small brown spots. In males, the ventral portion of the caudal fin, pelvic and anal fins are orange to fuchsia, with the base of this last fin yellow.



Trigonectes aplocheiloides (Huber, 1995)

Endemic species of western Chacoan (or semi-arid), medium size (10cm). The base of the dorsal fin is smaller than the base of the anal fin. The males have a greenish-grey color on the body and the pelvic fins, ventral part of the caudal fin and the anal fin red to orange, with the base of the latter with a yellow stripe. Females are greenish-grey and hyaline (no color) fins.



Neofundulus paraguayensis (Eigenmamm and Kennedy, 1903)

It is the only species shared between the eastern (or wet) Chacoan and the western (or semi-arid) Chacoan. It has a great variability of coloring patterns. They have a background coloration ranging from greenish grey to yellowish grey, with 3 longitudinal gray lines in the posterior portion of the body and a larger number in the anterior region, intercalated with longitudinal lines of orange spots. They have a longitudinal band at the base of the anal fin with dark edges that in males is orange or yellow and in females is lighter. Males have orange pelvic fins. Caudal fin with orange spots, which may or may not form a halfmoon shape and irregular white blotches. Some specimens have a dark grey spot behind the head.



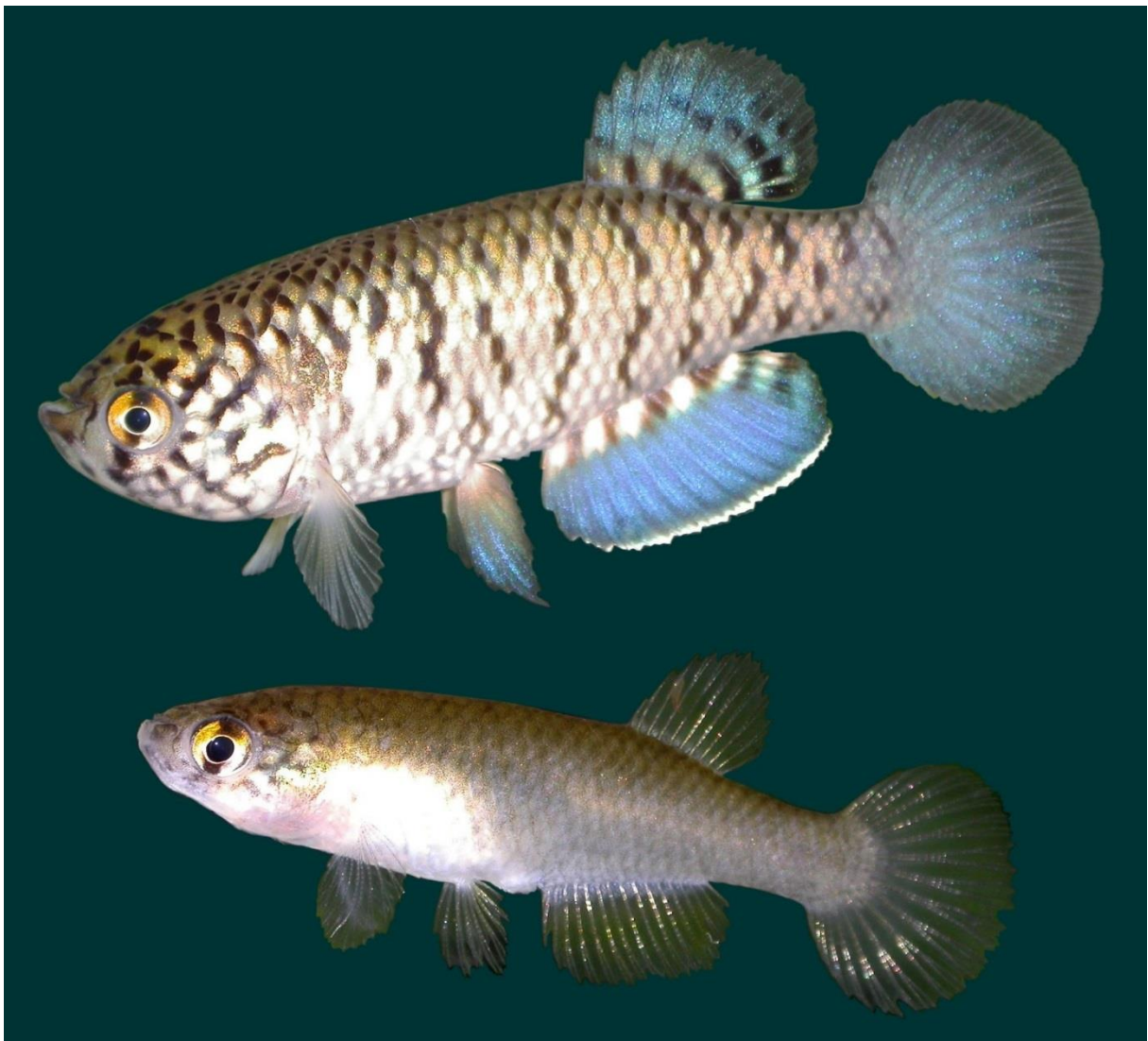
Pterolebias longipinnis Garman, 1895

It is the most widely distributed seasonal fish in the world. It is found from the mouth of the Amazon River to Bolivia and in Argentina has been recorded in the eastern Chacoan (wet) and the southernmost register corresponds to an island off the city of Rosario, Province of Santa Fe. Medium to large size (12 cm). Females grey with hyaline fins. Males, with a great color variability, usually brown body with some small iridescent golden dots and elongated and pointed unpair fins of brick to yellowish color with small subcircular and irregular brown blotches. Some specimens have some red spots posterior to the head.



