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Trophic niche overlap between two Chilean endemic species of *Trichomycterus* (Teleostei: Siluriformes)

Sobreposición de nicho alimentario de dos especies endémicas chilenas de *Trichomycterus*
(Teleostei: Siluriformes)

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ABSTRACT

Trichomycterus areolatus and *Trichomycterus chiltoni* are endemic siluriform fishes of Chile. They are the only Chilean species of this genus that live in sympatry and coexist in the Biobío basin. High trophic niche overlap between both species was found. Horn's index varied from 0.668 to 0.885 among seasons, without significant differences, and Schoener's index varied from 0.639 to 0.912. Also the discriminant analysis showed no significant differences in prey item between the two species. Trophic composition of *T. chiltoni* and *T. areolatus* consisted mainly in chironomid larvae and other aquatic invertebrates. At all seasons *T. chiltoni* showed the greatest prey richness. Principal component analysis (PCA) showed a high similarity between diets of *T. areolatus* and *T. chiltoni*. These diet scores were significantly related with body size in *T. chiltoni* whereas *T. areolatus* showed a significant relationship with seasons. This may indicate a generalist strategy in *T. areolatus* by varying its diet in function of available prey items in each season, whereas *T. chiltoni* would be specialized in relation to individual size and intraspecific habitat partitioning.

Key words: diet, sympatry, *Trichomycterus areolatus*, *Trichomycterus chiltoni*.

RESUMEN

Trichomycterus areolatus y *Trichomycterus chiltoni* son peces Siluriformes endémicos de Chile, siendo las únicas especies chilenas conocidas de este género que coexisten en simpatria. Se encontró alta sobreposición de nicho trófico entre estas dos especies. El índice de Horn varió de 0,668 a 0,885 entre estaciones, sin diferencias significativas, y el índice de Schoener varió de 0,639 a 0,912. Además el análisis discriminante no mostró diferencias significativas en las presas entre las dos especies. La composición de la dieta de *T. chiltoni* y *T. areolatus* consistió principalmente en larvas de chironómidos y otros invertebrados acuáticos. En todas las estaciones estudiadas *T. chiltoni* mostró una riqueza de presas mayor. El análisis de componentes principales (PCA) mostró una gran similitud entre las dietas de *T. areolatus* y *T. chiltoni*. Estos resultados se relacionaron significativamente con las medidas de tamaño corporal en *T. chiltoni* mientras que *T. areolatus* mostró una relación significativa con las estaciones. Esto podría indicar una estrategia generalista en *T. areolatus*, variando su dieta en función de las presas disponibles en cada estación, mientras que *T. chiltoni* estaría especializado en función del tamaño individual.

Palabras clave: dieta, simpatria, *Trichomycterus areolatus*, *Trichomycterus chiltoni*.

INTRODUCTION

Early notions of ecological relations of closely related species indicate that these species cannot occupy the same habitat unless they differ in resource utilization (Dumas 1964). Most studies compare closely related taxa that occur in allopatry. Nevertheless in sympatry, the stabilizing forces that promote niche conservatism,

inhibiting niche shifts, may be countered by natural selection favouring ecological divergence to minimize the intensity of interspecific interactions (Losos et al. 2003). This agrees with the competitive exclusion principle that indicates that if two or more non-interbreeding populations compete for the same limited resources, then all but one of them will be driven to extinction (Hutchinson 1965). In this paper we examine

trophic relationships of two congeneric freshwater fishes that inhabit the same basin.

In Chilean freshwater ecosystems sympatric coexistence of congeneric fishes is an unusual phenomenon (Vila et al. 1999, Dyer 2000, Vila & Pardo 2006), which may be explained in part by niche segregation through resource partitioning (i.e., diet, time and/or space, Schoener 1974). Habitat shift is a common mechanism for niche segregation in freshwater fishes (Werner & Hall 1977). However, niche partitioning may have an asymmetric effect among species, relegating the weakest competitor to marginal habitats (Nilson 1967, Werner & Hall 1976, 1977), where populations are more susceptible to local extinction (Zaret & Paine 1973).

