

## Antioch University AURA - Antioch University Repository and Archive

---

Dissertations & Theses

Student & Alumni Scholarship, including  
Dissertations & Theses

---


2015

# Scales of Resilience: Community Stability, Population Dynamics, and Molecular Ecology of Brook Trout in a Riverscape after a Large Flood

Erin V. Rodgers

*Antioch University - New England*

Follow this and additional works at: <http://aura.antioch.edu/etds>

 Part of the [Animal Sciences Commons](#), and the [Terrestrial and Aquatic Ecology Commons](#)

---

### Recommended Citation

Rodgers, Erin V., "Scales of Resilience: Community Stability, Population Dynamics, and Molecular Ecology of Brook Trout in a Riverscape after a Large Flood" (2015). *Dissertations & Theses*. 183.  
<http://aura.antioch.edu/etds/183>

This Dissertation is brought to you for free and open access by the Student & Alumni Scholarship, including Dissertations & Theses at AURA - Antioch University Repository and Archive. It has been accepted for inclusion in Dissertations & Theses by an authorized administrator of AURA - Antioch University Repository and Archive. For more information, please contact [dpenrose@antioch.edu](mailto:dpenrose@antioch.edu), [wmcgrath@antioch.edu](mailto:wmcgrath@antioch.edu).

# ANTIOCH UNIVERSITY NEW ENGLAND

Department of Environmental Studies

## DISSERTATION COMMITTEE PAGE

The undersigned have examined the dissertation entitled:

Scales of Resilience: Community stability, population dynamics, and molecular ecology of brook trout in a riverscape after a large flood

Presented by Erin V. Rodgers, candidate for the degree of Doctor of Philosophy and hereby certify that it is accepted\*.

Committee Chair: James Jordan, Ph.D., Department of Environmental Studies, Antioch University New England, Keene, NH

Committee Member: Beth Kaplin, Ph.D., Department of Environmental Studies, Antioch University New England, Keene, NH

Committee Member: Benjamin Letcher, Ph.D., Conte Anadromous Fish Research Laboratory, US Geological Survey, Turners Falls, MA

Defense Date: August 1, 2014

Date submitted to Registrar's Office:

\*Signatures are on file with the Registrar's Office, Antioch University New England.

**Scales of Resilience:  
Community stability, population dynamics, and  
molecular ecology of brook trout in a riverscape after  
a large flood**

by  
Erin Rodgers

A dissertation submitted in partial fulfillment of  
the requirements for the degree of

DOCTORATE OF PHILOSOPHY  
In  
Environmental Studies

at  
Antioch University New England

2014

## **Abstract**

Climate change in the northeastern United States currently and in future decadal predictions is characterized by warmer average temperatures and more frequent and intense storm events. Many aquatic organisms that thrive below a certain temperature threshold, such as brook trout, are being pushed towards their upper thermal limits, ultimately lowering their probability of survival and resilience to disturbance. In late-August and early-September 2011, Hurricane Irene and Tropical Storm Lee created an extended flood in the Delaware Water Gap region of Pennsylvania and New Jersey, as well as much of the northeast. This dissertation examines the effects of this flood on a network of naturally fragmented tributaries in the Delaware Water Gap National Recreation Area. All study sites showed significant changes in mesohabitat and in-stream large woody debris. Because of the area geology, downstream reaches of tributaries were more disturbed, exhibited significant changes in substrate composition, and had a greater loss of species richness. Abundance of all species varied significantly between years, in some locations increasing 500% between 2011 before the flood and 2012 after the flood. Displaced adults and massive increases in young-of-year recruitment should indicate a substantial change in genetic diversity and differentiation over time and space. In fact, pairwise  $F_{st}$  (a comparative measure of genetic differentiation) showed significant differences in nearly all study populations before and after the flood. Of even greater concern was an increase in fixed monomorphic loci in multiple populations. A rich and well-conserved landscape provides the resources necessary to build resilient stream communities and populations after a large disturbance. However, fine scale examination of population genetics show a much graver trend in species health due to fewer reproducing adults and higher offspring survival the following year. Such genetic homogenization increases the likelihood of inbreeding and susceptibility to disease and other long-term environmental stressors. The electronic version of this dissertation is at OhioLink ETD Center, [www.ohiolink.edu/etd](http://www.ohiolink.edu/etd)

## **Keywords**

Brook trout, *Salvelinus fontinalis*, flood, abundance, genetic divergence, community change, resilience, Delaware Water Gap National Recreation Area

## **Dedication**

Dedicated to the memory of Geraldine “Liza” Bissell Carroll,  
And of course to my parents, Peter and Molly Rodgers, for everything.

## **Acknowledgements**

I would like to acknowledge my committee for the time they have spent on me and my various drafts: To Jim for his effort and understanding; to Beth for her support and tact; to Ben for giving me the lab space, the funding, and especially all the opportunities these last many years.

I'd like to acknowledge my parents and all my pseudo-family in Pennsylvania and elsewhere for the unwavering pride and moral support, even, or especially, when they don't have any idea what I'm talking about. All the thanks in the world to Chuck for putting up with me throughout, and all the ups and downs that went with it.

Thank you to the staff and students at the Conte Anadromous Fish Research Center and Andrew Whiteley's genetic lab at University of Massachusetts – Amherst, for the consistent help over the years: Paul Schueller, Maili Page, Andrew Whiteley, Matt O'Donnell, Todd Dubreuil.

Amazing thanks to Maggie for her endless good cheer and writing support. Thanks to all the friends in NH and VT who have let me crash on couches and in guest rooms for class weekends over the last four years. Lastly, to the AUNE library staff who provided me with a steady stream of chocolate, baked goods, and a second home.

## Table of Contents

Abstract .....	2
Dedication .....	3
Acknowledgements .....	4
Chapter 1: Into the Gap: an introduction .....	7
Introduction .....	7
Literature Review .....	10
Climate Change .....	11
Catastrophic Floods .....	13
Scales of Influence .....	16
Statement of Problem and Objectives .....	22
Overview of Chapters .....	23
Conclusion .....	24
References .....	26
Chapter 2: The Delaware Water Gap Landscape: site description, methods, and initial results... 31	
Site and Landscape Description .....	31
Study Site .....	32
Geomorphic Landscape Differences .....	33
Historic Hydrologic Events .....	37
Data Collection Methods .....	40
Initial Results .....	42
Discussion .....	47
Conclusion .....	51
References .....	53
Appendix A – Field Collection Datasheets .....	56
Appendix B – Detailed Genetic Laboratory Protocol .....	58
I. Genomic DNA Extraction Protocol .....	58
II. PCR Reagent-Primer Recipe .....	60
III. PCR Steps .....	61
Chapter 3: Changes in brook trout population occupancy, abundance, and size structure following a massive flood .....	62
Abstract .....	62
Introduction .....	63
Methods .....	66

Results .....	69
Discussion .....	73
Conclusion.....	75
References .....	77
Tables and Figures.....	80
Chapter 4: The genetic consequences of a massive flood in a naturally fragmented landscape...	86
Abstract .....	86
Introduction.....	87
Methods.....	89
Analysis .....	91
Results .....	91
Discussion .....	94
Conclusion.....	96
References .....	98
Tables .....	100
Chapter 5: Conclusion.....	102
References .....	113



# Chapter 1

## Into the Gap: an introduction

### Introduction

What happens to fish during a flood? Do they swim strongly enough to remain in their territory? Do they find refugia? Are they swept away like the trees, hillsides, and substrate? Do the same fish return after a flood or do new species and individuals take their place? Large catastrophic floods are documented throughout cultural history, but their ecological repercussions remain fairly shrouded from our scientific understanding. Given the unpredictable nature of floods, research that includes both a priori and posteriori ecological data as well as the continued effects multiple years afterward is rare. While many studies examine the effects of floods on stream ecology (e.g. Hoopes 1975; Pearsons, et al. 1992; Letcher and Terrick 1998; Delong, et al. 2001; Schmidt, et al. 2001; Carline and McCullough 2003), a smaller number define their flood disturbance as “catastrophic” (Gibbins, et al. 2007; Herring, et al. 2004; Matthews 1986; Roghair, et al. 2002), and fewer of those catastrophic studies gathered detailed data on the location before the flood occurred (Dolloff, et al. 1994; Herbst and Cooper 2010; Roghair, et al. 2002). Without baseline data on species occupancy and abundance from before a flood, it is impossible to quantify the effect it had on the ecological system and therefore impossible to use those post-flood data to accurately predict the effects on fish communities of subsequent floods or floods in other watersheds.

The northeastern region of the United States, over the coming decades, is predicted to experience more precipitation over fewer storm events (Aber, et al. 1995; Hodgkins, et al. 2003; Groisman, et al. 2004). This means that large storms will become more common and will result

in an increase in the occurrence of large, catastrophic flood events (defined by Army Corps of Engineers as greater than a hundred-year recurrence event). Increasingly large and frequent disturbances will affect stream ecosystems that are not accustomed to regular extreme changes in flow and inundation, effects that ecologists cannot currently quantify accurately with the paucity of before-after type studies of large floods.

Climate change has already begun to affect cold water stream ecosystems in recent years. Regional temperature increases threaten thermally intolerant species such as brook trout (Meisner 1990; Perry and Ries 1995; Wenger, et al. 2011), especially those populations in smaller headwater streams. Indirectly, climate change has increased the range of certain invasive species, such as the hemlock woolly adelgid (Paradis, et al. 2007), that threaten forest stands associated with cold water stream systems. Such a large physical system change generates a cascade of other ecosystem changes: shifts in debris loading, invertebrate community composition (Snyder, et al. 2002), stream shading (Orwig and Foster 1998), and other forest processes (Stadler, et al. 2006).

Brook trout have been declining throughout much of their native range for the last several decades (Petty and Merriam 2012). It has only been recently noticed how rapidly their populations are declining, despite the efforts of fishery managers and conservation groups. Traditional means of monitoring and managing do not appear to be addressing the issue, and the traditional problems (degraded habitat, pollution) are no longer the only concerns. We can no longer assume that the “normal” climate conditions of the past will return or remain stable. We can only examine our assumptions, improve our methods, and adapt to the changing world in front of us. We must ask how vulnerable species in decline intersect with an increasing number, frequency, and extent of large natural disturbances. Such a variable climate can create unstable

and skewed populations which may lead to greater changes in stream communities and open more stream kilometers to invasion by non-native and generalist species.

Many areas are being confronted by a combination of these ecosystem changes, or confronted by all of them at once. This appears to be the case in the Delaware Water Gap National Recreation Area (DEWA) spanning northeastern Pennsylvania and northwestern New Jersey. High hemlock mortality caused by the hemlock woolly adelgid is causing complete forest stand changes in the landscape (Mahan, et al. 2004; Small, et al. 2005), streams not heavily influenced by groundwater are in danger of becoming too warm in the summer to support cold water communities, and native cold water stream fish are in precipitous decline throughout DEWA and much of their southern ranges (Hudy et al. 2004; Eastern Brook Trout Joint Venture 2005).

My study, which unintentionally spanned the years before and after a large flood resulting from hurricanes Irene and Lee that affected DEWA and much of the northeastern United States in late-summer 2011, examined the ecological effects of this flood at three scales: fish communities, the brook trout population across the landscape, and at the genetic level. The study began with the collection of detailed baseline data in eighteen sub-watersheds throughout the roughly 28,032 ha park. The large prolonged flood, with two discharge peaks over ten days, occurred immediately after the end of the first field season. Two additional years of community, population, and genetic data collection followed.

In the face of climate change, it can no longer be assumed that the “normal” conditions of the past will return or remain stable. Extreme weather events are creating more frequent ecological disturbances. Managing natural resources and ecological systems for such events is difficult. We can only examine our assumptions, improve our methods, and adapt to the changing

world in front of us. The following research examines the extent to which increasingly variable climate is creating unstable and highly skewed population dynamics, facilitating the colonization of more stream kilometers to warm water generalist communities over specialized cold water brook trout communities, and increasing genetic homogeneity throughout an extended landscape. This dissertation presents a more complete picture of before-and-after effects of a single catastrophic flood on three ecological scales within a single watershed.

## **Literature Review**

Coldwater stream communities are restricted to higher latitudes and elevations by their need for cold temperatures. Shifts in the climate and other environmental variables have begun to jeopardize these communities through much of the southern extent of their range. The historic range of brook trout, a cold water species, extended across much of the northeastern United States from Maine to Pennsylvania and, more narrowly, along the Appalachian Mountains south to Georgia (Karas 1997), but presently, the range of habitat where brook trout can sustainably persist is limited to the highest elevations of the Appalachians and is narrowing at the edges of their northern reaches where urbanization has increased warming.

Native eastern brook trout (*Salvelinus fontinalis*) have been a staple of eastern stream ecosystems for centuries. Since colonial days they have acted as both an economic and cultural touchstone (Karas 1997). Their populations have survived and returned following many environmental disturbances, including deforestation (Merten et al. 2010), urbanization (Marschall and Crowder 1996), industrialization (Canham 2011), and acid rain (Beggs and Gunn 1986). Recently, however, brook trout are facing multiple factors that negatively impact their survival and have caused a precipitous population decline. Climate change is warming streams past brook trout tolerance and is allowing competing species more access to primary brook trout

habitat (Clark, et al. 2001). Stocking and fishing pressure are altering the genetic structure and homogeneity of populations (Angers, et al. 1994). More frequent large-scale floods are regularly disturbing and dispersing brook trout populations as well as shifting geomorphic barriers (Roghair et al. 2002).

The following literature review will focus on changes in community ecology of cold water streams due to climate change; the effects of large scale floods on streams; and the scales of influence at which population disturbance is measured. From shifts of populations within a community, shifts of size and age classes within a single species' population, and shifts in the genetic structure of individuals, disturbances affect the health and resilience – as measured by population abundance and distribution across the landscape over time – of a species within nested ecological levels. Throughout this review, cold water stream communities and brook trout will be used as examples when necessary.

### **Climate Change**

The world's cold water streams face myriad unknown challenges as the global climate changes. There are direct climate-related challenges such as increased air and water temperatures, reduced snow fall and cover, and increased heavy precipitation (Groisman, et al. 2004). There are also indirect challenges such as changes in community assemblage (Eaton and Scheller 1996), forest canopy composition (Paradis, et al. 2007), and land-use changes that exacerbate the effects of climate change (Merten, et al. 2010). The impacts of climate change will go beyond warmer water - they will have cascading effects throughout ecosystems.

The published literature looks at the effects of climate shifts from two directions: some papers assess the historic and current shifts in cold water stream ecosystems while others model different climate scenarios into predicted changes we will see in the next twenty, fifty, or eighty-

five years. Hodgkins, et al. (2003) used sixty-eight years of historic flow data from throughout New England to show that spring high flows are peaking earlier in the year – advancing 1-2 weeks over the past thirty years. Groisman, et al. (2004) reviewed fifty years of hydrometeorologic data that historically verified trends of warming, less snow cover, and increases in thunderstorms and flood damage in the northeastern United States. They also found that minimum air surface temperatures have been increasing far more than maximum temperatures meaning that the air is not just getting warmer, it is getting far less cold as well. This last point is particularly important for cold tolerant and cold sensitive species.

Some studies projecting changes in temperature and flow focus on the effects on fish communities. Meyers, et al. (2012) were concerned with the size and temporal distribution of floods on a sympatric population of brook trout and rainbow trout at 2°C and 4°C regional warming scenarios. The projections showed a shift from spring floods to winter floods, which would disproportionately impact brook trout reproduction. Eaton and Scheller (1996) made projections of changes in tolerable habitat for fifty-seven fish species, and determined that coldwater species would lose roughly 50% of their current habitat while warmwater species could expect a 30% increase in available habitat. Clark, et al. (2001) agree with these projections for habitat change in the southern Appalachians, concluding that salmonids and sympatric coldwater species would lose roughly 42% of their habitat to unsuitable summer thermal maxima. Interestingly, while several studies attempt to predict shifts in community assemblage, few studies identify recent or ongoing shifts in community assemblage over multiple years.

Much of the literature focuses on the potential effects of climate change on cold water streams and their stream communities via increases in temperature, flow, and variable precipitation. Short term disturbances to habitat like increased flows, temporary drying, or

intolerable temperatures that displace fish might become long term trends in stream conditions that could help or hurt different organisms over time. Fausch et al. (2001) and Hitt and Roberts (2012) even identify how such environmental disturbances can lead to increased opportunity for invasion by new species – another indirect consequence of climate change. The changes in population size and species abundance after a large flood can present an opportunity for new fish and species to recolonize the habitat and alter the entire stream assemblage. It is one of the many ways in which temporary or sustained changes to the size and abundance of a population can be harmful to its persistence.

### **Catastrophic Floods**

The effects of large floods on river systems and their inhabitants are relatively unstudied because of their unpredictable nature. It is only when a flood passes through a river that is already under investigation that scientists can collect clear “before and after” data (Dolloff, et al. 1994). Such opportunism also influences what variables are studied based on the research being conducted before the site was flooded (Carline and McCullough 2003). Several studies attempt to document the changes caused by a large flood without substantial baseline data (Seegrist and Gard 1972). This does not lead to robust or highly reliable measurements of flood effects as scientists are left to describe the quality of the ecosystem post-hoc and its presumed return to a stable state.

The definition of a “catastrophic” flood, over and above the threshold of a large flood, varies between fields of study. In building infrastructure and determining risk management, the Army Corp of Engineers uses the one percent event (100-year recurrence interval) and storms of even lower frequency based a location’s annual exceedance probability as the benchmark for catastrophic flooding (National Research Council 2000). Erskine (2011) uses a flood frequency

analysis based on a log Pearson Type III scale to define catastrophic floods as those whose peak instantaneous discharge (in cubic meters per second,  $\text{cms}^{-1}$ ) has a ratio ten times as great as the mean annual flood discharge. However, many ecological studies of catastrophic floods give more vague definitions of “catastrophic”, if a definition is given at all. Roghair, et al. (2002) state that “so-called catastrophic events” have “return intervals measured in decades or centuries”, while Matthews (1986) wrote that “[a]ll available information indicated that this physically catastrophic flood was the worst in Piney Creek in this century”. Many descriptions of large catastrophic floods in ecology literature use qualitative descriptions of changes to riparian habitat, substrate movement, mesohabitat changes, and occasional changes to the biological community as well – most of which are often less quantitatively measured than those used in geology and hydrology literature.

There are several common metrics discussed in the flood ecology literature that include fish density (Pearsons, et al. 1992; Carline and McCullough 2003), invertebrate presence (Benke 2001; Herbst and Cooper 2010), community assemblage stability (Matthews 1986; Dolloff, et al. 1994), shifts in substrate (Roghair, et al. 2002; Carline and McCullough 2003), and mesohabitat change (Pearsons, et al. 1992; Dolloff, et al. 1994; Carline and McCullough 2003). What often goes unrecognized is the effect that all these changes have on ecosystem thresholds and resilience. For the purposes of this work, I talk about resilience in terms of Holling’s (1973) initial definition as “the ability of these systems to absorb changes of state variables, driving variables, and parameters, and still persist”. Operating under a similar definition Roghair, et al. (2002) add a note about resilience in relation to modern ecological conditions and considerations. They discuss the difference between system recovery – or the ability of the system to absorb changes – after chronic stream degradation versus less frequent catastrophic events in “proper”



ecosystem conditions; similar statements can be seen in other literature over time. Both Elwood and Waters (1969) and Seegrist and Gard (1972) noted that their respective systems returned to “normal” stream conditions and stable species assemblages within four years of multiple large-scale floods – these resilient systems absorbed changes, returned to normal, and continued to persist. Matthews (1986) did not see the same return time and questioned the accepted theory on species assemblage stability and persistence. In more recent years, the resulting damages of large catastrophic floods in single streams (Roghair, et al. 2002) and multiple streams (Carline and McCullough 2003) are more extreme than the observed effects of previous floods, and the time it took for various stream metrics to absorb and return to normal pre-flood conditions was more variable between studies. Healthy, less disturbed streams of the 1960s and before may have been able to return to previous conditions in a short period, but Roghair, et al.’s (2002) modern “chronically degraded” streams may not have the capacity to recover from catastrophic floods in the same way.

The timing of floods can have a drastic effect on the stream community, particularly on the spawning and hatching of various species. Several studies note that floods in different seasons have markedly different effects on sympatric species. Seegrist and Gard (1972) were the first to describe the timing effects of floods on the spawning and young-of-the-year brook trout and rainbow trout. Later, Fausch, et al. (2001) noted how the timing of floods facilitated or hindered upstream invasion of rainbow trout and brown trout. While these two studies hypothesized how floods shifted sediment that scoured salmonid redds and crushed young-of-the-year fish, Carline and McCullough (2003) had the opportunity to measure the direct effects of substrate movement from a large winter/spring flood on brook trout redds, adult brook trout density, and post-flood cohort survival. Adult brook trout cohorts had significantly reduced abundance and many young-

of-year cohorts throughout the study area failed to emerge after the flood. These results have serious implications for the future of stream ecosystems as models predict that continued climate change will cause extreme storm events more frequently throughout the year.

### **Scales of Influence**

Changes to a species can be measured at many levels: as species change within a community, as the age structure of individuals changes within a population, or as the molecular gene structure changes between generations. Each of these three scales of influence have been studied extensively under normal conditions resulting in a substantial body of literature; the challenge here is to determine how those studies relate to conditions under a changing climate previously described, and particularly in relation to a catastrophic flood. Coldwater stream communities are challenged by the warming climate and encroaching warm water tolerant fish (Eaton and Scheller 1996; Wenger et al. 2011); large shifts in the abundance of different age classes of brook trout due to flood mortality can create population boom and bust cycles (Hoopes 1975); and a crash in the number of reproducing adults – whether from an unsustainable warmer habitat or from a major flood – can lead to genetic bottlenecks or other reductions in genetic diversity (Garza and Williamson 2001). What may not visibly impact one level of scale may have significant repercussions at another level.

### ***Stream Communities***

Communities consist of many different species and guilds – different species that exploit the same resources – interacting in a defined area. River fisheries are often delineated by environmental variables such as water temperature and flow (Rahel and Hubert 1991). Water temperature is a key variable for cold water species such as the eastern brook trout. They prefer stream temperature at 19°C or cooler and cannot survive in water over 22°C (Cherry et al. 1977;

Trumbo et al. 2010). Few other fish in the northeast prefer such cold water temperature regimes, while warm water fish seek out temperatures of 25°C or higher and are able to tolerate very warm waters with low oxygen levels (Eaton and Scheller 1996). Generalist species can move between these two ranges.

The addition or subtraction of fish species to a community potentially creates cascading changes in the rest of the community. Rahel and Hubert (1991) looked at such changes in longitudinal stream reaches in the Rocky Mountains dominated by salmonids in the headwaters and eventually replaced by minnows and suckers at lower elevations. Those study streams were strongly zoned by temperature and the addition of species in other trophic guilds. Hitt and Roberts (2012) found that community structure and recolonization in naturally defaunated stream reaches were strongly influenced by the species that initially recolonize them. Certain fish can facilitate the establishment of some species while impeding that of others, whether during full recolonization of a reach or immigrating into a newly habitable one due to other environmental changes.

Significant changes to environmental or climate regimes can trigger entire shifts in aquatic community composition. While it is generally recognized that stream systems are both highly variable and have patchy resources, localized extinction and immigration of species are closely tied to environmental variables that allow strong local abundance (Taylor and Warren 2001). Whether it is caused by floods (Roghair et al. 2002) or fires (Howell 2006), partial or entire stream communities can be wiped out of a stream by a single disturbance. Interspecies interaction (Hanson and Waters 1974; Hitt and Roberts 2012) and pre-disturbance habitat conditions (Matthews 1986; Dolloff et al. 1994) can play a big role in the strength of population resilience and speed of recolonization.

Environmental variables, both within the stream and in the riparian area surrounding it, strongly influence the stability and resilience of stream communities. Fausch and Bramblett (1991) found that in four mid-western streams that regularly experienced quick shifts in extreme flow, species composition and abundance remained relatively stable as long as refuge pools contained complex habitat (see also Pearsons et al. 1992). Simple, shallow pool habitat had higher rates of extinction and colonization. Others have found that forest stand composition surrounding a stream reach influences the invertebrate and fish communities (Ross et al. 2003). Rapid changes to forest stands or other land use changes (Gomi et al. 2002) could ultimately result in a cascade of changes to understory aquatic communities.

### ***Populations***

The abundance of a species and the distribution of age and size classes are two of the broadest metrics of population dynamics, but are still indicative of many processes going on within the population over time. Population abundance can indicate adequate resources and carrying capacity of the habitat (Freckleton et al. 2005), as well as provide a source population for colonization assuming adequate connectivity for migration (Taylor and Warren 2001; Hilderbrand 2003). There is also a minimum population abundance, particularly if it is isolated, that will likely result in depensatory effects or local extinction (Freckleton et al. 2005). Within a population or metapopulation abundance, the abundance of individuals within a certain size or life-stage can influence the reproductive and migratory dynamics of the population.

The typical size structure of salmonid populations in headwater streams is often described as a log-normal distribution. During a normal year there are substantial numbers of young-of-year (YOY), with decreasing numbers of juveniles, reproductive adults, and a tailing end of large reproductive adults. A delineation between age-class cohorts can be made between smaller size

classes (i.e. between YOY and juveniles), but becomes increasingly difficult to distinguish as growth slows in adult classes. Because brook trout can reproduce even at relatively small sizes if necessary, abundant large juveniles and small adults are a key component of resilient populations even if large adult or YOY size classes are compromised by a disturbance (Marschall and Crowder 1996).

When a disturbance affects size-classes in a population unevenly, such changes can be visibly seen in a simple survey. Carline and McCullough (2003) showed significant losses of YOY and juveniles after a 1996 winter flood in Monongahela National Forest. Warren et al. (2009) also saw major losses of YOY after a 2005 spring flood in the Catskills. They also noted that the spring timing of the flood disproportionately affected fall-spawning salmonids more than spring-spawning salmonids, and opened habitat to shifts in the dominant fish species. Seegrist and Gard (1972) noted similar timing effects on trout streams in California over the course of ten years (also see Meyers et al. 2010). In another flood in Massachusetts that removed all YOY, Letcher and Terrick (1998) saw rapid growth and maturation of juveniles, thus substantially altering the life history of remaining fish.