Papiliolebias bitteri Costa, 1989

Endemic species of western Chacoan (or semi-arid), of small size (5 cm). Females grey with hyaline fins. Males are very colorful, with blue or light blue fins. They have a white band at the base of the anal fin with 4 or 5 sub-square brown blotches and a blue spot above the gill opening posterior to the head. Yellow operculum with a reticulated brown pattern. Greenish yellow body with brownish grey dorsal portion.



Annual or seasonal fish?

As we saw above it is common that there is more than one cycle of filling and drying puddles. For this reason, it is that the traditional name "annual" fish is not appropriate for these species and we prefer the use of seasonal fish. On the other hand, in some years we have observed in the Pampasic region cases in which puddles can last more than a year with water (in years with many rainfall and large puddles) so the cycles are also not strictly annual.

Can we find seasonal fish in permanent waters and vice versa?

In seasonal habitats permanent water species are found often. In general, they are species capable of breathing atmospheric air or tolerating low oxygen concentrations and with a high dispersion capacity that arrive from surrounding permanent environments, usually with surface runoff associated with heavy rains. The most common are "wolf fishes" (*Hoplias*, *Hoplerythrinus*, *Erythrinus*), callichthyids (*Callichthys*, *Hoplosternum*, *Lephtoplosternum*), catfishes (*Rhamdia quelen*) and some tetras (*Cheirodon interruptus*, *Astyanax lacustris*, *Hyphessobrycon anisitsi*) and livebearers (*Cnesterodon*, *Phalloceros*), and in many cases also the invasive alien species "mosquito fish" (*Gambusia* spp.) . However, when the puddle dries these fish will die, resetting the seasonal pond and freeing seasonal fish from competition and predators.



A catfish (*Rhamdia cf. quelen*) trapped in an almost dry temporary pond. This phenomenon "resets" the ponds of permanent water species and eliminates predators and competitors from seasonal fish.

On the other hand, seasonal fish may sometimes be found in permanent waters. This has a fundamental ecological and evolutionary value as the main route of dispersal and colonization of new

environments by seasonal fish is through permanent water bodies, usually during high-water times. For this reason, the temporary environments that they inhabit are frequently associated with floodplains of rivers or permanent streams.



Rio de Oro, Chacoan province. In this stream of permanent water in addition to the typical fish of these streams we recorded many *Pterolebias longipinnis*, the seasonal species of greatest worldwide distribution and that usually colonizes permanent environments.

Transport of fish on the legs of birds. Myth or reality?

There is a widespread myth that fish eggs are moved on the legs of birds. However, this is refuted by biogeography because, if we look at the distribution of the species, many of them are restricted to a single seasonal pond or micro-drainages and if this dispersal mechanism was effective these microendemisms would not be observed.

Aquarium hobby

There are some fundamental characteristics of this fish that makes many of them among the most popular aquarium fish in the world: the first is the diversified and striking color pattern exhibited by males and the second is, in the case of seasonal species, their particular type of reproduction that facilitates the exchange of eggs within aquarium enthusiast from all over the world. Since 2000, there was a great spread of these fish in Argentina, the product of the birth of the Killi Club Argentino (KCA), an association of aquarium hobbyist from which a group of enthusiasts emerged that began a wide survey of this family in Argentine territory, and contributed with observations of the ecology and behavior of these species, especially generating a strong diffusion of these fish in Argentina. This is

how some of us, who started as members of this group, within an association of aquarium enthusiasts,, decided to take a step further and then we formed the Killifish Research and Conservation Group (GICK, in spanish) composed of scientists and specialists in this group of fishes.

Responsible Aquarium Hobby



Biotope aquariums. Aquariums emulating seasonal fish environments of the Pampasic region in an exhibition held at the Argentine Museum of Natural Sciences (MACN).

Aquarium hobby can be a threat or an ally of fish conservation. It is important to promote a principled hobby that serves as a means of raising awareness in society about the importance of conserving these fish and their ecosystems, raise awareness on these species and economically support conservation and research projects for these species, as in fact already happens with some associations of aquarists throughout the world. Killifish, and seasonal species in particular, are species that by their size and characteristics can be relatively easily bred in aquarium, although they have some very particular specifications, once met the reproduction of most species is achieved without problems. Therefore, it is important that aquarium enthusiasts reproduce these fish in captivity to avoid their extraction from natural environments and that they commit to not to buy wild fish and avoid their extraction from nature. In turn, the knowledge generated by aquarium hobbyists about the biology of these species through the accumulation of breeding and maintenance experiences in aquariums, can be fundamental when it comes to conserving these species or studying them in laboratory. For this reason, we think it is important to promote responsible and environmentally conscious aquarium keeping hobby, away from a mere stamp collecting and closer to nature.

