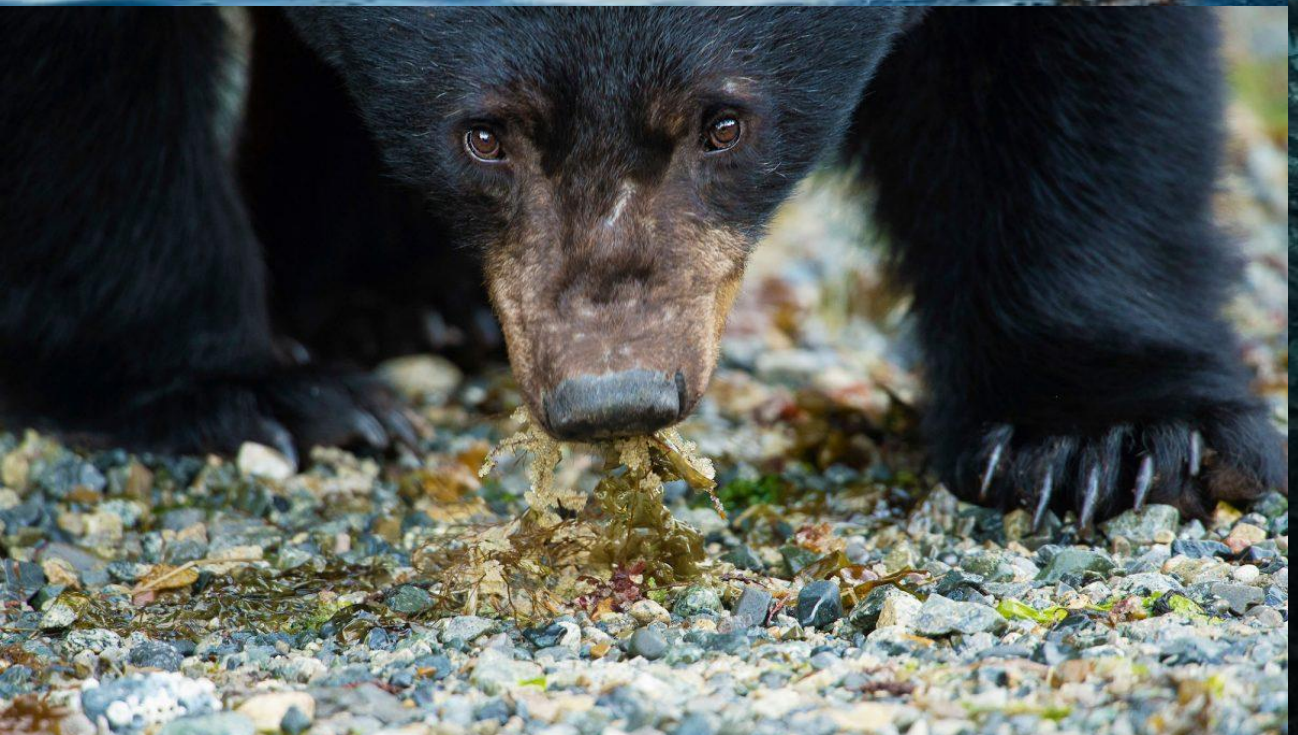
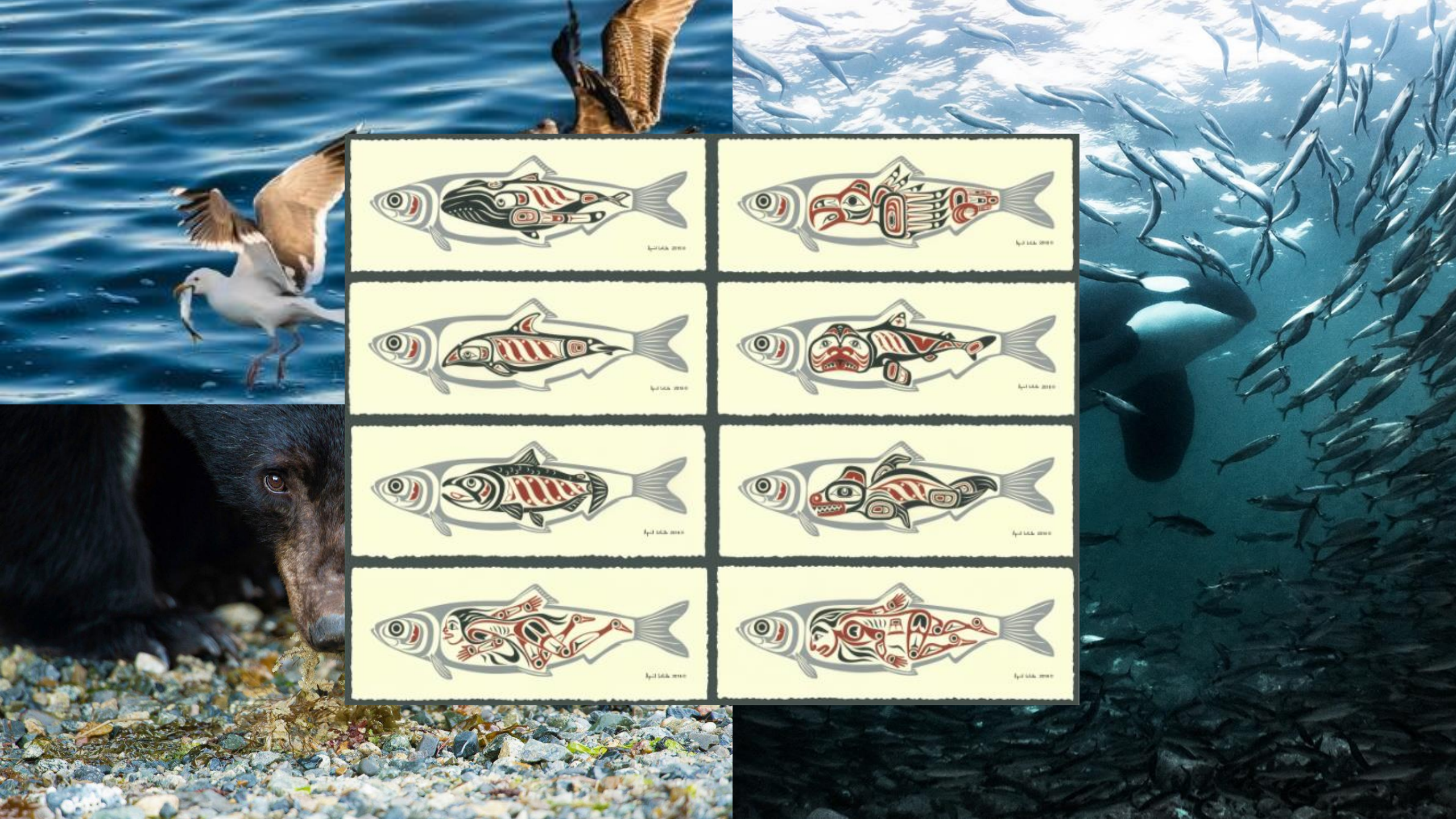
Temporal and spatial genomic contrasts of Pacific Herring populations

Joe McGirr





Pacific Herring and humans

Harvested by coastal indigenous communities

Main export:
dry-salted

Main export:
meal and oil

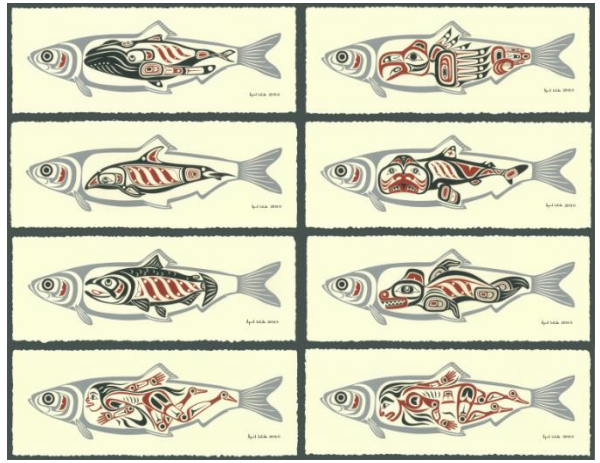
Main export:
roe/spawn on kelp and bait

1882
First commercial fisheries in Alaska

1930s

1960s

Present



Goal: Use genomics to understand how populations change over time

Part 1: Population collapse and recovery in Prince William Sound, Alaska

- What caused the PWS population to collapse?
- What is limiting population recovery?

Part 2: Local Adaptation

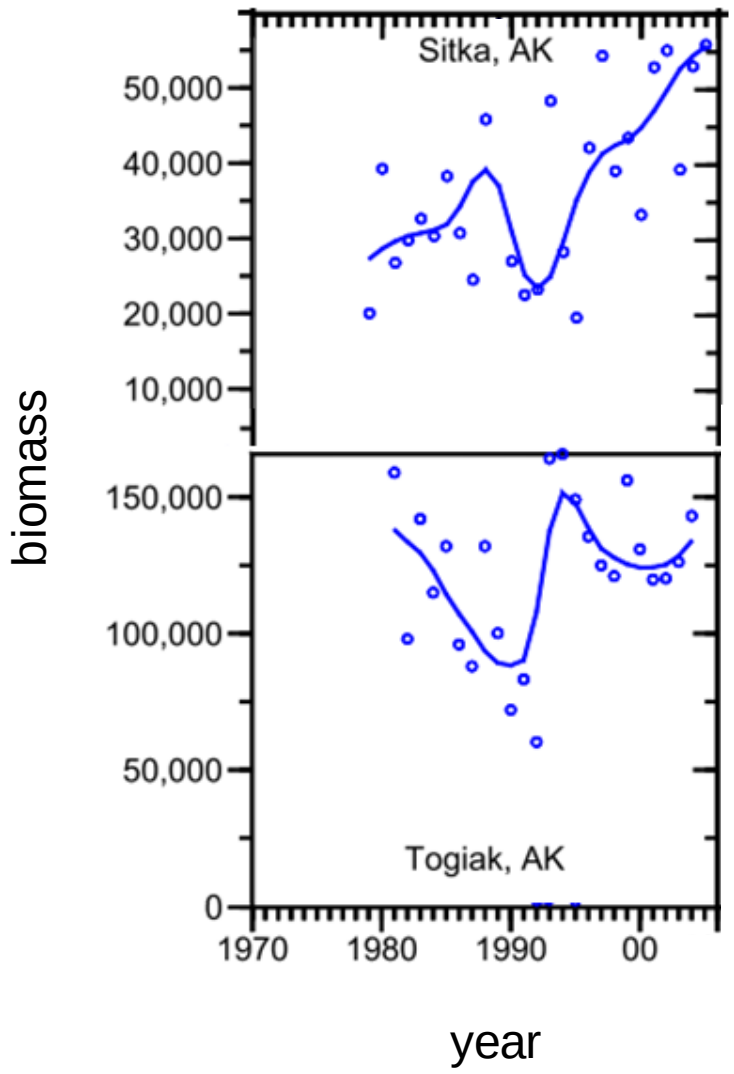
- What are the genetic differences between populations underlying locally adaptive phenotypes?
- How will populations respond to warming waters?

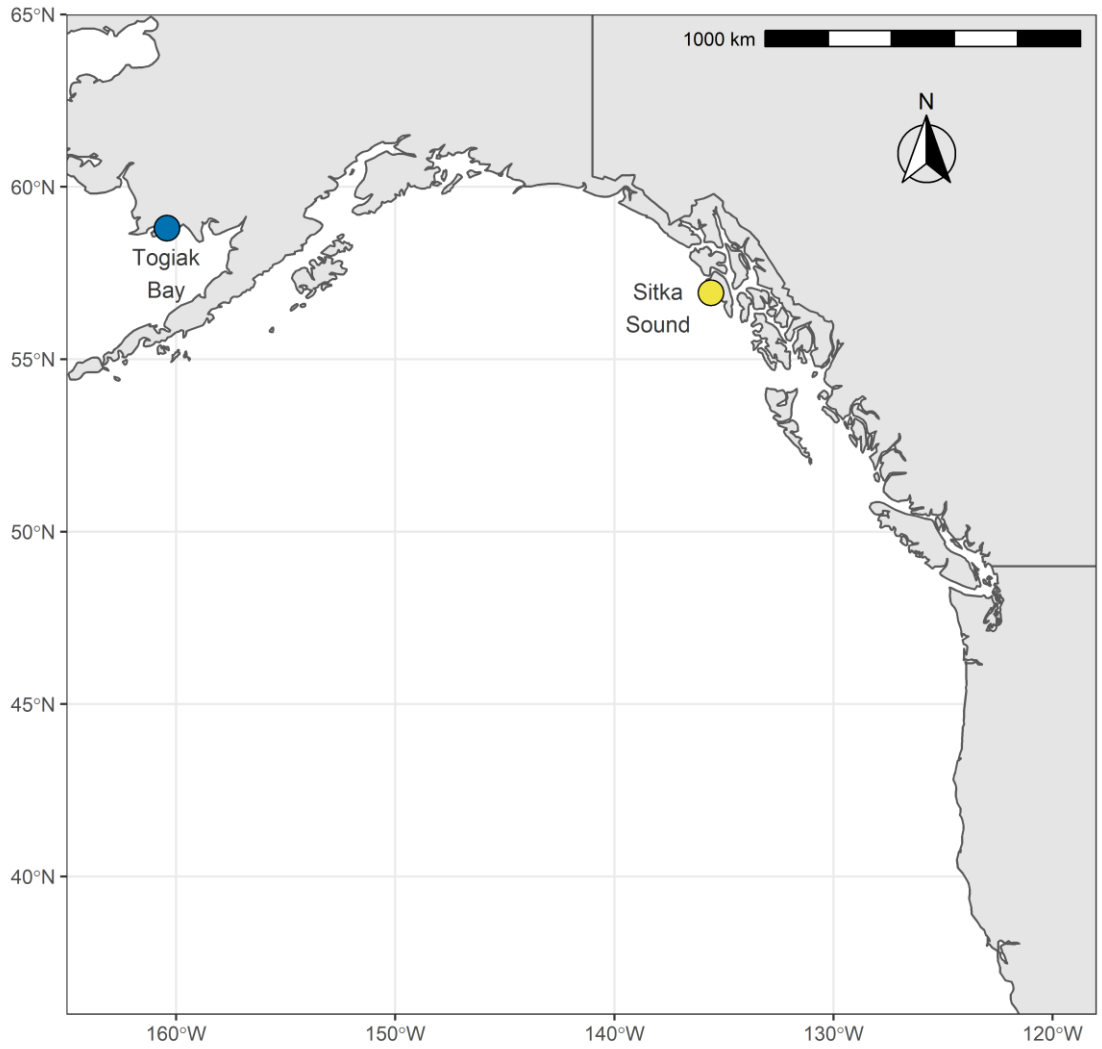
Population collapse and recovery

Clupeids, including Pacific herring, typically have boom or bust population cycles, even in unstressed populations

(Schweigert 2002, Trochta et al. 2020)

