FACTORS AFFECTING PREY CAPTURE AND OPTIMAL HOLDING VELOCITY OF WILD SOUTHERN AND HATCHERY NORTHERN BROOK CHARR (*SALVELINUS FONTINALIS*)

by

RIDGE SLIGER

(Under the Direction of Gary Grossman)

ABSTRACT

Identification of the factors affecting habitat selection is necessary for scientific management and conservation of at-risk fish populations. We tested the effects of 1) water velocity, 2) fish size, 3) days in captivity, 4) dominance, and 5) size rank, on prey capture success, holding velocity, and reactive distance of both hatchery Northern and wild Southern Brook Charr (*Salvelinus fontinalis*) using an experimental stream flume. In all experiments, prey capture success was negatively correlated with water velocity, holding velocity was positively correlated with water velocity, and dominant fish had greater prey capture success than did subordinate fish. None of the variables we measured had a strong, consistent effect on reactive distance. There were few behavioral differences between Southern Brook Charr and Northern Brook Charr. The Grossman et al. (2002) optimal foraging model successfully predicted the holding velocity of wild Southern Brook Charr in Lynn Camp Prong, Tennessee.

INDEX WORDS: Brook Trout, Microhabitat, Habitat selection, Net energy intake, Foraging models, Drift-feeding

FACTORS AFFECTING PREY CAPTURE AND OPTIMAL HOLDING VELOCITY OF WILD SOUTHERN AND HATCHERY NORTHERN BROOK CHARR (*SALVELINUS FONTINALIS*)

by

RIDGE SLIGER

BS, Lee University, 2018

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2020

FACTORS AFFECTING PREY CAPTURE AND OPTIMAL HOLDING VELOCITY OF WILD SOUTHERN AND HATCHERY NORTHERN BROOK CHARR (*SALVELINUS FONTINALIS*)

by

RIDGE SLIGER

Major Professor: Gary Grossman
Committee: Brian Irwin
Seth Wenger

Electronic Version Approved:

Ron Walcott
Interim Dean of the Graduate School
The University of Georgia
August 2020

DEDICATION

I dedicate this work to Chloe Bloom and the Sliger family, who have provided me with unwavering support in all my work and have always inspired me to explore the beauty of the natural world.

ACKNOWLEDGEMENTS

This research was made possible through the help of C. Bloom, B. Hilburn, C. Ellis, B. Bozeman, T. Simon, M. Tiller, G. Grossman, B. Irwin, S. Wenger, Great Smoky Mountains National Park, M. Kulp, C. Abramson, A. Walker, N. Goodman, J. Cary, the Georgia Department of Natural Resources, J. Thomson, J. Stewart, C. Cooksey, R. Herbison, R. Ratajczak, R. Chandler, the Warnell School of Forestry & Natural Resources, and a few who will remain anonymous.

TABLE OF CONTENTS

Page

CHAPTER

LIST OF TABLES

LIST OF FIGURES

Page

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

The spatial distribution of Brook Charr (*Salvelinus fontinalis*), ranges from Ontario, Canada in the north to northern Georgia, U.S. in the south (Stoneking et al. 1981). Brook Charr have been extirpated from much of their original range, and this decline is of particular conservation interest, given: 1) the species' desirability as a sport fish, 2) its status as the only Charr endemic to both lotic and lentic habitats in the Eastern United States, and 3) its status as the only salmonid native to the Southeastern United States. Hudy et al. (2008) summarized that the factors contributing to the decline of Brook Charr over its natural range include: 1) poor land use (King 1937, 1939; Lennon 1967; Nislow and Lowe 2003), 2) declines in water quality (Clayton et al. 1998; Hudy et al. 2000; Driscoll et al. 2001), 3) increases in water temperatures (Meisner 1990), 4) invasive fishes (Moore et al. 1983; Larson and Moore 1985; Strange and Habera 1998), 5) habitat fragmentation (Belford and Gould 1989; Gibson et al. 2005), and 6) other habitat degradation (Curry and MacNeill 2004). Similar to many other cold-water species, Brook Charr populations are expected to be reduced by anthropogenic climate change. Modeling conducted by Bassar et al. (2016) suggests that climate change induced decreases in stream flow and increases in temperature will cause population reductions greater than that for which density-dependent processes can compensate. Although there are some projects dedicated to the preservation and restoration of the Brook Charr throughout its range, such as those led by the Eastern Brook Trout Joint Venture (EBTJV) (Eastern 2005), there still remain significant information gaps that must be filled with continued research to ensure the conservation of the species.

One such knowledge gap concerns differences between Northern and Southern Brook Charr. As early as 1967, scientists suspected Southern and Northern Brook Charr were genetically distinct, given their differences in size, fecundity, susceptibilities to diseases, and survival and reproduction rates when exposed to similar environmental conditions (Lennon 1967). Stoneking et al. (1981) have since demonstrated that Northern and Southern Brook Charr are in fact genetically distinct strains. Because they respond differently to the same environmental disturbances, and because environmental disturbances differ over space, we need a more complete understanding of statuses and likely population trends of both strains of Brook Charr for their continued conservation. Although there is a significant body of literature on the Northern Brook Charr, little is known about the ecology of the Southern strain. Research on the Southern Brook Charr is especially important, as it is the only salmonid native to the Southern Appalachians. Research conducted by Hudy et. al (2013) indicates that at the catchment scale, the Southern Brook Charr is extant in only 14% of its original distribution. A review conducted by EBTJV indicates that in Georgia and South Carolina, the southern limit of the Southern Brook Charr's range, 96% of the subwatersheds historically inhabited by the strain have been significantly affected by the introduction of nonnative Rainbow Trout (*Oncorhynchus mykiss*), 91% by historical forestry practices, 87% by road sediment, 84% by urbanization, and 81% by poor land management (Eastern 2006). In addition to the above threats, given its more southern distribution, the Southern Brook Charr is at increased risk of reduction due to climate change. Modeling conducted by Flebbe et al. (2006) indicates that 53-97% of Charr and Trout habitat will be lost due to climate change. This would be expected to result in greater habitat fragmentation, as remaining habitat could be reduced to disconnected, high-elevation islands (Flebbe et al. 2006).

Successful conservation efforts typically require data from the population being managed, or from ecologically similar populations. Because the Southern Brook Charr is genetically distinct, and may be ecologically distinct as well, it is important to understand its habitat relationships. Given the reduction and fragmentation of waters originally inhabited by the Southern Brook Charr, and the presence of invasive salmonids in these waters, conservation efforts now must focus on small spatial scales (Habera and Moore 2005), such as subwatersheds. Consequently, it is important that we gain a mechanistic understanding of the conditions this strain requires to thrive in the streams it inhabits.

Net-Energy-Intake (NEI) microhabitat modeling is one method that has proved successful in providing mechanistic understandings of habitat requirement and selection of drift-feeding fishes such as the Brook Charr and similar species (Fausch 2014; Grossman 2014; Piccolo et al. 2014; Rosenfeld et al. 2014). NEI approaches are useful because they allow us to link an individual's microhabitat use to an estimation of its net-energy-intake (a surrogate of fitness). Typically, NEI models quantify the relationship between holding velocity and net-energy-intake, with the goal of identifying the "optimal" (i.e., high net energy gain) microhabitats in the stream. This approach has successfully been used to predict optimal holding positions for species including Arctic Grayling (*Thymallus arcticus*) (Hughes and Dill 1990; Bozeman and Grossman 2019a), Brown Trout (*Salmo trutta*) (Fausch 1984; Hayes et al. 2007), Northern Brook Charr (Fausch 1984), Coho Salmon (*Oncorhynchus kisutch*) (Fausch 1984), Rainbow Trout (Hill and Grossman 1993), and multiple stream minnows (Hill and Grossman 1993; Grossman et al. 2002).

In addition, quantifying the availability of high-quality holding positions in a stream facilitates inferences concerning the habitat that needs to be maintained to ensure population persistence.

Thus far, little research has focused on the ecology of the Southern Brook Charr. However, some recent research has identified relationships between this strain and its habitat. More specifically, in a typical Southern Appalachian stream, Southern Brook Charr tend to occupy deeper microhabitats with lower velocities and more erosional substrata (Anglin and Grossman 2013), and likely have small (<20m) home ranges (Anglin and Grossman 2018). While these findings are meaningful contributions to an understanding of Southern Brook Charr habitat use, more information is needed to acquire a better understanding of its habitat requirements and the energetic consequences of its habitat use. We tested the Grossman et al. (2002) NEI model in predicting the microhabitat use of Southern Brook Charr in Lynn Camp Prong, a third-order stream in the Tennessee portion of the Great Smoky Mountains National Park. We also quantified various factors affecting foraging behavior of Southern Brook Charr (e.g. prey capture success, holding velocity, and reactive distance). For comparative purposes, we also conducted experiments to quantify the same foraging parameters for hatchery Northern Brook Charr. Our data should fill information gaps concerning habitat requirements and selection of Southern Brook Charr and behavioral differences between the Southern and Northern strain, both of which may prove useful to their management.

CHAPTER 2

COMPARATIVE FORAGING DYNAMICS OF NORTHERN AND SOUTHERN BROOK CHARR (*SALVELINUS FONTINALIS*)[1]

---

[1] Sliger, R. and G.D. Grossman. To be submitted to Canadian Journal of Fisheries and Aquatic Sciences.

Abstract

Identification of the factors affecting habitat selection is essential for scientific management and conservation of fish populations. The majority of stream fishes in North America are drift-feeders, for which food acquisition is a primary component of habitat selection. We experimentally tested the effects of 1) water velocity, 2) fish size, 3) days in captivity, 4) dominance, and 5) size rank on prey capture success, holding velocity, and reactive distance of both hatchery Northern and wild Southern Brook Charr (*Salvelinus fontinalis*). For both strains: 1) prey capture success was negatively related to water velocity, 2) holding velocity was positively related to water velocity, and 3) dominant fish had greater prey capture success than did subordinate fish. Prey capture success was high up to 30cm/s, at which point it began to decline exponentially. Reactive distances were not strongly or consistently affected by any variables. Surprisingly, there were few differences in foraging behavior between Southern and Northern Brook Charr. Our data suggest that Brook Charr will forage well in streams with ample velocities up to 30cm/s.

Keywords: Brook Trout, Hatchery, Microhabitat, Drift-feeding, Reactive distance, Prey capture

Introduction

There is little ecological information concerning Southern Brook Charr (SBC; *Salvelinus fontinalis*), a genetically distinct strain endemic to the Southern Appalachian Mountains (Stoneking et al. 1981; McCracken et al. 1993; Danzmann et al. 1998), especially in contrast to Northern Brook Charr (NBC). Hudy et al. (2013) estimated that the SBC currently occupies only 14% of its historic range, likely due to the negative effects of: 1) invasive Rainbow Trout (*Oncorhynchus mykiss*), 2) stocking of NBC, and 3) increased sedimentation/erosion from poor forestry and construction practices, and urbanization (Eastern 2006). Furthermore, given that SBC are at the southern limit of the species' range, they also face the negative impacts of climate change (Flebbe et al. 2006). Consequently, it is important to quantify the ecological requirements of SBC for both conservation and management purposes.

Our knowledge of SBC is limited, as is our knowledge of hatchery NBC in Southern Appalachian habitat, where they have been stocked for many years. Consequently, Brook Charr populations in the Southern Appalachians are now represented by genetically mixed populations, and a few pure SBC and NBC populations. Population data for SBC from the Georgia and North Carolina mountains indicate that populations typically are limited to small-stream habitat located above barriers (Grossman et al. 2010; Anglin and Grossman 2013), preferentially occupy deeper microhabitats with lower velocity and higher amounts of erosional substrata, and have small (<20m) home ranges (Anglin and Grossman 2013, 2018). To our knowledge, nothing is known about the comparative foraging of SBC and hatchery NBC at either the individual or population level. Such information is essential for both conservation and management purposes of SBC. Consequently, we conducted experiments on the foraging behavior of both SBC and hatchery NBC using a laboratory stream flume. We quantified the effects of 1) water velocity, 2) fish size,

3) days in captivity, 4) behavioral dominance, and 5) size rank, on prey capture success, holding velocity, and reactive distance of these strains of Brook Charr.

Materials and Methods

Specimen Collection

We obtained NBC from the Lake Burton Fish hatchery (Clarkesville, Georgia, USA) on February 5, 2019 (n = 20, mean standard length [mm ± SD] = 188 ± 13) and on April 22, 2019 (n = 9, mean standard length [mm ± SD] = 225 ± 14). This hatchery is run by the Georgia Department of Natural Resources and supplies fish for stocking throughout the state. We collected SBC (n = 21, mean standard length [mm ± SD] = 147 ± 14) from an approximately 350m, third-order section of Lynn Camp Prong in the Tennessee portion of the Great Smoky Mountains National Park (lat. 35.6133 N; long. 83.6481 W) on May 21, 2019. We chose this stream because the SBC is the only salmonid present since its restoration in 2008, and because it is representative of Southern Appalachian streams historically inhabited by the strain (Kanno et al. 2016). We collected fish using electrofishers and dip nets, placed them into large coolers, and then transported them to our laboratory at the University of Georgia, Athens. Upon arrival, SBC were immediately placed in large holding tanks that were held at 11.5°C, similar to the temperature in Lynn Camp Prong. We fed NBC 0.5g/fish of thawed bloodworms daily. Initially, we fed the SBC 0.5g/fish of thawed bloodworms daily but switched their diet to 0.5g/fish of thawed brine shrimp in an attempt to reduce their reluctance to eat the bloodworms used in experimental feeding trials. Both food types had similar nutritional compositions (unpublished data), and we transitioned SBC to a diet of brine shrimp 13 days before beginning experimentation.

Experimental Tank Setup

We conducted experiments using a 3.5m L x 0.75m W x 1.0m H plexiglass tank and confined the fish to the top part of the flume in a 1.5m L x 0.75m W x 0.5m H chamber (henceforth experimental chamber). The experimental chamber was bounded upstream by a polyvinyl chloride (PVC) collimator (to increase flow homogeneity) and downstream by a mesh/PVC barrier. An illustration and complete description of the flume is presented in Bozeman and Grossman (2019a). We filled the experimental chamber to a depth of 40cm with dechlorinated tap water (turbidities < 0.001 NTUs, Athens-Clarke County) and refilled it approximately every 5 days. We attached thin bamboo strips to the downstream side of the collimator to mimic natural stream cover and to prevent specimens from occupying a holding position directly in front of the feeding tubes (6mm diameter). Feeding tubes were evenly spaced across the front of the experimental chamber at a depth of 8cm from the surface. We controlled water velocity with two 24V (80-pound thrust), continuous-speed trolling motors placed side-by-side, downstream of the experimental chamber, behind the mesh/PVC barrier, and in the lower portion of the flume. Water temperature was maintained at 15°C with an electronic chiller. The water temperatures of the holding tanks and the experimental tank differed by 3.5°C due to a thermometer discrepancy that we detected near the end of experimentation, but both temperatures are within the Brook Charr optimal growth range (Hartman and Sweka 2001). The flume was shielded with black plastic sheeting to cloak observers and reduce other disturbances to the test specimens.

