Assessing populations of eastern brook trout (Salvelinus fontinalis) above and below waterfalls in mountain streams of Virginia

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Assessing Populations of Eastern Brook Trout (Salvelinus fontinalis) Above and Below Waterfalls in Mountain Streams of Virginia

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ABSTRACT

Anthropogenically driven factors, such as increasing temperature and sediment in valley streams, acidification of mountain streams, and the introduction of non-native trout, are restricting habitat suitable for healthy populations of eastern brook trout (Salvelinus fontinalis) throughout their native Appalachian range. Brook trout are important as predators of insects in mountain streams and as a favorite of anglers. It is crucial that remaining populations in sustainable habitats be identified and preserved. Waterfalls are geologic knickpoints preventing base-level lowering that create unique, stable landscapes above them, which may alleviate the temperature-productivity/acidity “habitat squeeze” for populations of brook trout and could serve as potentially ideal targets for conservation efforts despite being isolated. This study investigates brook trout occurrence above waterfalls in Virginia and compares brook trout populations found above waterfalls to those below them. One-hundred meter reaches above and below seven waterfalls in Virginia’s George Washington and Jefferson National Forest were sampled for brook trout via 3-pass, block-netted, backpack electrofishing depletions. All brook trout were counted, weighed, and measured for fork length. The response variables are differences in 1) percent dominance, 2) population size, 3) biomass, and 4) length-weight index (Fulton’s Condition Factor) between brook trout above and below waterfalls. Brook trout dominance (100 vs. 36.9%) is greater above than below waterfalls, but not significantly (p = 0.1003). We found abundance (26 vs.12 individuals per 100m) and overall biomass (885.3 vs 284.6 grams per 100m) of brook trout populations above waterfalls to be significantly greater than their below waterfall counterparts (p = 0.078 for both). We also found brook trout above waterfalls to have a
higher condition factor (1.086g/cm$^3$ vs 1.0636g/cm$^3$) than those below waterfalls (p = 0.031). Lastly, we found populations above waterfalls where their occurrence was previously unknown. Despite being isolated, brook trout populations above waterfalls were just as if not more robust than those below and may be excellent targets for conservation.
INTRODUCTION

THE EASTERN BROOK TROUT

The great decline of native western fishes should be a warning to eastern states about the inadequacy of current conservation efforts for Southeastern fishes (493 species), which comprise 47 percent of the North American fish fauna and 62 percent of the fauna in the United States (Warren et al., 1997). The status of eastern brook trout is evidence of this; they are the only salmonid species native to the Appalachian Mountains, and they are declining across their entire native range from Maine to Georgia due to a variety of anthropogenic factors. Wild stream populations of eastern brook trout still occupy over 90 percent of their native habitat in only 5 percent of the watersheds assessed (70 percent of the United States range) by the Eastern Brook Trout Joint Venture (EBTJV) (Hudy et al., 2008). EBTJV also reported that wild stream populations of brook trout are greatly reduced or locally eradicated in nearly half of the watersheds. The majority of historically occupied large rivers no longer support self-reproducing populations of brook trout with genetic integrity (EBJV, 2011).

Taxonomy, Description, and Life History

The eastern brook trout, also known as the brook charr, is a beautiful and valuable fish. As a member of the Salmonidae family, brook trout are related to brown trout (Salmo trutta) and rainbow trout (Oncorhynchus mykiss), which have been introduced to the brook trout’s native range. Salmonids are ray-finned, stream-lined predators that spawn in freshwater. The appearance of brook trout varies greatly between different populations because they have been glacially separated into isolated breeding stocks and
diverse habitats that are now inconsistently impacted by humans (Power, 1980). Brook trout are distinguishable from other species by the black and white stripes along the edges of their lower body fins as well as by their “worm-like” coloring (vermiculation) on their back, which can range from olive, to dark blue-gray. They may also have red spots on their sides surrounded by bluish rings (Brasch et al., 1973). Brook trout have a robust head and a body that is about five times long as it is deep—they have deeper bodies than other charr species. The mouth of a brook trout is terminal with well-developed teeth and its tail is square or only slightly forked, which enables it to turn quickly in a confined space compared to other charrs (Power, 1980). These characteristics reflect the brook trout’s adaptation as a predator in highly variable mountain streams.

Some populations of brook trout are anadromous, meaning they migrate to the ocean to grow and back to freshwater streams to spawn, but the majority are only freshwater dwelling. Trout in the Southern Appalachian Mountains usually remain in the same approximate area for their entire lives and most spawn only once per year, beginning when they are two years old (Power, 1980). Brook trout spawn in autumn when temperature and daylight decrease, which happens to be October throughout most of their American range. A female brook trout will form a depression in the substrate, referred to as a “redd,” preferably where upwelling of groundwater occurs to oxygenate the eggs that she lays there. A male will then fertilize them, after which the parents do not provide any additional care for their offspring. Larval trout, referred to as alevins, hatch in the spring and remain in their protected redd until they have entirely consumed their egg yoke and need to feed. Adults feed on aquatic and terrestrial insects, molluscs, smaller fish, and crustaceans (Power, 1980). Size and longevity of adults vary greatly
between populations, but can grow to be 9 years old, but in many areas only live up to 4 years. They can grow up to 40 cm long in river systems (Power, 1980).

**Ecological Importance**

Brook are crucial to maintaining the balance of mountain stream ecosystems as predators. As insectivores, brook trout control macroinvertebrate species distribution and thus indirectly impact the rate of leaf detritus breakdown (Ruetz et al., 2002). Brook trout prefer drifting terrestrial insects, rely on them during stressful low flow conditions (Courtwright & May, 2013), but will prey on aquatic ones if less terrestrial are available, which makes them important to the riparian ecosystem as well as the instream ecosystem (Hubert & Rhodes, 1989; Courtwright & May, 2013).

Additionally, brook trout are important indicators of water quality in stream ecosystems. Biotic water quality indicators are important because water quality testing only captures the state of a water body at a given time—an analysis of the organisms that live in a water body indicates what conditions are like over those organisms’ lifetimes (Chovanec et al., 2003). Relationships between water quality and brook trout survival have been established. Brook trout cannot survive and reproduce in streams that have elevated temperatures (Hynes, 1970) and/or sediment loads (Marschall & Crowder, 1996). High acidity and heavy metal content have also been found to be coincident with high brook trout mortality (Schofield Jr., 1965; Baldigo & Murdoch, 1976). Thus, public resources managers can determine the presence or absence of brook trout in a stream where they should occur as an indication of overall water quality.
Economic and Social Importance

Brook trout are important game fish throughout their range. In Virginia, 110,000 anglers spend more than 1.1 million dollars per year on trout fishing alone. In and around the Shenandoah Valley, brook trout are a favorite of fly fisherman, and have historically been a source of food. Brook trout have a higher protein content than introduced rainbow trout (Rasmussen & Ostenfeld, 2000), which may also make them more favorable to fisherman than invasive rainbow trout.

EXPLAINING EASTERN BROOK TROUT RANGE RESTRICTIONS AND POPULATION DECLINES

A combination of anthropogenically driven factors is responsible for the decline of the eastern brook trout (Marschall & Crowder, 1996; Hudy et al., 2008). In Virginia, they are generally restricted to the western mountains, even though they were once prevalent in limestone spring creeks of the Shenandoah Valley region between the Blue Ridge and Allegheny mountain ranges (EBJV, 2011).

Increasing Temperature

Brook trout are coldwater fish. They require water less than 25.3 ºC to survive and less than 14.4 ºC reproduce (Hynes, 1970). The survival of young of the year brook trout in particular is strongly affected by temperature (Kanno et al., 2015). Benson’s work (1954) also demonstrated that brook trout growth likely depends on food availability during optimum temperatures, and these findings have been reinforced by McCormick et al. (1972) and well Xu et al. (2010). Rising water temperatures from climate change, urbanization, habitat fragmentation, and poor riparian management are largely
responsible for brook trout being restricted to upper elevation streams (Hudy et al., 2008). There are increasingly limited reaches of stream high enough in elevation for brook trout to experience suitable temperatures, but also large and productive enough for them to find enough food to grow and reproduce (Petty et al., 2014). An expected 3.8 °C rise in mean annual air temperature in the southern part of the native brook trout range in the next century would shift the lower boundary of their distribution up 714m (Meisner, 1990). This will exacerbate the reduction of suitable habitat for brook trout between warm downstream waters and acidic headwaters, resulting in a ‘habitat squeeze’ (McDonnell et al., 2015).

**Acidification**

Brook trout are also intolerant to low pH water, a problem that persists in otherwise pristine headwater streams protected from direct anthropogenic impacts, because of acid rain. Despite reductions in acidic emissions mandated by the Clean Air Act amendments of 1990, streams in western Virginia show little to no recovery because the region’s mountain geology has low Acid Neutralizing Capacity (ANC) retaining much of the acid deposited historically, unlike the limestone present in valley regions (Webb et al., 2005; Harmon, 2017). This is because the siliclastic and granitic rock types of the mountains are not as rich in acid neutralizing cations as basaltic and limestone rocks of the valley. This restricts the extent to which brook trout can use mountain streams as a refuge.

Acidic deposition in streams decreases egg to larval survival, juvenile survival, and adult growth rates of brook trout (Marschall & Crowder, 1996). It also results in
greater adult mortality when trout are exposed to acidic water for longer periods of time in poorly buffered streams (Baldivo & Murdoch, 1997), such as those in the Appalachian Mountains. Thus, the impending relaxation of air quality standards by the federal government and the subsequent increase in acid deposition could exacerbate the “habitat squeeze” between valley streams that are too warm and headwaters that are too acidic for Appalachian brook trout populations (McDonnell et al., 2015).

**Siltation**

Siltation, which stems from poor riparian management, habitat fragmentation, and urbanization, reduces brook trout survival. Cordone and Kelley (1961) describe multiple cases of brook trout populations declining with increased sedimentation. Specifically, increased sediment in streams decreases brook trout egg to larval survival rates (Marschall & Crowder, 1996) as well as survival rates throughout every stage of early development (Argent & Flebbe, 1999). Additionally, sedimentation can alter food webs from the bottom up. Macroinvertebrate density and diversity is directly related to substrate diversity (Gore, 1985), so if too much sediment settles into the interstitial spaces of the stream bed and the benthic habitat becomes homogenous, then the macroinvertebrate community will be smaller, less diverse, and therefore less of a food source for fish like trout (Henley et al., 2010).

**Introduced Rainbow, Brown, and Hatchery Trout**

The introduction of non-native rainbow trout, non-native brown trout, and brook trout reared in hatcheries from stocks of different regions for sport fishing, has had a profoundly negative effect on native, wild brook trout populations. Competition with
rainbow trout and brown trout for food resources and ideal habitat has decreased brook trout survival and distribution (Fausch & White, 1981; Larson & Moore, 1985). Adult brook trout prefer main channel habitats within the stream but are often forced into peripheral stream areas when sympatric with rainbow trout (Larson & Moore, 1985). Where rainbow trout and brook trout co-occur, rainbow trout are larger, about 1.8 times more massive than brook trout (Larson & Moore, 1985). This is problematic because they are then able to dominate smaller brook trout, which lose weight when subordinate (Cunjak & Green, 1984). The survival rate of small brook trout decreases when they cooccur with rainbow trout enough to cause a 50% reduction in overall brook trout population size (Marschall & Crowder, 1996). When rainbow trout are removed, brook trout populations grow (Moore & Larson, 1993).

Brown trout (*Salmo trutta*) also negatively affect brook trout populations; brook trout distribution between microhabitats changed when brown trout are introduced, and the brook trout lost weight (Dewald & Wilzbach, 1992). Brown trout not only outcompete brook trout for foraging habitat, but they also force brook trout into less favorable thermal areas of the stream (Hitt et al., 2017), so it is possible that the impacts of competition with rainbow and brown trout combined with the impacts of rising temperatures on brook trout populations are more than additive.