While large juveniles and smaller adults are necessary for continued immediate reproduction and sustained population abundance, a significant shift in size-classes can have lasting effects on the population dynamics for years afterward. The loss of any substantial portion of a population, whether small or large, releases resource competition for surviving individuals (Letcher and Terrick 1998) – although reduced competition and increased growth at one trophic level depend heavily on remaining prey availability and recovery post-flood as well (Elwood and Waters 1969). However, the release of intra-species competition potentially opens an area for increased inter-species competition and eventual displacement (Fausch et al. 2001).

Further, in instances where larger adults and juveniles are displaced by disturbance, there is a resulting decrease in effective breeders. This may encourage faster growth and maturation of YOY and smaller juveniles, but may still neutralize substantial recruitment for one or more spawning seasons (Carline and McCullough 2003) and potentially diminish genetic diversity in the overall population.

### ***Genetics***

Many ecologists agree that the population size and genetic heterogeneity of species can have a significant effect on the resilience and adaptability of that species (Hartl and Clark 1997). Genetic heterogeneity means there are a variety of allelic pairings at different loci and more unique genotypes. Genetic homogeneity can have deleterious effects and can result in the “fixation” of alleles (Allendorf and Phelps 1980). O’Grady, et al. (2006) show how inbreeding depression, a symptom of homogenization, strongly influences the potential for extinction. In this way, gene flow between populations of organisms is also important for genetic diversity (Hughes, et al. 2009).

Gene flow between populations can be interrupted in many ways. Some populations of organisms are fragmented by natural landscape barriers: mountains between plains, valleys between alpine peaks, or waterfalls in a stream; other populations are fragmented by man-made obstacles: urban areas, highways, or culverts. The effects of such fragmentation remain the same regardless of the cause: Carlsson and Nilsson (2001) and Moran, et al. (1995) explore natural fragmentation and reproductively isolated wild salmonid populations, while Neraas and Spruell (2001) and Gibbs (2001) examined genetic effects of anthropogenic fragmentation. Wofford, et al. (2005) teased apart the genetic differentiation caused by barriers and by demography – both of which play a role in gene flow –but emphasized the negative consequences low genetic

diversity has on population persistence. All of these studies showed that fragmentation, regardless of cause, created high genetic fragmentation between upstream and downstream populations separated by these barriers. Ironically, fragmented wild populations can also become refuges for wild genotypes that have not yet been impacted by the homogenized genotypes of artificially selected organisms (Araguas, et al. 2008).

A secondary factor affects the genetic composition of many game species: the addition of captive bred and raised animals into a wild population. In this case, the breeding and release of captive hatchery-raised fish is unparalleled by that of any other organism (Allendorf, 1988). Fish that are bred and raised in captivity undergo artificial selection that can produce significant genetic homogenization in just one or two generations (Hansen, et al., 2001), and the effects of hatchery fish on wild populations radiates in both the short and long term. Currens, et al. (1997) found that the genetic homogenization that occurred when wild rainbow trout bred with stocked trout caused the wild trout to become far more susceptible to disease, and Marie, et al. (2010) show that genetic homogenization was strongly related to how intensely Canadian lakes were stocked with brook trout. Krueger and Menzel (1979) showed that the genetic effects of intense stocking were still highly visible in brook trout streams twenty-five years later. Although researchers know how low heterogeneity reduces population health and adaptability, they do not yet know how it will influence the survival and resilience of trout populations as they confront changing environmental conditions due to climate change.

Gene transfer and flow in stream systems must be examined differently than in terrestrial systems. Instead of radiating between territories, patches, or individuals on land, genes in streams, and the individuals to which they belong, move only linearly upstream and downstream. When populations are impacted by floods and individuals are washed downstream, gene flow

can be unidirectionally skewed. Assuming washed-out individuals survive the forced migration, downstream populations would benefit the most from the increased diversity while upstream populations become increasingly limited by the genes of remaining individuals.

### **Statement of Problem and Objectives**

Initial questions arise in the literature regarding the use of the word “catastrophic” when describing a flood. As mentioned above, hydrologists share the most common definition and usage of catastrophic: a storm event with a greater than one-hundred-year recurrence interval (a “hundred-year storm or flood”). Often these storms create large amounts of damage to infrastructure, economy, and personal possessions, as well as geomorphic damage seen as bankside erosion, shifting substrate, and uprooted trees. But many ecological processes occur and aquatic organisms live below the easy view of the terrestrial landscape and may not be as catastrophically affected by the hundred-year or greater flood. The word “catastrophic”, however, is seemingly used almost interchangeably in the literature. My dissertation more deeply explores whether a hydrologically catastrophic flood is also an ecologically catastrophic flood.

There is a large gap in the flood literature about the marked changes before and after a flood based on pre-flood baseline data. Large floods are random and it is a rare opportunity that an ecological study of a population is conducted on a river or stream network that experiences catastrophic flood conditions. Such an opportunity presents several lines of inquiry to be detailed in three manuscripts, the underlying basis of which is: how do large floods affect riverine systems at different scales? My dissertation compares baseline data at twenty-four stream reaches in the Delaware Water Gap National Recreation Area collected in the months preceding a catastrophic flood in 2011 caused by Hurricane Irene and Tropical Storm Lee to the conditions of the following two years.



Part of the original rationale for conducting this research in DEWA was the precipitous decline of brook trout throughout the park (personal communication, R. Evans, Ecologist, National Park Service, DEWA). Although it appears to be an ecologically pristine landscape, myriad factors are degrading eastern brook trout habitat (EBTJV 2005; Hudy et al. 2004). This continued persistent species decline may indicate that current management policies are no longer appropriate under current conditions, nor are they likely to be under changing future conditions. A reasonable understanding of the responses of population dynamics to individual environmental variables as well as responses to interacting environmental variables will play a key role in the future of management decisions.

Large disturbances affect systems at many scales. This dissertation aims to examine three scales of influence in a landscape of streams affected by the 2011 flood in the Delaware Water Gap National Recreation Area. The following manuscripts will look at (1) the changes in stream fish community composition through stability, extirpation, and colonization, (2) the changes in eastern brook trout abundance and size structure within localized populations, and (3) shifts in the diversity and differentiation of eastern brook trout landscape population genetics. By combining these ecological scales, we begin to understand the additive effects of large catastrophic floods as well as the interactive effects such scales have on each other.

### **Overview of Chapters**

The following chapter (Chapter 2) is intended to set the context of the environmental conditions in the landscape historically, at the beginning of the study just prior to the 2011 flood, and in the years following the flood event. In it I will quantify some of the broad environmental changes that took place in the regions of the park including how the flood affected substrate, large woody debris, and stream mesohabitat.

Chapters 3-5 are presented as three manuscripts for publication. The first manuscript (Chapter 3) will look at how fish communities at twenty-four reaches in ten tributaries throughout the park influenced brook trout occupancy, abundance, and resilience. I will focus, in part, on changes to brook trout population abundance after the flood in relation to the richness and diversity of warm water fish species also present at each site. Localized colonization and extirpation, especially in landscapes characterized by natural barriers and fragmentation, can radically alter community structure.

Chapter 4 focuses on brook trout to examine changes in population abundance and size distribution within a landscape population at 24 reaches in 15 tributaries throughout the park. The timing of a flood will often affect adult, juvenile, and young-of-year fish differently and disproportionately. A metapopulation skewed to one size or reproductive maturity can alter the population dynamics for years.

Chapter 5 examines the fine scale molecular ecology of brook trout populations. A sudden decrease in the effective population of reproductive adults can reduce genetic diversity of brook trout throughout the park. Conversely, the unidirectional gene flow common to fragmented stream systems may benefit downstream metapopulations while increasing homogeneity of upstream metapopulations.

## **Conclusion**

There are many compound environmental changes taking place in the northeastern United States that are negatively impacting the persistence and resilience of native species. In the case of how fisheries react to large floods there are few clearly delineated a priori and posteriori data on which to base future scenarios. Moreover, there are slow persistent environmental changes like higher temperatures, invasive species altering forest stand composition, and non-native species competing with natives for primary resources to complement bigger environmental disturbances

that are coming more frequently. The combined effects of these environmental changes are largely unknown and the resilience of communities, species, and individuals is regularly tested. Yet knowing how stream communities respond to large floods is a necessary component of fishery management, especially as it relates to species already in decline such as the eastern brook trout.

## References

- Aber, J., Ollinger, S., Federer, C., Reich, P., Goulden, M., Kicklighter, D., Melillo, J., Lathrop Jr., R. (1995). Predicting the effects of climate change on water yield and forest production in the northeastern United States. *Climate Research*, 5, 207-222.
- Allendorf, F. (1988). Conservation biology of fishes. *Conservation Biology*, 2(2), 145-148.
- Allendorf, F., Phelps, S. (1980). Loss of genetic variation in a hatchery stock of cutthroat trout. *Transactions of the American Fisheries Society*, 109(5), 537-543.
- Angers, B., Bernatchez, L., Angers, A., Desgroseillers, L. (1995). Specific microsatellite loci for brook charr reveal strong population subdivision on a microgeographic scale. *Journal of Fish Biology*, 47, 177-185.
- Araguas, R., Sanz, N., Fernandez, R., Utter, F. M., Pla, C., Garcia-Marin, J.-L. (2008). Genetic refuges for a self-sustained fishery: experience in wild brown trout populations in the eastern Pyrenees. *Ecology of Freshwater Fish*, 17(4), 610-616.
- Beggs, G., Gunn, J. (1986). Response of lake trout (*Salvelinus namaycush*) and brook trout (*S. fontinalis*) to surface water acidification in Ontario. *Water, Air, and Soil Pollution*, 30, 711-717.
- Benke, A. (2001). Ecosystem importance of flood regime to invertebrate habitat in an unregulated river-floodplain ecosystem. *Journal of the North American Benthological Society*, 20(2), 225-240.
- Canham, H.O. (2011). Hemlock and Hide: The Tanbark Industry in Old New York. May 27<sup>th</sup>, 2011. *Northern Woodlands Magazine*.
- Carline, R., McCullough, B. (2003). Effects of floods on brook trout populations in the Monongahela National Forest, West Virginia. *Transactions of the American Fisheries Society*, 132(5), 1014-1020.
- Carlsson, J., Nilsson, J. (2001). Effects of geomorphological structures on genetic differentiation among brown trout populations in a northern boreal river drainage. *Transactions of the American Fisheries Society*, 130(1), 36-45.
- Cherry, D., Dickson, K., Cairns Jr., J., Stauffer, J. (1977). Preferred, avoided, and lethal temperatures of fish during rising temperature conditions. *Journal of the Fisheries Research Board of Canada*, 34(2), 239-246.
- Clark, M., Rose, K., Levine, D., & Hargrove, W. (2001). Predicting climate change effects on Appalachian trout: Combining GIS and individual-based modeling. *Ecological Applications*, 11(1), 161-178.
- Currens, K., Hemmingsen, A., French, R. A., Buchanan, D. V., Schreck, C. B., Li, H. W. (1997). Introgression and susceptibility to disease in a wild population of rainbow trout. *North American Journal of Fisheries Management*, 17(4), 1065-1078.
- Delong, M., Thorp, J., Greenwood, K., Miller, M. (2001). Responses of consumers and food resources to a high magnitude, unpredicted flood in the upper Mississippi River basin. *Regulated Rivers: Research and Management*, 17(3), 217-234.

- Dolloff, C., Flebbe, P., Owen, M. (1994). Fish habitat and fish populations in a southern Appalachian watershed before and after Hurricane Hugo. *Transactions of the American Fisheries Society*, 123(4), 668-678.
- Eastern Brook Trout Joint Venture (2005). Conserving the eastern brook trout: an overview of status, threats, and trends. Conservation Strategy Work Group, December, 1-14.
- Eaton, J., Scheller, R. (1996). Effects of climate warming on fish thermal habitat in streams of the United States. *Limnology and Oceanography*, 41(5), 1109-1115.
- Elwood, J. W., Water, T. F. (1969). Effects of flood on food consumption and production rates of a stream brook trout population. *Transactions of the American Fisheries Society*, 98(2), 253-262.
- Erskine, W. D. (2011). Geomorphic controls on historical channel planform changes on the lower Pages River, Hunter Valley, Australia. *Australian Geographer*, 42(3), 289-307.
- Fausch, K., Bramblett, R. (1991). Disturbance and fish communities in intermittent tributaries of a western Great Plains river. *Copeia*, 1991(3), 659-674.
- Fausch, K., Taniguchi, Y., Nakano, S., Grossman, G. D., Townsend, C. R. (2001). Flood disturbance regimes influence trout invasion success among five Holarctic regions. *Ecological Applications*, 11(5), 1438-1455.
- Freckleton, R. P., Gill, J. A., Noble, D., Watkinson, A. R. (2005). Large-scale population dynamics, abundance-occupancy relationships, and the scaling from local to regional population size. *Journal of Animal Ecology*, 74(2), 353-364.
- Garza, J. C., Williamson, E. G. (2001). Detection of reduction in population size using data from microsatellite loci. *Molecular Ecology*, 10, 305-318.
- Gibbins, C., Vericat, D., Battala, R. (2007). When is stream invertebrate drift catastrophic? The role of hydraulics and sediment transport in initiating drift during flood events. *Freshwater Biology*, 52(12), 2369-2384.
- Gibbs, J. (2001). Demography versus habitat fragmentation as determinants of genetic variation in wild populations. *Biological Conservation*, 100(1), 15-20.
- Gomi, T., Sidle, R., Richardson, J. (2002). Understanding processes and downstream linkages of headwater streams. *BioScience*, 52(10), 905-916.
- Groisman, P., Knight, R., Karl, T., Easterling, D., Sun, B., Lawrimore, J. (2004). Contemporary changes of the hydrological cycle over the contiguous United States: Trends derived from in-situ observations. *Journal of Hydrometeorology*, 5, 64-85.
- Hansen, M., Ruzzante, E., Nielsen, E., Mensberg, K.-L. (2001). Brown trout (*Salmo trutta*) stocking impact assessment using microsatellite DNA markers. *Ecological Applications*, 11(1), 148-160.
- Hanson, D., Waters, T. (1974). Recovery of standing crop and production rate of a brook trout population in a flood-damaged stream. *Transactions of the American Fisheries Society*, 103(3), 431-439.
- Hartl, D. L., Clark, A. G. (1997). *Principles of Population Genetics*. 3<sup>rd</sup> ed. Sunderland, MA: Sinauer Associates, Inc.

- Herbst, D., Cooper, S. (2010). Before and after the deluge: Rain-on-snow flooding effects on aquatic invertebrate communities of small streams in the Sierra Nevada, California. *Journal of the North American Benthological Society*, 29(4), 1354-1366.
- Hilderbrand, R. (2003). The roles of carrying capacity, immigration, and population synchrony on persistence of stream-resident cutthroat trout. *Biological Conservation*, 110(2), 257-266.
- Hitt, N., Roberts, J. (2012). Hierarchical spatial structure of stream fish colonization and extinction. *Oikos*, 121(1), 127-137.
- Hodgkins, G., Dudley, R., Huntington, T. (2003). Changes in the timing of high river flows in New England over the 20<sup>th</sup> century. *Journal of Hydrology*, 278, 244-252.
- Holling, C. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, 4, 1-23.
- Hoopes, R. (1975). Flooding as the result of Hurricane Agnes and its effect on a native brook trout population in an infertile headwater stream in central Pennsylvania. *Transactions of the American Fisheries Society*, 104(1), 96-99.
- Howell, P. (2006). Effects of wildfire and subsequent hydrologic events on fish distribution and abundance in tributaries of North Fork John Day River. *North American Journal of Fisheries Management*, 26(4), 983-994.
- Hudy, M., Thieling, T., Whalen, J., (2004). A large-scale risk assessment of the biotic integrity of native brook trout watersheds. *Wild Trout VIII Symposium*, 1-8.
- Hughes, J., Schmidt, D., Finn, D. (2009). Genes in streams: using DNA to understand the movement of freshwater fauna and their riverine habitat. *BioScience*, 59(7), 573-583.
- Karas, N. (1997). *Brook Trout*. New York, NY: Lyons & Burford.
- King, T. L., Julian, S. E., Coleman, R. L., Burnham-Curtis, M. K. (2003). Isolation and characterization of novel tri- and tetranucleotide microsatellite DNA markers for brook trout *Salvelinus fontinalis*: GenBank submission numbers AY168187, AY168192, AY168193, AY169194, AY168195, AY169197, AY168199. Available: [ncbi.nlm.nih.gov/nucleotide/](http://ncbi.nlm.nih.gov/nucleotide/). (February 2010).
- Krueger, C., Menzel, B. (1979). Effects of stocking on genetics of wild brook trout populations. *Transactions of the American Fisheries Society*, 108(3), 277-287.
- Letcher, B., Terrick, T. (1998). Maturation of male age-0 Atlantic salmon following a massive localized flood. *Journal of Fish Biology*, 53(1), 1243-1252.
- Mahan, C., Sullivan, K., Black, B., Kim, K., Yahner, R. (2004). Overstory tree composition of eastern hemlock stands threatened by the hemlock woolly adelgid at Delaware Water Gap National Recreation Area. *Castanea*, 69(1), 30-37.
- Marie, A., Bernatchez, L., Garant, D. (2010). Loss of genetic integrity correlates with stocking intensity in brook charr (*Salvelinus fontinalis*). *Molecular Ecology*, 19(1), 2025-2037.
- Marschall, E., Crowder, L. (1996). Assessing population responses to multiple anthropogenic effects: A case study with brook trout. *Ecological Applications*, 6(1), 152-167.

- Matthews, W. (1986). Fish faunal structure in an Ozark stream: Stability, persistence and a catastrophic flood. *Copeia*, 1986(2), 388-397.
- Meisner, J. (1990). Potential loss of thermal habitat for brook trout due to climatic warming in two southern Ontario streams. *Transactions of the American Fisheries Society*, 119(2), 282-291.
- Merten, E., Hemstad, N., Eggert, S., Johnson, L. B., Kolka, R., Newman, R., Vondracek, B. (2010). Relations between fish abundances, summer temperatures, and forest harvest in a northern Minnesota stream system from 1997 to 2007. *Ecology of Freshwater Fish*, 19(1), 63-73.
- Meyers, E., Dobrowski, B., Tague, C. (2010). Climate change impacts on flood frequency, intensity, and timing may affect trout species in Sagehen Creek, California. *Transactions of the American Fisheries Society*, 139(6), 1657-1664.
- Moran, P., Pendas, A., Garcia-Vazquez, E., Izquierdo, J. I., Lobon-Cervia, J. (1995). Estimates of gene flow among neighboring populations of brown trout. *Journal of Fish Biology*, 46(1), 593-602.
- National Research Council. (2000). *Risk Analysis and Uncertainty in Flood Damage Reduction Studies*. Washington, DC: The National Academies Press.
- O'Grady, J. J., Brook, B. W., Reed, D. H., Ballou, J. D., Tonkyn, D. W., Frankham, R. (2006). Realistic levels of inbreeding depression strongly affect extinction risk in wild populations. *Biological Conservation*, 133(1), 42-51.
- Orwig, D., Foster, D. (1998). Forest response to the introduced hemlock woolly adelgid in southern New England, USA. *Journal of the Torrey Botanical Society*, 125(1), 60-73.
- Paradis, A., Elkinton, J., Hayhoe, K., Buonaccorsi, J. (2007). Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. *Mitigation and Adaptation Strategies for Global Change*, 13(5-6), 541-554.
- Pearsons, T., Li, H., Lamberti, G. (1992). Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. *Transactions of the American Fisheries Society*, 121(4), 427-436.
- Perry, S., Ries, R. (1995). Potential effects of global climate warming on brook trout growth and prey consumption in central Appalachian streams, USA. *Climate Research*, 5(3), 197-206.
- Petty, J. T., Merriam, E.P. (2012) Brook Trout Restoration. *Nature Education Knowledge*, 3(7), 17.
- Rahel, F., Hubert, W. (1991). Fish assemblages and habitat gradients in a Rocky Mountain-Great Plains stream: Biotic zonation and additive patterns of community change. *Transactions of the American Fisheries Society*, 120(3), 319-332.
- Roghair, C., Dolloff, C., Underwood, M. (2002). Response of a brook trout population and instream habitat to a catastrophic flood and debris flow. *Transactions of the American Fisheries Society*, 131(4), 718-730.
- Ross, R., Bennet, R., Snyder, C., Young, J., Smith, D., Lemarie, D. (2003). Influence of the eastern hemlock (*Tsuga canadensis* L.) on fish community structure and function in headwater streams of the Delaware River Basin. *Ecology of Freshwater Fish*, 12(1), 60-65.

- Schmidt, J., Parnell, R., Grams, P., Hazel, J.E., Kaplinski, M.A., Stevens, L.E., Hoffnagle, T.L. (2001). The 1996 controlled flood in Grand Canyon: Flow, sediment transport, and geomorphic change. *Ecological Applications*, 11(3), 657-671.
- Seegrist, D., Gard, R. (1972). Effects of floods on trout in Sagehen Creek, California. *Transactions of the American Fisheries Society*, 101(3), 478-482.
- Small, M., Small, C., Dreyer, G. (2005). Changes in a hemlock-dominated forest following woolly adelgid infestation in southern New England. *The Journal of the Torrey Botanical Society*, 132(3), 458-470.
- Snyder, C., Young, J., Lemarie, D., Smith, D. (2002). Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 262-275.
- Stadler, B., Muller, T., Orwig, D. (2006). The ecology of energy and nutrient fluxes in hemlock forests invaded by hemlock woolly adelgid. *Ecology*, 87(7), 1792-1804.
- Taylor, C., Warren Jr., M. (2001). Dynamics in species composition of stream fish assemblages: environmental variability and nested subsets. *Ecology*, 82(8), 2320-2330.
- Trumbo, B., Hudy, M., Smith, E., Kim, D., Wiggins, B., Nislow, K., Dollof, C. (2010). Sensitivity and vulnerability of brook trout populations to climate change. USDA Forest Service, 10<sup>th</sup> Annual Wild Trout Symposium.
- Warren, D., Ernst, A., Baldigo, B. (2009). Influence of spring floods on year-class strength of fall- and spring-spawning salmonids in Catskill Mountain streams. *Transactions of the American Fisheries Society*, 138(1), 200-210.
- Wenger, S., Isaak, D., Dunham, J., Fausch, K., Luce, C., Neville, H., Reman, B., Young, M., Nagel, D., Horan, D., Chandler, G. (2011). Role of climate and invasive species in structuring trout distributions in the interior Columbia River Basin, USA. *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 988-1008.
- Wofford, J., Gresswell, R., Banks, M. (2005). Influence of barriers to movement on within-watershed genetic variation of coastal cutthroat trout. *Ecological Applications*, 15(2), 628-637.



## Chapter 2

### **The Delaware Water Gap Landscape: site description, methods, and initial results**

#### **Site and Landscape Description**

The physical landscape and structure of a place can play a vital role in how weather affects a location. The geology and slope affect how quickly rainfall moves through a drainage; the forest type and coverage does the same; human structures like dams can pointedly control the build-up and release of the river. The Delaware River is the last major un-dammed river east of the Mississippi, though not for lack of attempts to do so (Albert 2005). Extending 531 km from Hancock, NY to the Delaware Bay near Cape May, NJ, the Delaware River drains 35,066 km<sup>2</sup> in parts of Pennsylvania (51%), New Jersey (23%), New York (18%), and Delaware (18%).

The region has experienced a number of sweeping ecological changes from industries such as tanning, lumber, and recreation. Throughout the region's Euro-American history the forests have been cleared, floodplains farmed, and hillsides developed for tourism and trails. The Delaware River's proximity to several major metropolitan areas including New York City, NY, Philadelphia, PA, and Trenton, NJ, have made it the playground for urban vacationers and the subject of numerous political battles for more clean drinking water. However, colonial-era laws, political infighting, and an unstable geology have kept the river free-flowing and facilitated the creation of the Delaware Water Gap National Recreation Area, which was formally established in 1978 (Albert 2005).

This section provides an in-depth description of the Delaware Water Gap National Recreation Area region. It includes a description of the study site used for sampling, and brief geological and hydrological histories.

## **Study Site**

All field components of this research were conducted in the Delaware Water Gap National Recreation Area (DEWA) in partnership with the USGS-Leetown Science Center, USGS-Silvio Conte Anadromous Fish Research Center, and the National Park Service (NPS). DEWA encompasses 28,032 hectares of land and roughly 201 km of rivers, including 64 km of the Delaware River, within the park boundary in Pennsylvania and New Jersey. The study was conducted from July 5 – August 21, 2011, from July 9 – July 20, 2012, and from July 22 – August 2, 2013.

The study examined 16 sub-watershed tributaries that flow directly into the Delaware River. Eighty-three stream reaches were selected on these tributaries; each reach was 150m long and separated from other reaches on the same tributary by at least one natural barrier. Most man-made barriers and low-head dams within these sub-watersheds were removed by the NPS after the creation of the park. Tributaries ranged between first- and third-order streams between 1m and 18m wide (5m average).

In August and September 2011 two storm systems, Hurricane Irene and Tropical Storm Lee, passed over DEWA. These storms dropped a cumulative 33.83 cm of rain over ten days according to National Weather Service rain gauges near Milford, PA located at the northern terminus of the park (Aug 28: 13.51cm, Sept 5: 4.49cm, Sept 6: 5.03cm, Sept 7: 4.14cm, Sept 8: 6.65cm). Nearly half of all rain and flow gages in DEWA and surrounding areas recorded discharge peaks greater than or equal to a hundred-year recurrence interval storm event (Table 1). The hydrologic characteristics classify these paired storm events as “catastrophic” in geomorphological terms. Visual observation of the study area one month after the flood showed substantial changes to the substrate, natural in-stream barriers, and mesohabitat; erosion and large bankslides; and a demonstrable decline in adult brook trout populations. Some of these

changes were quantified the following summer. These environmental characteristics will be used to evaluate whether the paired storms were ecologically catastrophic as well.

