

## Evidence of Interactive Segregation between Introduced Trout and Native Fishes in Northern Patagonian Rivers, Chile

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**Abstract.**—Introduced rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta fario* are the most abundant fishes in the northern Chilean Patagonia, and their effect on native fishes is not well known. We tested for interactive segregation between trout and native fishes by using a before–after, control–impact design in which we deliberately reduced the density of trout and observed the response of the native fishes in their mesohabitat use (pool, run, riffle). Three native fish species, *Brachygalaxias bullocki*, *Galaxias maculatus* (inanga), and *Trichomycterus areolatus*, apparently had niche overlap with introduced trout and changed their mesohabitat use after trout reduction. The expansion of the three species into a wider range of mesohabitats after trout reduction suggests that these fishes occupy a broader spatial area when trout are reduced or possibly absent. However, some native fish species, such as *Geotria australis*, did not respond to the trout reductions. To protect Chilean native fishes, policy-makers need to consider providing legal protection for native fishes because native fishes currently have no protection in their catchments.

Interactive segregation (Nilsson 1967) and interspecific competition between introduced trout or salmon and native fishes occur in various rivers of the Southern Hemisphere (McDowall 1990; Ault and White 1994; Flecker and Townsend 1994; McIntosh et al. 1994). However, effects of introduced trout on native freshwater and diadromous fishes in rivers of the Patagonia, South America, have not yet been documented and are even less well understood (Campos 1970; Dyer 2000; Soto et al. 2006).

In Chile, rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta fario* were introduced beginning in the early 1900s by government initiatives to enhance

recreational fishing and early practices of aquaculture (Basulto 2003). It was thought that these areas in the Southern Hemisphere were suitable for and would benefit from the addition of trout (Campos 1970; Basulto 2003). Since their introduction, trout have formed naturalized populations and have become the most abundant fish species, accounting for over 95% of the total biomass in rivers of the Chilean Patagonia (Soto et al. 2006).

Trout introduction efforts were most intense in the Lakes District of the northern Patagonia (Basulto 2003), which makes effects from these introductions more likely to occur in this region. In total, 21 native freshwater and diadromous fishes have been described for the Lakes District (Campos et al. 1998), but 11 species are most commonly found (Soto et al. 2006). Most native fishes are described by their relatively small size, generally less than 20 cm in total length (Vila et al. 1999; Soto et al. 2006). Despite low native species richness the fauna is characterized by a high level of endemism (Campos 1985; Vila et al. 1999; Dyer 2000). Campos et al. (1998) also determined that in the Lakes District, 52% of fish species are listed at elevated conservation categories including at risk of extinction (14%), vulnerable (24%), and rare (14%). Not enough information is available for an additional 19% of the native fishes to be adequately categorized.

In areas with similar fish fauna and stream ecosystems, such as New Zealand, evidence suggests that predation by and competition for habitat with introduced trout are probably mechanisms for the reduction in native fish densities (McIntosh et al. 1994). In rivers of the Lakes District, predation is exerted only by large-sized rainbow trout (>17 cm) and brown trout (>10 cm; Gonzalez 2005). However, the possible effects that trout have on native fish habitat use are unknown. Additionally, basic quantitative information is lacking

