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Partial Migration in a Robust Brown Trout Population of a Patagonian River

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Abstract

Life history plasticity, particularly partial migration (i.e., coexistence of resident and anadromous forms), probably plays a major role in the ability of brown trout *Salmo trutta* to dominate food webs after introduction into Patagonian rivers. We documented brown trout establishment, distribution, and life history variation in relation to habitat features in the Rio Grande, Tierra del Fuego, Argentina. Results support the hypothesis that Rio Grande brown trout developed an anadromous life history form (“sea trout”) two decades after introduction in relation to localized food limitation as the population expanded throughout the basin. Tributary streams with only resident fish were narrower and had significantly higher levels of specific conductance and soluble reactive phosphorus than streams that were inhabited by both resident and anadromous brown trout. Invertebrate biomass was two to three times higher and juvenile brown trout density was significantly higher in resident-only sites than in streams with both life history forms. Density-dependent growth was not evident and juvenile condition was higher in resident-only streams. These findings suggest that food availability influences the individual decision to migrate, although genetic and other factors are probably also involved. Mark–recapture analysis showed that approximately 38,000–55,000 adult sea trout returned annually to the Rio Grande in 2006 and 2007, making it one of the most robust sea trout populations in the world. However, native fishes have apparently declined to near extirpation as the brown trout population has expanded.

Brown trout *Salmo trutta* and other salmonid fishes have been widely introduced in Patagonia, South America, where they dominate fish biomass in many rivers and in some cases have become anadromous (Pascual et al. 2002); however, the question of how nonnative salmonids affect the native fishes and food webs remains largely unresolved. Pervasive influences, often cascading over multiple trophic levels, are associated with invasion by brown trout and other salmonids in New Zealand streams, where native fish communities resemble those in Patagonia (Flecker and Townsend 1994; Huryñ 1996; Townsend 1996; McDowall 2006). While life history plasticity has often been noted as characteristic of successful invaders (Moyle and Light 1996; Townsend 1996; Alcaez et al. 2005), few studies have specifically addressed the role of life history variation in the invasion process (see Bohn et al. 2004; Bonsall and Mangel 2004; Alcaez et al. 2005).

Partial migration, the phenomenon of migratory and resident individuals coexisting in the same population, is a common expression of life history plasticity in fishes (Jonsson and Jonsson 1993; McDowall 1997). In brown trout, partial migration results in the presence of resident (or riverine) adults and anadromous adults (hereafter “sea trout”) in the same population. To be sustained, fitness benefits of migration, such as increased reproductive output, must outweigh mortality and other fitness costs (Gross 1987). The “decision” to migrate undoubtedly is a complex interaction involving genetic control of phenotypic plasticity and physiological (energetic) and environmental (food supply, physical habitat) correlates (Hindar et al. 1991; Jonsson and Jonsson 1993; Klemetsen et al. 2003). These tradeoffs are difficult to quantify, especially in remote settings where experimental opportunities are limited; therefore, determinants of partial migration are poorly understood. Nonetheless,

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environmental factors like the avoidance of adverse ambient conditions (e.g., extreme temperatures, poor reproductive habitat, or poor feeding habitat) must contribute considerably to an individual's decision to migrate (Nikolskii 1963).

Gross et al. (1988) argued that diadromous migrations evolved in relation to aquatic productivity. Their argument, known as the food availability hypothesis, is supported by the observation that anadromous fishes occur most frequently at higher latitudes where marine productivity exceeds freshwater productivity, whereas catadromous fishes occur most frequently at lower latitudes where freshwater productivity exceeds marine productivity. The food availability hypothesis has been corroborated experimentally in salmonid species by inducing migration via food deprivation and vice versa (Olsson et al. 2006). Thus, growth rate (Jonsson 1985) and ultimately body size (Bohlin et al. 1996) are associated with the tendency to migrate.

Partial migration is a notable expression of life history variation that could facilitate invasion when the supply of local resources is constraining. Indeed, if the food availability hypothesis applies in the introduced range of a species, the development of diadromy during invasion should be associated with a change in the food base. This implies potentially far-reaching impacts of the invader on the native food web. Although the effects of introduced fishes on native ecosystems have been

widely documented (Knapp and Matthews 2000; Schindler et al. 2001; Townsend 2003), such effects are rarely explored with respect to life history plasticity and are scarcely evaluated in South American rivers.

The purpose of this study was to determine the stocking history, current distribution, abundance, and life history variation of an introduced brown trout population in the Rio Grande within the province of Tierra del Fuego, Argentina; this river is touted for its high abundance of large sea trout. In the context of the food availability hypothesis, we expected to find both resident and anadromous forms, with residents occupying areas of greater food resources and having higher juvenile growth rates than sea trout. We also estimated the anadromous population size and inferred the effects of this invasive species on native fish populations.

STUDY AREA

The Rio Grande (57°47'S, 67°41'W) is the largest catchment on Isla Grande of Tierra del Fuego (Figure 1). It is approximately a fourth-order river originating in Chile from a headwater lake and a spring-fed Andean stream. The river flows 120 km to the South Atlantic Ocean through a large, shallow estuary at the city of Rio Grande, Argentina. The hydrograph is dominated by