Hybridization between hatchery trout and wild trout can be detrimental to wild populations. Hybrids between different species of salmonids are less developmentally stable than their parent species and therefore less fit to survive and reproduce (Leary, Allendorf, & Knudsen, 1985). Even hybrids between wild brook trout and hatchery trout of the same species are less likely to survive and reproduce because artificial selection
trains them to expect feeding and makes them less fit to survive in the wild (Flick & Webster, 1964). For example, in a study done by Vincent (1960), observed a 13% greater survival of wild trout stock than domestic trout stock in a mountain stream and observed that wild trout have greater resiliency to metabolites and high water temperatures than domestic trout stock. The results of Teears (2016) master’s thesis on the impacts of water hardness and acid-neutralizing capacity on the early development of brook trout fry indicated that genetic adaptations to water quality may give young brook trout with parents that spawned in the same stream a “home-field advantage” in early survival and growth over the offspring of trout that were not raised in the same environment. Additionally, wild strains of trout are inherently better at growing and surviving than their hatchery counterparts, regardless of their environment during development (Webster & Flick, 1981). Thus, introductions of non-native strains of brook trout into the Appalachian Mountains could reduce wild populations adaptability by simplifying the population structure and eliminating unique genotypes within it (Hayes et al., 1996).

Lastly, hatchery trout of any species can also introduce disease to wild populations. Whirling disease affects a variety of salmonid species by degrading their cartilage and giving them lesions containing toxic parasites (*Myxobolus cerebralis*). The disease has historically been introduced to wild trout populations through contact with hatchery raised trout like non-native rainbow trout (Bartholomew & Reno, 2002). Brown trout also introduce the fungus *Saprolegnia* sp. to brook trout, which results in the death of about 1/3 of their population (Dewald & Wilzbach, 1992).
WATERFALLS AS A COMPONENT OF CONSERVATION

Recent research indicates that above waterfall habitats are geomorphologically unique from other barriers to fish movement, such as dams and culverts, and may be more conducive to sustaining healthy salmonid populations (May et al., 2017). There is a conservation paradigm that isolated populations are at the highest risk for extirpation, but above waterfall populations of salmonids may not fit that paradigm.

Theory suggests that small isolated populations are subject to slow extirpation from inbreeding/ genetic drift (Guy et al., 2008) and/or rapid extinction from stochastic events (Letcher et al., 2007). However, a multitude of sizable trout populations have persisted above waterfalls for millennia (Carvalho, 1993; Guy et al., 2008; Whiteley et al., 2010), which suggests that isolated populations are not necessarily small in terms of abundance, despite occupying small spatial areas; and the tendency for above waterfall populations to stay instead of emigrating downstream, coupled with local adaptations, can “rescue” isolated populations from fragmentation threats (Letcher et al., 2007).
Waterfall Geomorphology

**Figure 1.** LIDAR map of the slopes in the Kentucky Falls, Oregon, basin (bottom), which exhibits much gentler slopes (blue) and wider floodplains than the basin on the other side of the ridge (top) that is not above a waterfall (May et al., 2017).

Waterfalls provide broad floodplains and low gradient habitat above them, allowing for large, stable populations to thrive (Fig 1). Waterfalls do this by preventing base-level lowering and channel incision (Fig A14); the erosion that doesn’t happen vertically above waterfalls occurs horizontally instead, creating broader floodplains and lower gradient channels (May et al., 2017).

Landslides and debris flows are events that impact steep headwater stream channels of the Appalachian Mountains (Eaton et al., 2003) as well as those in the Pacific Northwest. However, the lower gradient channels created above waterfalls may lessen the risk of landslides and debris flows in headwater streams (May et al., 2017). Debris flows and landslides can severely reduce or extirpate a population of trout so that the area must be recolonized for a population to persist (Roghair et al., 2002; Sato, 2006). Therefore,
the reduction of such risk improves the suitability of the habitat for the persistence of native salmonids, especially in naturally isolated habitats like those above waterfalls.

Brook trout prefer such lower gradient streams (Platts, 1976) with slower velocities (Cunjak & Green, 1983), because less energy is required to fight against the current than in a steep gradient habitat. Thus, they save metabolic energy for growth. Low-gradient, broad floodplains also retain nutrients longer than steep ones and therefore sustain more productive ecosystems overall (Wohl et al., 2012). Greater productivity above waterfalls may yield greater food availability for trout there than for trout below them. Additionally, wider channels provide more refuge for fish during high flow events (Schwartz & Herricks, 2005). Thus, the wider floodplains above waterfalls accommodate larger trout populations, which are less vulnerable to genetic drift and stochastic events than small populations. Habitat of sufficient size and productivity allows trout to successfully reside in their environment because they have enough food and less energy costs to grow more efficiently than migrant fish (Morinville & Rasmsusen, 2011). On a landscape scale, more suitable habitat available for salmonids in headwater streams is strongly correlated with greater genetic diversity and therefore greater evolutionary potential for isolated populations (Whiteley et al., 2010).

Brook trout are often the only fish species above waterfalls in Appalachia, so in their isolation, they are protected from interactions with non-native/hatchery trout. There is precedent on the west coast of the United States for intentionally isolating native salmonid species; artificial barriers to migration are often maintained to prevent cutthroat trout hybrids and competition with other non-native salmonids (Minckley & Deacon, 1991; Thompson & Rahel, 1998). The invasion of rainbow trout into Appalachian
streams historically occupied by brook trout is dynamic and continues to further restrict brook trout to higher and higher elevations (Larson & Moore, 1985), so the benefit of habitats above waterfalls for brook trout is heightened by the refuge from rainbow trout that these habitats offer.

A New Conservation Direction

Conservation efforts focused on populations above waterfalls may be advantageous for long-term conservation of not only brook trout, but a variety of native salmonid species in other regions. Upper reaches of streams usually have lower water temperature, higher dissolved oxygen, and greater clarity than lower reaches (Northcote & Hartman, 1988). Because small headwater tributaries often have ideal water temp, but insufficient food supply to match brook trout growth rates of downstream populations (Petty et al., 2014), above waterfall habitats that trap nutrients and are more productive than other upper reach habitats may be good places to relieve the “temperature-productivity squeeze.”

Additionally, trout isolated above waterfalls have a genetic tendency to reside there instead of migrating downstream, thus preserving the isolated population and representing important sources of genetic diversity that need protecting (Northcote, 1992; Carvalho, 1993). The unique genetic attributes occasionally feed genetic variation to downstream populations when straying individuals emigrate from above waterfall habitats; the fact that above waterfall populations are mostly isolated from downstream populations benefits the entire metapopulation in the long-run (Gresswell et al., 2006).
These naturally isolated populations of brook trout above waterfalls may therefore have the benefits of headwater streams being cold and clear, without some of the drawbacks such as high risk of landslides/debris flows and low productivity. Since mitigation efforts against acidification, such as liming, tend to be intensive, expensive, and not feasible to attempt for every stream containing brook trout, priority streams need to be established. Perhaps above waterfall stream habitats are ideal for the focus of such efforts and other conservation opportunities.

**OBJECTIVES AND HYPOTHESES**

The first objective of this study is to investigate occurrence of brook trout above waterfalls in Virginia’s George Washington National Forest (GWJNF). Above waterfall stream reaches are often remote and therefore not often investigated for the presence of brook trout. Often times, fish sampling does not occur above most barriers to fish movement, so communicating with professionals and fisherman about potential sites, as well as visiting waterfalls where brook trout occurrence above remains unknown is a key part of determining what waterfalls have brook trout above them and therefore can be considered for this study.

The second objective of this study is to compare brook trout populations above waterfalls to those below them in mountain streams of Virginia. The response variables are differences in 1) percent dominance 2) population size, 3) biomass, and 4) length-weight index between brook trout above waterfalls and brook trout below waterfalls.

It was hypothesized that brook trout populations would be more likely to exist above waterfalls on basaltic and granitic rock types with high ANC because such streams would be less acidic and therefore more habitable for brook trout than streams on
siliclastic rock types. It is also possible that waterfalls with a larger drainage basin above them may be more likely to have large populations of brook trout above them than those with a small drainage basin because a larger drainage basin holds a larger habitat for a population to utilize.

It was also hypothesized that populations above waterfalls will 1) have a greater percent dominance of brook trout over other species 2) a greater brook trout population biomass, 3) more brook trout individuals present overall, and 4) brook trout individuals that are more massive for their respective lengths than populations below. This is expected because waterfalls create unique, stable landscapes above them that may allow relatively large, healthy native trout populations to persist in cold, protected mountain streams without competition from non-native/hatchery trout.

**METHODS**

To determine where brook trout populations exist above waterfalls in Virginia, a list of sixteen waterfalls was compiled. To compare populations above waterfalls to their counterpart populations below waterfalls by measures of 1) percent dominance of brook trout 2) population size, 3) population biomass and 4) length-weight index, 100m reaches were sampled via three-pass block-netted backpack electrofishing depletions above and below seven waterfalls in Virginia’s George Washington and Jefferson National Forest (GWJNF). All fish collected in this way were identified, counted, and returned to the stream. All brook trout collected were counted, weighed, and measured for fork length before being returned to the stream (IACUC protocol #A18-A16).
SITE INVESTIGATION AND SELECTION

The selection process began with a list of over 40 known waterfalls in Virginia, but many of these were not considered for inclusion in this study because they lie within Shenandoah National Park, which requires separate permits for access that could not be obtained within the timeframe of this thesis. Waterfalls were discovered though the World Waterfall Database (https://www.worldwaterfalldatabase.com/) and/or Molloy et al. (2014) chapter on Virginia waterfalls. Waterfalls were then investigated that met the following criteria for sampling: they must 1) exist in GWJNF, 2) potentially have only wild native brook trout (no stocked and/or introduced non-native trout species) above them, 3) have a drainage basin above the falls between 2 and 40 km², and 4) be tall enough to be a barrier to trout movement upstream (at least 3m high) to have been considered for attempted sampling.

The world waterfall database was used to find the GPS coordinates and height of each waterfall. The USGS (United States Geological Survey) online Streamstats tool (https://streamstats.usgs.gov/ss/) was used to determine the size of the drainage basin above each waterfall. Streamstats map delineates the watershed above a selected point (each waterfall), and provides a report detailing the area, of that drainage basin. The occurrence of brook trout was determined through Virginia Department of Game and Inland Fisheries’ (VDGIF) brook trout area maps (https://www.dgif.virginia.gov/fishing/trout/area-maps/), EBTJV’s brook trout integrated special data (http://ecosheds.org:8080/geoserver/www/Web_Map_Viewer.html), the advice of Dawn Kirk, George Washington and Jefferson National Forest’s fisheries
biologist, and by communicating with VDGIF fisheries biologists Brad Fink, Jeff Williams, Steve Tanguay, Bill Kittrell, Steve Owens, and John Copeland.

Professionals from the US Forest Service and VDGIF have determined that no wild brook trout were found above Brumley Creek Falls, Tank Hollow Falls, Falling Water Cascades, Falling Spring Falls, and Devil’s Bathtub. They also confirmed that while wild brook trout do exist above Falls of Dismal, non-native rainbow trout are also stocked above it.

One of the objectives of this study is to determine the characteristics of waterfalls that have brook trout above them. As the basin size, rock type and height are known characteristics of these six waterfalls (Table 1), they were included, along with the ten waterfalls visited, in the analysis of characteristics of waterfalls and wild brook trout occurrence above them. These sixteen waterfalls were narrowed down from a list with eighteen additional waterfalls known to be outside of Shenandoah National Park, but where brook trout occurrence above could not be determined (Table 2). The basins above the sixteen waterfalls (ten visited plus six where brook trout occurrence above is known) were delineated using the watershed tool in Arc GIS. The predominant rock type in these basins were then determined using a shapefile of Virginia Geology from USGS (Fig 2).

In order to satisfy the second objective, to compare brook trout populations above and below waterfalls, ten waterfalls were selected from the list of sixteen to be sampled (Table 1) for meeting the criteria outlined above. The occurrence of trout above five of these waterfalls remained undetermined by professionals from the Forest Service and VDGIF until they were visited and sampled for this study. Brook trout were newly found through this study’s sampling above Overstreet Creek Falls and Little Cove Creek Falls,
but were not found above Apple Orchard Falls, Comer’s Creek Falls, and Mill Creek Falls (Table 1).

Table 1. The 16 waterfalls brook trout occurrence above is known, their location, and their characteristics analyzed in this study. These are listed by rock type and then alphabetically as on the map (Fig 2). Brook trout were found above 7 waterfalls and below 5 of those waterfalls via electrofishing. No brook trout were found above 3 of the 10 waterfalls visited, so sampling was not conducted below. Lastly, 6 waterfalls were not visited, but brook trout are known to either exist or not exist above the falls.