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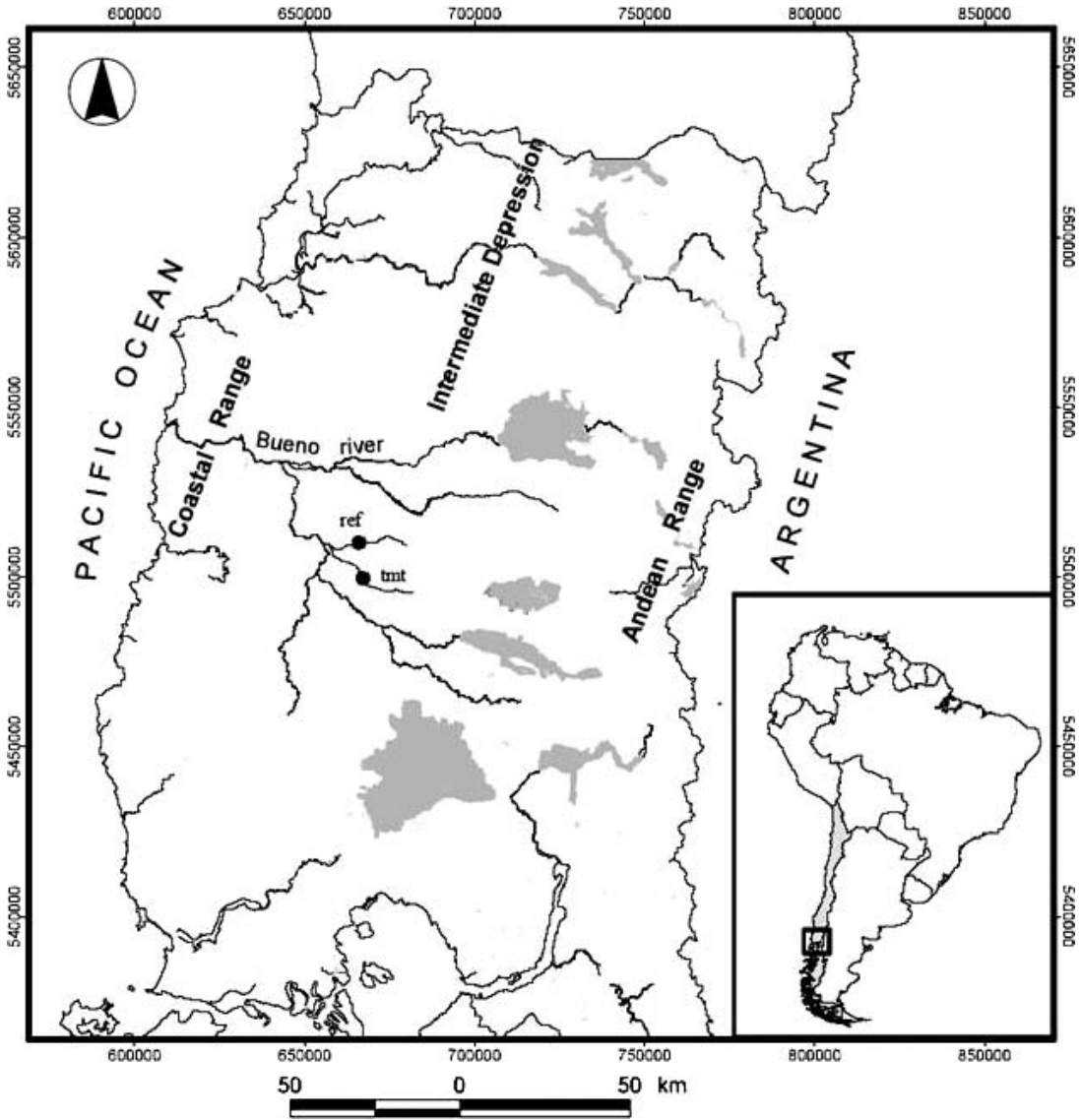


FIGURE 1.—Lakes District in northern Chilean Patagonia, with locations of the Bueno River catchment and letter indications of treatment (tmt) and reference (ref) rivers. Inset shows location of study region in Chile.

that would describe habitat conditions suitable for each native species (Pascual et al. 2002). Many potential ecological effects would be most easily measured if there were data on native fishes before the introduction of trout. Unfortunately, little information exists relating to native Chilean fishes before trout introduction.

Thus, our goal was to provide preliminary information that would quantify habitat use for native fishes by decreasing the nonnative trout density levels in a natural river stretch in the Lakes District of the northern Chilean Patagonia. We could then test for interactive

segregation between trout and native fishes by reducing the density of trout and observing the response of the native fishes. We hypothesized that the responses of native fishes to the reduction in trout density in a river stretch would reveal the preferred habitat for each native fish species.

