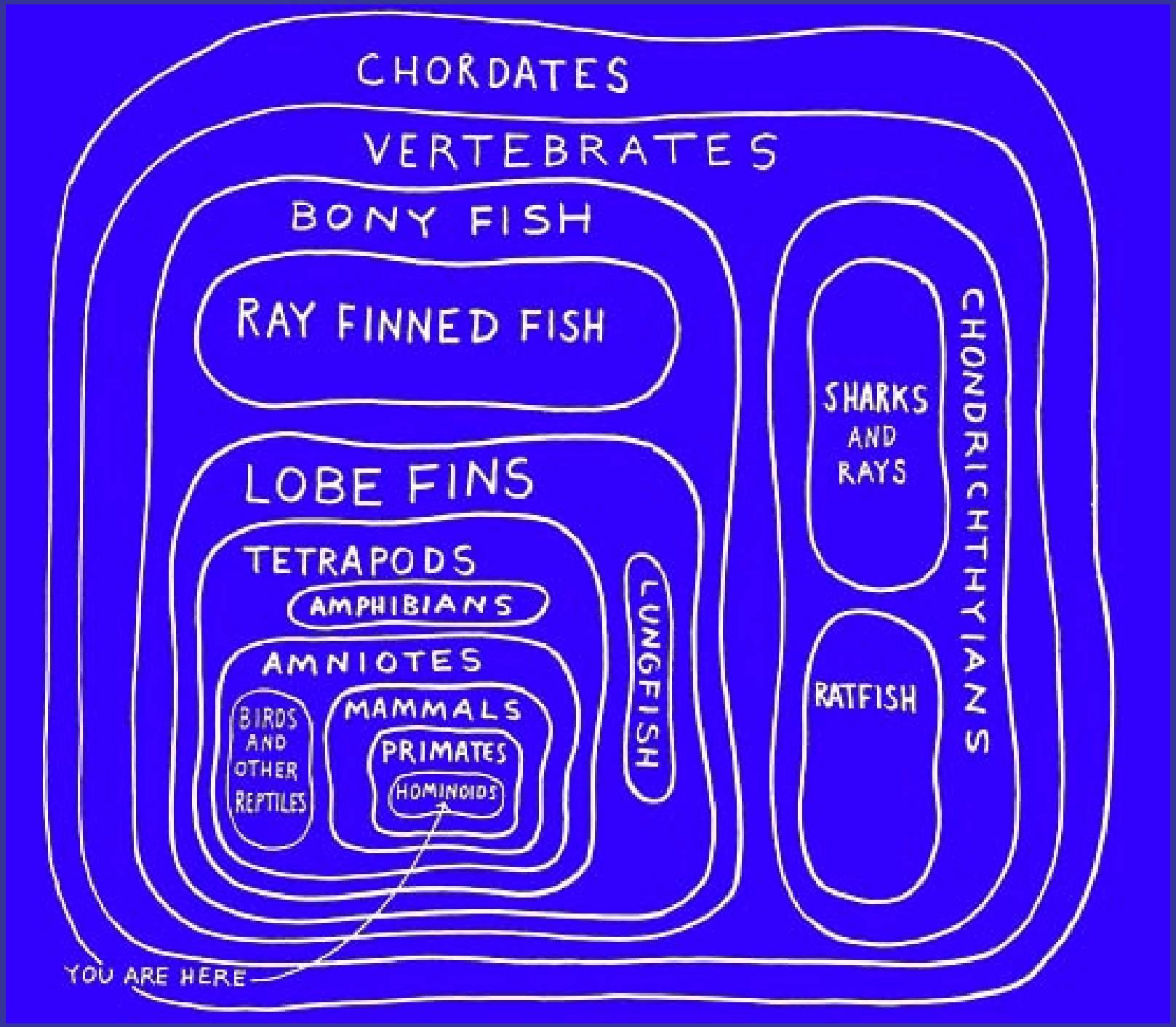

CHORDATES
VERTEBRATES
BONY FISH
RAY FINNED FISH
LOBE FINS
TETRAPODS
AMPHIBIANS
AMNIOTES
BIRDS AND OTHER REPTILES
MAMMALS
PRIMATES
HOMINOIDS
LUNGFISH
CHONDRICHTHYIANS
SHARKS AND RAYS
RATFISH
YOU ARE HERE

Adaptive versus Neutral Markers: Units of Conservation

Fred Allendorf

The University of Montana

Victoria
UNIVERSITY OF WELLINGTON
Te Whare Wānanga
o te Ūpoko o te Ika a Māui

Conservation Genetics Joke

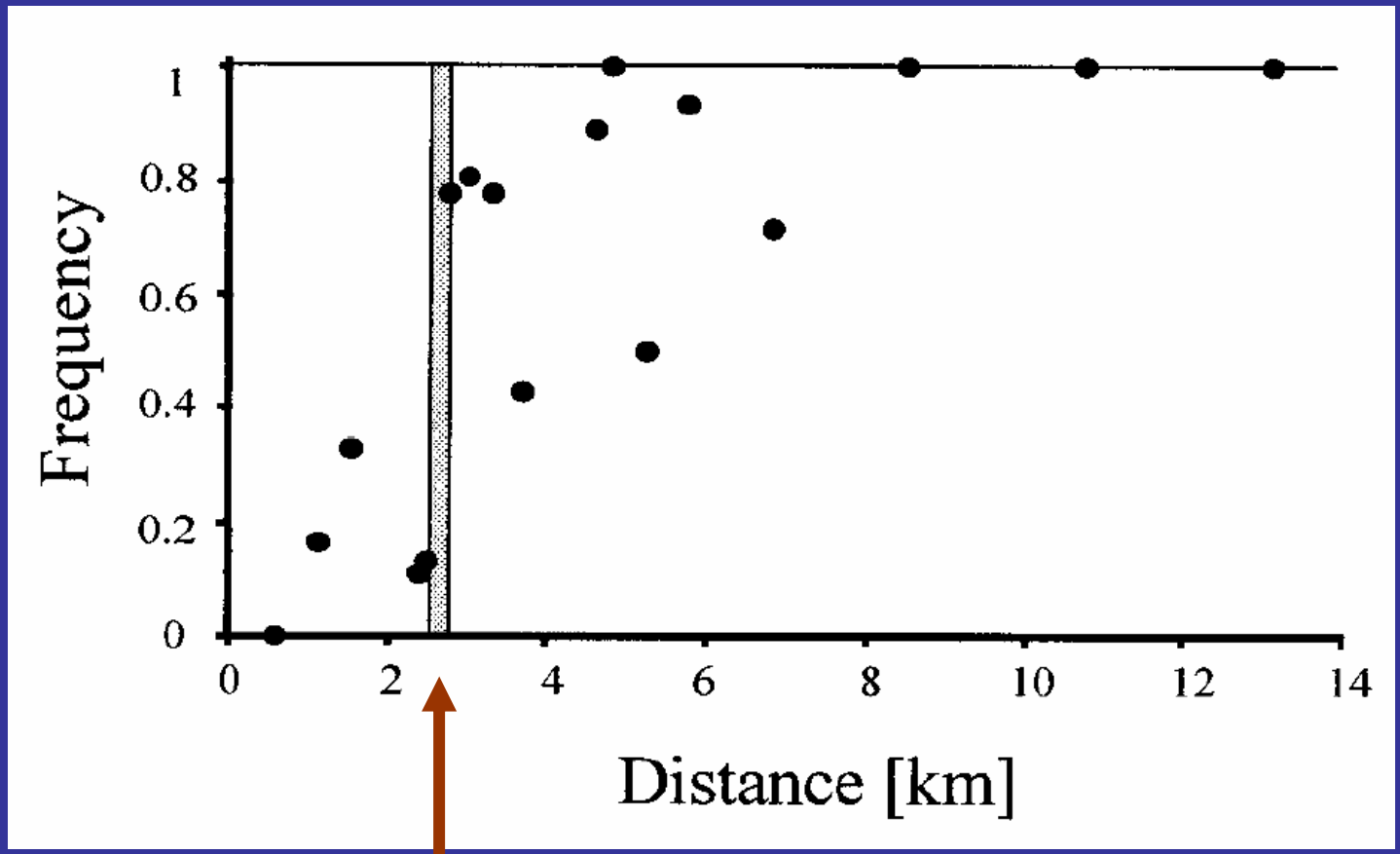
What did Custer say when he left South Dakota before the battle of the Little Bighorn in Montana?

Conservation Genetics Trivia

What is the correct term for a word or phrase that reads the same forward and backward, as in: “rats live on no evil star”?

