FISH & FILMS: MULTIDIMENSIONAL CONSERVATION OF FRESHWATER ECOSYSTEMS IN SOUTHERN APPALACHIA

by

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(Under the Direction of GARY D. GROSSMAN)

ABSTRACT

Streams and rivers in the Southern Appalachian Mountains support remarkably biodiverse ecosystems that are increasingly threatened by humans. Effective and durable freshwater conservation requires a comprehensive understanding of how fish and humans engage with streams. We conducted three studies to investigate the dynamics of human-stream-fish relationships in Southern Appalachia from multiple disciplinary perspectives and across multiple scales of time and space. First, we evaluated the validity of simplifying assumptions of a stream fish bioenergetics habitat selection model and compared performance of simplified and complex model variants to identify conservation applications. We found mixed support for the simplifying assumptions but observed that simplified models generally performed as well or better than complex models. Second, we used species distribution models to investigate the influence of geomorphology, climate, and land use on the distribution of Brook (*Salvelinus fontinalis*), Rainbow (*Oncorhynchus mykiss*), and Brown (*Salmo trutta*) Trout in Southern Appalachia. We found that slope and climate were important predictors of trout distribution in Southern Appalachia, that allopatric and sympatric populations of

Brook Trout were distributed along similar environmental gradients, and that trout distribution patterns were discernible at the stream-segment scale, but not the subwatershed scale. Third, we explored the potential for a conservation documentary film to generate support for conservation by showing the film to undergraduate students and measuring the relationship between shifts in conservation support and engagement with the film. We observed that a long and short conservation film increased conservation support among viewers, that film engagement was positively correlated with shifts in conservation support, and that these shifts persisted over time for viewers of the short film. Collectively, this body of work suggests that 1) refining our ability to quantify and model habitat characteristics of stream fish focal positions, 2) designing species-specific conservation strategies that prioritize habitat preservation at appropriate spatial scales, and 3) crafting compelling and engaging conservation narratives can help reconcile human use of the landscape with freshwater ecosystem integrity. Creative, integrative research programs that investigate multiple dimensions of fish-stream-human relationships can inform durable, pragmatic conservation approaches in a world where human activity continues to impact nature.

INDEX WORDS: Net energy intake, microhabitat selection, focal position, stream fish, science communication, transportation theory, narrative engagement, conservation support, species distribution models, trout distribution, land use, climate

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by

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DEDICATION

To my father, David Bozeman, who showed me the world and taught me to leave it better than I found it. May you live forever in the things you loved. Make it a great day.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Freshwater is perhaps the world's most precious and imperiled resource. It comprises just 2.5% of Earth's water, 0.3% of which is surface water in the form of rivers, lakes, and swamps (Garcia-Moreno et al., 2014; Mittermeier et al., 2011). Despite this relatively miniscule volumetric footprint, freshwater resources support an immense amount of biodiversity. Freshwater ecosystems are home to one-third of identified vertebrate species (Tickner et al., 2020), including approximately 10,000 fish species, an estimated 40% of global fish diversity (Dudgeon et al., 2006). Of surface waters, lotic rivers and streams are especially important reservoirs of freshwater species biodiversity due to their variety of physical, chemical, and biotic characteristics that provide critical habitat for many different species, and the longitudinal connections between these habitats (Meyer et al., 2007; Poff et al., 2001; Vannote et al., 1980).

Rivers and streams also provide myriad services to humans. We use them to supply water for municipal, household, and industrial needs, to irrigate cultivated crops, to generate hydroelectric power, and for transportation and recreation. We also interact with rivers and streams indirectly, and perhaps unwittingly, when they flow through landscapes that we have modified. Rivers are receivers; they are products of the watersheds they drain, and these products accumulate downstream (Allan, 2004; Dudgeon et al., 2006). Human activities in upland areas can influence stream quality by altering the quantity, quality, and timing of inputs to streams, or the pathways by which streams receive these inputs. Direct and indirect human influences on streams have compromised the integrity of the freshwater ecosystems they support through habitat degradation or fragmentation, introduction of exotic species, modification of flow regimes or stream channels, and increases in sedimentation, and nutrient and thermal pollution (Dudgeon et al., 2006; Paul & Meyer, 2001; Schlosser, 1991; Wang et al., 2001).

In the same way that rivers and streams support a disproportionate amount of freshwater biodiversity, so do they also bear a disproportionate amount of anthropogenic impairment. More than a quarter of described freshwater fish are listed as threatened or near threatened on the International Union for the Conservation of Nature's (IUCN) Red List (IUCN, 2021). There is evidence that freshwater biodiversity is deteriorating more rapidly than in marine or terrestrial systems (Turak et al., 2017). Despite thorough documentation of global threats to freshwater biodiversity, we have been slow to develop coordinated plans to reduce or reverse this decline (Tickner et al., 2020). The need for effective, durable, and equitable freshwater conservation has never been greater.

The above dynamics – remarkable freshwater biodiversity and concurrent stream degradation – are magnified in Southern Appalachia, which is a rugged, mountainous region encompassing portions of southwest Virginia, western North Carolina, eastern Tennessee, and northern Georgia and South Carolina. Streams and rivers in the Southern Appalachian Mountains support some of the highest rates of endemism and freshwater biodiversity in North America and the world (Collen et al., 2014; Jenkins et al., 2015). These streams and rivers form a fluvial network that flows through a patchwork landscape with federal and state publicly owned protected areas interspersed amongst small, privately owned parcels of land. The landscape is rapidly developing and is expected to continue to develop as the population grows in the coming years (Terando et al., 2014). This makes large-scale conservation challenging; many stakeholders with different objectives for their small part of the landscape mean that longitudinal, transboundary resources – such as streams – may pass through myriad types of landscapes, with concurrent climatic and landscape influences potentially accumulating downstream or within catchments. Therefore, it is critical that we understand direct and indirect human impacts on streams and identify opportunities to preserve the integrity of stream ecosystems in the face of ongoing and increasing change in this region.

Successful conservation strategies in the 21st century must embrace the inherent complexity of socioecological systems and consider system dynamics from multiple disciplinary, epistemological, or theoretical perspectives (Hart & Calhoun, 2010; Hirsch & Brosius, 2013; Newell et al., 2005). Integrative approaches to conservation that address a problem space from multiple directions are especially attractive in Southern Appalachia, where remarkable freshwater biodiversity intersects with complicated social-environmental dynamics (Burke et al., 2015; Panlasigui et al., 2018; Vercoe et al., 2014). Understanding how fish and humans perceive streams, which are an integral component of the Southern Appalachian landscape, can illuminate opportunities for successful, durable freshwater conservation by informing conservation strategies that account for both human-stream relationships and stream habitat quality, and thus characterize socioecological dynamics more comprehensively.

For the past five years, I have designed and conducted integrative research to investigate the dynamics of fish-stream-human relationships in Southern Appalachia from multiple disciplinary angles and across multiple scales of time and space. My first area of inquiry involved investigating how drift-feeding stream fish evaluate and select focal position habitats from a broad range of available options within temporally and spatially heterogeneous stream environments. This project provided critical insight into our ability to model and predict optimal habitats for stream fish, including which habitat variables are important for models and which models are useful for conservation initiatives. This project considered instantaneous fish-stream relationships within fine spatial scales (a few meters) from the disciplinary perspective of stream fish ecology.

My second area of inquiry involved investigating how geomorphology, land use, and climate influence the distribution of native Brook Trout (*Salvelinus fontinalis*) relative to nonnative Rainbow (*Oncorhynchus mykiss*) and Brown (*Salmo trutta*) Trout in Southern Appalachia. The goals of this study were to identify the landscape and climate context responsible for mediating longitudinal, differential distribution between native and nonnative trout and inform conservation strategies by identifying conditions suitable for the persistence of native trout in the face of nonnative invasion and continued land use modification and climate change. This project evaluated decade-long relative distribution patterns of ecologically, culturally, and economically valuable species on the basis of species-specific ecology and biology.

My third area of inquiry involved investigating the potential for a documentary film about freshwater biodiversity in Southern Appalachia to increase conservation support among viewers. Specifically, I explored whether watching a freshwater conservation film caused viewers to agree with pro-conservation beliefs expressed by the film or express interest in engaging in pro-conservation behaviors modeled by the film, and whether mental and emotional engagement with the film was related to shifts in conservation support. The goals of this project were to shed light on the potential for conservation films to be used as tools to generate conservation support amongst the public, identify mechanisms responsible for shifts in conservation support, and inform conservationists and communicators about how best to engage audiences on topics of conservation. This research approached freshwater biodiversity conservation from a regional perspective using theories and methodologies from the field of communication studies.

Given the remarkable biodiversity supported by freshwater resources in Southern Appalachia and the multifaceted and increasingly urgent threats to this biodiversity from direct and indirect anthropogenic influence, it is critical that we develop durable, equitable, and pragmatic conservation strategies that reconcile human use of the landscape with the ecological integrity of freshwater resources. The success of these conservation strategies will depend on 1) understanding how fish interact with habitat to maximize their fitness, 2) understanding the factors that predict or influence the quality and quantity of these habitats, and 3) understanding how people engage with conservation messages that attempt to persuade them to maintain or improve stream habitat quality for fish. In essence, what types of habitats do fish need to survive and reproduce, where do these habitats exist on the landscape, and how can we communicate fish habitat needs to stakeholders in Southern Appalachia? My three areas of inquiry collectively address this problem space more comprehensively than could any single disciplinary approach, and hopefully will enhance our ability to protect these systems and species in an uncertain future.

CHAPTER 2

THE USE OF NET ENERGY INTAKE MODELS TO PREDICT MICROHABITAT SELECTION BY DRIFT-FEEDING FISHES: ARE COMMON ASSUMPTIONS WARRANTED?[1]

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Abstract

Net energy intake (NEI) models are useful for quantifying mechanisms driving habitat selection in drift-feeding stream fishes; nonetheless, their complexity has limited their application in conservation. We evaluated the validity of assumptions and the performance of multiple variants of an exemplar NEI model for juvenile Chinook Salmon (*Oncorhynchus tshawytscha*), Dolly Varden Char (*Salvelinus malma*), and Arctic Grayling (*Thymallus arcticus*) in interior Alaska. We tested model assumptions that: 1) drift concentration, 2) fish visual reaction area, and 3) swimming cost do not vary meaningfully within the range of focal velocities occupied by drift-feeding stream fishes and can therefore be treated as constants or ignored. We compared the predictive success of complex and simplified model variants. Comparisons of literature and field data indicated model assumptions were: 1) plausible, 2) plausible, and 3) implausible, respectively. Simplified model variants generally performed as well or better than the complex model. Drift concentration, visual reaction field, and swimming cost are important components of drift-feeder habitat selection; however, the difficulty of accurately estimating these variables may currently limit the utility of complex NEI models. Simplified NEI models are pragmatic tools for addressing urgent conservation needs and can guide development of complex NEI models as estimation techniques improve.

Introduction

Rivers and streams are important habitats for many aquatic organisms, including the highly diverse fish assemblages of North America (Abell et al., 2008; Grossman et al., 1990; Poff et al., 2001). Many fishes in these lotic systems – including many if not most salmonids – feed on prey drifting downstream in the water column for all or a part of their lifetime and are known as drift-feeders (Quinn, 2018). Drift feeding is a distinct foraging strategy whereby: 1) individuals occupy a fixed focal position facing upstream, 2) pursue and intercept prey flowing downstream, and 3) return to their initial focal position after attack. The suite of physical and biological characteristics in the immediate vicinity (~ m^2) of a fish's focal position comprise its microhabitat (Grossman, 2014; Grossman & Freeman, 1987; Piccolo et al., 2014).

Given that streams are heterogeneous in space and time, the ability to discern and select favorable microhabitats from the mélange of available options within the broader habitat matrix has important implications for individual fitness (Hughes, 1992; LaPerriere, 1981; Vannote et al., 1980). Studies of the mechanisms affecting microhabitat choice of drift-feeders have long been of interest to ecologists, because of their relevance to community and behavioral ecology, habitat and population management, and conservation (Everest & Chapman, 1972; Grossman et al., 1998; Jenkins, 1969). Correlative habitat selection studies comparing abundance to physical and chemical habitat characteristics are common but are generally unable to identify specific characteristics that drive habitat use (Boyce & McDonald, 1999). Mechanistic models are a promising alternative to correlative studies because they quantify habitat characteristics relevant to a target species' physiology and behavior (e.g., energy balance) and, ultimately, fitness (Grossman, 2014; Naman et al., 2019; Rosenfeld et al., 2014).

Mechanistic net energy intake (NEI) models are useful tools that quantify the energetic benefits and costs associated with microhabitat use by drift-feeding stream fishes and then predict focal position selection or potential growth or abundance based on energy optimization criterion (Hayes et al., 2016; Hayes et al., 2007; Wall et al., 2015). By quantifying the energetic benefits and costs associated with a given focal position, NEI models can identify optimal focal positions where the difference between the energetic benefits and costs is the greatest (Figure 2.1). Drift-feeders are good candidates for mechanistic habitat use studies because they have been shown to preferentially select focal positions on the basis of energy optimization by occupying the stream position that affords the greatest energy intake that they can successfully defend in competitive hierarchies (Fausch, 1984; Hughes, 1998; Rosenfeld et al., 2014). Most NEI models assume drift-feeders maximize fitness by selecting focal positions that optimize energy intake (Fausch, 1984; Hill & Grossman, 1993; Hughes & Dill, 1990); however, newer models have begun incorporating elements of survival (e.g., predation risk) in addition to strict energy optimization (Railsback et al., 2021).

NEI model background

NEI models are grounded in optimal foraging theory, which connects habitat choice and foraging to fitness via energy optimization within the heterogeneous environmental matrix of a stream (MacArthur & Pianka, 1966; Pyke et al., 1977; Schoener, 1971). The many NEI models that have been developed and refined in the decades since Fausch's (1984) original model vary in predictive goals, information requirements, complexity, and realism (Piccolo et al., 2014; Rosenfeld et al., 2014). NEI models with different predictive goals have different input requirements and different sensitivities to potential biases of those inputs. Models that predict instantaneous microhabitat selection rank stream positions by their relative energetic potential (e.g., Grossman et al., 2002; Guensch et al., 2001). Therefore, slightly biased estimates of microhabitat energetic potential – via inaccurate estimates of input variables or structural errors in how the model estimates NEI – may still produce accurate predictions of optimal focal point velocities as long as the relative ranking of microhabitats is correct. Conversely, models that predict drift-feeder growth or abundance over entire stream reaches or fish lifespans (e.g., Hayes et al., 2007; Hayes et al., 2000; Wall et al., 2015) are dependent on accurate input variable estimates (e.g., drift abundance, swimming costs) to produce accurate estimates of absolute NEI. Therefore, NEI models that predict instantaneous microhabitat selection based on relative energetic potential may be more easily and appropriately simplified and generalized than NEI models which rely on more complete characterizations of absolute NEI to predict potential growth or carrying capacity at a given site.

NEI models also differ in terms of the variables they use to quantify energetic benefits and costs to predict habitat use. Variables associated with energetic gain include prey energy content, density of prey in the drift, and prey encounter and capture rates (e.g., Grossman et al., 2002; Jenkins & Keeley, 2010; Naman et al., 2019). Energetic cost variables include metabolic cost of swimming at focal positions, maneuvering costs for prey pursuit and capture, and prey processing costs, which often are estimated via equations from bioenergetic models for different species (Hayes et al., 2016; Hayes et al., 2000; Hughes & Kelly, 1996). Finally, NEI models with both instantaneous and long-term predictive goals frequently incorporate environmental and behavioral variables hypothesized to influence fish energetics, including velocity, depth at fish focal position, fish visual reaction area, foraging time, turbidity, presence of competitors, and amount of woody material (Harvey & Railsback, 2009; Kalb et al., 2018; Wall et al., 2017).

The variables included in a given NEI model are largely dependent upon the predictive goals of the model, the species or system it is to be applied to, and insights gained from previous modeling and parameter estimation efforts. Most contemporary NEI models are built on the shoulders of one or more foundational models (Piccolo et al., 2014). For instance, Dodrill et al. (2016) developed an NEI model based on a previous model adapted by Hayes et al. (2000) from one of the earliest NEI models (Hughes & Dill, 1990). The development of new NEI models is an incremental process incorporating more recent information, such as variable estimates or measurements that previously were held constant or neglected. For example, Hayes et al. (2016) incorporated the effects of velocity and turbidity on prey capture success, as well as prey pursuit costs across velocity gradients, which were not included in an earlier iteration of the model (Hayes et al., 2007). In general, mechanistic drift-foraging NEI models are better predictors of drift-feeder growth than correlative models and newer, more realistic NEI models ostensibly should be better predictors of drift-feeder habitat selection than their predecessors (Grossman, 2014; Naman et al., 2019). However, empirical comparisons of the performance of incrementally progressive NEI models are rare (Hughes & Dill, 1990; Jowett et al., 2021; Naman et al., 2019). Model parsimony generally is desirable, and more work is needed to assess how NEI models with differing amounts of complexity and biological realism perform in comparative studies with the same data.

In all modeling applications there is tension between ease of parameterization and use, and biological realism. Simplified NEI models contain few input variables and are relatively easy to parameterize and test. For instance, an NEI model that uses the relationship between prey capture success and velocity to predict optimal focal point velocity is easily parameterized via laboratory experiments that characterize this relationship (e.g., Hill & Grossman, 1993). However, the mechanistic insight and predictive value of these simplified models may be limited because they do not incorporate all variables that potentially influence focal position selection, such as the amount of available prey in the drift, metabolic costs of swimming and pursuing prey, or fish visual reaction area. This fact necessitates evaluation of simplified models under varying conditions and with varying species.

Conversely, complex NEI models incorporate a range of biological and physical variables to more accurately characterize biological reality. Because complex models may more closely approximate the actual habitat conditions and foraging processes that determine drift-feeder focal position selection, they potentially have greater ability to explain habitat use, growth or carrying capacity than simplified models. However, the predictive ability success of complex NEI models is dependent upon our ability to estimate input variables precisely and accurately. Each variable incorporated into a complex model has both a value and an error term; if variable error terms are large, models that incorporate greater realism may actually exhibit reduced ability to predict optimal focal velocities, growth, or reach-specific abundances. Furthermore, the high spatial and temporal heterogeneity of complex variables, such as macroinvertebrate drift dynamics, further complicates our ability to incorporate these processes in NEI models in useful ways (Brittain & Eikeland, 1988; Naman et al., 2016).

Species-specific data for some complex NEI model variables is limited, so researchers sometimes substitute data from different species to parameterize models. For example, Brett and Glass' (1973) swimming cost equations for Sockeye Salmon (*Oncorhynchus nerka*) and Rao's (1968) model of oxygen consumption of Rainbow Trout (*Oncorhynchus mykiss*) frequently are used to estimate some or all of the metabolic costs associated with drift-feeding for other salmonid species (e.g., Hayes et al., 2000; Hughes & Dill, 1990; Rosenfeld & Taylor, 2009) or are extrapolated beyond the range of temperatures, masses, and velocities to which the original models were fit. Species-borrowing is not inherently bad, but even closely related species can exhibit substantively different metabolic rates (Trudel & Welch, 2005). Therefore, the utility of complex NEI models that incorporate greater biological realism may be limited or negated by practical constraints associated with uncertainty regarding the quality and error of parameter estimates, or a lack of empirical data.

Simplified predictive models sometimes emerge when modelers, who set out to explain a natural phenomenon with as much biological realism as is practical, observe that one or a few model parameters exert disproportionate effects on model output, and condense the model to highlight those influential parameters. Hill and Grossman (1993) attempted to build a complex NEI model to explain focal position selection of Rainbow

Trout (*Oncorhynchus mykiss*) and Rosyside Dace (*Clinostomus funduloides*) as a function of standard and active metabolic rate (data from Facey & Grossman, 1990), food utilization efficiency, prey capture success, and prey abundance in a North Carolina stream. This model described focal position selection in terms of focal velocity, which is the velocity at the focal position as measured from the nose of the fish. They found, however, that prey capture success contributed disproportionately to the output of the complex model, and that the point at which prey capture success declined most rapidly with increasing velocity (i.e., the minima of the third derivative of the prey capture success-velocity function) was a better predictor of focal velocities occupied by these species in the stream than the complex model.

Consequently, Grossman et al. (2002) developed and field-tested a simplified NEI model for four cyprinid species based solely on the negative logistic relationship between focal velocity and prey capture success (Figure 2.2). The original, more complex version of their model included energy content of prey in the drift, fish visual reaction area, and swimming costs. However, many drift-feeding species in the study system (a 5th order stream in the Southern Appalachian Mountains) occupied focal positions within a relatively small range of low velocities (~5 - 20 cm/s; Facey & Grossman, 1992; Grossman & Freeman, 1987; Hill & Grossman, 1993), and previous work in the same system suggested there was little variation in energetic costs at these velocities (Facey & Grossman, 1990). This observation led to the removal of swimming costs, fish visual reaction area, and energy content of prey in the drift from the full model under the assumption that they varied minimally across the low and narrow range of velocities occupied by these drift-feeders, and could be considered constant (Facey & Grossman, 1990, 1992; Grossman et al., 2002).

The simplified Grossman et al. (2002) NEI model has been field tested on nine species in systems ranging from the Southeastern US to Alaska. The model has successfully predicted optimal habitat selection (via focal position velocity) for seven species, displayed marginal success for interior Dolly Varden Char, and failed to predict microhabitat selection by juvenile Chinook Salmon (Bozeman & Grossman, 2019a, 2019b; Donofrio et al., 2018; Grossman et al., 2002; Sliger & Grossman, 2021). Despite its success at predicting focal position velocities, the validity of the simplified Grossman et al. (2002) model assumptions has not been assessed, and the simplified version of the model has not been tested against the full, more complex version.

To our knowledge, there has not been a review, comparison, and field test of simplified and complex versions of an NEI model to assess potential differences in predictive abilities. The lack of understanding of the influence of complex variables on NEI model output – as well as the validity of simplifying assumptions – is a potential blind spot that hinders our ability to determine the utility and generality of these models. Consequently, we used full and simplified variants of the Grossman NEI models, empirical data, and data from the literature to evaluate the validity of model assumptions and compare predictive success of models with differing levels of complexity.

NEI model variants

Conceptually, the full NEI model explains focal position energetics for drift-feeders as a function of energy intake

(1) $$I_x = (E_x \times P_x) - S_x$$

Where *I* is net energy intake, *E* is prey encounter rate, *P* is the proportion of prey captured that enter the visual field of the fish, and *S* is swimming cost, all at microhabitat *x* (Grossman et al., 2002). Thus, net energy intake is a function of the number of prey that a fish encounters, pursues, and successfully captures at a specific focal position, minus the metabolic cost of maintaining that focal position.

Prey encounter rate, *E*, at a given microhabitat *x*, is expressed as

(2) $$E_x = D_x \times A_x \times V_x$$ (Hughes, 1998)

Where *D* is the abundance of prey in the drift converted to energy density (J/m^3), *A* is the visual reaction area of the fish (m^2), and *V* is velocity (m/s). The proportion of prey captured that enter the visual field of the fish (*P*) at a given microhabitat can be expressed as

(3) $$P_x = \frac{1}{(1 + e^{(b + cV_x)})}$$ (Hill & Grossman, 1993)

Where *b* and *c* are curve fitting constants as estimated by nonlinear least squares regression for the relationship between *P* and *V* at microhabitat *x*.

Therefore, given Equations 1, 2, and 3, net energy intake (*I*) at microhabitat *x* is mechanistically estimated via

(4) $$I_x = \left\{ (D_x \times A_x \times V_x) \times \left[\frac{1}{(1 + e^{(b + cV_x)})}\right]\right\} - S_x$$

Equation 4 is the full NEI model.

After simplifying the full NEI model based on the assumption that *D*, *A*, and *S* vary minimally across the range of drift-feeder focal velocities and thus can be dropped from the equation (Facey & Grossman, 1990, 1992; Grossman et al., 2002), we obtain

(5) $$I_x = V_x \times \left[\frac{1}{(1 + e^{(b + cV_x)})}\right]$$

which is solved iteratively to predict the velocity (*V*) at optimal microhabitat *x* (i.e., optimal focal velocity) where net energy intake (*I*) is maximized by a drift-feeder. Equation 5 is the simplified NEI model, which is dependent only on the relationship between prey capture success and velocity (Figure 2.2).

The velocity term in the simplified NEI model reflects the velocity at which the prey are traveling when captured (as driven by treatment velocities in the experimental stream flume). However, drift-feeding stream fish are known to occupy slower focal velocities and capture prey in nearby faster velocities (Hughes & Dill, 1990). Therefore, we used the experimentally-derived relationship between focal and foraging velocities to adjust the simplified NEI model output reflect observed differences in focal and foraging velocities; this is the adjusted NEI model (Sliger & Grossman, 2021). The third derivative of the negative logistic relationship between prey capture success and velocity (Figure 2.2) is the rate of increase of acceleration of prey capture success as velocity increases. We calculated the minima of the third derivative function – which is the maximum point of deceleration of the *P-V* curve – for each of our study species (Hill & Grossman, 1993). This is the third derivative NEI model.

Study objectives

We had two study objectives: 1) to assess the validity of the assumptions made by the simplified NEI model (Eq. 5) – that energy content of prey in the drift, fish visual reaction area, and swimming cost terms from the full model could be omitted; and 2) to compare the optimal focal velocity predictions of the full, simplified, adjusted, and third derivative NEI models. To satisfy these objectives, we used empirical field data and data from the literature to address the following questions: 1) Are energy content of prey in the drift, fish visual reaction area, and swimming cost correlated with focal position velocities occupied by juvenile Chinook Salmon (*Oncorhynchus tshawytscha*), Dolly Varden Char (*Salvelinus malma*), and Arctic Grayling (*Thymallus arcticus*) from interior Alaskan streams?, 2) What is the range of focal position velocities occupied by drift-feeding fishes as reported in the literature?, 3) Does the published literature reveal consistent correlations between commonly occupied focal velocities and energy content of prey in the drift, fish visual reaction area, and swimming cost?; and 4) What is the comparative performance of the original Grossman et al. (2002) full NEI model, simplified NEI model, adjusted NEI model, and third derivative model with respect to predicting optimal focal velocities?

Methods

We tested for correlations between energy content of prey in the drift (*D*), visual reaction area (*A*), and swimming cost (*S*) and focal velocities of juvenile Chinook Salmon, Dolly Varden Char, and Arctic Grayling using field observations and laboratory experiments. We also reviewed the primary literature to summarize the range of focal velocities commonly occupied by drift-feeders and the reported relationships between *D*, *A*, *S*, and stream velocity, within and beyond the range of common focal velocities. Finally, we used these data to evaluate the validity of simplified NEI model assumptions and parameterize and compare output of four NEI model variants.

Study species & systems

We studied populations of juvenile Chinook Salmon in the Chena River, Dolly Varden Char in Panguingue Creek, and Arctic Grayling in the Richardson Clearwater River in Alaska's Yukon River Drainage. Additional site and species information may be found in Donofrio et al. (2018), and Bozeman and Grossman (2019a, 2019b). These three species are ecologically, economically, and culturally important in interior Alaska. Chinook Salmon populations in the Chena River have been studied and monitored for several decades, and are in decline in some parts of the state (Barton, 1986; Schindler et al., 2013). Similarly, Arctic Grayling populations in the Richardson Clearwater River have been monitored for many years (Gryska, 2001; Ridder, 1988). Comparatively, little is known about the Dolly Varden Char population in Panguingue Creek or other interior populations of this species within its native range in the Pacific Northwest (Bozeman & Grossman, 2019b; Washington Department of Fish and Wildlife, 2000). Interior Dolly Varden Char are widely but patchily distributed throughout much of Alaska (Armstrong & Morrow, 1980). We chose these system-species combinations because they were representative of ideal habitats for the respective study species and had water clarity permitting extensive video observations.

Field observations

We conducted field observations during summer (June–August) of 2015 and 2016 in the Chena River (juvenile Chinook Salmon), Richardson Clearwater River (Arctic Grayling), and Panguingue Creek (Dolly Varden Char and Arctic Grayling). Mean standard length (± SD) of fish observed in the field for foraging behavior data collection was 4.7 cm (± 1.0) for juvenile Chinook Salmon (N = 24), 17.6 cm (± 2.8) for Dolly Varden Char (N = 32), and 42.4 cm (± 4.5) for Arctic Grayling (N = 29). Field data were obtained by identifying drift-feeding individuals via streamside observation, placing paired underwater video cameras near drift-feeding positions, and recording drift-feeding activity once fish had resumed normal foraging behavior, and then capturing videoed individuals via hook and line once videography data was collected for length and mass measurements and diet content analysis. Turbidity was low in study systems (visibility > 1m, see: https://www.youtube.com/watch?v=BJokgZrAi84&t=15s), and not dissimilar to conditions in the experimental flume (see: https://www.youtube.com/watch?v=RXcn1ew3KuM).

Energy density in the drift (D)

We estimated energy density in the drift (*D*, J/m^3) by placing fine mesh (100-micron, 47.7 x 29.2 cm opening, Chena River only), coarse mesh (243-micron, 49.5 x 29.5 cm opening), and ultra-coarse mesh (500 micron, 32 x 32 cm opening, 2016 Richardson Clearwater River only) drift nets in our study sites in habitat that contained drift-foraging fish. We measured velocity (m/s, electronic velocity meter) and water depth (straightedge, m) at net placement sites. We placed drift nets as close as possible (straight upstream or downstream) to drift-feeding fish without disturbing them (3 – 20 m away) for an average of 45 minutes (range: 10 – 186 minutes). After we removed drift nets from the stream, we split captured prey into 1mm size classes (1 – 10 mm) and estimated energy content based on prey identity and published length-mass regressions (e.g., Benke et al., 1999; Rogers et al., 1977; Sabo et al., 2002). We used the length and width of the net openings (m^2) along with water velocity measurements (m/s) at drift net placement positions to measure the volume of water filtered per sampling time. We estimated prey drift concentration (items/m^3) using the maximum observed value for either the fine or coarse net for each taxon to account for backwash bias (J. Neuswanger personal communication). Finally, we multiplied mean prey energy content (J) by prey drift concentration (items/m^3) for each size class and then summed across size classes to estimate energy content of prey in the drift (*D*, J/m^3) for use in analyses.

Visual reaction area of the fish (A)

We used videos of juvenile Chinook Salmon in the Chena River, Dolly Varden Char in Panguingue Creek, and Arctic Grayling in the Richardson Clearwater and VidSync 3D video analysis software to estimate several metrics of fish reaction distance (VidSync.org; Neuswanger et al., 2016). We reviewed field video footage for each of our study species and recorded the distance between a drift-foraging individual and a prey item when the fish first oriented toward the prey item to initiate a discrete foraging attempt. Reaction distance measurements were linear (cm) in three-dimensional space (i.e., straight line distance from fish snout to prey item in any direction). We used the 95th percentile of fish lateral reaction distance (i.e., cross-stream plane) as the radius to calculate a circular reaction area (cm^2) perpendicular to the direction of stream flow (Hughes & Dill, 1990) for use in our analysis. We truncated the circular reaction area when the radius was greater than the distance from fish focal position to the surface and/or stream bottom. Reaction distance values for each individual observed (juvenile Chinook Salmon N = 24, Dolly Varden Char N = 32, Arctic Grayling N = 29) were based on an average of 103 measurable foraging attempts (range: 46 – 180) per individual. Mean lengths (± SD) of prey items consumed during foraging attempts were 2.3 mm (± 0.4) for juvenile Chinook Salmon, 3.9 mm (± 0.6) for Dolly Varden Char, and 6.0 (± 0.9) for Arctic Grayling.