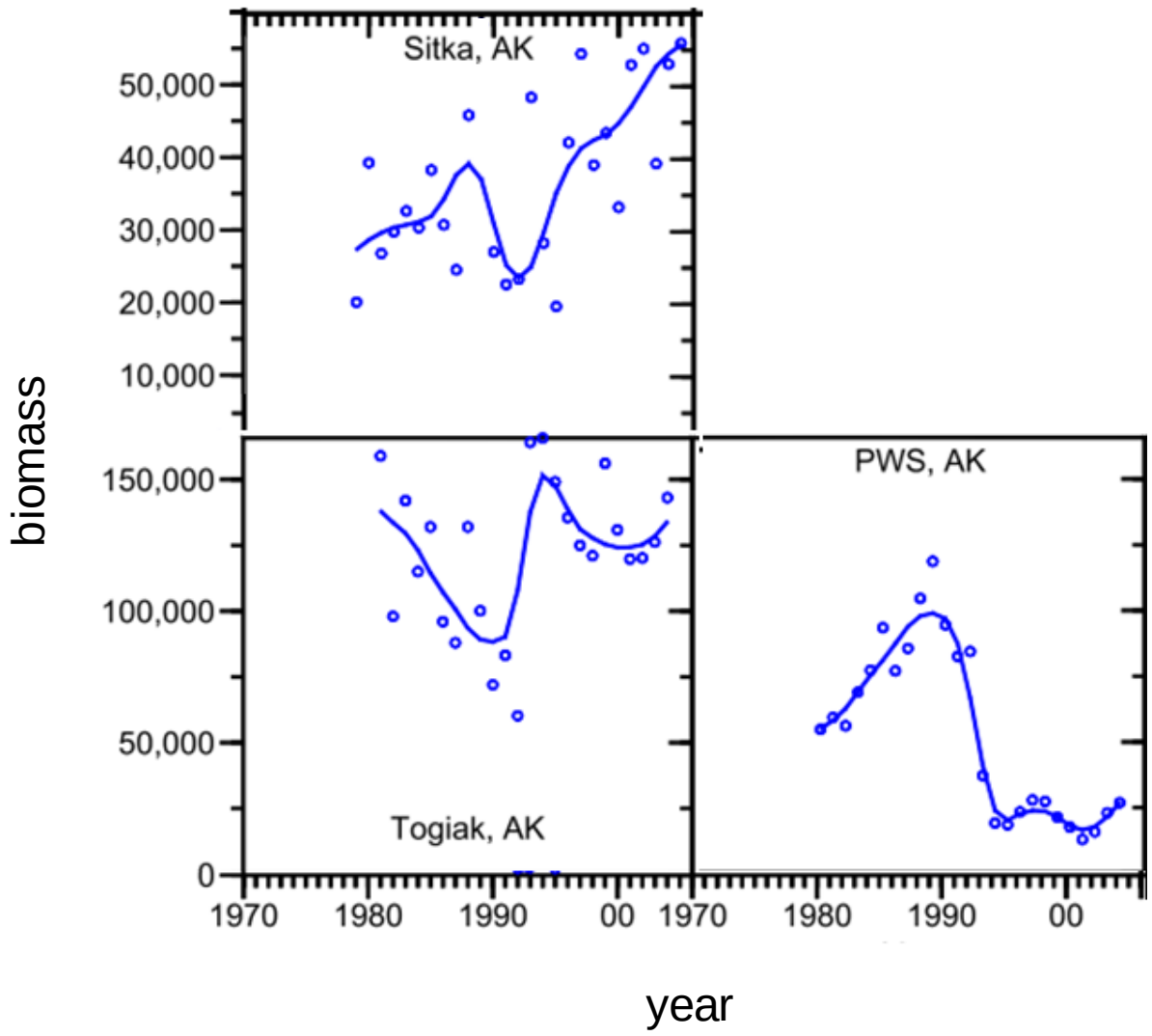
Population collapse and recovery

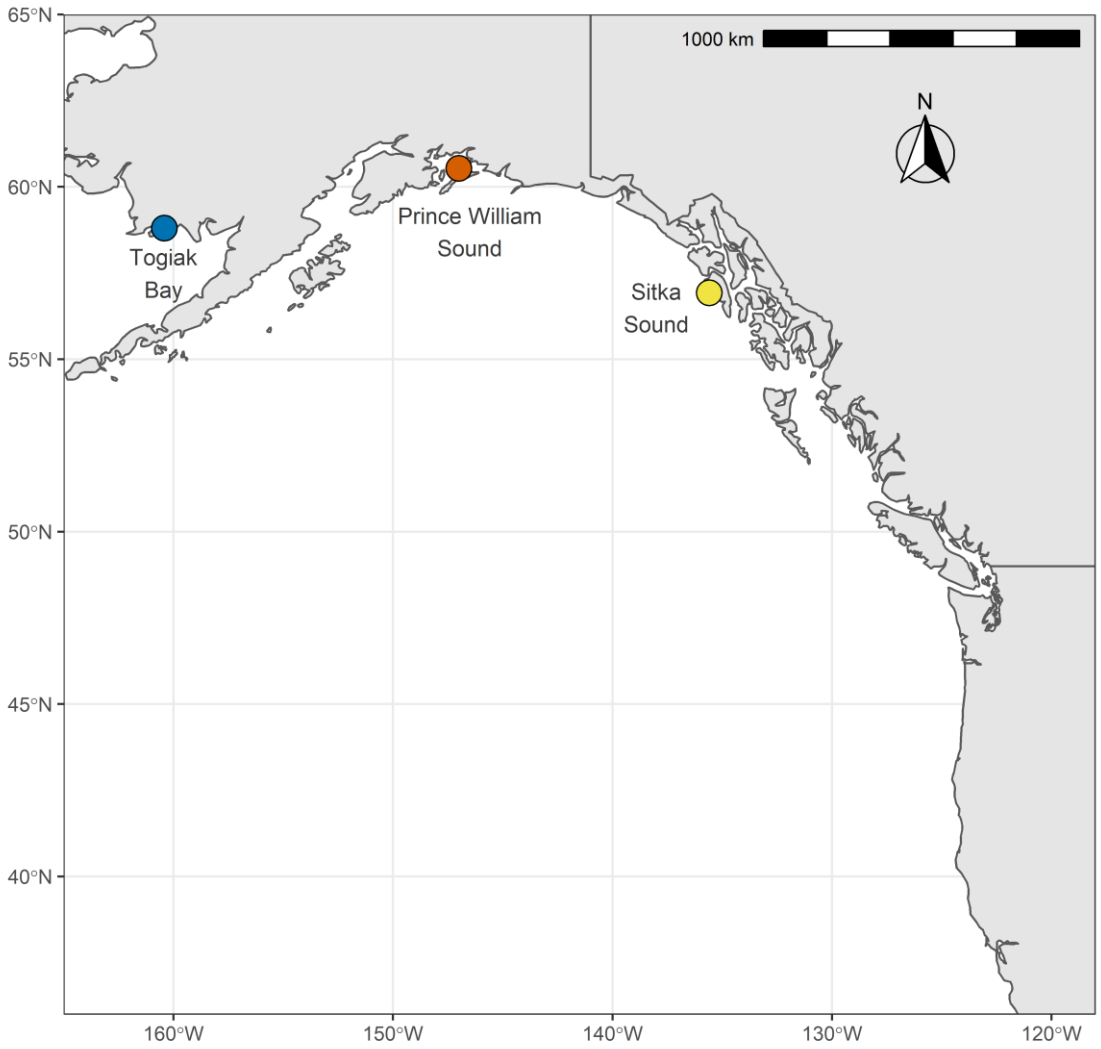




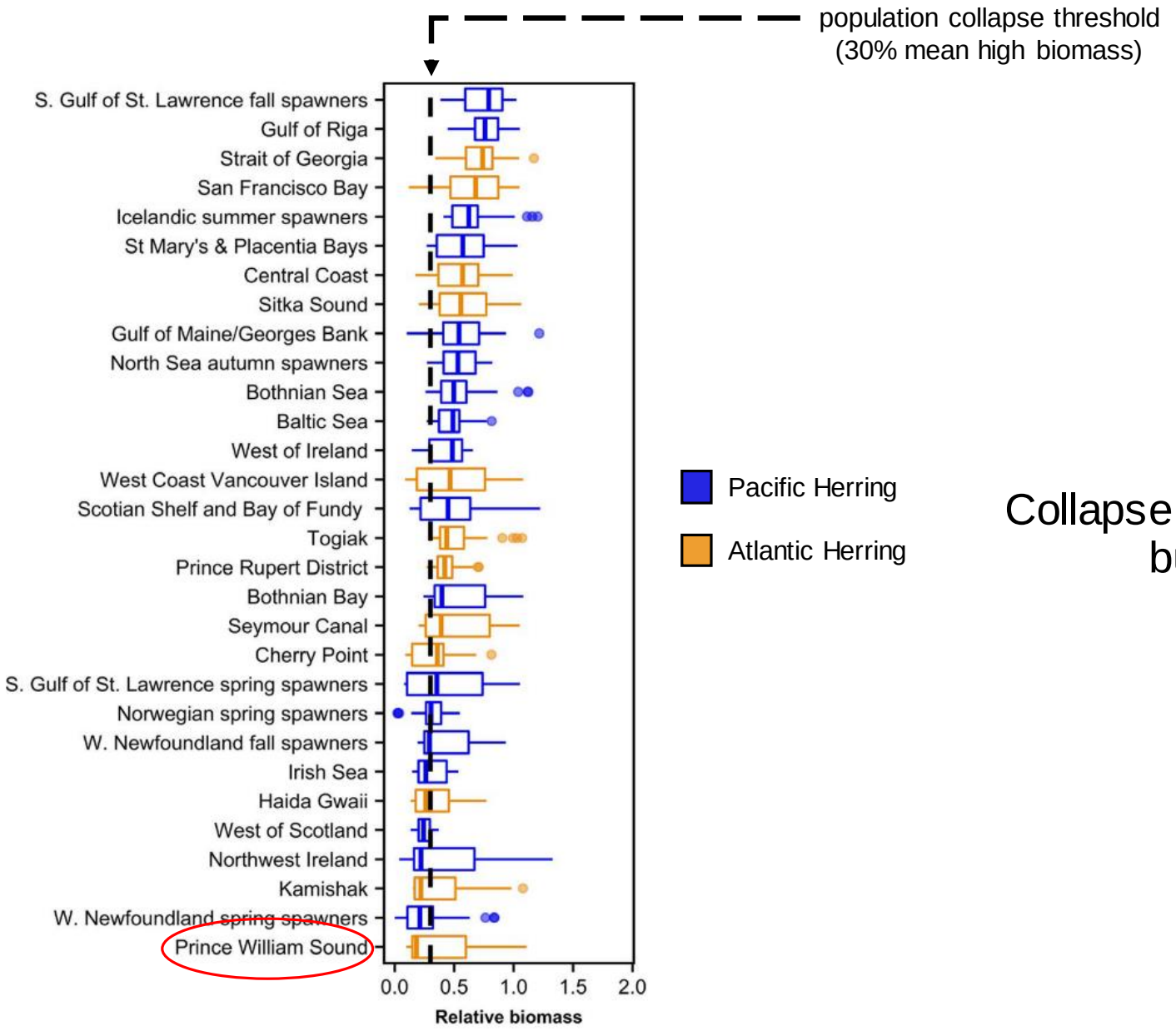
Rice and Carls 2007

No recovery in Prince William Sound (PWS)





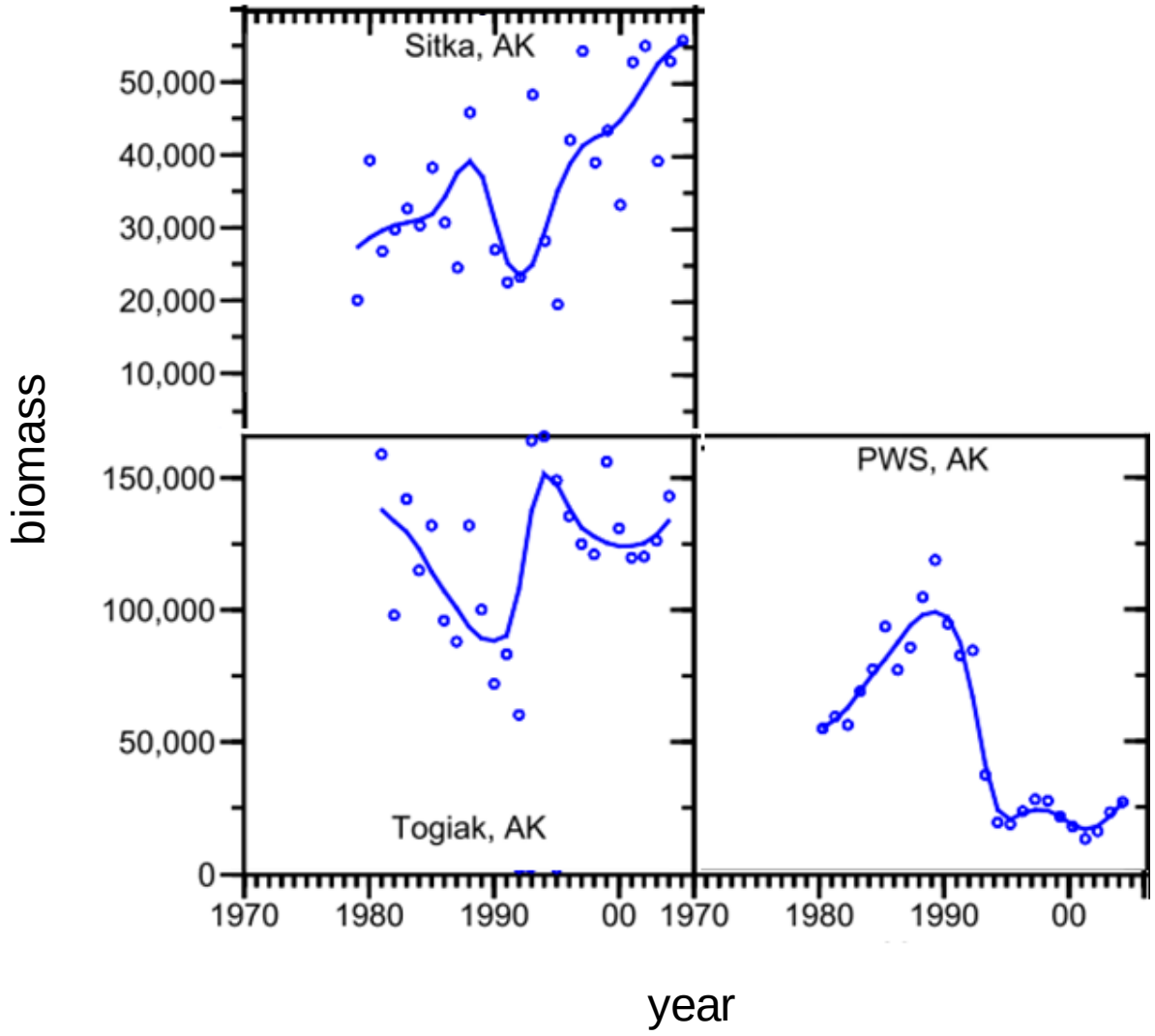
Rice and Carls 2007



Trochta et al. 2020

Collapse is geographically widespread but exceptional in PWS

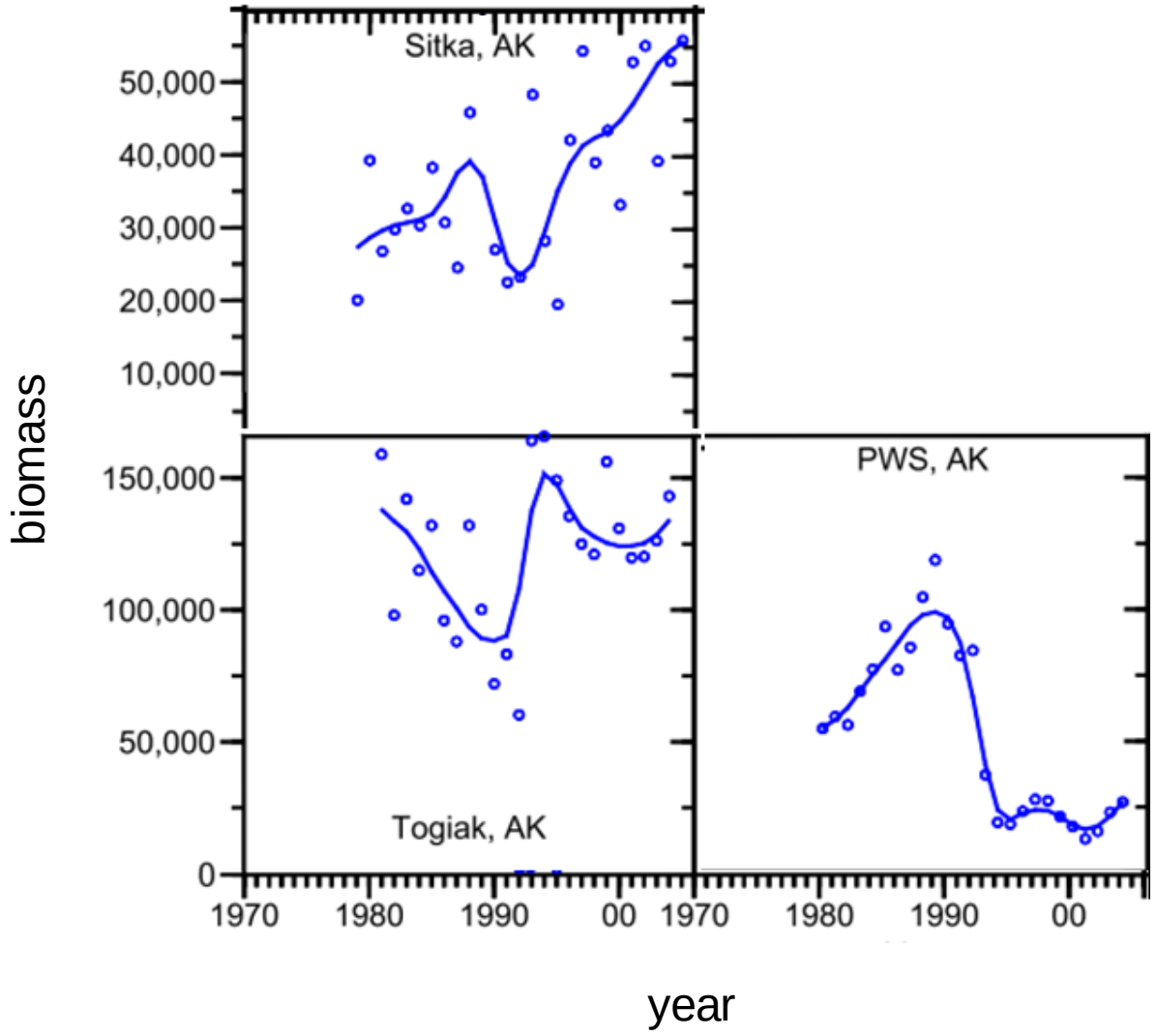
Many possible explanations



- Overfishing
- Pollution
- Climate Change
- Disease
- Predation
- Competition
- Complex interaction between several factors