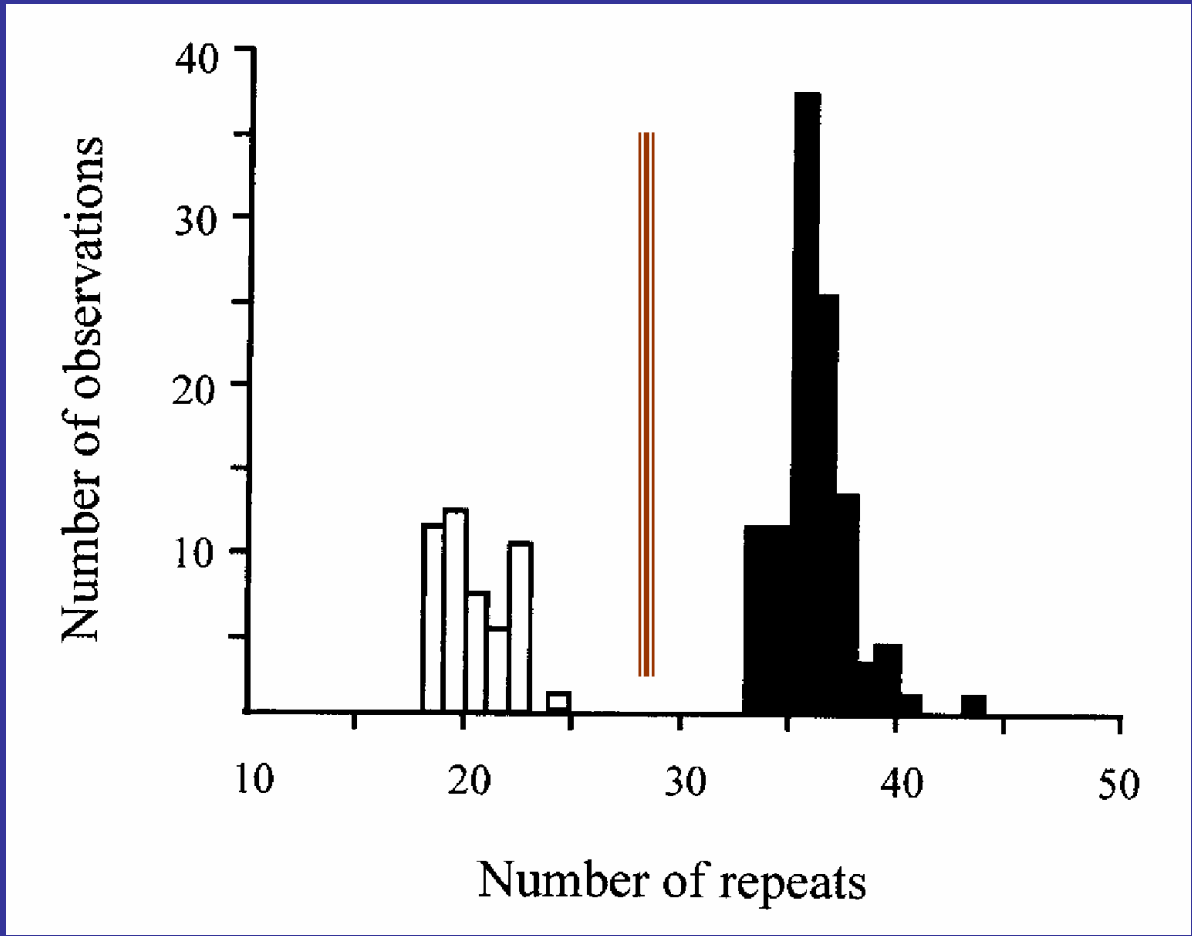
Common shrew in western France

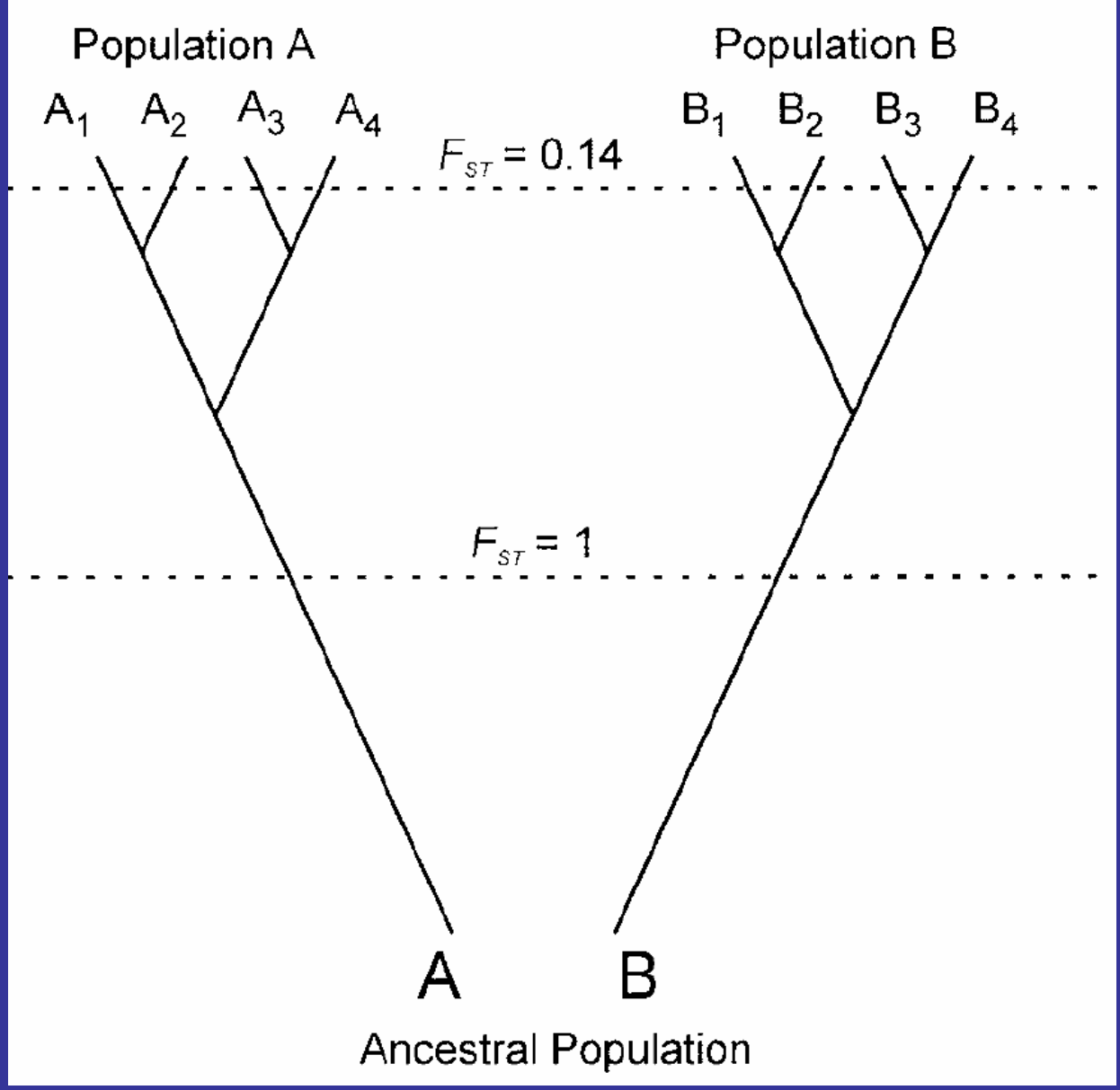
mtDNA



Hybrid zone

Y-linked microsatellite locus



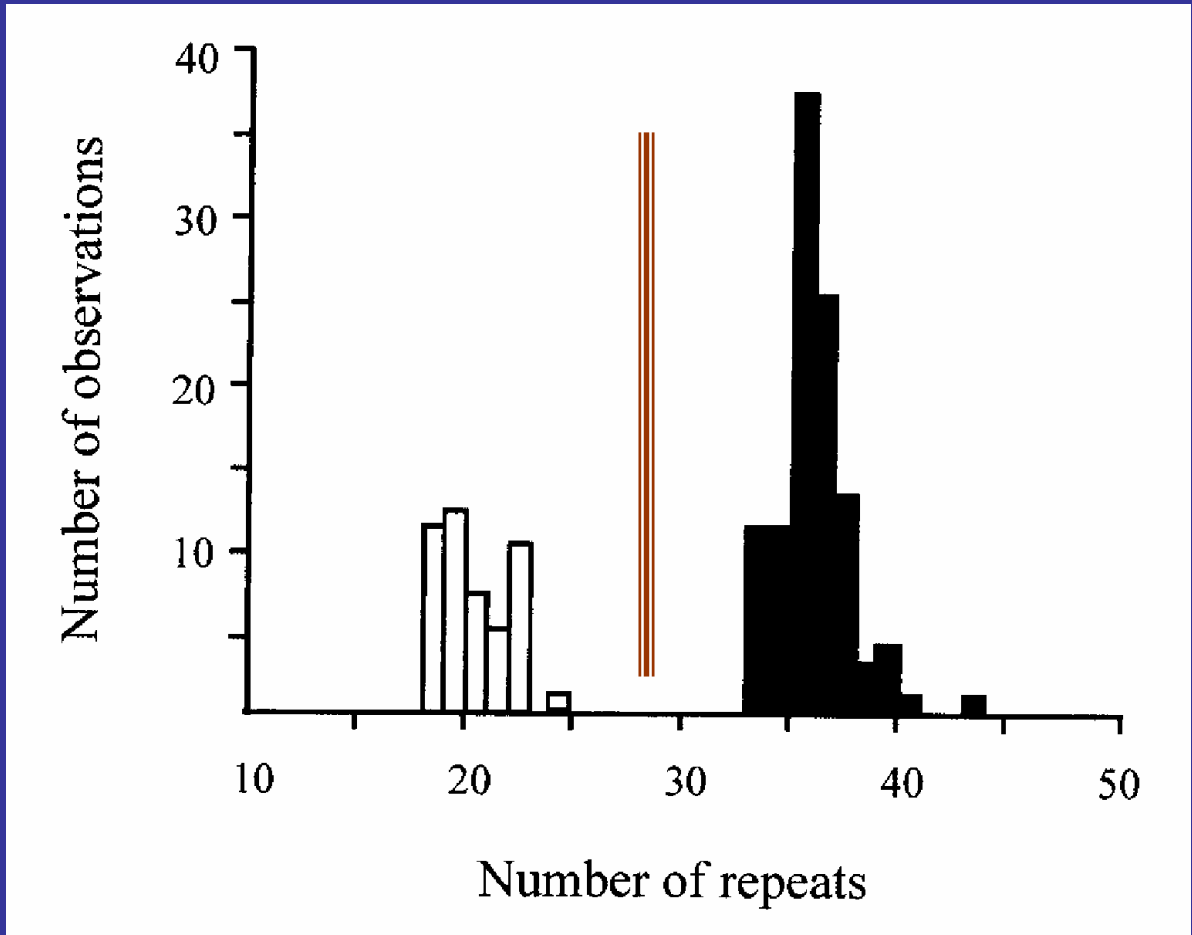


Allele genealogy

(coalescence)

R_{ST} is an analogue of F_{ST} that takes the relative size of alleles (i.e., allelic state) into consideration.

