Feeding ecology of the relict fish *Gymnocharacinus bergi*, a characid from southern South America

Alicia H Escalante[1,2] and Roberto C Menni[1,3*]

[1] Consejo Nacional de Investigaciones Científicas(CONICET) Argentina
[2] Universidad Nacional de Mar del Plata, Funes 3250, 3th floor, 7600 Mar del Plata, Argentina
[3] Museo de La Plata, Paseo del Bosque s/n,1900 La Plata, Argentina

Abstract

A food analysis was performed of the southernmost distributed Characidae, *Gymnocharacinus bergi*, the single species inhabiting the thermal headwaters of the Valcheta Creek in northern Patagonia. Chrysophyta were the dominant algae and chironomid larvae and testaceous amoebae the most abundant animal items. Few cladocerans and no copepods were consumed. The diet indicates a benthic feeding habit, though the species usually swims in the water column. Diversity and number of all items are more restricted than those of similar size characids from middle Argentina. The diet of *G. bergi* is similar to that of *Cheirodon interruptus* and *Bryconamericus iheringi* from mountain oligotrophic streams, but differs from tetragonopterine species occurring in richer plain habitats. Feeding traits appear to be related to the environment oligotrophy and agree with regressive traits in the species morphology, presumably associated with harsh environmental pressure.

Introduction
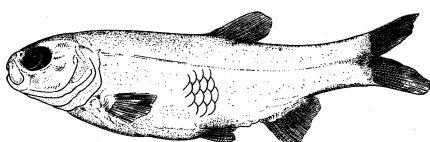
Figure 1
Gymnocharacinus bergi *from headwaters of Valcheta Creek. A juvenile specimen 40 mm in total length.*

Gymnocharacinus bergi is a characid fish (Fig. 1), remarkable in that the scales are reabsorbed in the adult (Miquelarena and Arámburu 1983; Cussac and Ortubay 1994). It is the only fish species inhabiting thermal headwaters of the endorrheic Valcheta Creek in the Somuncurá plateau in northern Patagonia (40º50'S, 66º40'W)(Fig. 2). The introduced trouts *Oncorhynchus mykiss* and *Salvelinus fontinalis* and the cyprinodontoids *Jenynsia* cf. *multidentata* and *Cnesterodon decemma-culatus* inhabit downstream waters at lower temperatures (Ortubay et al., 1997). Headwaters have a constant water temperature of between 18 and 22.6°C while the air temperature has an annual mean below 10°C with winter monthly mean maximum values less than 10°C and monthly mean minimum below 5°C (Menni and Gómez, 1995). *G. bergi* has a high lethal temperature (36.2 to 38.2°C), a para-nensean adaptation, similar to other Brazilian fishes. Its loss of equilibrium temperature (33.9 to 36.9°C) is higher than in some paranensean fishes and is related to the permanent warmth of its
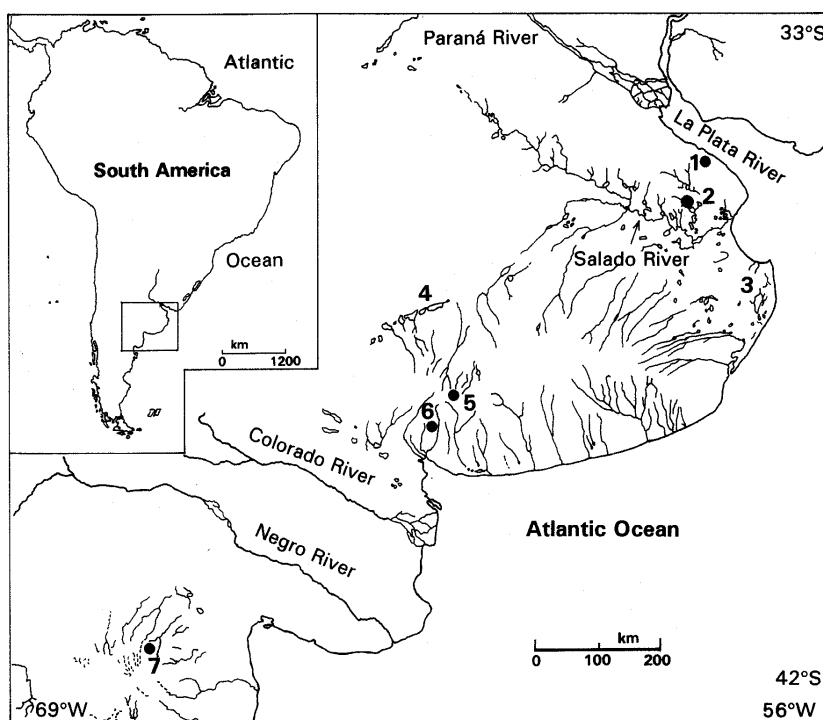
Figure 2
Argentinean "pampa" (northward of the Colorado River) and north of Patagonia (southward). 1: man-made ponds at Los Talas; 2, 3 and 4: pampean "lagunas"; 5, 6: highland environments in Sierra de La Ventana; 7: headwaters of the Valcheta Creek. Insert: position of the enlarged area in South America.

habitat. The species has partially lost its resistance to low tempera-tures and probably cannot extend its distribution to temperate nearby waters nor to water with large temperature fluctuations (Ortubay et al., 1994; 1997).