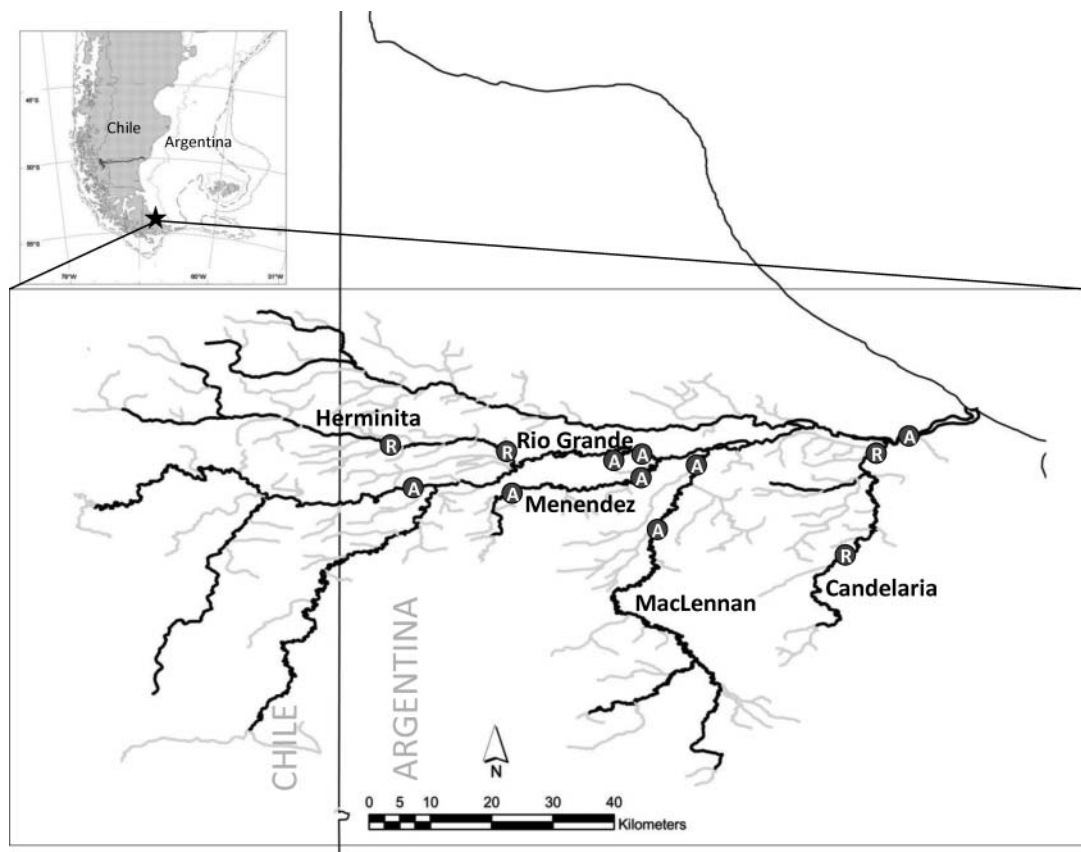


FIGURE 1. Map of the Rio Grande catchment in southern Patagonia, illustrating the sites (shaded circles) sampled for juvenile and adult brown trout and habitat metrics (A = locations where anadromous and resident fish were documented; R = locations where only resident fish were present).

rainfall. At base flow, the primary channel meanders or occasionally anastomoses (sensu Lorang and Hauer 2006) through an expansive flood plain (<1% slope; often >3 km wide). Average annual discharge is approximately 40 m³/s (Iturraspe et al. 1998). Major tributaries flowing into the Rio Grande include the Radman (or Rasmussen) River and the Menendez River. Smaller tributaries include the MacLennan (or Ona), Herminita (or Herminia), Moneta, and Candelaria rivers (Figure 1). The flood plain within the study reach is at a low elevation (from about 75 m to sea level), is characterized by a low gradient (~1%), and is dominated by small shrubs, grasses, and forbs.

Owing to the relative lack of human disturbance in the flood plain with respect to flow regulation, flood protection structures, point source pollution, and road development, ortho-fluvial and parafluvial spring brooks occur in the flood channels (sensu Stanford et al. 2005) and natural hyporheic flows appear to be undisturbed. However, extensive grazing by sheep and cattle has occurred throughout the catchment for over 100 years. Substratum in the channel varies in size from fine organics to bedrock (Wolman 1954), but main and secondary channels are dominated by large gravel to small cobble arrayed in riffle–pool–run–tailout sequences mediated by point-bar erosion and deposition characteristic of meandering channels. Historically, the river contained native creole perch *Percichthys trucha* and galaxiid species, including small puyen *Galaxias maculatus*, large puyen *G. platei*, and peladilla *Aplochiton* spp. (McDowall 1971).

METHODS

Retrospective analysis.—The history of native fishes and brown trout stocking and population expansion in the Rio Grande was determined from a limited literature base, documents from the Natural Resources Department of Tierra del Fuego, local knowledge, fishing records, and documents provided by Alejandro Menendez Behety (a fisher, fishing lodge owner, and local resident for 70 years). Additional fishing records dating back to 2000 were obtained from the five largest fishing lodges on the river. All retrospective data are archived at the Flathead Lake Biological Station (FLBS), Polson, Montana.

Site differentiation.—Sites on the main-stem Rio Grande and its main tributaries were selected to encompass the greatest possible extent of the Argentine portion of the river system. None of the tributaries had barriers that might limit adult or juvenile fish movement. Four sites were located on tributaries reported by local inhabitants as supporting resident fish only (Candelaria and Herminita rivers). Eight sites located on other tributaries (Menendez and MacLennan rivers) and the main-stem Rio Grande were reported to have low densities of resident fish that shared habitat with abundant sea trout spawners (Figure 1). This site differentiation was confirmed explicitly throughout the study.

Freshwater habitat characterization.—A suite of variables was measured seasonally in late December (hereafter, spring), late February (summer), and mid-April (fall) of 2007 as poten-

tial correlates to site-specific fish growth. Measured variables included average particle size on the river bottom (Wolman 1954); depth, wetted width, and thalweg velocity; specific conductance and pH (determined with an Oakton Model 10 pH meter; Oakton, Vernon Hills, Illinois); concentrations of total persulfate nitrogen, nitrate–nitrite, ammonium, total phosphorus, and soluble reactive phosphorus in grab samples from the thalweg (APHA 1998); standing crop of aufwuchs as chlorophyll-*a* concentration and ash-free dry mass (Steinman et al. 2006); and benthic invertebrate density and biomass determined by use of a 30- × 30-cm Surber sampler with 500-μm mesh (Hauer and Resh 2006). Additionally, water temperature was determined every 90 min with iButton temperature data loggers (Maxim Integrated Products, Sunnyvale, California). Thermistors were calibrated to correct for systematic bias or error. Temperature data were reduced to daily means. Analytical samples were shipped frozen to the Group of Anadromous Salmonid Studies (GESA, Argentina) laboratory and the FLBS and were analyzed according to routine protocols (APHA 1998). Assistance with invertebrate taxonomy was provided by the Laboratory of Ecological Investigations and Animal Systematics at the National University of Patagonia, Esquel, Argentina, and a reference collection was archived at FLBS.

Juvenile distribution, abundance, and diet.—Three-pass electrofishing with a Smith-Root Model LR-24 backpack electrofisher (Smith-Root, Vancouver, Washington) was conducted twice during the field season to determine densities of juvenile brown trout and native fishes. Electrofishing sites were blocked with a small-mesh net to control for migration. Brown trout growth was assessed via biomass accumulation and back-calculation from scale analysis (see below). All fish were measured for fork length (FL) and weighed in the field, and Fulton's condition factor (*K*) was calculated ($K = [\text{weight} \times 10^3]/\text{FL}^3$, where weight is in g and FL is in mm). Juvenile brown trout larger than 90 mm were sampled for stomach contents via gastric lavage, and the samples were preserved for analysis to compare with benthos data. Scales were removed from an area between the adipose and dorsal fins, 5–10 rows above the lateral line. Population densities of juveniles were determined by means of the Zippin (1958) estimation method based on the area of each reach.

