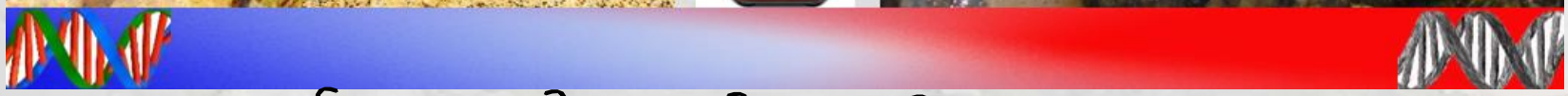
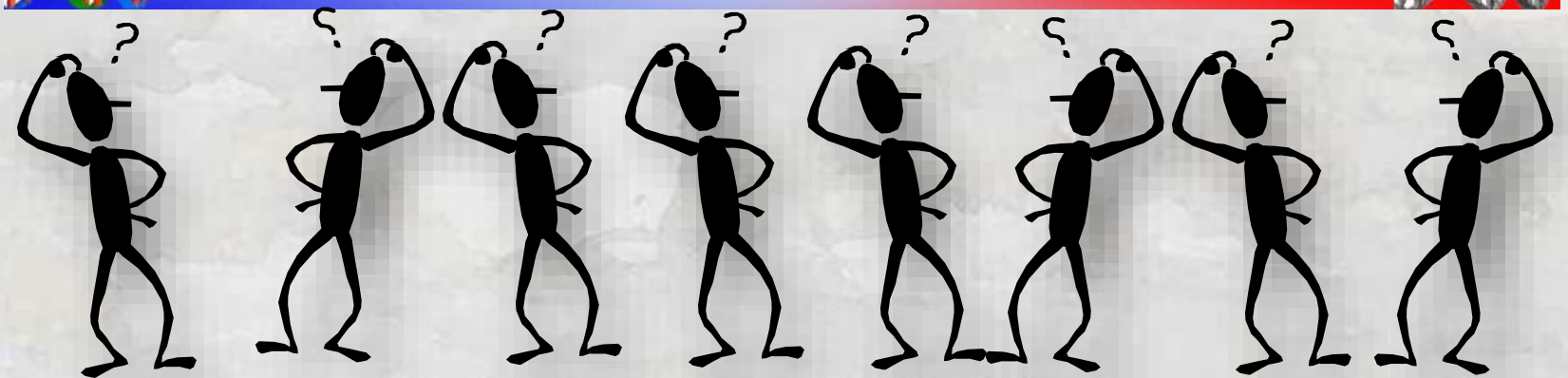
Whither the Hybrid Swarm?

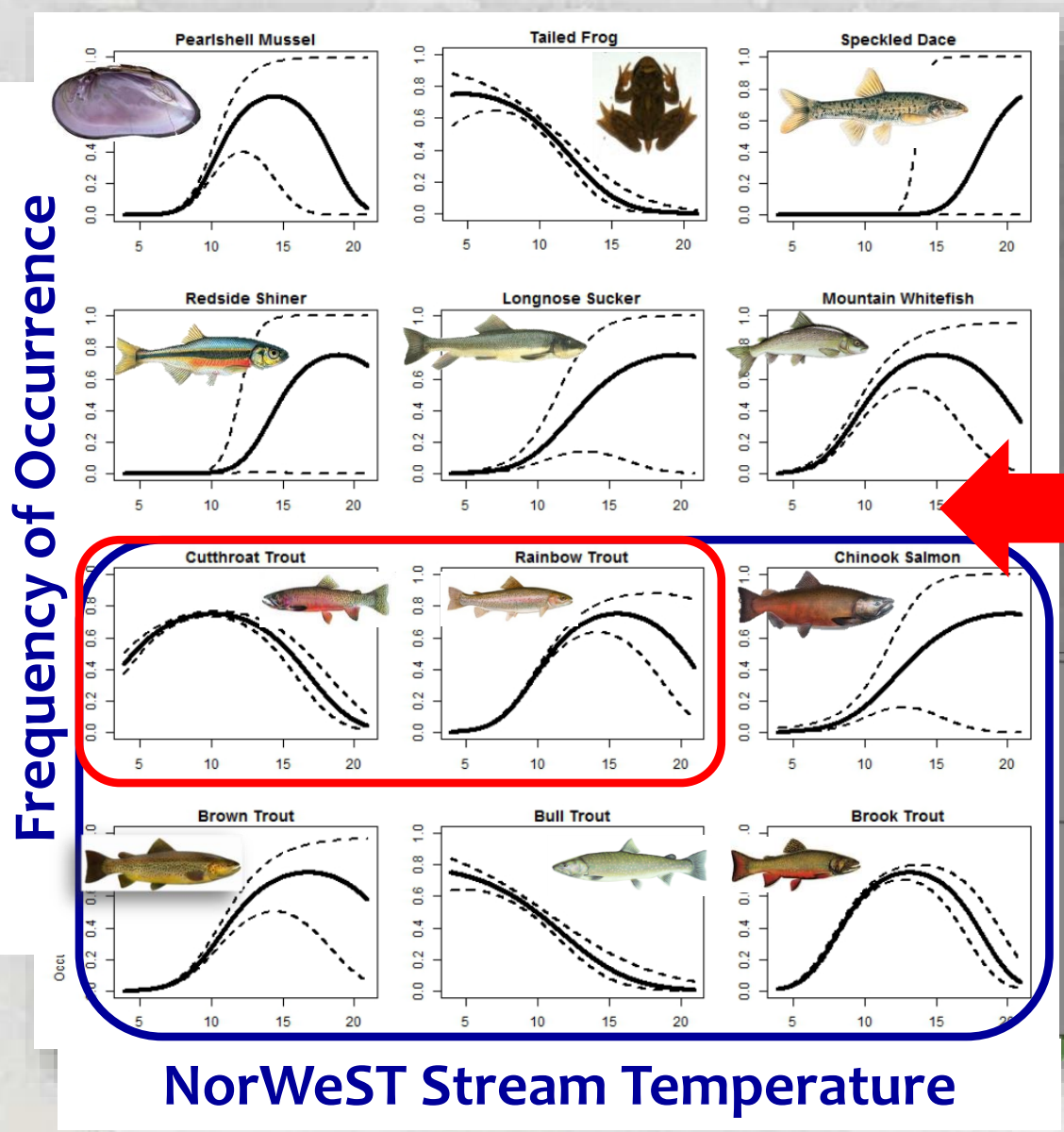
Stream environments segregate cutthroat and rainbow trout to control hybrid zone locations

