

Seasonal trophic activity of the aquatic morphotype of *Atelognathus patagonicus* (Anura, Neobatrachia) and prey availability in the littoral benthos of a permanent pond in Argentinean Patagonia

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Abstract

Seasonal trophic activity of the aquatic morphotype of *Atelognathus patagonicus* (Anura, Neobatrachia) and prey availability in the littoral benthos of a permanent pond in Argentinean Patagonia. The diet of the aquatic morphotype of *Atelognathus patagonicus* was studied in frogs collected from the Laguna Verde pond (Laguna Blanca National Park, Neuquén, Argentina). The content of 35 gastrointestinal tracts of post-metamorphic specimens from November 2003 to April 2006 was related to the composition of the benthos in their microhabitat. Number, size, occurrence and relative importance of preys, diversity of the diet, trophic niche breadth and electivity were estimated for each season of the year. The diet consisted of aquatic arthropods. The composition of both the benthos and the food (number and occurrence of organisms in the diet) were dominated by the amphipod *Hyaella* sp. The relative importance (IRI) of *Hyaella* sp. in the diet was over 99% in summer and autumn, and 100% in winter and spring. Diptera and Copepoda in summer, and Dytiscidae and Ostracoda in autumn, had seasonal IRI values $\leq 0.2\%$. Trophic niche breadth was very low in summer and autumn, and null (= 0) in winter and spring. The mean number of preys per individual was highest in spring (19 preys/frog) and lowest in winter (4 preys/frog). Frogs continued with their trophic activity in winter, even when the surface of the pond was frozen. There is a correspondence between the frogs' main food item and its presence in the benthos.

Keywords: Anura, Neobatrachia, *Atelognathus patagonicus*, seasonal diet, overwintering, benthos composition, Argentinean Patagonia.

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Resumo**Atividade trófica sazonal do morfótipo aquático de *Atelognathus patagonicus* (Anura, Neobatrachia) e disponibilidade de presas no bentos litorâneo de uma lagoa permanente da Patagônia argentina.**

Estudamos a dieta do morfótipo aquático de *Atelognathus patagonicus* com base em indivíduos coletados na lagoa Laguna Verde (Laguna Blanca National Park, Neuquén, Argentina). O conteúdo gastrointestinal de 35 indivíduos pós-metamórficos (novembro de 2003 a abril de 2006) foi correlacionado com a composição do bentos em seu micro-habitat. O número, o tamanho, a ocorrência e a importância relativa das presas, a diversidade da dieta, a amplitude do nicho trófico e a letividade foram estimados para cada estação do ano. A dieta consistiu de artrópodes aquáticos. A composição do bentos e da dieta (número e ocorrência de organismos na dieta) foram dominadas pelo anfípode *Hyalella* sp. A importância relativa (IRI) de *Hyalella* sp. na dieta foi maior que 99% no verão e no outono e de 100% no inverno e na primavera. Díptera e Copepoda no verão e Dytiscidae e Ostracoda no outono tiveram valores sazonais de $IRI \leq 0,2\%$. A amplitude do nicho trófico foi muito baixa no verão e no outono e nula ($= 0$) no inverno e na primavera. O número médio de presas por indivíduo foi maior na primavera (19) e menor no inverno (4). Os anuros continuaram a se alimentar no inverno, mesmo após o congelamento da superfície da lagoa. Há uma correspondência entre o principal item alimentar desses anuros e sua presença no bentos.

Palavras-chave: Anura, Neobatrachia, *Atelognathus patagonicus*, dieta sazonal, composição do bentos, Patagônia, Argentina.

Introduction

Atelognathus patagonicus, an endemic frog from north-western Argentinean Patagonia, is categorized as “Endangered” by IUCN (Úbeda *et al.* 2004); it was reported to have disappeared from Laguna Blanca, the main site, as a result of the introduction of fish (Administración de Parques Nacionales 1993, Fox *et al.* 2005). The species currently lives in permanent and temporary water bodies in a system of endorheic ponds located on the basalt plateaus of Laguna Blanca National Park and its surroundings (38°55'05" – 39°08'05" S, 70°05'00" – 70°30'00" W) (Cuello *et al.* 2009). The species has two morphotypes: aquatic and littoral (Cuello *et al.* 2008). The aquatic morphotype is the most common and lives mainly in permanent ponds (Fox *et al.* 2005).

Research on *A. patagonicus* began in Argentina in the 1960s (Ceí and Roig 1966, 1968, Daciuk 1968) and although there has been an increasing number of contributions in recent years, the knowledge of the biology of *A. patagonicus* is still limited. Some aspects of its natural history were studied by Cuello (2002), Fox *et al.* (2005), Cuello *et al.* (2006a,b). The

studies by Cuello *et al.* (2006a,b) analyzed the feeding behaviour of *A. patagonicus* in the ponds Laguna del Burro and Laguna del Hoyo using data collected during the summer months, which therefore do not provide information on seasonality in the frog's diet or on seasonal availability of preys in nature. Moreover, the overwintering biology of these frogs during the coldest months remains unknown.

Most adult anurans display one of three responses when winter approaches: 1) submersion, 2) permanence on land in a thermally isolated shelter, or 3) permanence on land tolerating freezing (Pinder *et al.* 1992). In permanent ponds, *Atelognathus patagonicus* remains submerged during winter, but it is not known whether it supports cold-induced lethargy or remains responsive according to the description by Hillman *et al.* (2009).

The aims of this study were to (i) record the feeding activity of the aquatic morphotype of *A. patagonicus* throughout the year in a permanent pond, investigating whether winter temperatures induce dormancy or torpor and fasting, (ii) determine whether there is correspondence among the items eaten by the frogs and the seasonal availability of food in

their microhabitat, and (iii) determine whether there are differences in diet according to the season.