<table>
<thead>
<tr>
<th>#</th>
<th>Waterfall</th>
<th>Rock Type</th>
<th>Basin Size (km²)</th>
<th>Height (m)</th>
<th>Visited</th>
<th>Brook trout occurrence</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Apple Orchard Falls</td>
<td>granitic</td>
<td>1.42</td>
<td>91</td>
<td>Yes</td>
<td>Not Above</td>
</tr>
<tr>
<td>2</td>
<td>Cabin Creek Falls</td>
<td>granitic</td>
<td>2.10</td>
<td>14</td>
<td>Yes</td>
<td>Above &amp; Below</td>
</tr>
<tr>
<td>3</td>
<td>Crabtree Falls</td>
<td>granitic</td>
<td>3.25</td>
<td>67</td>
<td>Yes</td>
<td>Above &amp; Below</td>
</tr>
<tr>
<td>4</td>
<td>Fallingwater Cascades</td>
<td>granitic</td>
<td>2.00</td>
<td>30</td>
<td>No</td>
<td>Not Above</td>
</tr>
<tr>
<td>5</td>
<td>Little Cove Creek Falls</td>
<td>granitic</td>
<td>3.37</td>
<td>6</td>
<td>Yes</td>
<td>Above &amp; Below</td>
</tr>
<tr>
<td>6</td>
<td>Overstreet Creek Falls</td>
<td>granitic</td>
<td>2.00</td>
<td>6</td>
<td>Yes</td>
<td>Above &amp; Below</td>
</tr>
<tr>
<td>7</td>
<td>Statons Creek Falls</td>
<td>granitic</td>
<td>14.25</td>
<td>42.5</td>
<td>Yes</td>
<td>Above &amp; Below</td>
</tr>
<tr>
<td>8</td>
<td>Brumley Creek Falls</td>
<td>siliclastic</td>
<td>16.27</td>
<td>6</td>
<td>No</td>
<td>Not Above</td>
</tr>
<tr>
<td>9</td>
<td>Comers Creek Falls</td>
<td>siliclastic</td>
<td>2.60</td>
<td>5</td>
<td>Yes</td>
<td>Not Above</td>
</tr>
<tr>
<td>10</td>
<td>Devil’s Bathtub</td>
<td>siliclastic</td>
<td>11.00</td>
<td>15</td>
<td>No</td>
<td>Not Above</td>
</tr>
<tr>
<td>11</td>
<td>Falls of Dismal</td>
<td>siliclastic</td>
<td>38.33</td>
<td>5</td>
<td>No</td>
<td>Above</td>
</tr>
<tr>
<td>12</td>
<td>Falling Spring Falls</td>
<td>siliclastic</td>
<td>32.00</td>
<td>21</td>
<td>No</td>
<td>Not Above</td>
</tr>
<tr>
<td>13</td>
<td>Little Stony Creek Cascades</td>
<td>siliclastic</td>
<td>39.00</td>
<td>20</td>
<td>Yes</td>
<td>Above, NO Below</td>
</tr>
<tr>
<td>14</td>
<td>Mill Creek Falls</td>
<td>siliclastic</td>
<td>17.50</td>
<td>3</td>
<td>Yes</td>
<td>Not Above</td>
</tr>
<tr>
<td>15</td>
<td>Rowland Creek Falls</td>
<td>siliclastic</td>
<td>5.93</td>
<td>15</td>
<td>Yes</td>
<td>Above, NO Below</td>
</tr>
<tr>
<td>16</td>
<td>Tank Hollow Falls</td>
<td>siliclastic</td>
<td>2.50</td>
<td>11</td>
<td>No</td>
<td>Not Above</td>
</tr>
</tbody>
</table>
Figure 2. The location and drainage basins of waterfalls in Southwestern Virginia as listed in Table 1. Yellow basins are on granitic rock types and red basins are on siliclastic rock types. They are numbered by rock type and then alphabetically. Stars indicate waterfalls visited and are dark blue if brook trout were found both above and below the falls, light blue if brook trout are found only above the falls, and yellow if no brook trout were found above the falls.
Table 2. The 18 waterfalls considered, but not analyzed because brook trout occurrence above is unknown. All exist outside of Shenandoah National Park. The counties in which each waterfall exists are listed and the waterfalls are organized by their reason for being excluded from attempted sampling.

<table>
<thead>
<tr>
<th>Waterfall</th>
<th>County</th>
<th>Reason for Excluding</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barnard Creek Falls</td>
<td>Patrick</td>
<td>difficult to access</td>
</tr>
<tr>
<td>Blue Suck Falls</td>
<td>Bath</td>
<td>difficult to access (6-mile hike)</td>
</tr>
<tr>
<td>Bent Mountain Falls</td>
<td>Montgomery</td>
<td>difficult to access (steep terrain)</td>
</tr>
<tr>
<td>Chestnut Creek Falls</td>
<td>Carroll</td>
<td>drainage basin too big (139.34 km²)</td>
</tr>
<tr>
<td>Panther Falls</td>
<td>Amherst</td>
<td>drainage basin too big (65.6 km²)</td>
</tr>
<tr>
<td>Barbours Creek Falls</td>
<td>Craig</td>
<td>drainage basin too big (81 km²)</td>
</tr>
<tr>
<td>Wigwam Falls</td>
<td>Nelson</td>
<td>drainage basin too small (0.83 km²)</td>
</tr>
<tr>
<td>Big Wilson Creek Falls</td>
<td>Grayson</td>
<td>in wilderness area</td>
</tr>
<tr>
<td>Saint Mary’s Falls</td>
<td>Augusta</td>
<td>in wilderness area</td>
</tr>
<tr>
<td>Abrams Falls</td>
<td>Washington</td>
<td>on private property</td>
</tr>
<tr>
<td>Crab Orchard Falls</td>
<td>Wise</td>
<td>on private property</td>
</tr>
<tr>
<td>Davis Mill Creek Falls</td>
<td>Amherst</td>
<td>on private property</td>
</tr>
<tr>
<td>Emerald Falls</td>
<td>Scott</td>
<td>on private property</td>
</tr>
<tr>
<td>Maidenhead Branch Falls</td>
<td>Nelson</td>
<td>on private property</td>
</tr>
<tr>
<td>Meadow Creek Falls</td>
<td>Craig</td>
<td>on private property</td>
</tr>
<tr>
<td>Shamokin Falls</td>
<td>Nelson</td>
<td>private property with golf course above</td>
</tr>
<tr>
<td>Roaring Run Falls</td>
<td>Botetourt</td>
<td>stocked trout above</td>
</tr>
<tr>
<td>Tumbling Creek Falls</td>
<td>Russell</td>
<td>stocked trout above</td>
</tr>
</tbody>
</table>

FISH COLLECTION

All fish were collected by backpack electrofishing depletions of a 100m reach above each of the ten waterfalls visited and a 100m reach below each of the seven waterfalls where brook trout were found above (Table 1 & Fig 2). The respective reaches began at least two pool-riffle sequences above the falls and two pool-riffle sequences below the falls, in order to avoid novel habitats created in close proximity to the waterfall itself. The reach below Overstreet Falls was an exception to this as the only place to access this area was part of a steep series of cascades below the main falls. A reel tape was used to set up each 100m reach, and block-nets were set at both upstream and downstream boundaries to prevent disturbance of sampling driving fish out of the sampling area, and thus create a closed system. Dimensions of the block nets were 5 to 7 mm bar mesh with lead bottom lines and were used as recommended by Dunham et al., (2009).
Three-pass, block-netted backpack electrofishing procedures were used to collect fish in accordance with methods outlined by American Fisheries Society for sampling populations of coldwater fish in wadeable streams. A pulsed DC backpack electrofishing unit (Smith Root LR-24) with a circular probe anode and a rat-tail cathode was operated by one person to shock fish, while one to four people used a dip net to collect the stunned fish. The number of dip netters was determined by the size of the stream and availability of assistants. The voltage was determined by the backpack from the conductivity of the water because a voltage too high would injure the fish and a voltage too low would result in a poor capture efficiency (Dunham et al., 2009). Shocking time was recorded and later used to calculate CPUE (Catch Per Unit Effort) of each 100m reach (Table A1). Reaches were sampled with a fourth pass if more brook trout were caught on the second pass than on the first or on the third pass than on the second. All individuals that were not brook trout were stored in a live-well, identified, and counted. All brook trout individuals collected were stored in a live-well, counted, wet weighed (g) and measured for fork length (cm). After counts and measurements were recorded, all fish were returned live to the stream. All aquatic equipment was rinsed in a 5% salt water solution between sampling each site to prevent the transfer of organisms between watersheds.

**CHARACTERIZING THE REACH**

Within each reach, five parameters were used to characterize the physical and chemical habitat. Above and below the waterfall at each site, the slope of each entire 100m stream reach was estimated by measuring the percent slope of each 25m section of the reach (four measurements) with a clinometer and then averaging those measurements. Wetted width was measured three times (at 25m, 50m, and 75m in the 100m reach) using
a reel tape and then averaged for each 100m reach. Pictures of the sampled streams were
taken and the top and bottom of each reach was recorded via AVENZA Maps App on a
smartphone. Slope and images were used to determine the reach scale classification of
each site as either cascade (slope > 6.5%), step pool (slope 3 - 6.5%), plane bed (slope 1.5
- 3%), or pool riffle (slope < 1.5%) as described by Montgomery & Buffington (1997).
These slope ranges and other visually assessed characteristics, such as the presence of
pools and/or riffles, were used to classify each reach (Frissell et al., 1986).

Water chemistry at each waterfall was analyzed by partnering with the University
of Virginia (UVA) Shenandoah Watershed Study (SWAS) program, a research network
focused on monitoring the chemical composition of trout streams in the headwaters of
Southwestern Virginia. Water samples were collected from the stream below each of the
seven waterfalls where brook trout were found above in accordance with the instructions
given by UVA’s Department of Environmental Sciences, which follow those outlined by
Webb et al., (2010). Their analyses determined the pH and ANC of each fully sampled
stream.

STATISTICAL ANALYSES

All statistical analyses were performed in R (v.3.4.4). An alpha value of 0.1 was
used to determine statistical significance because there are few waterfalls that had trout
above them and therefore, most comparisons had to be made with small sample sizes.
Analyses of normal distribution still use an alpha of 0.05.
Correlating Brook Trout Occurrence Above Waterfalls with Waterfall Characteristics

In order to better understand which characteristics of basins and waterfalls are most associated with the presence of wild brook trout above waterfalls, three logistic regressions were run with the sixteen waterfalls where brook trout are known to either exist or not exist above the falls (Table 1). The first logistic regression assessed the relationship between the size of basin above each waterfall (km²) and the occurrence of brook trout above it (0 = absent, 1 = present). The second logistic regression assessed the relationship between the rock type (siliclastic or granitic) of each waterfall’s drainage basin above it and the occurrence of brook trout above it. The third logistic regression assessed the relationship between waterfall height (m) and the occurrence of brook trout above it. These regressions were run separately because the sample size is small.

Comparing Brook Trout Populations Above and Below Waterfalls

The first comparison made between populations of brook trout above and brook trout populations below waterfalls is their percent dominance over other fish species. Percent dominance of brook trout in each habitat was calculated by dividing the number of brook trout caught by the total number of fish caught, and multiplying that ratio by 100. This ratio was calculated for all six waterfalls where fish were found above and below the falls. No fish of any species were found below Little Stony Creek Cascades, so this waterfall was excluded from this analysis. Populations above and below are distributed independently of each other, and so their normality was tested independently. Shapiro-Wilk Normality Tests indicate that the percent dominance data are not normally
distributed above the falls (p= 0.006) but are normally distributed below the falls (p=0.186). Therefore, a non-parametric analysis, a paired, two-sided Wilcoxon Rank-Sum Test, was used to compare the median percent dominance of brook trout in the reaches above waterfalls to the median percent dominance of brook trout in the below waterfall reach counterparts. Assuming the observed effect size, a total sample size of at least 12 waterfalls would be needed to reach a power level of 0.9 and see a significant difference between the means, while maintaining a significance level of 0.1.