Mike Young, Kevin McKelvey, Dan Isaak

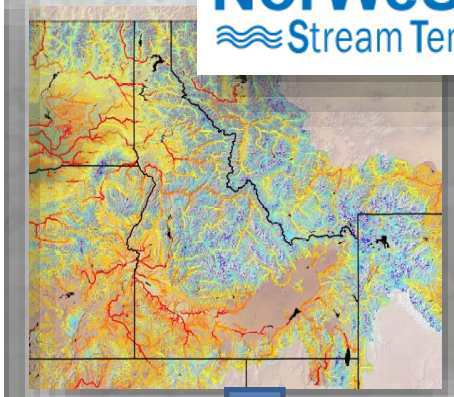




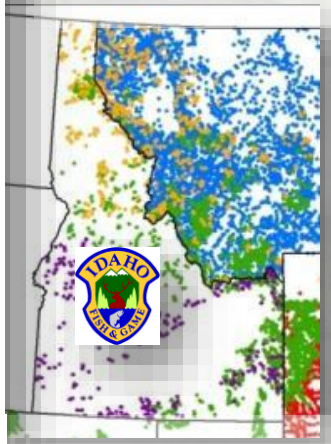
Stream Temperature & Species Distributions



NorWeST Stream Temp



BIG FISH Data



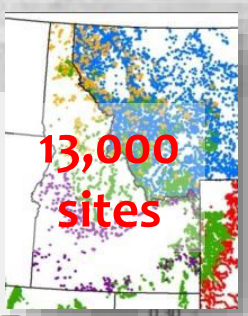
13,000 sites

Isaak et al. 2017. Big biology meets microclimatology. *Ecological Applications*

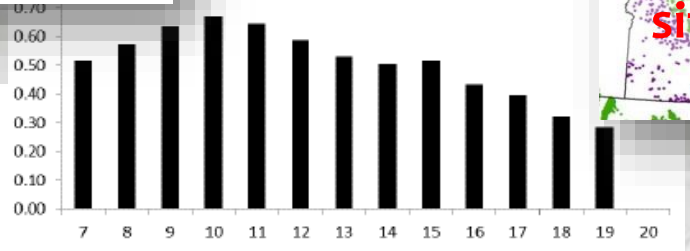
Cutthroat & Rainbow are Similar but Different

Sister species, diverged 2–10 million years ago

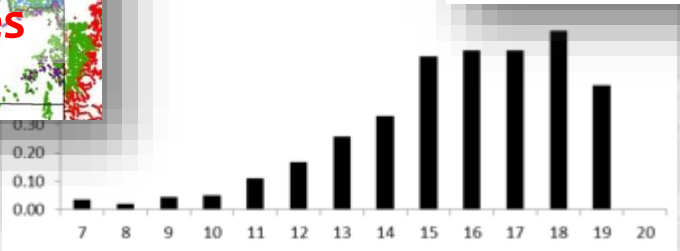
Fluvial, spring spawners



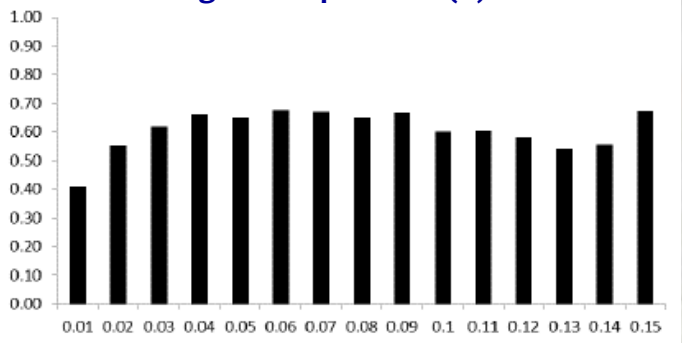
Proportion Occupied



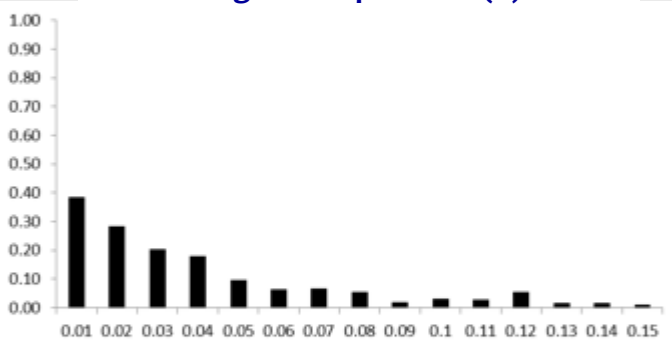
August temperature (C)



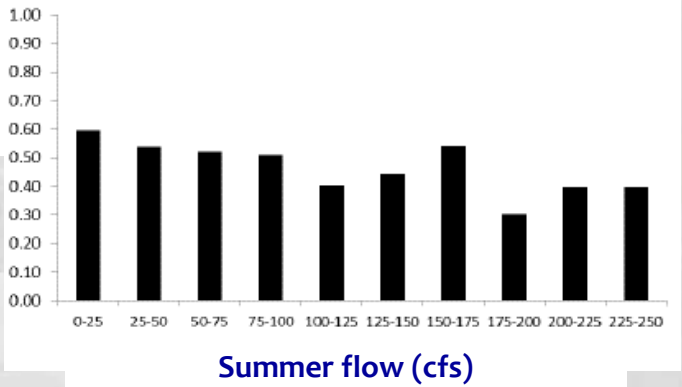
August temperature (C)



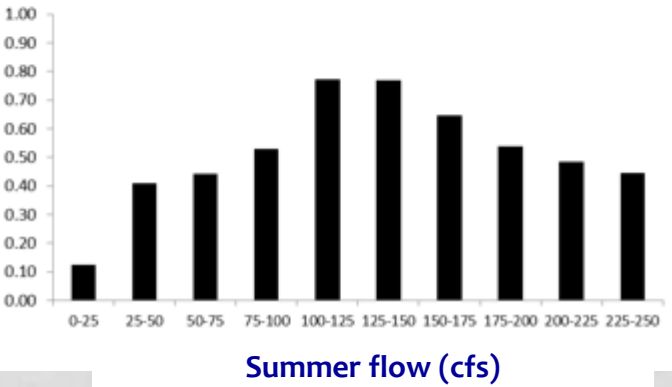
Reach slope (m/m)



Reach slope (m/m)



Summer flow (cfs)



Summer flow (cfs)

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"

