

University of Montana

## ScholarWorks at University of Montana

---

Graduate Student Theses, Dissertations, &  
Professional Papers

Graduate School

---

2008

### Lessons to learn from all out invasion: life history of brown trout (*Salmo trutta*) in a Patagonian River

Sarah Louise O'Neal  
*The University of Montana*

Follow this and additional works at: <https://scholarworks.umt.edu/etd>

**Let us know how access to this document benefits you.**

---

#### Recommended Citation

O'Neal, Sarah Louise, "Lessons to learn from all out invasion: life history of brown trout (*Salmo trutta*) in a Patagonian River" (2008). *Graduate Student Theses, Dissertations, & Professional Papers*. 1303.  
<https://scholarworks.umt.edu/etd/1303>

This Thesis is brought to you for free and open access by the Graduate School at ScholarWorks at University of Montana. It has been accepted for inclusion in Graduate Student Theses, Dissertations, & Professional Papers by an authorized administrator of ScholarWorks at University of Montana. For more information, please contact [scholarworks@mso.umt.edu](mailto:scholarworks@mso.umt.edu).

LESSONS TO LEARN FROM ALL OUT INVASION:  
LIFE HISTORY OF BROWN TROUT (*SALMO TRUTTA*)

IN A PATAGONIAN RIVER

By

SARAH LOUISE O'NEAL

B.S., University of Washington, Seattle, WA, 1999

Thesis

presented in partial fulfillment of the requirements

for the degree of

Master of Science  
in Organismal Biology and Ecology

The University of Montana  
Polson, MT

May 2008

Approved by:

---

Dr. Jack A. Stanford, Chair  
Flathead Lake Biological Station

---

Dr. David A. Strobel, Dean  
Graduate School

LESSONS TO LEARN FROM ALL OUT INVASION:  
LIFE HISTORY OF BROWN TROUT (*SALMO TRUTTA*)  
IN A PATAGONIAN RIVER

By

Sarah Louise O'Neal

B.S., University of Washington, Seattle, WA, 1999

M.S. Thesis

presented in partial fulfillment of the requirements  
for the degree of

Master of Science

The University of Montana  
Polson, MT

Spring 2008

Approved by:

Dr. David A. Strobel, Dean  
Graduate School

Dr. Jack A. Stanford, Chair  
Flathead Lake Biological Station

Dr. F. Richard Hauer  
Flathead Lake Biological Station

Dr. Lisa Eby  
Department of Conservation and Ecosystem Sciences

**Lessons to learn from all out invasion: life history of brown trout (*Salmo trutta*) in a Patagonian River**

Chairperson: Jack A. Stanford

**ABSTRACT**

Brown trout (*Salmo trutta*) are widely introduced throughout Patagonia, though their distribution and impact in the region remain poorly documented. Life history flexibility, and particularly partial migration play a major role in the ability of this species to adapt to Patagonian rivers. Consequently, this study explored habitat, distribution and life history of a partially migratory population of brown trout in the Rio Grande in Tierra del Fuego, Argentina. It described what is known of the history of the invasion. Physical, chemical, and biological habitat data were collected for comparison between sites supporting resident fish with those supporting anadromous fish. Additionally, brown trout and native fish distribution and abundance was described using a combination of local knowledge, angling, electrofishing, and netting.

Results indicate that brown trout developed an anadromous life history form several decades subsequent to their initial introduction, possibly after near extirpation of native galaxiid fish and reduction of invertebrate biomass. Sites supporting resident fish were narrower, and exhibited higher levels of specific conductance and soluble reactive phosphorous than those supporting both resident and anadromous fish. Resident sites additionally exhibited vastly higher invertebrate biomass. Significantly larger scale radii, suggesting faster juvenile growth was documented for fish in sites supporting resident fish versus those supporting anadromous fish, suggesting that food availability indeed may influence the individual 'decision' to migrate. The adult population proved to be exceptionally abundant and exhibited various life history traits which suggest that the Rio Grande supports one of the strongest remaining populations of anadromous brown trout worldwide.

Key words: sea trout, *Salmo trutta*, invasion, partial migration, Patagonia

## ACKNOWLEDGEMENTS

My acknowledgements could easily take nearly as much space as the rest of this document, as this project was about as far from a one-woman-show as a project can get. I first must thank my advisor, Jack Stanford, for sending me down to the land of fire, and for providing backup when things went south. For all practical purposes, I was co-advised by Ric Hauer, who bestowed invaluable encouragement and insight. My third committee member, Lisa Eby, has infallibly offered exceptional advice and genuine consideration, for which I cannot thank her enough. Doctors Fred Allendorf, Ray Callaway, and Winsor Lowe also helped immensely during the development of the project.

My labmates Michelle Anderson, Claudio Meier, Brian Reid, Aaron Hill, Kelly Crispen, Tyler Tappenbeck, Michael Morris, Lorrie Eberlee, Jake Chaffin, Nick Gayeski and Audrey Thompson have provided support, feedback, places to crash, and above all humor and friendship throughout this process.

All the staff at FLBS have taken incredible care of me, no matter how far away I was. In particular, Sue Gillespie, Judy Maseman, Joann Wallenburn, Diane Whited, Jeremy Nigon, Tom Bansak, Don Schenk, Bob Newell, Scott Relyea, Kristin Olson, and Marie Kohler, and more recently John Merritt and Tom Chandler helped with both short and long distance logistics.

Several other folks in Montana have provided valuable assistance, guidance, and equipment including David Schmetterling of Montana Fish Wildlife and Parks, Barry Hansen of the Confederated Salish and Kootenai Tribes, and Wade Fredenburg of the US Fish and Wildlife Service. Dr. John Graham of the University of Montana is my statistical hero. And I have been sheepishly honored to glean just a bit of the limitless wisdom of Dr. Robert Behnke from Colorado State University. Additionally, Dr. Sven Saltveit and his colleagues at the LFI laboratory at the University of Oslo, Norway assisted with scale reading and verification.

In Patagonia, I was graciously adopted by Miguel Pascual's GESA laboratory, where I found amazing colleagues and even better friends in Miguel, Ana Laura Liberoff (who also happens to be the best field assistant in at least two continents), Martín García Asorey, Julio Lanceoletti, Carla Riva Rossi, and Javier Ciancio. Laura Miserendino and her colleagues also provided generous assistance with invertebrate identification in one of the most beautiful places I've ever laid eyes on.

In Tierra del Fuego, I owe thanks to nearly every person I met. Gustavo Sanchez, whose friendship I prefer over his chauffer services, provided a great deal of assistance and an endless supply of stories. The fishing guides adorably endured my constant nagging, and even managed to collect a great dataset. Particularly Matt Breuer, German Pacho, Alejandro Martello, Paul Jones, Nick Thomson, Federico Zimmerman, Andrés Martín, Steve Estela, Marcelo Whidman, and Jorge Brigina provided information and field assistance without which the project would have flailed. Santiago Lesta and several other folks from Recursos Naturales helped me out in the field when I was in desperate need, and kindly helped with proper permits and permissions along the way. Pablo and Diego fed me what is most likely to be some of the best food I'll ever eat. Between my house, my finances, and rescuing Gustavo and me from the muddy floodplain time and

again, Margarita, Gloria, Pata, Pilar, The Other Gustavo, Omar, and Valentina looked after me like nobody's business.

And of course, my dear family and friends. My mom took over the practical aspects of my life, caring for the things I neglected when I went south (and yes, even when I was still up north). And miraculously never complained once. She also kept me warm in the unforgiving Fuegino climate with her magical knitting fingers. My father encouraged me forever and ever, and imparted critical negotiating skills like only he can. My sister has been my best editor and favorite person to talk to on a cell phone. Dylan has listened to me bitch and even helped me stop bitching more than anyone else on the planet. And Special Agent Hien Nguyen, Alison, Chad and Brian, Karen, Lindsey and Wayne, and so many other friends have put up with having a vagabond as a friend. I thank you all so very kindly.

This work was funded primarily by Estancia Maria Behety and Nervous Waters of Argentina. Alejandro Menendez provided quietly crucial support and added infinite color to a place that can otherwise be a bit drab. The Fly Shop and Frontiers International Travel also provided support, especially Ryan Peterson who figured out how to get everything from cryovials to coffee from one side of the world to another.

## TABLE OF CONTENTS

ABSTRACT.....	iii
ACKNOWLEDGEMENTS.....	iv
TABLE OF CONTENTS.....	vi
LIST OF FIGURES .....	vii
LIST OF TABLES.....	viii
INTRODUCTION .....	9
STUDY AREA .....	12
HISTORY OF BROWN TROUT IN RIO GRANDE.....	13
METHODS.....	14
FRESHWATER HABITAT CHARACTERIZATION.....	14
JUVENILE DISTRIBUTION, GROWTH, AND DIET .....	17
DISTRIBUTION AND ABUNDANCE OF ADULT TROUT.....	17
AGE AND GROWTH OF ADULT TROUT.....	18
STATISTICAL ANALYSES .....	20
RESULTS.....	21
FRESHWATER HABITAT CHARACTERIZATION.....	21
DISTRIBUTION AND ABUNDANCE OF ADULT TROUT.....	26
AGE AND GROWTH OF ADULT TROUT.....	27
DISCUSSION.....	29
REFERENCES .....	35
APPENDIX A.....	42

## LIST OF FIGURES

- Figure 1.** The Rio Grande watershed in southern Patagonia. Sites sampled for juvenile, resident, and habitat metrics are indicated by dark circles with an ‘A’ in locations where anadromous and resident fish are documented, and an ‘R’ in locations where only resident fish are documented (no anadromous fish were present). .... 12
- Figure 2.** Scale samples from anadromous (left) and resident (right) brown trout from the Rio Grande (images are not to scale). Circuli spacing is notably wider in the marine environment, and resorption due to spawning is evident in the third and fourth marine annuli of the anadromous fish. .... 19
- Figure 3.** Boxplots of habitat variables exhibiting significant differences between sites supporting solely resident fish (Resident only, gray) vs. sites supporting both anadromous and resident fish (Anadromy present, white). Boxes indicate first and third quartiles, while bars indicate maximum and minimum values. Outliers are shown separately. .... 22
- Figure 4.** Scud (a) and other invertebrate (b) biomass ( $\text{mg}/\text{m}^2$ ) in sites supporting resident fish only vs. sites supporting both resident and anadromous fish. .... 23
- Figure 5.** Density of juvenile brown trout in electrofished sites during summer (February) and fall (April) + 1 SE. Anadromous indicates sites which support both resident and anadromous adult fish (Grande, MacLennan and Menndez Rivers), while resident indicates sites which support resident fish only (Candelaria and Herminita Rivers). .... 24
- Figure 6.** Scale radius for the first and second annuli of adult residents residing in resident streams (black bars), adult residents residing in anadromous streams (gray bars), and anadromous adults (white bars) + 1 SE. Results indicate significantly higher growth of juvenile residents residing in resident streams than anadromous fish during the first year ( $p < 0.05$ ). .... 25
- Figure 7.** Proportion of juvenile trout with various diet items found in stomach contents between sites supporting both resident and anadromous vs. sites supporting only resident adult fish +1 SE. Most common diet items include scuds (*Hyaella araucana* G.); various chironimid (*Chironimidae*) taxa; snails (*Chilina patagonica* S.), Ephemoptera-Trichoptera-Plecoptera (EPT) taxa (*Andesiops sp.*, *cailloma sp.*, *Linoperla jaffueli* N., *Limnoperla sp.*, *Meridialaris chiloeensis* D., *Neatopsyche sp.*, *Rheochorema sp.*, and *Verger sp.*); terrestrial invertebrates, and brown trout (*Salmo trutta* L.). \*\* indicates a highly significant ( $p > 0.005$ ) difference, and \* indicates a significant difference at the  $p > 0.05$  level. .... 26
- Figure 8.** Mean back-calculated growth rates of anadromous and resident brown trout in the Rio Grande basin. Error bars represent  $\pm 1$  SE. .... 28



## LIST OF TABLES

<b>Table 1.</b> Summary of Floy tagged fish collected during January through April of 2006 and 2007 from the mainstem Rio Grande, including associated Schnable (1938) population estimate and associated 95% confidence intervals. ....	27
<b>Table 2.</b> Life history variables of resident and migrant brown trout in tributaries to as well as the mainstem Rio Grande including 95% confidence limits. Average number of spawning marks includes only fish exhibiting one or more mark.....	28
<b>Table 3.</b> Back-calculated growth (mean fork length, cm) and SE for anadromous and resident brown trout from scale measurements. ....	29
<b>Table 4.</b> Comparison of various life history traits of sea trout in their native range with those from the Rio Grande.....	31

## INTRODUCTION

Brown trout (*Salmo trutta* L.) are the second most widely distributed non-native fish introduced to Patagonia (Pascual et al. 2002), where documentation on the impacts that salmonids have on native communities is scarce and largely inconclusive. Because current distribution of native fish remains undocumented for most Patagonian rivers (Pascual et al. 2002), a call for research indicates that the most useful studies will examine native and nonnative fish distributional patterns which can contribute to an understanding of the nature and extent of invasions in the region (Habit et al. 2004). Macchi et al. state that while it is impossible to reconstruct the pre-salmonid fauna, it is possible to assess the probable impact of salmonids on native ecosystems. And Habit et al. (2004) add that because of the extent, complexity, and urgency of the situation of introduced salmonids in Patagonia, the most useful studies will contribute to theory on invasions and their impacts over several levels, from individual organisms to ecosystem processes such as trophic dynamics.