Trichomycterus is a catfish genus including about 120 species, commonly found in neotropical headwater streams (Eigenmann 1918, Pouilly & Miranda 2003). In Chile, *Trichomycterus* is represented by five endemic species with a wide altitudinal and latitudinal distribution (Pardo et al. 2005). These species inhabit the rhithronic zone of freshwater systems and show the highest relative abundance among native fishes. *Trichomycterus areolatus* Valenciennes, inhabits rivers from Huasco (28° 27' S) to Chiloé island (41° 27' S), and *Trichomycterus chiltoni* (Eigenmann) endemic at Biobío basin (36° 49' S) (Dyer 2000, Habit et al. 2006, Vila et al. 2006). These two species overlap extensively in the Biobio basin, and they are the only species of this genus that live in sympatry in Chile (Arratia 1981). The morphological differentiation between them is slight, however adults of *T. chiltoni* reach a larger total length (maximum length 170 mm) than *T. areolatus* (maximum length 116 mm) (Eigenmann 1927). This similarity probably increases their potential competitive interactions, mainly due to the high morphological resemblance (Eigenman 1927) and the similar bottom-dwelling behaviour (Arratia 1990). Besides, *T. areolatus* and *T. chiltoni* may be classified as strict insectivores, feeding mainly on aquatic insects (Habit et al. 2005), and these fishes, as do other siluroids, scrape organisms from plant and rock surfaces (Aranha et al. 1998).

The present study investigated the diet of *Trichomycterus* species from Biobio River, studying their mutual trophic interactions. The

purpose was to infer the ecological process that could ameliorate the competitive interaction between these species, thereby sustaining their present coexistence.

MATERIALS AND METHODS

Study area

Biobio basin (36°43'–38°55' S, 70°49'–73° 10' W) has an Andean origin, and its drainage area of 24,029 km² represents Chile's third largest river basin. It is a typical western Andean system characterized in having a length of ~380 km and a marked change in flow that varies between seasons from 300 to 1,200 m³ s⁻¹. Local climatic conditions are Mediterranean with 1,308.2 mm of mean annual precipitation and a mean annual temperature of 12.4 °C (Niemeyer & Cereceda 1984).

In this basin 14 endemic species of fishes have been reported, corresponding to 31.8 % of the Chilean native species (Campos 1985, Ruiz et al. 1993, Vila et al. 1999).

Diet analysis

From 1994 to 2000, bimonthly collections of *T. areolatus* and *T. chiltoni* specimens were made in the Biobio basin obtaining 452 specimens among which *T. chiltoni* was the most abundant (76.8 %). Fishes were captured using a Coffelt electrofishing backpack equipment and were preserved in 4 % buffered formalin. All esophagii and stomachs of captured specimens were analyzed and 70.4 % were empty, where *T. areolatus* shows the lowest proportion of empty stomachs (59.1 %), compared with *T. chiltoni* (79.2 %).

Prey items in the esophagus and stomach were analyzed under a dissecting microscope, and identified to order or family level whenever possible with available keys (Merritt & Cummins 1978, Lopretto & Tell 1995). Also, fishes were sexed and total body length measured with 0.1 mm precision. Total and eviscerated specimens were weighted with 0.01 g precision.

Horn's index of niche overlap (Krebs 1999) was calculated between *T. areolatus* and *T. chiltoni* on a seasonal basis. As a complement and due to the absence of quantitative data

concerning the resources, Schoener's overlap index (Schoener 1970, Wallace 1981, Kahl 2006) was determined. The confidence intervals of Horn's index were estimated using the percentile method by bootstrapping 10.000 individual diets (Manly 1997). A principal components analysis (PCA) was applied to individuals showing at least one prey item. For each species, the PCA scores of the first and second axes were related to date, body length, total and eviscerated weight, using Spearman's rank correlation (Zar 1996).

Also, to evaluate differences in trophic niche between *T. areolatus* and *T. chiltoni*, a Discriminant Analysis was performed, with a Jack-knifed classification matrix, that was complete using the first, second and third axis of PCA analysis of diet composition (Fisher, 1936).