In this paper we report the diet composition of *G. bergi* and show that feeding, as other traits of the naked characid, is related to its particular habitat. Additionally, we consider the hypothesis

TABLE 1
ABUNDANCE AND FREQUENCY OF FOOD ITEMS IN THE DIET OF *GYMNOCHARACINUS BERGI*
(33 INDIVIDUALS) DURING SPRING 1979 AND SUMMER 1980
(VA: VERY ABUNDANT, A: ABUNDANT, C: COMMON AND S: SCARCE)

	Absolute and/or relative abundance		Occurrences (Absolute frequency)	
	Spring 1979	Summer 1980	Spring 1979	Summer 1980
Testaceous amoeba	217	27	13 (86.7%)	4 (25.0%)
Algae	A	A	15 (100.0%)	2 (12.5%)
Fungi	no data	2	no data	1 (6.2%)
Vascular plants remains	VA	S	13 (86.7%)	3 (18.7%)
Seeds	8	no data	3 (20.0%)	no data
Acari	5	8	5 (33.3%)	4 (25.0%)
Cladocera	2	no data	1 (6.7%)	no data
Ostracoda	4	4	3 (20.0%)	2 (12.5%)
Anfipoda	no data	3	no data	3 (18.7%)
Chironomid larvae	221	141	15 (100.0%)	16 (100.0%)
Chironomid pupae	6	1	3 (20.0%)	1 (6.2%)
Dolichopodid larvae	no data	1	no data	1 (6.2%)
Staphilinid larvae	no data	22	no data	4 (25.0%)
Staphilinid pupae	no data	4	no data	2 (12.5%)
Hydrophilid larvae	no data	1	no data	1 (6.2%)
Insect fragments	A	C	5 (33.0%)	11 (68.7%)
Detritus	VA	A	7 (46.7%)	3 (18.7%)

that its diet should be similar to that of *Bryconamericus iheringi,* and especially to that of the eurytopic *Cheirodon interruptus* (Menni et al., 1996) because of anatomical similarities between them (Miquelarena and Arámburu, 1983). Feeding differences related to the lentic or lotic character of the habitats, and possible environmental influences in the evolution of the species are also discussed. In addition to its restricted distribution and limited habitat, *G. bergi* is probably affected by introduced salmon (Wegrzyn and Ortubay, 1991) which makes it the only fish species in danger of extinction in Argentina (Chebez, 1993).

Material and methods

Thirty-three specimens of *G. bergi* used for diet analysis were collected with handnets on November 1979 (spring) and on March 1980 (summer) from headwaters of the Valcheta Creek in the Somuncurá plateau. Specimens ranged from 30 to 50 mm standard length (mean 40.6 mm) and from 0.92 to 2.81 g mass (mean 1.6 g). We followed the advice that the sampling effort would require a compromise between the many benefits associated with a large sample and the negative impact that collecting without replacement might exert on some communities (Winemiller and Polis, 1995).

Each digestive tract was removed and preserved in 10% formalin and observations were made according to criteria described by Escalante (1982). To evaluate food composition a combination of numerical abundance, frequency occurrence, and volumetric methods was used (Berg 1979; Hyslop 1980). Relative abundance was described as VA = very abundant, A = abundant, C = common and S = scarce. Absolute abundance is the number of individuals in each item. Absolute frequency of occurrence indicates in which percentage of all digestive tracts analysed a given item is found. Relative frequency of occurrence shows in which percentage one prey species is found, considering as 100% the total

Results

Organisms found in the diet of *G. bergi* are listed in Table 1. Vascular plant remains were abundant. Algae were abundant during spring but scarce in summer, according to the normal cycle in temperate waters (Hutchinson, 1967). Periodicity in this case is probably proportional to light seasonality with around 11 sun hours in January (summer) and around 6 sun hours in July (winter). Ten diatom species (Chrysophyta) were found in *G. bergi* diet. Two species of Oscillatoria (Cyanophyta) and one Chlorophyta were also consumed (Table 2).