**Table 1:** Peak discharge from Hurricane Irene and Tropical Storm Lee events in the Delaware Water Gap National Recreation Area and average discharge for the same time period based on historic gage data. Gages are monitored, maintained, and verified by the National Weather Service and United States Geological Survey as part of the National Water Information System.

Gage Location	River	100-year Flood Discharge (cms <sup>-1</sup> )	Average Yearly Discharge (cms <sup>-1</sup> )	Record Flood Stage (cms <sup>-1</sup> )	2011 Peak H. Irene & T.S. Lee (cms <sup>-1</sup> ) (Aug 28-Sept 7)
Montague, NJ	Delaware River <sup>a</sup>	6400	167.4	7673 (1903)	3315
Flatbrook, NJ	Flat Brook	80	3.2	289 (2011)	289
Bushkill, PA	Bushkill	113	6.8	663 (1955)	154
Edgemere, PA	Little Bushkill	10	0.5	13 <sup>b</sup> (2011)	13

<sup>a</sup>Delaware River at this location is regulated by upstream control dams.

<sup>b</sup>Gage at Little Bushkill data only on record from 2006 to present.

### Geomorphic Landscape Differences

The geomorphology of a riverscape may ultimately play a key role in how certain tributaries are affected by flooding and the resilience of the populations within them. A stream that winds down a moderate slope will experience a different kind of flooding than a stream that cuts into a deep, high gradient ravine. Groundwater influence, a geomorphic trait as water flows through fissures and unconsolidated sediment, is an important factor in cold water community persistence and resilience because it keeps stream temperatures cooler throughout the year than streams fed by surface water alone (Mellina et al. 2002). The bedrock material in and around a stream also dictates variation in substrate material, conductivity, alkalinity, and siltation – all factors in trout production and survival (Scarnecchia and Bergerson 1987). Thus, the geological history of a landscape continues to play a role in present-day conditions and processes.

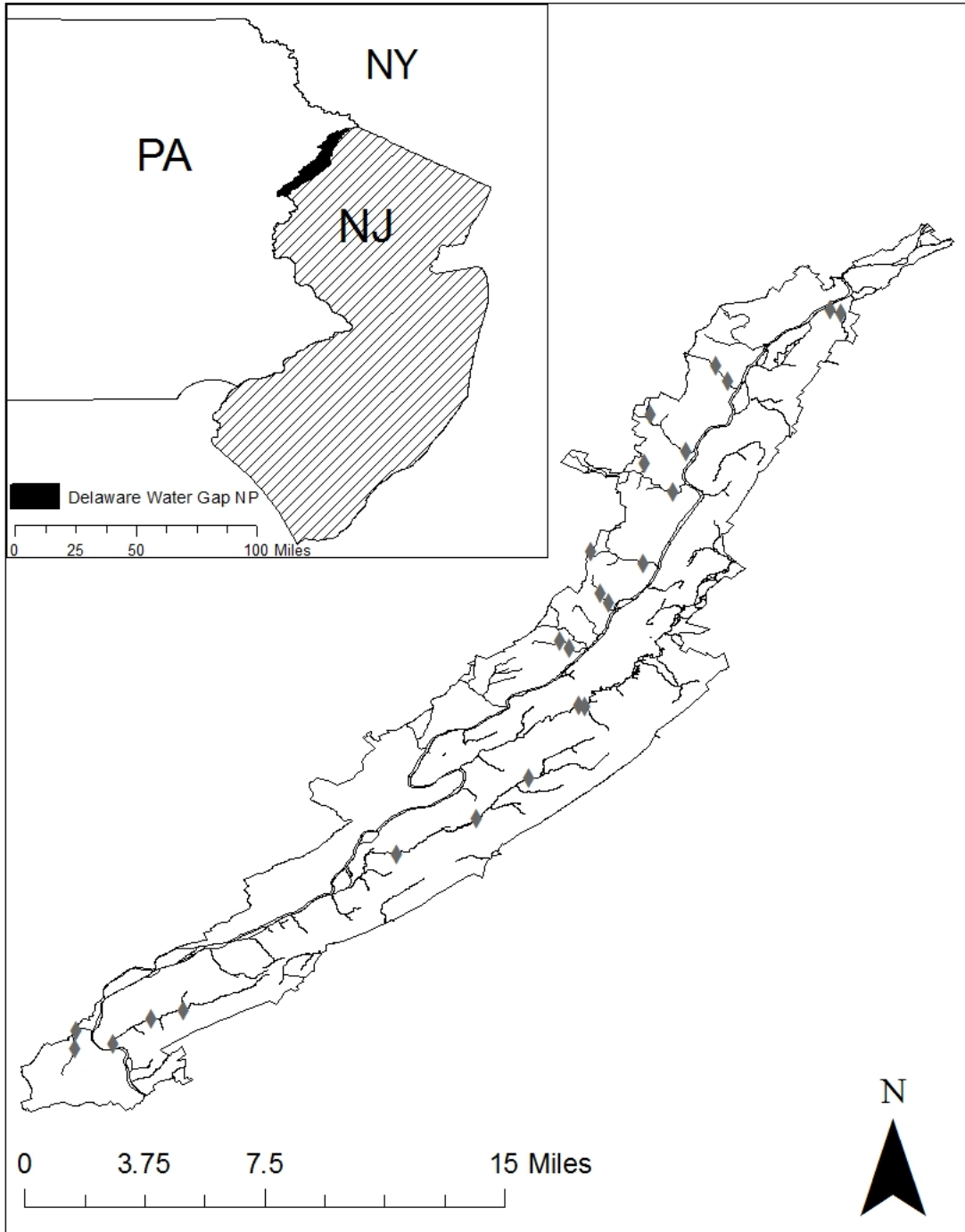
The rocks and substrate that underlie DEWA are part of a complex geological history that has been shaped and molded at long intervals by tectonic and glacial activity. Geologists have described the many processes that have formed the unique substrates of the region split between

the Pocono Plateau Province and the Valley and Ridge Province; the rocks ranging in time from the Ordovician, Silurian, and Devonian to the last two million years (Epstein 2006). This section will look at some of the geological processes and the effects they have had on the region's resources.

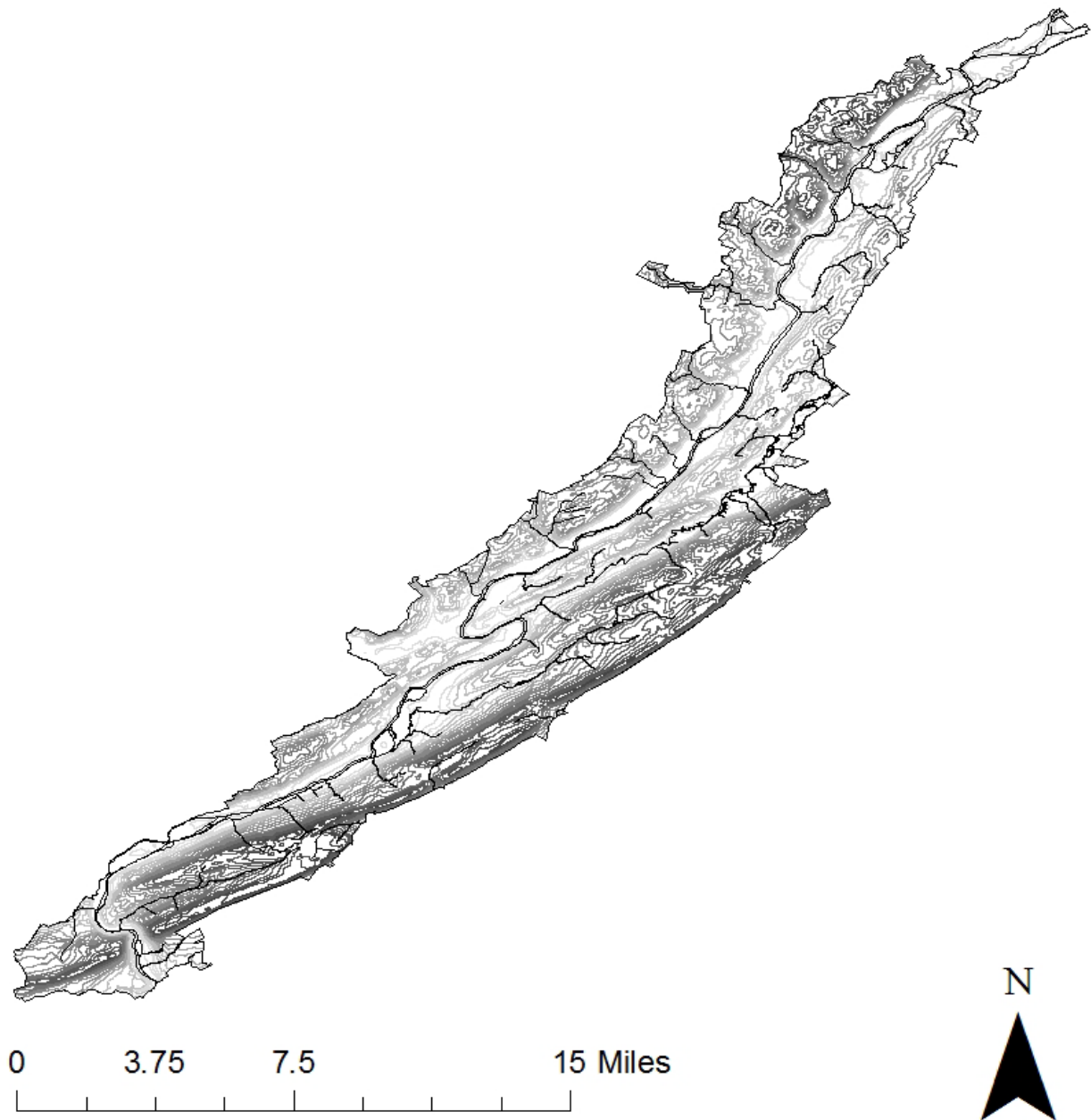
DEWA covers both the Pocono Plateau and the Valley and Ridge Province physiographies. The wide range of sediments are derived from three Paleozoic orogenies (Alleghenian, Taconic, and Acadian) with distinct depositional environments including deep-sea deposits, shallow marine deposits, and terrestrial deposits. The Plateau region at the northwest area of the park is mostly flat-lying sandstone and shale, while the Valley and Ridge region at the southeast of the park consists of complexly folded shale, sandstone, limestone, and dolomite. The shale and limestone, as well as sand and silt from the last glaciation, has controlled the downcutting of the Delaware River through the area (Epstein 2006) - geographically constrained by the mountain bedrock's natural resistance to wearing (Epstein 1966), but allowed sinuously meander through the sandy floodplain valley.

The topography of the river banks are quite different from one side of the river to the other: the Pennsylvania side consists of a gentle rise close to the river, a steep ledge, and a higher flatter plateau, while the New Jersey side rises slightly steeper and more consistently from the river before rising steeply to the Kittatinny Ridge (Figure 2). Pennsylvania appears to be most influenced by the Godfrey Ridge at the southern extent of the park and the Pocono Plateau at the north. The structure and angle of the Plateau bedrock where it sheers off before the Delaware River may influence the amount of cold groundwater seeps, which are found particularly in the northern regions of the park. New Jersey is mainly influenced by the Kittatinny Mountains at the southern extent of the park and the Walpack Ridge at the north extent (Epstein 2006). Both

Pennsylvania and New Jersey have substantial areas of broad flat flood plain – the silty deposition described above – at intervals throughout the park.



**Figure 1: Map of the Delaware Water Gap National Recreation Area which lies in both Pennsylvania to the west of the Delaware River and New Jersey to the east.**



**Figure 2: Topographic map of the Delaware Water Gap National Recreation Area. Note the steep rises in the northwest and southeast regions of the park.**

The Wisconsin glacial drift deposited a variety of glacial drift, carved out lakes, and altered river drainages. Although the time preceding the Wisconsin glacial drift produced much geological weathering and soil formation, glacial drift eroded much of the upland surface (Ridge et al. 1992). As ice retreated roughly 20,000 years ago it left large terminal moraine throughout the

Delaware Valley. The moraine created a large glacial meltwater lake, Lake Sciota, which facilitated lacustrine deposition that can be seen in the stratified layers of sand and gravel deposits through much of the lower elevation regions of the park. The lake remained until the glacier retreated past the Delaware Water Gap and the water was released, leaving an outwash terrace below the Gap (Epstein 2006). The lakebed deposition, through which the Delaware River now flows, left rich soils that would become prime farming land in the colonial era. However, the glacier left much exposed bedrock and thin soils across the ridges overall unsuitable for most trees except hemlock and white pine. In fact, the exposed bedrock also influences many tributaries on both sides of the Delaware River (Epstein 1966) as stream flow over large sections of bedrock with no overtopping substrate results in faster flows and unsuitable habitat for all but a few fish species.

The thin rocky soils influence where certain tree species may grow, the mineral composition of the rocks influences the pH and conductivity of the streams, and the presence of groundwater infiltration and cold water seeps dramatically alters water temperature in many small streams. Microclimates and geological history also create variation in erosion and sinuosity of streams across the landscape (Sharpe 2012). Even more, the shape of the landscape and surface composition affects the movement of water, how it collects, and the speed and severity of floods, as history has shown.

### **Historic Hydrologic Events**

The Delaware River, like most free-flowing rivers, encounters yearly spring floods locally called freshets – semi-regular small floods – and has experienced a range of historic large floods. In the colonial and early industrial eras, timber and freight companies relied on the regular spring freshets to bring massive quantities of goods from the upper Delaware Valley downstream to Trenton and Philadelphia (Dale 1996). In comparison, using the hydrological

definition of a catastrophic flood, there have been only a small handful of large catastrophic floods in the recorded history of the upper Delaware Valley upstream of the Water Gap. The 2011 flooding ranks among the top historic floods in tributary gages in or near the park, although it did not rank highly on any of the main-stem Delaware gages.

Hydraulic gaging stations have been in use along the Delaware River for nearly a century in some locations; some on the main stem of the Delaware have recorded flow data since 1903, although gaging stations on smaller nearby tributaries have become common only in recent decades. I have used four US Geological Survey gaging stations in or near the Delaware Water Gap National Recreation Area to provide hydraulic discharge data: one at Montague, NJ, on the Delaware River at the northernmost terminus of the park, one at Flatbrook, NJ, on Flat Brook at the east-central region of the park, and one each at Bushkill and Edgemere, PA, on the Bushkill and Little Bushkill at the south-western region of the park.

Average flow ( $\text{cms}^{-1}$ ) throughout DEWA varies in typical seasonal cycles. Spring snowmelt creates a high flow peak in late March through April. Often there is a second smaller peak in early fall as deciduous trees decrease transpiration, usually in September and early October. These two peak times appear to also be more vulnerable to incidents of high flooding; a third peak may appear in late winter as the river becomes susceptible to ice dams and sudden release. During the rest of the year, the Delaware River is more likely to experience low-flow conditions due to its wide shallow profile. Groundwater- and impoundment-fed tributaries are less likely to experience periods of low flow or stream drying during the same period.

Since federal agencies such as the United States Geological Survey (USGS) and National Weather Service (NWS) began monitoring the Delaware River in 1903, only a handful of very large floods have occurred, although written accounts of other historic large floods can be found



from as early as the 1810's (Dale 1996). Some of these include flooding in the late summer due mainly to hurricanes such as occurred in 1903, 1955, 2004, and 2011; and flooding in the winter caused by a combination of ice dams and rain in February and March such as occurred in 1875, 1904, and 1981 (Dale 1996).

The interesting aspect of this study in relation to the region's ecological history with catastrophic floods is that the closely paired storms of 2011 greatly mimic the paired storms of 1955 – the region's largest recorded flood. In the late summer of 1955, Hurricane Connie moved up the Atlantic coast, making landfall in North Carolina as a Category 1 storm on August 12 (Namais and Dunn 1955). Hurricane Diane followed closely on August 17, also making landfall in North Carolina as a major hurricane with sustained winds of 193kmph. The paired hurricanes dropped more than 76cm of rain on the northeastern United States, causing massive flooding and loss of life and property from Pennsylvania to New Hampshire.

Using the USGS and NWS historic flow data to create a recurrence-interval there is an exceedingly small chance such storms will be duplicated. Based on two flow gages on the main stem of the Delaware and three smaller tributaries within DEWA, there is a 0.002-0.003 percent chance that an event greater than the 1955 flood will reoccur and a 0.006-0.01 percent chance an event greater than the 2011 flood will reoccur. Of course this does not mean such events do not happen over short intervals; these two historic storms were only 56 years apart with at least two other large floods in between. The U.S. Environmental Protection Agency's multi-decadal climate forecasts indicate a rise in the frequency of such large storms (USGCRP 2009). While the consequences of most large catastrophic floods are generally recorded in terms of destruction, loss of property, and loss of life, the ecological study of the 2011 flood can also be used to convey the effects of large storm events on the natural landscape.

## Data Collection Methods

For this study 83 stream reaches in 16 tributaries to the Delaware River were examined between 2011-2013. The 150m long study reaches were processed in the following manner. A global positioning system (GPS) point was recorded electronically and the latitude and longitude recorded manually at the beginning of each reach. Water chemistry was collected at the upper terminus of the reach using an Oakton Waterproof PCTester 35 Multiparameter Meter (Oakton Instruments, Vernon Hills, IL) and included pH, conductivity ( $\mu\text{S}/\text{cm}$ ), and temperature ( $^{\circ}\text{C}$ ). The device was pH calibrated each morning. Three wet-widths of the reach were recorded at roughly the upper, middle, and lower ends of the reach.

The reach was then divided into 50m increments marked with removable orange flags along the bank. At each 50m mark, substrate cross-section, forest composition, and forest condition were recorded. Substrate was divided into categories based on a modified Wentworth classification (Wentworth 1922) including silt/fine sand (up to 2mm diameter), coarse sand (2-10mm), gravel (11-100mm), cobble (101-300mm), boulder ( $>300\text{mm}$ ), and bedrock. The field team estimated percent composition of substrate material at each cross-section. Forest composition of the riparian was estimated on each bank based on percent of deciduous trees and coniferous trees; at the same time eastern hemlock (*Tsuga canadensis*) mortality was ranked on a scale of 0-4 based on percentage of standing dead hemlocks (0 = no hemlock; 1 = 0-10% hemlock mortality; 2 = 10-25% mortality; 3 = 25-50% mortality; 4 = 50-100% mortality).

Throughout the reach, large woody material (LWM) and mesohabitat composition were recorded. LWM was characterized by counts of debris that were 0.1-0.3m diameter at the large end, 0.3-0.8m diameter, or  $>0.8\text{m}$  diameter, and 1.5m-5m, 5-15m, or  $>15\text{m}$  in length (see Appendix A). Mesohabitat was classified as riffle, run, or pool habitat measured as length

segments of the stream, and was later calculated to percent composition. These data were collected from the stream banks to minimize in-stream disturbance before electrofishing. The same personnel took all visual measurements each year of the study.

Electrofishing in each reach was conducted with one or two LR-24 backpack electroshockers (Smith-Root, Inc., Vancouver, WA) depending on the wet width at the time of sampling. If two backpacks were necessary, they were used in tandem. Reaches were shocked in a single continuous pass with no block nets (Peterson et al. 2005; Reid et al. 2009). Fish were netted and placed in a bucket; buckets were exchanged every 50m and the bucket of fish from the previous section was labeled and left in the shade with an air bubbler until the reach was completed. Eighty-three such reaches were sampled in 2011; 24 reaches were resampled in both 2012 and 2013.

At the end of the reach, buckets from each section were collected. Non-salmonid fish species were identified, counted, and released; brown trout and rainbow trout were measured to fork length ( $\pm 1$ mm) and released. Brook trout were measured to fork length ( $\pm 1$ mm), weighed ( $\pm 0.1$ g), and a subsample of 30 individuals was anesthetized and had their anal fin clipped. Brook trout were allowed to recover fully in fresh water before being released. Fin clips were placed in Wattman paper and labeled with an individual ID number for later genetic analysis. These were then dried and stored in an airtight container with a desiccant drying pouch until the fin clips were analyzed. In 2011, 630 such genetic samples were collected, dried, and analyzed, followed by 487 in 2012, and 620 in 2013.

Genetic analysis was conducted at University of Massachusetts-Amherst and the Conte Anadromous Fish Research Center in Turners Falls, MA, during the six months following the field season in which the fin clips were collected. DNA was extracted from the fin clips

following standard DNA extraction protocols and amplification conditions (King, et al., 2005; also see Appendix B). DNA extracted from fin clips were amplified at eight microsatellite loci which were used in previous brook trout studies (Hudy et al. 2010, Kanno et al. 2011): *SfoC-113*, *SfoC-88*, *SfoD-100*, *SfoC-115*, *SfoC-129*, *SfoC-24* (King et al. 2003), *SsaD-237* (King et al. 2005). Capillary electrophoresis of loci was performed on an ABI Prism 3130xl genetic analyzer, and allele positions were determined using GENEMAPPER version 4 and PEAK SCANNER version 1.0 software (Applied Biosystems Inc., Foster City, California, 2006). Detailed laboratory protocols can be found in Appendix B.

### **Initial Results**

The stream temperature between streams was highly variable, including one groundwater fed stream that was significantly colder than the rest ( $p < 0.001$ ). Most streams fell between 18-20°C with outliers at 14.5°C (Conashaugh Creek) and 24.5°C (Hornbecks Creek). The coldest stream was likely groundwater influenced; half of the warmest stream reaches, including Hornbecks, were subject to the influence of upstream impoundments just outside the park boundary. Although the average for all stream reaches in the study area each year fell well within a healthy range for coldwater streams (18.7-19.2°C), eight reaches were consistently over 20°C during the study. Four of these eight warm reaches did not contain any cold water species, and the other four reaches were among the lowest abundance throughout the park.

Of the 24 repeated sites, only five were in conifer-dominant forest stands, generally eastern hemlock (*Tsuga canadensis*). The other 19 stream reaches were in heavily deciduous-dominant forest stands (Table 2). The more eastern hemlock present in the forest composition, the greater percent would be subject to hemlock mortality. Two sites, which were conifer-dominant stands, showed greater than 50% eastern hemlock mortality. Reaches in >75% deciduous forest stands were far less likely to have high hemlock mortality; 9 out of 14 (64%) of such stands had less

than 10% hemlock mortality. Hemlock woolly adelgid (*Adelges tsugae*) was the main cause of hemlock mortality throughout the park (Snyder et al. 2002).

**Table 2: Forest composition and eastern hemlock mortality in repeat-sampled sites. Measurements were only taken immediately prior to stream sampling in 2011.**

Site	% Conifer	% Deciduous	% Hemlock Mortality
Adams – 1	34	66	50-100%
Adams – 5	43	24	0-10%
Adams – 6	67	33	0-10%
Dingmans – 7	9	91	NA
Dingmans – 9	7	93	0-10%
Hellers – 25	73	27	25-50%
Hellers – 26	30	70	10-25%
VCB – 30	33	67	0-10%
VCB – 33	20	80	NA
VCB – 36	72	28	25-50%
Hornbecks – 42	42	58	10-25%
Conashaugh – 48	28	72	25-50%
Conashaugh – 50	62	38	50-100%
White – 52	7	93	NA
White – 53	13	87	NA
Fuller – 56	37	63	0-10%
Fuller – 57	25	75	0-10%
Caledonia – 66	23	77	10-25%
Caledonia – 67	7	93	0-10%
Dunnfield – 70	0	100	NA
Dunnfield – 73	25	75	25-50%
Dunnfield – 75	53	47	25-50%
Spackman – 77	20	80	10-25%
Spackman – 83	0	100	NA

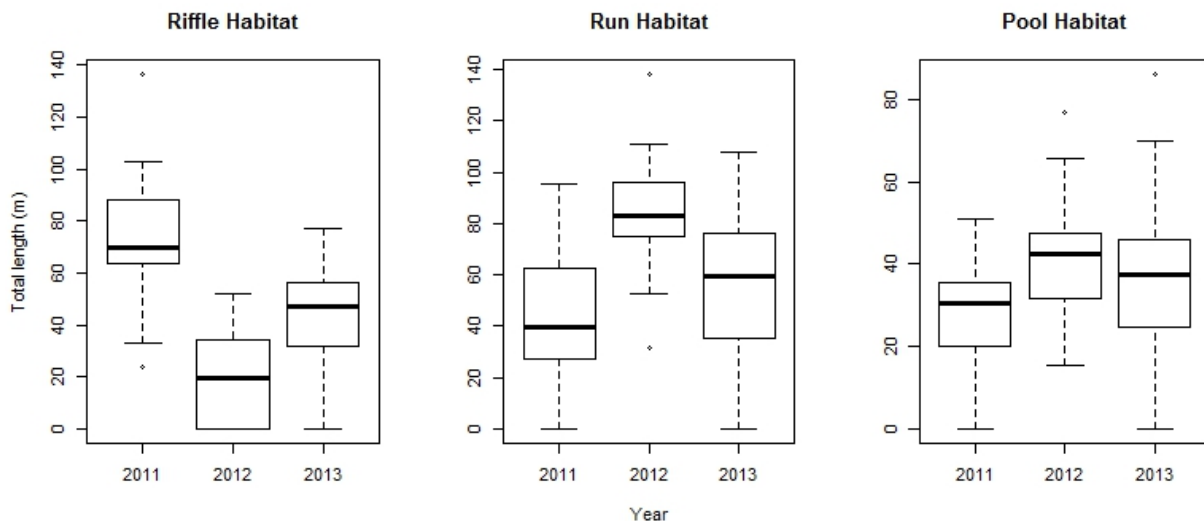
Large woody material (LWM) was analyzed for number of pieces and for estimated volume in each stream reach. Before the flood, streams generally ranged from 4-11 pieces of LWM per 150m reach (max = 20). The following year, much of the LWM was displaced by the flood (lower quantile = 3, upper quantile = 8, max = 15). By 2013 LWM had increased in all stream reaches with one site gaining over four times as many pieces (Table 3). Similarly, the volume of total LWM at that site increased over 400%. LWM volume in the rest of the study area mirrored LWM count: a reduction in volume the year after the flood, followed by a significant increase in 2013 (ANOVA:  $p = 0.04$ ).

