POPULATION STATUS AND ECOLOGY OF BROWN TROUT RIO GRANDE, TIERRA DEL FUEGO, ARGENTINA

Submitted to:

Nervous Waters of Argentina
&
Estancia Maria Behety

Sarah O'Neal and Jack A. Stanford
Flathead Lake Biological Station
The University of Montana
311 Bio Station Lane
Polson, MT 59860-9659
Phone: 406-982-3301
Fax: 406-982-3201
www.umt.edu/flbs

October 30, 2006

Flathead Lake Biological Station REPORT No. 193-06

Citation:
O'Neal, S., J.A. Stanford. 2006. Population status and ecology of brown trout Rio Grande, Tierra del Fuego, Argentina. FLBS Report 193-06. Prepared for Nervous Waters of Argentina and Estancia Maria Behety, by Flathead Lake Biological Station, The University of Montana, Polson, Montana. 18 pp.

INTRODUCTION

During the 2006 angling season, Nervous Waters of Argentina (NWA), Estancia Maria Behety (EMB), Frontiers Travel, and The Fly Shop contracted the Flathead Lake Biological Station (FLBS) to a begin a scientific assessment of the economically important sea trout population in the Rio Grande of Tierra del Fuego. The goals of the project are to understand 1) the status of the brown trout population, 2) the effect of sport fishing on population structure and productivity, and 3) what factors, other than angling, may limit trout productivity in different reaches of the river system.

The study entailed two major parts. The first involved working with NWA and EMB fishing guides and clients to collect mark-recapture data as well as size data, scale, tissue, and some stomach content samples from the adult sea run brown trout population. These data taken over several years will allow us to demonstrate the size, age and genetic structure of the population, including resident and sea run (anadromous) forms, and mortality associated with angling. The second part of the study concerned the basic ecology of the river, including the importance of various main channel, floodplain and tributary habitats for growth and survival of brown trout. This involved electrofishing to determine spatial distribution of juvenile and resident brown trout and collection of temperature, water chemistry, and food web data as basic river indicators and, hence, trout productivity. We present herein preliminary results from our first year of study.

METHODS

A thorough understanding of the Rio Grande brown trout population requires examination of aspects not only of sea run fish, but of their offspring as well as their riverine habitat. For this study, we initially investigated habitat use by adult brown trout, which allowed us to focus our efforts regarding juvenile fish and more habitat general attributes in areas important to the adult fishery.

Adult sea trout

Data from adult sea run fish were collected in cooperation with NWA and EMB guides. Guides were provided with sampling equipment from FLBS which included: a notebook and data sheets for recording information about each tagged fish and instructions on tagging procedures, envelopes including a scale card and ethanol-filled vial for tissue storage, Floy tags, extra needles, and guns for tagging fish. Guides were provided with a brief training course early in the season, and the graduate research assistant accompanied guides in the field for a minimum of one day (and usually more) in the field. The tagging procedure generally lasted less than five minutes, and involved measuring length and girth; insertion of a Floy tag for individual identification; collection of 10-20 scales from above the lateral line and between the dorsal and adipose fins using a knife or hemostats; and clipping a small portion of the adipose fin. Scale samples were stored on a scale card in an envelope labeled with the associated Floy tag number, length, girth, gender, and location of fish captured. Due to unreliable weight data, fish weights were calculated using the following equation (Gowans, A. personal communication):

$$\text{Weight (kg)} = 41.4*\text{length(kg)}*\text{girth(kg)}^{\wedge}2$$

Adipose fin samples were stored in 95% ethanol in cryovials, and later dried for airline transport. Some of the tagged fish were additionally analyzed for stomach contents. 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.

In addition to non-lethal sample collections, samples were collected from accidental mortalities, and from fish heads provided by the Rio Grande public access gate near the river mouth. When feasible, otolith (ear stone) samples were collected from the heads, as well as muscle samples for stable isotope analysis, fins for genetic analysis, and scales. Fin and scale samples were stored as described above. Otolith samples were dried and placed in labeled cryovials for transport. Muscle samples were stored on ice throughout the season, as well as during their transport back to Montana.

Mark-recapture data was analyzed using a Schnabel (1938) estimate which requires the following assumptions are met: 1) marked fish do not lose their marks; 2) marked fish are not overlooked in the recaptured sample; 3) marked and unmarked fish are equally vulnerable to capture; 4) marked and unmarked fish experience low to no mortality; 5) following release, marked fish become randomly mixed with unmarked fish; and 6) there are no additions to the population during the study interval. All assumptions were met with the exception of the last assumption regarding an open population, and potentially the second assumption if any recaptured fish were not reported to the graduate research assistant. An open population Joly-Seber model is likely more applicable to the Rio Grande population, due to near constant immigration and emigration. However, low recapture rates and other data gaps prohibited the use of an open population model.

Scale samples were processed and analyzed at FLBS. The process entails sorting through samples and discarding unusable regenerated scales. Rio Grande sea trout scales exhibit an unusually high rate of regeneration. After identifying complete, or the best available scales, they were cleaned in a solution of 10% mild detergent water. They were subsequently mounted to gum tape, and finally pressed into acetate sheets using a Carver Laboratory Press at moderate heat under pressure. The scale impressions were subsequently magnified for analysis, and digital images were taken for future measurement of growth rates, and back-calculated length-at-age data. Age determination was performed in accordance with Elliott and Chambers (1996) after instruction provided by Riva Rossi (GESA, Puerto Madryn, personal communication). The process involves projecting the magnified impression of the scale, and evaluating concentric circuli, several of which are deposited in a circular pattern around the scale center each year. During cold winter months, growth is slower, and circuli appear closer together, demarcating years of growth and allowing for age calculation. “Plus” growth, that indicated by an incomplete portion of an annulus, was rounded to the nearest half year (0.5 years).

Juvenile trout

Six sites were identified for more detailed data collection regarding juvenile growth and density in varying habitat types throughout the lateral extent of the floodplain. These sites were located in the mainstem, in upper and lower reaches of the river; in secondary channels within the regularly flooded (parafluvial) zone of the river; and in orthofluvial channels that are rarely flooded but are fed by upwelling ground water from the floodplain aquifer (Stanford et al. 2005). Rigorous three-pass electrofishing, using a Smith Root LR-24 backpack unit, was conducted twice during the season to determine juvenile densities and growth rates. All fish were weighed (to nearest 0.1 gram) and measured (to nearest millimeter). Fish more than 90 mm were sampled for stomach contents, scales, and tissue (fins) as described above. In addition, larger fish were individually marked with PIT Tags. Samples were preserved as described above. Accidental mortalities were collected for otolith and stable isotope samples, also preserved as described above. Electrofishing data was entered into Excel and densities were calculated using depletion estimates generated by MicroFish software.