The second comparison made between populations of brook trout above and below waterfalls is the size of their populations. Population size was analyzed in two ways: 1) by comparing the estimated population abundance of each 100m reach between reaches above waterfalls and reaches below waterfalls, and 2) by comparing population density (# of brook trout per 100m²) via a proxy of abundance per basin (km²) between reaches above and below waterfalls.

The Leslie Depletion Method was used for estimating population abundance within each 100m long reach via a step-by-step regression in R (Ogle, 2013). The information input was the number of brook trout caught per pass and the effort spent attempting to catch them (shock time in minutes).

The estimated abundance of brook trout above waterfalls was then compared to that of those below waterfalls via a paired, two-sided Wilcoxon Rank-Sum test. The data are normally distributed above (p = 0.105) and below (p = 0.153) the falls, but the nonparametric test was used instead of a t-test because the sample size of seven waterfalls is small. Assuming the observed effect size, a total sample size of at least 16 waterfalls
would be needed to reach a power level of 0.9 and see a significant difference between the means, while maintaining an alpha value of 0.1.

The population density per 100m² could be determined by dividing the estimated population abundance by the total area sampled (m²) and multiplying that by 100. The total sampled area = L*(W₁+W₂+W₃)/3, where L represents the length of the reach (always 100m) and W₁, W₂, and W₃ represent the three wetted-width measurements taken within the reach.

Virginia had an exceptionally rainy summer during 2018. The state experienced above average precipitation with some record rainfall in northwestern counties from May through July of 2018 (National Centers for Environmental Information, 2019). This caused flooding that may have elevated some of the measurements of wetted-width beyond what is typical of each stream for summer base-flow. This would make the calculation of sampled area inaccurate and therefore, the estimated population densities of some reaches not representative of their usual state. Because basin size (km²) is constant and a good indicator of stream size (Leopold & Miller, 1956), a proxy of population density was calculated using estimated abundance (# of individuals estimated to be in a 100m reach) divided by the size of the basin above the reach (km²) (Table A3). This ratio was used to compare brook trout density between reaches. A Shapiro-Wilk normality test indicates that the proxy population density data are normally distributed both above (p = 0.102) and below (p = 0.07) waterfalls. Again, a non-parametric, paired, two-sided Wilcoxon Rank-Sum Test was also conducted because the sample size is small (n = 7). A power analysis of a t-test assuming a power of 0.9 and an alpha of 0.1 indicates that a sample size of at least 29 would be needed to see a significant difference between
the means. These analyses of abundance and biomass were also repeated excluding data from Little Stony Creek Cascades as the lack of brook trout caught below this waterfall is suspected to be greatly influenced by heavy rain during the summer of sampling.

Measures taken to describe the reaches sampled, such as pH, ANC, water temp, basin size above, and stream slope, are each associated with brook trout population abundance of the reaches via linear regressions. The data for ANC is also associated with species richness in each stream (total number of fish species captured above and below the falls) via linear regression in combination with similar data from Harmon (2017). The pH and ANC data used for these regressions are those measured by SWAS from the water samples. For ANC and pH, there is only one measurement for each waterfall (Table A2). However, for water temperature, basin size, and slope, there is a measurement above separate from a measurement below each waterfall (Table A3). The basin sizes are determined by using the location of the bottom of each sample reach as the pour point instead of the location of the waterfall itself.

The third comparison made between brook trout populations above and below waterfalls is their biomass. Biomass was analyzed in three ways: 1) by comparing the average biomass of individual brook trout above all waterfalls to that of those below, 2) by comparing the total biomass of all brook trout in the reaches sampled above waterfalls to that of those below waterfalls, and 3) by comparing the estimated total brook trout biomass density (grams /100m²) above each waterfall to that below each waterfall via a proxy (grams of brook trout per km² of drainage basin). The biomasses of all brook trout individuals above waterfalls were compared to the biomasses of those below via non-
paired, Wilcoxon Rank-Sum test because the data are not normally distributed both above
(p < 0.0001) and below (p < 0.0001) waterfalls.

The estimated total brook trout biomass in each 100m reach was estimated by
multiplying the average biomass of individuals in a 100m reach by the estimated
abundance per 100m (calculated via the Leslie Depletion Method above) (Hayes et al.,
2007). A Shapiro-Wilk normality test indicates that the total biomasses in both above (p
= 0.086) and below reaches (p = 0.114) are normally distributed, but the sample size is
small (n=7) so a Wilcoxon Rank-Sum test was conducted to compare estimated total
brook trout biomass between reaches above and reaches below waterfalls. Assuming the
observed effect size, a total sample size of at least 60 waterfalls would be needed to reach
a power of 0.9 and see a significant difference between the means, while maintaining an
alpha value of 0.1.

The biomass density (g/100m²) could be calculated by dividing the estimated total
brook trout biomass in each 100m reach by the total sampled area of each reach (see area
calculation above). However, as with population density, a proxy of biomass density was
calculated using estimated biomass per basin above the reach (km²) because the stream
widths were likely atypical due to heavy rainfall this summer. This proxy was used to
compare brook trout density between reaches.

A Shapiro-Wilk normality test indicates that the density proxy data are normally
distributed both above (p = 0.23), and below the falls (p = 0.13). However, the sample
size is small (n = 7), so a non-parametric, paired, two-sided Wilcoxon Rank-Sum Test
was also conducted.
The fourth comparison made between populations of brook trout above and below waterfalls was the length-weight index of their individuals. The length and weight index, Fulton’s Condition Factor, was determined from the weights and lengths of each individual fish. Fulton’s Condition Factor: \( K = 100 \frac{W}{L^3} \), where \( W \) represents whole body wet weight in grams and \( L \) represents length in cm, was used as outlined by Froese (2006) to determine the condition of each brook trout collected. Length is cubed in this equation to comply with the cube law stated by Herbert Spencer in his Principles of Biology 1864–1867 (republished 2017), which states that “in similarly-shaped bodies the masses, and therefore the weights, vary as the cubes of the dimensions” (Froese, 2006). This index of length-weight relationships is accepted by American Fisheries Society (Quist et al., 2009).

The condition factor of brook trout in above waterfall populations were compared to that of those in below populations by comparing all brook trout individuals caught above seven waterfalls to all those caught below five of those waterfalls. A Shapiro-Wilk normality test indicates that the condition factor data of all book trout individuals above waterfalls \( p = 1.867e-14 \) and below waterfalls \( p = 2.462e-13 \) is not normally distributed. Therefore, individuals above were compared to individuals below via a nonparametric Wilcoxon Rank-Sum test.

The biomasses and length-weight indexes of brook trout above could also be compared to that of those below each of the five waterfalls where populations were found both above and below. The biomasses and length-weight indexes of all brook trout individuals above a given waterfall were compared to that of those below the same waterfall by Wilcoxon Rank-Sum tests, because the data were often not normal.
RESULTS

This study attained one-time measurements above and below seven waterfalls in George Washington and Jefferson National Forest during the summer of 2018. A total of 176 brook trout were caught above seven waterfalls and 114 brook trout were caught below five of those waterfalls. Twelve additional species were also captured above falls: longnose dace (Rhinichthys cataractae), blacknose dace (Rhinichthys atratulus), fantail darters (Etheostoma flabellare), torrent suckers (Thoburnia rothoeca), and northern hogsuckers (Hypentelium nigricans). Longnose dace, blacknose dace, fantail darters, torrent suckers, northern hogsuckers, rosy-sided dace (Clinostomus funduloides), rainbow trout (Oncorhynchus mykiss), brown trout (Salmo trutta), bluehead chub (Nocomis leptoccephalus), mountain redbelly dace (Chrosomus eos), red-lips shiners (Notropis chiliticus), and madtoms (Noturus sp.) were found below some of these falls (Table A4). The exact location of the sampled reaches as well as their characteristics can be found in Site Descriptions within the Appendix as well as Tables A1 and A2.

CORRELATING BROOK TROUT OCCURRENCE ABOVE WATERFALLS WITH WATERFALL CHARACTERISTICS

Three logistic regressions of these waterfalls revealed a lack of a statistically significant relationship between basin characteristics and the occurrence of brook trout above the waterfall (Table 3). This study found sixteen waterfalls for which data exists on the occurrence of brook trout above the waterfall, the size of the drainage basin above the waterfall, the rock type underlying the waterfall, and the height of the waterfall (Table 1). A larger basin size is not associated (p = 0.656) with brook trout being present above a waterfall. Likewise, waterfall height is not at all associated with brook trout occurrence
above (p = 0.938). Rock type has the smallest p-value (0.142) of the three characteristics, suggesting that granitic rock types instead of siliclastic ones may be associated with brook trout being present above waterfalls given a larger sample size.

**Table 3.** The parameter estimates of 3 logistic regressions analyzing the relationship between characteristics of 16 waterfalls and the occurrence of brook trout above them. For the variable Rock Type, waterfalls on granitic rock types were given a value of 1 while those on siliclastic rock types were given a value of 0.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Parameter Estimate</th>
<th>Logistic Regression P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basin Size (km²)</td>
<td>0.01759</td>
<td>0.656</td>
</tr>
<tr>
<td>Rock Type (granitic vs. siliclastic)</td>
<td>1.6094</td>
<td>0.142</td>
</tr>
<tr>
<td>Height (m)</td>
<td>-0.001614</td>
<td>0.938</td>
</tr>
</tbody>
</table>

**COMPARING PERCENT BROOK TROUT DOMINANCE BETWEEN POPULATIONS ABOVE AND BELOW WATERFALLS**

Four of the seven waterfalls sampled were estimated to have greater brook trout dominance in the sampled reach above them (median = 100%, 1st quartile = 72.92%, and 3rd quartile = 100%) than in the sampled reach below (median = 36.93%, 1st quartile = 9.77, and 3rd quartile = 86.96) (Fig 3). The other species found above and/or below each waterfall can be found under individual site descriptions in the Appendix as well as table A4. Two waterfalls had only brook trout found above and below them, and four waterfalls had only brook trout above them. While the percent dominance of brook trout above Little Stony Creek Cascades was calculable, the percent dominance of brook trout below is unknown because no fish at all were captured below (Fig 3a). Therefore, this site was excluded from the comparison of brook trout dominance above and below waterfalls. A non-parametric analysis via a paired, two-sided Wilcoxon Rank-Sum Test
revealed a large difference between the medians (63.07 % dominance); however, it was only marginally statistically significant (p= 0.1003) (Fig 3b).

**Figure 3.** Brook trout % dominance above and below waterfalls in GWJNF. The upper graph (A) displays this for each of the 7 waterfalls sampled (organized by rock type and then alphabetically). The lower graph (B) displays this for the 6 sites where fish were found both above and below, the median brook trout % dominance above, and the median brook trout % dominance below all 6 waterfall sites combined. In both graphs, blue bars represent the number of brook trout estimated above waterfalls and the orange bars represent that of those below waterfalls.
ESTIMATING BROOK TROUT ABUNDANCE AND COMPARING POPULATION SIZE (ABUNDANCE AND DENSITY) BETWEEN REACHES ABOVE AND REACHES BELOW WATERFALLS

It is estimated that there are twice as many brook trout on average in reaches above waterfalls (median = 25.62, 1st quartile = 21.48, and 3rd quartile = 37.99 brook trout) than in their below-waterfall counterpart reaches (median = 12.38, 1st quartile = 3.91, and 3rd quartile = 29.21 brook trout) (Fig 4). A paired, two-sided Wilcoxon Rank-Sum Test suggests the difference between the medians of estimated brook trout abundance of reaches above waterfalls and that of those below waterfalls (13.24 more brook trout per 100m reach above) to be statistically significant (p= 0.078) (Fig 4b). A total of 176 brook trout were caught above seven waterfalls and 114 brook trout were caught below. Five of the seven sites sampled were estimated to have more brook trout in the sampled reach above them than in the sampled reach below them (Fig 4). Only Overstreet Creek Falls and Cabin Creek Falls are estimated to more brook trout below them than above them. The reach above Crabtree falls is estimated to have the largest population, and the reach above Rowland Creek Falls is estimated to have the smallest population of brook trout, other than the reaches below Rowland Creek Falls and Little Stony Creek Cascades where brook trout were not found (Fig 4a).
Figure 4. Estimated brook trout abundance above and below 7 waterfalls in GWJNF. In both graphs, blue bars represent the number of brook trout estimated to be in the sampled reaches above waterfalls and the orange bars represent that of those below waterfalls. The upper graph (a) displays this for each individual waterfall (organized by rock type and then alphabetically). The lower graph (b) illustrates that brook trout are significantly more abundant in the reaches sampled above than in the reaches sampled below these 7 waterfalls (p = 0.078).