Experiments

Our experiments follow the design of Bozeman & Grossman (2019a,b). We conducted both single fish experiments (in which fish fed in isolation) and dominance experiments (in which fish fed in pairs). Our primary intent was to quantify the relationship between treatment velocity (cm/s; the controlled water velocity measured at three points spaced evenly across the width of the experimental chamber at a depth of 8cm) and: 1) prey capture success (success or failure), 2) holding velocity (cm/s; the water velocity at the stationary position held by the fish and to which it returned after capturing a prey), and 3) reactive distance (cm; the distance between the prey and the fish's nose when it first orients towards the prey, Bozeman and Grossman 2019a). We also tested whether prey capture success, holding velocity, and reactive distance were affected by fish size (standard length [mm]) and days in captivity. Given the strong correlation between our treatment velocity values and prey velocity (prey velocity = 0.02 + 0.98[treatment velocity], $n = 2620$, $R^2 = 0.88$, $p << 0.001$), we used treatment velocity values for all analyses. In addition to visual observations on fish during experiments, we recorded trials with two GoPro cameras, which allowed us to take accurate 3-D measurements of prey velocity and reactive distance with the video analysis software VidSync (www.vidsync.org; Neuswanger et al. 2016).

The day before a trial, we halted feeding, and after measuring standard length, placed the Charr in the experimental chamber. Water velocities were measured ($\pm$ 0.1cm/s) with a HACH FH950 flow meter. We began a trial by acclimating the fish to a 5cm/s current. We acclimated NBC and SBC for different amounts of time (15 minutes and 30 minutes respectively), because SBC required more time to initiate foraging behavior. A trial began by increasing water velocity to the first treatment velocity of 10cm/s. To assess the Charr's feeding motivation we released a few bloodworms (mm ± SD = 8.8 ± 1.4, n = 50, Bozeman and Grossman 2019a) down the middle feeding tube. If the fish initiated foraging behavior, we began the feeding trial. We released a prey from a randomly selected feeding tube and determined whether or not the prey was captured. After the fish's reaction was recorded, we released another prey, and continued this process until a total of nine prey items were released (a total of three prey from each randomly selected feeding tube). After the 10cm/s treatment was concluded, we reduced the water velocity to 5cm/s and allowed the fish to rest for 30min. We then slowly increased the treatment velocity to 20cm/s and repeated the procedure. We continued this procedure using 10cm/s increments until the specimen was unable to capture at least 3 of the 9 released prey, at which point we ended the trial.

To quantify the effects of behavioral dominance (i.e. dominant versus subordinate) and fish size rank (i.e. larger versus smaller) on prey capture success, holding velocity, and reactive distance, we conducted dominance experiments in which we repeated velocity trials with pairs of fish. Dominance trials were made only with two SBC or two NBC fish because we were only interested in within-group interactions, not between-group interactions. As per Bozeman and Grossman (2019a,b) the dominant fish was defined as the fish spending the greatest amount of time at the central holding position within the experimental chamber. To keep the ration of prey/fish constant between single fish and dominance experiments, we released 18 prey items per treatment velocity and ended the trial once the fish failed to capture a cumulative 6 prey items. All other methods were identical between experiments.

Statistical Analyses

We used generalized linear models (link = logit) to analyze the effects of predictor variables on prey capture success, and simple linear models to analyze the effects of the predictor variables on holding velocity and reactive distance in each of the four experiments (i.e. NBC single fish, NBC dominance, SBC single fish, SBC dominance). We constructed global models with these three predictor variables and constructed all possible reduced models. For the dominance experiments, we added dominance (dominant or subordinate) and size rank (larger or smaller) as categorical variables. We ranked models using Akaike's Information Criterion for small sample sizes (AICc) (Burnham and Anderson 2002). To calculate the effect sizes of treatment velocity, fish size, days in captivity, dominance status, and size rank, we performed model averaging over the full sets of models because we had a large sample size to predictor variable ratio, and our models were biologically realistic, reducing the possibility of spurious information (Burnham and Anderson 2002). To avoid loss of information caused by multicollinearity (Cade 2015), we standardized parameter coefficients by their partial standard deviations. All model averaging was conducted with the MuMIn package (Bartoń 2019) in R (R Core Team 2019).

All specimens were humanely treated under AUP# A2018 01-004-Y3-A3 approved by the IACUC of the University of Georgia.

Results

Prey Capture Success

Trials were terminated when fish failed to capture a minimum of three out of nine prey, which occurred at a maximum of 50cm/s for NBC and 60cm/s for SBC. Models with the greatest explanatory power for prey capture success varied across the experiments ($w_i = 0.27$-0.71), but the top model for each experiment always included a treatment velocity term (Table 2.1). Treatment velocity negatively affected prey capture success in all four experiments and had high effect sizes (slope $\beta_i \leq -0.824$, combined 95% CI range = -1.64/-0.70, $w+ = 1$ for all experiments, Table 2.2, Fig. 2.1-2.3). The remaining factors had little explanatory power across experiments. Fish size only affected prey capture success for the NBC single fish experiment ($\beta_i = -0.30$, 95% CI = -0.45/-0.16); whereas size rank only affected fish prey capture success in the SBC dominance experiment (β_i [small] = -0.21, 95% CI = -0.39/-0.058, Table 2.2). Finally, days in captivity only had a positive effect on prey capture success in the SBC single fish experiment ($\beta_i = 0.28$, 95% CI = 0.12/0.44, Table 2.2).

Holding Velocity

The models with the greatest explanatory power for holding velocity also all included treatment velocity, although only one had a $w_i \geq 0.36$ (Table 2.1, NBC single fish experiment $w_i = 0.71$). Holding velocity increased with treatment velocity in all experiments ($\beta_i = 7.57 - 8.78$, combined 95% CI range = 6.41/10.10, $w+ = 1$ for all experiments, Table 2.2, Fig. 2.4-2.6). The remaining predictors that significantly affected holding velocity only had explanatory power for one experiment each, with fish size affecting holding velocity only in the NBC single fish experiment ($\beta_i = 1.57$, 95% CI = 0.58/2.63, $w+ = 0.98$, Table 2.2), and days in captivity positively influencing holding velocity only in the SBC dominance experiment ($\beta_i = 1.46$, 95% CI = 0.30/3.08, $w+ = 0.87$, Table 2.2).

Reactive Distance

Reactive distance was weakly and inconsistently affected by the predictor variables (Fig. 2.7-2.9), with the models having the highest explanatory power still having low w_i values ranging from 0.10-0.41, Table 2.1). Days in captivity had a weak positive effect on reactive distance in the SBC single fish experiment (β_i = 0.0089, 95% CI = 0.0022/0.018, Table 2.2) but a weak negative effect on reactive distance in the SBC dominance experiment (β_i = -0.015, 95% CI = -0.024/-0.0067, Table 2.2). Fish size had a small negative effect on reactive distance only in the NBC single fish experiment (β_i = -0.0071, 95% CI = -0.015/-0.0014, Table 2.2), and size rank had a small effect on reactive distance in only the SBC dominance experiment (β_i [small] = -0.012, 95% CI = -0.022/-0.0039, Table 2.2).

Effects of Dominance

Dominant fish captured many more prey than did subordinates in both SBC and NBC dominance experiments (β_i [subordinates] = -1.08, 95% CI = -1.27/-0.88 and β_i [subordinates] = -2.05, 95% CI = -2.24/-1.86 and dominance had a $w+$ of 1 for both SBC and NBC, Table 2.2, Fig. 2.2-2.3). In addition, prey capture of dominant SBC in dominance experiments was higher at 30 and 40cm/s (87.8% and 74.4% respectively; Fig. 2.3) than prey capture of SBC in single fish experiments (64.0% and 37.0% respectively), but NBC did not display this difference. Generally, dominance behavior did not affect either holding velocity or reactive distance because the 95% CI of effect sizes overlapped zero for both SBC and NBC dominance experiments; although, dominant individuals had greater reactive distances at some of the higher velocities (Fig. 2.8-2.9).

Comparisons Between SBC and NBC

Most responses of SBC and NBC to treatments were similar, however several differential responses were observed. For example, in single fish experiments, SBC had greater reactive distances at 10-30cm/s velocities than NBC (Fig. 2.7). In addition, only SBC displayed a positive effect of days in captivity on prey capture success (β_i = 0.28, 95% CI = 0.12/0.44) and reactive distance (β_i = 0.0089, 95% CI = 0.0022/0.018; Table 2.2) in these experiments. Conversely, in single fish experiments, only NBC displayed a positive effect of fish size on holding velocity (β_i = 1.57, 95% CI = 0.58/2.63; Table 2.1-2.2). In dominance experiments, behavioral dominance had a larger effect on the prey capture success of NBC (β_i [subordinates] = -2.05, 95% CI = -2.24/-1.86) than on SBC (β_i [subordinates] = -1.08, 95% CI = -1.27/-0.88).

Discussion

Water velocity significantly affected prey capture success and holding velocity for both SBC and NBC. However, neither water velocity nor any other variables displayed a consistent effect on reactive distance for either strain. Dominance was important to foraging, with dominant fish having higher mean prey capture success than subordinates for both SBC and NBC. Finally, the differences observed between SBC and NBC were minor and inconsistent, which is perhaps surprising given that NBC are hatchery fish and not wild fish, and significant behavioral differences are often displayed between wild and hatchery fish of the same species (Weber and Fausch 2003). Our results represent a comparison between wild SBC and hatchery fish of NBC genetic stock.

Water velocity typically affects foraging of drift-feeding fishes, especially salmonids (Fausch 2014; Grossman 2014; Piccolo et al. 2014; Rosenfeld et al. 2014). At lower velocities, drift-feeders capture the majority of prey items present, but may not meet energy demands because prey availability is too low, given the well-known positive relationship between water velocity and drift prey abundance. Conversely, as velocities increase, eventually a point is reached at which fish become physically unable to detect and capture prey items (Hill and Grossman 1993). This typically results in a negative exponential relationship between treatment velocity and prey capture success (Grossman 2014), which we observed in all experiments. In addition, we expected to find a positive relationship between holding and treatment velocity based on previous work (Bozeman and Grossman 2019a,b). Although we tried to create laminar flow in the flume, fish were able to exploit small-scale heterogeneity within the experimental chamber, and hold at velocities lower than the treatment velocities. This phenomenon of drift-feeding salmonids holding at slightly lower velocities than those from which they forage, has been observed in both in laboratory and natural settings (Jenkins 1969; Everest and Chapman 1972; Hill and Grossman 1993; Liao 2007).

There were no clear patterns in the factors affecting reactive distance. Although days in captivity, fish size, and size rank were identified as factors having predictive power for reactive distance, their effect sizes were small and inconsistent. Our previous research has yielded similar results (Donofrio et al. 2018; Bozeman and Grossman 2019a,b), but these fishes were all from Alaskan lotic systems where an ability to identify and react to prey from a distance is at a premium. Nonetheless, reactive distance for other fishes is affected by factors such as: 1) light intensity (Vogel and Beauchamp 1999) and 2) turbidity (Barrett et al. 1992; Vogel and Beauchamp 1999; Hazelton and Grossman 2009). Although the reactive distance data are variable, SBC had significantly (non-overlapping 95% CIs) greater mean reactive distances than NBC for treatment velocities of 10-30cm/s. Although this difference was not large (mean reactive distance = 34.3 - 35.7cm for SBC fish vs. 27.5 - 28.2cm for NBC fish), it suggests that SBC, which commonly are found in low velocity microhabitats (Anglin and Grossman 2013), might experience a selective advantage in these microhabitats.

Dominance strongly affected prey capture success for both SBC and NBC, with dominants capturing considerably more prey items than subordinates. This finding provides a mechanism (intraspecific competition) for the strong effects of density-dependence previously identified in an SBC population (Grossman et al. 2010) and in other Appalachian Brook Charr populations (Utz and Hartman 2009; Huntsman and Petty 2014). Density-dependence commonly affects multiple aspects of salmonid populations (Grossman and Simon 2020). Although subordinate Charr experienced greatly reduced prey capture success, it must be noted that this effect might be diminished in stream habitats, where subordinates are likely better able to avoid dominants. For example, SBC in Lynn Camp Prong, were only observed once within approximately 2m of each other (Sliger, personal observation), a distance greater than the length of the experimental chamber.

Although dominance in other salmonids typically carries a cost (Bozeman and Grossman 2019a,b), prey capture success values for SBC in dominance trials and feeding alone were similar, except at intermediate velocities. At 30-40cm/s, dominant individuals had significantly greater prey capture success than SBC feeding alone. This was a surprising result, given that juvenile Chinook Salmon, interior Dolly Varden Charr, and Arctic Grayling all show a reduction in prey capture success when dominants are in the presence of a subordinate (Donofrio et al. 2018; Bozeman and Grossman 2019a,b). Nonetheless, laboratory studies on two marine species indicate that individuals increase feeding rates when conspecifics are present (Ryer and Olla 1991; Stoner and Ottmar 2004;). In addition, social facilitation of feeding also was observed in an estuarine goby, where dominant individuals displayed increased access to food but also stimulated feeding in subordinates (Grossman 1980).

Though we only observed small differences in foraging behavior between SBC and NBC, other investigators have noted that hatchery salmonids in general, typically display higher aggression (Moyle 1969; Weber and Fausch 2003), greater energy expenditure (Moyle 1969; Weber and Fausch 2003), and higher growth rates than their wild counterparts (Vincent 1960; Weber and Fausch 2003).

In conclusion, we have demonstrated that water velocity and behavioral dominance have significant impacts on the foraging behavior of both SBC and NBC. Given that little is known about the ecology of the SBC, our results should aid in conservation and management of this strain. For example, SBC have high foraging efficiency at velocities between 10 and 30cm/s, information that will aid managers in habitat restoration and flow management. Although, more research is needed to determine whether our results may be extrapolated to other populations of SBC.

Acknowledgements

This research was made possible through the help of C. Bloom, B. Hilburn, C. Ellis, B. Bozeman, T. Simon, M. Tiller, B. Irwin, S. Wenger, Great Smoky Mountains National Park, M. Kulp, C. Abramson, A. Walker, N. Goodman, J. Cary, the Georgia Department of Natural Resources, J. Thomson, J. Stewart, the Warnell School of Forestry & Natural Resources, and a few anonymous others.

REFERENCES

Anglin, Z.W., and Grossman, G.D. 2013. Microhabitat use by southern brook trout (*Salvelinus fontinalis*) in a headwater North Carolina stream. Ecol. Freshwat. Fish, **22**(4):567-577.

Anglin, Z.W., and Grossman, G.D. 2018. Movement of Southern Brook Charr in a North Carolina Headwater Stream. Southeast. Nat. **17**(3):476-483.