Rice and Carls 2007

Many possible explanations



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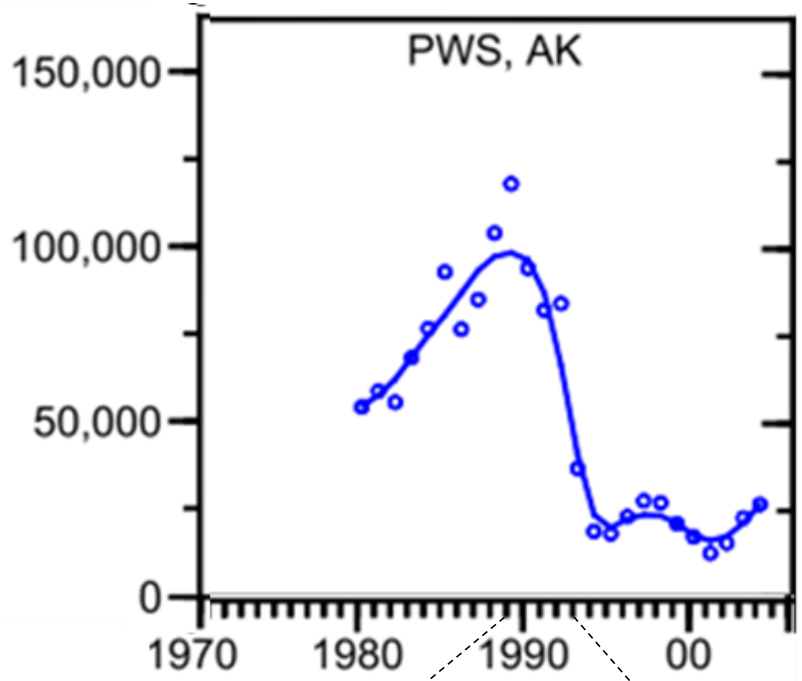
Exxon Valdez oil spill

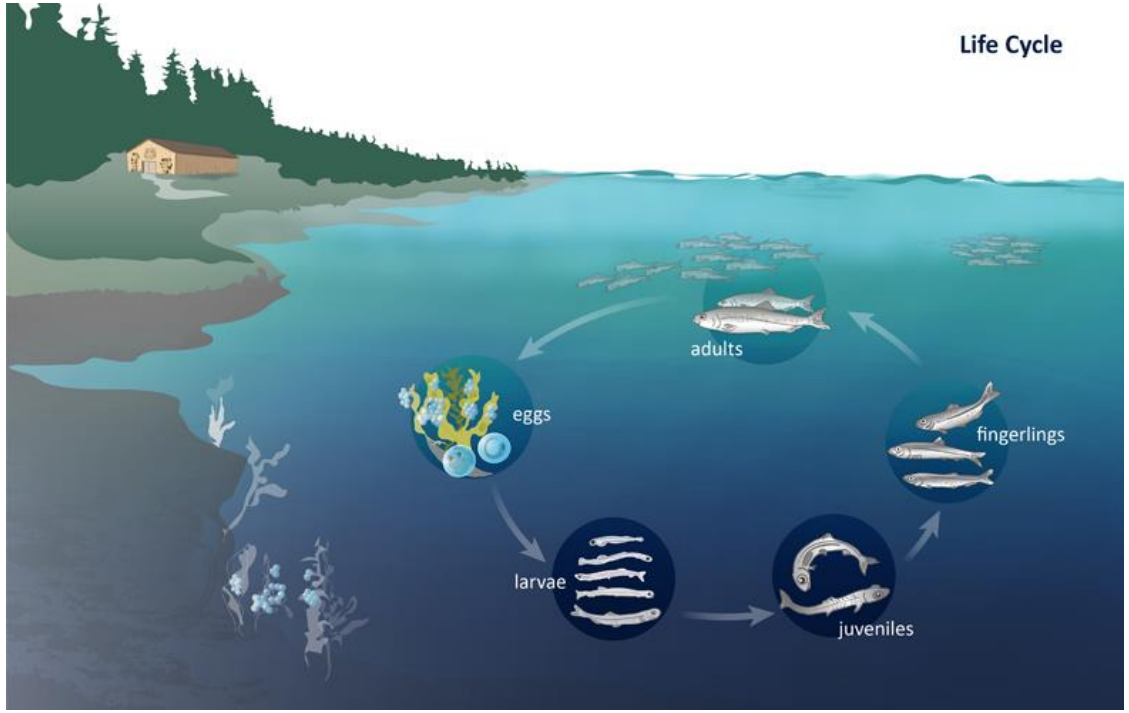
Exxon Valdez oil spill



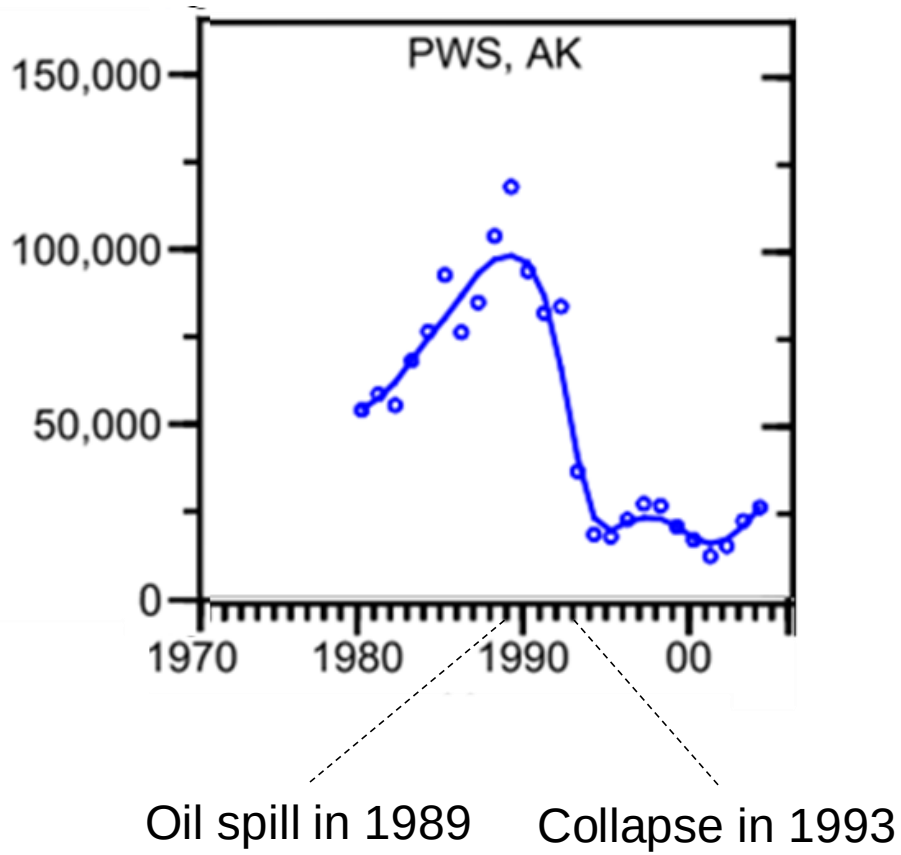
Oil spill in 1989

Collapse in 1993

3 year recruitment



Exxon Valdez oil spill



- Half of egg biomass deposited in 1989 was within the trajectory of the spilled oil
- The contribution of the 1989 year class to the 1993 spawning population was only 25% of that forecast.

(Carls et al. 2002, Marty et al. 2003).

Were Pacific Herring in PWS damaged by exposure to Exxon Valdez oil?

Controversy:

- Industry researchers (funded by Exxon) conclude that < 10% of herring embryos were damaged by oil.

- Government researchers (Natural Resource Damage Assessment) concluded that 25-33% of herring embryos were damaged.

Was the collapse of the PWS Herring population also related to Exxon Valdez oil?

Industry and government answers are more similar:

- Both concluded that the oil spill did not likely cause the collapse.
- Both agree that a decreased herring food supply (zooplankton) in 1992 stressed a population that was at a record high size, making ideal conditions for disease outbreaks that caused the collapse.

Disease: Viral hemorrhagic septicemia virus (VHSV) and *Ichthyophonus hoferi*

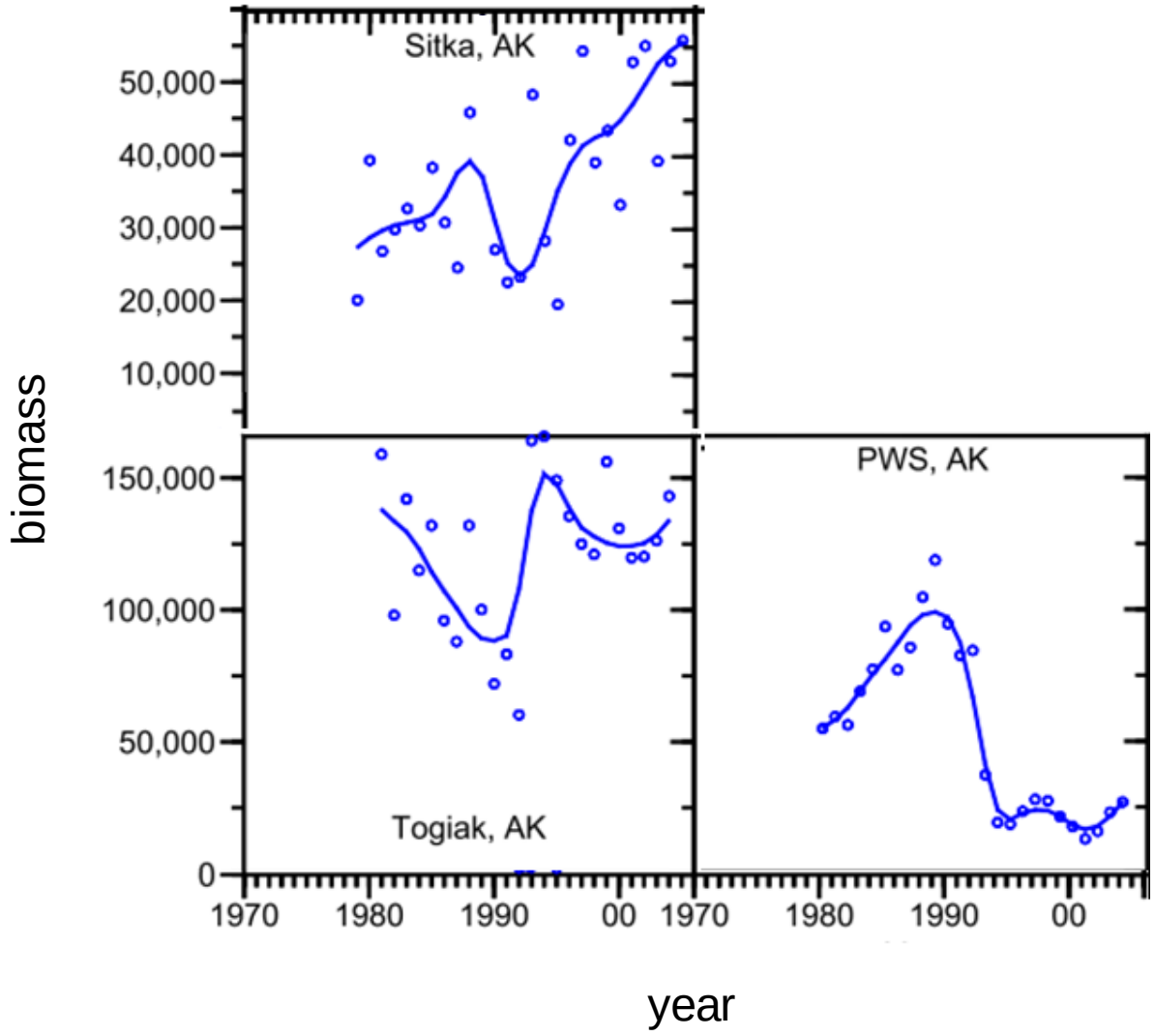
VHSV prevalence up to 14%
Deadly at early life stages

Ichthyophonus prevalence up to 51%
Deadly at later life stages

Data: Marty et al. 2010. Photos: Hershberger

Limited food in winter of 1992

Disease combined with limited food in winter of 1992



The 1993 disease outbreak affected all year classes equally, independent of their age at the time of the oil spill (Marty et al. 1998).

May explain collapse, but does not explain why the PWS population hasn't recovered.

PWS Salmon population also collapsed in 1993-94. (Have recovered since)

Rice and Carls 2007

Alternative hypothesis to explain collapse that also explains slow recovery

Given that:

1. Half of egg biomass deposited in 1989 was within the trajectory of the spilled oil.

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Alternative hypothesis to explain collapse that also explains slow recovery

Given that:

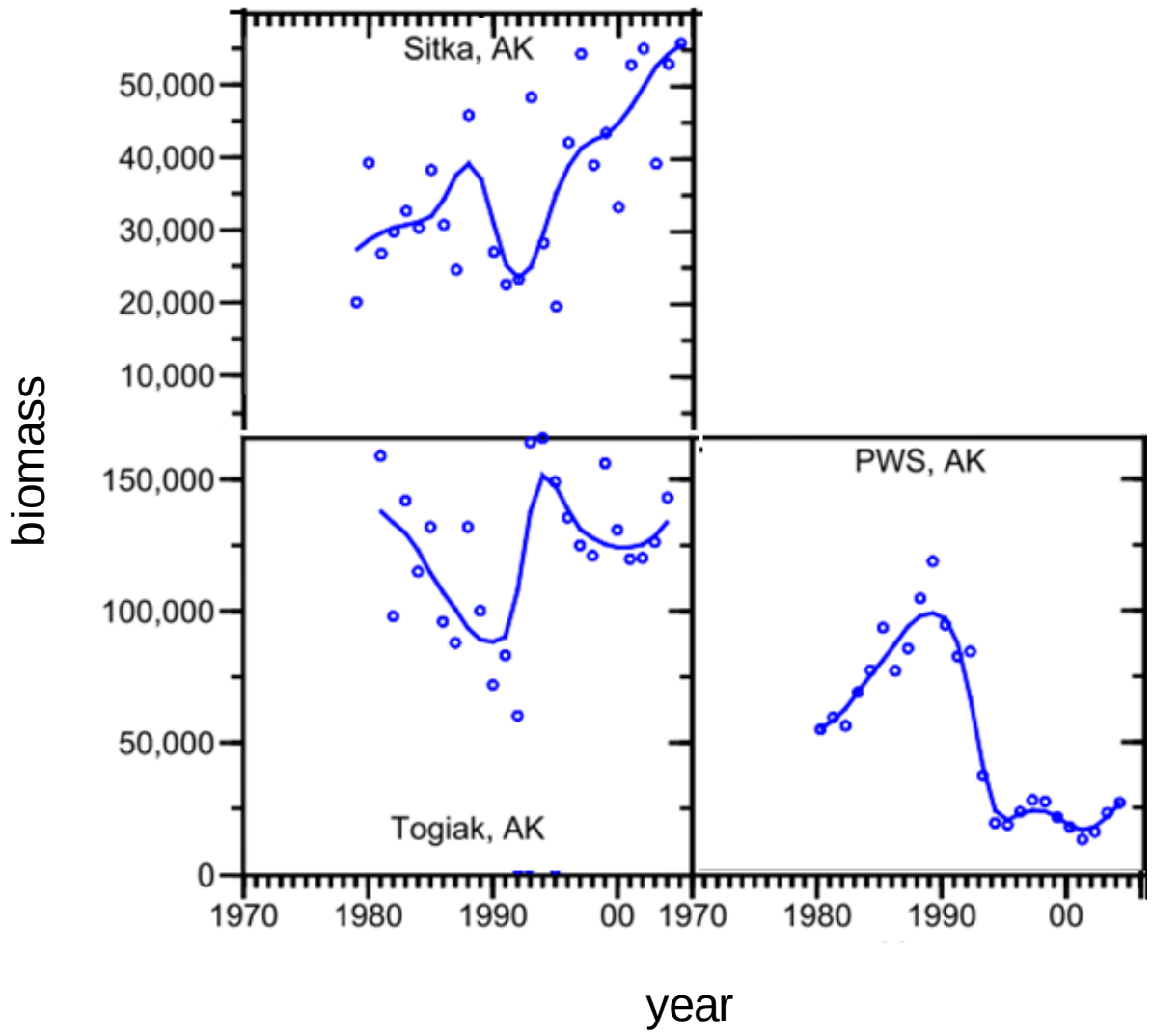
1. Half of egg biomass deposited in 1989 was within the trajectory of the spilled oil.
2. Crude oil impairs herring development at lower concentrations than previously appreciated in the ‘90s (Incardona 2015).
3. Rapid adaptation to pollutants can reduce genetic diversity in a population and favor genetic variants that impair the function of signaling pathways important for healthy immune systems (Reid et al. 2016).

