ABSTRACT

MOORMAN, MICHELLE CHATELAIN. The Conservation Implications of Introduced Trout and Beaver on Native Fish in the Cape Horn Biosphere Reserve, Chile. (Under the direction of David B. Eggleston.)

Introduced species are a threat to native species conservation worldwide and can cause an overall reduction in biodiversity. In the Cape Horn Biosphere Reserve in southern Chile, introduced beaver and trout are highly successful invaders in the landscape and alter stream ecosystem function. Our research suggests introduced beaver create favorable feeding habitats for native puye (*Galaxias maculatus)* by increasing available macrobenthic biomass and creating ideal feeding conditions for puye. A negative effect of trout on puye was only detectable in beaver-altered habitats where puye abundance was significantly reduced, a finding most likely due to the fact trout reduce prey availability in beaver-altered habitats. Our findings also show the presence of endangered *Aplochiton spp.* on Navarino and Hoste islands and the absence of brown trout completely from the southeast fringe of the Cape Horn Biosphere Reserve. Research in the Falkland Islands showed that if brown trout successfully invaded a watershed, *Aplochiton zebra* populations disappeared. Conservation measures should be taken to prevent the spread of brown trout into the area to protect rare *Aplochitons spp.* These results emphasize the need for understanding introduced species distributions and their influence on native biota and stream ecology so conservation measures to preserve native species and the pristine status of the Cape Horn Biosphere Reserve can be implemented.

THE CONSERVATION IMPLICATIONS OF INTRODUCED TROUT AND BEAVER ON NATIVE FISH IN THE CAPE HORN BIOSPHERE RESERVE, CHILE

By

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DEDICATION

To my mom, for giving me the encouragement and confidence to dream big.

To my husband, Chris Moorman, for providing patience, support and laughter through it all.

BIOGRAPHY

Michelle Moorman was born on a very hot July 9, 1977 in Richmond, Virginia to Yvonne Reid and Raymond Cienek. Her childhood was spent in Greensboro, NC where she was fascinated by nature and water and was commonly found playing in the woods, swimming in the creek, and climbing trees. It was her passion for the outdoors and the environment that led her to pursue a double major in Geography and Recreation Administration at the University of North Carolina at Chapel Hill. She often joked that she could tell people where to go to have fun with her degree, but it was during her summer internship with the U.S. Fish and Wildlife Service at Pea Island National Wildilfe Refuge that she fell in love with the field of environmental science and decided she wanted to study the environment rather then lead people to it.

After spending a year working and traveling, she obtained a job with the U.S. Geological Survey where she was surprised to learn she could get paid for her childhood passions of catching bugs and fish, riding around in boats, and playing in streams. During this time, she also traveled to Chile with her future husband, Chris Moorman on a three month backpacking trip. While they were in Chile, they volunteered with the Omora foundation where their friend Chris Anderson was completing his doctoral research. The following year the Omora foundation asked Michelle to return and help lead an ecological expedition in the Cape Horn Biosphere Reserve.

During this time, Michelle decided to return to graduate school and the Omora foundation encouraged her to write a grant so she could return to study the fish in Chile. She was contacted by Dr. David Eggleston who took her on as a graduate student and with excitement and nervousness allowed Michelle to pursue her graduate project in Chile while keeping a backup plan in case funding did not come through.. Michelle received funding from the Wildlife Conservation Society to return to Chile and the result of this work is documented in her master's thesis. During her time as a graduate student, Michelle has enjoyed being involved in the Student Fisheries Society and the MEAS Graduate Student Association, as well as her coursework and additional field experiences in marine science. She also has taken study breaks to travel, windsurf, sail, and mountain bike and looks forward to the new opportunities and adventures the future will bring.

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Above all, I would like to thank my advisor, Dave Eggleston, for his invaluable input, support, and guidance on this project. I want to thank Dave for taking a chance and allowing me to pursue my own research project in Chile even though he might have had reservations. Thank you, the experience was invaluable to me.

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I. INTRODUCTION

Invasions by nonnative species are a serious threat to freshwater ecosystems (Kolar and Lodge 2001; Rahel 2002; Dunham et al. 2002) and are a concern to conservation managers who are responsible for mitigating negative impacts (Parker et al. 1999). Invasive species are a principal component of global ecological change and can cause an overall reduction in biodiversity, even though they may enhance species richness at the regional and local level through interactions such as competitive displacement (Sax and Gaines 2003; Wilcove et al. 1998; Vitousek et al. 1997). Invasive species have demonstrated that they can be a problem in areas with limited human disturbance. For example, the relatively remote and pristine Cape Horn Biosphere Reserve, Chile harbors two successful invaders: beaver (Castor canadensis) and trout (Salmo trutta, Salvelinus fontinalis, and Oncorhynchus mykiss), which dominate the aquatic ecosystems on the fringes of the Reserve (Vila 1999, Lizarralde and Escobar 2000, Rozzi et al. 2004, Anderson et al. 2006). Historically, trout are one of the world's most successful invaders of cold water ecosystems (Townsend 1996; McIntosh et al. 1994; Flecker and Carrerra 2000; McDowall 2003). In their native habitats, beaver are well known ecosystem engineers capable of altering resources and habitat in a disproportionate manner, and have been speculated to alter non-native ecosystems significantly greater then other invasive species due to ecosystem engineering (Jones et al. 1996; Crooks 2002). While the negative consequences of an invasive species in an ecosystem are generally understood, complex interactions between multiple invasive species are often not. Theories of positive feedback loops between two invasive species suggest that the modification of a habitat by one invasive species facilitates the invasion of the habitat by another invasive species (Simberloff 1999, 2006); however solid evidence in support of these theories does not yet exist. In this study, we evaluate the interactive effects of two invasive species (beaver and trout) on native freshwater fish in the Cape Horn Biosphere Reserve Chile.

The introduction of non-native species presents one of the biggest threats to the Cape Horn ecosystem with approximately half of the terrestrial (12 of 22) and freshwater fish species (3 of 7) being introduced (Lizarralde and Escobar 2000; Rozzi et al. 2004; Anderson et al. 2006). In 1946, twenty-five pairs of the North American beaver, *Castor canadensis,* were introduced to Tierra del Fuego as a fur and food resource. Since then, beaver have proliferated and attained densities of approximately 1.1 colonies per a km of waterway in 75% of Tierra del Fuego and all of Navarino Island (Skewes et al. 1999; Anderson 2006). Beavers impact native fish by dramatically changing the stream ecosystem. For example, stream impoundments created by beavers enhance retention of organic matter (Naiman et al. 1986), sediment (Butler and Malanson 1995), and water (Burns and McDonnell 1998) which, in turn, affect a wide range of biotic and abiotic variables in a stream. Beaver impoundments can also alter available light, nutrient cycling and partitioning of resources (Naiman et al. 1988, 1994), current velocities, sediment deposition, (Butler and Malanson 1995) and macroinvertebrate biomass and diversity (McDowell and Naiman 1986; Anderson et al. 2006). In the Cape Horn Biosphere Reserve, macrobenthic biomass in beaver disturbed reaches is more then twice as much as macrobenthic biomass in undisturbed reaches, which, in turn, may be followed by increases in the biomass of macrobenthic predators (Pollock et al 1995; Anderson et al. 2006).

The effect of trout on native fish species is typically negative, since trout are known to be one of the most effective invaders world-wide and usually reduce native fish populations through competitive displacement and predation (Townsend 1996; Glova 2003; McDowall 2003). Three species of non-native trout, including *Oncorhynchus mykiss*, rainbow trout; *Salmo trutta,* brown trout; and *Salvelinus fontinalis,* brook trout were introduced to Tierra del Fuego in the early 1900's as a food and sport fishing resource (Vigliano and Darrigran 2002). Today, trout are an important economic resource in Southern Chile, supporting a recreational fishing industry (Soto et al. 2006). Studies examining competitive effects of introduced trout in southern Chile suggest the presence of trout in streams has displaced or reduced native fish densities through their predatory activities on native fish and their prey (Soto et al. 2006; Vila 1999).

Four native fish species currently listed on the Chilean red-list as either vulnerable or endangered, are expected to be present in the Cape Horn region (Cussac et. al 2004; Glade 1993). Little is known about native fish distributions in Tierra del Fuego, but all natives are members of the Osmeriform order and family Galaxiidae. *Galaxias spp.* are the most abundant with *Galaxias maculatus* or puye, being a stream dweller and *G. platei* being a specialized bottom dweller. *Aplochiton spp.* are rare with little documentation in southern Chile (Vila et al. 1999; Cussac et al. 2004; Soto et al. 2006). With the exception of *G. platei,* all species are catadromous fish that migrate to the estuaries to spawn, spend their juvenile existence at sea, and return to freshwater streams to live as adults, however, land-locked populations of all species exist (Cussac et al. 2004). A study of feeding preference conducted by Jowett (2002) showed catadromous puye prefer habitats downstream of flow constrictions, especially where food is concentrated and velocities are slow enough to hold a feeding position in the water column.