Materials and Methods

Study area

The Laguna Verde pond (in Laguna Blanca National Park, Neuquén Province, Argentina, 39°01' S, 70°23' W, 1,250 m a.s.l.) is a permanent water body that undergoes major variations in level. Its maximum surface area is 21.2 ha with a perimeter of 2.5 km (recorded in October 2005), and minimum surface area is 15.2 hectares, with a perimeter of 1.53 km (recorded in April 2006). It is located in a flat basin and its maximum depth (4.5 m) was recorded in February 2004 and January 2006. The pond freezes over in winter, while at midday in summer, the water temperature at the surface may be over 20 °C.

The landscape is characterized by basaltic plateaus with endorheic basins. The climate is arid; summers are warm with little or no rainfall; winters are cold, with heavy frost, snowfall and rain mainly from May to October. The vegetation is mainly low, thorny shrubby steppe. About 40% of the shore is gently sloping and covered in large overlapping blocks (≥ 45 cm), while 30% is covered in fine sediment; reeds and sedges grow on the rest of the littoral area.

The water is turbid due to suspended particles and microscopic algae. There are also spherical colonies of *Nostoc* sp. and submerged and rooted hydrophytes such as *Myriophyllum quitense* and *Zannichellia palustris*. The most outstanding vertebrates are the aquatic frog (*Atelognathus patagonicus*), which lives in the pond permanently, and from November to April there are many migratory aquatic birds: black-necked swans (*Cygnus melancoryphus*), flamingos (*Phoenicopterus chilensis*), grebes (*Podiceps occipitalis*), coots (*Fulica armillata*) and several species of Anatidae. There are no fish here.

Methods

Field work included seasonal sampling of frogs and benthos. It was performed during two days' work in summer (February), autumn (April), winter (July) and spring (November).

Samples of frogs were taken using plastic funnel traps (11 cm diameter, 30 cm long) with a single funnel (Smith and Rettig 1996). At each sampling, ninety traps were placed at the bottom of the pond, parallel to the shoreline, at three depths ranging from 0.2 m to 0.8 m, at 5 m intervals. These environments are considered suitable for the frogs (Fox *et al.* 2005). The traps were left undisturbed overnight.

As from November 2003, temperature was recorded at midday using a digital thermometer at the three depths. In April 2004, a data-logger (HOBO Water Temp Pro) was installed in the capture area at a depth of 0.5 to 0.8 m to provide hourly temperature records during the sampling period.

Benthos was sampled twice (once in winter and once in summer) along a section of the shore 50 m long by 2 m wide; in summer it was found that flat rocks provide an excellent microhabitat for the frogs (Cuello 2002, Fox *et al.* 2005). Three sites were selected at random and framed with a square of side 0.5 m. A flat rock was lifted at each site, its underside was brushed and the place where it had lain at the bottom was vacuumed. The sample was concentrated and fixed in ethanol 70%. In the laboratory, the surface area of the rock was calculated according to the measurements taken *in situ* (length and maximum and minimum width), taxa were identified, and the number and volume of each category recorded. The data were used to estimate the mean density of invertebrates in winter and summer at the sampling site.

A sub-sample of 40 *Atelognathus patagonicus* specimens was collected from Laguna Verde between November 2003 and April 2006: 19 males, mean snout-vent length (SVL) 33.74 ± 5.9 mm (23.5 - 45 mm); 18 females, mean SVL 30.93 ± 4.9 mm (24.9 - 39 mm) and 3

individuals of unidentified sex, mean SVL 26.70 ± 2.3 mm (24 - 28.2 mm). All specimens were immediately killed by euthanasia, fixed in 10% formalin directly after capture and preserved in ethanol 70%, measured (SVL) to the nearest 0.01 mm, and their sex was determined by direct observation of gonads.

The gastrointestinal tract was dissected and the content of the stomach and small intestine, which was considered as a unit, was isolated in order to study the diet.

The life stage and taxonomic category of preys, to the lowest possible level, were determined using a stereoscopic microscope. The whole or fragmented material present in the stomach and small intestine was used to quantify the prey items. The content of the large intestine was analyzed qualitatively to obtain additional information. Prey volume was estimated by water displacement (0.01 ml). For very small or incomplete preys, mean volume was calculated using reference specimens from the same taxon.

Percentage composition of number (% N), volume (% V) and frequency of occurrence (% FO) of preys eaten by the frogs in each season was calculated for each food category. Frequency of occurrence of each category was calculated as the number of gastrointestinal tracts in which a certain category was found divided by the total number of tracts examined. An estimate of the relative importance of each food category was obtained by the index of relative importance: $IRI = \% FO (\% N + \% V)$ (Pinkas *et al.* 1971). The food categories that made up 20% or more of the diet composition were considered primary; those that made up 1% to 19.9%, secondary, and less than 1%, incidental (King 1986).

Trophic niche breadth (B) was estimated by applying Levins (1968) index:

$$B = 1 / \sum_{i=1}^n p_i^2$$

where p_i is the proportion of the i th item (number) in the diet of *A. patagonicus*;

B takes on values between 1 and n , where n is total number of resource states (prey categories). The standardized Levins index (B') was estimated using the formula: $B' = B - 1 / n - 1$, where B is Levins index and n is the number of prey categories. The value of B' ranges from 0 to 1; becomes independent of the number of resources available and enables an absolutely equivalent comparison between two samples (Hurlbert 1978, Krebs 1989).

Per cent seasonal diet overlap was measured following Schoener (1970):

$$\alpha = 100 [1 - 0.5 \sum_{i=1}^n |p_{xi} - p_{yi}|],$$

where p_{xi} is the proportion of food category i in the diet of the season x , p_{yi} = proportion of food category i in the diet of the season y , and n = the number of food categories.