Biological invasions are a leading cause of species loss worldwide (Simberloff 2001), and there is a growing need to understand the invasion process because of the increasing number of aquatic ecosystems threatened by invasive species (Moyle and Light 1996). Invasions of non-native fishes can have far-reaching effects which may impact all levels of the foodweb (Townsend 1996). Indeed in New Zealand, where trout introductions have been extensively studied, researchers have documented significant declines in native galaxiid fish communities, as well as invertebrate communities subsequent to establishment of trout populations (Huryn 1996, Flecker and Townsend 1994, McDowall 1996, Townsend 1996). Life history plasticity has often been noted as a key characteristic of successful invaders (Moyle and Light 1996; Townsend 1996; Alcazar, Vila-Gispert, Garcia-Berthou 1996). However, few studies specifically address its role in the invasion process (but see Bohn et al. 2004; Bonsall and Mangel, 2004; and Vila-Gispert, Alcazar, and Garcia-Berthou 2005).

The occurrence of partial migration is one expression of life history plasticity which remains poorly understood even outside the context of invasion. Partial migration, the phenomenon of populations consisting of both migratory and resident individuals

(Jonsson and Jonsson 1993), is documented in animal taxa ranging from insects to higher vertebrates (Baker 1978), and is common among fish within freshwater and marine habitats (Jonsson and Jonsson 1993), as well as across the freshwater-saltwater boundary (McDowall 1997). Life history theory indicates that in order for individuals to migrate, the fitness benefits of migration (such as increased reproductive output) must outweigh the fitness costs (such as increased mortality) (Gross, 1987).

The role of environmental factors versus genetics on the ‘decision’ to migrate is still unknown. While genetics likely play an underlying role in the development of partially migratory populations, previous studies of fish species fail to differentiate genetically between resident and migratory individuals within a population, and in fact indicate that interbreeding often occurs between the migratory and resident individuals (Hindar et al. 1991, Jonsson and Jonsson 1993, Klemetsen et al. 2003). It thus follows that environmental factors contribute considerably to the decision by individuals to migrate. Environmental factors commonly associated with migration include avoidance of adverse ambient conditions such as extreme temperatures, as well as pursuit of preferable reproductive and feeding habitat (Nikolskii 1963).

Gross, Coleman, and McDowall (1988) argue that diadromous migrations evolved according to aquatic productivity. Their argument, known as the ‘food availability hypothesis,’ is supported by global patterns of diadromy whereby anadromous fish (which feed at sea but spawn in freshwater) occur most frequently at higher latitudes where marine productivity exceeds freshwater productivity and catadromous fish (which feed in freshwater but spawn at sea) 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 (Olsson et al. 2006 and others) and vice-versa, inducing residency by increasing food resources. Body size (Bohlin, Dellefors, and Farneo 1996) and growth rate (Jonsson 1985), are mechanisms that have additionally been postulated as drivers for migration, though studies regarding those mechanisms are often contradictory.

An assessment of the food availability hypothesis as it relates to an introduced partially migratory population may contribute not only to life history theory in general,

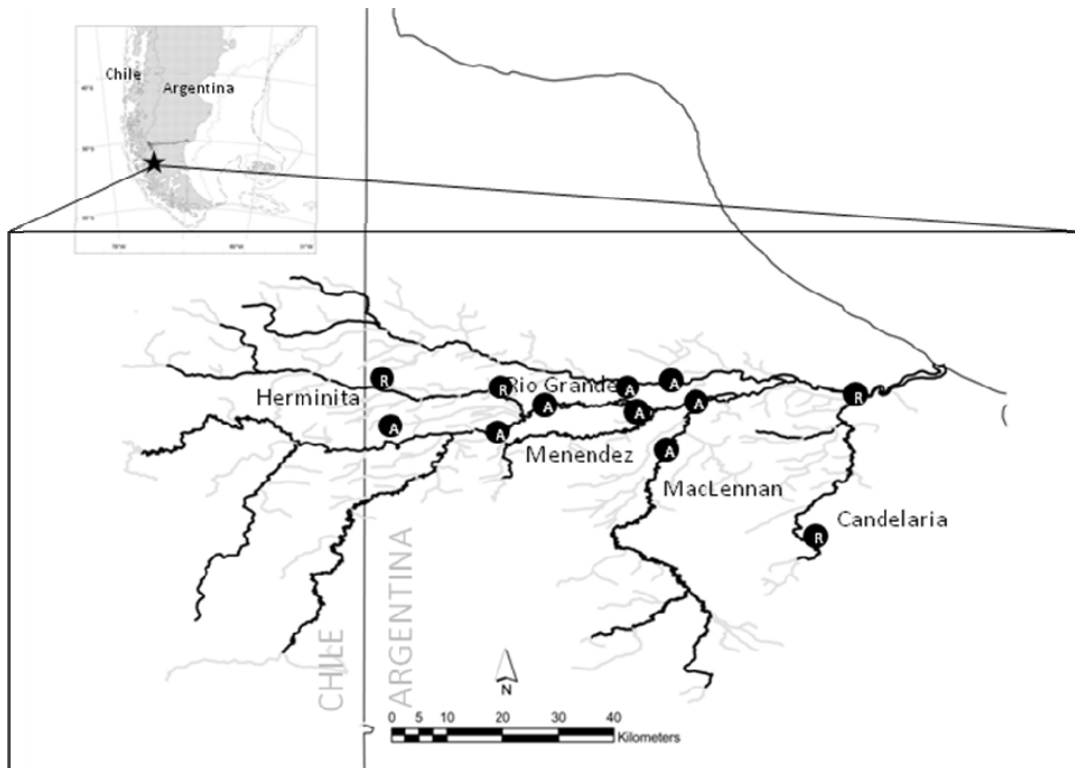
but also allow for inferences regarding the course of invasion. Indeed, if the food availability hypothesis appears to apply in the introduced range of a species, the evolution of diadromy during the course of an invasion implies a change in the food base, compelling some fish to migrate to an adjacent habitat exhibiting higher productivity. This implies potentially far-reaching impacts of the invader on the native foodweb. Certainly, the impact of introduced fishes on every trophic level of native ecosystems has been widely documented (Knapp and Matthews 2000; Schindler, Knapp, and Leavitt 2001; Townsend 2003). However, this effect has rarely been explored with respect to life history flexibility, and has never been evaluated in rivers on the south American continent.

Brown trout have been introduced into at least 24 countries outside their native European range (Elliott 1994). They proliferate throughout their introduced range, often forming sea-run migratory (sea trout) populations in the southern hemisphere (Frost and Brown 1967). Ironically, sea trout stocks in their native European range are in significant decline, largely due to overfishing, aquaculture activities, and river regulation (Harris and Milner 2006). The declines have instigated a proliferation of literature regarding habitat, life history characteristics, and population dynamics of native sea trout. Consequently, a more thorough understanding of the role of life history and environment in a successfully invading population may shed light on this growing conservation conundrum.

The overarching purpose of this study was to determine the distribution, abundance, and life history variation of an introduced brown trout population in the Rio Grande of Tierra del Fuego. In doing so, impacts of the invader were inferred and the following hypotheses were tested: the resident life history type dominates only where 1) sufficient instream food resources exist, and 2) juvenile growth rates are higher. Additionally, the adult sea run population was described in order to shed light on life history differences between declining native European populations and a successfully established introduced population.

## STUDY AREA

The study was conducted from December 2005 to March 2008 on the Argentine side of the Rio Grande (57° 47' S; 67° 41' W), the largest watershed on Isla Grande of Tierra del Fuego (Fig. 1) with average annual discharge of about 40 m<sup>3</sup>/s (Iturraspe, Gaviño, and Urciuolo 1998). The Rio Grande is a middle order, meandering river (Lorang and Hauer, 2006), originating from a headwater lake, as well as a spring fed Andean stream on the Chilean side of the border. It flows approximately 120 km to the South Atlantic. Major tributaries flowing into the Rio Grande include the Radman (or Rasmussen) and Menendez rivers. Smaller tributaries include the MacLennan (or Ona), Herminita (or Herminia), Moneta, and Candelaria Rivers (Fig. 1). The hydrograph exhibits a pluvial flow regime, dominated largely by rainfall. The floodplain within the study reach is low elevation (ranging from approximately 75m to sea level); low gradient (approximately 1%); and small shrub, grass, and forb dominated.



**Figure 1.** The Rio Grande watershed in southern Patagonia. Sites sampled for juvenile, resident, and habitat metrics are indicated by dark circles with an 'A' in locations where anadromous and resident fish are documented, and an 'R' in locations where only resident fish are documented (no anadromous fish were present).

Due to the relative lack of human disturbance in the floodplain with respect to flow regulation, point source pollution, road development, or flood protection structures, the orthofluvial and parafluvial catena (*sensu* Stanford, Lorang and Hauer 2005), and presumably natural hyporheic flows are undisturbed. Oxbows and abandoned channels occur throughout the floodplain, but maintain hyporheic connectivity to the river, thereby often forming orthofluvial springbrooks. However, extensive grazing by sheep and cattle occurs throughout the island. The river substratum varies in size from fine organics to bedrock, but is dominated by large gravel to small cobble.

Historically, the river contained native perch (*Percichthys sp.*), and galaxiid species including small puyen (*Galaxias maculatus* J.), large puyen (*Galaxias platei* S.), and peladilla (*Aplochiton sp.*) (McDowall 1971). As this study shows, the vast majority of native fish have been eliminated from the river. Resident rainbow trout are still found at low densities. Brown trout now clearly dominate the system. Migrating sea-run brown trout dominate the mainstem Rio Grande as well as the tributaries, the Menendez and MacLennan Rivers, though resident fish occur in those rivers as well. Sea-run fish do not reside in or use either the Herminita or the Candelaria Rivers, however, which are both dominated by resident brown trout.

#### *HISTORY OF BROWN TROUT IN RIO GRANDE*

Precise records describing the earliest introductions of brown trout to Tierra del Fuego as well as mainland Argentina are unavailable (C. Riva Rossi, personal communication). The first documented attempt at introduction of the species into Argentina occurred in 1906 when 6000 eggs were reportedly shipped, but died in transport, probably from the United Kingdom to the Santa Cruz Hatchery in mainland Patagonia (Marini and Mastrarrigo 1963). In 1927, brown trout stocking took place on the Chilean side of Tierra del Fuego in several rivers which may have included headwaters to the Rio Grande drainage (Basulto del Campo 2003). Those fish are of unknown European origin, but possibly from Hamburg, Germany and were marked “Meersforelle,” meaning “sea trout,” though the source population was not identified (Joyner 1980; R. Behnke, personal communication). Recent genetic studies regarding

parental stocks of southern Chilean brown trout suggest that the brown trout in southern Chile are of Atlantic as opposed to Mediterranean drainages (Colihueque, Vergara, and Parraguez 2003; Faundez et al. 1997).