Bartoń, K. 2019. MuMIn: Multi-Model Inference. R package version 1.43.15. https://CRAN.R-project.org/package=MuMIn.

Barrett, J.D., Grossman, G.D. and Rosenfeld, J. 1992. Turbidity induced changes in reactive distance in rainbow trout (*Oncorhynchus mykiss*). Trans. Am. Fish. Soc. **121**:437-443.

Bozeman, B.B., and Grossman, G.D. 2019a. Mechanics of foraging success and optimal microhabitat selection in Alaskan Arctic Grayling (*Thymallus arcticus*). Can. J. Fish. Aquat. Sci. **76**(5):815-830.

Bozeman, B.B., and Grossman, G.D. 2019b. Foraging behavior and optimal microhabitat selection in interior Dolly Varden Charr (*Salvelinus malma*) in Panguingue Creek, Alaska. Ecol. Freshwat. Fish, **28**:586-601.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, **2nd Edition**.

Cade, B.S. 2015. Model averaging and muddled multimodel inferences. Ecology, **96**(9):2370-2382.

Curry, R.A., and MacNeill, W.S. 2004. Population-level responses to sediment during early life in brook trout. J. N. Am. Benthol. Soc. **23**:140-150.

Danzmann, R.G., Morgan II, R.P., Jones, M.W., Bernatchez, L., and Ihssen, P.E. 1998. A major sextet of mitochondrial DNA phylogenetic assemblages extant in eastern North American brook trout (*Salvelinus fontinalis*): distribution and postglacial dispersal patterns. Can. J. Zool. **76**(7):1300-1318.

Donofrio, E., Simon, T., Neuswanger, J.R., and Grossman, G.D. 2018. Velocity and dominance affect prey capture and microhabitat selection in juvenile Chinook (*Oncorhynchus tshawytscha*). Environ. Biol. Fishes, **101**(4):609-622.

Eastern Brook Trout Joint Venture. 2006. Eastern brook trout: status and threats. Prepared by Trout Unlimited, Arlington, VA, for EBTJV.

Everest, F.H., and Chapman, D.W. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. J. Fish. Res. Board. Can. **29**(1):91-100.

Fausch, K.D. 2014. A historical perspective on drift foraging models for stream salmonids. Environ. Biol. Fishes, **97**(5):453-464.

Flebbe, P.A., Roghair, L.D., and Bruggink, J.L. 2006. Spatial modeling to project southern Appalachian trout distribution in a warmer climate. Trans. Am. Fish. Soc. **135**(5):1371-1382.

Grossman, G.D. 1980. Food, fights and burrows: the adaptive significance of intraspecific aggression in the Bay Goby (Pisces: Gobiidae). Oecologia, **45**(2):261-266.

Grossman, G.D. 2014. Not all drift feeders are trout: a short review of fitness-based habitat selection models for fishes. Environ. Biol. Fishes, **97**(5):465-473.

Grossman, G.D., and Simon, T.N. 2020. Density-dependent effects on salmonid populations: A review. Ecol. Freshwat. Fish, **29**:400-418.

Grossman, G.D., Ratajczak, R.E., Wagner, C.M., and Petty, J.T. 2010. Dynamics and regulation of the southern brook trout (*Salvelinus fontinalis*) population in an Appalachian stream. Freshwat. Biol. **55**(7):1494-1508.

Hartman, K.J., and Sweka, J.A. 2001. Development of a bioenergetics model for Appalachian brook trout. Proceedings of the Southeastern Association of Fish and Wildlife Agencies, **55**:38-51.

Hazelton, P.D., and Grossman, G.D. 2009. The effects of turbidity and an invasive species on foraging success of rosyside dace (*Clinostomus funduloides*). Freshw. Biol. **54**(9): 1977-1989.

Hill, J., and Grossman, G.D. 1993. An energetic model of microhabitat use for rainbow trout and rosyside dace. Ecology, **74**(3):685-698.

Hudy, M., Nislow, K., Smith, E.P., Cooper, A.R, and Infante, D.M. 2013. The Importance of Scale: Assessing and Predicting Brook Trout Status in Its Southern Native Range. https://easternbrooktrout.org/resources/science-publications/chesapeake-bay-brook-trout-management-strategy-references/the-importance-of-scale-assessing-and-predicting-brook-trout-status-hudy-et-al-2013/view.

Huntsman, B.M., and Petty, J.T. 2014. Density-dependent regulation of brook trout population dynamics along a core-periphery distribution gradient in a central Appalachian watershed. PloS one, **9**(3).

Jenkins Jr., T.M. 1969. Social structure, position choice and micro-distribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams. Anim. Behave. Monogr. **2:**55-123.

Kanno, Y., Kulp, M.A., and Moore, S.E. 2016. Recovery of native brook trout populations following the eradication of nonnative rainbow trout in southern Appalachian mountain streams. N. Am. J. Fish Manage. **36**(6):1325-1335.

Liao, J.C. 2007. A review of fish swimming mechanics and behaviour in altered flows. Philos. Trans. R. Soc. Lond., B, Biol. Sci. **362**(1487):1973-1993.

McCracken, G.F., Parker, C.R., and Guffey, S.Z. 1993. Genetic differentiation and hybridization between stocked hatchery and native brook trout in Great Smoky Mountains National Park. Trans. Am. Fish. Soc. **122**(4):533-542.

Moyle, P.B. 1969. Comparative behavior of young brook trout of domestic and wild origin. The Progressive Fish-Culturist, **31**(1):51-56.

Neuswanger, J.R., Wipfli, M.S., Rosenberger, A.E., and Hughes, N.F. 2016. Measuring fish and their physical habitats: Versatile 2-D and 3-D video techniques with user-friendly software. Can. J. Fish. Aquat. Sci. **73**(12):1861-1873.

Piccolo, J.J., Frank, B.M., and Hayes, J.W. 2014. Food and space revisited: The role of drift-feeding theory in predicting the distribution, growth, and abundance of stream salmonids. Environ. Biol. Fishes, **97**(5):475-488.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rosenfeld, J.S., Bouwes, N., Wall, C.E., and Naman, S.M. 2014. Successes, failures, and opportunities in the practical application of drift-foraging models. Environ. Biol. Fishes, **97**(5):551-574.

Ryer, C.H., and Olla, B.L. 1991. Information transfer and the facilitation and inhibition of feeding in a schooling fish. Environ. Biol. Fishes, **30**(3):317-323.

Stoneking, M., Wagner, D.J., and Hildebrand, A.C. 1981. Genetic evidence suggesting subspecific differences between northern and southern populations of brook trout (*Salvelinus fontinalis*). Copeia, 810-819.

Stoner, A.W., and Ottmar, M.L. 2004. Fish density and size alter Pacific halibut feeding: implications for stock assessment. J. Fish Biol. **64**(6):1712-1724.

Utz, R.M., and Hartman, K.J. 2009. Density-dependent individual growth and size dynamics of central Appalachian brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. **66**(7):1072-1080.

Vincent, R.E. 1960. Some influences of domestication upon three stocks of brook trout (*Salvelinus fontinalis* Mitchill). Trans. Am. Fish. Soc. **89**(1):35-52.

Vogel, J.L., and Beauchamp, D.A. 1999. Effects of light, prey size, and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. Can. J. Fish. Aquat. Sci. **56**(7):1293-1297.

Weber, E.D., and Fausch, K.D. 2003. Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition. Can. J. Fish. Aquat. Sci. **60**(8):1018-1036.

Tables

Table 2.1. AICc values, delta AICc values (ΔAICc), and Akaike weights (w_i) for interpretable models with explanatory power for all response variables (Resp. Var.) in all experiments. Experiments 1 and 2 are the NBC single fish experiment and dominance experiment respectively. Experiments 3 and 4 are the SBC single fish experiment and dominance experiment, respectively. Predictor variables are abbreviated as follows: treatment velocity = Velocity, fish size = Size, days in captivity = Days, dominance status= Dom, size rank = Rank. Models for each combination of predictor variables were evaluated, but only models with $w_i \geq 0.05$ are shown for brevity.

Resp. Var.	Experiment	Model	AICc	ΔAICc	w_i
Prey capture	Exp. #1	Global	1147.95	0	0.63
		Size + Velocity	1148.99	1.04	0.37
	Exp. #2	Dom + Velocity	1414.59	0	0.27
		Dom + Size + Velocity	1415.57	0.98	0.16
		Days + Dom + Size + Velocity	1415.59	1.00	0.16
		Global	1416.44	1.85	0.11
		Days + Dom + Velocity	1416.55	1.95	0.10
		Rank + Dom + Velocity	1416.60	2.01	0.10
		Rank + Dom + Size + Velocity	1417.43	2.84	0.06
	Exp. #3	Days + Velocity	861.35	0	0.71
		Global	863.24	1.89	0.28

	Exp. #4	Rank + Dom + Velocity	1675.77	0	0.32
		Days + Rank + Dom + Velocity	1675.93	0.17	0.30
		Global	1676.97	1.20	0.18
		Rank + Dom + Size + Velocity	1677.72	1.95	0.12
		Days + Dom + Size + Velocity	1678.61	2.84	0.08
Holding velocity	Exp. #1	Size + Velocity	759.88	0	0.71
		Global	761.87	1.99	0.26
	Exp. #2	Rank + Dom + Size + Velocity	776.61	0	0.22
		Dom + Velocity	778.26	1.65	0.10
		Dom + Size + Velocity	778.43	1.82	0.09
		Rank + Dom + Velocity	778.58	1.97	0.08
		Size + Velocity	778.79	2.18	0.07
		Global	778.84	2.23	0.07
		Days + Dom + Velocity	779.15	2.54	0.06
		Rank + Size + Velocity	779.18	2.57	0.06
		Days + Rank + Dom + Velocity	779.48	2.88	0.05
		Velocity	779.79	3.18	0.05
	Exp. #3	Velocity	624.35	0	0.36
		Size + Velocity	624.95	0.59	0.27
		Days + Velocity	625.31	0.96	0.22
		Global	626.02	1.67	0.16
	Exp. #4	Days + Size + Velocity	812.31	0	0.29

		Days + Dom + Size + Velocity	813.72	1.42	0.14
		Days + Dom + Velocity	813.79	1.48	0.14
		Days + Rank + Size + Velocity	814.30	1.99	0.11
		Global	814.35	2.05	0.10
Reactive distance	Exp. #1	Days + Size	-1272.74	0	0.41
		Size	-1271.27	1.47	0.20
		Global	-1270.86	1.88	0.16
		Size + Velocity	-1269.46	3.28	0.08
		Days	-1269.24	3.50	0.07
	Exp. #2	Days + Dom + Size	-1027.29	0	0.10
		Dom	-1026.92	0.37	0.08
		Null Model	-1026.42	0.87	0.06
		Dom + Rank	-1026.41	0.88	0.06
		Days + Dom + Size + Velocity	-1026.14	1.14	0.05
		Days + Dom	-1026.09	1.20	0.05
	Exp. #3	Days + Size	-1023.06	0	0.36
		Days	-1022.56	0.50	0.28
		Global	-1021.35	1.71	0.15
		Days + Velocity	-1020.75	2.31	0.11
		Size	-1018.93	4.13	0.05
	Exp. #4	Days + Rank + Size	-1161.51	0	0.32
		Days + Dom + Rank + Size	-1160.13	1.38	0.16

Days + Rank + Size + Velocity	-1159.96	1.55	0.15
Days + Rank	-1159.23	2.28	0.10
Global	-1158.55	2.96	0.07
Days + Dom + Rank	-1157.92	3.59	0.05
Days + Rank + Velocity	-1157.82	3.69	0.05

Table 2.2. Model-averaged parameter coefficients standardized by partial standard deviations (with 95% confidence intervals) and relative variable importance (*w*+) for all predictor variable (Pred. Var.) and response variable (Resp. Var.) combinations in all experiments. Abbreviations are consistent with those in Table 2.1. Confidence intervals marked by "†" overlap 0.

Resp. Var.	Pred. Var.	Experiment	Estimate (95% CI)	*w*+
Prey capture	Velocity	Exp. #1	-1.33 (-1.49/-1.16)	1.0
		Exp. #2	-1.05 (-1.19/-0.91)	1.0
		Exp. #3	-1.44 (-1.64/-1.24)	1.0
		Exp. #4	-0.82 (-0.95/-0.70)	1.0
	Days	Exp. #1	-0.080 (-0.27/0.016)†	0.63
		Exp. #2	0.030 (-0.082/0.23)†	0.41
		Exp. #3	0.28 (0.12/0.44)	0.99
		Exp. #4	0.056 (-0.031/0.23)†	0.55
	Size	Exp. #1	-0.30 (-0.45/-0.16)	1.0
		Exp. #2	0.053 (-0.049/0.26)†	0.50
		Exp. #3	-0.0083 (-0.19/0.13)†	0.28
		Exp. #4	0.030 (-0.11/0.26)†	0.38
	Dom (Subordinate)	Exp. #2	-2.05 (-2.24/-1.86)	1.0
		Exp. #4	-1.08 (-1.27/-0.88)	1.0
	Rank (Small)	Exp. #2	0.0096 (-0.12/0.19)†	0.31
		Exp. #4	-0.21 (-0.39/-0.058)	0.91
Holding velocity	Velocity	Exp. #1	7.57 (6.54/8.60)	1.0

		Exp. #2	7.67 (6.41/8.93)	1.0
		Exp. #3	8.68 (7.43/9.93)	1.0
		Exp. #4	8.78 (7.41/10.10)	1.0
	Days	Exp. #1	-0.061 (-1.26/0.81)†	0.27
		Exp. #2	-0.11 (-1.82/1.12)†	0.31
		Exp. #3	-0.26 (-1.93/0.57)†	0.38
		Exp. #4	1.46 (0.30/3.08)	0.87
	Size	Exp. #1	1.57 (0.58/2.63)	0.98
		Exp. #2	0.67 (-0.19/2.44)†	0.60
		Exp. #3	-0.33 (-2.03/0.48)†	0.42
		Exp. #4	1.12 (-0.066/3.23)†	0.71
	Dom (Subordinate)	Exp. #2	-0.92 (-2.57/0.0036)†	0.71
		Exp. #4	-0.61 (-2.94/0.53)†	0.50
	Rank (Small)	Exp. #2	0.57 (-0.31/2.39)†	0.54
		Exp. #4	0.039 (-1.99/2.23)†	0.34
Reactive distance	Velocity	Exp. #1	0.00043 (-0.0054/0.0084)†	0.28
		Exp. #2	0.0012 (-0.0050/0.012)†	0.34
		Exp. #3	-0.00057 (-0.0098/0.0059)†	0.29
		Exp. #4	-0.00092 (-0.011/0.0052)†	0.32
	Days	Exp. #1	-0.0044 (-0.013/0.00032)†	0.68
		Exp. #2	-0.0035 (-0.016/0.0027)†	0.52
		Exp. #3	0.0089 (0.0022/0.018)	0.90

	Exp. #4	-0.015 (-0.024/-0.0067)	0.99
Size	Exp. #1	-0.0071 (-0.015/-0.0014)	0.85
	Exp. #2	-0.0022 (-0.016/0.0054)†	0.43
	Exp. #3	-0.0036 (-0.014/0.0014)†	0.57
	Exp. #4	-0.0060 (-0.017/0.00037)†	0.72
Dom (Subordinate)	Exp. #2	-0.0050 (-0.016/0.00085)†	0.64
	Exp. #4	-0.0016 (-0.014/0.0051)†	0.37
Rank (Small)	Exp. #2	0.0014 (-0.0059/0.013)†	0.36
	Exp. #4	-0.012 (-0.022/-0.0039)	0.94

List of Figures

Figure 2.8: There was no strong, consistent difference between the reactive distances of subordinate and dominant NBC, although those for dominant Charr were greater at the highest velocities. Error bars represent 95% confidence intervals. Point labels represent sample sizes. The treatment velocities at which reactive distances for dominant and subordinate Charr were different are marked by “*”.