River ecology

At each of the electrofishing sites, we determined temperature patterns, water chemistry and invertebrate community composition relative to juvenile diet. Temperature data was collected on an hourly basis using VEMCO temperature data loggers deployed at the six primary sampling sites, as well as a few other locations. Temperatures are averaged on a daily basis for the purposes of this report. Water chemistry grab samples were frozen for transport to FLBS in Montana for analysis of primary plant growth nutrients, nitrogen and phosphorus. This is done on an “autoanalyzer” using a routine protocol (Lenore et al. 1998). Specific conductance and pH were measured using an electronic meter (Oakton model 10) that was calibrated with standard solutions before each field day.

The pH of water is a measure of the “acidity” ($pH < 7$) or “basicity” ($pH > 7$). The pH determines the solubility and biological availability of chemical constituent such as plant growth nutrients. Conductivity reflects the total ion content of water, and higher conductivity values in some locations than others may be related to either to groundwater influence or differences in geology. Nutrient concentrations indicate the relative “richness” of the aquatic environment. These water chemistry variables taken together are strong indicators of the productive potential of the river, providing temperature and flow patterns are suitable.

Qualitative benthic invertebrate samples were collected at each of the six sites, and quantitative invertebrate drift samples were collected at each site. Benthic invertebrate samples are collected by kicking invertebrates from the bottom gravel into a net, and subsequently preserving them. Drift samples are collected by placing a net in an area of moderate flow within the site to collect invertebrates from the water column. These samples could not be transported on airlines owing to the caustic preservative and therefore remain onsite in Rio Grande. We intend to analyze the samples in Rio Grande during the upcoming season.

RESULTS AND DISCUSSION

Physical characteristics of the Rio Grande

The Rio Grande is a middle order, meandering brown water river, originating from a headwater lake and a spring-fed Andean stream on the Chilean side of the border. Major tributaries flowing of the Rio Grande include the Radman, Menendez, and McLellan (or Ona) Rivers. Smaller tributaries include the Hermanita (or Herminia), Moneta, and Candelarias. The total river length, including these tributaries, is about 200km. We focused our work on the most downstream 60km of the river (above the estuary) with some sampling in tributaries of this reach.

The river within the study reach is low gradient, meandering through grasslands with very low relief and almost no woody riparian vegetation. The river is free flowing (no dams) and has a very low human population density. Oxbows and abandoned channels are clearly visible throughout the flood plain. Many of the abandoned channels contain upwelling ground water from the alluvial aquifer. These spring channels or floodplain spring brooks (Figure 1) are key attributes of gravel bed rivers with expansive flood plains (Stanford et al., 2005). They typically exhibit “dampened” thermal regimes; water temperatures are cooler than the main river during the summer and warmer than the main river during the winter. Consequently, these areas provide ideal habitat for growth of juvenile salmonids. Big floods like the one in winter, 2006 (see photo below), can fill these channels with sediment, or may scour new ones. Hence, habitat is created and maintained naturally by flooding. Flood scour also creates and maintains pools in the main channel that are preferred habitat for the sea trout as they prepare for spawning. The effects of the recent flood on the full range of trout habitats should be a primary consideration during future data collection efforts.

Figure 1. Meandering landscape of the Rio Grande (left). Winter 2006 flood, re-shaping the floodplain (middle). Example of an orthofluvial springbrook (right).

Within the floodplain, the river is dominated by pool-riffle reaches, which are common in mid-sized, low gradient, alluvial streams (Bisson and Montgomery, 1996) like the Rio Grande. Pools within the river clearly serve as critical holding habitat for adult sea trout as they migrate upstream for spawning. This is true of sea trout populations worldwide (Le Cren, 1984).

The river bottom varies from fine organics to cobble, but is dominated by gravel and small cobble (Figure 2). Thus the river bottom in many places seems ideal for sea trout spawning owing to good circulation of surface and ground water over the eggs. However, we need to measure hydraulic transmissivity in known spawning areas to verify this.

Figure 2. Medium-sized cobble typical of the Rio Grande floodplain that should be ideal for sea trout spawning.

River temperature is a primary determinant of the distribution and growth of trout and their forage. Consequently, we documented temperature patterns in a variety of habitat types: main channel, spring brooks and tributaries (Figure 3). Summer temperatures for most sites, particularly during the early part of the season, fell within the ideal range for brown trout growth, from, that is from 13 to 19° (Klemetsen et al. 2003). Although brown trout can thrive in temperatures ranging from from 0 to 25°C, their growth and metabolism tends to slow particularly below a temperature of 8°C (Heggens and Dokke 2001). One of the spring brooks, named “Guides” due to its proximity to Guides pool on La Retranca property, exhibited the classic summer cool pattern caused by the moderating effect of groundwater upwelling from the alluvial aquifer (Stanford et al., 2005). All of the spring brooks supported dense populations of juvenile trout, however. We concluded that temperature patterns generally were not limiting the sea trout population.

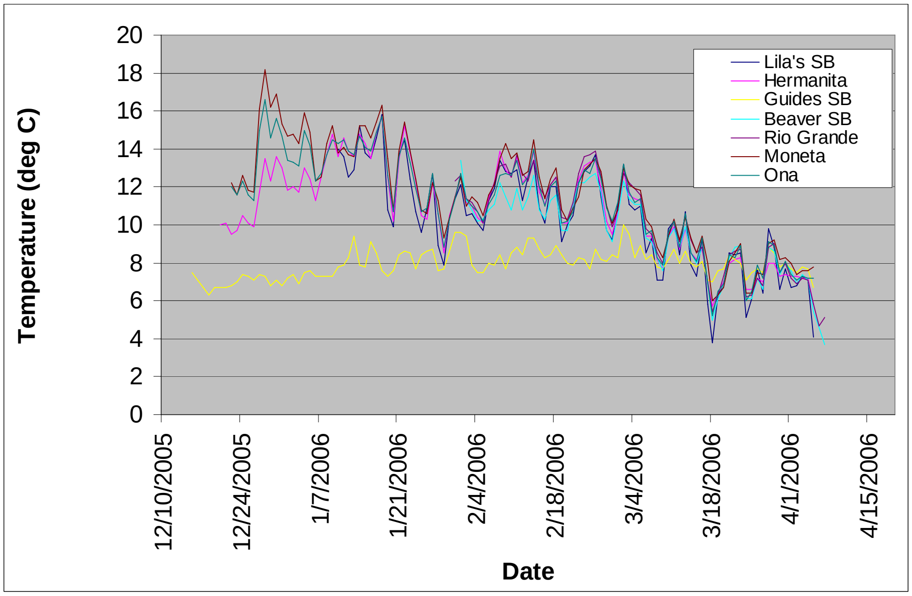

Figure 3. Thermal patterns in main stem, selected tributaries and spring brooks.

The waters of the Rio Grande exhibited moderate (basic) pH and moderate to low specific conductance values (Figure 4). The river is well buffered and is slightly on the "hard" side suggesting ample basic ion content to support rapid trout growth. Higher values in some of the spring brooks reflect ion accumulation in ground water that is supplying most or all of the flow in these environments except during extreme flooding. Variation among the tributaries most likely is due to different bedrock geologies.