From 1935 to 1937, English settler John Goodall received and reared brown trout ova from Puerto Montt, Chile before releasing them into the Candelaria, Herminita, MacLennan, and Menendez Rivers (Bruno Videla 1978). Potential sources of those ova include Hamburg, Germany or other locations in Europe (Valiente et al. 2007). Rainbow trout (*Onchoryncus mykiss* W.) and Atlantic salmon (*Salmo salar* L.) were stocked during the same period throughout tributaries to the Rio Grande. Stocking of brown trout in the watershed resumed in 1976 (Bruno Videla 1978), and with the exception of 1979-1981, continued annually through at least 2000 (S. Lesta, personal communication).

The first recorded catch of resident brown trout in the river appears in Goodall's records in 1937. Records from 1948 document catches of all three introduced species (resident brown trout, resident rainbow trout, and Atlantic salmon) in the mainstem Rio Grande. Evidently brown trout remained in the stream as a resident population for decades, until local anglers report the emergence of 'large, silver,' apparently sea run fish in the mid- to late-1950s (A. Menendez Behety, personal communication). Local net and rod fishing, with a loosely enforced bag limit of five sea trout per fisherman per day, developed later in the century until catch-and-release angling tourism started in 1986 (Solomon and Czerwinski 2006). As angling tourism grew, public access to the river diminished. Currently, less than 10 stream kilometers are open to angling only by local anglers with an enforced bag limit of one fish per fisherman per day. There is additional access to the river for the general public one day per week. Access to the vast majority of the Argentine section of the river, however, is controlled by private landowners who lead primarily foreign anglers on a daily basis for strictly catch-and-release fishing during the summer and early fall.

## **METHODS**

### ***FRESHWATER HABITAT CHARACTERIZATION***

In order to characterize freshwater habitat, several habitat variables were collected throughout the watershed. Habitat variables were additionally used to evaluate factors

limiting juvenile growth and thus to test the food availability hypothesis. They included physical (temperature, average depth, width, and velocity), chemical (specific conductance, pH, total persulfate nitrogen, nitrate-nitrite, ammonia, total phosphorus, and soluble reactive phosphorus), and biological (chlorophyll *a*, ash-free dry mass, and invertebrate density and biomass) variables, and were measured three times during the season at twelve sites (Figure 1). Sites were selected to encompass as much of the Argentine portion of the basin as possible. Duplicate sites within tributaries were located as far as possible from one another in order to minimize spatial correlation, though accessibility was a major factor in site selection as well. Four sites were located in tributaries known by local anglers and landowners to support resident fish only (Candelaria and Herminita Rivers). Eight additional sites were located in tributaries (Menendez and MacLennan Rivers) and the mainstem Rio Grande known to support both low densities of resident fish as well as migrating and spawning anadromous fish (Figure 1). Measurements were taken within ten days of one another across the floodplain in late December (hereon referred to as spring), late February (hereon referred to as summer), and mid-April (hereon referred to as fall) of 2007.

Average particle size of the river bottom was determined using the Wolman (1954) method in riffles where algae and invertebrate samples were additionally collected. During each habitat sampling event, an approximate discharge measurement was collected. Cross-sectional area was determined across three transects in which depth and width were measured to the nearest centimeter. Approximate velocity between transects was measured using a neutrally buoyant object.

All water chemistry sampling equipment was acid-washed between sites and subsequently rinsed with sample water prior to grab sample collection. Dissolved nutrient samples were filtered through 0.45 $\mu$ m mesh membrane filters. Samples were frozen until analysis of primary plant growth nutrients, nitrogen and phosphorus. This was performed using an autoanalyzer according to routine protocol (APHA 1998). Specific conductance and pH were additionally measured using an Oakton model 10 meter (Vernon Hills, IL, US) that was calibrated with standard solutions before and after each sampling period.



Algal biomass was quantified using both ash-free dry mass (AFDM) methodology as well as analysis for the pigment Chlorophyll *a*. Prior to AFDM sample collection, glass fiber filters were pre-ashed and weighed. Three replicate samples for both parameters were collected from randomly selected rocks (for a total of six rocks per site) within riffles, using a 4-cm<sup>2</sup> sampling template. Algal material was scraped from the sampling area and placed onto a glass fiber filter (pre-ashed and weighed for AFDM only). Water was extracted using a Nalgene (Rochester, NY, US) hand vacuum pump. Filters with samples were subsequently placed into vials, wrapped in aluminum foil to prevent penetration of light, and frozen until analysis. All AFDM samples were dried to a constant weight at 105°C and weighed to the nearest 0.1 milligram (mg), oxidized at 500°C, rewetted and re-dried to a constant weight at 105°C, and finally re-weighed to the nearest 0.1 mg. Dry mass was calculated as the weight of dried material plus filter weight minus the original filter weight, divided by the area of the sampled rocks (4-cm<sup>2</sup>). AFDM was calculated as the weight of the dry mass minus the residual ash, divided by the area of the sampled rocks, according to Steinman and Lamberti (1996). All Chlorophyll *a* samples were analyzed within ninety days of sample collection. Chlorophyll *a* was measured using the fluorometric method described in APHA *et al.* (1998).

Benthic macroinvertebrate samples were collected in triplicate from a riffle within each sampling site using a Surber sampler with 500 µm mesh. For each sample, river bottom substrate was cleaned and organisms were kicked from a 0.3 m<sup>2</sup> area into the sampling net. The sample was subsequently decanted in a bucket, filtered through a 250 µm sieve, transferred to a sampling jar, and preserved using ethanol diluted to approximately 70% (Hauer and Resh 1996). Samples were later identified to the lowest taxonomic level possible, and enumerated using a dissecting microscope. Assistance with identification was provided by local experts from the Laboratory of Ecological Investigations and Animal Systematics at the National University of Patagonia in Esquel, Argentina. After identification, samples were dried in pre-weighed aluminum cups at 60° C for 48 hours before re-weighing. Weights were determined to the nearest mg. Scud (*Hyalella araucana* G.) specimens were weighed separately due to their apparent

importance in trout diets as revealed by preliminary data. All other invertebrate taxa were pooled.

Additionally, temperature was collected every ninety minutes using iButton temperature data loggers (Maxim Integrated Products, Inc., Sunnyvale, CA, US). Loggers were pre- and post-calibrated using controlled temperature baths to correct for any systematic bias or error. Temperatures were averaged on a daily basis for the purposes of this paper.

#### *JUVENILE DISTRIBUTION, GROWTH, AND DIET*

Three-pass electrofishing, using a Smith Root LR-24 (Vancouver, WA, US) backpack unit, was conducted twice during the season to determine juvenile densities and growth rates at the twelve sites shown in Figure 1. Block nets (5 mm mesh) were used whenever possible. All fish were weighed to the nearest 0.1 g and measured to the nearest mm. Fish over 90 mm were sampled for stomach contents and scales. Using a syringe and wide diameter plastic tubing with sufficient length to reach the stomach, water was flushed into the stomach cavity to force evacuation of its contents. Scales were removed 5 - 10 rows above the lateral line between the adipose and dorsal fins. All scale samples were dried and preserved. Population densities were determined using the Zippin (1958) estimation method divided by the unit area of each reach.

In addition to electrofishing, investigative fyke netting was conducted to shed light on juvenile freshwater migration patterns between tributaries and the mainstem. Fyke nets (6.3-mm mesh) were installed facing both up and downstream, and attached to each other and the river bank in all tributaries for a minimum of 48 hours during the summer and the fall. Nets were monitored twice daily, and migrants were sampled as described above for electrofishing.

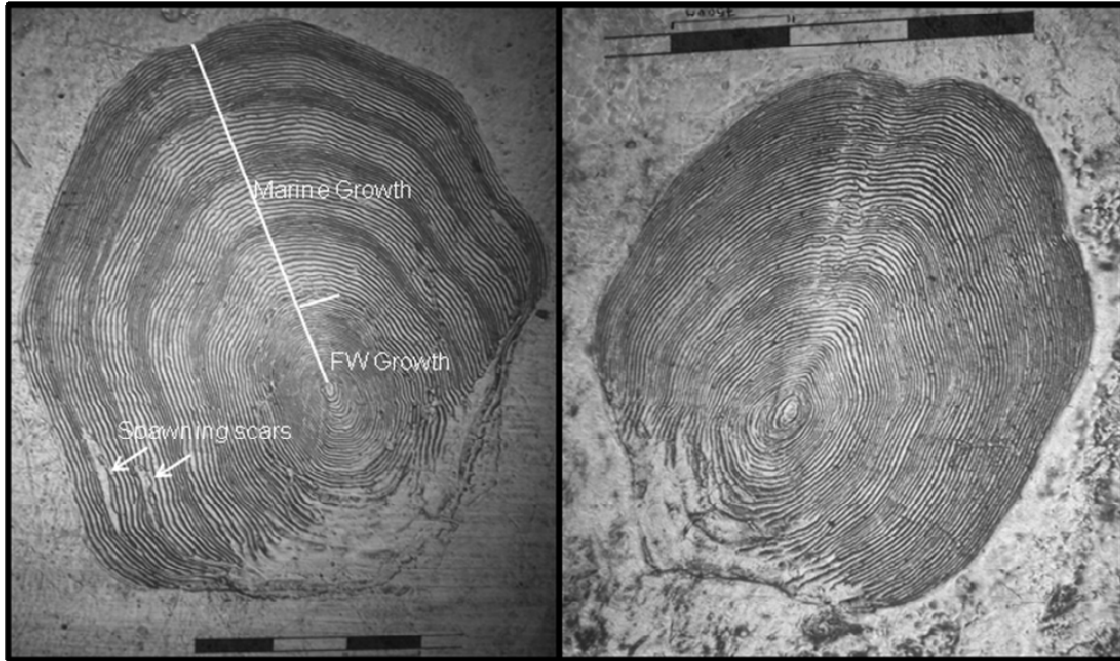
#### *DISTRIBUTION AND ABUNDANCE OF ADULT TROUT*

Adult resident and anadromous brown trout were collected by hook and line from January through April of 2006 through 2008 by tourism anglers as well as scientists. Adult fish were collected from throughout the Argentine section of the mainstem Rio Grande and samples were taken by both scientists and trained guides. Additional angling took place on accessible tributaries. Floy T-bar anchor tags were inserted underneath the

dorsal fin of fish >30 cm due to the size of the tag. Fork length and girth anterior to the dorsal fin were measured to the nearest five centimeters for all fish, and scale samples were taken from between the dorsal and adipose fins, above the lateral line. Adipose fins were clipped during the 2006 season for genetic analysis as well as a measure of tag retention. Because fish were not killed, sex was generally determined by morphology. Males exhibit a slight kype or a precursory kype while females do not. In order to evaluate freshwater feeding habits of returning migratory fish, some of the tagged fish were additionally analyzed for stomach contents as described above for juvenile sampling.

#### *AGE AND GROWTH OF ADULT TROUT*

Scale samples were cleaned and acetate impressions were made using a heated hydraulic press. Impressions were subsequently magnified under a dissecting microscope and digital images were taken for later analysis using Spot software (Diagnostic Instruments, Sterling Heights, MI, US). ImageJ image analysis software (<http://rsb.info.nih.gov/ij>) was used to inspect each scale sample. Annuli were counted, and their radii measured along the anterior-posterior axis of the scale. Ages at spawning events were inferred by the degree of scarring on the annuli (Figure 2). The absence of spawning marks, however, does not confirm the absence of spawning behavior (Elliott and Chambers 1996) such that reported numbers of spawning events serve as a minimum estimate. Resident and anadromous brown trout were distinguished both by morphology as well as scale growth patterns. Resident brown trout are generally smaller, darker colored with a more densely spotted pattern, and exhibited a fusiform body shape relative to that of sea trout. Additionally, circuli spacing on scales is wider during the post-smolt phase due to higher growth rates in the marine vs. freshwater environment (Figure 2).