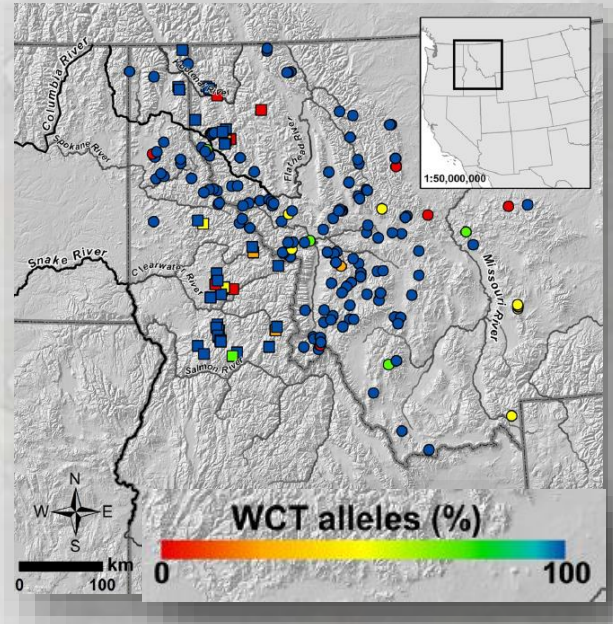
"Dark Power of the Genomic Ratchet"

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"



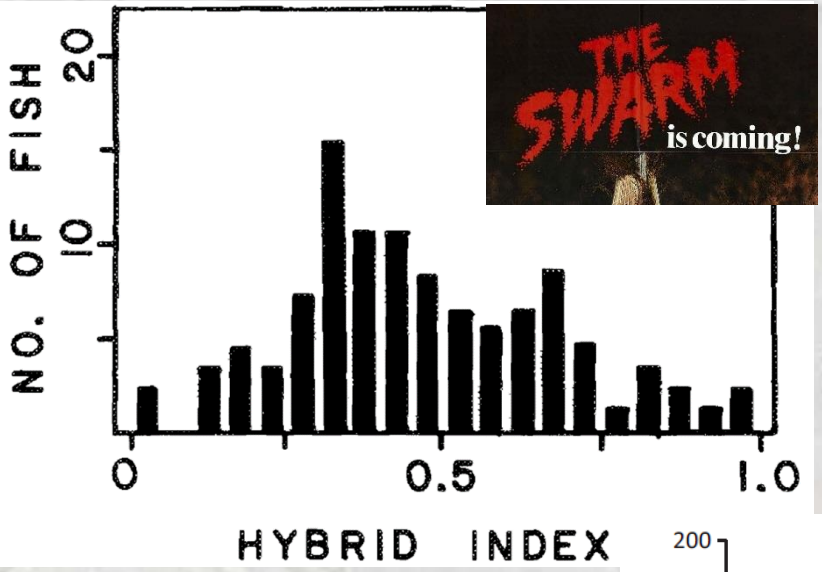
- 188 sites in 129 streams (2nd – 4th Order)
- 3,865 fish genotyped

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

McKelvey et al. 2016. Patterns of hybridization among cutthroat trout and rainbow trout in northern Rocky Mountain streams. *Ecology and Evolution*. **6**:688–706.

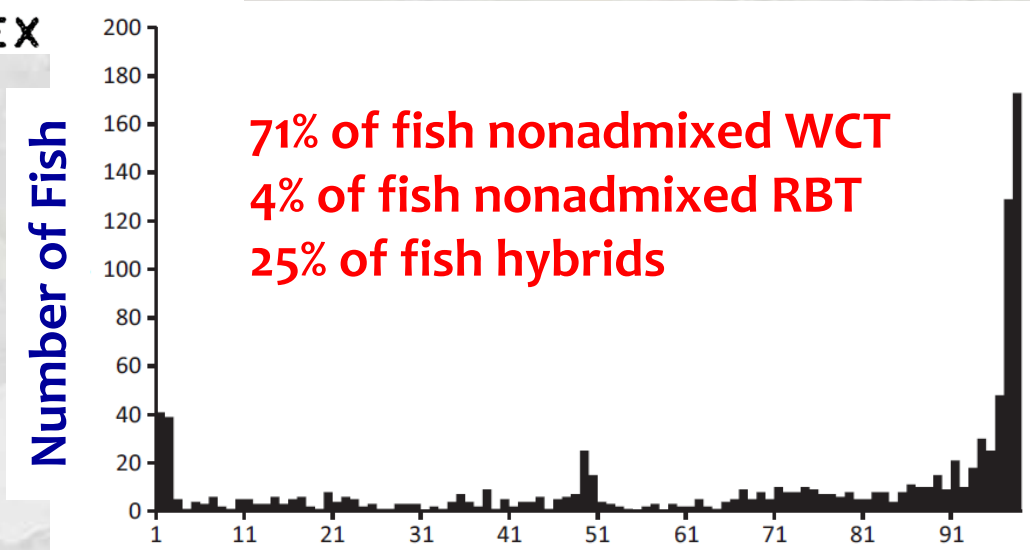
Admixture Patterns in Individual Fish

Prediction: Extensive admixture



Hybrid swarms at 8 sites but 7 involved Yellowstone CT stocking

Observation: Limited admixture at 188 sites



71% of fish nonadmixed WCT
4% of fish nonadmixed RBT
25% of fish hybrids

McKelvey et al. 2016

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

The LINNEAN SOCIETY of London
BIOLOGICAL Journal of the Linnean Society

Biological Journal of the Linnean Society, 2012, **105**, 56–72. With 7 figures

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

JOSEPH B. RASMUSSEN[1]*, MICHAEL D. ROBINSON[1], ALICE HONTELA[1] and DANIEL D. HEATH[2]