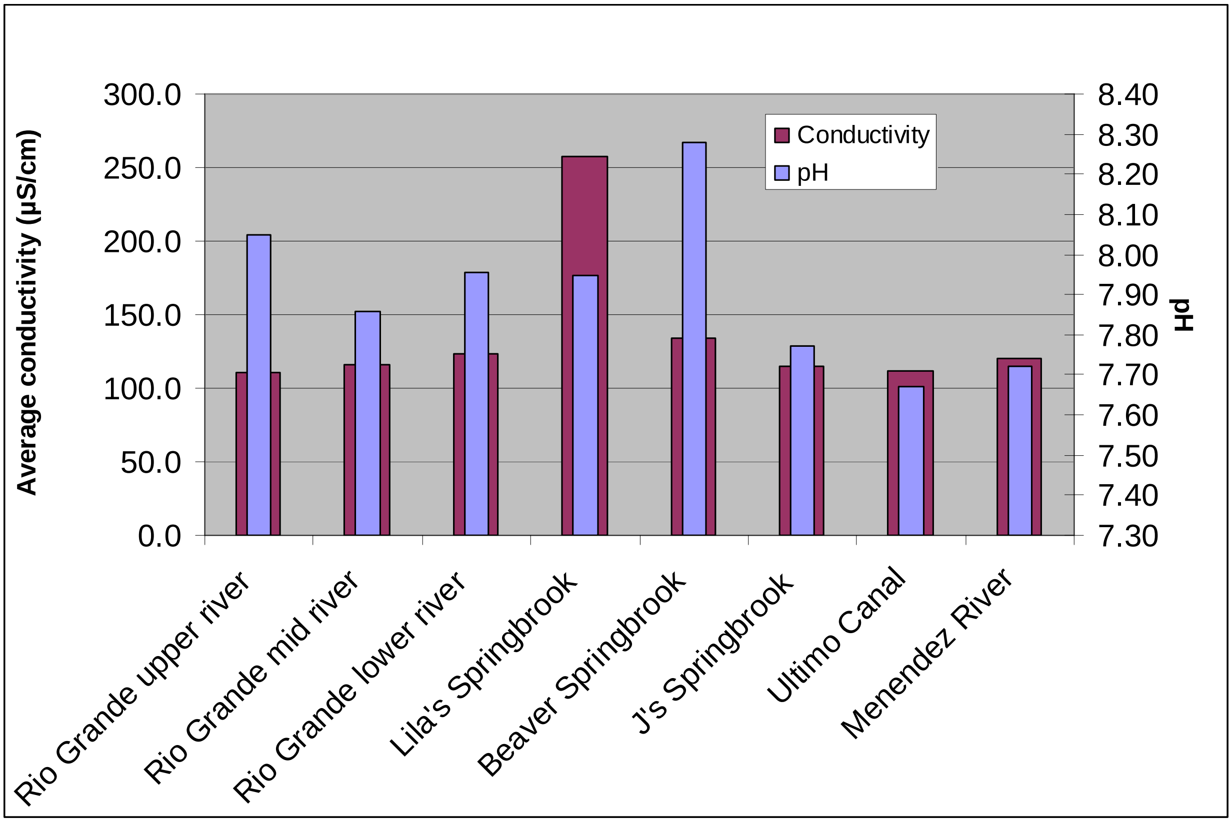

Figure 4. Average pH and specific conductance (=conductivity) at the main sampling sites in the study reach.

Nitrate and ammonium (NH$_3$) are the biologically available forms of nitrogen and SRP is the labile form of phosphorus. Values were quite high overall, as were the total concentrations (Figure 5 and 6). Highest nitrogen values were in the spring brooks (Lila's and Beaver). Ground water typically is high in nitrogen. Also these channels receive pasture runoff that likely has elevated nutrient content owing to the concentrations of sheep along in the riparian zone of the river. In any case, the Rio Grande has ample nutrients to support very high productivity. On the basis of the water chemistry, the Rio Grande should be considered eutrophic or highly productive (Wetzel 2001).

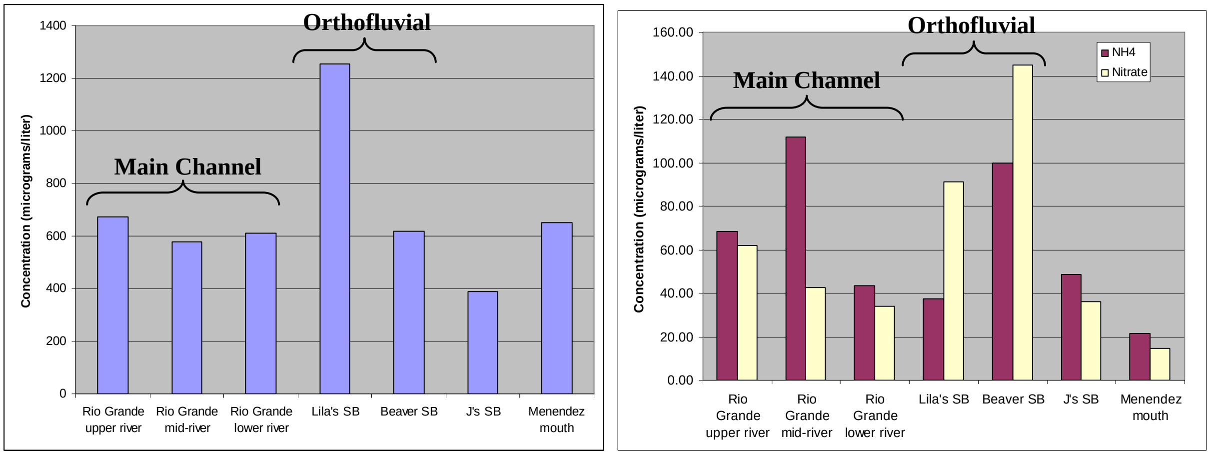

Figure 5. Average total nitrogen (left graph) and ammonia and nitrate (right graph) concentrations for various sites during the 2005-6 sampling season.