Trophic diversity (H) of the "aquatic morphotype" was calculated following Hurtubia (1973), who estimates trophic diversity for each predator following Brillouin (1965): $H = (1/N) (\log_2 N! - \sum \log_2 N_i!)$.

Prey item data from frogs taken at random were used to calculate the accumulated trophic diversity (H_k) and determine the minimum sample following Pielou (1966), as modified by Hurtubia (1973).

Electivity in feeding was calculated by Ivlev's Index (E_i) (Ivlev 1961): $E_i = (n_i - r_i) / (n_i + r_i)$, where n_i is the proportion of each prey item found in the diet and r_i is the proportion of each prey item in the environment. E_i can vary between -1 and 1. A threshold of 0.5 was used following Cogalniceanu *et al.* (1998): prey taxa with $E_i > 0.5$ are considered preferred (positive electivity) and those with $E_i < -0.5$ are considered avoided (negative electivity). Ivlev's Index (E_i) is zero when the organism is taking a food category in direct proportion to the relative abundance or likelihood of encountering the food category (Lechowicz 1982).

Results

According to the midday records taken with the digital thermometer, water temperature had well-defined seasonality (Figure 1). The coldest months were May, June and July, while the warmest were December, January and February.

With the data-logger, the mean minimum water temperature was recorded in June 2005 (2.28 ± 0.77 °C) and the mean maximum in February 2005 (19.94 ± 2.84 °C). The absolute minimum value was 0.55 °C, recorded in July 2004; the absolute maximum was 26.96 °C, recorded in February 2005. The hourly temperature during the ten days prior to the winter frog sampling (July 15, 2005) ranged from 1.02 °C to 4.4 °C.

Every year the surface of the pond freezes over partly or totally from June to August.

There was content in the digestive tract of thirty-five specimens of the aquatic morphotype of *A. patagonicus* (87.5% of the material collected). The greatest number of empty stomach-small intestine (n=3) was recorded in spring. In winter, 83.3% of the frogs analyzed had food in the stomach-small intestine.

The SVL of the frogs with some gut content ranged from 23.5 mm to 45 mm. The latter value approaches the highest known SVL (50 mm) for the species (Figure 2). The lowest SVL value was observed in summer, whereas the highest was in winter.

Five categories of food were identified in the stomach-small intestine of males and females;

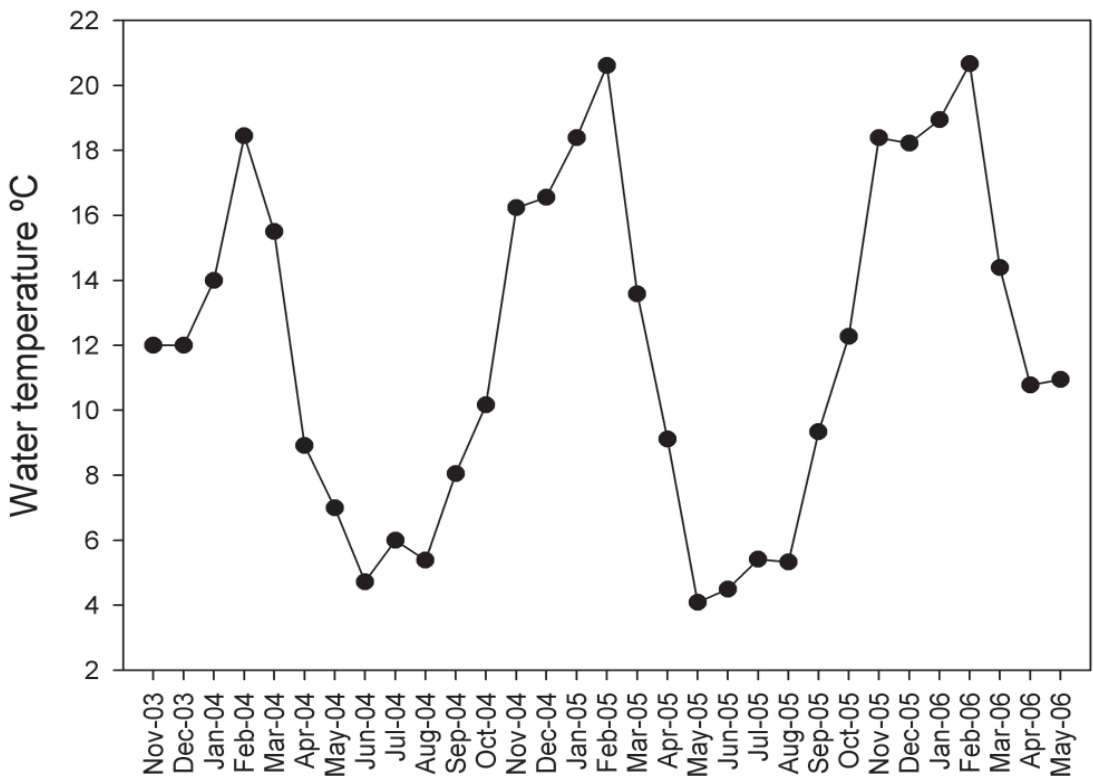


Figure 1 - Monthly water temperature record at Laguna Verde, Neuquén, Argentina, during the period November 2003 – May 2006. Temperatures (average for three depths between 0.2 and 0.8 m), recorded at midday in the area where frogs were captured.