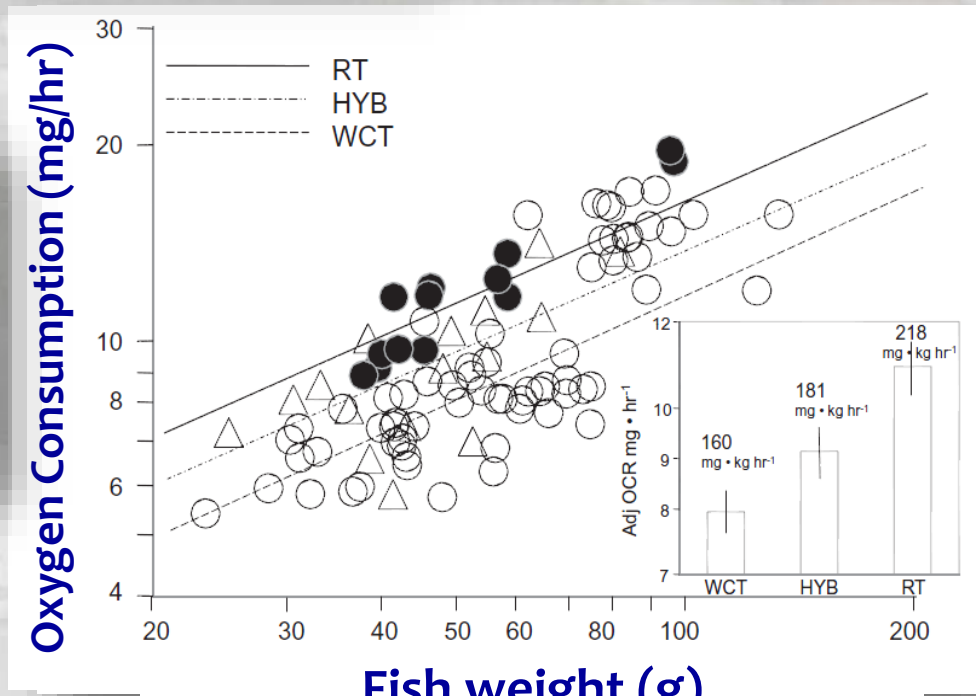
& other fishes…

JOURNAL OF Evolutionary Biology

doi: 10.1111/j.1420-9101.2

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

nature climate change

LETTERS

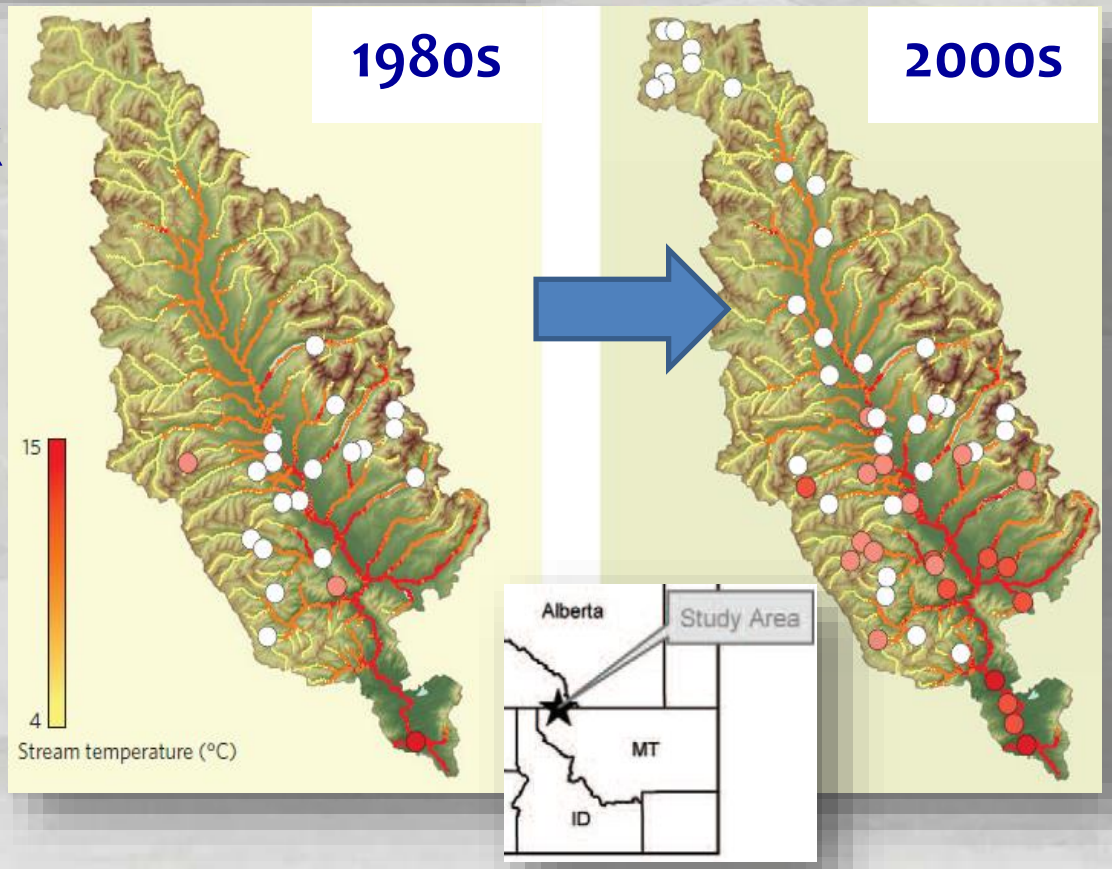
PUBLISHED ONLINE: 25 MAY 2014 | DOI: 10.1038/NCLIMATE2252

Invasive hybridization in a threatened species is accelerated by climate change

Clint C. Muhlfeld[1,2*], Ryan P. Kovach[2], Leslie A. Jones[1,3], Robert Al-Chokhachy[4], Matthew C. Boyer[5], Robb F. Leary[6], Winsor H. Lowe[3], Gordon Luikart[2] and Fred W. Allendorf[3]

Genomic extinction is inevitable!

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



Motivation: Continued Misperception

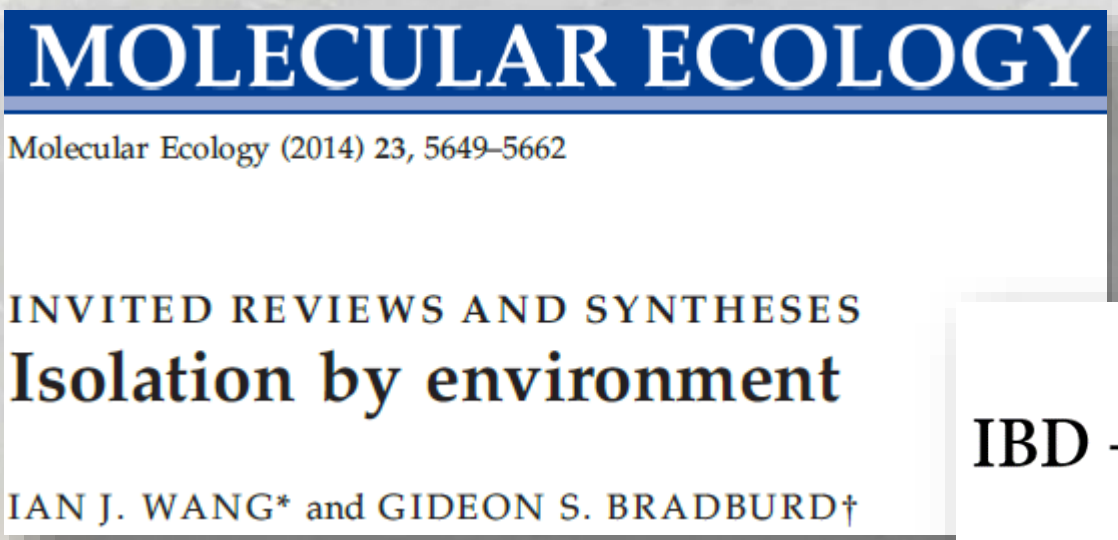
nature LETTERS

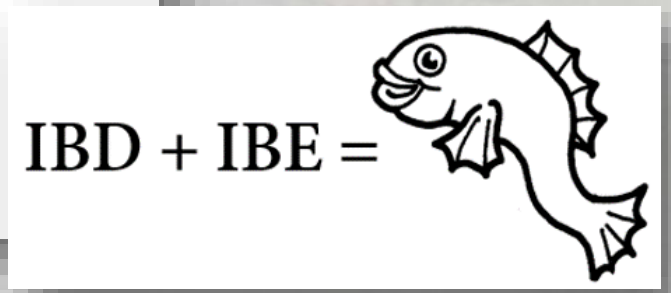
Muhlfeld et al. 2014. data plotted vs. NorWeST baseline

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.