Y-linked microsatellite locus

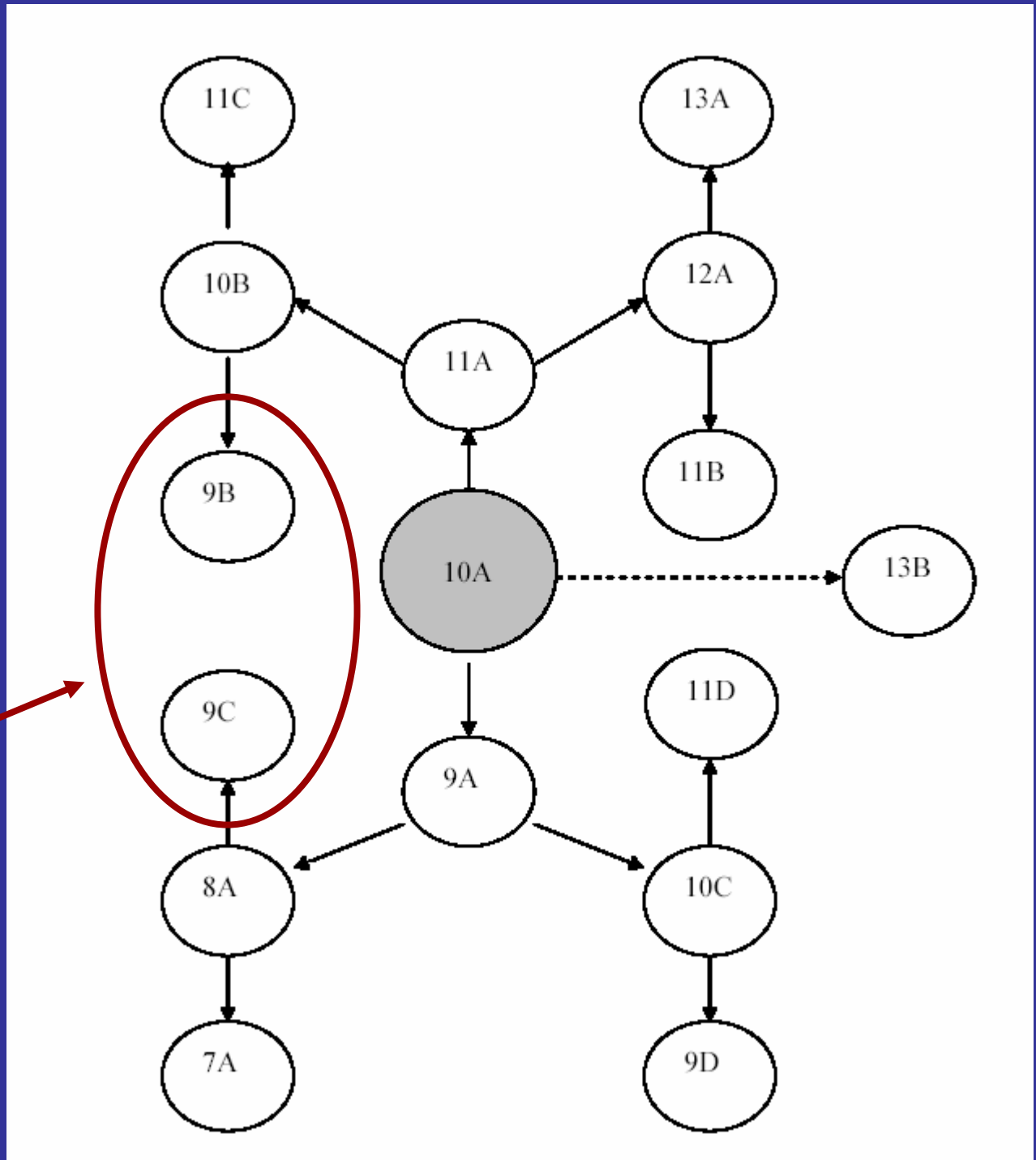


$H_S = 0.71$

$F_{ST} = 0.19$; $R_{ST} = 0.98$

Microsatellite mutation network

Homoplasy



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Te Whare Wānanga
o te Ūpoko o te Ika a Māui

Setting priorities for conservation efforts

Preserving the Tree of Life

Georgina M. Mace,[1] John L. Gittleman,[2] Andy Purvis[3]

Science 300:1707-1709. (2003)

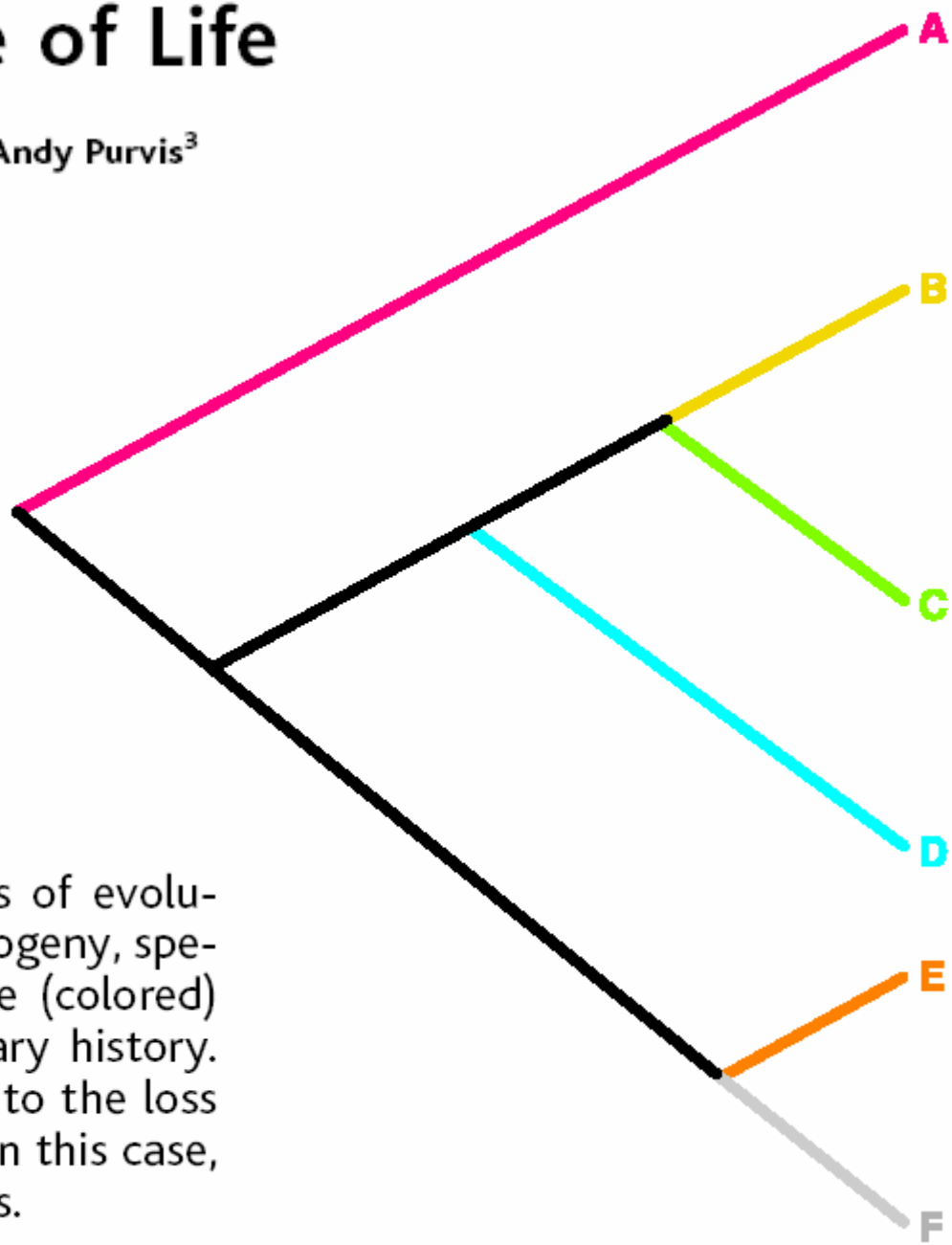
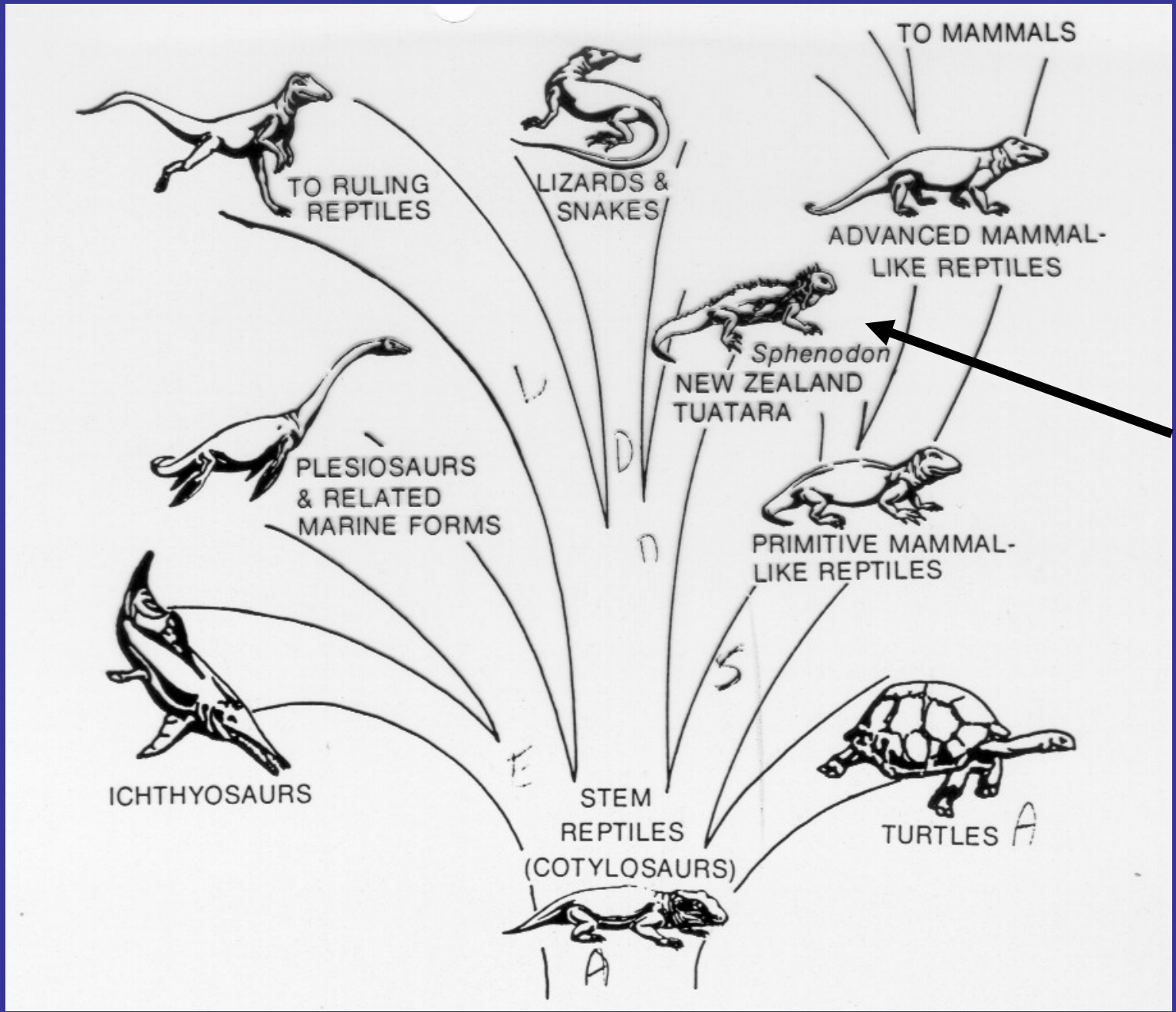
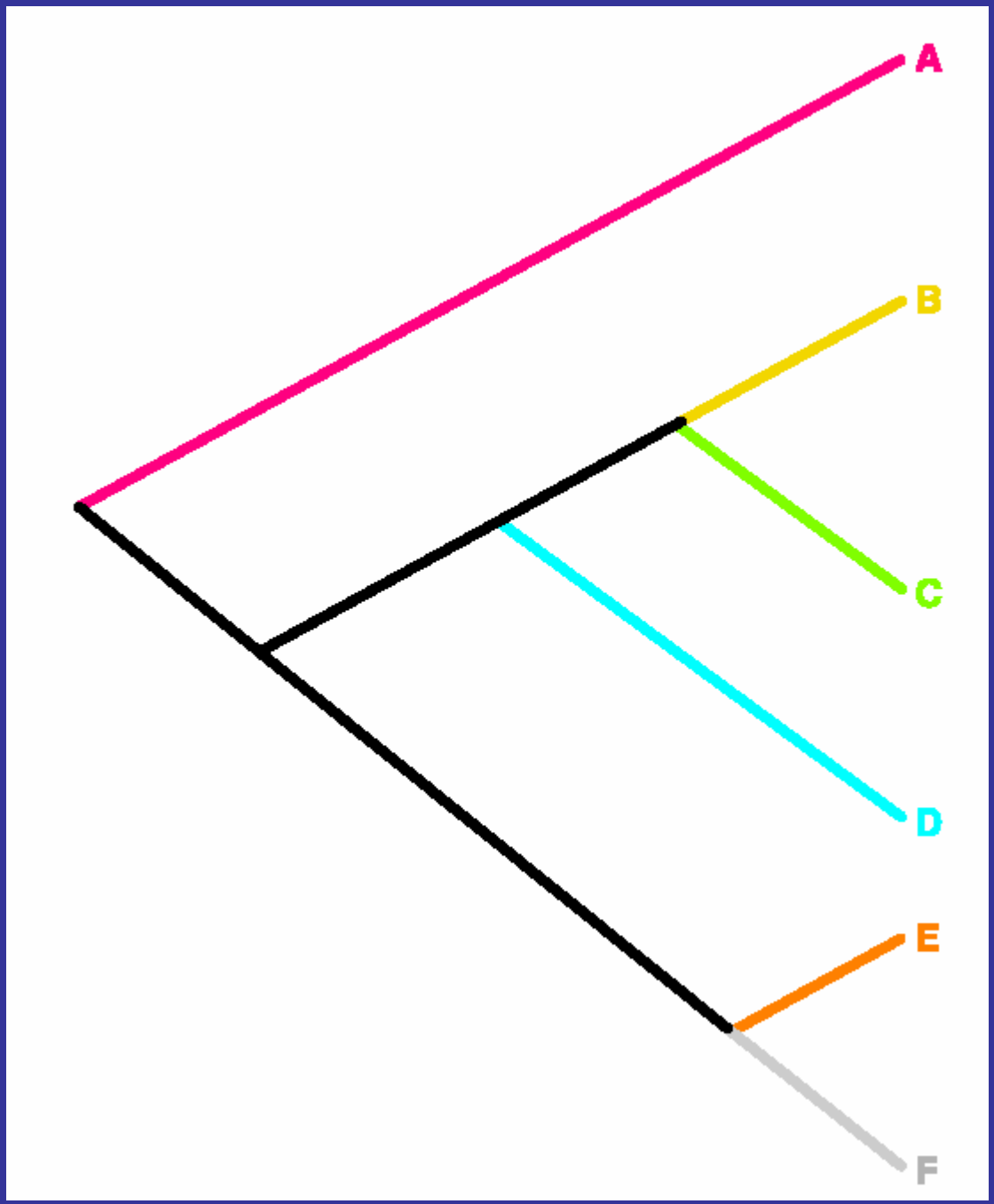