Figure 2.9: Reactive distances for dominant and subordinate SBC were not different, except at one treatment velocity. Error bars represent 95% confidence intervals. Point labels represent sample sizes. The treatment velocity at which reactive distances for dominant and subordinate Charr were different is marked by “*”.

Figure 2.1

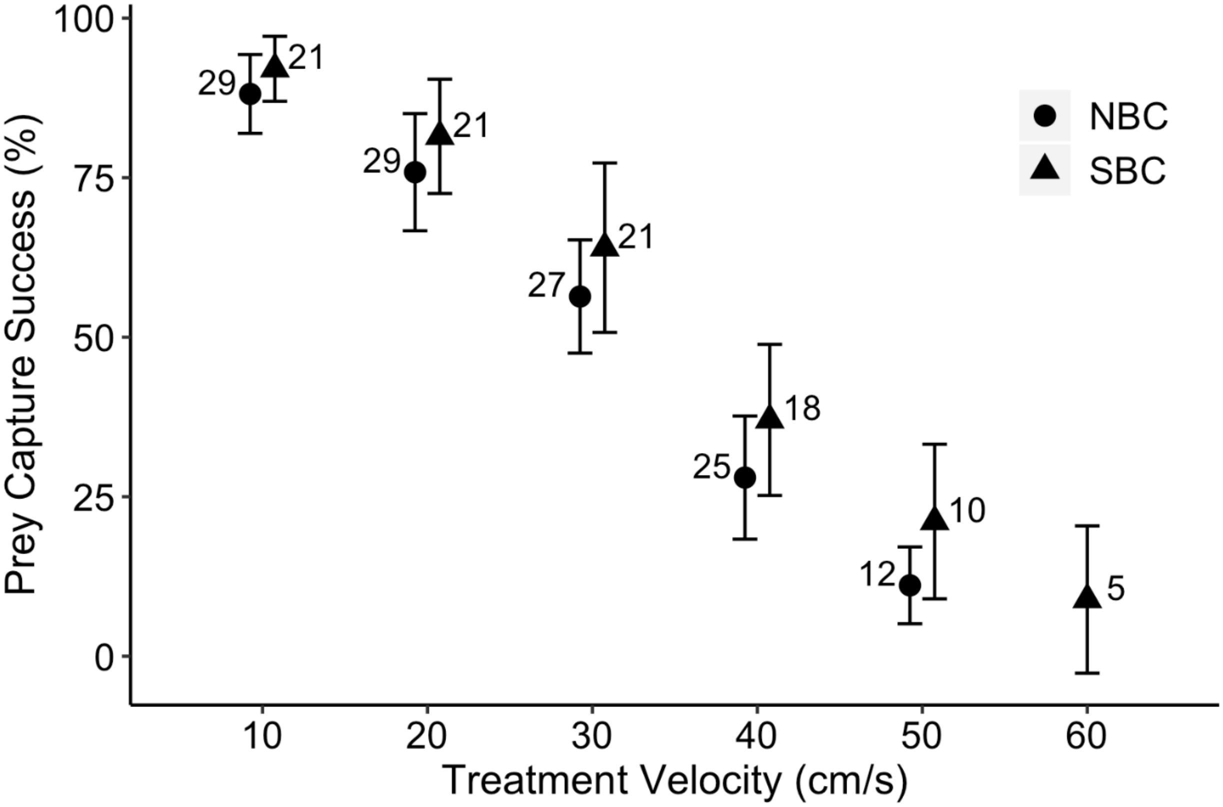

100
75
50
25
0
Prey Capture Success (%)
10
20
30
40
50
60
Treatment Velocity (cm/s)
● NBC
▲ SBC
29
21
29
21
27
21
25
18
12
10
5

Figure 2.2

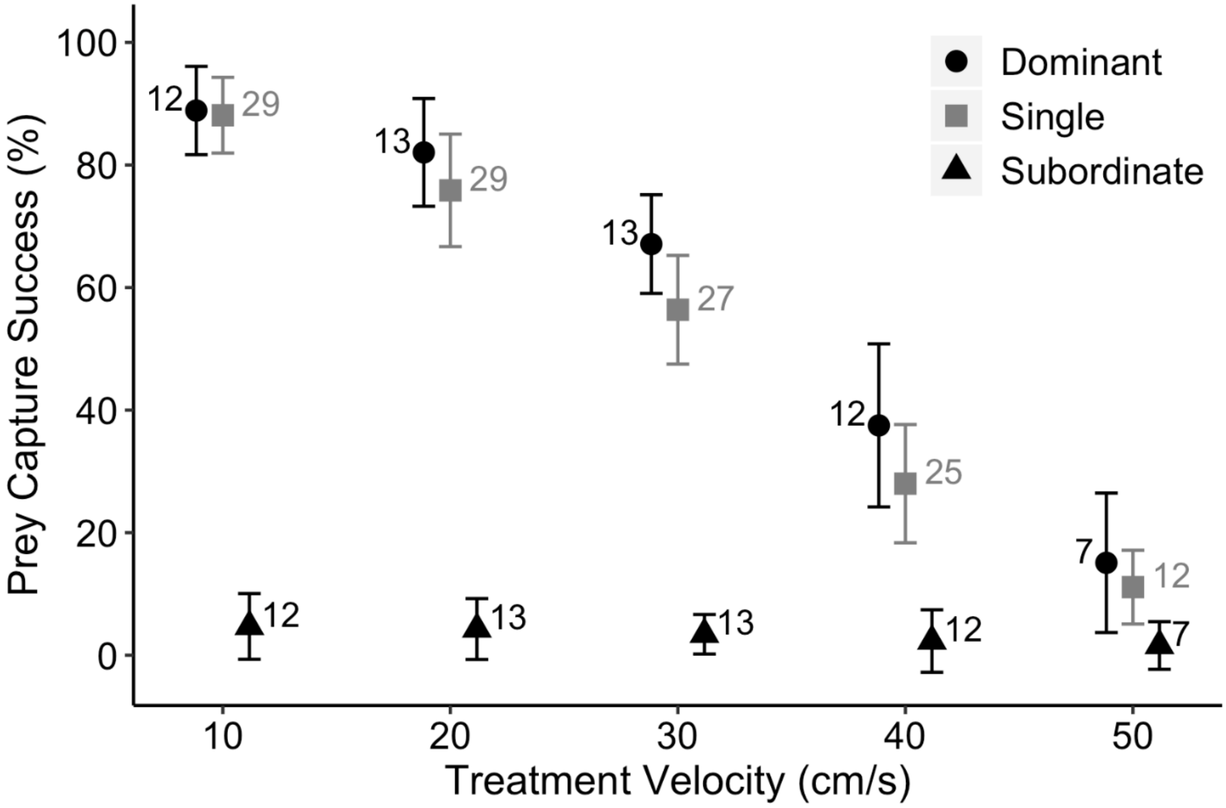

Prey Capture Success (%)
0
20
40
60
80
100
10
20
30
40
50
Treatment Velocity (cm/s)
● Dominant
■ Single
▲ Subordinate
12
29
13
29
13
27
12
25
7
12
12
13
13
12
7

Figure 2.3

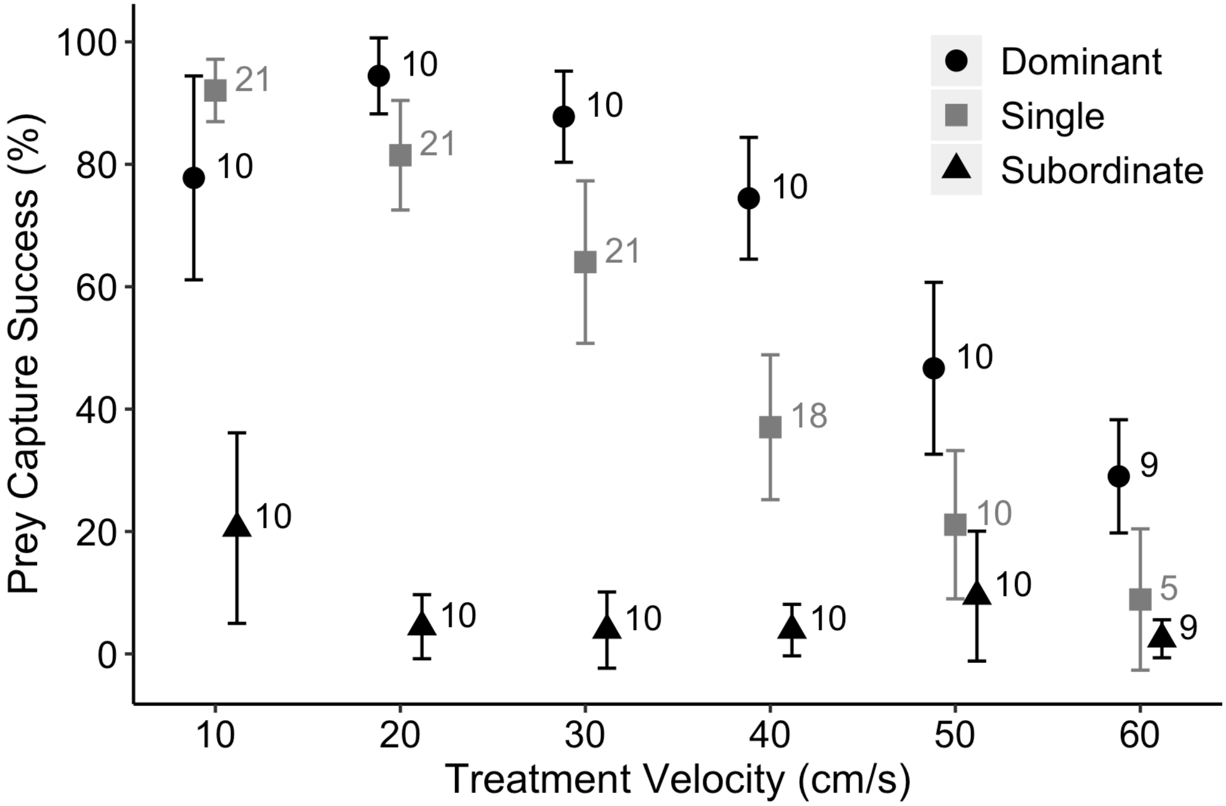

Prey Capture Success (%)
100
80
60
40
20
0
10
20
30
40
50
60
Treatment Velocity (cm/s)
Dominant
Single
Subordinate
21
10
10
21
10
21
10
18
10
10
9
10
5
9
10
10
10
10
10
9

Figure 2.4

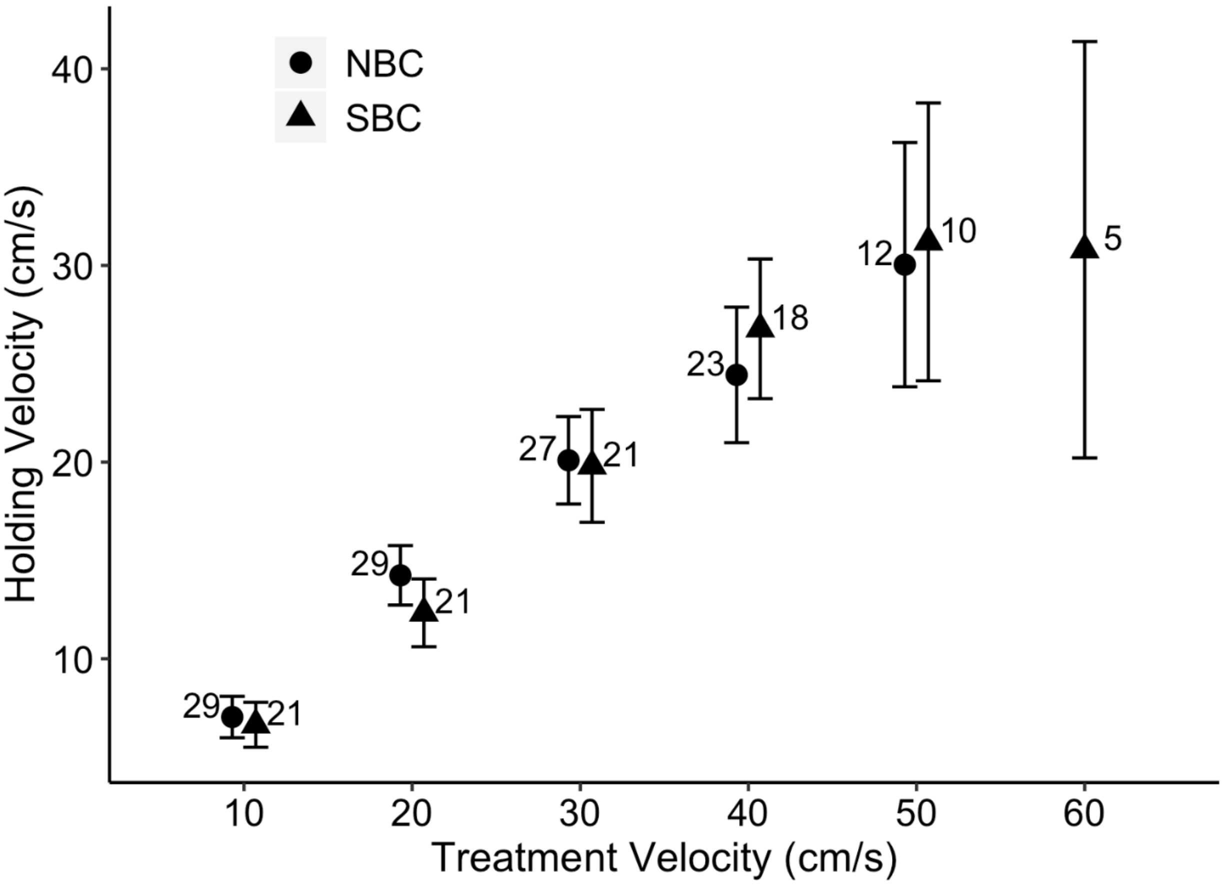

● NBC
▲ SBC
Holding Velocity (cm/s)
40
30
20
10
Treatment Velocity (cm/s)
10
20
30
40
50
60
29
21
29
21
27
21
23
18
12
10
5