Brook trout density is also estimated to be twice as great above waterfalls (median = 7.4, 1\textsuperscript{st} quartile = 1.77, and 3\textsuperscript{rd} quartile = 16.49 brook trout per km\textsuperscript{2}) as below them (median = 3.5, 1\textsuperscript{st} quartile = 0.13, and 3\textsuperscript{rd} quartile = 8.04 brook trout per km\textsuperscript{2}) (Fig 5). A paired, two-sided Wilcoxon Rank-Sum Test suggests the medians (3.9 more brook trout per km\textsuperscript{2} above than below) are significantly different (p= 0.016) (Fig 5b). All seven
waterfalls are estimated to have a greater density of brook trout above them than below them. The area above Crabtree Falls is estimated to have the greatest density of brook trout, and other than the below-falls reaches where no brook trout were found, the area below Statons Creek Falls is estimated to have the lowest density of brook trout (Fig 5a).

Figure 5. Brook trout population density proxy: estimated abundance divided by the km² of drainage basin above and below 7 waterfalls in GWJNF. In both graphs, blue bars represent the number of brook trout estimated per 100m² above waterfalls and the orange bars represent that of those below waterfalls. The upper graph (a) displays this for each individual waterfall (organized by rock type and then alphabetically). The lower graph (b) illustrates that sampled reaches above waterfalls have a significantly higher density of brook trout than those below waterfalls (p = 0.016).
ANALYSES OF COVARIATES TO POPULATION SIZE

There is no clear relationship between pH or ANC and brook trout abundance of the streams sampled. According to two linear regressions, there is no significant correlation between pH and estimated brook trout abundance above (p = 0.743) or below (p = 0.757) waterfalls (Fig 6a). The pH of the seven streams fully sampled ranges from 6.145 at Rowland Creek to 6.897 at Statons Creek (Table A2). This is a narrow range within the tolerance range of brook trout (Marschall & Crowder, 1996). Virginia experienced much above average rainfall during May, June, and July of 2018 (National Centers for Environmental Information, 2019), and this range likely reflects the heavy rain at most of the basins sampled this summer (Carline, Sharpe, & Gagen, 1992).

The ANC of seven study streams ranges from 27.72 μeq/L at Cabin Creek to 209.55 μeq/L at Statons Creek Falls (Table A2), all streams being almost above the threshold of 30 μeq/L, above which trout populations remain undamaged (Lien et al., 1995). A linear regression indicates that there is also no significant correlation between ANC measurements and estimated brook trout abundance above (p = 0.447) and below (p = 0.399) waterfalls (Fig 6b). Additionally, a logistic regression indicates that there is no statistically significant correlation between the rock type and the ANC of the seven streams where brook trout were found above a waterfall (parameter estimate = 0.007, p = 0.716). A linear regression between ANC and pH of the seven sampled streams indicates a statistically significant positive correlation (p = 0.078, Fig 7).

To compare with previous studies, Harmon (2017) also found a significant positive relationship between median ANC and species richness. The seven data points from this study analyzed in combination with Harmon’s thirteen data points appear to
follow the same trend, with greater species richness associated with greater acid neutralizing capacity ($R^2 = 0.787, p < 0.0001$, Fig 9).

**Figure 6.** Estimated brook trout abundance vs. stream pH (a) and vs. ANC (μeq/L) (b) as measured by SWAS above (blue dots) and below (orange dots) 7 waterfalls in GWJNF. The regression lines for data above waterfalls is blue and the regression lines for data below waterfalls is orange. pH is not significantly correlated with brook trout abundance in sampled reaches above ($p = 0.743$) or below ($0.757$) waterfalls. ANC is also not significantly correlated with brook trout abundance in sampled reaches above ($p = 0.447$) or below ($p = 0.399$) waterfalls.
Figure 7. ANC (μeq/L) vs. pH measured below each of the seven waterfalls sampled in GWJNF. As ANC increases, pH significantly increases ($p = 0.078$).

Figure 8. Fish species richness vs. ANC from Harmon (2017) and the 7 streams sampled in GWJNF. Harmon (2017) determined fish species richness in 300m reaches sampled in 2016 and correlated richness to the median ANC of those streams from 1996 to 2015. The ANC and species richness of the streams sampled in this study are plotted on this figure as triangles. All red points indicate measurements from streams on siliclastic rock types, all yellow points indicate that of those on granitic rock types, and all green points indicate that of those on basaltic rock types. The thick line represents the regression line of the combined data while the thin line represents data of only Harmon (2017), and the dotted line represents data of only this study.
As temperature increases, brook trout abundance decreases. A linear regression of estimated brook trout population abundance above and below each of the seven waterfalls and the temperature (°C) of each stream reach sampled revealed this negative correlation is statistically significant (p = 0.015, Fig 9). Still, all these measurements are below 25.3 °C, the lethal limit for brook trout (Hynes, 1970).

![Graph showing the relationship between temperature and brook trout abundance.](image)

**Figure 9.** The stream temperature (°C) vs. the estimated abundance of brook trout above and below 7 waterfalls in GWJNF. Points in blue represent data from reaches above waterfalls while points in orange represent data from reaches below waterfalls. As temperature increases, brook trout abundance significantly decreases (p = 0.015).

As basin size increases, brook trout abundance decreases. However, a linear regression of each sampled reach’s basin size (km²) and the estimated abundance of brook trout indicates that this trend is not significantly (p = 0.11, Fig 10). As stream slope increases, brook trout abundance increases. However, a linear regression of each sampled reach’s slope (%) and the estimated abundance of brook trout indicates that this trend is not significant (p = 0.386, Fig 11).
Figure 10. The drainage basin (km²) determined from the bottom of each sampled reach vs. estimated abundance of brook trout above and below 7 waterfalls in GWJNF. Points in blue represent data from reaches above waterfalls while points in orange represent data from reaches below waterfalls. As drainage basin increases, brook trout abundance decreases, but not significantly so (p = 0.11).

Figure 11. Slope (%) vs. estimated brook trout abundance above and below 7 waterfalls in GWJNF. Points in blue represent data from reaches above waterfalls while points in orange represent data from reaches below waterfalls. The correlation between slope and the estimated abundance of brook trout is not significant (p = 0.386).
COMPARING BROOK TROUT BIOMASS ABOVE AND BELOW WATERFALLS

There is little difference between the average biomass of a brook trout above and the average biomass of a brook trout below waterfalls. According to a Wilcoxon Rank-Sum test, the average (median) biomass of individual brook trout above \((n = 176)\) waterfalls, 24.82g, is not significantly greater than that of those below \((n = 114)\) waterfalls, 24.85g \((p = 0.712, \text{Fig 12})\).

![Boxplot](image.png)

**Figure 12.** The average biomass of brook trout individuals caught above (blue) 7 waterfalls and below (orange) 5 of those waterfalls in GWJNF. The average biomass of brook trout above waterfalls is not significantly greater than that of brook trout below \((p = 0.712)\).

Total biomass of all brook trout estimated to be in a 100m reach is over three times greater in reaches above \((\text{median} = 885.3g, \text{1}^{\text{st}}\) quartile = 448.3g, and \text{3}^{\text{rd}}\) quartile = 951.4g) than in reaches below waterfalls \((\text{median} = 284.6g, \text{1}^{\text{st}}\) quartile = 100.3g, and \text{3}^{\text{rd}}\) quartile = 829.7g) \((\text{Fig 13})\). A two-sided Wilcoxon Rank-Sum Test suggests the medians are significantly different \((600.7g \text{ more above, } p = 0.078, \text{Fig 13b})\). Five of the seven waterfalls sampled were estimated to have a greater total estimated biomass of brook
trout in the sampled reach above them than in the sampled reach below them. Only Cabin Creek Falls and Overstreet Creek Falls had more biomass of brook trout below them than above them. No brook trout were found below Rowland Creek and Little Stony Creek Falls, and therefore no brook trout biomass (Fig 13a).

Figure 13. Total estimated biomass per 100m reach above and below 7 waterfalls in GWJNF. In both graphs, blue bars or boxes represent the biomass of all brook trout estimated to be within 100m² above waterfalls and the orange bars or boxes represent that of those below waterfalls. The upper graph (a) displays this for each individual waterfall (organized by rock type and then alphabetically). The lower graph (b) illustrates that the total biomass of brook trout in sampled reaches above waterfalls is significantly greater than that of brook trout in sampled reaches below waterfalls (p = 0.078).
Brook trout biomass density is estimated to be over four times greater above waterfalls (median = 286.63 g/km², 1st quartile = 51.16 g/km², 3rd quartile = 493.76 g/km²) than below them (median = 64.48 g/km², 1st quartile = 6.02 g/km², 3rd quartile = 242.7 g/km²) (Fig 14). A paired, two-sided Wilcoxon Rank-Sum Test reveals the difference between the medians (222.15 g/km²) to be statistically significant (p= 0.031, Fig 14b). Six of the seven waterfalls sampled are estimated to have a greater density of brook trout biomass above them than below them. Only Cabin Creek Falls has a greater density of brook trout biomass below it than above it (Fig 14a).
Figure 14. Brook trout biomass density proxy (total biomass /km² of drainage basin) above and below 7 waterfalls in GWJNF. In both graphs, blue bars represent the biomass of brook trout estimated per km² above waterfalls and the orange bars represent that of those below waterfalls. The upper graph (a) displays this for each individual waterfall (organized by rock type and then alphabetically). The lower graph (b) illustrates that the biomass density of brook trout in reaches above waterfalls is significantly greater than that in reaches below waterfalls (p = 0.031).
COMPARING THE LENGTH-WEIGHT INDEX OF BROOK TROUT ABOVE WATERFALLS TO THAT OF THOSE BELOW WATERFALLS

Brook trout above waterfalls have a slightly greater condition factor (median = 1.086g/cm³) than those below waterfalls (1.064g/cm³). However, according to a non-paired Wilcoxon Rank-Sum test this difference (0.0224 g/cm³) is statistically significant (p = 0.031, Fig 15b). The populations above and below are also similarly distributed. The brook trout in the reach above Cabin Creek Falls have the lowest average condition factor (1) while those in the reach below Crabtree Falls have the highest average condition factor (1.27). Of the five waterfalls where brook trout were found both above and below the falls, only Overstreet Falls has brook trout above that have a greater condition factor on average than those below it (Fig 15a).
Figure 15. Fulton’s Condition Factor of all brook trout individuals caught above (blue) 7 waterfalls and below (orange) 5 of those waterfalls in GWJNF. The top graph (a) displays this for each individual waterfall (organized by rock type and then alphabetically). The bottom graph (b) illustrates that the average condition factor of brook trout captured above waterfalls is significantly greater than that of those captured below waterfalls (p = 0.031).
DISCUSSION

This study seeks to determine where populations of brook trout have managed to persist in isolation above waterfalls in Virginia despite how prone Appalachian headwaters are to disturbance and acid-impairment. Two new populations of brook trout have been discovered above Overstreet Falls and Little Cove Creek Falls. It also seeks a pattern for habitat characteristics of waterfalls where brook trout occur above compared to those that do not have brook trout above. No such pattern was found. Lastly, it seeks to determine if the populations of brook trout found above waterfalls are more dominant over other species, larger with greater biomass, and have individuals of greater condition factor than their below waterfall counterparts. By these measures, populations of brook trout above waterfalls seem to be just as if not more robust than their below waterfall counterparts.

