

Ecological significances of ontogenetic shifts in the stream-dwelling catfish, *Hatcheria macraei* (Siluriformes, Trichomycteridae), in a Patagonian river

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Abstract – The relationship between ontogenetic changes and both feeding and habitat preferences was studied in a stream catfish population of Argentine Patagonia. Fish capture, as well as habitat data recording, was performed during a 1-year long period. Larvae–juvenile transition was determined between 22.4 and 29.4 mm standard length (SL), on the basis of the relative growth changes and morphogenesis, and juvenile–adult shift was established between 61 and 65 mm SL using a macroscopic criterion of gonadal development and gonadosomatic index. Spawning period was estimated to be in the summer season, from December to February. Larvae preferred shallow marginal pools and fed mainly on small Chironomidae larvae, while juveniles and adults inhabited riffles and preyed on Ephemeroptera nymphs and Chironomid larvae. Morphological constraints during the larval period were related to habitat and feeding preferences. A complete development of fins allowed juveniles to colonise faster water habitats while a bigger mouth gape permitted them to prey on new items and on a larger size prey range.

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Key words: allometric changes; habitat use; diet shift; morphological constraints

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Introduction

During ontogeny, body size increases and new functional systems are acquired continuously in order to reach adequate performance levels for survival (Osse 1990). Mainly, early life stages of indirect development undergo very complex processes of morphogenesis and differentiation (Balon 1984). The challenges that fish larvae must face are numerous and especially arduous due to their relatively small size, which on many occasions constrains their ability to avoid predators, capture preys and withstand starvation. In this context, changes in ontogenetic states often coincide with niche shifts (Balon 1990, 1999). Therefore, the comprehension of these changing relationships between organism and environment

is crucial not only for ecological knowledge of a species, but also for its future conservation.

The saltatory ontogeny theory (Balon 1999) considers development as a sequence of stabilised states separated by rapid changes. These fast changes have been confirmed at morphological, anatomical and growth level (Osse 1990; Osse & van den Boogart 1995; Loy et al. 2001), and have been related to behavioural (Gisbert & Ruban 2003), habitat (Simonović et al. 1999; Barriga et al. 2002) and diet (Balon 1984) shifts. Transition from one period or phase (*sensu* Balon 1975) to the next one has usually been detected employing relative growth analyses (Gisbert 1999; Kováč et al. 1999; Simonović et al. 1999). Allometric growth changes have been more frequently detected at larvae–juvenile transition (Coop

et al. 1999) than at juvenile–adult transition, as juveniles have already acquired the definitive phenotype.

The native ichthyofauna of Patagonia is very scarce (Baigún & Ferriz 2003); however, basic traits of several species are nowadays still unknown. Particularly, in relation to Siluriform fishes, little is known about their life cycles and early ontogeny (Ludberg et al. 2004). *Hatcheria macraei* (Girard 1855) is a rheophilic and negatively phototactic catfish (Menni 2004) that inhabits fast flowing, clear, cold and well-oxygenated waters (Ringuelet et al. 1967). An important size-related habitat shift has been reported for this species (Arratia & Menu-Marque 1981), which makes *H. macraei* a good subject to evaluate whether this shift is related to ontogenetic periods.

The relationship among life-history traits, such as reproductive characters, is other important point to consider in order to understand how a given species maximises its fitness in a particular habitat (Matthews 1998). The Trichomycteridae life-history strategies seem to be very variable, from precocial type in troglobitic catfishes (Trajano 1997, 2001) to altricial forms in other *Trychomicterus* of Brazil (Casatti 2003). Small changes in life traits can trigger great changes in fitness (Hutchings 1997) and also alternative life histories (e.g., Salmonidae fishes, Klemetsen et al. 2003). Consequently, the generation of basic population data in *H. macraei* is the first step towards a general species understanding.

The focus of this study was on a *H. macraei* population from Patagonia, the southernmost distribution for Trichomycteridae species (Arratia & Menu-Marque 1981). The main goals of this work were: (i) to estimate the ontogenetic periods by means of relative growth, morphogenesis changes and gonad examination, (ii) to establish both the habitat and diet preferences during the development and (iii) to relate these niche shifts to morphological and functional constraints.

Materials and methods

Study area

Hatcheria macraei individuals were collected from the Caleufú River in the northern Patagonian steppe. This river is originated by the confluence of Meliquina and Filo-Hua-Hum Rivers, and empties its water into the Piedra del Águila Reservoir on the Limay River (Atlantic basin). The Caleufú annual mean discharge is $64.5 \pm 49.7 \text{ m}^3 \cdot \text{s}^{-1}$, with a wide fluctuation in the year from $4 \text{ m}^3 \cdot \text{s}^{-1}$ in February to $173 \text{ m}^3 \cdot \text{s}^{-1}$ in October (AEPN (Anuario Estadístico de la Provincia del Neuquén) 2003). The sampling stations on the Caleufú River were located in the steppe, where the

climate is arid (200 mm rainfall per year), approximately 4 km upstream from the reservoir (at $40^\circ 20' 10'' \text{S}$, $70^\circ 45' 12'' \text{W}$; 595 m.a.s.l.). The riparian vegetation consists mainly of shrubs such as *Discaria chacaye* (G. Don) and *Berberis buxifolia* Lam. and the grass *Cortaderia araucana* Stapf.