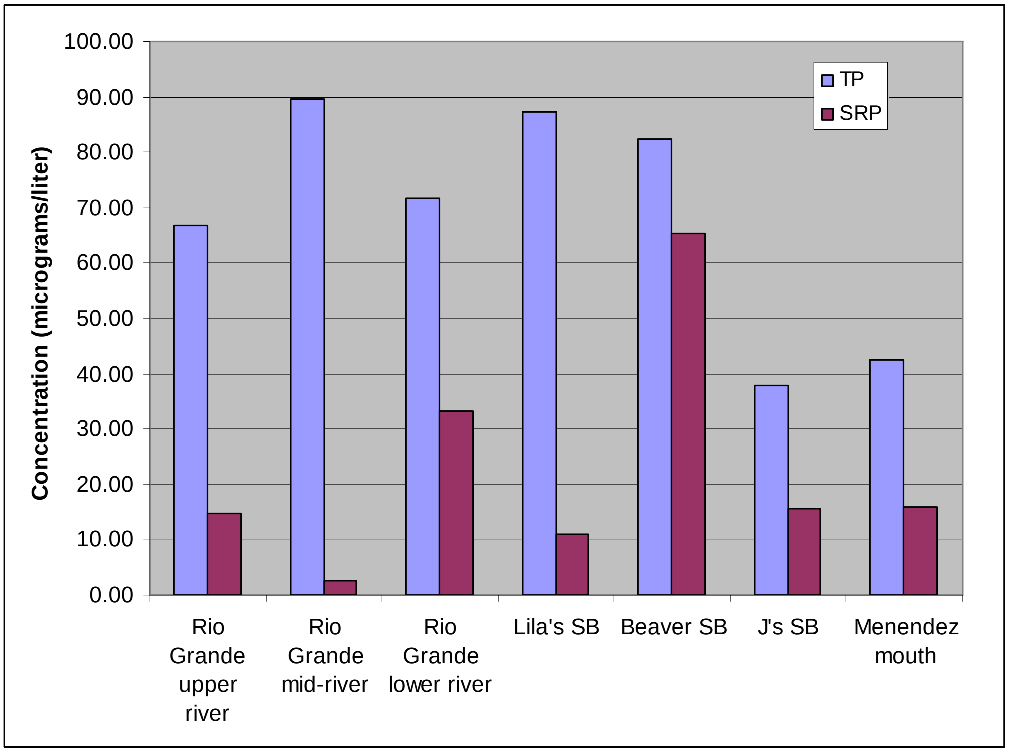

Figure 6. Average total nitrogen (left graph) and ammonia and nitrate (right graph) concentrations for various sites during the 2005-6 sampling season.

Adult sea trout population

During the course of the season, guides and others tagged a total of 1043 (19.9%) fish out of the 5233 fish caught between the five participating lodges. Of the 1043 marked fish, only twenty (0.02% of tagged fish) were recaptured, or recorded as recaptured, during the season. The Schnabel method produced a population estimate of 37,803 brown trout, with a 95%

confidence interval of 24,808 and 79,389. The confidence interval indicates that there is a 95% chance the population lies somewhere between 24,808 and 79,389 fish. The wide confidence interval is due to the low recapture rate. Confidence in the population estimate can (and should) be increased by increased tagging and careful reporting of recaptures. Because of the groundwork laid during the 2006 season, and a commitment to more rigorous tagging efforts, we think that a much more definitive population estimate will be forthcoming.

From a purely statistical perspective, due to the violation of the closed population assumption inherent in the Schnabel population estimate, our calculated population number should be an UNDER-estimate of the numbers of sea trout in the river. However, a run of 40,000 large sea trout into a river the size of the Rio Grande seems improbable based on experience in salmon rivers. On the other hand, looking at the estimate another way, consider that the Rio Grande has about 200km of river (including the larger tributaries) where sea trout have been observed or caught according to local people. This works out to about 200 fish per kilometer of river using our estimate. This seems plausible, but if so the Rio Grande has a VERY robust population and it must be a VERY productive river. So, we emphasize that our initial estimate is not robust owing to the sampling problems described above. We need greater guide participation in the future to verify the population estimate. We also strongly recommend adding a DIDSON Sonar unit with currently planned work as has been discussed. JAS had used a DIDSON on a steelhead river in Russia during fall 2006 with great success. We were able to enumerate large fish holding in deep pools with high confidence in a situation nearly identical to the Rio Grande. By coupling tagging with sonar, we can really nail down the numbers of fish returning to the river.

The size distribution of tagged fish is given in the histogram below (Figure 7). From the histogram, it appears there are more, large (and presumably older) fish than smaller ones. This suggests a declining population trend in an unbiased sample. However, it is likely this is an artifact of guides' sampling larger than smaller fish, and, consequently, we cannot reliably deduce population trends. There was no correlation between time of season and size of fish caught. A wide range of sizes was caught throughout the summer.

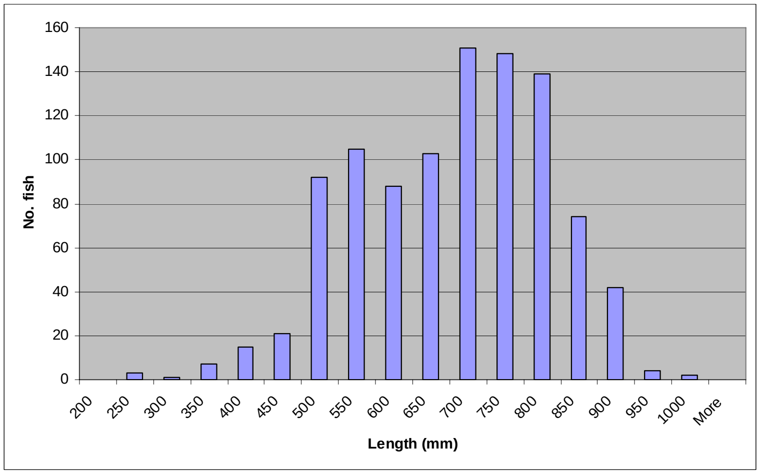

Figure 7. Size distribution of fish tagged during the 2006 season.

The ratio of female to male sea trout captured was 2.77:1 (Figure 8). This is similar to the ratio typically found in European trout populations (Elliott, 1994).

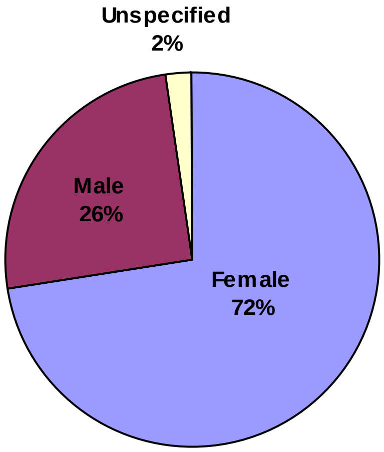

Figure 8. Genders of tagged fish

The low recapture rate of tagged fish (0.02%) certainly suggests a minimal impact of the recreational fishery in the Rio Grande; that is, almost all fish caught were only handled once by fishermen and, given the careful catch and release tactics used on the river, mortality should be minimal. Again, however, because of potentially biased sampling methodology, the recapture rate may be underestimated. But, dead fish were rarely observed on the river and if the population estimate is anywhere near right, mortality due to fishing cannot be significant. If rate of marking and recapture is suitable increased in future years, combined with the data we have in hand, we will be able to estimate mortality rates of the Rio Grande sea trout. One year of mark-recapture data, however, is not sufficient. We can say however, that the numbers of large sea run fish are quite large given the size of this relatively small river system. That of course is corroborated by the high success rate for fly fishermen that makes the Rio Grande famous.

On the other hand, the recapture data does provide useful information regarding fish movement. The average distance traveled by the twenty recaptured fish was 9.8 kilometers, and ranged from 0 km, for five fish that were captured twice in the same pool, to a maximum of 42.7 km. Travel distances are represented in Figure 9. Values are based on the assumption that fish swam a direct route to their recapture location.