**Methods**

*Study sites.*—We selected two rivers (Figure 1) from the Bueno River watershed (40°10'S, 73°08'W); these rivers sustain the highest richness (eight species) and

TABLE 1.—Mean characteristics of reference and treatment rivers in the northern Chilean Patagonia from January to April 2005. Mean values are in bold text.

Site	Mesohabitat	Depth (m)	Flow (m <sup>3</sup> /s)	Area (m <sup>2</sup> )	Velocity (m/s)	Temperature (°C)	Conductivity (μS/cm)	pH	Transparency
Reference before reduction	Pool ( <i>n</i> = 37)	0.33		16.0	0.1	15.0	146.4	7.6	3.6
	Rapids ( <i>n</i> = 10)	0.15		8.9	0.4	14.5	150.7	7.7	3.1
	Run ( <i>n</i> = 16)	0.15		15.1	0.2	14.8	141.5	7.7	3.3
	Mean	<b>0.25</b>	<b>0.03</b>	<b>14.7</b>	<b>0.1</b>	<b>14.9</b>	<b>145.8</b>	<b>7.6</b>	<b>3.4</b>
Reference after reduction	Pool ( <i>n</i> = 40)	0.47		11.9	0.0	11.7	171.4	6.9	2.6
	Rapids ( <i>n</i> = 12)	0.11		11.3	0.4	11.6	171.3	6.9	2.5
	Run ( <i>n</i> = 16)	0.13		21.9	0.1	11.8	171.6	6.9	2.5
	Mean	<b>0.33</b>	<b>0.02</b>	<b>14.1</b>	<b>0.1</b>	<b>11.7</b>	<b>171.4</b>	<b>6.9</b>	<b>2.5</b>
Treatment before reduction	Pool ( <i>n</i> = 20)	0.26		14.6	0.0	14.0	237.4	7.6	4.2
	Rapids ( <i>n</i> = 15)	0.27		11.1	0.7	13.5	239.3	7.1	3.8
	Run ( <i>n</i> = 15)	0.34		23.0	0.1	13.4	241.3	7.3	3.9
	Mean	<b>0.28</b>	<b>0.05</b>	<b>16.1</b>	<b>0.3</b>	<b>13.7</b>	<b>239.1</b>	<b>7.4</b>	<b>4.0</b>
Treatment after reduction	Pool ( <i>n</i> = 24)	0.30		17.5	0.1	12.4	225.6	6.9	2.6
	Rapids ( <i>n</i> = 20)	0.29		11.0	0.6	12.2	226.3	6.9	2.6
	Run ( <i>n</i> = 20)	0.26		21.0	0.1	12.2	226.3	6.9	2.5
	Mean	<b>0.28</b>	<b>0.04</b>	<b>16.6</b>	<b>0.3</b>	<b>12.3</b>	<b>226.0</b>	<b>6.9</b>	<b>2.5</b>

density levels of native fishes in the Lakes District of the northern Chilean Patagonia (Soto et al. 2006). The climate of the study area is rain-dominated (1,200 mm/year), and the area is classified as a mesotemperate and humid bioclimate (Amigo and Ramirez 1998). The typical streamflow for this area is at a maximum in winter (June to August) and a minimum in summer (February to April; Niemeyer and Cereceda 1984). Also, the two study rivers have similar physiography, geology, soil, and slope characteristics (<10% incline) and they have no physical barriers to fish movement.

Our study was performed under natural field conditions in segments of the two study rivers, one as a reference river and the other a treatment river, which were located approximately 10 km upstream from their downstream union. Each segment was approximately 70 m in length, 100 m<sup>2</sup> in area, and located at 50-m elevation. Both segments were blocked with 2-mm-mesh netting for the duration of the experiment, which prevented fish movement out of the segment. Block nets were cleaned regularly due to plant litter buildup.