Swimming cost (S)

We estimated the total metabolic costs of drift feeding as the sum of standard metabolic rate, swimming activity at the focal position, and foraging maneuvers to capture prey. We estimated standard metabolic rate as a function of temperature and mass using models parameterized for species closely related to our study species; Baikal Grayling (*Thymallus baikalolenensis*; Hartman & Jensen, 2017) for Arctic Grayling, Bull Trout (*Salvelinus confluentus*; Mesa et al., 2013) for Dolly Varden Char, and an *Oncorhynchus* spp. model that is widely used for Chinook Salmon (Stewart & Ibarra, 1991; Stewart et al., 1983). We used a mass- and swimming speed-dependent equation from Trudel and Welch (2005) parameterized for Sockeye Salmon (Brett & Glass, 1973) to estimate swimming cost associated with holding a fixed focal position in the stream. Finally, we used a maneuver model (Neuswanger et al., 2022) to estimate the metabolic cost of maneuvering to capture prey in the drift and returning to the focal position. Accounting for standard metabolic rate, swimming cost, and foraging maneuvers likely is a more accurate characterization of metabolic costs incurred by drift-feeders than steady swimming costs alone (Hughes & Kelly, 1996).

Focal position velocity (V)

We quantified focal velocity using *in situ* stream velocity measurements at fish focal positions and field videos and VidSync. Focal velocity is the velocity at the nose of a drift-feeding stream fish. For juvenile Chinook Salmon in the Chena River, Dolly Varden Char in Panguingue Creek, and Arctic Grayling in the Richardson Clearwater, we estimated focal velocities by observing drift-feeding individuals via the cameras and releasing pre-soaked, neutrally buoyant Israeli couscous upstream of the individual. During video analysis, we used the cous-cous particles as velocity tracers and averaged the velocities of the six tracers nearest to the drift-feeding fish. For Arctic Grayling in

Panguingue Creek, we identified drift-feeding individuals (N = 25) in the camera viewfinders, observed each individual pursue and capture at least five prey items and return to the same fixed focal position between foraging attempts, and then measured focal position velocity with a Marsh McBirney Model 201 electronic flow meter.

To evaluate the assumption that energy content of prey in the drift (*D*), visual reaction area (*A*), and swimming cost (*S*) could be held constant across the range of velocities occupied by drift-feeders, we regressed values of *A* and *S* against focal velocities from each species-stream combination. Because *D* was sampled in locations that did not necessarily correspond to stream fish focal positions, we regressed values of *D* with velocities taken at drift-net placement positions, which were well within the range of focal velocities occupied by drift-feeders in the same stream. We used a t-test to test the null hypothesis that the slope of the regression line does not differ significantly from zero.

Laboratory experiments

We captured specimens for laboratory experiments from the same streams and in the same seasons as field observations and shipped them to the University of Georgia for prey capture success – velocity experiments (Fall 2014 – Fall 2016). Mean standard length (± SD) of fish used in laboratory experiments was 6.2 cm (± 1.1) for juvenile Chinook Salmon (N = 43), 16.5 cm (± 2.4) for Dolly Varden Char (N = 20), and 16.8 cm (± 3.0) for Arctic Grayling (N = 40). A full description of laboratory experiment protocol can be found in Donofrio et al. (2018) and Bozeman and Grossman (2019a, 2019b).

We fed individual subjects 9 prey (frozen bloodworms, 8.8 $\pm$1.4 mm) per specimen per velocity treatment (10 – 70 cm/s in 10 cm increments) in an experimental stream flume and recorded the proportion of those prey captured (prey capture success, *P*). We also measured the velocity at the focal position occupied by the subject during the trial to assess potential differences in treatment velocity in the stream flume (*V*) and focal velocity. Turbidity in the stream flume was negligible (Bozeman & Grossman, 2019b). We then used nonlinear least squares regression (package 'nlstools' in R; Baty et al., 2015) to estimate species-specific curve-fitting constants *b* and *c* to best describe the negative logistic relationship between prey capture success (*P*) and treatment velocity in the stream flume (*V*) (Figure 2.2; Eq. 3).

Literature review

We reviewed the published literature to quantify the patterns of focal velocities occupied by drift-feeders as well as patterns in relationships between *D*, *A*, and *S* and stream velocity. We searched Google Scholar and Web of Science for relevant papers using combinations of the terms "microhabitat," "stream fish," "habitat use," "stream velocity," "fish metabolism," "focal position," "reaction area," and "energy content of prey in the drift." We also identified relevant papers by checking the reference sections of published NEI studies and other articles identified in the review. In our review of focal velocities, we only included sources that reported focal velocities measured *in situ* directly at a drift-feeder's focal position following observations of active, undisturbed feeding. We did not include information from sources that reported average velocities at locations where fish were collected or embedded focal velocities within PCA or habitat suitability curves instead of reporting them directly.

Parameterizing and testing NEI model variants

We parameterized and tested: 1) the full NEI model that includes data for *D*, *A*, and *S* (Eq. 4), 2) the simplified NEI model (Eq. 5), 3) the adjusted NEI focal model, and 4) the third derivative NEI model. To parameterize and run the simplified NEI model, we used nonlinear least squares regression in R package "nlstools" (Baty et al., 2015) to estimate species-specific *b* and *c* values for the relationship between prey capture success and velocity (Eq. 3). We then solved Equation 5 iteratively to produce the optimal foraging velocity prediction of the simplified NEI model. Note that the simplified NEI model is based on the relationship between velocity and prey capture success as characterized in the experimental stream flume, where velocity refers to the speed prey were traveling at when captured. Therefore, the simplified NEI model predicts optimal foraging velocities, which may or may not be different from focal velocities, depending on the species and system. The simplified NEI model is the variant tested by Donofrio et al. (2018), and Bozeman and Grossman (2019a, 2019b).

Because drift-feeders are known to select focal positions at slower velocities and forage for prey in nearby faster velocities (Fausch, 1984; Fausch & White, 1981), we used the experimentally-derived relationship between foraging velocities (i.e., water velocity treatment levels in stream flume experiments) and focal velocities (generally less than foraging velocity, see Bozeman & Grossman, 2019a, 2019b) to predict the optimal focal velocity. We ran a simple linear model to characterize the relationship between focal and foraging velocities from our laboratory experiments and used model coefficients and the simplified NEI model prediction to obtain the optimal focal velocity prediction of the adjusted NEI model.

To test the third derivative model, we calculated the third derivative of our experimentally-derived prey capture success-velocity relationship and identified the minima of the resulting function – the maximum point of deceleration of the curve describing the negative logistic *P*-*V* relationship – as the optimal velocity predicted by the third derivative model. Finally, we used a combination of nonlinear least squares and simple linear regression to parameterize and solve the full NEI model (Eq. 4): we related model variables *D*, *A*, and *S* (*P* already is incorporated as a function of *V* with curve-fitting constants *b* and *c* estimated in parameterization of the simplified NEI model) to fish focal position velocity via regression and then identified the focal position velocity at which *I* was maximized.

The Grossman NEI model was developed in a system where predation and competition were not important drivers of microhabitat selection (Grossman et al., 1998), and drift-feeders were assumed to select focal positions solely based on NEI maximization (Grossman et al., 2002; Hill & Grossman, 1993). Accordingly, we tested NEI model variants by comparing model predictions with the velocities of focal positions occupied by fish in their respective study streams. If model predictions fell within the 95% confidence interval of field focal position velocities, we considered them successful. Predictions that fell outside of this interval were considered unsuccessful.

Statistical analyses

All statistical analyses were performed in R statistical software version 4.0.2 (R core team, 2020) and alpha for frequentist statistics was 0.05. Potential outliers in regression analyses were identified via a combination of Cook's Distance and studentized and standardized residuals (R package 'olsrr' version 0.5.3; Hebbali, 2020). We removed outliers with a Cook's Distance value greater than 4x the mean of Cook's Distance and an absolute studentized and standardized residual greater than two (Kutner et al., 2005). To limit data loss, we removed outliers identified during evaluation of the full data set, but not during subsequent evaluation of the data (i.e., new outliers were not identified after removal of outliers from the full data set). This outlier removal protocol resulted in the removal of no more than two data points in any species/system-variable combination.

Results

Literature review of drift-feeder focal velocities

Our search of the literature for focal velocity measurements for drift-feeders revealed 21 peer-reviewed articles containing 50 independent reports of focal velocity from 7113 individual records encompassing a wide range of age classes, seasons, geographic locations, and seasons (Table 2.1). Our literature review indicated that mean focal velocity for drift-feeding stream fish species was 16.5 cm/s ($\pm$ 8.5 SD) (Figure 2.3). More than 75% of stream fish held position at velocities below 20 cm/s, and more than 90% occupied microhabitats with velocities below 35 cm/s. The assumptions of the simplified NEI model state that *D*, *A*, and *S* can be considered constant across the range of focal velocities occupied by most stream fishes (Grossman et al., 2002). Consequently, we evaluate our NEI model assumptions in the context of this summary of common drift-feeder focal point velocities.

Energy content of prey in the drift (D)

Empirical analysis: energy content of prey in the drift (D)

There were no significant relationships between drift-net velocity and energy density of prey in the drift for any of the three systems observed (Figure 2.4, $p = 0.33$ (A), 0.96 (B), 0.10 (C), respectively). Linear models described only a small proportion of the variation of D ($R^2 < 0.15$). The relationship between drift-net velocity and energy density in the drift generally was negative for the Chena River and Richardson Clearwater; there was no relationship observed between these variables in Panguingue Creek. The three species occupied focal velocities over the lower range of drift-net velocities.

Literature review, energy content of prey in the drift (D)

Our literature review revealed a generally positive relationship between velocity and drift. Multiple studies have shown that various measures of drift abundance (e.g., concentration, rate, proportion) increase across velocities of 10 – 80 cm/s (Brittain & Eikeland, 1988; Ciborowski, 1983; Elliott, 1971; Gibbins et al., 2010; LaPerriere, 1983; Smith & Li, 1983; Townsend & Hildrew, 1976). This encompasses the range of focal velocities occupied by most drift-feeders (8.0 – 25.0 cm/s) and argues for inclusion of drift abundance metrics in microhabitat models.

However, the drift-velocity relationship is complex and mediated by several other factors. Macroinvertebrate drift mechanics are driven by a combination of hydraulics (i.e., passive drift) and behavior (i.e., active drift), the balance of which shifts as a function of environmental conditions and species-specific traits (Naman et al., 2016). Positive relationships between drift and flow observed between streams or habitat types (pools, riffles, runs) may disappear at smaller spatial and temporal scales (e.g., within a single habitat type in a single stream) relevant to drift-feeder ecology and habitat use (LaPerriere, 1983; Leung et al., 2009). Numerous studies have shown that in addition to velocity, drift processes are dependent upon many interacting factors including: season; time of day; macroinvertebrate species, body size and origin (terrestrial or aquatic); presence of predators; stream alkalinity; and substrate type (Brittain & Eikeland, 1988; Ciborowski, 1983; Everest & Chapman, 1972; Hoover & Richardson, 2010; Wankowski & Thorpe, 1979).

Drift-flow relationships vary based on which metrics of flow are considered; increases in drift concentration may be positively correlated with increasing velocity, a linear measurement, and concurrently negatively correlated with increasing discharge, a volumetric measurement, via dilution (LaPerriere, 1981; 1983). Heavy rainfall events that cause flows to increase at a given stream station may result in lower drift concentration per flow volume, but an overall increase in drift concentration export longitudinally downstream. Drift-feeding fishes upstream also may deplete drift concentrations immediately downstream (Hayes et al., 2007; Hughes, 1992). These relationships may shift at velocity extremes; at high velocities (> 40 cm/s) some macroinvertebrates may reduce drift rates and shelter in substrate and at low velocities

(< 10 cm/s) macroinvertebrates may increase drift rates to escape drying streams (Elliott, 1971; Hoover & Richardson, 2010). Finally, drift rates also may depend on previous flow conditions, with taxa responding differently to the same flow conditions based on whether flow is increasing or decreasing (Gunderson, 2000; Naman et al., 2016).

Constant drift versus velocity assumption

In summary, the relationship between metrics of drift and flow is complicated, but *D* and *V* generally appear to be positively correlated. The observed relationship depends on which metrics of drift (e.g., concentration, abundance, rate, etc.) are compared to which metrics of flow (e.g., discharge, filtered volume, velocity, etc.), in addition to other potentially correlated factors (e.g., season, time of day, macroinvertebrate species, alkalinity, drift-feeder depletion, etc.). Sampling techniques also may affect the observed relationship between drift and flow due to phenomena such as net clogging and backwash at high velocities.

Nonetheless, data from our study streams show no significant relationships between drift-net velocities and drift concentrations (Figure 2.4). Despite the nuance in previously reported drift-flow relationships, the consensus in the literature is that flow and drift concentration are positively related, even at the focal velocities of 8.0 – 25.0 cm/s occupied by most drift-feeders (Brittain & Eikeland, 1988). The discrepancy between our empirical observations and the literature may be due to the complexity and subtlety of the flow-drift relationship (e.g., mediating factors of season, daylight, species, substrate, dilution, habitat type, etc.), the fact that this relationship may become homogenized at small scales of time and space relevant to the drift-feeders in our study, or methodological issues such as net backwash or net clogging. Nonetheless, the assumption of constant *D* over the range of focal velocities occupied by drift-feeders is plausible for models predicting instantaneous microhabitat selection within many systems although in general it may be context-specific.

Fish visual reaction area (A)

<u>Empirical analysis: fish visual reaction area (A)</u>

There were no significant relationships between focal velocity and visual reaction area for any of our study species (Figure 2.5, $p = 0.06$ (A), 0.34 (B), and $p = 0.89$ (C), respectively). Linear models were poor fits to the data in each case (Figure 2.5, all R^2 values were < 0.16). Arctic Grayling reaction areas were nearly two orders of magnitude greater than those of juvenile Chinook Salmon and one order of magnitude greater than Dolly Varden Char reaction areas.

<u>Literature review, fish visual reaction area (A)</u>

Our literature review revealed few papers that directly measured the relationship between *A* and velocity or prey density, and the studies that measured these variables yielded mixed results. Most studies measured reaction distance, which is the straight-line distance between a drift-feeder’s nose and the prey item at the moment the fish initiates prey pursuit. Godin and Rangley (1989) observed decreases in reaction distance across velocities from 4 – 14 cm/s for juvenile Atlantic Salmon (*Salmo salar*); however, they also noted that fish oriented to prey items prior to pursuing them in faster velocities, concluding that fish minimized pursuit costs by delaying attack maneuvers at faster velocities. This implies that fish visual reaction distance remained high at fast velocities. Piccolo et al. (2008) reported declining prey detection distances across velocities ranging from 30 – 60 cm/s for juvenile Coho Salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss irideus*), which is faster than most drift-feeder focal velocities (Figure 2.3). O'Brien and Showalter (1993) likewise found that the prey search window decreased with increasing velocities for Arctic Grayling; however, this decrease primarily occurred at velocities greater than 32 cm/s and was offset by increased prey encounter rates at velocities up to 46 cm/s. O'Brien et al. (2001) found that increasing velocities from 25 – 40 cm/s (near the high end of typical focal velocities) resulted in decreased location distance and efficiency for Arctic Grayling, although feeding rate remained unchanged, which suggests a trade-off between increasing prey encounter rates and reaction area. It is possible that at faster velocities, drift-feeders alter foraging strategies and intercept prey predominately by moving laterally rather than hurriedly pursuing prey upstream before returning downstream to the focal position (Wankowski & Thorpe, 1979).

Early models conceptualized reaction distance as a positive function of prey size, fish size, turbidity, and light conditions (Hughes et al., 2003; Schmidt & Obrien, 1982; Sweka & Hartman, 2001), rather than velocity. Laboratory experiments that hold prey size, prey density, light, and turbidity constant have shown that reaction distance increases slightly from 10 – 70 cm/s or remains unchanged and is not strongly correlated with fish size (Bozeman & Grossman, 2019a; Donofrio et al., 2018; Sliger & Grossman, 2021). Holding prey density constant in experiments is important because prey encounter rate increases with velocity, which may confound a potential relationship between velocity and reaction distance (Fausch, 1984; Hughes & Dill, 1990). Are fish traveling shorter distances to capture prey because reaction area is decreased at higher velocities, or because more prey is available nearer the focal position?

Constant visual reaction area versus velocity assumption

Our field data displayed no significant relationships between focal velocity and visual reaction area for our study species, which parallels results of our past laboratory experiments (Bozeman & Grossman, 2019a, 2019b; Donofrio et al., 2018; Sliger & Grossman, 2021) as well as assumptions of original reaction distance models (Hughes & Dill, 1990; Hughes et al., 2003; Schmidt & Obrien, 1982). The relationships reported in the literature contradict these results but are confounded by correlations with other variables (i.e., declining reaction distances at velocities greater than those commonly occupied by drift-feeders or observations of fish noticing prey prior to initiating capture maneuvers). Functionally, accounting for visual fields of drift-feeders in NEI models explains – in conjunction with *D* and *V* – the amount of prey a drift-feeder encounters at its focal position, which is important for energy intake. Our data suggest visual field does not decrease with increasing velocity. The literature suggests that visual field decreases with velocity, but drift-feeders do not exhibit concurrent decreases in prey consumption. In both circumstances, *A* values have little effect on energy intake across focal velocities generally occupied by drift feeders. Therefore, we suggest that the assumption of constant *A* across the range of velocities occupied by drift-feeders is plausible for NEI models predicting microhabitat selection based on relative energetic potential between available focal positions.

Swimming cost (S)

Empirical analysis: swimming cost (S)

We observed a significant positive relationship between focal velocity (cm/s) and total swimming cost (J/s) for juvenile Chinook Salmon (Figure 2.6A, $p = 0.01$), Dolly Varden Char (Figure 2.6B, $p = 0.02$), and Arctic Grayling (Figure 2.6C, $p = 0.04$). Linear models fit the data poorly (R^2 values: 0.18 – 0.27); however, residual patterns did not suggest that nonlinear functions would be better descriptors. Average swimming cost increased by 500%, 240%, and 150% across the range of relatively low focal velocities occupied by juvenile Chinook Salmon, Dolly Varden Char, and Arctic Grayling, respectively (Figure 2.6). Note that total swimming costs increase from juvenile Chinook Salmon to Dolly Varden Char to Arctic Grayling such that swimming cost estimates differ by approximately one order of magnitude between species.

Literature Review, swimming cost (S)

Our literature review revealed that drift-feeder swimming costs generally are positively related to water velocity as well as fish mass and water temperature (Boisclair & Tang, 1993; Trudel & Welch, 2005; Ware, 1978). Drift-feeder swimming costs (as estimated via equations and constants derived from oxygen consumption studies; e.g., Brett & Glass, 1973) largely are exponentially related to velocity within and beyond the range of velocities occupied by drift-feeders (Feldmeth & Jenkins Jr., 1973; Lee et al., 2003; Rao, 1968), though for some species and seasons this relationship is linear (Facey & Grossman, 1990). Dickson and Kramer (1971) observed an asymptotic relationship between velocity and active metabolism for Rainbow Trout; however, this only occurred at velocities of 40 – 100 cm/s, which is greater than the range of velocities occupied by most drift-feeders (8.0 – 25.0 cm/s, Figure 2.3) including Rainbow Trout in other natural systems (Grossman & Freeman, 1987; Grossman & Ratajczak, 1998).

The relationship between velocity and swimming costs is mediated by many factors, including water temperature, fish mass, turbulence, and fish swimming activity (Enders et al., 2005; Jowett et al., 2021; Trudel & Welch, 2005). In cooler months, swimming costs may only increase linearly with velocity, or not at all (Facey & Grossman, 1990). The effects of temperature on metabolism are greatest at low velocities (i.e., < 30 cm/s where most drift-feeders are found), and temperature becomes less important relative to velocity as velocities approach critical swimming speeds (Brett & Glass, 1973). Models that estimate fish metabolism based on steady swimming at a fixed velocity within flumes with no turbulence and neglect the additional costs of foraging maneuvers and prey assimilation may dramatically underestimate actual metabolic costs incurred by drift-feeders in turbulent streams with considerable velocity heterogeneity (Facey & Grossman, 1990; Hughes & Kelly, 1996; Tang et al., 2000). Additionally, applications that estimate swimming costs by extrapolating models beyond the ranges of fish masses, velocities, and temperatures at which they were parameterized, or those that use parameters developed for different species, may be vulnerable to bias (Trudel & Welch, 2005).

Constant swimming cost versus velocity assumption

Our data (Figure 2.6) and the literature clearly indicate that there is a significant positive relationship between swimming costs and the range of velocities occupied by drift-feeding fish. The literature suggests this relationship generally is exponential (e.g., Lee et al., 2003). When pooled, our data show a positive exponential relationship between velocity and swimming cost, largely due to the considerable discrepancies in species-specific swimming cost estimates; however, this relationship is linear when separated by species. Drift-feeders often select focal velocities near the low (i.e., flat) end of the exponential relationship, yet may still experience potentially meaningful increases in swimming costs even at those focal velocities. Our data and the literature suggest that the assumption of constant *S* over the range of velocities occupied by drift-feeding stream fishes is not valid for NEI models predicting microhabitat selection.

NEI Model Variant Predictions

We compared model output for the four NEI models to quantify their comparative ability to predict the optimal focal velocities of juvenile Chinook Salmon, Dolly Varden Char, and Arctic Grayling in natural systems. We judged model performance by comparing predicted optimal velocities with the 95% confidence interval of velocities of focal positions occupied by drift-feeders in their respective study streams.

Model performance varied between species and model variant. The 95% confidence interval of focal velocities occupied by juvenile Chinook Salmon (N = 24) in the Chena River was 9.7 – 13.9 cm/s. All four models over-estimated optimal focal velocities of juvenile Chinook Salmon in the Chena River; the adjusted NEI model was the closest to field focal velocities (< 5 cm/s from the upper CI), with the other three models producing worse predictions (Table 2.2). The 95% confidence interval of focal velocities of Dolly Varden Char (N = 32) in Panguingue Creek was 25.1 – 29.2 cm/s. The adjusted NEI model and full NEI model each missed the 95% CI of Dolly Varden Char focal velocities in Panguingue Creek by less than one cm/s, which is well within the range of measurement error. In addition, a potential competitor (Arctic Grayling) was present in Panguingue Creek at the time of our study. The third derivative and simplified NEI models under- and overestimated optimal microhabitat, respectfully (Table 2.2). Finally, the 95% confidence interval for Arctic Grayling was 34.0 – 42.3 cm/s in the Richardson Clearwater (N = 29) and 20.8 – 27.2 cm/s in Panguingue Creek (N = 25). Three of the four model variants were successful for Arctic Grayling, albeit in different contexts. The simplified NEI model successfully predicted microhabitat selection of Arctic Grayling in the Richardson Clearwater, but not in Panguingue Creek, where a potential competitor (Dolly Varden Char) was present. Both the adjusted NEI model and the third derivative model successfully predicted microhabitat selection in Panguingue Creek, but not in the Richardson Clearwater (Table 2.2). The full NEI model prediction fell between the optimal focal velocities observed in Panguingue Creek and the Richardson Clearwater (Table 2.2), and thus was unsuccessful in both contexts.

Discussion

Investigations of the factors affecting habitat selection are essential for our understanding of how animals behave, which is a requirement for effective, science-based conservation and management. A key challenge for aquatic ecologists is identifying the fitness consequences of habitat selection. Mechanistic NEI models for drift-feeding stream fish are potentially useful tools for this task because they connect habitat use to fitness via energetics. Our evaluation of the assumptions of a simplified NEI model and comparison of complex and simplified models illuminates the mechanics of these models, highlights potential shortcomings associated with input variable estimation and parameterization, and provides important insight into how such models might be improved in the future.

Our empirical analysis demonstrated no relationships between velocity and energy content of prey in the drift or fish visual reaction area for any of our study species and a positive relationship between velocity and swimming cost for all of our study species. In conjunction with our review of the literature for each of these variables, we concluded that energy content of prey in the drift and fish visual reaction area could plausibly be considered constant within the range of drift-feeder focal position velocities, but swimming cost could not. When we parameterized and tested the four model variants, we found the adjusted NEI model was the best predictor of focal velocities occupied by the drift-feeders in this study; it was successful for Arctic Grayling in Panguingue Creek and was consistently closer to the 95% CI focal velocity window for Dolly Varden Char and juvenile Chinook Salmon than the other variants. These findings have important implications for how we theorize and estimate the various components of drift-feeder energetics and habitat use.

NEI model variable estimation: challenges & implications

Our data suggests the Grossman et al. (2002) simplifying assumption for energy content of prey in the drift (*D*) is plausible, because we observed no significant correlations between these *D* and *V* for any of our study species. However, it is possible we did not observe a significant relationship between these variables due to high natural variability in the drift process, biased sampling techniques, or some combination of these things. The lack of observed relationship between *D* and *V* in our empirical analysis stands in contrast to the majority of the published literature, which suggests a positive relationship between velocity and metrics of drift (see Brittain & Eikeland, 1988 for a review). Drift at any focal velocity is a complex function of lateral and vertical hydrodynamics, entry point (i.e., benthos, drift from upstream, or terrestrial sources), settling rate, abundance, and depletion by drift-feeders upstream. Drift processes also are influenced by macroinvertebrate species-specific traits, whereby macroinvertebrates actively enter or exit the drift based on abundance, season, time of day, and velocity (Nakano & Murakami, 2001; Naman et al., 2016; Stark et al., 2002). The amount of energy in the drift available to drift-feeders is a complex function of the interaction between the abiotic dynamics of the stream and the ecological and biological characteristics of the invertebrate species themselves; any estimate of that amount is dependent on the time, place, and techniques used to sample this phenomenon.

There are a few potential biases which may have affected our estimates of energy concentration of prey in the drift. Sampling drift concentrations 3 – 20m away from drift-feeders may not be reflective of drift concentrations encountered by drift-feeders at their focal positions given that drift can be highly spatially heterogeneous

(Brittain & Eikeland, 1988). Backwash due to net clogging and drift-net placement in the water column (the typical method of sampling macroinvertebrate drift) may underestimate drift concentrations, especially in fast velocities, which could potentially explain the negative trends observed in our data. However, removing the five fastest velocity data points from our velocity-drift concentration analyses did not change the observed relationship between drift and velocity in any of the three study systems. In addition, it possible that we did not observe a relationship between drift and velocity, because the velocity at drift-net positions potentially did not reflect flow conditions upstream that produced drift conditions.

Our field data showed no significant relationships between fish reaction area (*A*) and focal velocity, which matches results from laboratory experiments on these same species (Bozeman & Grossman, 2019a, 2019b; Donofrio et al., 2018). These results stand in contrast to the negative relationships between metrics of reaction field and velocity frequently reported in the literature. One possible explanation of these differences is that our method of recording reaction distance (for both laboratory experiments and field videos), which was the basis of our reaction area estimates, may not accurately capture the visual field of drift-feeding fish. We measure reaction distance between a drift-feeder and a prey item at the moment the drift-feeder initiates movement towards the prey. However, it is possible that drift-feeders visually observe prey prior to orienting towards it, thus decoupling the moment of prey recognition from the initiation of prey pursuit (Godin & Rangeley, 1989). This phenomenon would bias our reaction area estimates such that they underestimate the true size of the visual window within which drift-feeders are foraging for prey items.

It is unclear how true visual reaction areas could be detected and measured because of the difficulties associated with discerning when a fish sees a prey item versus when it initiates pursuit of that prey item. Feeding in faster currents may necessitate that drift-feeders initiate foraging maneuvers earlier than they would in slower currents despite visually observing prey items at similar distances from their focal position. Published reports of decreased reaction distances for drift-feeders with increasing velocity either reported this relationship at velocities greater than most drift-feeders occupy (O'Brien & Showalter, 1993; Piccolo et al., 2008) or observed constant or increasing prey encounter rates (O'Brien et al., 2001). Additionally, drift-feeders must discriminate between similarly sized prey items and inedible debris, the latter of which can vastly outnumber consumable prey especially for small-bodied drift-feeders (Neuswanger et al., 2014). The presence of potential competitors also may influence reaction distance, whereby drift-feeders are more likely to pursue prey on sight rather than let it drift closer and risk losing it to competition. Collectively, these dynamics make it difficult to know whether fish travel shorter distances to capture prey due to decreased prey recognition ability, large quantities of inedible debris, or increased prey availability nearer their focal position.

Original reaction distance models conceptualized reaction distance as a function of fish size, prey size, and light conditions (Hughes & Dill, 1990; Hughes et al., 2003; Schmidt & Obrien, 1982). Fish size was not significantly correlated with reaction distance in past laboratory experiments (Bozeman & Grossman, 2019a, 2019b; Donofrio et al., 2018) despite a wide range of experimental specimen lengths (4 – 27 cm) including many fish within the range of sizes at which are hypothesized to influence reaction distance (< 19 cm; Hughes & Dill, 1990). Light intensity may influence reaction distance (Hansen et al., 2013; Mazur & Beauchamp, 2003), but it is unlikely that light conditions affected our reaction distance measurements, because laboratory measurements were conducted in a well-lit facility, and field observations were conducted during the Alaskan summer (> 16 hours in a day of daylight). Turbidity has been shown to be positively associated with stream velocity and negatively associated with fish reaction distance and foraging success (Hansen et al., 2013; Sweka & Hartman, 2001; Vogel & Beauchamp, 1999), but was negligible in our laboratory experiments (stream flume < 0.001 NTUs) and low in our field observations (visibility greater than 1m). We are hopeful that advances in underwater videography (e.g., VidSync) will continue to improve our understanding of three-dimensional fish foraging areas – including how fish visual field shifts in response to fish and prey size, light, turbidity, and presence of competitors – to address shortcomings of early foraging models (Dunbrack & Dill, 1984; Neuswanger et al., 2016).

Unsurprisingly, swimming costs were positively related to focal velocities for all three species; a trend also observed in our literature review (e.g., Feldmeth & Jenkins Jr., 1973; Rao, 1968). Nonetheless, several studies have shown that the incorporation of swimming costs in NEI models – a parameter that is logistically difficult to quantify and highly variable – does not necessarily improve the predictive ability of NEI models (Hill & Grossman, 1993; Hughes & Dill, 1990). Indeed, the full NEI model did not outperform the more simplified model variants despite being the only model containing this information. It is possible that drift-feeders occupy focal positions where energetic benefits overwhelm even considerable energetic costs, which would explain why costs did not improve the predictive ability of our full NEI model that ranks focal position based on relative energetic potential. However, this does not mean costs associated with swimming and foraging are unimportant for drift-feeder energetics modeling, because NEI models that calculate absolute NEI require accurate estimates of swimming cost even when costs are small relative to benefits.

The relative importance of energetic benefits (e.g., prey capture success) and costs in determining focal velocity selection via NEI is dependent on fish size. Jowett et al. (2021) found that swimming cost was more important for predicting optimal velocities of large fish (> 96g, 20 cm) than prey capture success, but that prey capture success was more important than costs for small fish optimal velocity predictions. It is widely known that fish metabolism is dependent on mass, especially for small fish (Rosenfeld & Taylor, 2009; Trudel & Welch, 2005). Finally, most NEI models that include energetic costs – including our full NEI model – estimate this variable using equations that were parameterized for different species using swimming trials in laminar flow swimming chambers (e.g., Trudel & Welch, 2005), or extrapolate the models beyond the ranges of fish sizes, temperatures, or velocities for which they were parameterized. This may or may not be appropriate depending on the modeled species and the severity of the extrapolation.