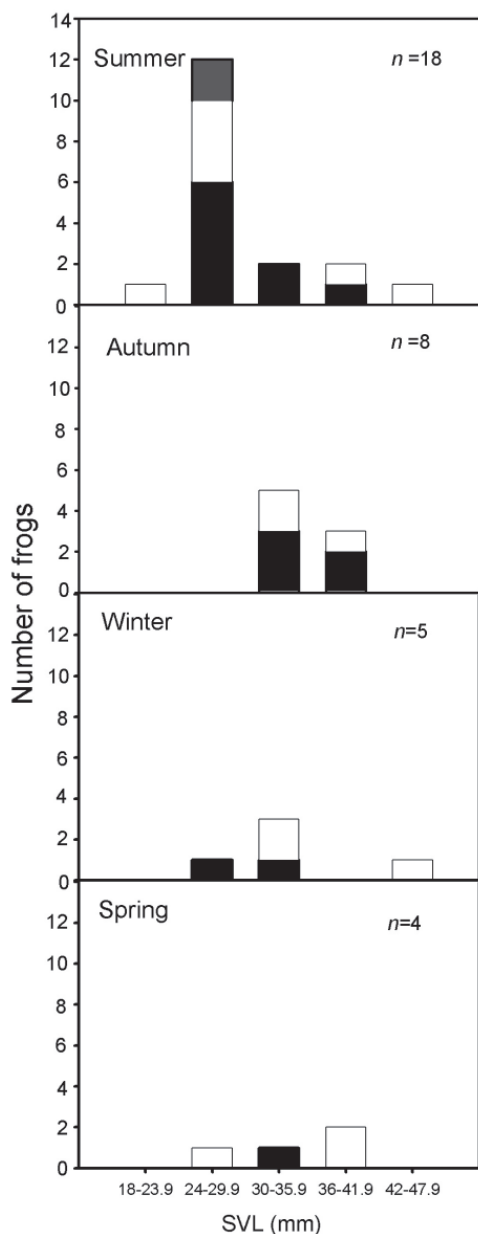


Figure 2 - Number of *Atelognathus patagonicus* (aquatic morphotype) males, females and individuals of unidentified sex with preys in the stomach-small intestine for each season, for five length classes, $n = 35$; Laguna Verde, Neuquén, Argentina. White bars = males; black bars = females; grey bar = specimens of unidentified sex.

three categories were listed in summer, three in autumn, one in winter and one in spring (Table 1). The taxonomic categories found in the large intestine were the same as the ones found in the stomach-small intestine during the study period. Mean trophic diversity and accumulated trophic diversity were $\bar{H} = 0.05 \pm 0.14$ and $H_k = 0.13$ in summer, and they were $\bar{H} = 0.1 \pm 0.19$ and $H_k = 0.26$ in autumn. In winter and spring, diet diversity was null ($= 0$). The minimum sample was 11 digestive tracts in summer, seven in autumn, and one in winter and in spring.

Average intake was 7 preys/frog (range 1–22) in summer, 7 preys/frog (2–17) in autumn, 4 preys/frog (2–7) in winter and 19 preys/frog (5–32) in spring. The diet was made up of aquatic arthropods in all seasons. The amphipod *Hyalella* sp. had the greatest occurrence and was a constant prey item all year round; the relative importance of *Hyalella* sp. in the diet was 100% in winter and in spring, 99.95% in summer and 99.66% in autumn (Table 1). *Hyalella* sp. is identified as the primary food item, and Dytiscidae (Coleoptera), Brachycera (Diptera), Copepoda and Ostracoda as incidental food.

Seasonal diets were similar (overlap $\geq 99\%$, Table 2); trophic niche breadth was low in summer ($B = 1.03$; $B' = 0.02$) and autumn ($B = 1.08$; $B' = 0.04$), and null in winter and spring (Table 1).

Hyalella sp. prey length ranged from 3 to 14 mm. The largest amphipods, with mean estimated length of 10.83 ± 1.61 mm, were eaten in autumn. Modal length was 9 mm in summer and spring, and 11 mm in autumn. Amphipods measuring 3 to 5 mm were the least frequent preys and were found only in winter and summer (Figure 3).

The individual volume of amphipod preys eaten by the frogs did not exceed 0.04 ml.

The analysis of the benthic composition in the frogs' feeding area showed that *Hyalella* sp. was predominant in both summer and winter. Summer samples were made up of *Hyalella* sp. (95.4%), ostracods (1.8%), copepods (1.7%)

Table 1 - Components of the diet of *Atelognathus patagonicus* (aquatic morphotype) expressed in percentages of number (N), volume (V) and frequency of occurrence (FO), and index of relative importance (IRI) and percentage of IRI (% IRI), grouped according to seasons. For each season, the values for trophic niche breadth and standardized niche breadth are provided (B and B') respectively. 1 = larva.

Prey categories		% N	% V	% FO	IRI	% IRI	B	B'
Summer							1.03	0.02
Amphipoda	<i>Hyalella</i> sp.	98.32	99.89	94.44	18719.70	99.95		
Diptera	Brachycera (1)	0.84	0.01	5.56	4.70	0.03		
Copepoda		0.84	0.10	5.56	5.20	0.03		
Autumn							1.08	0.04
Amphipoda	<i>Hyalella</i> sp.	96.30	98.46	100	19476	99.66		
Coleoptera	Dytiscidae (1)	1.85	1.52	13	42	0.22		
Ostracoda	Podocopa	1.85	0.02	13	23	0.12		
Winter							0	0
Amphipoda	<i>Hyalella</i> sp.	100	100	100	20000	100		
Spring							0	0
Amphipoda	<i>Hyalella</i> sp.	100	100	100	20000	100		

and a series of organisms whose individual representation was lower than 1%: odonate naiades of the genus *Rhionaeschna*, chironomid, corixid and dytiscid larvae, cladocerans of the genus *Daphnia*, hirudineans, hydras and nematodes. Winter samples were made up of *Hyalella* sp. (86.5%), chironomid larvae (5.3%), hirudineans (4.5%), ostracods (3.7%) and adult corixids (0.06%). The frogs' primary food, amphipods, was always the most

plentiful item in the microhabitat (Figure 4). Amphipods of sizes ≤ 4 mm, which were rarely eaten, represented 82.6% and 71.3% of the benthic organisms in summer and winter, respectively. Estimated mean densities of invertebrates in the frogs' feeding area were 0.84 specimens per sq. cm in summer and 0.64 specimens per sq. cm in winter.