Our experimental study was designed as a before–after, control–impact (BACI) manipulation (Stewart-Oaten et al. 1986). The reference and treatment rivers naturally displayed a reduction in native fish density from the before to after observations. Thus, we can assume that the effects seen in our study are specifically due to the reduction of the trout species and not from a decrease in overall fish density. We sampled the reference and treatment rivers eight times (four times before trout reduction in the treatment river and four times after trout reduction) during daylight in the summer of 2005 (January through April). Before trout reduction our four sampling times were 10 d apart

in January and February. After trout reduction, our four sampling times in March and April were 4 d, 10 d, 20 d, and 1 month after the initial reduction. We estimated fish abundance using single-pass electrofishing with a Smith-Root Model 12B backpack electrofisher (Vancouver, Washington), which probably was an underestimation of population abundance and an overestimation of removal efficiency (e.g., Rosenberger and Dunham 2005).

In each river segment, we identified different mesohabitat units (riffle, run, and pool) classified by Hawkins et al. (1993) and river characteristics each time that we sampled for fishes (Table 1). The number of mesohabitat units sampled in each river varied from 13 to 18 between sampling sessions. River characteristics included water velocity, which was measured using a current meter (Hydro-Bios 445 500–033, Kiel, Germany). Mean water depth was measured using a meter stick, and water flow was calculated using the mid-section method. Water temperature (Thermo Orion 830A, Waltham, Massachusetts), conductivity (Thermo Orion 130A), and pH (Thermo Orion 265A) were measured using handheld field meters. Water transparency was observed on a point scale, with 1 being clear and 5 being opaque. Riffle mesohabitat was described by shallow, lower-gradient sections with moderate current velocity over cobble-like substrate. Run mesohabitat was defined by shallow water flowing at a slow-to-moderate velocity over a variety of substrates. Pool mesohabitat was identified by slow sections with nearly flat water surface gradient. In each river segment we determined species presence, species density, and the size (total length, cm) of captured individuals for each mesohabitat unit. After each sampling period, we returned all native species

TABLE 2.—Classification of fishes in the northern Chilean Patagonia from January to April 2005, with pooled chi-square goodness-of-fit test results for select native fishes, comparing before trout reduction (expected) and after trout reduction (observed) patterns of mesohabitat use (Bonferroni-adjusted  $\alpha = 0.0125$ ; significant *P*-values are in bold text; ref = reference; tmt = treatment).

Species	Origin	Conservation category	Size range (cm)	Mean size (cm)	Chi-square test df	Chi-square test, ref river
<i>Geotria australis</i>	Native	Unlisted	4.0–11.0	8.8	2	4.5
<i>Cheirodon australe</i>	Endemic	Not at risk	2.3–6.7	4.5		
<i>Trichomycterus areolatus</i>	Native	Vulnerable	2.0–11.0	7.2	2	175.79
<i>Galaxias maculatus</i>	Native	Not at risk	2.0–10.0	5.4	2	199.79
<i>Galaxias platei</i>	Endemic	Vulnerable	4.0–10.6	6.1		
<i>Brachygalaxias bullocki</i>	Endemic	Undetermined	1.5–10.0	3.7	2	368.84
Brown trout	Introduced	Unlisted	2.0–37.0	13.1	2	1.13
Rainbow trout	Introduced	Unlisted	3.0–29.0	9.3	2	3.06

back into their respective mesohabitat units. Trout also were returned to their respective mesohabitat units, except in the treatment river when they were removed after the trout reduction phase of the study.

*Data analysis.*—Fish abundance was assessed based on the number of individuals captured per specific mesohabitat unit for each species. The fish abundance data were analyzed using Statistica 6.0 software (StatSoft, Tulsa, Oklahoma). We used nonparametric chi-square goodness-of-fit analysis on the fish count data to determine differences between expected (before trout reduction) and observed (after trout reduction) patterns of mesohabitat use for four native fish species and both trout species (Table 2). *Galaxias platei* and *Cheirodon australe* were found in too few numbers in the treatment river to be included in the chi-square analysis.