In addition to electrofishing, fyke-netting was conducted to estimate juvenile freshwater migration patterns between tributaries and the main stem. Fyke nets (6.3-mm mesh) were installed facing both upstream and downstream and were attached to each other and the riverbank in all tributaries for a minimum of 72 h during the summer and fall. Nets were monitored twice daily, and migrants were measured (FL) and weighed. Mortality due to all sampling procedures was less than 1% of the total number of fish handled.

Adult distribution and abundance.—Adult sea trout and resident brown trout in the main-stem Rio Grande and the Menendez River were landed by sport anglers and scientists during January–April in 2006–2008; fish were measured, weighed, and

tagged and their scales were collected by scientifically trained guides. Researchers conducted angling on the other tributaries. Fork length and girth anterior to the dorsal fin were measured for all fish, and scale samples were taken as described above for juveniles. Floy T-bar anchor tags were inserted underneath the dorsal fins of fish exceeding 30 cm FL ($N = 3,976$). Adipose fins were clipped during the 2006 season to measure tag retention. Because fish were not killed, sex was generally determined by morphology. Males exhibit a slightly hooked jaw or a precursory hooked jaw, whereas females do not. To evaluate freshwater feeding habits of returning migratory fish, some of the tagged fish were analyzed for stomach contents obtained by gastric lavage ($N = 40$). Data were recorded by guides and later verified.

Adult age and growth.—Scale samples were cleaned and pressed into acetate by means of a heated hydraulic press. Impressions were magnified under a dissecting microscope and were digitally photographed for analysis with Spot software (Diagnostic Instruments, Sterling Heights, Michigan). Image analysis software (ImageJ) was used to examine and photo-record each scale sample. Annuli were counted to estimate the age of the fish. The radii of annuli were measured along the anterior–posterior axis of the scale to determine scale length at a specific age. Ages at spawning events were inferred by the degree of scarring on the annuli. The absence of spawning marks, however, does not confirm the absence of spawning behavior (Elliott and Chambers 1996); thus, the reported number of spawning events serves as a minimum estimate. Sea trout and resident brown trout were distinguished by morphology and scale growth patterns. Relative to sea trout, the resident brown trout were smaller and darker in color, had a more densely spotted pattern, and exhibited a fusiform body shape. Circuli spacing on scales was used to confirm morphological life history characterization. For sea trout, spacing is wider in the circuli of scales during the postsmolt phase owing to higher growth rates in the marine versus freshwater environment. Individual back-calculated length at age was determined from scale analyses using the Fraser-Lee method (Fraser 1916; Lee 1920). The biological intercept of 3.8 cm was determined with linear least-squares regression ($r = 0.81$, $df = 201$, $P < 0.05$). The assumption of homogeneity of variances was met, and the linearity of the relationship between scale radius and fork length was confirmed. Growth rates of male and female sea trout were not significantly different, and thus the samples were pooled. Blind verification of aging techniques was performed on 75 scale samples by the Inland Fisheries Laboratory at the University of Oslo, Norway. Age agreement between data sets was 85%. Samples for which there was no agreement were from old fish (≥ 8 years) and did not exhibit consistent bias in overestimation or underestimation.

Statistical analyses.—To test the food availability hypothesis, binomial logistic regression of site variables by site type (resident sites = sites supporting only adult resident brown

trout; anadromous sites = sites supporting adults of both anadromous and resident forms) was initially used with values from each season treated as replicates after no significant effect of season was demonstrated ($P = 0.316$ – 0.988). In the logistic regression model, the explanatory habitat data exhibited both quasi-complete and complete separation, precluding the development of maximum likelihood estimates. Quasi-complete or complete separation occurs when there is little or no overlap (i.e., a large difference without commonality) between explanatory data points of the response variable categories (Hosmer and Lemeshow 2000). Consequently, a fully parameterized model could not be developed, and differences in site variables between site types were subsequently analyzed with nonparametric exact Mann–Whitney U -tests. The Mann–Whitney U -test was selected because of the small sample sizes and the nonnormal distribution of data (Landau and Everitt 2004). Additional comparisons were made between back-calculated growth rates of juvenile fish in resident streams and anadromous streams by means of univariate analysis of variance (ANOVA). Subsequent multiple comparisons were performed with post hoc Tukey's pairwise procedure (Landau and Everitt 2004). All statistical calculations were carried out with the Statistical Package for the Social Sciences version 16.0 GP (SPSS, Inc., Chicago, Illinois). An α level of 0.05 was used.

Mark–recapture data were analyzed with a Schnabel (1938) estimator. This estimator is used for multiple mark–recapture events occurring over a short period of time and assumes the absence of immigration, emigration, recruitment, or mortality. Although the assumption of no immigration was violated in this migratory population, a more appropriate model would have required more data than we could collect. The goal of the analysis was to generate a reasonable estimate of the brown trout population in the Rio Grande.

RESULTS

Retrospective Analysis

The Rio Grande historically was inhabited by native creole perch, small puyen, large puyen, and peladilla (McDowall 1971). The galaxiids are catadromous species. The native fishes apparently were abundant before the expansion of brown trout (A. Matias, local resident of Rio Grande, personal communication), but only 12 specimens (all galaxiids) were observed during our study.

Precise records describing the earliest introductions of brown trout to Tierra del Fuego and mainland Argentina are unavailable (C. Riva Rossi, GESA, Puerto Madryn, personal communication). The first documented attempt at introducing brown trout to mainland Patagonia occurred in 1906, when 6,000 eggs were reportedly shipped (probably from the UK) but died in transport (Marini and Mastrarrigo 1963). The first documented stockings of brown trout in Tierra del Fuego occurred in 1927 in several rivers on the Chilean side of the island that may

have included headwaters to the Rio Grande drainage (Balsulto del Campo 2003). The egg containers were marked *meerforelle* (i.e., sea trout) and may have originated near Hamburg, Germany, although the source population was not definitively identified (Joyner 1980; R. Behnke, Colorado State University, Fort Collins, personal communication). Genetic analyses of parental stocks of southern Chilean brown trout suggest that the source populations were Atlantic rather than Mediterranean in origin (Faundez et al. 1997; Colihueque et al. 2003).

From 1935 to 1937, English settler John Goodall hatched and reared brown trout obtained from Puerto Montt, Chile. He released hundreds of thousands of juveniles into the Candelaria, Herminita, MacLennan, and Menendez rivers (Bruno Videla 1978). Those fish were of unknown European origin (Valiente et al. 2007). Goodall also stocked rainbow trout *Oncorhynchus mykiss* and Atlantic salmon *S. salar* throughout the Rio Grande during the same period. Documented stocking of brown trout in the catchment occurred again in 1976 (Bruno Videla 1978) and continued annually (except during 1979–1981) through at least 2000 from hatcheries (in Bariloche and Ushuaia, Argentina) that reared fish of unknown European origin. Annual stocking of brown trout in the Rio Grande catchment from 1982 to 2000 averaged about 60,000 juveniles or eggs (S. Lesta, Department of Natural Resources of Tierra del Fuego, personal communication).