Ivlev's index is 0.02 in summer and 0.05 in winter for amphipod preys (intake according to abundance), and it is -1 (negative selectivity) for the rest of the organisms, which were poorly represented in the environment, in both summer and in winter (Figure 4).

Discussion

This study enabled us to collect information on the feeding activity of *Atelognathus patagonicus* throughout the year. In particular, it revealed the feeding-related behaviour of the aquatic morphotype during winter.

The water temperature in Laguna Verde is markedly seasonal. In winter it depresses,

Table 2 - Matrix of Schoener (1970) index values measuring percent diet overlap of *Atelognathus patagonicus* (aquatic morphotype) among seasons at Laguna Verde, Neuquén, Argentina.

	Winter	Spring	Summer
Autumn	99.66	99.66	99.66
Winter	-	100	99.95
Spring	-	-	99.95

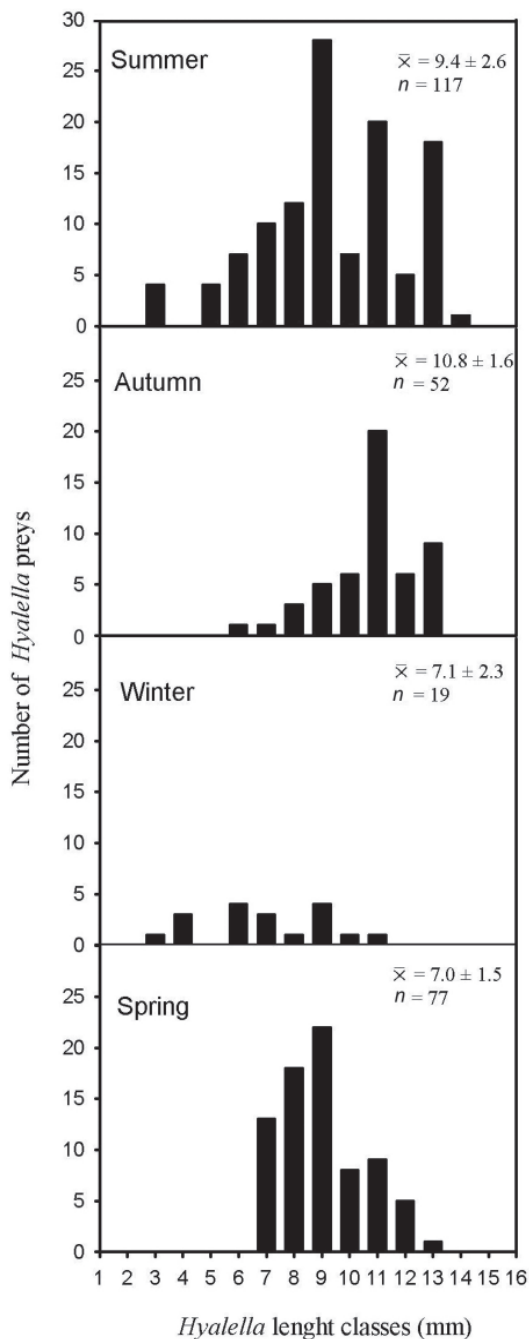


Figure 3 - Distribution according to length classes of *Hyalella* preys eaten by *Atelognathus patagonicus* (aquatic morphotype) in each season. Laguna Verde, Neuquén, Argentina.

though does not inhibit, frogs' feeding activity. Low temperatures during the cold season depress the activity of many anurans in cold-temperate climates, including the green frog, *Rana clamitans* (Martof 1956), the leopard frog, *R. pipiens* (Rand 1950, Emery et al. 1972, Cunjak 1986) and the Columbia spotted frog, *R. luteiventris* (Bull and Hayes 2002), among others. In general, Pinder et al. (1992) recognize that when amphibians hibernate there is a reduction of the metabolic rate due to the decline in environmental temperature.

There is some information available on the activity of frogs overwintering in ice-covered ponds. In the northern hemisphere, Martof (1956) showed that hibernating adult green frogs remain inactive for over 145 days. Bull and Hayes (2002) have shown that Columbia spotted frog maintains discreet mobility in water below 3°C to make use of areas with greater oxygen content. Emery et al. (1972) observed leopard frogs resting in small pits in an ice-covered pond, sometimes lightly covered with silt and all capable of some movement. In the southern hemisphere, frogs and tadpoles of *Alsodes gargola* inhabiting harsh Andean-Patagonian alpine environments are active or respond to manual stimulation during real or simulated overwintering conditions, and are in good physical condition at the beginning of the thaw (Logares and Úbeda 2004, 2006).

Corbalán et al. (2008) proposed that *Alsodes pehuenche* tadpoles overwinter at least twice in the west of Mendoza Province, Argentina, in high mountain habitats where the climate is harsh, with long winters and a short favourable season.

