# Major processes that shape Brook Trout genetic structure



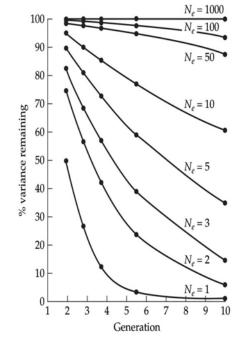
Eric Hallerman and Dave Kazyak

#### Brook trout and population genetic processes

- At all points in their natural history, Brook Trout would be subject to population genetics processes:
  - Mutation
  - Migration
  - Selection
  - Random genetic drift
  - Inbreeding
  - Coadaptation
- Let's consider these processes in the context of the natural (and un-natural) history of Brook Trout

#### Random genetic drift

- As they hung on in their glacial refugia, they would have been subject to random genetic drift...
- Random changes in allele frequency due to:
  - Founder effects
  - Sampling of breeders
  - Sampling of gametes
- Small populations lose genetic variation more rapidly than large populations.



RINCIPLES OF CONSERVATION BIOLOGY, Third Edition, Figure 11.3 @ 2005 Sinauer Associates, Inc.

#### Random genetic drift

- Recolonization of the deglaciated landscape likely involved rather few individuals, leading to founder effects.
  - These few founders could not have had all the genetic variation that was in the population from which they dispersed.
- Random drift is a non-selective force.
  - Populations tend to lose rare alleles.
  - Some of these lost alleles may have adaptive value.

#### Random genetic drift

- Concept of effective population size,  $N_{\rm e}$ .
  - Relates to how much genetic variation a population can transmit, given sex ratio among breeders, variation in breeding success and occurrence of any demographic bottlenecks.
- Estimation of  $N_{\rm e}$ :
  - N<sub>e</sub> can be estimated directly if we know these demographic parameters.
  - $N_{\rm e}$  can be estimated indirectly from genotype frequencies

#### Population genetic processes

- Finite populations *lose* genetic variation how can they *gain* new variation?
  - Mutation
  - Gene flow

#### Mutation

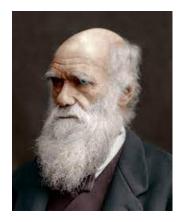
- = Spontaneous change in genetic coding
- The *ultimate* source of all genetic variation
- Most mutations are *not* adaptive in the ecological or genetic contexts in which they arise
- Most mutations are *lost* to selection or drift
- Some mutations *are* adaptive and critical to evolutionary adaptation
- Note that large populations lose fewer mutations to drift, which aids in their persistence

### Migration

- *Genetically effective* migration = movement from population of birth to another population, followed by reproduction
- Sometimes termed *gene flow*



- Links populations genetically
- Often contributes variation of adaptive value



#### Selection

- = Differential survival and reproductive success of different phenotypes and underlying genotypes
- *Critical* to adaptive evolution!
- The *rate* of adaptive evolution depends on:
  - selection intensity,
  - heritability of trait,
  - allele frequencies at fitness-related loci,
  - mode of selection...
- We don't generally know which genes are acted upon by selection (though we are making progress on that!)

#### Coadaptation

- Sometimes, fitness depends upon expression of certain combinations of alleles at fitness-related loci, termed coadapted gene complexes.
- Combinations arise by chance, and are retained by natural selection, a process termed *coadaptation*.

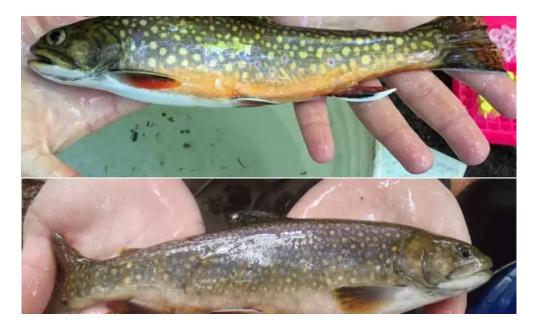
Coadaptation may be driven by:



- Adaptation to local ecological conditions (more on that later)
- Combinations of alleles across genome that simply work best together

#### **Outbreeding depression**

- When differentially coadapted populations interbreed, it can lead to *breakdown* of coadapted gene complexes, or *outbreeding depression* 
  - E.g., following interbreeding of stocked with wild trout



