VELOCITY, PREY CAPTURE SUCCESS, AND MICROHABITAT SELECTION IN ARCTIC GRAYLING (*THYMALLUS ARCTICUS*)

by

BRYAN BOZEMAN

(Under the Direction of Gary Grossman)

ABSTRACT

Our knowledge of factors affecting microhabitat selection for drift feeding salmonids is incomplete. We quantified relationships between water velocity, fish size, days in captivity, and dominance (predictor variables) and prey capture success, holding velocity, and reactive distance (response variables) experimentally for three sets of fluvial Alaskan Arctic Grayling. Water velocity had a negative effect on prey capture success and a positive effect on holding velocity in all experiments. Holding velocity increased at a slower rate than capture velocity and plateaued at 30 cm/s at velocities of 30 cm/s and greater. Reactive distance displayed a weak (positive) or nonexistent relationship with velocity. Dominant fish captured more prey than subordinate fish, but had similar holding velocities and reactive distances. Holding velocity predictions from Grossman *et al.*'s (Grossman *et al.*, 2002) foraging model (41.2 cm/s, 36.2 cm/s, 34.7 cm/s) were greater than Arctic Grayling holding velocities measured in Panguingue Creek, AK (95% CI: 20.7 – 27.9 cm/s).

INDEX WORDS: Arctic Grayling, Microhabitat, Habitat selection, Net energy gain, Foraging models, Drift-feeding, Holding velocity

VELOCITY, PREY CAPTURE SUCCESS, AND MICROHABITAT SELECTION IN ARCTIC GRAYLING (*THYMALLUS ARCTICUS*)

by

BRYAN BOZEMAN

BS, The University of Tennessee, 2014

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

MASTER OF SCIENCE

ATHENS, GEORGIA

2017

VELOCITY, PREY CAPTURE SUCCESS, AND MICROHABITAT SELECTION IN ARCTIC GRAYLING (*THYMALLUS ARCTICUS*)

by

BRYAN BOZEMAN

Major Professor:	Gary Grossman
Committee:	Richard Chandler Brian Irwin

Electronic Version Approved:

Suzanne Barbour
Dean of the Graduate School
The University of Georgia
August 2017

DEDICATION

This thesis is dedicated to my loving and supportive parents, who inspired my love for the natural world and encourage me daily in my pursuit of knowledge.

ACKNOWLEDGEMENTS

This research was completed with the help of many individuals including: D. Bullock, R. Chandler, B. Grossman, B. Irwin, J. Neuswanger, T. Simon, Jittery Joes, Two Story, and Creature Comforts Brewing Company. The North Pacific Research Board was the primary funding source for this research via grant #1424 and the Graduate School and Daniel B. Warnell School of Forestry and Natural Resources of the University of Georgia provided additional funding. A version of the manuscript was reviewed by E. Donofrio, R. Chandler, J. Cullen, B. Irwin, J. Neuswanger, and T. Simon.

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

GENERAL INTRODUCTION AND LITERATURE REVIEW

Net Energy Gain Approaches

Drift-feeding is a foraging strategy employed by many fishes in temperate, lotic systems that involves holding a steady position in the current and consuming prey as they flow downstream. Drift-feeding fishes, especially Salmonids, have been the subject of much habitat research, likely due to their interesting foraging strategy, prominent roles in aquatic ecosystems and economic importance (Deegan *et al.*, 1997; Grossman, 2014; Piccolo, Frank & Hayes, 2014). Traditionally, researchers have sought to understand drift-feeding fish microhabitat (i.e., the suite of physical and biological characteristics possessed by the habitat at the fish's position) selection by relating stream habitat availability to habitat use (Grossman, 2014). However, descriptive studies of physical habitat generally cannot identify specific mechanisms driving habitat selection because they do not include biological factors such as prey or predator abundance and cannot quantify the differential effects of habitat quality on selection.

Net energy gain approaches to drift-feeding fish habitat selection studies are an alternative to traditional descriptive approaches because they link individual fitness to habitat selection (Fausch, 2013; Grossman, 2014). These approaches quantify physical habitat characteristics (e.g., depth, velocity, turbidity, substratum composition) occupied by drift-feeding fishes (alternatively, drift-feeders) to identify a suite of factors potentially affecting habitat selection in these species. Optimal foraging theory suggests that animals likely select microhabitat based on optimizing net energy gain (Schoener, 1971; Charnov, 1976; Pyke, Pulliam & Charnov, 1977). Net energy gain for drift-feeding fish can be calculated by quantifying costs (e.g., swimming cost) and benefits (e.g., prey encounter, energy intake) incurred by selecting a holding position in the current (Fausch, 1984; Hughes & Dill, 1990; Hill & Grossman, 1993). By quantifying fitness-based functions associated with occupying specific locations in a stream or river, net energy gain approaches can more precisely determine mechanisms influencing drift-feeder habitat selection than descriptive studies.

The water velocity at the position occupied by drift-feeding fish—here termed holding velocity—is a prominent aspect of drift-feeder habitat selection because benefits and costs should both increase with water velocity. Salmonids are excellent subjects for microhabitat selection studies because they have been observed holding in positions of slow velocities (i.e., minimizing swimming costs) while foraging in nearby positions of higher velocities (i.e., maximizing prey encounter and energy intake; Jenkins 1969; Hughes & Dill, 1990; Hill and Grossman 1993). This apparent optimization of net energy gain combined with ease of quantifying both holding and foraging positions explain the focus of mechanistic microhabitat selection studies on this group.

A review of drift-feeding models for stream salmonids (Piccolo, Frank & Hayes, 2014) cites the work of Fausch (1984), Hughes and Dill (1990) and Hill and Grossman (1993) as the three cornerstone quantitative models for drift-feeding fish habitat selection. Fausch (1984) is widely credited with publishing the first cost-benefit model for drift-feeding salmonids which was later refined and improved by Hughes and Dill (1990) and Hill and Grossman (1993; Piccolo, Frank & Hayes, 2014). Fausch's (1984) model used parameters of water velocity and invertebrate drift to predict potential net energy gain as a function of specific growth rates of

Brook Trout (*Salvelinus fontinalis*), Brown Trout (*Salmo trutta*) and juveniles of Coho Salmon (*Oncorhynchus kisutch*). Fausch (1984) hypothesized that the potential net energy gain for salmonids occupying a particular stream location could be determined by the energy available from drift invertebrates minus the metabolic cost of swimming at that position and that the position at which net energy gain was maximized was the optimal stream position (Table 1.1). Fausch's results supported his hypothesis that juvenile salmonids selected positions within an experimental stream that maximized net energy gain (Fausch, 1984). Fausch (1984) also noted that dominant fish selected the optimal position during trials with multiple fish in the experimental stream, and thus exhibited the highest specific growth rates.

Hughes and Dill (1990) refined Fausch's (1984) model by speculating that a fish's ability to react to and capture prey declined with increasing water velocity as well as noting that fish may see and capture more prey with increasing water depth (Table 1.1). Specifically, this revised model added realism to Fausch's (1984) novel foraging model by incorporating prey size-frequency distribution, reactive distances, stream depth, and flow patterns to estimate net energy intake associated with occupying a specific microhabitat (Hughes & Dill, 1990). Hughes and Dill's (1990) model was a better predictor of microhabitat selection than Fausch's (1984) model when both were applied to Arctic Grayling (*Thymallus arcticus*) in Twelvemile Creek, AK. Additionally, Hughes and Dill (Hughes & Dill, 1990) noticed that removing swimming costs from their model did not change microhabitat selection predictions.

Hill and Grossman's (1993) microhabitat selection model for Rainbow Trout (*O. mykiss*) and Rosyside Dace (*Clinostomus funduloides*) further refined net energy gain microhabitat selection approaches by incorporating more realistic details in models such as activity levels, and seasonal and size effects. They also included actual prey availability, utilization, and capture success rates (Table 1.1). The specificity of this newer model allowed Hill and Grossman (1993) to more precisely tease apart the mechanisms by which these fishes selected microhabitats. Additionally, they discovered that prey capture success rates had a disproportionate impact on drift-feeding fish microhabitat selection. The third derivative (point of maximum decline) of prey capture success curves provided a better fit to holding velocities selected by fish in their natural habitat than the complete model whose physiological cost parameters were minimal and added more variance than predictability (Hill & Grossman, 1993).

Grossman *et al.* (2002) used information gained from Hill and Grossman's (1993) findings to construct a new net energy gain model based entirely on the relationship between prey capture success and water velocity. These authors hypothesized that variables included in the original Hill and Grossman (1993) foraging model (i.e., energy in the drift, visual reactive area, and swimming costs) could be held constant across habitats occupied by stream fishes in their study. Therefore, they constructed prey capture success – water velocity curves, and used curve-fitting constants (*b* and *c*, Table 1.1) derived from the maximum point of decline to yield optimal focal point velocity predictions (Grossman *et al.*, 2002). The optimal focal point velocity is the position in the stream at which net energy gain is potentially maximized. The new foraging model produced accurate predictions of focal point velocities for Rosyside dace (*C. funduloides*), Warpaint shiner (*Luxilus coccogenis*), Tennessee shiner (*Notropis leuciodus*) and Yellowfin shiner (*N. lutipinnis*) in a southern Appalachian stream. This mechanistic foraging model is easily transferrable across systems and species, but has not been tested outside of southern Appalachian streams (Grossman, 2014). Further testing is needed to determine the scope of the model's applicability; hence, we test the optimal focal point velocities predicted by Grossman *et al.*'s (2002) against focal point velocities occupied by Arctic Grayling (*T. arcticus*) in Panguingue Creek, AK. Hill and Grossman (1993) and Grossman *et al.* (2002) use the terminology of focal point velocity to refer to the water velocity at the position selected by an actively foraging drift-feeder. Focal point velocity is synonymous with our terminology of holding velocity and we will use holding velocity henceforth for brevity.

General Arctic Grayling Biology and Life History

The Arctic Grayling (*Thymallus arcticus*; henceforth, Grayling) is a cold-water, iteroparous salmonid found in streams, lakes, and rivers from central Asia to eastern Canada (Scott & Crossman, 1973; Stamford & Taylor, 2004). Grayling is the only species in the genus *Thymallus* that occurs in North America (Scott & Crossman, 1973; Armstrong, 1986) and has a historic continental distribution from Hudson Bay west throughout the Northwestern Territories and Alaska (Sawatzky *et al.*, 2007; Stewart *et al.*, 2007). Fossil records and DNA analyses suggest that Grayling colonized North America between 3 and 5 million years ago via the Bering land bridge and survived Pleistocene glaciations in multiple refugia in modern day Canada and northern U.S.A. (Redenbach & Taylor, 1999; Stamford & Taylor, 2004; Artym, 2016). The southernmost natural populations of Grayling in the contiguous United States are extirpated (Michigan) or severely limited (Montana) by development and other anthropogenic disturbances (Northcote, 1993; Magee, Rens & Lamothe, 2006).

Arctic Grayling have elongated, trout-like body forms and range in color from dark gray to silvery-blue to taupe with black spots along their sides. Grayling are easily identified by their large, sail-like dorsal fin, which can be brightly colored on large individuals and lends to their popularity as a sport fish and aids in competition and spawning behaviors (Tack, 1971; Alaska Department of Fish and Game, 2013). Age at maturity, growth rate and lifespan of Grayling vary regionally based on length of growing season, food availability, and density. Generally, high latitudes and/or densities result in slower growth rates, smaller maximum lengths, older maturation and longer lifespans (Hubert *et al.*, 1985; Kaya, 1990). Grayling populations in Montana and Wyoming mature as early as age 3 (Kruse, 1959; Kaya, 1990), can grow up to 90 mm per year, and rarely exceed 375 mm in length (Liknes, 1981; Hubert *et al.*, 1985). Grayling found in a high elevation (2800 m) Montana lake reach 10 years of age; however, maximum life spans in Montana typically are only 5 – 7 years of age (Brown, 1943; Nelson, 1953). Conversely, Grayling populations in Alaska usually reach maturity at 5 – 9 years of age at approximately 275 mm long and grow approximately 40 mm per year (Armstrong, 1986; Clark, 1992*b*). Alaskan Grayling can live up to 22 years and exceed 500 mm total length in extreme cases (de Bruyn & McCart, 1974; Hubert *et al.*, 1985). Grayling from the Tanana River drainage in Alaska (near our study site) typically mature at age 7 and 300 mm length, and have a lifespan of approximately 12 years and maximum length of 430 mm (Tack, 1980).

Similar to many other salmonids, Grayling have a highly specialized migratory life history, and exhibit seasonal and ontogenetic shifts in habitat use and migratory behavior (Vascotto, 1970; Tack, 1980; Hughes & Reynolds, 1994). Grayling populations display stream resident, fluvial, adfluvial and lacustrine life histories across their geographical range (Stewart *et al.*, 2007). Migratory life histories (i.e., fluvial and adfluvial) are common because Arctic Grayling require different overwintering, spawning, and feeding habitats, which rarely are found in the same river, stream, or lake (Northcote, 1993; Buzby & Deegan, 2000). Each of these migrations is precisely timed because seasonal habitats utilized by Grayling are often unavailable (e.g., summer feeding sites freeze during the winter and overwintering sites are too turbid and fast during the summer) during the rest of the year (Tack, 1980).

Grayling spawn in the spring and begin a reproductive migration from overwintering refugia upstream to suitable spawning habitat just after ice breakup (April – June depending on latitude) once water temperatures reach 1°C (Tack, 1980; Northcote, 1993). This migration typically occurs when rivers are at flood stage and Grayling can utilize low flow eddies in floodplains and expanded river margins that do not exist at normal flow levels (Tack, 1980). In Alaska, Grayling commonly spawn on riffle habitats with mixed sand and gravel substratum in bog or mountain streams, or lake outlets or inlets (Warner, 1955; Tack, 1980). The length and time of spawning migrations vary regionally; most Alaskan Grayling populations spawn between mid-May and mid-June when water temperatures reach 4°C and some may migrate up to 100 km before spawning (Warner, 1955; Armstrong, 1986; West *et al.*, 1992). Riffle habitats in mountain streams are ideal spawning locations because they warm earliest in spring and remain warm throughout the summer which shortens incubation time and maximizes the summer feeding season for yearlings (Tack, 1980; Northcote, 1993). Unlike many other salmonids, Grayling do not construct redds; however, physical spawning activity occurs on top of the substratum (i.e., male pressing female into substratum) and heavy, adhesive eggs settle below the substratum (Tack, 1971; Armstrong, 1986). The distribution and behavior of spawning Grayling is influenced by homing behaviors, temperature, and density (Tack, 1980).

Once spawning is completed, Grayling migrate to summer feeding grounds. The distribution of fluvial Grayling in summer habitats follows a general pattern of large adults in headwaters of clear, cool rapid runoff rivers or their tributaries, and progressively smaller fish downstream with yearlings remaining in margins and side channels of spawning streams (Stuart & Chislett, 1979; Northcote, 1993). Larger Grayling occupy optimal foraging locations in deep pools near the center of the current in upstream mountain stream reaches, and competitively exclude smaller fish from these positions (Hughes & Reynolds, 1994). Smaller subadults occupy either the farthest upstream position they are capable of defending or are displaced into small headwater tributaries incapable of supporting adults (Vascotto, 1970; Tack, 1980). Grayling fry spend a few days living in the substratum, and then migrate to nearby river margins and side-channels where they spend their first summer growing rapidly in relatively warm, slow waters (Kratt & Smith, 1977; Alt, 1980; Hubert *et al.*, 1985). During their second summer feeding season, juvenile Grayling join the upstream trophic migration cycle and progress farther upstream each subsequent year (Tack, 1971). Previous studies indicate that homing to summer feeding sites does occur (Tack, 1980; Northcote, 1993; Ridder, 2000), which may be an adaptation to a short summer feeding season with little time to explore alternative feeding locations (Buzby & Deegan, 2000).

Mature Grayling in headwaters of mountain streams in Alaska preferentially occupy positions in the center of the stream, typically in deeper microhabitats far from overhead cover, for up to 24 hours a day during the short three-month growing season (Armstrong, 1986; Hughes & Dill, 1990). Grayling are gape-limited predators that feed primarily on aquatic insects, although terrestrial insects also are important food sources, especially in narrow mountain streams with heavy riparian vegetation (Reed, 1964; Craig & Poulin, 1975; Armstrong, 1986). Large Grayling also are known to opportunistically feed on salmon eggs, small fish, or even rodents (Alaska Department of Fish and Game, 2013). Grayling in lotic habitats forage primarily in the drift or near the surface (Vascotto, 1970), although they have been observed to shift to a benthic foraging strategy when drift prey abundance is low (Morrow, 1980). The landscape-level pattern of larger Grayling occupying upstream habitats also is present on the pool scale, with larger Grayling holding position near the head of the pool with first access to drift prey and smaller individuals occupying positions progressively downstream and to the side (Hughes, 1992*a; *1992*b*). This pattern also has been observed in other salmonids (Newman, 1956; Fausch, 1984).

The third and final annual movement is a downstream refuge migration in autumn and is present in all age groups (Craig & Poulin, 1975; Tack, 1980). Because summer feeding habitats may be unavailable (e.g., frozen solid) to Grayling in the winter, they must return to overwintering refugia in the fall while conditions permit (Armstrong, 1986; Stewart *et al.*, 2007). These refugia typically are large river side channels and pools, spring-fed rivers and pools, or lakes (Tack, 1980; Northcote, 1993; Stewart *et al.*, 2007). Refuge migrations are less concentrated than reproductive or trophic migrations and may occur in Alaska from September through December (Tack, 1980), although Grayling may return to overwintering habitat earlier if feeding habitat conditions become unfavorable (Hughes, 2000). Grayling remain in overwintering habitat until the following spring when water temperatures increase to 1°C and spawning migrations commence.

We studied a population of fluvial Arctic Grayling from Panguingue Creek, Alaska. Panguingue Creek is a combination bog-fed, rapid runoff mountain stream (Wojcik, 1955) that flows Northeast from the Northeastern border of Denali National Park into the Nenana River and is within the Tanana River drainage (Figure 1.1). Panguingue Creek waters are sometimes stained brown due to leached tannins from the upstream boggy tundra region; however, this coloration is slight and is not present in periods of no rainfall. The Grayling population in Panguingue Creek likely overwinters in side channels or deep pools of the Nenana River and spawns in side channels of the Nenana River or lower reaches of Panguingue Creek before migrating roughly 8 km upstream to our study site to feed (J. Neuswanger pers. comm.). Apart from a population of fluvial Arctic Grayling, Panguingue Creek supports a stream resident population of Dolly Varden charr (*Salvelinus malma*) and occasional Slimy Sculpin (*Cottus cognatus*). The stretch of Panguingue Creek where we captured Grayling runs through a steep-sided, forested valley similar to the unsilted rapid runoff mountain rivers described by Wojcik (1955). As such, it provides excellent spawning and feeding habitat and fluvial Grayling usage of Panguingue Creek should be very similar to Grayling habitat usage in the innumerable similar systems throughout interior Alaska.