Overwintering *Atelognathus patagonicus* tadpoles have been reported by Cuello and Perotti (2006) as a result of observations at Laguna Verde from June to August 2004 (austral winter), under the harshest winter climatic conditions. Our study found that in the 1.2 – 4.4 °C interval, adult *A. patagonicus* specimens overwinter submerged in the rocky littoral maintaining their mobility, as noted by

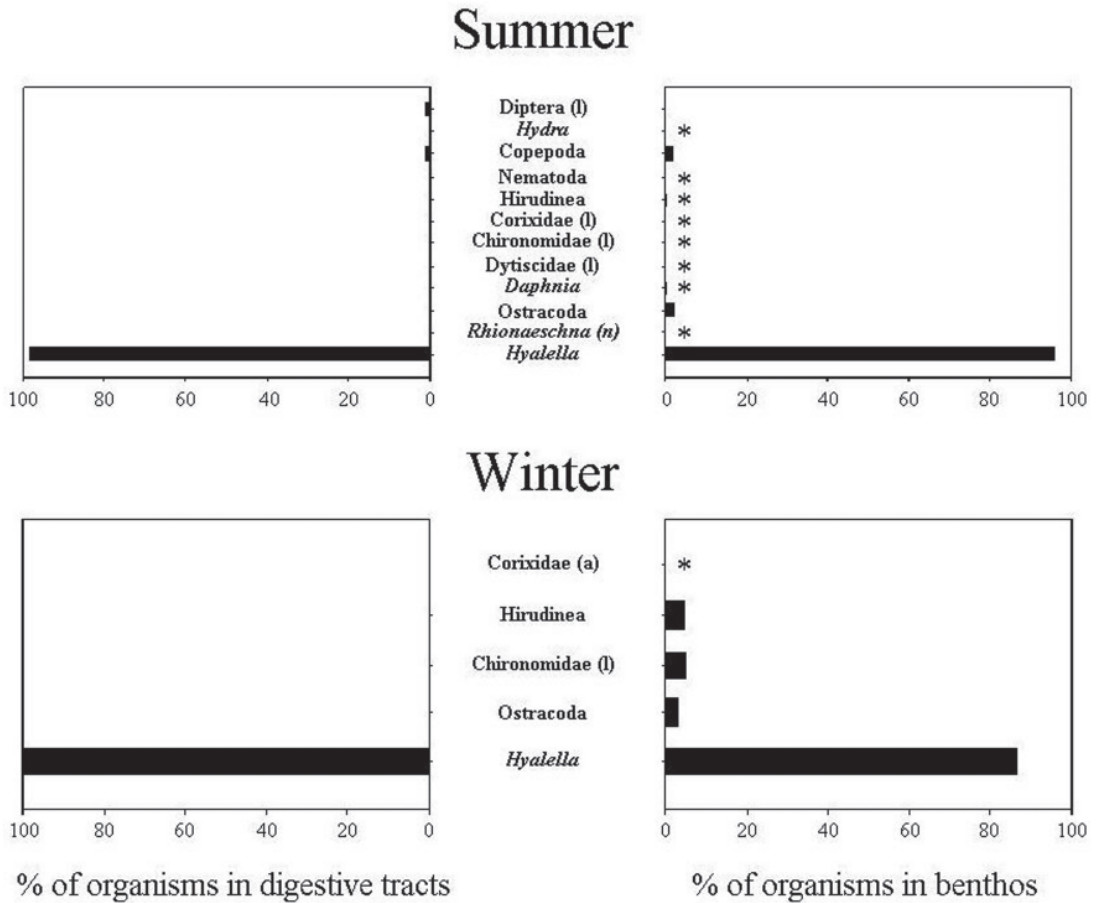


Figure 4 - Percentages of organisms found in the digestive tract of *Atelognathus patagonicus* (aquatic morphotype) and in the benthos samples taken in summer and winter in the frogs' microhabitat. Laguna Verde, Neuquén, Argentina. Insect stages: *l*, *n* and *a* = larvae, naiads and adults; * = occurrence with values lower than 1%.

their entering into the funnel traps. Most of the specimens examined sustained their foraging activity during winter, even though the individual capture of preys declined. This information on the overwintering habits of post-metamorphic *A. patagonicus* is the first contribution of data on the subject, and the information could be taken into account when conservation action is proposed.

Larsen (1992) tried to find an explanation for the seasonal differences observed in

amphibian intake rate and linked the amount of food eaten to changes in the structure and function of the digestive system caused by changes in environmental conditions, specifically, maximum development of the gastrointestinal tract towards mid-summer and its decline before hibernation in *Rana temporaria* (Juszczuk *et al.* 1966). Towards the end of hibernation, Geuze (1971) found signs of activation in the gastric mucosa of *Rana sculentia*. Thus, it is not surprising that the

number of prey organisms eaten by *A. patagonicus* in spring was comparatively high. Subsequently, in summer and autumn, the intake rates recorded in frogs at Laguna Verde were moderate and approached those recorded for the population at Laguna del Hoyo during summer (Cuello *et al.* 2006b).

In contrast to other aquatic anurans, *Atelognathus patagonicus* does not include plant matter in its diet. The Titicaca frog, *Telmatobius culeus*, eats species of *Chara*, *Potamogeton*, *Myriophyllum* and *Schoenoplectus* (Pérez-Bejar 1998) and the African clawed frog, *Xenopus laevis*, in four aquatic environments in Chile, often includes microalgae when it eats (Lobos *et al.* 1999).

Regarding type of prey, the aquatic morphotype of *A. patagonicus* was found to eat only arthropods from the benthos. The trophic fidelity of aquatic anurans to their environment has been noted by Pérez-Bejar (1998) on recording the preys eaten by *Telmatobius culeus* in Lake Titicaca, and by McCoid and Fritts (1980) in Southern Californian waters, Schoombee *et al.* (1992) in South Africa, and Lobos *et al.* (1999) in central Chile, on analyzing the stomach content of *Xenopus laevis*.

Other species of aquatic anurans of the genera *Pseudis* and *Lysapsus*, which inhabit subtropical environments in South America, have a mixed diet of aquatic and terrestrial organisms (Duré and Kehr 2001, Miranda *et al.* 2006). *Pseudis bolbodactyla* preys mainly on insects detected above the water surface, on the leaves of plants found inside and at the margins of the pond (Teixeira *et al.* 2004).