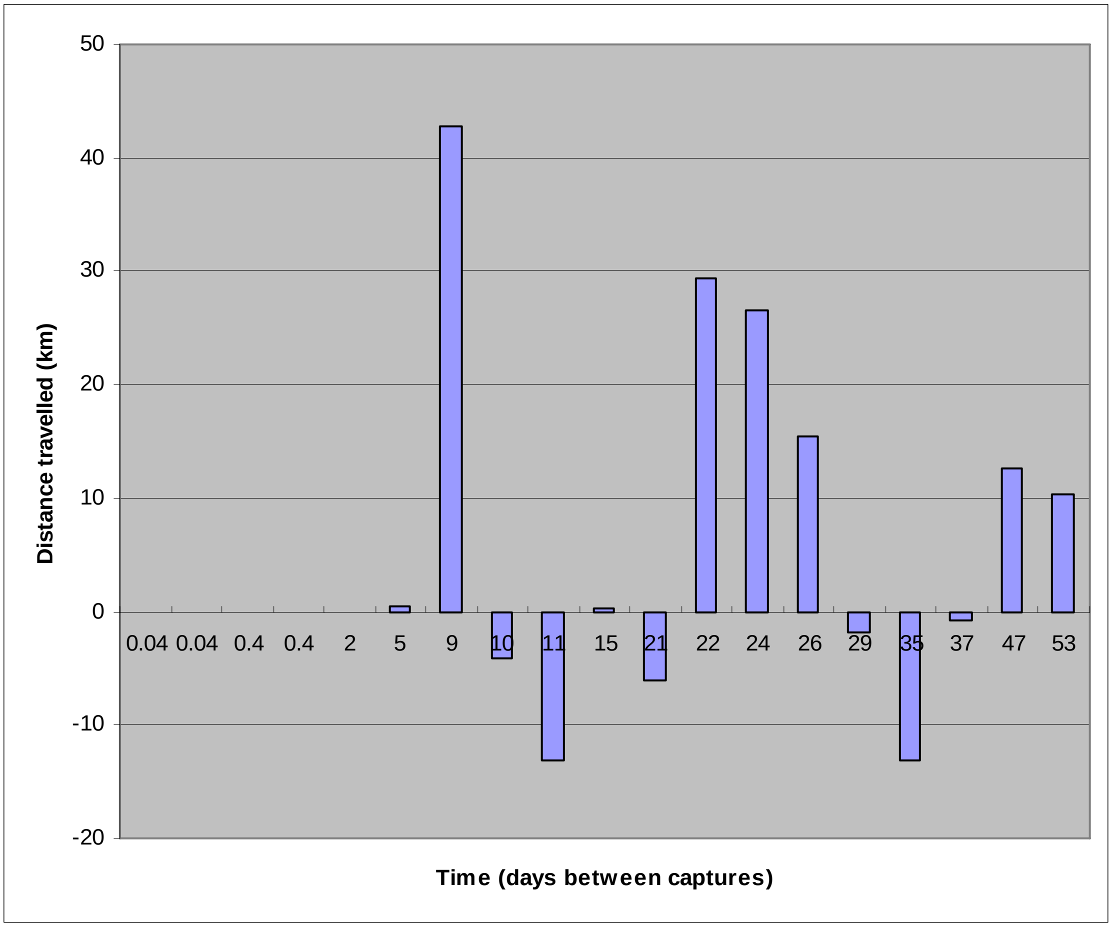

Figure 9. Distances traveled by each recaptured fish. Negative values indicate downstream movement and this presentation assumes that fish swam a direct route to their recapture location. Only 4 fish did not move from original capture location.

The average travel speed for fish was 0.56 km per day, ranging from 0 km to up to 4.74 kilometers per day. Most fish traveled 0.1 km per day or less (Figure 10) and probably stay for long periods in the deep pools of the main river in the study reach. This is typical of what is found in European sea trout populations as well (Le Cren 1984). The data also indicates both up- and downstream movement of fish, suggesting that all will not be simultaneously present in the river.

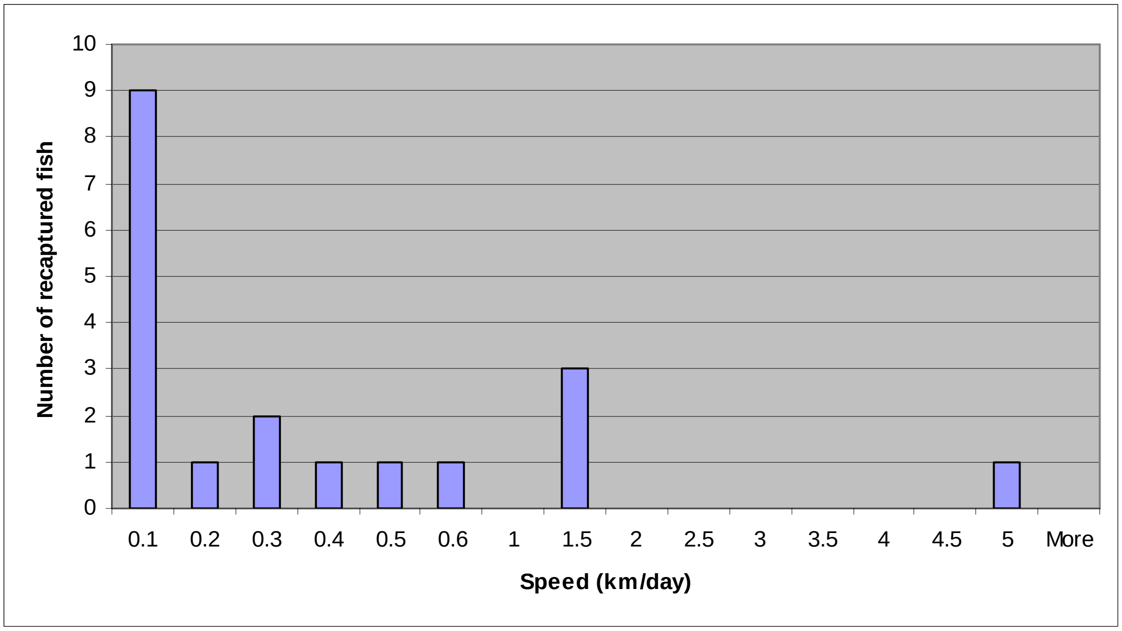

Figure 10. Frequency distribution of travel speeds. Most of the fish were moving at fairly slow rates, perhaps due to low water.

Spawning surveys proved to be much more difficult than anticipated due to very low visibility in the river. Consequently, information regarding spawning was collected largely from guides who are intimately familiar with fishing pools and the bottom formation. Guides began reporting spawning activity in the lower river as early as the second week of March, moving upriver and continuing through (and most likely beyond) the end of the season in April. Pools listed by guides as supporting dense redds (nests) include: La Roca, Arturo, Monster, Julia, No Cigar, Poacher's, Jackie's. There are undoubtedly additional key spawning locations. The DIDSON sonar described above for enumeration of fish also would allow direct observation of spawning activities. In Russia JAS and colleagues were able to record a large steelhead taking a fly using this sonar system including clearly recording the fly approaching the stationary fish.