The first recorded catch of resident brown trout in the river appears in John Goodall's records in 1937. Records from 1948 document catches of all three introduced salmonids in the main-stem Rio Grande, and the popularity of sportfishing in the area began to increase. No evidence of anadromy existed until local anglers reported large, silver, apparently sea-run fish in the lower section of the river in the mid- to late 1950s (A. Menendez Behety, local fisher and lodge owner, Rio Grande, personal communication). In-river netting and angling under a loosely enforced bag limit of 5 sea trout·fisher⁻¹·d⁻¹ increased as sea trout proliferated. Catch-and-release angling tourism started in 1986 (Solomon and Czerwinski 2006). As angling tourism grew, public access to the river diminished due to private riverbank ownership by a few large ranch owners. Access is now controlled by landowners that market strictly enforced catch-and-release angling during the summer and early fall to mostly foreign fishers. Less than 10 km of stream at the downstream-most end of the river are open to public angling, and the enforced bag limit is 1 sea trout·fisher⁻¹·d⁻¹. Additional access to the river for the general public occurs 1 d/week. In 2008, the private sea trout sport fishery on the Rio Grande was conducted by seven exclusive lodges and generated over US\$5 million.

During the course of our study, brown trout dominated the Rio Grande fish community, with both resident and anadromous forms abundant. Sea trout and resident brown trout were routinely caught in the main-stem Rio Grande and in the Menendez and MacLennan rivers. Sea trout were not observed in the Herminita River or the Candelaria River, whereas resident brown trout were common. This distributional dichotomy was clear

throughout the course of fieldwork and provided a natural experimental design with which to examine partial migration as a factor driving brown trout population expansion.

Freshwater Habitat Characterization

Several habitat variables exhibited significant differences between resident sites and anadromous sites. Resident sites had narrower wetted channels on average than anadromous sites (Mann–Whitney *U*-test: $N = 35$, $z = -3.2$, $P = 0.001$; Figure 2). Specific conductance was significantly higher in resident streams than in anadromous streams (Mann–Whitney *U*-test: $N = 34$, $z = -3.4$, $P < 0.001$), as was soluble reactive phosphorus ($N = 35$, $z = -4.0$, $P < 0.001$; Figure 2). Likewise, the density of scuds *Hyaella araucana* (Amphipoda; Mann–Whitney *U*-test: $N = 36$, $z = -3.7$, $P < 0.001$), biomass of *H. araucana* ($N = 36$, $z = -2.4$, $P < 0.001$), and biomass of other invertebrates ($N = 36$, $z = -2.92$, $P = 0.003$) were significantly higher at resident sites (Figure 3). *Hyaella araucana* were analyzed separately because they were notably abundant in the Rio Grande. Habitat data were pooled and are presented in Table 1.

Juvenile Distribution, Abundance, and Diet

Densities of brown trout young of the year (age 0) and parr (age 1) across all sites ranged from 0 to 0.71 fish/m² in the spring and from 0 to 1.88 fish/m² in the fall (Figure 4). Resident sites exhibited significantly higher juvenile densities than anadromous sites ($t = 2.107$, $df = 22$, $P < 0.047$; Figure 4).

No migration was documented based on fyke-net deployment at any site during summer sampling. During fall, age-0 (96%) and age-1 (4%) fish were documented as migrating upstream from the main stem into the resident tributaries, the Herminita River ($N = 18$) and Candelaria River ($N = 7$), but there were no downstream captures. These findings provided some confidence for the closed-population assumption used in calculating site-specific growth rates based on cohort biomass change.

Diets consumed by juvenile brown trout ($N = 185$) were dominated (in order of decreasing frequency) by *H. araucana*, various Chironomidae taxa, snails *Chilina patagonica*, Ephemeroptera–Trichoptera–Plecoptera taxa (i.e., mayflies *Andesiops* spp. and *Meridialaris chiloeensis*; caddisflies *Cailloma* spp., *Nectopsyche* spp., *Rheochorema* spp., and *Verger* spp.; and stoneflies *Limnoperla jaffueli* and *Limnoperla* spp.), terrestrial invertebrates, and other juvenile brown trout. Proportions of stomachs that contained *H. araucana* (ANOVA: $F = 10.589$; $df = 1, 17$; $P < 0.005$) and *Chilina patagonica* ($F = 8.358$; $df = 1, 17$; $P < 0.01$) were significantly higher at resident sites than at anadromous sites, and juveniles from anadromous sites had a greater frequency of empty stomachs and a greater presence of terrestrial invertebrates than those at resident sites (Figure 5). Finally, K was higher in brown trout from resident sites ($K = 0.07$ – 5.43) than in fish from anadromous sites ($K = 0.08$ – 3.49). While the difference in K was not significant, it was