Fish collection and habitat preference

Fish were captured by means of a 24 V DC backpack electrofishing unit, model 12-B (Smith-Root, Inc., Vancouver, WA, USA), and always in upstream direction. In the marginal areas of the riffles, where water was the shallowest, fish were found hidden beneath rocks and then caught using a hand net (1 mm mesh size). Captured fish were sacrificed in a carbon dioxide-saturated water solution and stored in 4% formaldehyde. Fourteen sampling sessions were conducted from September 2002 to August 2003, and were performed at least every 3 weeks from November to April, and at least once every 6 weeks for the rest of the year.

To evaluate habitat preferences, data were grouped into three habitat categories: pools, riffles and marginal riffles. Pool areas were characterised as having slow and deep water (from 30 to 70 cm deep), with a smooth-surface appearance and patches of aquatic macrophytes, mainly *Myriophyllum* sp., on silty bottom. This habitat was not considered in the analysis because a single individual was caught. Riffle areas were distinguished by fast and shallow water (from 10 to 40 cm deep), with a broken-surface appearance and a rocky bottom substrate characterised by cobbles (64–256 mm) and boulders (>256 mm). Marginal riffle areas were present during the drought season and were characterised by having the shallowest water (<10 cm depth) at the edge of the river with nearly still water with the same riffle bottom substrate.

Conductivity was registered by means of a Multi-range portable conductivity meter, HI 8733 (Hanna Instruments Inc., Buenos Aires, Argentina) ($\pm 0.1 \mu\text{S} \cdot \text{cm}^{-1}$), and water temperature ($\pm 1^\circ \text{C}$) was measured using a TES 1302 digital thermometer (TES Electrical Electronic Corp., Taipei, Taiwan). Average water velocity was recorded with a digital flowmeter with back-run stop, model 438 115 (Hydro-bios, Kiel, Germany) in the riffle areas where fish were caught.

Life periods assessment

Three approaches were applied to estimate the size range of each ontogenetic period: by means of relative growth, morphogenesis and gonadal examination.

All captured fish ($N = 117$) were photographed in dorsal, ventral and left lateral views, and 26 body measurements were recorded (Fig. 1) using an image

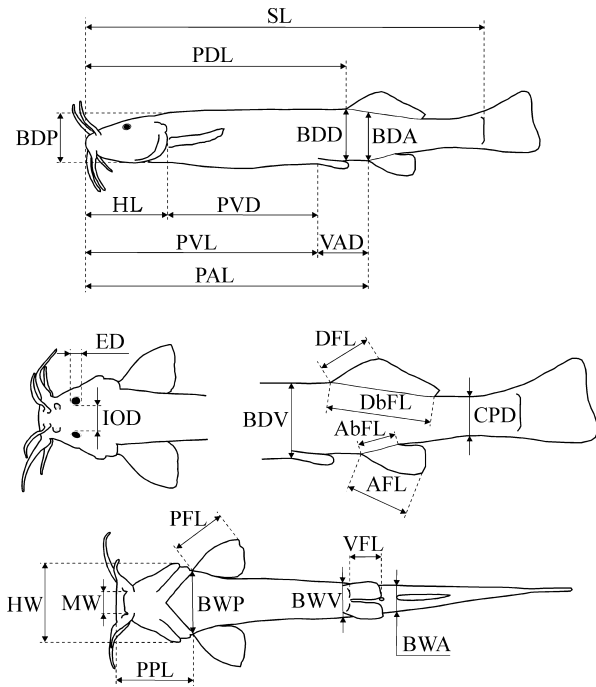


Fig. 1. Measurements used in *Hatcheria macraei* morphometric analysis. Standard length (SL), head length (HL), head width (HW), interorbital distance (IOD), eye diameter (ED), mouth width (MW), prepectoral length (PPD), predorsal length (PDD), preanal length (PAL), pre-ventral length (PVL), pectoral-ventral distance (PVD), ventral-anal distance (VAD), pectoral fin length (PFL), ventral fin length (VFL), dorsal fin length (DFL), anal fin length (AFL), dorsal base fin length (DbFL), anal base fin length (AbFL), caudal peduncle depth (CPD), body width in pectoral fin (BWP), body width in ventral fin (BWV), body width in anal fin (BWA), body depth in pectoral fin (BDP), body depth in dorsal fin (BDD), body depth in ventral fin (BDV) and body depth in anal fin (BDA).

analysis software, Image-Pro Plus[®], version 4.0 for windows (Silver Spring, Maryland, USA). Relative growth (*sensu* Fuiman & Higgs 1997) of *H. macraei* was calculated as a power function (Fuiman 1983) of standard length (SL) using nontransformed data: $y = ax^b$, where y is the independent variable (each measurement other than LS), x the dependent variable (LS), a the intercept and b the relative growth coefficient. When proportions between measurements remain constant (isometric relative growth) $b = 1$, and when proportions change (allometric relative growth) $b \neq 1$, resulting positive or negative when it is greater or minor than 1, respectively.

Thresholds in the life history of fishes (e.g., larvae-juvenile transition) have commonly been estimated by means of inflexion points (IPs) in relative growth analysis (see Kováč et al. 1999; Simonović et al. 1999). With this aim, linear regressions were performed on log-transformed data using the SL as the independent variable. Inflexion points growth curves were determined according to van Snik et al. (1997) and Gisbert (1999) and relative growth coefficients were compared statistically by means of the t -test (Zar 1999).