#### Multiple processes can act simultaneously!

- These processes may be in dynamic tension within a population, e.g.:
  - Mutation and drift how many alleles may be maintained in a population
  - Selection and migration clinal variation of allele frequency
  - Selection and random drift loss of variation due to random drift can overwhelm natural selection and lead to loss of adaptive potential

### Processes may be mutually reinforcing!

- Small, isolated populations may lose variation by drift and also be subject to inbreeding
  - <u>Case study</u>: Florida panther showed kinked tails, cryptorchid males, low breeding success

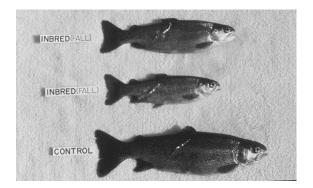




- Introduction of new genetic material increased genetic variation, led to outcrossing, reversed these problems
- Termed *genetic rescue*

# Inbreeding

- = Mating among relatives
- Can lead to loss of fitness = *inbreeding depression*, affecting:
  - Survival
  - Growth
  - Reproductive traits
  - Disease resistance
  - Etc.



- Can be calculated for individuals if the pedigree is known
- Can be estimated for populations from genotype frequencies at genetic marker loci

#### Inbreeding

• Over deep time, an isolated population can adapt to inbreeding by purging maladaptive alleles.



Owens pupfish



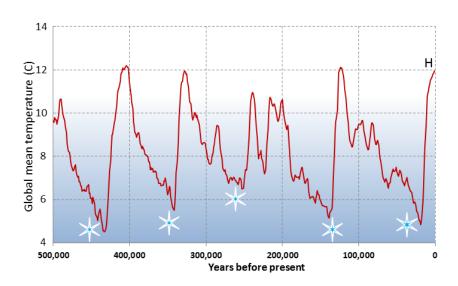
• Recently isolated populations, however, would be expected to suffer from inbreeding depression.

## Natural history of Brook Trout

Population genetic processes are superimposed on deeper patterning from natural history

#### Natural history of Brook Trout

• North America has been subject to a cycle of glaciation and deglaciation, affecting all life



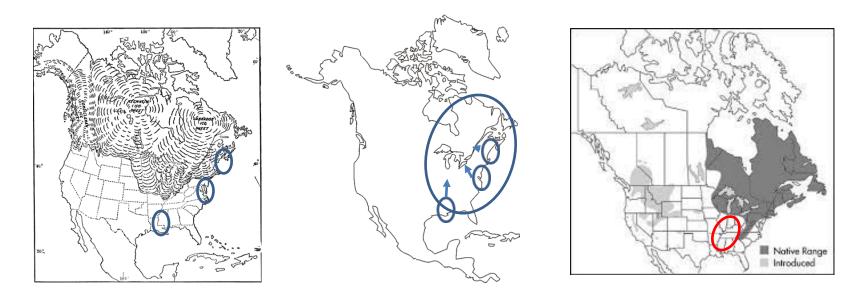
Historical temperature variation and ice ages



#### North America 18,000 YBP

# Natural history of Brook Trout

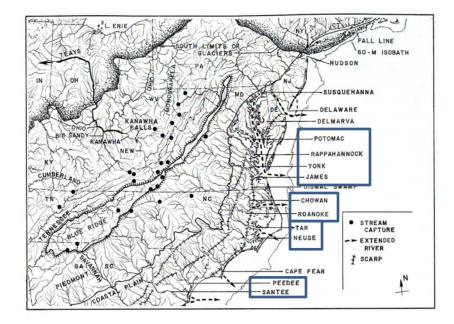
- Glaciation contraction of distribution into glacial refugia
- Deglaciation recolonization of the landscape



• This dynamic has shaped the deepest patterning of the population genetic structure of brook trout

#### Post-glacial dispersal of Brook Trout

- How did Brook Trout cross drainage divides?
- Stream capture:
  - The dots show locations of over twenty known stream-capture events in our region
- Local inland flooding
- Coastal dispersal:
  - Brook trout are marine dispersers
  - Some now-separate rivers were joined during the Pleistocene:
    - All rivers entering Chesapeake Bay
    - Roanoke and Chowan rivers
    - Tar and Neuse rivers
    - Pee Dee and Santee rivers

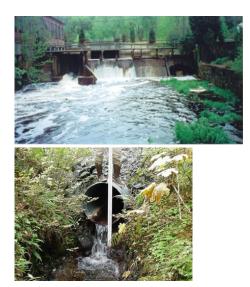


#### Population genetic patterning

- "Deep" patterning comes from natural historical processes...
- …Onto which recent population genetic processes add their signatures…
- ...And onto which anthropogenic impacts add their own signatures...

