Whither the Hybrid Swarm?

Stream environments segregate cutthroat and rainbow trout to control hybrid zone locations

Mike Young, Kevin McKelvey, Dan Isaak
Stream Temperature & Species Distributions

Contribution of Big Fish Data

NorWeST Stream Temperature

Frequency of Occurrence

Isaak et al. 2017. Big biology meets microclimatology. Ecological Applications
Cutthroat & Rainbow are Similar but Different
Sister species, diverged 2–10 million years ago
Fluvial, spring spawners
Hybridization in Fish is Common

- External fertilization
- Incomplete reproductive isolation may lag for millions of years after species divergence

Cutthroat & Rainbow Trout (a.k.a. the Poster Children for Invasive Hybridization)

- Presence of post-F1 hybrids after stocking
- Ubiquity of hybrids at some locations
- Movement of hybrids away from stocking locations
- Hybrids beget more hybrids...

Spawned Fears of:
- "The Swarm" & "Genomic Extinction"
- "Dark Power of the Genomic Ratchet"
A Random Sample to Document the Demise of Westslope CT

A priori Expectations:
1) Widespread hybridization,
2) Cutthroat trout would be rare

“...have been extirpated from 90% of historical habitat”

• 188 sites in 129 streams  
  (2\textsuperscript{nd} – 4\textsuperscript{th} Order)
• 3,865 fish genotyped

• 137/188 sites (73%) <5% RBT alleles
• 109/188 sites (58%) <1% RBT alleles

Admixture Patterns in Individual Fish

**Prediction:** Extensive admixture

**Observation:** Limited admixture at 188 sites

- **McKelvey et al. 2016**
  - 71% of fish nonadmixed WCT
  - 4% of fish nonadmixed RBT
  - 25% of fish hybrids

Hybrid swarms at 8 sites but 7 involved
Yellowstone CT stocking
Rainbow Trout Stocking is Pervasive
Montana has stocked 400,000,000 in 60 years

Real Question Should be
“How Do So Many Cutthroat Populations Persist Despite the Onslaught?”
Mechanism: Physiological Differences Among Cutthroat, Rainbows, & Hybrids

Metabolic traits of westslope cutthroat trout, introduced rainbow trout and their hybrids in an ecotonal hybrid zone along an elevation gradient

JOSEPH B. RASMUSSEN1*, MICHAEL D. ROBINSON1, ALICE HONTELA1 and DANIEL D. HEATH2

& other fishes...

Physiological adaptation along environmental gradients and replicated hybrid zone structure in swordtails (Teleostei: Xiphophorus)

Z.W. CULUMBER†, D.B. SHEPARD‡, S.W. COLEMAN‡, G.G. ROSENTHAL†1 & M. TOBLER†1
Motivation: Continued Misperception

- 20 million rainbow trout stocked in NFK Flathead River (& private hatchery releases)
- Flathead Lake rainbow trout source immediately downstream

Invasive hybridization in a threatened species is accelerated by climate change

Genomic extinction is inevitable!
Motivation: Continued Misperception

Muhlfeld et al. 2014. data plotted vs. NorWeST baseline

% Rainbow Alleles vs. NorWeST August Stream Temp (°C)
Let’s Test the Alternative Hypotheses:

1) Isolation By Distance (IBD; Wright 1943): Genetic patterns controlled only by dispersal & distance. If true, hybridization shouldn’t be predictable from stream habitat characteristics. “Hybrid Ratchet Effect”

2) Isolation By Environment (IBE; Wang & Bradburd 2014): Genetic patterns controlled by environment. If true, genetic patterns will be predictable from stream habitat characteristics.
A Definitive Hybridization Dataset

- Data aggregated from 12 previous Westslope studies
- 558 stream sites, 13,315 genotyped fish

~20,000 years of coexistence

~100 years of coexistence

PRTA 10 (%)
- △ ≤1
- ▲ 1–10
- ○ 10–20
- ● >20

Rainbow trout range
Link Data to Reach-Scale Habitat Descriptors

Consistent GIS datasets for all streams in West

NorWeST
Stream Temp

VIC flow metrics

3,000,000 stream kilometers

NHDPlus

Many others...
- Forest canopy
- Elevation
- Slope
- %Landuse
- Precipitation
- Etc...