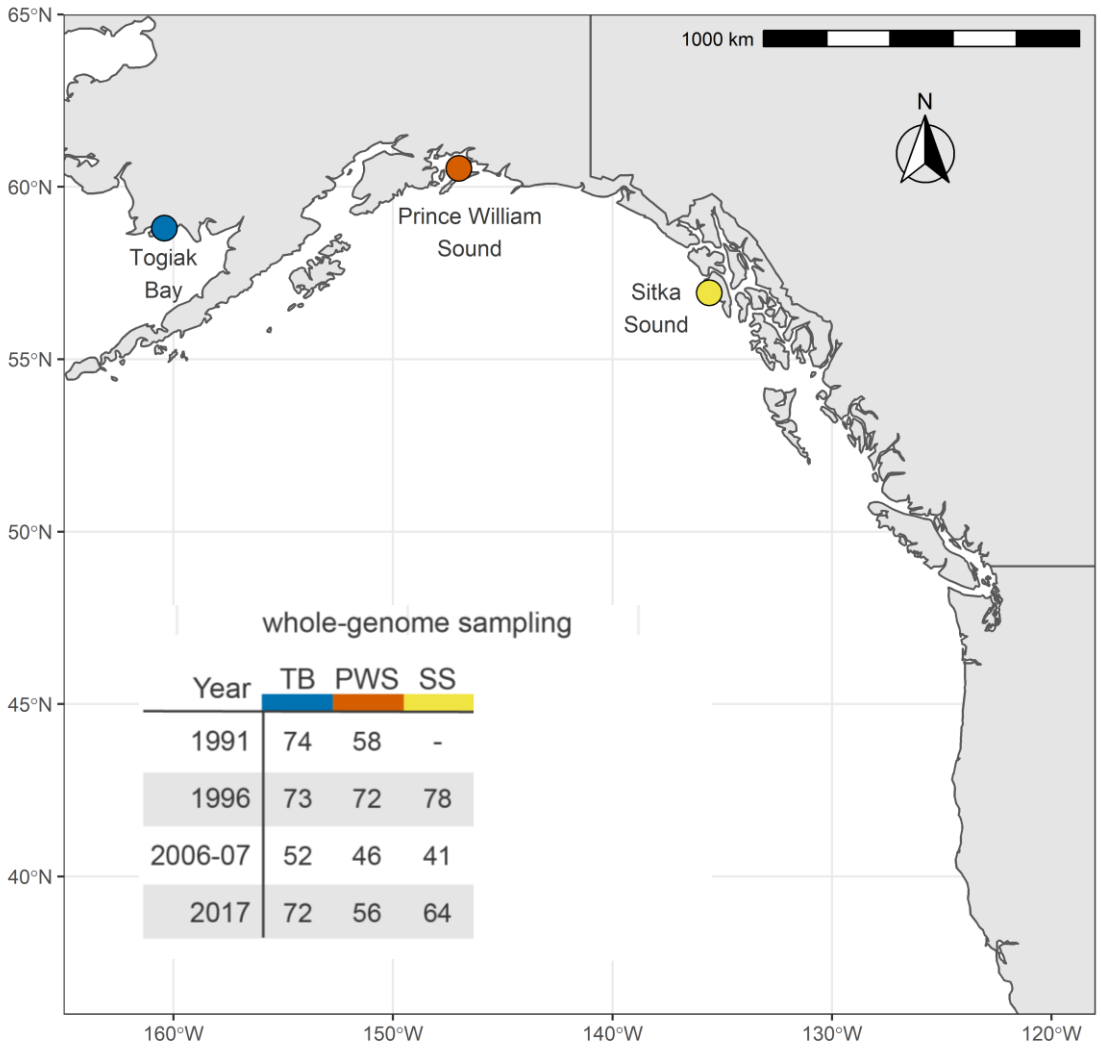
Alternative hypothesis to explain collapse that also explains slow recovery

We predict that:

1. Exposure to oil was a major selective event.
2. Genetic variants were favored that conferred resistance to oil exposure at the cost of impaired immune function.
3. The frequency of individuals with impaired immune function increased, enabling disease outbreak that contributed to population collapse.
4. Recovery has been slow because due to limited genetic diversity genome-wide, or at genes involved in immune function.

Whole genome sequencing across time and space





whole-genome sampling

Year	TB	PWS	SS
1991	74	58	-
1996	73	72	78
2006-07	52	46	41
2017	72	56	64

Rice and Carls 2007

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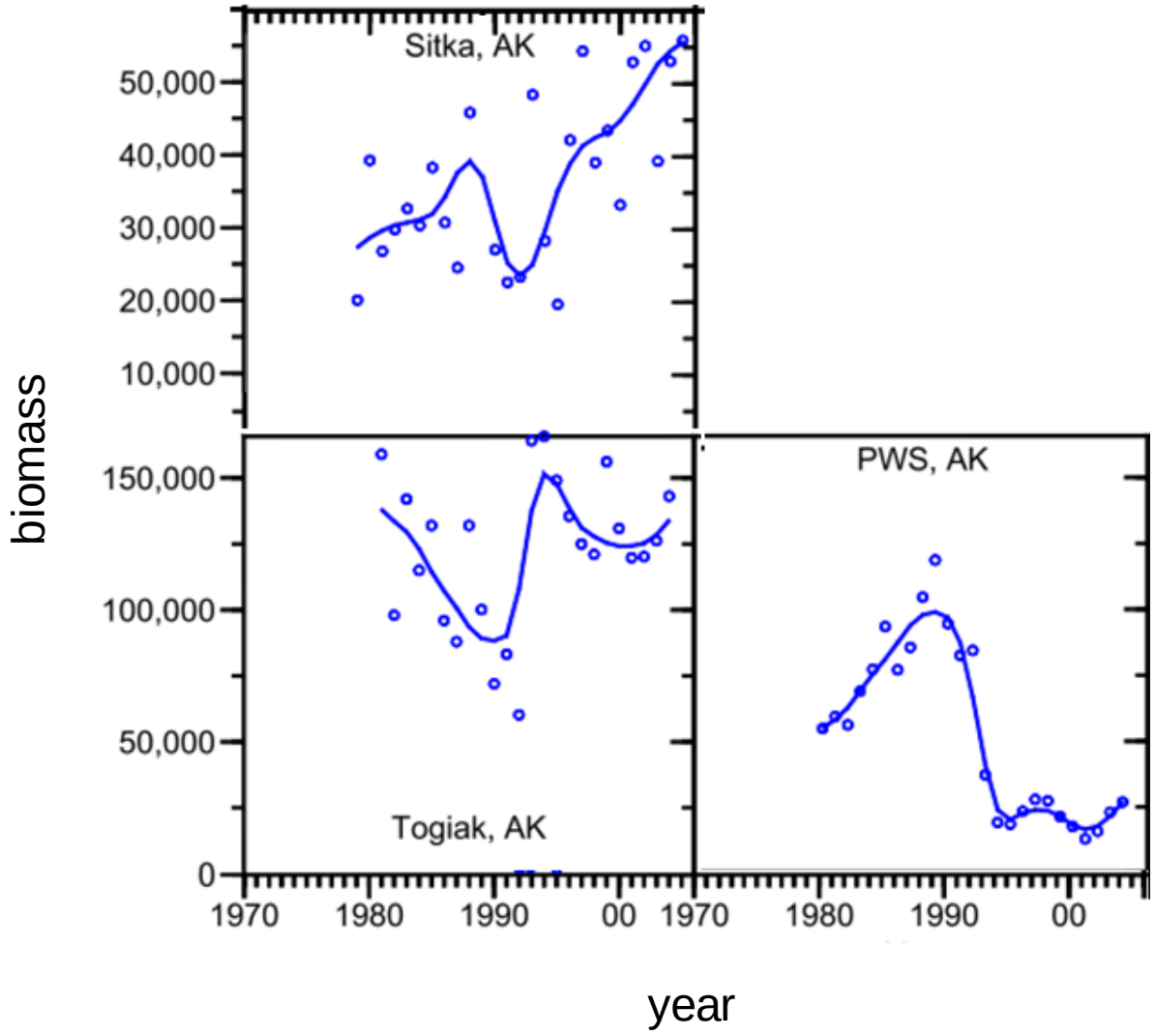
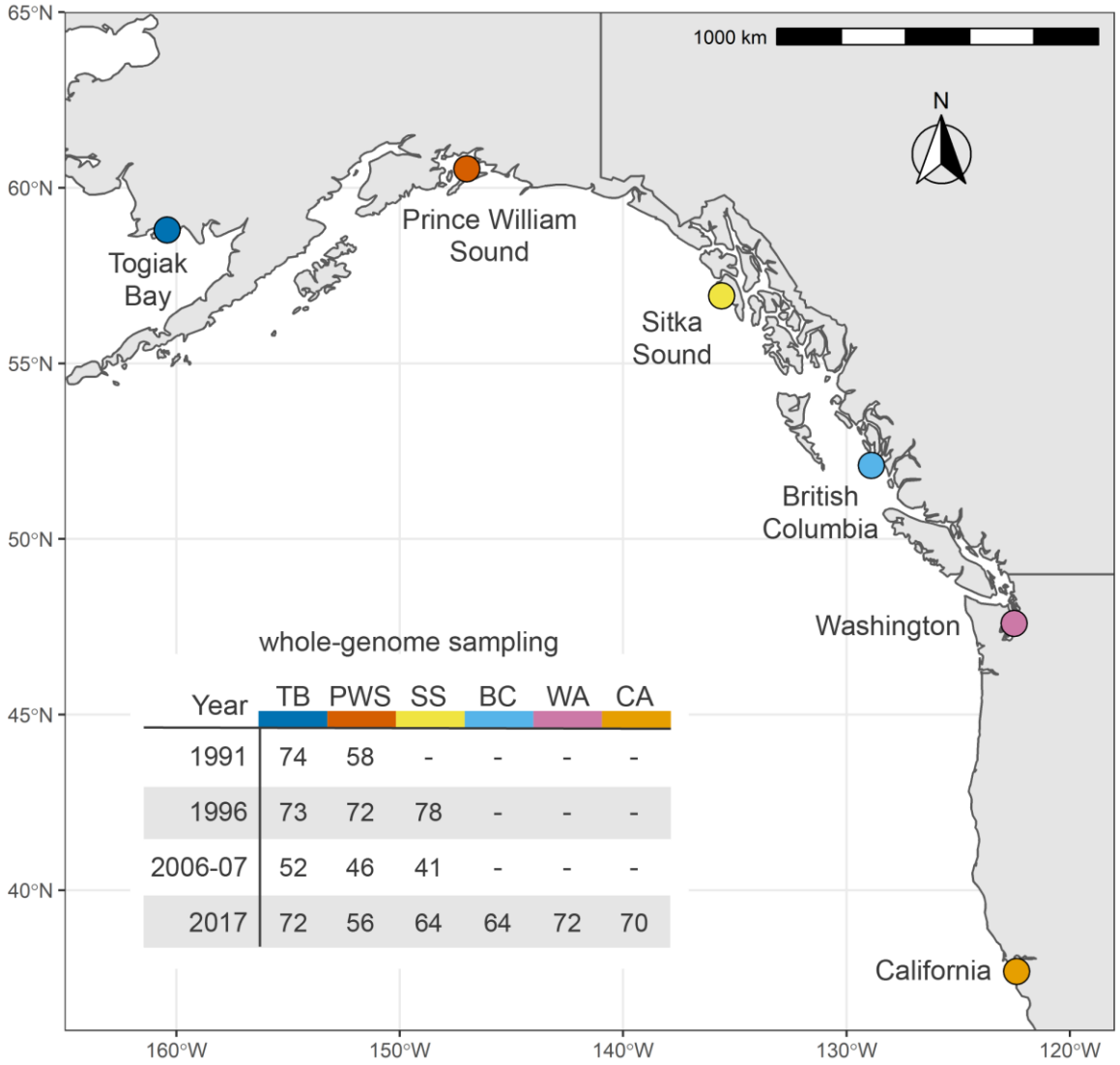


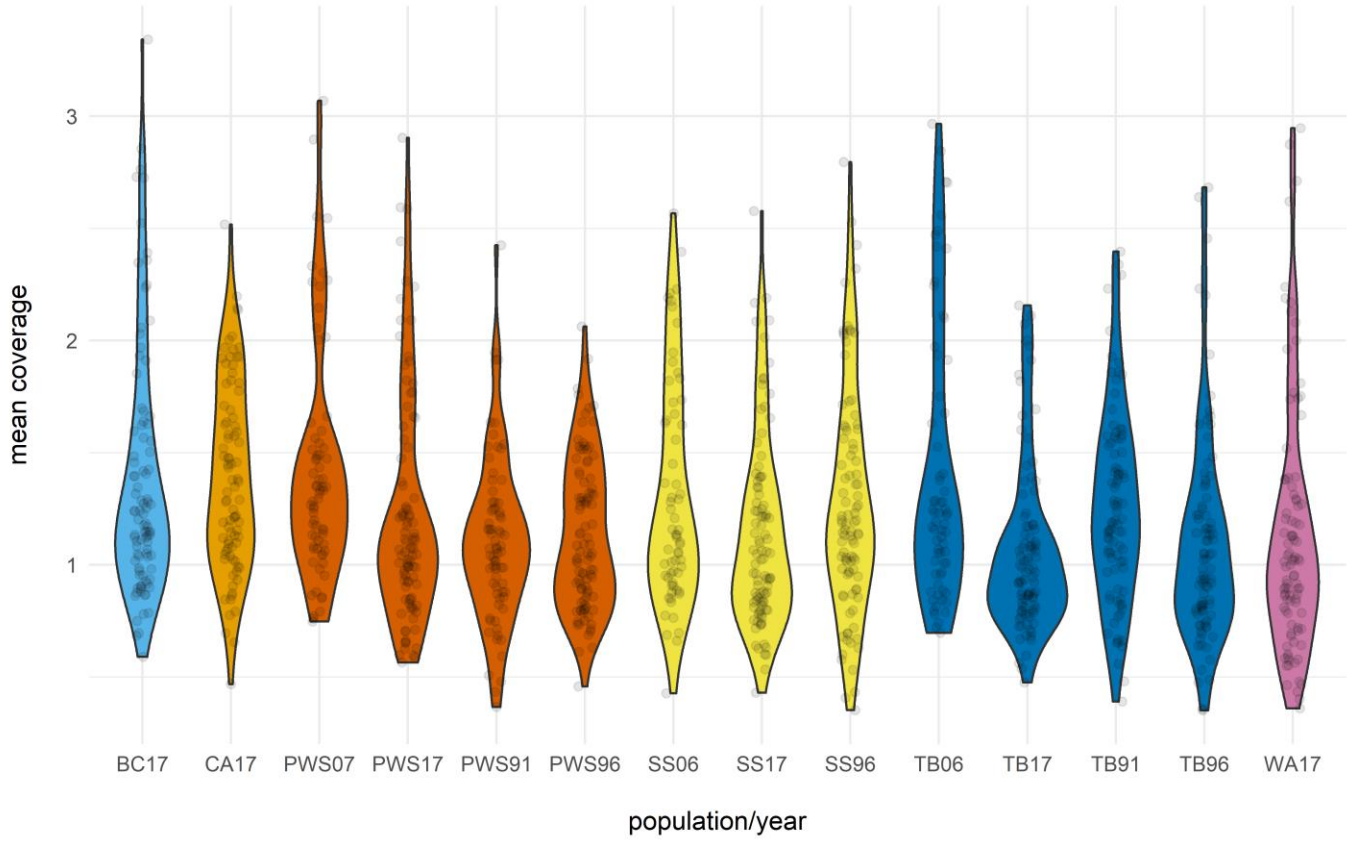


whole-genome sampling

Year	TB	PWS	SS	BC	WA	CA
1991	74	58	-	-	-	-
1996	73	72	78	-	-	-
2006-07	52	46	41	-	-	-
2017	72	56	64	64	72	70

Rice and Carls 2007

Low coverage sequencing (mean ~1.2x)