**Figure 2. Scale samples from anadromous (left) and resident (right) brown trout from the Rio Grande (images are not to scale). Circuli spacing is notably wider in the marine environment, and resorption due to spawning is evident in the third and fourth marine annuli of the anadromous fish.**

Back-calculated length at age was determined using the Fraser-Lee method (Fraser 1916, Lee 1920). The biological intercept ( $c$  in the equation below) of 3.83 cm ( $r=0.81$ ,  $d.f.=201$ ,  $p<0.05$ ) was determined using linear least-squares regression. The Fraser-Lee model back-calculates individual body length as:

$$L_i = c + (L_c - c)(S_i/S_c);$$

$L_i$  = back-calculated fish length at annulus  $i$ ;

$L_c$  = fish length at capture;

$S_i$  = scale radius to annulus  $i$ ;

$S_c$  = total scale radius to annulus  $i$ ;

$c$  = the Fraser-Lee correction factor (the intercept point at the y-axis).

Significant differences between growth rates of male and female sea trout were not found, and thus samples were pooled. Blind verification of aging techniques was performed on 75 scale samples by the LFI laboratory at the University of Oslo, Norway. Eighty-five percent of determined ages agreed between datasets. Those that did not agree

were for old fish ( $\geq 8$  years) and did not indicate consistent bias in over- or underestimation.

### *STATISTICAL ANALYSES*

In order to test the food availability hypothesis, binomial logistic regression was initially used. Binomial logistic regression was chosen due to the categorical nature of the response variable (i.e., the presence or absence of anadromy). This analysis was first conducted using the variable 'season' as a factor, as habitat variables were collected three times during the year. However, because the model revealed no significant effect of season (p values ranging from 0.316 to 0.988), values from each season were treated as replicates for subsequent analyses. In the logistic regression model, the explanatory habitat data exhibited both quasicomplete and complete separation, precluding the development of maximum likelihood estimates. Quasicomplete and complete separation occur when there is respectively little to no overlap (i.e., a large difference without commonality) between explanatory data points of the categories of the response variable (Hosmer and Lemeshow 2000). Consequently, a fully parameterized model could not be developed and differences between site types were subsequently analyzed using nonparametric Mann-Whitney exact U tests. The Mann-Whitney test was selected due to small sample sizes as well as nonnormal distribution of data (Landau and Everitt 2000).

Additional comparisons were made between resident and anadromous individuals using univariate analysis of variance (ANOVA). Subsequent multiple comparisons were performed using post hoc Tukey pairwise procedures (Landau and Everitt 2004).

Mark-recapture data was analyzed using a Schnable (1938) estimator. This estimator is used for multiple marking and recapture samples over a short period of time and assumes no immigration, emigration, recruitment, or mortality. While the assumption of no immigration was clearly violated by this migratory population, a third year of data is required for a more appropriate, robust design model. The goal of the analysis was to generate an estimate of the order of magnitude of sea trout in the Rio Grande.

Linear regression was used to determine the biological intercept for the Fraser-Lee back-calculation equation. The assumption of homogeneity of variances was met, and the linearity of the relationship between scale radius and total length confirmed.

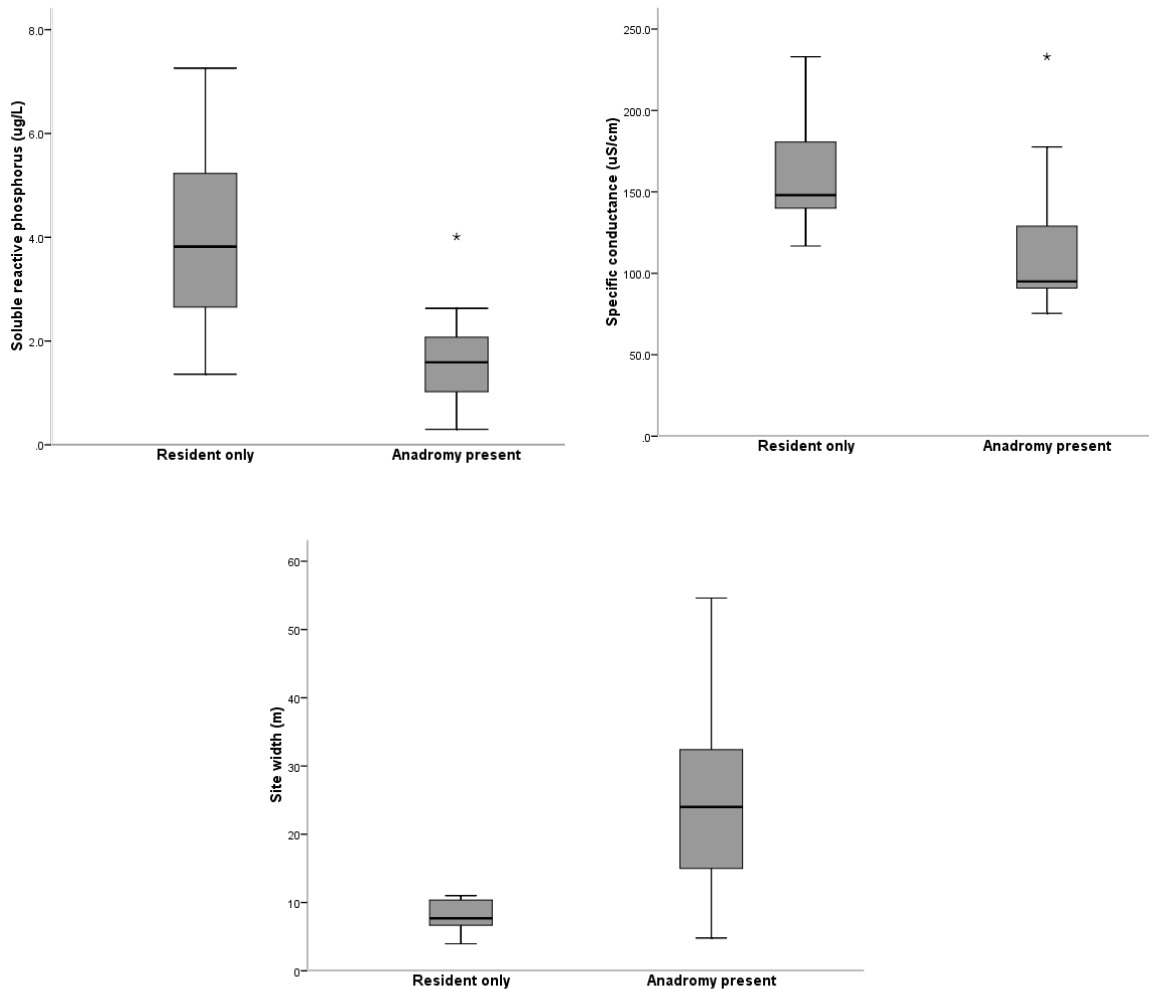
All statistical calculations were carried out using SPSS 16.0 GP (SPSS Inc., Chicago, IL, US). A rejection level of 0.05 was used in all tests.

## **RESULTS**

### *FRESHWATER HABITAT CHARACTERIZATION*

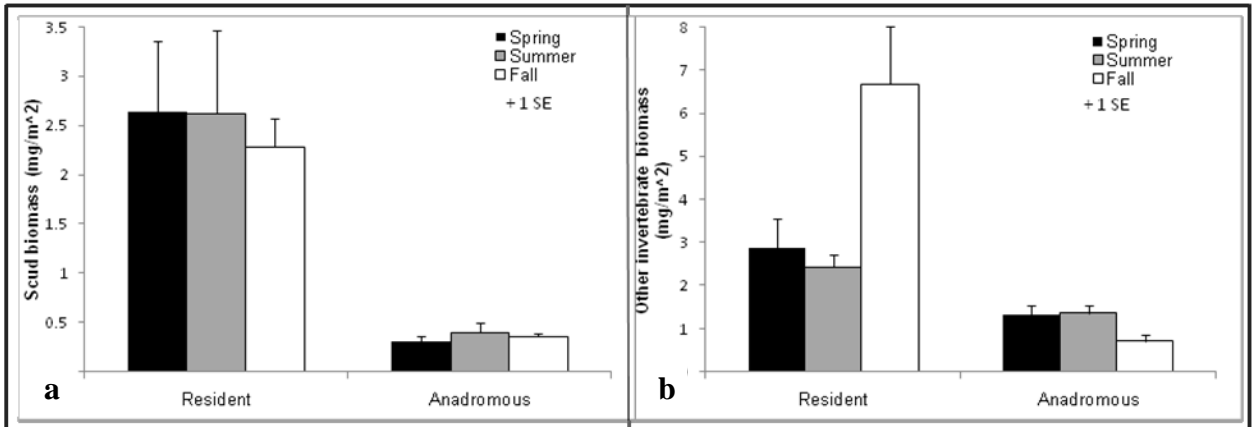
Physical variables including stream width, average depth, current velocity, river bottom particle size, and stream temperature were compared between sites used by resident and anadromous fish and sites used only by resident fish. Only stream width significantly differed between resident and anadromous sites. Streams supporting only resident fish were narrower on average than those supporting resident and anadromous fish (Mann-Whitney U test,  $z = -3.2$ ,  $p = 0.001$ , Figure 3).

Nutrient concentrations were low, at levels characteristic of unpolluted streams (Wetzel 2001). Only SRP was significantly different between sites supporting solely resident vs. sites supporting both resident and anadromous fish (Mann-Whitney U test,  $z = -4.0$ ,  $p < 0.001$ ), with higher values in resident sites (Figure 3). While pH values did not differ significantly between site types, specific conductance was also higher in streams supporting only resident trout (Mann-Whitney U test,  $z = -3.4$ ,  $p < 0.001$ , Figure 3).



**Figure 3. Boxplots of habitat variables exhibiting significant differences between sites supporting solely resident fish (Resident only, gray) vs. sites supporting both anadromous and resident fish (Anadromy present, white). Boxes indicate first and third quartiles, while bars indicate maximum and minimum values. Outliers are shown separately.**

Measures of primary productivity, AFDM and chlorophyll *a*, were highly variable, and did not exhibit statistical significance with respect to the presence or absence of anadromy. Separate analyses conducted for scuds and for all other invertebrates indicated that scud density (Mann-Whitney U test,  $z = -3.7$ ,  $p < 0.001$ ), scud dry mass (Mann-Whitney U test,  $z = -2.4$ ,  $p < 0.001$ ), and other invertebrate biomass (Mann-Whitney U test,  $z = -2.92$ ,  $p = 0.003$ ) were significantly different between site types, with sites supporting only resident trout exhibiting higher levels of scud and invertebrate biomass (Figure 4), as well as scud density. Habitat data is summarized according to site and season in Appendix A.

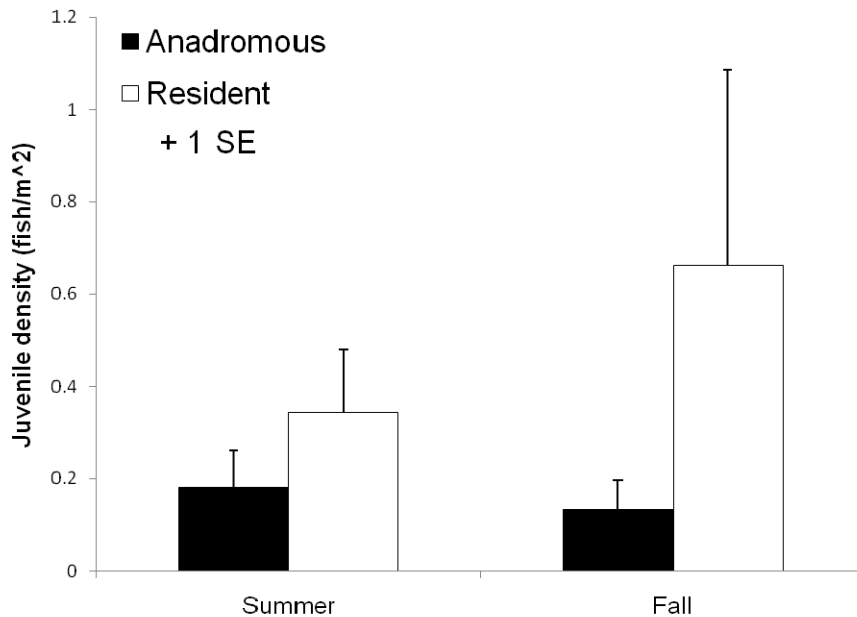


**Figure 4. Scud (a) and other invertebrate (b) biomass (mg/m<sup>2</sup>) in sites supporting resident fish only vs. sites supporting both resident and anadromous fish.**

#### *JUVENILE DISTRIBUTION, GROWTH, AND DIET*

Juvenile population density assessed throughout the watershed at sites indicated in Figure 1 ranged from 0 to 0.71 fish/m<sup>2</sup> in the spring, and 0 to 1.88 fish/m<sup>2</sup> in the fall (Figure 5). Tributaries supporting only resident fish exhibited significantly higher juvenile densities than those supporting both resident and anadromous fish (2.107, df = 22, p < 0.05). Specific growth rate for both young-of-the-year (YOY) and parr did not significantly differ between resident and anadromous sites. Fulton's condition factor (K), however, was higher in sites supporting resident fish than in those supporting resident and anadromous fish with a difference approaching statistical significance (t = 1.730, df = 22, p = 0.098).