Figure 2.5

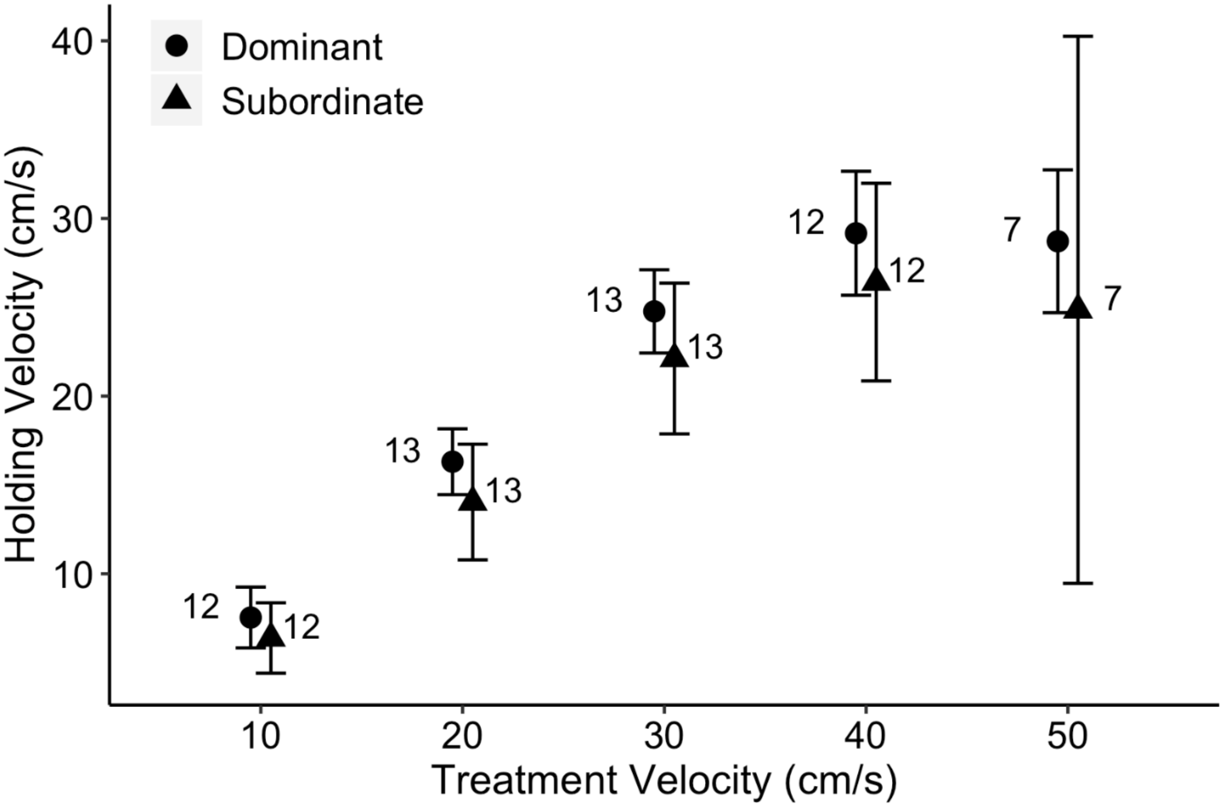
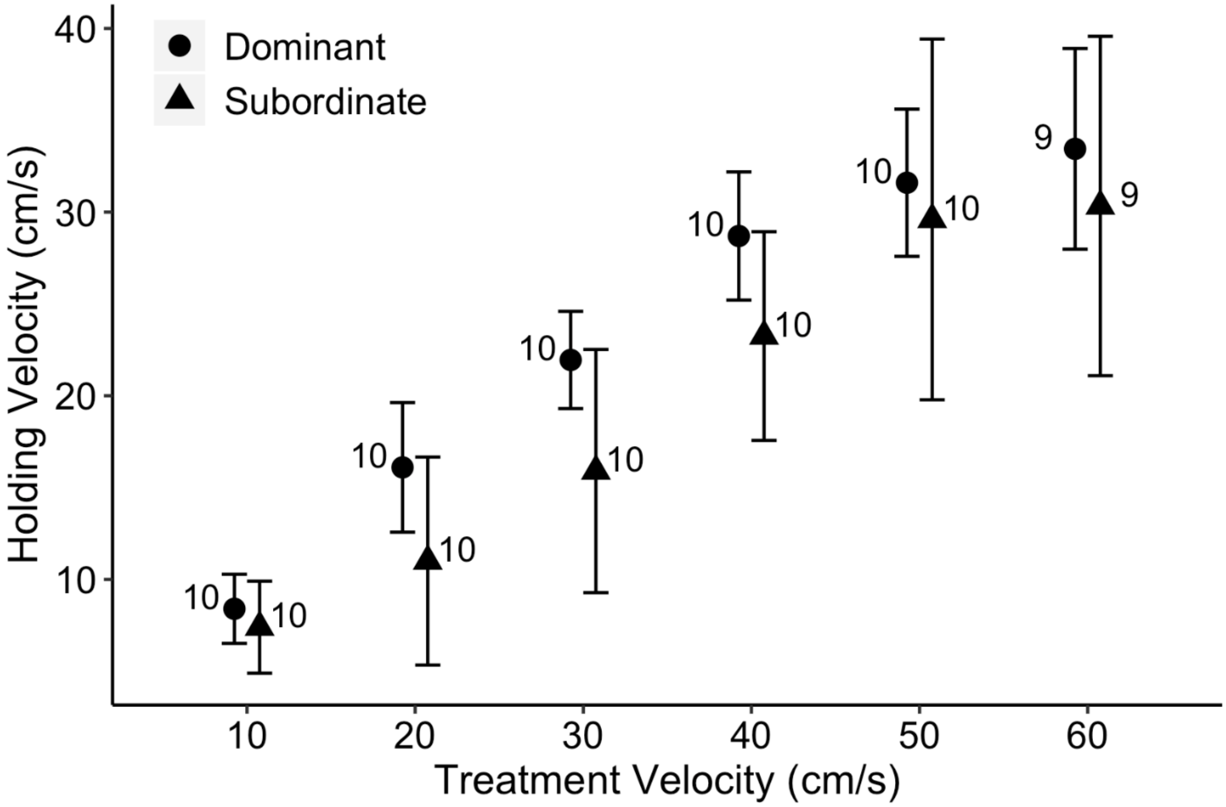

Dominant
Subordinate
Holding Velocity (cm/s)
Treatment Velocity (cm/s)
40
30
20
10
10
20
30
40
50
12
12
13
13
13
13
12
12
7
7

Figure 2.6



● Dominant
▲ Subordinate
Holding Velocity (cm/s)
Treatment Velocity (cm/s)
10
20
30
40
10
20
30
40
50
60
10
10
10
10
10
10
10
10
10
10
9
9

Figure 2.7

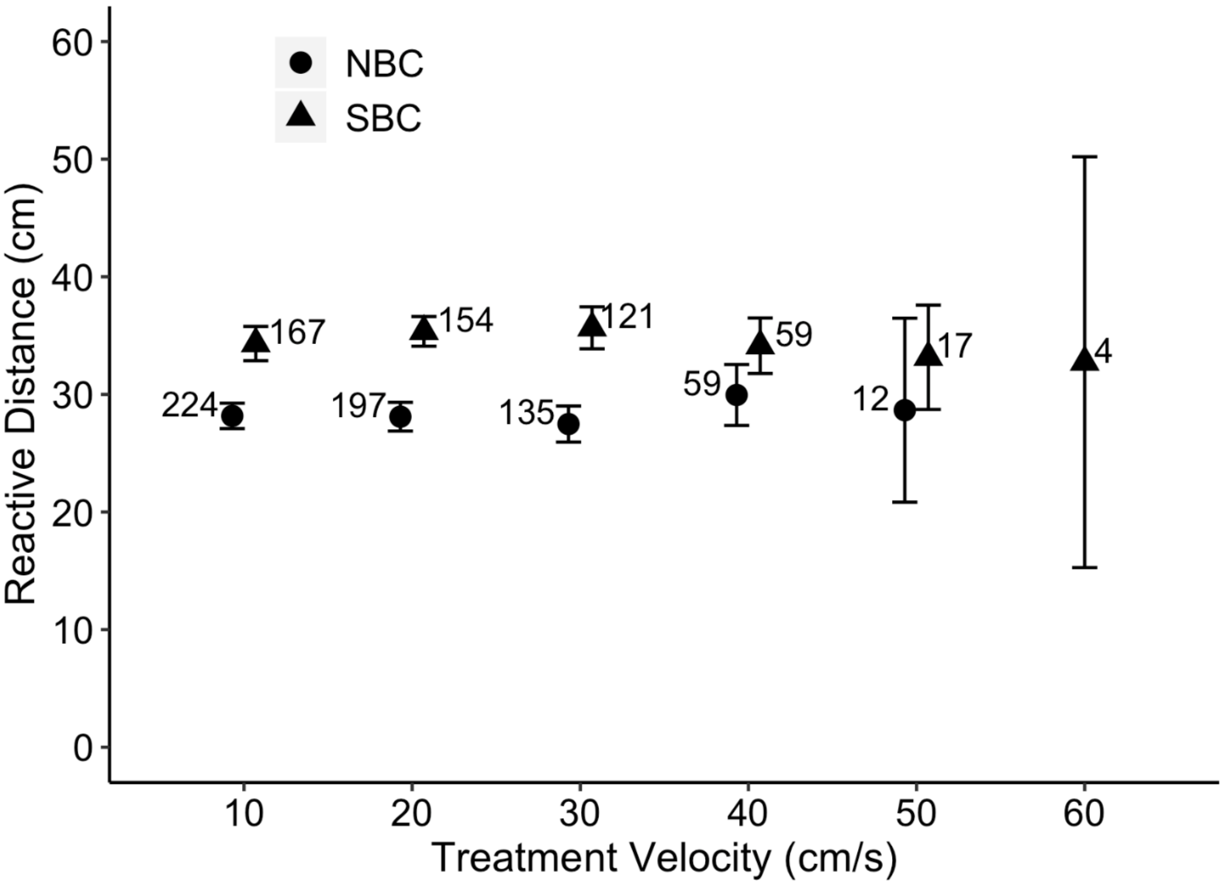

● NBC
▲ SBC
Reactive Distance (cm)
Treatment Velocity (cm/s)
0
10
20
30
40
50
60
10
20
30
40
50
60
224
167
197
154
135
121
59
59
12
17
4

Figure 2.8

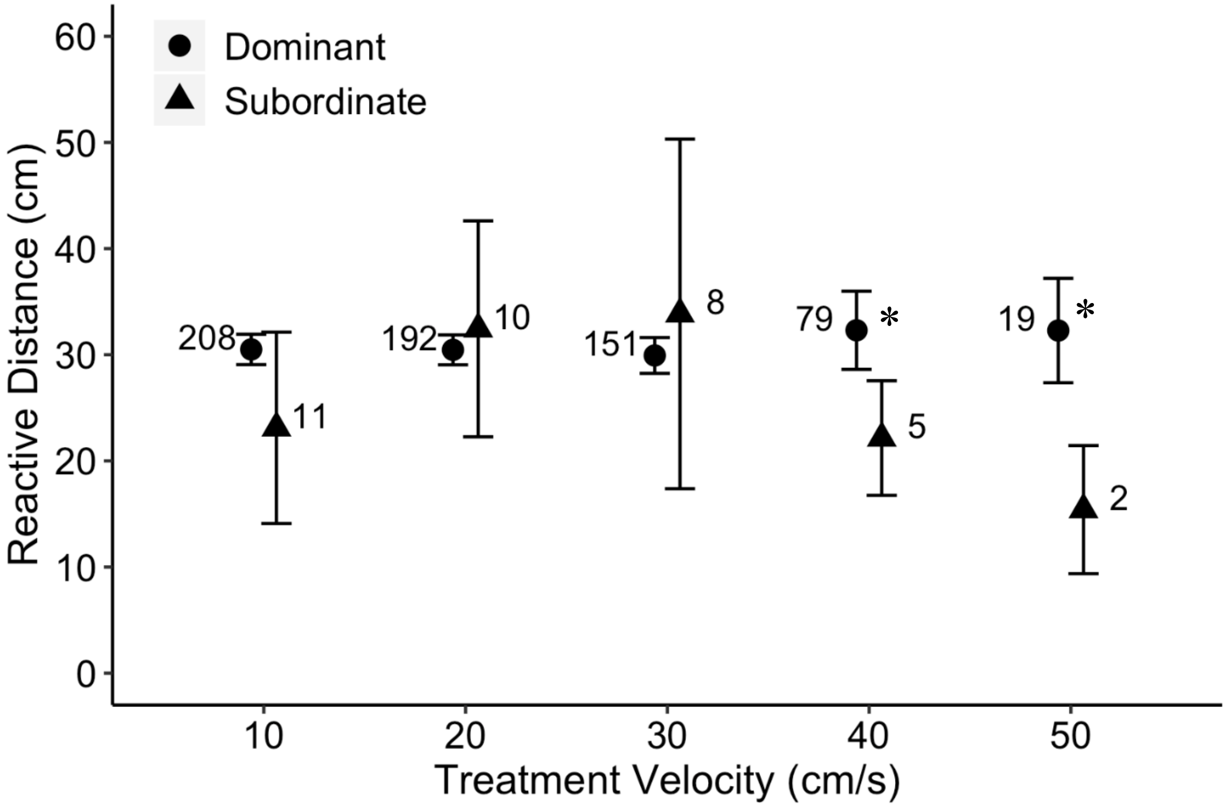
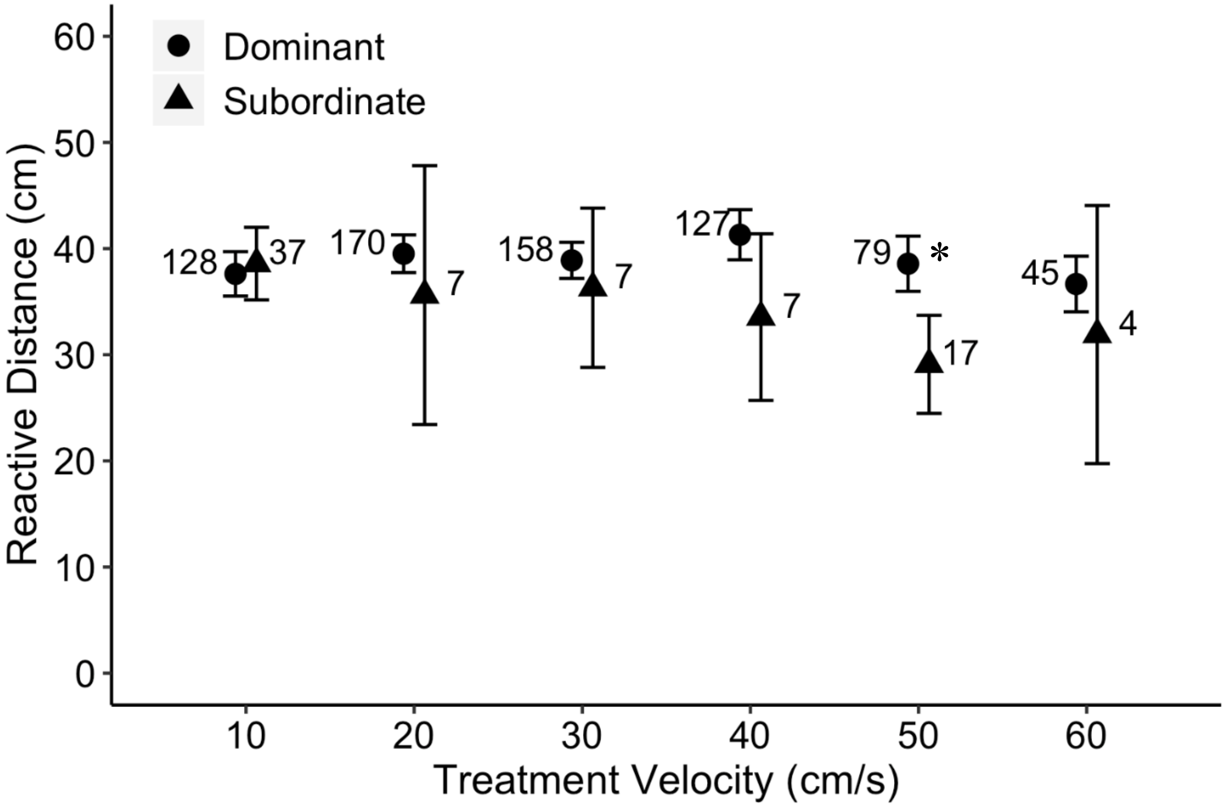