Seeds were scarce and detritus was abundant. Animal prey included both chironomid larvae and pupae, testaceous amoebae, Cladocera and Ostracoda, Acari and insect fragments. Chironomid larvae were the most abundant animal item, followed by testaceous amoebae, together comprising 97.6% of ingested animal items (chironomid larvae 49.9%, testaceous amoebae 47.7%, Acari 1.1%, Ostracoda 0.9%, benthic and/or littoral Cladocera 0.4%). Individual numbers of chironomid larvae and testaceous amoebae were quite similar; however, larvae ($3.3 \ mm^3$ each) imply a larger volume. The same occurs with plant remains and algae. The fish did not eat copepods and just a few cladocerans. Individuals of a non-planktonic *Chydorus* sp. (Cladocera) occasionally appeared. Larval dolichopodids (Diptera) and hydrophilids, as well as larval and pupal staphilinids (Coleoptera), ostracods, amphipods and fungi were consumed. The volume of insect larvae, namely $1310 \ mm^3$ (99.2%), is much larger than those of amphipods ($9 \ mm^3$, 0.7%), ostracoda ($0.8 \ mm^3$, 0.06%) and cladocerans ($0.04 \ mm^3$, 0.003%) (Table 3).

The Morisita index was calculated for five pairs of species, taking into account only the animal prey species (Table 4). The "overlap" index has a value of 0.84 for the pair *G. bergi* vs *C. interruptus* and 0.68 for the pair *G. bergi* vs. *B. iheringi*, both from creeks.

Discussion

Care must be taken when attributing diets to South American fish species or groups, based on studies conducted in tropical areas, because many temperate environments differ from tropical ones, e.g. regarding flood cycle or plant cover. Piranhas in temperate Argentina are exclusively carnivorous, in spite of the frugivory or seed-eating behaviour observed in the tropics (Menni and Almirón, 1994). In the upper Amazonian (Ecuador), seven species of

TABLE 2
ABUNDANCE AND FREQUENCY OF ALGAE PRESENT IN THE DIET OF *GYMNOCHARACINUS BERGI*
(33 INDIVIDUALS) DURING SPRING 1979 AND SUMMER 1980.
(VA: VERY ABUNDANT, A: ABUNDANT AND C: COMMON)

	Relative abundance	Absolute frequency	Relative frequency	Mean cell size (μ)
Chrysophyta				
Amphora ovalis var. *pediculus*	A	1 (6.7%)	1.3%	25 x 11
Biddulphia laevis	VA	14 (93.3%)	17.7%	100 x 80
Cocconeis sp.	C	10 (66.7%)	12.7%	50 x 15
Cymbella affinis	A	10 (66.7%)	12.7%	50 x 8
Denticula sp.	A	6 (40.0%)	7.6%	22 x 7
Gomphonema sp.	C	3 (20.0%)	3.8%	40 x 9
Melosira sp.	A	1 (6.7%)	1.3%	15 x 10
Navicula pupula	A	14 (93.3%)	17.7%	30 x 8
Nitzschia sp.	A	6 (40.0%)	7.6%	50 x 6
Synedra ulna var. *ulna*	A	14 (93.3%)	17.7%	200 x 6
Cyanophyta				
Oscillatoria sp.	C	4 (26.7%)	50.0%	no data
Oscillatoria princeps	C	4 (26.7%)	50.0%	5 x 25
Chlorphyta				
Filamentous	A	6 (40.0%)	100.0%	no data

TABLE 3
VOLUMES OF ANIMAL ITEMS (AS PERCENTAGES) IN THE DIET OF *GYMNOCHARACINUS BERGI* AND OTHER CHARACID FISH. 1: VALCHETA HEADWATERS, 2: PAMPEAN 'LAGUNAS', 3: LOS TALAS PONDS.

	Chironomid larvae	Cladocera	Amphipoda	Ostracoda
Gymnocharacinus bergi 1	99.20	<0.01	0.70	0.06
Astyanax eigenmanniorum 2	16.70	71.30	5.30	2.50
Bryconamericus iheringi 2	14.90	79.40	2.10	0.20
Cheirodon interruptus 2	12.50	75.60	6.50	0.90
Hyphessobrycon anisitsi 2	9.50	58.40	29.30	no data
Hyphessobrycon meridionalis 3	88.70	5.30	no data	no data

Bryconamericus (a common genus in Argentina) feed on formicids, ephemeroptera, chironomids and other insects (Saul, 1975). By contrast, *B. iheringi* from several environments in the Buenos Aires plain exhibits a diet composed mainly of algae and microcrustaceans, and the seasonal variation is low.