The influence of an invasive species is dependent on how their presence affects available resources for native species (Vitousek at al. 1987) and how their numbers dominate the landscape (Strayer et al. 1999). The effects of non-native trout and beaver in the pristine Cape Horn Biosphere Reserve are of particular concern due to their invasive history and pervasiveness throughout the landscape in Southern Chile. Puye usually occur in reduced abundance and along stream shallows when brown and rainbow trout are present (Vila et al. 1999; Glova 2003; Soto et al. 2006). Despite this claim, the extent of trout introductions in the Cape Horn Biosphere Reserve was not previously known for Navarino and Hoste Islands, and the effect of trout on native fish in southern Chile is not well studied (Vila et al. 1999, Soto et al. 2006). The impact of beaver on native puye densities is less understood, with one previous study showing puye densities significantly higher in streams with beaver ponds present than without (Vila et al. 1999). Because beaver disturbances enhance macrobenthic biomass, and trout are predicted to reduce available prey, we expecte puye densities to be highest in the presence of beaver disturbances and in the absence of competitive trout (Glova 2003; McDowall 2003; Anderson, 2006).

In addition to evaluating the influence of invasive species on native fish, we also examined environmental variables that influence fish distribution and abundance. For example, factors such as riparian habitat and instream variables including velocity, depth, substrate, and percent pool can influence puye distributions (Jowett 2002, Jowett et al. 2003). We carried out a stream assessment of each reach which provided a synopsis of the environmental conditions present in a stream to assess streams and determine naturally occurring differences. The Stream Visual Assessment Protocol (SVAP) is a simple rapid assessment tool that can be used to assess the ecological conditions of low-order streams and is a suitable tool for initial in-stream assessments (Bjorkland et al. 1999).

II. HYPOTHESES

This study assessed the impact of non-native trout and beaver on native fish and their benthic prey, as well as the potential effects of habitat characteristics and environmental variables on native stream fish in the Cape Horn Biosphere Reserve, Chile. Five *a-priori* hypotheses were tested:

H1: The mean density of native puye fish and non-native trout in streams will vary by riparian habitat since stream morphology and riparian landcover influence the distribution of fish.

H2: The mean density of native puye fish in streams will be highest in beaver-disturbed reaches, determined by the presence of a beaver dam within 50 m upstream of the end of the sampled reach, and lowest in the presence of non-native trout which compete for food resources with native puye.

H3: There will be a negative relationship between the macrobenthic biomass and the density of non-native trout because non-native trout prey on aquatic macroinvertebrates.

H4: The density of native puye fish will be higher in streams with a higher Stream Visual Assessment Protocol (SVAP) score because high SVAP scores are an index of favorable stream conditions for fish.

H5a: The density of native puye fish will increase as the percent soft substrate increases because puye prefer reaches with a higher percentage of soft substrate.

H5b: The density of native puye fish will increase as the percent pool habitat increases because puye prefer to feed in deeper and slower streams.

H5c: The density of native puye fish will increase as average depth increases because puye prefer streams with deeper water columns.

H5d: The density of native puye fish will decrease as stream velocities increase because puye prefer low velocity waters for feeding.

III. METHODS

Study systems

This study was conducted on the eastern edge of the Cape Horn Biosphere Reserve on Navarino and Hoste Islands, Tierra del Fuego, Chile (Fig. 1). The vegetation of these islands consist of a forested, steep north slope, dominated by broad-leafed deciduous forests of the genus *Nothofagus,* and Magellanic tundra and bog habitat on the more gently sloping south-side of the islands. Temperature decreases and precipitation increases from northeast to southwest across the islands. Human populations and associated human disturbances are concentrated on Navarino Island (est. 2500 people) in the regional capital, Puerto Williams. Human disturbance on Hoste Island is minimal, with a few ranches and navy outposts (pop. i.c. <10) (Rozzi et al. 2004). Introduced beavers are altering the forested north-slope of both islands by deforesting riparian areas and creating beaver dams.

Site selection

A total of 23 watersheds consisting of 22 streams and one lake, were sampled from January to March 2006 to characterize habitat and fish communities (Table 1 and Fig. 2).

For this study, the term "site" will be used to describe each discrete watershed sampled and "reach" will be used to refer to each discrete length of stream that was sampled. Site selection was based on an initial analysis of landcover using GIS, discussion with local scientists, and field reconnaissance of the selected sites before data collection.

Four different riparian habitats were sampled (e.g., beaver-disturbed, scrub, forest, and meadow) with 4-14 sites sampled for a given habitat type (Table 1 and see "Habitat Classification" section below). An unbalanced design with respect to riparian habitat type and beaver disturbance was utilized because access in the region is limited. There is a dirt road on the north side of Navarino Island that can be used to access all watersheds on the north side of the island, but all other destinations have to be reached by boat. A boat was hired for one week, but the watersheds and riparian habitat types available to be sampled were limited by accessibility. We also recorded whether or not a beaver dam was located upstream of the sampled stream reach (<50 m), as an indicator of beaver disturbance. Since catadromous native fish were the focus of this study, we located stream reaches close to the coast where densities would be greatest. All sites were initially sampled for fish using double-pass electro-fishing techniques (Lyons 1993; Moulton et al. 2000), starting 50 meters upstream from the road or from the coast to avoid any impact the road or saltwater could have on the stream fish assemblages. All sampled reaches covered a distance that was 20 times the mean channel width, or roughly one meander wavelength, since this distance should adequately represent one riffle, pool, run sequence or all available geomorphic units in the stream reach (Fitzpatrick et al. 1998). Specific conductivity measurements were recorded at each site to ensure we were sampling freshwater systems.

Habitat classification

Stream characteristics and riparian land cover in the watershed are thought to influence the distribution of native fish (Jowett et al. 2003). We used a general classification of the riparian habitat along a sampled reach based on the general habitat classifications outlined by Moore (1983), with the addition of a category to represent beaver disturbed habitats. These habitat classification categories included forest, scrub, meadow, and beaver disturbed. All reaches were measured in meters and the total length of each riparian habitat type present was recorded. Riparian habitat classification was designated according to the riparian habitat type with the greatest percent coverage along the reach. Forested habitats are composed primarily of mature evergreen or deciduous *Nothofagus* species and are the dominant habitat on the north-slope of the island. The introduction of beavers is disturbing these forested habitats through the construction of beaver dams. Beaver dams impound the water and create a stagnant pool and much of the riparian vegetation dies due to flooding of the riparian zone. Sediment and organic detritus accumulates in an impounded reach and the stream directly downstream of a beaver dam is termed beaver disturbed (Butler and Malanson 1995). Beaver disturbances alter the riparian ecology by increasing aquatic macroinvertebrate density, decreasing aquatic macroinvertebrate diversity, creating a more homogenous bottom substrate, and reducing stream velocity (Anderson 2006). In time, the dam will breach and the river can begin to return to its natural state. The previously impounded system will initially be re-colonized by grasses and other plants progressing into a meadow habitat. Meadows are dominated by native and non-native grasses and often coincide with areas deforested in the past by beavers or loggers (Anderson et al. 2006, Martínez Pastur et al. 2006). Scrub is a transitional habitat between beaver meadow and forest when the meadow begins to be re-colonized by larger plants and small trees. Scrub habitats represent transitional zones between the forests, and bog or meadow communities (Moore 1983).

Fish sampling

Freshwater fish fauna were sampled using double-pass, backpack electrofishing with a LR-24 Smith-Root Backpack unit. Length of reaches was set to 20 times their average width, with a minimum length of 100 meters to insure adequate sampling of all in-stream habitat features for each reach (Fitzpatrick et al. 1998; Moulton 2002). Block-nets of 0.5 cm knotless mesh measuring 2 m deep X 15 m long enclosed the upstream and downstream ends of the reach during electro-fishing. Based on the depth (wadeable, <1 m) and width (1 - 10 m) of these streams, as well as the average conductivity of these streams (slightly less than 100 µs; Moorman et al. 2006), backpack electrofishing was the most effective method for sampling and determining fish community structure in these streams (Bagenal, 1978; Plafkin et al. 1989; Lyons 1993; Moulton et al. 2000). Voltage settings for the backpack electrofisher ranged from 200-600 and Frequency settings ranged from 20-70 Hz.

Once collected, each fish was identified, weighed, and measured. Length measurements were determined by using a measuring board with a linear metric scale on a flat wooden base with a stop at the zero point. Both standard length (measurement from tip of the closed mouth to the estimated posterior end of the caudal peduncle) and total length (the distance from the closed mouth to the extreme tip of the caudal fin, when the lobes of the caudal fin are squeezed together) were recorded to the nearest millimeter. Weight was recorded in grams using an Aculab portable electronic scale rated to the nearest 0.1 gram. The scale was calibrated weekly to insure proper performance. Clove oil was used as a fish anesthetic to calm the fish while they were measured and weighed (Iverson et al. 2003, Pirhonen & Schreck 2003). It was necessary to euthanize a small sub-sample of each species to keep for future reference and to ensure the proper identification of all species present. Fish were preserved in 10% formalin for two weeks and then transferred to a 70% ethanol solution. Fish vouchers were incorporated into the Chilean Museum of Natural History or the North Carolina Museum of Natural Science's permanent collections.