Scale samples were collected from 968 fish. We aged 348 of these fish. Aging from scales was not easy because a surprisingly high percentage were regenerated scales, resulting from prior scale loss. Regenerated scales do not contain the complete life history of the fish and therefore cannot be used for aging. Consequently, we had to carefully search scales from each fish to find a suitable scale. For some fish, none of the scales were usable.

The sea trout varied in age from 1.5 to 13.5 years of age (Figure 11). The average age was 6.2 years. Interestingly, age does not appear highly correlated with fish weight (Figure 12). This may indicate that these fish experience a "patchy" food supply and/or that adult size is significantly determined by size and age at smoltification. Fish rearing in areas of higher food resources may grow more than fish rearing in areas of lower food resources, regardless of age. Additionally, there may be a sex bias in these data or the equation we used to estimate weight from length measurements is inaccurate.

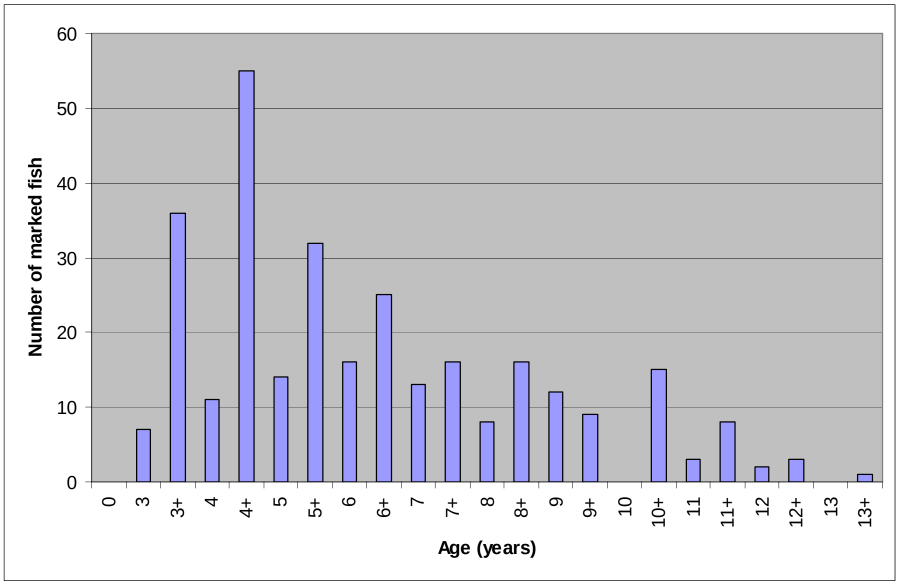

Figure 11. Age distribution for 348 adult sea trout in the Rio Grande, 2006.

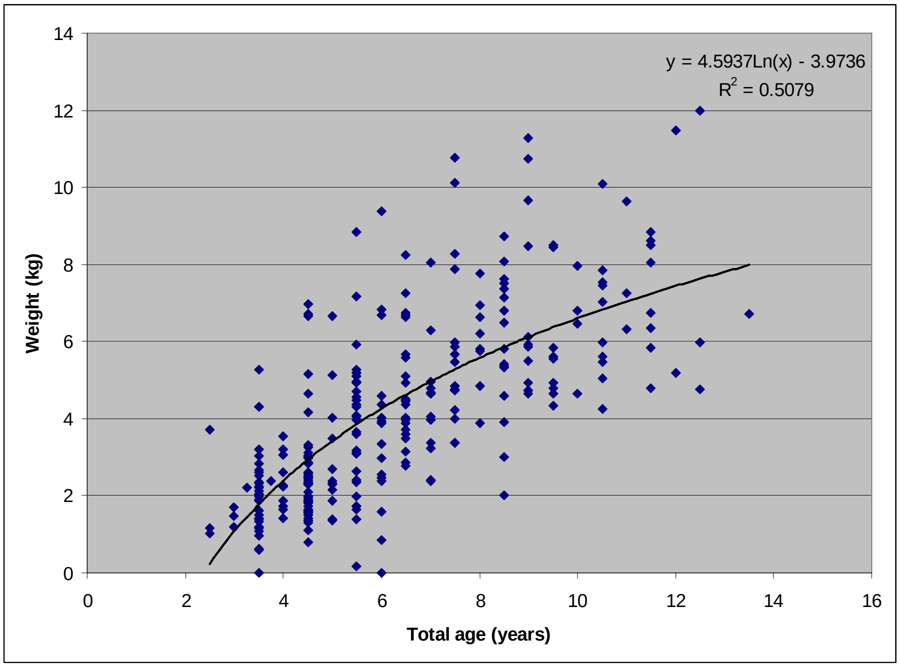

Figure 12. Weight in relation to age for Rio Grande sea trout, 2006

When the fish first enter the estuary or ocean, the growth rates increase substantially and thus the age at smoltification can be determined at the point where the width between annuli on the scales initially increases. Nearly half (49%) of fish in the sample smoltified at age two (Figure 13). Le Cren (1984) reviewed studies on smolt age for European sea trout and reported that two-thirds of fish enter the ocean after two years in freshwater, and approximately one-third migrate after three years in freshwater.

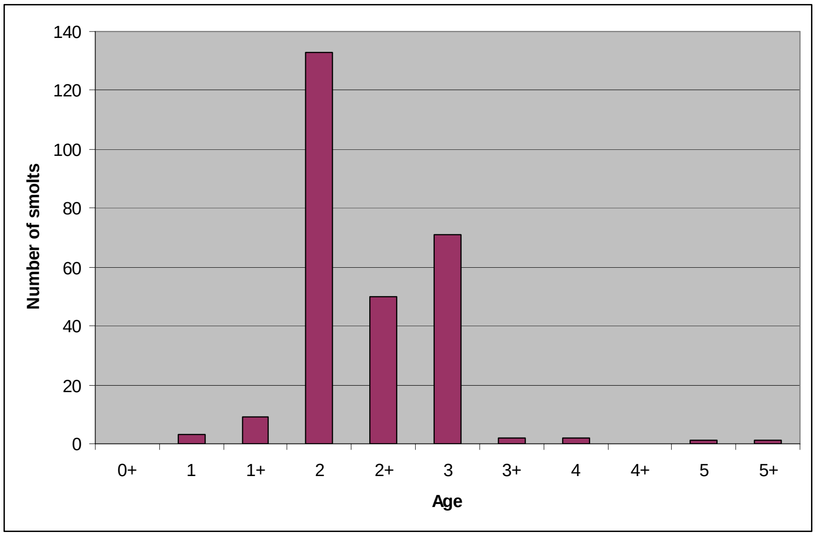

Figure 13. Age distribution for sea trout smolts in the Rio Grande, 2006.