When chi-square tests resulted in significant differences between mesohabitat use before and after trout reduction, we used Jacobs’ (1974) selectivity index *D*, a modification of Ivlev’s electivity index, as a nonstatistical indication of where differences between mesohabitat use and availability of mesohabitat units occurred. The index is calculated as:

$$D = (r - p) / (r + p - 2rp),$$

where *r* is the proportion of individuals of one species observed in a particular mesohabitat and *p* is the proportion of a given mesohabitat to total available stream habitat. To ensure that our statistical test results would be considered to be significant at an  $\alpha$  of 0.05, we made a Bonferroni’s adjustment (four tests, 2 df) resulting in an adjusted  $\alpha$  of 0.0125. Trout density (fish/m<sup>2</sup>) was assessed based on the number of individuals per stream reach using eight values for the reference river, four values for the treatment river before trout reduction, and four values for the treatment river after trout reduction.

**Results**

A total of eight fish species were captured from the families Petromyzontidae, Characidae, Trichomycteridae, Galaxiidae, and Salmonidae (Table 2). In both rivers, introduced brown trout and rainbow trout were present. In the reference river, five native fishes were captured, including *Brachygalaxias bullocki*, *Galaxias maculatus*, *Galaxias platei*, *Geotria australis* (captured only as juveniles in ammocoetes and metamorphous stages), and *Cheirodon australe*. In the treatment river, six native fishes were captured including the previously listed five species and *Trichomycterus areolatus*. The percent of total area represented by the three mesohabitat units in each river were (1) reference river: riffle (24%), run (27%), and pool (49%); and (2) treatment river: riffle (31%), run (31%), and pool (38%). In the reference river, trout density was  $0.46 \pm 0.08$  fish/m<sup>2</sup> (mean  $\pm$  SD) for the duration of the study. In the treatment river, trout density before reduction was  $1.01 \pm 0.09$  fish/m<sup>2</sup> and  $0.21 \pm 0.03$  fish/m<sup>2</sup> after trout reduction. Trout densities were manually reduced by an estimated 79% because complete removal was not possible.

Native fishes and trout in the reference river did not change their mesohabitat use during the study (chi-square analysis; Table 2). Jacobs’ *D* ranges from  $-1$ , which indicates complete avoidance of mesohabitat, to  $+1$ , which indicates exclusive use of mesohabitat. Jacobs’ *D* also indicated that *B. bullocki* used all mesohabitats during the duration of the study (before reduction: pool = 0.76, run = 1.00, riffle = 0.52; after reduction: pool = 1.00, run = 1.00, riffle = 0.80), as did *G. maculatus* (before reduction: pool = 0.51, run = 0.90, riffle = 0.67; after reduction: pool = 0.69, run = 1.00, riffle = 0.80). In the treatment river, however, *B. bullocki*, *G. maculatus*, and *T. areolatus* changed their mesohabitat use after trout reduction (Figure 2). *Galaxias maculatus* changed their habitat use within 4 d after trout reduction (chi-square = 7.75, df = 2, *P* <

TABLE 2.—Extended.

Species	Ref river <i>n</i>	<i>P</i> -value, ref river	Chi-square test, tmt river	Tmt river <i>n</i>	<i>P</i> -value, tmt river
Pouched lamprey <i>Geotria australis</i>	96	0.92	4.5	8	0.11
Pocha <i>Cheirodon austral</i>					
Pencil catfish <i>Trichomycterus areolatus</i>			175.79	32	<0.0001
Inanga <i>Galaxias maculatus</i>	80	0.39	199.79	226	<0.0001
Tollo <i>Galaxias platei</i>					
Puye <i>Brachygalaxias bullocki</i>	142	0.13	368.84	60	<0.0001
Brown trout	13	0.51	1.13	10	0.57
Rainbow trout	12	0.41	3.06	28	0.22