Threats to Arctic Grayling

Stream ecosystems inhabited by drift-feeding fishes around the globe are increasingly threatened due to climate- and other human-induced changes (Sorg *et al.*, 2012; Shah *et al.*, 2015; Williams *et al.*, 2015). These stressors combine to limit native drift-feeding fish populations whose attempts at tracking suitable habitats are thwarted by habitat fragmentation (Heino, Virkkala & Toivonen, 2009; Isaak *et al.*, 2011). Headwater streams at higher latitudes and elevations are at greater risk of climate-induced changes due to their sensitivity to changes in precipitation and thermal regimes and may become unsuitable for salmonids if warmed or otherwise altered (Jacobsen *et al.*, 2012; Prowse *et al.*, 2012; Immerzeel, Pellicciotti & Bierkens, 2013; Betts & Kane, 2015). Despite the severity of these known and impending perils and the high diversity of freshwaters, the biological effects of climate change on freshwater systems remain poorly understood (Shah *et al.*, 2015).

North American Arctic Grayling populations are negatively affected by numerous anthropogenic disturbances, the most severe of which is overfishing (Holmes, 1985; Armstrong, 1986; Northcote, 1993). Arctic Grayling are interior Alaska’s most valuable sport fish and the

Tanana River drainage supports the largest Grayling fishery in North America (Clark & Ridder, 1987). Strong angling pressure combined with relative ease of capture and increased accessibility renders Grayling highly susceptible to overfishing (Northcote, 1993; Walker, 2005). Reports of tens of thousands of Grayling taken from systems in a single year, even by inexperienced anglers, are not uncommon (Vincent, 1962; Mills, 1981; Armstrong, 1986). Declines in Grayling populations due to overfishing were recorded as early as the 1950s (Wojcik, 1955). Stock assessments on the Chena River, AK Arctic Grayling population in the late 1980s indicated a 50% decline in abundance that prompted managers to establish emergency reduced bag limit angling regulations for the 1987 fishing season that were eventually strengthened to catch-and-release status in the 1990s (Ridder, 2000). Apart from general stock declines, other effects of overfishing include earlier age at maturation (Tack, 1974) and reductions in average size and age (Falk & Gillman, 1974). Larger Grayling are more attractive to anglers, more readily caught, and have higher annual mortality rates than smaller individuals, potentially contributing to population-level effects of overfishing (Carl, Walty & Rimmer, 1992; Northcote, 1993; Stewart *et al.*, 2007). Arctic Grayling angling regulations for the 2017 fishing season on the Chena River and many other streams remain catch-and-release only (Alaska Department of Fish and Game, 2017).

Climate change and high discharge also negatively affect Arctic Grayling populations, although their impacts are not equal over all age classes. High temperatures and low flows associated with climate change negatively affect mature Arctic Grayling, which have been observed to undertake short-term migrations to avoid unusually high water temperatures (Wojcik, 1955; Schallock, 1966). Unusually low discharge also may cause decreased growth for mature Grayling that rely on discharge for prey delivery (Deegan *et al.*, 1999; Hobbie *et al.*, 1999). Conversely, conditions of low flow and warm water temperatures may improve growth and survival in young-of-the-year, which are weak swimmers and grow rapidly in warm river and stream margins during their first summer of life (Clark, 1992*a;* Deegan *et al.*, 1999). Years with generally high discharge or Spring flood events may potentially destroy entire age classes by flushing eggs and juveniles out of nursery habitat and downstream to waiting predators (Tack, 1971; Deegan *et al.*, 1999). The differential responses of Grayling age groups to warming temperatures and increased flow variability may compound the effects of overfishing because these conditions also encourage earlier maturation and decreased overall size and age. Wedekind *et al.* (2013) suggest that warming temperatures also may shift sex ratios by increasing the proportion of male yearlings in Grayling and further contribute to population decline. How Grayling will adapt to continued increases in water temperature and flow variability remains to be seen but the evidence suggests that overall populations likely will decline (Reist *et al.*, 2006; Stewart *et al.*, 2007).

In addition to overfishing and climate change, Arctic Grayling populations also are impaired by habitat degradation in the form of placer mining sediment and nutrient enrichment. Buhl and Hamilton (1991) found Arctic Grayling alevins to be more sensitive to inorganic compounds from placer mining sediment than other salmonids tested. The introduction of placer mining sediment may cause physiological damage, slower maturation, and general displacement of Grayling in streams where they once thrived (Simmons, 1984; Reynolds, Simmons & Burkholder, 1989). Tack (1971) observed increased growth in Grayling found in a section of the Chena River where sewage and other wastes had been introduced. Although nutrient enrichment increased Grayling growth via an increase in invertebrate volume (Frey, Mueller & Berry, 1970), Tack (1971) warns of a possible drastic reduction in Grayling numbers due to either: 1) anoxic conditions or 2) disease or disturbance wiping out a homogenous food source. Although not prevalent in interior Alaska, impoundments also have been shown to negatively affect populations of Arctic Grayling in southern regions of their native range via habitat alteration and fragmentation (Wojcik, 1955; Northcote, 1993).

If healthy populations of Arctic Grayling are to persist throughout their historic range, it is important that we recognize and minimize current and future threats and learn from past management failures. Arctic Grayling once existed as far south and east as Michigan, but were extirpated in the 1930s due to overfishing, logging, invasive species introductions (i.e., *Salmo trutta*) and development (Hubbs & Lagler, 1958; McPhail & Lindsey, 1970). A fluvial population of Arctic Grayling still exists in Big Hole River, Montana, but is threatened by warming temperatures (Lohr *et al.*, 1996; Magee, Rens & Lamothe, 2006). Many Arctic Grayling populations in southern regions of their historic range in Alberta, Canada, also are in decline due to the suite of factors mentioned above (Walker, 2005). Past and present trends in Arctic Grayling populations throughout the scope of their range clearly indicate that this species is susceptible to human-driven disturbances. It is imperative that we continue to study, monitor, and manage these populations with an eye towards past management shortcomings as development and climate change continually modify northern North America.

Impetus for Study

Our ability to manage and conserve declining salmonid species is only as robust as our knowledge of their habitat requirements (Anglin & Grossman, 2013). In this study, we quantified the effects of velocity, fish size, and days in captivity on prey capture success, holding velocity and reactive distance in a population of Arctic Grayling from Panguingue Creek, AK.

We also quantified the effects of dominance on these three response variables expressed by holding position selection (a fitness-based process). Finally, we tested holding velocity predictions of Grossman *et al.*'s (2002) mechanistic foraging model against holding velocities occupied by individuals in Panguingue Creek. This study should provide managers with useful information on specific mechanisms that drive Arctic Grayling microhabitat selection that should enhance management and conservation initiatives. Furthermore, this study contributes to the overall body of knowledge on net energy gain approaches for drift-feeding fish habitat studies, and tests the generality of a proven mechanistic foraging model.

Tables

Table 1.1. Evolution of drift-feeding fish microhabitat selection models. A side-by-side comparison of variables, parameters, and study species used in the three cornerstone models for drift-feeding fish habitat selection. Grossman *et al.*'s (2002) net energy gain model (used in this study) emboldened and included at the bottom.

Evolution of Drift Feeding Fish Microhabitat Selection Models

Author **Year**	**Models & Variables**	**Parameters of Interest**	**Species**	**Study Area**
Fausch 1984	$P = D - S$ Potential profit (P) Energy from drift (D) Swimming cost (S)	Velocity, invertebrate drift, specific growth rate	*O. kisutch* *S. fontanalis* *S. trutta*	East Lansing, MI, USA (lab only)
Hughes & Dill 1990	$NEI = GEI - SC$ Net energy intake (Hobbie *et al.*) Gross energy intake (GEI) Swimming cost (SC)	Velocity, capture area, prey concentration, energy content of prey	*T. arcticus*	Twelvemile Creek, AK, USA
Hughes & Dill 1990	$MCD = \sqrt{RD^2 - (V \times RD/VMAX)^2}$ Max. capture distance (Reist *et al.*) Reaction distance (RD) Velocity (V) Max. sustainable speed to prey ($VMAX$)	Velocity as it relates to decreased prey capture success	*T. arcticus*	Twelvemile Creek, AK, USA
Hill & Grossman 1993	$E_x = (I_x \times 0.68) - C_x$ Net energy gained (E_x)	Total energy intake, utilization inefficiency	*O. mykiss* *C. funduloides*	Coweeta Creek, NC, USA

	Total energy intake (Brix *et al.*) Estimation of prey utilization efficiency (0.68) Cost of holding position (C_x)	(specific dynamic action, egestion rate, excretion rate), all at velocity *x*		
Grossman *et al.* 2002	$\boldsymbol{e^{(b+cV)} = 1/(cV - 1)}$ Prey capture success curve fitting constants (*b* & *c*) Velocity (*V*)	Energy from drift, visual reactive area, and swimming costs held constant, optimal velocity from *b* and *c*	*C. funduloides* *L. coccogenis* *N. leuciodus* *N. lutipinnis*	Coweeta Creek, NC, USA

Figures

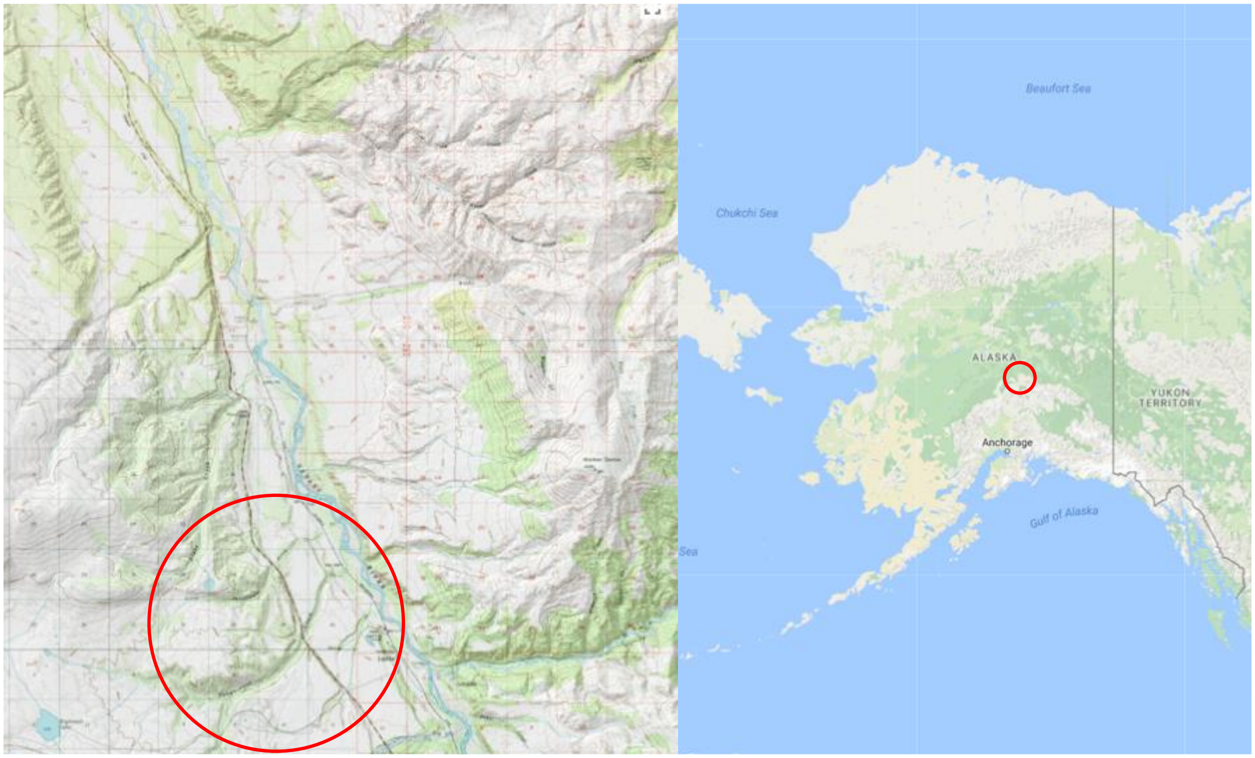


Figure 1.1. Map of Panguingue Creek, Alaska. Sources: www.topozone.com (left) and Google Maps (right).

CHAPTER 2

VELOCITY, PREY CAPTURE SUCCESS, AND MICROHABITAT SELECTION IN ARCTIC GRAYLING (*THYMALLUS ARCTICUS*)

Bozeman, B. B. and G. D. Grossman. To be submitted to *Freshwater Biology*.

Abstract

Our knowledge of factors affecting microhabitat selection for drift feeding salmonids is incomplete. We quantified the relationship between water velocity and prey capture success, holding velocity, reactive distance, and dominance experimentally for three sets of fluvial Alaskan Arctic Grayling. Velocity had a negative effect on prey capture success (β_i = -1.79 – -0.55) and a positive effect on holding velocity (β_i = 0.42 – 0.48) in all experiments. Holding velocity increased at a slower rate than capture velocity and plateaued at 30 cm/s at velocities of 30 cm/s and greater. Reactive distance displayed a weak (positive) or nonexistent relationship with velocity (β_i = 0.065 – 0.12). Dominant fish captured more prey than subordinate fish, but had similar holding velocities and reactive distances. Holding velocity predictions from Grossman et al.'s (2002) foraging model (41.2 cm/s, 36.2 cm/s, 34.7 cm/s) were greater than Arctic Grayling holding velocities in Panguingue Creek, AK (95% CI: 20.7 – 27.9 cm/s).

Introduction

Most research on lotic fish-habitat relationships correlates fish abundance to physical characteristics of stream reaches (Grossman, 2014). Although useful, these studies are only capable of identifying associations between habitat and abundance, and hence, cannot identify the actual mechanisms driving habitat selection. Alternatively, net energy gain studies (Fausch, 1984; Hughes & Dill, 1990; Hill & Grossman, 1993) attempt to identify the mechanism(s) driving habitat selection by quantifying currencies directly linked to individual fitness (i.e., cost of holding position versus the benefits of holding position) in specific microhabitats (Grossman, 2014). For drift-feeding fishes (fishes that hold position and wait for the current to bring them prey) these approaches test the hypothesis (mechanism) that fish maximize net energy gain by selecting holding positions in the stream where benefits (i.e., prey encounter and capture rates) are highest relative to costs (Fausch, 1984; Hughes & Dill, 1990; Urabe *et al.,* 2010). Drift-feeders in general are excellent subjects for studying net energy gain habitat selection because several aspects of holding position choice (i.e., swimming costs and prey encounter rates) are quantifiable and the relationships between water velocity and these variables are well known (Fausch & White, 1981; Hill & Grossman, 1993; Piccolo, Frank & Hayes, 2014). Besides the fact that net energy gain approaches test a specific mechanism driving habitat selection, they also have the potential to be transferable across lotic systems. Consequently, they represent a potentially powerful approach to a critical aspect of fish biology and fisheries; identification of the causal mechanisms producing habitat selection in species (Grossman, Hill & Petty, 1995; Urabe *et al.*, 2010; Fausch, 2013).

Drift-feeding fishes occur in many fish assemblages in Northern Hemisphere streams and include economically important species (Grossman, 2014). Members of the Cyprinidae, Salmonidae, and Percidae are all common drift feeders as are some centrarchids. The behaviors involved in drift-feeding by most of these species are fairly consistent including: 1) facing upstream into the current, 2) occupying a steady holding position, 3) identifying prey as it drifts downstream, 4) orienting towards the prey (termed reactive distance), 5) capturing prey and 6) returning to the holding position.

The Arctic Grayling (*Thymallus arcticus*, henceforth Grayling) is a salmonid drift-feeder widely distributed across Holarctic freshwaters, from eastern Canada west to central Asia (Scott & Crossman, 1973; Stewart *et al.*, 2007). Grayling live in cold (i.e., typically below 14°C) freshwater streams, rivers and lakes and have a maximum lifespan of 32 years (Clark, 1992*b;*

U.S. Fish and Wildlife Service, 2012). Grayling reach maturity between 6 and 10 years of age and at a length of between 276 and 376 mm fork length (Clark, 1992). Seasonal and ontogenetic shifts in habitat use by fluvial Grayling populations are well-documented (Tack, 1971; 1980; Alt, 1980; Hughes, 1992*a;* 1992*b*), and include: 1) spawning by adults in the spring just after ice breakup, 2) migration upstream to cool, clear tributaries for summer and early fall foraging, and 3) a return to deeper, slower rivers for overwintering (Tack, 1980; Armstrong, 1986; Northcote, 1993; Alaska Department of Fish and Game, 2013). In interior Alaskan fluvial populations, almost all growth occurs from mid-May thru mid-August (Armstrong, 1986). Grayling in these streams often occupy a single position for multiple days (Reed, 1964; Hughes & Dill, 1990; Northcote, 1993), which makes them excellent subjects for microhabitat selection studies.

Microhabitat use by Grayling during the summer feeding season varies by each age class. In general, fluvial Grayling habitat use after spawning follows the pattern of: 1) large adults in upper reaches of unsilted or spring fed rivers, 2) subadults in middle reaches of these systems, 3) juveniles in clear tributaries or lower reaches of unsilted rivers and 4) young-of-the-year individuals in side channels and stream margins (Tack, 1980; Northcote, 1993; Hughes & Reynolds, 1994). Young-of-the-year and juvenile Grayling forage primarily in warm, calm stream margin and side-channel riffle microhabitats (Stuart & Chislett, 1979) and adults and subadults select microhabitats in deep pools near the center of the current (Northcote, 1993; Hughes & Dill, 1990). Hughes and Dill (1990) and Hughes (1992*a*) found that behavioral rank (i.e., competitive foraging ability) affected microhabitat choice by adult Grayling in Twelvemile Creek, Alaska, more than simple estimates of costs and benefits.

Although Hughes and Dill (1990) and Hughes (1992*b*) tested a net-energy gain model for Grayling, their calculations were made using assumed rather than quantified values for the relationship between prey-capture and velocity. Nonetheless, estimates of swimming cost had little impact on calculations of optimal microhabitat choice; a finding also observed by Hill and Grossman (1993) and Grossman *et al.* (2002). These authors found that quantifying prey capture success – velocity relationships could be used to successfully predict optimal microhabitat use (holding velocity) for five species of drift-feeders in a Southern Appalachian stream. Consequently, we used Grossman *et al.*'s (2002) approach to test the mechanistic hypothesis that Grayling in Panguingue Creek, Alaska were selecting microhabitats (velocity at the holding position) on the basis of their potential for net energy gain. Specifically, we quantified the relationship between water velocity and: 1) prey capture success, 2) holding velocity, 3) reactive distance and 4) behavioral dominance prey capture success. Additionally, we compared optimal holding velocity predictions produced by Grossman *et al.*'s (2002) net energy gain model to holding velocities occupied by Grayling in Panguingue Creek. Given their importance as sport fishes (Northcote, 1993; Alaska Department of Fish and Game, 2013), tests of the relationship between foraging success and velocity and development of a net energy gain microhabitat model should aid managers in predicting potential effects of both climate change and increasing development on Grayling populations in Alaska and beyond.