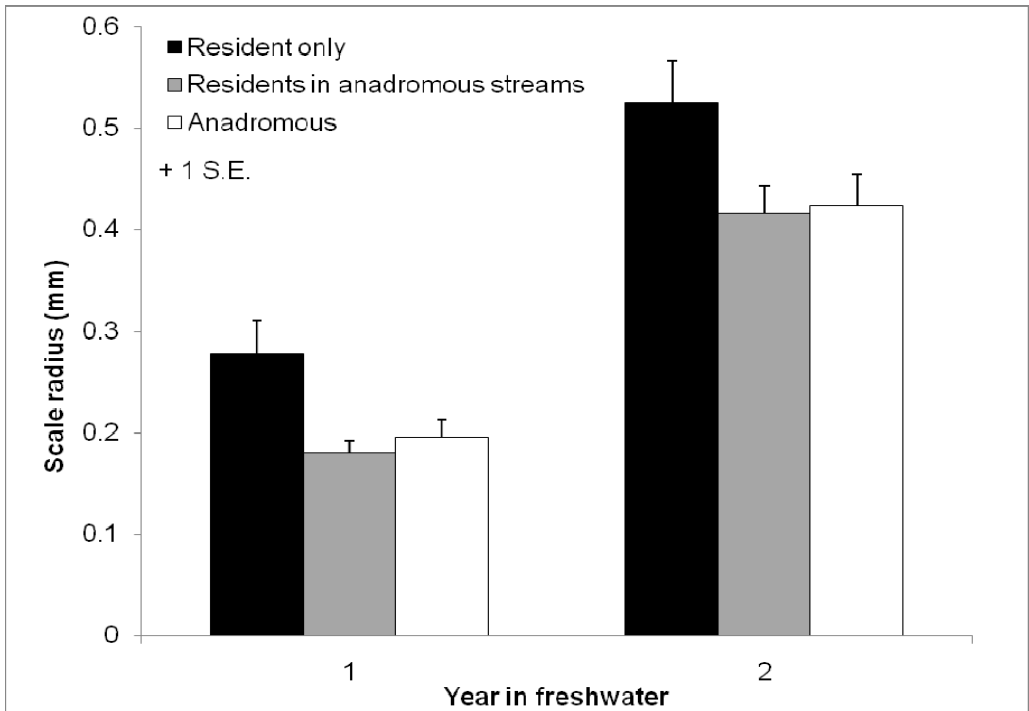




**Figure 5. Density of juvenile brown trout in electrofished sites during summer (February) and fall (April) + 1 SE. Anadromous indicates sites which support both resident and anadromous adult fish (Grande, MacLennan and Menndez Rivers), while resident indicates sites which support resident fish only (Candelaria and Herminita Rivers).**

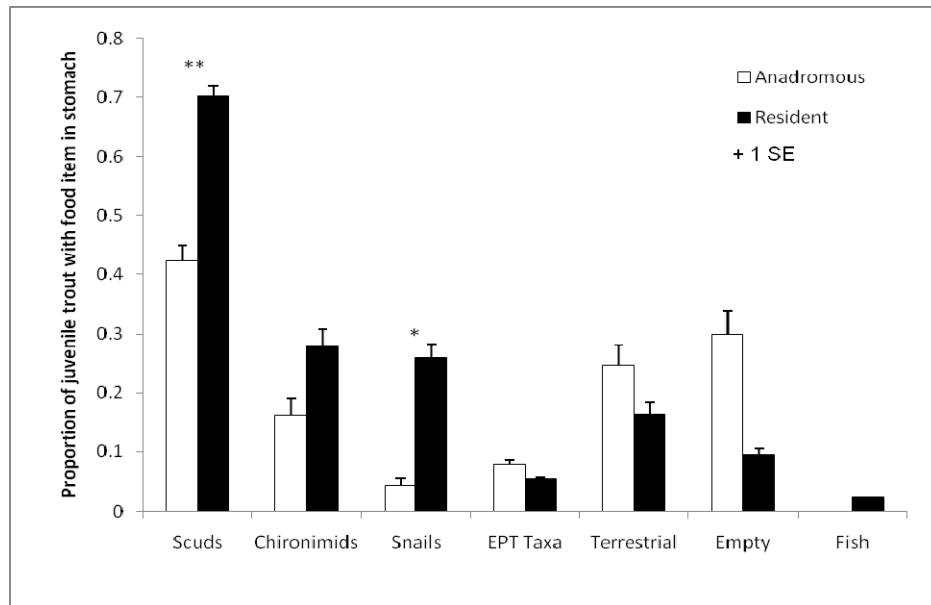
Fyke netting for juveniles in freshwater suggested very low levels of summer migration between the mainstem Rio Grande and its tributaries, at zero to two 1+ fish per day or less moving upstream into tributaries supporting resident fish. During fall fyke netting, however, 0+ (96%) and 1+ (4%) fish were documented migrating upstream into tributaries supporting solely resident fish (Herminita (N = 18) and Candelaria (N = 7) Rivers).

Adult residents residing in resident streams exhibited significantly wider annuli spacing during the first year in freshwater versus adult anadromous fish during the first year in freshwater (ANOVA followed by Tukey's test,  $F(2, 202) = 6.349$ ,  $p < 0.05$ ), suggesting higher juvenile growth of residents in those streams. Interestingly, adult residents residing in anadromous streams exhibited narrower annuli spacing than residents in resident streams, though differences were not statistically significant (Figure 6).



**Figure 6.** Scale radius for the first and second annuli of adult residents residing in resident streams (black bars), adult residents residing in anadromous streams (gray bars), and anadromous adults (white bars) + 1 S.E. Results indicate significantly higher growth of juvenile residents residing in resident streams than anadromous fish during the first year ( $p < 0.05$ ).

Stomachs of 185 juvenile (0+ and 1+) trout were evacuated, 73 from sites supporting resident and anadromous fish and 112 from sites supporting only resident fish. Most common diet items found in stomachs included scuds (*Hyaella araucana* G.); various chironomid (*Chironimidae*) taxa; snails (*Chilina patagonica* S.), Ephemoptera-Trichoptera-Plecoptera (EPT) taxa (*Andesiops* sp., *cailloma* sp., *Limnoperla jaffueli* N., *Limnoperla* sp., *Meridialaris chiloeensis* D., *Neatopsyche* sp., *Rheochorema* sp., and *Verger* sp.); terrestrial invertebrates, and juvenile brown trout (*Salmo trutta* L.). Juvenile fish in sites supporting both resident and anadromous fish were more frequently found to have empty stomachs and to have terrestrial invertebrates within stomach contents (Figure 6). Cannibalism was documented only in sites supporting solely resident fish. Statically significant differences were found between sites supporting anadromous and resident fish vs. those supporting only resident fish for the proportion of juveniles with scuds in their stomachs (ANOVA  $F(1, 17) = 10.589$ ,  $p < 0.01$ ); and for the proportion of juveniles with snails in their stomachs (ANOVA  $F(1, 17) = 8.358$ ,  $p < 0.05$ ), as shown in Figure 6.



**Figure 7. Proportion of juvenile trout with various diet items found in stomach contents between sites supporting both resident and anadromous vs. sites supporting only resident adult fish +1 SE. Most common diet items include scuds (*Hyalella araucana* G.); various chironimid (*Chironimidae*) taxa; snails (*Chilina patagonica* S.), Ephemoptera-Trichoptera-Plecoptera (EPT) taxa (*Andesiops sp.*, *cailloma sp.*, *Linoperla jaffueli* N., *Limnoperla sp.*, *Meridialaris chiloeensis* D., *Neatopsyche sp.*, *Rheochorema sp.*, and *Verger sp.*); terrestrial invertebrates, and brown trout (*Salmo trutta* L.). \*\* indicates a highly significant ( $p > 0.005$ ) difference, and \* indicates a significant difference at the  $p > 0.05$  level.**

In addition to brown trout, rainbow trout, and two native galaxid species (*Galaxias maculatus* J. and *Galaxius platei* S.) were documented in very low densities in electrofishing sites. Galaxiids were present only in sites in the lower mainstem Rio Grande, and the lower Candelaria River at densities varying from 0.04 - 0.05 fish/m<sup>2</sup>, an order of magnitude lower than brown trout densities.

#### ***DISTRIBUTION AND ABUNDANCE OF ADULT TROUT***

During the summer of 2006, 1043 adult trout were tagged, and adipose fins removed. Of those, twenty (1.9%) were recaptured. During the summer of 2007, 2933 adult trout were tagged. Of those, 66 (2.3%) were recaptured. Tag loss based on 2007 recaptures of fish tagged in 2006 was determined to be minimal (<3%). Because the closed-population assumption of the Schnabel estimate was violated, the estimate should serve as an underestimation of the true population size (Table 1). About 72% of

returning anadromous fish were female, while the percentage of female resident fish varied between 25-40% in tributaries where adult residents were collected. The majority of anadromous fish examined for stomach contents (N=89) were not feeding in freshwater as determined by the lack of food in their stomachs or a clean digestive tract. Three notable exceptions, which had small numbers of freshwater macroinvertebrates in their stomachs, were all on their first return to freshwater.

**Table 1. Summary of Floy tagged fish collected during January through April of 2006 and 2007 from the mainstem Rio Grande, including associated Schnable (1938) population estimate and associated 95% confidence intervals.**

Year	N	% recaptured	% anadromous	Female: male (anadromous)	Female: male (resident)	Anadromous population estimate	95% Confidence interval
2006	1043	20 (2.5%)	98.7%	1:0.3	1:3	37,803	24,808 – 79,389
2007	2933	66 (1.9%)	98.1%	1:0.3	1:1.5	55,058	44,784 – 71,448

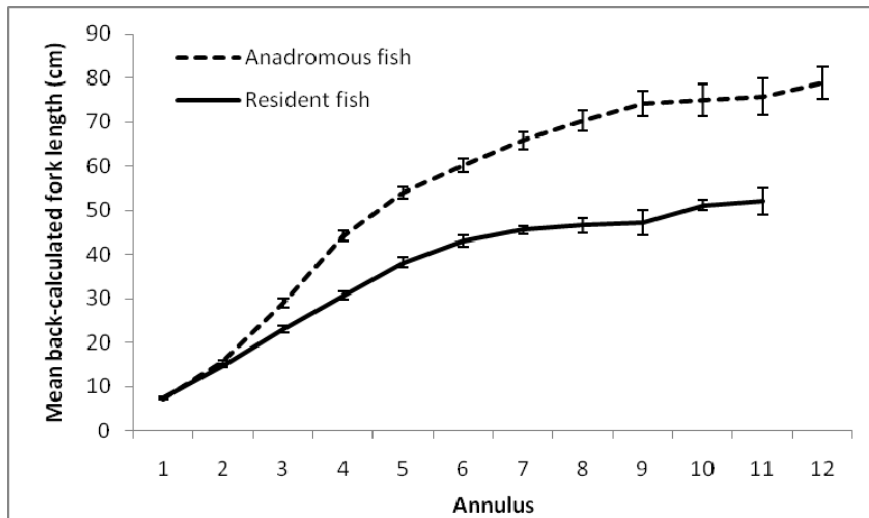
#### *AGE AND GROWTH OF ADULT TROUT*

Scales of both resident and anadromous brown trout were analyzed for freshwater age, marine age (in anadromous fish), spawning marks, and growth rates. Resident fish sampled were predominantly male (63%, N = 74, Table 2) and ranged in age from 2+ to 11 years (Table 3). Spawning marks on resident scale samples ranged in frequency from 0 to 4. Anadromous fish sampled were predominantly female (72% N = 129, Table 2) and ranged in total age from 2+ to 12 years. Spawning marks ranged in frequency from 0 to 6. Fish migrated to sea at two and three years in similar proportions (45.7% and 40.3%, respectively), though seaward migration varied from age 1+ to 4 years. Between rivers, annual growth rates of residents were significantly lower in the Candelaria River than in the Herminita and Menendez Rivers (ANOVA followed by Tukey's test,  $F(4,73) = 3.56$ ,  $p < 0.05$ ). No significant differences were found between growth rates of anadromous fish between rivers where they were captured.