Gear efficiency

Abundance estimates for stream fish often rely on active capture of fish by methods such as electrofishing (Murphy and Willis 1996), and it is well known that these methods are not 100% effective (Rosenberger and Dunham 2005). Electrofishing techniques that use removal models to estimate fish abundance are often negatively biased, especially when capture efficiency is low (Peterson et al. 2004). Removal estimates are biased by factors such as fish species and size (Buttiker 1992), the number of removal passes, the statistical estimator (White et al. 1982), the real abundance of the target species, and environmental characteristics of the sampled stream (Kennedy and Strange 1981; Riley et al. 1993). All removal models present biased estimates, with only slight decreases in the width of the confidence interval of the estimator as the number of sampling passes increases (Rosenberger and Dunham 2005).

Since this study represents an initial sampling effort in a previously unexplored area, we sacrificed estimator precision, as might be achieved through triple-pass depletion sampling or mark-recapture techniques, for double-pass depletion sampling so more sites could be sampled. Fish abundance and capture probability were computed from the double-pass electrofishing data (Table 2, Fig. 4) using the constant capture probability estimator (Zippin 1956), (Model M_b) in the program CAPTURE which estimated species abundance and capture probability at each sampled reach (White et al. 1982, Rexstad et al. 1991). These estimates could then be converted into estimates of fish density by dividing estimated abundance within a sampled reach by estimated area of the sampled reach. The removal model generally overestimates sampling efficiency (Rosenberger and Dunham 2005) and negative bias of removal-based estimation increases when first pass capture efficiency decreases (Peterson et al. 2004). Estimates of capture probability in this study (45%-100%) were similar to those reported for other stream dwelling trout (Table 2) (Riley and Fausch 1992), and there was no evidence capture probabilities varied significantly by species or between habitat types (Fig. 4). Since the goal of this study was to compare how native puye densities varied due to the presence or absence of invasive trout and beaver, as well as other environmental variables, and how macroinvertebrate densities varied due to estimated trout densities, it is important that there was no significant difference in capture probability between study sites—which was the case. Therefore, we conclude our estimates of fish density and capture probability were adequate for testing the study hypotheses.

Aquatic macroinvertebrate data

Aquatic macroinvertebrates were sampled seasonally in four streams (Table 1) during January, May, and October of 2003 by Chris Anderson for his doctoral dissertation

(University of Georgia). The present study makes use of these previously collected benthic data to begin to assess the potential impacts of habitat type and presence of non-native trout on macrobenthic communities. Seven of our sampled reaches corresponded to Anderson's study sites. Anderson computed macrobenthic biomass at these sample sites and reported mean annual values of benthic biomass for each sample site (Anderson 2006).

Habitat surveys

The following habitat data were collected for each stream reach sampled: (1) stream width, length, and depth (m), (2) percent of riffle, pool, and run habitat present, (3) types of substrate present (e.g., boulder, gravel, sand, silt, mud), and (4) latitude and longitude. In addition, a diagram of each site was made detailing stream orientation along the landscape, the location and lengths of riffle, pool, and run segments, and any other important in-stream habitat characteristics. Detailed photographs were also collected at each sampled reach for future reference of riparian habitat characteristics.

Average stream depth and width were determined for each stream by measuring the width and depth at transects every 20 meters using a measuring stick and measuring tape (Peterson 2004). These data were used to compute an average depth and width for a given stream reach that could be used to calculate average stream volume for the sampled reach, as well as a minimum density of each fish species present. Dissolved oxygen (mg/L), pH, specific conductance (µs), ambient conductance (µs), temperature (^{o}C), nitrate (ppm), nitrite (ppm), and phosphate (ppm) were measured at each reach.

A habitat index for each stream reach was computed using a Stream Visual Assessment Protocol (SVAP) developed at the University of Georgia (Bjorkland 1999). This protocol assesses parameters related to channel condition, hydrologic alteration, riparian zone, bank stability, water appearance, nutrient enrichment, barriers to fish movement, in-stream fish cover, pools, invertebrate habitat, canopy cover, and riffle embeddedness. Each parameter is scored on a scale of 1-10 with <6 representing poor, 6.1-7.4 representing fair, 7.5 – 8.9 representing good, and >9 representing excellent condition. When this index was evaluated across streams in the United States, it correlated well with Fish Index of Biotic Integrity scores computed from the same streams (Bjorkland 1999). One concern with the application of the SVAP in determining in-stream habitat suitability scores is that it is qualitative and can vary with the person making the assessment. Therefore, all of the assessments were completed by M. Moorman to ensure the SVAP scores were similar in how they were estimated across streams. The other issue with the SVAP is that it was developed as an index in the United States to help rapidly assess water quality in urban areas. It is possible that the SVAP index may not be sensitive to subtle changes in habitat in the Cape Horn Biosphere Reserve.

Response and independent variables

The primary response variables in this study were the (1) density of native puye fish, (2) the density of invasive trout, and (3) biomass of aquatic benthic invertebrates. The density of a fish species was computed by dividing the estimated abundance of the fish species in a sampled stream reach by the average area of the reach (W x L where W = average width and L = average length) (Table 3).

The independent variable used to test if fish density by species varied by riparian habitat type since in-stream characteristics and available canopy cover vary by riparian habitat type. The independent variables used to evaluate the relationship between native puye and non-native trout and beaver were (1) the presence or absence of rainbow or brook trout, and (2) the presence of beaver dams. The independent variables used to evaluate the relationship between total in-stream biomass of aquatic benthic invertebrates and trout density was the density of brook trout, since only brook trout were present in these seven sampled reaches for which the benthic data were available. The independent variables used to measure the response of puye densities to abiotic factors were (1) riparian habitat type, (2) percent soft substrate, (3) percent pool, (4) estimated stream velocity, (5) stream depth, and (6) a Stream Visual Assessment Protocol (SVAP) score. Percent soft substrate was calculated by adding the percent sand, percent silt, and percent mud estimates for each stream. Substrate estimates, falling into the categories of boulder, gravel, sand, silt, and mud, were made along 20 meter transects by determining the percentage composition of each substrate type at the transect and then determining average percent substrate for each stream reach. Percent pool was calculated by dividing the total length of a pool in a given reach by the total length of the stream reach. Estimated stream velocity was calculated by timing how quickly a ball floated 10 m in seconds at 3 points along a stream cross-section at the terminus of the reach, taking the estimate of these three numbers, and multiplying the estimate by 0.85 since the surface velocity of the stream multiplied by 0.85 can be used to estimate total stream velocity within the water column (Rantz 1982).

Data analysis

One-way ANOVA model was used to test the variability of fish density by species between riparian habitats (H1). Two-way ANOVA model tested the variability of native puye densities due to the presence of beaver, trout, and the interaction of beaver and trout (H2). Regression models tested if a negative relationship existed between total biomass of aquatic macroinvertebrates and trout density (H3). Linear regression was used to test (H4) if a positive relationship existed between estimated puye density in a reach and the Stream Visual Assessment (SVAP) score, (H5a) if a positive relationship existed between estimated puye density and the percent soft substrate (H5b) percent pool, or (H5c) average stream depth in a sample reach, or (H5d) if a negative relationship existed between estimated puye density and estimated velocity in a sampled reach.

IV. Assumptions

We expected native puye to respond to the presence of trout in a manner similar to their responses in other parts of Tierra del Fuego and New Zealand, whereby the presence of non-native trout significantly decreased the density of puye or eliminated them completely. A comprehensive study on abundance and density patterns of native fish and non-native trout in Chile found very few native puye south of 42° (Soto et al. 2006). Similarly, a comprehensive review of 1030 fish samples in New Zealand found that native puye did coexist with trout, but puye densities were relatively low at these sites compared to sites without trout (Jowett et al. 2003). Second, we assumed the Stream Visual Assessment Protocol developed at the University of Georgia was an appropriate habitat index to identify fish habitat of varying quality for the streams sampled in this study. Bjokland et al. (1999) found the SVAP had a correlation coefficient of 0.63 when correlated with Fish IBI scores at 56 sites in Virginia. It is unclear whether or not the SVAP is an appropriate tool for application to relatively pristine streams. Third, we assumed the aquatic benthic invertebrate data collected in 2003 represented the general benthic community present in each sampled reach during January/February 2006 when the stream fish density data were collected for this study. Aquatic benthic invertebrate communities are relatively constant annually, as long as environmental conditions in a particular stream are constant (Brown et al. 2006). Since there has been little change in the riparian habitats on Navarino and Hoste islands since the aquatic benthic invertebrate sampling, the aquatic benthic invertebrate communities sampled in 2003 should be a reasonable approximation of macrobenthos in 2006. Fourth, we assumed double-pass removal electro-fishing in an enclosed area is an effective method for determining the biomass and density of each fish species present in each stream reach. Backpack electro-fishing has been deemed the most effective and least intrusive method for sampling fish in small, wadeable streams (Lyons 1993, Moulton et al. 2000). We used a constant capture probability estimator (Zippin 1956) (Model M_b) in program CAPTURE to estimate species abundance for all sites (White et al. 1982, Rexstad et al. 1991). The constant probability estimator assumes sampling of a closed population and equal capture probability for all fish of the same species in a given sampling location (White et al. 1982). The closed population assumption was easily met in this study by placing block-nets on the upstream and downstream ends of a sampled reach. The equal probability of capture assumption is more difficult to satisfy, but is most likely to hold true when identical collection effort and methods are applied during each removal (Dorazio et al. 2005). Use of this estimator for estimating fish abundance from two-pass removal sampling has its difficulties, but is the most robust method available (Pollock et al. 1990).