Each fish was examined under stereomicroscope, model Wild M3C (Leica AG Corp., Heerbrugg, Switzerland), to verify the morphogenesis and differentiation status (the formation, transformation or loss of different external body structures) in relation to the size. The presence/absence of the following structures was recorded: dorsal and ventral median finfold, splitted into anterior (from anterior to dorsal or anal fins) and posterior (from dorsal or anal fins to caudal fin) sections, anlagen of hypural bones, pterigiophores and rays of each fin, anlagen of ventral fin and caudal fin shape (from rounded to truncated) as well as pigmentation. The presence of a stomach was recorded after dissection. A binary logistic regression model was used (Norusis 1986) to establish at what size these ontogenetical shifts occur. In this model, the dependent variable takes binary values, presence or absence (1 and 0, respectively) of each structure and the independent variable is the SL.

$$Y = [e^{(cX)+d}] [1 + e^{(cX)+d}]^{-1},$$

where Y represents values between 0 and 1, X is the SL, and c and d are the parameters estimated by the model. The point where $Y = 0.5$ represents the transition size for a specific body structure. When the transition was recorded in individuals of consecutive size we calculated the mean point between their respective sizes.

Sex and gonad condition (GC) of fish without any external larval structure, bigger than 30 mm SL, were recorded on the basis of macroscopic examination of the gonads. The GC was staged according to the criteria of Marraro et al. (2005) and Chapman et al. (2006) simplifying five or seven states into two categories: 0 for virgin or maturing virgin individuals, and 1 for developing, developed, mature or gravid, spawning and spent individuals. As in the morphogenesis analysis, the juvenile-adult size transition was estimated using a binary logistic regression model based on GC. Due to the small number of individuals captured (female = 34, male = 41), this analysis was carried out using individual LS-GC data rather than the classical approach that uses percentages of size ranges. To estimate the spawning season, the gonadosomatic index for *H. macraei* was calculated as $GSI = 100 \times \text{gonad mass} \times (\text{total body mass})^{-1}$. Both gonad and total body (TM) masses were recorded with an electronic balance (± 0.002 g; Ohaus Corp., Florham Park, NY, USA).

Diet analysis

The stomach, or the first portion of the gut in larvae, of each specimen from the Caleufú River was dissected for examination of its food contents under a

stereomicroscope fitted with an ocular micrometer. Empty guts (15%) were registered but not considered into the diet analysis. Recently eaten preys (appeared undigested) were identified up to the minor taxa as was possible following Fernández & Domínguez (2001). Prey width was measured in the broadest rigid part of each consumed prey excluding all appendages; e.g., on the thorax in Ephemeroptera nymphs or on the cephalic capsule in Chironomidae larvae. Also prey volume was estimated by means of volumetric displacement of water (for big preys, ± 0.001 ml) or estimated according to Botrell et al. (1976) using different body lengths. To describe diet we calculated the frequency of occurrence ($\%F_i$), percentage by number ($\%N_i$) and percentage by volume ($\%V_i$) as,

$\%F_i = 100 n_i/n_t$, where n_i is the number of fish containing prey category i in the stomach, and n_t is the total number of fish containing food in the stomach.

$\%N_i = 100 N_i/N_t$, where N_i is the total number of items of prey category i , and N_t is the total number of items of all prey categories.

$\%V_i = 100 V_i/V_t$, where V_i is the total volume of items of prey category i , and V_t is the total volume of items of all prey categories.

Next, we estimated the index of relative importance (Pinkas et al. 1971) as, $IRI_i = (\%N_i + \%V_i) \times \%F_i$. This index was then expressed in percentage as, $\%IRI_i = (IRI_i / \sum IRI_i) \times 100$. Diet overlaps were estimated by the Schoener Index, $SI = 1 - 0.5[\sum(\%IRI_{x_i} - \%IRI_{y_i})]$, where $\%IRI_{x_i}$ is the index of relative importance of the prey category i in the life period x diet and $\%IRI_{y_i}$ is the index of relative importance of the prey category i in life

period y diet (Schoener 1970). Values equal or higher than 0.6 were considered biologically significant (Wallace 1981).

Shannon–Weaver diversity Index (Townsend et al. 2003) was calculated for each life period as, $H' = -\sum p_i \ln(p_i)$, where p_i is the relative abundance of each prey category.

Results

Life periods

The size range of the captured *H. macraei* ($N = 117$) was from 9 to 127.4 mm SL. All individuals could be grouped into larval, juvenile and adult periods according to their relative growth, anatomical changes and gonadal development.

Significant changes were not detected in the weight–length log–log plot throughout the ontogeny (regression, $y = 2.97x - 5.02$, $R^2 = 0.994$). However, significant (t -test, $P < 0.05$) IPs were found from the log-transformed data, 19/25 measures showed an allometric growth change (Fig. 2, Table 1). Eighteen of these characters presented a positive allometric growth ($b > 1$) up to the IP, after which the growth changed to isometric ($b \approx 1$) or negative allometric ($b < 1$). The ventral–anal distance was the only measurement that showed negative to positive change in the relative growth. The six remaining characters without IP presented a relative growth close to the isometry with the exception of the mouth width that showed a negative allometric relative growth ($b = 0.666$). All the IPs were registered between 9.8 and 22.4 mm SL.