Materials and Methods

Experimental Procedures

We captured wild Arctic Grayling (*Thymallus arcticus*) via hook and line from Panguingue Creek in central Alaska (Tenana River drainage, WGS84 Coordinates: 63.906 N, 149.095 W) in August 2015 and July 2016. Grayling were shipped to the University of Georgia within two days of capture. Fish typically arrived in excellent condition and there was no mortality or signs of distress from handling and shipping. We shipped 3 separate groups of 15 individuals for three replicate experiments (1 – 3) with individual fish (termed single-fish experiments). Individuals from Experiments 2 and 3 also were used in a two-fish dominance experiment (4). Mean standard lengths (mm ± SD) and mean masses (g ± SD) of individuals in Experiments 1 – 3 were 162 ± 31 mm and 44.6 ± 36.5 g, 184 ± 19 mm and 75.7 ± 20.6 g, and 153 ± 31 mm and 44.8 ± 25.0 g, respectively. Fish were kept in holding tanks at water temperatures approximating capture temperatures (10° C) for 162 (Exp.1), 34 (Exp. 2) and 14 (Exp. 3) days before beginning single-fish experiments. We fed individuals frozen blood worms (*Glycera*) ad libitum during the holding period; however, we withheld rations on the day preceding a trial to increase feeding motivation (Grossman *et al.*, 2002).

We conducted experiments in a 3.5 m L x 0.75 m W x 1.0 m H artificial stream flume (Figure 2.1). The flume consisted of a test chamber section (top half) and a water return section (bottom half), which were bisected horizontally by a plexiglass shelf. Individuals were confined to the test chamber section, which measured 1.5 m L x 0.75 m W x 1 m H and was bounded upstream by a polyvinyl chloride (PVC) collimator and downstream by a mesh and PVC barrier. The PVC collimator served to reduce flow heterogeneity and the barrier served to keep individuals in the trial space (in view of observer and cameras) and prevent them from approaching the trolling motors. We filled the stream flume with filtered, dechlorinated tap water (turbidities > 0.001 NTUs, Athens-Clarke County) so that the test chamber had a water depth of 40 cm. We minimized debris and turbidity levels in the experimental stream flume by draining and refilling the tank approximately every five days. We used two 24V, 80-lbs. thrust, variable speed trolling motors to achieve the desired current velocity. The trolling motors propelled water through the return chamber and the PVC collimator into the test chamber where the individuals were located. We replicated natural stream habitat in the test chamber by attaching several thin lengths of bamboo to the downstream side of the collimator, which facilitated fish orientation. The bamboo structures also prevented fish from holding positions at the front of the test chamber and compromising reactive distance measurements. A chiller downstream of the test chamber maintained appropriate water temperatures during prey capture trials. We measured water velocity with an electronic velocity meter and made observations of fishes from behind a plastic blind to minimize disturbance.

It was logistically impossible to use natural Alaskan invertebrates for experiments; therefore, we used frozen bloodworms (8.8 ± 1.4 mm, N = 50) for trial prey because they elicited natural foraging behaviors in Grayling and were readily visible in real time and on video. We delivered prey to the test chamber via one of three flexible plastic tubes (6 mm diameter). The tubes were attached to the collimator at evenly spaced intervals (~19 cm) across the width of the flume and delivered prey at 8 cm below the water's surface via a flush of tank water administered by a trial assistant. To minimize confusion over terminology in the following sections, experimental layers are as follows: each fish was subjected to a series of velocity *treatments*, the sum of which comprised a *trial*, and each *experiment* consisted of a series of fish *trials* (e.g., Grayling #4 was the fourth *trial* of *experiment* #1, and consisted of velocity *treatments* 10 cm/s – 60 cm/s; Table 2.1).

Single-Fish Experiments

We conducted experiments to quantify the relationship between water velocity and: 1) prey capture success, 2) holding velocity and 3) reactive distance for Grayling. To do this, we subjected individual fish to trials consisting of a series of treatment velocities beginning at 10 cm/s and increasing in 10 cm/s increments with 30 minute breaks between at low flow (~5 cm/s). We recorded prey capture success, holding velocity, and reactive distance for each individual at each velocity and ended trials when the fish exhibited a large reduction in prey capture success (≤ 22%, capture of two or less than nine prey) at a given velocity treatment. To ensure accurate treatment velocities, we took cross-sectional velocity measurements at ~ 8 cm depth from the surface prior to releasing prey for each treatment velocity.

All individuals were acclimated via a two-step process prior to being subjected to a trial that included an overnight acclimation in the test chamber with no flow and a 15-minute acclimation period at low flow (~5 cm/s) immediately preceding the first velocity treatment. After the second acclimation period, we slowly increased the velocity to the first treatment level of 10 cm/s. Once this velocity was achieved, we released several prey into the test chamber to initiate foraging behavior and began trials when the individual captured one of the initial prey. Occasionally, an individual failed to capture one of the first five prey released or behaved unusually (e.g., erratic swimming). In these rare circumstances, we allowed the individual to rest for 30 minutes at low flow levels and then retested. If the individual again exhibited similar behavior, it was eliminated from experiments.

For each velocity treatment, we delivered nine prey to the test chamber via the feeding tubes in a randomized order unique to each experiment. We used visual or video observations to record: 1) the proportion of prey captured (prey capture success), 2) holding velocity (water velocity of position most frequently occupied by individual throughout treatment), and 3) reactive distance (distance between prey and individual's nose when first orienting toward prey) at each velocity treatment. If the individual held in multiple locations throughout the test chamber, we recorded the velocity and depth of each position and took the average for holding velocity measurements. On rare occasions, we eliminated a prey release from the presentation count of nine if the observer deemed the prey to be outside the individual's field of vision, or if the individual was engaged in another foraging attempt (e.g., distracted by a previously missed worm) during a release, although this was uncommon. After the delivery of nine prey, we allowed the individual to rest at low flow (~5 cm/s) for 30 minutes before beginning the next velocity treatment. Velocity treatments increased in 10 cm/s increments following each 30-minute rest period until the fish captured less than three of the nine prey at which point we ended the trial and returned the fish to a holding tank. The maximum treatment velocity reached was 70 cm/s.

We recorded prey capture success and holding velocity measurements following each velocity treatment and measured reactive distances and capture velocities using VidSync after all experiments had been completed (www.vidsync.org, Neuswanger *et al.* 2016). We assessed flow heterogeneity within the test chamber by taking an additional 18 water velocity measurements at 3 cross-sections: 25%, 50%, and 75% test chamber lengths following each velocity treatment for Experiments 2 and 3. At each cross-section, we measured velocity at three width increments (25%, 50%, and 75%) and at two depths (8 cm and 32 cm below the surface). We used VidSync capture velocity measurements to compare actual prey velocities to the intended treatment velocity. Because capture velocity measurements were highly correlated to intended treatment velocities ($R^2 = 0.968$, slope = 0.942, Table 2.1), we used the treatment velocity variable for statistical analyses.

Effects of Dominance

We quantified the effect of dominance on prey capture success, holding velocity, and reactive distance by running trials with two Grayling in the test chamber (multi-fish Experiment 4) and assessing their behavioral rank. To reduce the probability of potential artifacts from holding fish for long periods we only used individuals from single-fish Experiments 2 and 3. Individuals were rested an average of 88 days (range 54 – 122 days) between single- and multi-fish experiments. This experiment consisted of 22 individuals (N = 11 pairs) with an average standard length of 175 mm (SD ± 30 mm) and an average mass of 60.3 g (SD ± 28.2 g). Individuals within pairs differed in standard length by an average of 48 mm (range 117 – 1 mm) and in mass by an average of 45 g (range 110.3 – 4.7 g).

We selected individuals for Experiment 4 to maximize the range of size differences within and between pairs. We began by selecting the largest and smallest individuals from the holding tank for the first pair and proceeded in that manner until all individuals had been selected (i.e., 117 mm size difference in pair 1 and 1 mm size difference in pair 11). We measured and weighed two fish and acclimated them overnight in the artificial stream flume. We held methods constant between single- and multi-fish trials, except we released 18 prey per treatment velocity in Experiment 4 to keep our prey-per-fish ratio consistent across experiments. We ended trials when 6 or more of the 18 prey released (≥ 33%) were missed cumulatively between fish.

For each fish in each velocity treatment, we recorded: 1) proportion of prey captured (prey capture success), 2) velocity and depth of holding position, and 3) reactive distance. We noted instances of aggression—including aggressor, victim, and displacement, if it occurred. We recorded the holding positions of both fish throughout each velocity treatment trial for use in data analysis. Holding positions were classified as “central” (approximate mid-portion of the test chamber on the x, y, and z axes) and “peripheral” (a departure from the central position in any direction). This classification was based on personal observation of over 320 single-fish treatment velocity trials where individuals consistently held a location in the central position of the tank across all treatment velocities when competition was not present. We observed similar behavior during multi-fish trials whereby one individual occupied this central position and the other individual selected a position at the margins of the test chamber. Previous studies have shown that Salmonids form linear dominance hierarchies with the dominant individual occupying the ideal stream position preferred by all fish and subordinate individuals occupying positions progressively downstream and to the side (Jenkins, 1969; Fausch, 1984). Consequently, we used fish holding position as an independent means of classifying dominance, with the fish that held the central position classified as dominant and the fish that held a peripheral position classified as subordinate.

Because we used individuals from Experiments 2 – 3 in multi-fish Experiment 4, we determined the cost of dominance by subtracting prey capture success for the corresponding individual in single-fish Experiment 2 or 3 from prey capture success from the dominant (i.e., centrally-holding) fish in each pair for each velocity. We determined cost of being subordinate (i.e., peripherally-holding) by subtracting paired dominant individual prey capture success from subordinate individual prey capture success for each treatment velocity. We calculated costs of behavioral rank on prey capture success in this way so that they would be graphically displayed in an intuitive manner (i.e., difference in prey capture success between dominant and subordinate individuals as a negative value rather than positive; Figure 2.8).

Optimal Foraging

We used the net energy gain model developed by Grossman *et al.* (2002) to predict optimal holding velocities for Grayling. The model predicts stream fish microhabitat selection as a function of velocity (*V*), visual reactive area of the fish (*A*), energy content of prey in the drift (*D*), prey capture success (*P*), and the cost of swimming at a given velocity (*S*). We estimated parameters (i.e., *b* & *c*) relating prey capture success (*P*) to treatment velocity (*V*) using the data from our experiments. Hill and Grossman (1993) describe the relationship between prey capture success and velocity as

(1)

$$P = 1/(1 + e^{(b+cV)})$$

where *b* and *c* are curve-fitting constants obtained from the prey capture success curve. The full habitat selection model for net energy gain (*I*) at velocity *x* is expressed as

(2)

$$I_x = \left\{(D \times A \times V) \times \left[\frac{1}{1 + e^{(b+cV)}}\right]\right\} - S_x$$

Because *D*, *A*, and *S* can be held constant across the range of microhabitats occupied by drift-feeding stream fishes (Grossman *et al.*, 2002), the model simplifies to

(3)

$$e^{(b+cV)} = 1/(cV - 1)$$

which can be solved to yield a single optimal holding velocity prediction using curve-fitting constants (*b* and *c*) obtained from our prey capture success curve (note that focal point velocity terminology used by Grossman *et al*. 2002 is synonymous with holding velocity terminology used throughout this document; Table 2.1).

We compared the net energy gain model's optimal holding velocity predictions to observations made in Panguingue Creek during July of 2016. In the field, we measured holding velocities occupied by drift-feeding Grayling (N = 25) *in situ* using an electronic velocity meter. We selected positions for in-stream holding velocity measurements under the following criteria: 1) we located a drift-feeding Grayling using an underwater paired camera apparatus and 2) we observed the individual pursue and capture at least five prey items while returning to the same holding position between foraging attempts. Once this behavioral criterion had been met, we directed a field assistant to the specific holding position using the camera viewing window to record the velocity and depth of that location. Additionally, we measured the range of velocities available to drift-feeding Grayling via mid-water column cross-sectional velocity measurements (N = 72) made along a ~115m reach of Panguingue Creek in July 2016 where Grayling were present. We then used these measurements to determine whether the model-predicted optimal holding velocity was available in Panguingue Creek. We considered the model predictions to be successful if they fell within the 95% confidence interval of the holding velocities occupied by Grayling while drift-feeding in their natural habitat and unsuccessful if they did not (Grossman *et al.,* 2002).

Statistical Analysis

We used an information-theoretic inference approach (Burnham & Anderson, 2002) to quantify the relative effects of three continuous, fixed predictor variables on three response variables. Our predictor variables were treatment velocity, fish size and days in captivity. Our response variables were prey capture success, holding velocity and reactive distance. For each single-fish experiment and response variable combination, we constructed simple linear models containing all three predictor variables (i.e., global models) and all possible reduced versions including intercept-only models. For multi-fish dominance Experiment 4, we added categorical predictor variables of size rank (i.e., larger or smaller) and dominance status (i.e., dominant or subordinate based on holding position) to our candidate model sets. We did not include interaction terms in our candidate model sets because we were predominantly interested in main effects. Furthermore, interaction terms cannot be included in equal numbers of models as main effects making model averaging coefficients questionable. All predictor variables were of *a priori* biological interest (Burnham & Anderson, 2002).

We used Akaike's Information Criterion for small sample sizes (AICc) and the criteria of Burnham and Anderson (2002) for model selection. AICc is a measure of the relative information lost by using a given model in a candidate set (Burnham, Anderson & Huyvaert, 2010). Consequently, the best model has the lowest information loss and the lowest AICc value with subsequent models typically having progressively higher AICc scores (i.e., greater information loss). We ranked the models based on delta AICc ($\Delta AICc$) values and Akaike weights (w_i). Akaike weights are easily interpretable and range from 1.0 (zero information loss) to 0.0 (complete information loss) (Grossman *et al.*, 2006; Grossman, Sundin & Ratajczak, 2016). Because w_i values sum to 1.0 within a candidate model set, w_i can be viewed as the probability that a model is true given the data and the competing models (Burnham & Anderson, 2002; Grossman *et al.*, 2006). We divided the w_i value of the best model (lowest information loss) by the w_i of subsequent models to assess their comparative explanatory power (Grossman *et al.*, 2006). As per Burnham and Anderson (2002), we did not evaluate models with w_i values of less than 10% of the top model. We calculated all AICc, ΔAICc, w_i, and comparative likelihood values manually using R 3.2.3 (https://www.R-project.org/).

Because there were several instances in our analyses where model selection uncertainty existed (i.e., top model w_i < 0.60), we used a model-averaging approach to produce robust parameter estimates and 95% confidence intervals (Burnham & Anderson, 2002; Grueber *et al.*, 2011). We obtained model-averaged parameter estimates for each variable by averaging parameter estimates across all evaluated models, including those where the variable was not present (Lukacs, Burnham & Anderson, 2009). To elucidate the relative importance of each predictor variable (w_+), we summed the model weights (w_i) across all models containing the predictor variable of interest (Burnham & Anderson, 2002). Model-averaging techniques were performed using R package 'MuMIn' (Barton, 2016).

Results

Prey Capture Success

Trial treatment velocities ranged from 10 cm/s to as high as 70 cm/s (Table 2.1) depending on individual prey capture successes. Treatment velocity was a strong predictor of prey capture success in all experiments (Tables 2.1 – 2.2). Treatment velocity was the sole predictor variable in each of the top candidate models for single-fish experiments (w_i = 0.42 – 0.47) and was included in every model evaluated across all experiments (w_+= 1.0, Table 2.2). Prey capture success decreased sharply with increasing treatment velocity in all single-fish experiments ($\beta_i \leq -1.16$, Figure 2.2, Table 2.3) and decreased at a lesser rate for all fish in dominance Experiment 4 (β_i = -0.55, Figure 2.3, Table 2.3). The effects of other predictor variables were small and inconsistent across experiments. For all single-fish experiments, days in captivity and treatment velocity models (the second-ranked model in all single-fish experiments) had lower Akaike weights ($w_i \leq 30$) and were at least 1.5 × less likely to be true than top-ranked treatment velocity-only models (Table 2.2). For multi-fish Experiment 4, dominance was included in all evaluated models (w_+= 1.0), but the model-averaged parameter estimate for subordinate behavior showed very little effect on prey capture success (β_i = $-$0.0035, Table 2.3). Model-averaged parameter estimates for days in captivity and fish size (all experiments) and size rank (multi-fish experiment) had 95% confidence intervals that overlap zero (Table 2.3), suggesting that these predictors had little explanatory power for prey capture success data.

Holding Velocity

We recorded holding velocities based on the position occupied by the individual throughout the treatment velocity. Treatment velocity was a strong predictor of holding velocity in all experiments and was present in all evaluated models (w_+= 1.0, Tables 2.1 – 2.2). For single-fish Experiments 1 and 2, the strongest candidate model contained only the treatment velocity predictor variable (w_i = 0.50 – 0.54, Table 2.2). For Experiment 3, no competing models had w_i values of at least 10% of the global model; hence, the global model was the only model evaluated (Table 2.2). Holding velocity was positively related to treatment velocity in all experiments (β_i = 0.42 – 0.48, Figures 2.4 – 2.5, Table 2.3), but increased at a lesser rate than capture velocity (Figures 2.4 & 2.5). The effects of other predictor variables on holding velocity were small and differed across experiments. For example, the addition of fish size and days in captivity to treatment velocity in second-ranked models for Experiments 1 and 2, respectively, caused a 50% decrease in Akaike weights (w_i = 0.25 – 0.21); therefore, these models were at least 2 × less likely to be true than top-ranked treatment velocity-only models (Table 2.2). In Experiment 3, fish size had a positive effect on holding velocity ($\beta_i = 0.052$) and days in captivity had a negative effect on holding velocity ($\beta_i =$ -0.31), and no 95% confidence intervals overlapped zero, suggesting important, albeit slight, influence on holding velocity (Table 2.3). For multi-fish Experiment 4, days in captivity had a small positive effect on holding velocity ($\beta_i = 0.14$), but neither size rank, nor dominance, nor fish size strongly influenced holding velocity (Table 2.3, Figure 2.5). Fish size and days in captivity in single-fish Experiments 1 and 2, and fish size, dominance and size rank in multi-fish Experiment 4 have 95% confidence intervals that overlap zero, hence these effects must be interpreted with caution (Table 2.3).