IV. RESULTS

During our study, three native species of stream fish (*G. maculatus, A. zebra,* and *A. taeniatus*) and two species of introduced trout (brook trout, *S. fontinalis* and rainbow trout, *O. mykiss)* were collected. The reported presence of brown trout (*S. trutta)* on Navarino Island by local recreational fishermen was not confirmed, despite sampling 16397 m^2 of streams. Densities of puye, as well as brook and rainbow trout, were calculated for all sampled reaches (Table 3). The presence of native *Aplochiton* species was so rare in streams that we did not compute densities for this species (*A. taeniatus*: n = 1). Similarly, only four specimens of *A. zebra* were found in a lake on the southeastern end of the island using hook and line fishing techniques. This study extends the known range of *Aplochiton spp.*, verifies the presence of brook and rainbow trout as well as puye and the absence of brown trout on Navarino and Hoste islands which helps to improve our knowledge of fish distributions in the poorly studies south of Chile (Fig. 3 and 4). Do to the small numbers of *Aplochiton spp.* found, we did not compute densities for these species, and only consider native puye to evaluate the relationships between native fish and invasive beaver and trout.

The mean density of native puye in streams varied significantly by riparian habitat type, whereas the density of non-native trout did not (ANOVA, puye: F = 4.66, df = 3,18, p = 0.01; brook trout: F=0.36, df = 3,18, p = 0.78; rainbow trout: F= 1.74, df = 3,18, p=0.19). A subsequent multiple comparisons test indicated the mean density of native puye was significantly higher in beaver-disturbed, riparian habitats than other habitat types (Student-Newman-Kuels test, $p = 0.05$; Fig. 5). Thus, habitat disturbance by non-native beaver, such as dam building and flooding, create favorable habitats for native puye populations. The positive response of native puye to beaver-disturbed streams, however, was most apparent in the absence of non-native trout. For example, the mean density of native puye varied significantly with the presence/absence of non-native trout in beaver-disturbed habitats; however, a significant trout by beaver interaction effect precluded contrasts across the treatment means (2-way ANOVA; trout: $F = 10.02$, $df = 3,18$, $p = 0.0054$; beaver: $F = 15.69$, $df = 3,18$, $p = 0.0009$; interaction: $F = 12.65$, $df = 3,18$, $p = 0.0023$; Fig. 6). The interaction effect was due to significantly higher puye densities in beaver-disturbed habitats in the absence of trout than in the presence of trout. A LSD multiple comparisons procedure indicated that in the presence of trout, average puye density in reaches disturbed by beavers was significantly lower than the average puye density in beaver-disturbed reaches without trout. Puye densities were lowest in reaches not disturbed by beavers, regardless of whether trout were present (Fig. 6). Thus, in the case of native puye, the effects of invasive species is mixed, with non-native beaver apparently having a positive effect on puye density and non-native trout having a negative effect on native puye densities.

Mean macrobenthic biomass did not vary with mean trout density (least squares regression; $R^2 = .35$, $p = 0.3$). Although the relationship was not statistically significant, likely due to low sample size (n=7), it is important to note the site with the highest trout density had the lowest macrobenthic biomass (Fig. 7). Future studies should test if there is a negative relationship between macrobenthic prey biomass and increasing trout density since trout prey heavily on aquatic macroinvertebrates.

We found significant relationships between puye density and two of our environmental variables, percent soft substrate and velocity. There was a positive relationship between native puye density and percent soft substrate (least squares regression; $F=16.18$, $df=1$; $p < 0.0001$) (Fig. 8) and a negative relationship between native puye density and estimated stream velocity ($F=98.77$, $df=1$, $p<0.0001$; Fig. 8). Both these relationships were strong (R-squared = 0.44 and 0.82, respectively) and best represented by an exponential growth or decay model, respectively when model fit of a linear, quadratic, and exponential model was compared using Akaike information criteria (AIC) (Table 4). These relationships may be indicative of the changes caused by beaver disturbances in the streams since beaver dams can decrease stream velocities and increase soft substrate. The mean density of native puye in streams did not show significant variation across any of the other natural environmental gradients we measured. For example, there was no relationship between puye density and percent pool present (least squares regression; $R^2 = 0.022$; $p = 0.07$), average depth ($R^2 = 0.046$, $p = 0.5132$), or the Stream Visual Assessment Protocol score ($R^2 = 0.09$, $p=0.1743$) calculated for each reach (Fig. 8).

VI. DISCUSSION

Potential interactions between native fish and non-native beaver and trout

Both beaver and trout were introduced to Tierra del Fuego in the early 1900's and are successful invaders (Lizarralde and Escobar 2000; Vila 1999; Anderson et al. 2006).

Native puye fish had relatively high densities directly downstream from beaver ponds compared to streams surrounded by relatively unmodified riparian habitat. When brook trout were present in beaver ponds, puye densities were reduced, but not as low as in the absence of beaver. Beaver dams may provide an opportunistic feeding habitat for puye by increasing food availability and creating favorable feeding habitat. For example, in the same study system as ours, chironomid biomass, a preferred food of puye, was significantly higher in the presence of beaver ponds than without, and higher in the relatively slow waters around beaver impoundments than in faster moving streams not impacted by beaver (Anderson 2006). Puye prefer habitats downstream of flow constrictions, especially where food is concentrated and velocities are slow enough for puye to hold a feeding position (Jowett 2002). Young trout show similar feeding behavior to drift-feeding puye, in that they prefer to feed where food delivery is maximized and swimming energy minimized (Bachman 1984; Hayes et al. 2000), but studies indicate trout populations in some New Zealand streams can consume all available benthic production (McDowell 2003). Thus, invasive beaver appear to enhance the abundance of native puye, whereas invasive trout appear to negate the benefits of beaver ponds to puye.

An alternative mechanism for the apparent enhancement of puye in the presence of beaver dams is that dams may serve as a barrier to upstream trout migration, thereby concentrating these predators below dams and allowing puye densities to flourish upstream of the barrier, as suggested by Vila et al. (1999). However, puye are poor climbers and tend to be lowland pool and run dwellers, are catadromous, with migratione to the estuaries to spawn in the fall, and normally have a life span of one year (R.M. McDowall, pers. comm).

Thus, it is more likely that beaver dams concentrate catadromous puye below the dams, preventing their further migration upstream. Therefore, beaver likely have a positive localized effect on native puye densities by creating favorable feeding habitats at the scale of the stream reach, but may cause a negative effect over the entire stream reach by preventing upstream migration of catadromous puye. The scale-dependent effects of invasive beaver and trout on native puye requires further testing.

<u>Freshwater fish assemblages of the Cape Horn Biosphere Reserve</u>

During January and February 2006, non-native fish assemblages were composed of brook and rainbow trout, while native fish assemblages were dominated by puye. Puye appear widespread and abundant in the study area, even though they have been listed as vulnerable on the Chilean red list (Glade 1993). In contrast, both *Aplochiton* species appear to be much rarer and few specimens were encountered in our study or in other recent studies in southern Chile (Vila et al. 1999; Cussac et. al. 2004; Soto et al. 2006). It is important to reiterate that brown trout were completely absent from our study area, but *A. zebra* was present and cohabitating with brook and rainbow trout. Work in the Falkland Islands, suggests *A. zebra* disappears from a river system following the appearance of brown trout (Clark et al. 1994). Since *A. zebra* is listed as a species of concern and *A. taeniatus* is listed as endangered (Glade 1993), immediate precautions should be taken to prevent the spread of brown trout to Navarino and Hoste Islands. In contrast to puye, both *Aplochiton* spp. were extremely rare in our study, similar to other parts of southern Chile. Measures such government regulations that prevent the accidental or intentional introduction of brown trout and educational campaigns that promote the native fish species present should be taken to conserve *Aplochiton* spp. on Navarino and Hoste Islands (Vila et al. 1999; Soto et al. 2006). One native fish species documented for the Fuegian Archipelago, which was not found in this study, but is probably present on Navarino and Hoste Islands was *Galaxias platei* (Jenyns 1842; Cussac et al. 2004; McDowall pers comm.). *Galaxias platei* prefers deep benthic lake habitats and would not be expected to exist in coastal streams (Cussac et. al. 2004).