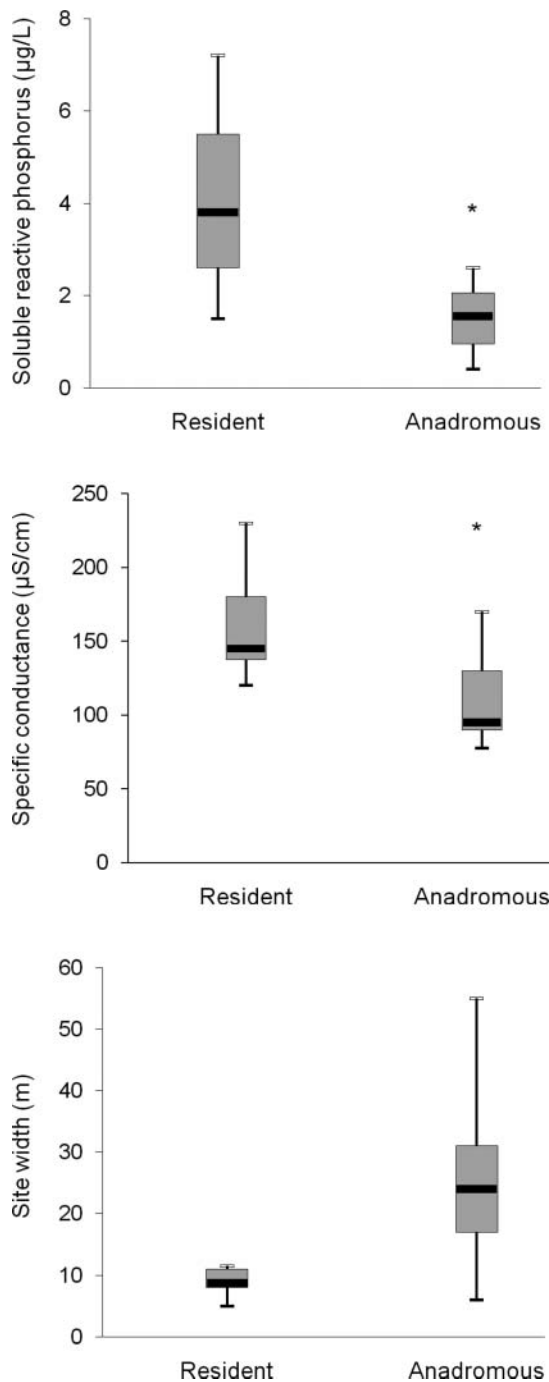


FIGURE 2. Box-and-whisker plots of Rio Grande habitat variables exhibiting significant differences between sites that supported only resident adult brown trout (resident) and sites that supported both anadromous and resident adults (anadromous). Boxes indicate first and third quartiles, solid black bars within boxes indicate means, and whiskers indicate maximum and minimum values. Outliers are shown separately (indicated by asterisks).

close ($t = 1.730$, $df = 22$, $P = 0.098$) and may be biologically relevant.

Of the native fishes, the small puyen and large puyen were documented in low densities (0.04–0.05 fish/m²) during the elec-

trofishing surveys in the lower main-stem Rio Grande ($N = 10$) and the lower Candelaria River ($N = 2$). Rainbow trout juveniles also occurred rarely (their densities were not calculated). No other fishes were observed.

Adults Distribution, Abundance, and Diet

Sea trout were routinely landed and tagged throughout the main-stem Rio Grande and the Menendez River. During summer 2006, 1,043 adult sea trout were tagged; of those, 20 fish (1.9%) were recaptured in that season. During summer 2007, 2,933 adult sea trout were tagged and 66 (2.3%) of those fish were recaptured in that season. Tag loss was less than 3% based on 2007 recaptures of fish that were tagged and fin-clipped in 2006. Based on the mark–recapture data, the population size of sea trout in the Rio Grande was estimated to be 37,803 fish in 2006 and 55,058 fish in 2007 (Table 2). Because the closed-population assumption of the Schnabel estimate was violated, the true population size was underestimated (Williams et al. 2002).

Most of the sea trout examined for stomach contents ($N = 89$) were not feeding in freshwater; all except three fish had empty stomachs and clean digestive tracts. The three exceptions had sparse amounts of freshwater macroinvertebrates in their stomachs, and each of those fish was on its first return to freshwater from the marine environment.

Age and Growth

Site-specific growth rates based on changes in cohort biomass of juvenile brown trout captured by electrofishing for age-0 fish did not significantly differ between resident and anadromous sites ($t = -0.639$, $df = 10$, $P = 0.269$). During the second year in freshwater, sea trout were significantly larger than resident brown trout occupying resident streams (ANOVA followed by Tukey's test: $F = 3.468$, $df = 2, 202$, $P = 0.033$; Figure 6).

The sampled resident adults were predominantly male (63%, $N = 74$; Table 3) and ranged in age from 2 to 11 years. Spawning marks ranged in frequency from 0 to 4. Conversely, the sampled sea trout adults were predominantly female (72%, $N = 129$; Table 3), ranged in age from 2 to 12 years, and had a spawning mark frequency of 0–6. Fish migrated to sea at ages 2 and 3 in similar proportions (45.7% and 40.3%, respectively), although the age at seaward migration varied from age 1 to age 4.

Back-calculated growth at age confirmed that upon reaching the ocean, sea trout grew faster than residents (ANOVA followed by Tukey's test: $F = 18.3$, $df = 3, 113$, $P < 0.001$; Figure 7). Among tributaries, annual back-calculated growth rates of resident brown trout were significantly lower in the Candelaria River than in the Herminita and Menendez rivers (ANOVA followed by Tukey's test: $F = 3.56$; $df = 4, 73$; $P < 0.007$). Average growth rates for the first year at sea varied from 17.8 cm for 2-year-old smolts to 21.7 cm for 1-year-old smolts (Table 4).

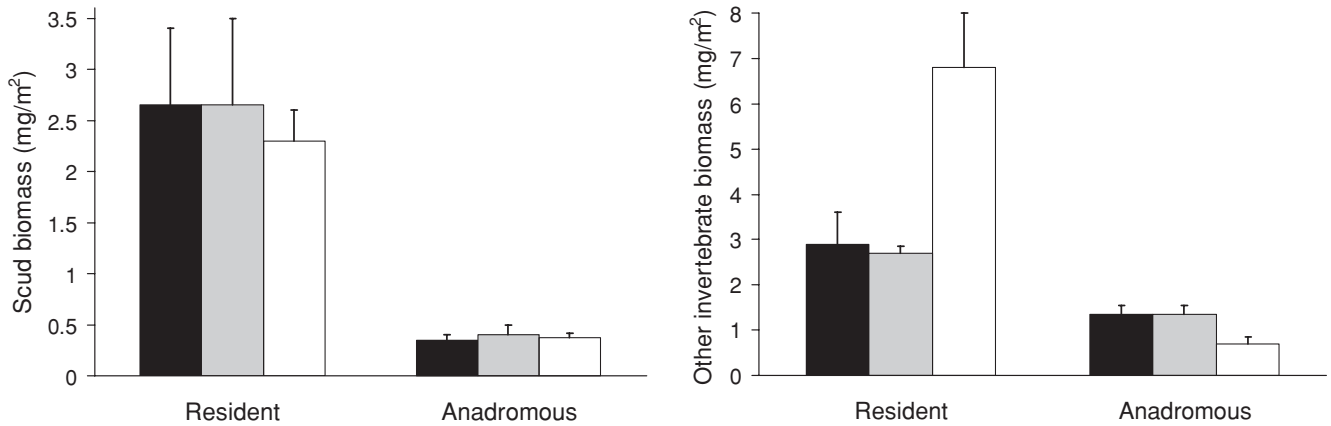


FIGURE 3. Mean (+SE) biomass (mg/m^2) of scuds *Hyaella araucana* (left panel) and other invertebrates (right panel) at Rio Grande sites supporting only resident adult brown trout (resident; $N = 12$) versus sites supporting both resident and anadromous adults (anadromous; $N = 24$). Biomass is separated by seasons (black bars = spring; gray bars = summer; unshaded bars = fall).