Ideally, we would like to be able to quantify and include each element of swimming metabolism potentially affecting and affected by focal position choice by drift feeders. However, the complexity and logistical difficulties of accurately and precisely measuring multi-faceted metabolic costs (e.g., standard metabolism, active metabolism, anaerobic foraging burst maneuvers, digestive costs, etc.) may limit their utility to NEI models, at least those which rank focal positions based on relative NEI. Previous studies demonstrated that estimates of swimming cost that do not incorporate the effects of turbulence or the energetic demands of burst foraging maneuvers may considerably underestimate the full energetic costs of drift-feeding in streams (Enders et al., 2003; Hughes & Kelly, 1996; Tang et al., 2000). Therefore, although foraging maneuvers certainly inflate swimming costs it remains to be seen whether the inclusion of the complete energetic costs associated with drift-feeding can be incorporated in NEI models with sufficient precision to increase their predictive ability (see Facey & Grossman, 1990, 1992). Clearly, more work is needed to reliably and precisely estimate swimming costs and incorporate them into NEI habitat selection models, and our results illustrate the difficulty of including accurate energetic cost data in these models.

Prey capture success is the most important determinant of output of the NEI models tested in this study. Prey capture success was the only model input variable derived from laboratory experiments, and as such, likely is the most precise variable included in the models. Nonetheless, there are several potential biases associated with our protocol for estimating prey capture success that could influence the output of each of our NEI model variants.

The experimental stream flume we used to measure prey capture success differed from natural stream environments in serval important ways. The stream flume received consistent lighting during all experiments, and contained very little visual complexity, outside of a small clump of bamboo placed at the upstream end of the flume to facilitate fish orientation. We regularly cleaned the stream flume to minimize debris and turbidity, and only presented prey items to fish one at a time. Each of these departures from the natural stream environment were necessary to facilitate laboratory experiments (whose scope extended beyond simple prey capture success measurements) and keep fish healthy; however, these simplifications of the stream environment potentially result in prey capture success being overestimated at a given velocity. Clearly, this would have serious implications for model output given the importance of the prey capture success-velocity function to the formulation of the NEI models. However, this bias has not apparently been reflected in the past success of our simplified and adjusted NEI models (Bozeman & Grossman, 2019a, 2019b; Donofrio et al., 2018; Grossman et al., 2002; Sliger & Grossman, 2021). Future experiments focusing purely on prey capture success (and not other processes that require flume water clarity or bright lighting, e.g., video recording for reaction distance) under more natural conditions of turbidity, turbulence, prey-like inedible debris, and variable lighting conditions may more appropriately characterize prey capture success of drift-feeders in natural systems and improve foraging models.

Implications of simplified versus complex NEI model success

The predictive ability of the four variants of the Grossman NEI model varied among species and systems. Overall, the adjusted NEI model outperformed the other model variants by successfully predicting Arctic Grayling optimal focal velocities in Panguingue Creek, underestimating Dolly Varden Char optimal focal velocities in Panguingue Creek by less than 1 cm/s, and being the closest of the variants to the 95% confidence interval of juvenile Chinook Salmon focal velocities in the Chena River (< 5 cm/s away). There was no clear-cut second-best model, with the simplified, full, and third derivative model variants performing differentially for different species. This observation indicates parameter estimates for *D*, *A*, and *S* did not increase the predictive ability of the full NEI model in our study.

Except for juvenile Chinook Salmon, which likely are selecting habitat for reasons other than energy optimization (e.g., predator avoidance via strong association with shelter), our NEI models performed reasonably well and were able to yield insights into the process of microhabitat focal velocity selection. The performance of the models for Dolly Varden Char and Arctic Grayling was impressive given that model predictions fell within ~10 cm/s of the 95% CI of field focal velocities for these species in the Richardson Clearwater and Panguingue Creek despite water column velocities in our study sites ranging from negligible to at least 120 cm/s. These insights are important because many NEI models have been developed in the 40 years since their inception (Fausch, 1984; Piccolo et al., 2014), but few if any studies have directly assessed the predictive ability of various forms of an NEI model, and the majority of NEI models have not undergone rigorous testing with multiple species and in multiple years and seasons.

Given that the Grossman et al. (2002) NEI model was developed for systems in which interspecific competition and predation were not strong driving factors affecting microhabitat selection (Grossman et al., 1998), it is not surprising that the model and its variants performed poorly for juvenile Chinook Salmon in the Chena River (Donofrio et al., 2018). Juvenile Chinook Salmon in the Chena River typically were observed in shallow areas near or underneath shelter (e.g., within root balls of fallen trees), which suggests that the proximity to shelter from predators may be an important component of microhabitat selection (Quinn, 2018). This habitat preference is evidenced by lower focal velocities and swimming costs (by one and two orders of magnitude) for Chinook Salmon compared to Dolly Varden Char and Arctic Grayling, respectively. However, this observation is unsurprising, because juvenile Chinook Salmon in this study were very small (4.7 $\pm$ 1.0 SD SL), and focal velocity typically increases with length (Everest & Chapman, 1972; Grossman & Ratajczak, 1998). Larger individuals often select microhabitats nearer the center of the channel with greater focal velocities and are not as vulnerable to potential predators (Bozeman & Grossman, 2019a; Hughes, 1998; Hughes & Reynolds, 1994).

One interesting aspect of model variant performance is that the simplified NEI model successfully predicted optimal microhabitats of Arctic Grayling in the Richardson Clearwater, whereas the adjusted NEI model (and the third derivative NEI model) successfully predicted Arctic Grayling optimal microhabitats in Panguingue Creek. We observed that these systems differ markedly in depth, velocity heterogeneity, habitat complexity and the presence of a potential competitor (Dolly Varden Char). It is important to consider the possibility that model variants may perform differentially based on the systems in which they are applied. For instance, it is well known that drift-feeders may occupy slightly slower focal velocities adjacent to higher velocity microhabitats in which they forage for drifting prey (Everest & Chapman, 1972; Fausch & White, 1981; Naman et al., 2021). In systems with considerable velocity heterogeneity with potentially large differences between focal and foraging velocities (e.g., Panguingue Creek), models that predict optimal focal velocity (as discounted from foraging velocity) may outperform models that predict optimal foraging velocity. By contrast, optimal foraging velocity models may perform better in systems with less velocity heterogeneity and fewer focal and foraging velocity shears. Some NEI models address this issue by accounting for vertical or lateral velocity differentials in foraging areas (Dodrill et al., 2016; Hayes et al., 2000). Understanding how different models (or different versions of models that account for spatial velocity heterogeneity) perform in different systems is an important area of research for the development and application of future NEI models.

From a logistical point of view, it is encouraging that the simplified, adjusted, and third derivative models performed just as well or better than the full NEI model because model parsimony generally is desirable and estimates for *D*, *A*, and *S* are costly and difficult to obtain. However, from a NEI model development and managerial perspective, it is discouraging that our estimates of these additional variables do not improve model output given that many NEI models calculate absolute NEI, which is dependent on *D*, *A*, and *S*, to predict potential growth, abundance, or carrying capacity for applied management strategies. One potential explanation for the underwhelming performance by the full model is that the linear models we used to relate *D*, *A*, and *S* to velocity and subsequently parameterize the full model explain very little of the variation in *D*, *A*, and *S* due to velocity (R^2 ranged from 0.00 – 0.27). This is not a particularly robust or elegant way to parameterize the full NEI model; however, this is the first attempt to parameterize and test this model, and inspection of the data suggested that nonlinear functions would not be better descriptors than linear functions.

Another potential and related reason for underperformance of some variants is bias associated with our data collection. In each application of the model variants, the full and simplified NEI model predictions were greater than the third derivative and adjusted NEI model predictions. This pattern suggests we likely are overestimating drift-feeder NEI. Two potential sources of overestimation of NEI are underestimation of swimming costs and overestimation of prey capture success (it seems less likely that drift density and visual reaction area would be biased high). Improved estimation techniques for both of these variables, as previously discussed, will provide additional insight into the dynamics of these models.

Our NEI model comparison has important implications for NEI models with different predictive goals. For NEI models that rank instantaneous optimal microhabitat selection based on relative NEI, parsimonious models that do not account for energy content of prey in the drift, visual reaction area, and swimming cost perform reasonably well. This conclusion is supported by the finding that the full model rarely outperforms the adjusted or simplified models despite incorporating more biological realism by including additional variables.

However, parsimony is inappropriate for models that predict potential growth or carrying capacity via absolute NEI; these models require accurate estimates and arrangements of energetics variables to produce reasonable results. For instance, swimming costs may be overwhelmed by energetic benefits in NEI models that predict instantaneous habitat selection via ranking of available focal positions (Hill & Grossman, 1993; Hughes & Dill, 1990), but even small swimming cost estimates may be highly influential in NEI model applications that predict potential growth or carrying capacity over space or time (e.g., Hayes et al., 2016; Naman et al., 2019). Likewise, temporal (diel) and spatial (within or between habitats) variation in drift may hinder our ability to detect patterns at scales relevant to modeling of instantaneous focal position selection by drift-feeders (LaPerriere, 1981; Leung et al., 2009; Naman et al., 2016). Drift density may also interact with predation risk to explain focal position selection. If predation risk is high, drift-feeders may forage in faster velocities to achieve satiation in less time compared to foraging all day in slower velocities absent predation risk (Naman et al., 2021; Railsback et al., 2021). Drift dynamics certainly are critical components of drift-feeder habitat quality given that drifting macroinvertebrates, both terrestrial and aquatic, comprise most of the food for drift-feeding fishes (Elliott, 1973; Quinn, 2018).

Looking forward

Variables that regulate energetic gain (prey quantity and quality, fish visual reaction field, prey capture success) and expenditure (cost of holding a fixed focal position in the stream, cost of foraging) certainly are important determinants of drift-feeder habitat selection, ecology, and fitness. This observation is evidenced by the inclusion of these variables in the vast majority of NEI models, including the earliest and latest applications (e.g., Fausch, 1984; Naman et al., 2019; Rosenfeld & Taylor, 2009), and is substantiated by our review of the relevant literature. More sophisticated methods of parameter estimation for energy content of prey in the drift, visual reaction area, and swimming costs will improve our understanding of the intricacies of drift-feeder microhabitat selection and may ultimately improve the power, tractability, and utility of complex NEI models that use these and other variables to estimate absolute NEI.

Our results indicate that prey capture success is the variable with the most influence on the predictions made by our NEI model variants. Future research should parameterize prey capture success-velocity functions for additional species and age classes that could be incorporated into user-friendly habitat suitability estimation software (e.g., Naman et al., 2020) or generalized across populations. Developing prey capture success-velocity functions specific to species, age classes, or even types of systems (e.g., stream size), especially through methods that guard against overestimation of prey capture success in oversimplified stream flumes, will provide important insight into model formulation and drift-feeder foraging behavior for absolute and relative NEI models alike. Understanding species-specific foraging performance also will help us predict how species may respond in the face of shifts in habitat quality or quantity, or the presence of competitors (e.g., Nakano et al., 1999).

Global climate change and other anthropogenic stressors necessitate that we develop practical conservation and management strategies to mitigate threats to freshwater biodiversity (Dauwalter et al., 2011; Jenkins et al., 2015; Williams et al., 2011). One of the most promising aspects of NEI models is their potential ability to be linked to hydrodynamic models to predict microhabitat quality and quantity at broader spatial scales (Hayes et al., 2007; McHugh et al., 2017; Railsback, 2016), or incorporated into software that can readily estimate absolute NEI based on user-selected fish species, mass, water depth, velocity, and other variables (Hayes et al., 2020; Naman et al., 2020). Global climate change will affect drift-feeder habitat quality and quantity through many mechanisms, including altering metabolic rates (Trudel & Welch, 2005) and availability of prey in the drift. Although simplified variants of NEI models can be linked to climate modeling based on predicted changes in flow, complex NEI models that predict absolute NEI will be necessary to capture the full suite of effects of climate change on drift-feeder populations.

In conclusion, our results demonstrate that energy content of prey in the drift and fish visual reaction area potentially can be considered constant across the range of velocities occupied by drift-feeders, but swimming cost cannot. Nonetheless, we found that simplified variants of an NEI model based on the prey capture success-velocity function performed as well or better than a more complex NEI model, which is more difficult to parameterize. In the short term, this is encouraging because we can use simplified NEI models to predict instantaneous habitat selection by drift-feeders. However, complex NEI models that predict potential growth, abundance, or carrying capacity via absolute NEI ultimately are needed for robust management and conservation applications. We support the continued improvement of complex habitat variable estimation techniques, as well as the parameterization of species-specific prey capture success-velocity functions to advance our understanding of drift-feeding foraging behavior and our ability to evaluate stream fish habitat quality and quantity in an uncertain future.

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Tables

Table 2.1. Sources, species, age classes, seasons, reported focal velocities (mean ± SD, cm/s), and sample sizes from literature review of focal velocities of drift-feeding stream fishes. Season abbreviations are as follows: Sp = Spring, Su = Summer, Fa = Fall. Sources with no focal velocity standard deviation did not directly report a measure of precision with mean focal velocity.

Source	Species	Age Class	Season	Focal Velocity (cm/s)	N
Baltz et al. 1987	Rainbow Trout (*Oncorhynchus mykiss*)	Adult	Su/Fa	14.7 (14.0)	137
	Hardhead (*Mylopharodon conocephalus*)	Adult	Su/Fa	19.6 (14.0)	27
	Sacramento Pikeminnow (*Ptychocheilus grandis*)	Adult	Su/Fa	12.6 (11.8)	56
Baltz et al. 1991	Rainbow Trout (*O. mykiss*)	YOY	Su/Fa	5.0 (7.7)	166
		Juvenile	Su/Fa	8.0 (9.0)	101
		Adult	Su/Fa	13.0 (11.9)	32
Bozeman and Grossman 2019a	Arctic Grayling (*Thymallus arcticus*)	Adult	Su	36.7 (8.7)	20
				24.3 (7.8)	25
Bozeman and Grossman 2019b	Dolly Varden Char (*Salvelinus malma*)	Adult	Su	27.1 (5.8)	29
Donofrio et al. 2018	Chinook Salmon (*Oncorhynchus tshawytscha*)	Adult	Su	12.0 (4.9)	28
Enders et al. 2005	Atlantic Salmon (*Salmo salar*)	Juvenile	Su	36.4 (8.7)	8
Facey and Grossman 1992	Rainbow Trout (*O. mykiss*)	Adult	Sp/Su	14.8 (40.7)	94
	Rosyside Dace (*Clinostomus funduloides*)	Adult	Sp/Su/Fa	10.6 (46.2)	347
Fausch and White 1981	Brook Trout (*Salvelinus fontinalis*)	Juvenile	Su	16.6 (11.8)	96
		Adult	Su	16.4 (9.5)	18
Grossman et al. 2002	Rosyside Dace (*C. funduloides*)	Adult	Su	14.7 (18.6)	214
	Warpaint Shiner (*Luxilus coccogenis*)	Adult	Su	15.3 (13.2)	44
	Tennessee Shiner (*Notropis luciodus*)	Adult	Su	16.0 (7.3)	25
	Yellowfin Shiner (*Notropis lutipinnis*)	Adult	Su	11.0 (10.0)	38
Hayes and Jowett 1994	Brown Trout (*Salmo trutta*)	Adult	Su	23.5	189
Healy and Lonzarich 2000	Coho Salmon (*O. kisutch*)	Juvenile	Su	5.0	80
Heggenes 2002	Brown Trout (*Salmo trutta*)	All	Su	14.0 (11.0)	1598

Hill and Grossman 1993	Rainbow Trout (*O. mykiss*)	Juvenile	All	14.7 (20.4)	85
		Adult	All	19.3 (19.2)	133
	Rosyside Dace (*C. funduloides*)	Juvenile	All	13.2 (16.0)	441
		Adult	All	13.2 (16.3)	319
Hillman et al. 1987	Chinook Salmon (*O. tshawytscha*)	Juvenile	Su	11.7 (6.0)	281
			Fa	9.5 (3.5)	120
Hughes and Dill 1990	Arctic Grayling (*T. arcticus*)	Adult	Su	37.5 (17.6)	8
Moyle and Baltz 1985	Rainbow Trout (*O. mykiss*)	YOY	Su/Fa	7.3 (8.6)	82
		Juvenile	Su/Fa	19.4 (16.1)	108
		Adult	Su/Fa	28.6 (18.0)	108
	Sacramento Pikeminnow (*P. grandis*)	Juvenile	Su/Fa	12.1 (13.0)	149
		Adult	Su/Fa	18.3 (14.5)	49
	Hardhead (*M. conocephalus*)	Juvenile	Su/Fa	14.0 (14.0)	81
		Adult	Su/Fa	21.7 (17.9)	57
	Tule Perch (*Hysterocarpus traskii*)	Juvenile	Su/Fa	7.4 (6.0)	12
		Adult	Su/Fa	6.1 (5.8)	19
Naman et al. 2021*	Rainbow Trout (*O. mykiss*)	Juvenile	Su	17.3 (16.6)	92
	Bull Trout (*S. confluentus*)	Juvenile	Su	10.8 (13.0)	60
Nielsen 1992	Coho Salmon (*O. kisutch*)	Juvenile	Su	14.0 (3.3)	107
				12.0 (1.3)	216
Rimmer et al. 1984	Atlantic Salmon (*Salmo salar*)	YOY	Su	16.8	501
			Fa	7.8	117
		Juvenile	Su	29.8	218
			Fa	9.4	48
		Adult	Su	38.4	146
			Fa	7.1	28
Rincon and Lobon-Cervia 1993	Brown Trout (*Salmo trutta*)	Adult	All	22.8	193
Sliger and Grossman 2021a	Brook Trout (*S. fontinalis*)	Adult	Su	17.0 (8.6)	26

Table 2.2. NEI model variant optimal microhabitat predictions and field focal velocities (mean and 95% CI) for each study species. Focal velocities are mean (95% confidence interval, cm/s). Model predictions falling within the 95% CI are marked with an asterisk and those falling just outside the CI (< 1 cm/s) are marked with a †. RC = Richardson Clearwater, PC = Panguingue Creek.

Species	Field Focal Velocity	Model	Prediction (cm/s)
Chinook Salmon (N = 24)	11.8 (9.7 – 3.9)	Simplified NEI	34.0
		Adjusted NEI	18.5
		Third derivative	20.7
		Full NEI	34.4
Dolly Varden Char (N = 32)	27.2 (25.1 – 29.2)	Simplified NEI	36.4
		Adjusted NEI	24.4†
		Third derivative	17.2
		Full NEI	29.5†
Arctic Grayling (N = 29, 25)	37.6 (34.0 – 41.2) (RC)	Simplified NEI	37.2*
	24.0 (20.8 – 27.2) (PC)	Adjusted NEI	23.0*
		Third derivative	25.1*
		Full NEI	32.5

Figures

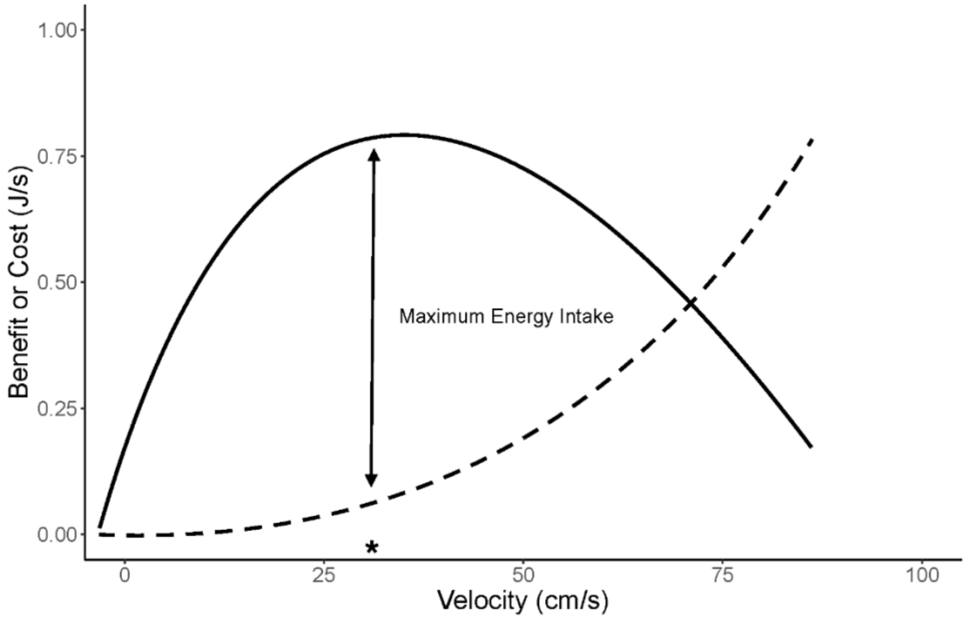

Figure 2.1. Conceptual depiction of a cost-benefit NEI model for microhabitat use (via focal position velocity). The broken line is energetic cost; the solid line is energetic benefit. The maximum difference between cost and benefit lines is the optimal focal position velocity (denoted with an asterix) where NEI is maximized.

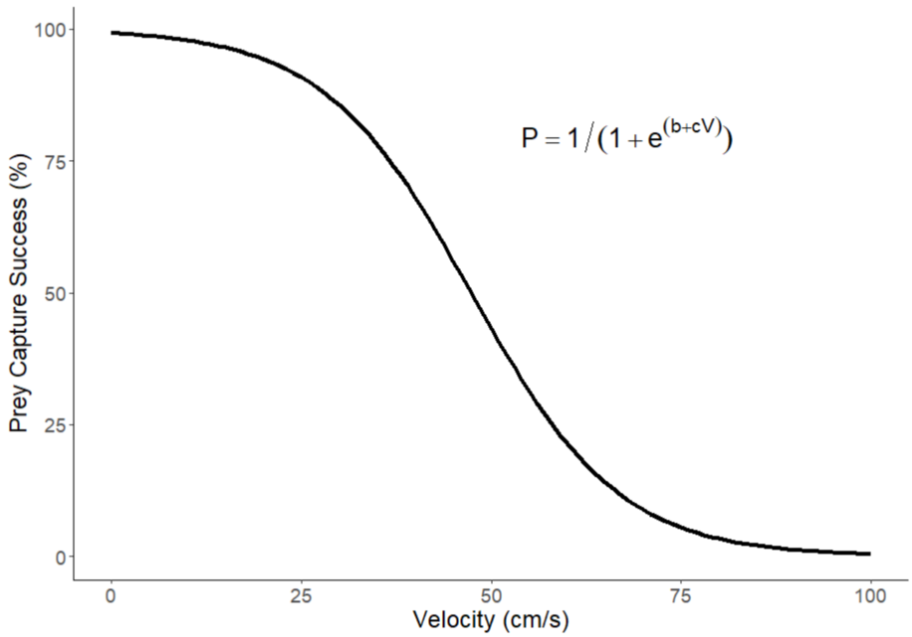

Figure 2.2. The negative logistic relationship between prey capture success and velocity with Hill and Grossman's (1993) equation that describes the relationship between prey capture success and velocity (Eq. 3).

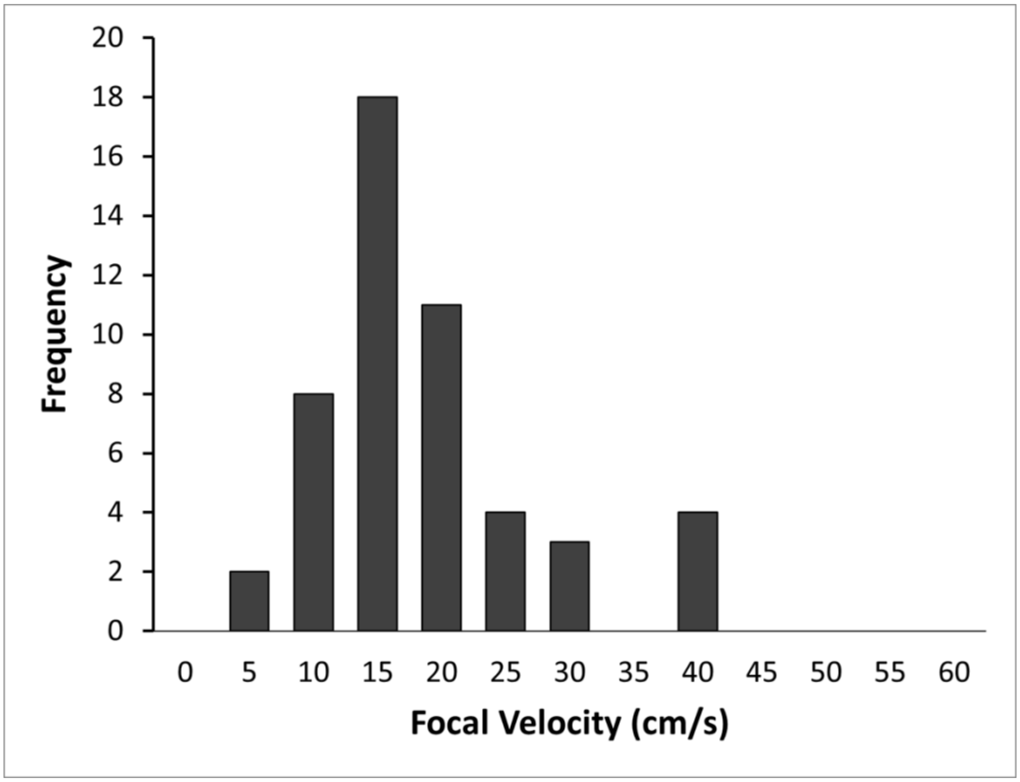

Figure 2.3. Frequency distribution histogram of published focal velocities (N = 50 data sets representing 7113 individual measurements, Table 2.1) for stream fishes.

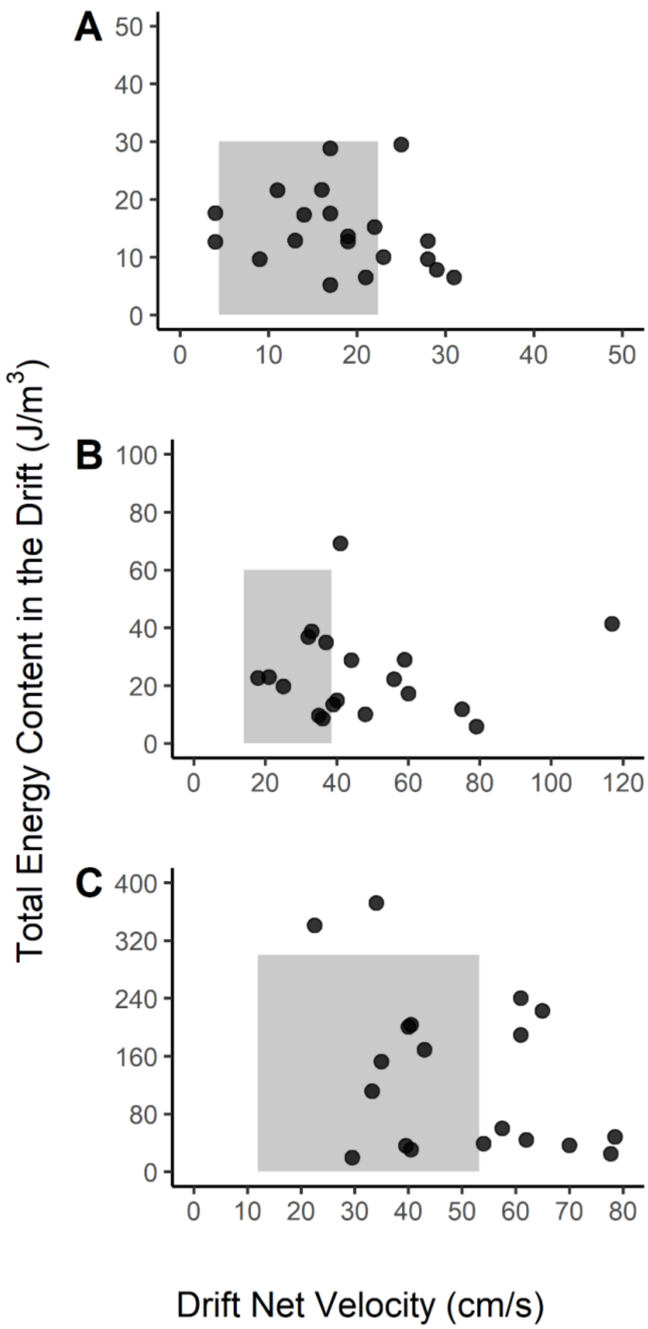

Figure 2.4. Mean drift net velocity (cm/s) versus total energy density in the drift (J/m^3) in habitats occupied by: (A) juvenile Chinook Salmon (Chena River), (B) Dolly Varden Char (Panguingue Creek), and (C) Arctic Grayling (Richardson Clearwater). Note differences in axis scales. The gray shaded areas are the focal velocities of the respective species in their respective streams.

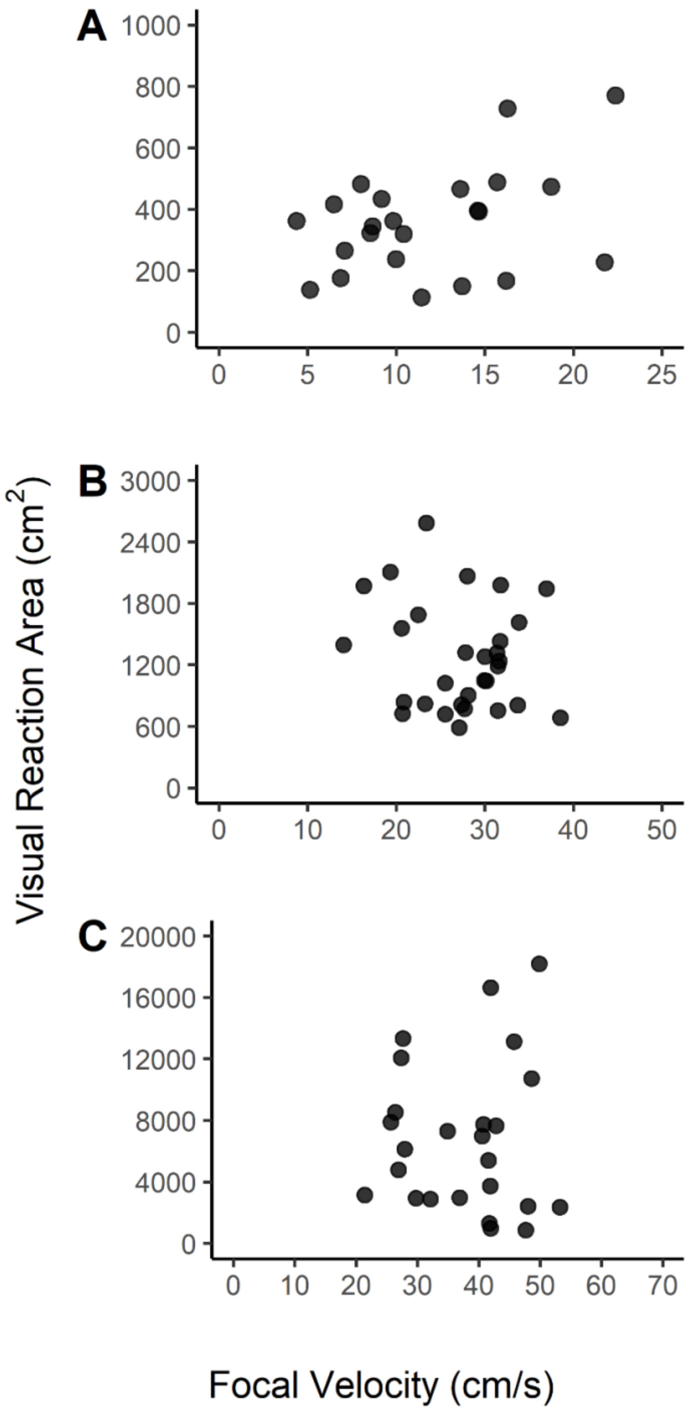

Figure 2.5. Focal velocity (cm/s) versus visual reaction area (cm^2) for: (A) juvenile Chinook Salmon, (B) Dolly Varden Char, and (C) Arctic Grayling. Note the differences in axis scale.