**Table 2. Life history variables of resident and migrant brown trout in tributaries to as well as the mainstem Rio Grande including 95% confidence limits. Average number of spawning marks includes only fish exhibiting one or more mark.**

	N	Ratio females: males	Average length (cm)	Average age (years)	Average smolt age (years)	Average sea age (years)	Average no. spawning marks
<b>Candelaria River</b>							
Resident	19	0.2	23.6 ± 2.3	4.4 ± 0.4			
<b>Herminita River</b>							
Resident	16	0.3	39.2 ± 5.7	6.2 ± 1.0			
<b>MacLennan River</b>							
Resident	16	0.2	29.8 ± 5.7	5.3 ± 2.1			
Anadromous	4	3.0	63.8 ± 17.0	7.4 ± 0.6	2.9 ± 0.7	4.5 ± 1.8	2.8 ± 1.2
<b>Menendez River</b>							
Resident	5	0.5	40.6 ± 15.5	5.7 ± 1.4			
Anadromous	9	2.0	57.1 ± 8.9	6.1 ± 1.1	2.8 ± 0.3	3.5 ± 0.9	1.4 ± 0.3
<b>Grande River</b>							
Resident	31	0.7	42.2 ± 2.7	6.8 ± 0.4			2.7 ± 0.4
Anadromous	104	3.6	59.4 ± 3.2	7.0 ± 0.9	2.6 ± 0.1	4.6 ± 0.5	2.6 ± 0.3

Back-calculated growth indicated that amongst anadromous trout, larger parr migrated to sea earlier (ANOVA followed by Tukey’s test  $F(3,113) = 18.3, p < 0.001$ ). 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 8. Mean back-calculated growth rates of anadromous and resident brown trout in the Rio Grande basin. Error bars represent ±1 SE.**

**Table 3. Back-calculated growth (mean fork length, cm) and SE for anadromous and resident brown trout from scale measurements.**

ANNULUS	Anadromous			Resident		
	N	Mean back-calculated length (cm)	Range (cm)	N	Mean back-calculated length (cm)	Range (cm)
1	117	7.2	4.7-12.7	88	7.4	5.3-13.3
2	117	15.7	6.4-36.3	88	14.7	80.8-24.6
3	116	29.0	79.2-53.4	87	23.0	10.5-40.1
4	114	44.1	17.6-73.3	75	30.6	12.0-54.2
5	101	54.0	23.0-85.0	55	38.1	14.4-65.0
6	70	60.2	26.0-86.1	35	43.0	26.0-61.0
7	50	65.8	38.0-89.1	23	45.6	33.0-50.0
8	34	70.4	42.7-91.6	9	46.5	35.1-50.9
9	23	74.2	43.9-94.7	5	47.1	36.0-52.6
10	14	74.9	45.0-96.0	4	51.1	48.3-54.0
11	8	75.8	50.0-86.0	2	52.0	49.0-55.0
12	3	78.8	72.0-84.5			

## DISCUSSION

Life history plasticity appears to have played a particularly crucial role in the successful establishment and spread of brown trout in the Rio Grande. The fact that this population consisted for decades of solely resident brown trout before shifting to the marine environment suggests a change in the food base in the freshwater environment. In New Zealand rivers where brown trout are also introduced, they are known to feed directly on native galaxiids, as well as significantly deplete invertebrate communities (Townsend 2003, Waters 1988). While the original freshwater foodweb of the Rio Grande is undocumented, it can be inferred that there was a sufficient food base to support the formerly resident population. The paucity of native fish remaining in the system combined with local accounts of much higher densities of galaxiids in the past (A. Matias, personal communication) suggests that indeed brown trout likely caused the near extirpation of the native fish through both competition and direct predation.

Further, significantly lower invertebrate biomass in sites supporting anadromous vs. resident brown trout, combined with the higher incidence of terrestrial invertebrates in the diets of juvenile fish as well as the more frequent occurrence of empty stomachs in those sites implies that the food base may indeed be limiting brown trout in sites

supporting anadromous fish. Huryn (1996) determined that introduced brown trout may consume more than 80% of benthic prey production in New Zealand rivers. Thus it appears possible, if not likely, that the formerly resident Rio Grande brown trout population subsisted on substantially higher densities of both native galaxiid fish as well as invertebrates, and may have begun seaward migration after depleting those resources.

In other partially migratory salmonid populations where the food availability hypothesis has been tested, growth data suggest that fish which grow more during their first years of life in freshwater residualize in streams as residents, while those that grow less tend to migrate (Olsson and Greenberg 2004, Thériault and Dodson 2003). Indeed, analysis of freshwater annuli spacing of adult resident trout in resident streams was higher than that of adult resident trout in anadromous streams, and significantly higher than that of adult anadromous trout during the first year of life suggesting higher growth. Additionally, in the Rio Grande, higher fall juvenile densities in resident streams as well as fyke netting data suggest that some fish which residualize, largely males, likely migrate into tributaries with higher invertebrate and juvenile trout densities which can sustain them. It is probable that these resident fish descend tributaries and spawn with returning anadromous trout (Klemetsen et al. 2003). It is unknown whether the Rio Grande brown trout population has reached a relatively stable state, or if it will continue to shift toward higher levels of anadromy. Higher conductivity and SRP levels in tributaries supporting resident fish indeed suggest generally higher fertility of those locations (Wetzel 2001).

Regardless of the mechanisms leading to the occurrence of seaward migration in Rio Grande brown trout, comparison of the population with those from Europe clearly indicate that it is amongst the strongest anadromous populations in the world (Table 5). Mark-recapture data collected from the adult sea trout population of the Rio Grande revealed its exceptional size. The closed-population assumption of the Schnabel estimate is violated by this migratory population. However, based on catch records and other observations, immigration into the study reach exceeds both emigration and mortality.

**Table 4. Comparison of various life history traits of sea trout in their native range with those from the Rio Grande.**

Location	Sources	Parr Density (no./m <sup>2</sup> )	Freshwater growth (year 2, cm)	Mean Smolt Age (years)	Saltwater growth (first year at sea, cm)	Repeat spawners (%)	Maximum age (years)	Maximum length reported (cm)	Average annual declared catch
England	Davidson et al. 2006, Fahy 1978, Harris 2006, Mann et al. 1989, Nall 1930	0.10 – 0.80	3.7 – 6.8	2.0 – 3.4	4.4 - 12.5	12.5 - 39.6	8	62.4	1181 (416 – 5692)
Germany	Roche 1992	n/a	n/a	n/a	n/a	26	n/a	n/a	
Ireland	Fahy 1978, Gargan et al. 2006, Nall 1930	n/a	n/a	2.1 – 2.8	n/a	n/a	8	n/a	320 (37 – 1175)
Norway	Berg and Jonsson 1990, Jonsson 1985, L'Abée-Lund et al. 1989, L'Abée-Lund et al. 1991	0.11	3.6 – 7.5	1.2 - 5.6	7.9 – 20.4	5 – 69	11	69	n/a
Scotland	Butler and Walker 2006, Egglshaw and Shackley 1977, Nall 1930	n/a	n/a	2.1 – 3.4	n/a	16.5 - 65.1 <sup>b</sup>	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	Leeuw 2007	n/a	n/a	n/a	n/a	21	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	Fahy 1978, Nall 1930	n/a	n/a	2.1 – 2.5	n/a	n/a	8	n/a	n/a
Kerguelen Islands <sup>a</sup>	Davaine and Beall 1992	n/a	4 – 10	n/a	5 – 20	n/a	n/a	n/a	n/a
Rio Grande <sup>a</sup>	This study	0.02 – 1.8	8.5	2.47	17.8 – 21.7	62.9	12	116.0	>>5455 <sup>c</sup>

<sup>a</sup> The Kerguelen Islands and the Rio Grande are southern hemisphere locations where sea trout have been introduced

<sup>b</sup> The highest repeat spawning rate in Scotland occurred prior to 1980

<sup>c</sup> This value accounts for only 80% of the rods on the river and thus is considered an underestimate



Catch rates in upper reaches of the study area are low, and the occurrence of sea trout on the Chilean side of the border is rare (G. Pacho., personal communication). Immigration causes underestimation of true population size (Williams, Nichols, and Conroy 2002). It is thus apparent that the Rio Grande supports tens of thousands of adult anadromous brown trout. Reasons for the large population are likely to include strict harvest limits and inaccessibility of the estuary to commercial fishing as well as few natural predators in the freshwater environment.

Few published population estimates of sea trout in European rivers exist, though rod catch statistics for studied rivers in Ireland, where average annual catch equals 320 sea trout (Gargan et al. 2006, Table 5), England and Wales, where declared catch averages 1181 (Harris 2006, Table 5), and France where run estimates do not exceed 3000 (Euzenat, Fournel, and Fagard 2006) indeed suggest much smaller populations than that in the Rio Grande. Catch records for only 80% of the anglers on the river during the course of the study indicate an average annual catch in the river of well over 5500 sea trout.

Not only do data indicate a surprisingly large population size, various other life history traits of this population suggest the Rio Grande and adjacent marine environment may indeed support one of the strongest existing sea trout populations in the world. While Rio Grande juvenile trout exhibit freshwater growth rates comparable to those in the southern portion of their European range (Mann, Blackburn, and Beaumont 1989; LeCren 1985; L'Abée-Lund et al. 1989; Table 5), growth rate at sea is more than twice as high as that in English rivers (Davidson, Cove, and Hazlewood 2006; Fahy 1978; Harris 2006; Mann et al. 1989; Nall 1930; Table 5), and on the high end of the range of marine growth rates for Norwegian sea trout (Jonsson and Jonsson 2006, Table 5). Back-calculated growth rates indicated a 17.8 to 21.7 cm increment (Table 5) during the first year at sea, amongst the highest documented rates in the literature from The Netherlands, France (de Leeuw, ter Hofstede, and Winter 2007), and Germany (Roche 1992). Total length of fish collected from the Rio Grande similarly exceeds that of documented European fish. The largest male and female in the Rio Grande dataset were 120 cm and 99 cm in fork length, respectively. The highest values for body length located in the literature were in the 85-90 cm range (LeCren 1985, L'Abée-Lund et al. 1989, de Leeuw

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

Additionally, repeat spawning rates and longevity of Rio Grande sea trout exceed those of many European populations (Table 5). Southern European populations tend to live fewer (3-5) years, but spawn more times, with a repeat spawning rate of up to 60%; and northern populations tend to live longer (up to 8 years), but spawn fewer times with 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 (64%) as well as remarkable longevity (living up to at least twelve years).