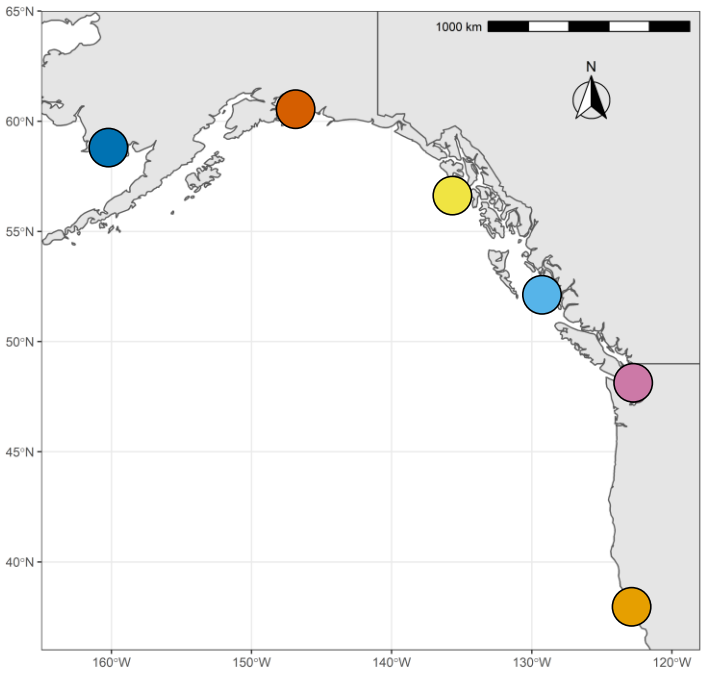


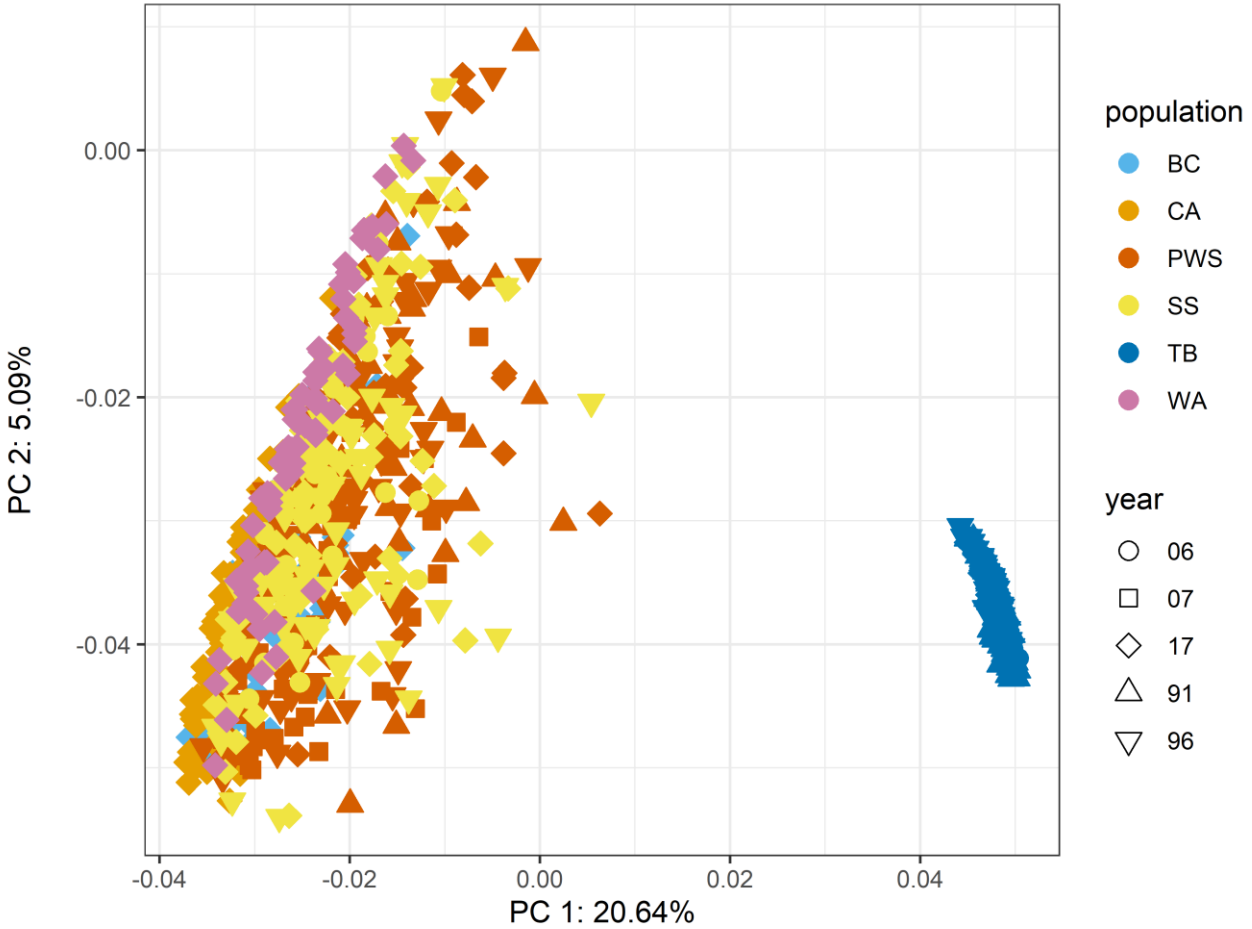
Final VCF filter:

- minimum depth = 600
- maximum depth = 2000
- minimum base quality = 20
- minimum mapping quality = 30
- minor allele frequency >= 5%
- genotyping rate >= 50% for each population (grouped by samping location and year)

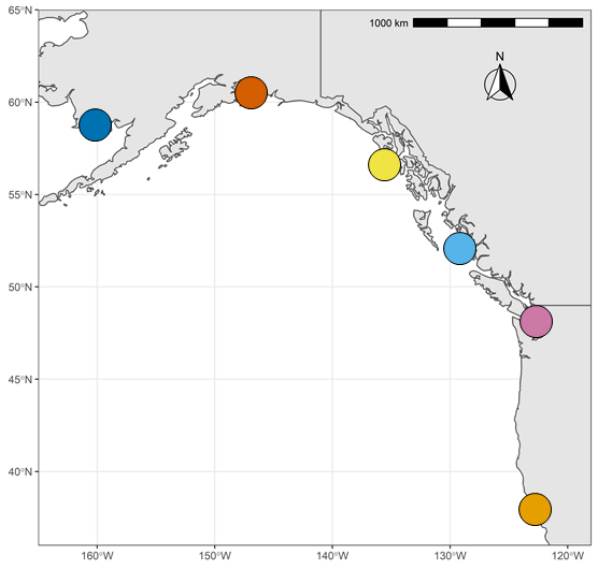
~3 million SNPs

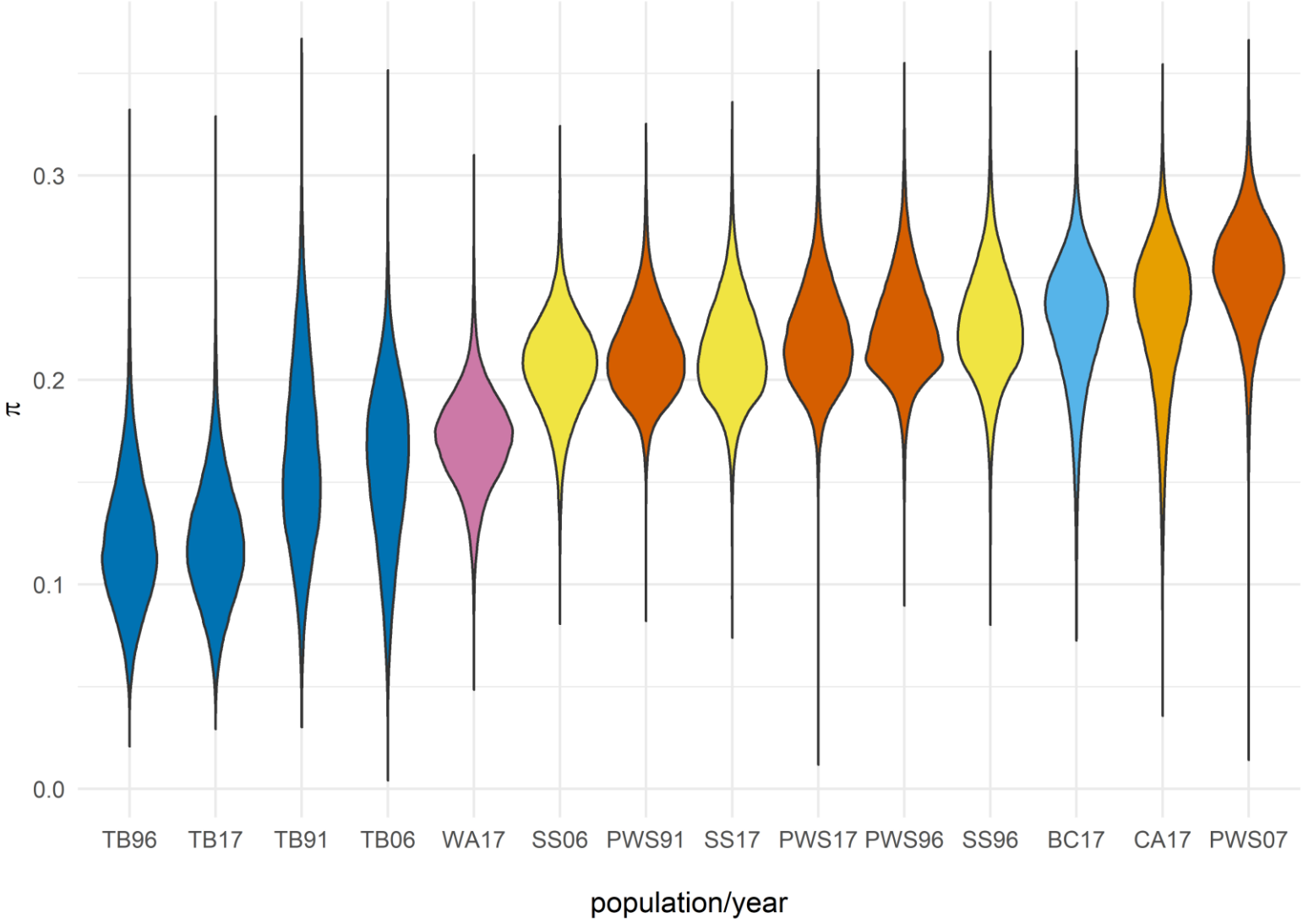
Whole genome sequencing across time and space





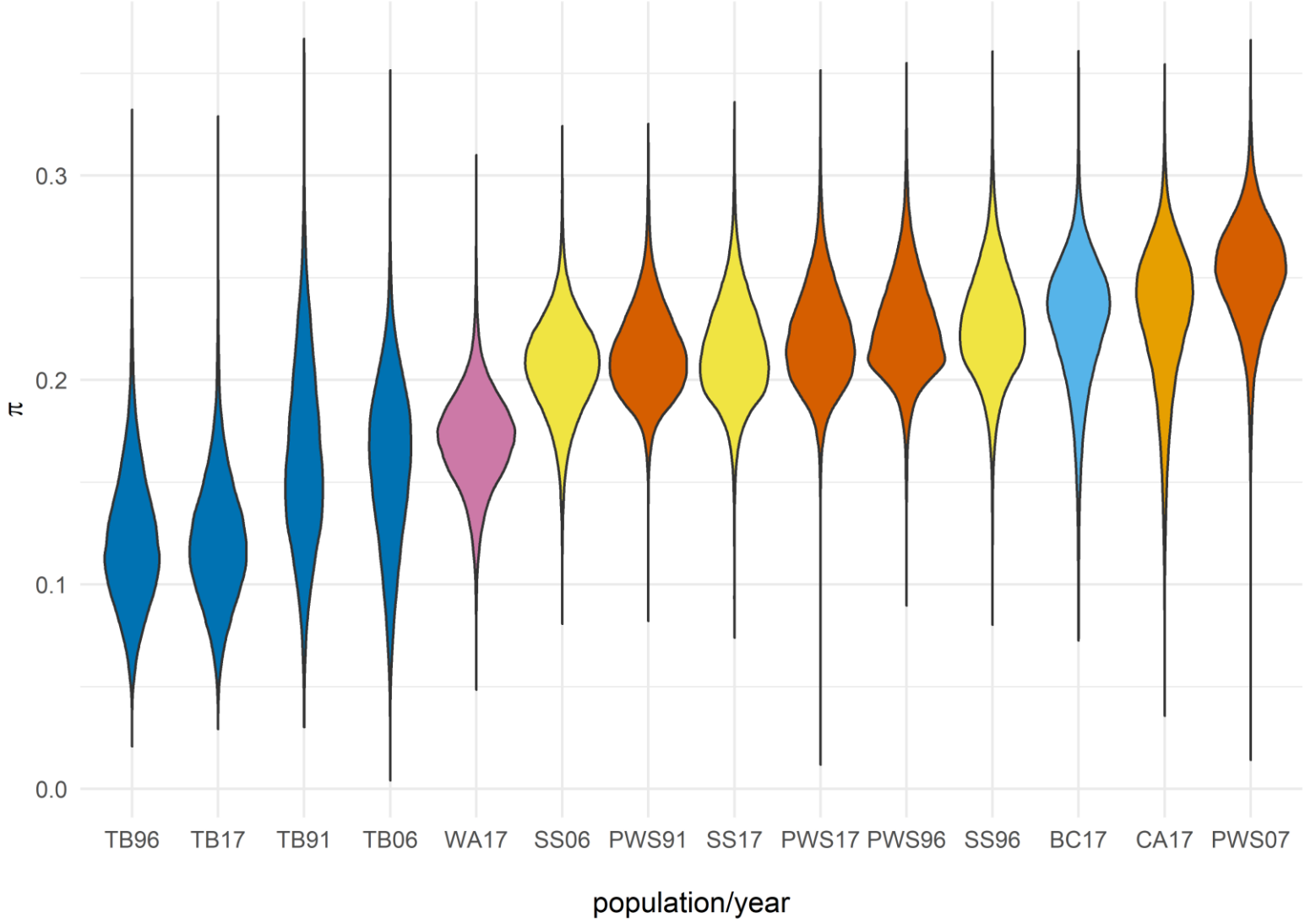
Genetic diversity (pairwise nucleotide diversity π)





Genetic diversity (pairwise nucleotide diversity π)