**Table 3: Quantity and volume of large woody material in repeat-sampled sites over the course of the study.**

Site	2011		2012		2013	
	Count	Volume	Count	Volume	Count	Volume
1	1	2.4	3	5.03	11	12.16
5	13	3.2			11	13.8
6	3	4.8	5	3.45	2	4.75
7	11	12.6	14	15.03	22	31.59
9	1	0.1	2	0.2	2	0.87
25	8	9.2	8	5.36	35	27.57
26	20	15.1	7	11.36		
30	0	0.0	9	7.67	3	6.85
33	3	6.8	3	4.36	3	7.31
36	8	6.7	4	7.41	13	17.32
42	11	15.5			21	22.03
43			8	18.51		
45	0	0.0	6	9.64	5	11.6
48	0	0.0	3	1.65	2	0.2
50	11	10.8	0	0	16	13.13
52	5	5.5	5	2.06	1	0.31
53	11	8.8	6	8.27	5	6.18
56	6	5.6	0	0	2	0.87
57	19	12.1	10	7.93	8	9.16
66	4	0.8	13	1.96	13	8.57
67	2	0.6	2	0.2	5	0.93
70	4	6.9	5	2.06	8	10.04
73	5	6.1	1	0.77	3	1.4
75	10	8.9	11	4.49	18	19.41
77	11	11.2	1	2.38	14	25.41
78	0	0.0	6	19.54		
83	8	3.3			2	4.75

There were significant shifts in the mesohabitat of streams throughout Delaware Water Gap National Recreation Area between 2011 before the flood and 2012 after the flood (pool:  $p < 0.001$ , run:  $p = 0.01$ , riffle:  $p < 0.001$ ). Riffle habitat made up a large proportion of mesohabitat in most stream reaches throughout the park during the first year of the study, up to 73% of mesohabitat in some reaches. By the second year nearly all sites had decreased riffle habitat and mesohabitat was instead dominated by runs and pools. By 2013, the third year of the study, mesohabitat had shifted again towards a more equal composition of riffle, run, and pool habitats in most streams (Figure 3). All but three stream reaches regained riffle habitat and no single mesohabitat type comprised more than half the mesohabitat in any given reach.

**Figure 3: Meters of riffle, run, and pool habitat in 150m long stream sections. Yearly variation of habitat types were all significantly different (ANOVA, pool:  $p < 0.001$ , run:  $p = 0.01$ , riffle:  $p < 0.001$ ).**



The flood significantly altered the substrate composition throughout the park. Using a permutational multivariate analysis of variation (perMANOVA, vegan package, R), average substrate composition at each study site was analyzed for variation between years, rivers, study sites, and whether the site was an upstream or downstream reach. This initial analysis showed that substrate between rivers was the only source of significant variation ( $p < 0.01$ ). Secondary

analysis using reach location (upstream versus downstream) to stratify the data showed significant variation between years ( $p = 0.03$ ), rivers ( $p < 0.01$ ), and the combined effects of river and study site ( $p < 0.01$ ). The largest shift in substrate type was caused by the movement of cobble and gravel, particularly in downstream reaches.

Because of the timing of the field work and the flood, we were unable to quantify the loss of individuals from subpopulations immediately after the hurricanes passed over the area; however we are able to qualify some of the loss. In August 2011 we resampled three 150m sections in the same manner described above: Conashaugh 48, Conashaugh 50, and Adams 6. During the resample, we additionally inserted passive integrated transponder (PIT) tags into brook trout larger than 60mm (see Appendix B for full PIT tag methods). In total 154 fish were tagged: 53 brook trout from Adams 6, 27 brook trout from Conashaugh 48, and 74 brook trout from Conashaugh 50 (Table 4).

In late October 2011 I was allowed to return to the three sites with tagged fish and use a BioMark BP portable antenna (BioMark, Inc., Boise, ID) to identify the location of individual brook trout, scanning the original 150m sections plus 50-100m up- and downstream. At that time no tagged individuals were located in Conashaugh 48, two individuals were located in Conashaugh 50, and eight individuals were located in Adams 6. During the 2012 sampling, we used an Avid PowerTracker handheld scanner (Avid Identification Systems, Inc., Norco, CA) to attempt to find previously tagged individuals in those three sections and in the sections immediately downstream. At that time one tagged individual was located in Conashaugh 48, four tagged individuals were located in Conashaugh 48, and six tagged individuals were located in Adams 6. All recaptured brook trout were found in the section they were initially tagged. We did not scan for tagged fish in 2013.



**Table 4: PIT tagged brook trout in three 150m stream sections.**

Stream Section	Initial Capture – Aug 2011	Recapture – October 2011	Recapture – July 2012
Adams 6	53	4	6
Conashaugh 48	27	0	4
Conashaugh 50	74	1	1

Such a loss of the brook trout population should have remained apparent in population trends across the park’s landscape in the 2012 field season. However, few other subpopulations were affected as drastically as the three tagged sections above. Of the 24 sections resampled in 2012 only five had a net decrease in age 1+ brook trout – which would include adults and young-of-year that survived from 2011. Conashaugh 48 and 50 ranked as the two greatest decreases. Conversely, Conashaugh 48 also ranks as the third greatest increase of total population between 2011 and 2012.

## **Discussion**

Warming stream temperature is the main challenge presented by climate change to cold water streams and fish. Water temperature relates directly to cold water species' health, energetics, and overall resilience to other disturbances, and summer water temperature is a key threshold to consider (Beschta 1997; Boyd and Sturdevant 1997). Throughout DEWA, 38 of the original 83 stream reaches sampled were too warm to support cold water fish species. These reaches were not generally in open or deforested areas, but more often near the border of the park where water temperature might be more influenced by land use factors beyond the park's boundaries. For example, several stream reaches resampled during the study and which consistently were too warm, as noted above, were in the downstream influence of an impoundment. This agrees with the findings of Lessard and Hayes (2003) which showed that

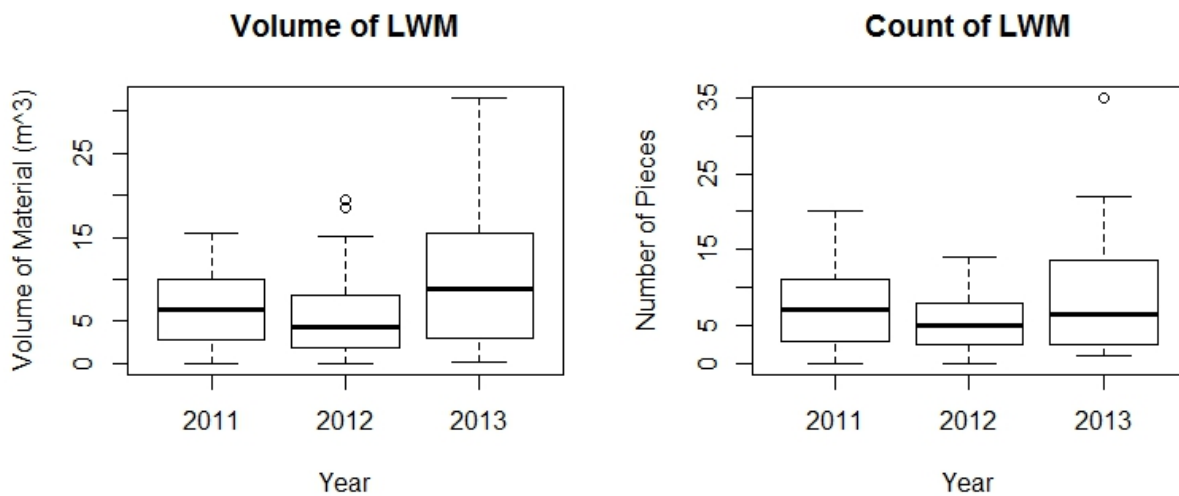
upstream impoundments can account for up to 5°C increase in cold water streams.

Six stream reaches were identified that are potentially influenced by cold groundwater seeps; these reaches remained under 17°C at the height of summer and could be highly localized. One such reach was located between two other reaches on the same stream that were 2-3°C warmer. Cold groundwater seeps play a vital role in cold water species survival and persistence during climate change (Torgersen et al. 2012). These cold seeps were not exclusive to upstream or downstream reaches and were found in both PA and NJ streams, but all reaches contained moderate to robust populations of brook trout.

The forest stands around study reaches reflect the history and changing conditions within the park. Once dominated by eastern hemlock and white pine forests, past logging operations left the landscape open to deciduous recolonization (Burgi et al. 2000) The dominant forest is now beech, red oak, and other deciduous hardwoods as eastern hemlock continue to decline due to the invasive hemlock wooly adelgid (Paradis et al. 2008). Ross et al. (2003) showed that such a change in forest type leads to changes in species composition, functional diversity, and trophic structure in streams throughout DEWA, and cautioned that continued eastern hemlock declines threaten cold water streams. The characterization of the forests around the current study reaches is congruent with previous findings and realizes the continued changes to the forest landscape over the last decade.

Changes to forests around streams have precipitated a shift in large woody debris in the DEWA headwater streams. The age and composition of the surrounding forest obviously impacts the size and type of LWM found in streams; LWM is also redistributed by floods – sometimes removed from a reach and sometimes adding to it by large debris dams. For instance, Dolloff et al. (1994) found a large increase in LWM after flooding caused by Hurricane Hugo in North

Carolina. The changes to in-stream LWM during the course of the study indicate a shift from more pieces of LWM that were generally smaller, 10-40cm diameter and 1.5-10m in length, in 2011 to fewer pieces of larger LWM, 40-100cm diameter and 5-15m long, in 2012. This was followed by a significant increase in the volume of LWM in 2013, a large portion of which was dead eastern hemlock trees (Figure 4). This lag in tree fall after the flood could have been the result of eastern hemlock mortality from the hemlock woolly adelgid combined with hillside destabilization caused by the storm.



**Figure 4: The number of pieces of in-stream large woody material (LWM) and volume of LWM throughout the Delaware Water Gap National Recreation Area preceding and following the flood.**

Such a significant restructuring of the size and quantity of LWM in streams has implications on both substrate and mesohabitat. Brooks et al. (2004) monitored the effects of engineered log jams and added woody debris on river morphology and substrate after a series of floods; LWM increased complexity through variable scouring and deposition, and helped retain finer substrate bed materials as compared to a control reach. Maintaining sand and gravel is an important factor in appropriate spawning conditions for salmonids as well as young-of-year survival throughout the winter and spring (Curry and MacNeill 2004). The changes to substrate

material after the flood in DEWA could not be linked to changes to LWM during the study years, but the 2013 increase in LWM will likely have continued effects on both the substrate and mesohabitat complexity.

The flood caused significant changes to stream mesohabitat throughout the park. This variation was not localized to any particular region within the park, stream, or reach location within a stream. Before the flood in 2011 most stream reaches displayed good habitat complexity, dominated slightly by riffle habitat. In 2012, after the flood, riffle habitat had decreased significantly while run and pool habitat both increased significantly, homogenizing the mesohabitat. The flood also exposed more bedrock, mostly in upstream reaches. Some stream complexity increased by 2013 as overall riffle habitat increased and there was more variation in all three types of habitat across the landscape. Increased habitat complexity is thought to be a component of increased species and guild diversity (Billman et al. 2012). Pearsons et al. (1992) also showed that habitat complexity increases community resilience after a flood. This is a good indicator of future resilience as both LWM and habitat complexity appear to be increasing, and also has positive associations with the resilience of current fish communities.

The amount of change in substrate seen after the 2011 flood in DEWA is not uncommon after large floods. Roghair et al. (2002) found that large stream sections had been entirely scoured in Shenandoah National Park after a flood and massive debris flow (see also Elwood and Waters, 1969). In less catastrophic cases, Dolloff et al. (1994) and Carline and McCullough (2003) both noted a significant shift from smaller sized substrate to a dominance of larger sized substrate material after large floods. The latter study particularly noted the lack of spawning gravel preferred by salmonids. However, gravel was not significantly reduced in DEWA in the years after the flood, which likely benefitted reproductive adults and increased species

recruitment in 2012.

Initial analysis of data across the landscape shows that the abundance of fish communities in nearly all stream reaches went through significant changes after the 2011 flood event. The loss of PIT tagged individuals indicates that larger adults may have been more susceptible to being displaced by the flood than smaller young of the year (YOY) trout. Displacement and loss of key adult brook trout may have released competition the following year and allowed significantly higher recruitment in 2012. Such a mechanism would help recovery and resilience of fish communities following such a disturbance assuming adequate resources are available. However, recruitment trends across the landscape were fairly consistent even after accounting for visually assessed differences in physical flood disturbance. The lack of difference between localized areas, especially between highly disturbed and minimally disturbed regions, may indicate that populations cycles synchronically increased throughout the park rather than being a result of flood disturbance. These trends will be discussed is more broadly below.

## **Conclusion**

The force of large floods, especially over prolonged periods of time, has catastrophic effects on a river and surrounding resources that can be mitigated or increased by the natural landscape. Once dominated by eastern hemlock-white pine forests, historic logging and the infestation of the invasive hemlock woolly adelgid beginning in 1989 altered most of the study sites in DEWA to hardwood dominated forest stands. Study sites were situated in mostly 2<sup>nd</sup>- and 3<sup>rd</sup>-order streams. Initial measurements of physical environmental characteristics in 2011 showed an abundance of good in-stream habitat, containing an average of seven pieces of LWM per study reach. Mesohabitat was predominantly riffle interspersed with run and pool habitat.

The late summer 2011 flood in DEWA caused significant changes to river structure and

habitat, and such changes continued for the following two years of the study. LWM was reduced to less than five pieces per reach, then in 2013 increased in both count and volume as standing dead eastern hemlock fell from eroded, unstable banks. Mesohabitat became more homogenous, dominated by long stretches of runs; and more bedrock was exposed within stream beds. By 2013, mesohabitat had begun to regain complexity, perhaps due in part to increases in LWM.

The physical changes documented in DEWA after the 2011 flood appear to be similar to disturbance documented in other previous flood studies, but the presence of so much hemlock mortality in riparian stands could continue to influence in-stream and riparian habitat. While falling dead hemlock may continue to destabilize and erode stream banks, such in-stream LWM contributes to the formation of pools, increased habitat complexity, and an abundance of detritivores and other invertebrates, all of which create excellent habitat for brook trout and other cold water fish.

The physical disturbance caused by the 2011 flood could have been detrimental to displacement and survival of some individuals within the brook trout population, as indicated by the loss of PIT tagged brook trout from their original study reaches. However, substrate composition, in-stream habitat, and LWM appear to be returning to baseline conditions as they were recorded before the flood. The additional LWM may continue to improve in-stream habitat beyond pre-flood conditions. The following chapters will help to illustrate the larger role the physical environment may have played in further brook trout population structure and dynamics in DEWA before and after the flood.

## References

- Albert, R.C. (2005). *Damming the Delaware: The rise and fall of Tocks Island Dam*. University Park, PA: Pennsylvania State University Press.
- Beschta, R. (1997). Riparian shade and stream temperature: an alternative perspective. *Rangelands*, 19(2), 25-28.
- Billman, E. J., Kreitzer, J. D., Creighton, J. C., Habit, E., McMillan, B., Belk, M. C. (2012). Habitat enhancement and native fish conservation: can enhancement of channel complexity promote the coexistence of native and introduced fishes? *Environmental Biology of Fishes*, 96(4), 555-566.
- Boyd, M., Sturdevant, D. (1997). The scientific basis for Oregon's temperature standard: common questions and straight answers. Oregon Department of Environmental Quality, Salem, OR.
- Brooks, A. P., Gehrke, P. C., Jansen, J. D., Abbe, T. B. (2004). Experimental reintroduction of woody debris on the Williams River, NSW: geomorphic and ecological responses. *River Research and Applications*, 20(5), 513-536.
- Burgi, M., Russell, E.W.B., Motzkin, G. (2000). Effects of post-settlement human activities on forest composition in the north-eastern United States: A comparative approach. *Journal of Biogeography*, 27(5), 1123-1138.
- Curry, R. A., MacNeill, W. S. (2004). Population-level responses to sediment during early life in brook trout. *Journal of the North American Benthological Society*, 23(1), 140-150.
- Dale, F. (1996). *Delaware Diary: Episodes in the life of a river*. New Brunswick, NJ: Rutgers University Press.
- Dolloff, C., Flebbe, P., Owen, M. (1994). Fish habitat and fish populations in a southern Appalachian watershed before and after Hurricane Hugo. *Transactions of the American Fisheries Society*, 123(4), 668-678.
- Elwood, J. W., Water, T. F. (1969). Effects of flood on food consumption and production rates of a stream brook trout population. *Transactions of the American Fisheries Society*, 98(2), 253-262.
- Epstein, J. B. (1966). Structural control of wind gaps and water gaps and of stream capture in the Stroudsburg area, Pennsylvania and New Jersey. *US Geological Survey Professional Paper*, 550, B80-B86.
- Epstein, J. B. (2006). Geology of Delaware Water Gap National Recreation Area, New Jersey–Pennsylvania. *Field Guides*, 8, 47-63.
- Hudy, M., Coombs, J. A., Nislow, K., Letcher, B. H. (2010). Dispersal and within-stream spatial population structure of brook trout revealed by pedigree reconstruction analysis. *Transactions of the American Fisheries Society*, 139(5), 1276-1287.
- Kanno, Y., Vokoun, J., Letcher, B. H. (2011). Fine-scale population structure and riverscape genetics of brook trout (*Salvelinus fontinalis*) distributed continuously along headwater channel networks. *Molecular Ecology*, 20(18), 3711-3729.
- King, T. L., Julian, S. E., Coleman, R. L., Burnham-Curtis, M. K. (2003). Isolation and characterization of novel tri- and tetranucleotide microsatellite DNA markers for brook trout *Salvelinus fontinalis*: GenBank submission numbers AY168187, AY168192, AY168193, AY169194, AY168195, AY169197, AY168199. Available: [ncbi.nlm.nih.gov/nucleotide/](http://ncbi.nlm.nih.gov/nucleotide/). (February 2010).

- King, T. L., Eackles, M. S., Letcher, B. H. (2005). Microsatellite DNA markers for the study of Atlantic salmon (*Salmo salar*) kinship, population structure, and mixed-fishery analysis. *Molecular Ecology Notes*, 5(1), 130-132.
- Lessard, J.L., Hayes, D.B. (2003). Effects of elevated water temperature on fish and macroinvertebrate communities below small dams. *River Research and Applications*, 19(7), 721-732.
- Mellina, E., Moore, R.D., Hinch, S.G., Macdonald, J.S., Pearson, G. (2002). Stream temperature responses to clearcut logging in British Columbia: the moderating influences of groundwater and headwater lakes. *Canadian Journal of Fish and Aquatic Sciences*, 59, 1886-1900.
- Namais, J., Dunn, C. (1955). The weather and circulation of August 1955: Including the climatological background for hurricanes Connie and Diane. *Monthly Weather Review*, August, 163-183.
- Paradis, A., Elkington, J., Hayhoe, K., Buonaccorsi, J. (2008). Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. *Mitigation and Adaptation Strategies for Global Change*, 13(506), 541-554.
- Pearsons, T., Li, H., Lamberti, G. (1992). Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. *Transactions of the American Fisheries Society*, 121(4), 427-436.
- Peterson, J., Banish, N., Thurow, R. (2005). Are block nets necessary?: Movement of stream-dwelling salmonids in response to three common survey methods. *North American Journal of Fisheries Management*, 25(2), 732-743.
- Reid, S., Yunker, G., Jones, N. (2009). Evaluation of single-pass backpack electric fishing for stream fish community monitoring. *Fisheries Management and Ecology*, 16(1), 1-9.
- Ridge, J., Evenson, E.B., Sevon, W.D. (1992). A model of late quaternary landscape development in the Delaware Valley, New Jersey and Pennsylvania. *Geomorphology*, 4(5), 319-345.
- Roghair, C., Dolloff, C., Underwood, M. (2002). Response of a brook trout population and instream habitat to a catastrophic flood and debris flow. *Transactions of the American Fisheries Society*, 131(4), 718-730.
- Ross, R. M., Bennett, R. M., Snyder, C. D., Young, J. A., Smith, D. R., Lemarie, D. P. (2003). Influence of eastern hemlock (*Tsuga canadensis* L.) on fish community structure and function in headwater streams of the Delaware River basin. *Ecology of Freshwater Fish*, 12, 60-65.
- Scarnecchia, D.L., Bergersen, E.P. (1987). Trout production and standing crop in Colorado's small streams, as related to environmental features. *North American Journal of Fisheries Management*, 7(3), 315-330.
- Sharpe, D. (2012). Variations in river longitudinal profiles along the Kittatinny Ridge, Appalachian Mountains. *Geological Society of America Abstracts with Programs*, 44(7), 417.
- Snyder, C. D., Young, J. A., Lemarie, D. P., Smith, D. R. (2002). Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams. *Canadian Journal of Fisheries and Aquatic Sciences*, 59, 262-275.
- Torgersen, C. E., Ebersole, J. L., Keenan, D. M. (2012). Primer for identifying cold-water refuges to protect and restore thermal diversity in riverine landscapes. United States Environmental Protection Agency, Office of Water and Watersheds, EPA 910-C-12-001.



USGCRP (2009). *Global Climate Change Impacts in the United States*. Karl, T. R., J. M. Melillo, and T. C. Peterson (eds.). United States Global Change Research Program. Cambridge University Press, New York, NY, USA.

## Appendix A – Field Collection Datasheets

Sheet 1: Physical habitat including substrate transects, forest stand composition, and large woody debris tally.

Site:

Date:

Data collector:

Wetted width (m):

	Transect (m)						
	0	25	50	75	100	125	150
	Substrate (within 0.5m upstream/downstream of each transect)						
Clay/silt (%)							
Sand (%)							
Gravel (%)							
Cobble (%)							
Boulder (%)							
Bedrock (%)							
	Forest type/condition: stream-right (within 5m upstream/downstream of each transect and 10m depth)						
Coniferous (%)							
Deciduous (%)							
Hemlock mortality: 0-10%							
Hemlock mortality: 10-25%							
Hemlock mortality: 25-50%							
Hemlock mortality: >50%							
	Forest type/condition: stream-left (within 5m upstream/downstream of each transect and 10m depth)						
Coniferous (%)							
Deciduous (%)							
Hemlock mortality: 0-10%							
Hemlock mortality: 10-25%							
Hemlock mortality: 25-50%							
Hemlock mortality: >50%							

### Large woody debris tally

(> 10 cm small end diameter  
and > 1.5 m length)

Diameter large end	L = 1.5 - 5m	5 - 15 m	> 15 m
0.1 to < 0.3 m			
0.3 - 0.8 m			
> 0.8 m			



## Appendix B – Detailed Genetic Laboratory Protocol

### I. Genomic DNA Extraction Protocol

#### Step 1

*Preparation:*

Prepare 48 1.5mL microcentrifuge tubes, labeled with sample identifiers.

Add (500 $\mu$ L of Cell Lysis Buffer) x (number of individuals + 3) to 50mL conical tube.

Add (3 $\mu$ L of Proteinase K) x (number of individuals) to cell lysis solution

\*Thaw proteinase K in hand. As ice melts, gently flick the sample.

Utensil rinse = One (1) 5-mL conical tube of 10% bleach and two (2) 50ml conical tubes of deionized (DI) water

*Procedure:*

Remove dry tissue samples from filter paper in tiny pieces and place them in prepared 1.5mL microcentrifuge tubes.

\*Close tubes tightly, do not use tubes that pop open.

\*If the tissue is cut into very small pieces it will digest quickly; if it is left in larger pieces it will still digest, but it will take longer and will require more vortexing throughout the digestion process.

Thoroughly rinse utensils between each sample in 10% bleach followed by two rinses in DI water.

Add 500 $\mu$ L of cell lysis + proteinase K to each 1.5mL tube containing tissue

Incubate at ~55°C approximately 24 hours until all of the tissue is dissolves.

\*The process can be sped up by vortexing the samples every 30 minutes or so.

\*Make sure tissue is well digested. The next day, more proteinase K (~1-2 $\mu$ L per sample) can be added if need be.

---

#### Step 2

*Preparation:*

Label a second set of empty 1.5mL microcentrifuge tubes as before. Add 500 $\mu$ L 100% isopropanol and store in freezer for Step 3.

Obtain and pour Protein Precipitation Solution (Ammonium Acetate 7.5M) into 50mL conical tube

Prepare ice block

*Procedure:*

Remove digested samples from incubator and place in ice block. Flick tubes to break up tissue if needed

Add 168 $\mu$ L of Protein Precipitation Solution (Ammonium Acetate 7.5M) to each sample

Vortex each sample for 20 seconds; thorough mixing is very important.

\*vortex setting ~6: samples should look milky white

Place samples back on ice while you go through all the tubes

---

### Step 3

#### *Preparation:*

Obtain and prepare labeled waste beakers: liquid and tips

#### *Procedure:*

Remove samples from ice and centrifuge at 13,000RPM for 6 minutes

Remove second set of microcentrifuge tubes of 100% isopropanol prepared during the previous step from freezer.

Transfer supernatant from centrifuged tubes to tubes with isopropanol

\*Don't wait too long to do this step as the pellet can loosen

\*Discard the tubes containing the protein pellets.

Invert tubes gently ~50 times. Mixing at this step is extremely important, but do not vortex.

Place samples in freezer for ~1 hour.

\*You should be able to see whitish globs floating in your tubes before you proceed

\*If you cannot see the DNA at this point, you need to invert tubes again and leave them in the freezer for another hour, or consider that your DNA concentration is very low and more tissue should be used.

---

### Step 4

#### *Preparation:*

Obtain and pour 70% ethanol into 50mL conical tube

Fold ~2ft length piece of paper towel in half and lay on bench top. One will be used to lay out the samples when you decant the isopropanol supernatant and the other will be used when you lay out the samples when you decant the ethanol supernatant

#### *Procedure:*

Remove samples from freezer and centrifuge at 13,000RMP for 3 minutes

Pour off and discard supernatant very carefully; do not lose the DNA pellet

Blot each tube on paper towel and lay tubes on towel as you go through the samples

Add 500 $\mu$ L of 70% ethanol to each sample

Invert tubes GENTLY several times to wash pellet

\*Do not vortex. Pellet may or may not dislodge, it is not essential that it does

Centrifuge at 11,000RPM for 8 minutes

Pour off and discard supernatant very carefully; do not lose the DNA pellet

Remove excess EtOH by pressing the rim of the tube onto a paper towel.