RESULTS

Trophic composition of *T. chiltoni* and *T. areolatus* consisted mainly of chironomids in all seasons (Fig. 1). Ephemeroptera was almost absent in both species during winter, but represented almost 20 % of prey items the rest of the year. Prey organisms that represented less than five percent (Others), include the following insects: Coleoptera, Diptera, Baetidae, Tipulidae, Simuliidae and Odonata;

crustaceans: Decapoda and Amphipoda; Hirudinea and molluscs. Prey items of the class Others (Fig. 1) in *T. areolatus* were less diverse but more abundant. *Trichomycterus chiltoni* showed the greatest niche breadth.

Horn's trophic niche overlap between *T. chiltoni* and *T. areolatus* varied from 0.668 to 0.885, among seasons. Higher values were found during summer and spring, but 95 % bootstrap confidence interval overlapped between all seasons (Fig. 2), showing non-significant differences between them. On the other hand, Schoener's overlap index presented similar variation from 0.639 to 0.912 in summer and autumn, respectively. Intermediate values were found in winter (0.814) and spring (0.835).

The first two PCA factors, performed using the diet composition of *T. areolatus* and *T. chiltoni* at all seasons, explained over 85 % of the variance. That would indicate a strong similarity between diets of these species (Fig. 3). However, in *T. areolatus* the first PCA factor was correlated significantly with the sampling date, whereas the first and second factors of *T. chiltoni* showed a strong relationship with body size (Table 1). PCA was more effective in classifying *T. chiltoni* than *T. areolatus* (Table 2). The discriminant analyses showed no significant differences in prey items between the two species (Wilks' lambda = 0.98, $F_{4,137} = 0.75$, $P = 0.56$).

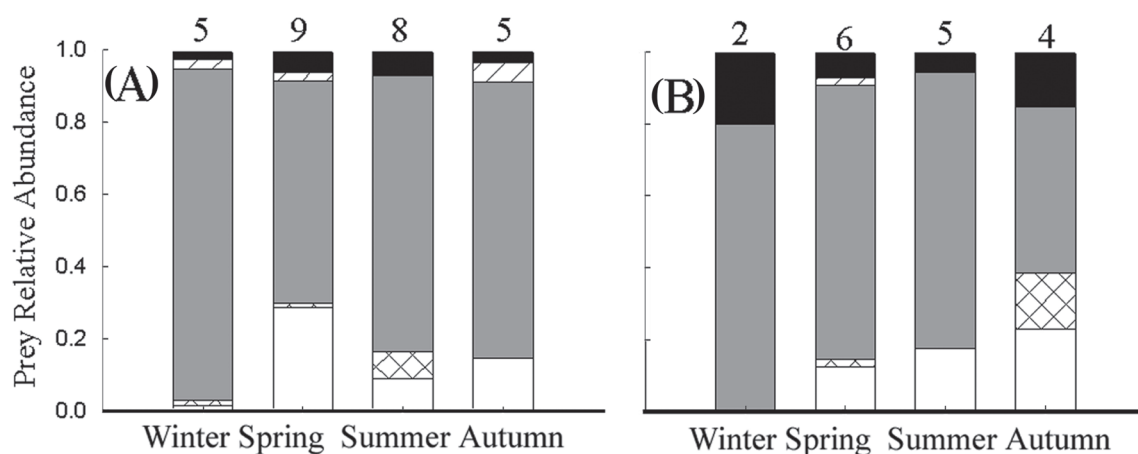


Fig. 1: Summary of seasonal diet composition of (A) *T. chiltoni* and (B) *T. areolatus*. Bars represent prey items: (▨) Trichoptera, (□) Ephemeroptera, (■) Chironomidae, (▤) Plecoptera and (■) Others. Number of prey items is displayed over bars.

Resumen de la composición dietaria estacional de (A) *T. chiltoni* y (B) *T. areolatus*. Las barras representan los ítemes de presa: (▨) Trichoptera, (□) Ephemeroptera, (■) Chironomidae, (▤) Plecoptera y (■) Otros. El número de ítemes presa son mostrados sobre las barras.