DISCUSSION

Life history plasticity had a considerable role in the successful establishment and spread of brown trout in the Rio Grande. The population consisted solely of resident brown trout for at least two decades before fish began to migrate to the marine environment; this suggests a change in the food base within the river. In New Zealand rivers, introduced brown trout feed directly on native galaxiids and deplete the invertebrate communities (Waters 1988; Townsend 2003). Although the native food web of the Rio Grande cannot be documented, native food resources were sufficient to foster rapid establishment and expansion of resident brown trout. The paucity of native fishes remaining in the system combined with local accounts of much higher galaxiid densities in the past suggest that brown trout substantially reduced the populations of native fishes, probably by direct predation as well as by competition for invertebrate

food resources. It is likely that anadromy in these brown trout began as instream food resources were depleted.

Further, the significantly lower invertebrate biomass at anadromous sites versus resident sites, the higher incidence of terrestrial invertebrates in the diets of juvenile fish at anadromous sites, and the more frequent occurrence of empty stomachs in juveniles at anadromous sites support the concept of food limitation as a determinant of the juveniles' decision to migrate downstream. Also, specific conductance and soluble reactive phosphorus levels were higher at resident sites, indicating that fertility is elevated at these sites in comparison with

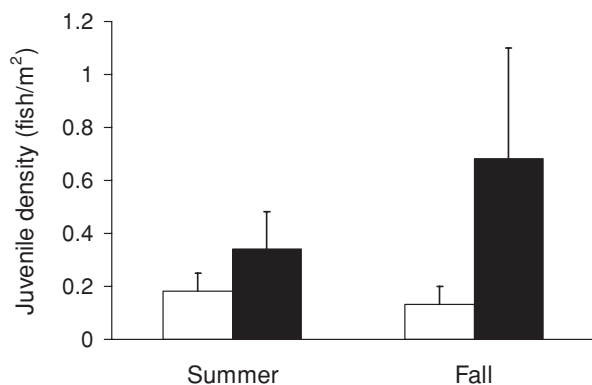


FIGURE 4. Mean (+SE) density of juvenile brown trout at electrofished Rio Grande sites during summer (February) and fall (April), presented for sites that supported both resident and anadromous adult brown trout (Grande, MacLennan, and Menendez rivers; unshaded bars; summer $N = 22$, fall $N = 23$) and sites that supported only resident adults (Candelaria and Herminita rivers; black bars; summer $N = 12$, fall $N = 12$).

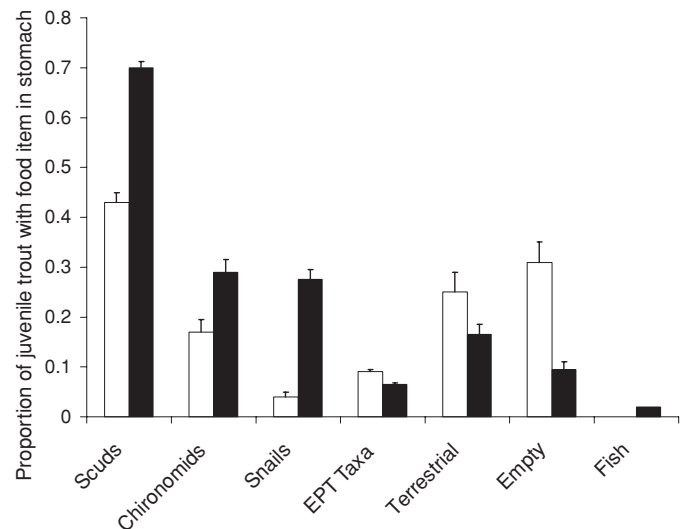


FIGURE 5. Mean (+SE) proportion of juvenile brown trout with various diet taxa represented in their stomach contents (scuds = *Hyaella araucana*; snails = *Chilina patagonica*; EPT = Ephemeroptera-Trichoptera-Plecoptera) compared between Rio Grande sites supporting both resident and anadromous adults (unshaded bars; $N = 40$) and sites supporting only resident adults (black bars; $N = 82$).

TABLE 1. Mean, SD, and range of habitat variables examined for Rio Grande (Argentina) sites containing only resident adult brown trout (resident sites) and sites containing both anadromous and resident adult brown trout (anadromous sites); asterisks indicate variables exhibiting significant differences between site types ($P < 0.05$).

Variable	Resident sites				Anadromous sites			
	N	Mean	SD	Range	N	Mean	SD	Range
Average water temperature (°C)	12	10.9	1.5	8.7–12.1	21	10.8	1.3	8.7–12.1
Growing degree-days	12	379	52	303–424	21	363	93	306–424
Discharge (m ³ /s)	12	1.33	0.79	0.03–2.53	20	9.61	9.43	0.02–33.46
Average wetted width (m ³ /s)*	12	8.1	2.3	3.9–11.0	23	24.0	14.1	4.8–54.6
Average velocity (m/s)	12	0.53	0.24	0.01–0.81	20	0.61	0.42	0.01–1.50
Average depth (m)	12	0.3	0.1	0.2–0.5	24	0.4	0.1	0.1–0.6
Average substrate size (mm)	6	37	35	10–104	12	39	13	18–58
Specific conductance (µS/cm)*	11	163	38	117–233	23	112	38	76–233
pH (units)	12	8.2	0.4	7.4–8.8	22	7.8	0.4	7.1–8.4
Total persulfate nitrogen (µg/L)	12	507.91	165.35	318.26–824.06	23	383.57	165.06	205.01–842.33
Nitrate–nitrite (µg/L)	12	5.78	5.36	0.92–15.80	23	5.36	5.76	0.70–20.59
Ammonium (µg/L)	12	56.58	46.22	28.84–194.13	23	45.92	16.18	24.90–91.69
Total phosphorus (µg/L)	12	14.05	3.16	9.24–19.16	23	14.40	24.97	4.58–118.2
Soluble reactive phosphorus (µg/L)*	12	3.97	1.74	1.36–7.26	23	1.60	0.86	0.30–4.01
Chlorophyll <i>a</i> (µg/cm ²)	12	0.46	0.60	0.03–1.98	24	0.37	0.44	0.00–1.59
Ash-free dry mass (µg/cm ²)	12	3.77	6.40	0.00–20.68	23	4.41	6.66	0.38–21.69
Scud (<i>Hyalella araucana</i>) density (number/m ²)*	12	12.01	12.34	0.66–37.62	24	0.98	1.51	0–7.00
Scud biomass (mg/m ²)*	12	2.51	2.08	0.43–6.94	24	0.36	0.39	0.00–1.52
Other invertebrate density (number/m ²)	12	7.71	6.26	1.29–19.32	24	14.15	10.85	2–40
Other invertebrate biomass (mg/m ²)*	12	3.99	3.40	0.59–10.84	24	1.15	0.85	0.17–3.30

anadromous sites (Wetzel 2001). Huryn (1996) showed that introduced brown trout may consume more than 80% of benthic prey production in New Zealand rivers. Thus, it appears likely that the resident brown trout population in the Rio Grande expanded until the food supply began to limit growth, thus forcing fish to migrate to the ocean.