Conservation status of seasonal fish species present in Argentina

In the last 12 years, 2.8 million hectares (6.9 million acres) of native forests were lost in Argentina according to Greenpeace. The advance of the agricultural border has been massive in Argentina, especially in the Chacoan region, where only during the last year (2019) about 80 thousand hectares (about 200 thousand acres) of woods have been cut, with the province of Chaco ahead. According to a report by the Refugio Foundation, more than one million hectares (about 2.5 million acres) of Chacoan forest were cut down in the province of Salta in the period 2004-2015. This gives us an idea of the great impact of these activities in this region. Due to their biological characteristics, seasonal fish are particularly vulnerable to environmental disturbances. As they live in shallow seasonal wetlands it is very common for these environments to be channeled or filled with earth for agricultural use, which is reflected in a considerable decrease in the environments available to these species. In addition, in the case of monocultures, such as soybeans, we have observed a kind of "sterilization" of environments surrounding these crops and the total disappearance of seasonal fish, even when those environments are not within a field but surrounding it (see below), since the agrochemicals used are cured towards the depressions that form from the terrain, where a total loss of the aquatic vegetation is observed and almost not aquatic life is observed in these ponds.



Temporary environment in the western Chacoan region in Salta province, where there were seasonal fish and that after the implantation of soybeans was "sterilized", without aquatic plants, neither fish nor invertebrates.

There is a species that we have recently described in the western Chacoan region in Salta province, in the Bermejo River basin, which we have named *Austrolebias wichi* (Alonso *et al.* 2018). Although we have made numerous surveys in that area since 2005, we have only been able to register this species

in a single puddle, which is a paleochannel (old riverbed that is filled with rainwater), which is surrounded by soybean plantations and monocultures. In recent years we have recorded very few specimens of this species in this environment, and in fact many years we have not been able to detect even one. Although we have informed the authorities of the province regarding the critical conservation status of this species until our knowledge, no action has been taken in pursuit of its conservation. The area where this species inhabits has suffered a huge impact in recent years due to large deforestation and the implantation of monocultures and we have also observed the channeling of a large portion of the area's characteristic wetlands. Urgent action is needed to conserve this species and these unique wetlands, and to review these types of agricultural practices that, in addition to degrading the environment, have shown to generate very marked patterns of social exclusion that appear in the media every now and then, such as the death from malnutrition of children of local ethnicities. It is essential that we review this productive model in depth both for its ecological and social consequences that are intimately linked.



Austrolebias wichi and its habitat, a species in critical conservation status due to the advance of the agricultural border and the use of agrochemicals in the area of the Western Chacoan region in Salta.

Killis Research and Conservation Group (GICK).



Analyzing newly collected specimens and taking tissue samples for DNA analysis in a sampling trip in the Chacoan region.

From 2005, together with other colleagues, we formed a group dedicated to the research of the Rivulidae that we would later call **killis Research and Conservation Group (or Grupo de Investigación y Conservación de Killis, GICK, in Spanish)**. "Knowing to transmit and conserve" and "always beyond" are our mottos that define us in values and attitude. We believe in the generation of knowledge and its dissemination as essential tools for the conservation and development of our societies. Seasonal fish are a paradigmatic case in Biology for their particular characteristics, with potential applications of research on these species at the level of biotechnology, medicine, aquaculture and conservation, with their importance as flag species or umbrella species, which are charismatic or emblematic species that serve to mobilize society to protect a certain ecosystem and thus all species that inhabit in it. That is why we have formed a team of a group of biologists and specialists to study this group of fish and turn our passion and dedication. We believe in a science committed to society, in education, and in knowledge as tools of change.



Sampling in the Pampasic region.

As a result of the formation of this working group we have carried out several scientific publications and popular science articles, with the description of new species and studies of ecology and evolution. We have also held numerous popular science talks and exhibitions in various places such as the Argentine Museum of Natural Sciences (MACN), University of Buenos Aires, Universidad Nacional de Salta, Feria del Libro, Nights of museums, Veterinary Expo, etc. We collaborate in various publications of dissemination in various newspapers such as Pagina/12, Infobae, Clarín, Exactamente, and specialized aquarium magazines. The team is composed of specialists of these fish from Argentina (Felipe Alonso, IBIGEO; Ignacio García, UNLP; Guillermo Terán, FML-UEL; Martín Miguel Montes, CEPAVE-UNLP, Marcos Waldbillig, UNLP, Tomás Acuña, Facundo Bozza; and Pablo Calviño, MACN), Uruguay (Wilson Sebastián Serra Alanís, Museo Nac. Hist. Nat. (Francisco Severo Neto, UNESP).



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