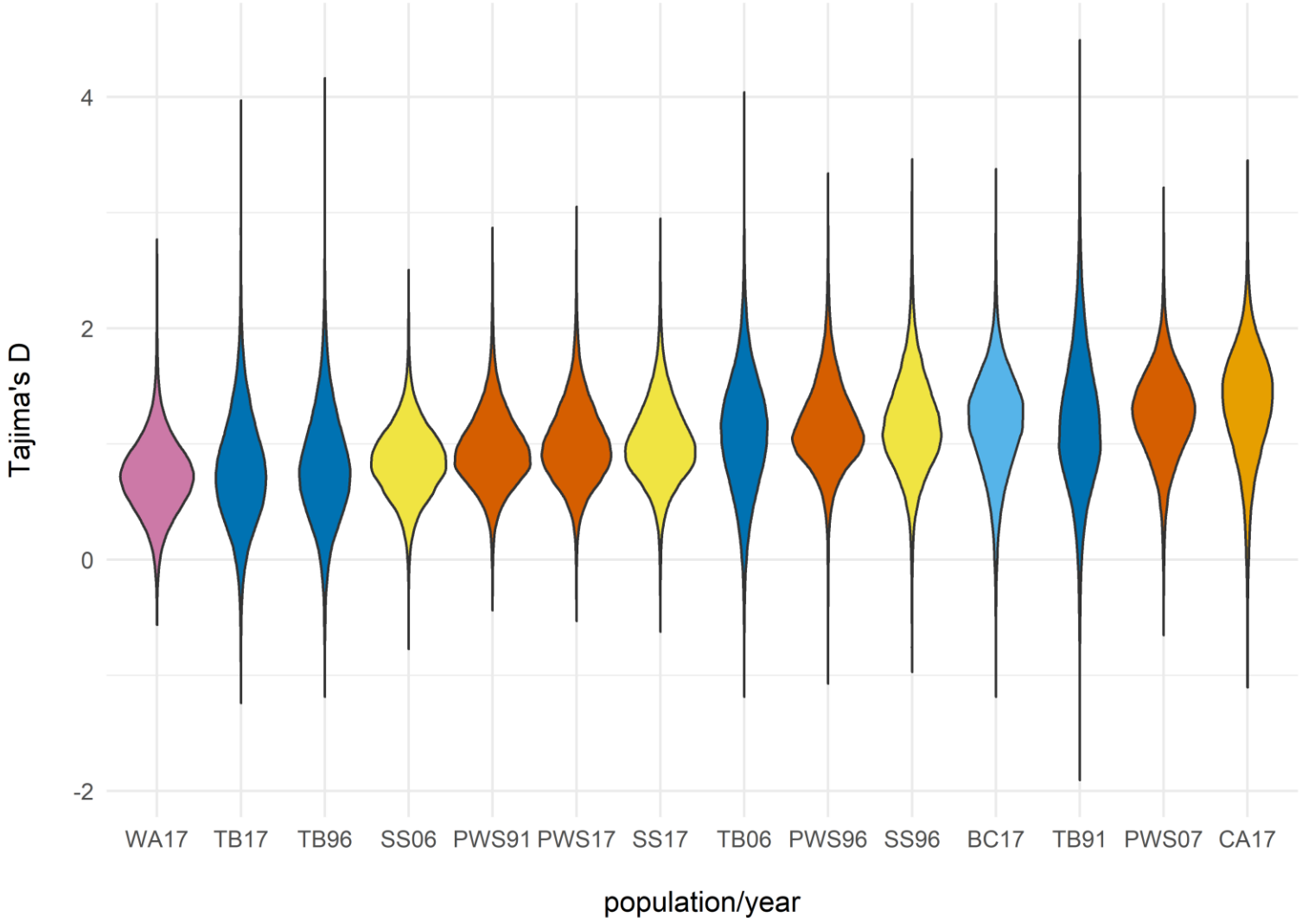
No evidence for reduced genetic diversity genome-wide in PWS relative to SS



Demographic History: Tajima's D

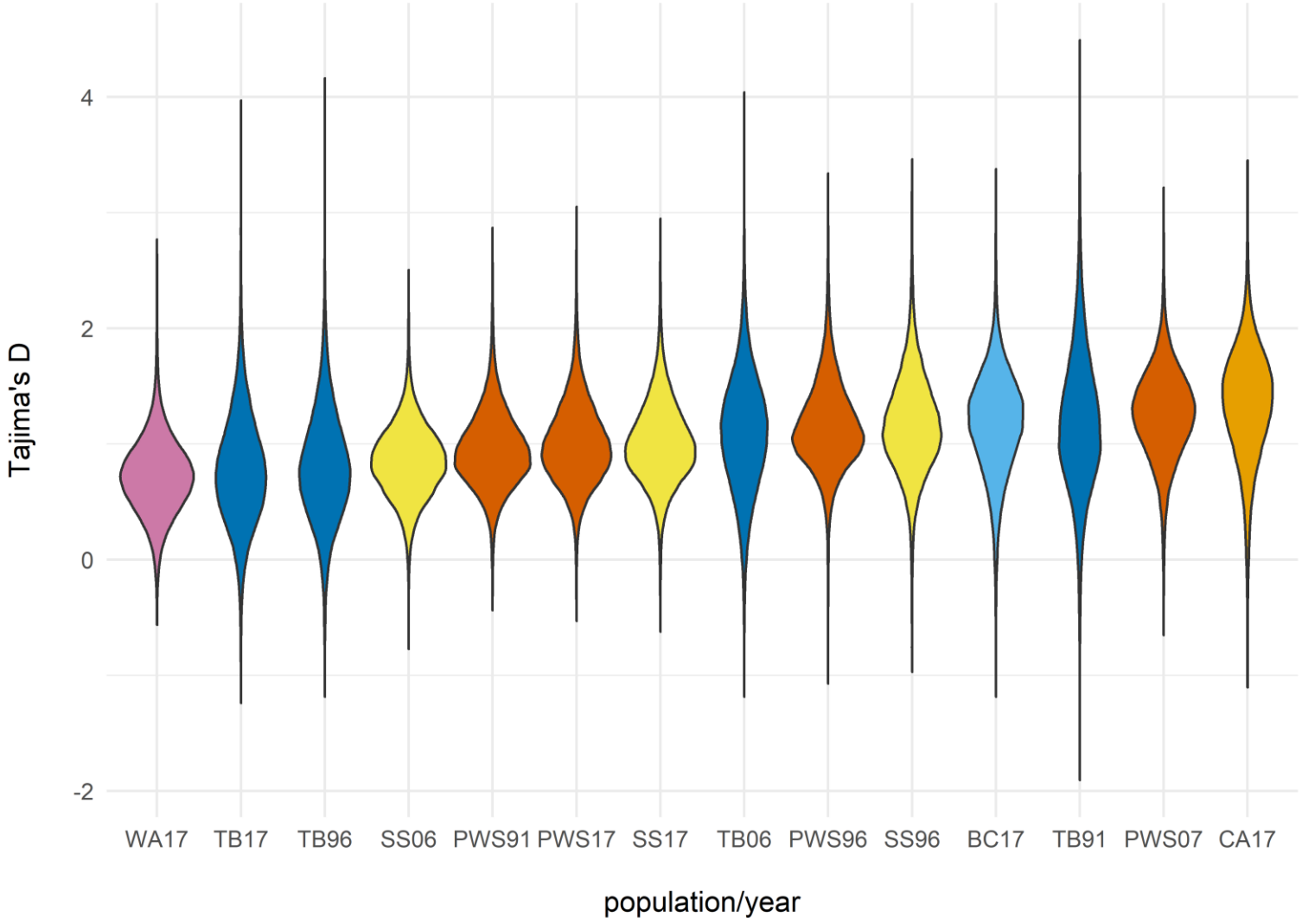
D > 0
Rare alleles scarce
Sudden population contraction

D < 0
Rare alleles abundant
Recent selective sweep
Recent population expansion

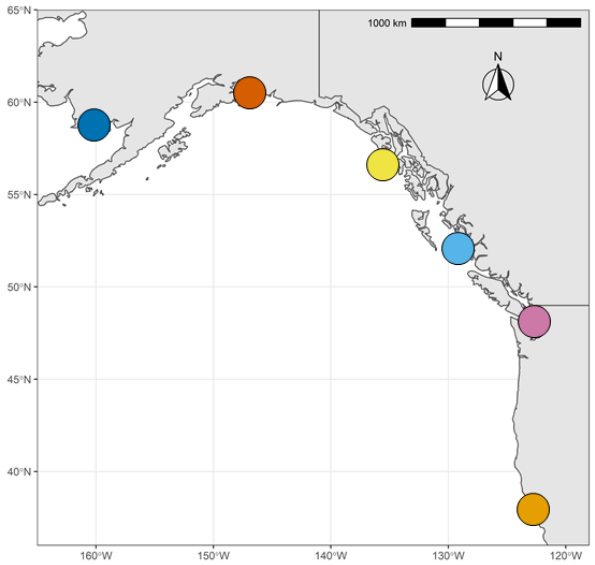


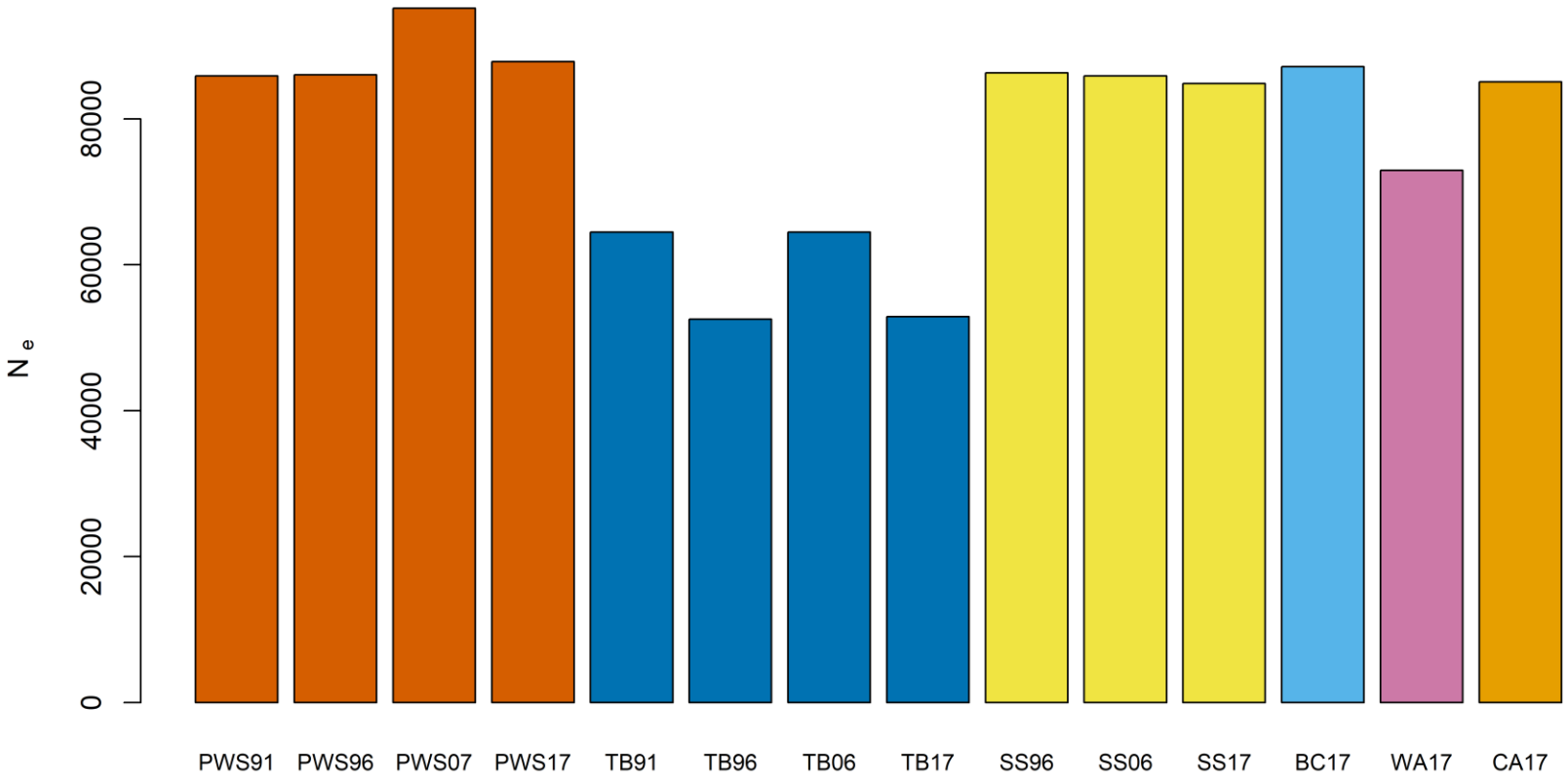
Demographic History: Tajima's D

Some evidence for population contraction in PWS relative to SS



Demographic history: Effective population size (Ne)





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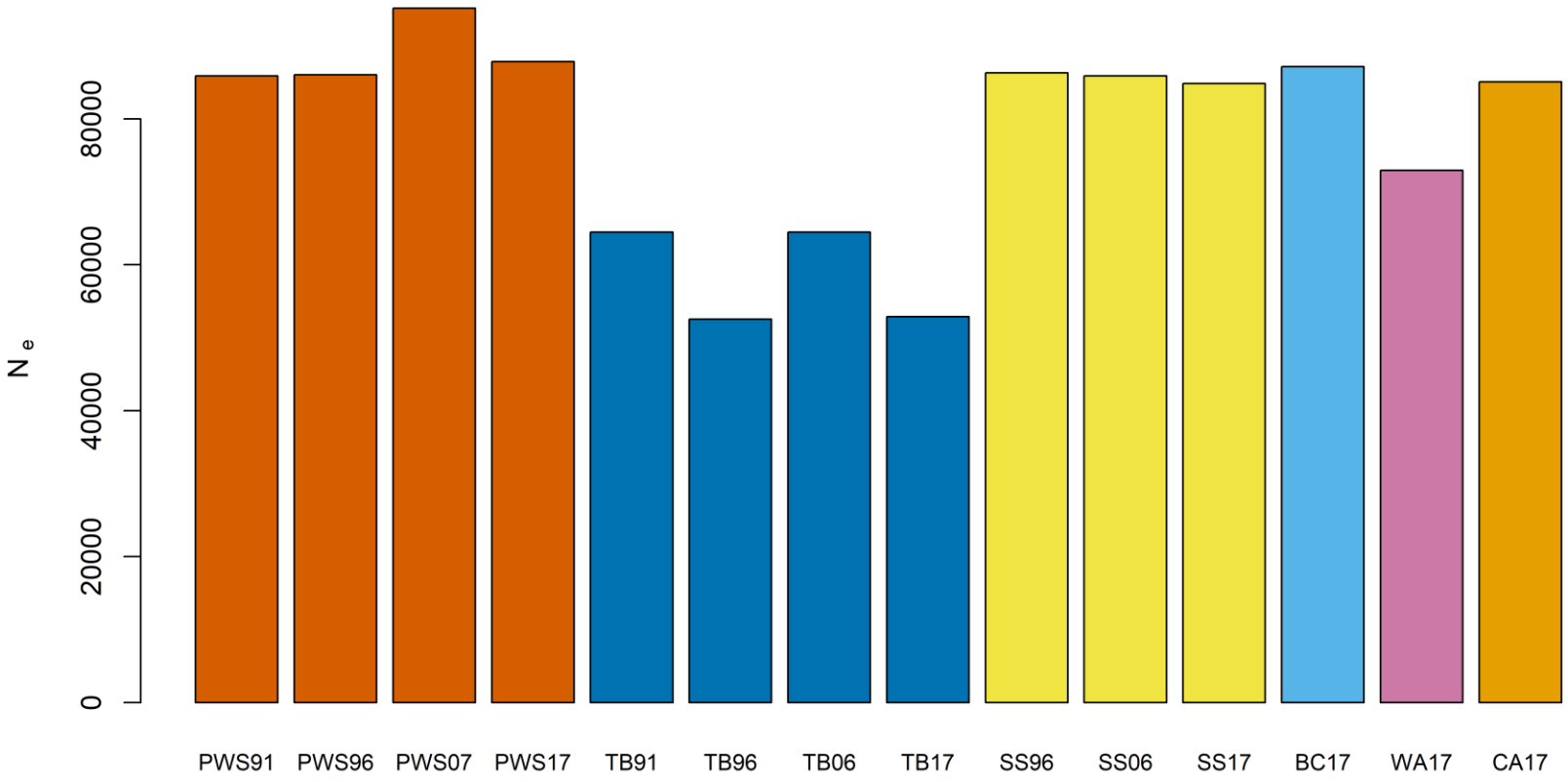
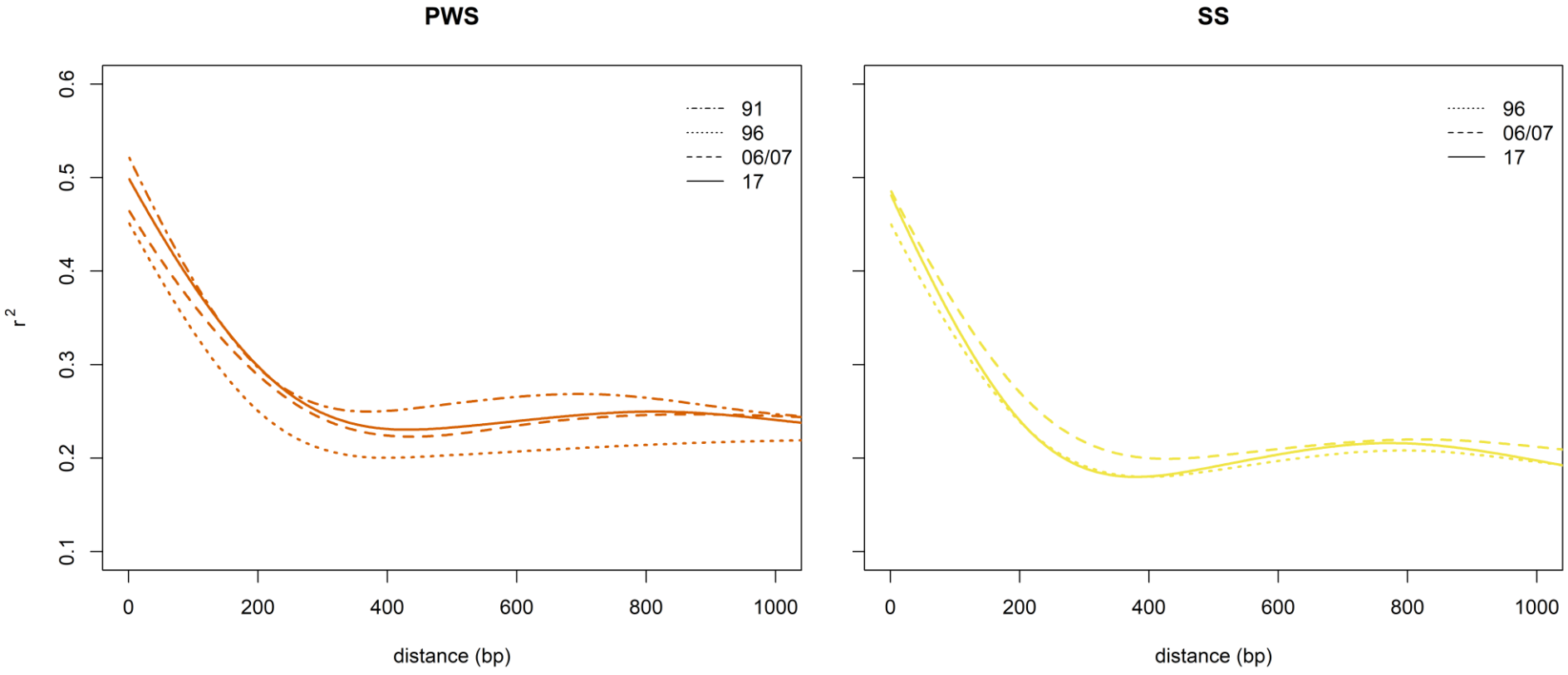