Reactive Distance

We made reactive distance measurements using VidSync 3D video analysis software (www.vidsync.org, Neuswanger *et al.* 2016). The effects of all included predictor variables on reactive distance were mostly small and inconsistent across experiments (Tables 2.1 – 2.2). Reactive distance ranged from 19.2 to 60.6 cm across all treatment velocities for all single-fish experiments. Treatment velocity had a slight positive effect on reactive distance in Experiment 1 (Figure 2.6A) and was included in all evaluated models ($\beta_i = 0.12, w_+ = 1.0,$ Table 2.3). However, 95% confidence intervals of treatment velocity parameter estimates overlap zero in Experiments 2 – 4, and this limits our ability to evaluate its impact on reactive distance (Figures 2.6B&C – 2.7). Although the candidate models provided moderate explanatory power for reactive distance, none of the models had greater than 50% of the Akaike weight ($w_i \leq 0.49$, Table 2.2). For Experiments 2 and 3, 95% confidence intervals for all coefficient estimates overlap zero (Table 2.3), suggesting that none of our predictor variables considerably influence reactive distance in these experiments. For multi-fish Experiment 4, fish size and days in captivity were included in all evaluated models ($w_+ = 1.0$). Reactive distance was positively affected by fish size ($\beta_i = 0.11$) and negatively affected by days in captivity ($\beta_i = -0.29$). Treatment velocity, size rank, and dominance parameter estimate 95% confidence intervals all overlap zero in Experiment 4 suggesting little to no relationship with reactive distance (Table 2.3).

Effects of Dominance

Dominance (via holding position selection) was a much better predictor of prey capture success than size rank (i.e., larger or smaller) in multi-fish Experiment 4 (Table 2.3, Figure 2.3). For prey capture success, size rank was approximately half as important as dominance, which was included in all evaluated candidate models ($w_{+(dominance)} = 1.0$ vs. $w_{+(size\ rank)} = 0.47$, Table 2.3). Size rank was a poorer predictor of prey capture success as larger individuals had higher prey capture success percentages than their smaller counterparts in just 64% of multi-fish velocity treatment trials. Conversely, dominant individuals exhibited higher prey capture success percentages than subordinate individuals in 93% of multi-fish velocity treatment trials. Smaller individuals were dominant in 36% of multi-fish velocity treatments and captured a greater percentage of prey on average than larger individuals at treatment velocities 10 – 20 cm/s (Figure 2.3A) while subordinate individuals captured fewer prey on average than dominant individuals across all treatment velocities (Figure 2.3B). There was little to no effect of size rank or dominance on holding velocity or reactive distance (Figures 2.5 & 2.7). Candidate models containing size rank and/or dominance had little explanatory power for these two response variables ($w_i \leq 0.17$, Table 2.2) and neither variable was very important ($w_+ \leq 0.29$, Table 2.3).

Additionally, 95% confidence intervals for size rank and dominance overlapped zero (Table 2.3), suggesting they had little to no effect on holding velocity and reactive distance.

Cost of Dominance

As expected, dominant individuals captured a greater average proportion of prey than subordinate individuals in most of the Experiment 4 trials. Our calculations showed that both dominant and subordinate individuals exhibited a reduction in prey capture success in the presence of a competitor. The cost of dominance was moderate (i.e., ~30% reduction in prey capture success) at lower velocities, but was beneficial (i.e., ~30% gain in prey capture success) at higher velocities (Figure 2.8). The cost of being subordinate was greater than the cost of dominance at all velocities, and dominant fish captured more prey on average than subordinate fish at all velocities (Figures 2.1B & 2.8).

Optimal Microhabitat Prediction

We fit our data from single-fish Experiments 1 – 3 to Grossman *et al.*'s (2002) empirical fitness-based model. Parameter b and c produced by equation (1) values were similar across Experiments 1, 2, and 3 (b = -4.2, -6.8, -4.4 and c = 0.08, 0.15, 0.1, respectively). We used these estimates in equation 2 to solve for optimal holding velocity predictions of 41.2 cm/s, 36.2 cm/s, and 34.7 cm/s for our three single-fish experiments. The average holding velocity selected by Grayling (N = 25) in Panguingue Creek in July 2016 was 24.3 cm/s with a 95% confidence interval of 20.7 cm/s – 27.9 cm/s. Because Grossman *et al.*'s (2002) net energy gain model optimal holding velocity predictions for all three single-fish experiments fall outside of the 95%

confidence interval of field holding velocities, we considered these predictions unsuccessful. Mid-water column cross-sectional water velocity measurements (N = 72) from a 115m stretch of Panguingue Creek where Grayling were present and feeding showed that the average available velocity was 55.8 cm/s (range: 4 cm/s – 126 cm/s). Approximately 25% of available velocity measurements in this stretch of Panguingue Creek were 35 cm/s or less, and velocities in the central portion main pool where many Grayling were holding were ~ 25 cm/s. Therefore, the failure of Grossman *et al.*'s (2002) model to predict velocities occupied by Grayling in the field was not due to a lack of predicted velocity availability, but because the fish clearly selected holding positions with slower velocities.

Overall, our results indicate that prey capture success was higher at slower water velocities, while holding velocity increased with water velocity. The relationship between velocity and reactive distance was less clear; reactive distance increased slightly with velocity in Experiment 1, but was not affected by velocity in the other experiments. Our dominance experiment results suggest that dominance via holding position selection is a better predictor of prey capture success than size rank. The effects of fish size and days in captivity on all response variables were small and inconsistent across experiments. Model-predicted optimal holding velocities, based on lab experiments, were greater than holding velocities of Graying observed in Panguingue Creek.

Discussion

Habitat selection of lotic fishes in streams has long intrigued ecologists, fishers, and other resource users. Descriptions of drift-feeding behavior and habitat preference in trout appear in the fly-fishing literature as early as the mid-fifteenth century (Berners, 1496), but humans likely observed intentional habitat selection patterns in lotic fishes since their first encounters with these potential food sources (Piccolo, Hughes & Bryant, 2008). Rivers and streams are complex systems containing multiple habitat types in the form of pools, riffles, rapids and slack water. Quantifying aspects of fish behavior in these habitats (e.g., prey capture success, holding velocity, and reactive distance) should help identify specific mechanisms driving microhabitat selection and enhance our understanding of these species.

Our experiments demonstrate that velocity had an overarching impact on foraging behavior of small Grayling, including a consistently high level of explanatory power for prey capture success (negative) and holding velocity (positive). The response of reactive distance to increasing treatment velocities was less clear; there were weak (positive) or nonexistent relationships between these variables in all experiments. Furthermore, dominance was a better predictor of prey capture success than size rank (i.e., size differences within pairs). Finally, the Grossman *et al.* (2002) optimal holding velocity model did not yield successful predictions of Grayling holding velocities in Panguingue Creek, AK.

Treatment velocity was the strongest, most consistent predictor variable in our laboratory experiments (included in 87% of all evaluated models). Previous fitness-based models for drift feeders have documented the importance of this variable for predicting net energy gain and habitat selection in drift-feeding salmonids (Fausch, 1984; Hughes & Dill, 1990; Hill & Grossman, 1993). Velocity is strongly tied to both energy expenditure (e.g., swimming cost) and energy gain (e.g., prey encounter rate). However, these costs and benefits are not necessarily simple linear functions (Grossman, 2014), and prey capture success may decline via nonlinear relationships including asymptotes and negative exponential phases (Hill & Grossman; Grossman *et al.*; Grossman).

Early investigations of habitat selection by salmonids showed that individuals occupy areas of low velocity and foraged in nearby areas of high velocity where it is assumed prey encounter rates are higher (Kalleberg, 1958; Jenkins, 1969; Everest & Chapman, 1972). Our results support these conclusions because Grayling maintained holding velocities of approximately 30 cm/s, even as capture velocity (i.e., prey speed; Table 2.1) and treatment velocity approached 60 cm/s. Interestingly, holding velocities occupied by individuals in the Dominance experiment differ little between size rank or dominance. Although there were a few instances where aggression forced peripherally holding fish to shelter directly beneath the bamboo structure (velocity ~ 5 cm/s, personal observation), most pairs occupied similar holding velocities throughout trials. This likely is due to the fact that we attempted to minimize flow variation within the test chamber as well as the relatively small area available to fish. One indicator that our experimental flume was a good simulation of natural habitats is that mean holding velocities for Grayling in Panguingue Creek (24 cm/s) were similar to values observed in the artificial stream (21 cm/s), even though nearly 80% of available velocities were 30 cm/s or greater.

Although prey capture success (negative) and holding velocity (positive) were affected by increasing velocity, there were few variables that affected reactive distance values. We identified three weak relationships (treatment velocity [positive] in Experiment 1 and fish size [positive] and days in captivity [negative] in the Dominance experiment 4), which varied among replicates. Although the lack of decline in reactive distance with increasing treatment velocity may seem unusual, similar trends were observed in previous laboratory experiments with juvenile Chinook salmon (*Oncorhynchus tshawytscha*) (Donofrio *et al.* in review). Conversely, O'Brien and Showalter (1993) found that reactive distance (location distance) in Grayling decreases with increasing velocity and suspended debris. It is unlikely that suspended debris influenced reactive distance in our laboratory experiments due to our efforts to minimize turbidity and suspended debris in the experimental stream flume. The slight positive relationship between fish size and reactive distance in Dominance Experiment 4 has been observed in Grayling previously (Schmidt & Obrien, 1982; Hughes & Dill, 1990). Reactive distances of other drift-feeding stream fishes are negatively affected by turbidity including: Rosyside dace (*Clinostomus funduloides*), Rainbow trout (*Oncorhynchus mykiss*) (Barrett, Grossman & Rosenfeld, 1992; Zamor & Grossman, 2007). Given the status of turbidity of as a major water contaminant world-wide, more research is needed on this topic (Henley *et al.*, 2000; Hazelton & Grossman, 2009).

It is reasonable to expect that behavioral dominance would lead to increased access to food resources (Grossman, 1980). Relative fish size frequently is a strong predictor of dominance in Salmonids (Newman, 1956; Jenkins, 1969; Nakano, 1994), including Grayling (Hughes, 1992*a;* Hughes & Reynolds, 1994; Hughes, 1998). Results from our dominance experiment suggest that size is not a strong predictor of dominance in Grayling from Panguingue Creek given that larger individuals exhibited higher prey capture success in just 64% of our trials. Furthermore, smaller individuals captured more prey on average than larger individuals at 10 and 20 cm/s. This result is similar to the findings of Huntingford *et al.* (1990) who observed weak or nonexistent relationships between size and dominance in Atlantic salmon parr (*Salmo salar*). Abbott *et al.* (1985) suggest that behavioral rank (i.e., dominant or subordinate) is determined in early life stages based on size and that individuals maintain rank statuses even when size relationships change. This could potentially explain our results given Grayling display agonistic and territorial behavior within four weeks of emergence (Kratt & Smith, 1979) and individuals in our sample surely had varying early-life experiences regardless of their relative size within pair at time of trial.

Our results indicate that dominance is a stronger predictor of prey capture success than size rank, with fish in central holding positions (i.e., dominant) exhibiting higher prey capture success than those in peripheral positions (i.e., subordinate) in 93% of our trials. This makes sense because holding position selection is a behavior that influences fitness, rather than a physical characteristic such as fish size, which is a result of fitness-based behavior. As trial treatment velocities increased, instances of aggression decreased and differences in holding position and prey capture success increased (personal observation), indicating that detectable relationships between competing individuals can be established on short, hours-long time scales. This observation suggests that early-life behavioral dominant and subordinate impressions may be compounded by short-term experiences (Abbott, Dunbrack & Orr, 1985; Thornton, Duda & Quinn, 2017).

Similar to observations by Gowan and Fausch (2002), we noticed that smaller fish were more likely to capture a greater proportion of prey than larger fish when size differences within pairs were small (i.e., ≤ 16 mm). Additionally, in the pair with the largest size difference (117 mm), the smaller individual captured more prey than the larger individual, indicating that either: 1) the size difference between competing fish was so great that the larger individual did not recognize the smaller individual as a competitor, or 2) early-life behavioral impressions can supersede current conditions, which also might be maladaptive (Abbott, Dunbrack & Orr, 1985). Due to constraints on fish collection, we could only test 11 pairs of Grayling and could not replicate the within-pairs size difference gradient.

The optimal holding velocity predictions produced by fitting our data to Grossman *et al.*'s (2002) net energy gain model (34.7 – 41.2 cm/s) were considerably faster than velocities occupied by Grayling in Panguingue Creek, AK (95% CI: 20.7 – 27.9 cm/s). There are a few tenable explanations for these discrepancies. First, other fitness-based mechanisms (e.g., predator avoidance) may be driving Grayling position selection rather than maximization of energy gain. While plausible, it is unlikely that predator avoidance is influencing position choice by Grayling in Panguingue Creek for a number of reasons. Mature Grayling likely are top predators in their headwater summer feeding grounds. Previous studies have shown that proximity to overhead cover can influence position selection of salmonids (Newman, 1956; Jenkins, 1969); however, field observations of Grayling habitat usage in Panguingue Creek in 2016 revealed that most Grayling occupied positions in the center of pools, far from places of shelter. Similar observations led Hughes and Dill (1990) to conclude that Grayling do not trade off energy gain for predation risk when selecting foraging positions. Interspecific competition with Dolly Varden charr (*Salvelinus malma*) (the other drift-feeder present in Panugingue Creek), possibly could influence Grayling position selection; however, the effects of these interactions are unknown, despite evidence that Grayling are strong interspecific competitors (Northcote, 1993).

Model-predicted optimal holding velocities were inaccurate; however, holding velocities in the artificial stream (mean = 21.1 cm/s) very closely matched holding velocities of Grayling in Panguingue Creek (20.7 – 27.9 cm/s). This indicates that overestimates of predicted optimal holding velocities could be due to Grayling in Panguingue Creek holding positions in slower velocities and foraging in nearby faster velocities, similar to energy gain optimization behavior we observed in laboratory experiments. The mean capture velocity of Grayling (N = 13) in the

Richardson Clearwater (a large river in the Tanana River drainage) was 44 cm/s, which closely matches optimal holding velocities predicted by the net energy gain model (35 – 41 cm/s). However, this river is much larger than Panguingue Creek and the Grayling observed were larger than our experimental individuals. We did not have capture velocity (i.e., foraging velocity) data for Grayling in Panguingue Creek; however, the mean capture velocity of Dolly Varden charr (drift-feeder with similar size, habitat usage, and diet; N = 13) in Panguingue Creek (30 cm/s) still was slower than model-predicted optimal holding velocities. Our comparisons of model velocity predictions with foraging velocities of the same species in a different system and a different species in the same system are speculative; more research is needed to determine the similarity between foraging velocities and optimal holding velocity predictions produced by Grossman *et al.*'s (2002) net energy gain model.

Further examination of the failure of the optimal foraging model suggests that variables other than velocity may affect the choice of holding velocities in Grayling such as suspended materials in the water column. For example, O'Brien and Showalter (1993) found that suspended debris reduces the angle and distance at which Grayling first detect prey. This could lead to Grayling occupying slower holding velocities than the optimum. A reduction in foraging success with increased turbidity has been documented in other drift-feeding fishes (Barrett, Grossman & Rosenfeld, 1992; Zamor & Grossman, 2007; Hazelton & Grossman, 2009). In addition, Panguingue Creek is light brown in color due to tannins leached from upstream tundra bogs, although this coloration is slight and very likely does not obscure fish vision (J. Neuswanger, pers. comm.). Consequently, the effects of suspended materials on the over estimates of the optimal foraging model are unknown.

A final possible reason for the difference between model predictions and field holding velocities of Grayling lies in potential undetected differences between our experimental stream flume (Figure 2.1) and Panguingue Creek. Analysis of Dolly Varden charr stomach contents ($N = 13$) from Panguingue Creek in 2015 indicated that the average size of prey consumed by these fish was 3.9 ± 0.7 mm. We do not have field Grayling diet samples, but it is highly likely that Grayling are consuming the same prey given their similar size, feeding behavior, and habitat usage. By contrast, bloodworm prey used in our laboratory experiments were 8.8 ± 1.4 mm. Consequently, experimental prey were slightly larger than prey consumed by Dolly Varden charr in Panguingue Creek, although experimental prey often contracted when flushed into the test chamber and may have appeared smaller than their actual length (personal observation). Regardless, this larger prey size could have contributed to higher prey capture success rates and thus higher model predictions of optimal velocity. Additionally, our test chamber environment (flat white right sides, white collimator, unbroken black plastic barrier left side) was less complex visually than the underwater environment of Panguingue Creek. The sharp contrast between bright red bloodworms and white backdrop and collimator compared to dark colored macroinvertebrates against natural stream substrate potentially resulted in improved prey identification abilities. Furthermore, our attempts to minimize suspended debris and flow heterogeneity in the water column likely reduced the number of distractions that might challenge fish in natural systems. Each of these departures in realism from the natural state of Panguingue Creek could have contributed to our unsuccessful model predictions by inflating prey capture success abilities across a range of velocities.

Although our test of Grossman *et al.*’s (2002) empirical fitness-based model yielded unsuccessful optimal velocity predictions when compared to field observations, our study produced useful and interesting results. Velocity is clearly an important predictor of prey capture success and position selection; however, there are likely other, unmeasured variables at play. Additionally, our results indicate that behavioral dominance via holding position selection, a fitness-based process, is a stronger predictor of prey capture success than fish size, a physical descriptor. Our field observations of habitat availability and usage suggest that velocities of approximately 25 cm/s are important, as fish preferentially choose to occupy these habitats even while foraging in much faster velocities (Figures 2.4 & 2.5, Lab field video observation). Furthermore, dominant (i.e., centrally holding) fish in Experiment 4 exhibited higher prey capture success than the same individuals in single-fish Experiments 2 and 3 (Figure 2.8), which suggests that competition could work to optimize dominant fish position selection in addition to the traditional negative effects on subordinate individuals (e.g., decreased growth, increased stress, etc.). These findings should help identify critical Grayling microhabitat and inform policy development, which are relevant to the management of this popular sportfish (Northcote, 1993; Alaska Department of Fish and Game, 2013).

Tables

Table 2.1: Velocity terminology and experimental layer definitions.