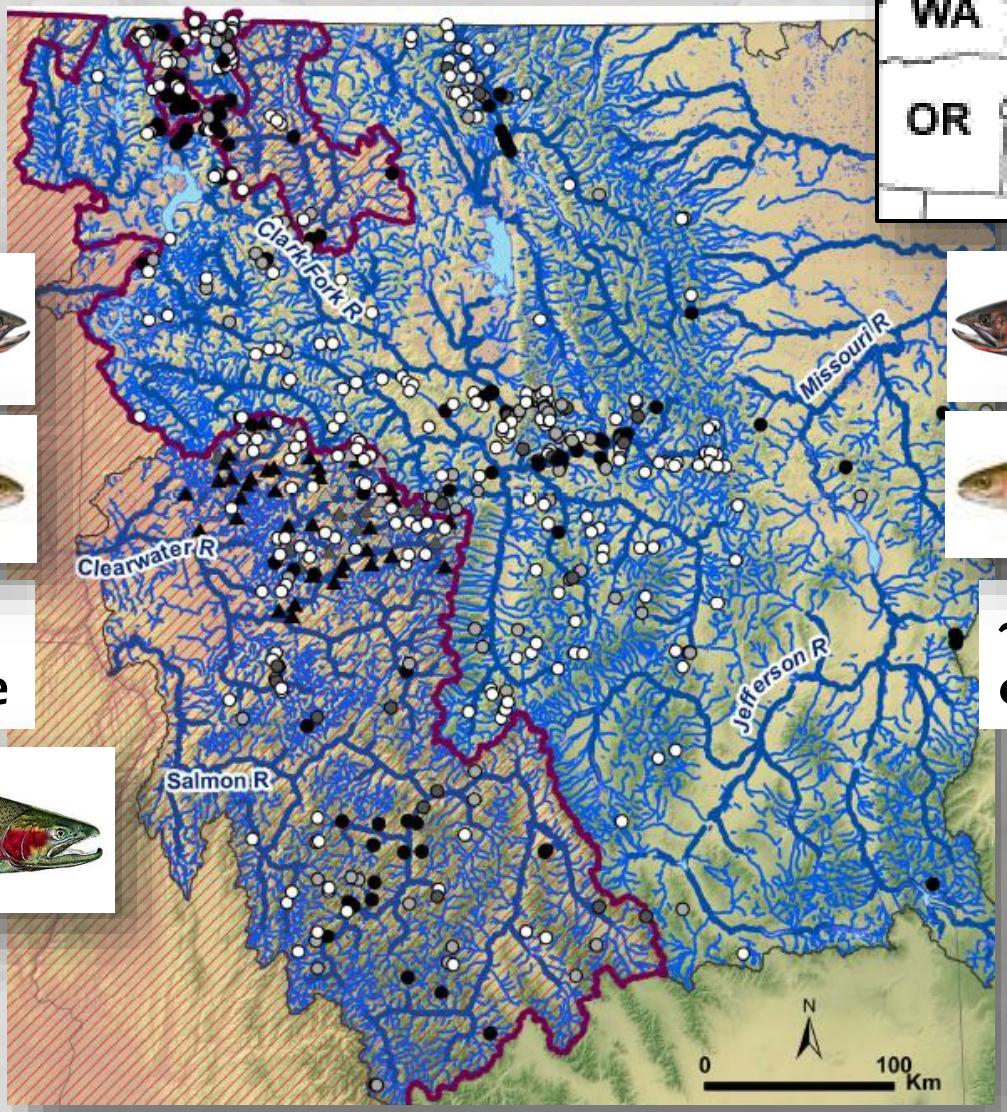




A Definitive Hybridization Dataset

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

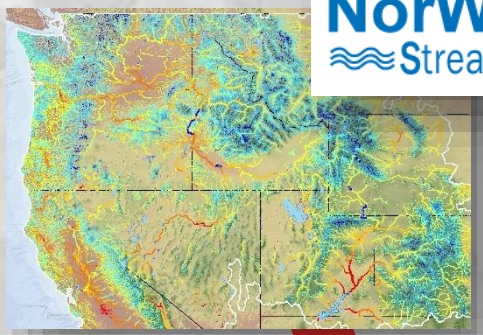
~20,000 years of coexistence



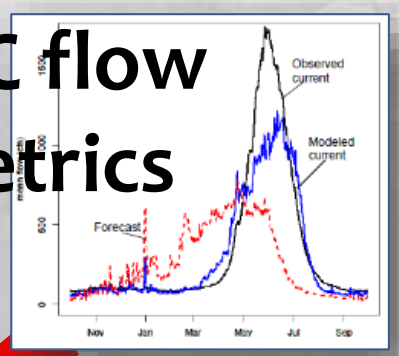
~100 years of coexistence

Link Data to Reach-Scale Habitat Descriptors

Consistent GIS datasets for all streams in West



VIC flow metrics



3,000,000 stream kilometers

NHDPlus

Many others…

- Forest canopy
- Elevation
- Slope
- %Landuse
- Precipitation
- Etc…

Cooter et al. 2010. A nationally consistent NHDPlus framework for identifying interstate waters: Implications for integrated assessments and interjurisdictional TMDLs. *Environmental Management* **46**:510-524.