Comparisons of dietary overlap in *Atelognathus patagonicus* between seasons show that the feeding pattern does not undergo many changes during the year. Amphipods were a primary food item all year round; nevertheless, in other environments, *A. patagonicus* can also include other types of arthropods outstanding for their size in its diet. For example, frogs captured at Laguna del

Burro showed that naiads of *Rhionaeschna* sp. (Odonata, Aeshnidae) (> 20 mm) were the primary food items (IRI% = 86.57), and *Hyaella* sp. were the secondary food items (IRI% = 12.89) (Cuello *et al.* 2006a).

Moreover there are differences between environments regarding the size of the food items identified as primary. At Laguna del Burro *Rhionaeschna* reached a length of 30 mm; at Laguna Verde, in agreement with the findings for Laguna del Hoyo (Cuello *et al.* 2006b), the amphipod preys of intermediate sizes were the most numerous. Small, recently recruited amphipods were avoided at Laguna Verde, which is noteworthy because there was a much higher proportion of small amphipods than of adult specimens in the littoral benthos samples.

The presence of amphipods in the diet of aquatic anurans is common and well-documented (Schoombee *et al.* 1992, Pérez-Bejar 1998, Lobos *et al.* 1999). Amphipods have always been recorded in the diet of the aquatic morphotype of *Atelognathus patagonicus* (Ceï and Roig 1966, 1968, Cuello *et al.* 2006a,b). As *Hyaella* sp. is available as a potential prey in Laguna Verde, the diet of the aquatic morphotype of *A. patagonicus* can consist basically of these arthropods all year round. There are personal observations of the permanent abundance of *Hyaella* sp. in Laguna Verde, particularly in areas frequented by the aquatic morphotype of *A. patagonicus*. The density of invertebrates under rocks in the littoral area, in which the proportion of *Hyaella* sp. was outstanding, was almost as high in winter as in summer. Therefore, the diet of these frogs in Laguna Verde is made up of the dominant organisms in their trophic habitat and consequently, the frogs are identified as opportunistic consumers. Ivlev's electivity Index indicates that amphipods are eaten in direct proportion to their relative abundance, both in winter and in summer.

The present diet analysis suggests that the amphipods are essential as food for the frog

population in Laguna Verde due to their high demand as preys and the high nutritional value afforded by their high percentage of protein (78% in dry weight) (E. Dorsch pers. com.). Furthermore, these results are useful for understand the role of these frogs as predators in ecosystems where they are the only vertebrates in permanent residence and therefore contribute constantly to maintaining ecological balance. Thus, *Atelognathus patagonicus* might be considered a key species in the system of endorheic ponds in the Laguna Blanca National Park.

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References

- Administración de Parques Nacionales. 1993. *Plan General de Manejo del Parque Nacional Laguna Blanca*. Buenos Aires, Argentina. Delegación Técnica Regional Patagónica, Administración de Parques Nacionales. Resolución 65/94. 63 pp.
- Brillouin, L. 1965. *Science and Information Theory*. New York. Academic Press. 245 pp.
- Bull, E. L. and M. P. Hayes. 2002. Overwintering of Columbia spotted frogs in Northeastern Oregon. *Northwest Science* 76: 141–147.
- Cei, J. M. and V. G. Roig. 1966. Los caracteres biocenóticos de las lagunas basálticas del oeste del Neuquén. *Boletín de Estudios Geográficos* 13: 182–201.
- Cei, J. M. and V. G. Roig. 1968. Telmatobiinos de las lagunas basálticas de Neuquén (Anura, Leptodactylidae). *Physis* 27: 265–284.
- Cogalniceanu, D., F. Aioanei, C. Ciubuc, and A. Vadineanu. 1998. Food and feeding habits in a population of common spadefoot toads (*Pelobates fuscus*) from an island in the lower Danube floodplain. *Alytes* 15: 145–157.
- Corbalán, V., G. Debandi and C. A. Úbeda. 2008. *Alsodes pehuénche* (NCN). Larval biology. *Herpetological Review* 39: 457–458.
- Cuello, M. E. 2002. *Atelognathus patagonicus* (Anura, Leptodactylidae): distribución, hábitat, fenología y estado de conservación en el Parque Nacional Laguna Blanca y alrededores. Unpublished Biol. Lic. Thesis. Centro Regional Universitario Bariloche, Universidad Nacional del Comahue, Argentina.
- Cuello, M. E. and M. G. Perotti. 2006. *Atelognathus patagonicus* (Rana Acuática de Laguna Blanca). Overwintering tadpoles. *Herpetological Review* 37: 441.
- Cuello M. E., M. G. Perotti and G. J. Iglesias. 2009. Dramatic decline and range contraction of the endemic patagonian frog, *Atelognathus patagonicus* (Anura, Leptodactylidae) *Oryx* 43: 443–446.
- Cuello, M. E., C. A. Úbeda and M. T. Bello. 2008. Relationship between morphotypes of *Atelognathus patagonicus* (Anura, Neobatrachia) and environmental conditions: evidence and possible explanation. *Phyllomedusa* 7: 35–44.
- Cuello, M. E., M. T. Bello, M. Kun, and C. A. Úbeda. 2006a. Feeding habits and their implications for the conservation of the endangered semiaquatic frog *Atelognathus patagonicus* (Anura, Neobatrachia) in a northwestern Patagonian pond. *Phyllomedusa* 5: 67–76.
- Cuello, M. E., C. A. Úbeda, M. T. Bello, and M. Kun. 2006b. *Atelognathus patagonicus* (NCN). Diet. *Herpetological Review* 37: 198–199.
- Cunjak, R. A. 1986. Winter habitat of northern leopard frogs, *Rana pipiens*, in a southern Ontario stream. *Canadian Journal of Zoology* 64: 225–257.
- Daciuk, J. 1968. La fauna del Parque Nacional Laguna Blanca. (Estudio zoo-ecológico preliminar). *Anales de Parques Nacionales* 11: 225–304.
- Duré, M. and A. I. Kehr. 2001. Differential exploitation of trophic resources by two pseudid frogs from Corrientes, Argentina. *Journal of Herpetology* 35 340–343.