Trophic habits of several characid species in the size range of *G. bergi* are well known (Escalante 1982, 1983 a,b, 1984, 1987 a,b, 1993), including studies in different kinds of habitats, namely 'lagunas' (lakes without persistent stratification) in the Buenos Aires plain, and comparing man-made ponds of the Río de La Plata (34° 58'S, 58°W), with colder highland creeks in Sierra de La Ventana (38S, 62W), located near the south-eastern border of the distribution of the Brazilian fish fauna. Differences observed among diets of *Bryconamericus iheringi, Hyphessobrycon anisitsi, H. meridionalis,* and *Cheirodon interruptus* from these different habitats, are determined by the dominance of particular prey instead of by a whole change in food composition (Escalante, 1983a).

Though the number of items is considerably less than in species quoted above, *G. bergi* has a relatively wide omnivorous diet including algae, vascular plants and animal organisms. The Chrysophyta are dominant among algae consumed. Its number suggests a wide use of the available algal resources, but the number of genera and species (overall diversity) is markedly less than in other characid species. As in related species, chironomid larvae are a substantial item. On the contrary, planktonic crustaceans are extremely rare.

Algae consumed by *G. bergi* are mostly benthic, and together with the abundance of chironomid larvae and other items, particularly abundant detritus, point to a benthic feeding habitat. In spite of this, the fish is normally observed in the water column, and can swim against strong currents (pers. obs. November 1979).

Cheirodon interruptus is a small characid widely occurring in eutrophic pampean 'lagunas' where it is the species with the wider trophic range among five Tetragonopterinae and one Characinae (Escalante 1983a; Escalante, 1987a). However, in Sierra de La Ventana oligotrophic highland creeks *C. interruptus* preyed upon chironomid larvae and plant remains, a diet similar to that of *G. bergi*. This similarity is probably related in part to morphological traits; for example, although the naked characid has more developed cusps, its teeth are very similar (Miquelarena and Arámburu, 1983; Miquelarena, 1986).

Environmental influence is suggested by the fact that *C. interruptus* feeds upon a larger proportion of chironomid larvae in creeks than in ponds where plankton is more abundant. Also *Hyphessobrycon meridionalis* is less zooplanktophagous in man-made ponds at Los Talas where zooplankton is scarce (Solari, 1983; Escalante 1983a). In Sierra de la Ventana *B. iheringi* preys heavily upon chironomid larvae, while in the pampean 'lagunas' it feeds on algae and microcrustaceans. In Sierra de La Ventana and Valcheta, scarcity of plankton appears to force the fishes toward a more restricted, benthophagous feeding.

Volumes of animal items show the predominance of chironomid larvae in *G. bergi* and of cladocerans in other characid species. The Morisita index based on the number of animal items was low when comparing *G. bergi* with small characids from pampean 'lagunas', but high compared with those from creeks (Table 4), showing that *G. bergi* has a diet composition more similar to individuals from harsh environments than to others. Further confirmation is given by

TABLE 4
MORISITA INDEX VALUES AMONG *GYMNOCHARACINUS BERGI* AND CHARACIDS FROM DIFFERENT ENVIRONMENTS (ANIMAL ITEMS ONLY), 1: FROM PONDS, 2: FROM CREEKS.

	Gymnocharacinus bergi
Cheirodon interruptus 1	0.005
Bryconamericus iheringi 1	0.005
Hyphessobrycon anisitsi 1	0.005
Astyanax eigenmanniorum 1	<0.001
Hyphessobrycon meridionalis 1	0.100
Cheirodon interruptus 2	0.660
Bryconamericus iheringi 2	0.790

Horn's index values of 0.84 for the pair *G. bergi* and *C. interruptus* and 0.68 for *C. interruptus* and *B. iheringi*, both from creeks.

Loss of scales in *G. bergi* required an extended period, during which time the scales stopped their development, followed by a quick process of reabsorption. This trait can be considered as a morphological regression, allowed by the absence of predators, particularly piscivorous fish (Cussac and Ortubay, 1994). Besides the loss of scales, the anatomy of *G. bergi* shows several regressive characteristics, including a low number of orbital bones, reduced extrascapula and reduction of some caudal elements (Miquelarena and Arámburu, 1983). Modifications of body structures, like reduction in the scales, diminution of sculpturing in head bones and miniaturisation, have also been considered paedomorphic traits (Weitzman and Vari, 1988). These traits could result from ecological pressures, such as selection for small size in food-poor environments (Moore, 1994). This is the case at Valcheta Creek, and has been observed in the deep sea and in cave fishes (Peters and Peters, 1983; Langecker and Longley, 1993). These mechanisms, together with the framework posed by the peculiar traits of the habitat (thermal water, oligotrophy, isolation), relate feeding characteristics of *G. bergi* to some of the more obvious apomorphies of the species.

Acknowledgements

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