Habitat Descriptors Considered in Models

Variable	Rationale	Source
Abiotic		
T: mean August temperature (°C)	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.	NorWeST
S: slope (%)	Increasing slope may lead to greater bioenergetic costs for upstream migrating rainbow trout. Many salmonid species show reductions in habitat occupancy with greater slope.	NHDPlus
MAF: mean annual flow (m^3/s)	Larger, more productive streams are associated with rainbow trout, and smaller, less productive streams are associated with cutthroat trout.	VIC flow metrics
CFM: center of flow mass, the date when 50% of the mean annual flow has been discharged	High snowmelt-driven flows in late spring and early summer are associated with declines in rainbow trout recruitment.	
W95: number of winter days with flows among the top 5% for the year	High winter flows are positively related to rainbow trout presence and negatively related to cutthroat trout presence.	
E, N: easting and northing (m)	Geographic location can serve as a surrogate for climatic and geological covariates not otherwise represented.	
Biotic		
DT13: Distance (m) to mean August temperature > 13 °C	Warmer streams may favor rainbow trout. Occurrence of rainbow trout peaked at this temperature in this region.	Custom GIS script
DF3: Distance (m) to mean annual flow > 2.83 m^3/s	Larger streams may favor rainbow trout. This threshold exceeds those habitats generally suitable for cutthroat trout spawning.	
DS: Shortest distance (m) to rainbow trout	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.	
RTrange: historical range of rainbow trout (yes/no)	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	

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 2. Model selection results.

Introgression metric	Model	AIC
PRTA > 1%	T + RTrange + DS + E + MAF + DT13 + W95 + S	575.87
	T + RTrange + DS + E + MAF + DT13 + W95 + YCTI + S	576.23
	T + RTrange + DS + MAF + E + DT13 + YCTI + S	576.72
	T + RTrange + DS + E + MAF + W95 + S	576.88
PRTA > 10%	**T + RTrange + DS + DT13 + MAF + E**	433.13
	T + RTrange + DS + DT13 + MAF + E + YCTI	433.51
	T + RTrange + DS + DT13 + MAF + E + W95	434.27
	T + RTrange + DS + DT13 + MAF + E + S	434.32
PRTA > 20%	**T + RTrange + DT13 + MAF + E + DS**	387.75
	T + RTrange + DT13 + MAF + E	388.40
	T + RTrange + DT13 + MAF + E + DS + S	389.23
	T + RTrange + DT13 + MAF + E + DS + W95	389.35

Young et al. 2016. Climate, demography, and zoogeography predict thresholds in salmonid hybrid zones in Rocky Mountain streams. *PLoS ONE* **11:** e0163563

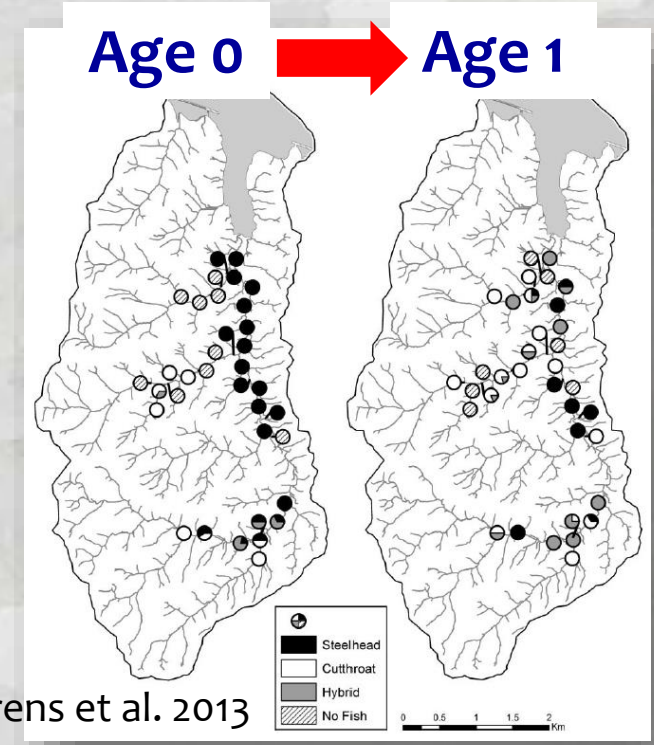
Models Make Accurate Predictions & Are Robust

PRTA > 10%

						Classification accuracy		
Predictor	b_x	SE	z	p	AUC	Threshold[a]	Training data	10-fold CV
Intercept	-1.34E+01	2.65E+00	-5.07	<0.01	0.85	0.384	81.2%	81.0%
T	2.66E-01	1.00E-01	2.65	<0.01				
RTrange	1.34E+00	2.94E-01	4.57	<0.01				
DS	-1.34E-04	4.24E-05	-3.16	<0.01				
DT13	-6.18E-05	2.35E-05	-2.63	<0.01				
MAF	5.12E-01	1.90E-01	2.69	<0.01				
E	6.75E-06	1.51E-06	4.46	<0.01				