Spawning marks are visible on fish scales as dark areas caused by cessation of growth as the fish stop feeding during migration and spawning. However, the absence of a spawning mark does not signify that fish did not spawn (Elliott and Chambers, 1996). Consequently, only a minimum possible number of spawning events can be counted from scale samples. Spawning marks were positively identified on only 105 scales. Of those, 47 (45% of scales with spawning marks), contained one spawning mark, ranging in age between one year at sea and six years at sea. Twenty three scales (22%) contained two spawning marks, signifying a minimum of two spawning events during the life history of those fish; 19 (18%) contained three spawning marks, 14 (13%) contained four spawning marks; and only one contained five, and one contained six spawning marks, signifying a minimum of five and six spawning events respectively. So, some of the Rio Grande fish were oldsters that were coming back for the 4th-7th time when we caught and tagged them. The earliest spawning mark was seen after only one summer at sea (sea age 0+), and the latest was seen after nine summers at sea (sea age 9). The majority of fish with spawning marks spent two or three full years at sea before returning to spawn for the first time at an average total age of 4+. This correlates with the highest frequency of tagged fish (Figure 5), indicating a high number of what were likely first time spawners were in the river. Unlike the length-frequency relationship (Figure1), this is indicative of a more stable population structure. A population with a higher number of younger, first time spawners is more likely to be either growing or stable.

Stomach contents of some adult sea trout were analyzed using lavage (n=46), in order to confirm the assumption that adult sea trout are not feeding in the river. Indeed, the majority of fish analyzed had empty stomachs and several dead fish that we gutted had no evidence of any recent feeding. However, approximately 25% of adult fish that were stomach pumped regurgitated a small amount (relative to resident adults and juveniles). Food items consisted mainly of scuds (87.5%), and, in one case, a mostly digested unidentifiable fish. Those fish with a small amount of food in their stomachs appear to be first time spawners based on the scale analysis.

Juvenile trout

Spring fed, off-channel habitat, termed "springbrooks" clearly had the highest density of brown trout juveniles (Figure 14). Densities were very low in the main channel, probably because food or cover was less available. We intend to investigate this aspect of brown trout ecology more thoroughly in 2007.

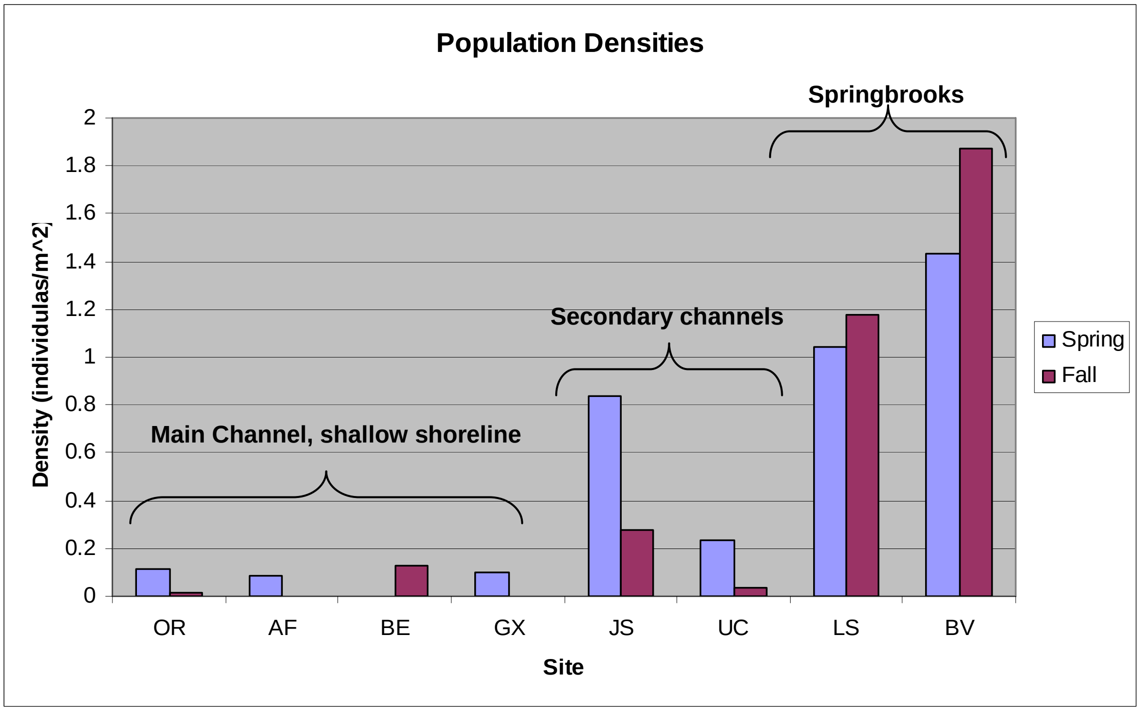

Figure 14. Juvenile densities in various habitat types where three-pass electrofishing was conducted.

Scuds (freshwater shrimps or Amphipoda) proved to be the most important food of juvenile trout in all habitat types. Scuds were found in 59% of all juvenile stomachs pumped. Terrestrial insects, caddisflies, and mayflies were also important food items, though to a lesser extent (Figure 15). Brown trout are known as opportunistic feeders (Klemetsen et al. 2003), and consequently, their diet is likely simply a reflection of what is available for feeding within the system.

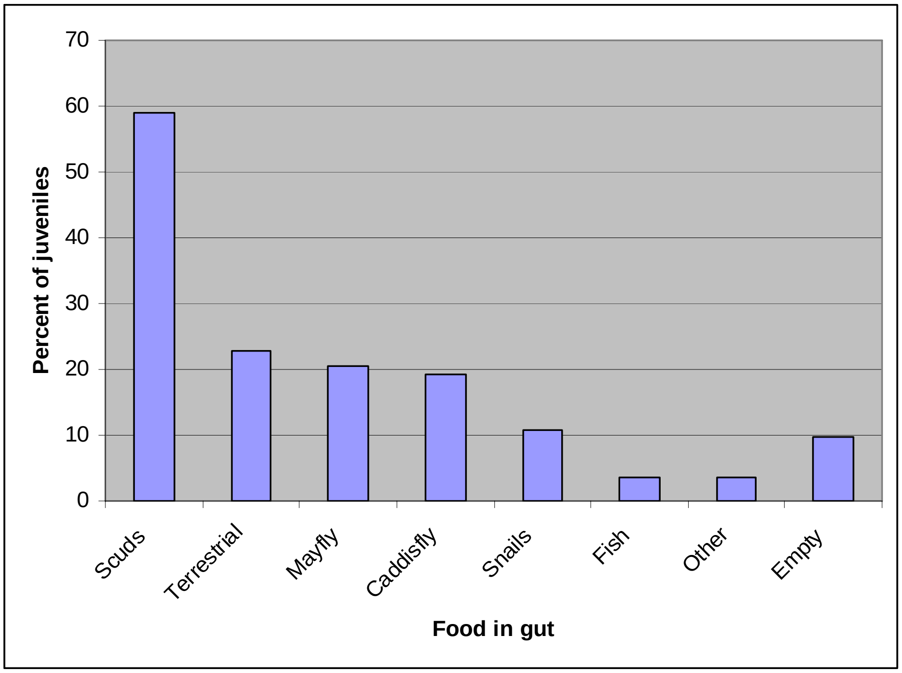

Figure 15. Percent of juvenile fish examined with food item in gut.