Fig. 1. Loss of species leads to loss of evolutionary history. In this example phylogeny, species A to F each have some unique (colored) and some shared (black) evolutionary history. Extinction of any one species leads to the loss of the unique history it represents. In this case, loss of species A is the most serious.


TO MAMMALS
TO RULING REPTILES
LIZARDS & SNAKES
ADVANCED MAMMAL-LIKE REPTILES
Sphenodon
NEW ZEALAND TUATARA
PLESIOSAURS & RELATED MARINE FORMS
PRIMITIVE MAMMAL-LIKE REPTILES
ICHTHYOSAURS
STEM REPTILES (COTYLOSAURS)
TURTLES



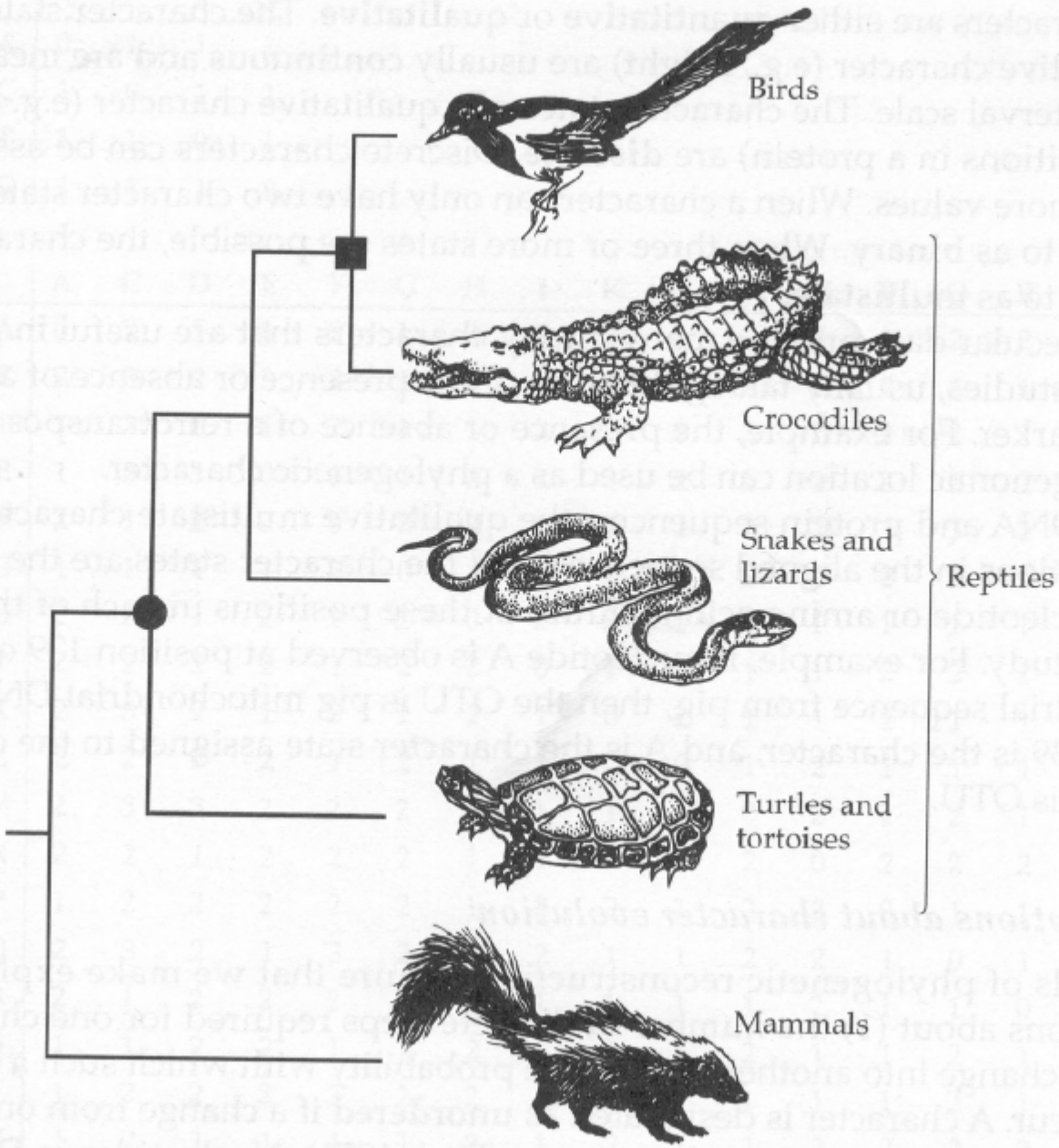
Tuatara

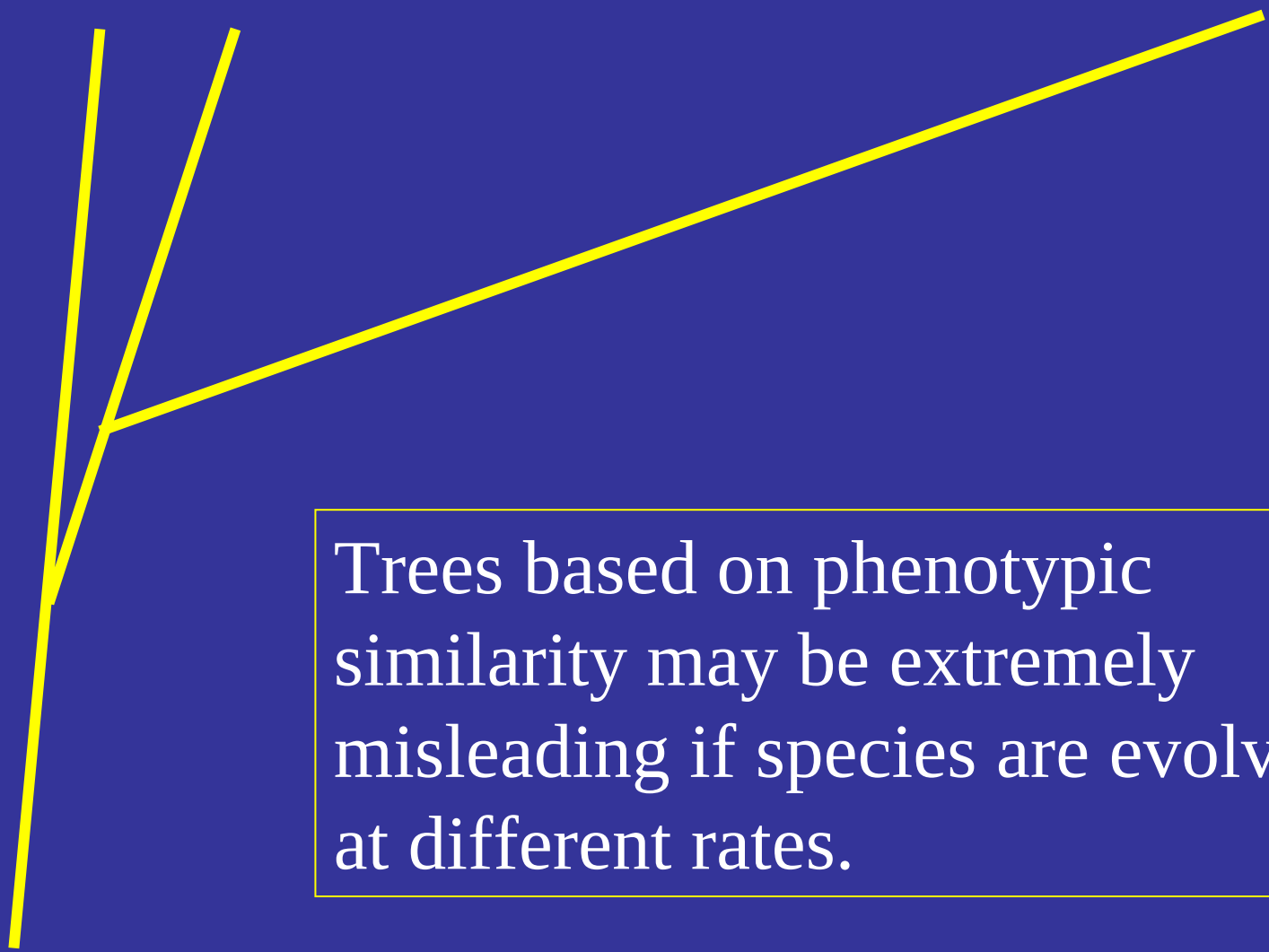
Lizards & snakes

Turtles

Dinosaurs

Birds

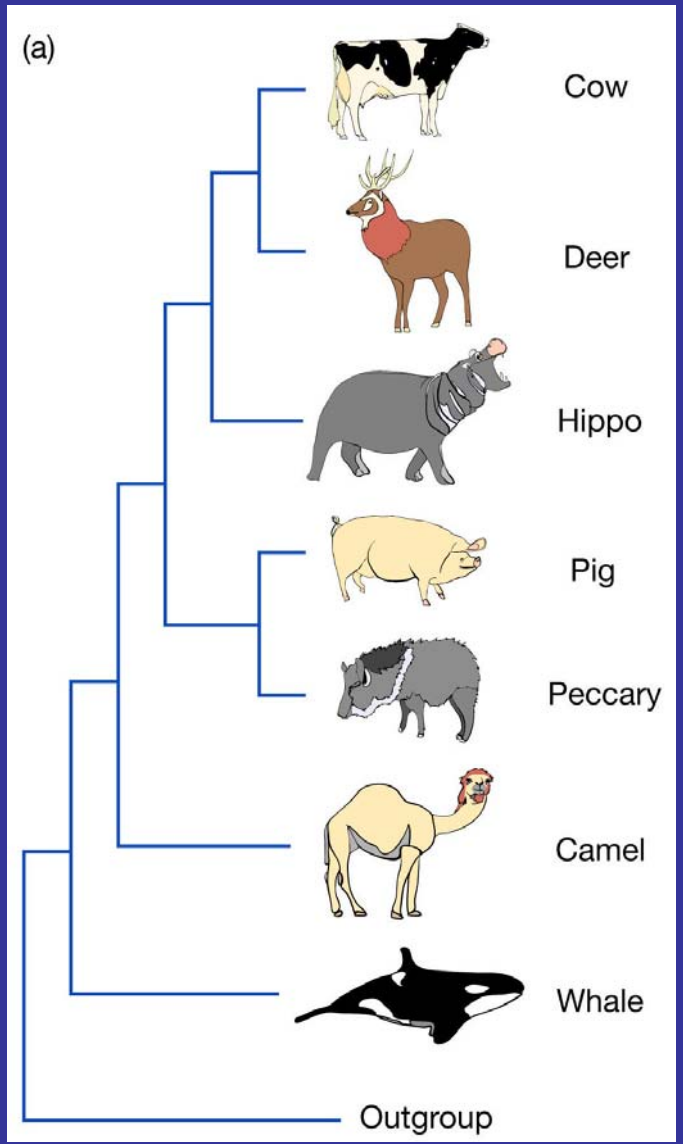

Birds
Crocodiles
Snakes and lizards
Reptiles
Turtles and tortoises
Mammals



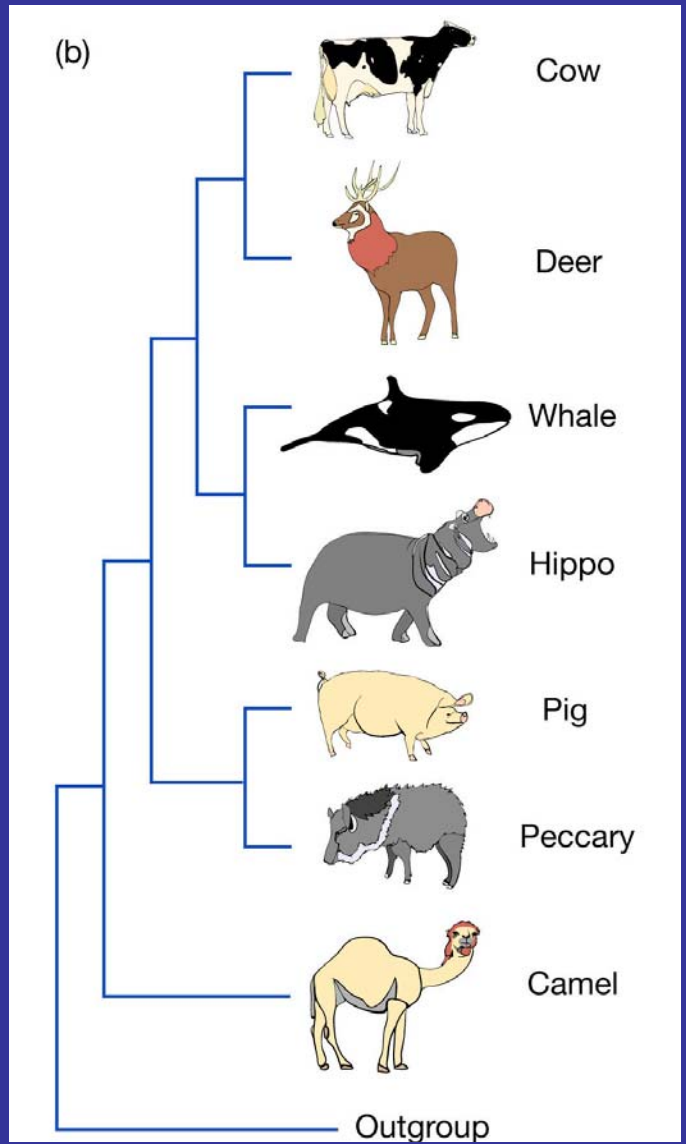
Trees based on phenotypic similarity may be extremely misleading if species are evolving at different rates.