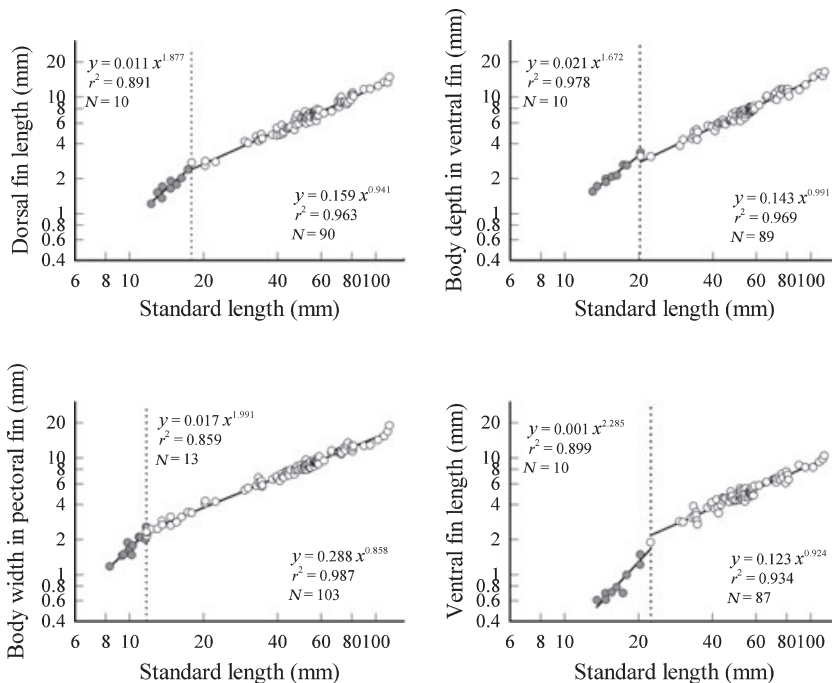


Fig. 2. Allometric growth equations for those selected measurements with the most abrupt IPs (highest t -values). Dotted lines represent IPs for dorsal fin length (17.9 mm SL), body depth in ventral fin (20.3 mm SL), body width in pectoral fin (11.7 mm SL) and ventral fin length (22.4 mm SL). Pre (grey) and post (white) IP individuals are also indicated. Axes are in logarithmic scale.

Ecological significances of ontogenetic shifts in *Hatcheria macraei*

Table 1. Parameters of allometric growth model ($Y = aX^b$) for *Hatcheria macraei* using no-transformed data, standard length (mm) as independent variable and each measurement as dependent variable.

Measurement	$X_{\min} - IP$				$IP - X_{\max}$				IP
	<i>b</i>	<i>a</i>	<i>r</i> ²	<i>n</i>	<i>b</i>	<i>a</i>	<i>r</i> ²	<i>n</i>	
Head length	1.267	0.113	0.945	20	0.825	0.365	0.972	96	13.6
Head width	1.356	0.085	0.924	23	0.884	0.361	0.979	93	15.5
Interorbital distance	1.201	0.043	0.908	12	0.838	0.105	0.972	104	11.7
Eye diameter	1.145	0.025	0.863	21	0.747	0.075	0.946	95	14.7
Mouth width†	0.666	0.254	0.953	115	–	–	–	–	NS
Prepectoral length	1.302	0.100	0.946	19	0.834	0.356	0.98	97	13.5
Predorsal length†	0.998	0.653	0.999	106	–	–	–	–	NS
Preanal length†	1.007	0.685	0.998	106	–	–	–	–	NS
Preventral length†	0.985	0.584	0.997	97	–	–	–	–	NS
Pectoral-ventral distance†	1.069	0.288	0.987	98	–	–	–	–	NS
Ventral-anal distance	0.478	0.592	0.522	11	1.109	0.099	0.942	87	22.4
Pectoral fin length	1.668	0.029	0.888	18	0.907	0.215	0.979	98	13.0
Ventral fin length	2.285	0.001	0.899	10	0.924	0.123	0.934	87	22.4
Dorsal fin length	1.877	0.011	0.891	10	0.941	0.159	0.963	90	17.9
Anal fin length	1.716	0.017	0.921	13	0.925	0.174	0.945	87	22.4
Dorsal base fin length†	1.075	0.155	0.977	93	–	–	–	–	NS
Anal base fin length	1.831	0.011	0.964	5	0.927	0.156	0.922	89	20.3
Caudal peduncle depth	1.470	0.017	0.952	26	0.996	0.076	0.953	88	20.3
Body width in pectoral fin	1.991	0.017	0.859	13	0.858	0.288	0.987	103	11.7
Body width in ventral fin	1.491	0.019	0.966	10	1.119	0.059	0.947	89	20.3
Body width in anal fin	1.876	0.011	0.786	12	1.066	0.095	0.984	95	14.7
Body depth in pectoral fin	1.701	0.027	0.873	4	0.897	0.183	0.988	112	9.8
Body depth in dorsal fin	1.722	0.019	0.448	7	1.008	0.125	0.986	99	12.3
Body depth in ventral fin	1.672	0.021	0.978	10	0.991	0.143	0.969	89	20.3
Body depth in anal fin	1.783	0.007	0.798	10	1.105	0.047	0.973	95	13.5

b represents the growth coefficient, *a* the intercept with *Y* axis, *n* the number of individuals and NS indicates no significant inflexion point (IP) found. The IP on standard length (mm) is only indicated for significant cases (*t*-tests, $P < 0.05$).

†parameters estimated with all indicated individuals.

Larval structures were registered in all individuals up to 22.4 mm SL (Table 2, Fig. 3). These fish were characterised by the presence of a median finfold and no dark pigmentation on the body. An early development of the sensory system was also registered, all individuals had barbels and dark pigmented eyes. The anlagen of caudal fin rays were the first to be detected (9.4 mm SL) on the median finfold, then dorsal and anal fin pterigiophores (10.4 mm SL), dorsal and anal fin rays (a.c.11.2 mm SL), the pelvic fin primordium (12.9 mm SL) and finally the pelvic fin rays (20.3 mm SL). The absence of finfold was registered in individuals equal or larger than 29.4 mm SL as well as the presence of a pouch-like stomach. Based on the morphological changes registered in *H. macraei*, larvae–juvenile transition was calculated at 25.9 mm SL, being the mean value between the larger individual captured with larval structures (22.4 mm SL) and the smaller one with a juvenile phenotype or without any larval structures (29.4 mm SL). Individuals larger than 25.9 mm SL were considered as juveniles (Table 2).