### Habitat Descriptors Considered in Models

<table>
<thead>
<tr>
<th>Variable</th>
<th>Rationale</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Abiotic</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T: mean August temperature (°C)</td>
<td>Declining temperature (or its surrogate, increasing elevation) is related to decreases in rainbow trout presence and introgression. Rainbow trout have metabolic rates, growth efficiencies, oxygen consumption rates, and life histories that are better adapted to warmer, more productive habitats.</td>
<td>NorWeST</td>
</tr>
<tr>
<td>S: slope (%)</td>
<td>Increasing slope may lead to greater bioenergetic costs for upstream migrating rainbow trout. Many salmonid species show reductions in habitat occupancy with greater slope.</td>
<td>NHDPlus</td>
</tr>
<tr>
<td>MAF: mean annual flow (m³/s)</td>
<td>Larger, more productive streams are associated with rainbow trout, and smaller, less productive streams are associated with cutthroat trout.</td>
<td>VIC flow metrics</td>
</tr>
<tr>
<td>CFM: center of flow mass, the date when 50% of the mean annual flow has been discharged</td>
<td>High snowmelt-driven flows in late spring and early summer are associated with declines in rainbow trout recruitment.</td>
<td>VIC flow metrics</td>
</tr>
<tr>
<td>W95: number of winter days with flows among the top 5% for the year</td>
<td>High winter flows are positively related to rainbow trout presence and negatively related to cutthroat trout presence.</td>
<td>VIC flow metrics</td>
</tr>
<tr>
<td>E, N: easting and northing (m)</td>
<td>Geographic location can serve as a surrogate for climatic and geological covariates not otherwise represented.</td>
<td>Custom GIS script</td>
</tr>
<tr>
<td><strong>Biotic</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DT13: Distance (m) to mean August temperature &gt; 13 °C</td>
<td>Warmer streams may favor rainbow trout. Occurrence of rainbow trout peaked at this temperature in this region.</td>
<td>Custom GIS script</td>
</tr>
<tr>
<td>DF: Distance (m) to mean annual flow &gt; 2.83 m³/s</td>
<td>Larger streams may favor rainbow trout. This threshold exceeds those habitats generally suitable for cutthroat trout spawning. The shortest distance among: 1) the two previous variables, 2) habitat known to support a naturally reproducing population of rainbow trout, or 3) habitat stocked with rainbow trout within 10 years of the time of genetic sampling. Proximity to any of these four habitats is a surrogate for proximity to rainbow trout propagules.</td>
<td>Custom GIS script</td>
</tr>
<tr>
<td>DS: Shortest distance (m) to rainbow trout</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RRange: historical range of rainbow trout (yes/no)</td>
<td>Occupancy over evolutionary time enabled rainbow trout to colonize a larger portion of a watershed, for hybrid zones to stabilize at their highest longitudinal point, and for levels of introgression to achieve a quasi-equilibrium. In some cases, being in the range of rainbow trout</td>
<td></td>
</tr>
</tbody>
</table>

**Not considered:** road density, precipitation, elevation, wildfire
Developed 3 Logistic Regression Models
Probability Hybridization > 1% / 10% / 20% thresholds

\[
p = \frac{\exp(a + bx \ldots ny)}{1 + \exp[a + bx \ldots ny]}
\]

PRTA = Percent RBT alleles

<table>
<thead>
<tr>
<th>Introgression metric</th>
<th>Model</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>PRTA &gt; 1%</td>
<td>T + RTrange + DS + E + MAF + DT13 + W95 + S</td>
<td>575.87</td>
</tr>
<tr>
<td></td>
<td>T + RTrange + DS + E + MAF + DT13 + W95 + YCTI + S</td>
<td>576.23</td>
</tr>
<tr>
<td></td>
<td>T + RTrange + DS + MAF + E + DT13 + YCTI + S</td>
<td>576.72</td>
</tr>
<tr>
<td></td>
<td>T + RTrange + DS + E + MAF + W95 + S</td>
<td>576.88</td>
</tr>
<tr>
<td>PRTA &gt; 10%</td>
<td>T + RTrange + DS + DT13 + MAF + E</td>
<td>433.13</td>
</tr>
<tr>
<td></td>
<td>T + RTrange + DS + DT13 + MAF + E + YCTI</td>
<td>433.51</td>
</tr>
<tr>
<td></td>
<td>T + RTrange + DS + DT13 + MAF + E + W95</td>
<td>434.27</td>
</tr>
<tr>
<td></td>
<td>T + RTrange + DS + DT13 + MAF + E + S</td>
<td>434.32</td>
</tr>
<tr>
<td>PRTA &gt; 20%</td>
<td>T + RTrange + DT13 + MAF + E + DS</td>
<td>387.75</td>
</tr>
<tr>
<td></td>
<td>T + RTrange + DT13 + MAF + E</td>
<td>388.40</td>
</tr>
<tr>
<td></td>
<td>T + RTrange + DT13 + MAF + E + DS + S</td>
<td>389.23</td>
</tr>
<tr>
<td></td>
<td>T + RTrange + DT13 + MAF + E + DS + W95</td>
<td>389.35</td>
</tr>
</tbody>
</table>

Models Make Accurate Predictions & Are Robust

**PRTA > 10%**

<table>
<thead>
<tr>
<th>Predictor</th>
<th>$b_x$</th>
<th>SE</th>
<th>$z$</th>
<th>$p$</th>
<th>AUC</th>
<th>Threshold$^a$</th>
<th>Training data</th>
<th>10-fold CV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-1.34E+01</td>
<td>2.65E+00</td>
<td>-5.07</td>
<td>&lt;0.01</td>
<td>0.85</td>
<td>0.384</td>
<td>81.2%</td>
<td>81.0%</td>
</tr>
<tr>
<td>T</td>
<td>2.66E-01</td>
<td>1.00E-01</td>
<td>2.65</td>
<td>&lt;0.01</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RTrange</td>
<td>1.34E+00</td>
<td>2.94E-01</td>
<td>4.57</td>
<td>&lt;0.01</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DS</td>
<td>-1.34E-04</td>
<td>4.24E-05</td>
<td>-3.16</td>
<td>&lt;0.01</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DT13</td>
<td>-6.13E-05</td>
<td>2.35E-05</td>
<td>-2.63</td>
<td>&lt;0.01</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MAF</td>
<td>5.12E-01</td>
<td>1.90E-01</td>
<td>2.69</td>
<td>&lt;0.01</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>6.75E-06</td>
<td>1.51E-06</td>
<td>4.46</td>
<td>&lt;0.01</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Accurate despite...**