Keep the tubes on their side on the paper towel and allow to dry.

---

### Step 5

#### *Preparation:*

Obtain TE solution (elution buffer)

Group samples by similar pellet size, see rough classes below:

(small) size 1 – add 50 $\mu$ L of TE

(medium) size 2 – add 75µL of TE

(large) size 3 – add 100µL of TE

When you are sure that the samples are COMPLETELY DRY, rehydrate with the appropriate volume of TE and leave at room temp overnight.

Store DNA samples in -20°C freezer the next morning.

## II. PCR Reagent-Primer Recipe

BKT MasterMix 1 - Group 1					No. of Samples		100
	Stock Conc		Final Conc		Volume		Rxn 2
dH2O	***		***		2.7	<b>dH2O</b>	<b>270</b>
X Buffer	10	X	1	X	1	<b>X Buffer</b>	<b>100</b>
MgCl2	25	mM	2	mM	0.8	<b>MgCl2</b>	<b>80</b>
dNTPs	10	mM	0.25	mM	1	<b>dNTPs</b>	<b>100</b>
PRIMER 1 F	5	uM	0.45	uM	0.8	<b>C113 F</b>	<b>80</b>
PRIMER 1 R	5	uM	0.45	uM	0.8	<b>C113 R</b>	<b>80</b>
PRIMER 2 F	5	uM	0.45	uM	0.9	<b>D 75 F</b>	<b>90</b>
PRIMER 2 R	5	uM	0.45	uM	0.9	<b>D 75 R</b>	<b>90</b>
Taq Pol	5	units/ul	0.05	units/ul	0.1	<b>Taq Pol</b>	<b>10</b>
DNA	100	ng/ul			1	<b>DNA</b>	<b>100</b>
<b>TOTAL</b>					<b>10</b>		1000

BKT MasterMix 1 - Group 2					No. of Samples		100
	Stock Conc		Final Conc		Volume		Rxn 2
dH2O	***		***		2.7	<b>dH2O</b>	<b>270</b>
X Buffer	10	X	1	X	1	<b>X Buffer</b>	<b>100</b>
MgCl2	25	mM	2	mM	0.8	<b>MgCl2</b>	<b>80</b>
dNTPs	10	mM	0.25	mM	1	<b>dNTPs</b>	<b>100</b>
PRIMER 1 F	5	uM	0.45	uM	1	<b>C 88 F</b>	<b>100</b>
PRIMER 1 R	5	uM	0.45	uM	1	<b>C 88 R</b>	<b>100</b>
PRIMER 2 F	5	uM	0.45	uM	0.7	<b>D 100 F</b>	<b>70</b>
PRIMER 2 R	5	uM	0.45	uM	0.7	<b>D 100 R</b>	<b>70</b>
Taq Pol	5	units/ul	0.05	units/ul	0.1	<b>Taq Pol</b>	<b>10</b>
DNA	100	ng/ul			1	<b>DNA</b>	<b>100</b>
<b>TOTAL</b>					<b>10</b>		1000

<b>BKT MasterMix 2 - Group 1</b>						<b>No. of Samples</b>	100
<b>Stock Conc</b>			<b>Final Conc</b>		<b>Volume</b>		<b>Rxn 2</b>
dH2O	***		***		3.1	<b>dH2O</b>	<b>310</b>
X Buffer	10	X	1	X	1	<b>X Buffer</b>	<b>100</b>
MgCl2	25	mM	2	mM	0.8	<b>MgCl2</b>	<b>80</b>
dNTPs	10	mM	0.25	mM	1	<b>dNTPs</b>	<b>100</b>
PRIMER 1 F	5	uM	0.45	uM	0.8	<b>C 24 F</b>	<b>80</b>
PRIMER 1 R	5	uM	0.45	uM	0.8	<b>C 24 R</b>	<b>80</b>
PRIMER 2 F	5	uM	0.45	uM	0.7	<b>C 129 F</b>	<b>70</b>
PRIMER 2 R	5	uM	0.45	uM	0.7	<b>C 129 R</b>	<b>70</b>
Taq Pol	5	units/ul	0.05	units/ul	0.1	<b>Taq Pol</b>	<b>10</b>
DNA	100	ng/ul			1	<b>DNA</b>	<b>100</b>
<b>TOTAL</b>					<b>10</b>		<b>1000</b>

<b>BKT MasterMix 2 - Group 2</b>						<b>No. of Samples</b>	100
<b>Stock Conc</b>			<b>Final Conc</b>		<b>Volume</b>		<b>Rxn 2</b>
dH2O	***		***		2.3	<b>dH2O</b>	<b>230</b>
X Buffer	10	X	1	X	1	<b>X Buffer</b>	<b>100</b>
MgCl2	25	mM	2	mM	0.8	<b>MgCl2</b>	<b>80</b>
dNTPs	10	mM	0.25	mM	1	<b>dNTPs</b>	<b>100</b>
PRIMER 1 F	5	uM	0.45	uM	0.7	<b>C 115 F</b>	<b>70</b>
PRIMER 1 R	5	uM	0.45	uM	0.7	<b>C 115 R</b>	<b>70</b>
PRIMER 2 F	5	uM	0.45	uM	1.2	<b>D 237 F</b>	<b>120</b>
PRIMER 2 R	5	uM	0.45	uM	1.2	<b>D 237 R</b>	<b>120</b>
Taq Pol	5	units/ul	0.05	units/ul	0.1	<b>Taq Pol</b>	<b>10</b>
DNA	100	ng/ul			1	<b>DNA</b>	<b>100</b>
<b>TOTAL</b>					<b>10</b>		<b>1000</b>

### III. PCR Steps

Programed steps for polymerase chain reaction for DNA amplification in an MJ Research PTC DNA Engine Dyad (Waltnam, MA):

1. Incubate at 94°C for 2 min
2. Incubate at 94°C for 45sec
3. Incubate at 56°C for 45sec
4. Incubate at 72°C for 2 min
5. Cycle steps 2-4 for 34 more times
6. Incubate at 72°C for 10 min
7. Store at 6°C forever

## **Chapter 3**

### **Changes in brook trout population occupancy, abundance, and size structure following a massive flood**

#### **Abstract**

In late August 2011 a pair of large storms, Hurricane Irene and Tropical Storm Lee, passed over the Delaware Water Gap National Recreation Area in eastern Pennsylvania and western New Jersey. The storms collectively dropped over 33cm of precipitation on the park which created massive flows through much of the region. This study encapsulates the stream community, abundance, and response of brook trout in ten streams across the landscape the year before and two years following the 2011 flood event. Age 1+ brook trout abundance remained steady while young-of-year (YOY) trout abundance increased up to 840%, particularly in isolated reaches upstream of large natural barriers. While most species responded to the flood with increased abundance across the landscape, brook trout populations showed little to no population growth in well-connected downstream locations in tributaries with high community diversity. Brook trout size and cohort structure was highly skewed during the two years after the flood and significantly reduced the mean and median trout length. These findings may demonstrate the initial stages of a cold water to warm water regime shift due to climate change in peripheral populations of brook trout.



## Introduction

Climate change results in warmer air and water temperatures in many parts of the world which can lead to species range shifts, facilitate an increase in invasive species, and increase the likelihood of large storm events (Eaton and Scheller 1996; Poff 2002; Paradis et al. 2007).

Singly, any of these changes have been known to disrupt native species; combined, these changes may have significant consequences for the long-term stability and persistence of some native species, such as the eastern brook trout (*Salvelinus fontinalis*). Brook trout rely on cold water stream habitat, which is threatened throughout the northeastern United States. Notable changes to stream temperature have been documented as well as a regional increase in precipitation (Groisman et al. 2004; Kaushal et al. 2010). Both trends are expected to continue in the coming decades. Species such as eastern brook trout that are declining over much of their original habitat as streams warm and experience greater competition for stream resources from generalist and warm water tolerant fish able to colonize new reaches (EBTJV 2006; Hudy et al. 2008).

Small, regular floods are a necessary and healthy component of lotic systems, but large floods are spatially and temporally unpredictable, as are the ways stream ecosystems respond to them (Reice et al. 1990). This also makes the ecological effects of floods difficult to quantify. Matthews (1986) reported little change to stream community composition and increased species abundance after a large 1982 flood in the Ozarks. After a winter and spring flood in Monongahela National Forest in early 1996, young-of-year trout were reduced by 98% and adult trout by 84% (Carline and McCullough 2003).

In late August and early September 2011, Hurricane Irene and Tropical Storm Lee passed through the Delaware Water Gap National Recreation Area (DEWA; Figure 1) of Pennsylvania and New Jersey as well as much of the northeastern United States. The flood was one of the

largest recorded in that area and resulted in two sustained flood-stage peaks approximately 10 days apart as recorded by US Geological Survey gaging stations located in and around DEWA; I will refer to these paired events as a single flood from here on forward.

Before the flood, a brook trout tagging study and population survey was being conducted throughout the park; the resulting shifts in brook trout population dynamics and demographic structure are presented here. Early expectations following the 2011 flood were that most brook trout populations would be washed out during the repeated high flows and lead to an overall decreased abundance within brook trout populations due to loss of age 1+ brook trout and subsequent lost reproductive potential. This study examines fish communities in twenty-four tributary reaches across the park's landscape in the year before and for two years after the 2011 flood (Figure 1). In particular, I looked at the interaction between warming stream temperatures, encroaching generalist communities, and the flood on the abundance and resilience of brook trout populations. I hypothesize that, in this region, fish community richness and diversity, as measured by the Shannon Index, limit brook trout abundance and reduce brook trout population resilience – or the ability of a population to “absorb changes of state variables, driving variables, and parameters, and still persist” (Holling 1973) – in response to the 2011 flood.

Most similar to the current study, Dolloff et al. (1994) completed a basin-wide fish and habitat survey of the Basin Cove watershed along the Blue Ridge Parkway in North Carolina just before Hurricane Hugo spurred a large flood in September 1989. That flood resulted in significant homogenization and scouring of stream habitat; there was very little change in species composition, and many common species saw an increase in population abundance throughout the study area. However, the only salmonids in the Basin Cove watershed were rainbow trout (*Oncorhynchus mykiss*), which spawn in the spring and are more severely affected by large

spring floods than fall floods (Warren et al. 2009; Meyers et al. 2010). In that study, young-of-year (YOY) rainbow trout density increased in downstream reaches and overall abundance in the landscape remained similar to pre-flood records.

Many studies that examine the effects of floods on salmonids note that the timing of the flood is an important factor in how the abundance of different ages and species of fish are affected (Hoopes 1975; Ottoway and Clark 1981; Carline and McCullough 2003; Meyers et al. 2010). High flows, especially in spring, severely reduce fry survival (Ottoway and Clark, 1981). Winter and spring floods scour redds and severely decrease young-of-year recruitment (Carline and McCullough 2003). Hoopes (1975) found that young-of-year brook trout (*Salvelinus fontinalis*) were reduced by 96% after a large June flood, while other year classes were far less impacted. Changes in climate that would favor larger storm events in the late summer and fall would be detrimental to fall-spawning of adult brook trout (Meyers et al. 2010).

Cold water fish species such as brook trout face an increasing amount of edge habitat – stream habitat where water temperatures gradually but regularly reach the upper limit of brook trout tolerance (Wenger et al. 2011). Edge effects generally result in the decline of species losing habitat to the edge permeability, in this case thermal permeability, while other species gain from their ability to permeate new habitat. This loss and gain can lead to long-term shifts in community and population dynamics (Ries et al. 2004). When streams are viewed in this way, with the temperature gradient acting as the “edge”, decreased thermal habitat suitability and increased negative interactions between species at the edge of cold water and warm water habitat occur. Although brook trout interactions with other salmonids have been studied (Whitworth and Strange 1983; Hearn 1987; Carlson et al. 2007; Korsu et al. 2009), no studies have measured

brook trout interactions within a more diverse community setting – possibly because cold water brook trout habitat is not optimal habitat for many other fish species.

Ecological regime shifts tend to happen over long temporal periods identified after the shift has been initiated (Ripple and Beschta 2006; Poff and Allan 1995; Helle and Hoffman 1998). Climate change is already creating a slowly shifting habitat edge for peripheral populations (Haak et al. 2010) of cold water species. Given spatial and thermal constraints, cold water communities may presently be undergoing such a change as downstream limits continue to warm and allow generalist fish species the opportunity to infiltrate and out-compete extant communities in connected riverscapes. A large sustained flood, such as the 2011 flood event in DEWA, disturbs physical habitat while potentially displacing individuals, reducing overall abundance, or disrupting spawning events, all of which opens unoccupied edge habitat to other infiltrating fish species.

## **Methods**

The Delaware Water Gap National Recreation Area consists of over 28,000 hectares surrounding the Delaware River from Montague, NJ at the north end of the park to Delaware Water Gap, PA at the south end. In 2011, during the first year of the study, 83 reaches on 16 tributaries to the Delaware River were selected for electrofishing surveys based on NPS survey prioritization (R. Evans, DEWA NPS ecologist, personal communication). Streams in DEWA are highly fragmented by natural barriers often greater than 3m high. Twenty-four of these original 83 sites were selected for resampling in 2012 and 2013 (Figure 1) based on 2011 brook trout presence and on initial visual estimates of physical disturbance caused by the flood in order to create a post-hoc modified before-after-control-impact design.

Each of the 83 study reaches were 150m long and were processed in the following manner. A global positioning system (GPS) point was recorded electronically and the latitude and longitude recorded manually at the beginning of each reach. Water chemistry was collected at the upper terminus of the reach using an Oakton Waterproof PCTester 35 Multiparameter Meter (Oakton Instruments, Vernon Hills, IL) and included pH, conductivity ( $\mu\text{S}/\text{cm}$ ), and temperature ( $^{\circ}\text{C}$ ). The device was pH calibrated at the beginning of each field day. Three wet-widths of the reach were recorded at roughly the upper, middle, and lower ends of the reach.

Reaches were then subdivided into 50m increments marked with removable orange flags along the bank. At each 50m mark a substrate cross-section was measured, and forest composition and forest condition were estimated. Substrate cross-section was divided into categories based on a modified Wentworth classification (Wentworth 1922) including silt/fine sand (up to 2mm diameter), coarse sand (2-10mm), gravel (11-100mm), cobble (101-300mm), boulder ( $>300\text{mm}$ ), and bedrock. Percent composition of substrate material was estimated at each cross-section. Forest composition was estimated on each bank based on percent of deciduous trees and coniferous trees; at the same time eastern hemlock (*Tsuga canadensis*) mortality was ranked on a scale of 0-4 based on percentage of standing dead hemlocks (0 = no hemlock presence; 1 = 0-10% hemlock mortality; 2 = 10-25% mortality; 3 = 25-50% mortality; 4 = 50-100% mortality).

Throughout each reach, large woody material (LWM) and mesohabitat composition were recorded. LWM was characterized by counts of debris that were 0.1-0.3m diameter, 0.3-0.8m diameter, or  $>0.8\text{m}$  diameter at the large end, and 1.5m-5m, 5-15m, or  $>15\text{m}$  in length (see Appendix A). Mesohabitat was classified into riffle, run, or pool categories; each habitat unit was measured and later calculated as percentage of habitat composition within the reach. These data

were collected from the stream banks to minimize in-stream disturbance before electrofishing. The same personnel took all visual measurements each year of the study.

Electrofishing in each reach was conducted with one or two LR-24 backpack electroshockers (Smith-Root, Inc., Vancouver, WA) depending on the wet width at the time of sampling. If two backpacks were necessary, they were used in tandem. Reaches were shocked in a single continuous pass with no block nets (Peterson, et al., 2005; Reid, et al., 2009). Fish were netted and placed in a bucket; buckets were exchanged every 50m and the bucket of fish from the previous section was labeled and left in the shade with an air bubbler until the reach was completed.

A further passive integrated transponder (PIT) tag study began in 2011 at three study reaches chosen for abundant brook trout populations. At these three sites, electrofishing took place again approximately eight weeks after the initial electrofishing sample beginning using the same methods and beginning at the same point in the stream. At the end of the 150m reach 30 brook trout over 60mm long were anaesthetized. A 12mm PIT tag was inserted into the abdominal cavity of each fish, which was then put in a bucket of fresh water to recover before being replaced in the stream.

To relocate PIT tagged fish, I walked the study stream with a BP portable antenna (Biomark, Boise, ID) once a month for three months following the August/September 2011 flood. During the 2012 field season, all sampled brook trout were scanned with a Power Tracker V handheld PIT tag scanner (AVID Identification Systems, Norco, CA) during data collection and any PIT tag IDs were recorded.

I calculated community abundance, richness, and Shannon diversity (H) at each site for each year. To test for initial differences in community composition between sites and years I used

a dissimilarity matrix in a permutational multivariate analysis of variance (perMANOVA; vegan package in R). I modeled brook trout population abundance relative to Shannon diversity, year, and reach location as defined by being upstream or downstream of a natural barrier in the landscape. I also used analysis of variation (ANOVA) to compare site abundance, richness, and diversity between years, upstream or downstream reach location, stream temperature, and brook trout abundance.

For all age and size analysis, brook trout were divided into two size-related age classes: young of the year (YOY) and age 1+ fish. Age groups were determined for each year based on breaks in the size distribution of the metapopulation across the entire park (Figure 2). YOY typically were <96mm in length; age 1+ fish were all other brook trout >97mm and could potentially be reproductively active in the fall spawning season of that year.

## **Results**

In the months immediately following the flood, six tagged fish were found in the three PIT tagged study sections using the portable antenna; eleven fish tagged in 2011 were recaptured during the summer 2012 sampling. These recaptured brook trout account for only 5% of tagged individuals one to three month after initial capture and fewer than 10% of individuals were recaptured up to one year after initial tagging. Of the recaptured fish, one was a surviving 2011 YOY; all others were 105-173mm long when first captured in 2011 (Table 1). Growth amongst these individuals was moderate, averaging 38mm and 24.4g (SD = 14.4mm and 13.3g).

The loss of the brook trout population in the three reaches indicated by the remnants of the PIT tag study were localized and do not seem to have affected populations throughout the park with the same severity. In much of the rest of DEWA age 1+ brook trout abundance showed little change or even increased slightly. Of the resampled reaches in 2012 only five populations

had a net decrease in age 1+ brook trout. Because tagged fish were not caught in any other sampled section, it is not known if they were displaced to other areas of the stream or if there was high mortality after the flood. Based on the abundance of age 1+ brook trout in PIT tagged sections and non-tagged sections the greatest loss of age 1+ fish was in the northwest region of the park where the PIT tag streams were located.

Across the landscape, upstream reaches above barriers tended to be colder and have less diverse fish communities than downstream reaches which were warmer and had a more diverse fish community. Diversity was significantly lower in reaches upstream of large natural barriers throughout the park (F model = 3.95,  $p = 0.001$ ). Increased diversity was almost exclusively due to the presence of warm water and generalist fish species such as fallfish (*Semotilus corporalis*) and largemouth bass (*Micropterus salmoides*) (Table 2). Stream temperature was generally warmer in downstream reaches and correlated well with community richness (F = 9.295,  $p = 0.003$ ;  $r^2 = 0.34$ ).

Abundance of most reproductively sustaining species populations increased the year following the flood. Total abundance in both generalist and brook trout communities rose as much as 900% in some reaches between 2011 and 2012 ( $t = -2.75$ ,  $p = 0.01$ ; Figure 2). Increased species abundance was limited to species with more than five individuals in a reach. Species with few adult fish in the study area generally did not experience the same trend, and some species with very low abundance were absent from previous locations entirely after the flood.

All subpopulations throughout DEWA experienced a marked increase in brook trout abundance in 2012, the summer immediately following the 2011 flooding (paired t-test,  $t = -2.75$ ,  $df = 23$ ,  $p = 0.01$ ). Abundance throughout the park increased 193% from the previous year and individual subpopulation abundance increased from 23% to 963% (Figure 2).



YOY brook trout accounted for the dramatic increase in population abundance. In 2011, YOY represented 20%-45% of individuals in most subpopulations (Figure 3). In 2012, YOY abundance increased significantly ( $t = -3.29$ ,  $p = 0.003$ ) and accounted for the majority of individuals at a site, often as much as 80%-95% of a subpopulation (Table 3). By 2013, total population abundance declined slightly from the 2012 peak, but YOY recruitment remained significantly higher than before the flood ( $t = -2.06$ ,  $p = 0.05$ ).

The flood did not significantly alter community richness or diversity. Although several generalist species were extirpated from several study sites after the 2011 flood, the trend was neither strong nor consistent across sites (Figure 4). Brook trout experienced no extirpation from previously occupied sites in the years following the flood, and one site was briefly colonized by a single adult.

The flood greatly altered the mean and median size of fish within the study area. There was a substantial reduction in the density of larger age 1+ brook trout while number and density of YOY increased significantly ( $t = -4.74$ ,  $p < 0.001$ ). This change in size shifted the length distribution in the population and created a distinct break between cohort years in 2012 and 2013 (Figure 5). Kolmogorov-Smirnov tests to compare distributions of fish length showed that length distributions were significantly greater in 2012 ( $D = 0.46$ ,  $p < 0.001$ ), then was significantly reduced the following year ( $D = 0.31$ ,  $p < 0.001$ ). Average length of YOY brook trout decreased from 72.5mm (SD = 11.3mm) in 2011 to 65mm (SD = 8.4mm) in 2012 and did not increase much in 2013 rising to only 65.6mm (SD = 8.9mm). Both YOY and age 1+ brook trout length changed significantly over the years (both age classes,  $p < 0.001$ ) and the break between size classes, typically at 96mm, shifted downwards in 2013 cohorts to 92mm.

Brook trout abundance was negatively related to the diversity of the whole fish community of the stream reach. This effect was particularly noticeable when comparing fish communities in upstream and downstream reaches. In this highly fragmented landscape, “upstream” and “downstream” reaches are defined by their location in relation to those natural stream barriers. Thus downstream reaches are downstream of the barrier and well connected to the main stem of the Delaware River while upstream reaches are separated from downstream reaches by one or more significant waterfalls. A linear model of all reaches showed a significant negative association between community diversity and brook trout abundance both before and after the flood ( $t$  value = 2.67,  $p$  = 0.01). Separating the negative interaction between diversity and brook trout by those communities in upstream and downstream reaches revealed that the post-flood response of brook trout abundance was significantly and negatively impacted by high community diversity in downstream locations ( $t$  value = 2.89,  $p$  = 0.005; Figure 6). Downstream reaches with high community diversity showed either no change or loss of brook trout population abundance after the flood while brook trout populations in both upstream and downstream reaches with low community diversity had much higher increase in abundance.

Brook trout abundance in reaches upstream of natural barriers increased proportionally throughout the DEWA landscape and appeared to be minimally influenced by the flood. In these reaches, all brook trout populations increased abundance in 2012 regardless of community diversity, unlike downstream populations in which brook trout experienced no increased abundance in high-diversity stream reaches (Figure 6). While there was a significant increase in the abundance of all populations in 2012 ( $t$  = -2.75,  $p$  = 0.001), brook trout in downstream reaches were disproportionately affected by the species diversity of surrounding community.

## **Discussion**

At the southern edge of their thermal tolerance, cold water fish species are confronted by both changing climate and species more suited for the new environment. High fish community diversity was generally due to more warm water tolerant species (Table 2). These communities occurred in warmer stream reaches downstream of large natural barriers with good connectivity to the main stem of the Delaware River. The limitations of temperature and community on brook trout presence and abundance were visible during normal conditions before the 2011 flood and continued to affect brook trout abundance in response to the flood (Figure 6). Temperature and diversity have reduced standing brook trout stocks over time such that brook trout abundance before the flood was low (< 30 individuals) at all sites. These factors created a negative feedback that appear to have contributed to the reduction and loss of brook trout throughout DEWA.

Comparing the before- and after-effects of the flood on brook trout abundance (Figure 6), the response of brook trout in upstream and downstream study sites was markedly different. High fish community diversity severely limited any increase in brook trout abundance after the flood in downstream reaches. Because many other warm water and generalist species also significantly increased abundance after the flood (Figure 3) the competition for resources, habitat, or optimal spawning locations may have excluded brook trout reproduction in the fall or YOY recruitment the following spring.

Upstream reaches, where stream temperature was consistently cooler and overall fish community diversity was lower than downstream reaches, did not have similar effects. Population abundance after the flood increased in all upstream study sites, apparently not limited by high community diversity. In this way, fragmentation between upstream and downstream reaches within the same stream may benefit brook trout by keeping generalist species from moving into warming streams and competing with native cold water species.

The proportion of size classes and the overall cohort structure was dramatically changed after the flood. Post-flood recruitment of YOY brook trout was high for two years following the flood compared to recruitment immediately before the flood (Figure 4). There was no significant loss of age 1+ brook trout in 2012, but YOY accounted for a much larger percentage of the total population in both 2012 and 2013 than they had previously. This proportional change was accompanied by a downward shift in brook trout fork length throughout DEWA. These years of a high density of much smaller trout may have negative consequences for such a highly recreational fishery including loss of revenue or demands for more fish stocking in the park.

The timing of the 2011 storms may have been one of the biggest factors influencing population abundance and recruitment after the flood. Winter and early spring floods cause the greatest potential mortality in brook trout YOY (Ottoway and Clark 1981; Carline and McCullough 2003; Warren et al. 2009; Meyers et al. 2010), but late fall flooding can disrupt spawning by removing substrate, scouring redds, reducing prey and other trophic resources, or by displacing mature adults thereby decreasing the number of effective breeders. The timing of the flood examined in this study, approximately 6-10 weeks before probable spawning, may have allowed enough time for displaced mature brook trout to repopulate reaches and locate good spawning areas.