The transition between immature and mature individuals was estimated at 64.4 mm SL for females and 61.4 mm SL for males using the logistic regressions. These transition points were consistent with the

Table 2. Formation (A → P), transformation (T) or loss (P → A) of different body structures of *Hatcheria macraei* in relation to the size (SL, mm).

Morphological structure	Shift	SL (mm)			Method
		TP	Min	Max	
Caudal fin rays	A → P	9.4	9.5	10.2	Logistic
Dorsal fin pterigiophores	A → P	10.4	9.9	10.3	Logistic
Anal fin pterigiophores	A → P	10.4	9.9	10.3	Logistic
Anal fin rays	A → P	11.2	11.1	11.7	Logistic
Dorsal fin rays	A → P	11.6	11.1	11.8	Logistic
Pelvic fin anlagen	A → P	12.9	12.3	13.6	Logistic
Caudal fin shape†	T	18.2	14.7	17.9	Logistic
Anterior dorsal finfold	P → A	19.1	17.9	20.3	Mean
Anterior ventral finfold	P → A	20.3	20.3	20.3	Mean
Pelvic fin rays	A → P	20.3	20.3	20.3	Mean
Pigmentation	A → P	20.3	20.3	20.3	Mean
Posterior dorsal finfold	P → A	25.9	22.4	29.4	Mean
Posterior ventral finfold	P → A	25.9	22.4	29.4	Mean
Stomach	A → P	25.9	22.4	29.4	Mean

The transition point (TP) of each structure was calculated using a logistic regression, $Y = [e^{(cX)+d}][1 + e^{(cX)+d}]^{-1}$ or the mean value when the change was observed in individuals of consecutive sizes. The smaller and larger individuals that delimit the transition range are also indicated.

†From rounded to truncated.

GSI. Adult individuals showed the greater GSI while juvenile values were not higher than GSI = 1 for females and GSI = 0.5 for males (Fig. 4). Sex ratio did not differ significantly from 1:1 ratio ($z = 0.451$,

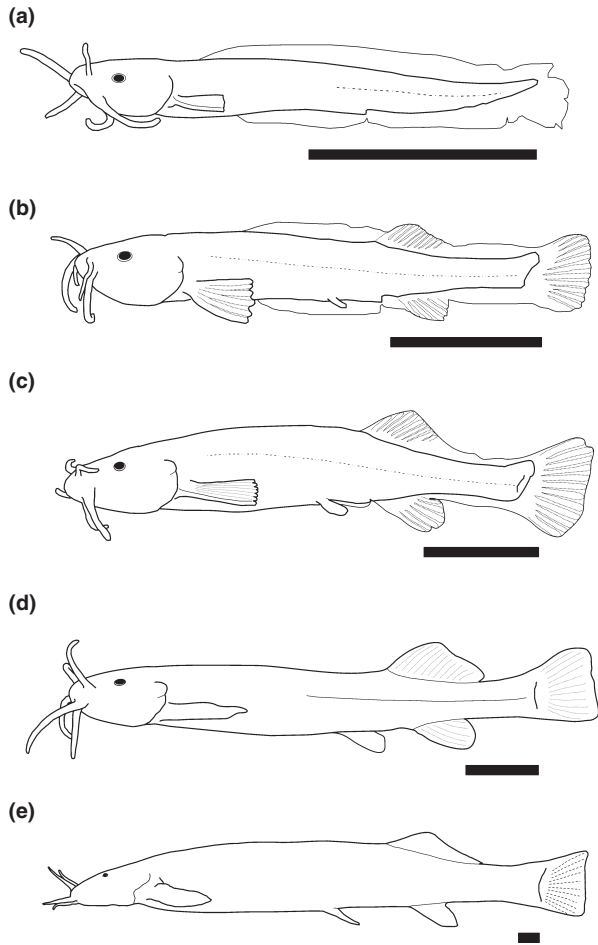


Fig. 3. External morphology (schematic drawings from photographs of fixed individuals) of *Hatcheria macraei*: (a) larva (SL = 10.2 mm SL), (b) larva (SL = 15.5 mm SL), (c) larva (SL = 20.3 mm SL), (d) juvenile (SL = 32.8 mm SL) and (e) adult (SL = 110.9 mm SL). Bar = 5 mm.

$P = 0.652$), 54% of captured individuals were males and 46% females.

In spite of the insufficient adults captured to plot a monthly GSI, the spawning period could roughly be estimated by means of the highest GSI (both female and male) and the larval presence throughout the year. Females and males in the most advanced stage of gonadal development were captured in January and December, respectively while the larval individuals were captured in January and February, after maximum daylight hours (Fig. 5). The percentage of larvae were significantly correlated with water temperature (Spearman, $\rho = 0.59$, $P < 0.05$) but not with water velocity (Spearman, $P > 0.05$, Fig. 5).