Phenotypic Divergence ------>

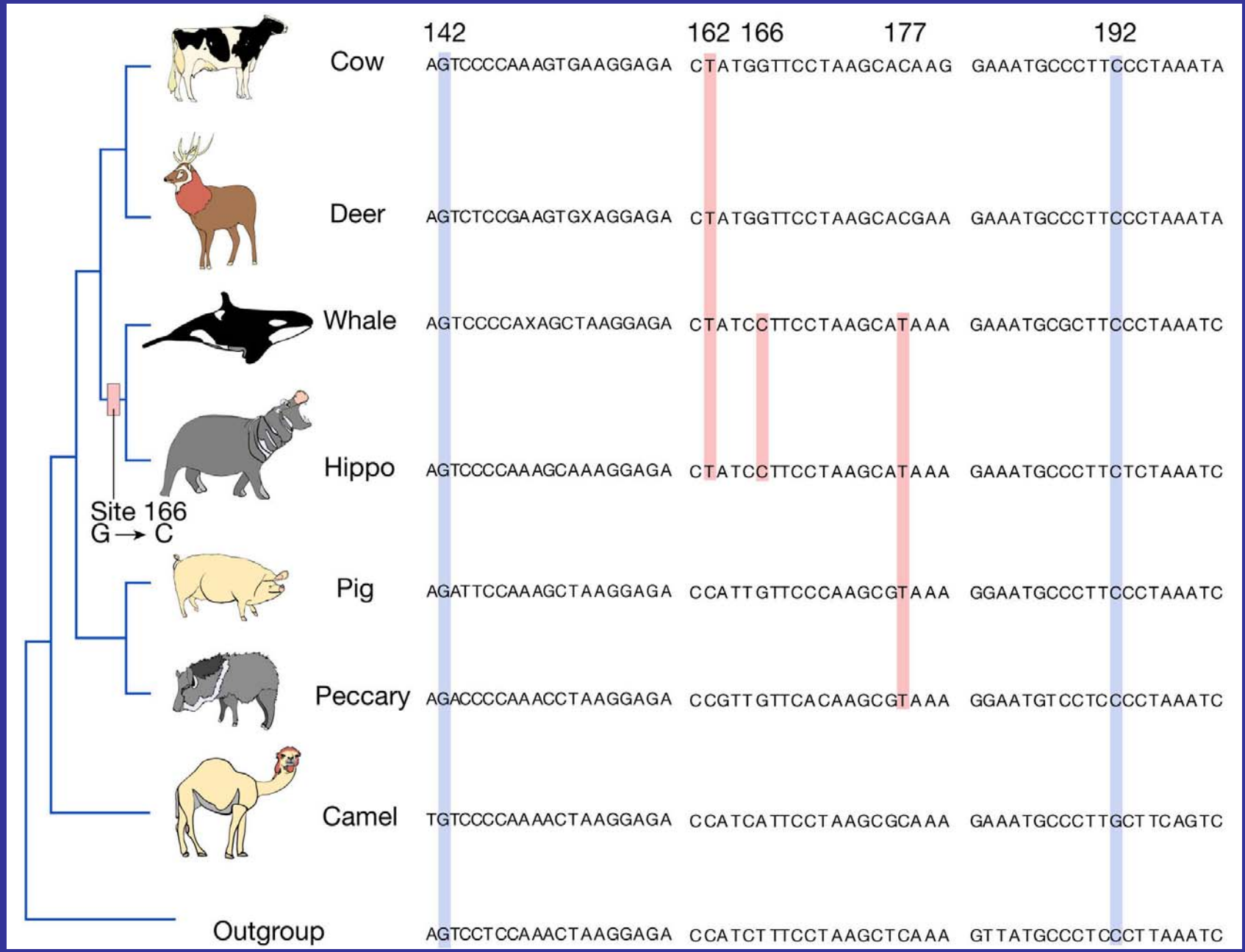
The Evolution of Whales and Dolphins



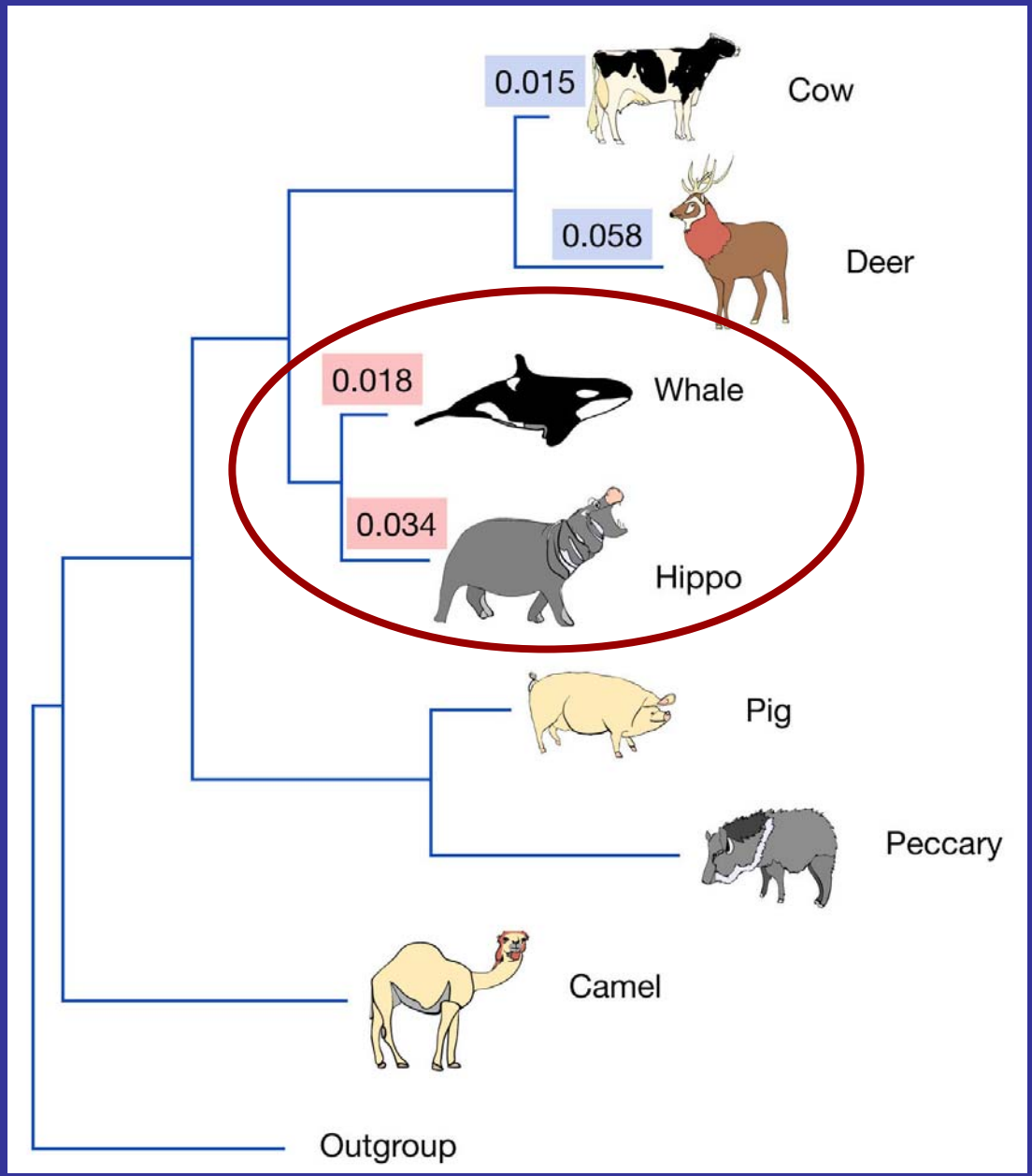
Traditional



Alternative

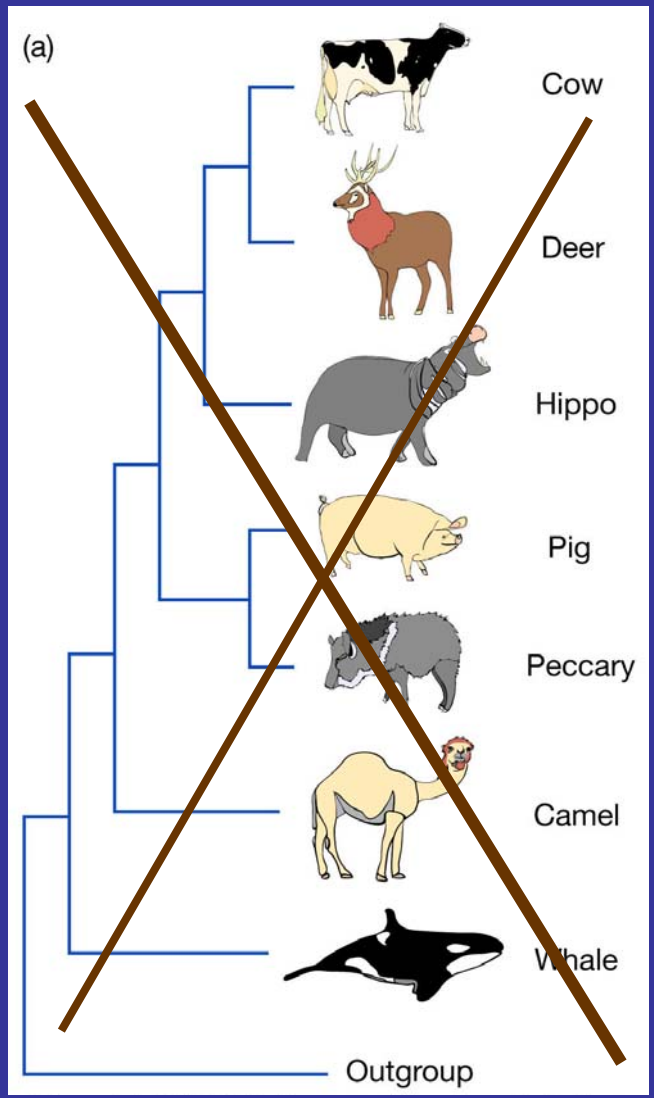


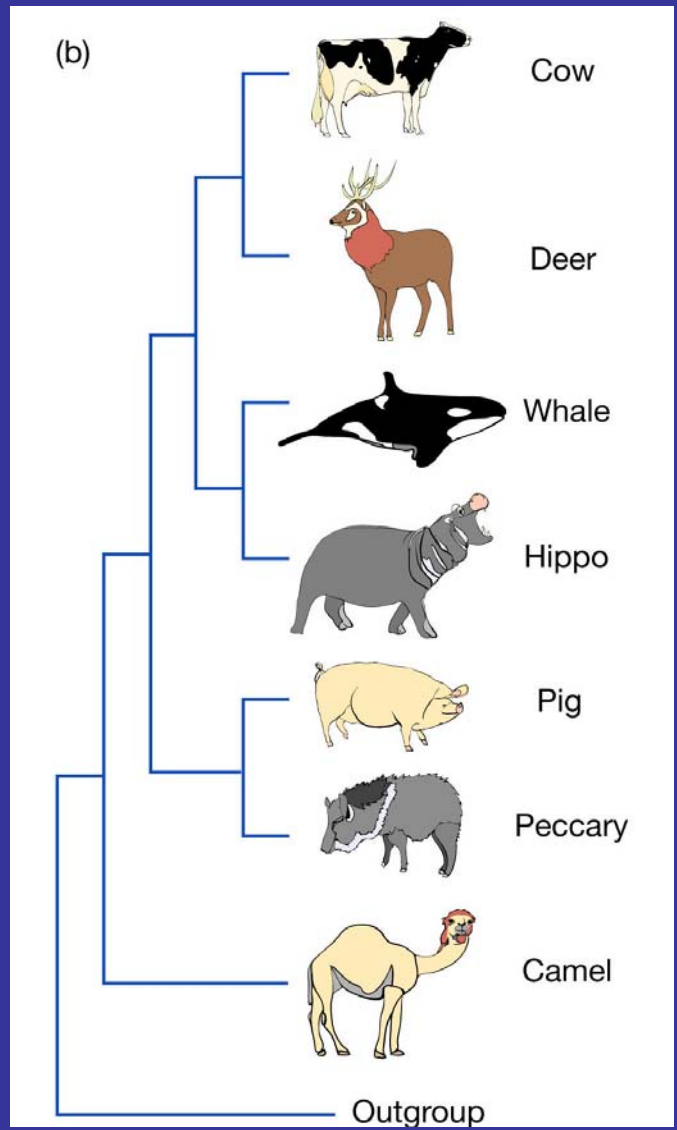
Parsimony analysis of sequence data for beta-casein gene

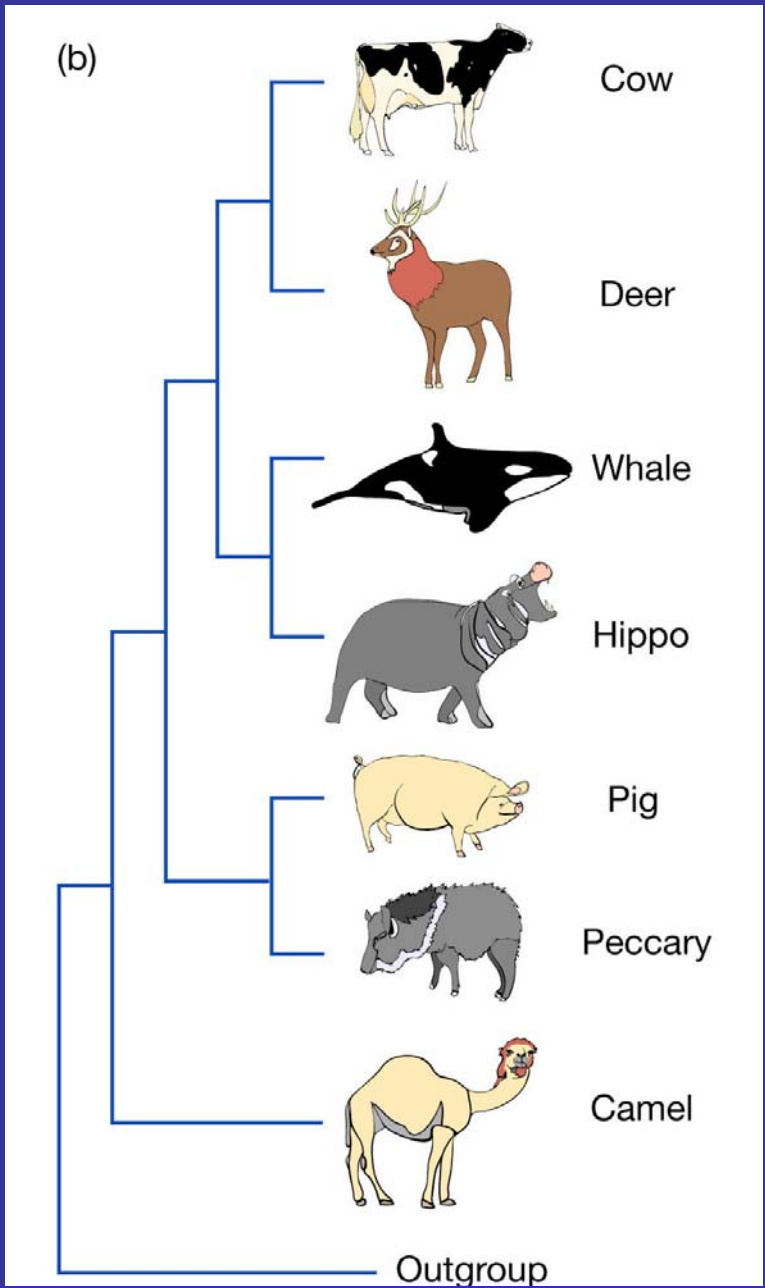


Cluster analysis of genetic distances

Phenetic and cladistic analysis of all of the available molecular data support the hypothesis that hippos and whales are sister taxa.







Systematics is not taxonomy.

Steve Chambers

Taxonomy

Should whales be classified as an ungulate???