Trends in the increase of population abundance lead me to suggest a disconnect between hydrologically catastrophic and ecologically catastrophic floods. The sustained flood event created by the paired storms in 2011 was nearly record-breaking at several stream gage locations and fit within the parameters of a hydrologically-defined catastrophic flood event. However, despite visual observation of severe disturbance in and around study sites, biological processes appeared relatively undisturbed as evidenced by the massive increase in overall abundance of

species throughout the landscape (Figure 2). This agrees with at least two other publications describing stream systems pre- and post-flood (Matthews 1986; Dolloff et al. 1994). If floods do not create additional disturbance like scouring or debris flows (Roghair et al. 2002; Howell 2006) that defaunate streams, these massive flood events may not have the ecological impact to stream communities they are often assumed to have.

DEWA's status as a highly conserved landscape is both a positive and negative in its ability to mitigate the effects of climate change. Climate change is predicted to increase air and stream temperatures and increase the frequency and intensity of storm events in the northeastern United States (Eaton and Scheller 1996; Kaushal et al. 2010). The protected state of the landscape in DEWA appears to have acted as a buffer to potential flood damage such that brook trout and other species were able to maintain and increase population abundance after massive disturbance. On the other hand, without adequate means of preventing cold water streams from the warming influence of climate change, warm water and generalist species will encroach upon the thermal limits of brook trout habitat and gradually exclude them.

This study only examined the effects of the flood at one ecological scale of population and demographic dynamics, which could in turn affect the population at other ecological scales such as the genetic diversity of populations or divergence within metapopulations. Population genetics are not often considered when species abundance appears to rebound after a major disturbance. It would be worthwhile to investigate this metapopulation at a finer scale to examine the repercussions of population boom and bust cycles on brook trout molecular ecology.

## **Conclusion**

The late-summer 2011 flood caused by Hurricane Irene and Tropical Storm Lee did not appear to diminish the abundance of age 1+ brook trout despite the majority of previously tagged fish being displaced from their study sections. Instead, there was a large increase in abundance in

brook trout and many generalist fish species due to recruitment and survival of young-of-year during the following spring and summer of 2012. This high recruitment of YOY altered the size structure and lowered the mean and median length of brook trout populations throughout the park.

Peripheral populations of brook trout in the Delaware Water Gap National Recreation Area contend with warming stream temperatures, invading warm water fish communities, and recent large flood events. Brook trout populations in stream reaches downstream of large natural barriers and well connected to the main stem of the Delaware River had very low abundance before and after the 2011 flood when those reaches also had high fish community diversity. Conversely, well connected downstream reaches with low community diversity had large increases in brook trout abundance. However, this effect was not a significant factor in study sites upstream of barriers.

## References

- Billman, E., Kreitzer, J., Creighton, J., Habit, E., McMillan, B., Belk, M.C. (2012). Habitat enhancement and native fish conservation: can enhancement of channel complexity promote the coexistence of native and introduced fishes? *Environmental Biology of Fishes*, 96(4), 555-566.
- Brana, F., Nicieza, A., Toledo, M. (1992). Effects of angling on population structure of brown trout, *Salmo trutta* L., in mountain streams of northern Spain. *Hydrobiologia*, 237, 61-66.
- Cardinale, B.J., Palmer, M.A, Collins, S.L. (2002). Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature*, 415(6870), 426-429.
- Carline, R., McCullough, B. (2003). Effects of floods on brook trout populations in the Monongahela National Forest, West Virginia. *Transactions of the American Fisheries Society*, 132(5), 1014-1020.
- Carlson, S.M., Hendry, A.P., Letcher, B.H. (2007). Growth rate differences between resident native brook trout and non-native brown trout. *Journal of Fish Biology*, 71(5), 1430-1447.
- Carlson, S.M., Letcher, B.H. (2003). Variation in brook and brown trout survival within and among seasons, species, and age classes. *Journal of Fish Biology*, 63(3), 780-794.
- Dolloff, C., Flebbe, P., Owen, M. (1994). Fish habitat and fish populations in a southern Appalachian watershed before and after Hurricane Hugo. *Transactions of the American Fisheries Society*, 123(4), 668-678.
- Eastern Brook Trout Joint Venture. (2006). Eastern brook trout: status and threats. Technical Report, January, 2006.
- Eaton, J. Scheller, R. (1996). Effects of climate warming on fish thermal habitat in streams of the United States. *Limnology and Oceanography*, 41(5), 1109-1115.
- Elmqvist, T., Folke, C., Nystrom, M., Peterson, G., Bengtsson, J., Walker, B., Norberg, J. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, 1(9), 488-494.
- Groisman, P.Y.A, Knight, R.W., Karl, T.R., Easterling, D.R, Sun, B., Lawrimore, J.H. (2004). Contemporary changes of the hydrological cycle over the contiguous United States: Trends derived from in-situ observations. *Journal of Hydrometeorology*, 5, 64-85.
- Grossman, G.D., Ratajczak, Jr., R.E., Crawford, M., Freema, M.C. (1998). Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. *Ecological Monographs*, 68(3), 395-420.
- Haak, A.L., Williams, J., Neville, H., Dauwalter, D.C., Colyer, W.T. (2010). Conserving peripheral trout populations: The values and risks of life on the edge. *Fisheries*, 35(11), 530-549.
- Harding, J.S., Benfield, E.F., Bolstad, P.V., Helfman, G.S., Jones, B.D. (1998). Stream biodiversity: the ghost of land use past. *Ecology*, 148, 702-709.
- Hearn, W. (1987). Interspecific competition and habitat segregation among stream-dwelling trout and salmon: A review. *Fisheries*, 12(5), 24-31.
- Helle, J.H., Hoffman, M.S. (1998). Changes in size and age at maturity of two North American stocks of chum salmon (*Oncorhynchus ketal*) before and after a major regime shift in the North Pacific Ocean. *North Pacific Anadromous Fish Community Bulletin*, No.1: 81-89.
- Hobbs, R.J., Huenneke, L.F. (1992). Disturbance, diversity, and invasion: Implications for conservation. *Conservation Biology*, 6(3), 324-337.

- Holling, C. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, 4, 1-23.
- Hoopes, R. (1975). Flooding as the result of Hurricane Agnes and its effect on a native brook trout population in an infertile headwater stream in central Pennsylvania. *Transactions of the American Fisheries Society*, 104(1), 96-99.
- Howell, P. (2006). Effects of wildfire and subsequent hydrologic events on fish distribution and abundance in tributaries of North Fork John Day River. *North American Journal of Fisheries Management*, 26(4), 983-994.
- Hudy, M., Thieling, T.M., Gillespie, N., Smith, E.P. (2008). Distribution, status, and land use characteristics of subwatersheds within the native range of brook trout in the eastern United States. *North American Journal of Fisheries Management*, 28(4), 1069-1085.
- Johnson, S.L., Rahel, F., Hubert, W. (1992). Factors influencing the size structure of brook trout populations in beaver ponds in Wyoming. *North American Journal of Fisheries Management*, 12(1), 118-124.
- Kauschal, S.S., Likens, G.E., Jaworski, N.A., Pace, M.L., Sides, A.M., Seekell, D., Belt, K.T., Secor, D.H., Wingate, R.L. (2010). Rising stream and river temperatures in the United States. *Frontiers in Ecology and the Environment*, 8(9), 461-466.
- Korsu, K., Huusko, A. Muotka, T. (2009). Invasion of north European streams by brook trout: hostile takeover or pre-adapted habitat niche segregation? *Biological Invasions*, 12(5), 1363-1375.
- Larscheid, J.G., Hubert, W.A. (1992). Factors influencing the size structure of brook trout and brown trout in southeastern Wyoming mountain streams. *North American Journal of Fisheries Management*, 12(1), 109-117.
- Letcher, B., Terrick, T. (1998). Maturation of male age-0 Atlantic salmon following a massive localized flood. *Journal of Fish Biology*, 53(1), 1243-1252.
- Matthews, W. (1986). Fish faunal structure in an Ozark stream: stability, persistence, and a catastrophic flood. *Copeia*, 1986(2), 388-397.
- Meisner, J.D. (1990). Effect of climatic warming on the southern margins of the native range of brook trout, *Salvelinus fontinalis*. *Canadian Journal of Fisheries and Aquatic Sciences*, 47, 1065-1070.
- Meyers, E., Dobrowski, B., Tague, C. (2010). Climate change impacts on flood frequency, intensity, and timing may affect trout species in Sagehen Creek, California. *Transactions of the American Fisheries Society*, 139(6), 1657-1664.
- Ottoway, E., Clark, A. (1981). A preliminary investigation into the vulnerability of young trout (*Salmo trutta* L.) and Atlantic salmon (*S. salar* L.) to downstream displacement by high water velocities. *Journal of Fish Biology*, 19, 135-145.
- Paradis, A., Elkington, J., Hayhoe, K., and Buonaccorsi, J. (2007). Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. *Mitigation and Adaptation Strategies for Global Change*. 13(5-6), 541-554.
- Peterson, G., Allen, C.R., Holling, C.S. (1998). Ecological Resilience, biodiversity, and scale. *Ecosystems*, 1, 6-18.
- Poff, N. L., Allan, J. D. (1995). Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology*, 76(2), 606-627.



- Poff, N.L. (2002). Ecological response to and management of increased flooding caused by climate change. *Philosophical Transactions: Mathematical, Physical, and Engineering Sciences*, 360(1796), 1497-1510.
- Reice, S., Wissmar, R., Naiman, R. (1990). Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. *Environmental Management*, 14(5), 647-659.
- Ries, L., Fletcher, Jr., R.J., Battin, J., Sisk, T.D. (2004). Ecological responses to habitat edges: Mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics*, 34, 491-522.
- Ripple, W. J., Beschta, R. L. (2006). Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. *Biological Conservation*, 133(4), 397-408.
- Roghair, C.N., Dolloff, C., Underwood, M. (2002). Response of a brook trout population and instream habitat to a catastrophic flood and debris flow. *Transactions of the North American Fisheries Society*, 131(4), 718-730.
- Ross, R., Bennet, R., Snyder, C., Young, J., Smith, D., Lemarie, D. (2003). Influence of the eastern hemlock (*Tsuga canadensis* L.) on fish community structure and function in headwater streams of the Delaware River Basin. *Ecology of Freshwater Fish*, 12(1), 60-65.
- Vincenzi, S., Crivelli, A., Jesensek, D., DeLeo, G. (2010). Individual growth and its implications for the recruitment dynamics of stream-dwelling marble trout (*Salmo marmoratus*). *Ecology of Freshwater Fish*, 19(3), 477-486.
- Warren, D., Ernst, A., Baldigo, B. (2009). Influence of spring floods on year-class strength of fall-and spring-spawning salmonids in Catskill mountain streams. *Transactions of the American Fisheries Society*, 138(1), 200-210.
- Wagner, T., Deweber, J., Detar, J., Kristine, D., Sweka, J. (2014). Spatial and temporal dynamics in brook trout density: Implications for population monitoring. *North American Journal of Fisheries Management*, 32(2), 258-269.
- Wenger, S.J., Isaak, D., Dunham, J., Fausch, K., Luce, C.H., Neville, H.M., Reman, B.E., Young, M.K., Nagel, D.E., Horan, D.L., Chandler, G.L. (2011). Role of climate and invasive species in structuring trout distributions in the interior Columbia River Basin, USA. *Canadian Journal of Fisheries and Aquatic Sciences*, 68, 988-1008.
- Whitworth, W.E and Strange, R.J. (1983). Growth and population of sympatric brook and rainbow trout in an Appalachian Stream. *Transactions of the American Fisheries Society*, 112(4), 469-475.
- Wismer, D.A., Christie, A.E. (1987). Temperature relations of Great Lakes fishes: A data compilation. Great Lakes Fishery Commission Special Publication No 87-3. 165p.

## Tables and Figures

**Table 1:** The length and weight of all PIT tagged brook trout captured in 2011 and recaptured in 2012.

Stream	Tag Number	2011		2012	
		Length	Weight	Length	Weight
Adams	2121	117	16.3	139	26.4
Adams	2197	105	12.4	145	34.1
Adams	2248	114	15.6	171	54.6
Adams	0B10	145	34.0	182	57
Adams	1B81	129	23.8	155	38.5
Adams	21A8	173	60.0	192	78.8
Conashaugh 1	21D9	138	30.1	196	85.8
Conashaugh 2	2190	149	31.0	185	60.9
Conashaugh 2	2472	114	17.1	160	44
Conashaugh 2	18D3	134	25.3	156	39.3
Conashaugh 2	23CB	70	3.3	123	17.9

**Table 2:** Common and scientific names of fish with cold water, generalist, and warm water temperature range preferences.

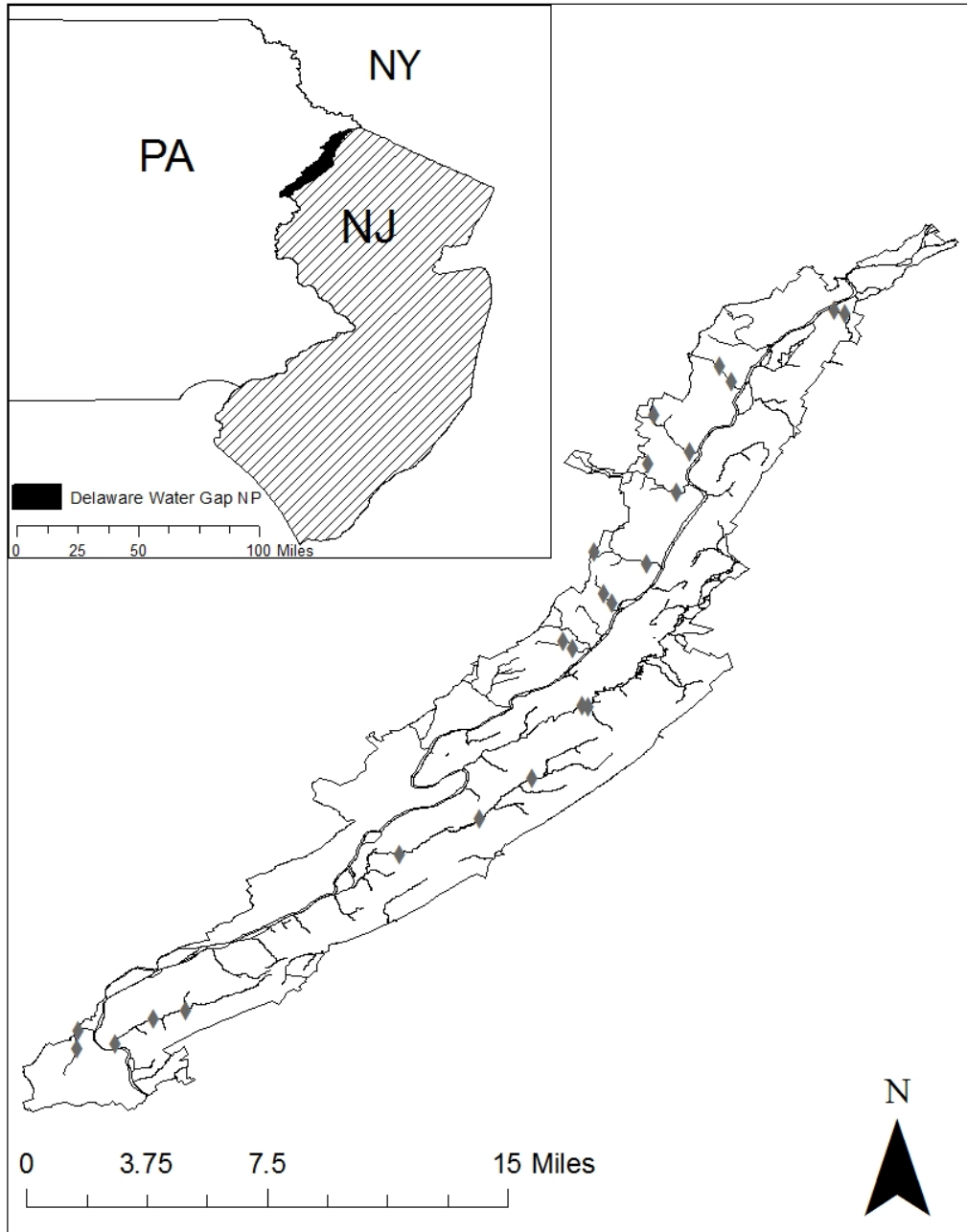
Warm Water		Generalist		Cold Water	
Common Name	Scientific Name	Common Name	Scientific Name	Common Name	Scientific Name
American Eel	<i>Anguilla rostrata</i>	Bluntnose	<i>Pimephales</i>	Brook Trout	<i>Salvelinus fontinalis</i>
Black Crappie	<i>Pomoxis nigromaculatus</i>	Minnnow	<i>notatus</i>	Brown Trout	<i>Salmo trutta</i>
Bluegill	<i>Lepomis macrochirus</i>	Common			<i>Oncorhynchus mykiss</i>
Brown	<i>Ameiurus</i>	Shiner	<i>Luxilus cornutus</i>	Rainbow Trout	<i>Salmo trutta</i>
Bullhead	<i>nebulosus</i>		<i>Semotilus atromaculatus</i>	Blacknose	<i>Rhinichthys atratulus</i>
Chain		Creek Chub	<i>Exoglossum maxillingua</i>	Dace	<i>Rhinichthys cataractae</i>
Pickrel	<i>Esox niger</i>	Margined		Longnose Dace	<i>Cottus bairdii</i>
Golden Shiner	<i>Notemigonus crysoleucas</i>	Madtom	<i>Noturus insignis</i>	Mottled	
Green Sunfish	<i>Lepomis cyanellus</i>		<i>Nocomis micropogon</i>	Sculpin	<i>Cottus bairdii</i>
Hog Sucker	<i>Hypentelium nigricans</i>	River Chub		Mudminnow	<i>Umbra limi</i>
Largemouth	<i>Micropterus salmoides</i>	Shield			
Bass		Darter	<i>Percina peltata</i>		
Pumpkinseed	<i>Lepomis gibbosus</i>	Spottail	<i>Notropis hudsonius</i>		
Satinfin	<i>Cyprinella analostana</i>	Shiner	<i>Etheostoma olmstedi</i>		
Shiner		Tesselated			
		Darter			

White Sucker	<i>Catostomus commersonii</i>		
Yellow Bullhead	<i>Ameiurus natalis</i>		
Yellow Perch	<i>Perca flavescens</i>		
Fallfish	<i>Semotilus corporalis</i>		

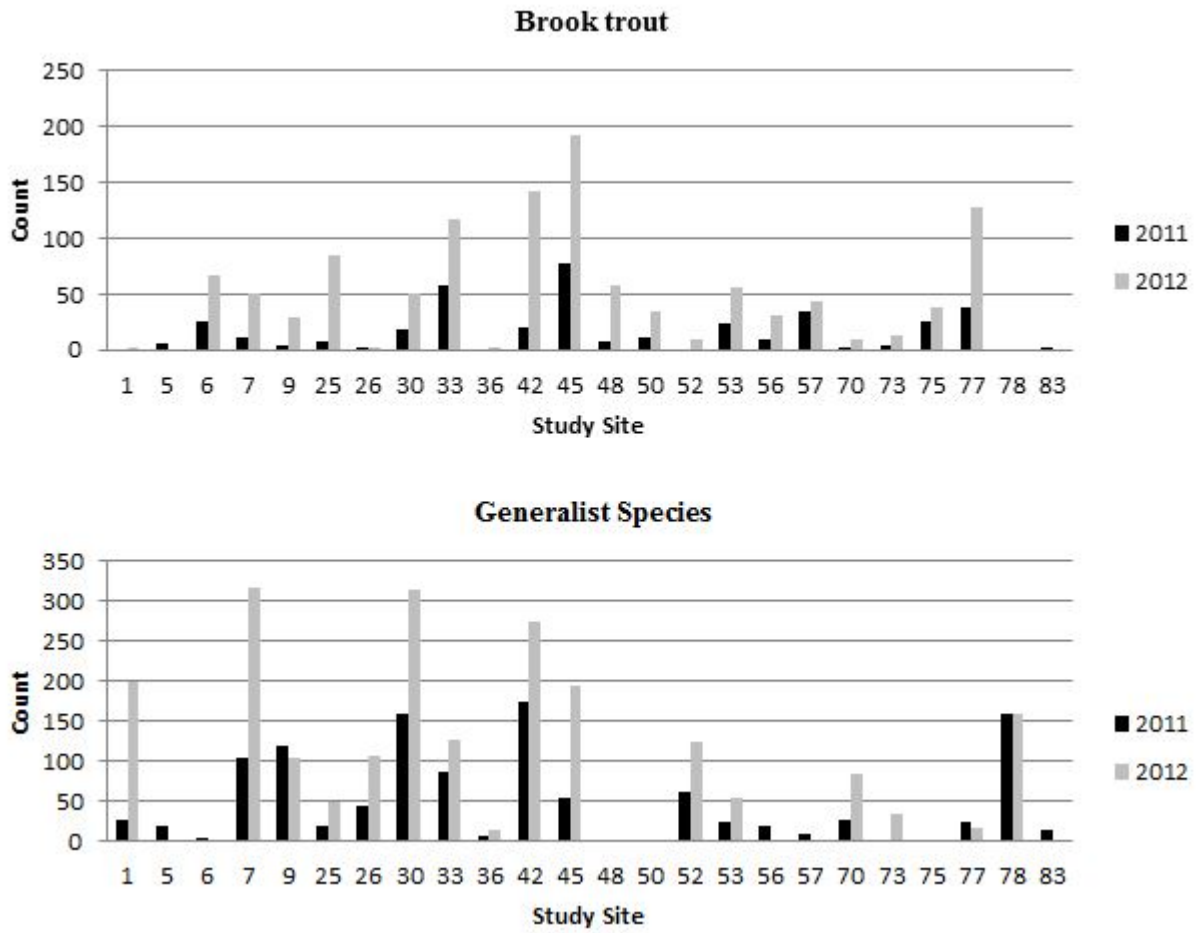
**Table 3:** Number of young-of-year (YOY) and age 1+ brook trout at each reach in the study area.

Site	2011		2012		2013	
	YOY	Age 1+	YOY	Age 1+	YOY	Age 1+
1	0	0	0	1	0	0
5	0	6	-	-	1	15
6	8	17	39	27	5	28
9	7	4	22	29	15	18
25	0	4	25	5	18	11
26	8	4	75	10	-	-
30	0	1	0	2	0	1
33	4	15	33	18	11	35
36	15	42	60	43	24	43
48	1	19	129	13	23	110
50	33	44	171	22	48	90
52	3	4	57	1	3	6
53	3	8	31	3	0	19
57	10	13	36	20	15	25
66	4	6	18	13	19	12
67	7	28	15	28	17	14
70	0	3	6	4	2	2
73	1	4	9	4	1	0
75	9	15	22	17	19	10
77	18	21	108	20	62	25
83	3	0	-	-	84	6

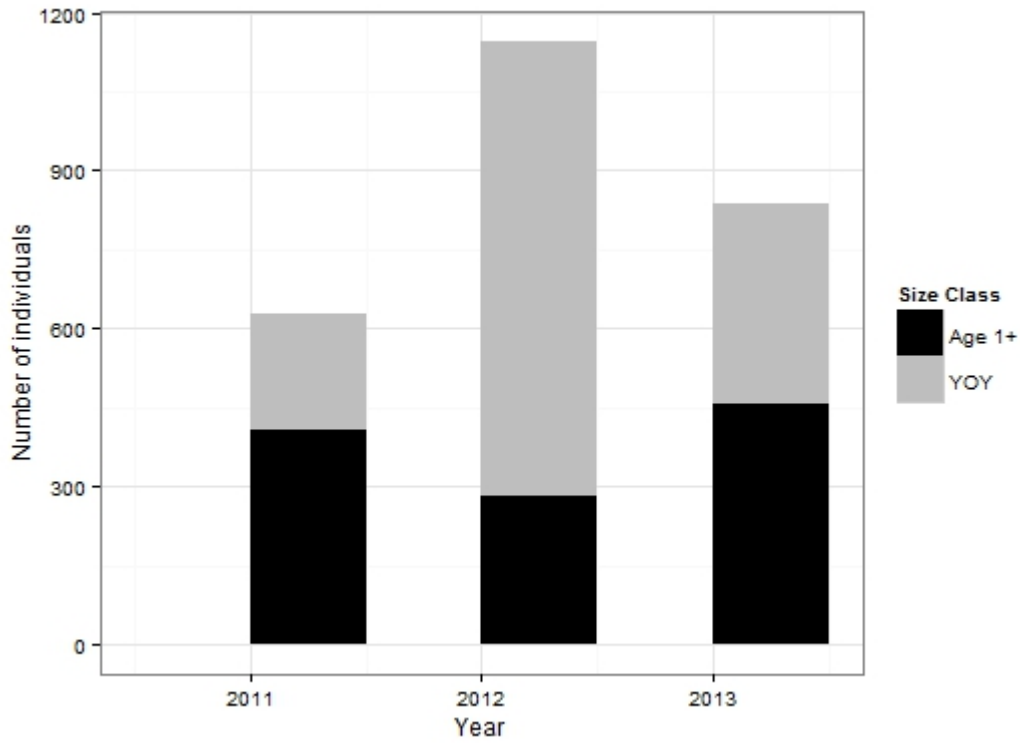
**Figure 1:** Map of Delaware Water Gap National Recreation Area, its rivers, and the 24 sites resampled between 2011-2013.



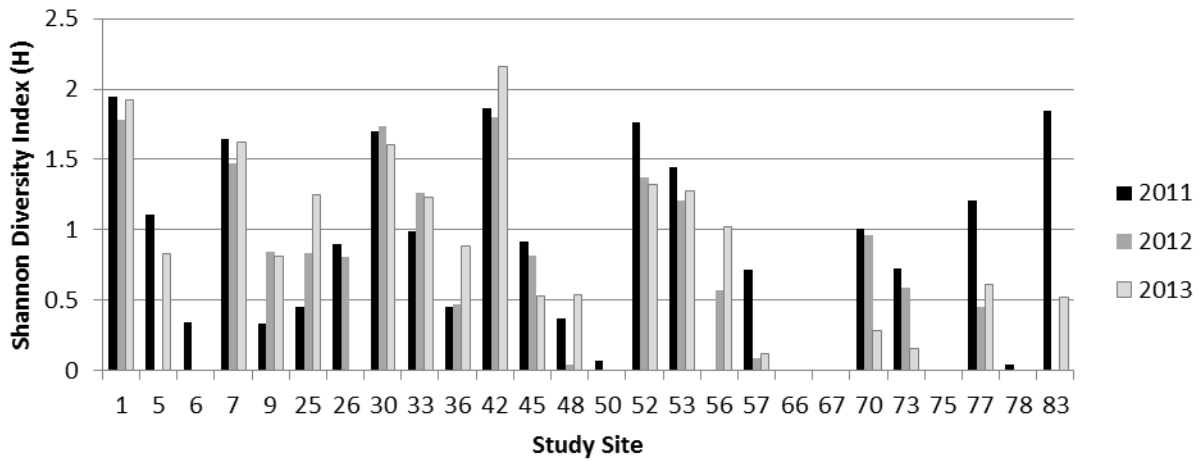
**Figure 2:** Increase in brook trout and generalist species abundance between 2011 before the massive flood and 2012 after.