Dominant
Subordinate
Reactive Distance (cm)
0
10
20
30
40
50
60
Treatment Velocity (cm/s)
10
20
30
40
50
208
11
192
10
151
8
79
*
5
19
*
2

Figure 2.9



Dominant
Subordinate
Reactive Distance (cm)
0
10
20
30
40
50
60
Treatment Velocity (cm/s)
10
20
30
40
50
60
128
37
170
7
158
7
127
7
79
*
17
45
4

CHAPTER 3

A GENERALIZED OPTIMAL HABITAT SELECTION MODEL FOR DRIFT-FEEDING FISHES: SOUTHERN BROOK CHARR (*SALVELINUS FONTINALIS*)[2]

---

[2] Sliger, R. and G.D. Grossman. To be submitted to Freshwater Biology.

Abstract

Optimality theory has been a useful foundation for predictive models of habitat use, although few habitat selection models have been tested on multiple species. We tested the ability of the fitness-based, energy maximization, optimal holding velocity model developed by Grossman et al. (2002) to predict velocity use by Southern Brook Charr (SBC; *Salvelinus fontinalis*) in a Southern Appalachian stream. We conducted laboratory foraging experiments in a stream flume to construct a prey capture success versus water velocity curve, and measured holding velocities of SBC in experiments. We then parameterized the Grossman et al. (2002) model which yielded an optimal holding velocity prediction for SBC of 18.5cm/s. A successful model prediction requires a value that falls within the 95% confidence interval of the mean holding velocity occupied by SBC in Lynn Camp Prong, Tennessee, which was 13.5-20.5cm/s (mean = 17.0cm/s). Consequently, the model successfully predicted the holding position of SBC in Lynn Camp Prong, and SBC are choosing holding positions on the basis of maximizing energy intake. Although further testing is necessary, this result increases the number of drift-feeding stream species whose holding velocities have been successfully predicted by the model. Many drift-feeding stream fishes appear to choose holding velocities (i.e. microhabitats) that maximize their net energy gain. Given the paucity of information on SBC our results will aid conservation and management of this genetically distinct strain of native Charr.

Keywords: Brook Trout, Microhabitat, Net energy intake, Foraging models, Drift-feeding, Holding velocity

Introduction

Studies of habitat selection have provided important insights into both theory and praxis in ecology (Stephens and Krebs 1986). A productive way of examining habitat selection is to ask whether individuals are behaving in a manner that maximizes fitness or some proxy of fitness such as growth, mortality, or reproductive output. There is a long and productive history of such approaches beginning with Fry's (1947) paper "Effects of the environment on animal activity" (Evans 1990; Grossman 2014) and progressing through the fitness-based, optimality habitat selection models of Fretwell and Lucas (1970), Rosenzweig (1981), Werner and Hall (1979), Gilliam (1982) and Werner and Gilliam (1984). Nonetheless, there are few optimality models for habitat selection studies that have been tested with multiple species, seasons, or years.

For aquatic species, there was a long hiatus between Fry's early habitat selection work (Fry 1947) and the optimal-fitness based papers of Werner and Hall (1979) both of which focused on lentic rather than lotic species. Fausch (1984) appears to be the first investigator to apply a fitness-based habitat selection model to stream fishes, in a study of competition among native and invasive salmonids. Studies of habitat selection in stream fishes have focused on drift-feeders, that is, fishes that hold position in the current and feed on prey that drift by (Grossman 2014). These fishes represent the majority of species inhabiting temperate streams and include many economically important species such as trout and salmon (Grossman 2014). A crucial factor influencing habitat selection in these fishes is food acquisition (Fausch 2014; Grossman 2014; Piccolo et al. 2014), especially in habitats in which prey are drifting by at varying velocities. In many cases, predation does not appear to have a major impact on habitat selection in stream fishes residing in fast, cold-water streams.

One useful optimality approach to quantifying habitat quality and selection in drift-feeders is via the use of Net-Energy-Intake (NEI) models (Hill and Grossman 1993; Grossman et al. 2002; Piccolo et al. 2014). These models typically estimate the amount of energy (a fitness surrogate) a fish gains from occupying a given holding position and may be used to predict the holding positions individuals should occupy if they are maximizing energy intake (Fausch 1984, Hughes and Dill 1990, Grossman et al. 2002). Net-Energy-Intake models also may be scaled up to test whether a specific habitat is saturated (Hayes et al. 2007, Wall et al. 2016). In this paper we test the ability of the NEI model developed by Grossman et al (2002) to predict the optimal holding velocity (i.e., position) of Southern Brook Charr (SBC; *Salvelinus fontinalis*) in a Southern Appalachian Mountain stream. The Grossman et al. (2002) optimality model is mechanistic, NEI-based, and has a number of advantages including simplicity, logistical tractability, and success in predicting holding positions of multiple species of drift-feeding fishes (Grossman et al. 2002; Bozeman and Grossman 2019a,b).

Given that habitat alteration and invasive species are the two main causes of population declines and extinctions in stream fishes, the importance of understanding the processes driving habitat selection cannot be overstated. This highlights the need for development and tests of mechanistic models such as the Grossman et al. (2002) model, that assess habitat selection through the lens of fitness and natural selection. Habitat selection studies for species such as SBC that have limited ranges or are at the southern-most distribution of salmonid fishes in the Eastern United States are particularly important, given the potential effects of global climate change (Flebbe et al. 2006).

Materials and methods

Study Species

Our study species was the SBC, the only salmonid native to the Southern Appalachian Mountains (Grossman et al. 2010). Little is known about this genetically distinct strain of Charr, which now displays a fragmented distribution due to habitat change and invasive competitors (Eastern 2006; Hudy et al. 2013). This species has a short lifespan (≤ 3 years) and displays strong density-dependence in the per-capita rate of population increase and individual growth (Grossman et al. 2010). In western North Carolina, SBC are over-represented in deeper microhabitats with lower velocity and higher amounts of erosional substrata (Anglin and Grossman 2013). The species also displays both short and long movement patterns, although a majority of individuals have small (<20m) home ranges (Anglin and Grossman 2018).

Net Energy Intake Model Test

The Grossman et al. (2002) model requires quantification of the relationship between prey capture success and water velocity and is described in detail in (Bozeman and Grossman 2019a,b; with data for SBC in Sliger and Grossman 2020). In brief, experiments were conducted in a stream flume using the experimental design of Bozeman and Grossman (2019a). An illustration and complete description of the flume is presented in Bozeman and Grossman (2019a). Feeding trials began at a water velocity of 10cm/s. Nine prey (blood worms) were individually introduced through one of three randomly selected tubes at the front of the experimental chamber (portion of the flume that held the fish). A total of three prey were presented through each of the tubes. After all prey were released, the tank velocity was decreased to 5cm/s for 30 minutes so the specimen could rest and then raised to 20cm/s for the next trial.

Trials were continued, by increasing water velocity at 10cm/s intervals, until SBC missed more than six out of nine prey, which occurred at a maximum of 60cm/s. Water temperature was maintained at 15°C with an electronic chiller, and maintained within a several degree range within the optimal growth range for Brook Charr (Hartman and Sweka 2001). We used increasing water velocities as treatments rather than randomly chosen velocities because they represented a more ecologically realistic treatment strategy (i.e., fish typically experience water velocities as gradients rather than as abrupt changes), and because of concern over potential carry-over effects (i.e., it is likely that conducting the 10cm/s treatment after the 60cm/s treatment would lead to biased values). All specimens were humanely treated under AUP# A2018 01-004-Y3-A3 approved by the IACUC of the University of Georgia.

We parameterized and tested the Grossman et al. (2002) NEI optimal foraging model using data collected from the SBC water velocity versus prey capture success curve (Fig. 3.1). The NEI at a specific microhabitat (x), written as I_x, can be expressed in the following manner:

(**Equation 1**) $I_x = (E_x * P_x) - S_x$,

where E is the prey encounter rate, P is prey capture success, and S is the metabolic swimming cost. The prey encounter rate may also be expressed as

(**Equation 2**) $E_x = D_x * A_x * V_x$,

where D is the energy content of the prey in the drift (J/m^3), A is the visual reactive area of the fish (cm^2) (Hughes and Dill 1990), and V is water velocity (cm/s) (Hughes 1998). Prey capture success can also be expressed as

(**Equation 3**) $P_x = 1/[1 + e^{(b + cVx)}]$, where V is water velocity and b and c are fitting constants derived from the prey capture success versus water velocity (P vs. V) curve (Hill and Grossman 1993). Therefore, the NEI at microhabitat x may be expressed as

(**Equation 4**) $I_x = \{(D_x * A_x * V_x) * (1 / [1 + e^{(b+cV_x)}])\} - S_x$.

The variables D, A, and S generally are constant across the range of microhabitats used by drift-feeding fishes (Grossman et al. 2002; Bozeman and Grossman 2019a); consequently, they may be dropped from the equation, which yields

(**Equation 5**) $I_x = V_x * (1 / [1 + e^{(b+cV_x)}])$.

We used the R package nlstools (Baty et al. 2015) to obtain the b and c curve fitting constants for the nonlinear relationship between prey capture success (P) and water velocity (V) (Equation 3), and then we iteratively calculated the optimal foraging velocity (the value of V in Equation 5 that maximizes I, from which fish would be expected to forage) (R Core Team 2019). Because fish often hold at lower velocities than the main currents from which they forage (Hill and Grossman 1993; Liao 2007), to obtain an optimal holding velocity prediction (the velocity within which fish would be expected to hold to maximize I), we input the optimal foraging velocity prediction as the treatment velocity (the controlled, experimental water velocity) term in the linear equation for the relationship between the treatment velocity and holding velocity (the velocity at the stationary point at which fish held) from the SBC experiment. The resulting value was our optimal holding velocity prediction.

Model Test

We conducted a field test of the Grossman et al. (2002) model by comparing the predicted optimal holding velocity to the observed holding velocity of SBC in Lynn Camp

Prong, a stream in the Tennessee portion of the Great Smoky Mountains National Park. We considered the model successful if its prediction fell within the 95% confidence interval of the estimated mean holding velocity of SBC (Grossman et al. 2002). We quantified holding velocity for SBC (n = 26, mean standard length = 9.6 cm ± 4.1 SD) by snorkeling slowly in an upstream direction, locating an undisturbed, drift-feeding individual, visually estimating its size, and measuring holding velocity (velocity at the fish's nose) and the mean water column velocity (measured at 60% depth for depths <75cm; the mean of measurements made at 20% and 80% depth for depths ≥75cm) with an electronic flow meter (Marsh-McBirney Flow-Mate Model 2000 (Grossman and Freeman 1987).

We intended to compare mean SBC holding velocity to randomly available velocities in Lynn Camp Prong but erroneously used the method of Grossman and Skyfield (2009) designed for benthic fishes with small home ranges. This method constrained velocity availability measurements to a radius within two meters of a specimen and almost certainly yielded non-independent values, given that the mean distance from an SBC was 1m with a range of 21-200cm. Consequently, we did not compare mean velocities in the stream with those occupied by SBC.

Results

Optimal Holding Velocity

We fit the mean prey capture percentage values from each treatment velocity of the SBC single fish experiment to Equation 3 of the Grossman et al. (2002) optimal foraging model (RSS = 1.42), which yielded curve fitting values of b = -3.41 and c = 0.0963. Inputting these values into Equation 5, and iteratively solving for the value of V that maximizes I, yielded a value of

29.2cm/s. Inputting this value as the treatment velocity term in the linear equation of the relationship between treatment and holding velocity for the SBC single fish experiment (holding velocity = 1.38 + 0.59[treatment velocity], n = 96, $R^2 = 0.67$, $p \ll 0.001$) yielded an optimal holding velocity value of 18.5cm/s. The mean holding velocity of individuals at Lynn Camp Prong was 17.0cm/s with a 95% confidence interval of 13.5-20.5cm/s. Given that the predicted optimal holding velocity fell within the confidence interval of observed holding velocities, SBC appear to be foraging in a manner that maximizes NEI, and the Grossman et al. (2002) model successfully predicted the holding velocities occupied by this species in Lynn Camp Prong.

Discussion

In addition to successfully predicting the holding velocity of SBC, the Grossman et al. (2002) model has successfully predicted the holding velocities of two species of salmonids (Arctic Grayling [*Thymallus arcticus*; Bozeman and Grossman 2019a] and Dolly Varden Charr [*Salvelinus malma*; Bozeman and Grossman 2019b]) and four species of cyprinids (Rosyside Dace [*Clinostomus funduloides*]; Warpaint Shiner [*Luxilus coccogenis*]; Tennessee Shiner [*Notropis leuciodus*]; and Yellowfin Shiner [*Notropis lutipinis*; Hill and Grossman 1993; Grossman et al. 2002]). This suggests that many stream fishes are choosing holding velocities based on maximizing their NEI. However, the Grossman et al. (2002) model requires further testing because it has failed to predict holding velocities of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*; Donofrio et al. 2018) as well as holding velocities for Tennessee and Yellowfin Shiners in some seasons (Grossman et al. 2002) and Arctic Grayling in one stream (Bozeman and Grossman 2019a). Nevertheless, this NEI-based, habitat selection model is one of the few models that has been tested with multiple species, in multiple sites and in multiple years (Grossman et al. 2002).