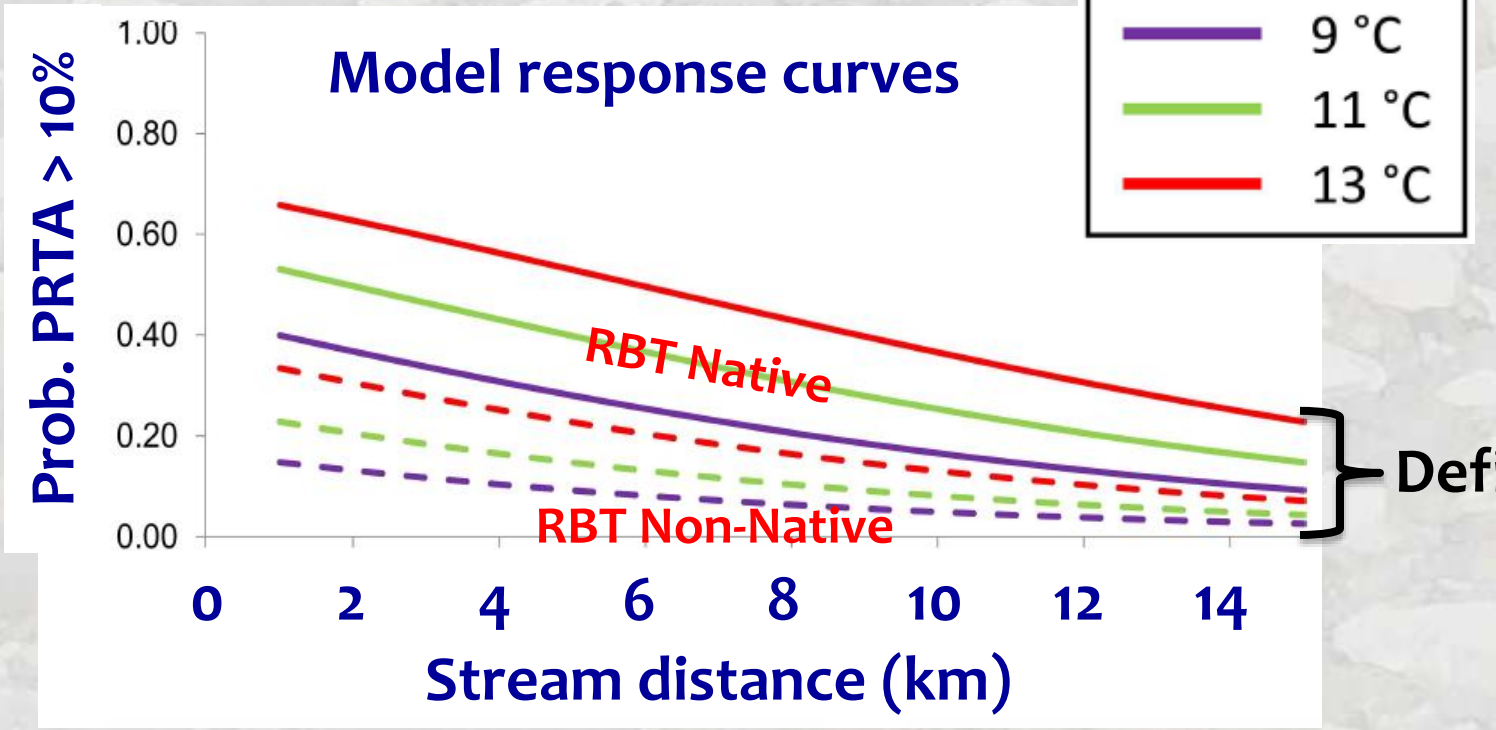
Accurate despite…

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

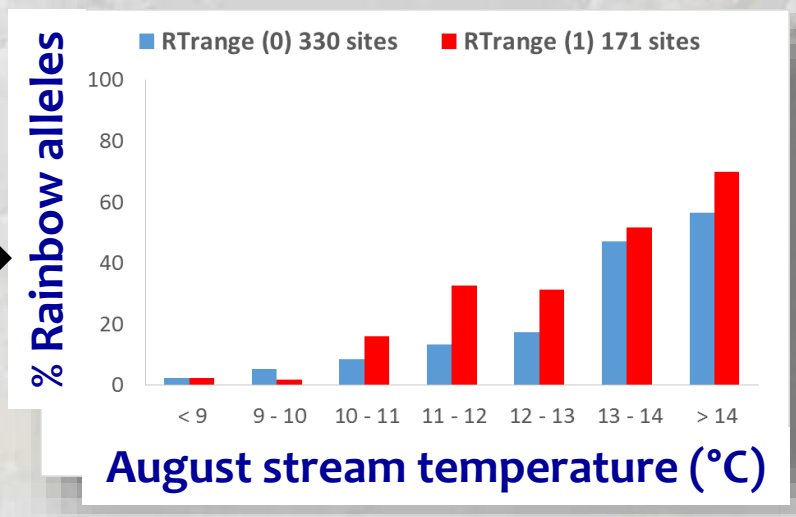


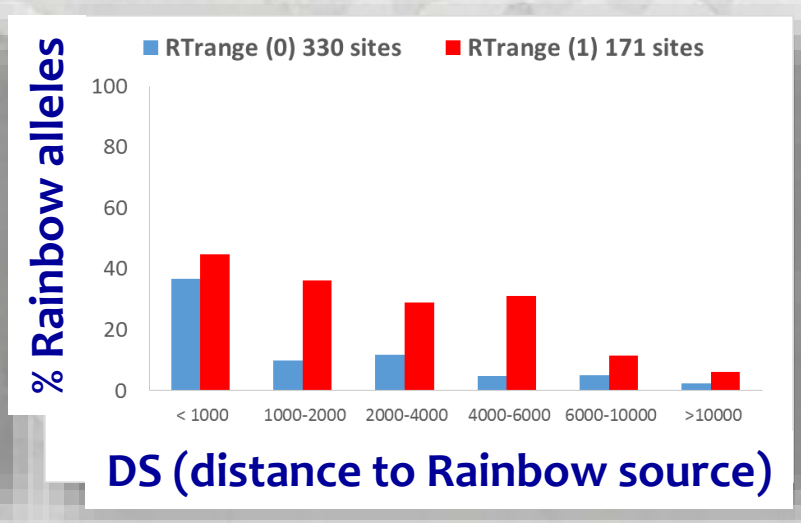
Buehrens et al. 2013

A Hybrid Deficit?



& in data summaries





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?

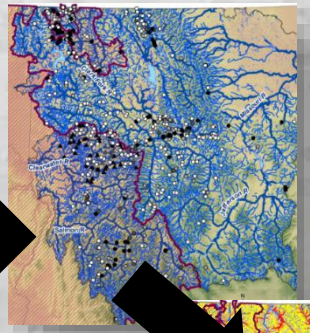
3) Perhaps large anadromous steelhead enhance propagule pressure throughout the native range of rainbow trout in the Pacific Northwest?

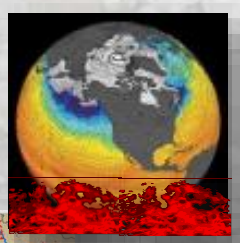
"Relaxation" Hypothesis:

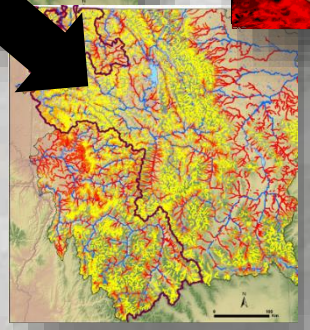
1) Hybridization will decrease once local propagule pressure is reduced & could be reversible in some environments (e.g., small cold streams)

Model Scenarios Span the Possibilities (& Climate Change)

55,000 kilometer stream network







PRTA < 10%

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)