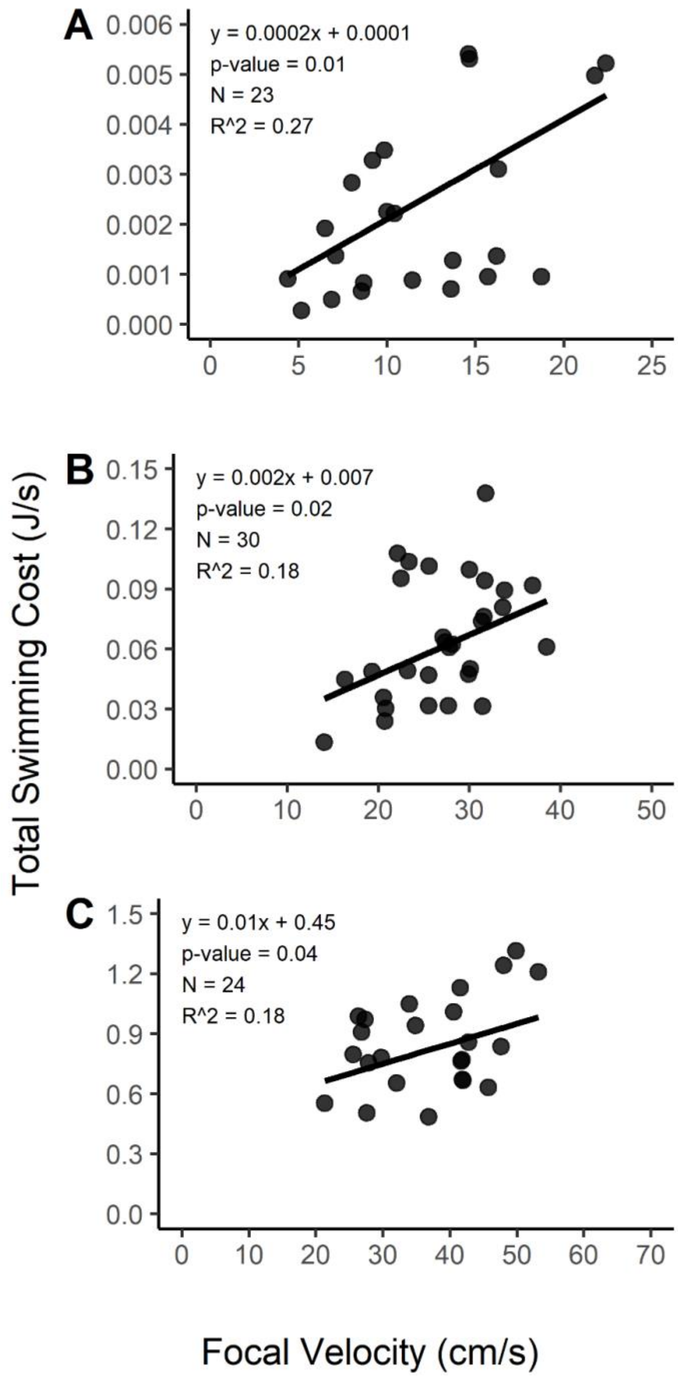

Figure 2.6. Focal velocity (cm/s) versus estimated total swimming costs (J/s) for (A) juvenile Chinook Salmon, (B) Dolly Varden Char, and (C) Arctic Grayling. Note the differences in axis scales.

CHAPTER 3

LANDSCAPE AND CLIMATE INFLUENCES ON TROUT SYMPATRY IN SOUTHERN APPALACHIA, USA[2]

[2] Bozeman, B.B., S.J. Wenger, N.P. Nibbelink and G.D. Grossman. To be submitted to *Ecology of Freshwater Fish*.

Abstract

In Southern Appalachia, historic and contemporary landscape modification and encroachment of nonnative Rainbow (*Oncorhynchus mykiss*) and Brown (*Salmo trutta*) Trout have limited Brook Trout (*Salvelinus fontinalis*) populations to high elevation headwater streams. Brook Trout have managed to persist, despite predictions that they would eventually become extirpated from this region. We evaluated the effects of geomorphologic, land use, and climate variables on the distribution of populations of Brook Trout (*Salvelinus fontinalis*), Rainbow Trout (*Oncorhynchus mykiss*), and Brown Trout (*Salmo trutta*) using two methods. First, we constructed species distribution models for each species and for allopatric Brook Trout populations to evaluate distribution patterns at the stream segment scale. Second, we compared the relative balance of native and nonnative trout per subwatershed to subwatershed-scale predictor variables. Brook Trout were more likely to occur in high elevation (918 $\pm$ 224 m), steep streams with cool summer temperatures (26 $\pm$ 1.6 C) and ample annual rainfall (1714 $\pm$ 248 mm). By contrast, Rainbow and Brown Trout were more likely to occur in low elevation (763 $\pm$ 198 m), low gradient streams in warmer (27 $\pm$ 1.5 C) and dryer areas (1616 $\pm$ 221 mm). Land use characteristics of forest, agriculture, development, and change were not important predictors of trout distribution at the stream segment scale. General and allopatric Brook Trout distributions were similarly related to predictor variables. Relationships between environmental gradients and relative trout distribution detected at the stream segment scale were not discernible at the subwatershed scale. General trout management approaches in Southern

Appalachia can be implemented at the subwatershed-scale, but targeted conservation efforts for native Brook Trout populations likely should focus on stream segments.

Introduction

Coldwater streams in the Blue Ridge Mountains of North Carolina, Tennessee, and Georgia support populations of Brook Trout (*Salvelinus fontinalis*), Rainbow Trout (*Oncorhynchus mykiss*), and Brown Trout (*Salmo trutta*). The Brook Trout is the southeastern United States' only native salmonid; populations of Rainbow and Brown Trout have become naturalized throughout the region via stocking that began in the early 1900s (Grossman et al., 2010; MacCrimmon, 1971; MacCrimmon & Marshall, 1968). Southern Appalachian Brook Trout populations are near the edge of their native geographic range and therefore are of special conservation interest because of their potential to maximize intraspecific genetic diversity and enhance adaptation in the face of climate change or other stressors (DeRolph et al., 2015; Haak et al., 2010). To better manage trout populations in areas with rapid land use change and ongoing and future climate change, it is critical to identify factors that may influence differential longitudinal distributions of these three species, including factors that may allow native Brook Trout populations to persist in the face of abiotic and biotic stressors.

Prior to 1900, Brook Trout ostensibly occupied all streams with suitable trout habitat in the Southern Appalachian Mountains. However, logging, introduction of nonnative Rainbow and Brown Trout, and high angling pressure in the early 1900s reconfigured both local and regional trout distributions. Brook Trout became relegated to high elevation headwater streams due to widespread logging, overfishing, and other landscape modification that caused heavy siltation and loss of stream shading (Kelly et al., 1980; King, 1937). As stream habitat recovered in the years following heavy logging operations, introduced Rainbow and Brown Trout claimed lower elevation streams that formerly were Brook Trout habitat, and Brook Trout remained confined to higher elevation streams (Bivens, 1984; Lennon, 1967). Today, Brook Trout occupy an estimated 5 – 20% of their original Southern Appalachian habitat (Bivens, 1984; Hudy et al., 2013; Hudy et al., 2008).

In the decades following their introduction, Rainbow and (to a lesser degree) Brown Trout increased their upstream distributions, possibly displacing Brook Trout (Larson & Moore, 1985). Some researchers suggested that Brook Trout would become extirpated from Southern Appalachian streams via upstream encroachment of Rainbow and Brown Trout as soon as 2030 (Bivens, 1984; Kelly et al., 1980). This does not appear to be happening. Instead, the three trout species seem to have settled into the apparently stable longitudinal pattern described above: Brown and Rainbow Trout downstream, Brook Trout upstream, frequently with an overlapping sympatric zone between (Flebbe, 1994; Habera et al., 2021; Habera et al., 2001; Strange & Habera, 1998). This longitudinal distribution pattern also has been observed outside of Appalachia (Fausch, 1989; Fausch & White, 1981; Gard & Flittner, 1974; Rahel & Nibbelink, 1999). Impassible barriers may be implicated in the upstream limits of some Rainbow Trout populations, but barriers (i.e., cascades or waterfalls greater than ~2 m in height) are present only in an estimated 30% of Brook Trout streams in some parts of Southern Appalachia (e.g., Great Smoky Mountains National Park; Bivens, 1984; Kelly et al., 1980).

There are multiple mechanisms capable of explaining the differences in distribution among Brook, Rainbow, and Brown Trout operating separately or in tandem, and at varying spatial and temporal scales**.** Relatively immutable geomorphologic characteristics like elevation and slope may regulate trout distributions locally via their effects on temperature (e.g., de la Hoz Franco & Budy, 2005; DeWeber & Wagner, 2015), available habitat, stream size, or longitudinal mobility (e.g., Adams et al., 2000; Fausch, 1989; Rahel & Nibbelink, 1999). Other, more dynamic environmental characteristics such as climate and land use also may regulate relative trout distribution via their impact on species-specific biological characteristics. For example, different spawning seasons of Brook and Rainbow Trout (fall versus late winter/spring) means that eggs, young-of-the-year and, subadults of each species are differentially affected by seasonal climate patterns. Brook Trout young-of-the-year are more vulnerable to high flow events caused by heavy precipitation in winter and spring months before, during, or shortly after fry emergence than Rainbow Trout who emerge later and grow rapidly (Clark & Rose, 1997; Fausch, 2008; Fausch et al., 2001; Kanno et al., 2017).

The three trout species also have differential thermal requirements; Brook Trout are more tolerant of cooler stream temperatures compared to Rainbow and Brown Trout (Gard & Flittner, 1974; Peterson et al., 1979; Rahel & Nibbelink, 1999; Vincent & Miller, 1969). Seasonal climate patterns – both temperature and precipitation – may differentially affect age-classes and influence population dynamics by altering recruitment (Kanno et al., 2016), especially in short-lived populations like Southern Appalachian Brook Trout. Finally, conversion of land use from forest to agriculture or development often results in elevated nutrient concentrations, fine sediment, and stream temperature as well as shifts in stream energetics and trophic webs (Niyogi et al., 2007). Brook Trout typically are negatively associated with agriculture, impervious surfaces, development, and land use change within riparian zones or subwatersheds (e.g., DeWeber & Wagner, 2015; Hudy et al., 2008; Kanno et al., 2015; Stranko et al., 2008). Land use also may interact with presence of nonnative competitors to further influence relative trout distribution (Wagner et al., 2013).

Decades of anthropogenic stream and landscape alteration combined with potential competitive pressures from introduced nonnative Rainbow and Brown Trout make understanding of the factors affecting the differential longitudinal distributions of the three species important for both management and conservation of trout in the Southern Appalachians. In this study, we assessed the relative importance of geomorphology, climate, and land use on the probability of occurrence of native Brook Trout and nonnative Rainbow, and Brown Trout.

Materials & methods

Study area and species

Southern Appalachia is a rugged, mountainous region extending from southwestern Virginia through eastern Tennessee and western North Carolina and into northern Georgia and South Carolina (Figure 3.1). These mountains have steep slopes with mixed hardwood – conifer forests and many clear, cold mountain streams (Bivens, 1984). The Southern Appalachians receive the greatest amount of annual precipitation in the eastern United States, with average annual precipitation values ranging from 890 mm to 2,040 mm, depending on local topography (Gaffin & Hotz, 2000; U.S. Forest Service, 2020). The average annual temperature is 18 C (range = -5 – 30 C). Elevation ranges from ~90 m to 2,040 m above sea level, with a maximum elevation of 2037 m atop Mount Mitchell in North Carolina.

The native range of the Brook Trout extends from northeastern Canada west to Minnesota and south to northern Georgia (Stoneking et al., 1981). Individuals in the Southern Appalachians rarely exceed 200 mm in standard length and live for about three years (Grossman et al., 2010; Raleigh, 1982). Rainbow Trout are native west of the North American continental divide, from as far south as Mexico to as far north as northwestern Canada and Alaska (MacCrimmon, 1971). Like Brook Trout, Rainbow Trout have been widely introduced far beyond their native range and are now naturalized in many parts of the eastern United States, including Southern Appalachia (MacCrimmon, 1971). Rainbow Trout in Southern Appalachia tend to grow faster, reach larger sizes, and live longer than Brook Trout (Kelly et al., 1980; Larson & Moore, 1985). Finally, Brown Trout are native to Europe and Asia, though they have been introduced and have become naturalized on every continent but Antarctica (MacCrimmon & Marshall, 1968). Brown Trout in Appalachia also tend to grow much larger and live longer than smaller-bodied, shorter-lived Brook Trout (Burrell et al., 2000).

Trout dataset

We used trout data provided by the Georgia Department of Natural Resources (GADNR), Tennessee Wildlife Resources Agency (TWRA), North Carolina Wildlife Resources Commission (NCWRC), and Great Smoky Mountains National Park (GSMNP) to characterize the distribution of Brook, Rainbow, and Brown Trout in the Southern Appalachian Mountains (Figure 3.1).

Our trout dataset was organized hierarchically as individuals of each species detected per sampling event per sampling site. We filtered the dataset to include only samples that were influenced by natural processes (i.e., no stocking influence, population restoration or maintenance, or artificial impassible barriers) from 2010 – 2020. Specifically, we snapped trout sampling site points to the nearest stream flowline from the National Hydrography Dataset (NHD) using the spatial join tool in ESRI ArcMap 10.8 (ESRI, 2019; henceforth ArcMap), which allowed us to inspect longitudinal (temporal and spatial) abundance patterns at sites within connected stream segments. We omitted sampling sites that displayed dramatic shifts in abundance between species in consecutive years (e.g., where abundant Rainbow Trout were removed and Brook Trout were restored), as well as those with notes from state or federal agency personnel indicating presence of barrier or population maintenance. This process produced a final filtered trout dataset containing information based 98,691 trout observed in 1,425 sampling events across 430 sampling sites within 84 subwatersheds (sixth-level USGS hydrologic units, or HUC12s).

Environmental data & hypotheses

We characterized biologically and ecologically relevant environmental data to explain trout distribution data using a geographic information systems (GIS) framework. The full suite of predictor variables included two geomorphic, five land use, and four climate variables (Table 3.1). Our trout dataset was built on observations of individuals of at least one of the three trout species, and therefore did not contain any sampling sites with zero trout present. Accordingly, the hypotheses below describe our expectations for how selected environmental gradients relate to the *relative* distribution of the three trout species within habitat that is suitable for trout in Southern Appalachia. For instance, we might expect Rainbow Trout to occupy streams at lower elevations *relative* to Brook Trout, but high elevations relative to regional availability given that all naturally occurring trout populations in the South occur in the Southern Appalachian Mountains.

<u>Geomorphic hypotheses</u>

We developed two hypotheses related to stream geomorphology. We hypothesized that Brook Trout probability of occurrence would be positively associated with elevation, and that Rainbow and Brown Trout probability of occurrence would be negatively associated with elevation (Flebbe, 1994; Strange & Habera, 1998; Vincent & Miller, 1969). We also hypothesized that Brook Trout would be more likely to occur in stream segments with steeper slopes, and that Rainbow and Brown Trout would be less likely to occur in steeply sloped streams (Fausch, 1988, 1989; Gard & Flittner, 1974; Kanno et al., 2015).

We used 10-m digital elevation models (DEM) obtained from the NHDPlus High Resolution Dataset Digital Elevation Program (3DEP; U.S. Geological Survey, 2020) to estimate elevation at each sampling site by extracting values to points in ArcMap. To obtain the slope of each sampling site stream segment, we snapped sampling sites to the nearest stream flowline from NHDPlus V2 medium resolution data (U.S. Environmental Protection Agency, 2012), which includes segment slope estimates derived from 30-m DEMs.

Land use hypotheses

We hypothesized that Brook Trout probability of occurrence would be positively associated with subwatershed percent forest, and negatively associated with subwatershed percent agriculture and development, as well as the total percentage of subwatershed land use change over the last twenty years (DeWeber & Wagner, 2015; Hudy et al., 2008; Kanno et al., 2015; Stranko et al., 2008). We hypothesized that Rainbow and Brown Trout probability of occurrence would be inversely affected by those same variables. We used land cover data from the National Land Cover Database (NLCD; Dewitz, 2019) and zonal statistics in ArcMap to calculate the percent of each subwatershed in classes of development (NLCD classes 21 – 24), agriculture (NLCD classes 81 – 82), and forest (NLCD classes 41 – 43) using NLCD 2016 land cover data, which we selected to represent land cover for the full 2010 – 2020 trout dataset. To capture land use change, we also calculated the percent of each subwatershed that had shifted land use classification at least once from 2001 – 2019 using NLCD's Land Cover Change Index (Dewitz, 2021). NLCD land use and change index models were 30-m raster files. We characterized land use at the subwatershed scale as opposed to finer spatial scales because regional land use has been shown to more appropriately capture landscape effects on stream ecosystems than local conditions (Roth et al., 1996).

Climate hypotheses

We hypothesized that Brook Trout probability of occurrence would be negatively associated with temperature (Clark & Rose, 1997; DeWeber & Wagner, 2015; Fausch,

1988) and precipitation because of fry vulnerability to high winter and spring flow events, especially over prolonged periods (Fausch et al., 2001; Habera et al., 2018; Strange & Habera, 1998; Wenger et al., 2011). We hypothesized that Brown Trout probability of occurrence would be positively associated with temperature and negatively associated with precipitation (because they also are fall spawners), and that Rainbow Trout probability of occurrence would be positively associated with both precipitation and temperature. (Note: these hypothesized correlations are relative between trout species, and not relative to conditions more broadly.)

We used data from the PRISM Climate Group (PRISM Climate Group, 2021) to characterize long-term climate patterns for our study area. We used the 30-year Normal dataset from PRISM with a resolution of 800m x 800m and the extract values to points tool in ArcMap to estimate the average annual temperature (C) and precipitation (mm) per sampling site from 1991 – 2020. We also calculated the average March precipitation and average maximum August temperature per sampling site to capture seasonal climate extremes (e.g., months with especially high flows or temperatures).

Species distribution models

We constructed four separate species distribution models (SDMs) to explain relative trout distribution in Southern Appalachia: one each for Brook (including populations that are allopatric and sympatric with other trout), Rainbow, and Brown Trout. The SDMs classified each sampling site (N = 430) based on modified presence-absence (P/A) for each species. We designated a species as being present at a given site if it comprised at least 10% of the total population observed during any sampling event from 2010 – 2020, and absent if it comprised less than 10% of the observed population during each sampling event. The allopatric Brook Trout SDM was more restrictive. In order for a sample to be included in the present category, neither Rainbow nor Brown Trout abundance could exceed 5% of the total observed population during any sampling event. We used this modified, proportion-based P/A designation as opposed to absolute P/A to try to capture persistent habitat use over the last decade for each species and preclude the equivalency of one or two individuals of one species scoring the same as tens or hundreds of individuals of another species. This method is similar to population status classifications in previous trout surveys in Southern Appalachia (Bivens, 1984; Whitworth & Strange, 1979). Based on this classification method, there were 249 sites with Brook Trout, 235 sites with Rainbow Trout, 113 sites with Brown Trout, and 152 sites with allopatric Brook Trout. Each SDM included all 430 sampling sites classified from the perspective of the target species.

Prior to constructing and evaluating SDMs for each species, we screened our full suite of predictor variables to identify and remove highly correlated variables. Unsurprisingly, several of our predictor variables were highly correlated, especially those within the same category (Table 3.2). Accordingly, we constructed single-variable models containing variables with a Pearson correlation coefficient absolute value of at least 0.6 and retained the variable that had the greatest explanatory power for the most species. This resulted in a global model with no predictor variable correlations greater than 0.6. The global model included slope, mean maximum August temperature, mean annual precipitation, percent agriculture, percent development, and percent change.

We constructed generalized linear mixed models to evaluate the relative explanatory power of our continuous predictor variables on the binary P/A response for each species with subwatershed as a random effect (DeRolph et al., 2015; Steen et al., 2006) with R package ‘lme4’ version 1.29 (Bates et al., 2015; R core team, 2020). We standardized all predictor variables by subtracting the mean and dividing by the standard deviation to facilitate direct comparison of the magnitude and direction of predictor variable coefficients (Faraway, 2016).

We compared the global model with all subsets using Akaike’s information criterion adjusted for small sample size (AICc) using R package ‘MuMIn’ (Barton, 2016). We selected models with delta AICc values of less than 5, and discarded lower-ranked models that were more complex versions of a better supported model (i.e., those that included one or two additional variables and were within 2 – 4 delta AICc from the best-supported model; Arnold, 2010). The remaining models comprised the “confidence set” of models. Finally, we evaluated the performance of the best-supported model given the data and the candidate set using area under the receiver operating characteristic curve (AUC) and plotted the odds ratio (OR) marginal effects of each variable included in best-supported models for each species on the original scale of the respective predictor variables.

Trout balance model

We also assessed whether there were discernible differences between subwatershed characteristics and the relative balance between native Brook Trout and nonnative Rainbow and Brown Trout at the subwatershed scale. We summarized the total number of individuals of each species observed from 2010 – 2020 per subwatershed (N = 84), and classified trout population status as the ratio of native Brook Trout to nonnative Rainbow and Brown Trout. This variable, which we term trout balance, ranged from 0.0 (entirely Rainbow and/or Brown Trout) to 1.0 (entirely Brook Trout). We used beta regression (R package 'Betareg' version 3.4; Cribari-Neto & Zeileis, 2010) to evaluate potential relationships between subwatershed scale predictor variables and the trout balance response variable.

Because trout balance was classified per subwatershed, we also characterized all predictor variables by subwatershed for this analysis using the same data sources as the SDMs. We calculated minimum, mean, and maximum elevation per subwatershed. We calculated average stream slope per subwatershed as the average slope of all NHDPlus V2 stream segments within each subwatershed weighted by stream segment length. We also calculated average values for mean annual and mean March precipitation and mean annual and mean maximum August temperature per subwatershed. Land use predictor variables of percent agriculture, development, agriculture and development, forest, and change were already summarized at the subwatershed scale for the SDM analyses.

Because beta regression with logit transformation is not possible for true 0 and 1 values, we re-scaled the trout balance response variable to fall between 0 and 1 via

(1) $$x_i^* = \frac{x_i(n-1)+0.5}{n}$$

Where x_i^* is the transformed value of x_i and *n* is the total number of observations in the dataset (Douma & Weedon, 2019).

Following the same AICc protocol in the SDM analysis, we evaluated the full suite of potential subwatershed-scale predictor variables for collinearity, and removed correlated predictor variables (Pearson's correlation coefficient absolute value ≥ 0.6) that ranked second in pairwise AICc single-variable model comparisons. We constructed an exhaustive set of candidate models with all remaining variables and evaluated the relative performance of the global model and all simplified variations using AICc. The global model for the trout balance analysis included maximum elevation, slope, mean March precipitation, percent agriculture, percent development, and percent change. We used the same model selection process as the SDM analysis to prune the candidate model set such that it contained models with a delta AICc of ≤ 5 and did not contain slightly more complex versions of the best model with very similar likelihood estimates.

Results

Species distribution models

<u>Brook Trout</u>

The best-supported model for general Brook Trout probability of occurrence included slope, maximum August temperature, and mean annual precipitation. This was the only model in our confidence set based on our evaluation and pruning criteria (Table 3.3). Consistent with our hypotheses, Brook Trout probability of occurrence was positively correlated with slope (β = 1.81, Odds Ratio [OR] = 6.1) and negatively correlated with August temperature (β = -1.46, OR = 0.23). However, contrary to our expectations, Brook Trout occurrence was positively correlated with annual precipitation (β = 1.18, OR = 3.3) (Table 3.4, Figures 3.2 & 3.3). Slope was the most important predictor of Brook Trout occurrence, followed by temperature and precipitation; land use metrics were not strongly related to Brook Trout occurrence.

Results of our allopatric Brook Trout SDM were very similar to those of our general Brook Trout model. The best-supported model for allopatric Brook Trout included slope, August temperature, and annual precipitation, and was the only model in the confidence set (Table 3.3). Allopatric Brook Trout probability of occurrence was positively correlated with slope (β = 1.13, OR = 3.1) and annual precipitation (β = 1.13, OR = 3.1), and negatively correlated with August temperature (β = -1.01, OR = 0.36) (Table 3.4, Figures 3.2 & 3.3). Slope and annual precipitation were equally important predictors of allopatric Brook Trout occurrence; August temperature was of lesser importance. Distributions of allopatric Brook Trout are determined by the same variables as sympatric Brook Trout, with allopatric populations being slightly more sensitive (Figure 3.2).

Rainbow Trout

As with the general and allopatric Brook Trout models, the best-supported model for Rainbow Trout occurrence included slope, August temperature, and annual precipitation (Table 3.3). Our model selection process revealed a second model that shared explanatory power for Rainbow Trout probability of occurrence that included slope, August temperature, and percent agriculture (delta AICc = 4.18, w = 0.11, Table

3.3). The best-supported model revealed that Rainbow Trout probability of occurrence was positively correlated with August temperature (β = 0.93, OR = 2.5) and negatively correlated with slope (β = -0.88, OR = 0.41) and precipitation (β = -0.91, OR = 0.40) (Table 3.4, Figures 3.2 & 3.3). These variables were of basically equal importance. Our hypotheses that Rainbow Trout occurrence would be negatively related to slope and positively related to temperature were supported; our hypotheses for positive associations with land use and precipitation were not supported.

Brown Trout

Our model selection process revealed a candidate set of three models that shared explanatory power (Table 3.3). The best-supported model for Brown Trout probability of occurrence included slope, annual precipitation, percent agriculture, and percent change (*w* = 0.511). The second-best model included slope, mean annual precipitation, and percent agriculture (delta AICc = 0.91, *w* = 0.32) and the third-best model included slope and mean annual precipitation (delta AICc = 2.27, *w* = 0.17) (Table 3.3). Brown Trout probability of occurrence was negatively correlated with slope (β = -1.56, OR = 0.21), annual precipitation (β = -1.14, OR = 0.32), and percent agriculture (β = -0.85, OR = 0.43), and positively correlated with percent change (β = 0.59, OR = 1.8) (Table 3.4).

Although it was included in the best-supported model, the relationship between percent change and Brown Trout occurrence was not significant at the 0.05 level. Parameter estimates for variables included in the best-supported model suggest that the order of importance of predictor variables was – from most to least – slope, precipitation, agriculture, and change (Table 3.4). Our hypotheses that Brown Trout occurrence would be negatively related to slope and annual precipitation were supported; our hypotheses that Brown Trout occurrence would be positively related to subwatershed agriculture and percent change were not supported.

Trout balance model

None of the variables in the trout balance global model were significantly correlated with trout balance at the subwatershed scale (Figure 3.4). P-values for single-variable models ranged from 0.08 (percent agriculture) to 0.96 (slope). Pseudo R^2 values were generally very low (0.049 – 0.000; Figure 3.4). Model selection results were similar to the conclusions of single-variable models. The best supported model for trout balance was percent agriculture (w = 0.36), followed by the null model (w = 0.21, Table 3.5). Following our model selection process of selecting models with delta AICc of less than 5 and removing slightly more complex versions of better performing models (Arnold, 2010), seven models remained: single-variable models for each predictor variable, and the null model (Table 3.5). Collectively, the high p-values and low pseudo R^2 values of single-variable models and the final candidate model set from our model selection process indicate that none of our subwatershed-scale predictor variables were meaningfully related to trout balance. None of our hypotheses for geomorphology, climate, or land use were supported at the 0.05 level.

Discussion

Our species distribution models revealed interesting patterns in the relative distribution of Brook, Rainbow, and Brown Trout in the southern extent of these species' ranges in the eastern United States. Brook Trout – in sympatry and allopatry – were more likely to occur in steeper streams that received greater annual rainfall and had lower maximum August temperatures relative to Rainbow and Brown Trout, who were associated with flatter streams in warmer, dryer microclimates. These patterns were evident at the sampling site scale; however, they completely disappeared in the trout balance analysis.

Our finding that Brook Trout were more likely to occur in steep, high elevation streams in cooler microclimates relative to Rainbow and Brown Trout is consistent with past studies in Appalachia (e.g., Bivens, 1984; Hudy et al., 2008; Larson & Moore, 1985) and elsewhere (e.g., Gard & Flittner, 1974; Vincent & Miller, 1969). Our predictor variable correlation analysis revealed that temperature and elevation were so highly correlated in this dataset (r = -0.96) that they can be considered essentially interchangeable, which has been observed in other studies in Southern Appalachia (Flebbe et al., 2006).

The commonly accepted hypothesis explaining the restriction of Brook Trout to the upper portions of watersheds and dominance of Rainbow and Brown Trout downstream is that, absent impassible barriers, Rainbow and Brown Trout are superior competitors in downstream reaches, and environmental gradients shift the competitive pendulum to favor Brook Trout in headwaters (Fausch, 1988, 1989; Larson & Moore, 1985; Vincent & Miller, 1969). Streams within high elevation subwatersheds typically become less hospitable with increasing elevation within the subwatershed. Brook Trout generally are more tolerant of cold temperatures than Rainbow or Brown Trout (Gard & Flittner, 1974; Rahel & Nibbelink, 1999; Vincent & Miller, 1969) and are more aggressive toward Rainbow Trout in colder temperatures (Cunjak & Green, 1986; Magoulick & Wilzbach, 1998) and may competitively exclude Rainbow Trout from cold headwaters outside of the latter's preferred thermal window.

Conversely, in warmer downstream habitats, Rainbow Trout may competitively exclude Brook Trout from optimal feeding positions, which potentially reduces juvenile Brook Trout growth during the critical first summer after fry emerge from the substrate (Cunjak & Green, 1983; Magoulick & Wilzbach, 1997; Rose, 1986). Rainbow Trout in Great Smoky Mountains National Park grow faster than Brook Trout; juvenile Rainbow Trout are the same size as juvenile Brook Trout by summer, despite emerging several months later (Kelly et al., 1980). When Rainbow Trout are removed from stream segments where they co-occur with Brook Trout, Brook Trout increase in abundance (Moore et al., 1983) and select focal positions previously occupied by the Rainbow Trout (Lohr & West, 1992). Thus, condition-specific competition (Taniguchi & Nakano, 2000) may affect the distribution of Brook, Rainbow, and Brown Trout populations longitudinally based on (closely related) elevation and temperature.

Slope was the most important predictor of probability of occurrence for three of our four SDMs and was included in every candidate model selected under our model selection and pruning process. Obviously, a critical consideration for our study is whether slope is correlated with impassible barriers, which would confound our analyses. Extensive surveys of Brook Trout streams in Great Smoky Mountains

National Park (Kelly et al., 1980) and Tennessee (Bivens, 1984) (far beyond streams included in our dataset) estimated that approximately 30% of Brook Trout streams contained impassible barriers. Sampling sites from Tennessee and Great Smoky Mountains National Park comprised 54% of our dataset. We extensively inspected the dataset and removed any samples that displayed abnormally large shifts in abundance between species in adjacent sites, as well as those with annotations from stream sampling teams that mentioned barriers or cascades. We are confident that this screening process removed all or nearly all barrier-influenced samples from our analysis and that the vast majority of our observed slope-distribution relationships are driven by environmental characteristics other than barriers.