We modified the model test by using holding velocities measured in experiments, rather than treatment velocities themselves, and this resulted in a more accurate prediction. Without this modification, the model would have produced a prediction that was positively biased, which may have resulted in partial (Bozeman and Grossman 2019a) or complete (Donofrio et al. 2018) model failure as seen in other studies. Multiple studies, including some on salmonids, have shown that these species often hold position in lower velocity water adjacent to a patch with higher velocity (McMahon and Hartman 1989; Shuler et al. 1994; Everest and Chapman 1972; Hill and Grossman 1993). This likely is an energy minimization strategy (Facey and Grossman 1990, 1992) although in many cases the holding velocities occupied in the field are on the asymptotic portion of the energetic cost versus holding velocity curve (Facey and Grossman 1992). Liao (2007) suggests that holding position adjacent to a faster velocity is the most common form of flow exploitation described in the fisheries literature.

In conclusion, fitness-based optimality models have contributed greatly to our understanding of how animals choose habitats. Our findings suggest that high quality SBC habitat will have a variety of velocities, centered on the optimal holding velocity of 18.5cm/s. This information will be useful for quantifying essential habitat and evaluating the potential effects of habitat alterations, especially in a time of global climate change.

Acknowledgements

This research was made possible through the help of C. Bloom, B. Hilburn, C. Ellis, B. Bozeman, T. Simon, M. Tiller, B. Irwin, S. Wenger, Great Smoky Mountains National Park, M.

Kulp, C. Abramson, A. Walker, N. Goodman, J. Cary, the Georgia Department of Natural Resources, J. Thomson, J. Stewart, the Warnell School of Forestry & Natural Resources, and a few who will remain anonymous.

REFERENCES

Anglin, Z.W., and Grossman, G.D. 2013. Microhabitat use by southern brook trout (*Salvelinus fontinalis*) in a headwater North Carolina stream. Ecol. Freshwat. Fish, **22**(4):567-577.

Anglin, Z.W., and Grossman, G.D. 2018. Movement of Southern Brook Charr in a North Carolina Headwater Stream. Southeast. Nat. **17**(3):476-483.

Baty, F., Ritz, C., Charles, S., Brutsche, M., Flandrois, J., Delignette-Muller, M. 2015. A Toolbox for Nonlinear Regression in R: The Package nlstools. J. Stat. Softw. **66**(5), 1-21. URL http://www.jstatsoft.org/v66/i05/.

Bozeman, B.B., and Grossman, G.D. 2019a. Mechanics of foraging success and optimal microhabitat selection in Alaskan Arctic Grayling (*Thymallus arcticus*). Can. J. Fish. Aquat. Sci. **76**(5):815-830.

Bozeman, B.B., and Grossman, G.D. 2019b. Foraging behavior and optimal microhabitat selection in interior Dolly Varden Charr (*Salvelinus malma*) in Panguingue Creek, Alaska. Ecol. Freshwat. Fish, **28**:586-601.

Donofrio, E., Simon, T., Neuswanger, J.R., and Grossman, G.D. 2018. Velocity and dominance affect prey capture and microhabitat selection in juvenile Chinook (*Oncorhynchus tshawytscha*). Environ. Biol. Fishes, **101**(4):609-622.

Eastern Brook Trout Joint Venture. 2006. Eastern brook trout: status and threats. Prepared by Trout Unlimited, Arlington, VA, for EBTJV.

Evans, D.O. 1990 Introduction to the proceedings of the symposium “From environment to fish to fisheries, a tribute to F.E.J. Fry”. Trans. Am. Fish. Soc. **119**:567-570.

Everest, F.H., and Chapman, D.W. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. J. Fish. Res. Board. Can. **29**(1):91-100.

Facey, D.E., and Grossman, G.D. 1990. The metabolic cost of maintaining position for four North American stream fishes: effects of season and velocity. Physiol. Zool. **63**(4):757-776.

Facey, D.E. and Grossman, G.D. 1992. Do metabolic constraints influence microhabitat use in four North American stream fishes? Hydrobiologia, **239**:1-6.

Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Can. J. Zool. **62**:441-451.

Fausch, K.D. 2014. A historical perspective on drift foraging models for stream salmonids. Environ. Biol. Fishes, **97**(5):453-464.

Flebbe, P.A., Roghair, L.D., and Bruggink, J.L. 2006. Spatial modeling to project southern Appalachian trout distribution in a warmer climate. Trans. Am. Fish. Soc. **135**(5):1371-1382.

Fretwell, S.D. and Lucas Jr., H.L. 1970. On territorial behavior and other factors influencing habitat distributions of birds. Acta Biotheoretica, **19**:16-36.

Fry, F.E.J. 1947. Effects of the environment on animal activity. Univ. Toronto Stud. Bio. **55**:1-52

Gilliam, J.F. 1982. Habitat use and competitive bottlenecks in size-structured fish populations. PhD thesis, Michigan State University, 107pp.

Grossman, G.D. 2014. Not all drift feeders are trout: a short review of fitness-based habitat selection models for fishes. Environ. Biol. Fishes, **97**(5):465-473.

Grossman, G.D., and Freeman, M.C. 1987. Microhabitat use in a stream fish assemblage. J. Zool. **212**(1):151-176.

Grossman, G.D., Ratajczak, R.E., Wagner, C.M., and Petty, J.T. 2010. Dynamics and regulation of the southern brook trout (*Salvelinus fontinalis*) population in an Appalachian stream. Freshwat. Biol. **55**(7):1494-1508.

Grossman, G.D., Rincon P.A., Farr M.D., and Ratajczak, R.E. 2002. A new optimal foraging model predicts habitat use by drift-feeding stream minnows. Ecol. Freshw. Fish, **11**:2-10.

Hartman, K.J., and Sweka, J.A. 2001. Development of a bioenergetics model for Appalachian brook trout. Proceedings of the Southeastern Association of Fish and Wildlife Agencies, **55**:38-51.

Hayes, J.W., Hughes, N.F., and Kelly, L.H. 2007. Process-based modelling of invertebrate drift transport, net energy intake and reach carrying capacity for drift-feeding salmonids. Ecol. Model. **207**(2-4):171-188.

Hill, J., and Grossman, G.D. 1993. An energetic model of microhabitat use for rainbow trout and rosyside dace. Ecology, **74**(3):685-698.

Hudy, M., Nislow, K., Smith, E.P., Cooper, A.R., and Infante, D.M. 2013. The Importance of Scale: Assessing and Predicting Brook Trout Status in Its Southern Native Range. https://easternbrooktrout.org/resources/science-publications/chesapeake-bay-brook-trout-management-strategy-references/the-importance-of-scale-assessing-and-predicting-brook-trout-status-hudy-et-al-2013/view.

Hughes, N.F. 1998 A model of habitat selection by drift-feeding stream salmonids at different scales. Ecology, **79**:281-294.

Hughes, N.F. and Dill, L.M. 1990. Position choice by drift-feeding salmonids: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Can. J. Fish. Aquat. Sci. **47**:2039-2048.

Liao, J.C. 2007. A review of fish swimming mechanics and behaviour in altered flows. Philos. Trans. R. Soc. Lond., B, Biol. Sci. **362**(1487):1973-1993.

McMahon, T.E., and Hartman, G.F. 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. **46**(9):1551-1557.

Nislow, K.H., and Lowe, W.H. 2003. Influences of logging history and stream pH on brook trout abundance in first-order streams in New Hampshire. Trans. Am. Fish. Soc. **132**:166-171.

Piccolo, J.J., Frank, B.M., and Hayes, J.W. 2014. Food and space revisited: The role of drift-feeding theory in predicting the distribution, growth, and abundance of stream salmonids. Environ. Biol. Fishes, **97**(5):475-488.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rosenzweig, M.L. 1981. A theory of habitat selection. Ecology, **62**:327-335.

Shuler, S.W., Nehring, R.B., and Fausch, K.D. 1994. Diel habitat selection by brown trout in the Rio Grande River, Colorado, after placement of boulder structures. N. Am. J. Fish Manage. **14**(1):99-111.

Sliger, R. and Grossman, G.D. 2020. Comparative foraging dynamics of Northern and Southern Brook Charr (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci.: submitted.

Stephens, D.W., Krebs, J.R. 1986. Foraging theory. Princeton University Press, Princeton.

Wall, C.E., Bouwes, N., Wheaton, J.M., Saunders, W.C., and Bennett, S.N. 2016. Net rate of energy intake predicts reach-level steelhead (*Oncorhynchus mykiss*) densities in diverse basins from a large monitoring program. Can. J. Fish. Aquat. Sci. **73**(7):1081-1091.

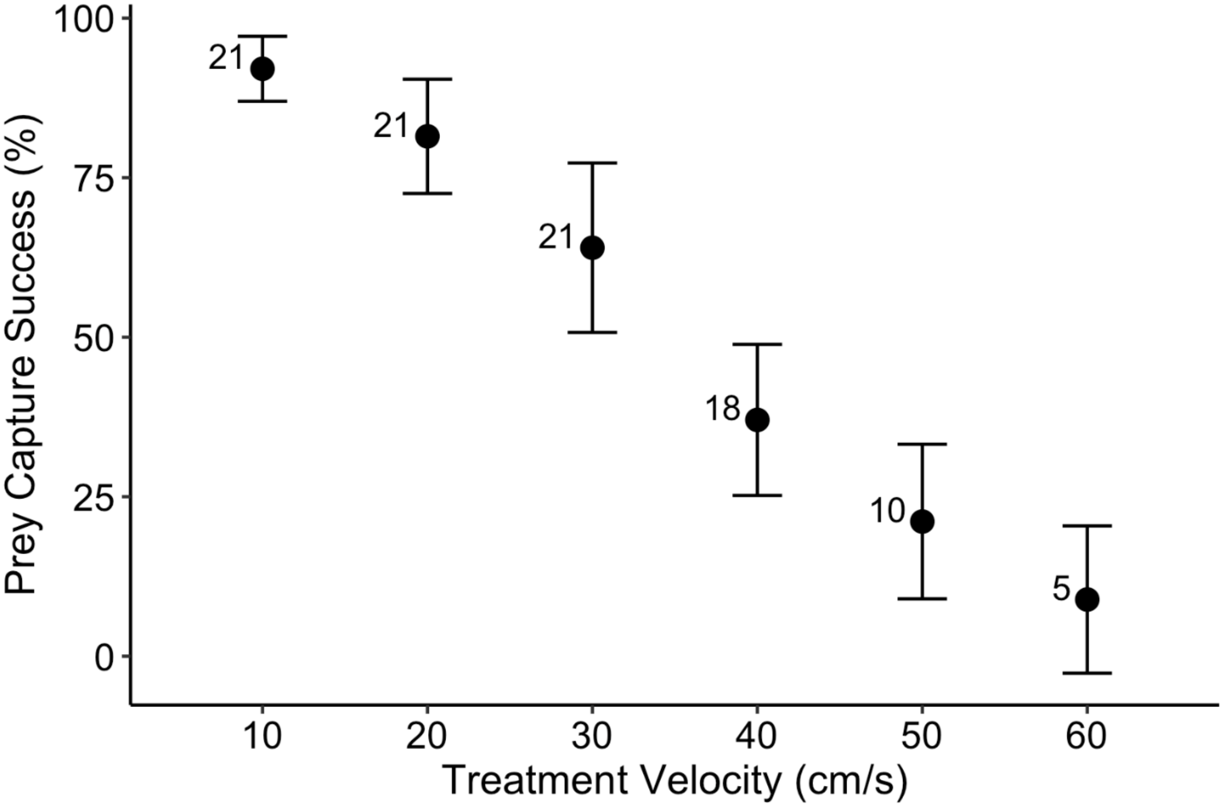
Werner, E.E., and Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. **15**:393-425.

Werner, E.E., and Hall, D.J. 1979. Foraging efficiency and habitat switching in competing sunfishes. Ecology, **60**:256-264.

List of Figures

Figure 3.1: The relationship between prey capture success and treatment velocity for SBC. Error bars represent 95% confidence intervals. Point labels represent sample sizes.

Fig 3.1


Prey Capture Success (%)
100
75
50
25
0
21
21
21
18
10
5
10
20
30
40
50
60
Treatment Velocity (cm/s)

CHAPTER 4

GENERAL CONCLUSIONS

To most efficiently manage and conserve drift-feeding stream fishes, we need to fill knowledge gaps concerning their foraging dynamics and the energetic consequences of their habitat use. Net-Energy-Intake (NEI) modeling has been useful in filling these knowledge gaps because it allows researchers to use NEI as a surrogate of fitness to mechanistically determine the suitability of certain habitat types for various stream fishes (Grossman 2014; Fausch 2014; Piccolo et al. 2014; Rosenfeld et al. 2014). Given that little is known about the ecology of the Southern Brook Charr, and that it faces significant threats (Hudy et al. 2013; Eastern 2006), applying NEI modeling to this strain is particularly critical. In this work, we have applied the Grossman et al. 2002 optimal foraging model to wild Southern Brook Charr from Lynn Camp Prong in the Tennessee portion of the Great Smoky Mountains National Park in an attempt to predict their microhabitat use in regards to the water velocity at the point in the water column where they hold to drift feed (holding velocity). The data collection necessary for us to parameterize the model allowed us to quantify the effects of 1) water velocity, 2) fish size, 3) days in captivity, 4) dominance, and 5) size rank, on prey capture success, holding velocity, and reactive distance of the Southern Brook Charr in an experimental stream flume. In addition, we collected the same data for hatchery Northern Brook Charr to determine if there were any foraging behavior differences between the two strains.

Taking into account the difference between experimental holding velocity and treatment velocity, the Grossman et al. (2002) optimal foraging model correctly predicted the optimal holding velocity of individual Southern Brook Charr in Lynn Camp Prong. Without considering this difference, the model prediction would have failed. This finding further demonstrates the usefulness of the Grossman et al. (2002) optimal foraging model to predicting microhabitat use of drift-feeding stream fishes and suggests that the model may make successful predictions in more scenarios than previously thought, when considering velocity differences between positions in which fish hold, and the main currents from which they forage.

From the other data we collected, we were able to determine that 1) water velocity had a strong effect on prey capture success and holding velocity; 2) dominant individuals had higher prey capture success rates than did subordinate individuals; 3) no variables had a consistent strong effect on reactive distance, but Southern Brook Charr had greater reactive distances at treatment velocities of 10-30cm/s, and 4) there were few foraging differences between Southern and Northern Brook Charr

In conclusion, this work contributes to a further understanding of factors affecting foraging aspects of both wild Southern and hatchery Northern Brook Charr. In addition, it highlights the importance of distinguishing between holding velocity and foraging velocity when creating NEI models, and the need to understand how the factors we have studied affect the foraging of Brook Charr in natural stream settings. The research we have conducted will be useful to continued successful conservation and restoration of the Southern Brook Charr throughout its range.