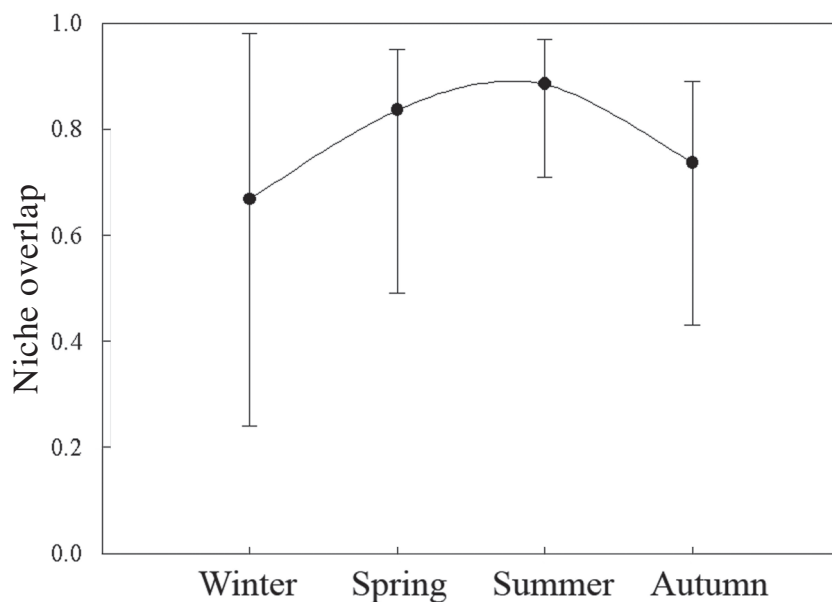


Fig. 2: Horn's indices of niche overlap between *T. chiltoni* and *T. areolatus* calculated for all seasons. Error bars represent bootstrap 95 % confidence intervals.

Índices de Horn para la sobreposición de nicho entre *T. chiltoni* y *T. areolatus* calculados para todas las estaciones. Las barras de error representan los intervalos de confianza al 95 % obtenidos por Bootstrap.

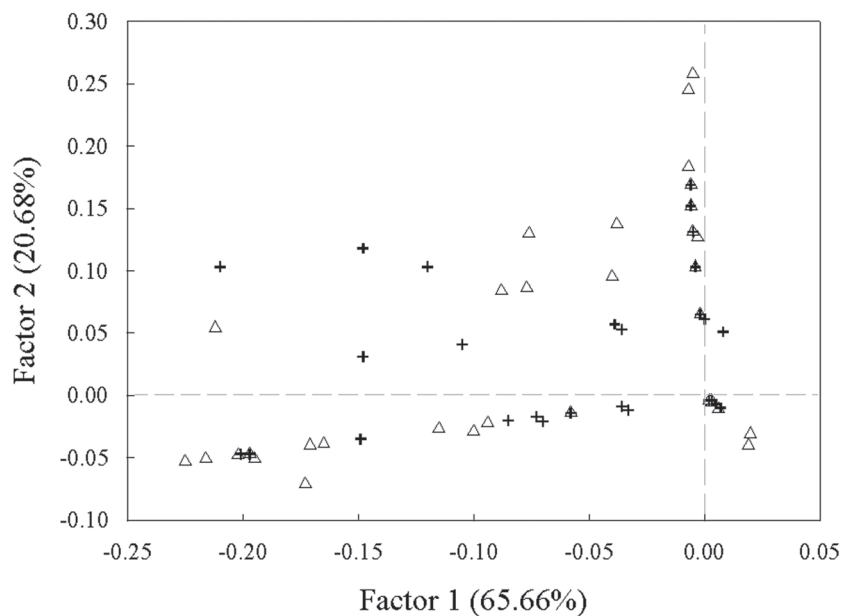


Fig. 3: Plot representing the first two factors of a principal components analysis performed on the diet composition of *T. chiltoni* (Δ) and *T. areolatus* (+), between 1994 and 2000 in all seasons. Percentage of the total variance of each factor is shown in parenthesis.