Velocity Terminology	
Holding Velocity	The water velocity encountered by a drift-feeding Arctic Grayling at the position occupied by the individual from which foraging attempts are initiated (i.e., holding position). Synonymous with focal point velocity terminology used by Grossman *et al.* 2002.
Capture Velocity	The water velocity at which a drift-feeding Arctic Grayling captures prey. Synonymous with prey speed and foraging velocity.
Experimental Layers	
Experiment	A unit composed of a series of fish *trials* (e.g., Experiment 1 consisted of 15 Arctic Grayling trials). The largest experimental layer.
Trial	A series of *treatment velocities* to which individuals (Experiments 1 – 3) or pairs of individuals (Experiment 4) were exposed (e.g., Arctic Grayling #4 was a trial comprised of treatment velocities 10 – 60 cm/s). The intermediate experimental layer.
Treatment Velocity	The water velocity to which laboratory individuals were exposed in the experimental stream flume as measured from the central cross section of the test chamber at 8 cm depth from the water surface. Additionally, the intended velocity of prey items introduced to the test chamber, although not necessarily equal to capture velocity (slope = 0.942). Treatment velocities ranged from 10 – 70 cm/s in 10 cm/s increments. The smallest experimental layer.

Table 2.2: AICc values, delta AICc values ($\Delta AICc$), and Akaike weights (w_i) for all experiments and response variables. The comparative likelihood that the top-ranked model is true compared to subsequent models given the data is in parenthesis beside Akaike weight value (e.g., Velocity model is 1.9 X more likely to be true given the data than Velocity + Days model for prey capture success in Experiment #1). Experiments 1 – 3 are single-fish experiments and Experiment 4 is multi-fish dominance experiment. Predictor variables are abbreviated as follows: Treatment Velocity = Velocity, Days in Captivity = Days, Fish Size = Size, Size Rank = Rank, Holding Dominance = Dom.

Response Var.	Experiment	Candidate Model	AICc	$\Delta AICc$	w_i
Capture Succ.	Exp. #1	Velocity	655.96	0	0.47
		Velocity + Days	657.22	1.26	0.25 (1.9)
		Velocity + Size	657.75	1.79	0.19 (2.5)
		Global	659.47	3.51	0.08 (5.9)
	Exp. #2	Velocity	728.98	0	0.42
		Velocity + Days	730.52	1.54	0.20 (2.1)
		Global	730.54	1.56	0.19 (2.2)
		Velocity + Size	730.61	1.63	0.19 (2.2)
	Exp. #3	Velocity	566.41	0	0.44
		Velocity + Days	567.16	0.75	0.30 (1.5)
		Velocity + Size	568.67	2.25	0.14 (3.1)
		Global	569.06	2.64	0.12 (3.7)
	Exp. #4	Velocity + Size + Rank + Dom	-86.33	0	0.29
		Velocity + Size + Dom	-85.51	0.82	0.19 (1.5)
		Velocity + Dom	-85.4	0.93	0.18 (1.6)
		Global	-84.07	2.26	0.09 (3.1)
		Velocity + Days + Dom	-83.95	2.38	0.09 (3.3)
		Velocity + Size + Days + Dom	-83.38	2.95	0.07 (4.4)
		Velocity + Rank + Dom	-83.23	3.1	0.06 (4.7)
		Velocity + Days + Rank + Dom	-81.72	4.61	0.03 (10.0)
Holding Vel.	Exp. #1	Velocity	456.67	0	0.50
		Velocity + Size	458.05	1.38	0.25 (2.0)
		Velocity + Days	458.87	2.21	0.17 (2.9)

		Global	460.28	3.61	0.08 (6.3)
	Exp. #2	Velocity	482.41	0	0.54
		Velocity + Days	484.27	1.86	0.21 (2.6)
		Velocity + Size	484.61	2.2	0.18 (3.0)
		Global	486.36	3.95	0.07 (7.7)
	Exp. #3	Global	337.79	0	1.00
	Exp. #4	Velocity + Days	762.33	0	0.36
		Velocity + Days + Dom	763.82	1.49	0.17 (2.1)
		Velocity + Days + Rank	763.92	1.58	0.16 (2.3)
		Velocity + Size + Days	764.32	1.99	0.13 (2.8)
		Velocity + Days + Rank + Dom	765.72	3.39	0.07 (5.1)
		Velocity + Size + Days+ Dom	765.99	3.66	0.06 (6.0)
		Velocity + Size + Days + Rank	766.08	3.75	0.06 (6.0)
Reactive Dist.	Exp. #1	Velocity	498.53	0	0.47
		Velocity + Size	499.67	1.14	0.27 (1.7)
		Velocity + Days	500.45	1.93	0.18 (2.6)
		Global	501.97	3.44	0.08 (5.9)
	Exp. #2	Velocity + Size	549.28	0	0.23
		Global	549.34	0.06	0.22 (1.0)
		Velocity + Days	549.37	0.09	0.22 (1.0)
		Size	550.18	0.91	0.14 (1.6)
		Size + Days	550.81	1.53	0.11 (2.1)
		Days	551.3	2.02	0.08 (2.9)
	Exp. #3	Velocity + Size	386.03	0	0.49
		Size	388.34	2.31	0.15 (3.3)
		Global	388.4	2.38	0.15 (3.3)
		Velocity	389.49	3.46	0.09 (5.4)
		Velocity + Days	389.78	3.75	0.07 (7.0)
		Size + Days	390.55	4.52	0.05 (9.8)
	Exp. #4	Velocity + Size + Days	707.13	0	0.41
		Size + Days	709.05	1.92	0.16 (2.6)
		Velocity + Size + Days + Dom	709.21	2.08	0.14 (2.8)
		Velocity + Size + Days + Rank	709.28	2.15	0.14 (2.9)
		Size + Days + Dom	711.07	3.94	0.06 (7.2)
		Size + Days + Rank	711.17	4.04	0.05 (7.5)
		Global	711.39	4.26	0.05 (8.4)

Table 2.3: Model-averaged parameter estimates, 95% confidence intervals, and relative variable importance for all experiments. Confidence intervals that overlap zero are denoted with an asterisk.

Response Variable	Predictor Variable	Experiment	Estimate ± 95% CI	w+
Capture Succ.	Treatment Velocity	Exp. #1	-1.16 ± 0.28	1.0
		Exp. #2	-1.79 ± 0.21	1.0
		Exp. #3	-1.53 ± 0.41	1.0
		Exp. #4	-0.55 ± 0.062	1.0
	Days in Captivity	Exp. #1	0.079 ± 0.37*	0.33
		Exp. #2	-0.073 ± 0.28*	0.39
		Exp. #3	-0.33 ± 1.11*	0.42
		Exp. #4	-0.00017 ± 0.0016*	0.28
	Fish Size	Exp. #1	0.011 ± 0.095*	0.27
		Exp. #2	0.046 ± 0.18*	0.38
		Exp. #3	0.0074 ± 0.13*	0.26
		Exp. #4	-0.00097 ± 0.0021*	0.64
	Dominance	Exp. #4	-0.0035 ± 0.0020	1.00
	Size Rank	Exp. #4	-0.033 ± 0.11*	0.47
Holding Vel.	Treatment Velocity	Exp. #1	0.46 ± 0.073	1.00
		Exp. #2	0.45 ± 0.049	1.00
		Exp. #3	0.48 ± 0.061	1.00
		Exp. #4	0.42 ± 0.088	1.00
	Days in Captivity	Exp. #1	-0.00037 ± 0.068*	0.25
		Exp. #2	0.0064 ± 0.044*	0.29
		Exp. #3	-0.31 ± 0.22	1.00
		Exp. #4	0.14 ± 0.12	1.00
	Fish Size	Exp. #1	-0.0064 ± 0.030*	0.33
		Exp. #2	00.00083 ± 0.025*	0.25
		Exp. #3	0.052 ± 0.039	1.00
		Exp. #4	0.0013 ± 0.031*	0.24
	Dominance	Exp. #4	-0.31 ± 1.75*	0.29
	Size Rank	Exp. #4	-0.31 ± 1.97*	0.28
Reactive Dist.	Treatment Velocity	Exp. #1	0.12 ± 0.097	1.00
		Exp. #2	0.065 ± 0.12*	0.66
		Exp. #3	0.094 ± 0.14*	0.79
		Exp. #4	0.079 ± 0.13*	0.73
	Days in Captivity	Exp. #1	0.0092 ± 0.098*	0.26
		Exp. #2	0.091± 0.19*	0.63
		Exp. #3	0.013 ± 0.23*	0.27
		Exp. #4	-0.29 ± 0.14	1.00

Fish Size	Exp. #1	0.0096 ± 0.042*	0.35
	Exp. #2	0.070 ± 0.12*	0.70
	Exp. #3	0.055 ± 0.07*	0.84
	Exp. #4	0.11 ± 0.08	1.00
Dominance	Exp. #4	-0.16 ± 1.76*	0.24
Size Rank	Exp. #4	0.19 ± 2.74*	0.24

Figures

Figure 2.1: Diagram of the experimental stream flume used in all laboratory experiments. Figure is not to scale.

Figure 2.2: Mean prey capture successes vs. treatment velocity for single-fish Experiments 1 – 3 (A – C). Error bars represent SD. N represents sample size (number of fish trials completed) at each treatment velocity.

Figure 2.3: Mean prey capture successes vs. treatment velocity for multi-fish Experiment 4 by fish size rank (A) and dominance (B). Error bars represent SD. N represents sample size (number of fish pair trials completed) at each treatment velocity.

Figure 2.4: Mean holding velocities vs. treatment velocity for single-fish Experiments 1 – 3 (A – C). Mean capture velocities are also displayed. Error bars represent SD. N represents sample size (number of fish trials completed) at each treatment velocity.

Figure 2.5: Mean holding velocities vs. treatment velocity for multi-fish Experiment 4 by fish size rank (A) and dominance (B). Mean capture velocities are also included. Error bars represent SD. N represents sample size (number of fish pair trials completed) at each treatment velocity.

Figure 2.6: Mean reactive distances vs. treatment velocity for single-fish Experiments 1 – 3 (A – C). Error bars represent SD. N represents sample size (number of fish trials completed) at each treatment velocity.

Figure 2.7: Mean reactive distances vs. treatment velocity for multi-fish Experiment 4 by fish size rank (A) and dominance (B). Error bars represent SD. N represents sample size (number of fish pair trials completed) at each treatment velocity.

Figure 2.8: Mean cost of competition in multi-fish Experiment 4. The cost of dominance is the prey capture success for corresponding individuals in single-fish Experiment 2 or 3 subtracted from prey capture success of the dominant (i.e., centrally-holding) fish in each pair for each velocity. The cost of being subordinate (i.e., peripherally-holding) paired dominant individual prey capture success subtracted from subordinate individual prey capture success for each treatment velocity.

Figure 2.1

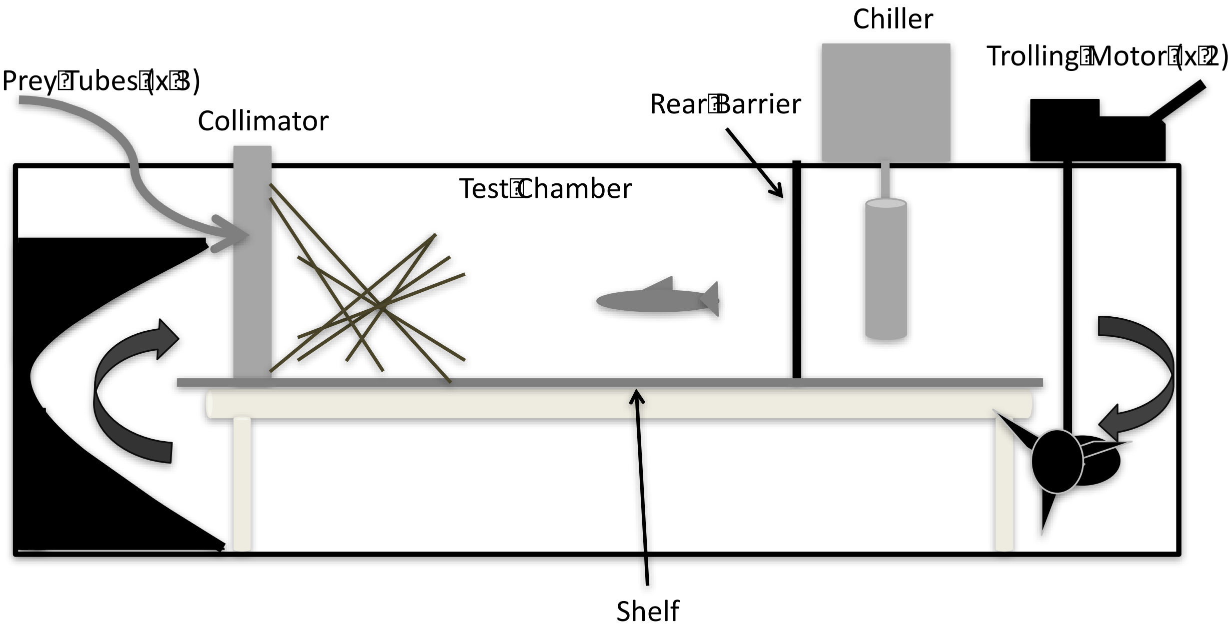
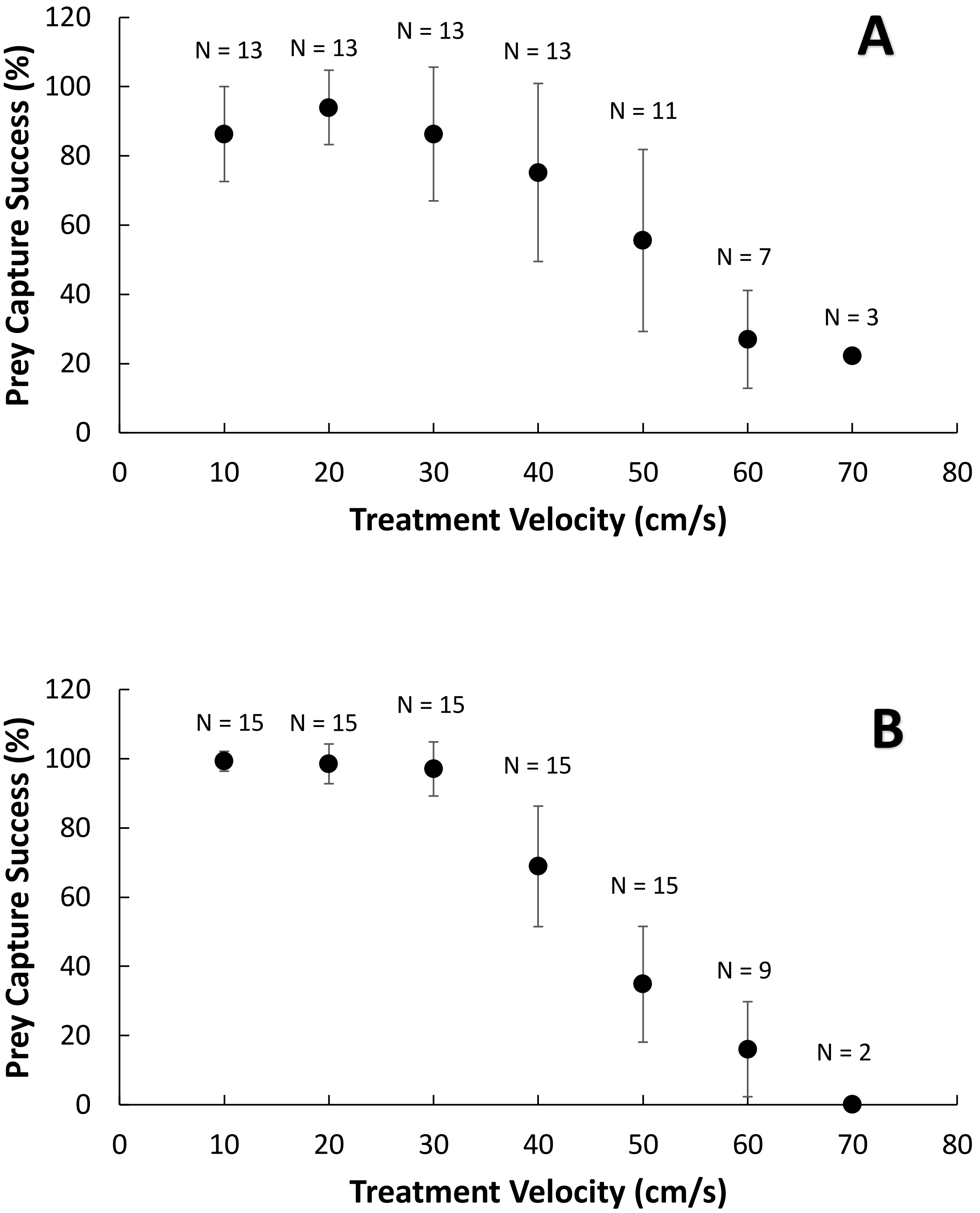

Chiller
Trolling Motor (x 2)
Prey Tubes (x 3)
Rear Barrier
Collimator
Test Chamber
Shelf

Figure 2.2


A
Prey Capture Success (%)
120
100
80
60
40
20
0
N = 13
N = 13
N = 13
N = 13
N = 11
N = 7
N = 3
0
10
20
30
40
50
60
70
80
Treatment Velocity (cm/s)
B
Prey Capture Success (%)
120
100
80
60
40
20
0
N = 15
N = 15
N = 15
N = 15
N = 15
N = 9
N = 2
0
10
20
30
40
50
60
70
80
Treatment Velocity (cm/s)