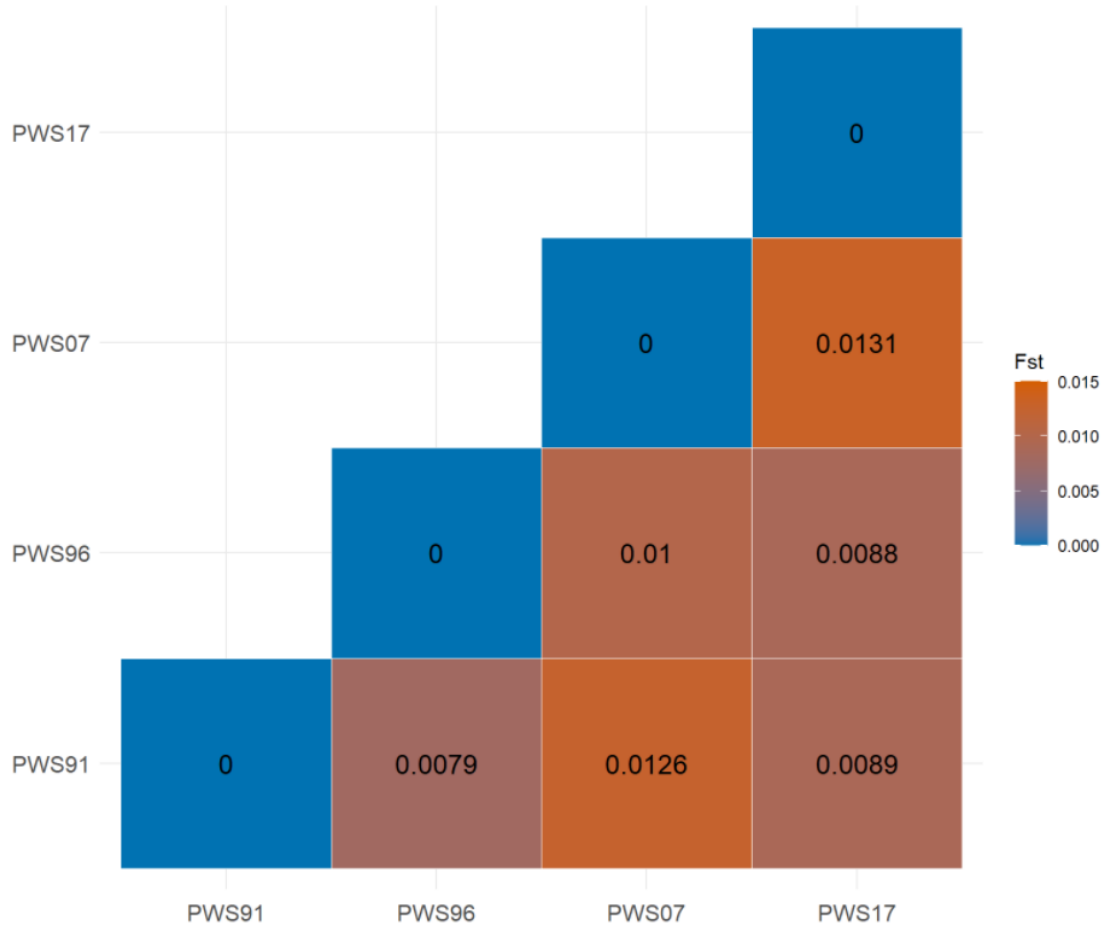
Demographic history: Linkage disequilibrium



Similar LD decay between PWS and SS suggest no population contraction drastic enough to influence Ne

Population differentiation: Temporal comparisons

Fst is low between 1991 (unexposed to oil) and all other years.



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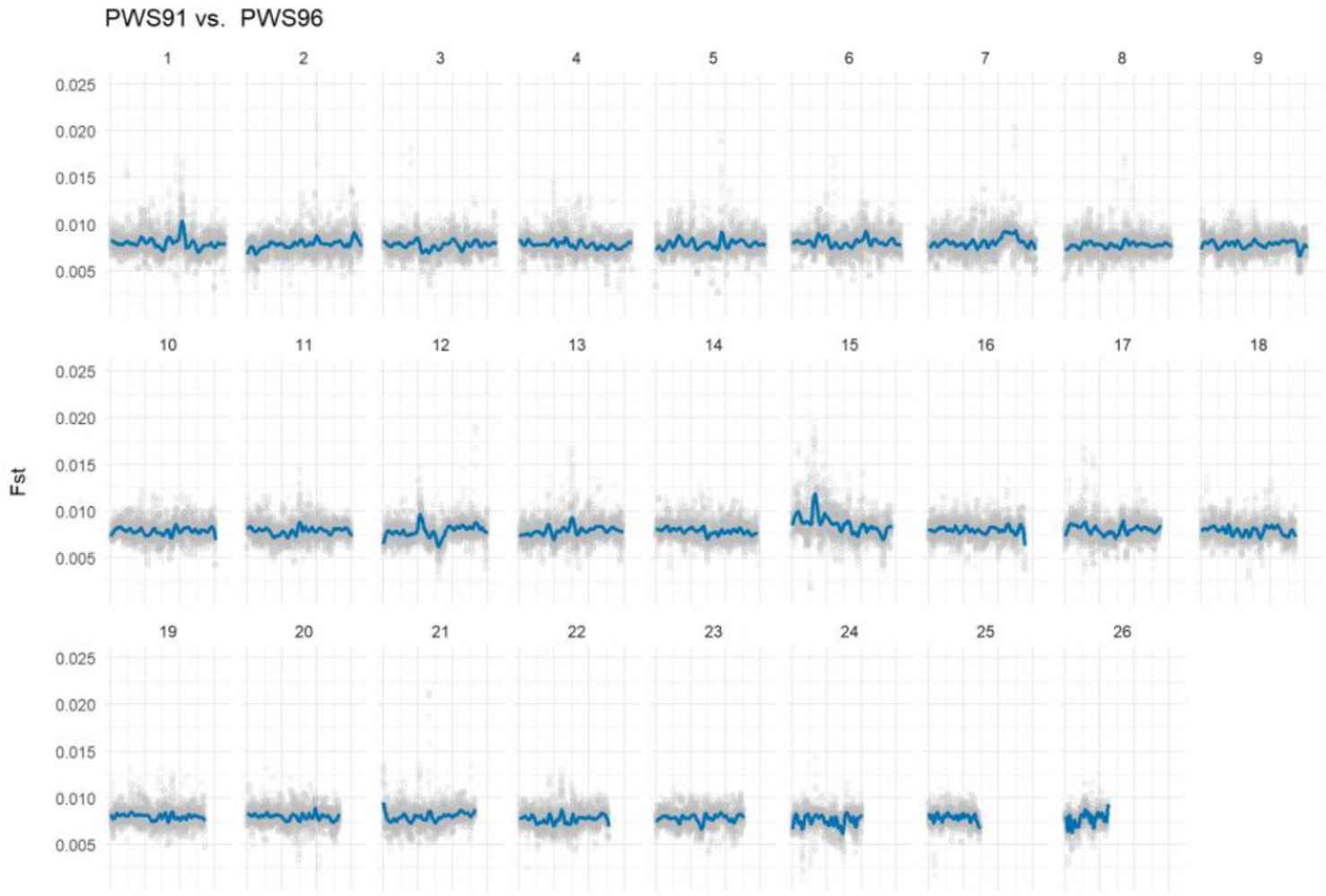
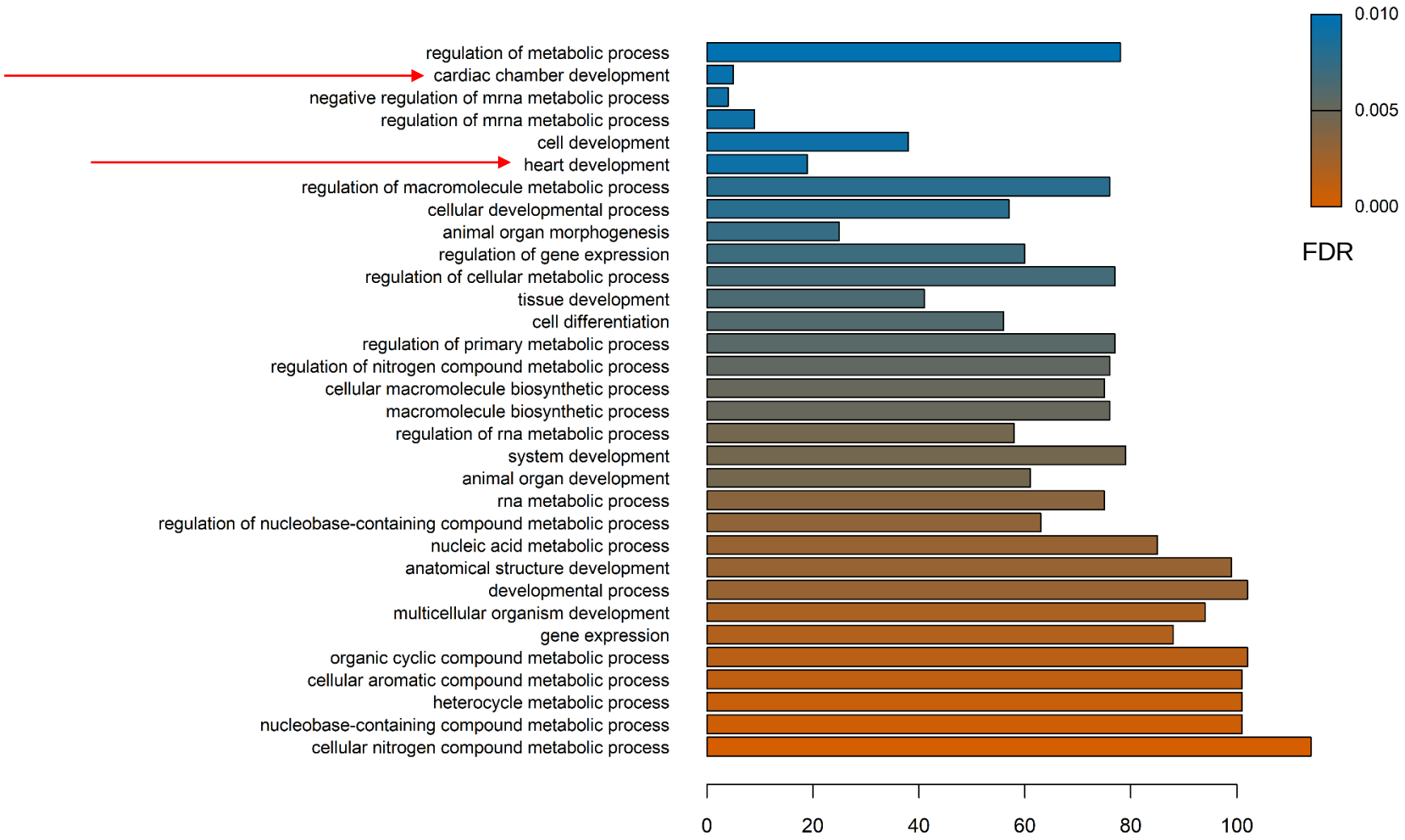
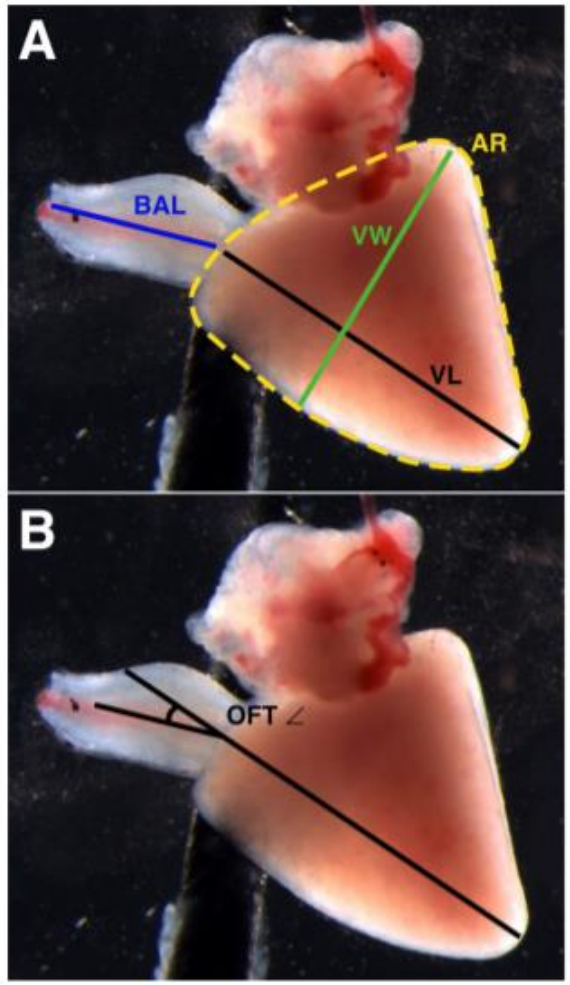


GO enrichment for 450 genes in top 99% Fst outlier regions



Very low embryonic crude oil exposures cause cardiac defects in herring (Incardona et al. 2015)



measure	control	oil exposed	*P* oil effect[b]
Fork length (cm)	5.3 ± 0.1	5.6 ± 0.1	0.0005
Mass (g)	1.26 ± 0.07	1.65 ± 0.10	0.0003
Condition factor	0.82 ± 0.01	0.87 ± 0.01	0.01
Ventricle length—lateral[a]	69.5 ± 1.0	69.8 ± 1.2	0.2
Ventricle width—lateral[a]	51.3 ± 0.9	49.8 ± 0.7	0.7
Aspect ratio—lateral	1.45 ± 0.02	1.52 ± 0.02	0.04
Ventricle length—ventral[a]	64.0 ± 1.0	63.6 ± 1.5	0.6
Ventricle width—ventral[a]	63.5 ± 0.9	64.3 ± 1.0	0.07
Aspect ratio—ventral	1.14 ± 0.01	1.13 ± 0.01	0.2
Ventricle volume (mm^3)	0.042 ± 0.003	0.050 ± 0.002	0.007
BA length (relative to ventricle)	0.45 ± 0.01	0.47 ± 0.01	0.6
OFT angle (degrees)	21.9 ± 1.8	15.4 ± 1.4	0.004

Conclusions part 1: Population collapse and recovery in PWS

- Oil exposure did not cause a drastic reduction in effective population size in PWS.
- Genome-wide genetic diversity results mirror previous studies using microsatellites and mtDNA:
  - Diversity in PWS herring collected in 1996 is comparable to that of other healthy Pacific herring populations in Alaska and British Columbia (Liu et al. 2012; Seeb et al. 1999; Bentzen et al. 1997).
- While genetic diversity genome-wide is similar across time in PWS and similar to diversity in healthy populations, oil exposure may have selected for variants at key loci.