Several other studies have described marked longitudinal shifts in trout distribution attributable to slope (Fausch, 1989; Gard & Flittner, 1974; Kocovsky & Carline, 2005; Larson & Moore, 1985; Vincent & Miller, 1969). Longitudinal movement for trout in steep sloped streams is difficult (Kruse et al., 1997) and slope may limit upstream distribution of Brook (Dunham et al., 2002; Macphee, 1966), Rainbow (Larson & Moore, 1985), and Brown Trout (Diana et al., 2004; Kennedy & Strange, 1982). There are also potentially dramatic habitat differences in high gradient streams relative to low gradient streams, such as colder temperatures and different ratios of pools to riffles (Gard & Flittner, 1974; Vincent & Miller, 1969). Our slope metric potentially captures several important elements of the physical stream habitat and immediate surroundings not available or quantified in our dataset (e.g., stream size, order, width, depth, discharge, riparian vegetation, habitat composition, woody cover, substrate; Flint, 1974; Hubert & Kozel, 1993), which are known to be important components of trout habitat quality and regulators of trout distribution (DeRolph et al., 2015; Rahel & Nibbelink, 1999; Rashleigh et al., 2005).

We hypothesized that precipitation would be negatively correlated with Brook and Brown Trout probability of occurrence and positively correlated with Rainbow Trout probability of occurrence because of well-documented impacts of winter and spring high flow events on Brook Trout eggs or recently emerged fry (e.g., Fausch, 2008; Kanno et al., 2017). We observed the opposite pattern. We characterized mean precipitation during March per sampling site to attempt to capture stressful high flow events surrounding Brook and Brown Trout emergence; however, March and annual precipitation were highly correlated and mean annual precipitation was a stronger predictor of occurrence for all species, hence March precipitation was not included in global models.

In some cases, Brook Trout upstream distribution is thought to be limited by small stream sizes and insufficient pool habitat to survive winter freezes (Fausch, 1988; Gard & Flittner, 1974). Relative to Rainbow and Brown Trout, Brook Trout prefer slower velocities and deeper pools (Cunjak & Green, 1983; Kanno et al., 2012; Magoulick & Wilzbach, 1997; Rose, 1986) and are adapted to low-gradient streams (Larson & Moore, 1985; Platts, 1976). Therefore, it is plausible that we observed Brook Trout occurrence as positively associated with annual precipitation because greater annual rainfall enhances pool habitats in upstream reaches where Brook Trout are relegated.

Allopatric Brook Trout distribution did not appear to differ meaningfully from the distribution of more general Brook Trout populations. Although percent combined agriculture and development and percent forest were not included in the global model for any species due to high correlations within land use variables and lower explanatory power than percent agriculture, allopatric Brook Trout were significantly negatively related to percent combined agriculture and development ($p = 0.03$, $\beta = -0.52$) and positively related to percent forest ($p = 0.04$, $\beta = 0.50$) in single-variable models; no other species were significantly related to these variables. This indicates that although sympatric and allopatric Brook Trout seem to be similarly affected by geomorphology, land use, and climate, allopatric populations are more sensitive to subwatershed land use characteristics than general Brook Trout populations. In general, it does not appear that presence of nonnative species causes substantial changes in distribution of Brook Trout at the southern extent of their range (as assessed via comparisons of the general and allopatric Brook Trout SDMs), despite interspecific interaction effects being exhibited elsewhere (e.g., Wagner et al., 2013; Wenger et al., 2011).

It is interesting that land use variables generally were not important predictors of occurrence for any of our SDMs. Land use is widely known to influence trout distribution, including several of the same characteristics used in this study (e.g., DeWeber & Wagner, 2015; Hudy et al., 2008; Kanno et al., 2015; Wagner et al., 2013). Our results suggest that geomorphic and climate variables characterized at the sampling site are better predictors of the relative distribution of trout species in Southern Appalachia than subwatershed land use. It is possible that we did not observe patterns in land use and trout distribution because of the coarse spatial scale of subwatershed land use characterization relative to stream sampling site characterization of geomorphologic and climate variables. However, subwatershed-scale models perform better than watershed- or catchment-scale models for assessing Brook Trout occurrence (Hudy et al., 2013), and spatial scales much coarser than subwatershed (e.g., state-wide characteristics or ecological drainage units) have revealed important patterns between environmental gradients and stream fish populations (Angermeier & Winston, 1999; DeWeber & Wagner, 2015). In general, land use in high elevation Southern Appalachian subwatersheds is similar across spatial scales (e.g., 50 km stream buffer, catchment, subwatershed; Bozeman unpublished data).

The lack of observed relationship between our subwatershed-scale land use predictors and occurrence of trout species in SDMs mirrors the results of our trout balance model, where all predictor variables were summarized at the subwatershed scale. The trout populations included in this study are at the far southern extent of perennial self-sustaining trout habitat in the eastern United States. As a function of this far-South distribution, Southern Appalachian trout populations are condensed into relatively few watersheds at high elevations with highly similar land use characteristics. Subwatersheds with trout populations in our study display relatively little variation in land use characteristics included in this study (Table 3.1); most are heavily forested with marginal agriculture, development, or change. By comparison, studies that have shown land use influences on trout distribution have either covered a larger spatial extent with far greater land use variation (e.g., Hudy et al., 2008), or studied less concentrated populations nearer the center of their distribution in more variable landscapes (e.g., Connecticut; Kanno et al., 2015).

Site-level geomorphologic and climate variables dominated the best-supported models for our SDMs, but they were the least important variables in our subwatershed trout balance analysis. For example, slope was the most important predictor of probability of occurrence for individual species SDMs and the least important predictor in the trout balance model. Calculating slope at the stream sampling site captures important elements of the habitat that fish experience directly. Condensing slope to mean segment slope per subwatershed collapses critical within-subwatershed nuance important for characterizing relative trout distribution. For regional studies of relatively spatially condensed populations, fine-scale predictor variable characterization may do a better job of capturing important and interesting variation in predictor and response variables than subwatershed-scale analyses.

Our trout dataset did not contain true absence values, and thus we were restricted to modeling relative trout distribution for each species using samples where at least one trout was observed. Future modeling approaches should consider investigating relationships between predictor variables and trout distribution over a more complete range of stream habitats and subwatersheds – and not just those that contain trout – in Southern Appalachia. This approach would provide a more comprehensive understanding of the nature of the effect of environmental gradients on trout distribution and may reveal unimodal responses of trout distribution to environmental gradients that provide additional insight into the responsiveness of trout to these gradients. For example, it would be useful to understand how downstream limits of Rainbow and Brown Trout are affected by the environmental and biological characteristics of lower sites. Likewise, understanding how Brook Trout distribution is limited upstream could provide important insight into potential consequences of climate change if downstream distributional limits shift due to warming stream temperatures and encroaching Rainbow and Brown Trout.

We used mean maximum August temperature in our models as a surrogate for stream temperature, which may not be an accurate depiction of actual water temperature. Many streams in Appalachia are influenced by groundwater, which could decouple air and stream temperatures, especially during high seasonal temperatures (Kanno et al., 2014). Groundwater influence in mountain streams may provide important thermal refugia in the face of climate change (Briggs et al., 2018), and mountain streams may remain cold due to local topographical controls (Isaak et al., 2016). To properly capture the effects of temperature (current and projected) on trout distribution, it will be important to include stream temperature (if available) in modelling strategies, or at least quantify the expected relationship between air and stream temperature (e.g., Snyder et al., 2015).

Our characterization of mean March precipitation from 1991 – 2020 and the temporal scale of our trout dataset (2010 – 2020) likely precluded our ability to detect the potential effects of seasonal high flow events that may take place over the span of a few consecutive days that can destroy entire age classes (e.g., Kanno et al., 2017; Wenger et al., 2011). Although our results revealed an interesting and unexpected positive relationship between mean annual precipitation and Brook Trout probability of occurrence, future modelling approaches should explore the dynamics and trade-offs of damaging pulse high flow events compared to the positive effects of annual precipitation at finer temporal (and possibly spatial) scales. Lastly, future modelling strategies should compare relationships between environmental gradients and trout distribution across spatial scales in populations nearer the center of their natural distribution to determine if our lack of observed patterns between subwatershed trout balance and predictor variables was an artifact of spatially condensed populations near the edge of their distribution, or if trout distribution-environmental gradient relationships generally are better described at finer spatial scales.

Conservation implications & conclusions

Our results have important implications for the conservation and management of trout populations in Southern Appalachia. Subwatershed (or larger) conservation strategies that emphasize the importance of preserving subwatershed-scale processes that maintain ecological integrity and stream community biodiversity for all life stages of all species (i.e., Native Fish Conservation Areas; Williams et al., 2011) are promising and productive, especially in Southern Appalachia where globally significant freshwater biodiversity and landscape development are at odds (Little Tennessee NFCA Designation 2015) (Jenkins et al., 2015). However, targeted conservation strategies for native Brook Trout populations should focus on maintaining or restoring specific stream segments with known native, allopatric populations, rather than at the subwatershed scale where habitat differences are not discernible from other trout.

In high elevation, steep-sloped streams where most Southern Appalachian Brook Trout are found, local geomorphology and climate are critical factors that maintain Brook Trout habitat for both allopatric and sympatric populations. Brook Trout restoration efforts should prioritize stream segments with cold water temperatures and habitat complexity that provides or creates pools as refugia from stressful high and low flows. Stream warming due to climate change could potentially harm Brook Trout populations beyond the compensatory effects of density-dependence (Bassar et al., 2016; Grossman et al., 2010; Huntsman & Petty, 2014) and likely would shift the competitive advantage to Rainbow and Brown Trout who prefer warmer stream temperatures. Prioritizing headwater stream segments with considerable groundwater influence and/or local topographic control may insulate Brook Trout populations from the effects of climate change (Briggs et al., 2018; Isaak et al., 2016) and preserve their competitive superiority over nonnative trout. Lastly, special priority should be given to stream segments with high connectivity that potentially allow for Brook Trout movement between cold headwater tributaries via mainstems with thermal refugia, which maintains genetic diversity and generally supports larger individuals who potentially enhance connected metapopulations via greater fecundity (Huntsman et al., 2016; Petty et al., 2012; Petty et al., 2005).

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Tables

Table 3.1. Summary and descriptive statistics of all predictor variables.

Metric	Abbrev.	Category	Description	Units	Range	Mean
Elevation	Elev	Geomorphic	Elevation at sampling site	m	310.0 - 1588.4	827.6
Stream Slope	Slope	Geomorphic	Slope of sampling site NHDFlowline segment	m/m	0.0 - 0.2	0.07
Percent Agriculture	Ag	Land use	Percent of HUC12 classified as Agriculture in 2016	%	0.0 - 29.2	2.7
Percent Developed	Dev	Land use	Percent of HUC12 classified as Developed in 2016	%	0.0 - 34.2	4.8
Percent Developed + Agriculture	DevAg	Land use	Percent of HUC12 classified as Developed or Agriculture in 2016	%	0.0 - 42.6	7.5
Percent Forest	Forest	Land use	Percent of HUC12 classified as Forest in 2016	%	56.2 - 99.6	90.9
Percent Change	Change	Land use	Percent of HUC12 that has shifted from one land use class to another from 2001 - 2019	%	0.3 - 15.0	4.0
Mean Annual Precipitation	Ann Ppt	Climate	Average annual precipitation from 1991 - 2020	mm	1102 - 2484	1661
Mean March Precipitation	Mar Ppt	Climate	Average March precipitation from 1991 - 2020	mm	94.9 - 215.9	143.3
Mean Annual Temperature	Ann Tmp	Climate	Average annual temperature from 1991 - 2020	C	8.6 - 14.9	12.0
Mean Maximum August Temperature	Aug Tmp	Climate	Average maximum August temperature from 1991 - 2020	C	21.6 - 30.5	26.6

Table 3.2. Pearson correlation coefficients for the full suite of predictor variables.

	Elev	Slope	Ann Tmp	Aug Tmp	Ann Ppt	Mar Ppt	Dev	Ag	DevAg	Forest
Slope	0.43									
Ann Tmp	-0.87	-0.42								
Aug Tmp	-0.96	-0.44	0.91							
Ann Ppt	0.33	0.06	0.00	-0.26						
Mar Ppt	0.31	0.07	0.01	-0.23	0.95					
Dev	0.16	0.00	-0.24	-0.21	-0.20	-0.29				
Ag	-0.10	-0.02	-0.07	0.08	-0.53	-0.60	0.39			
DevAg	0.04	-0.01	-0.19	-0.09	-0.43	-0.52	0.86	0.81		
Forest	-0.06	0.02	0.18	0.10	0.40	0.50	-0.83	-0.79	-0.97	
Change	0.14	-0.05	-0.21	-0.18	-0.13	-0.19	0.39	0.42	0.48	-0.52

Table 3.3. Global and best-supported models for each species as ranked by Akaike's information criterion (AICc) and filtered by delta values and uninformative parameter rules (Arnold 2010).

Global Model	**Slope + Aug Tmp + Ann Ppt + Ag + Dev + Change**			
Species	**Models (delta < 5)**	**delta**	**w**	**AUC**
Brook Trout	Slope + Aug Tmp + Ann Ppt	0	1.00	0.969
Allopatric Brook Trout	Slope + Aug Tmp + Ann Ppt	0	1.00	0.950
Rainbow Trout	Slope + Aug Tmp + Ann Ppt	0	0.89	0.939
	Slope + Aug Tmp + Ag	4.18	0.11	
Brown Trout	Slope + Ann Ppt + Ag + Change	0	0.511	0.953
	Slope + Ann Ppt + Ag	0.91	0.324	
	Slope + Ann Ppt	2.27	0.165	

Table 3.4. Parameter estimates for predictor variables included in the best-supported model for each species. Values are mean ± SE. Note that elevation and development have been removed from the table because they were not included in any of the best-supported models.

Model	Slope	Aug Tmp	Ann Ppt	Ag	Change
Brook Trout	1.81 ± 0.33	-1.46 ± 0.40	1.18 ± 0.38		
Allo. Brook Trout	1.13 ± 0.23	-1.01 ± 0.32	1.13 ± 0.33		
Rainbow Trout	-0.88 ± 0.21	0.93 ± 0.30	-0.91 ± 0.31		
Brown Trout	-1.56 ± 0.29		-1.14 ± 0.37	-0.85 ± 0.40	0.59 ± 0.35

Table 3.5. Best performing models for subwatershed trout balance analysis as identified by model selection, filtered by delta ≤ 5. We also removed models within two delta AICc of the best model if they were slightly more complex versions of the best model based on Arnold's (2010) recommendation.

Model	delta	w
Global: Max Elev + Slope + Mar Ppt + Ag + Dev + Change	13.36	
Ag	0.00	0.36
Null	1.08	0.21
Mar Ppt	2.00	0.13
Max Elev	3.08	0.08
Change	3.16	0.07
Dev	3.22	0.07
Slope	3.22	0.07

Figures

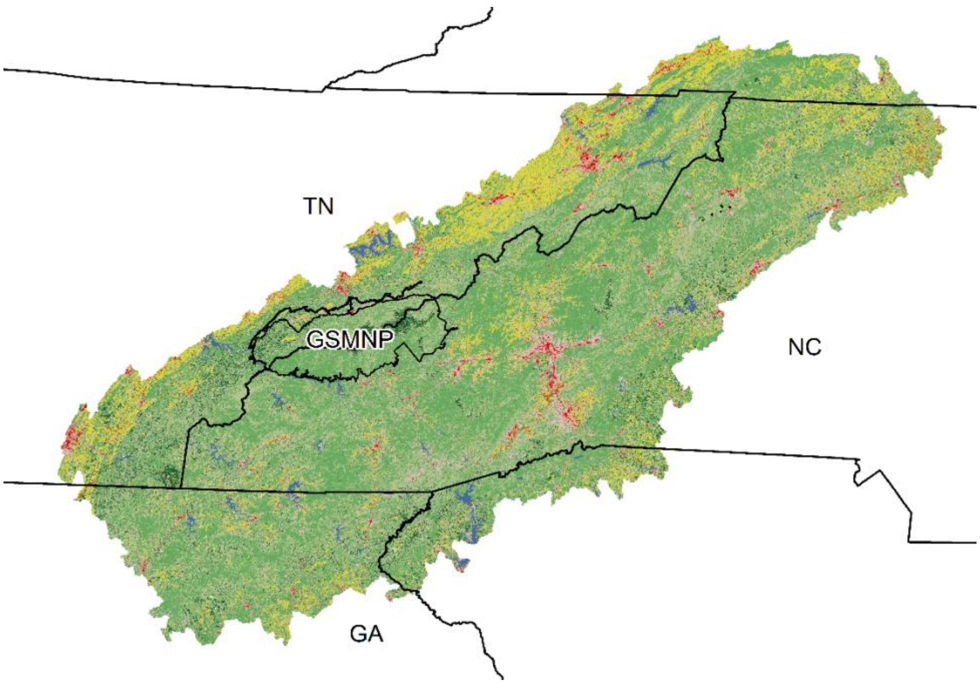

Figure 3.1. Map of the study area in Southern Appalachia with trout data regions labelled. This map displays land use classifications in 2016. GSMNP = Great Smoky Mountains National Park.

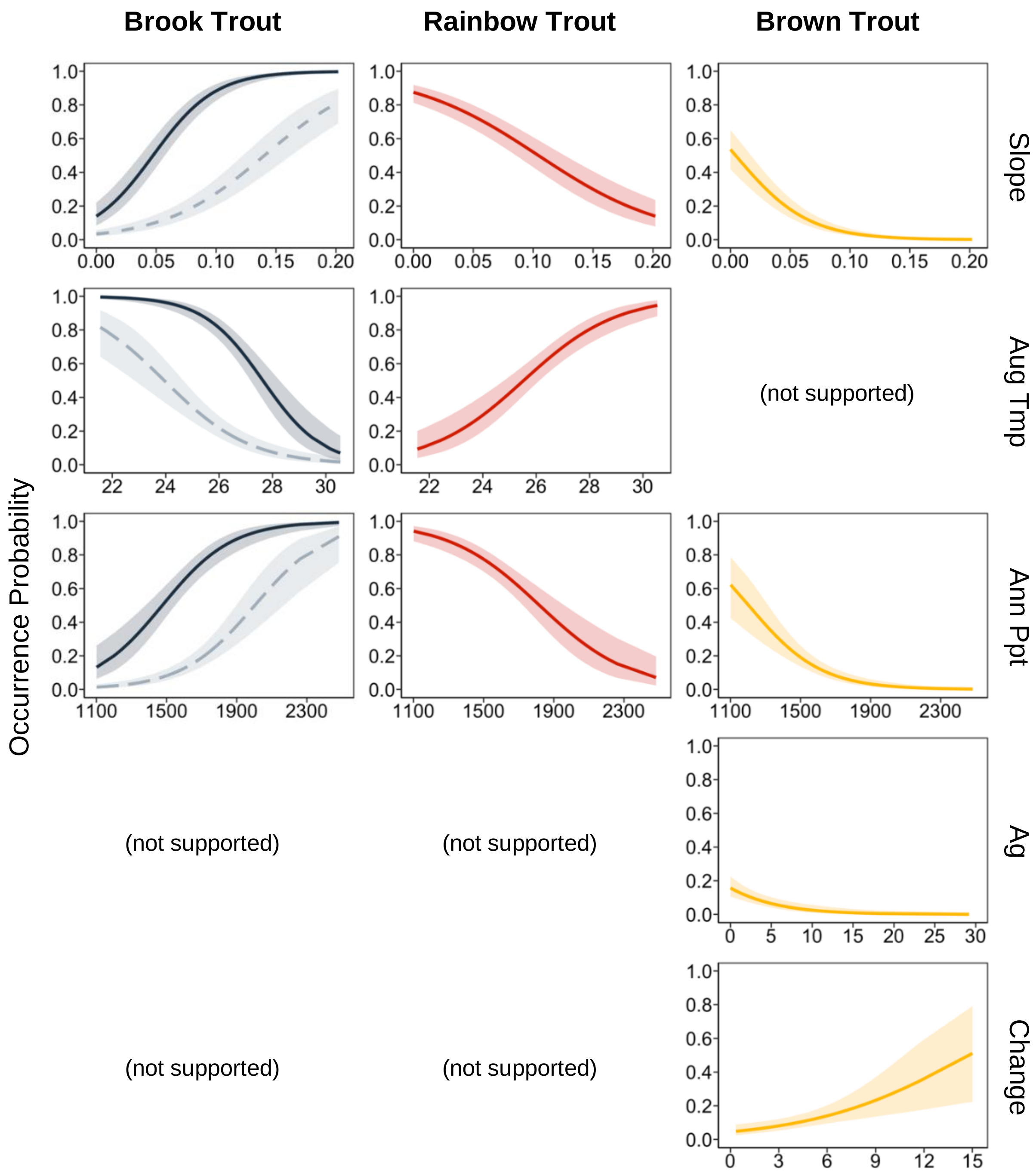

Figure 3.2. Marginal effects (± SE) of predictor variables included in the best-supported models. Allopatric Brook Trout model predictions are dashed lines.

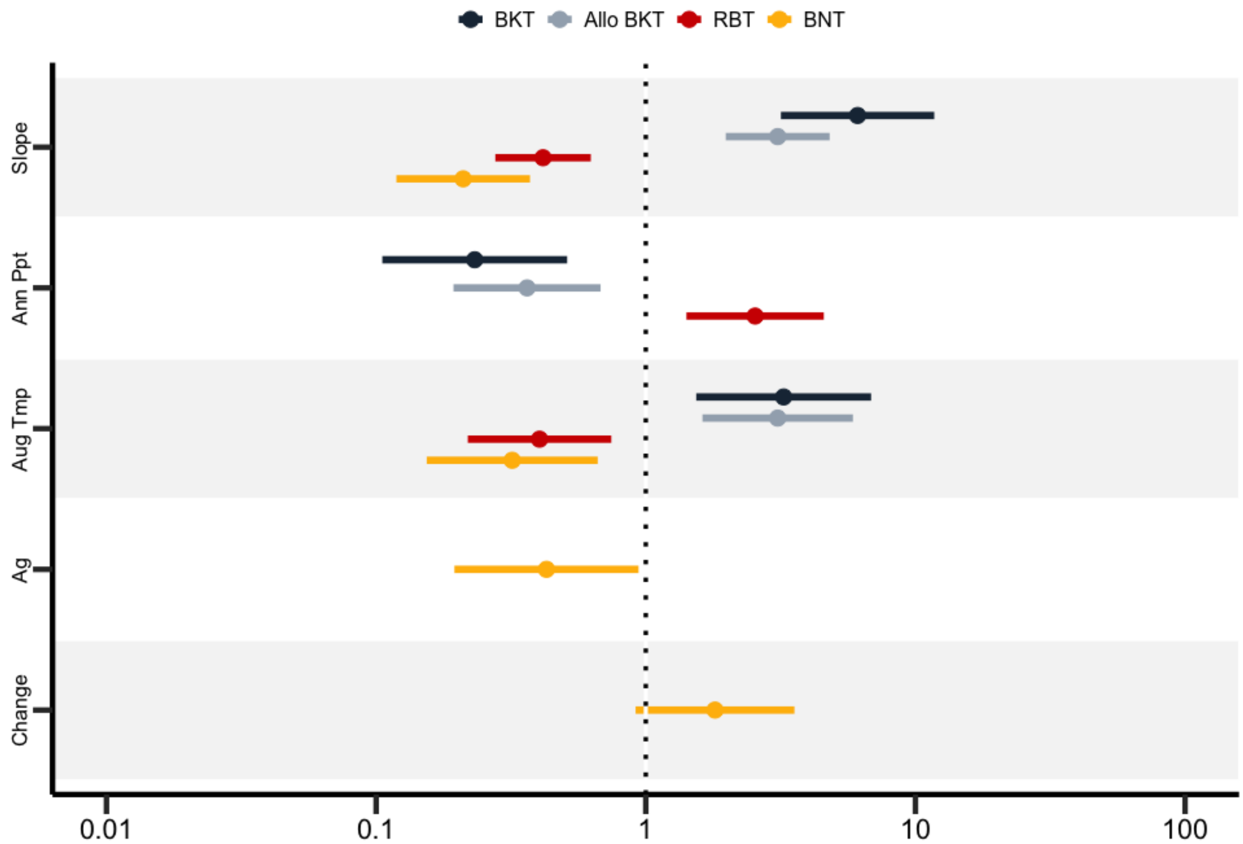

Figure 3.3. Odds ratios for predictor variables included in best-supported models for each species. Values are means ± 95% confidence intervals. Values below the y-intercept of 1 indicate negative effects; values above 1 are positive effects.

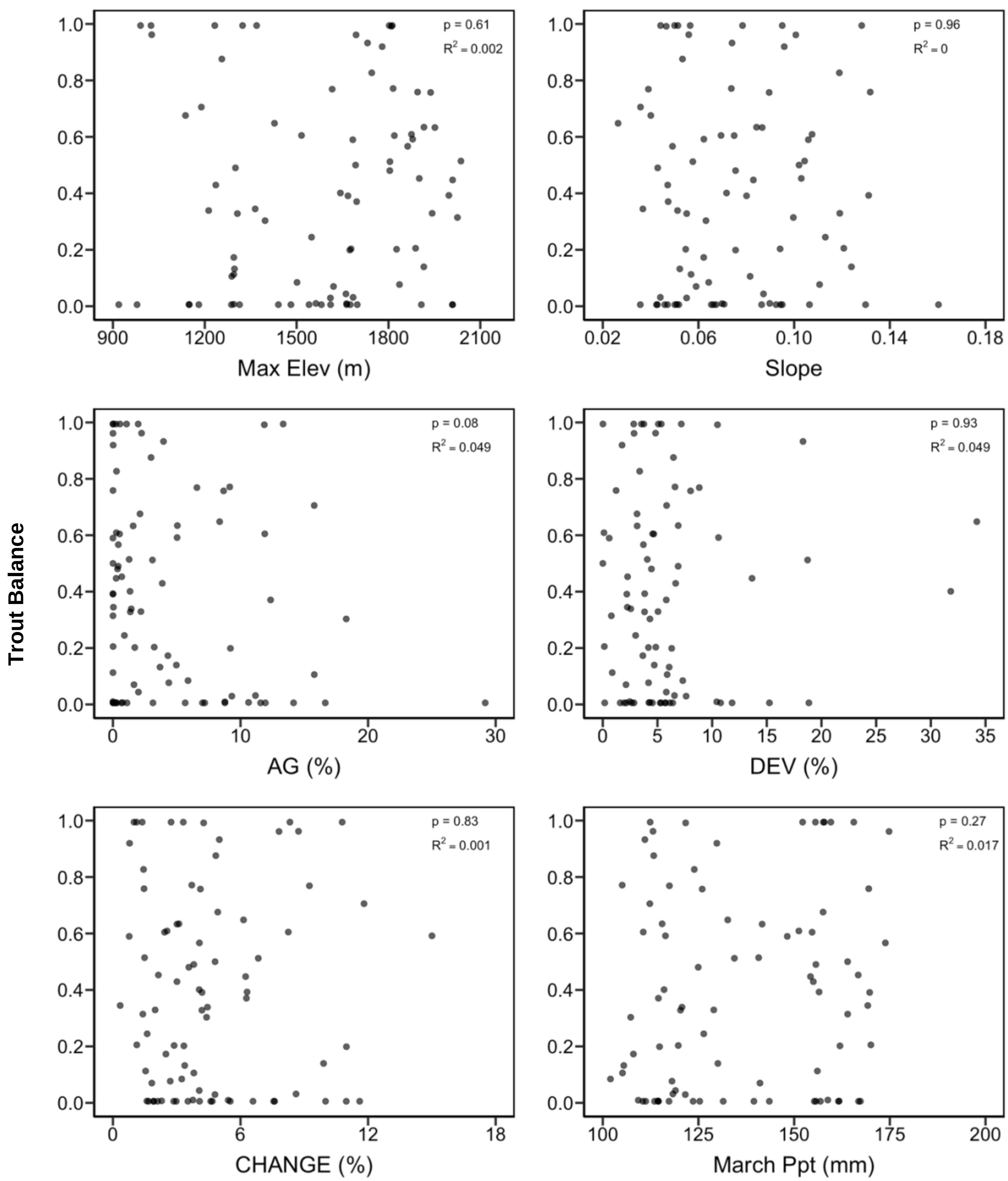

Figure 3.4. Relationships between final predictor variables and subwatershed trout balance. Beta regression p-values and pseudo R^2 values reported.

CHAPTER 4

DO CONSERVATION FILMS GENERATE SUPPORT FOR CONSERVATION? A CASE STUDY USING TRANSPORTATION THEORY AND *HIDDEN RIVERS*[3]

[3] Bozeman, B.B., C.M. Condit, and G.D. Grossman. Revised and resubmitted to *Science Communication*, 6/28/22

Abstract

We conducted an experiment to determine if watching a conservation film motivated people to support conservation and if transportation and emotion were correlated with shifts in conservation support. Viewers of a short or feature length conservation film exhibited greater alignment with story-centric beliefs and conservation behavior interest than individuals who viewed a control film. Transportation was correlated with conservation belief alignment and behavior interest; emotion was correlated with behavior interest. Conservation films can be engaging and persuasive and are potentially powerful tools for generating conservation support among audiences not previously interested in this topic. Future research should continue to explore engagement and persuasion dynamics within this growing and important genre.

Introduction

We are in the midst of a human-driven environmental crisis. The effects of anthropogenic alteration of the environment are increasingly apparent and are realized in many related forms, including global climate change (IPCC, 2021), biodiversity loss and mass extinctions (Ceballos et al., 2015; Koh et al., 2004), and the collapse of ecosystem services, including food production (Mehrabi, 2020). Urgent, creative conservation is needed to address these issues and reconcile human resource use with natural system integrity (Bennett et al., 2017; Jenkins et al., 2015; Moon & Blackman, 2014).

Science communication focused on the environment can potentially support conservation initiatives by motivating the public to engage in environmentally responsible behavior (Bieniek-Tobasco et al., 2019; Vaske & Kobrin, 2001), support environmental policy (Cooper & Nisbet, 2016; Vasi et al., 2015), improve environmental literacy (Bickford et al., 2012), and strengthen science-public relationships (Nisbet & Scheufele, 2009). One potentially promising method of engaging with the public on environmental issues is through narratives, which are engaging, informative, and persuasive (Busselle & Bilandzic, 2009; Moyer-Gusé & Nabi, 2010; Singhal & Rogers, 2012).

Conservation narratives are messages designed to engage the public on topics relating to the state of the natural world with implicit or explicit attempts to change the way people feel or act towards the resource of interest. Conservation issues fit nicely within narrative frameworks; they have characters (resources and users, human and non-human), conflict (threat or active decline), and some attempt at resolution (a success story, a conservation plan, a call to action) woven together in a meaningful series of events that occur in fixed space and time (Kreuter et al., 2007). Films are a particularly promising medium for conservation narratives because they have been shown to be more persuasive than print media (Shen et al., 2015), can connect viewers with species, ecosystems, and landscapes in emotionally engaging ways, and can be widely disseminated via box office releases, community showings, streaming services, and websites (Howell, 2014; Manzo, 2017; Silk et al., 2018; Whiteman, 2003). Increases in smartphone and social media usage (Holt, 2016; Van Laer et al., 2019) are providing new opportunities for digital storytelling and some conservation organizations have devoted considerable resources to creating films easily viewed on personal devices (e.g., American Rivers' Film Collection).