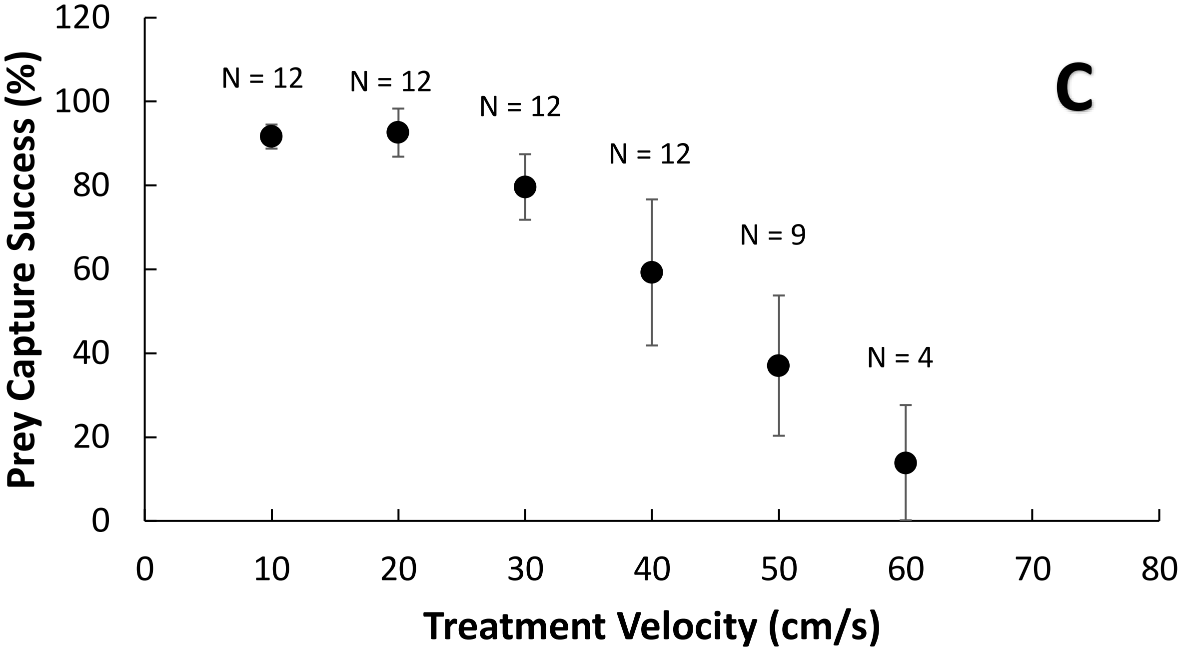
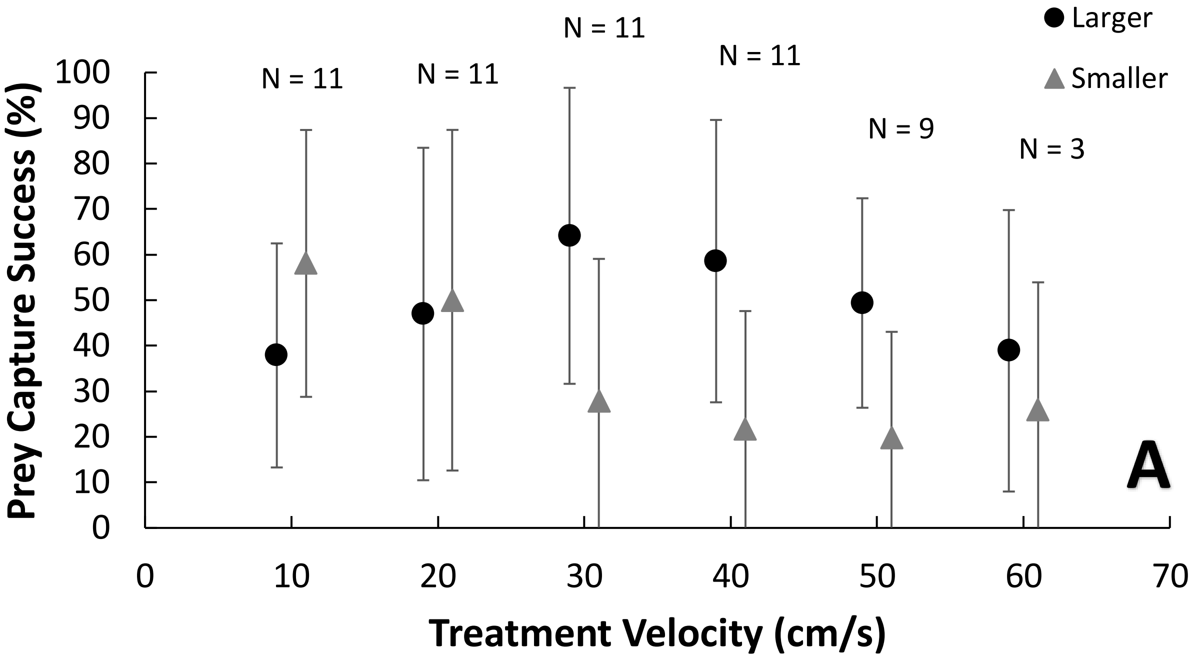
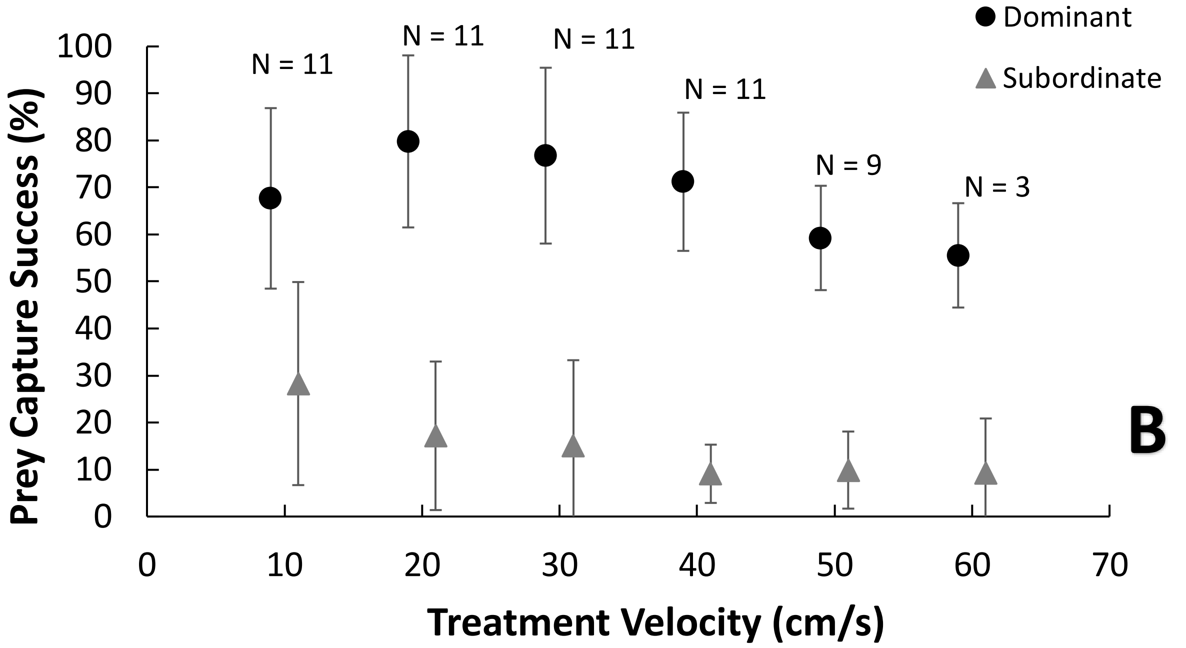

C
Prey Capture Success (%)
Treatment Velocity (cm/s)
0
20
40
60
80
100
120
0
10
20
30
40
50
60
70
80
N = 12
N = 12
N = 12
N = 12
N = 9
N = 4

Figure 2.3

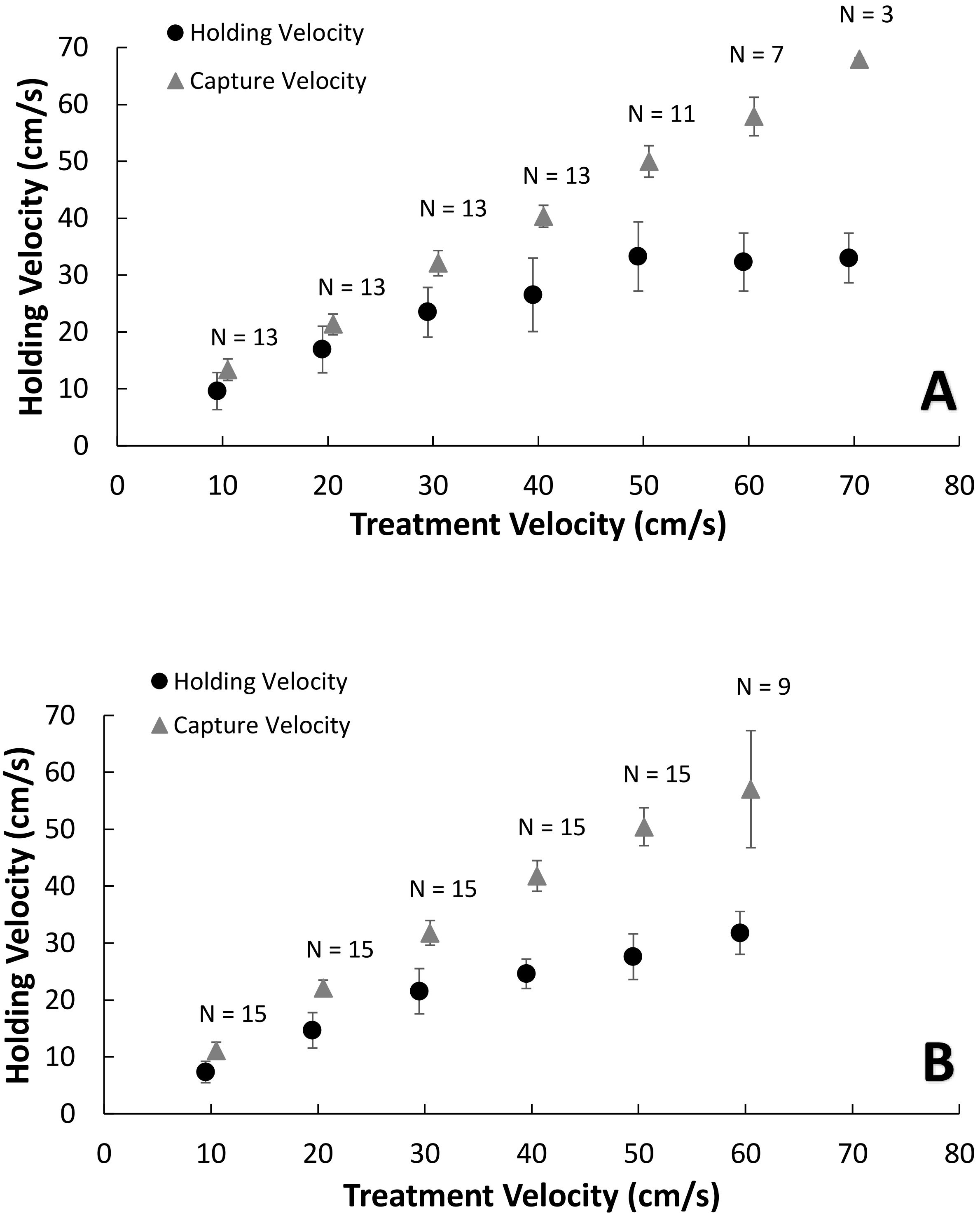


● Larger
▲ Smaller
N = 11
N = 11
N = 11
N = 11
N = 9
N = 3
Prey Capture Success (%)
100
90
80
70
60
50
40
30
20
10
0
0
10
20
30
40
50
60
70
Treatment Velocity (cm/s)
A



● Dominant
▲ Subordinate
N = 11
N = 11
N = 11
N = 11
N = 9
N = 3
Prey Capture Success (%)
100
90
80
70
60
50
40
30
20
10
0
0
10
20
30
40
50
60
70
Treatment Velocity (cm/s)
B

Figure 2.4


● Holding Velocity
▲ Capture Velocity
Holding Velocity (cm/s)
Treatment Velocity (cm/s)
N = 13
N = 13
N = 13
N = 13
N = 11
N = 7
N = 3
A
0
10
20
30
40
50
60
70
80
● Holding Velocity
▲ Capture Velocity
Holding Velocity (cm/s)
Treatment Velocity (cm/s)
N = 15
N = 15
N = 15
N = 15
N = 15
N = 9
B

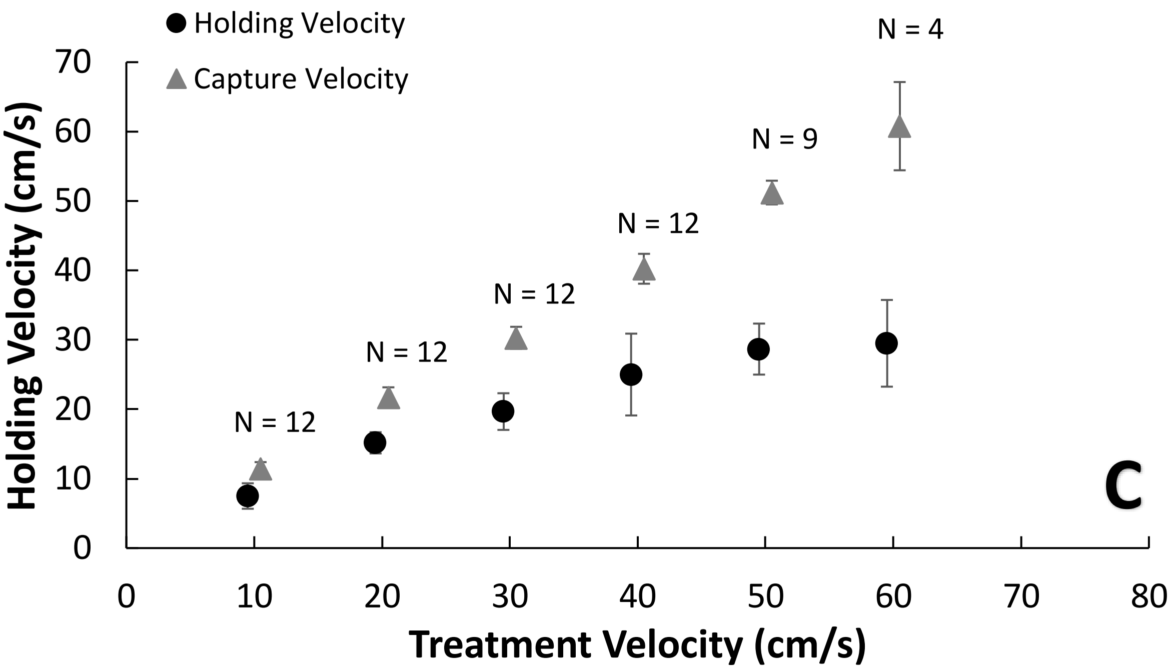
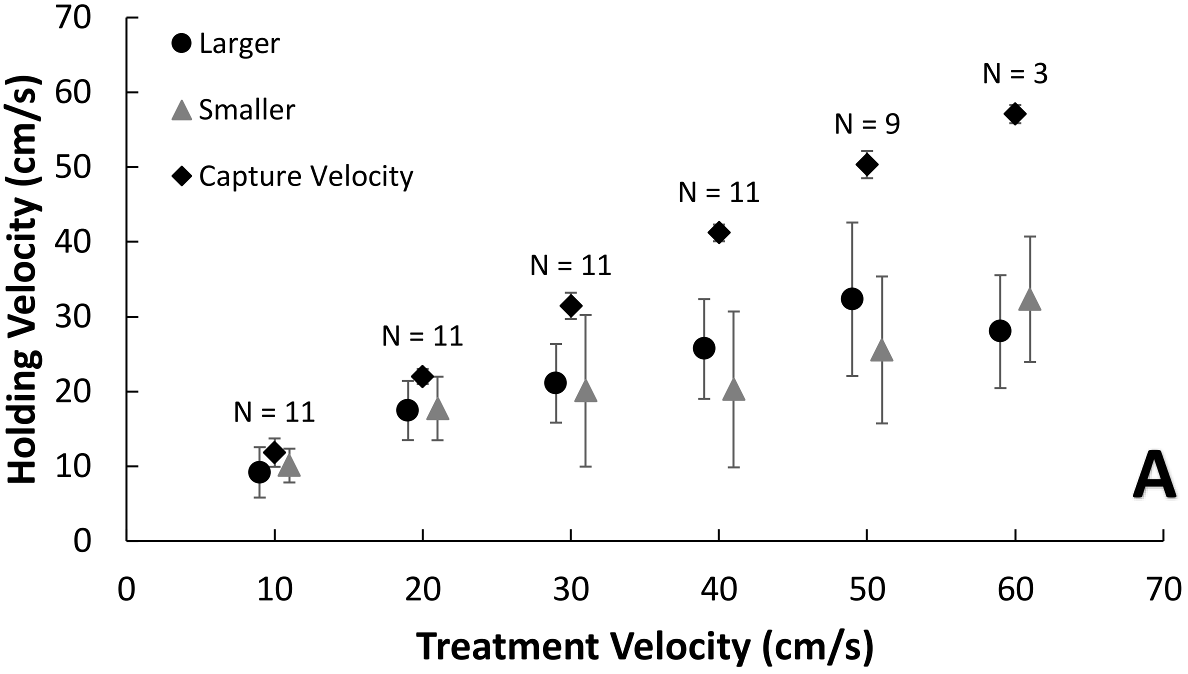

● Holding Velocity
▲ Capture Velocity
N = 12
N = 12
N = 12
N = 12
N = 9
N = 4
C
Holding Velocity (cm/s)
0
10
20
30
40
50
60
70
Treatment Velocity (cm/s)
0
10
20
30
40
50
60
70
80

Figure 2.5


Holding Velocity (cm/s)
Treatment Velocity (cm/s)
0
10
20
30
40
50
60
70
● Larger
▲ Smaller
◆ Capture Velocity
N = 11
N = 11
N = 11
N = 11
N = 9
N = 3
A