In other partially migratory salmonid populations for which the food availability hypothesis has been tested, fish that grow more during their first years of life in freshwater have a strong tendency to remain in streams as residents, while those that grow less tend to migrate (Thériault and Dodson 2003; Olsson and Greenberg 2004). In the Rio Grande, we observed significantly higher juvenile brown trout densities at resident sites (Figure 4), but the back-calculated growth rates during the first year in freshwater did not differ as expected among sites (Figure 6).

Thus, the choice to migrate to the ocean or remain as a resident in freshwater did not appear to be a function of density-dependent growth, which is in contrast to studies of brown trout elsewhere (Elliott 1994). Nonetheless, juveniles emigrated from the main-stem river into resident streams at higher rates, suggesting a relationship between the tendency to stay in the river as residents and a higher food supply. Resident fish were mostly males, which probably descend tributaries and spawn with returning sea trout, as has been observed elsewhere (Klemetsen et al. 2003). Studies examining brown trout fidelity to natal streams, however, are warranted in the Rio Grande to verify that adult residents remain in their rearing streams, as was assumed for the course of this study. Whether the Rio Grande brown trout population has reached a relatively stable state or will continue to shift toward higher levels of anadromy remains uncertain.

TABLE 2. Summary of Floy-tagged brown trout collected from the main-stem Rio Grande during January–April 2006–2007, including the Schnabel (1938) population estimate and associated 95% confidence interval (CI).

Year	N tagged	Recaptured (%)	Anadromous (%)	Female : male ratio (anadromous)	Female : male ratio (resident)	Anadromous population estimate	95% CI
2006	1,043	20 (2.5)	98.7	1.0:0.3	1:3	37,803	24,808–79,389
2007	2,933	66 (1.9)	98.1	1.0:0.3	1.0:1.5	55,058	44,784–71,448

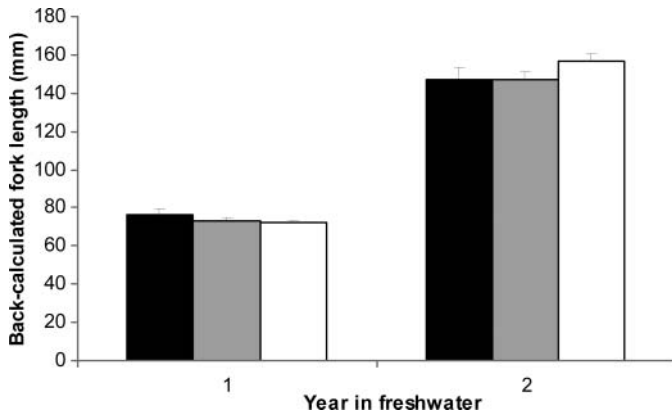


FIGURE 6. Back-calculated fork length (+SE) in the first and second years for adult resident brown trout inhabiting sites that supported only residents (black bars; $N = 36$); adult residents inhabiting sites that supported both anadromous and resident adults (gray bars; $N = 52$); and anadromous adults (unshaded bars; $N = 117$).

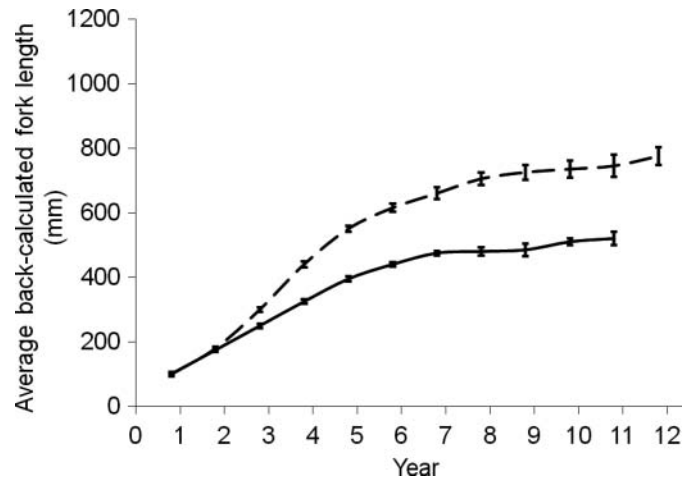


FIGURE 7. Mean (\pm SE) back-calculated growth in fork length for anadromous brown trout (dashed line; $N = 169$) and resident brown trout (solid line; $N = 63$) in the Rio Grande basin.

Regardless of the mechanisms leading to their anadromy, the current Rio Grande sea trout population is robust as about 38,000–55,000 sea trout spawners returned annually during the study period (Table 2). Few published estimates of sea trout population size exist. In Ireland, the average annual rod catches reportedly were around 320 sea trout/river, suggesting very small runs (Gargan et al. 2006; Table 4). Anglers participating in the present study caught an average of well over 5,500 sea trout annually. The run size estimated for England and Wales was 1,181 sea trout/river (Harris 2006; Table 4), and in France the runs do not exceed 3,000 (Euzenat et al. 2006), an order of magnitude lower than the run size in the Rio Grande.

Rio Grande juvenile sea trout exhibited freshwater growth rates that were comparable with those observed in the southern portion of the species' European range (Le Cren 1984;

L'Abée-Lund et al. 1989; Mann et al. 1989; Table 4); however, growth rate at sea was more than twice as high as that seen in English rivers (Nall 1930; Fahy 1978; Mann et al. 1989; Davidson et al. 2006; Harris 2006; Table 4) and was high relative to marine growth rates reported for Norwegian sea trout (Jonsson and Jonsson 2006; Table 4). Back-calculated growth rates (17.8–21.7 cm) for Rio Grande sea trout during the first year at sea are among the highest reported (Table 4), similar to values for sea trout in The Netherlands, France (de Leeuw et al. 2007), and Germany (Roche 1992). The length of Rio Grande fish similarly exceeded that of documented European fish. The largest male and female captured during the course of this study were 120 and 99 cm FL, respectively. The highest values for body length in the literature range from 85 to 90 cm (Le Cren 1984; L'Abée-Lund et al. 1989; de Leeuw et al.

TABLE 3. Life history variables (mean \pm 95% confidence interval) for resident and anadromous brown trout in the main-stem Rio Grande and tributaries. Average number of spawning marks only includes fish that exhibited at least one mark.