0.02); *B. bullocki* changed their habitat use within 10 d after trout reduction (chi-square = 10.79, *df* = 2, *P* < 0.0045); and *T. areolatus* changed their habitat use within 20 d after trout reduction (chi-square = 175.79, *df* = 2, *P* < 0.0001). Before trout reduction in the treatment river, *B. bullocki* predominately used run mesohabitats and avoided riffles and pools, but after trout reduction puye occupied riffle, run, and pool mesohabitats. *Galaxias maculatus* inhabited runs followed by pools and avoided riffle mesohabitats before trout reduction in the treatment river, whereas after trout reduction *G. maculatus* used all mesohabitats with preferential order as run, pool, and riffle. *Trichomycterus areolatus* mainly used riffle mesohabitats in the treatment river before trout reduction and avoided runs and pools. However, after trout reduction, *T. areolatus* substantially occupied mainly runs and a smaller amount of riffles while still avoiding pools.

### Discussion

Despite the intrinsic limitations of our BACI field experiment (e.g., lack of spatial replication), our results show a change in mesohabitat use by *B. bullocki*, *G. maculatus*, and *T. areolatus*, which suggests that trout restrict the mesohabitat range of these native fishes, leading to interactive segregation during the austral summer. This change in mesohabitat use is most likely because *B. bullocki*, *G. maculatus*, and *T. areolatus* have more of a niche overlap with trout than do other native fishes, such as *G. australis*, which did not display changes in mesohabitat use. The results of our study are in agreement with the idea that interspecific competition is the driving factor for determining fish hierarchy at the mesohabitat scale (Fausch et al. 1994).

Results from field experiments, such as our study, account for natural and stochastic forces occurring in real ecosystems. However, field experiments have limitations because it can be difficult to separate

measured effects from individually occurring natural conditions and interactions. For example, in our study indirect effects from species assemblage interactions (Wootton 1994) may have influenced habitat use changes. Also, the addition of *T. areolatus* in the treatment river adds an extra species to the assemblage, increasing interactions and possible indirect effects. Additional sources of error may be accounted for by net-blocking of the stream reach. Trout or native fishes may have moved past the barriers, and because we did not tag fish inside or outside of the blocked area we cannot be completely certain that there was no movement. We chose not to block between mesohabitats because we thought there would be an equal amount of evasion by fishes during the net installation. However, we observed that fish did not move from one mesohabitat unit to another. The effects of the presence or absence of trout were not assessed by species or their size, which may be important distinctions for future studies.

*Brachygalaxias bullocki* use a diverse range of mesohabitat units, as seen by Berra et al. (1995), and not just runs that they inhabited before trout reduction. Riffles probably allow puye to maximize their desired feeding position where they are able to maintain a wider trophic range than other native fishes (Campos 1985). Most likely due to their mesohabitat displacement, *B. bullocki* eat fewer items and substantially less allochthonous prey, and less larger-sized autochthonous prey in the presence of a high density of brown trout (Gonzalez 2005).

*Galaxias maculatus*, similar to *B. bullocki*, occupy waters with a wide range of mesohabitat units after trout reduction, and not just runs and pools, which they inhabited before trout reduction. McDowall (1971) indicated that *G. maculatus* use a varied range of habitats from rocky to sandy bottoms and at varying temperature levels. Also, because *G. maculatus* eat both allochthonous and autochthonous prey