No brown trout were found during our surveys, even though Anderson et al. (2006) reported this species based on fishermen accounts. Apparently, what is often called "brown trout" by the locals on Navarino Island, is actually brook trout. When brook trout are absent from reaches downstream from beaver dams, native puye densities (μ=0.62 puye/m^2, s.e.=0.45 puye/m^2, n=2) are higher then puye densities reported in other stream studies in southern Chile. When brook trout are present in these favorable systems, mean puye densities (μ=0.36 puye/m^2, s.e.=0.26 puye/m^2, n=3) are equivalent to other stream reaches where puye are present. When no beaverdam is present, puye densities (μ=0.11 puye/m^2, s.e.=0.05 puye/m^2, n=12) are lower than other stream reaches (Soto et al. 2006). This study extends the southern documented range of *Aplochiton* spp. and identified three species of native fish co-occurring with the presence of invasive brook and rainbow trout.

<u>Implications for management of the Cape Horn Biosphere Reserve</u>

This study identified potential positive and negative effects of invasive beaver and trout on native puye. It also provides valuable information for the management of the newly created Cape Horn Biosphere Reserve by quantifying fish species composition, density, and distribution patterns, as well as habitat characteristics of watersheds on the southeastern fringe of the Reserve. This information will aid managers in predicting the impacts of non-native trout and beaver on native fish and benthos, as well as the potential ecosystem response to removal of these non-native species. One life-history trait to be considered for native fish in the study area is that they are all, with the exception of *G. platei*, catadromous and their life histories include a regular migration between freshwater and the sea, even though some landlocked populations do exist (Cussac et al. 2004). If beaver prevent the upstream migration of native puye and other native fish, the formation of beaver dams could negatively impact native fish by restricting their upstream distribution and abundance patterns. This aspect should be considered and investigated before it is concluded that the overall impact of beavers is positive on native puye densities. While our study suggests beaver dams increase puye densities at the scale of a given stream reach, these putative benefits could disappear at the scale of the entire stream. Moreover, trout are an important sport fishing resource in southern Chile, but conservation of native fish biodiversity is also important. Efforts such as education of locals on native fish and their importance and a ban on the accidental or intentional introduction of brown trout on Navarino and Hoste Islands should be taken to prevent the spread of brown trout into the study system since they are currently not present, and rainbow and brook trout are available for sportfishing. This measure could protect the rare *Applochiton spp.* that are present in the biosphere reserve.

We suggest the consequences of invasive trout and beaver on native fish in the Cape Horn Biosphere Reserve be explored further by testing the following interactions.

First, determine if beavers impede the upstream migration of puye and trout during both high and low flow periods. Upstream migration of trout and puye could be examined through mark-recapture or bio-telemetry studies. This information will clarify if beaver dams protect native fish by preventing the upstream migration of trout or restrict migration of catadromous native fish. Second, the relationship between trout, beaver and available benthic prey should be explored further by looking at prey availability in beaver disturbed reaches versus non-beaver disturbed reaches. It is necessary to identify and sample reaches that lack trout completely. We expect that macrobenthic prey biomass will be highest in beaver disturbed reaches versus non-beaver disturbed reaches since this trend was shown by Anderson (2006), but that the presence of predatory trout in the beaver disturbed reaches will reduce macrobenthic prey biomass as compared to beaver disturbed reaches lacking trout. This information could explain why puye densities are observed in reduced numbers in beaver disturbed reaches when trout are present, and further provide an example of a negative feedback loop between two invasive species where the positive effect of one invasive species reduces the negative effect of a second invasive species in an ecosystem. Further defining the relationship between native puye and invasive trout will elucidate interactive effects of multiple invasive species within a study system and aid conservation managers on the ecosystem effects of invasive trout and beaver in the Cape Horn Biosphere Reserve.

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Table 1: Sampling site information. Locations, sampling dates, dominant riparian habitat type, and availability of aquatic macroinvertebrate data listed.

Site ID	Date Sampled	Latitude (◦S)	Longitude (◦W)	Dominant Riparian Habitat Type	Aquatic macroinvertebrate data available
1	2/21/2006	54.94253	68.59322	Forest	
2	2/21/2006	54.94515	68.58818	Beaver disturbed	
3	2/22/2006	54.94517	68.56557	Meadow	
4	2/20/2006	54.98108	68.37537	Beaver Disturbed	
5	2/20/2006	55.00914	68.33566	Forest	
6	2/18/2006	54.97471	68.21794	Forest	
7	2/18/2006	55.04669	68.14683	Forest	
8	2/19/2006	55.17771	68.04876	Scrub	
9	2/19/2006	55.17072	68.10589	Beaver disturbed	
10	1/30/2006	54.90881	68.10902	Forest	
11	1/30/2006	54.90296	68.0822	Forest	X
12	1/30/2006	54.90535	67.99854	Forest	X
12	2/15/2006	54.90495	67.98884	Meadow	X
13	1/28/2006	54.9128	67.84845	Forest	
13	1/28/2006	54.91751	67.84961	Scrub	
14	2/14/2006	54.9217	67.78075	Forest	X
15	1/29/2006	54.94114	67.70274	Scrub	
15	2/28/2006	54.94548	67.70835	Forest	
16	2/10/2006	54.94172	67.65759	Meadow	
16	1/29/2006	53.31723	71.96811	Forest	X
16	1/29/2006	54.95391	67.64672	Scrub	X
17	2/24/2006	54.93866	67.62344	Beaver disturbed	
18	2/1/2006	54.93914	67.60118	Forest	
19	1/29/2006	59.92994	67.55711	Meadow	
20	2/8/2006	54.93423	67.52342	Forest	
21	1/29/2006	54.9367	67.46533	Forest	
21	3/1/2006	54.93589	67.4659	Meadow	
22	2/12/2006	54.92786	67.42028	Beaver disturbed	
23	2/25/2006	55.01144	67.28656	Lake (hook and line)	

Table 2: Estimates of fish species abundance by site. Associated standard error (SE) and capture probabilities are given. Sites with failed capture probabilities represent sites where more fish were captured in the second pass than the first pass.

Site #	Puye Abund	Puye Abund SE	Puye Capture Prob	Brook Abund	Brook Abund SE	Brook Capture Prob	Rainbow Abund	Rainbow Abund SE	Rainbow Capture Prob
1	92	9.1	0.614	16	4.0	0.605	0		
2	2597	210	0.346	0			0		
3	96	2.5	0.823	10	0.7	0.833	0		
4	41	2.9	0.743	13	0.6	0.867	0		
7	41	6.5	0.601	0			0		
8	45	7.6	0.578	14	1.0	0.824	8	2.5	0.621
9	161	5.3	0.754	15	0.6	0.882	0		
10	38		Failed	16	9.8	0.433	0		
11	45	7.1	0.593	11	0.7	0.846	0		
12	36	8.9	0.527	17	1.3	0.794	0		
13	3	0.7	0.75	0			36	12.0	0.472
14	1	0	0.999	67	3.1	0.770	0		
15	29		Failed	18	1.2	0.809	28	11.1	0.463
16	27	9.0	0.502	135	3.4	0.808	0		
17	108		Failed	0			0		
18	0			173	75.8	0.294	29	5.1	0.613
19	0			132	20.7	0.492	4		Failed
20	0			252	28.7	0.492	0		
21	39	2.4	0.769	40	8.6	0.546	0		
22	3		Failed	20	4.9	0.587	0		

Table 3: Computed fish densities. Density (#/m^2) equals the estimated species abundance in a sampled reach divided by the estimated reach area. In streams where multiple reaches were sampled, the reach located 50 m upstream from the coast is indicated. * Densities could not be computed due to hook and line sampling.

Site ID	Puye	Rainbow Trout	Brook Trout	Other	Coastal Reach
1	0.032	0.000	0.006		
2	6.819	0.000	0.000		
3	0.620	0.000	0.067		
4	0.214	0.000	0.071		
5	0.000	0.000	0.000		
6	0.000	0.000	0.000		
7	0.083	0.000	0.000	A. taeniatus*	
8	0.043	0.008	0.016		
9	0.981	0.000	0.097		
10	0.181	0.000	0.013		
11	0.095	0.000	0.028		
12	0.078	0.000	0.047		X
12	0.006	0.000	0.016		
13	0.003	0.027	0.000		X
13	0.000	0.020	0.000		
14	0.004	0.000	0.229		
15	0.056	0.038	0.035		X
15	0.000	0.000	0.000		
16	0.029	0.000	0.181		X
16	0.000	0.000	0.000		
16	0.000	0.000	0.000		
17	0.864	0.000	0.000		
18	0.000	0.016	0.055		
19	0.000	0.010	0.330		
20	0.000	0.000	0.935		
21	0.123	0.000	0.107		X
21	0.000	0.000	0.000		
22	0.007	0.000	0.040		
23	0	Present*	Present*	A. zebra*	

Table 4: AIC Results

	MODEL TYPE	PARAMETERS	SS RES	AIC
% SOFT SUBSTRATE	linear	1	0.619	-76.5552
	quadratic	2	0.5008	-79.217
	exponential	1	0.5358	-79.7308
VELOCITY	linear	1	0.61	-76.8775
	quadratic	2	0.3656	-86.1397
	exponential	2	0.1597	-104.361