Reasons behind the great success of the Rio Grande fishery remain to be explored. It is likely due to a combination of both hereditary and environmental factors. The estuary at the mouth of the Rio Grande may be one of the most important environmental factors in their success. It is large and shallow, providing the benefits of both high productivity and shelter from large commercial fishing boats. The estuary is adjacent to the highly productive South Patagonian Shelf Ecosystem (Ciancio et al. 2008; Rivas, Dogliotti, and Gagliardina 2006) where sea trout feed largely on sprats (*Sprattus fuegensis*, Ciancio et al. 2008). Additionally, as opposed to other anadromous salmonids, sea trout do not generally travel far from coastal areas (Klemetsen et al. 2003), a behavior corroborated by their reported lack of appearance in offshore fishing nets in the area (A. Matias, personal communication). The absence of significant aquaculture activities, and the relative lack of human induced disturbance also likely contribute to the robust nature of the fishery. Further, a strict no kill policy imposed on the vast majority of the river since the mid-1980s appears to have resulted in increased catch rates, average size, and longevity of fish (Solomon and Czerwinski 2006).

This study is the first rigorous analysis of anadromous sea trout on the south American continent clearly documenting their distribution as well as what little remains of the distribution of native galaxiid fish. It implies far-reaching impacts of brown trout in the Rio Grande system, suggesting that severe depletion of native galaxiid and invertebrate communities compelled a shift toward a migratory life history. Juvenile

growth rates, as inferred from scale data supports the food availability hypothesis as seen in other studies of partially migratory brown trout populations. Indeed, the individual 'decision' to migrate to sea appears to be associated with lower growth rates and fewer available instream food resources. Regardless of the mechanisms compelling migration, the combination of fresh and saltwater habitat available to the Rio Grande population appears to support what may indeed be one of the strongest anadromous populations of the species remaining in the world.

## REFERENCES

- Alcaez, C., Vila-Gispert A., Garcia-Berthou E. (2005) Profiling invasive fish species: the importance of phylogeny and human use. *Diversity and Distributions*, **11**, 289-298.
- American Public Health Association (1998) *Standard methods for the Examination of Water and Wastewater*. 20<sup>th</sup> ed. APHA, Washington, D.C.
- Baker, R.R. (1978) *The Evolutionary Ecology of Animal Migration*. Hodder and Stoughton. London.
- Basulto del Campo, S. (2003). *El Largo Viaje de los Salmones, Una Crónica Olvidada: Propagación y Cultivo de Species Acuáticas en Chile*. Maval Ltda. Chile.
- Baxter, C.V., Fausch, K.D., Murakami, M., Chapman, P.L. (2004) Fish invasion restructures stream and forest food web by interrupting reciprocal prey subsidies. *Ecology*, **85**, 2565-2663.
- Behnke, R.J. (1986) Brown trout. *Trout*, **27**, 42-47.
- Berg, O.K. and Jonsson, B. (1990) Growth and survival rates of the anadromous trout, *Salmo trutta*, from the Vardnes River, northern Norway. *Environmental Biology of Fishes*, **29**, 145-154.
- Bisson, P.A., and D. R. Montgomery (1996) Valley segments, stream reaches, and channel units. In: *Methods in Stream Ecology* (Eds F.R. Hauer and V.H. Resh), pp. 23-52. Academic Press. San Diego.
- Bohlin, T., Dellefors, C. and Farneo, U. (1996) Date of smolt migration depends on body-size but not age in wild sea-run brown trout. *Journal of Fish Biology*, **49**, 157-164.
- Bohn, T., Sandlund, O.T., Amundsen, P., and Primicerio, R. (2004) Rapidly changing life-history during invasion. *Oikos*, **106**, 138-150.
- Bonsall, M.B. and Mangel, M. (2004) Life-history trade-offs and ecological dynamics in the evolution of longevity. *Proceedings of the Royal Society of London*, **271**, 1143-1150.
- Bruno Videla, P.H. (1978). *Los Salmónidos en Tierra del Fuego*. Gobernación del Territorio Nacional de la Tierra del Fuego, Antártida e Islas del Atlántico Sud. Dirección de Intereses Marítimos.

- Butler, J.R.A. and Walker, A.F. (2006) Characteristics of the Sea Trout *Salmo trutta* (L.) Stock Collapse in the River Ewe (Wester Ross, Scotland), 1988-2001. In: *Sea Trout Biology, Conservation & Management* (Eds G. Harris and N. Milner), pp. 45-59. Blackwell Publishing, Oxford.
- Caballero, P., Cobo, F., and González, M.A. (2006) Life history of a sea trout (*Salmo trutta* L.) population from the North-West Iberian Peninsula (River Ulla, Galicia, Spain). In: *Sea Trout Biology, Conservation & Management* (Eds G. Harris and N. Milner), pp. 234-247. Blackwell Publishing, Oxford.
- Ciancio, J.E., Pascual, M.A., Botto, F., Frere, E., and Iribarne, O. (2008) Trophic relationships of exotic anadromous salmonids in the southern Patagonian Shelf as inferred from stable isotopes. *Limnology and Oceanography*, **53**, 788-798.
- Colihueque, N., Vergara, N., and Parraguez, M. (2003) Genetic characterization of naturalized populations of brown trout *Salmo trutta* L. in southern Chile using allozyme and microsatellite markers. *Aquaculture Research*, **34**, 525-533.
- Cussac, V., Ortubay, S., Iglesias, G., Milano, D., Lattuca, M.E., Barriga, J.P., M. Battinin, and Gross, M. (2004) The distribution of South American galaxiid fishes: the role of biological traits and post-glacial history. *Journal of Biogeography*, **31**, 103-121.
- Davaine, P. and Beall, E. (1992) Relationships between temperature, population density, and growth in sea trout population (*S. trutta* L.) of the Kerguelen Islands. *ICES Journal of Marine Science*, **49**, 445-451.
- Davidson, I.C., Cove, R.J., and Hazlewood, M.S. (2006) Annual variation in age composition, growth and abundance of adult sea trout returning to the River Dee at Chester, 1991-2003. In: *Sea Trout Biology, Conservation & Management* (Eds G. Harris and N. Milner), pp. 401-416. Blackwell Publishing, Oxford.
- de Leeuw, J.J., ter Hofstede, R., and Winter, H.V. (2007) Sea growth of anadromous brown trout (*Salmo trutta*). *Journal of Sea Research*, **58**, 163-165.
- Egglishaw, H.J. and Shackley, P.E. (1977) Growth, survival and production of juvenile salmon and trout in a Scottish stream, 1966-75. *Journal of Fish Biology*, **11**, 647-672.
- Elliott J.M. (1994) *Quantitative Ecology and the Brown Trout*. Oxford University Press. Oxford.
- Elliott, J.M. and Chambers, S. (1996) *A Guide to the Interpretation of Sea Trout Scales*. Institute of Freshwater Ecology. Windermere Laboratory. R&D Report 22.

- Euzenat, G., Fournel, F., and Fagard, J.-L. (1996) Population Dynamics and Stochastic Recruitment of Sea Trout in the River Bresle, Upper Normandy, France. In: *Sea Trout Biology, Conservation & Management* (Eds G. Harris and N. Milner), pp. 307-326. Blackwell Publishing, Oxford.
- Fahy, E. (1978) Variation in some biological characteristics of British sea trout *Salmo trutta* L. *Journal of Fish Biology*, **13**, 123-138.
- Faundez, V., Blanco, G., Vázquez, E., and Sánchez, J.A. (1997). Allozyme variability in brown trout *Salmo trutta* in Chile. *Freshwater Biology*, **37**, 507-514.
- Flecker, A.S. and Townsend, C.R. (1994) Community-wide consequences of trout introduction in New Zealand streams. *Ecological Applications*, **4**, 798-807.
- Fraser, C.M. (1916) Growth of the spring salmon. *Transactions of the Pacific Fisheries Society*, **1915**, 29-29.
- Frost, W.E. and Brown, M.E. (1967) *The Trout*. Collins, London.
- Gargan, P.G., Roche, W.K., Forde, G.P., and Ferguson, A. (2006) Characteristics of the Sea Trout (*Salmo trutta* L.) Stocks from the Owengowla and Invermore Fisheries, Connemara, Wester Ireland, and Recent Trends in Marine Survival. In: *Sea Trout Biology, Conservation & Management* (Eds G. Harris and N. Milner), pp. 25-44. Blackwell Publishing, Oxford.
- Gross, M.R. (1987) Evolution of diadromy. *American Fisheries Society Symposium*, **1**, 14-25.
- Gross, M.R., Coleman, R.M., and McDowall, R.M. (1988) Aquatic productivity and the evolution of diadromous fish migration. *Science* 239: 1291-1293.
- Habit E. 2004. Introduced species in Chile's freshwaters—the need for research. Introduced Fish Section Newsletter. American Fisheries Society 21(1):3-4.
- Harris, G. (2006) Sea Trout Stock Descriptions in England and Wales. In: *Sea Trout Biology, Conservation & Management* (Eds G. Harris and N. Milner), pp. 441-456. Blackwell Publishing, Oxford.
- Harris, G. and N. Milner (Eds) (2006) *Sea Trout Biology, Conservation and Management*. Blackwell Publishing. Oxford.
- Hauer, F.R., and V.H. Resh (1996) Benthic macroinvertebrates. In: *Methods in Stream Ecology* (Eds F. R. Hauer and G. A. Lamberti). Academic Press. San Diego.

- Hindar, K., Jonsson, B., Ryman, N., Stahl, G. (1991) Genetic relationships among landlocked, resident, and anadromous brown trout, *Salmo trutta* L. *Heredity* **66**, 83-91.
- Hosmer, D.W. and Lemeshow, S. (2000) *Applied Logistic Regression*, Ed. 2. John Wiley and Sons, Inc., New York.
- Huntington, H.P. (2000) Using Traditional Ecological Knowledge in Science: Methods and Applications. *Ecological Applications*, **10**, 1270-1274.
- Hurn, A.D. (1996) An appraisal of the Allen paradox in a New Zealand trout stream. *Limnology and Oceanography*, **41**, 243-252.
- Hynes, H.B.N. (1970) *The Ecology of Running Waters*. University of Toronto Press. Toronto.
- Iturraspe R., Gaviño M., and Urciuolo A. (1998) Caracterización hidrológica de los valles de Tierra Mayor y Carbajal, Tierra del Fuego. *Anales del XVII Congreso Nac. del Agua y II Simposio de Rec. Hídricos del Cono Sur*. **I**, 147-156
- Jonsson, B. (1985) Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. *Transactions of the American Fisheries Society*, **114**, 182-194.
- Jonsson, B. and Jonsson, N. (1993) Partial Migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries*, **3**, 348-365.
- Jonsson, B. and L'Abée-Lund, J.H. (1993) Latitudinal clines in life-history variables of anadromous brown trout in Europe. *Journal of Fish Biology*, **43** (Supplement A), 1-16.
- Jonsson, B. and Jonsson, N. (2006) Life history of the anadromous trout *Salmo trutta*. In: *Sea Trout Biology, Conservation & Management* (Eds G. Harris and N. Milner), pp. 196-223. Blackwell Publishing, Oxford.
- Jonsson, N. and Jonsson, B. (2002) Migration of anadromous brown trout *Salmo trutta* in a Norwegian River. *Freshwater Biology*, **47**, 1391-1401.
- Joyner, T. (1980) Salmon ranching in South America. In: *Salmon Ranching* (Ed. J.E Thorpe), pp. 261-276. Academic Press, London.
- Klemetsen A, Amundsen P.-A., Dempson J.B., Jonsson B., Jonsson N., O'Connell M.F., Mortensen E. (2003) Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* L.: a review of aspects of their life histories. *Ecology of Freshwater Fish*, **12**, 1-59.