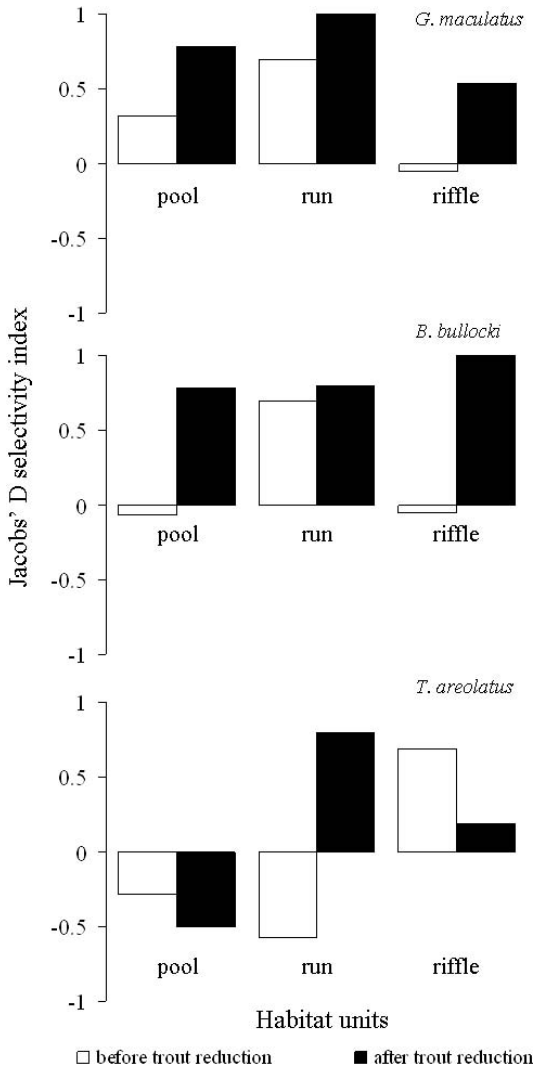


FIGURE 2.—Mesohabitat use by native Chilean fishes (*Galaxias maculatus*, *Brachygalaxias bullocki*, and *Trichomyxerus areolatus*) before and after rainbow trout and brown trout reduction in the treatment river from January to April 2005, using Jacobs' selectivity index  $D$ , which ranges from  $-1$  (complete avoidance of mesohabitat) to  $+1$  (exclusive use of mesohabitat).

items (Campos 1985; Gonzalez 2005), they have access to all mesohabitat units and a wide range of food sources.

After trout reduction, *T. areolatus* used runs followed by riffles. This species has the ability to take shelter between and on the underside of rocks and boulders (Campos 1985), and has a specialized feeding behavior with a low trophic range, eating only autochthonous prey associated with rocky benthic substrates (Habit et al. 2005). Relative to riffles, runs

maintain higher periphyton cover that autochthonous prey grazers would potentially feed upon, possibly leading to more abundant food resources for *T. areolatus*. Thus, it is likely that a position in run habitat allows *T. areolatus* to maintain their desired food resources and exert less energy than is required to maintain position in riffle habitat. This specialized mesohabitat use is probably the reason for the wide distribution of pencil catfish in rivers that are fast-to-medium flowing with large cobbles and boulders (Arratia 1983; Habit et al. 2005).

However, not all native fishes changed their mesohabitat use after trout reduction. Juvenile *G. australis* used pool mesohabitats regardless of trout density levels. This species may not exploit enough of the same mesohabitat resources as trout or they may maintain an evolutionary adaptation that allows them to succeed against trout. It also is not known whether *G. platei* or *C. australe* changed their mesohabitat use after trout reduction because they were left out of the comparison analysis. In our study, *G. platei* were most often captured in pools and runs that provided darkness either due to cover or shade. This result is supported by Chusca et al. (2004) who classified *G. platei* as deepwater bottom dwellers, with tolerances for lower dissolved oxygen and higher turbidity levels. In our study, *C. australe* were captured exclusively in pools, mainly with the aquatic plant *Callitriche lechleri*. It is probable that this type of vegetation sustains a higher density of microcrustaceans, such as Cladocera, and the relatively small autochthonous prey that constitute the highly specialized diet of *C. australe* (Campos 1985; Gonzalez 2005).

Understanding changes in habitat use by certain native fishes after trout reduction will provide insight into which species has the most niche overlap with trout and allow for predictions as to which native fish species are at the most risk for competition. Native species classified with higher risks could receive heightened levels of priority and protection in their catchments. However, there is currently no law that provides legal protection for native fishes, whereas introduced trout do have this protection, which makes current fisheries management of unprotected native fishes difficult and challenging.

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