Future directions part 1: Population collapse and recovery in PWS

- Collaborate!
- Temporal sampling allows us to identify alleles under selection (covariance in allele frequency change over time).

RESEARCH ARTICLE

Estimating the genome-wide contribution of selection to temporal allele frequency change

Vince Buffalo and Graham Coop

PNAS August 25, 2020 117 (34) 20672-20680; first published August 12, 2020 https://doi.org/10.1073/pnas.1919039117

Edited by Montgomery Slatkin, University of California, Berkeley, CA, and approved July 13, 2020 (received for review October 31, 2019)

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- Search for reduced diversity and signatures of selection at specific loci (AHR signaling and immune signaling genes).

Future directions part 1: Population collapse and recovery in PWS

- Collaborate!
- Use more sophisticated tools that use coalescent models to estimate changes in population size over time (dadi / fastsimcoal / moments).
- Perform simulations informed by demographic modeling to define significance thresholds for candidate adaptive loci.
- Search for reduced diversity and signatures of selection at *a priori* candidate loci (AHR signaling and immune signaling genes).

Goal: Use genomics to understand how populations change over time

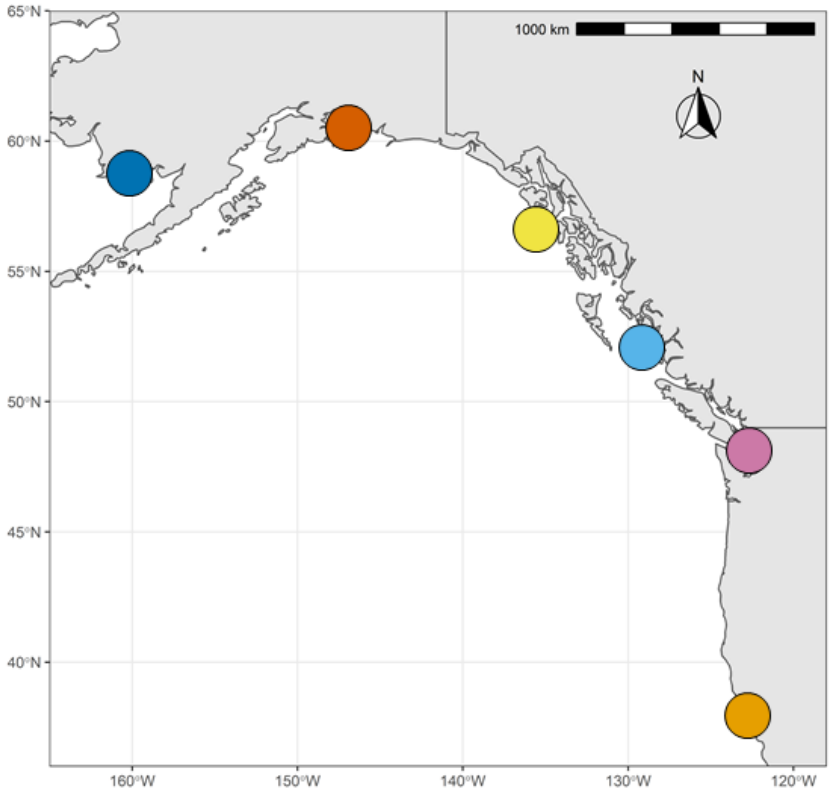
Part 1: Population collapse and recovery in Prince William Sound, Alaska

- What caused the PWS population to collapse?
- What is limiting population recovery?

Part 2: Local Adaptation

- What are the genetic differences between populations underlying locally adaptive phenotypes?
- How will populations respond to warming waters?

Latitudinal differences between populations

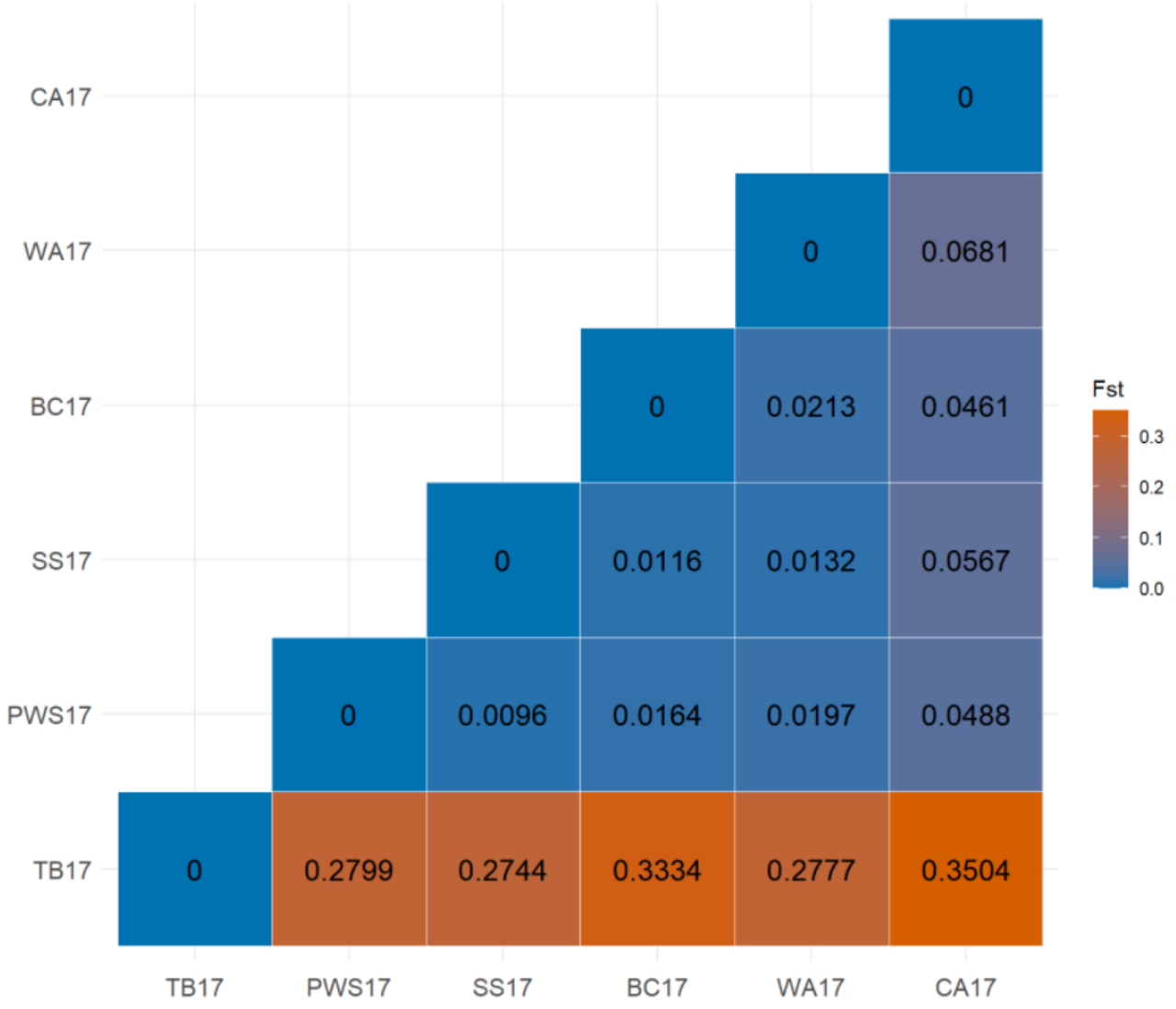


Trends from North to South

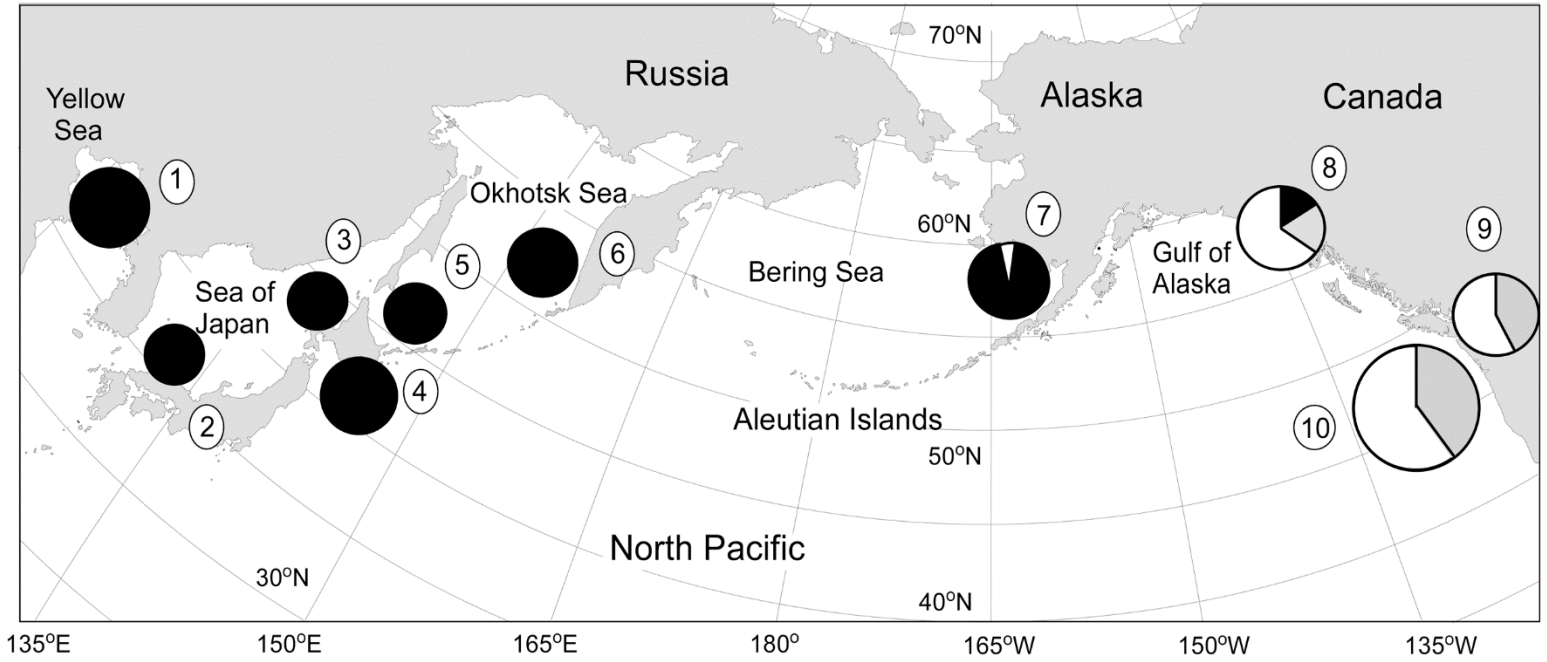
- smaller size
- sexually mature earlier
- spawn earlier in the year
- die younger

(Hay et al. 2008)

Population differentiation: 2017 comparisons



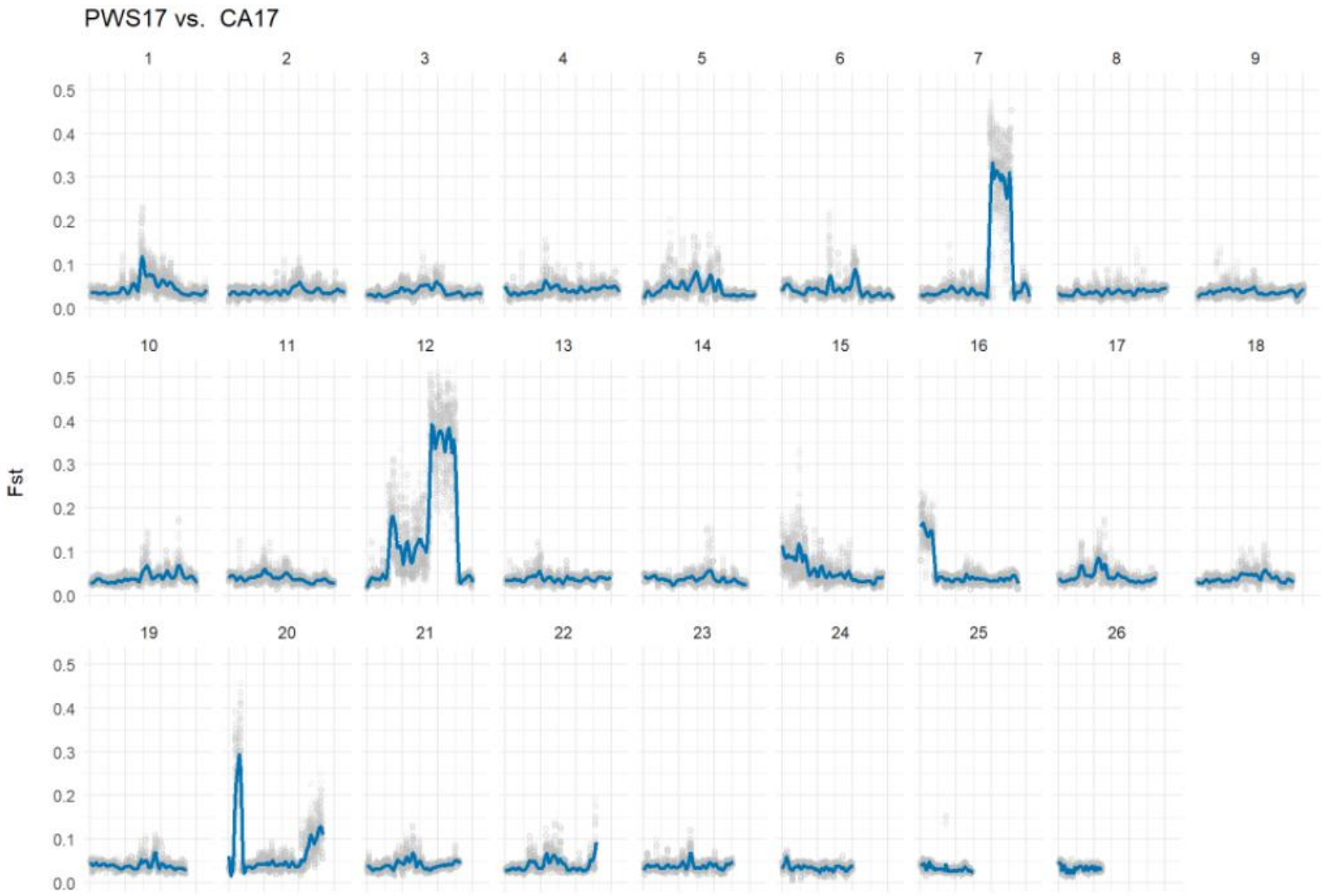
Consistent with previous microsatellite and mtDNA data



(Liu et al. 2012)

Population differentiation: Togiak Bay vs PWS 2017

Population differentiation: California vs PWS 2017



Conclusions part 2: Local adaptation across a latitudinal gradient

- Whole genome sequencing confirms previous findings that herring in the Bering Sea are significantly diverged from other populations in the East Pacific.

- California population shows low genome-wide divergence compared to other Eastern Pacific populations, but high divergence concentrated in small regions of a few chromosomes. Potential inversions may harbor genetic variation important for adaptive phenotypes.