Ungulate = hoofed mammals

Setting priorities for conservation efforts

The contemporary view of a "Living Fossil"

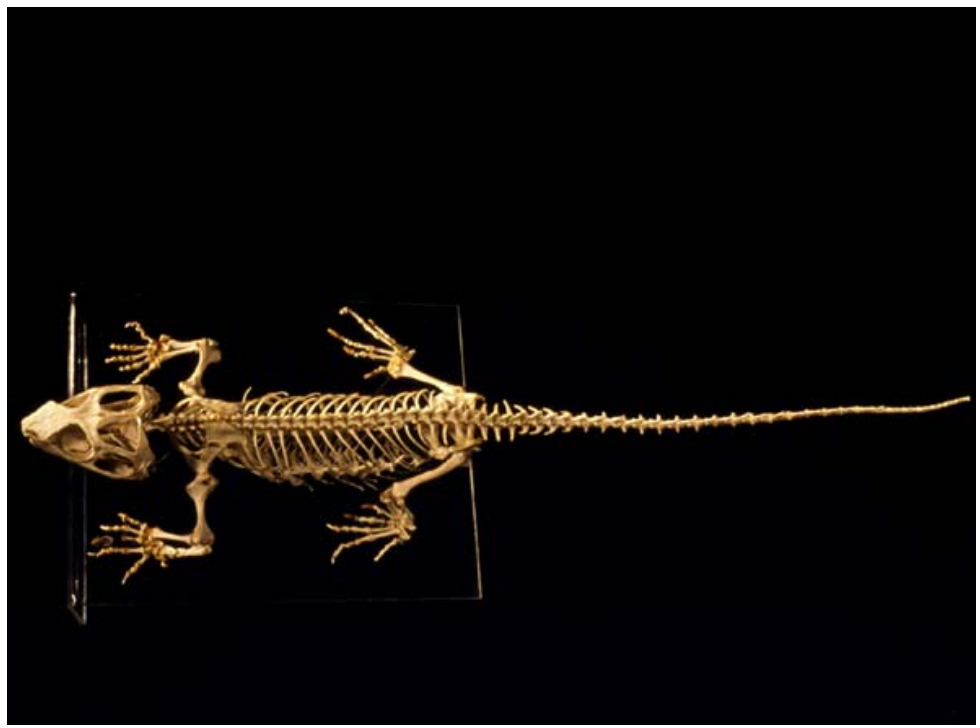
- Order Sphenodontia
- 1 or 2 extant species
- Lineage originated > 225 MYA
- Extinct following the K-T event (65 MYA) except in New Zealand

Why do tuatara and other living fossils matter?

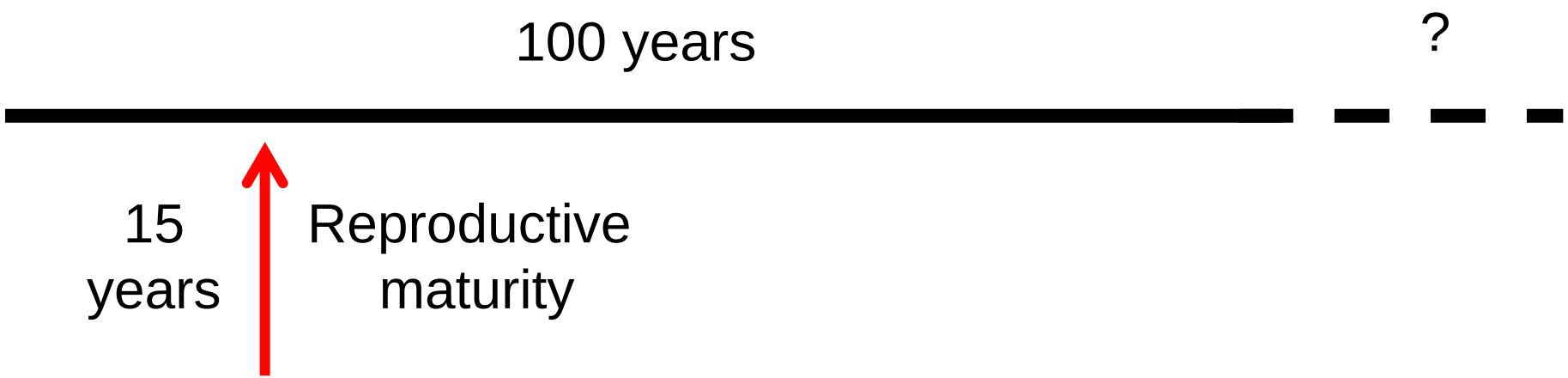
- A window to the past
- A glimpse of the possibilities of life
- As good as finding a living dinosaur

Very distinctive biology

- No penis or hemipenes in male
- Uncinate processes on ribs
- Amphicoelous vertebrae
- Unique hemoglobin
- Fully diapsid skull