BROOK TROUT OCCURRENCE ABOVE WATERFALLS

Because many of the waterfalls visited in this study are remote and difficult to access, the occurrence of brook trout above them has been unknown. The presence or absence of brook trout above half of the waterfalls selected for attempted sampling could not be determined before visitation. Therefore, trout occurrence above Little Cove Creek Falls, Overstreet Falls, Apple Orchard Falls, Comer’s Creek Falls, and Mill Creek Falls was only determined via attempted sampling in the area above each of them. While no brook trout were found above Apple Orchard Falls, Comers Creek Falls, and Mill Creek Falls, populations of brook trout were newly discovered above Little Cove Creek Falls and Overstreet Falls.
The logistic regressions analyzing the height, rock type, and basin size of sixteen waterfalls (ten visited plus six where VDGIF knows brook trout occurrence above) indicates that the correlations between each of these characteristics and the presence of brook trout above waterfalls are not statistically significant, failing to support the hypothesis that brook trout populations would be found more commonly above waterfalls with large drainage basins on granitic rock types than above waterfalls with small drainage basins and/or on siliclastic rock types.

Rock type is the characteristic with the lowest p-value in its association with brook trout occurrence above waterfalls. Therefore, with a larger sample size, it may be determined that brook trout are more likely to exist above waterfalls on granitic and basaltic rock types than on siliclastic ones. The lack of correlation between waterfall height and brook trout above was expected and smaller falls not being more likely to have brook trout above them simply reinforces that the waterfalls chosen for analysis are all tall enough to be barriers to fish movement upstream.

**Rock Type, ANC, and pH as Factors**

Despite the lack of statistical significance, rock type may be more closely related to brook trout presence above waterfalls than the other two characteristics ($p = 0.142$, Table 3). With a greater number of waterfalls sampled, it may be determined that brook trout are more likely to occur above waterfalls on granitic rock types than above waterfalls on siliclastic rock types. The suspected relationship between rock type and brook trout occurrence may be attributable to granitic rock types having a greater ANC than siliclastic ones (Harmon, 2017). A linear regression shows a statistically significant
positive relationship between the ANC and pH of the seven streams fully sampled for brook trout \( (R^2 = 0.5, p = 0.0776, \text{Fig 7}) \) and is closely aligned with the relationship developed by Harmon (2017). This result agrees with other literature demonstrating that greater ANC results in less acid-impaired streams (Lawrence, 2002). Trout populations are undamaged by ANC greater than 30 μeq/L (Lien et al., 1995) and such a buffer against acidification would increase the likelihood that a population of brook trout can survive, reproduce, and therefore persist in headwater streams (Marschall & Crowder, 1996) like those above waterfalls.

Greater average ANC resulting in more brook trout in granitic watersheds over siliclastic ones agrees with Jastram et al. (2013), which found lower brook trout abundances, particularly of young of the year, in the siliclastic streams than in the granitic or the basaltic watersheds of Shenandoah National Park. The ANC and pH of streams without brook trout above their waterfalls should be determined and compared to those already sampled in this study and known to have brook trout above. Perhaps with a larger sample size including waterfalls on basaltic rock types as well as those on granitic and siliclastic ones, a predictive relationship between the underlying rock type and the occurrence of brook trout above waterfalls would be detected.

Although linear regressions indicate no correlation between ANC or pH and brook trout abundance above or below the seven waterfalls sampled, only two, Rowland Creek Falls and Little Stony Creek Cascades, were on siliclastic instead of granitic rock types. These are also the only two that were found to have brook trout present above but not below the falls. Another waterfall, Devil’s Bathtub, is on a stream in a shale rock type known to be too acidic to have any fish in it. Rowland Creek Falls, has brook trout
above it, but only rainbow trout below it. This result suggests that Rowland Creek’s the level of acid-impairment is low enough for brook trout to persist in alone, but perhaps not when coupled with the additional pressure of competition from other trout species. Therefore, rock type may still be a key factor in predicting where brook trout populations exist, especially when combined with other pressures on brook trout such as the presence of non-native trout species.

**Drainage Basin Size as a Factor**

Brook trout populations were found in this study to have persisted in some habitats that are not only isolated by waterfalls but are also limited by small drainage basins. It was hypothesized that waterfalls with large drainage basins above them would be more likely to have brook trout above them than those with smaller drainage basins because larger available habitat above waterfalls has been correlated with greater genetic variation in the salmonid populations above them, which should improve their potential to adapt and evolve with change in the environment (Whiteley et al., 2009). Additionally, a study of bull trout in the Pacific Northwest found that the likelihood of populations occurring in watersheds smaller than 10km$^2$ is less than 0.1, indicating that trout are more likely to persist in large, connected habitats than in small, fragmented ones (Rieman & McIntyre, 2011).

Contradictory to such studies on other trout species and what was hypothesized, there is no significant correlation between larger drainage basins above waterfalls and brook trout occurrence above waterfalls ($p = 0.656$, Table 3). Only three of the eight waterfalls in this study with watersheds greater than 10km$^2$ have brook present above
them while five do not have brook trout present above them (Table 1). The habitats where brook trout populations were newly discovered above waterfalls are also small: less than 10km². Specifically, the drainage basin above Overstreet Falls is the second smallest of all waterfalls analyzed in this study (Table 1). It was therefore surprising to find large populations of brook trout above and below these waterfalls. Despite its small drainage basin, Overstreet Falls has the second greatest population density above it of all reaches sampled (Fig 5). These paradoxical findings may be explained by brook trout adaptation to these isolated, but stable, often spring-fed habitats above natural barriers. Letcher (2007) found that local adaptation of brook trout can rescue their populations from the threats of fragmented habitats, so it is possible that they are able to thrive in small isolated drainage basins above waterfalls like Overstreet Falls and Little Cove Creek Falls because populations there are well adapted to those environments, especially if such streams are spring-fed, like Crabtree Creek, and therefore thermally ideal for brook trout.

The reaches above Apple Orchard, Comers Creek, and Mill Creek Falls may each lack brook trout for different reasons. Apple Orchard Falls has the smallest drainage basin of all the waterfalls analyzed (Table 1) and may simply not have enough flow year-round to support a population of trout. Comers Creek winds through a boggy field and over a gravel road very shortly before entering a gorge and becoming a waterfall (Fig A12). The habitat above it may be too close to the road and too unshaded upstream of the road to support brook trout. Mill Creek Falls is located just downstream of the Fenwick Mines Recreation Area (Fig A13), which was an iron mine during the 19th century. The stream is very straight and without much complexity, woody debris or heterogenous substrate, which could result in insufficient habitat complexity not only for brook trout to
reproduce, but also for their macroinvertebrate prey to persist (Henley et al., 2010). Mill Creek still has a reddish tinge characteristic of iron mining in the area, the impacts of which are often lethal to native fish (Wohl, 2006), and may have eradicated any brook trout population historically inhabiting Mill Creek. Thus, land use and habitat size above waterfalls may be limiting factors for brook trout to persist there, even on protected, public land.

**Stream Slope/ Waterfall Geomorphology**

While brook trout may be well adapted to survive in steep headwater streams under their normal conditions, such habitats are also prone to stochastic events, such as shallow landslides and debris flows, capable to decimating a population (Roghair et al., 2002; Brayshaw & Hassan, 2009). Although headwaters of the Rocky Mountains experience more frequent landslides and debris flows than those of the Appalachian Mountains, any habitat with steep slopes is prone to such events and they occur annually in the Southern Appalachians (Eaton et al., 2003). The hypothesis that populations of brook trout populations isolated above waterfalls would be able to persist in headwater streams stems from the studies that have found waterfalls on both the west coast and the east coast of the United States to create gentler stream slopes less prone to landslides in the basins above them (Gallen et al., 2011; May et al., 2017).

The slope of all streams analyzed for brook trout occurrence above waterfalls could not be determined and the slopes of the seven streams fully sampled were only 100m snapshots of the slopes in the entire drainage basin impacting the trout in the sampled reach. Therefore, the drainage basins of the areas above these waterfalls may
still have overall gentler slopes than that of the areas below, which may play a role in not only the greater abundance of brook trout found above waterfalls, but also which waterfalls have brook trout above them at all. Future studies could determine this by comparing LIDAR images of the drainage basins above waterfalls where brook trout population sizes have been measured to that of those above waterfalls where brook trout are known to not exist and to those of similar headwater basins not above a waterfall at all. A greater understanding of these isolated habitats where brook trout persist are crucial as such isolated populations of salmonids are estimated to be valuable conservation sources for genetic and therefore adaptive variability (Northcote & Hartman, 1988).

**BROOK TROUT POPULATIONS ABOVE COMPARED TO BELOW WATERFALLS**

It was hypothesized that compared to below waterfall populations of brook trout, populations above waterfalls 1) have a greater percent dominance over other species 2) a greater population biomass, 3) more individuals present overall, and 4) individuals that are more massive for their respective lengths than populations below. Results support these hypotheses.

**Greater Dominance of Brook Trout Over Other Species Above Waterfalls than Below**

Brook trout are more dominant over other fish species above waterfalls than they are below, but this trend is not statistically significant \( p = 0.1003 \), Fig 3. None of the waterfalls sampled have a population of brook trout below that is more dominant than the population above. Reduced overall fish species richness has been documented above
waterfalls and cascades in southern Appalachian streams (Robinson & Rand, 2005), and as barriers to fish movement, waterfalls prevent new and non-native fish species from migrating above them. Rainbow trout in particular reduce the population size and therefore dominance of brook trout when they co-occur (Moore & Larson, 1993; Marschall & Crowder, 1996). Rowland Creek Falls has rainbow trout below it (41% dominant) and Statons Creek Falls has brown trout below it (0.6% dominant). Little Stony Creek Falls is also known to have rainbow trout below the waterfall, though none were captured via this study’s sampling. By simply excluding the invasion of such non-natives as rainbow trout, waterfalls may encourage greater brook trout dominance above them. It is possible that if more than six waterfalls could be analyzed for brook trout percent dominance, the difference between above and below waterfalls would be statistically significant.

Greater dominance over other species in these habitats would be beneficial to brook trout, especially if they are not competing with other trout species above when they would otherwise have to below. The only two sites where non-native trout were caught waterfall, Rowland Creek and Statons Creek, have these non-natives only below their waterfall, not above. These are both sites where the population size of brook trout is estimated to be larger above the falls than below (Fig 4 & Fig 5). It is possible that their greater dominance of brook trout over other species above these waterfalls is also part of the cause for greater brook trout abundance above waterfalls than below them.
Larger Brook Trout Populations & Population Biomasses Above Waterfalls than Below

In support of the original hypothesis, brook trout populations above waterfalls were found to have both a greater abundance ($p = 0.078$, Fig 4) and density ($p = 0.016$, Fig 5) of individuals than those below waterfalls. It is also apparent that populations are reproducing as trout shorter than 6 cm in length (presumably young of the year), were captured both above and below waterfalls (Fig A16). However, the small sample size and irregular weather conditions during the sampling period must be accounted for. High flows give fish much more habitat and deeper water in which to escape from capture. Specifically, although this study was unable to capture any brook trout below Little Stony Creek Cascades, they are known to be there by many anglers. This was by far the largest stream sampled, so the high water from the consistent rain this summer made the reach below this waterfall too flooded to effectively sample. If this waterfall is excluded from analysis, the density of brook trout above waterfalls is still greater than below waterfalls ($p = 0.031$, Fig A15b), but the overall abundance, while still greater above waterfalls than below them, is not significantly so ($p = 0.156$, Fig A15a).

The stream most dramatically exhibiting greater brook trout population size above the waterfall than below it is Crabtree Creek, where it is estimated that the 100m reach above its waterfall has 73 more brook trout in it than that below the waterfall. This agrees with the findings of Studio (2018) who also found brook trout to be more abundant above the waterfall than below it (an estimated 23 more brook trout per 100m above the waterfall than below it). However, most of the literature comparing populations of salmonids above and below waterfalls examine those on the western side of the United
States and focus on their genetic divergence instead of their comparative size. Few other studies have compared the estimated abundance or density of brook trout above natural barriers in the Appalachian Mountains to that of the populations directly below those barriers.

The larger brook trout total biomass in reaches above than in reaches below waterfalls ($p = 0.078$, Fig 13) as well as the greater brook trout biomass density (by proxy of #/km²) in reaches above waterfalls than in those below waterfalls ($p = 0.031$, Fig 14), are both likely directly resulting from the greater population size and density of brook trout populations above waterfalls, as the average biomass of individual brook trout above is not significantly different from that of those below a waterfall ($p = 0.712$, Fig 12). This greater abundance and density of brook trout above waterfalls may indicate that those habitats are more fertile than the habitats below (Cooper & Scherer, 1967).