Habitat preferences

A clear preference for running waters was registered. Almost all *H. macraei* individuals were captured in the

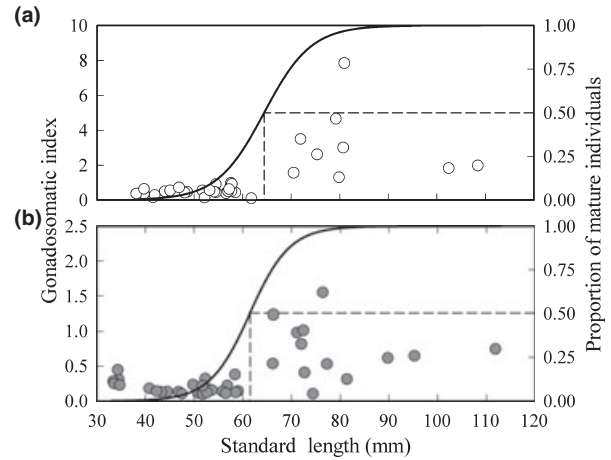


Fig. 4. Gonadosomatic index (left axis) and proportion of mature individuals (right axis) in relation to size (SL, mm) for females (a) and males (b) of *Hatcheria macraei*. Dash line indicates juvenile–adult transition size (64.4 mm SL for females and 61.4 mm SL for males) estimated from sigmoid regressions [females, $y = (e^{0.207x+13.307}) / (1 + e^{0.207x+13.307})^{-1}$ and males, $y = (e^{0.243x+14.908}) / (1 + e^{0.243x+14.908})^{-1}$].

riffle and marginal areas ($N = 116$) and only one was caught in a pool. All larvae ($N = 30$) and four juveniles were caught in the marginal areas of the riffles, while the remaining individuals (57 juveniles and 25 adults) were captured in the riffles. Adults were detected only in the deeper areas of the riffles. Fish up to 33 mm SL were caught in the marginal riffles while individuals longer than 35 mm SL were only captured in riffles (Fig. 5).

Diet analysis

A diet shift was found during the *H. macraei* ontogeny as well as a progressive increment in the total items consumed (TIC). The main prey for the catfish larvae was Chironomidae larvae (%IRI = 99.41). All larvae had preyed on this Diptera (%F = 100). The remaining categories were rarely eaten ($\sum \%IRI < 0.6$). During the juvenile period, the main preys consumed were two ($H' = 2.09$): Ephemeroptera nymphs and Chironomidae larvae. The presence of other preys like Trichoptera larvae and pupae was also registered. In the adult period, Chironomidae larvae and Ephemeroptera nymphs were still important in the diet ($H' = 1.94$). Other categories were incorporated, like Plecoptera nymphs, Dytiscidae larvae and also *Galaxias maculatus* juveniles, other native fish present in the Caleufú River (Table 3). Diet overlap was greater comparing the diet of juveniles versus adults (SI = 0.81); and larvae versus adults (SI = 0.62) than between larvae and juveniles fish (SI = 0.47).

Significant differences were found in the width of the ingested Chironomidae larvae among ontogenetical

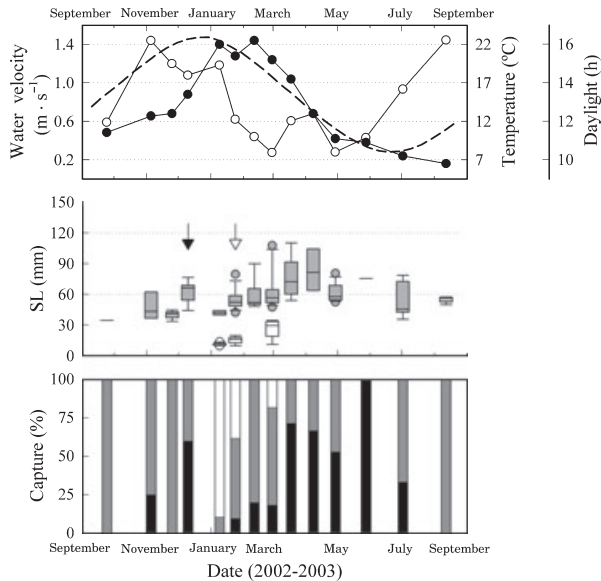


Fig. 5. Water velocity ($\text{m}\cdot\text{s}^{-1}$, white circles), water temperature ($^{\circ}\text{C}$, black circles) and daylight time (hours, dashed line, data from Groenenberg & Cussac 1993) in riffles of the Caleufú river (top panel). Size (SL, mm) annual variation for *Hatcheria macraei* captured in riffle (grey) and in shallow marginal areas (white). Median, quartiles and data outside 10th and 90th percentiles are indicated per sampling date. Arrows indicate dates with higher GSI registered for males (black) and females (white) (middle panel). Percentage of larvae (white), juveniles (grey) and adults (black) captured in riffles per sampling day (lower panel).

periods of *H. macraei* (ANOVA, $P < 0.001$). Catfish larvae preyed on the smallest Diptera (mean \pm SD; $0.095 \text{ mm} \pm 0.074$, $N = 267$), juveniles on the intermediates sizes ($0.213 \text{ mm} \pm 0.068$, $N = 291$) and adults on the largest Chironomidae ($0.287 \text{ mm} \pm 0.089$, $N = 173$). On the other hand,

no significant differences were found among periods for the sizes of the other important prey, Ephemeroptera nymphs (ANOVA, $P = 0.280$).

A different size range of consumed prey was recorded. Chironomidae larvae showed a narrow width size, from 0.057 to 0.716 mm, while Ephemeroptera nymphs had the widest range, from 0.086 to 2.148 mm (Fig. 6). The increasing mouth width of adults was not associated with an augmentation of the prey items' size (Fig. 6). Furthermore, in spite of the small size of Diptera larvae for *H. macraei* adults, this item showed to be an important component of the diet.