- Emery, A. R., A. H. Berst and K. Kodaira. 1972. Under-ice observations of wintering sites of leopard frogs. *Copeia* 1972: 123–126.
- Fox, S. F., J. H. Yoshioka, M. E. Cuello, and C. Úbeda. 2005. Status, distribution, and ecology of an endangered semi-aquatic frog (*Atelognathus patagonicus*) of northwestern Patagonia, Argentina. *Copeia* 2005: 921–929.
- Geuze, J. J. 1971. Light and electron microscope observations on the gastric mucosa of the frog (*Rana esculenta*): 2. Structural alternations during hibernation. *Zeitschrift für Zellforschung* 117: 103–117.
- Hillman, S. S., P. C. Withers, R. C. Drewes, and S. D. Hillyard. 2009. *Ecological and Environmental Physiology of Amphibians*. New York. Oxford University Press Inc. 469 pp.
- Hurlbert, S. H. 1978. The measurement of niche overlap and some relatives. *Ecology* 59: 67–77.
- Hurtubia, J. 1973. Trophic diversity measurement in sympatric predatory species. *Ecology* 54: 885–890.
- Ivlev, V. S. 1961. *Experimental Ecology of the Feeding of Fishes*. New Haven. Yale University Press. 302 pp.
- Juszczyk, W., K. Obrzut and W. Zamachowski. 1966. Morphological changes in the alimentary canal of the common frog (*Rana temporaria* L.) in the annual cycle. *Acta Biologica Cracoviensia (Zoology)* 9: 239–246.
- King, R. P. 1986. Observations on *Liza grandisquamis* (Pisces: Mugilidae) in Bonny River, Nigeria. *Hydrobiologie Tropical* 19: 61–66.
- Krebs, C. J. 1989. *Ecological Methodology*. New York. Harper Collins Publishers. 654 pp.
- Larsen L. O. 1992. Feeding and digestion. Pp. 378–394 in M. E. Feder and W. W. Burggren (eds.), *Environmental Physiology of the Amphibians*. Chicago and London. The University of Chicago Press. 646 pp.
- Lechowicz, M. J. 1982. The sampling characteristics of electivity indices. *Oecologia* 52: 22–30.
- Levins, R. 1968. *Evolution in Changing Environments*. Princeton. Princeton University Press. 120 pp.
- Lobos, G., P. Cattán and M. López. 1999. Antecedentes de la ecología trófica del sapo africano *Xenopus laevis* en la zona central de Chile. *Boletín del Museo Nacional de Historia Natural (Chile)* 48: 7–18.
- Logares, R. E. and C. A. Úbeda. 2004. *Alsodes gargola* (Rana del Catedral). Overwintering tadpoles. *Herpetological Review* 35: 368–369.
- Logares, R. E. and C. A. Úbeda. 2006. First insights into the overwintering biology of *Alsodes gargola* frogs and tadpoles inhabiting harsh Andean-Patagonian alpine environments. *Amphibia Reptilia* 27: 263–267.
- Martof, B. 1956. Factors influencing size and composition of populations of *Rana clamitans*. *American Midland Naturalist* 56: 224–245.
- McCoid, M. J. and T. H. Fritts. 1980. Observations of feral populations of *Xenopus laevis* (Pipidae) in southern California. *Bulletin of the Southern California Academy of Sciences* 79: 82–86.
- Miranda, T., M. Ebner, M. Solé, and A. Kwet. 2006. Spatial, seasonal and intrapopulation variation in the diet of *Pseudis cardosoi* (Anura: Hylidae) from the Araucaria Plateau of Rio Grande do Sul, Brazil. *South American Journal of Herpetology* 1: 121–130.
- Pérez-Bejar, M. E. 1998. Dieta y ciclo gametogénico anual de *Telmatobius culeus* (Anura: Leptodactylidae) en el Lago Titicaca (Huíñaimarca). Unpublished Biol. Lic. Thesis. Universidad Mayor de San Andrés, La Paz, Bolivia. 140 pp.
- Pielou, E. C. 1966. Species-diversity and pattern-diversity in the study of ecological succession. *Journal of Theoretical Biology* 10: 370–383.
- Pinder, A. W., K. B. Storey and G. R. Ultsch. 1992. Estivation and hibernation. Pp. 250–274 in M. E. Feder and W. W. Burggren (eds.), *Environmental Physiology of the Amphibians*. Chicago and London. The University of Chicago Press. 646 pp.
- Pinkas, L., M. S. Oliphant and Z. L. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. *California Department of Fish and Game, Fish Bulletin* 152: 1–105.
- Rand, A. S. 1950. Leopard frogs in caves in winter. *Copeia* 1950: 324.
- Schoener, T. W. 1970. Non-synchronous spatial overlap lizards in patchy habitats. *Ecology* 51: 408–418.
- Schoonbee, H. J., J. F. Prinsloo and J. G. Nxiweni. 1992. Observations on the feeding habits of larvae, juvenile and adult of the African clawed frog, *Xenopus laevis*, in impoundments in Transkei. *Water SA* 18: 227–236.
- Smith, G. R. and J. E. Rettig. 1996. Effectiveness of aquatic funnel traps for sampling Amphibian larvae. *Herpetological Review* 27: 190–191.
- Teixeira, R. L., D. Vrcibradic and J. A. P. Schneider. 2004. Food habits and ecology of *Pseudis bolbodactyla* (Anura: Pseudidae) from a flood plain in southeastern Brazil. *Herpetological Journal* 14: 153–155.
- Úbeda, C., E. Lavilla and N. Basso. 2004. *Atelognathus patagonicus* in IUCN 2009. *IUCN Red List of Threatened Species. Version 2009.1*. URL: www.iucnredlist.org. Captured on 27 June 2009.