REFERENCES

Anglin, Z.W., and Grossman, G.D. 2013. Microhabitat use by southern brook trout (*Salvelinus fontinalis*) in a headwater North Carolina stream. Ecol. Freshwat. Fish, **22**(4):567-577.

Anglin, Z.W., and Grossman, G.D. 2018. Movement of Southern Brook Charr in a North Carolina Headwater Stream. Southeast. Nat. **17**(3):476-483.

Bartoń, K. 2019. MuMIn: Multi-Model Inference. R package version 1.43.15. https://CRAN.R-project.org/package=MuMIn.

Bassar, R.D., Letcher, B.H., Nislow, K.H., and Whiteley, A.R. 2016. Changes in seasonal climate outpace compensatory density-dependence in eastern brook trout. Global Change Biology, **22**(2), 577-593.

Baty, F., Ritz, C., Charles, S., Brutsche, M., Flandrois, J., Delignette-Muller, M. 2015. A Toolbox for Nonlinear Regression in R: The Package nlstools. J. Stat. Softw. **66**(5):1-21. URL http://www.jstatsoft.org/v66/i05/.

Barrett, J.D., Grossman, G.D., and Rosenfeld, J. 1992. Turbidity induced changes in reactive distance in rainbow trout (*Oncorhynchus mykiss*). Trans. Am. Fish. Soc. **121**:437-443.

Belford, D.A., and Gould, W.R. 1989. An evaluation of trout passage through six highway culverts in Montana. N. Am. J. Fish Manage. **9**:437-445.

Bozeman, B.B., and Grossman, G.D. 2019a. Mechanics of foraging success and optimal microhabitat selection in Alaskan Arctic Grayling (*Thymallus arcticus*). Can. J. Fish. Aquat. Sci. **76**(5):815-830.

Bozeman, B.B., and Grossman, G.D. 2019b. Foraging behavior and optimal microhabitat selection in interior Dolly Varden Charr (*Salvelinus malma*) in Panguingue Creek, Alaska. Ecol. Freshwat. Fish, **28**:586-601.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, **2nd Edition**.

Cade, B.S. 2015. Model averaging and muddled multimodel inferences. Ecology, **96**(9):2370-2382.

Clayton, J.L., Dannaway, E.S., Menendez, R., Rauch, H.W., Renton, J.J., Sherlock, S.M., and Zurbuch, P.E. 1998. Application of limestone to restore fish communities in acidified streams. N. Am. J. Fish Manage. **18**:347-360.

Curry, R.A., and MacNeill, W.S. 2004. Population-level responses to sediment during early life in brook trout. J. N. Am. Benthol. Soc. **23**:140-150.

Danzmann, R.G., Morgan II, R.P., Jones, M.W., Bernatchez, L., and Ihssen, P.E. 1998. A major sextet of mitochondrial DNA phylogenetic assemblages extant in eastern North American brook trout (*Salvelinus fontinalis*): distribution and postglacial dispersal patterns. Can. J. Zool. **76**(7):1300-1318.

Donofrio, E., Simon, T., Neuswanger, J.R., and Grossman, G.D. 2018. Velocity and dominance affect prey capture and microhabitat selection in juvenile Chinook (*Oncorhynchus tshawytscha*). Environ. Biol. Fishes, **101**(4):609-622.

Driscoll, C.T., Lawrence, G.B, Bulgur, A.J., Butler, T.J., Cronan, C.S., Eagar, C., Lambert, K.F., Likens, G.E., Stoddard, J.L., and Weathers, K.C. 2001. Acidic deposition in the northeastern United States: sources and inputs, ecosystem effects, and management strategies. BioScience, **51**:180-198.

Eastern Brook Trout Joint Venture. 2005. Conserving the Eastern brook trout: An overview of status, threats, and trends. *Conservation Strategy Work Group, Eastern Brook Trout Joint Venture, International Association of Fish and Wildlife Agencies Washington (DC)*.

Eastern Brook Trout Joint Venture. 2006. Eastern brook trout: status and threats. Prepared by Trout Unlimited, Arlington, VA, for EBTJV.

Evans, D.O. 1990 Introduction to the proceedings of the symposium “From environment to fish to fisheries, a tribute to F.E.J. Fry”. Trans. Am. Fish. Soc. **119**:567-570.

Everest, F.H., and Chapman, D.W. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. J. Fish. Res. Board. Can. **29**(1):91-100.

Facey, D.E., and Grossman, G.D. 1990. The metabolic cost of maintaining position for four North American stream fishes: effects of season and velocity. Physiol. Zool. **63**(4):757-776.

Facey, D.E., and Grossman, G.D. 1992. Do metabolic constraints influence microhabitat use in four North American stream fishes? Hydrobiologia, **239**:1-6.

Fausch, K.D. 1984. Profitable stream positions for salmonids: relating specific growth rate to net energy gain. Can. J. Zool. **62**:441-451.

Fausch, K.D. 2014. A historical perspective on drift foraging models for stream salmonids. Environ. Biol. Fishes, **97**(5):453-464.

Flebbe, P.A., Roghair, L.D., and Bruggink, J.L. 2006. Spatial modeling to project southern Appalachian trout distribution in a warmer climate. Trans. Am. Fish. Soc. **135**(5):1371-1382.

Fry, F.E.J. 1947. Effects of the environment on animal activity. Univ. Toronto Stud. Bio. **55**:1-52

Gibson, R.J., Haedrich, R.L., and Wernerheim, C.M. 2005. Loss of fish habitat as a consequence of inappropriately constructed stream crossings. Fisheries, **30**(1):10-17.

Gilliam, J.F. 1982. Habitat use and competitive bottlenecks in size-structured fish populations. PhD thesis, Michigan State University, 107pp.

Grossman, G.D. 1980. Food, fights and burrows: the adaptive significance of intraspecific aggression in the Bay Goby (Pisces: Gobiidae). Oecologia, **45**(2):261-266.

Grossman, G.D. 2014. Not all drift feeders are trout: a short review of fitness-based habitat selection models for fishes. Environ. Biol. Fishes, **97**(5):465-473.

Grossman, G.D., and Freeman, M.C. 1987. Microhabitat use in a stream fish assemblage. J. Zool. **212**(1):151-176.

Grossman, G.D., and Simon, T.N. 2020. Density-dependent effects on salmonid populations: A review. Ecol. Freshwat. Fish, **29**:400-418.

Grossman, G.D., Ratajczak, R.E., Wagner, C.M., and Petty, J.T. 2010. Dynamics and regulation of the southern brook trout (*Salvelinus fontinalis*) population in an Appalachian stream. Freshwat. Biol. **55**(7):1494-1508.

Grossman, G.D., Rincon, P.A., Farr, M.D., and Ratajczak, R.E. 2002. A new optimal foraging model predicts habitat use by drift-feeding stream minnows. Ecol. Freshw. Fish, **11**:2-10.

Habera, J., and Moore, S. 2005. Managing southern Appalachian brook trout: a position statement. Fisheries, **30**(7):10-20.

Hartman, K.J., and Sweka, J.A. 2001. Development of a bioenergetics model for Appalachian brook trout. Proceedings of the Southeastern Association of Fish and Wildlife Agencies, **55**:38-51.

Hayes, J.W., Hughes, N.F., and Kelly, L.H. 2007. Process-based modelling of invertebrate drift transport, net energy intake and reach carrying capacity for drift-feeding salmonids. Ecol. Model. **207**(2-4):171-188.

Hazelton, P.D., and Grossman, G.D. 2009. The effects of turbidity and an invasive species on foraging success of rosyside dace (*Clinostomus funduloides*). Freshw. Biol. **54**(9): 1977-1989.

Hill, J., and Grossman, G.D. 1993. An energetic model of microhabitat use for rainbow trout and rosyside dace. Ecology, **74**(3):685-698.

Hudy, M., Downey, D.M., and Bowman, D.W. 2000. Successful restoration of an acidified native brook trout stream through mitigation with limestone sand. N. Am. J. Fish Manage. **20**:453-466.

Hudy, M., Nislow, K., Smith, E.P., Cooper, A.R., and Infante, D.M. 2013. The Importance of Scale: Assessing and Predicting Brook Trout Status in Its Southern Native Range. https://easternbrooktrout.org/resources/science-publications/chesapeake-bay-brook-trout-management-strategy-references/the-importance-of-scale-assessing-and-predicting-brook-trout-status-hudy-et-al-2013/view.

Hudy, M., Thieling, T.M., Gillespie, N., and Smith, E.P. 2008. Distribution, status, and land use characteristics of subwatersheds within the native range of brook trout in the eastern United States. N. Am. J. Fish Manage. **28**(4), 1069-1085.

Hughes, N.F. 1998 A model of habitat selection by drift-feeding stream salmonids at different scales. Ecology, **79**:281-294.

Hughes, N.F. and Dill, L.M. 1990. Position choice by drift-feeding salmonids: model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. Can. J. Fish. Aquat. Sci. **47**:2039-2048.

Huntsman, B.M., and Petty, J.T. 2014. Density-dependent regulation of brook trout population dynamics along a core-periphery distribution gradient in a central Appalachian watershed. PloS one, **9**(3).

Jenkins Jr., T.M. 1969. Social structure, position choice and micro-distribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams. Anim. Behave. Monogr. **2:**55-123.

King, W. 1937. Notes on the distribution of native speckled and rainbow trout in the streams of Great Smoky Mountains National Park. Journal of the Tennessee Academy of Science, **12**:351-361.

King, W. 1939. A program for the management of fish resources in Great Smoky Mountains National Park. Trans. Am. Fish. Soc. **68**(1):86-95.

Kanno, Y., Kulp, M.A., and Moore, S.E. 2016. Recovery of native brook trout populations following the eradication of nonnative rainbow trout in southern Appalachian mountain streams. N. Am. J. Fish Manage. **36**(6):1325-1335.

Larson, G.L., and Moore, S.E. 1985. Encroachment of exotic rainbow trout into stream populations of native brook trout in the southern Appalachian Mountains. Trans. Am. Fish. Soc. **114**:195-203.

Lennon, R.E. 1967. Brook trout of Great Smokey Mountains National Park. U.S. Fish and Wildlife Service Technical Paper 15.

Liao, J.C. 2007. A review of fish swimming mechanics and behaviour in altered flows. Philos. Trans. R. Soc. Lond., B, Biol. Sci. **362**(1487):1973-1993.

McCracken, G.F., Parker, C.R., and Guffey, S.Z. 1993. Genetic differentiation and hybridization between stocked hatchery and native brook trout in Great Smoky Mountains National Park. Trans. Am. Fish. Soc. **122**(4):533-542.

McMahon, T.E., and Hartman, G.F. 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. **46**(9):1551-1557.

Meisner, J.D. 1990. Effect of climatic warming on the southern margins of the native range of brook trout, Salvelinus fontinalis. Can. J. Fish. Aquat. Sci. **47**:1065-1070.

Moore, S.E., Ridley, B., and Larson, G.L. 1983. Standing crops of brook trout concurrent with removal of rainbow trout from selected streams in Great Smoky Mountains National Park. N. Am. J. Fish Manage. **3**:72-80.

Moyle, P.B. 1969. Comparative behavior of young brook trout of domestic and wild origin. The Progressive Fish-Culturist. **31**(1):51-56.

Neuswanger, J.R., Wipfli, M.S., Rosenberger, A.E., and Hughes, N.F. 2016. Measuring fish and their physical habitats: Versatile 2-D and 3-D video techniques with user-friendly software. Can. J. Fish. Aquat. Sci. **73**(12):1861-1873.

Piccolo, J.J., Frank, B.M., and Hayes, J.W. 2014. Food and space revisited: The role of drift-feeding theory in predicting the distribution, growth, and abundance of stream salmonids. Environ. Biol. Fishes, **97**(5):475-488.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rosenfeld, J.S., Bouwes, N., Wall, C.E., and Naman, S.M. 2014. Successes, failures, and opportunities in the practical application of drift-foraging models. Environ. Biol. Fishes, **97**(5):551-574.

Rosenzweig, M.L. 1981. A theory of habitat selection. Ecology, **62**:327-335.

Ryer, C.H., and Olla, B.L. 1991. Information transfer and the facilitation and inhibition of feeding in a schooling fish. Environ. Biol. Fishes, **30**(3):317-323.

Shuler, S.W., Nehring, R.B., and Fausch, K.D. 1994. Diel habitat selection by brown trout in the Rio Grande River, Colorado, after placement of boulder structures. N. Am. J. Fish Manage. **14**(1):99-111.

Sliger, R. and Grossman, G.D. 2020. Comparative foraging dynamics of northern and Southern Brook Charr (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci.: submitted.

Stephens, D.W., and Krebs, J.R. 1986. Foraging theory. Princeton University Press, Princeton.

Stoneking, M., Wagner, D.J., and Hildebrand, A.C. 1981. Genetic evidence suggesting subspecific differences between northern and southern populations of brook trout (*Salvelinus fontinalis*). Copeia, 810-819.

Stoner, A.W., and Ottmar, M.L. 2004. Fish density and size alter Pacific halibut feeding: implications for stock assessment. J. Fish Biol. **64**(6):1712-1724.

Strange, R.J., and Habera, J.W. 1998. No net loss of brook trout distribution in areas of sympatry with rainbow trout in Tennessee streams. Trans. Am. Fish. Soc. **127**:434-440.

Utz, R.M., and Hartman, K.J. 2009. Density-dependent individual growth and size dynamics of central Appalachian brook trout (*Salvelinus fontinalis*). Can. J. Fish. Aquat. Sci. **66**(7):1072-1080.

Vincent, R.E. 1960. Some influences of domestication upon three stocks of brook trout (*Salvelinus fontinalis* Mitchill). Trans. Am. Fish. Soc. **89**(1):35-52.

Vogel, J.L., and Beauchamp, D.A. 1999. Effects of light, prey size, and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. Can. J. Fish. Aquat. Sci. **56**(7): 1293-1297.

Wall, C.E., Bouwes, N., Wheaton, J.M., Saunders, W.C., and Bennett, S.N. 2016. Net rate of energy intake predicts reach-level steelhead (*Oncorhynchus mykiss*) densities in diverse basins from a large monitoring program. Can. J. Fish. Aquat. Sci. **73**(7):1081-1091.

Weber, E.D., and Fausch, K.D. 2003. Interactions between hatchery and wild salmonids in streams: differences in biology and evidence for competition. Can. J. Fish. Aquat. Sci. **60**(8):1018-1036.

Werner, E.E., and Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. Ann. Rev. Ecol. Syst. **15**:393-425.

Werner, E.E., and Hall, D.J. 1979. Foraging efficiency and habitat switching in competing sunfishes. Ecology, **60**:256-264.