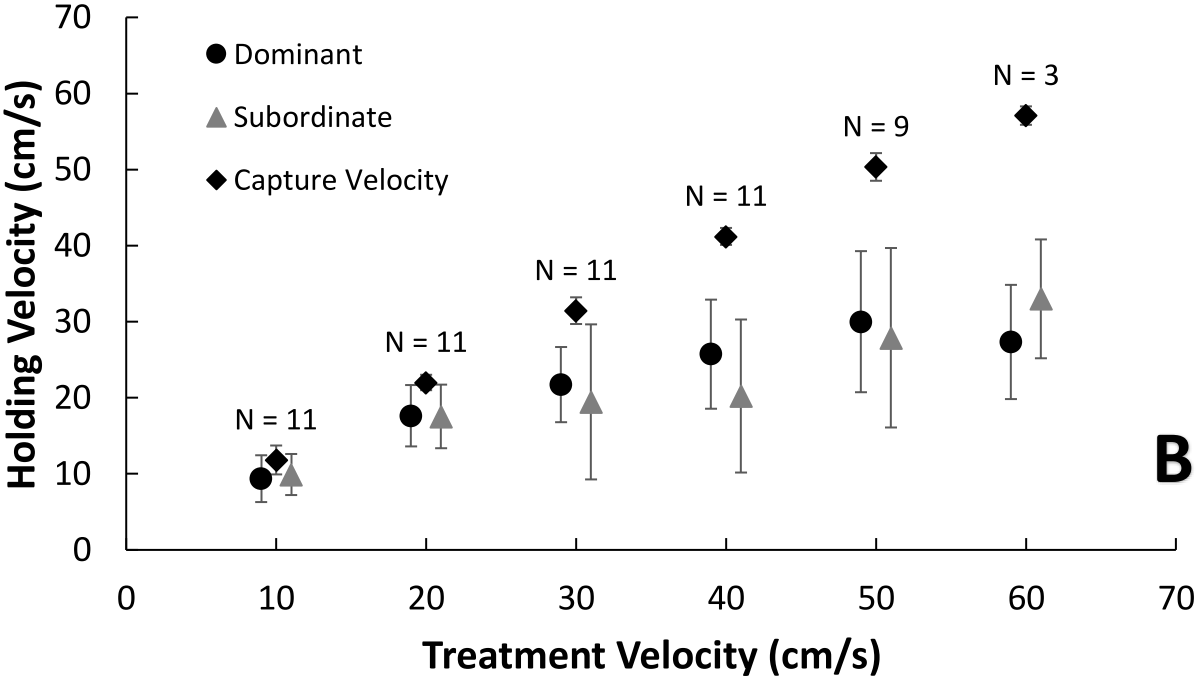
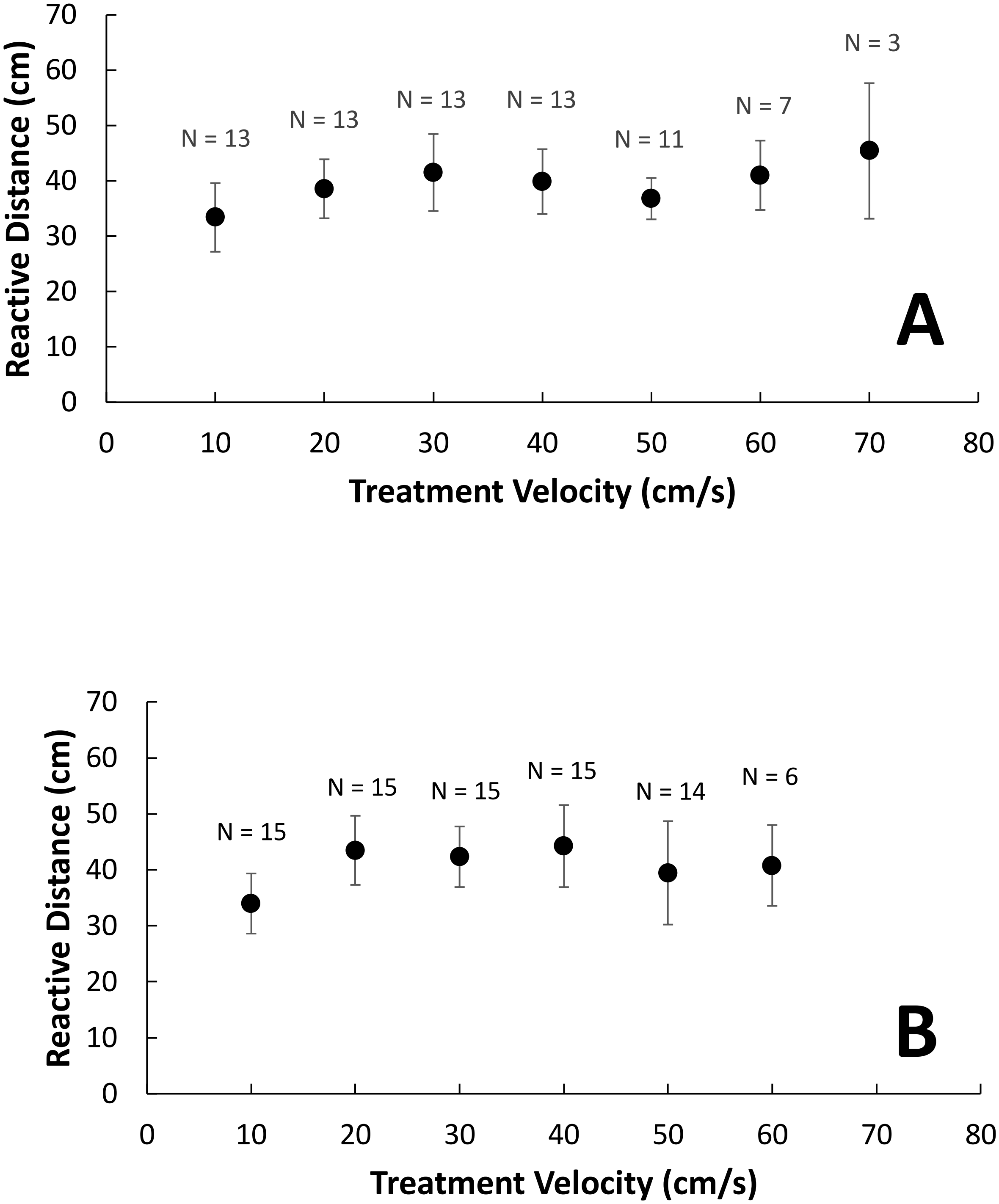

Holding Velocity (cm/s)
Treatment Velocity (cm/s)
0
10
20
30
40
50
60
70
● Dominant
▲ Subordinate
◆ Capture Velocity
N = 11
N = 11
N = 11
N = 11
N = 9
N = 3
B

Figure 2.6


70
60
50
40
30
20
10
0
Reactive Distance (cm)
N = 13
N = 13
N = 13
N = 13
N = 11
N = 7
N = 3
A
0
10
20
30
40
50
60
70
80
Treatment Velocity (cm/s)
70
60
50
40
30
20
10
0
Reactive Distance (cm)
N = 15
N = 15
N = 15
N = 15
N = 14
N = 6
B
0
10
20
30
40
50
60
70
80
Treatment Velocity (cm/s)

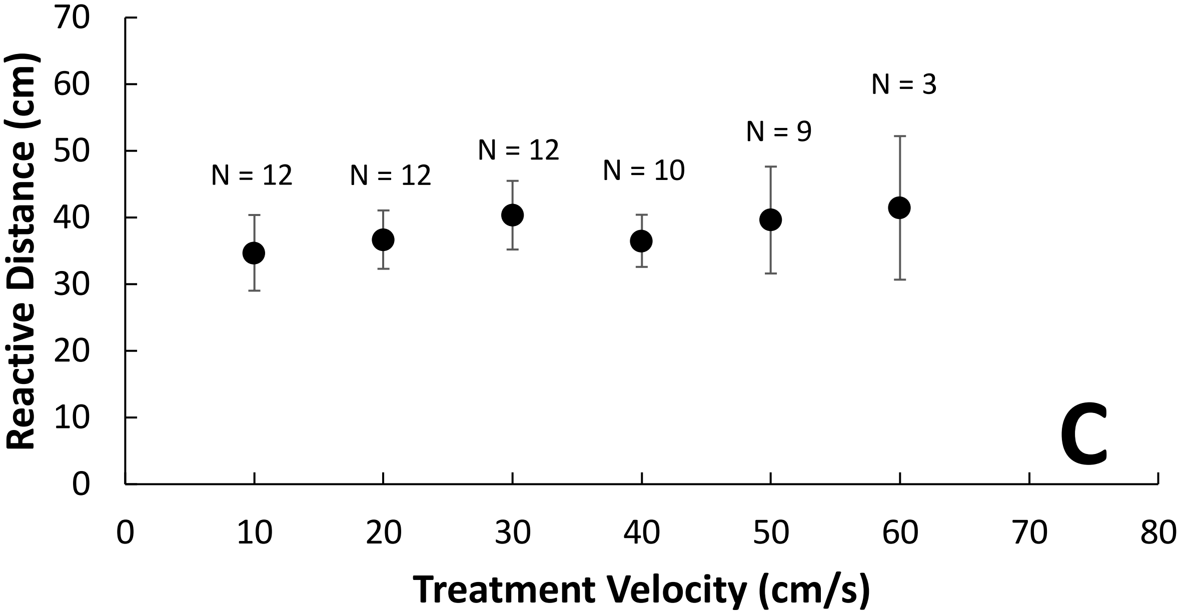

Reactive Distance (cm)
0
10
20
30
40
50
60
70
N = 12
N = 12
N = 12
N = 10
N = 9
N = 3
C
0
10
20
30
40
50
60
70
80
Treatment Velocity (cm/s)

Figure 2.7

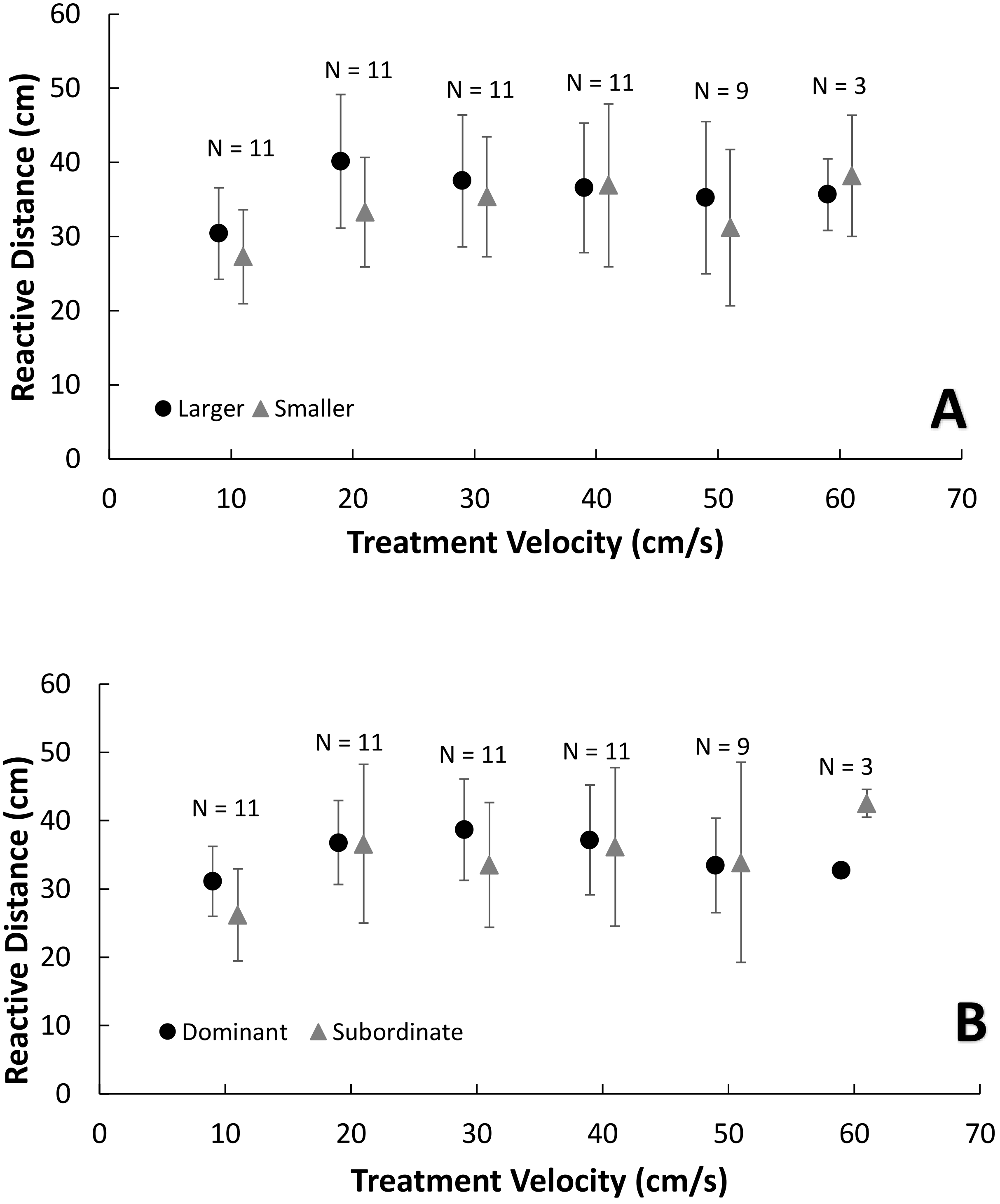
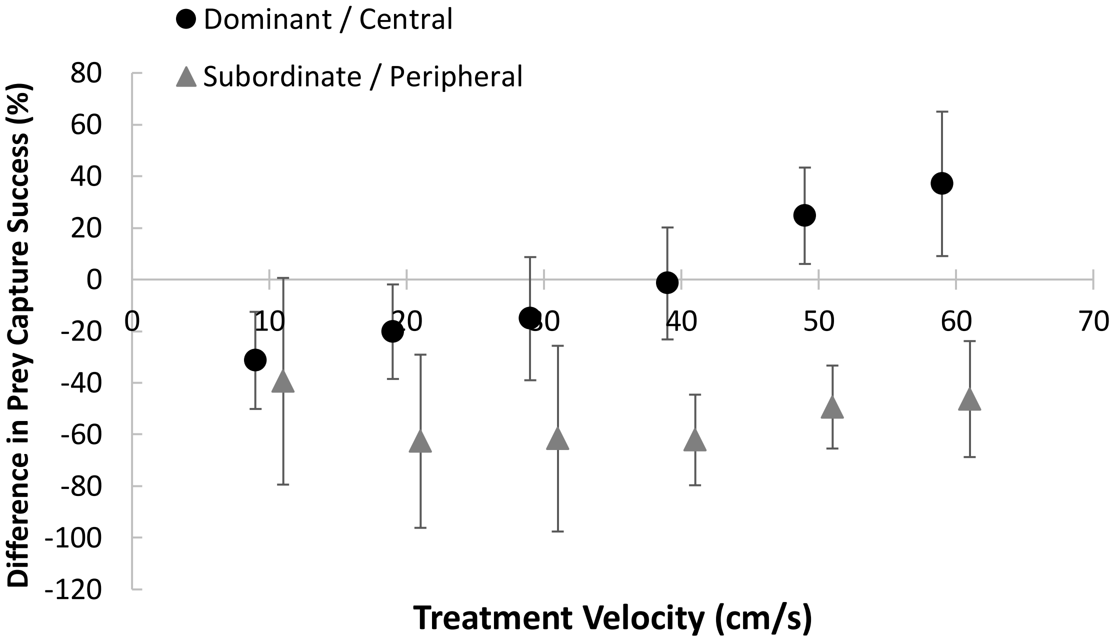

60
50
40
30
20
10
0
Reactive Distance (cm)
N = 11
N = 11
N = 11
N = 11
N = 9
N = 3
● Larger ▲ Smaller
A
0
10
20
30
40
50
60
70
Treatment Velocity (cm/s)
60
50
40
30
20
10
0
Reactive Distance (cm)
N = 11
N = 11
N = 11
N = 11
N = 9
N = 3
● Dominant ▲ Subordinate
B
0
10
20
30
40
50
60
70
Treatment Velocity (cm/s)

Figure 2.8


● Dominant / Central
▲ Subordinate / Peripheral
80
60
40
20
0
-20
-40
-60
-80
-100
-120
Difference in Prey Capture Success (%)
0
10
20
30
40
50
60
70
Treatment Velocity (cm/s)

REFERENCES

Abbott J.C., Dunbrack R.L. & Orr C.D. (1985) The interaction of size and experience in dominance relationships of juvenile Steelhead Trout (*Salmo gairdneri*). *Behavior,* **92,** 241-253.

Alaska Department of Fish and Game. (2013) Species profile: Arctic Grayling (*Thymallus arcticus*).

Alaska Department of Fish and Game. (2017) Sport Fishing Regulations.

Alt K.T. (1980) Inventory and cataloging of sport fish and sport fish waters of Western Alaska. *Alaska Department of Fish and Game,* **21**.

Anglin Z.W. & Grossman G.D. (2013) Microhabitat use by southern brook trout (Salvelinus fontinalis) in a headwater North Carolina stream. *Ecology of Freshwater Fish,* **22,** 567-577.

Armstrong R.H. (1986) A review of the Arctic Grayling studies in Alaska, 1952 - 1982. *Biol. Pap. Univ. Alaska,* **23**.

Artym K. (2016) Determining the habitat occupancy of young of the year Arctic Grayling (*Thymallus arcticus*) in sub-arctic tunda streams while accounting for imperfect detection.

Barrett J.C., Grossman G.D. & Rosenfeld J. (1992) Turbidity-induced changes in reactive distance of Rainbow Trout. *Transactions of the American Fisheries Society,* **121,** 437 - 443.

Barton K. (2016) Package ‘MuMIn’: Model selection and model averaging based on information criteria (AICc and alike).

Berners J. (1496) A treatyse of fysshynge wyth an angle. Boke of St. Albans, Westminister, UK.

Betts E.D. & Kane D.L. (2015) Linking North Slope of Alaska climate, hydrology, and fish migration. *Hydrology Research*, **46,** 578.

Brix K.V., Gerdes R., Curry N., Kasper A. & Grosell M. (2010) The effects of total dissolved solids on egg fertilization and water hardening in two salmonids--Arctic Grayling (Thymallus arcticus) and Dolly Varden (Salvelinus malma). *Aquat Toxicol*, **97,** 109-115.

Brown C.J.D. (1943) Age and growth of Montana Grayling. *The Journal of Wildlife Management*, **7,** 353 - 364.

Buhl K.J. & Hamilton S.J. (1991) Relative sensitivity of early life stages of Arctic Grayling, Coho Salmon, and Rainbow Trout to 9 inorganics. *Ecotoxicology and Environmental Safety*, **22,** 184-197.

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

Burnham K.P., Anderson D.R. & Huyvaert K.P. (2010) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology,* **65,** 23-35.

Buzby K.M. & Deegan L.A. (2000) Inter-annual fidelity to summer feeding sites in Arctic Grayling. *Environmental Biology of Fishes*, **59,** 319-327.

Carl L.M., Walty D. & Rimmer D.M. (1992) Deomgraphy of spawning Grayling (*Thymallus arcticus*) in the Beaverlodge River, Alberta. *Hydrobiologia*, **243/244,** 237-247.

Charnov E.L. (1976) Optimal Foraging, the Marginal Value Theorem. *Theoretical Population Biology,* **9,** 129-136.

Clark R.A. (1992) Age and Size Maturity of Arctic Grayling in Selected Waters of the Tanana Drainage. (Ed D.O.S.F. Alaska Department of Fish and Game). Fisheries Manuscript, Anchorage.

Clark R.A. (1992*a*) Influence of stream flows and stock size on recruitment of Arctic Grayling (*Thymallus arcticus*) in the Chena River, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences,* **49,** 1027-1034.

Clark R.A. (1992*b*) Age and size at maturity of Arctic Grayling in selected waters of the Tanana Drainage. *Alaska Department of Fish and Game, Div. Sport Fish. Man.,* **92**.

Clark R.A. & Ridder W.P. (1987) Abundance and length composition of selected Grayling stocks in the Tanana Drainage during 1986. *Alaska Department of Fish and Game, Division of Sport Fish,* **Fishery Data Series No. 26**.

Craig P.C. & Poulin V.A. (1975) Movements and growth of Arctic Grayling (Thymallus arcticus) and juvenile Arctic Char (Salvelinus alpinus) in a small arctic stream, Alaska. *Journal of the Fisheries Research Board of Canada,* **32,** 689-697.