- Fish movement & age class mixing
- DS, DT13 are proxies for propagule pressure
- NorWeST model imprecision (+/- 1.0°C)
- Decadal trends ignored

Buehrens et al. 2013
A Hybrid Deficit?

Model response curves

Prob. PRTA > 10%

Stream distance (km)

% Rainbow alleles

August stream temperature (°C)

% Rainbow alleles

DS (distance to Rainbow source)

& in data summaries

Deficit?
Deficit Explanations:

1) Perhaps introduced rainbow trout have lower fitness outside their native range, are unable to spread as extensively, and have already reached their environmentally-mediated distribution?

2) Perhaps there are additional environments rainbow trout will colonize & hybridization will spread, but if so the establishment of hybrid zones takes a long time?

3) Perhaps large anadromous steelhead enhance propagule pressure throughout the native range of rainbow trout in the Pacific Northwest?

“Relaxation” Hypothesis:

1) Hybridization will decrease once local propagule pressure is reduced & could be reversible in some environments (e.g., small cold streams)
Scenario 1. Current: 31,600 km
Scenario 2. Equilibrium: 23,500 km (26% loss)
Scenario 3. Current +0.5°C: 27,500 km (13% loss)
Scenario 4. Equilibrium +0.5°C: 19,200 km (39% loss)
Scenario 5. Current +1.0°C: 23,900 km (24% loss)
Scenario 4. Equilibrium +1.0°C: 15,200 km (52% loss)

PRTA < 10%

- Also PRTA < 1% & <20%
- By stream length & volume

Table 4. Cutthroat trout habitat amounts relative to rainbow trout range.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>PRTA</th>
<th>Length</th>
<th>% change</th>
<th>Volume</th>
<th>% change</th>
</tr>
</thead>
<tbody>
<tr>
<td>Current</td>
<td></td>
<td>7,869</td>
<td>—</td>
<td>1,656</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>&lt;1%</td>
<td>9,863</td>
<td>2,854</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>&lt;10%</td>
<td>10,887</td>
<td>3,394</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Equilibrium</td>
<td></td>
<td>7,869</td>
<td>1,656</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>&lt;1%</td>
<td>9,863</td>
<td>2,854</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>&lt;10%</td>
<td>10,887</td>
<td>3,394</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Current + 0.5°C</td>
<td></td>
<td>6,302</td>
<td>-19.9%</td>
<td>1,245</td>
<td>-24.8%</td>
</tr>
<tr>
<td></td>
<td>&lt;1%</td>
<td>8,121</td>
<td>-17.7%</td>
<td>2,099</td>
<td>-26.5%</td>
</tr>
<tr>
<td></td>
<td>&lt;10%</td>
<td>9,939</td>
<td>-14.2%</td>
<td>2,582</td>
<td>-23.9%</td>
</tr>
<tr>
<td>Equilibrium+0.5°C</td>
<td></td>
<td>6,302</td>
<td>—</td>
<td>1,245</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>&lt;1%</td>
<td>8,121</td>
<td>—</td>
<td>2,099</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>&lt;10%</td>
<td>9,939</td>
<td>—</td>
<td>2,582</td>
<td>—</td>
</tr>
<tr>
<td>Current + 1.0°C</td>
<td></td>
<td>4,902</td>
<td>-36.9%</td>
<td>911</td>
<td>-45.0%</td>
</tr>
<tr>
<td></td>
<td>&lt;1%</td>
<td>6,723</td>
<td>-31.8%</td>
<td>1,615</td>
<td>-43.4%</td>
</tr>
<tr>
<td></td>
<td>&lt;10%</td>
<td>7,820</td>
<td>-28.2%</td>
<td>1,982</td>
<td>-41.6%</td>
</tr>
<tr>
<td>Equilibrium+1.0°C</td>
<td></td>
<td>4,902</td>
<td>—</td>
<td>911</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>&lt;1%</td>
<td>6,723</td>
<td>—</td>
<td>1,615</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>&lt;10%</td>
<td>7,820</td>
<td>—</td>
<td>1,982</td>
<td>—</td>
</tr>
</tbody>
</table>

Young et al. 2016. Climate, demography, and zoogeography predict thresholds in salmonid hybrid zones in Rocky Mountain streams. PLoS ONE 11: e0163563
Scenarios Formatted as User-Friendly Digital Maps for Conservation Planning

Look before leaping...

BIG
Website: Cutthroat-Rainbow Trout Hybridization

Cutthroat trout-rainbow trout hybridization

Papers

Dataset

Scenario Maps