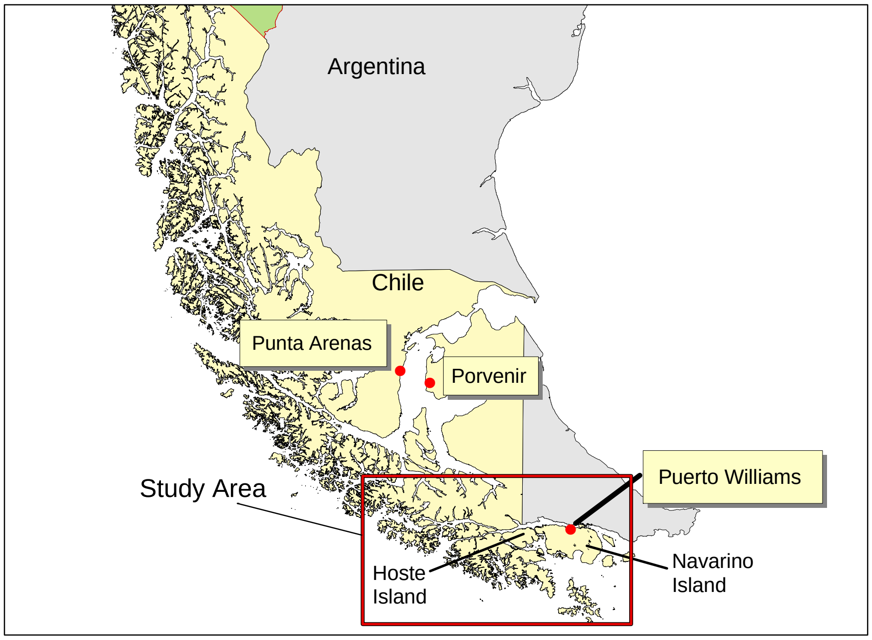


Figure 1: Map of southern South America indicates location of Puerto Williams, Navarino and Hoste Islands, and the Cape Horn Biosphere Reserve study area.

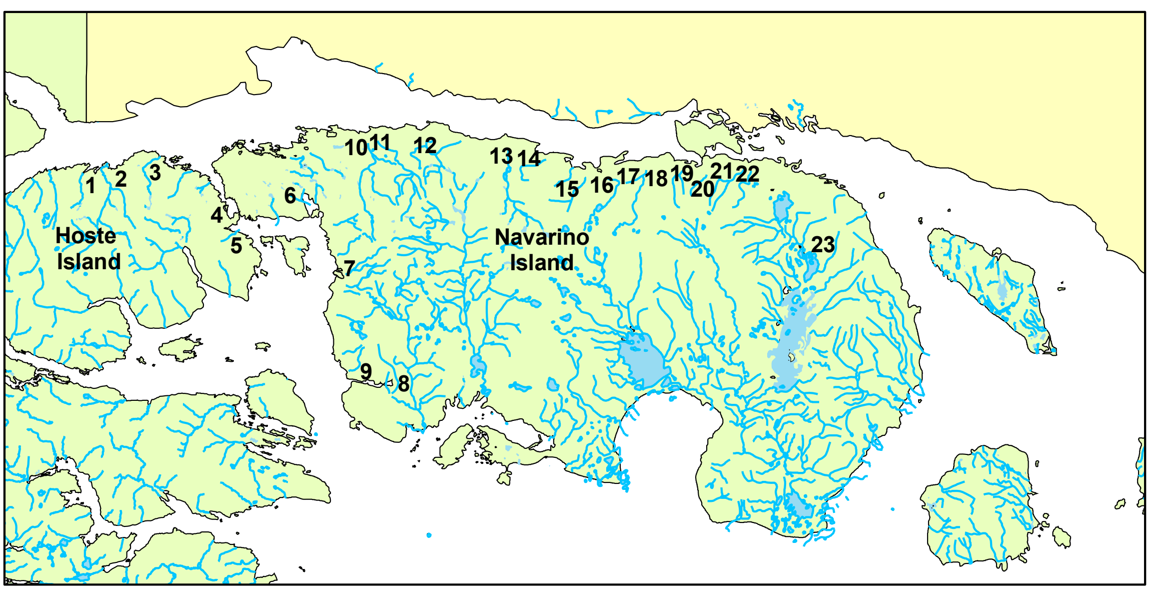
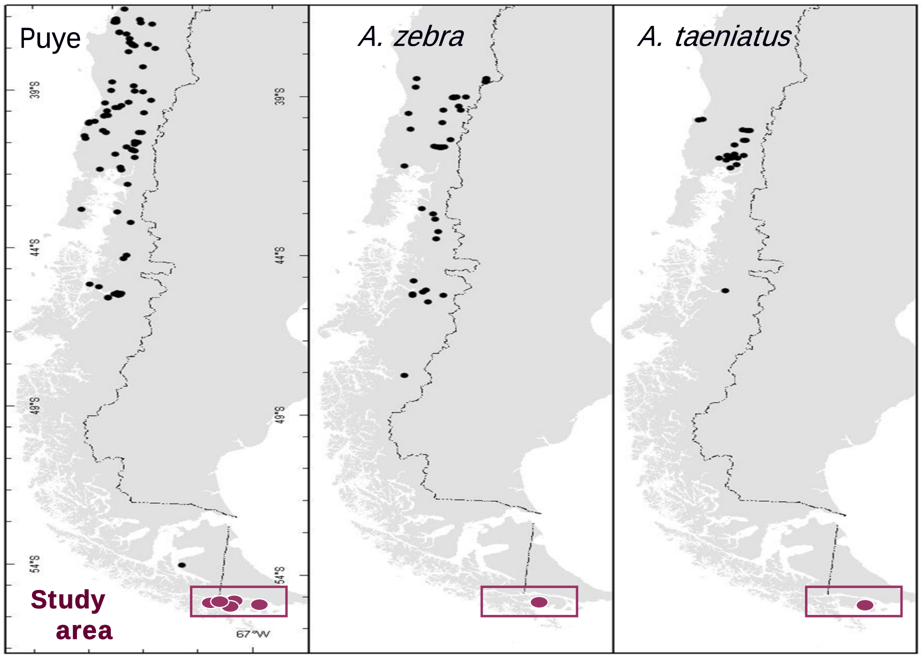
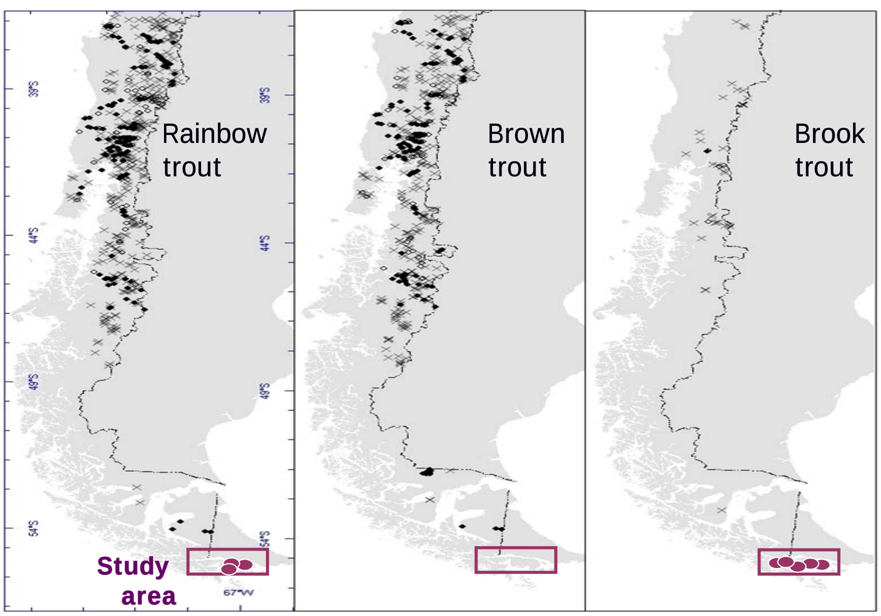


Figure 2: Map of study sites sampled for fish during February of 2006. Site numbers correspond to site numbers in Table 1.



Map Courtesy Cristian Correra



Map Courtesy Cristian Correra

Figure 3: Known distributions of native fish (Puye, *A.taeniatus and zebra)* and introduced trout (rainbow, brown, and brook) in S. Chile (38' to 55'). Distributions confirmed by this study are highlighted in the purple box. Maps courtesy of Cristian Correra.