Discussion

In this paper, we could estimate the size range of each life period of *H. macraei* (larva, juvenile and adult; *sensu* Balon 1999) on the basis on the relative growth, morphogenesis and gonadal status. The larva–juvenile transition was registered between 22.4 and 29.4 mm SL, and juvenile–adult transition between 61 and 65 mm SL. Changes from positive allometric to isometric relative growth in *H. macraei* reflected the larva–juvenile transition. All the IPs in the relative growth occurred up to 22.4 mm SL showing evidence of this shift. In addition, the complete loss of larval structures as well as the differentiation of all juvenile systems was registered shortly after the IPs found at larger size (22.4 mm SL). The positive allometric growth in larvae affected mainly the head region, locomotion structures and body robustness, also including the trunk region. These regions are mostly related with respiration, feeding and swimming skills (Osse & van den Boogart 1995; Osse et al. 1997;

Table 3. Diet composition as: frequency of occurrence (%F), percentage by number (%N), percentage of volume (%V) and percentage of relative importance index (%IRI) of *Hatcheria macraei* in each life period.

Ingested prey	Larvae (n = 26)				Juveniles (n = 57)				Adults (n = 23)			
	$H' = 1.1$		TIC = 5		$H' = 2.09$		TIC = 8		$H' = 1.94$		TIC = 10	
	%F	%N	%V	%IRI	%F	%N	%V	%IRI	%F	%N	%V	%IRI
Copepoda (A)	7.69	0.66	12.83	0.56	1.75	0.07	0.01	0.00	–	–	–	–
Chironomidae (L)	100.00	98.52	87.06	99.41	77.19	70.64	24.50	47.03	86.96	79.01	22.62	61.91
Chironomidae (P)	3.85	0.16	0.06	0.00	24.56	1.61	0.69	0.36	17.39	1.18	1.37	0.31
Other diptera (L)	7.69	0.33	0.02	0.01	–	–	–	–	13.04	0.26	0.45	0.07
Ephemeroptera (N)	7.69	0.33	0.03	0.01	84.21	26.49	70.59	52.35	82.61	17.70	41.42	34.21
Ephemeroptera (A)	–	–	–	–	1.75	0.07	0.49	0.01	–	–	–	–
Plecoptera (N)	–	–	–	–	–	–	–	–	8.70	0.13	0.68	0.05
Trichoptera (L)	–	–	–	–	8.77	0.49	2.87	0.19	21.74	0.72	13.11	2.11
Trichoptera (P)	–	–	–	–	7.02	0.28	0.58	0.04	4.35	0.07	0.15	0.01
Coleoptera, Dytiscidae (L)	–	–	–	–	–	–	–	–	4.35	0.07	0.14	0.01
Fish, <i>Galaxias maculatus</i> (J)	–	–	–	–	–	–	–	–	8.70	0.39	19.59	1.22
Algae, <i>Nostoc</i> sp.	–	–	–	–	5.26	0.35	0.28	0.02	17.39	0.46	0.48	0.11

Shannon–Weaver diversity index (H') and total items consumed (TIC) are also indicated. L, larvae; P, pupae; N, nymphs; J, juvenile; A, adults.

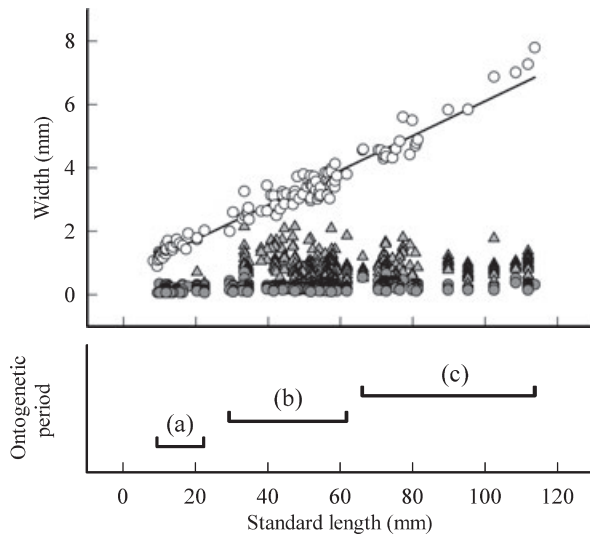


Fig. 6. Standard length (SL, mm) of *Hatcheria macraei* in relation to mouth (white circles) and prey (triangles for Ephemeroptera nymphs and grey circles for Chironomidae larvae) width (mm) consumed. Solid line represents a linear regression ($y = 0.638x + 0.055$, $r^2 = 0.95$) between SL and mouth width (upper panel). Size ranges of larvae (a), juveniles (b) and adults (c) are indicated (lower panel).

Gisbert 1999). Differential relative growth in this early period reflects the larval basic functions or skills that have to be achieved for increasing chances of survival (Osse 1990). Starvation and predation are the main factors for high mortality rate in early life history (Chambers & Trippel 1997). In this sense, a fast development of sensorial organs (e.g., eye size) and fins potentially enhance both prey detection and predator evasion. On the other hand, juvenile and adults' isometric growth registered in *H. macraei* has also been registered in a close-related species, *Trichomycterus areolatus* in Chile (Habit et al. 2005). The juvenile–adult transition did not show any inflexion in the relative growth.