- Knapp, R.A., and Matthews, K.R. (2000) Non-native fish introductions and the decline of the mountain yellow-legged frog from within protected areas. *Conservation Biology*, **14**, 428-438.
- L'Abée-Lund, J.H., Jonsson, B., Jensen, A.J., Sættem, L.M., Heggberget, T.G. Johnsen, B.O. and Naesje, T.F. (1989) Latitudinal variation in life-history characteristics of sea-run migrant brown trout (*Salmo trutta*). *The Journal of Animal Ecology*, **58**, 525-542.
- L'Abée-Lund, J.H. (1991) Variation within and between rivers in adult size and sea age at maturity of anadromous brown trout, *Salmo trutta*. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 1015-1021.
- Landau, S. and Everitt, B.S. (2004) *A Handbook of Statistical Analyses using SPSS*. Chapman & Hall/CRC, Florida.
- Le Cren, E.D. (1984) *The Biology of the Sea Trout*. Atlantic Salmon Trust and Welsh Water Authority.
- Lee, R.M. (1920) A review of the methods of age and growth determinations in fishes by means of scales. *Fishery Investigations, Series II*, Marine Fisheries, Great Britain Ministry of Agriculture, Fisheries and Food, **4**(2), 1-35.
- Lorang, M.S., and F.R. Hauer. (2006) Fluvial geomorphic processes. In: *Methods in Stream Ecology*, 2<sup>nd</sup> Ed. (Eds F.R. Hauer and G.M. Lamberti), pp. 145-168. Academic Press/Elsevier. San Diego.
- Macchi P.J., Cussac, V.E., Alonso, M.F., Denegri, M.A. (1999) Predation relationships between introduced salmonids and native fish fauna in lakes and reservoirs of northern Patagonia. *Ecology of Freshwater Fish*, **8**, 227-236.
- Mann, R.H.K, Blackburn, J.H. and Beaumont, W.R.C. (1989) The ecology of brown trout *Salmo trutta* in English chalk streams. *Freshwater Biology*, **21**, 57-70.
- Marini, T.L. and Mastrarrigo, V. (1963) *Piscicultura, Recursos Naturales Vivos, Evaluación de los Recursos Naturales de la Argentina*. Ministerio de Agricultura de la Nación, Tomo 7(2), Buenos Aires.
- McDowall, R.M. (1971) The galaxiid fishes of South America. *Zoological journal of the Linnean Society*, **50**, 33-73.
- McDowall, R.M. (1997) The evolution of diadromy in fishes (revisited). *Reviews in Fish Biology and Fisheries* **7**, 443-462.



- McDowall, R.M. (2006) Crying wolf, crying foul, or crying shame: alien salmonids and a biodiversity crisis in the southern cool-temperate galaxioid fishes? *Reviews in Fish Biology and Fisheries* **16**, 233-422.
- Menzies, W.J.M. (1936) *Sea Trout and Trout*. Edward Arnold and Company. London.
- Moyle, P.B. and Light, T. (1996) Biological invasions of freshwater: empirical rules and assembly theory. *Biological Conservation*, **78**, 149-161.
- Nall, H.E. (1930) *The Life of the Sea Trout Especially in Scottish Waters; With Chapters on the Reading and Measuring of Scales*. Seeley, Service & Co. Ltd., London.
- Nikolskii, G.V. (1963) *The Ecology of Fishes*. Academic Press, London.
- Olsson, I.C. and Greenberg, L.A. (2004) Partial migration in a landlocked brown trout population. *Journal of Fish Biology*, **65**, 106-121.
- Olsson, I.C., Greenberg, L.A., Bergman, E., and Wysujack, K. (2006) Environmentally induced migration: the importance of food. *Ecology Letters*, **9**, 645-651.
- Pascual M., P. Macchi, J. Urbanski, F. Marcos, C. Riva Rossi, M. Novara, P. Dell'Arciprete. (2002) Evaluating potential effects of exotic freshwater fish from incomplete species presence-absence data. *Biological Invasions*, **4**, 101-113.
- Rivas, A.L., Dogliotti, A.I., and Gagliardina, D.A. (2006) Seasonal variability in satellite-measured surface chlorophyll in the Patagonian Shelf. *Continental Shelf Research*, **26**, 703-720.
- Roche, P. (1992) Mise en évidence de l'écotype truite de mer dans les captures de grandes truites (*Salmo trutta* L.) du Rhin supérieur, *Bull. Fr. Pêche Piscic.*, **324**, 36-44.
- Rubin, J.-F., Glimsäter, C, and Jarvi, T. (2005) Spawning characteristics of the anadromous brown trout in a small Swedish stream. *Journal of Fish Biology*, **66**, 107-121.
- Schindler, D.E., Knapp, R.A., and Leavitt, P.R. (2001) Alteration of nutrient cycles and algal production resulting from fish introductions into mountain lakes. *Ecosystems*, **4**, 308-321.
- Schnabel, Z.E. (1938) The estimation of the total fish population of a lake. *American Mathematical Monographs*, **45**, 348-368.
- Simberloff, D. (2001) Biological invasions – how are they affecting us and what can we do about them? *Western North American Naturalist*, **61**, 308-315.

- Simon, K.S., Townsend, C.R., Biggs, B.J.F., Bowden, W.B., and Frew, R.D. (2004) Habitat-specific nitrogen dynamics in New Zealand streams containing native or invasive fish. *Ecosystems*, **7**, 777-792.
- Solomon, D.J. and Czerwinski, M. (2006) Catch and Release, Net Fishing and Sea Trout Fisheries Management. In: *Sea Trout Biology, Conservation & Management* (Eds G. Harris and N. Milner), pp. 434-440. Blackwell Publishing, Oxford.
- Stanford, J.A., Lorang, M.S., and Hauer, F.R. (2005) The shifting habitat mosaic of river ecosystems. *Verh. Internat. Verein. Limnol.*, **29**, 123-136.
- Steinman, A.D. and Lamberti, G.A. (1996) Biomass and pigments of benthic algae. In: *Methods in Stream Ecology*, 2<sup>nd</sup> Ed. (Eds F.R. Hauer and G.M. Lamberti), pp. 295-314. Academic Press/Elsevier. San Diego.
- Townsend, C.R. (1996) Invasion biology and ecological impacts of brown trout *Salmo trutta* in New Zealand. *Biological Conservation*, **78**, 13-22.
- Townsend, C.R. (2003) Individual, population, community and ecosystem consequences of a fish invader in New Zealand streams. *Conservation Biology*, **17**, 38-47.
- Valiente, A.G., Juanes, F., Nuñez, P. and Garcia Vazquez, E., (2007). Is genetic variability so important? Non-native salmonids in South America. *Journal of Fish Biology*, **71 (Sup. D.)**, J.A.136-147.
- Vila-Gispert, A., Alcaraz, C., and Garcia-Berthou E. (2005) Life-history traits of invasive fish in small Mediterranean streams. *Biological Invasions*, **7**. 107-116.
- Waters, T.F. (1988) Fish production-benthos production relationships in trout streams. *Pol. Arch. Hydrobiol.*, **35**, 545-561.
- Wetzel, R.G. (2001). *Limnology: Lake and River Ecosystems*. Ed. 3. Academic Press, San Diego.
- Williams, B.K., Nichols, J.D., Conry, M.J. (2002) *Analysis and Management of Animal Populations: Modeling, Estimation and Decision Making*. Academic Press, San Diego.
- Wolman, M. G. (1954) A Method of Sampling Coarse River-Bed Material. *Transactions of the American Geophysical Union*, **35**, 951-956.
- Zippin, C. (1958) Removal method of population estimation. *Journal of Wildlife Management*, **22**, 83-90.

## APPENDIX A

**Average (minimum, maximum) values for water chemistry, primary productivity, and secondary productivity related variables by river and season.**

		Total phosphorus (µg/L)	Soluble reactive phosphorus (µg/L)	Total persulfate nitrogen (µg/L)	Nitrate-nitrite (µg/L)	Ammonium (µg/L)	Chlorophyll a (µg/cm <sup>2</sup> )	Ash-free dry mass (mg/cm <sup>2</sup> )	Invertebrate density (no./m <sup>2</sup> )
<b>Candelaria (resident only)</b>									
	Spring	13.5 (12.4-14.5)	5.0 (4.0-6.0)	505.3 (448.5-562.0)	4.5 (3.1-5.6)	126.6 (59.0-194.1)	0.52 (0.03-2.77)	1.08 (0.00-2.03)	8.6 (2.1-13.2)
	Summer	10.7 (9.2-12.2)	3.2 (2.8-3.6)	396.1 (364.9-427.3)	1.4 (0.9-1.8)	39.4 (35.2-43.6)	0.81 (0.00-3.65)	11.33 (0.42-60.07)	8.3 (2.2-16.1)
	Fall	13.7 (10.3-17.0)	1.8 (1.4-2.2)	607.7 (391.3-824.1)	1.9 (1.4-2.4)	30.6 (28.8-32.4)	0.12 (0.00-0.19)	1.50 (0.65-3.60)	15.2 (8.5-29.3)
<b>Herminita (resident only)</b>									
	Spring	13.3 (11.7-14.8)	2.9 (2.5-3.2)	357.0 (318.3-395.7)	8.9 (2.0-15.8)	55.5 (30.2-80.8)	0.29 (0.06-0.82)	5.64 (0.00-33.00)	36.4 (8.6-66.6)
	Summer	14.6 (12.4-16.8)	4.4 (4.2-4.6)	628.9 (439.3-818.5)	5.9 (1.6-10.2)	34.7 (32.6-36.7)	0.78 (0.03-3.35)	0.47 (0.00-2.85)	29.4 (12.9-50.6)
	Fall	18.5 (17.9-19.6)	6.6 (5.9-7.3)	552.5 (545.0-560.0)	12.2 (1.0-13.5)	52.7 (40.1-65.4)	0.08 (0.00-0.25)	1.25 (0.00-3.20)	20.0 (3.2-33.7)
<b>MacLennan (resident and anadromous)</b>									
	Spring	6.7 (n/a)	2.0 (n/a)	282.8 (274.4-291.2)	2.4 (n/a)	36.5 (n/a)	0.78 (0.32-1.60)	2.40 (0.03-5.60)	9.2 (4.4-20.2)
	Summer	6.7 (6.3-7.2)	0.7 (0.7-0.8)	224.9 (205.0-244.8)	3.6 (2.3-4.9)	44.1 (43.2-45.0)	1.36 (0.00- 3.35)	10.12 (1.48-45.93)	12.1 (10.4-13.8)
	Fall	6.6 (6.1-7.2)	0.3 (n/a)	409.6 (364.1-455.1)	1.6 (0.8-2.3)	51.0 (30.9-71.1)	0.09 (0.00-0.03)	1.15 (0.05-3.93)	27.0 (16.5-37.6)
<b>Menendez (resident and anadromous)</b>									
	Spring	7.0 (n/a)	1.4 (1.3-1.4)	282.8 (274.4-291.2)	3.3 (2.1-4.4)	44.4 (24.9-63.9)	0.12 (0.03-0.20)	10.26 (0.10-57.13)	5.6 (22.2-28.7)
	Summer	5.4 (4.6-6.2)	1.0 (1.0-1.1)	224.9 (205.0-244.8)	1.1 (1.0-1.2)	51.7 (43.4-60.0)	0.41 (0.06-0.73)	1.50 (0.00-4.63)	22.2 (10.3-34.1)
	Fall	32.9 (8.3-57.5)	0.9 (0.5-1.3)	409.6 (364.1-455.1)	3.1 (2.8-3.4)	50.3 (47.6-53.0)	0.01 (0.00-0.05)	1.38 (0.65-3.25)	28.7 (15.8-41.6)
<b>Grande (resident and anadromous)</b>									
	Spring	7.0 (6.2-8.0)	2.1 (1.7-2.6)	496.6 (349.4-752.5)	8.9 (3.6-20.6)	49.4 (25.7-91.7)	0.21 (0.03-0.64)	1.16 (0.18-4.05)	13.4 (5.0-21.6)
	Summer	10.7 (9.2-12.2)	2.5 (1.6-4.0)	347.3 (266.5-464.5)	5.8 (0.7-17.2)	47.7 (36.6-72.8)	0.58 (0.00-2.04)	7.79 (0.00-62.42)	12.6 (10.7-14.0)
	Fall	13.7 (10.3-17.0)	1.9 (1.4-2.3)	559.3 (371.9-842.3)	9.2 (3.8-18.6)	37.2 (34.0-40.4)	0.03 (0.00-0.08)	4.16 (0.00-45.15)	12.3 (4.0-31.3)