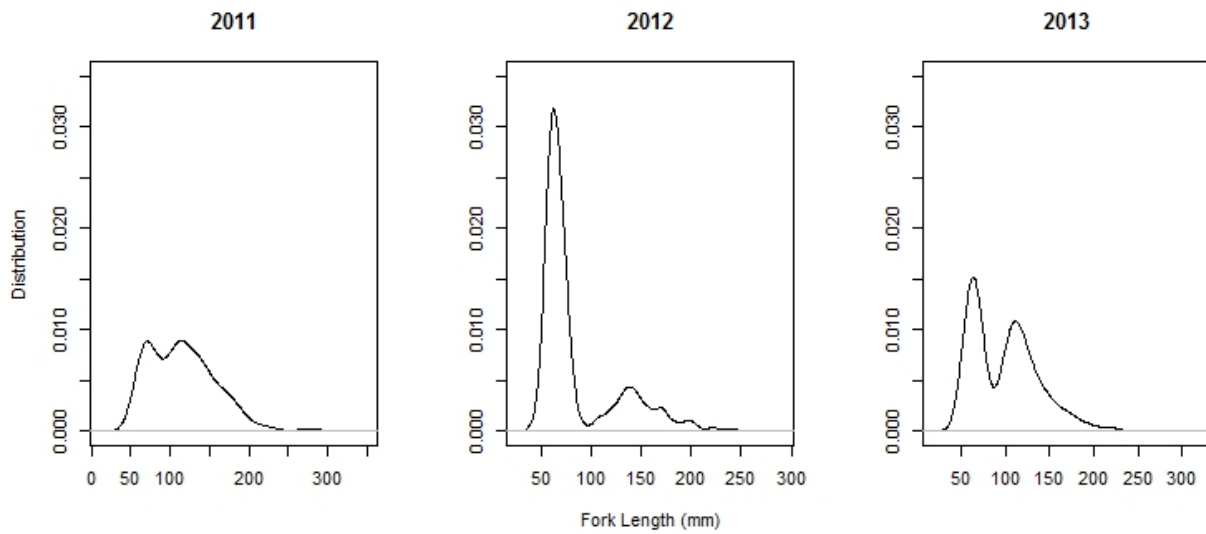
**Figure 3:** Abundance of young-of-year and age 1+ brook trout throughout DEWA between 2011-2013.



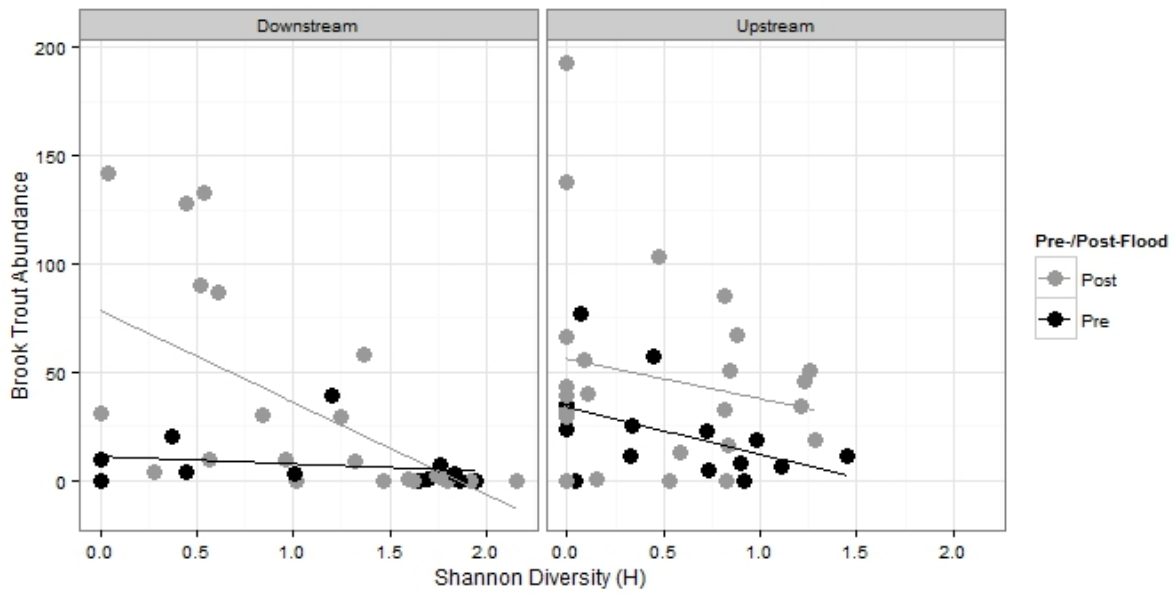
**Figure 4:** The Shannon Diversity Index value for each site during the study.



**Figure 5:** Frequency distribution of brook trout length during the study period.



**Figure 6:** Linear models of brook trout abundance relative to fish community diversity in reaches downstream and upstream of large natural barriers.



## Chapter 4

### **The genetic consequences of catastrophic flooding in a naturally fragmented landscape**

#### **Abstract**

In late summer 2011 a large sustained flood passed through the Delaware Water Gap National Recreation Area. The pre-flood population of brook trout, which was largely naturally fragmented, can be defined as spatially hierarchically structured: genotypes in individual streams were significantly differentiated from all others, and genotypes in individual stream reaches that were divided by large barriers within the same stream were often significantly differentiated from each other as well. This strong genetic structure was temporarily interrupted by gene flow among brook trout that appeared to be displaced from upstream populations into downstream populations. Temporally, the flood had a significant effect on population genetics of sites compared between years. Site genotypes of brook trout populations compared before and after the flood (2011-2012) were significantly altered. These temporal effects did not last: several study sites identified with monomorphic loci in 2011 did not show any fixation in 2012, but over half of these sites were identified with monomorphic loci again in 2013. This indicates that a sudden genetic influx of individuals into a population did not create a sustained increase in allelic diversity of brook trout populations in a fragmented landscape. Genetic problems may be linked to lower population resilience after a large natural disturbance.



## **Introduction**

Major disturbances in stream systems have the potential to alter habitat, displace individuals from populations, and increase mortality – all of which may affect the genetic structure and diversity of stream-dwelling fish (Carlsson and Nilsson 2001; Diener et al. 2006; Gibbs 2001). However, there are surprisingly few studies that link the effects of large ecosystem disturbances, such as floods, to genetic changes of populations. Other studies recognize the importance of disturbance and refugia on the natural regimes of fish population abundance. Reeves et al. (1995) argued that regular disturbance regimes need to be considered when designing salmonid restoration projects in the Pacific Northwest, but they were accounting for many small or modest disturbances to affect more resilient population dynamics and maintain reproduction, not considering the effects of disturbances on the genetic mixing of their study populations. Single high-disturbance events often create significant, though not necessarily negative, changes in population abundance, movement, and fecundity (Reeve et al. 1995). Such events may remove individuals poorly adapted to those conditions, but they may also reduce overall genetic variability within the population.

It is uncommon to have adequate baseline presence or abundance data for a flood-affected fish population (Dolloff et al. 1994), and it is even rarer to have baseline genetic data for a flood-affected fish population. A few studies have examined the effects of floods without data on pre-flood conditions (Seegrism and Gard 1972; Snyder and Johnson 2006), while many studies were established in areas both before and after a flood in order to collect historic or baseline data (Hoopes 1975; Dolloff et al. 1994; Roghair et al. 2002; Carline and McCullough 2003). These studies look broadly at survival and recolonization at a species or community level, but have not collected genetic data.

In late August 2011, Hurricane Irene passed over the Delaware Water Gap National Recreation Area (DEWA) in Pennsylvania and New Jersey, depositing over 20.3cm of rain in two days and causing a large flood peak recorded by USGS flow gages on the Delaware River and several nearby tributaries. Eight days later this storm event was followed by Tropical Storm Lee, which deposited another 12.7cm of rain over the area and created a second flood peak. The pair of storms, which I will refer to as a singular collective flood from here forward created significant damage to in-stream and terrestrial habitat and dramatically altered the abundance and demography of brook trout populations across the landscape (see chapter 3).

In this study, I examine the consequences of the flood on the molecular ecology of brook trout, both spatially across the landscape and temporally before and after the flood. First I will look at the hierarchical structuring of populations to identify spatial breaks between populations. Because of downstream displacement during the flood and significant natural barriers to upstream movement, I hypothesize that dispersal and redistribution caused by the flood will increase overall genetic diversity in downstream reaches. Meanwhile the displacement of adults from upstream to downstream study reaches within the same stream will decrease the genetic distance between sites, homogenizing them.

Genetic mixing and diversity are important elements in countering natural genetic drift, but highly fragmented and genetically structured populations do not always carry negative connotations. Araguas et al. (2008) identified the need for genetic refuges in headwater streams for native brown trout against stocked competition in order to retain diverse wild genetic traits. A large isolated population can retain important traits and fitness without much gene flow, but small isolated populations are susceptible to inbreeding, fixed alleles, and an overall loss of biological fitness (Whitlock 2000).

## Methods

Research was conducted in the Delaware Water Gap National Recreation Area (DEWA) in partnership with the USGS-Leetown Science Center, the USGS-Silvio Conte Anadromous Fish Research Center, and the National Park Service (NPS). DEWA encompasses 28032 ha of land and roughly 200 km of rivers, including 64 km of the Delaware River, within the park boundary in Pennsylvania and New Jersey. The study was conducted from July 5 – August 21, 2011, from July 9 – July 20, 2012, and from July 22 – August 2, 2013.

In 2011, 16 sub-watershed tributaries in DEWA were identified that flow directly into the Delaware River. Eighty-three stream reaches were selected on these tributaries (2-5 per stream); each reach was 150m long and separated from other reaches on the same tributary by at least 300m and one natural barrier. Most man-made barriers and low-head dams within these sub-watersheds were removed by the NPS after the creation of the park in 1978. Tributaries comprised first- and second-order streams between 1m and 18m wide (5m average). During 2012 and 2013, 24 reaches were resampled from the original 83 in the same manner to identify both spatial and temporal genetic variation between reaches over time, as well as any genetic redistribution caused by a 2011 flood.

The DEWA landscape has high natural fragmentation. The natural geology of the landscape creates large waterfalls > 3m high that are entirely impassable by fish in an upstream direction between sections. Downstream fish movement over these barriers may be possible, but is unlikely (Letcher et al. 2007). Of the 83 streams sampled the first year of the study, 11 contained brook trout. One of these streams had only one individual brook trout during the first year of the study; no brook trout were observed during the subsequent the other two years and so this stream was struck from analysis.

The 150m long study reaches were analyzed in the following manner: a global positioning system (GPS) point was recorded electronically and the latitude and longitude recorded manually at the beginning of each reach. Electrofishing in each reach was conducted with one or two LR-24 backpack electro-shockers (Smith-Root, Inc., Vancouver, WA) depending on the wet width at the time of sampling. If two backpacks were necessary, they were used in tandem. Reaches were shocked in a single continuous pass with no block nets (Peterson, et al., 2005; Reid, et al., 2009). Fish were netted and placed in a bucket; buckets were exchanged every 50m and the bucket of fish from the previous section was labeled and left in the shade with an air bubbler until the reach was completed. Eighty-three reaches were sampled in 2011; twenty-four reaches were resampled in 2012 and 2013.

At the end of the reach, buckets from each section were collected and non-salmonid fish species were released. Brook trout were measured to fork length ( $\pm 1$ mm), weighed ( $\pm 0.1$ g), and a subsample of thirty individuals was anesthetized and had their anal fin clipped. Brook trout were allowed to recover fully in fresh water before being released. Fin clips were placed in Wattman paper and labeled with an individual ID number for later genetic analysis. These were then dried and stored in an airtight container with a desiccant drying pouch until the fin clips were analyzed. In 2011, 630 such genetic samples were collected, dried, and analyzed, 487 in 2012, and 620 in 2013.

Genetic analysis was conducted at University of Massachusetts-Amherst and the Conte Anadromous Fish Research Center in Turners Falls, MA, during the autumn and winter following the field season in which the fin clips were collected. DNA was extracted from the fin clips following standard DNA extraction protocols and amplification conditions (King, et al., 2005). DNA extracted from fin clips were amplified at eight microsatellite loci which were used

in previous brook trout studies (Hudy et al. 2010, Kanno et al. 2011): *SfoC-113*, *SfoC-88*, *SfoD-100*, *SfoD-75*, *SfoC-115*, *SfoC-129*, *SfoC-24* (King et al. 2003), *SsaD-237* (King et al. 2005).

Electrophoresis of loci was performed on an ABI Prism 3130xl genetic analyzer, and alleles were scored using GENEMAPPER version 4 and PEAK SCANNER version 1.0 software (Applied Biosystems Inc., Foster City, California, 2006).

### **Analysis**

Microsatellite analysis was conducted using Arlequin version 3.1 (Excoffier 2006), the hierfstat R package (Goudet 2013), and GenoDive version 2.0b32 (Meirmans 2013). Pairwise  $F_{st}$  comparisons, analysis of molecular variation (AMOVA) and hierarchical grouping within AMOVA were computed with Arlequin; observed heterogeneity ( $H_o$ ), within-population gene diversity ( $H_s$ ), overall gene diversity ( $H_t$ ), gene diversity among samples ( $D_{st}$ ), and differentiation within and between variables were computed with the hierfstat R package. Allele frequencies, inbreeding coefficient ( $G_{is}$ ), and individual population assignment were calculated with GenoDive. Spatial differences in brook trout genetic structure and diversity were analyzed at several levels in order to determine the appropriate scale to look for changes in genetic diversity caused by their redistribution after the flood. Across the landscape, genetic differentiation was analyzed between tributaries, between sections within the same tributary, and within populations in individual sections.

### **Results**

Genetically, brook trout populations between and within streams appeared to be completely unconnected. Between-stream pairwise  $F_{st}$  ranged from 0.05-0.23; these scores indicate that populations within streams were significantly differentiated from all other streams in the study area ( $p < 0.01$ ). Study sites within the same stream had slightly lower  $F_{st}$  values ( $F_{st}$

= 0.03-0.17), but still indicated significant differentiation between such populations ( $p < 0.01$ ). All but one stream showed this significant differentiation between upstream and downstream reaches in 2011 before the flood – a common finding in highly fragmented streams.

Hierarchical spatial structuring within DEWA was corroborated using a nested-group AMOVA and k-means clustering. The AMOVA showed that populations within study sections accounted for 88% of variation; 9% of variation was accounted for by between-stream variation, and only 3% was accounted for by within-stream variation. Cluster analysis consistently grouped populations into the smallest populations possible: those of individual sites.

The flood created a distinct temporal change in genetic differentiation when comparing the same populations at individual study sites between two years. Comparing populations between 2011 and 2012, pairwise  $F_{st}$  values were significantly different in fifteen of the twenty sites comparing pre- and post-flood genotypes ( $F_{st} = 0.002-0.13$ ). Populations in two study sites showed significant differentiation between 2012 and 2013, but the rest of the stream reaches showed little significant differentiation from 2012 to 2013.

Because within-stream spatial variation between study reaches was already highly differentiated, it is difficult to tell whether sites in the same stream became more or less genetically similar after the flood. Table 1 compares two stream reaches within the same tributary for each year of the study. Within-stream pairwise  $F_{st}$  in 2011 was similar to pairwise  $F_{st}$  in 2012 ( $F_{st} = 0.01-0.16$ ); comparing the two within-stream reaches – separated upstream and downstream by a large natural barrier – showed significant differentiation each year. One stream proved to be an exception as it did not exhibit significant within-stream variation between sites in 2011, and remained genetically similar throughout the study period. By 2013, within-stream pairwise differentiation was no longer significant in many of the previously differentiated

streams. Only four of the twelve pairwise within-stream comparisons were significantly different during the final year of the study.

Genetic diversity throughout the park was moderately high at all but the most human-influenced streams. The stream with the lowest diversity (Dingmans Creek,  $H_o = 0.469$ ), is also one of the few remaining stocked streams in DEWA. During the course of the study, diversity did not significantly increase or decrease at individual reaches (Figure 1). The location of the stream reach upstream or downstream of natural barriers was not related to the amount or variability of diversity over time.

Basic gene flow between streams was limited, but within-stream gene from upstream to downstream populations was evident based on population assignment analysis. Using likelihood ratios across per-population thresholds to infer the originating genetic population for individuals, eighteen brook trout out of nearly 500 individuals in 2012 were calculated as having likely originated in a different study site in 2011. More than half of those identified were likely redistributed from upstream populations (likelihood ratios = 2.1-43.9).

Regardless of potential gene flow in several streams, fixed alleles were present in multiple study sites. In 2011, five populations in four streams had one or more monomorphic loci (Table 2) – most commonly *SfoC-129* and *SfoC-24*. Most of these populations were notably small with total captured populations comprising less than 10 individuals, but at least one population had 22 captured individuals in the site. As part of the population assignment analysis indicated, four individual brook trout were displaced from more abundant upstream populations into very low abundance populations downstream which in 2011 had fixed alleles at a minimum of one locus. These low-abundance populations did not show any monomorphism in 2012 after abundance increased significantly in all populations, but the presence of fixed loci was detected

again in three populations in two streams in 2013. All three populations with monomorphic loci in 2013 also had monomorphic loci in 2011 before the flood. These populations were again notably small in 2013 and had fewer than 10 individual brook trout captured in the study section.

## **Discussion**

The significant genetic differences between streams and between most stream sections were not unexpected given that there was a high degree of natural fragmentation between sections. Natural fragmentation, while not necessarily limiting the persistence of populations, does create a high degree of genetic differentiation (Letcher et al. 2007; Whiteley et al. 2013). Individuals cannot move between populations to stimulate gene flow, thereby creating a distinct genetic structuring between stream populations as well as between individual study sites across the DEWA landscape.

The 2011 flood facilitated redistribution of several individual brook trout from upstream populations to downstream populations which evident through population assignment analysis. The analysis shows only a small number of displaced brook trout because individuals must both survive the disturbance and forced migration, and then successfully reproduce as well. Displaced individuals may add to the genetic diversity of downstream populations, but the significance of this contribution depends on the size and heterogeneity of the population they enter. The addition of upstream individuals to very small downstream populations may increase diversity and release fixed loci, but often only temporarily, as described in the results above.

When washed into abundant downstream populations, redistributed individuals may not make any noticeable contribution to the genetic diversity unless the downstream population is already greatly homogenous. Because DEWA brook trout populations appear to have maintained genetic heterogeneity, this would explain why population assignment most confidently identified



individuals displaced into small (>10 individuals) and modest (10-20 individuals) downstream populations, and did not identify such redistributed individuals into downstream sections with abundant brook trout. Thus, the areas where displaced individuals could be most influential are in modest but reproductively viable populations of 10-20 individuals.

The presence of monomorphic loci in multiple locations is common in very small, isolated populations (Whitlock 2000). While fixed alleles have been found to be both harmful or beneficial in different contexts, they are often deleterious in small populations and are associated with reduced fitness. They occurred most frequently in DEWA populations with fewer than ten individual brook trout captured in downstream study sections (Table 2). These small peripheral populations were often subject to marginal quality habitat and high competition from other species (chapter 3). Young of year brook trout were observed and sampled in roughly half of these downstream sites with fixed loci in 2012, yet the small increase in abundance did not appear to influence genetic diversity over time.

The location, quantity, and composition of the fixed alleles were not consistent over the course of the study. In 2012, a year of highly increased recruitment, no monomorphic loci were present in any of the study sites. Increased recruitment was not sustained in 2013, nor was the absence of fixed alleles. Two of the 2011 populations with monomorphic loci benefitted from temporarily increased abundance and appeared to resolve the monomorphic loci through 2013. The other three populations with monomorphic loci in 2011 did not similarly benefit and two of these sites showed multiple fixed loci in the 2013 sample.

Temporally, the 2011 flood created significant genetic shifts to singular populations within a year. Nearly all populations, regardless of population size, experienced a significant change in genetic composition based on pairwise  $F_{st}$  between years; the genetic distance between

a 2011 population and the 2012 population in the same location appeared to be significantly different. However, there is no clear indication as to whether this change in  $F_{st}$  was caused by genotypes becoming more distinct through the addition of individuals to the population or less distinct through the loss of individuals and increased inbreeding.

The spatial differentiation within streams decreased between 2011 and 2013. Nearly half of within-stream differentiation between reaches exhibited reduced  $F_{st}$  and were no longer significantly differentiated from the other. This indicates gene flow between populations that, based on presence and location of large natural barriers, were likely the result of displacement and survival from upstream to downstream study areas. Further it indicates that a significant number of individuals that were displaced from upstream reaches also survived in downstream reaches until the following sample and could have potentially reproduced as well.

High year-to-year variation in terms of abundance (Wagner et al. 2014) and genetic variability should not discount a study covering only two years of genetic analysis after a flood. The overall changes seen in brook trout population genetics after a massive flood can still influence how ecologists and managers view disturbance-affected populations. Movement and redistribution of individuals between stream populations was evident, but immigrating individuals did not contribute significantly to any site's genetic diversity. Redistribution as a function of disturbance in fragmented landscapes does not increase genetic diversity. Declining populations with few reproducing adults and low genetic diversity can become fixed at one or more loci, which may have a negative effect on the population's fitness (Whitlock, 2000).

## **Conclusion**

Every landscape is divided into differently sized ecologically significant units based on fragmentation, connectivity, and movement of individuals between populations. A hierarchical

analysis of brook trout genotypes in DEWA suggests that populations are best defined by individual reaches separated from each other by large natural barriers, even within the same stream. With both high between-stream and within-stream differentiation, this suggests that there is very little connectivity and movement between most populations.

Forced downstream redistribution of individuals due to a large flood in 2011 was apparent in several streams using population assignment analysis. The temporary addition of these highly differentiated individuals into new downstream populations did not affect gene diversity but did create significant changes to within-site differentiation over time. This created a slight within-stream homogenization as pairwise differentiation – although still very high – declined by the 2013.

Upstream study sites were highly isolated, however they maintained moderately high genetic diversity and no monomorphic loci. Instead downstream sites, which often had much smaller populations, were subject to fixed alleles. The addition of individuals displaced from upstream populations appeared to add some allelic diversity, but the effect was short lived and half of the study sites with monomorphic loci in 2011 were again fixed in 2013. A sudden large natural disturbance may have forced brief mixing between isolated populations, but it was not enough to cause any long-lasting genetic changes.

## References

- Araguas, R., Sanz, N., Fernandez, R., Utter, F. M., Pla, C., Garcia-Marin, J.-L. (2008). Genetic refuges for a self-sustained fishery: experience in wild brown trout populations in the eastern Pyrenees. *Ecology of Freshwater Fish*, 17(4), 610-616.
- Carline, R., McCullough, B. (2003). Effects of floods on brook trout populations in the Monongahela National Forest, West Virginia. *Transactions of the American Fisheries Society*, 132(5), 1014-1020.
- Carlsson, J, Nilsson, J. (2001). Effects of geomorphological structures on genetic differentiation among brown trout populations in a northern boreal river drainage. *Transactions of the American Fisheries Society*, 130(1), 36-45.
- Deiner, K., Garza J.C., Coey, R., Girman, D.J. (2006). Population structure and genetic diversity of trout (*Oncorhynchus mykiss*) above and below natural and man-made barriers in the Russian River, California. *Conservation Genetics*, 8(2), 437-454.
- Demarais, B.D., Dowling, T.E., Minckley, W. (1993). Post-perturbation genetic changes in populations of endangered Virgin River chubs. *Conservation Biology*, 7(2), 334-341.
- Dolloff, C.A., Flebbe, P.A., Owen, M.D. (1994). Fish habitat and fish populations in a southern Appalachian watershed before and after Hurricane Hugo. *Transactions of the American Fisheries Society*, 123(4), 668-678.
- Gibbs, J.P. (2001). Demography versus habitat fragmentation as determinants of genetic variation in wild populations. *Biological Conservation*, 100(1), 15-20.
- Hoopes, R. (1975). Flooding as the result of Hurricane Agnes and its effect on a native brook trout population in an infertile headwater stream in central Pennsylvania. *Transactions of the American Fisheries Society*, 104(1), 96-99.
- Hudy, M., Coombs, J. A., Nislow, K., Letcher, B. H. (2010). Dispersal and within-stream spatial population structure of brook trout revealed by pedigree reconstruction analysis. *Transactions of the American Fisheries Society*, 139(5), 1276-1287.
- Kanno, Y., Vokoun, J., Letcher, B. H. (2011). Fine-scale population structure and riverscape genetics of brook trout (*Salvelinus fontinalis*) distributed continuously along headwater channel networks. *Molecular Ecology*, 20(18), 3711-3729.
- King, T. L., Julian, S. E., Coleman, R. L., Burnham-Curtis, M. K. (2003). Isolation and characterization of novel tri- and tetranucleotide microsatellite DNA markers for brook trout *Salvelinus fontinalis*: GenBank submission numbers AY168187, AY168192, AY168193, AY169194, AY168195, AY169197, AY168199. Available: [ncbi.nlm.nih.gov/nucleotide/](http://ncbi.nlm.nih.gov/nucleotide/). (February 2010).
- King, T. L., Eackles, M. S., Letcher, B. H. (2005). Microsatellite DNA markers for the study of Atlantic salmon (*Salmo salar*) kinship, population structure, and mixed-fishery analysis. *Molecular Ecology Notes*, 5(1), 130-132.
- Letcher, B.H., Nislow, K.H., Coombs, J.A., O'Donnell, M.J., Dubreuil, T.L. (2007). Population response to habitat fragmentation in a stream-dwelling brook trout population. *PloSOne*, 2(11), e1139. DOI:10.1371/journal.pone.0001139

- Peterson, J., Banish, N., Thurow, R. (2005). Are block nets necessary?: Movement of stream-dwelling salmonids in response to three common survey methods. *North American Journal of Fisheries Management*, 25(2), 732-743.
- Reeves, G.H., Benda, L.E., Burnett, K.M., Bission, P.A., Sedell, J.R. (1995). A disturbance-based ecosystem approach to maintaining and restoring freshwater habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. *American Fisheries Society Symposium*, 17, 334-349.
- Reid, S., Yunker, G., Jones, N. (2009). Evaluation of single-pass backpack electric fishing for stream fish community monitoring. *Fisheries Management and Ecology*, 16(1), 1-9.
- Roghair, C., Dolloff, C., Underwood, M. (2002). Response of a brook trout population and instream habitat to a catastrophic flood and debris flow. *Transactions of the American Fisheries Society*, 131(4), 718-730.
- Seegrist, D., Gard, R. (1972). Effects of floods on trout in Sagehen Creek, California. *Transactions of the American Fisheries Society*, 101(3), 478-482.
- Snyder, C., Johnson, Z. (2006). Macroinvertebrate assemblage recovery following a catastrophic flood and debris flows in an Appalachian mountain stream. *Journal of the North American Benthological Society*, 25(4), 825-840.
- Wagner, T., Deweber, J., Detar, J., Kristine, D., Sweka, J. (2014). Spatial and temporal dynamics in brook trout density: Implications for population monitoring. *North American Journal of Fisheries Management*, 32(2), 258-269.
- Whiteley, A.R., Coombs, J.A., Hudy, M., Robinson, Z., Colton, A, Nislow, K.H., Letcher, B.H. (2013). Fragmentation and patch size shape genetic structure of brook trout populations. *Canadian Journal of Fisheries and Aquatic Sciences*, 70(5), 678-688.
- Whitlock, M.C. (2000). Fixation of new alleles and the extinction of small populations: drift load, beneficial alleles, and sexual selection. *Evolution*, 54(6), 1855-1861.