De Bruyn M. & Mccart P. (1974) Life history of the Grayling (*Thmallus arcticus*) in Beaufort Sea Drainages in the Yukon Territory. *Biometrics,* **2,** 1 - 42.

Deegan L.A., Golden H.E., Harvey C.J. & Peterson B.J. (1999) Influence of environmental variability on the growth of age-0 and adult Arctic Grayling. *Transactions of the American Fisheries Society,* **128,** 1163-1175.

Deegan L.A., Peterson B.J., Golden H., Mcivor C.C. & Miller M.C. (1997) Effects of fish density and river fertilization on algal standing stocks, invertebrate communities, and fish production in an arctic river. *Canadian Journal of Fisheries and Aquatic Sciences,* **54,** 269-283.

Everest P.H. & Chapman D.W. (1972) Habitat selection and spatial interaction by juvenile Chinook salmon and Steelhead trout in two Idaho streams. *Journal Fisheries Research Board of Canada,* **29,** 91-100.

Falk M.R. & Gillman D.V. (1974) Impact of a sport fishery on Arctic Grayling in the Brabant Island area, Northwest Territories. *Can. Fish. and Mar. Serv. Tech. Rep. Series,* **no. CEN/T-74-7,** 21.

Fausch K.D. (1984) Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Canadian Journal of Zoology,* **62,** 441-451.

Fausch K.D. (2013) A historical perspective on drift foraging models for stream salmonids. *Environmental Biology of Fishes,* **97,** 453-464.

Fausch K.D. & White R.J. (1981) Competition between Brook Trout (*Salvelinus fontinalis*) and Brown Trout (*Salmo trutta*) for positions in a Michigan Stream. *Canadian Journal of Fisheries and Aquatic Sciences,* **38,** 1220 - 1227.

Frey P.J., Mueller E.W. & Berry E.C. (1970) The Chena River, the study of a subarctic stream. (Ed N.R. Federal Water Quality Administration, U.S. Dept. Of the Interior), p. 96. Alaska Water Laboratory, College, Alaska.

Gowan C. & Fausch K.D. (2002) Why do foraging stream salmonids move during summer? *Environmental Biology of Fishes,* **64,** 139-153.

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

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

Grossman G.D., Hill J. & Petty J.T. (1995) Observations on habitat structure, population regulation, and habitat use with respect to evolutionarily significant units: a landscape perspective for lotic systems. *American Fisheries Society Symposium*, **17,** 381 - 391.

Grossman G.D., Ratajczak R.E., Petty J.T., Hunter M.D., Peterson J.T. & Grenouillet G. (2006) Population dynamics of Mottled Sculpin (*Pices*) in a variable environment: information theoretic approaches. *Ecological Monographs*, **76,** 217 - 234.

Grossman G.D., Rincon P.A., Farr M.D. & Ratajczak R.E. (2002) A new optimal foraging model predicts habitat use by drift-feeding stream minnows. *Ecology of Freshwater Fish*, **11,** 2-10.

Grossman G.D., Sundin G. & Ratajczak R.E. (2016) Long-term persistence, density dependence and effects of climate change on Rosyside Dace (Cyprinidae). *Freshwater Biology,* **61,** 832-847.

Grueber C.E., Nakagawa S., Laws R.J. & Jamieson I.G. (2011) Multimodel inference in ecology and evolution: challenges and solutions. *J Evol Biol*, **24,** 699-711.

Hazelton P.D. & Grossman G.D. (2009) Turbidity, velocity and interspecific interactions affect foraging behaviour of rosyside dace (Clinostomus funduloides) and yellowfin shiners (Notropis lutippinis). *Ecology of Freshwater Fish,* **18,** 427-436.

Heino J., Virkkala R. & Toivonen H. (2009) Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biol Rev Camb Philos Soc*, **84,** 39-54.

Henley W.F., Patterson M.A., Neves R.J. & Lemly A.D. (2000) Effects of sedimentation and turbidity on lotic food webs: a concise review for natural resource managers. *Reviews in Fisheries Science,* **8,** 125 - 139.

Hill J. & Grossman G.D. (1993) An energetic model of microhabitat use for rainbow trout and rosyside dace. *Ecological Society of America,* **74,** 685-698.

Hobbie J.E., Peterson B.J., Bettez N., Deegan L., O'brien W.J., Kling G.W., Kipphut G.W., Bowden W.B. & Hershey A.E. (1999) Impact of global change on the biogeochemistry and ecology of an Arctic freshwater system. *Polar Research,* **18,** 207-214.

Holmes R. (1985) Population structure and dynamics of the Arctic grayling with emphasis on heavily fished stocked. *Alaska Department of Fish and Game, Division of Sport Fish,* **26**.

Hubbs C.L. & Lagler K.F. (1958) *Fishes of the Great Lakes region,* University of Michigan Press, Ann Arbor, Michigan.

Hubert W.A., Helzner R.S., Lee L.A. & Nelson P.C. (1985) Habitat suitability index models and instream flow suitability curves: Arctic Grayling riverine populations. *U.S. Fish Wildl. Serv. Biol. Rep.,* **82,** 34.

Hughes N.F. (1992*a*) Ranking of feeding positions by drift-feeding Arctic Grayling (*Thymallus arcticus*) in dominance hierarchies. *Canadian Journal of Fisheries and Aquatic Sciences,* **49,** 1994 - 1998.

Hughes N.F. (1992*b*) Selection of positions by drift-feeding salmonids in dominance hierarchies: model test for Arctic Grayling (*Thymallus arcticus*) in subarctic mountain streams, Interior Alaska. *Canadian Journal of Fisheries and Aquatic Sciences,* **49,** 1999 - 2008.

Hughes N.F. (1998) A model of habitat selection by drift-feeding stream salmonids at different scales. *Ecological Society of America,* **71,** 281-294.

Hughes N.F. (2000) Testing the abillity of habitat selection theory to predict interannual movement patterns of a drift-feeding salmonid. *Ecology of Freshwater Fish,* **9,** 4-8.

Hughes N.F. & Dill L.M. (1990) Position choice by drift-feeding salmonids: model and test for Arctic Grayling (*Thymallus arcticus*) in subarctic mountain streams, Interior Alaska. *Canadian Journal of Fisheries and Aquatic Sciences,* **47,** 2039 - 2048.

Hughes N.F. & Reynolds J.B. (1994) WHY DO ARCTIC GRAYLING (THYMALLUS-ARCTICUS) GET BIGGER AS YOU GO UPSTREAM. *Canadian Journal of Fisheries and Aquatic Sciences,* **51,** 2154-2163.

Huntingford F.A., Metcalfe N.B., Thorpe J.E., Graham W.D. & Adams C.E. (1990) Social dominance and body size in Atlantic Salmon parr, *Salmo salar* L. *J. Fish Biol.,* **36,** 877 - 881.

Immerzeel W.W., Pellicciotti F. & Bierkens M.F.P. (2013) Rising river flows throughout the twenty-first century in two Himalayan glacierized watersheds. *Nature Geoscience,* **6,** 742-745.

Isaak D.J., Wollrab S., Horan D. & Chandler G. (2011) Climate change effects on stream and river temperatures across the northwest U.S. from 1980–2009 and implications for salmonid fishes. *Climatic Change,* **113,** 499-524.

Jacobsen D., Milner A.M., Brown L.E. & Dangles O. (2012) Biodiversity under threat in glacier-fed river systems. *Nature Climate Change,* **2,** 361-364.

Jenkins T.M. (1969) Social structure, position choice and micro-distribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams. *Animal Behaviour Monographs,* **2,** 55-123.

Kalleberg H. (1958) Observations in a stream tank of territoriality and competition in juvenile salmon and trout (Salmo salar L. and S. trutta L.). *Institute of Freshwater Research Drottningholm Report,* **39,** 55-98.

Kaya C.M. (1990) Status report on fluvial Arctic Grayling. *Montana State Library*.

Kratt L.F. & Smith R.J.F. (1977) Post-hatching sub-gravel stage in life-history of Arctic Grayling (Thymallus arcticus). *Transactions of the American Fisheries Society,* **106,** 241-243.

Kratt L.F. & Smith R.J.F. (1979) Agonistic behavior of age 0, age 1 and non-breeding adult Arctic Grayling (Thymallus arcticus, Pallas). *Journal of Fish Biology,* **15,** 389-404.

Kruse T.E. (1959) Grayling of Grebe Lake, Yellowstone National Park, Wyoming. *Washington, U.S. Govt. Print. Off., Fishery bulletin of the Fish and Wildlife Service,* **59**.

Liknes G.A. (1981) The fluvial Arctic Grayling (*Thymallus arcticus*) of the upper Big Hole River drainage, Montana. *M.SC. thesis, Montana State Univ., Bozeman, Montana*.

Lohr S.C., Byorth P.A., Kaya C.M. & Dwyer W.P. (1996) High-temperature tolerances of fluvial Arctic Grayling and comparisons with summer river temperatures of the Big Hole River, Montana. *Transactions of the American Fisheries Society,* **125,** 933 - 939.

Lukacs P.M., Burnham K.P. & Anderson D.R. (2009) Model selection bias and Freedman's Paradox. *Annals of the Institute of Statistical Mathematics,* **62,** 117-125.

Magee J., Rens E. & Lamothe P. (2006) Fluvial Arctic Grayling monitoring report 2005: Big Hole River and reintroduction efforts. *Montana Department of Fish, Wildlife, and Parks*.

Mcphail J.D. & Lindsey C.C. (1970) Freshwater fishes of northwestern Canada and Alaska. *Fish. Res. Board Can. Bull.,* **173,** 381.

Mills M.J. (1981) Alaska statewide sport fish harvest studies. (Ed D.O.S.F. Alaska Department of Fish and Game, Federal Aid in Fish Restoration, Annual Performance Report 1980-1981), p. 107, Juneau, Alaska.

Morrow J.E. (1980) *The freshwater fishes of Alaska,* Alaska Northwest Publishing Company.

Nakano S. (1994) Variation in agonistic encounters in a dominance hierarchy of freely interacting red-spotted Masu Salmon (*Oncorhynchus masou isikawai*). *Ecology of Freshwater Fish,* **3,** 153-158.

Nelson P.H. (1953) Life history and management of the American Grayling (*Thymallus signifer tricolor*) in Montana. *Theses, Dissertations, Professional Papers.,* **Paper 6170**.

Newman M.A. (1956) Social behavior and interspecific competition in two trout species. *Physiological Zoology,* **29,** 64 - 81.

Northcote T.G. (1993) A review of management and enhancement options for the Arctic Grayling (*Thymallus arcticus*) with special reference to the Willison Reservoir Watershed in British Columbia. *British Columbia Ministry of Environment, Lands and Parks, Fisheries Management Report,* **101,** 69.

Obrien W.J. & Showalter J.J. (1993) Effects of current velocity and suspended debris on the drift feeding of Arctic Grayling. *Transactions of the American Fisheries Society,* **122,** 609-615.

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

Piccolo J.J., Hughes N.F. & Bryant M.D. (2008) Water velocity influences prey detection and capture by drift-feeding juvenile Coho Salmon (*Oncorhynchus kisutch*) and Steelhead

(*Oncorhynchus mykiss irideus*). *Canadian Journal of Fisheries and Aquatic Sciences,* **65,** 266 - 275.

Prowse T., Alfredsen K., Beltaos S., Bonsal B.R., Bowden W.B., Duguay C.R., Korhola A., Mcnamara J., Vincent W.F., Vuglinsky V., Walter Anthony K.M. & Weyhenmeyer G.A. (2012) Effects of Changes in Arctic Lake and River Ice. *Ambio,* **40,** 63-74.

Pyke G.H., Pulliam H.R. & Charnov E.L. (1977) Optimal Foraging: a selective review of theory and tests. *The Quarterly Review of Biology*, **52,** 137-154.

Redenbach Z. & Taylor E.B. (1999) Zoogeographical implications of variation in mitochondrial DNA of Arctic Grayling (*Thymallus arcticus*). *Molecular Ecology,* **8,** 23 - 35.

Reed R.J. (1964) Life history and migration patterns of Arctic Gryaling, *Thymallus arcticus* (Pallas), in the Tanana River drainage of Alaska. (Ed R.R. Alaska Department of Fish and Game), p. 30.

Reist J.D., Low G., Johnson J.D. & Mcdowell D. (2002) Range extension of Bull Trout, Salvelinus confluentus, to the Central Northwest Territories, with notes on identification and distribution of Dolly Varden, Salvelinus malma, in the Western Canadian Arctic. *Arctic Institute of North America,* **55,** 70-76.

Reist J.D., Wrona F.J., Prowse T.D., Power M., Dempson J.B., Beamish R.J., King J.K., Carmichael T.J. & Sawatzky C.D. (2006) General effects of climate change on Arctic fishes and fish populations. *Ambio,* **35,** 370 - 380.

Reynolds J.B., Simmons R.C. & Burkholder A.R. (1989) Effects of placer mining discharge on health and food of Arctic Grayling. *Water Resour. Bull. Am. Water Resour. Assoc.,* **25,** 625 - 635.

Ridder W.P. (2000) Characteristics of the spring population of Arctic Grayling in the Chena River in 1998 and 1999. *Alaska Department of Fish and Game, Fishery Data Series,* **00-39**.

Sawatzky C.D., Michalak D., Reist J.D., Carmichael T.J., Mandrak N.E. & Heuring L.G. (2007) Distributions of freshwater and anadromous fishes from the Mainland Northwest Territories, Canada. *Can. Manuscr. Rep. Fish. Aquat. Sci.,* **2793,** 255.

Schallock E.W. (1966) *Grayling life history related to a hydroelectric development on the Chatanika River in Interior Alaska.* M.Sc. thesis, University of Alaska, Fairbanks, AK.

Schmidt D. & Obrien W.J. (1982) Planktivorous feeding ecology of Arctic Grayling (Thymallus arcticus). *Canadian Journal of Fisheries and Aquatic Sciences,* **39,** 475-482.

Schoener T.W. (1971) Theory of Feeding Strategies. *Annual Review of Ecology and Systematics,* **2,** 369 - 404.

Scott W.B. & Crossman E.J. (1973) Freshwater Fishes of Canada. *Fisheries Research Board of Canada Bulletin,* **184,** 1-966.

Shah R.D.T., Sharma S., Haase P., Jähnig S.C. & Pauls S.U. (2015) The climate sensitive zone along an altitudinal gradient in central Himalayan rivers: a useful concept to monitor climate change impacts in mountain regions. *Climatic Change,* **132,** 265-278.

Simmons R.C. (1984) *Effects of placer mining sedimentation on Arctic Grayling in interior Alaska.* M.Sc. thesis, University of Alaska, Fairbanks, AK.

Sorg A., Bolch T., Stoffel M., Solomina O. & Beniston M. (2012) Climate change impacts on glaciers and runoff in Tien Shan (Central Asia). *Nature Climate Change,* **2,** 725-731.

Stamford M.D. & Taylor E.B. (2004) Phylogeographical lineages of Arctic Grayling (Thymallus arcticus) in North America: divergence, origins and affinities with Eurasian Thymallus. *Mol Ecol,* **13,** 1533-1549.

Stewart D.B., Mochnacz N., Reist J.D. & Carmichael T.J. (2007) Fish life history and habitat use in the Northwest Territories: Arctic Grayling (*Thymallus arcticus*). *Can. Manuscr. Rep. Fish. Aquat. Sci.,* **2797,** 64.

Stuart K.M. & Chislett G.R. (1979) Aspects of the life history of Arctic Grayling in the Sukunka drainage. *Prov. B.C., Fish. Br., Prince George, Internal Rep.***,** 111.

Tack S.L. (1971) Distribution, abundance and natural history of the Arctic Grayling in the Tanana River drainage. *Alaska Department of Fish and Game, Division of Sport Fish,* **12**.

Tack S.L. (1974) Distribution, abundance, and natural history of the Arctic Grayling in the Tanana River drainage. (Ed F.a.I.F.R. Alaska Department of Fish and Game, Annual Performance Report), Juneau, Alaska.

Tack S.L. (1980) Migrations and distributions of Arctic Grayling, *Thymallus arcticus* (Pallas), in Interior and Arctic Alaska. *Alaska Department of fish and Game, Sport Fish Division,* **21**.

Thornton E.J., Duda J.J. & Quinn T.P. (2017) Influence of species, size and relative abundance on the outcomes of competitive interactions between brook trout and juvenile coho salmon. *Ethology Ecology & Evolution,* **29,** 157-169.

U.S. Fish and Wildlife Service. (2012) Arctic Grayling. In: *Endangered Species*.

Urabe H., Nakajima M., Torao M. & Aoyama T. (2010) Evaluation of habitat quality for stream salmonids based on a bioenergetics model. *Transactions of the American Fisheries Society,* **139,** 1665-1676.

Vascotto G.L. (1970) Summer ecology and behavior of the Grayling of McManus Creek, Alaska. *M.Sc. thesis, Univ. Alaska, College, AK*.

Vincent R.E. (1962) *Biogeographical and ecological factors contributing to the decline of Arctic Grayling, Thymallus arcticus Pallas, in Michigan and Montana.* Ph.D. thesis, University of Michigan, Ann Arbor, Michigan.

Walker J. (2005) Status of the Arctic Grayling (*Thymallus arcticus*) in Alberta. *Alberta Sustainable Resource Development, Fish and Wildlife Division, and Alberta Conservation Association, Wildlife Status Report No. 57, Edmonton, AB***,** 41.

Warner G.W. (1955) Spawning habits of grayling in interior Alaska. *U.S. Fish Wildl. Serv., Quarterly Prog. Rep., Proj. F-1-R-5:10p*.

Wedekind C., Evanno G., Szekely T., Pompini M., Darbellay O. & Guthruf J. (2013) Persistent unequal sex ratio in a population of Grayling (Salmonidae) and possible role of temperature increase. *Conserv Biol,* **27,** 229-234.

West R.L., Smith M.W., Barber W.E., Reynolds J.B. & Hop H. (1992) Autumn migration and overwintering of Arctic Grayling in coastal streams of the Arctic National Wildlife Refuge, Alaska. *Transactions of the American Fisheries Society*, **121,** 709-715.

Williams J.E., Haak A.L., Fesenmyer K., Dauwalter D.C., Neville H.M., Barney M. & Mayfield M. (2015) State of the Trout. p. 77. Trout Unlimited, http://www.tu.org/stateofthetrout.

Wojcik F.J. (1955) Life history and management of the Grayling in interior Alaska. *M.sc. thesis, University of Alaska*.

Zamor R.M. & Grossman G.D. (2007) Turbidity affects foraging success of drift-feeding Rosyside Dace. *Transactions of the American Fisheries Society,* **136,** 167-176.