When diet data are parsed by habitat, it appears that off channel habitat (including backwaters, springbrooks, and tributaries) are important feeding locations (Figure 16). The highest percentage of empty stomachs occurred in the main channel of the Rio Grande.

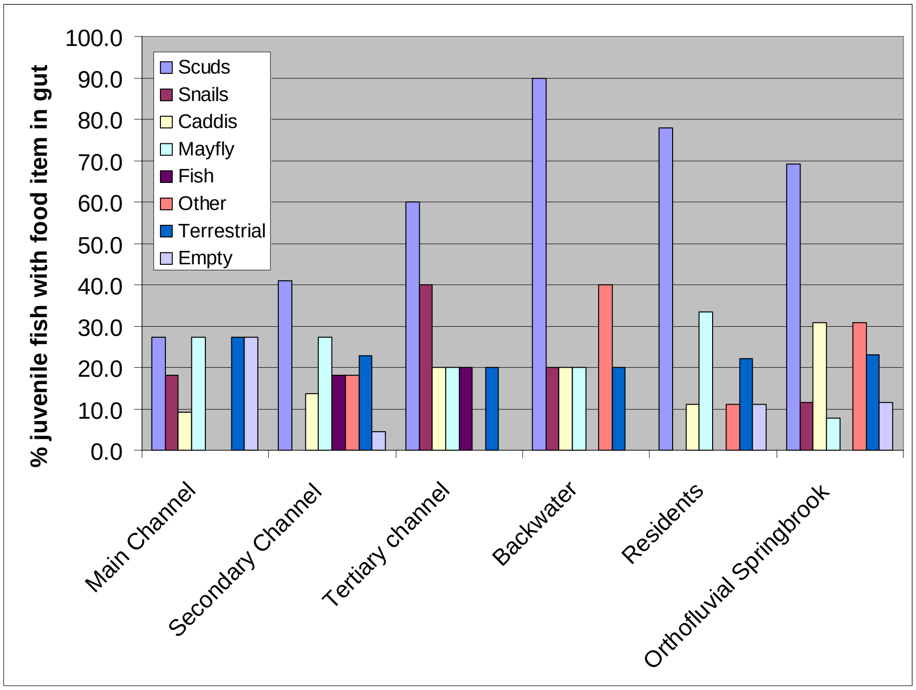

Figure 16. Percent of juvenile fish with food item in gut by habitat types.

SUMMARY AND RECOMMENDATIONS

The low gradient, meandering nature of the Rio Grande, combined with extensive areas of unconsolidated gravel and cobble, ideal temperatures, and high ion and nutrient content of the water, is ideal brown trout habitat. We found juvenile fish in every main channel, flood plain and tributary site that we sampled. Numbers of juveniles were much higher in the spring brooks and tributary streams. These environments, not the main channel, apparently are the rearing habitats for sea trout. The young fish feed preferentially on scuds that appear to be very abundant in the rearing habitats; but, more analysis of the food web is needed. Resident brown trout were collected and are often caught by anglers. All of the resident fish we examined were males, whereas 72% of the sea trout were females. Probably sea trout females often mate with resident males. This can be determined from otolith (ear stone) analyses in the future. Average age of sea trout returning to spawn in 2006 was 6.2 years and they typically went to the ocean after 2-3 years in the river. Spawning apparently begins in late March.

Overall, the sea population appears robust and the run size in 2006 certainly numbered in thousands, probably many thousands. Indeed, our mark-recapture estimate was 37,803 fish. But we are not at all confident of that number because only 20% of the fish caught by anglers were tagged only 20 recoveries were reported. Continued data collection is required for a more accurate population estimate in addition to mortality estimates, and quantification of population trends. If the true re-catch rate is only 20 out of 1000 as indicated by the tagging program in 2006, there is no impact on the fishery by the catch-and-release activity. The only potentially negative aspect of the fishery that we noted is that the fishing season in 2006 continued into the spawning period. Treading on redds by anglers and guides may disturb spawning behavior. We have no evidence that this is problematic for sustaining the population however.

We have obtained a very basic understanding of this important trout fishery. We recommend continued study of the population in order to solidify population estimates, clearly quantify population structure and stability, precisely delineate spawning areas (tributaries included), and understand factors influencing juvenile distribution, growth and smoltification. This requires full participation from all contributing lodges and guides in the tagging program. We have recruited participation by Dr. Miguel Pascuel, an Argentine scientist of considerable repute in fish ecology, to work with us on the Rio Grande in 2007, significantly increasing project capacity. We also are very interested in the rainbow and steelhead (*Oncorhynchus mykiss*) in the Rio Grande, as potential competitors with the sea trout if the mykiss population is expanding. Finally, we strongly recommend using a DIDSON Sonar for direct observation of the adult sea trout. This proven methodology would corroborate the tagging work and this particular sonar is the only way we know of to observe spawning behavior owing to the characteristic dark color and often high turbidity at high flows during spawning season.

CITATIONS

Elliott, J.M. 1994. Quantitative Ecology and the Brown Trout. Oxford University Press. Oxford.

Elliott, J.M. and S. Chambers. 1996. A Guide to the Interpretation of Sea Trout Scales. Institute of Freshwater Ecology. Windermere Laboratory. R&D Report 22.

Heggenes, J. & Dokk, J.G. 2001. Contrasting temperatures, waterflows, and light: Seasonal habitat selection by young Atlantic salmon and brown trout in a boreonemoral river. *Regulated Rivers: Research and Management* 17: 623–635.

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* 2003: 12: 1–59.

Le Cren, E.D. 1984. The biology of the sea trout. Atlantic Salmon Trust and Welsh Water Authority.

Lenore, S.C., A.E. Greenberg, A.D. Eaton. 1998. Standard Methods for the Examination of Water and Wastewater (20th Ed.). American Public Health Association

Lorang, M.S., and F.R. Hauer. 2006. Fluvial geomorphic processes. Chapter 7 in F. R. Hauer and G. A. Lamberti (Eds.) 2nd Edition. *Methods in Stream Ecology*. Academic Press/Elsevier. San Diego.

Schnabel, Z.E. 1938. The estimation of the total fish population of a lake. *American Mathematical Monographs* 45: 348-368.

Stanford, J.A. M.S. Lorang, and F.R. Hauer. 2005. The shifting habitat mosaic of river ecosystems. *Verh. Internat. Verein. Limnol.* 29: 123-136.

Wetzle, R.G. 2001. Limnology: Lake and River Ecosystems. Third Ed. Academic Press. San Diego.