Conservation narrative films are increasingly popular. A search on the popular online streaming service Netflix for films related to 'conservation' returns greater than 30 films and series about the human-natural world relationship. Hollywood blockbusters (e.g., *The Day After Tomorrow,* 2004), feature length documentaries (*e.g., An Inconvenient Truth*, 2006), and films produced by environmentally conscious corporations and conservation nongovernmental organizations underscore the popularity of narrative films for conservation communication. However, the research base remains thin on how or if they achieve their goals of shifting public perception about the natural world and inspiring conservation behavior.

There is much published research on the efficacy of environmental communications, but only a small portion of this research has investigated the influence of films (Schäfer & Schlichting, 2014), most of which focuses on climate change films.

Viewers of *The Day After Tomorrow* and *An Inconvenient Truth* have been shown to express concern about global climate change and show interest in engaging in environmentally friendly behavior (Beattie et al., 2011; Jacobsen, 2011; Leiserowitz, 2004; Lowe et al., 2006; Nolan, 2010). These films also increased concerns for other environmental issues (Lowe et al., 2006), caused viewers to support film distribution (Lin, 2013), and generated internet traffic on climate change websites (Hart & Leiserowitz, 2009). Viewers of *The Age of Stupid*, a feature length climate change film, exhibited greater concern for global climate change, motivation to act, and sense of agency, but these effects did not persist over time (Howell, 2011, 2014). Climate change films may cause viewers to be more likely to engage in ecofriendly behavior out of a sense of personal obligation (Bilandzic & Sukalla, 2019); however, they also may decrease intent to engage in ecofriendly behavior if viewers do not believe the behavior will make a difference (Bieniek-Tobasco et al., 2019).

Research on the impact of conservation films on topics other than climate change is sparse. Viewers of films about water conservation (Kantola et al., 1983), eco-friendly home renovations (Rhodes et al., 2016), and aquaculture (Rickard et al., 2021) generally were shown to display greater interest in environmental issues and behaviors compared to people who had not viewed these films. Environmental films about potential human risks associated with hydrofracturing and genetically modified organisms increased support for regulatory policies among viewers (Cooper & Nisbet, 2016) and contributed to greater online discourse about the environment and increased political activism (Vasi et al., 2015). Lastly, embedding pro-environmental messaging in comedic television shows can increase conservation behavior intent (Moyer-Gusé et al., 2019).

Research investigating the effects of biodiversity or wildlife conservation films is especially sparse, despite the proliferation of such films in recent years (Silk et al., 2018) and the severity and urgency of the ongoing biodiversity crisis (Ceballos et al., 2015; Jenkins et al., 2015). Viewers of *Fly Away Home*, a documentary film about bird migrations, expressed greater conservation beliefs and behavior intent than people who did not view the film (Chen & Lin, 2014). Researchers have debated how artistry and emotional framing of biodiversity conservation films might influence their impact on the public (Jones et al., 2019; Silk et al., 2018; Wright, 2010), but the consensus is that more research is needed to assess the role of biodiversity conservation films in shifting public perception about this critical issue.

The growing body of research on the impact of environmental films on audience beliefs and behaviors is encouraging; however, the insight gained from most of these studies is limited because: 1) they rely on data collected from individuals who willfully sought out the films (and thus are likely already supportive of conservation), and 2) they do not consider the mechanisms that potentially predict belief and behavior shifts (Bilandzic & Sukalla, 2019; Jones et al., 2019). We addressed these shortcomings by conducting an experiment to investigate if and how dimensions of narrative engagement are correlated with the effects of viewing a conservation film on a population of university students.

Narrative Engagement & Transportation Theory

Narratives can persuade people to feel or act differently because of characters, events, or phenomena depicted in the story (Avraamidou & Osborne, 2009). The persuasive effects of narratives are dependent upon engagement with the story. There are multiple dimensions of narrative engagement including transportation (Green & Brock, 2000), identification (Cohen, 2001), and emotional engagement and attentional focus (Busselle & Bilandzic, 2009). Studies of narrative engagement and persuasion typically assess beliefs of individuals before and after exposure to a narrative and compare shifts in beliefs to measures of engagement (e.g., Beattie et al., 2011; Cooper & Nisbet, 2016; Green & Brock, 2000).

In this study, we focused on the relationship between transportation and emotion and the persuasive effects of a conservation film. Moreover, this study targets audience members who have moderate to low alignment with conservation beliefs and intentions. This is presumably a primary audience that advocacy-oriented filmmakers wish to reach. Previous research in narrative transportation has not segmented audiences by prior belief alignment. This may mask both the persuasive effects on these desired target audiences and also the underlying mechanisms responsible for these dynamics, as suggested by recent research on fear appeals by Shen and Dillard (2014). Their work showed that "audience segmentation reveals different curves for different groups as well as differential associations between those curves and persuasion" (p. 95). Their methodological and theoretical analysis is likely to apply to other emotions and persuasive mechanisms such as transportation. Their work indicates that strong increases in belief alignment among those who are already in agreement with a position may mask the patterns (including boomerang effects) among other groups. Targeted attention to people who disagree with a message has also become a locus of research attention in climate change communication regarding the “Gateway Belief Model” (GBM) regarding scientific consensus as a driver of beliefs (Dixon et al., 2017; Van der Linden, 2021). This study therefore provides a novel and potentially fruitful contribution by directing studies of narrative transportation effects toward dissenting target audiences. Because narrative transportation is presumed in the literature to operate through mechanisms that may include emotions (such as fear) but also extend beyond mechanisms such as group consensus (GBM), if this study provides evidence that narrative transportation is linked to persuasive effects among conservation skeptics, this would provide a firm basis for more complex theoretical and methodological explorations analogous to those currently taking plce in GBM and fear appeal research.

Transportation into a narrative world is a convergent mental process that involves the integration of imagery, emotion, and attentional focus on the events and characters in a story (Green & Brock, 2000; 2002). Being transported into a story involves losing awareness of oneself and immediate physical and psychological surroundings, experiencing emotions and stimuli relevant to the story, and then returning to the real world, perhaps with altered beliefs or values (Gerrig, 1993; Green & Brock, 2000; Nell, 1988). Because being transported involves losing awareness of oneself and becoming entirely cognitively engaged in an alternate world, transportation is thought to be incompatible with counterarguing (de Graaf et al., 2009; Slater & Rouner, 2002) (but see Moyer-Gusé & Nabi, 2010). Individuals who are completely immersed in a story are deterred from actively refuting the beliefs expressed in the story, even if those beliefs are inconsistent with personal beliefs. This has important implications for conservation narratives, which overtly or subtly seek to persuade people to feel or act differently about the natural world, potentially at a cost to resource use or economic development.

Transportation is one of the most studied dimensions of narrative engagement (Busselle & Bilandzic, 2009; de Graaf et al., 2009; Murphy et al., 2011). Transportation into film has been shown to predict shifts in knowledge, attitudes, and behavior toward public health initiatives (Moyer-Gusé & Nabi, 2010; Williams et al., 2010), regulatory environmental policy (Cooper & Nisbet, 2016), aquaculture (Rickard et al., 2021), and avian conservation (Chen & Lin, 2014). Transportation usually is assessed with Green and Brock's (2000) original scale, which measures transportation as a function of emotional involvement, cognitive attention, feelings of suspense, lack of awareness of surroundings, and mental imagery. This scale was developed for use with written text, and accordingly pays special attention to the role of imagery as a subcomponent of transportation (Green & Brock, 2000; 2002). The transportation scale has been extended (e.g., Appel et al., 2015; Busselle & Bilandzic, 2009; de Graaf et al., 2009; van Laer et al., 2014) and adapted for different mediums (e.g., film; Williams et al., 2010), but each iteration retains key elements of transportation: imagery, emotion, and attention.

Emotion is an important element of how we engage with narratives, both within and beyond the context of transportation (Green et al., 2012; Mazzocco et al., 2010). Emotional engagement is story-specific, and may include vicariously experiencing the emotions of a character (Cohen, 2001), feeling emotions for a character (Moyer-Gusé, 2008), or experiencing discrete emotions – alone or in sequence – due to events depicted in the story (e.g., Green et al., 2012; Nabi, 2002; 2015). Emotional engagement has been shown to influence persuasive outcomes of narratives (Busselle & Bilandzic, 2009; de Graaf et al., 2009), including inspiring pro-environmental beliefs and behavior following exposure to environmental messages (Nabi et al., 2018; Ojala, 2012). Eliciting a strong emotional reaction from the public may increase their perception of risks associated with environmental degradation (Beattie et al., 2011; Weber, 2006).

Hidden Rivers is of particular interest for the study of the workings of emotion in films because its focus on the ecosystem as a whole is a desirable theme in many persuasive efforts regarding conservation. However, if emotional engagement requires identification with individual characters, then conservation films – and other ecosystem-oriented films – that do not rely heavily on devices such as personification of individual animals – might not be able to achieve the persuasive effects sought. Certainly, many film makers turn heavily to personifying individual animals and telling their individual stories (an elephant and its child crossing a drought-stricken landscape; a polar bear mother and its cub trying to navigate depleted ice floes or a pair of penguin mates re-finding each other after the annual separation). If *Hidden Rivers* is able to elicit the targeted emotional effects, this would demonstrate that this kind of emotional effect is not dependent on heavy personification of individual animals.

Another characteristic of narratives that potentially impacts audience engagement or persuasion is length. Message length – via increased number of arguments – has been shown to be positively correlated with persuasion for audiences with low topic interest, who evaluate messages using peripheral or heuristic cues

(Johnson & Eagly, 1989; Petty & Cacioppo, 1984; Wood et al., 1985). Narrative engagement, which is cognitively disparate from these elaborative or systematic processing modes (Green & Brock, 2000; Slater & Rouner, 2002), also is potentially affected by message length. Longer narratives increase exposure to characters and duration of story-evoked emotions, and they provide more opportunities for immersion in the story for longer periods of time (Green et al., 2004; Green et al., 2008; Nabi & Green, 2015; Tal-Or & Cohen, 2010; Warren, 2020), which may subsequently influence persuasion (Leventhal & Niles, 1965; McKinley, 2013). Even in studies that do not explicitly evaluate the role of length in narrative engagement and transportation, researchers take care to select message interventions of similar length or otherwise control for length differences (e.g., Alam & So, 2020; Bezdek & Gerrig, 2017; Chen & Chang, 2017; Das et al., 2017; Han & Fink, 2012), which implicitly recognizes the potential influence of message length on reception.

Although the literature therefore leads to the hypothesis that greater length would be correlated with greater transportation, the value of extended viewing cannot be taken for granted. There does not appear to be a minimum temporal requirement for transportation. Audiences can be transported and persuaded with static one-page advertisements (Escalas, 2004; Phillips & McQuarrie, 2010) or over several consecutive hours of television (Warren, 2020). There is therefore a need for an empirical test, as whether engagement and persuasion are influenced by message length. Such a test is warranted because length can be one of the most critical considerations for communicators.

Narrative engagement theory confirms that transportation and emotion are important for persuasion. Individuals who are exposed to pro-conservation beliefs and behaviors by being transported and emotionally engaged by a conservation film should be more likely to align with those beliefs and express interest in engaging in those behaviors than individuals who have not viewed the film or who have been exposed to those beliefs and behaviors in a didactic, overtly persuasive format (Chen & Lin, 2014; Green & Brock, 2000; Moyer-Gusé et al., 2019; Slater & Rouner, 2002). Additionally, longer pro-conservation messages should provide greater opportunities for viewers to engage with the story, internalize pro-conservation beliefs, and observe pro-conservation behaviors (Green, 2008). We applied transportation theory to the growing genre of conservation films and evaluated the relationship between message length and engagement and persuasion. We explored three questions: 1) Can a conservation film increase conservation support by generating pro-conservation beliefs and/or interest in engaging in conservation behavior among moderate to low alignment audiences?, 2) Are transportation and emotion related to the persuasive effects of a conservation film that does not have high personification?, and 3) Does film length influence narrative engagement or persuasive effects of a conservation film? We were interested in duration of persuasive effects, so we also included a second, delayed assessment. To address these questions, we evaluated the following hypotheses:

Hypothesis 1: Alignment with pro-conservation beliefs will be greatest for viewers of a feature length conservation film, intermediate for viewers of a short conservation film, and least for viewers of a non-conservation film both immediately after film exposure (H1a) and several days-weeks later (H1b).

Hypothesis 2: Interest in engaging in conservation behavior will be greatest for viewers of a feature length conservation film, intermediate for viewers of a short conservation film, and least for viewers of a non-conservation film both immediately after film exposure (H2a) and several days-weeks later (H2b).

Hypothesis 3: Transportation (H3a) and emotional engagement (H3b) will be significantly greater for viewers of the feature length conservation film than the short conservation film or the non-conservation film.

Hypothesis 4: Alignment with pro-conservation beliefs will be positively correlated with transportation (H4a) and emotion (H4b).

Hypothesis 5: Interest in engaging in conservation behavior will be positively correlated with transportation (H5a) and emotion (H5b).

Materials and Methods

Participants

Undergraduate students (n = 280) at a large public university in the US South participated in our study in exchange for course credit and a chance to win a gift card. We screened our sample population for individuals with low to moderate conservation support. Our sample was equal parts male and female (M = 139, F = 140, one participant preferred not to answer) with an average age of 19 (range: 18 – 30). On a scale from very conservative (1) to very liberal (7) our sample was slightly conservative (mean = 3.7, SD = 1.6, self-reported).

Stimuli

Our primary treatment was exposure to *Hidden Rivers* (HR, 56:00 min.), a feature length film about freshwater biodiversity in the Southern Appalachian region of the United States. *Hidden Rivers* details the rare and threatened nature of aquatic ecosystems in this region and emphasizes the urgent need for conservation. We selected *Hidden Rivers* as the primary treatment because it was of high cinematic and narrative quality, expressed pro-conservation beliefs, depicted conservation behaviors that could reasonably be adopted by participants, and is accessible in online formats for viewing on personal computers. After selection, we noted that the film does not include intense personification of animals, in contrast to many environmentally oriented films. We received permission from the filmmakers to use the film in the study.

The second treatment film was a shortened version of *Hidden Rivers* (SHR, 13:50 min.). We shortened the feature length version of *Hidden Rivers* with help from the filmmakers. Specifically, we used the final 13:00 minutes of the feature film, added the same introduction and opening credits, and added character name subtitles that appeared the first time each character was shown on the screen (to match the full film). Shortened *Hidden Rivers* maintained the same narrative quality as the full film, introduced characters in the same way, and depicted the same pro-conservation beliefs and behaviors. The filmmakers have since used similar versions of the shortened film in educational settings where feature length films are not practical.

The third treatment film was a short film about the Baja 1000, an outdoor motorsports race that takes place on the Baja Peninsula. This short film features activities occurring outdoors, but there are no pro-conservation beliefs or behaviors expressed in this film. In fact, this film depicts people engaged in activities that are detrimental to the environment. This film was our Content Control treatment (CC, 12:47 min) against which to compare the effects of HR and SHR, the conservation films. For more information about *Hidden Rivers*, visit: https://www.freshwatersillustrated.org/hidden-rivers.

Procedure

Participation in this study involved completing three surveys and viewing one of three treatment films. First, prospective participants completed a screening survey to determine preexisting conservation support. To mask the nature of the study, the screening survey asked students to indicate their level of support for a wide range of topics, including conservation of wildlife and natural resources in the United States. Students who indicated low to moderate support for conservation were invited to participate in the study within 24 hours of completing the screening survey. This screening was necessary because our focus was on *shifting* conservation support and so we wished to target an audience with low-to-moderate conservation support. Students in a pilot trial expressed strong conservation support, necessitating a screening step.

In the primary survey, participants were first asked to provide some basic demographic information and then were randomly assigned to one of the three treatment films (embedded within the survey software). Participants viewed the assigned film, and then immediately completed the remainder of the primary survey. To ensure that participants viewed their respective film, we included five multiple choice film-specific attentional questions and a timer function on the survey. Survey responses with more than one wrong attentional question answer or a survey duration less than the length of the treatment film were discarded from analyses.

The primary survey included several sections. We recorded participant self-reported political orientation on a 7-point Likert scale from very conservative to very liberal with a midpoint of neither conservative nor liberal (Petrocik, 2009). We estimated transportation using an 11-item scale (adapted for film) comprised of questions from Green and Brock (2000), Busselle and Bilandzic (2009), and deGraaf et al. (2009) scales (Table 4.1). We measured each transportation scale item on a 7-point Likert scale from strongly disagree to strongly agree. For emotional engagement, we asked participants to indicate the degree to which they experienced seven discrete emotions on a 7-point scale anchored by not at all and very much. The emotions were: anger, sadness, disgust, fear, happiness, surprise, and hope.

We measured shifts in conservation beliefs and behavior interest by asking participants to indicate the degree to which they agreed with beliefs expressed in HR and SHR and their interest in participating in conservation behaviors depicted in these films. We measured alignment with nine story-centric beliefs expressed in both HR and SHR on a 7-point Likert scale from strongly disagree to strongly agree (Table 4.2). We measured interest in engaging in six conservation behaviors (four behaviors modeled in HR and SHR, two behaviors associated with discussing or promoting the conservation films) on a 7-point scale from not at all to very much. Finally, we included the conservation support question from the screening survey to compare participant responses to the same question before and after film exposure.

We invited participants to complete the follow-up survey several days to weeks later (mean = 18 days, SD = 13). The follow-up survey contained the same questions on story-centric belief alignment, conservation behavior interest, and conservation support as the primary survey. Because participants received course credit for participating in the study, we were only able to collect survey response data until the end of the academic semester. More time elapsed between primary and follow-up survey responses for participants who signed up for the study earlier in the semester compared to those who signed up near the end of the semester. We timed the invitations for follow-up survey participation to maximize the time between surveys.

We summed transportation, emotion, story-centric belief, and conservation behavior interest responses, respectively, per study participant and then characterized responses per treatment film group. Item sequence within each question block (i.e., transportation, emotion, story-centric beliefs, and conservation behaviors) was randomized for each participant, but question block order was not. All elements of the study (participant recruitment, treatment films, and surveys) were administered online via the university's research participant portal and Qualtrics survey software during October – December 2020. We compared differences in survey responses between treatment film groups (unpaired) and within groups over time (paired, repeated measures) using analyses of variance. We evaluated relationships between predictor and response variables using simple linear regression. All statistical analyses were performed in R statistical software (R core team, 2020). Survey response data were anonymized during analysis. This project was approved by the University of Georgia institutional review board under approval code PROJECT00001084.

Results

We received 280 primary survey responses. We removed 54 untrustworthy samples with more than one wrong attentional question response or whose duration was less than the length of the assigned treatment film (HR = 33, SHR = 15, CC = 6). Of the resulting 226 trustworthy primary survey responses, 56 students viewed *Hidden Rivers* (25%), 80 students viewed Shortened *Hidden Rivers* (35%), and 90 students viewed Content Control (40%). We received 190 responses to our follow-up survey, consisting of 46 students in the *Hidden Rivers* group (24%), 68 students in the Shortened *Hidden Rivers* group (36%), and 76 students in the Content Control group (40%). Our retention rate between primary and follow-up surveys was 84%. A post-hoc power analysis revealed that our power to detect a moderate effect size was 0.93 in the primary survey, and 0.87 in the follow-up survey.

Alignment with Story-Centric Beliefs

There were significant differences in alignment with story-centric beliefs between treatment film groups in the primary survey ($p < 0.001$) and the follow-up survey ($p = 0.001$). In the primary survey, mean alignment with story-centric beliefs was 54.5 (6.4

SD) for *Hidden Rivers*, 54.3 (4.8 SD) for Shortened *Hidden Rivers*, and 49.6 (5.2 SD) for Content Control. Alignment with story-centric beliefs was 4.9 (95% CI: 2.8 – 7.1) and 4.7 (95% CI: 2.7 – 6.7) points greater for *Hidden Rivers* and Shortened *Hidden Rivers* groups, respectively, than the Content Control group ($p < 0.001$, Figure 4.1). Alignment with story-centric beliefs did not differ between *Hidden Rivers* and Shortened *Hidden Rivers* groups ($p = 0.97$). Hypothesis 1a was partially supported; alignment with story-centric beliefs was significantly greater immediately after film exposure for individuals who viewed either conservation film than for individuals who viewed the control film, but did not differ significantly between short and feature length conservation film viewers.

In the follow-up survey, mean alignment with story-centric beliefs was 52.0 (6.9 SD) for *Hidden Rivers*, 53.2 (4.7 SD) for Shortened *Hidden Rivers*, and 49.7 (5.2 SD) for Content Control. Shortened *Hidden Rivers* group alignment with story-centric beliefs was significantly greater than Content Control group belief alignment ($p < 0.001$, Figure 4.1). However, *Hidden Rivers* group belief alignment was not significantly different than the Content Control group ($p = 0.08$) or the Shortened *Hidden Rivers* group ($p = 0.46$); therefore, hypothesis 1B was partially supported. There were slight shifts in alignment with story-centric beliefs within treatment groups between primary and follow-up surveys (Figure 4.2). Alignment with story-centric beliefs declined by 2.5 points in the *Hidden Rivers* group ($p < 0.001$) and 1.1 points in the Shortened *Hidden Rivers* group ($p = 0.003$) and was virtually unchanged in the Content Control group (0.1 increase, $p = 0.82$).

Interest in Engaging in Conservation Behavior

There were significant differences in conservation behavior interest between treatment film groups in the primary survey ($p = 0.001$) and follow-up survey ($p = 0.04$). In the primary survey, mean conservation behavior interest was 24.4 (8.5 SD) for the *Hidden Rivers* group, 23.8 (7.4 SD) for the Shortened *Hidden Rivers* group, and 20.4 (6.7 SD) for the Content Control group (Figure 4.3). Interest in engaging in conservation behavior was significantly greater in the *Hidden Rivers* group ($p = 0.004$) and the Shortened *Hidden Rivers* group ($p = 0.008$) compared to the Content Control group. Conservation behavior interest in the primary survey did not differ significantly between the *Hidden Rivers* and Shortened *Hidden Rivers* groups ($p = 0.86$). Hypothesis 2a was partially supported; viewers of either conservation film expressed significantly greater interest in engaging in conservation behaviors immediately after film exposure than control film viewers, but there were no significant differences in behavior interest between short and feature length conservation film viewers.

In the follow-up survey, mean conservation behavior interest was 23.2 (9.0 SD) for the *Hidden Rivers* group, 24.0 (8.1 SD) for the Shortened *Hidden Rivers* group, and 20.8 (7.1 SD) for the Content Control group. The Shortened *Hidden Rivers* group exhibited significantly greater interest in engaging in conservation behavior than the Content Control group ($p = 0.04$). However, there were no other significant differences in conservation behavior between the other groups; thus, hypothesis 2b was partially supported. There were no significant differences in conservation behavior interest within treatment groups between the primary and follow-up surveys. Interestingly, conservation behavior interest increased slightly from the primary to the follow-up surveys in the Shortened *Hidden Rivers* (+0.2) and Content Control groups (+0.3) but decreased in the *Hidden Rivers* group (-1.3) (Figure 4.4). Hypothesis 2b was partially supported.

Conservation Support

There were no significant differences in responses to the conservation support question between treatment film groups in the screening survey ($p = 0.19$). The average screening survey response was 3.94 (1.0 SD), which corresponds to conservation of resources even when there are substantial costs to economic growth and development. There were significant differences in responses to the conservation support question in the primary survey ($p = 0.03$). Conservation support question mean responses were 4.41 (1.2 SD) for *Hidden Rivers*, 4.32 (0.8 SD) for Shortened *Hidden Rivers*, and 4.0 (1.0 SD) for Content Control groups. Mean responses were significantly greater for the *Hidden Rivers* group than the Content Control group ($p = 0.04$). There were no other significant differences between groups. Finally, there also were no significant differences in conservation support question responses between groups in the follow-up survey, or within treatment groups between surveys.

Narrative Engagement

There were significant differences in transportation between treatment groups in the primary survey ($p < 0.001$). Mean transportation levels were 53.6 (12.7 SD) for the *Hidden Rivers* group, 53.7 (9.7 SD) for the Shortened *Hidden Rivers* group, and 43.9 (11.1 SD) for the Content Control group. Individuals in the *Hidden Rivers* and Shortened

Hidden Rivers groups were significantly more transported than individuals in the Content Control group ($p < 0.001$, Figure 4.5). Hypothesis 3a was partially supported; viewers of the feature length conservation film were significantly more transported than viewers of the control film, but not viewers of the short conservation film.

Treatment groups responded differently to transportation scale items, driven primarily by differences in responses between conservation film groups and the Content Control group (Figure 4.6). Compared to the conservation film groups, Content Control viewers: did not picture themselves in the story as much (item 2), were not as affected emotionally (item 6), did not find the film as moving (item 10), did not have their emotions stirred (item 11), and reported greater mind wandering (item 7). The *Hidden Rivers* and Shortened *Hidden Rivers* groups shared the five highest ranking transportation scale items of mental involvement (item 3), picturing themselves in the film (item 2), being moved by the film (item 10), wanting to learn how the story ended (item 5), and being completely immersed in the story (item 9), albeit in slightly different orders.

Our 11-item transportation scale displayed good internal consistency, with a Cronbach's alpha of 0.89 (95% CI: 0.87 – 0.91).

There were significant differences in emotional engagement between treatment film groups ($p < 0.001$). Mean emotional engagement was 23.9 (6.1 SD) for the *Hidden Rivers* group, 22.2 (5.7 SD) for the Shortened *Hidden Rivers* group, and 16.1 (4.8 SD) for the Content Control group. The *Hidden Rivers* and Shortened *Hidden Rivers* groups were significantly more emotionally engaged than the Content Control group ($p < 0.001$,

Figure 4.7). *Hidden Rivers* and Shortened *Hidden Rivers* groups did not exhibit significantly different emotional engagement. Hypothesis 3b was partially supported; viewers of the feature length conservation film were significantly more emotionally engaged than viewers of the control film, but not more emotionally engaged than viewers of the short conservation film.

We also classified emotions into two groups based on valence. Positive emotions were happiness, hope, and surprise. Negative emotions were sadness, fear, anger, and disgust. When evaluated by valence, mean response per positive emotion (4.1, 1.3 SD) was significantly greater than mean response per negative emotion (mean = 2.0, 1.0 SD) for all study participants, as well as within each treatment film group (all p-values < 0.001, Figure 4.8).

Linear Models

We ran simple linear models to identify correlations between story-centric belief alignment, interest in engaging in conservation behavior, treatment film, transportation, emotional engagement, political orientation, age, and sex. Alignment with story-centric beliefs was positively correlated with transportation ($p < 0.001$, $\beta = 0.32$) in the *Hidden Rivers* group, transportation ($p = 0.002$, $\beta = 0.18$) and political orientation ($p = 0.008$, $\beta = 0.84$) in the Shortened *Hidden Rivers* group, and political orientation ($p = 0.01$, $\beta = 0.90$) in the Content Control group (Figure 4.9, Table 4.3). The effects of age and sex on alignment with story-centric beliefs were weak and inconsistent. Our hypothesis that narrative engagement would be positively correlated with alignment with story-centric beliefs was partially supported; transportation (H4a) was a significant predictor of belief alignment, but emotion was not (H4b).

Interest in engaging in conservation behavior was positively correlated with transportation ($p < 0.001$, $\beta = 0.34$) and emotion ($p = 0.03$, $\beta = 0.38$) in the *Hidden Rivers* group, transportation ($p < 0.001$, $\beta = 0.39$) and emotion ($p = 0.03$, $\beta = 0.28$) in the Shortened *Hidden Rivers* group, and emotion ($p = 0.02$, $\beta = 0.36$) in the Content Control group (Figures 4.10 & 4.11, Table 4.3). The effects of political orientation, age, and sex were weak and inconsistent. Our hypothesis that narrative engagement would be positively correlated with interest in engaging in conservation behavior was supported; transportation (H5a) and emotion (H5b) were significant predictors of conservation behavior interest.

We evaluated the effect of time between surveys on changes in alignment with story-centric beliefs and conservation behavior interest by calculating net shifts in belief alignment and behavior interest (follow-up – primary) and regressing those values against days between survey submissions. The average time between surveys for our sample was 18 days (range: 0 – 46 days). Time between surveys was negatively related to net shift in story-centric belief alignment ($p = 0.03$, $\beta = -0.05$, Figure 4.12A). Net shift in conservation behavior interest was not significantly related to time between surveys ($p = 0.40$, $\beta = -0.02$, Figure 4.12B).

Discussion

Our results suggest that conservation films can increase pro-conservation beliefs and intent to engage in conservation behavior for audiences with low to moderate preexisting conservation support, and that these shifts are correlated with film engagement. Even films that do not rely on identification with animals or other agents can produce these transportation effects. Study participants who viewed conservation films were more likely to agree with the pro-conservation beliefs expressed in the films and more interested in engaging in conservation behaviors exhibited in the films than participants who viewed a non-conservation film. Participants who reported greater engagement with their respective treatment film exhibited stronger belief and behavior interest. Crucially, we observed that the short conservation film was as engaging as the feature length film, and produced equal short-term and greater long-term shifts in conservation support. This did not support our hypothesis that the longer film would be more engaging and subsequently cause greater shifts in conservation support. To our knowledge, this is the first study to empirically test the effects of message length on narrative engagement and corresponding shifts in beliefs and behavioral intent.

There are a few plausible reasons for these results. Long messages could exceed audience attention span and increase distraction and fatigue (Kim et al., 2012). Short messages are able to transport and persuade viewers (Escalas, 2004; Phillips & McQuarrie, 2010), but these phenomena also occur over extended periods of exposure (Warren, 2020). Some research has implied that slight differences in message length may not have much effect on engagement (e.g., Kim et al., 2012; McKinley, 2013; Redondo et al., 2018), but these studies did not empirically test for the effects of length. Engagement ebbs and flows over the duration of a story as the plot becomes more or less intense which can influence persuasive outcomes (Bezdek & Gerrig, 2017; Nabi & Green, 2015). It is possible that the intense plot events and emotions evoked by the short conservation film were diluted over time in the feature length film, resulting in similar levels of engagement due to the same intense moments driving engagement in both films. Clearly, more work is needed to characterize the relationship between message length and engagement and persuasion, particularly with message lengths relevant to communicators (e.g., 10 min. versus 60 min.).

Our results have important implications for future conservation communication strategies because message length is a critical consideration for filmmakers with limited resources. Compared to feature films, short films require considerably less time, money, and effort to produce, and are more likely to be encountered and viewed by more people across more platforms (J. Monroe & S. Eberle personal communication). Repeated exposure to advertisements has produced to lasting effects (Howell, 2011; Manzo, 2017) and repeated exposure to the same story via a different medium may increase transportation (Green et al., 2008). Short films are more easily viewed multiple times in succession compared to feature films; serialized short films about the same topic may provide viewers with opportunities for extended engagement without taxing attention spans (Warren, 2020). Indeed, seeking out similar stories was the third most popular behavior in our study, and the only behavior with greater reported interest in the follow-up survey than the primary survey.

It is interesting that viewers of the shortened version of *Hidden Rivers* still expressed significantly greater conservation support in the follow-up survey than viewers of the control film. Previous research on environmental film efficacy has shown that shifts in beliefs, attitudes, or intended behaviors tend to decay over time (Howell, 2014; Jacobsen, 2011; Leiserowitz, 2004; Nolan, 2010). This has been attributed to complexities underlying the relationships between attitudes and intended and actual behavior (e.g., Ajzen, 1991; Bamberg & Möser, 2007; Kollmuss & Agyeman, 2002), a lack of clear depictions or suggestions for specific action at the end of films (Lowe et al., 2006; Nolan, 2010) and concern about the ability to make a difference given the scale of the problem depicted (e.g., global climate change; Bieniek-Tobasco et al., 2019). However, the conservation films in this study explicitly modeled multiple conservation behaviors and featured imperiled ecosystems near the sample population where behaviors ostensibly would be effective. More research is needed to determine the roles that film length and engagement play in the persistence of persuasive effects – do short stories have long influences?