Waterfalls creating more productive, stable habitats above them than is typical of other surrounding headwaters would be consistent with the findings of May et al. (2017). However, this study does not attempt to establish causation for this correlation between greater population size and areas above waterfalls.

The suspected relationship between the habitats that waterfalls create above them and the relatively large brook trout populations this study finds above them does not fit the current conservation paradigm that isolated populations are the most prone to extinction (Miyazono & Taylor, 2013; Sato & Harada, 2018). Still, this is not the first study to suggest that large, potentially stable populations of salmonids can persist in isolation. Cook et al. (2010), determined that even populations of cutthroat trout (*Oncorhynchus clarkii*) isolated above artificial barriers are able to persist for decades,
provided they have a large enough population size to maintain genetic variability.

However, such artificial sources of isolation do not geomorphologically alter the habitat above them to be more favorable to large populations of salmonids as waterfalls do (May et al., 2017). Salmonid populations above waterfalls in Oregon and Alaska, though less genetically diverse than downstream populations, have been large enough for them to persist in isolation for not just decades, but for millennia: from 8,000 to 12,500 years (Guy et al., 2008; Whiteley et al., 2010). Therefore, populations of brook trout above waterfalls may not fit the conservation paradigm of isolated populations being small and doomed to eventual extinction. However, much more information is needed to better understand what other factors and habitat characteristics influence the population size and viability of brook trout naturally isolated above waterfalls in Appalachia.

In addition to brook trout populations above waterfalls tending to be larger than their below Falls counterparts, brook trout in warmer stream reaches are estimated to be significantly less abundant ($p = 0.015$, Fig 9). This result is consistent with literature indicating that high stream temperatures negatively impact brook trout populations (Kanno et al., 2015), because they are unable to reproduce at temperatures warmer than 14.4 °C and unable to survive at temperatures warmer than 25.3 °C (Hynes, 1970). The seven streams sampled are relatively well-shaded and cool because the canopy of their drainage basins is managed on the protected public land of GWJNF. Even on such well-protected streams, slightly warmer temperatures may be limiting the population size of brook trout. Therefore, temperature may be limiting populations above waterfalls with basins that have been impacted by deforestation, agricultural, residential, or urban land
use despite the otherwise more favorable landscape a waterfall creates above it for brook trout.

There is no correlation between other covariates and brook trout abundance. The size of the drainage basin above a reach is not correlated with the abundance of trout estimated to be in it for those above waterfalls \( (p = 0.501, \text{Fig 10}) \) and for those below waterfalls \( (p = 0.158, \text{Fig 10}) \). The lack of correlation in this study may partially be the result of a small sample size and the weather conditions during the summer sampling took place. Only two of the seven streams sampled have a reach with drainage basins larger than 10km² (Table A3), so perhaps a study of waterfalls with a greater range of drainage basins sizes would find a difference between the abundance of trout in reaches located within large drainage basins than that of those in small ones. Additionally, the streams with larger drainage basins are bigger and therefore more difficult to deplete of fish when flow is high, as it was during this summer. This may have resulted in an underestimation of brook trout population size within large drainage basins.

Additionally, no correlation was found between stream slope and brook trout abundance of the seven waterfalls where trout are found above (Fig 11). The genetics of brook trout populations in headwater streams analyzed by Kanno, Vokun, & Letcher (2011), indicate that steep stream slope may have little influence on brook trout as they are particularly adept in navigating upstream of step pools and steep gradients compared to other species. Therefore, brook trout may be so well adapted to steep headwater streams that if the habitat within the entire basin is not so steep as to be prone to landslides and debris flows, they are just as capable of thriving in steep streams as they are in more gently sloped stream channels.
Greater Condition Factor of Brook Trout Above Waterfalls than Below

Greater condition factor indicates that the fish is heavier for its length. In general, trout with condition factors greater than one are “fat” while those with condition factors less than one are considered to be “skinny” (Lamaze et al., 2013). Hakala and Hartman (2004), found adult brook trout in well-forested headwater streams of West Virginia to have an average condition factor of 1.01 ± 0.04 g/cm$^3$ during a non-drought summer, such as the sampling period of this study. The condition factor of brook trout above waterfalls (1.086 g/cm$^3$) is similar if not slightly greater than that of those below waterfalls (1.064 g/cm$^3$) ($p = 0.03$, Fig 15). This could indicate that the areas above waterfalls may be productive enough to alleviate the “productivity squeeze” in headwater streams (Petty et al., 2014). However, Northcote and Hartman (1988) observed the opposite trend, that salmonids below a waterfall in Colorado have a greater condition factor than those above a different waterfall in Colorado. Still, their study was also conducted on different species, in a different region, on fewer waterfalls with larger drainage basins than this study. To shed more light on the relation between trout body condition and the landscapes waterfalls create above them, perhaps the condition factor of brook individuals above Appalachian waterfalls should be compared not only to that of those directly below, but to the condition factor of brook trout in comparable streams without a waterfall.

CONCLUSIONS

While many individual analyses within this study are limited by their sample size (only seven waterfalls could be fully sampled), and by the fact that they are based on one-time measurements (each waterfall was sampled only once during an extraordinarily wet
year), a holistic consideration of all analyses together may still offer valuable insight into the relationship between waterfalls and populations of brook trout in headwater streams. Populations of brook trout were found above remote waterfalls with small drainage basins and steep terrain, but that also have complex habitats in well shaded streams on granitic rock types. Some such waterfalls, Overstreet Falls and Little Cove Creek Falls, were not previously known to have brook trout above them. In general, the overall increased dominance of brook trout over other species, greater abundance and density of brook trout, and comparable condition factor of brook trout in reaches above compared to that of those below the seven waterfalls sampled in this study indicates that populations of brook trout above waterfalls can be just as if not more robust than their below waterfall counterparts.

The impacts of landscape attributes on salmonid populations may be species specific and context dependent (Gomez-Uchida et al., 2009; Rieman & Dunham, 2009). Further investigation of brook trout above Appalachian waterfalls is needed to better understand the relationship between the landscapes that waterfalls create above them and the size of the native brook trout species above them. In particular, populations above waterfalls have co-evolved to the geologically unique landscapes waterfalls form, while manmade barriers to fish movement, such as dams and culverts are unable to alter the morphology of the landscapes upstream of them as waterfalls do (May et al., 2017), and may therefore not be able to support resilient populations as those above waterfalls.

As brook trout are increasingly threatened by warmer streams and acid-impaired headwaters throughout their native range, it is important to prioritize target populations for conservation efforts. For example, liming is intensive, but improves the survival,
growth, and population density of brook trout in acid-impaired streams (Simmons, et al., 1996). Such measures may result in greater success for populations isolated above waterfalls that only face these abiotic pressures, than for those brook trout populations connected not only to the metapopulation, but also to the additional abiotic pressures of landslides and biotic pressures of competition, disease, and hybridization with non-native trout species. Naturally isolated populations in headwater streams are potentially excellent candidates for conservation efforts also because their habitats feed the rest of the stream network and they themselves may serve as a source of colonists to downstream habitats (Meyer, et al., 2007). The existing paradigm about isolated populations dictates that brook trout populations above waterfalls should be smaller and more prone to extirpation than those below. However, even the analyses within this study that find no significant difference between populations of brook trout above and below waterfalls defy this paradigm and suggest that brook trout populations isolated above natural waterfalls should be investigated further for their conservation potential.
LITERATURE CITED


APPENDIX

A. SITE DESCRIPTIONS & WITHIN SITE COMPARISONS

Cabin Creek Falls

This was the seventh site visited, sampled on July 8\textsuperscript{th} and 9\textsuperscript{th}, 2018. It is located within Grayson Highlands State Park and its drainage basin is comprised of granitic rhyolite. The stream is well shaded, has large boulders, and appears to have a cascade morphology (Fig A1). Only Brook trout were found both above and below the falls. Capturing brook trout was difficult in such complex habitat, and a fourth pass had to be conducted above the falls.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{cabin_creek_falls.png}
\caption{Photographs of Cabin Creek: the bottom of the reach above the falls (left), and the bottom of the reach below the falls (right). There was a very large boulder that brook trout would have to jump to breach about 25m into the reach below the falls and it can be seen in the back of the picture on the right.}
\end{figure}

The median condition factor of trout above Cabin Creek Falls, 1.004 (g/cm\textsuperscript{3}), is not significantly lower than the median condition factor of trout below, 1.024 (g/cm\textsuperscript{3}), according to a non-paired Wilcoxon Rank-Sum test (p-value = 0.365). The median
biomass of trout above, 24.70g, is not significantly lower than the median biomass of trout below, 25.6g, according to a non-paired Wilcoxon Rank-Sum test (p-value = 0.783).

**Crabtree Falls**

This was the first site visited, sampled on June 14th, 2018. At 67m high Crabtree is the tallest waterfall in Virginia (Fig A2). The drainage basin above the falls is comprised of granitic rock types including granite, mylonite, gneiss, and granitic gneiss. The stream appears to have a step-pool morphology above the waterfall and a cascade morphology below. Only Brook trout were found above the falls, but american eel, blacknose dace, longnose dace, and northern hogsucker, were found below the falls.
Figure A2. Photographs of Crabtree Creek: parts of Crabtree Falls (below) and the bottom (upper left) and top (upper right) of the 100m reach above the Falls.

The median condition factor of brook trout above Crabtree Falls, 1.166 (g/cm³), is not significantly lower than the median condition factor of trout below, 1.273 (g/cm³), according to a non-paired Wilcoxon Rank-Sum test (p-value = 0.08). The median biomass of brook trout above, 16.6g, is also not significantly less than the median biomass of trout below, 20.5g, according to a non-paired Wilcoxon Rank-Sum test (p-value = 0.768).
Little Cove Creek Falls

This was the sixth site visited, sampled on July 5\textsuperscript{th}, 2018. The height of Little Cove Creek Falls has not been documented, but it is at least 6m high (Fig A3). The drainage basin is comprised of granite. The stream appears to have a cascade morphology. Brook trout and blacknose dace were the only two fish species found both above and below the falls. Very bright orange crayfish are also prevalent both above and below the waterfall (Fig A3).

Figure A3. Photographs of Little Cove Creek: the falls (left), a pool in the reach below the falls (center), and a crayfish found below the falls (right).

The median condition factor of trout above Little Cove Creek Falls, 1.077 (g/cm\textsuperscript{3}), is not significantly lower than the median condition factor of trout below, 1.093 (g/cm\textsuperscript{3}), according to a non-paired Wilcoxon Rank-Sum test (p-value = 0.328). The median biomass of trout above, 37.9g, is significantly greater than the median biomass of trout below, 26.7g, according to a non-paired Wilcoxon Rank-Sum test (p-value = 0.034) (Fig A4).
Figure A4. Biomass of brook trout above and below Little Cove Creek Falls in GWJNF. The blue box represents the biomass of all 33 brook trout caught in a 100m reach above the waterfall and the orange box represents that of all 19 brook trout caught in a 100m reach below the waterfall.

Overstreet Falls

This was the third site visited, sampled on June 18th, 2018. The terrain was very steep, especially below the falls (Fig A5, Table A2). Like Little Cove Creek Falls, Overstreet Falls’ height has not been formally documented, but it is at least 6m high (Fig A5). The drainage basin above the falls is comprised of granulite. The stream appears to have a cascade morphology. Brook trout were the only species found both above and below the falls.
Figure A5. Photographs of Overstreet Creek: the falls (top left), bottom of the above reach looking up (top center), top of above looking down (top right), top of below looking down (bottom left), and bottom of below looking up (bottom right.)

The median Condition Factor of brook trout above Overstreet Falls, 1.08 (g/cm³), is significantly greater than the median Condition Factor of brook trout below, 1.034 (g/cm³), according to a non-paired Wilcoxon Rank-Sum test (p-value = 0.009) (Fig A6).
Figure A6. Fulton’s Condition Factor of brook trout above and below Overstreet Falls GWJNF. The blue box represents the condition of all 31 brook trout caught in a 100m reach above the waterfall and the orange box represents that of all 41 brook trout caught in a 100m reach below the waterfall.

The difference between the median biomass trout above, 27.2g, is not significantly greater than the median biomass of trout below, 24.6g, according to a non-paired Wilcoxon Rank-Sum test (p-value = 0.597).