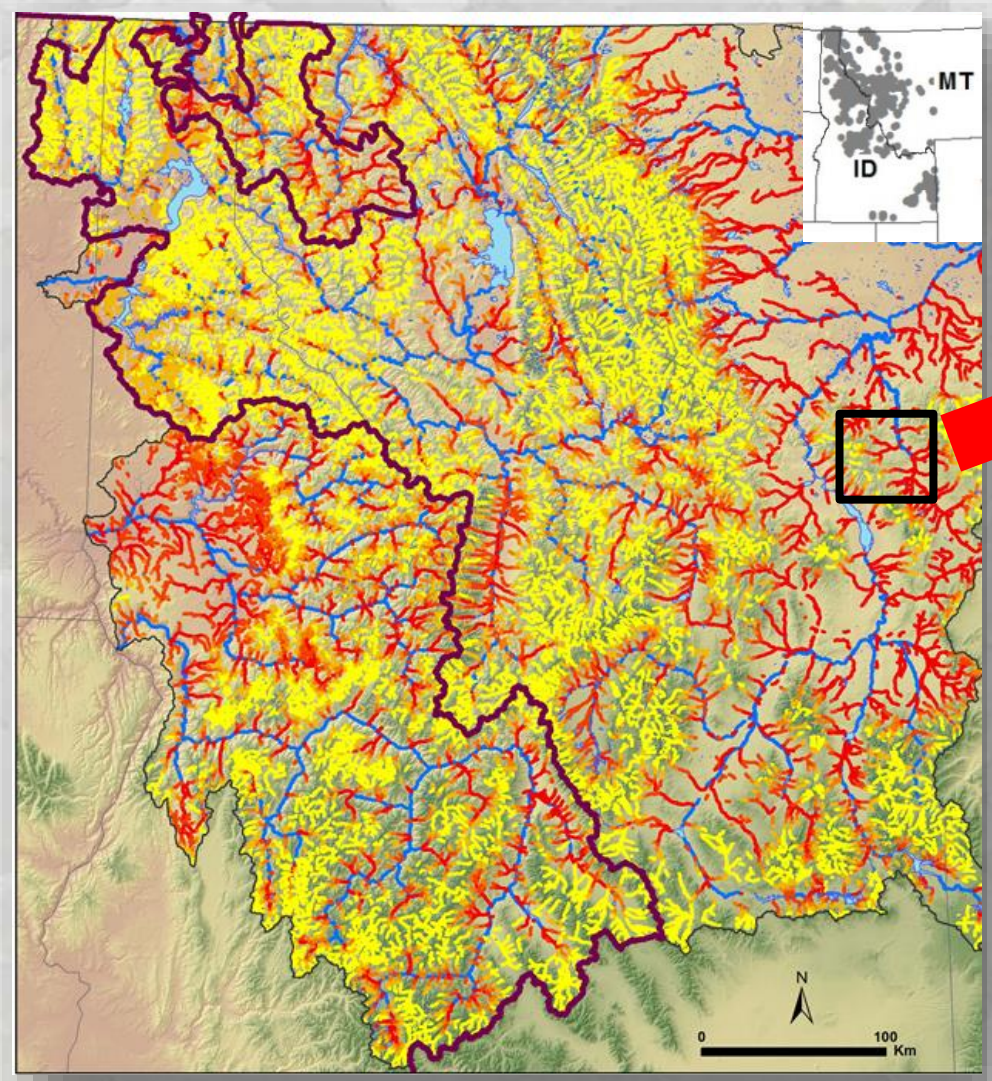
- Also PRTA < 1% & <20%
- By stream length & volume

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

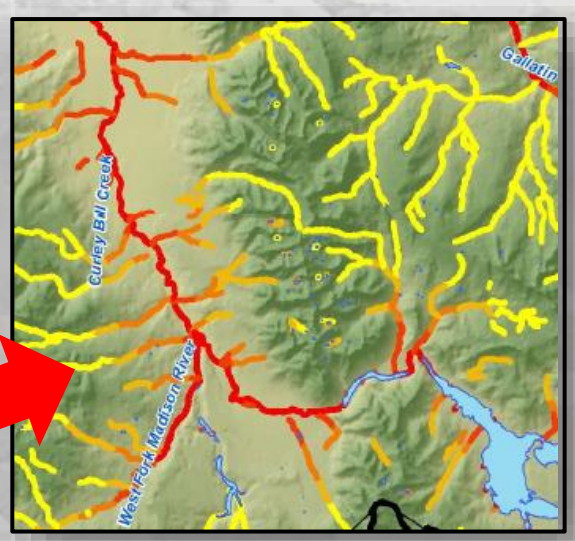
		Inside range of rainbow trout				Outside range of rainbow trout			
Scenario[a]	PRTA	Length	% change	Volume	% change	Length	% change	Volume	% change
Current	<1%	7,869	—	1,656	—	16,186	—	4,117	—
	<10%	9,863	—	2,854	—	21,760	—	7,925	—
	<20%	10,887	—	3,394	—	23,290	—	9,051	—
Equilibrium	<1%	7,869	—	1,656	—	9,472	-41.5%	2,070	-49.7%
	<10%	9,863	—	2,854	—	13,643	-37.3%	4,479	-43.5%
	<20%	10,887	—	3,394	—	16,588	-28.8%	5,922	-34.6%
Current + 0.5°C	<1%	6,302	-19.9%	1,245	-24.8%	13,855	-14.8%	116,017	-18.8%
	<10%	8,121	-17.7%	2,099	-26.5%	19,391	-10.2%	227,997	-16.0%
	<20%	9,339	-14.2%	2,582	-23.9%	20,882	-9.5%	264,298	-14.6%
Equilibrium + 0.5°C	<1%	6,302	—	1,245	—	7,163	-55.7%	1,495	-63.7%
	<10%	8,121	—	2,099	—	11,110	-48.9%	3,402	-57.1%
	<20%	9,339	—	2,582	—	13,855	-40.5%	4,711	-47.9%
Current + 1.0°C	<1%	4,962	-36.9%	911	-45.0%	11,240	-30.6%	2,620	-36.4%
	<10%	6,723	-31.8%	1,615	-43.4%	17,165	-21.1%	5,506	-30.5%
	<20%	7,820	-28.2%	1,982	-41.6%	18,746	-19.5%	6,438	-28.9%
Equilibrium + 1.0°C	<1%	4,962	—	911	—	5,122	-68.4%	1,043	-74.7%
	<10%	6,723	—	1,615	—	8,455	-61.1%	2,475	-68.8%
	<20%	7,820	—	1,982	—	11,038	-52.6%	3,546	-60.8%

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

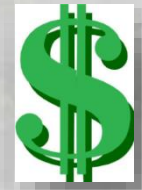


1-km resolution



Look before leaping…

BIG



Website: Cutthroat-Rainbow Trout Hybridization

Papers

PLOS ONE

RESEARCH ARTICLE

Climate, Demography, and Zoogeography Predict Introgression Thresholds in Salmonid Hybrid Zones in Rocky Mountain Streams

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Patterns of hybridization among cutthroat trout and rainbow trout in northern Rocky Mountain streams

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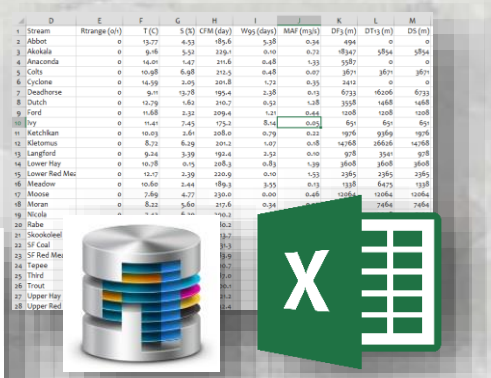
Dataset



Scenario Maps