Gráfico representando los dos primeros factores del análisis de componentes principales realizados con la composición de la dieta de *T. chiltoni* (Δ) y *T. areolatus* (+), entre 1994 y 2000 en todas las estaciones. El porcentaje de la varianza total de cada factor es mostrado entre paréntesis.

TABLE 1

Spearman correlation between first and second axis of PCA analysis against biological variables for *T. chiltoni* (n = 102) and *T. areolatus* (n = 40); Lt = total length, Wt = total weight, We = eviscerated weight

Correlaciones de Spearman entre el primer y segundo eje del análisis de PCA versus variables biológicas para *T. chiltoni* (n = 102) y *T. areolatus* (n = 40); Lt = largo total, Wt = peso total, W = peso eviscerado

Species		Lt	Wt	We	Date
<i>T. areolatus</i>	Factor 1	0.104	0.049	0.072	*-0.363
	Factor 2	-0.134	-0.069	-0.074	0.071
<i>T. chiltoni</i>	Factor 1	*0.219	*0.204	*0.226	-0.008
	Factor 2	*0.307	**0.343	*0.322	-0.055

* P < 0.05; ** P < 0.001

TABLE 2

Jack-knifed classification matrix, using first, second and third axis of PCA analysis of diet composition

Matriz de clasificación corregida con jackknife, utilizando los tres primeros ejes del análisis de PCA de la composición de la dieta

	<i>T. areolatus</i>	<i>T. chiltoni</i>	% correct
<i>T. areolatus</i>	15	28	35
<i>T. chiltoni</i>	25	74	75
Total	40	102	63

Wilks' lambda = 0.978, $F_{4,137} = 0.753$, P = 0.5579

DISCUSSION

According to previous works (Habit et al. 2005) and to our results, *Trichomycterus areolatus* and *T. chiltoni* are mainly benthic feeders, preying mostly on insect larval stages. Our estimates of resource partitioning between *T. areolatus* and *T. chiltoni* in the Biobío River, revealed high Schoener's niche overlap, which is consistent with Horn's overlap values in the trophic niche throughout the year. Also, the discriminant analysis does not show significant differences between these two species, indicating a greater discrimination by *T. chiltoni* individuals than by *T. areolatus* ones, showing the highest overlap at smaller sizes. These results led us to consider that these fishes should present mechanisms to avoid competitive interactions when the resources are

scarce (Hutchinson 1965). Feeding results of *T. areolatus* and *T. chiltoni* suggest these two species may coexist mainly due to differences in their observed diet patterns. *Trichomycterus areolatus* correlates its diet with seasonal changes, and this would be related to the well described yearly changes shown by insect abundance and diversity (Fernández et al. 2001, Sabando 2004). We speculate that this implies generalist behaviour, associated to seasonal resource changes. On the other hand *T. chiltoni* shows a differential diet at different body sizes as intraspecific habitat partitioning (Arratia 1983). The prey items captured by *T. chiltoni* showed a greater taxa richness, what could be explained by the larger size that this fish reaches, allowing consumption of all preys eaten by *T. areolatus* plus bigger items such as decapods and dragonfly larvae that are absent in the stomach contents of *T. areolatus*. This widening in the trophic niche could be related with morphological characteristics such as mouth and body size that determine, in many cases, the types of prey consumed by fishes (Keeley & Grant 1997, Karpouzi & Stergiou 2003). Size range in these catfishes would have a constraining influence on the kind of trophic niche and therefore, on the feeding mechanism as well (Adriaens 2003). Thus, we suggest that the higher relative abundance of *T. chiltoni* in the Biobío river can be attributable to interspecific competition, with an asymmetric competitive feeding relationship that clearly favours *T. chiltoni* and suggests that *T. areolatus* is the weakest competitor. Future work should consider exclusion experiments

that could support the suggested competitive relationship between *T. chiltoni* and *T. areolatus* described herein.

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