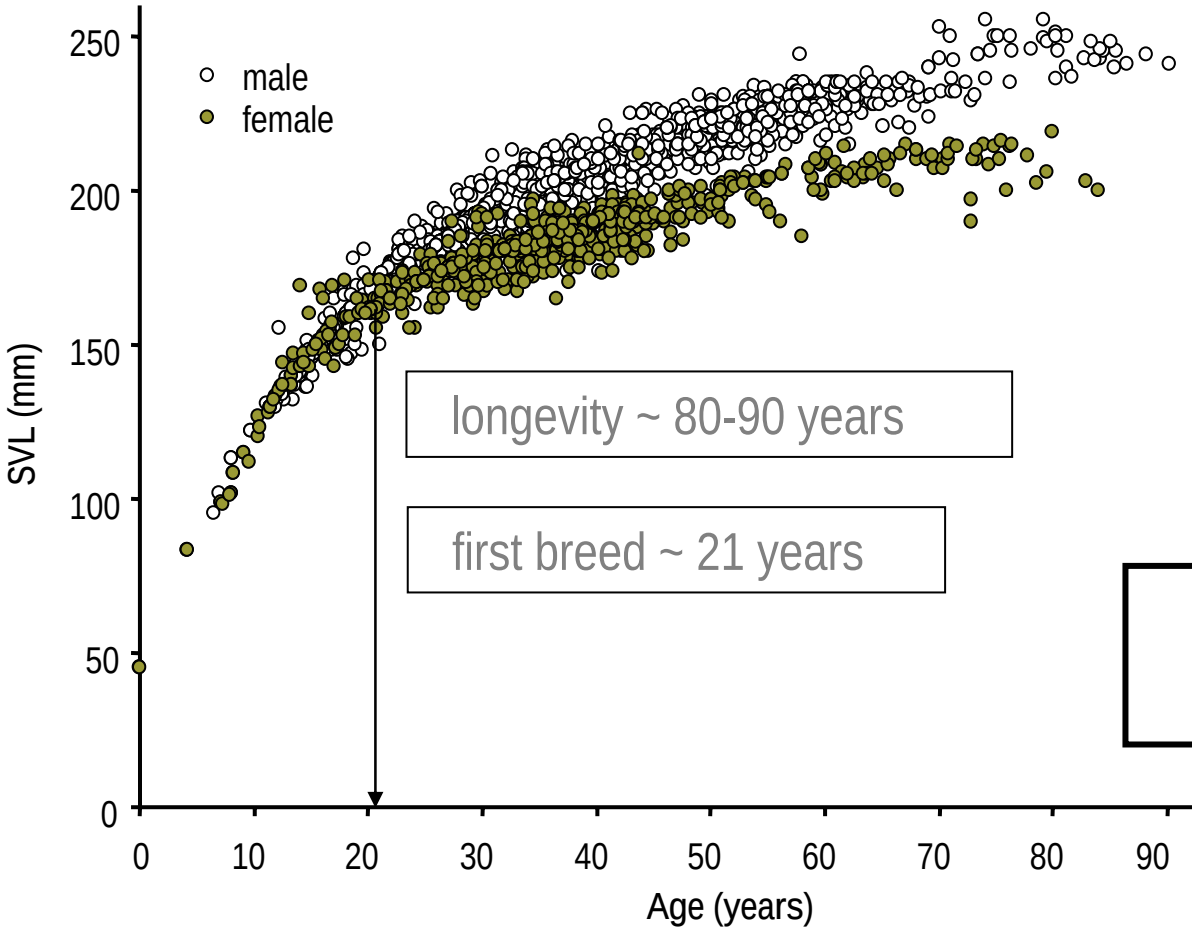
Lengthy life history



Annual adult survivorship > 0.95

Highly territorial and philopatric

Life history characters of *S. guntheri*



longevity ~ 80-90 years

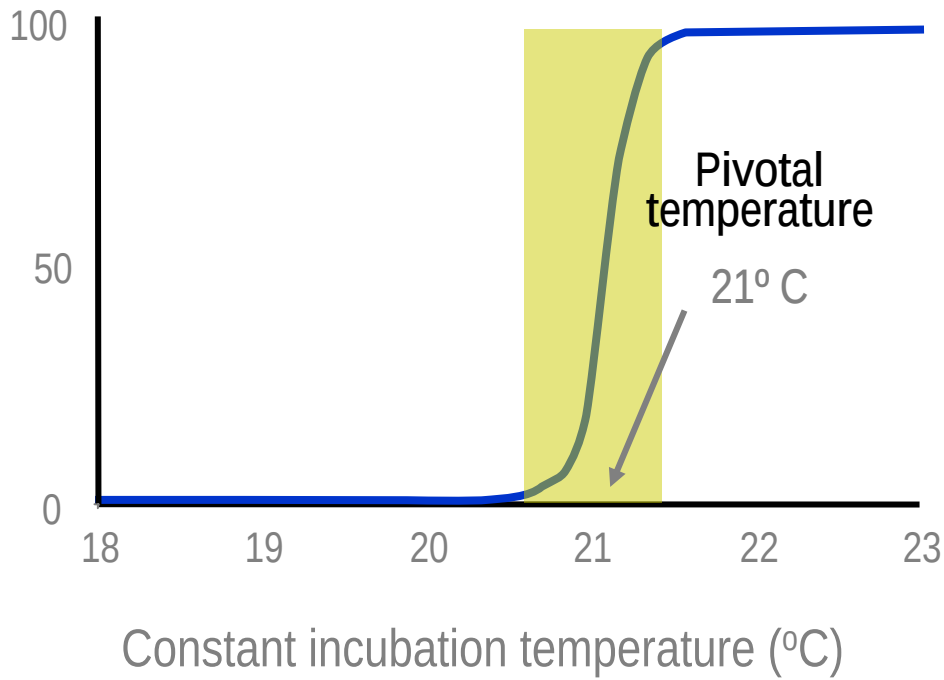
first breed ~ 21 years

skewed sex ratio
60% male

~ 13% of females breed each year ⟶ interclutch interval: ~7-8 years

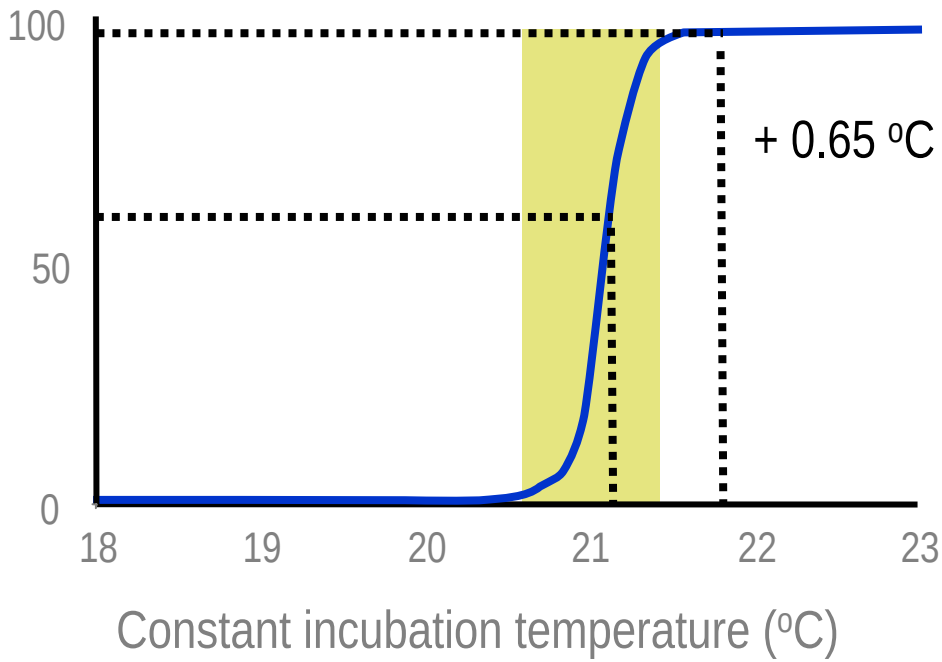
Sexually dimorphic with TSD

Tuatara have temperature-dependent sex determination

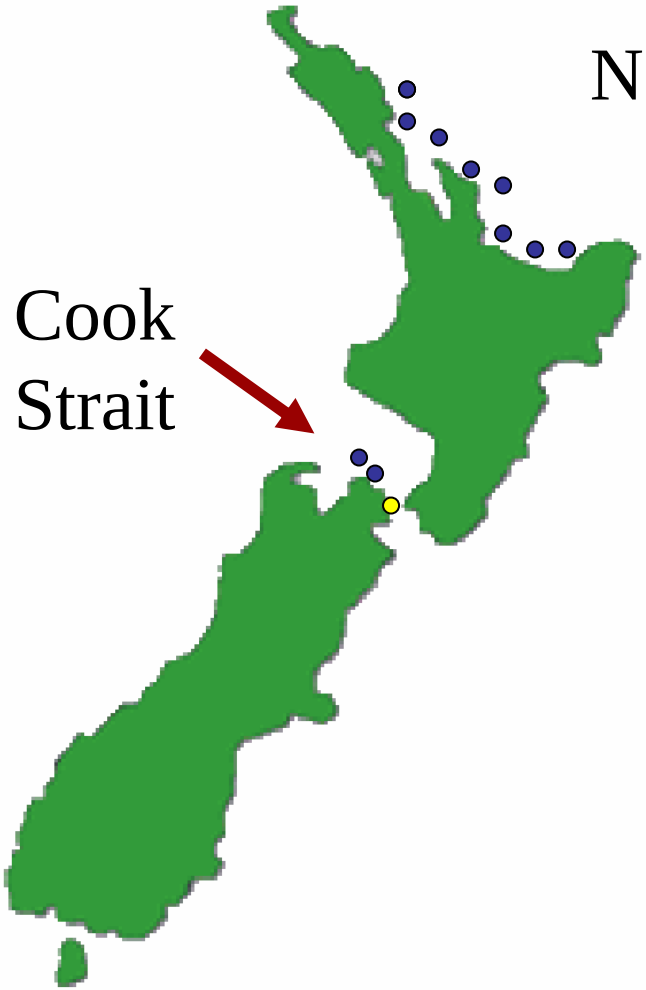


How might climate change affect hatchling sex ratios?

Prediction for Cook Strait: in 50 years