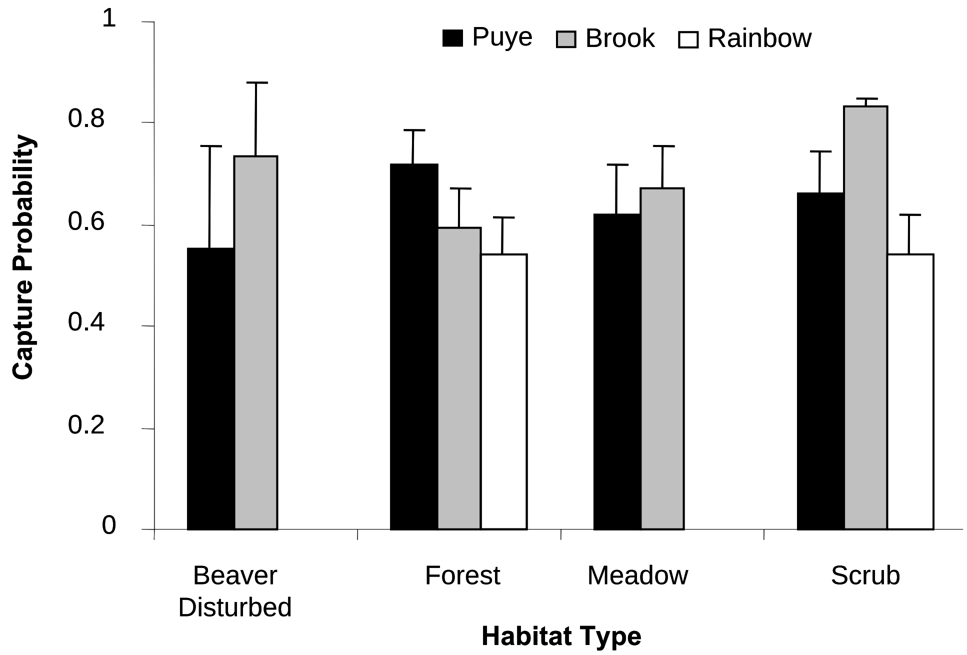


Figure 4: Mean capture probability of puye, brook trout, and rainbow trout (± SE) between habitats.

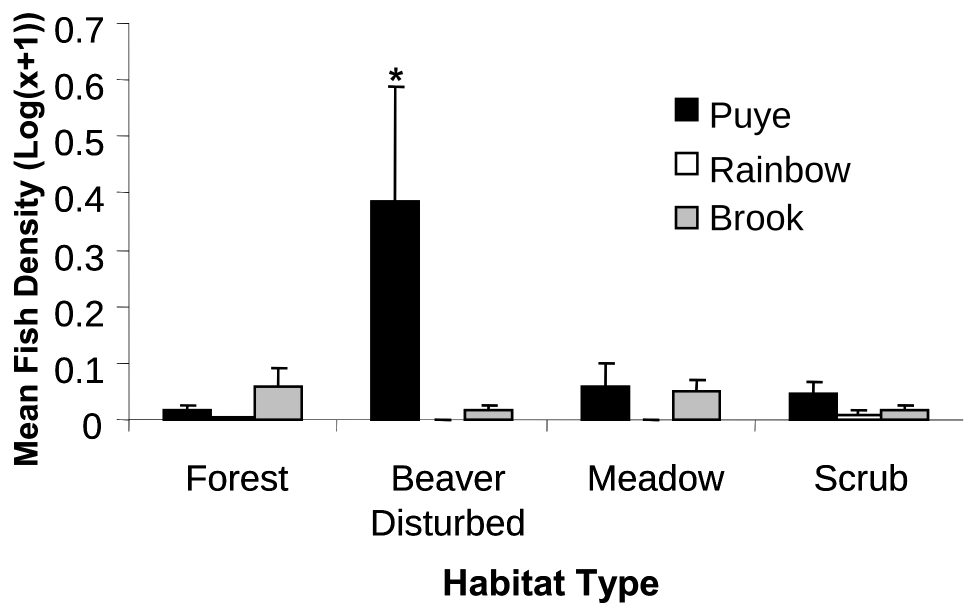


Figure 5: Mean puye, brook trout, and rainbow trout density (± SE) within each habitat type. * indicates puye densities were significantly different

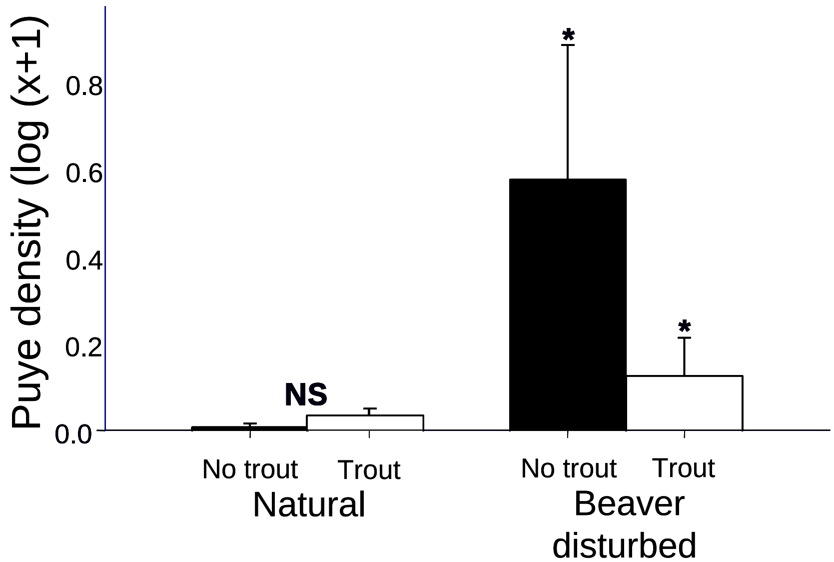


Figure 6: Mean puye density in response to the presence or absence of invasive beaver and trout. * indicates densities were significantly different, NS indicates no significant difference

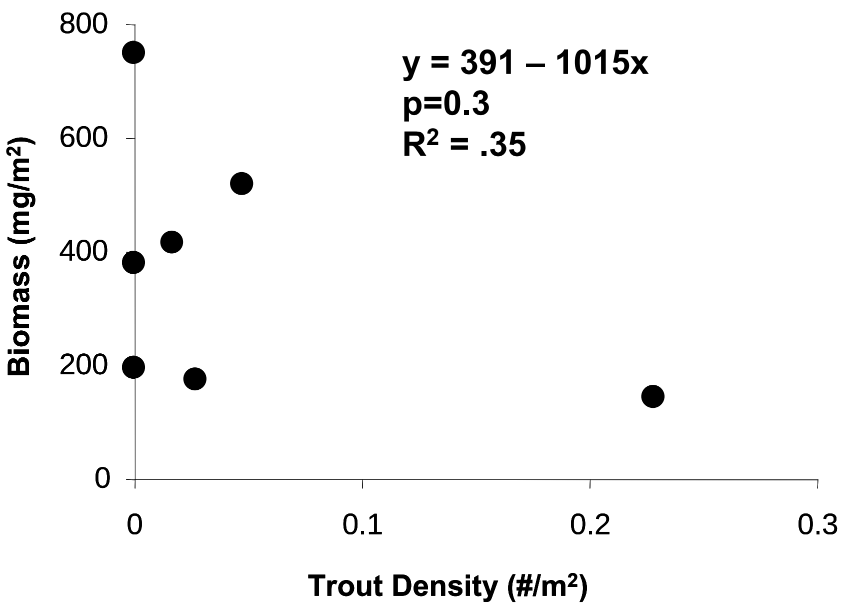
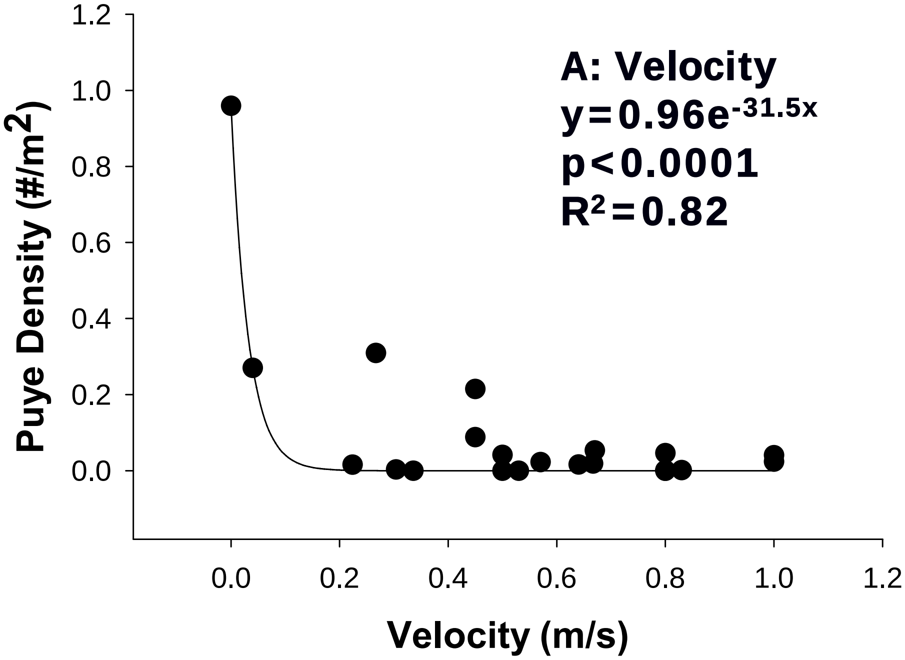
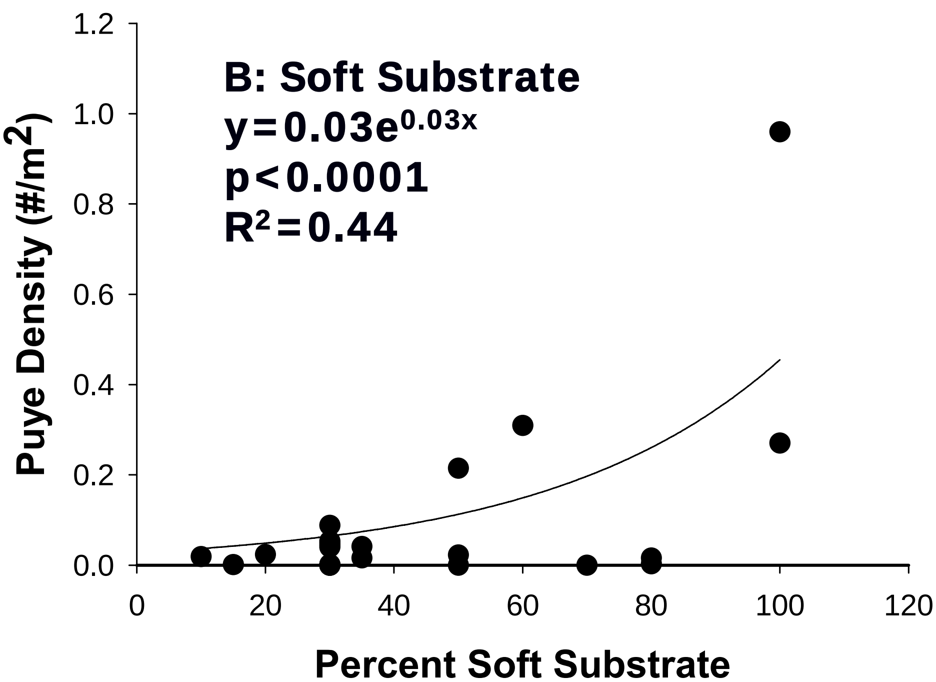