Statons Creek Falls

This was the second site visited, sampled on June 15th, 2018. Statons Creek Falls is also known as Deadman’s Falls (Fig A7). The drainage basin above the falls is comprised of granulite. The stream appears to have a plane-bed morphology. The stream was not very steep (Table A2) and the reach below the falls was set up after the confluence with the Pedlar river because any farther upstream was too difficult to access
and still a part of the falls. Brook trout, northern hogsucker, blacknose dace, and torrent suckers were found above the falls, while brook trout, rosy-sided dace, brown trout, bluehead chub, northern hogsuckers, mountain redbelly dace, red-lips shiners, blacknosed dace, torrent suckers, fantail darters, and madtoms were found below the falls.

Figure A7. Photographs of Statons Creek: the falls from above (top left), the reach above the falls (top center), part of the reach below the falls with Adam Landry holding a large brown trout (top right), a large brook trout above the falls (bottom left) and a large brook trout below the falls (bottom right).

The median Condition Factor of brook trout above Statons Creek Falls, 1.073 (g/cm³), is significantly less than the median Condition Factor of brook trout below, 1.206 (g/cm³), according to a non-paired Wilcoxon Rank-Sum test (p-value = 0.009) (Fig A8).
Figure A8. Fulton’s Condition Factor of brook trout above and below Statons Creek Falls in GWJNF. The blue box represents the condition factor of all 19 brook trout caught in a 100m reach above the waterfall and the orange box represents that of all 6 brook trout caught in a 100m reach below the waterfall.

The median biomass trout above, 27.84g, is not significantly less than the median biomass of trout below, 32.265g, according to a non-paired Wilcoxon Rank-Sum test (p-value = 0.437).

**Little Stony Creek Cascades**

This was the tenth and last site visited. The reach above the falls was sampled on July 22nd, 2018, and the reach below was attempted on July 23rd, but thunderstorms prevented a full sampling event from occurring. Therefore, the reach below was fully sampled on August 9th. This was the largest stream sampled and the cascade is 20m tall (Fig A9). The drainage basin above the falls is comprised of sandstone and shale. The
stream appears to have a lane-bed morphology above the falls, and a step-pool morphology below. Brook trout, blacknose dace, fantail darters, and longnose dace were caught above the waterfall, but no fish were caught below the falls.

**Figure A9.** Photographs of Little Stony Creek: the bottom of the reach above the cascade (left) and the waterfall itself (right).

**Rowland Creek Falls**

Rowland Creek was the ninth site visited on July 13th, 2018. The waterfall (Fig A10) is the uppermost of a series of waterfalls. The drainage basin above the falls is comprised of sandstone and quartzite. The stream appears to have a step-pool morphology. Brook trout were the only species caught above the falls. Only rainbow trout, blacknose dace, fantail darters, and longnose dace were caught below the waterfall.
Figure A10. Photographs of Rowland Creek: the bottom of the reach sampled above Rowland Creek Falls (upper left), the waterfall itself (upper right), a brook trout above the falls (lower left), and a rainbow trout caught below the falls (lower right).

Apple Orchard, Comer’s Creek, and Mill Creek Falls

Apple Orchard Falls was the fifth site visited on June 23rd, 2018. It has the smallest drainage basin of all the sites selected for attempted sampling and was therefore a very small stream (Fig A11). No fish were captured at all above the waterfall.
Comer’s Creek Falls was the eighth site visited on July 12th, 2018. The area directly upstream of the reach above the falls was boggy and unforested (Fig A12). Only blacknose and longnose dace were found above the waterfall.
Mill Creek Falls (Fig A13) was the fourth site visited on June 23rd, 2018. It is located downstream of the Fenwick Mines Recreation Area and the stream lacked complex habitat. There was very little woody debris, large boulders, pools, or riffles. Only longnose dace were found above the waterfall.

Figure A13. Mill Creek Falls and its proximity to Fenwick Mines Recreation Area upstream
B. SUPPLEMENTAL FIGURES

Figure A14. Theoretical landform differences between stream slopes without a waterfall (black dotted line) and those with a waterfall (blue dotted line).
Figure A15. Brook trout population size above (blue boxes) and below (orange boxes) 6 waterfalls (Little Stony Cascades excluded) in GWJNF. With Little Stony Cascades excluded from the analysis, estimated abundance of brook trout (a) is no longer significantly greater above waterfalls than below ($p = 0.156$). However, the brook trout population density proxy ($#/km^2$) (b) is still significantly greater above waterfalls than below them ($p = 0.031$).

Figure A16. The frequency of lengths (cm) of brook trout caught above 7 waterfalls (blue) and below 5 of those waterfalls (orange) in GWJNF. The young of the year are circled in red.
### C. SUPPLEMENTAL TABLES

**Table A1.** Catch per unit effort (CPUE) of brook trout with each electrofishing pass at each 100m reach sampled.

<table>
<thead>
<tr>
<th>Waterfall and Reach Type</th>
<th>Pass #</th>
<th>CPUE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Above Cabin Creek Falls</td>
<td>1</td>
<td>0.9619589</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.2612103</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.3490401</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Below Cabin Creek Falls</td>
<td>1</td>
<td>1.0212418</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.4739336</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Above Crabtree Falls</td>
<td>1</td>
<td>0.3827751</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.8280015</td>
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<td></td>
<td>3</td>
<td>0.3539254</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>0.2154399</td>
</tr>
<tr>
<td>Below Crabtree Falls</td>
<td>1</td>
<td>0.2227880</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.1451906</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Above Little Cove Creek Falls</td>
<td>1</td>
<td>1.2597481</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.4383562</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.4046243</td>
</tr>
<tr>
<td>Below Little Cove Creek Falls</td>
<td>1</td>
<td>3.1724138</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>1.2543554</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.6419401</td>
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<tr>
<td>Above Overstreet Falls</td>
<td>1</td>
<td>0.5191434</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.2910737</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.1938611</td>
</tr>
<tr>
<td>Below Overstreet Falls</td>
<td>1</td>
<td>1.0482180</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.2139495</td>
</tr>
<tr>
<td></td>
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</tr>
<tr>
<td></td>
<td>4</td>
<td>0.2132196</td>
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<tr>
<td>Above Statons Creek Falls</td>
<td>1</td>
<td>0.4174573</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.1447702</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.1286174</td>
</tr>
<tr>
<td>Below Statons Creek Falls</td>
<td>1</td>
<td>0.0994365</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.0627156</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.0352982</td>
</tr>
<tr>
<td>Above Little Stony Cascades</td>
<td>1</td>
<td>0.0836820</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.1170275</td>
</tr>
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<td></td>
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<td>0.0573065</td>
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<tr>
<td>Below Little Stony Cascades</td>
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</tr>
<tr>
<td></td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Above Rowland Creek Falls</td>
<td>1</td>
<td>0.3362152</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Below Rowland Creek Falls</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0</td>
</tr>
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</table>
Table A2. All waterfalls visited in GWJNF, listed by rock type, then alphabetically their location, and the ANC, and pH of the stream determined by SWAS from samples taken below the waterfall of sites fully sampled.

<table>
<thead>
<tr>
<th>Waterfall</th>
<th>County</th>
<th>Watershed (River)</th>
<th>Coordinate (decimal degrees)</th>
<th>ANC (μeq/L)</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apple Orchard Falls</td>
<td>Botetourt</td>
<td>North</td>
<td>37.5162, -79.5329</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Cabin Creek Falls</td>
<td>Grayson</td>
<td>New</td>
<td>36.6335, -81.5193</td>
<td>22.7</td>
<td>6.2</td>
</tr>
<tr>
<td>Crabtree Falls</td>
<td>Nelson</td>
<td>James</td>
<td>37.8440, -79.0750</td>
<td>65.4</td>
<td>6.5</td>
</tr>
<tr>
<td>Little Cove Creek Falls</td>
<td>Amherst</td>
<td>James</td>
<td>37.7278, -79.2024</td>
<td>111.8</td>
<td>6.3</td>
</tr>
<tr>
<td>Overstreet Falls</td>
<td>Bedford</td>
<td>Roanoke</td>
<td>37.4971, -79.5291</td>
<td>87.3</td>
<td>6.6</td>
</tr>
<tr>
<td>Statons Creek Falls</td>
<td>Amherst</td>
<td>James</td>
<td>37.7684, -79.2363</td>
<td>209.5</td>
<td>6.9</td>
</tr>
<tr>
<td>Comers Creek Falls</td>
<td>Grayson</td>
<td>New</td>
<td>36.714, -81.4738</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Little Stony Cascades</td>
<td>Giles</td>
<td>New</td>
<td>37.3726, -80.5743</td>
<td>92.4</td>
<td>6.6</td>
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<td>Mill Creek Falls</td>
<td>Craig</td>
<td>James</td>
<td>37.5652, -80.0545</td>
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<td>-</td>
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<tr>
<td>Rowland Creek Falls</td>
<td>Smyth</td>
<td>Holston</td>
<td>36.7218, -81.5646</td>
<td>75.9</td>
<td>6.1</td>
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Table A3. The location, basin size (km²), water temperature (°C), and slope (%) of the bottom of reaches sampled above and below 7 waterfalls in GWJNF, listed by rock type, then alphabetically.

<table>
<thead>
<tr>
<th>Waterfall and Reach Type</th>
<th>Coordinate (decimal degrees)</th>
<th>Basin Size (km²)</th>
<th>Temp (°C)</th>
<th>Slope (%)</th>
<th>Reach-Scale Classification</th>
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</thead>
<tbody>
<tr>
<td>Above Cabin Creek Falls</td>
<td>36.6352, -81.52</td>
<td>3</td>
<td>15</td>
<td>8.8</td>
<td>Cascade</td>
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<tr>
<td>Below Cabin Creek Falls</td>
<td>36.6306, -81.5181</td>
<td>3.7</td>
<td>13.2</td>
<td>9</td>
<td>Cascade</td>
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<td>Above Crabtree Falls</td>
<td>37.835, -79.079</td>
<td>2.28</td>
<td>11.7</td>
<td>3.3</td>
<td>Step-pool</td>
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<td>Below Crabtree Falls</td>
<td>37.851, -79.078</td>
<td>3.5</td>
<td>17.3</td>
<td>8.8</td>
<td>Cascade</td>
</tr>
<tr>
<td>Above Little Cove Creek Falls</td>
<td>37.7266, -79.2017</td>
<td>3.44</td>
<td>20</td>
<td>11.3</td>
<td>Cascade</td>
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<tr>
<td>Below Little Cove Creek Falls</td>
<td>37.7257, -79.1997</td>
<td>3.5</td>
<td>20.8</td>
<td>9.5</td>
<td>Cascade</td>
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<td>Above Overstreet Falls</td>
<td>37.498, -79.529</td>
<td>1.89</td>
<td>14.8</td>
<td>10.8</td>
<td>Cascade</td>
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<td>37.496, -79.53</td>
<td>2.02</td>
<td>15.9</td>
<td>22.5</td>
<td>Cascade</td>
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<td>Above Statons Creek Falls</td>
<td>37.768, -79.236</td>
<td>14.32</td>
<td>13.5</td>
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<td>Plane-bed</td>
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<td>Below Statons Creek Falls</td>
<td>37.767, -79.25</td>
<td>30.82</td>
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<td>1.5</td>
<td>Plane-bed</td>
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<td>37.3752, -80.5706</td>
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<td>16.5</td>
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<td>Plane-bed</td>
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<td>17.1</td>
<td>5.3</td>
<td>Step-pool</td>
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<td>16.7</td>
<td>3.8</td>
<td>Step-pool</td>
</tr>
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<td>6.58</td>
<td>18.2</td>
<td>3</td>
<td>Step-pool</td>
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Table A4. The number of each species caught in each habitat sampled

<table>
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<tr>
<th>Waterfall and Reach Type</th>
<th>brook trout</th>
<th>rainbow trout</th>
<th>black nose dace</th>
<th>long nose dace</th>
<th>torrent sucker</th>
<th>northern hog sucker</th>
<th>fantail darter</th>
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*Additionally, 5 rosy-sided dace, 1 brown trout, 36 bluehead chub, 8 mountain red-belly dace, & 23 madtoms were also caught below Statons Creek Falls.

Table A5. The fork-lengths and wet-weights of all brook trout caught in each of the sampled habitats.

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