The size of maturity is very variable within the Trichomycteridae family. Casatti (2003) registered the smallest mature individuals of a *Trichomycterus* species in the South of Brazil of 37.7 and 31.0 mm SL for females and males, respectively. In Colombia, the size of maturity of *Trichomycterus caliense* was registered at 74 and 92 mm SL for females and males, respectively (Roman-Valencia 2001). The adulthood in *H. macraei* of the Caleufú River was reached at smaller sizes in males (61.4 mm SL) than in females (64.4 mm SL). These results are similar to those of *T. areolatus* in Chile where the maturity size ranges from 50 mm TL (Habit et al. 2005) to 56.7 mm SL (Manriquez et al. 1988).

The spawning period for *H. macraei* was roughly estimated in the summer season from December to February, taking into account the highest GSI and the

larvae presence dates. This period overlaps in part with data reported by Marraro et al. (2005) for *Trichomycterus corduvensis*, by Habit et al. (2005) for *T. areolatus* and also with data reported by Trajano (1997) for *Trichomycterus itacarambiensis*, a troglolitic catfish. In general, fishes inhabiting high latitudes show seasonal patterns of reproduction related with changes in temperature and hours of daylight (Wootton 1998). In this sense, the spawning season in *H. macraei* showed to be related to rising temperatures but not with water velocity (Fig. 5). In contrast, reproduction of some *Trichomycterus* populations at low latitudes ($<5^\circ$) has been related to rainy seasons (Roman-Valencia 2001; Chará et al. 2006). However, in another low-latitude *Trichomycterus* populations (Casatti 2003; Chará et al. 2006), the presence of mature individuals throughout the year has also been reported as an alternative and more opportunistic reproductive style (Casatti 2003).

In the life-history model (Balon 1999), the change from one ontogenetic period to the next one entails morphogenesis; growth or differentiation generating new functional system/s. Acquisition of new functions produces a change in the organism–environmental interaction that ultimately can generate a niche shift. A clear spatial segregation was found in *H. macraei* depending on the ontogenetic period of life. All larvae were captured in the shallow marginal riffles where the maximum depth registered was 10 cm, water velocity was almost zero and a rocky bottom substrate was found, while juveniles and adults were caught in deeper riffles. This pattern could be associated to the swimming constrains because the fins are still in development in the larval period. The ecological outcome is to reduce the predation risk by the exclusion of a wide size range of fish predators, like trout and the creole perch, *Percichthys trucha*, of the shallow waters. Microhabitat preferences related to the ontogenetic period have been reported by Arratia & Menu-Marque (1981). Also ontogenetic shift in bottom composition preference has been found in *Trichomycterus chiltoni* (Arratia 1983) and *T. areolatus* (Arratia 1983; Manriquez et al. 1988) in Chilean rivers, where the juveniles prefer soft bottom while adults live in gravel bottom.

There is scant information about the diet of *H. macraei*, as other trichomycteridae (Habit et al. 2005; Chará et al. 2006; Scott et al. 2007), this species demonstrated to be a benthic feeder preying mostly on insect larval stages. The main prey of *H. macraei* was Chironomidae larvae during all the ontogeny. But larvae, juveniles and adults preyed upon different, and incrementing, size classes of this prey. Furthermore, Ephemeroptera nymphs were incorporated since the juvenile period. An increment of TIC was registered from larvae to adults. During the adult period, the

presence of a native fish, *G. maculatus*, was registered in the stomach contents. This is consistent with the migration of *G. maculatus* at larva–juvenile transition registered from February to early April in the Caleufú River (Barriga et al. 2007).

The change of both the relative importance of some preys and size classes represents an ontogenetical shift in the diet of *H. macraei*. An abrupt prey size increment from larvae to juveniles was registered, as well as the presence of small Ephemeroptera nymphs in the juveniles' stomachs that could have been eaten by larvae (see Fig. 6). This is more probably due to the habitat shift detected at larva–juvenile transition than a constraint because of mouth size. In addition, greater diet overlap between juveniles and adults individuals also indicates that prey electivity could be driven mainly by microhabitat use.

Adaptations to a benthic life style can be inferred from *H. macraei* morphology. This elongated fish has a flattened head with small dorsal eyes and three pairs of barbels. Its mouth is subterminal, moderately wide and has a prognathous upper lip (Arratia & Menu-Marque 1981; see Fig. 1). Probably, the negative allometric growth of mouth width found in this species ($b = 0.666$) could be related to its benthic feeding behaviour and the small size of the main preys consumed during all ontogeny. The optimal foraging theory predicts that optimal prey size is approximately 0.6 times the fish's mouth (Gill 2003). Prey size eaten by *H. macraei* till 60 mm SL adjusts to this theory, but beyond this length, prey size did not show any increment (Fig. 6). This fact can be simply explained as a consequence of prey availability in the habitat, or indirectly as a result of predation forces on catfish that restrict its microhabitat use. Despite this, no differences in weight–length relationship during the ontogeny indicates no detrimental condition due to a suboptimal feeding.

In conclusion, the results of this work suggest that morphological changes during the ontogeny of *H. macraei* have important ecological consequences, mainly in the larva–juvenile transition. At that moment, the most critical functions, crucial for surviving, such as feeding, swimming and respiration (Osse & van den Boogart 1995; Gisbert 1999) are still developing. Marginal riffle areas seem to be the nursery habitat where early stages of *H. macraei* have low probability of being predated due to the exclusion of predators from these shallow areas. Future works on population size and density are needed to evaluate the conservation status of this and other populations of *H. macraei*. Moreover, as very little is known about the effect of introduced trouts in lotic environments (Pascual et al. 2007; Aigo et al. 2008), catfish population data will improve our understanding about native–exotic fish interactions to develop management

and conservation strategies of the Patagonian native fauna.

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