Transportation clearly was the strongest predictor of conservation support; it was significantly, positively correlated with both elements of support and overwhelmed other predictor variables in our models. Of secondary importance was emotional engagement, which was correlated with conservation behavior interest. It is interesting that study participants exhibited significantly greater positive emotional engagement than negative emotional engagement given that both conservation films clearly expressed the critical conditions of freshwater resources in Southern Appalachia. However, both films conclude on a hopeful note, and it is possible that our study participants were biased in reporting positive emotions felt at the end of the films compared to negative emotions elicited earlier in the stories. An emerging area of research suggests that the sequence in which people experience emotions has important implications for the persuasive effects of narratives (Nabi et al., 2018). Future research on conservation communication efficacy should investigate the role of emotional flow on belief and behavior outcomes.

Limitations & Directions for Future Research

One challenge for research that seeks to investigate potential shifts in beliefs, attitudes, and behaviors due to message exposure is accessing a representative population without preexisting topic interest. We filtered our sample population for individuals who expressed low to moderate support for conservation; however, our sample of university students is not representative of the broader US population. Young people are critical for the future of conservation and young, highly educated Americans show greater levels of environmental concern than older, less-educated citizens (Howell, 2011; Reinhart, 2018). Approximately 40% of the students who completed our screening survey were ineligible based on high conservation support. Future research should investigate how broader age groups, political orientations, and educational backgrounds potentially interact with film-driven shifts in conservation support.

We had limited access to our sample population, which constrained the time between primary and follow-up surveys. In general, it is difficult to gain long-term access to a sample population in communications research as evidenced by the dearth of studies with longitudinal data. However, interesting patterns emerged within this time frame. Alignment with pro-conservation beliefs decayed at different rates between treatment groups, and belief alignment decayed more rapidly than interest in conservation behavior. These observations are contrary to the expected relationship between strong beliefs and weak behavior (Barr, 2006), which is interesting given that several of the conservation behaviors viewers expressed interest in are service-oriented. Therefore, more research is needed to understand the how message-induced shifts in attitudes, beliefs, and behaviors persist or decay over time.

The importance of narrative engagement and length are largely unexplored in the context of the persuasive effects of conservation films. There is a growing understanding in related persuasion research that persuasion dynamics need to be investigated in terms of specific audience belief alignments, as the persuasion pathways and outcomes may vary. Accordingly, we designed this case study to explore the possibility that these dimensions potentially influenced the persuasive effects of a conservation film specifically among those with moderate-to-low conservation beliefs. We used two versions of a story about freshwater biodiversity conservation in Southern Appalachia, USA. Although our results are encouraging and suggest that these films, even when they do not include intense personification to build identification, may have the potential to shift public perception about the environment, we cannot extrapolate these results beyond the scope of *Hidden Rivers*. Future research should extend and apply these questions to the growing genre of conservation films to understand the audience-specific dynamics involved in the use of these types of messages to generate conservation support amongst the public. Specifically, future studies should incorporate multiple conservation and control treatment films and employ models that explore pathways that include non-identification-based engagement for transportation to ascertain whether conservation films generally influence conservation support, or if there are film-specific elements that affect persuasive outcomes.

Another promising area of future research is investigating the role that messages accompanying conservation films might play in shifting conservation support. For instance, presenting accompanying educational material with films may potentially operationalize persuasive effects (Schneider-Mayerson et al., 2020; Wright, 2010). However, these materials may also reduce motivation to act if deemed overtly persuasive by the audience (Moyer-Gusé et al., 2019). Finally, given that we found that a short conservation film engaged audiences and motivated them to seek out similar stories, it would be interesting to explore the potential for conservation films to encourage viewers to watch similar (or serialized) films and thus leverage the effects of exposure to one message into long-term, concrete shifts in conservation belief and behavior. This could have important implications for this genre of films and conservation in general, especially if viewers did not previously seek out these types of messages.

Conclusion

In summary, conservation films are potentially powerful tools for shaping public perception about the natural world and motivating people to engage in conservation behavior, including for audiences without previous interest in this topic. Study participants with low to moderate conservation beliefs who were more transported and emotionally engaged by the conservation films exhibited significantly greater change toward alignment with conservation beliefs and intent to engage in conservation behaviors. Importantly, the short film was equally as engaging as the feature film and elicited more persistent shifts in conservation beliefs and intended behaviors over time. This is encouraging news, given that conservation films featuring a wide variety of topics are increasingly popular and accessible. We look forward to the growing body of research on conservation film efficacy and for their potential as conservation tools to be fully realized.

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Declaration of Interest

There are no conflicts of interest for any of the authors of this study.

Tables

Table 4.1. Transportation scale used in this study as adapted from Green & Brock (2000), deGraaf et al. (2009), and Bussellee & Bilandzic (2009). Reverse coded items are labeled (–). Scale internal validity, α = 0.89.

Transportation Scale Items
1) While I was watching the film, activity going on in the room around me was on my mind. (–)
2) I could picture myself in the scene of the events depicted in the film.
3) I was mentally involved in the film while watching it.
4) Once the film ended, I found it easy to put it out of my mind. (–)
5) I wanted to learn how the film ended.
6) The film affected me emotionally.
7) I found my mind wandering while watching the film. (–)
8) I forgot my own problems and concerns during the film.
9) While viewing the film, I was completely immersed in the story.
10) I found the film moving.
11) The film stirred emotions in me.

Table 4.2. Story-centric beliefs and conservation behavior interests assessed in the primary and follow-up surveys. Reverse coded items are labeled (–). Aquatic life was defined in the question prompt as the fish, mussel, salamander, and other animal populations that live in rivers and streams.

Story-Centric Beliefs
The aquatic life in Southern Appalachian rivers is ecologically important.
The aquatic life in Southern Appalachian rivers is culturally important.
The aquatic life in Southern Appalachian rivers is threatened due to human activities.
The aquatic life in Southern Appalachian rivers should be protected.
The aquatic life in Southern Appalachian rivers should be a conservation priority throughout the next decade.
Scientists and conservation professionals play an important role in helping us understand and protect rivers and aquatic organisms in Southern Appalachia.
Anyone can experience and act as a steward of Southern Appalachian rivers and their ecosystems through river snorkeling, volunteering with conservation groups, and everyday decisions.
We should not spend time and money protecting aquatic life in Southern Appalachian rivers since most people do not know these species exist.
We should prioritize economic growth and development, not conservation, in Southern Appalachia in the next decade. (–)
Conservation Behaviors
Participate in a river clean-up event (i.e., remove trash or debris from local streams or streambanks)
Swim or wade in a river or stream to view underwater life
Visit a fish or mussel hatchery to learn about the biology and ecology of aquatic species
Assist state and federal agencies or conservation organizations with the reintroducing native species into streams, rivers, or lakes
Read, listen to, and/or watch more stories similar to this film
Talk about this film with friends, family, or acquaintances

Table 4.3. Linear model output per type of conservation support and treatment group.

Alignment with Story-Centric Beliefs				
Film	**Predictor**	**Estimate (β)**	**95% CI**	**p-value**
Hidden Rivers	Transportation	0.32	0.19 – 0.45	< 0.001
	Emotion	0.03	-0.23 – 0.30	0.80
	Political Orientation	0.72	-0.15 – 1.59	0.10
	Age	-0.04	-0.74 – 0.67	0.92
	Sex (M)	-2.14	-4.92 – 0.63	0.13
Shortened Hidden Rivers	Transportation	0.18	0.07 – 0.29	0.002
	Emotion	0.02	-0.17 – 0.21	0.84
	Political Orientation	0.84	0.23 – 1.46	0.01
	Age	-0.65	-1.55 – 0.26	0.16
	Sex (M)	-1.24	-3.23 – 0.75	0.22
Content Control	Transportation	0.06	-0.05 – 0.16	0.29
	Emotion	-0.06	-0.30 – 0.18	0.60
	Political Orientation	0.90	0.20 – 1.60	0.01
	Age	0.36	-0.44 – 1.15	0.37
	Sex (M)	-2.12	-4.30 – 0.07	0.06
Conservation Behavior Interest				
Film	**Predictor**	**Estimate (β)**	**95% CI**	**p-value**
Hidden Rivers	Transportation	0.34	-0.18 – 0.50	< 0.001
	Emotion	0.38	0.05 – 0.72	0.03

	Political Orientation	0.54	-0.57 – 1.65	0.33
	Age	0.28	-0.62 – 1.18	0.53
	Sex (M)	-1.43	-4.96 – 2.10	0.42
Shortened Hidden Rivers	Transportation	0.39	0.25 – 0.54	< 0.001
	Emotion	0.28	0.02 – 0.54	0.03
	Political Orientation	0.43	-0.39 – 1.25	0.30
	Age	-0.41	-1.62 – 0.81	0.51
	Sex (M)	1.44	-1.22 – 4.10	0.28
Content Control	Transportation	0.07	-0.06 – 0.21	0.27
	Emotion	0.36	0.06 – 0.67	0.02
	Political Orientation	0.50	-0.40 – 1.39	0.27
	Age	0.28	-0.73 – 1.29	0.58
	Sex (M)	2.10	-0.69 – 4.89	0.14

Figures

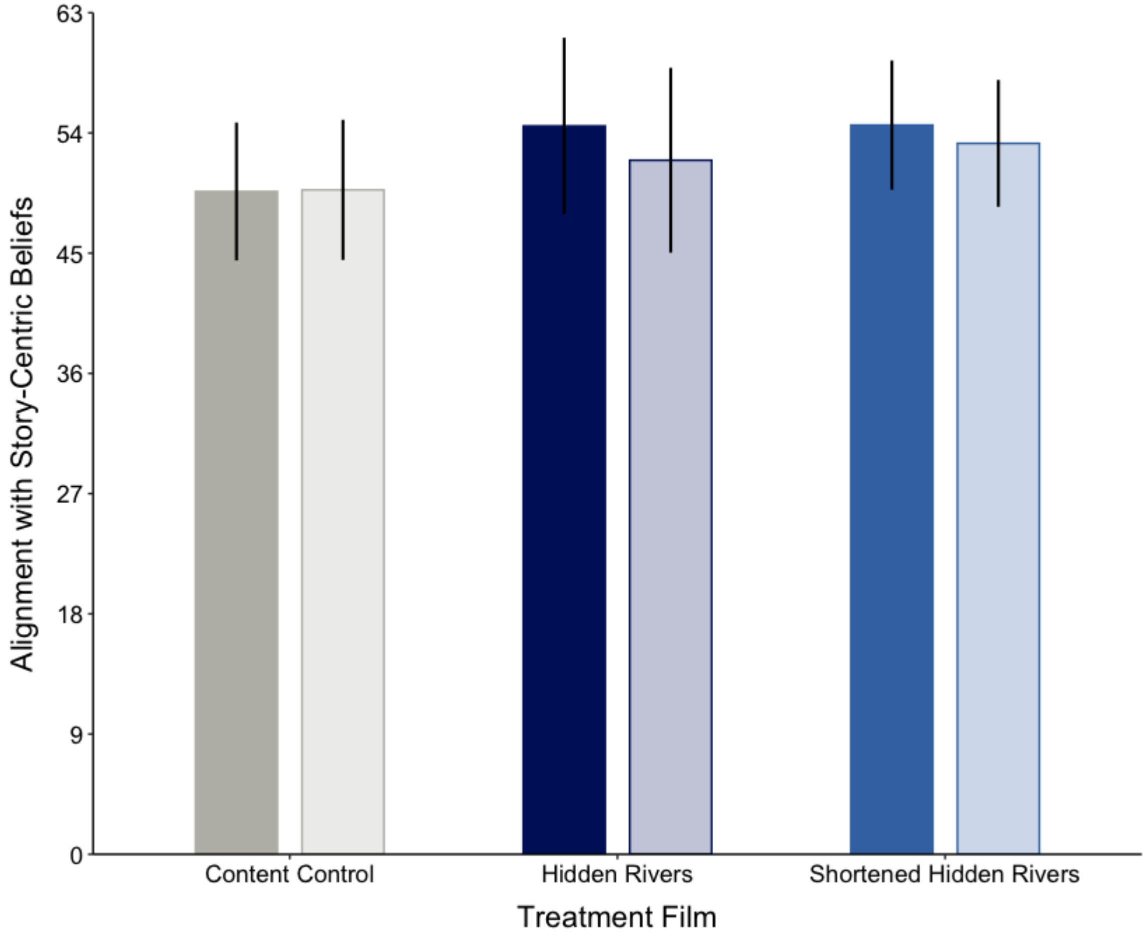

Figure 4.1. Mean percent alignment with story-centric beliefs per treatment group in the primary survey (darker, left bars) and follow-up survey (lighter, right bars). Error bars are plus/minus one standard deviation.

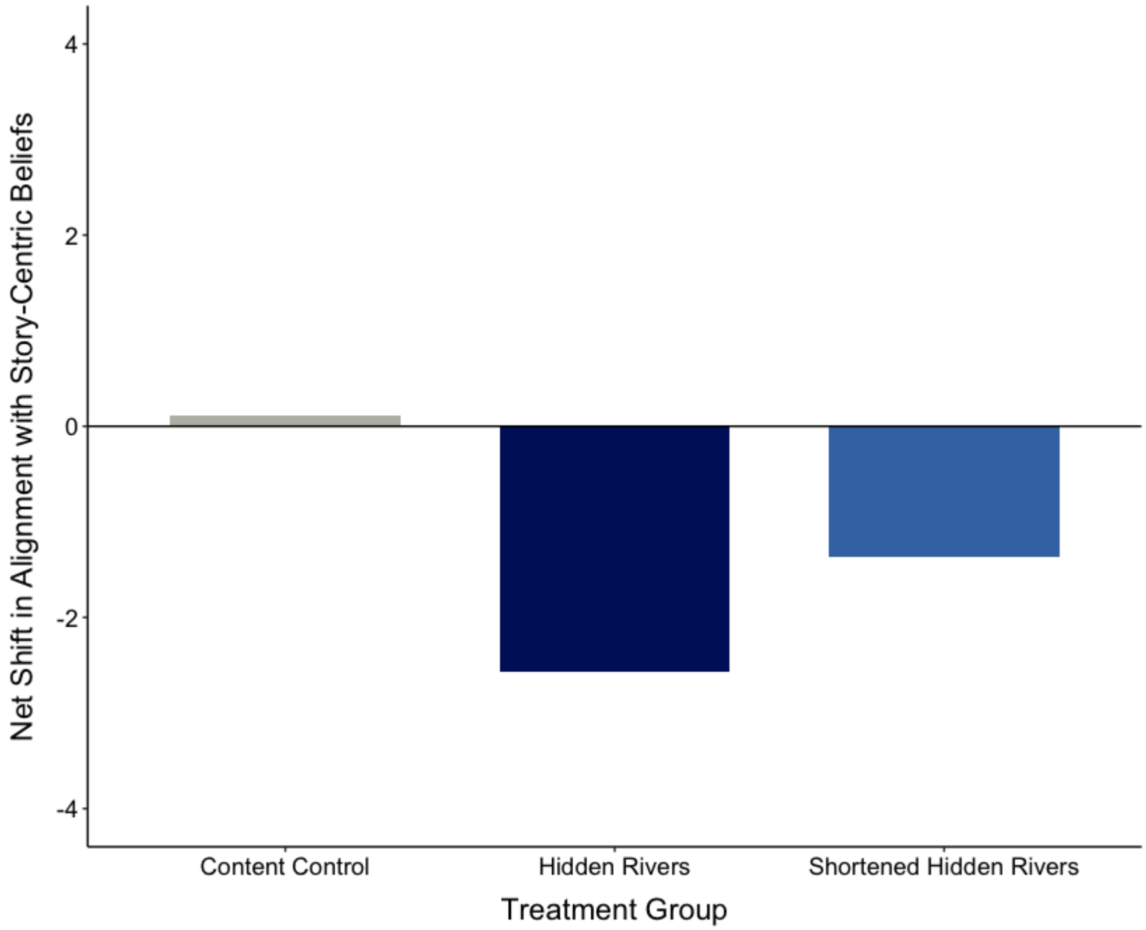

Figure 4.2. Net shift in percent alignment with story-centric beliefs between primary and follow-up surveys per treatment group.

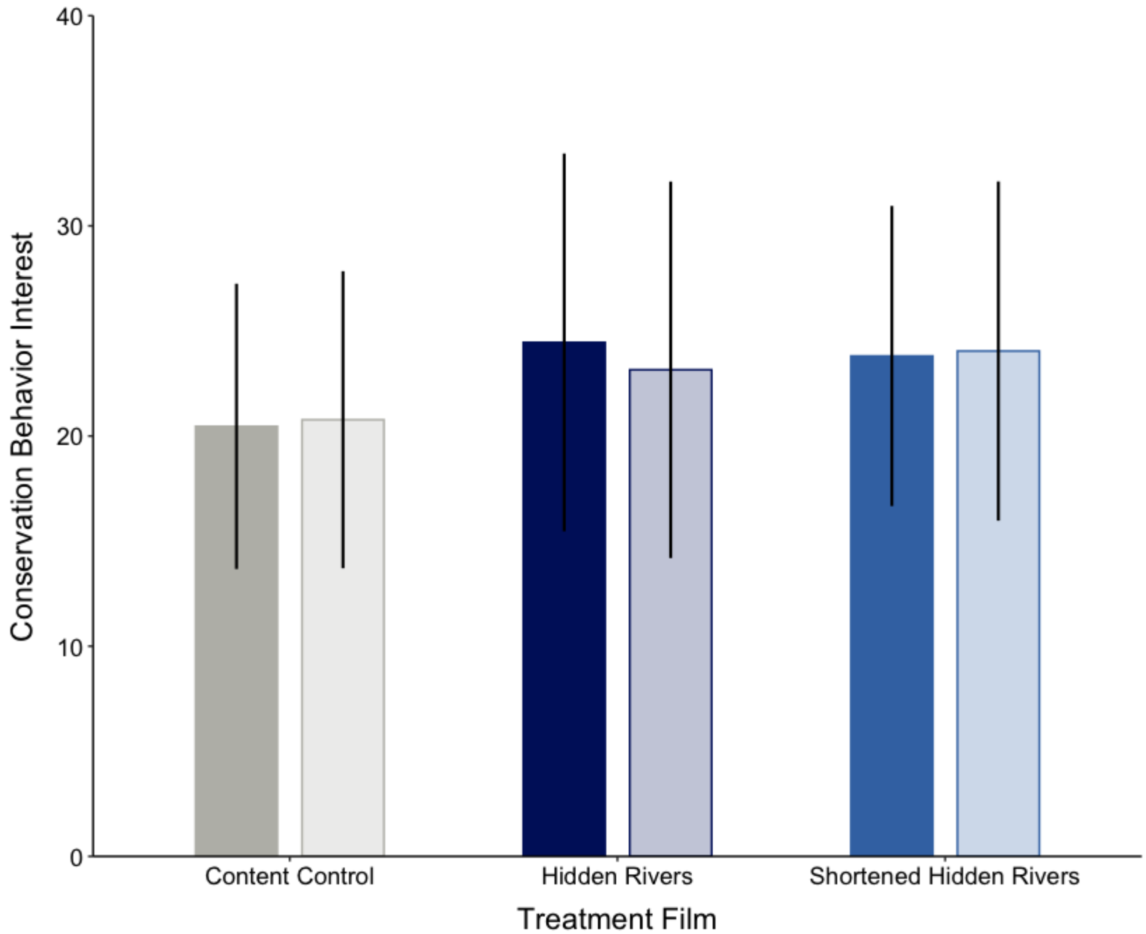

Figure 4.3. Mean conservation behavior interest per treatment group in the primary survey (darker, left bars) and follow-up survey (lighter, right bars). Error bars are plus/minus one standard deviation.

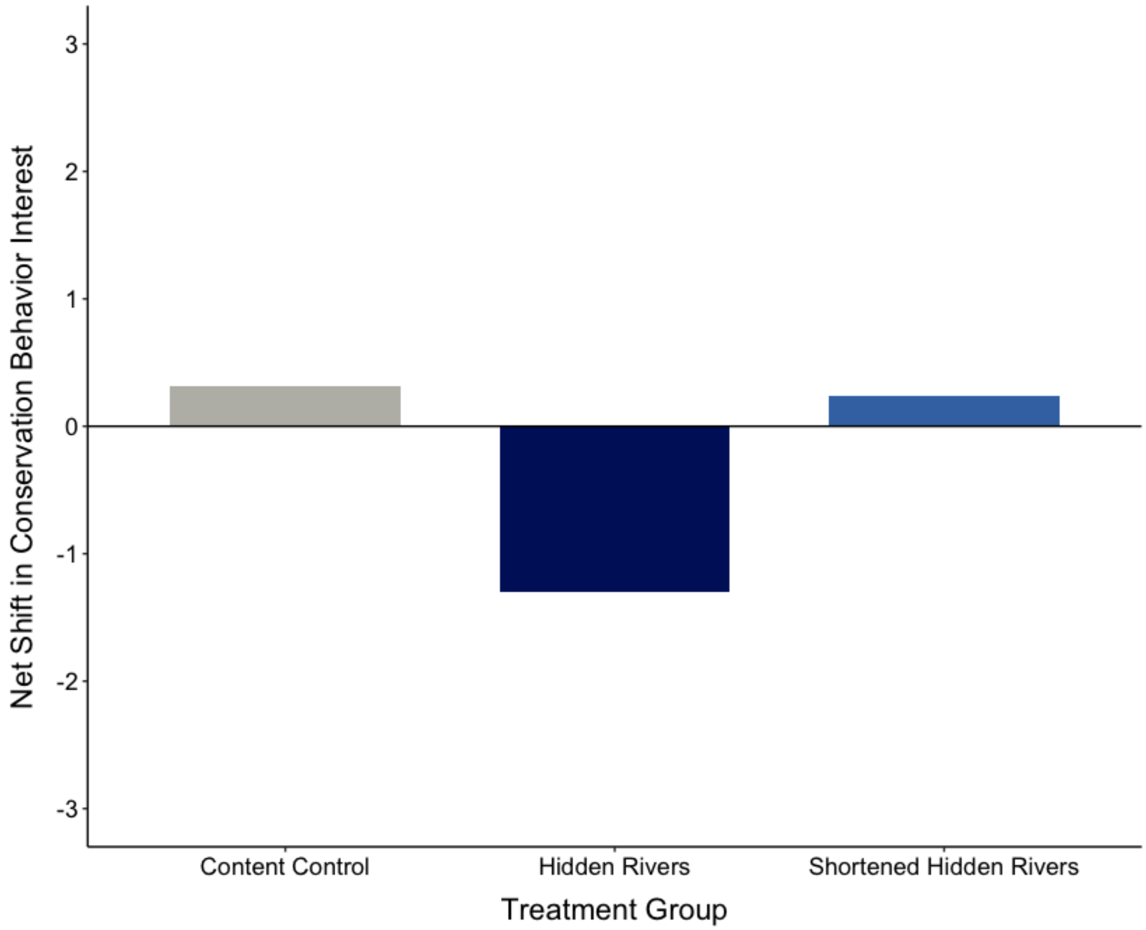

Figure 4.4. Net shift conservation behavior interest between primary and follow-up surveys per treatment group.

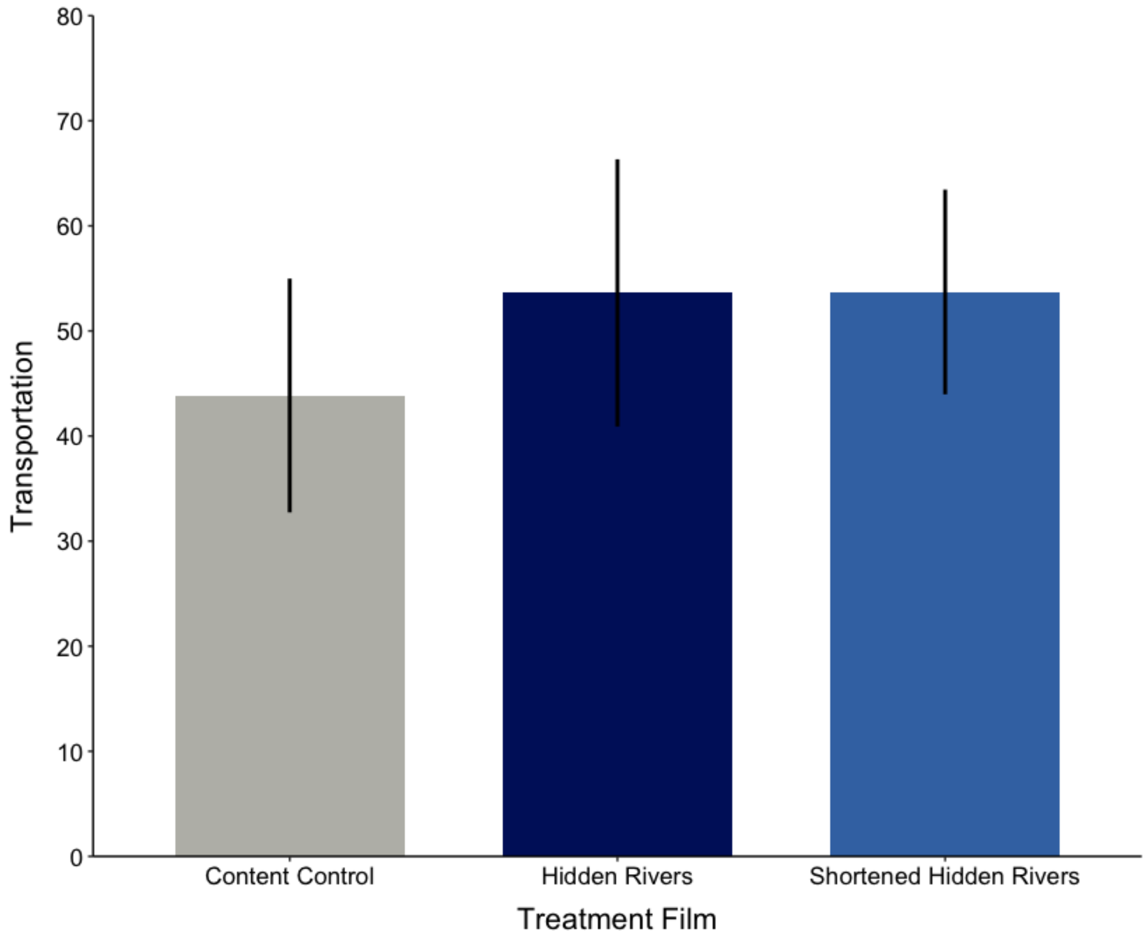

Figure 4.5. Mean transportation level per treatment group in the primary survey. Error bars are plus/minus one standard deviation.

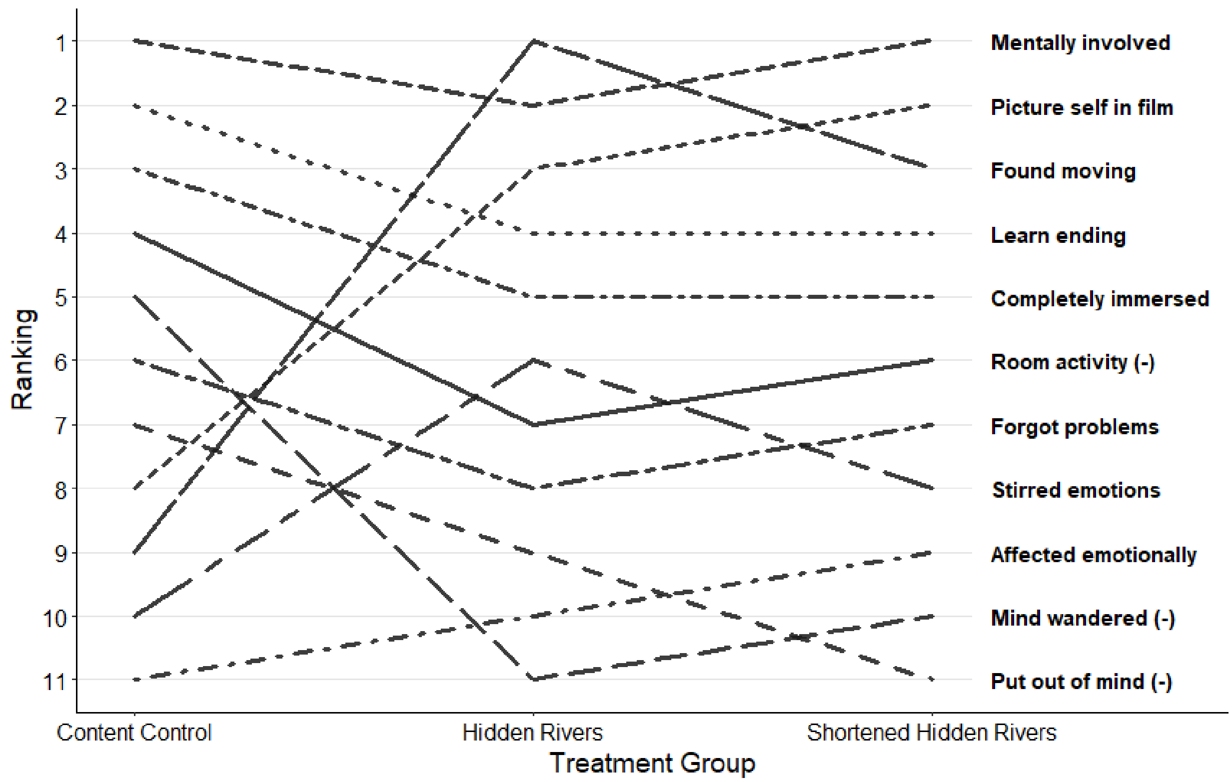

Figure 4.6. Rank of mean transportation scale item score across each treatment group. Note the fewer line crossings between *Hidden Rivers* and Shortened *Hidden Rivers* groups compared to many line crossings between the *Hidden Rivers* and Content Control group. Scale item shorthand is listed to the right next to corresponding lines, which can be traced left to determine that item's ranking per respective treatment film group.