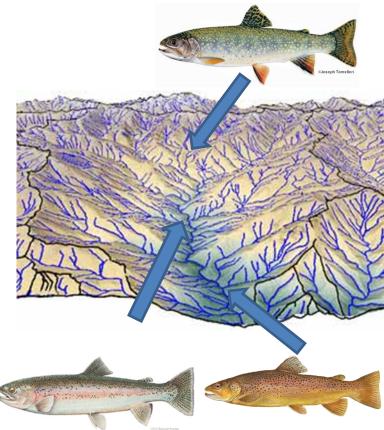
### Un-natural history of Brook Trout

- European colonization of North America, population growth, overexploitation, habitat alteration, introduction of non-native species
  - fragmentation of habitat
  - loss of populations
  - isolation of populations

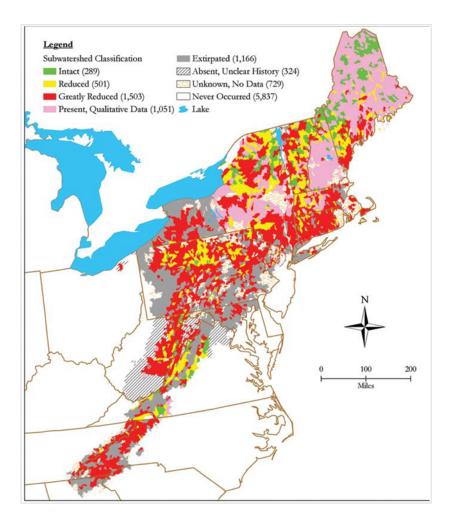








# The distribution and genetic structure of Brook Trout have been impacted by these anthropogenic effects



- EBTJV Brook Trout extirpated from 21% of historic range
- Many local populations now isolated
  - Heightened drift and inbreeding
  - Smaller populations have less capacity for evolutionary adaptation.
- And there's another issue...

#### Stocking of Brook Trout

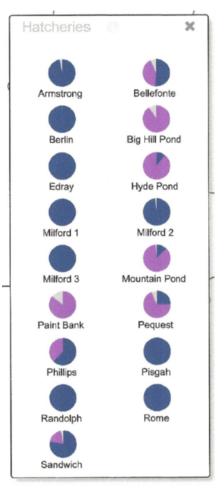
• To reverse the decline of the species, wide-spread stocking began in the mid-1800s





#### Hatchery strains of Brook Trout

- What is a "strain"?
  - Not a population genetic concept
  - It's a *breeder's* concept a population that has been held in culture for at least three generations that has predictable performance under specified conditions.
  - There's a Brook Trout strain registry (H. Kincaid, 1990s) laying out founding resources, breeding history, and key performance characters
  - Strains often transferred between hatcheries, crossed, ...
- Most Brook Trout strains are from the Northeast
- Before genetic differentiation was recognized, brook trout of a few narrow origins were widely stocked...



Origins of Brook Trout hatchery strains, *K* = 10

### Impacts of hatchery Brook Trout

- Ecological impacts from competition?
- Interbreeding?
  - Effects can range from eventual loss of hatchery background, to stable introgression, to replacement of native populations.
  - Insights from recent data...
- Genetic impacts from introgression?
  - Loss of local adaptation?
  - Results from Rainbow Trout suggest that this is plausible:
    - Araki et al. 2007. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science, 318:100–103.
    - Araki et al. 2009. Carry-over effect of captive breeding reduces reproductive fitness of wild-born descendants in the wild. Biol. Lett., 5:621–624.
  - Could introgression compromise the viability of native populations?



#### A view to the future

- From a genetic viewpoint, what are our goals for management of Brook Trout?
  - Maintain short-term viability
  - Maintain long-term adaptive potential
    - Especially in the face of anthropogenic impacts, including climate change
    - Note that mutation is just too slow to replace variation lost to drift in small, isolated populations