## Tables and Figure

**Table 1:** Pairwise  $F_{st}$  between study site reaches within the same stream each year. \* denotes statistically significant differences in the genetic heterogeneity between the two compared sites.

Stream	Sites Compared	$F_{st}$	$F_{st}$	$F_{st}$
		2011	2012	2013
Adams	5 & 6	0.081*	<sup>a</sup>	0.149*
Hellers	25 & 26	<sup>a</sup>	0.168*	<sup>a</sup>
Conashaugh	48 & 50	0.079*	0.052*	0.032*
White	52 & 53	0.055*	0.059*	0.017
Caledonia	66 & 67	0.009*	0.058*	0.071*
Spackman	77 & 83	0.059*	<sup>a</sup>	0.036*
VanCampen	30 & 33	0.048	0.043	0.099
VanCampen	33 & 36	0.032*	0.013*	0.008
VanCampen	30 & 36	0.030	0.029	0.123
Dunnfield	70 & 73	0.095*	0.082*	0.083
Dunnfield	73 & 75	0.043	0.031*	-0.062
Dunnfield	70 & 75	0.064*	0.051*	0.090

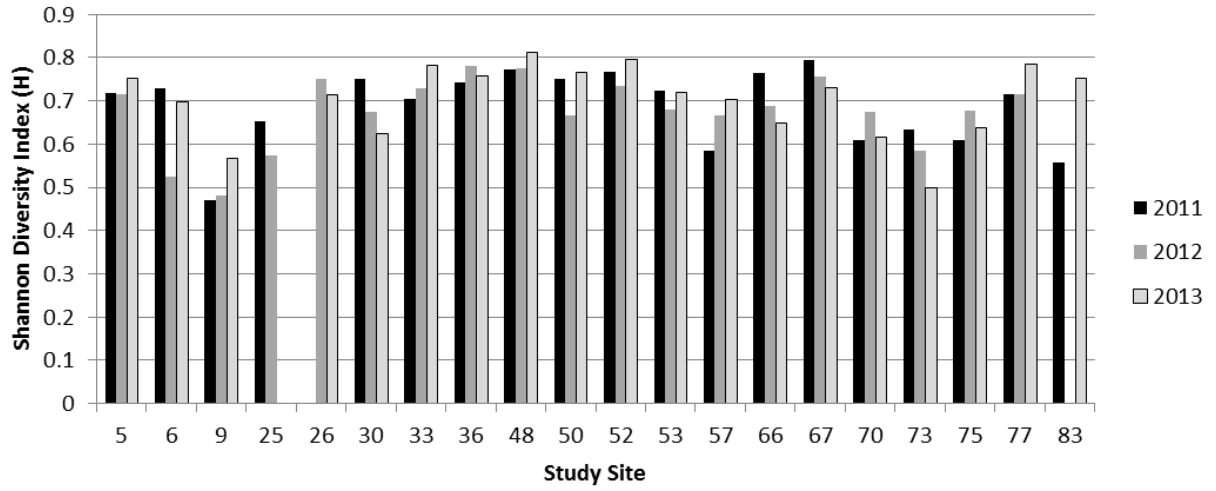
<sup>a</sup> indicates a site that was not sampled that year.

**Table 2:** Sampled population, average diversity, and number of fixed alleles at each site during the study.

Stream	Site	N			Avg Diversity			Monomorphic Loci		
		2011	2012	2013	2011	2012	2013	2011	2012	2013
Adams	5	6	<sup>a</sup>	16	0.71780	0.71596	0.75126			
Adams	6	24	30	28	0.72954	0.52493	0.69765			
Dingmans	9	11	30	30	0.46969	0.47980	0.56744	1		
Hellers	25	4	30	<sup>a</sup>	0.65178	0.57465	<sup>a</sup>			
Hellers	26	<sup>a</sup>	16	32	<sup>a</sup>	0.75000	0.71366			
VCB	30	1	2	1	0.75000	0.67514	0.62500	NA	NA	NA
VCB	33	19	30	30	0.70448	0.72853	0.78248			
VCB	36	30	30	31	0.74273	0.78115	0.75608			
Conashaugh	48	20	<sup>a</sup>	30	0.77308	0.77521	0.81052			
Conashaugh	50	30	30	30	0.74986	0.66568	0.76589			
White	52	7	30	9	0.76648	0.73411	0.79575			
White	53	11	30	19	0.72294	0.68026	0.72013			
Fuller	57	23	30	30	0.58551	0.66695	0.70261			
Caledonia	66	10	30	30	0.76307	0.68912	0.64887			
Caledonia	67	32	30	30	0.79343	0.75678	0.73015			
Dunnfield	70	3	10	3	0.60952	0.67368	0.61666	1		1
Dunnfield	73	5	13	1	0.63333	0.58500	0.50000	1		NA
Dunnfield	75	25	30	28	0.60928	0.67748	0.63831			
Spackman	77	30	30	30	0.71384	0.71411	0.78389			
Spackman	83	3	<sup>a</sup>	31	0.55833	<sup>a</sup>	0.75324	2		

<sup>a</sup> indicates a site that was not sampled that year.

**Figure 1:** The average community diversity as calculated by the Shannon Diversity Index (H) at each site during the study.



## **Chapter 5**

### **Conclusion**

This research began as a project between the National Park Service, the Leetown Science Center (US Geological Survey), and the Conte Anadromous Research Center (USGS) as an investigation of the effects of stocked fish and warming stream temperatures on the presence and genetic integrity of brook trout within Delaware Water Gap National Recreation Area. A fish community survey and a brook trout movement study using passive integrated transponder (PIT) tags were also associated with the study.

The research began in July 2011; a group of six people surveyed 83 stream reaches in eighteen unconnected tributaries to the Delaware River. We used two backpack electroshockers, half a dozen 5-gal buckets, half a dozen nets, a portable scale, and measuring board to complete the surveys. At each site with brook trout, we used anesthetic, surgical scissors, and a scalpel to take a piece of anal fin from 30 brook trout and insert a PIT tag into individuals at three select sites. The field team finished the work in the second week of August 2011.

Ten days after field work was completed the Hurricane Irene came up the Atlantic coast and inland toward the northeastern United States. A week later Tropical Storm Lee followed a similar path through the region. The pair of storms dropped over 33cm of precipitation on the Delaware Water Gap region and caused near-record high flooding in several locations in or near the park. The Delaware River itself was fairly unaffected because two upstream control dams on the East and West Branches maintain the main stem of the river at a base flow of  $50 \text{ cms}^{-1}$ .

Re-examination of the study area one and two months after the flood subsided to scan for PIT tagged fish yielded only six individuals from the original 165 tagged only a few weeks



before. The vast majority of brook trout that were larger than 60mm had been displaced from their original 150m long reaches or otherwise not recaptured. Additional scanning with the portable antenna above and below the tagged reaches yielded no additional tagged individuals, but I did observe untagged adult brook trout in these above- and below-reach areas. Local populations had been redistributed but not entirely removed.

The three reaches were chosen for the PIT tag part of the study based on the abundance of the brook trout populations, which were higher than other areas of the park. However, it resulted that the three PIT tag reaches were all located in the northwestern region of the park. Visual and quantitative assessment described in chapter two shows that the northwestern region had the highest physical disturbance compared to other regions in the park. Thus, I do not know how high flows affected young of the year and age 1+ brook trout in other regions immediately after the flood.

I attempted to extrapolate some of the larger trends in brook trout occupancy and abundance in relation to changes in the physical environment and surrounding fish community. Occupancy and abundance were compared with characteristics and changes in the physical environment with two-way analysis of variance and multivariate analysis. They were compared with fish community richness and diversity by linear modeling. Full descriptions of the applied analysis can be found in the first and second manuscripts (chapters three and four).

I also looked at the apparent gain, loss, and redistribution of brook trout populations through the lens of spatial and temporal genetic changes. I used eight microsatellite loci to measure molecular variance, heterozygosity, allelic frequency, and linkage disequilibrium within and between populations. I hierarchically structured populations both spatially and temporally to

determine how populations differentiated from each other. Again, the full description of genetic analysis is described in the third manuscript (chapter five).

Brook trout occupancy was associated with several environmental characteristics that fit with much of the previous literature. Brook trout were strongly related to colder stream temperatures and heterogeneous substrate and mesohabitat. They were also moderately associated with eastern hemlock forests, which agrees with Ross et al. (2002) who documented the occurrence relationship between brook trout and hemlock forests. The count and volume of large woody material (LWM) poorly related to changes in brook trout abundance. This agrees with literature such as Neumann and Wildman (2002) and Warren and Kraft (2003) who suggest that LWM plays little consistent role in the growth and survival of salmonids, and that stream dimensions and habitat have a larger effect on trout (Neumann and Wildman 2002) – a relationship that was also agreed with our current findings. In flood scenarios, LWM and other large individual objects are thought act as potential refugia (Shirvell 1990), although it is not a necessary component of post-flood survival and resilience (Dolloff et al. 1994). None of these results are surprising, but it does suggest that other results are based on systems set in very different conditions.

Brook trout occupancy appeared to be fairly stable over the course of the study. The flood did not extirpate any populations, regardless of population abundance, location, or apparent disturbance. After the flood, occupancy changed at only two study reaches that experienced temporary colonization by single age 1+ brook trout. Both of these colonizations were short-lived and the reaches were devoid of brook trout again in 2013.

Overall brook trout occupancy across DEWA was lower than originally anticipated by the park ecologist even before the flood (R. Evans, personal communication). Of the original 83 sites

in 18 streams chosen for the study, 36 sites in 10 streams maintained brook trout populations. The implication is that brook trout populations are declining across the park over time. However, any population decline in the park is more likely a slowly occurring change that is not the result of large one-time disturbance, but the result of something much more persistent.

Brook trout abundance did not reflect the same kind of stability as occupancy did over the course of the study. Before the flood, abundance in the park was low in nearly all locations; we found populations with more than thirty brook trout at only four of twenty-one 150m-long sites. Brook trout density was very low. High post-flood recruitment led to abundance increases of 20-900% in brook trout populations in 2012. Between 2012-2013, brook trout abundance decreased 3-90%. However, the abundance in 2013 was still an increase over the 2011 baseline abundance.

Increased brook trout abundance was not evenly distributed across size classes. Of course, age 1+ brook trout (> 96mm) cannot recruit into all study sites across a landscape at once. Overall, age 1+ trout declined slightly in just three study sites and remained relatively stable throughout the rest of the region. The vast majority of increased abundance was the result of high young-of-year (YOY) recruitment.

The large shifts in abundance indicate a good overall resilience to disturbance in the system. Stream resources and habitat have the capacity to contain and potentially sustain high brook trout density and biomass. Population abundance did decline in the third year of the study, but YOY overwintering survival is highly variable and high mortality has been linked to small YOY length (Hunt 1969). Brook trout YOY made up a high proportion of total abundance in 2012 and were on average smaller than the 2011 baseline. Moderate YOY mortality over the

2011-2012 winter would appear as overall population decline but still fall within normal overwinter mortality.

This all brings to question the resilience (Holling 1973) within the park surrounding the 2011 flood. Brook trout did not appear to have any particularly negative response to the flood, but this may be an example how populations in DEWA absorbed a major disturbance. The physical disturbance to the environment was apparent in chapter 2, but no other analysis showed that the flood affected the biological processes of brook trout. Although the lack of brook trout response to the flood could indicate a natural species adaptation to high flows in headwater streams, not all brook trout populations in other areas affected by the same flood had such a positive response in 2012 and 2013.

The resilience of brook trout abundance in DEWA appeared to be more influenced by the surrounding fish community than by any environmental factor. Stream temperature is often cited as the biggest factor limiting brook trout abundance and occupancy both in the past (Hudy et al. 2008) and modeled into the future (Trumbo et al. 2010; Wenger et al. 2011), but community richness and diversity, measured by the Shannon Index (H), was more closely related to post-flood population growth than stream temperature was. Where community diversity was high there was little to no increase in brook trout abundance, but where diversity was very low there was massive increase in brook trout abundance, over 900% in some places.

The relationship between post-disturbance abundance response and community diversity may be indicative of the multi-faceted problems causing brook trout declines in a warming climate. The cold water fish are less tolerant of warmer stream temperatures, which better suit a host of generalist and warm water fish species. Additional species and fish density increase competition for food and habitat resources, while some generalist species are more aggressive

and piscivorous than the brook trout and dace common to most brook trout communities. Brook trout not only face degraded environmental conditions that put them at an energetic disadvantage, but also face increased competition and predation. Such negative interspecies interactions have been previously noted and modeled between different species of trout (Hearn, 1987; Wenger et al. 2011), but similar negative interactions arise from increased competition with a variety of different generalist fish.

Across the landscape, this pattern of negative diversity interaction was most visible in downstream reaches that were wider, more open, and were well connected to the main stem of the Delaware River. Initial landscape analysis showed the strong influence of reach location between sites located upstream or downstream of natural barriers that prevented upstream movement by generalist fish. Downstream reaches, while not always significantly warmer than upstream reaches in the same tributary, nearly always had much higher community diversity.

The connectivity of the landscape played a big role in how the fish community, and therefore brook trout abundance, was structured in the park. The geology of the region creates a highly fragmented riverscape divided by large waterfalls and significant quantities of exposed bedrock streambed. Other studies tell us that large barriers such as waterfalls generally prevent downstream fish migration (Letcher et al. 2007) and they certainly prevent upstream fish migration. This ensures that, although stream temperatures may warm, generalist fish communities will not infiltrate upstream reaches naturally. Downstream brook trout populations are subjected to both rising temperature and invasive fish communities while upstream brook trout populations are only subject to confronting rising temperature and therefore appear to be more resilient after a major disturbance.

Upstream brook trout populations are not entirely protected from generalist species invasion regardless of natural fragmentation. Many of the man-made barriers in the park were removed in the past fifty years, however many small impoundments remain outside of the park boundary. These small warm ponds are subject to the same washout and population redistribution during floods as stream populations are and possibly occur more frequently depending on spring high water. Fish washed out of impoundments result in many of these warm water lentic species being found in stream pools in upstream headwaters as well. These upstream warm water washouts are not as diverse or abundant as those found in downstream reaches, but chapter 3 shows they still have a strong negative impact in cool headwater streams.

Because community diversity has a strong negative effect on the increase of population abundance and all abundance increased due to brook trout YOY recruitment while age 1+ brook trout abundance remained stable, it would logically follow that a diverse warm water community most directly impacts brook trout YOY survival. Such an effect would also be responsible for a persistent brook trout decline. Very low YOY recruitment and survival that can no longer compensate for natural adult mortality and emigration drains population abundance slowly over time. Peripheral brook trout populations (Haak et al. 2010) at the edges of their range and habitat are the most at risk to this influence.

Peripheral populations are some of the most important populations to monitor because they tend to contend with a range of biotic and environmental stressors. Their persistence and survival in adverse conditions may indicate traits or adaptations that will help maintain brook trout populations into the future. Such populations may not have experienced the same high resilience as other brook trout populations in DEWA, but still doubled or tripled their abundance

after the flood from very low abundance (< 10 individuals) to more sustainable levels (> 30 individuals).

The increase in brook trout abundance appears at first glance to be a benefit to populations, but the genetic consequences of such a population explosion from a small effective breeding population may lead to other problems including inbreeding, genetic temporal instability, and increased differentiation between populations. Based on the genetic analysis in chapter five, populations were already highly structured and differentiated throughout the landscape before the flood occurred. The 2011 flooding may have actually displaced individuals and increased gene flow between populations in the same stream.

The genetic temporal stability of brook trout populations varied in the two intervals between years of the study. Comparing population genotypes of study sites between 2011 and 2012, the years directly before and immediately after the flood event, showed significant changes in  $F_{st}$  values in ten of the seventeen sites. Two of the non-significant sites had negative pairwise  $F_{st}$  values likely caused by population samples that contained too few individuals. The following time interval comparing genotypes between 2012 and 2013 were instead quite stable; only two sites showed significant change in  $F_{st}$ .

It is difficult to interpret a trend with only two time-steps. If genetic variability within sites was consistent in the years before the flood, then the 2011 storm event was a significant break in the trend and altered the genotypic composition of within-site populations. Alternatively, the changes in genetic variability could be similar to the results found by Heath et al. (2002) in steelhead trout whereby multi-decadal genetic analysis showed no long term genetic temporal stability.

The changes to genetic diversity in brook trout populations before and after the storm, potentially influenced by individual displacement within the stream, also altered within-stream heterozygosity. In both 2011 and 2012, study sites located in the same stream and separated by a large natural barrier were significantly differentiated from each other. Only one stream did not have this level of differentiation. However, in 2013 half of the streams were no longer significantly different. The downstream displacement and temporary gene flow increased genetic similarity within the same stream.

A final genetic concern is the result of monomorphic or fixed loci within a population. In 2011, brook trout populations at five study sites in four streams had at least one monomorphic locus. Populations at these sites each had fewer than ten individuals caught during sampling, and the monomorphic loci indicate these populations have probably maintained very low abundance for a number of generations. Interestingly, while all of these sites exhibited the same increased population abundance in 2012 none of them were found with monomorphic loci. This is a strong indication that at least a portion of the 2012 brook trout population originated in another part of the stream that did not have the same combination of fixed alleles.

Most released fixation was temporary. By 2013 three of the initial five brook trout populations with monomorphic loci were again fixed. These populations started with extremely low abundance (< 5 individuals) and any increased abundance still left a small population of brook trout (< 15 individuals) in peripheral edge habitat with stream temperatures at the warmer end of brook trout thermal maxima and moderate to high community diversity. Brook trout displaced into these sites did not survive and fixed loci returned. This may indicate the presence of genetic traits in peripheral populations that allow them to persist in poor habitat conditions, or



it could indicate that these peripheral brook trout populations are demonstrably less resilient and may soon be extirpated.

Whether it is in terms of flow or precipitation recurrence intervals, the monetary cost of damages, or loss of human life, references to catastrophic floods are usually defined by some kind of numeric metric. By many of those metrics, the extended flooding caused by Hurricane Irene and Tropical Storm Lee were indeed catastrophic. Ecologically, however, I would be hesitant to call it such. The flooding caused significant changes to several abiotic environmental factors including substrate movement, mesohabitat composition, and the volume of in-stream large woody debris. Biotic communities also underwent significant changes after the flood, but not of a generally negative nature. Community composition and brook trout occupancy were stable and nearly all species abundance increased. Brook trout population resilience was high, and even though population size structure is significantly skewed it is a temporary effect; young trout will grow and the typical size distribution will return. The long-term effects on population genetics remain as the most substantial unknown problem going forward.

Not all brook trout populations respond as well to large floods such as the event precipitated by Hurricane Irene and Tropical Storm Lee in DEWA (Elwood 1969; Seegrist and Gard 1972; Hanson and Waters 1974; Hoopes 1975; Roghair et al. 2002; Carline and McCullough 2003; Howell 2006) and the population resilience exhibited there is a testament to the value of a conserved landscape, regardless of its connectivity. However, stable or increased population abundance does not indicate a stronger population from a management perspective. Brook trout populations examined in this dissertation have been severely altered in length and age distribution and genetic structure. I believe most of these brook trout populations will maintain higher abundance for several years, but other persistent factors like warmer stream

temperatures and invading warm water fish species will continue to diminish these populations over time. Populations that are resilient in response to one kind of disturbance are still affected by multiple persistent stressors that will invariably reduce their overall resilience as well, as seen in the peripheral populations.

## References

- Carline, R., McCullough, B. (2003). Effects of floods on brook trout populations in the Monongahela National Forest, West Virginia. *Transactions of the American Fisheries Society*, 132(5), 1014-1020.
- Dolloff, C., Flebbe, P., Owen, M. (1994). Fish habitat and fish populations in a southern Appalachian watershed before and after Hurricane Hugo. *Transactions of the American Fisheries Society*, 123(4): 668-678.
- Elwood, J. W., Water, T. F. (1969). Effects of flood on food consumption and production rates of a stream brook trout population. *Transactions of the American Fisheries Society*, 98(2), 253-262.
- Haak, A., Williams, J., Neville, H., Dauwalter, D., Colyer, W. (2010). Conserving peripheral trout populations: the values and risks of like on the edge. *Fisheries*, 35(11): 530-549.
- Hanson, D., Waters, T. (1974). Recovery of standing crop and production rate of a brook trout population in a flood-damaged stream. *Transactions of the American Fisheries Society*, 103(3). 431-439.
- Hearn, W. (1987). Interspecific competition and habitat segregation among stream-dwelling trout and salmon: a review. *Fisheries*, 12(5): 24-31.
- Heath, D., Busch, C., Kelly, J., Atagi, D. (2002). Temporal change in genetic structure and effective population size in steelhead trout (*Oncorhynchus mykiss*). *Molecular Ecology*, 11(2): 197-214.
- Holling, C. (1973). Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, 4, 1-23.
- Hoopes, R. (1975). Flooding as the result of Hurricane Agnes and its effect on a native brook trout population in an infertile headwater stream in central Pennsylvania. *Transactions of the American Fisheries Society*, 104(1), 96-99.
- Howell, P. (2006). Effects of wildfire and subsequent hydrologic events on fish distribution and abundance in tributaries of North Fork John Day River. *North American Journal of Fisheries Management*, 26(4), 983-994
- Hudy, M., Thieling, T., Gillespie, N., Smith, E.P. (2008). Distribution, status, and land use characteristics of subwatersheds within the native range of brook trout in the eastern United States. *North American Journal of Fisheries Management*, 28(4): 1069-1085.
- Hunt, R.L. (1969). Overwinter survival of wild fingerling brook trout in Lawrence Creek, Wisconsin. *Journal of the Fisheries Research Board of Canada*, 26(6): 1473-1483.
- Letcher, B., Nislow, K., Coombs, J., O'Donnell, M., Dubreuil, T. (2007). Population response to habitat fragmentation in a stream-dwelling brook trout population. *PloS one*, 2(11): e1139.  
DOI: 10.1371/journal.pone.0001139
- Neumann, R., Wildman, T. (2002). Relationships between trout habitat use and woody debris in two southern New England streams. *Ecology of Freshwater Fish*, 11(4): 240-250.
- Roghair, C., Dolloff, C., Underwood, M. (2002). Response of a brook trout population and instream habitat to a catastrophic flood and debris flow. *Transactions of the American Fisheries Society*, 131(4), 718-730.
- Ross, R. M., Bennett, R. M., Snyder, C. D., Young, J. A., Smith, D. R., Lemarie, D. P. (2003). Influence of eastern hemlock (*Tsuga canadensis* L.) on fish community structure and function in headwater streams of the Delaware River basin. *Ecology of Freshwater Fish*, 12: 60-65.

Seegrist, D., Gard, R. (1972). Effects of floods on trout in Sagehen Creek, California. *Transactions of the American Fisheries Society*, 101(3), 478-482.

Shirvell, C. S. (1990). Role of instream rootwads as juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) cover habitat under varying streamflows. *Canadian Journal of Fisheries and Aquatic Sciences*, 47: 852-861.

Trumbo, B., Hudy, M., Smith, E.P., Kim, D.Y., Wiggins, B.A., Nislow, K.H., Dolloff, C.A. (2010). Sensitivity and vulnerability of brook trout populations to climate change. In *Proceedings of the 10<sup>th</sup> Annual Wild Trout Symposium, West Yellowstone, MT*.

Warren, D., Kraft, C. (2003). Brook trout (*Salvelinus fontinalis*) response to wood removal from high-gradient streams of the Adirondack Mountains (NY, USA). *Canadian Journal of Fisheries and Aquatic Sciences*, 60: 379-389.

Wenger, S., Isaak, D., Dunham, J., Fausch, K., Luce, C., Neville, H., Reman, B., Young, M., Nagel, D., Horan, D., Chandler, GL. (2011). Role of climate and invasive species in structuring trout distributions in the interior Columbia River Basin, USA. *Canadian Journal of Fisheries and Aquatic Sciences*, 68: 988-1008.