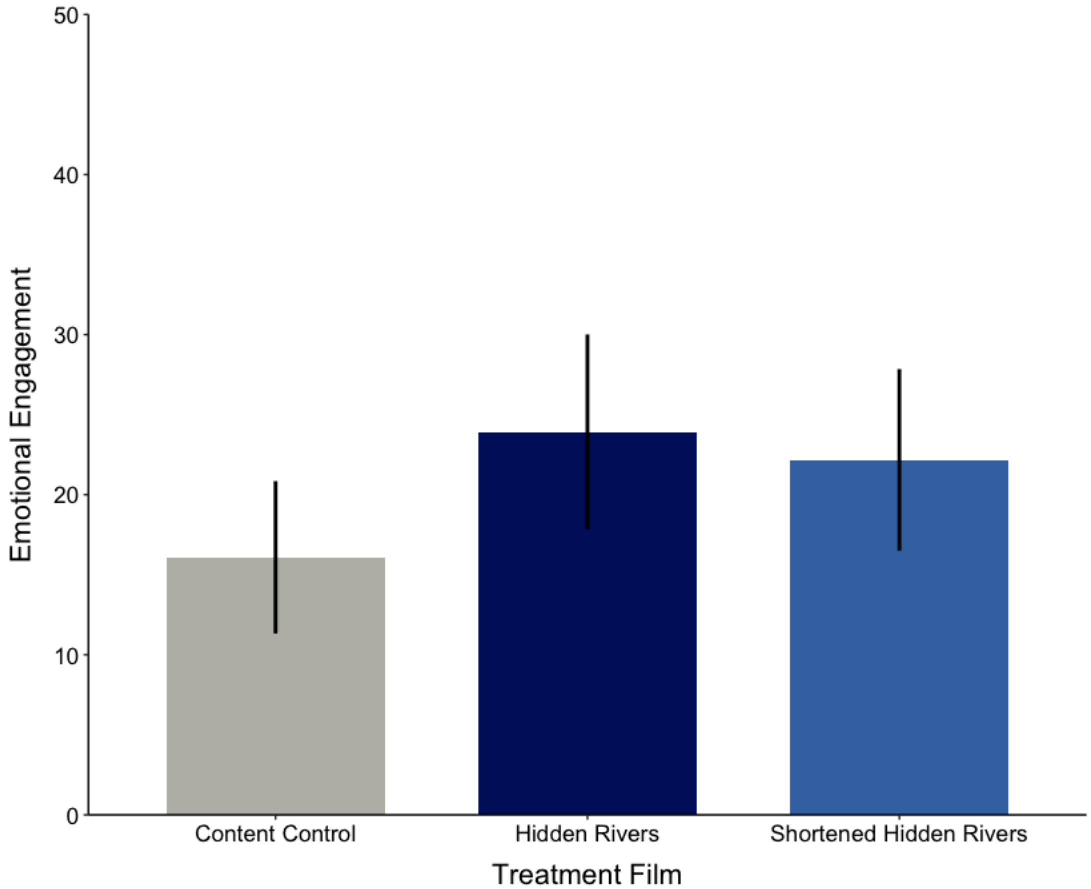

Figure 4.7. Mean emotional engagement per treatment group in the primary survey. Error bars are plus/minus one standard deviation.

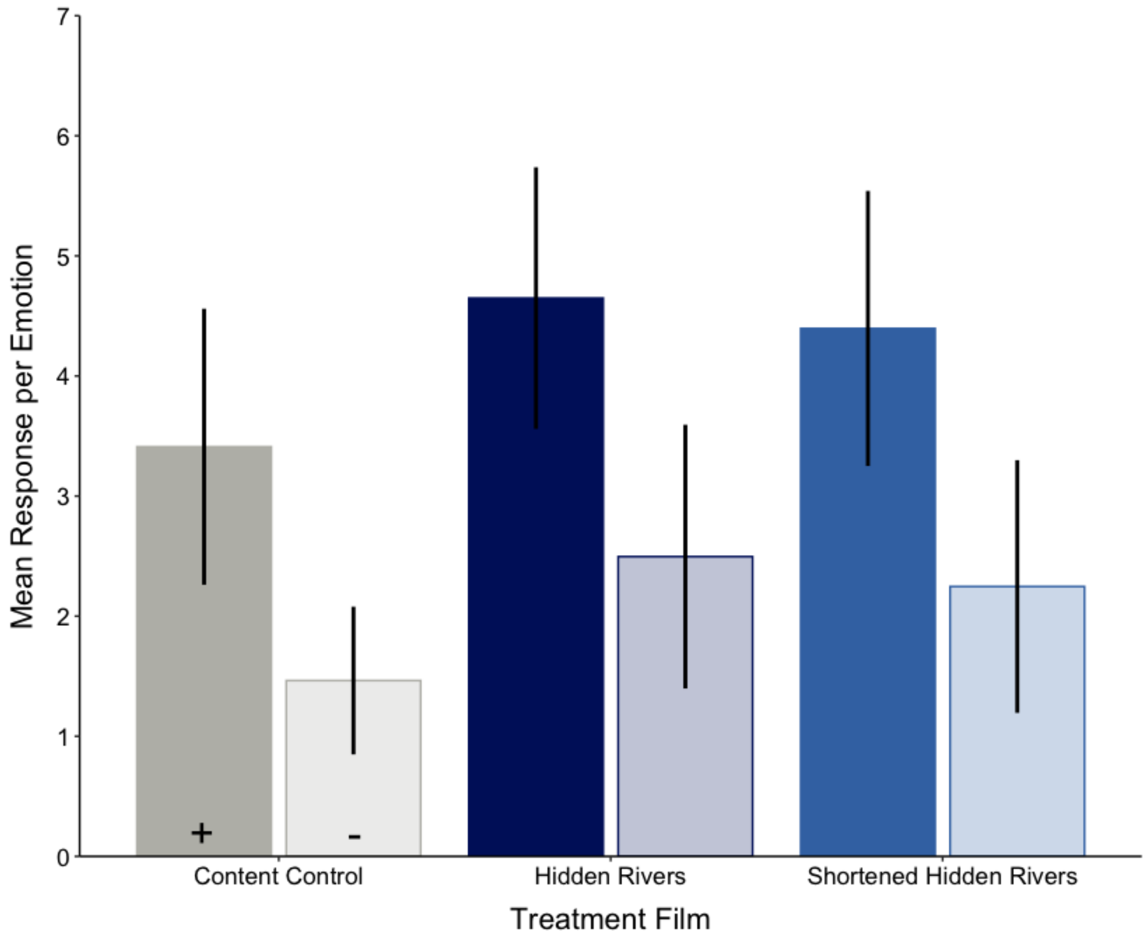

Figure 4.8. Mean response for positive (left, darker bars) and negative (right, lighter) discrete emotions per treatment group. Error bars are plus/minus one standard deviation.

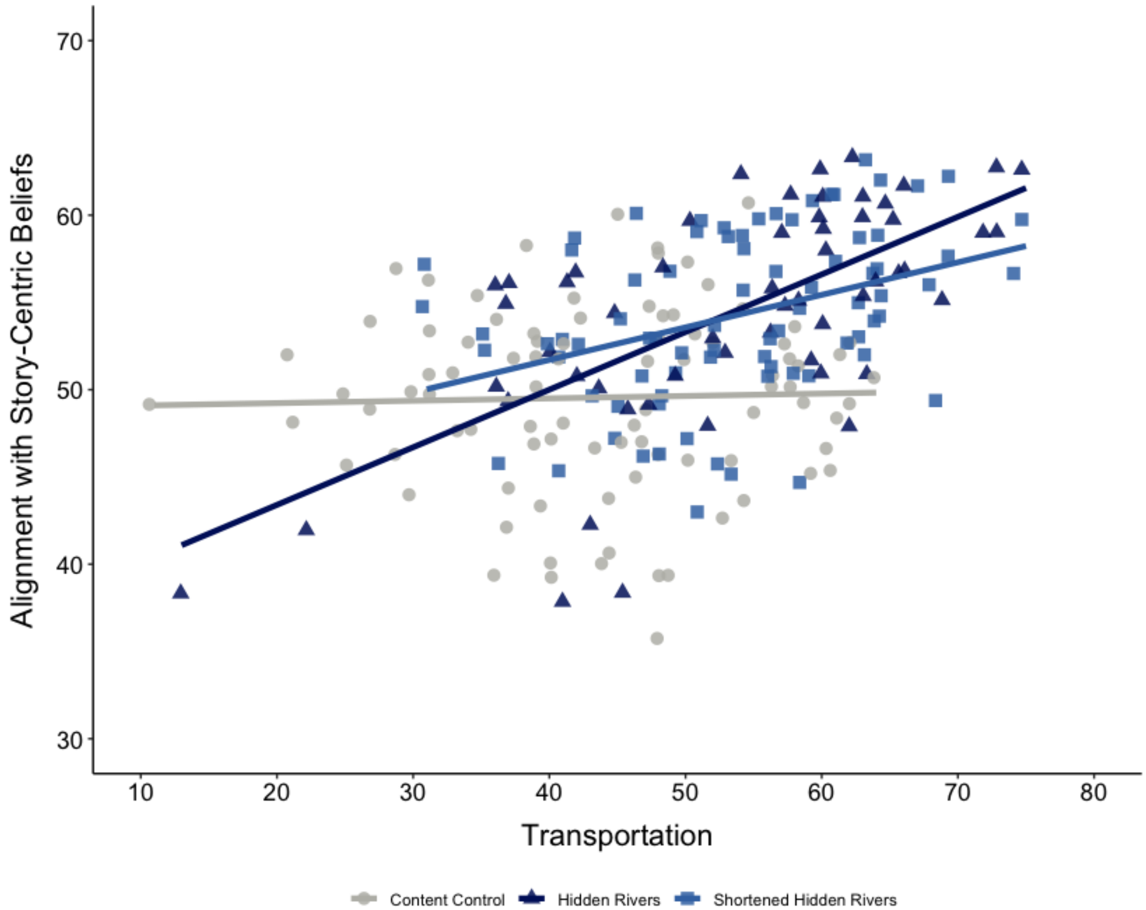

Figure 4.9. Transportation vs. percent alignment with story-centric beliefs per treatment group.

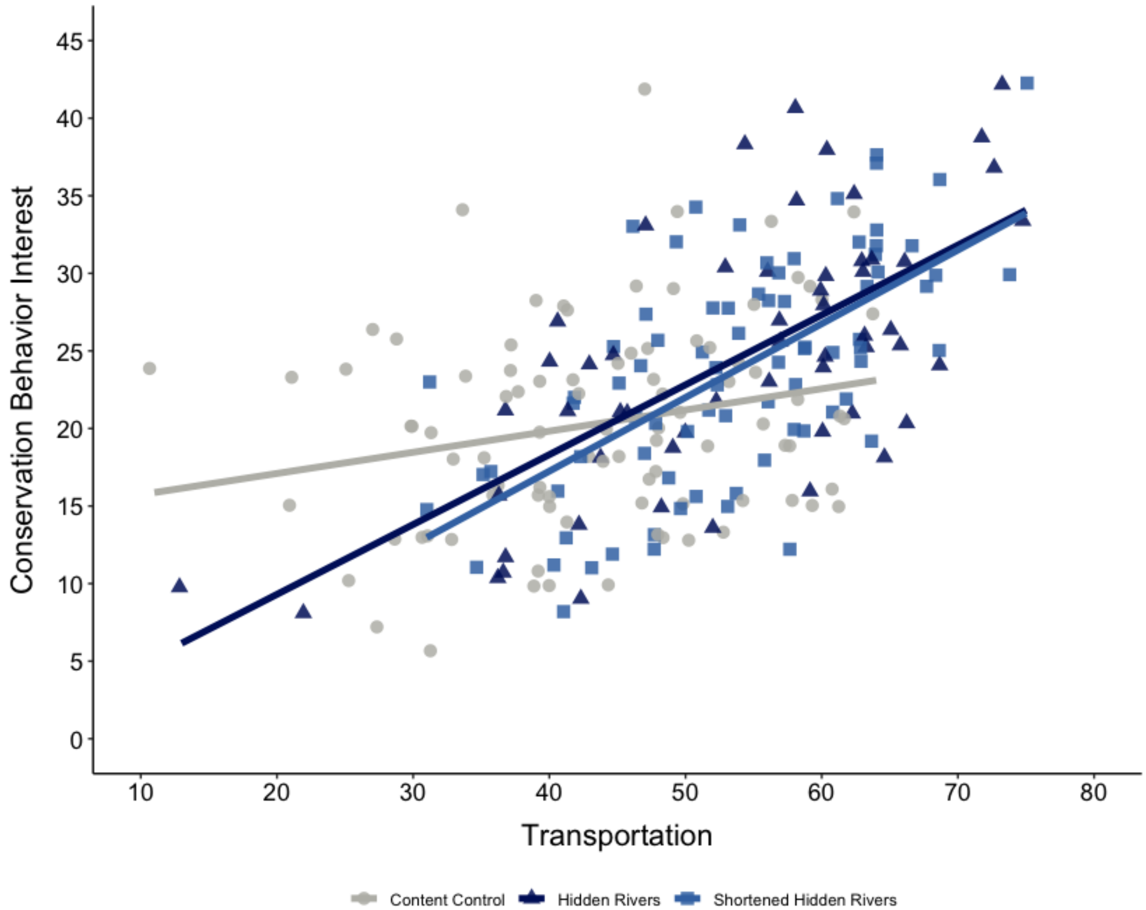

Figure 4.10. Transportation vs. conservation behavior interest per treatment group.

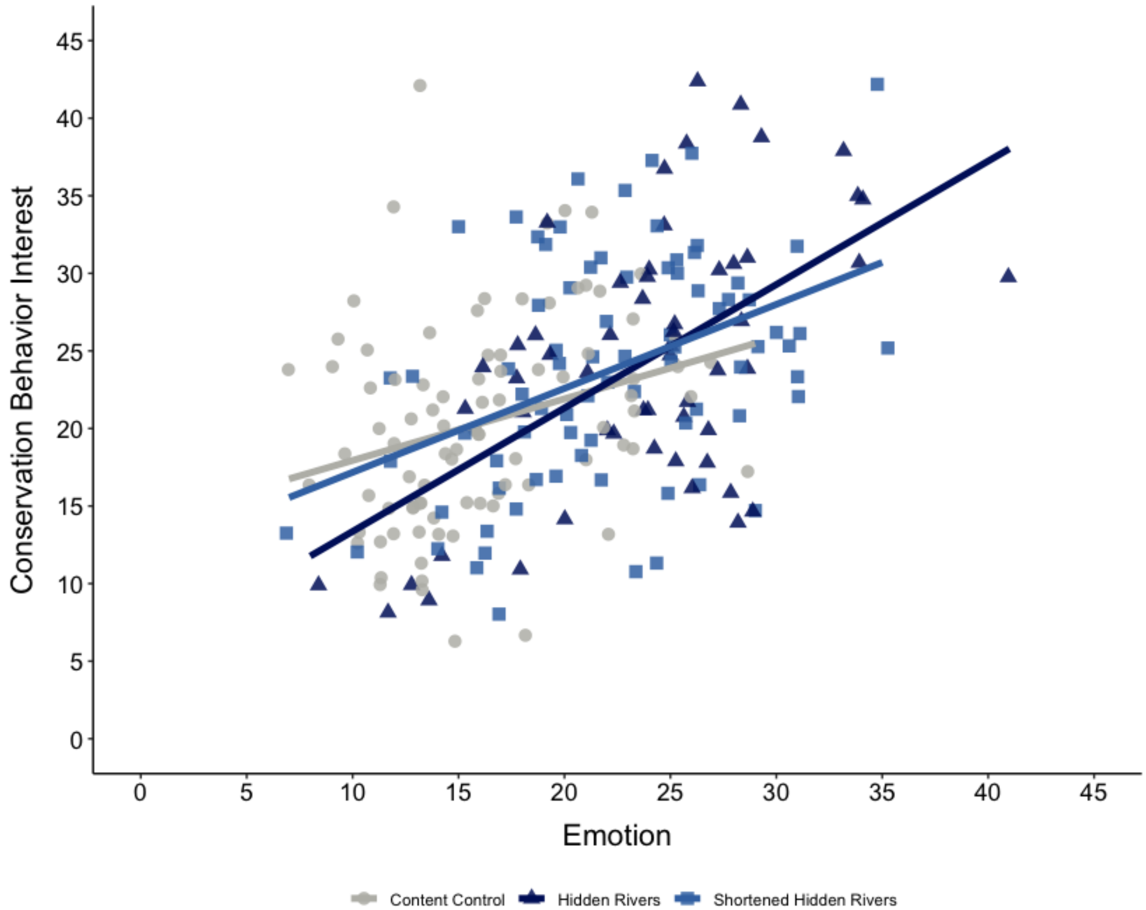

Figure 4.11. Emotion vs. conservation behavior interest per treatment group.

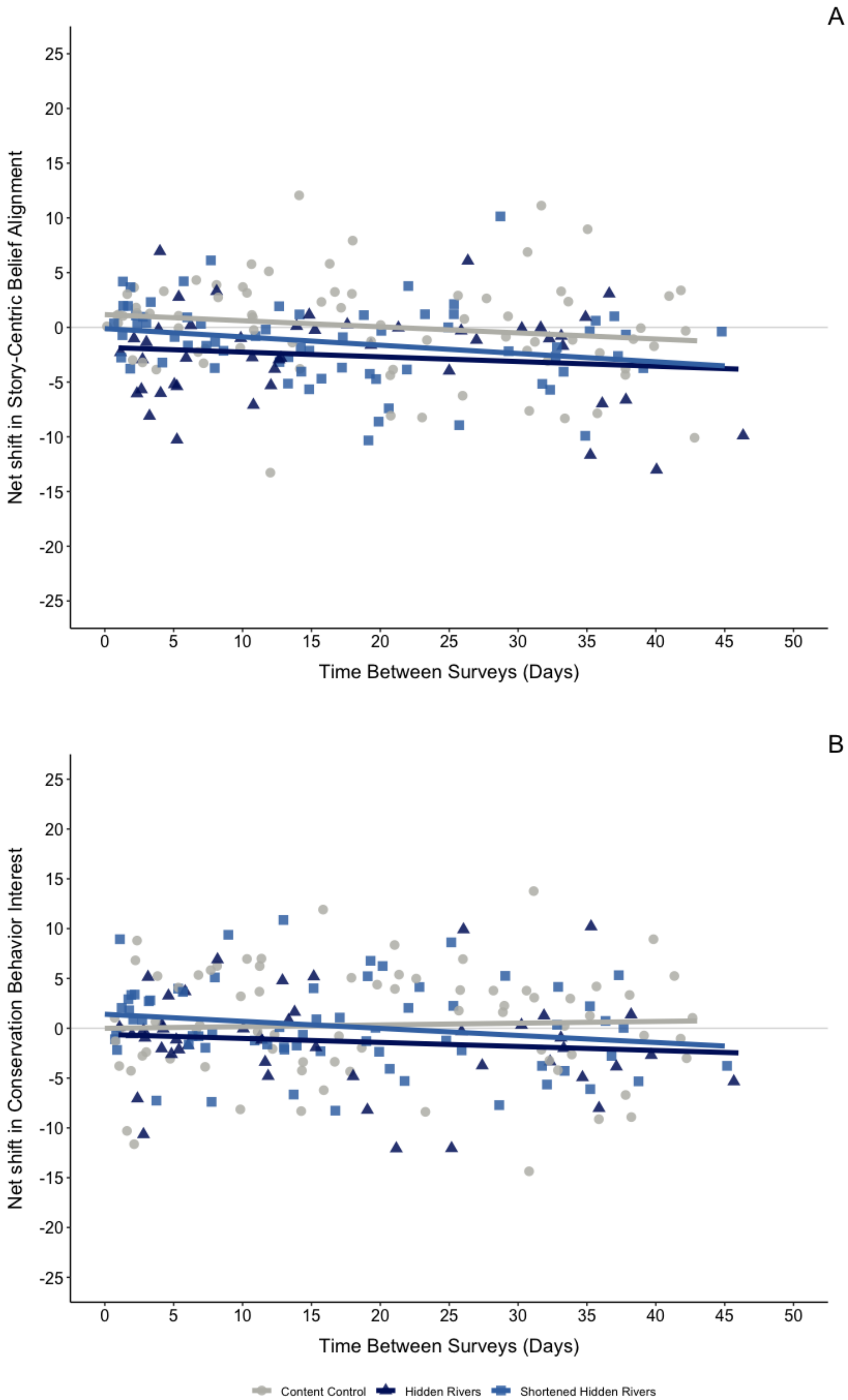

Figure 4.12. Time between surveys (days) vs. net shift in alignment with story-centric beliefs (A) and conservation behavior interest (B) per treatment group.

CHAPTER 5

SYNTHESIS AND CONCLUSIONS

Origins of interest

It all starts with a stream. When you're knee-deep in a mountain stream, you get the sense that you're straddling two connected but distinct worlds. You feel the cold water swirling around your ankles on its way downstream, you see the pockets of slower and faster current. You watch as leaves and twigs swirling on the surface, getting temporarily caught on boulders before continuing their journey downstream. You notice deep, slow pools blending into shallow, quick runs. You begin to appreciate these complexities and think about how different sizes or ages or species of fish rely on different types of habitats. You consider for a moment that fish must navigate these habitat complexities in search of food or shelter.

As you look up from the stream, you also notice how leaves or twigs from overhanging trees or shrubs sometimes fall into the stream. You notice that some sections of the stream receive more sunlight than others where trees and undergrowth have been cleared all the way to the streambank. You notice how, just beyond the line of trees next to the stream, a farmer is cutting this year's hay from a 20-acre pasture. You might think about how land use near streams might impact the quality or quantity of the rainfall that drains into the stream from the landscape, and how clearing vegetation on the streambank might make the water warmer, or muddier. You realize that activities beyond the streambank might affect the habitat within the stream, and subsequently, the fish.

It all starts with a stream. For me, that stream is the Middle Prong of the Little Pigeon River in Sevier County, Tennessee. I spent many warm days knee-deep in that mountain stream, a few miles downstream of where it flows north out of Great Smoky Mountains National Park. The 20-acre farm on the left is the Hurst family's property. The undercut banks where the stream flows past the farm's riparian clearing will sometimes yield a Smallmouth Bass. The deep pool shaded by a grove of hemlock trees – the spot my dad and I nicknamed the Honey Hole – is usually good for a few Rainbow Trout. A bit further downstream and around the bend where big slabs of bedrock funnel the current through small channels of cobble are where the Bluehead Chubs build their nests in springtime. In late May, these nests become balls of red and yellow fury, color that rivals any coral reef, as Yellowfin shiners, Rosyside dace, Warpaint shiners, and more descend on these nests in search of a meal or a spot to lay their own eggs.

The Little Pigeon River is my version of John Prine's *Paradise*. It's not in danger of being devastated by a coal company, but nearby land use, stream-side rental and vacation properties, and high angling pressure threaten stream habitat quality and biodiversity. My experiences of standing knee-deep in the Little Pigeon River inspired a curiosity that fueled this dissertation and will guide my career. How do fish decide which stream position is best from all the available options? How do our activities on the landscape affect habitat quality and quantity within watersheds? Can we depict these remarkable resources in articles or films in ways that make people want to conserve them? These ideas form the crux of my dissertation research. They all started in a stream.

Summary of findings

In this dissertation, my main objective was to explore relationships between fish, streams, and humans in Southern Appalachia from multiple disciplinary perspectives in order to identify opportunities for successful freshwater conservation. We investigated these relationships from two disciplinary perspectives and across multiple scales of space and time. Specifically, we studied: 1) fine-scale fish habitat selection processes, 2) conservation communication engagement and efficacy, and 3) land use and climactic influences on the relative distribution of trout species.

In Chapter 1, I introduce the problem space – remarkable freshwater biodiversity within a patchwork, increasingly modified landscape – and present an argument for the importance of pragmatic, durable freshwater biodiversity conservation in Southern Appalachia. In Chapter 2, we evaluated simplifying assumptions made by fish habitat selection models and compared the performance of models with differing levels of complexity. We found that some of the assumptions were likely not robust; however, simplified models still performed as well or better than more complex models. We concluded that simplified models currently are useful tools for predicting stream fish habitat selection based on relative habitat quality at fine spatial scales, but that improved estimation techniques of input variables (e.g., swimming cost, energy content of prey in the drift) will enable complex models to predict potential growth or carrying capacity at larger spatial scales, which will enhance the utility of complex models for conservation.

In Chapter 3, we explored the relationship between broad-scale environmental gradients of geomorphology, land use, and climate and the relative distribution of three co-occurring trout species in Southern Appalachia. We found clear patterns at the stream segment scale driven by slope, precipitation, and temperature. However, these patterns disappeared when summarized at the subwatershed scale. Finally, in Chapter 4 we assessed the ability of a conservation film about freshwater biodiversity in Southern Appalachia, *Hidden Rivers*, to generate conservation support among viewers. Our results suggest that two versions of *Hidden Rivers* – a feature-length version and a shortened ~13-minute version – generated significant shifts in conservation support, and that greater engagement with the films via transportation and emotion resulted in stronger shifts in conservation support. Interestingly, we found that the short and long version of *Hidden Rivers* were equally impactful immediately following film viewing, but that shifts in conservation support were more persistent for viewers of the short film several weeks after film viewing.

Interdisciplinary perspectives & insight

It is important to reflect on how the integrative approach outlined in this dissertation contributed to our results and ideally will inform applied conservation strategies for freshwater ecosystems in Southern Appalachia. I identified a single problem space – remarkable and threatened freshwater biodiversity in Southern Appalachia – and investigated it from multiple disciplinary angles. This approach provided me with opportunities to engage with theory and methodologies in multiple, disparate disciplines, and also painted a more comprehensive picture of fish-stream-human dynamics in Southern Appalachia than possible via any single area of inquiry. Insight gained from each chapter can be used to inform the others and illuminate opportunities for creative, synergistic conservation or future research.

Studies of relationships between broad-scale environmental gradients and trout distribution can identify variables important for fine-scale habitat requirements (Poff, 1997). Our findings that Brook Trout are more likely to occupy streams with steep gradients and cold temperatures could inform fine-scale habitat selection models by identifying new input variables (e.g., substrate composition as influenced by steep gradients and high flow) or highlighting the importance of previously uninformative or secondary parameters (e.g., the role of temperature in swimming cost estimates). Likewise, fine-scale studies of habitat selection can identify the mechanisms that make landscape-scale variables important (e.g., steep slopes could produce flows facilitate energy optimization; Grossman et al., 2002; Piccolo et al., 2014) and illuminate how habitat selection mechanisms might shift due to changes in environmental gradients or reveal new gradients important for habitat selection that were previously unknown.

Of course, a refined understanding of the ecological dimensions of fish-stream relationships at both fine and coarse scales also informs communication strategies to reshape stream-human relationships. Understanding how fish evaluate and select focal positions in streams (e.g., in pools or behind boulders or logs) as well as how climate and land use patterns (e.g., precipitation or agriculture within a watershed) influence fish distribution can help communicators and scientists better characterize fish-stream-human relationships in communication and outreach strategies. Our observations that trout select focal positions in specific velocities to maximize prey capture and that Brook Trout prefer cooler, steeper streams that receive ample rainfall can help communicators tell compelling stories about the critical habitat needs of trout in Southern Appalachia.

Additionally, understanding how audiences engage with conservation narratives and which sorts of conservation behaviors (e.g., participating in clean-up or restoration events, donating to a conservation organization, or seeking out additional pro-conservation messages) they are motivated to engage in can inform conservation strategies to maximize public engagement and support. Our observation that viewers of conservation films believed that scientists and conservation professionals play important roles the protection of aquatic life and that this life is ecologically and culturally valuable (specific story-centric beliefs expressed in the short and full version of *Hidden Rivers*) could bode well for establishing dialogue and trust between scientists and community members (Burke et al., 2016; Metcalfe, 2019). Furthermore, our observation that viewers of these conservation films were interested in attending river clean-up events and assisting with species reintroductions (specific conservation behaviors modeled in both versions of *Hidden Rivers*) could translate into meaningful changes in fish-habitat relationships that ultimately show up in fine and coarse scale modeling outcomes.

In summary, the integrative approach used to design and implement the research detailed in this dissertation results in chapter conclusions and contributions that are more than the sum of their parts. Each chapter is oriented around a single, shared problem space. Each chapter provides insight into freshwater ecosystem dynamics in Southern Appalachia from a specific disciplinary perspective and a specific spatial and temporal scope; each chapter also potentially feeds back into the other chapters to more comprehensively characterize fish-stream-human relationships in a complex socioecological landscape.

Conservation opportunities

A core objective of this body of work was to identify opportunities for successful and durable freshwater conservation in Southern Appalachia. Simplified NEI models are adequate and useful tools for predicting stream fish habitat use based on the relative energetic potential of stream focal positions. We recommend that fisheries managers consider these models when evaluating stream habitat at small spatial scales (e.g., within reaches). However, broader-scale applications of these simplified models are limited because they are unable to predict potential growth or carrying capacity, which depend on reasonable estimates of absolute energy potential of habitats (as opposed to relative). We also recommend that researchers develop improved techniques for sampling and modeling complex variables like drift dynamics and swimming cost, which will enhance the utility of complex models by improving their estimates of absolute NEI.

We observed that Brook Trout are more likely to occur in streams with steeper gradients and in wetter and cooler microclimates than Rainbow or Brown Trout in Southern Appalachia. We recommend that fisheries managers consider Brook Trout conservation strategies that prioritize maintaining or restoring populations in specific stream reaches known to have these conditions, as opposed to subwatershed-scale strategies (though this would be beneficial to all trout species; Williams et al., 2011). We also recommend that managers assess Brook Trout streams for groundwater influence and local topographic climate control to identify potential refugia in the face of ongoing and impending climate change.

Lastly, Conservation films are potentially powerful tools for generating conservation support. We recommend that conservation filmmakers carefully consider message length when producing films, including potentially separating long feature-length films into several shorter, episodic films that audiences could engage with at their own pace. We also recommend that conservation filmmakers provide viewers with opportunities to act on their motivations (e.g., donate to a conservation organization, sign up to participate in a conservation event, or access or share other similar conservation stories) immediately after viewing the films to capitalize on short-term pulse effects.

Future directions

Each of these areas of inquiry could support an entire career's worth of research. Our analyses of fine-scale fish-habitat relationships, landscape-scale influences on relative trout distribution, and conservation communication efficacy provided important insights into fish-stream-human relationships in Southern Appalachia, but also revealed many opportunities for future research. The future of NEI models and our ability to harness them to hydro-dynamic models to predict stream fish energetics across broader scales of space and time largely depends on our ability to model drift dynamics. Improved estimates of drift density as a function of flow, season, substrate type, and other important covariates will greatly enhance the quality of NEI models and their utility to managers beyond simple relative habitat quality rankings. Future research on NEI model mechanics also should investigate the relative importance of input variables on model predictions via sensitivity analyses.

Future studies of relative trout distribution should continue to compare observed patterns between different spatial scales. It is possible that we observed no meaningful differences in relative trout distribution at the subwatershed scale because of the spatial concentration of all trout species into relatively few, similar subwatersheds at the southern extent of their range. It would be interesting and productive to see if these patterns remained in more central regions of trout distribution or if species-specific differences in habitat use become apparent at broader spatial scales. Of course, future research should continue to consider potential changes in relative trout distribution due to climate change, especially in peripheral populations likely to be more strongly impacted (DeRolph et al., 2015).

Future research on conservation communication efficacy should explore the role of time in influencing message engagement and response. Understanding how message length influences audience engagement with films will inform future filmmaking and communication strategies. Likewise, exploring how film-precipitated shifts in conservation support decay with time since viewing will inform longitudinal communication strategies. At the very least, future conservation communication scholarship should extend our study framework to other conservation films to determine whether our conclusions are supported beyond *Hidden Rivers*. Conservation films are increasingly popular; there are ample opportunities to extend communication science theories developed for other types of messages (e.g., public health) to this rapidly growing genre.

Conclusion

Integrative approaches to conservation are a process of gaining perspective, which involve identifying and embracing problem complexity and context rather than reducing it (Hirsch & Brosius, 2013; Newell et al., 2005). We asked and answered questions regarding fine-scale fish habitat selection, landscape and climate influences on trout distribution in Southern Appalachia, and the potential for conservation films to shift public perception of the natural world. Collectively, these projects evaluated each component of fish, stream, and human relationships in Southern Appalachia. How do we reconcile human use of the landscape with the integrity of freshwater ecosystems? We can do this, at least in part, through refining our ability to identify optimal habitat for stream fishes and preserving it, through species-specific conservation strategies that prioritize habitat preservation at relevant and appropriate spatial scales, and through telling compelling stories about these remarkable resources that engage and move audiences to care and act. Southern Appalachia is a complicated landscape that contains remarkable biodiversity and a growing human footprint. Integrative approaches that consider human and fish perspectives provide the best opportunity for successful, durable conservation in a world where human activity continues to impact nature.

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