Figure 7: Relationship between total macrobenthic biomass and trout density. Included are regression equations, as well as p and R^2 values.

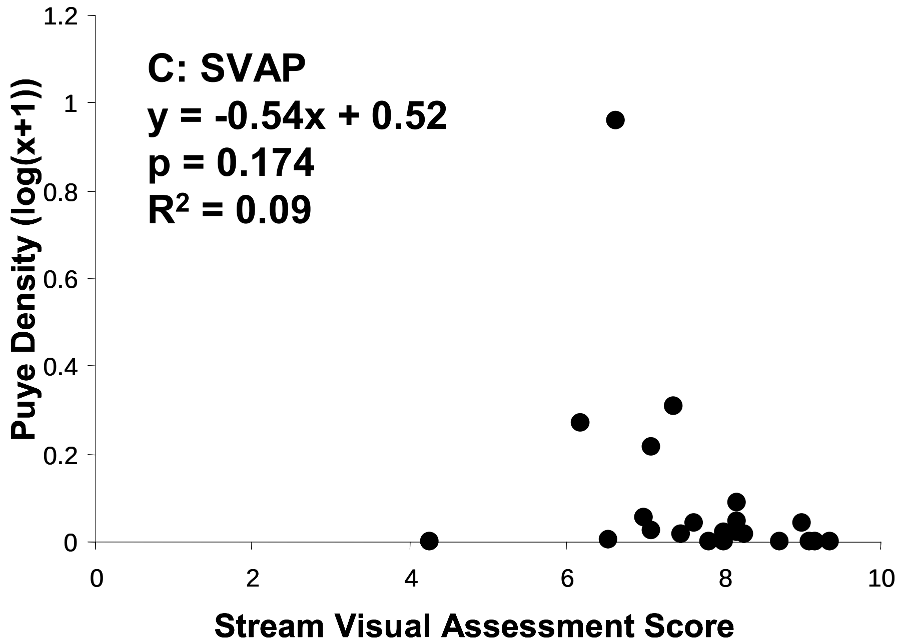
Figure 8: Relationship between abiotic factors (A: velocity, B: soft substrate, C: SVAP score, D: depth, and E: percent pool) and log transformed normalized puye densities. Lines are significant least square regression trends; included are regression equations, as well as p and R^2 values.

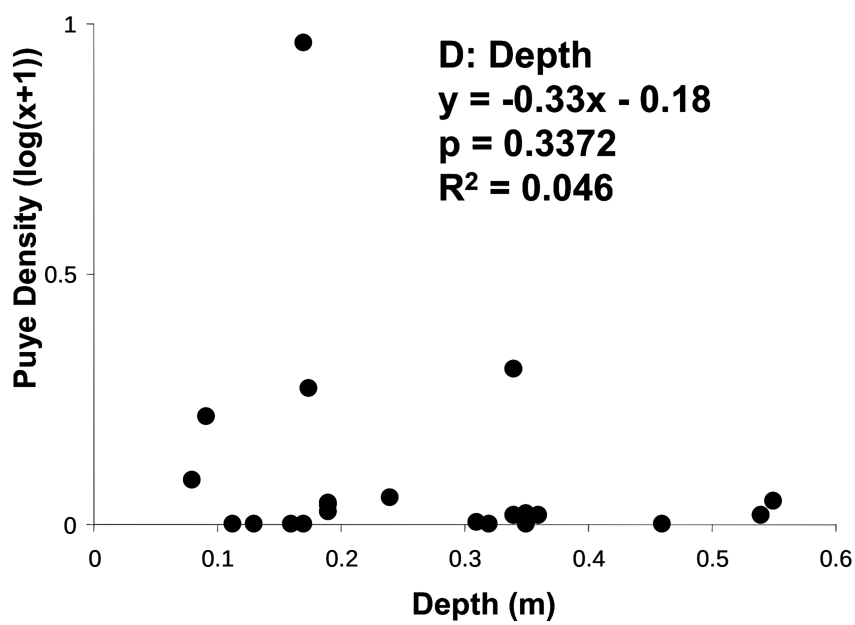


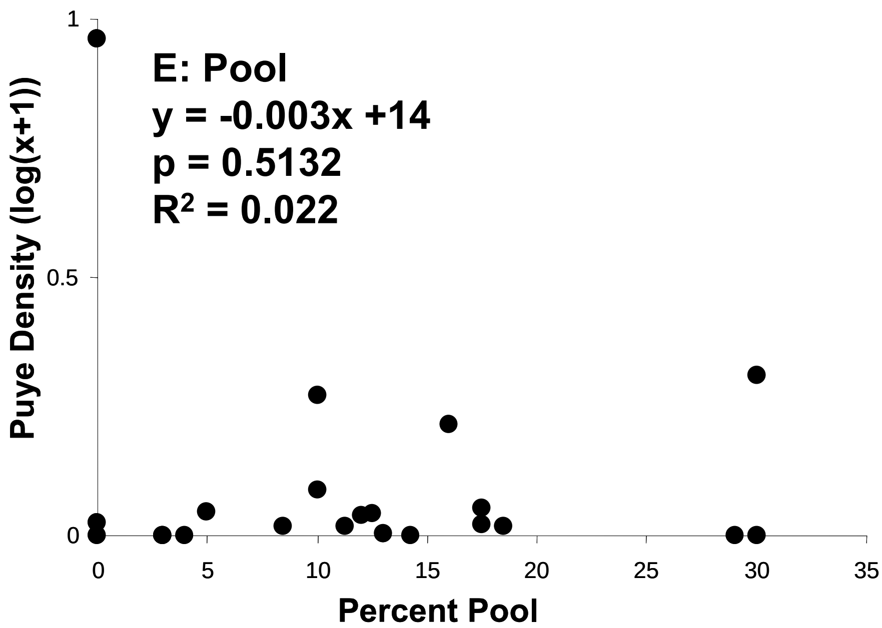
A: Velocity
$y=0.96e^{-31.5x}$
$p<0.0001$
$R^2=0.82$
Puye Density (#/m2)
Velocity (m/s)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
1.2



B: Soft Substrate
$y=0.03e^{0.03x}$
$p<0.0001$
$R^2=0.44$
Puye Density (#/m2)
Percent Soft Substrate
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0
20
40
60
80
100
120


C: SVAP
y = -0.54x + 0.52
p = 0.174
R2 = 0.09
Puye Density (log(x+1))
Stream Visual Assessment Score
1.2
1
0.8
0.6
0.4
0.2
0
0
2
4
6
8
10


D: Depth
y = -0.33x - 0.18
p = 0.3372
R2 = 0.046
Puye Density (log(x+1))
Depth (m)
1
0.5
0
0
0.1
0.2
0.3
0.4
0.5
0.6


E: Pool
y = -0.003x +14
p = 0.5132
R2 = 0.022
Puye Density (log(x+1))
1
0.5
0
0
5
10
15
20
25
30
35
Percent Pool

VIII. APPENDICES

1. Forested Habitats

Site 1

Site 5


Site 6


Site 7


Site 10


Site 11


Site 12


Site 13


Site 14


Site 15


Site 16


Site 18


Site 20


Site 21

2. Beaver Disturbed Habitats

Site 2

Site 4


Site 9


Site 17


Site 22

3. Meadow Habitats


Site 3


Site 12


Site 16

4. Scrub Habitats

Site 8

Site 13


Site 15


Site 16

5. Lake Habitats

Site 23