Population	N	Female : male ratio	Fork length (cm)	Age (years)	Smolt age (years)	Sea age (years)	Number of spawning marks
Candelaria River							
Resident	19	0.2	23.6 \pm 2.3	4.4 \pm 0.4			
Herminita River							
Resident	16	0.3	39.2 \pm 5.7	6.2 \pm 1.0			
MacLennan River							
Resident	16	0.2	29.8 \pm 5.7	5.3 \pm 2.1			
Anadromous	4	3.0	63.8 \pm 17.0	7.4 \pm 0.6	2.9 \pm 0.7	4.5 \pm 1.8	2.8 \pm 1.2
Menendez River							
Resident	5	0.5	40.6 \pm 15.5	5.7 \pm 1.4			
Anadromous	9	2.0	57.1 \pm 8.9	6.1 \pm 1.1	2.8 \pm 0.3	3.5 \pm 0.9	1.4 \pm 0.3
Rio Grande							
Resident	31	0.7	42.2 \pm 2.7	6.8 \pm 0.4			2.7 \pm 0.4
Anadromous	104	3.6	59.4 \pm 3.2	7.0 \pm 0.9	2.6 \pm 0.1	4.6 \pm 0.5	2.6 \pm 0.3

TABLE 4. Comparison of various life history traits for sea trout (anadromous brown trout) in the Rio Grande with values reported from their native range (n/a = not available).

Location	Source(s)	Parr density (fish/m ²)	Freshwater growth in year 2 (cm)	Mean smolt age (years)	Saltwater growth, first year at sea (cm)	Repeat spawners (%)	Maximum age (years)	Maximum fork length reported (cm)	Average annual declared catch
Rio Grande ^a	Present study	0.02–1.8	8.5	2.47	17.8–21.7	62.9	12	116.0	>5,455 ^b
Kerguelen Islands ^a	Davaine and Beall 1992	n/a	4–10	n/a	5–20	n/a	n/a	n/a	n/a
England	Nall 1930; Fahy 1978; Mann et al. 1989; Davidson et al. 2006; Harris 2006	0.10–0.80	3.7–6.8	2.0–3.4	4.4–12.5	12.5–39.6	8	62.4 ^c	1,181 (416–5,692)
Germany	Roche 1992	n/a	n/a	n/a	26	n/a	n/a	n/a	n/a
Ireland	Nall 1930; Fahy 1978; Gargan et al. 2006	n/a	n/a	2.1–2.8	n/a	n/a	8	n/a	320 (37–1,175)
Norway	Jonsson 1985; L'Abée-Lund et al. 1989; Berg and Jonsson 1990; L'Abée-Lund 1991	0.11	3.6–7.5	1.2–5.6	7.9–20.4	5–69	11	69	n/a
Scotland	Nall 1930; Egglisshaw and Shackley 1977; Butler and Walker 2006	n/a	n/a	2.1–3.4	n/a	16.5–65.1 ^d	11 (up to 1980); 5 (1997–2001)	n/a	n/a
Spain	Caballero et al. 2006	n/a	n/a	2.2–2.4	n/a	n/a	n/a	71.0	n/a
Sweden	Rubin et al. 2005	n/a	n/a	n/a	n/a	n/a	8	89.0	n/a
The Netherlands	de Leeuw et al. 2007	n/a	n/a	n/a	21	n/a	n/a	n/a	n/a
Turkey	Okumuş et al. 2006	n/a	6.5–19.5	n/a	n/a	n/a	n/a	n/a	n/a
Wales	Nall 1930; Fahy 1978	n/a	n/a	2.1–2.5	n/a	n/a	8	n/a	n/a

^aThe Rio Grande and Kerguelen Islands are Southern Hemisphere locations where sea trout have been introduced.

^bThis value accounts for only 80% of the rods on the river and thus is considered an underestimate.

^cThis value is total length rather than fork length.

^dThe highest repeat spawning rate in Scotland occurred before 1980.

2007), similar to values calculated for the asymptotic length of sea trout based on historical data describing intact Scottish populations (Butler and Walker 2006). Sea trout of the sizes attained in the Rio Grande have historically only been reported for Baltic populations (R. Behnke, personal communication).

Additionally, iteroparity (repeat spawning rates) and longevity of Rio Grande sea trout exceed those of many European populations (Table 4). Southern European sea trout populations tend to live for fewer (3–5) years but spawn more often, exhibiting a repeat spawning rate of up to 60%; northern European populations tend to live longer (up to 8 years) but spawn less often and have a repeat spawning rate of about 30% (Jonsson and L'Abée-Lund 1993). In contrast, Rio Grande sea trout exhibit both a high degree of iteroparity (63%) and remarkable longevity of up to 12 years or more.

Although the genetic legacy of brown trout is undoubtedly important and remains to be more closely examined along with physiological correlates (*sensu* Roff 1992), environmental circumstances clearly were critical to the success of brown trout in the Rio Grande. The estuary at the mouth of the Rio Grande is large, shallow, and apparently very productive; this estuary is contiguous with the notably productive South Patagonian Shelf Ecosystem (Rivas et al. 2006; Ciancio et al. 2008), where sea trout feed largely on abundant Patagonian sprat *Sprattus fuegensis* (Ciancio et al. 2008). As opposed to other anadromous salmonids, sea trout do not generally travel far from coastal areas (Klemetsen et al. 2003) and are not caught in commercial fisheries offshore of Tierra del Fuego (A. Matias, personal communication). The absence of significant aquaculture activities, commercial fishing, and other human-induced disturbances (e.g., dams or large urban centers) in the catchment also probably contributes to the robust nature of the fishery. Finally, a strict no-kill policy imposed on the vast majority of the river since the mid-1980s appears to have increased the catch rates, average size, and longevity of these fish (Solomon and Czerwinski 2006).

This study is the first analysis on the South American continent that documents in-river distribution of sea trout and resident brown trout as well as what little remains of the distribution of native galaxiid fishes. The demise of the native fish community is coincident with brown trout expansion; given the demonstrated strong association of resident fish in the more productive tributaries, it seems likely that a severe depletion of fish and invertebrate forage compelled a shift toward a migratory life history in brown trout. Juvenile brown trout density and invertebrate density support the food availability hypothesis as seen in other studies of brown trout populations that are partially migratory. Indeed, the individual decision to undergo seaward migration appears to be associated with fewer available instream food resources. Regardless of the mechanisms compelling migration, the Rio Grande supports one of the strongest anadromous populations of brown trout in the world due to favorable habitat throughout their life cycle and low mortality resulting from management practices.

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