0.65ºC increase in mean temperature



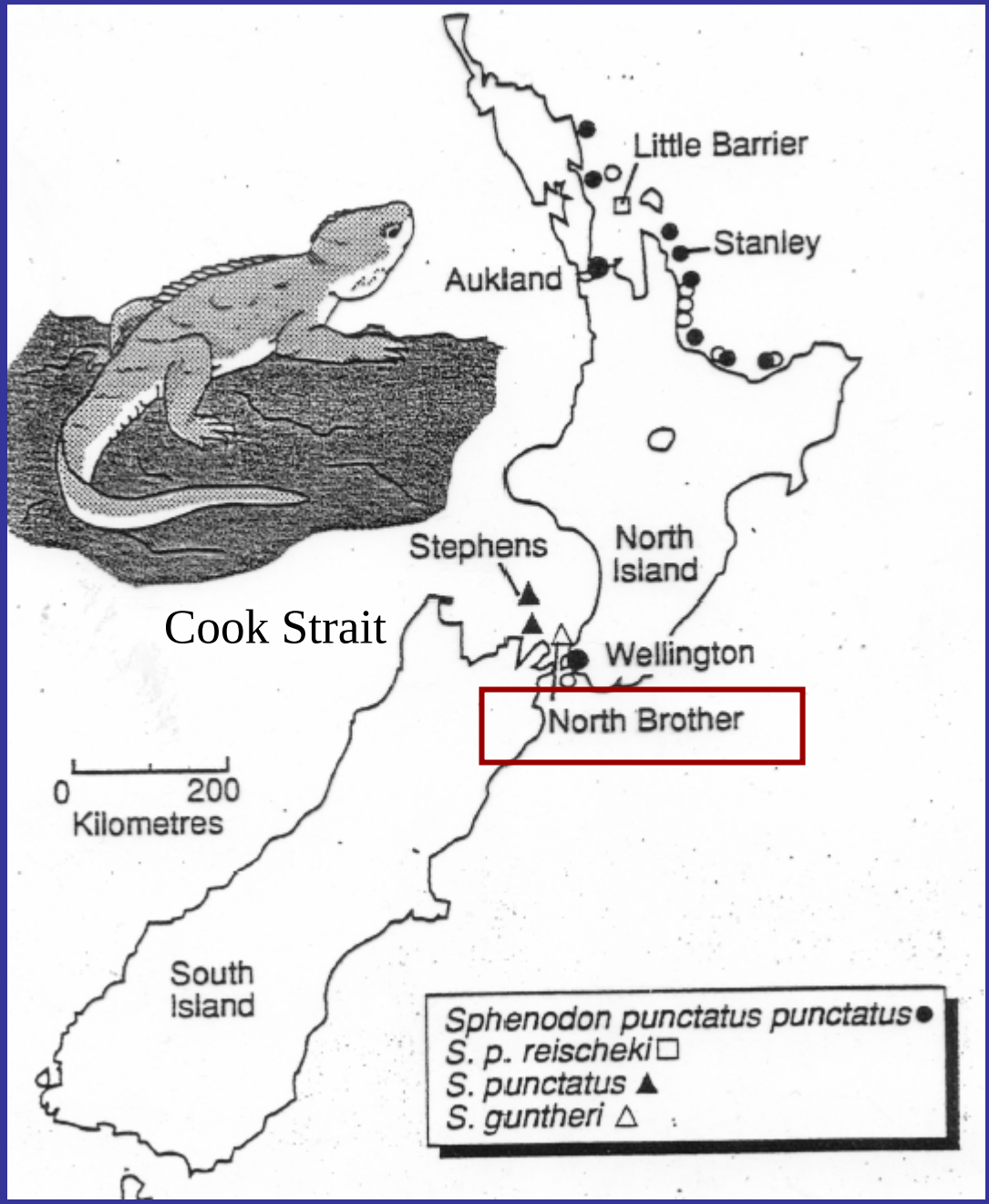
The distribution of tuatara



Restricted to ~30 offshore islands around New Zealand

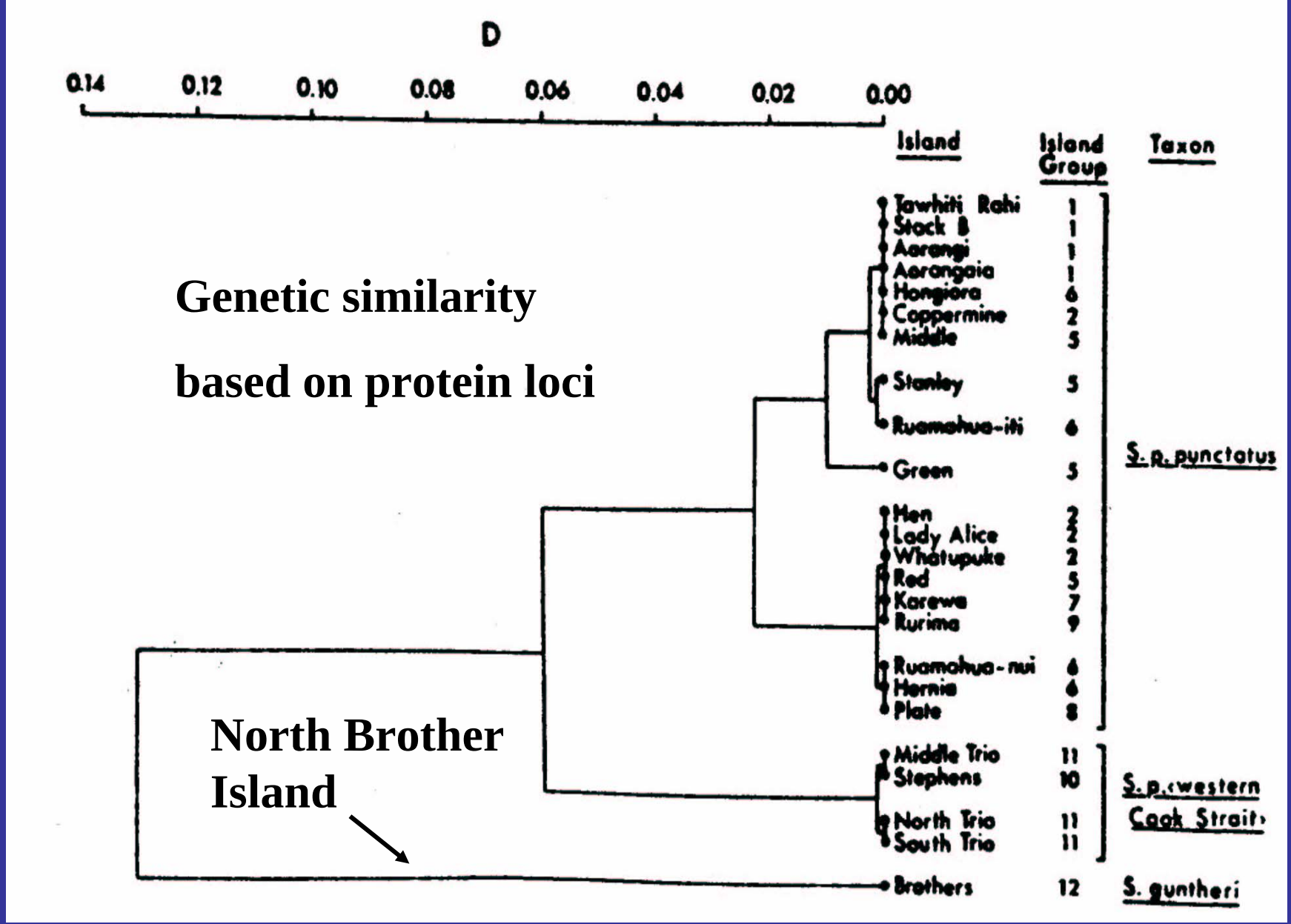
Estimated tuatara population sizes (Recovery Plan 1993).

N	*No. islands*
<100	12 (40%)
100-1,000	14 (47%)
1,000-10,000	3 (10%)
30,000	1 (3%)


Little Barrier
Stanley
Aukland
Stephens
North Island
Cook Strait
Wellington
North Brother
0
200
Kilometres
South Island
Sphenodon punctatus punctatus
S. p. reischeki
S. punctatus
S. guntheri

North Brother Island

- Only natural population of *S. guntheri*
- 4 ha
- 350 adults
- 63% male



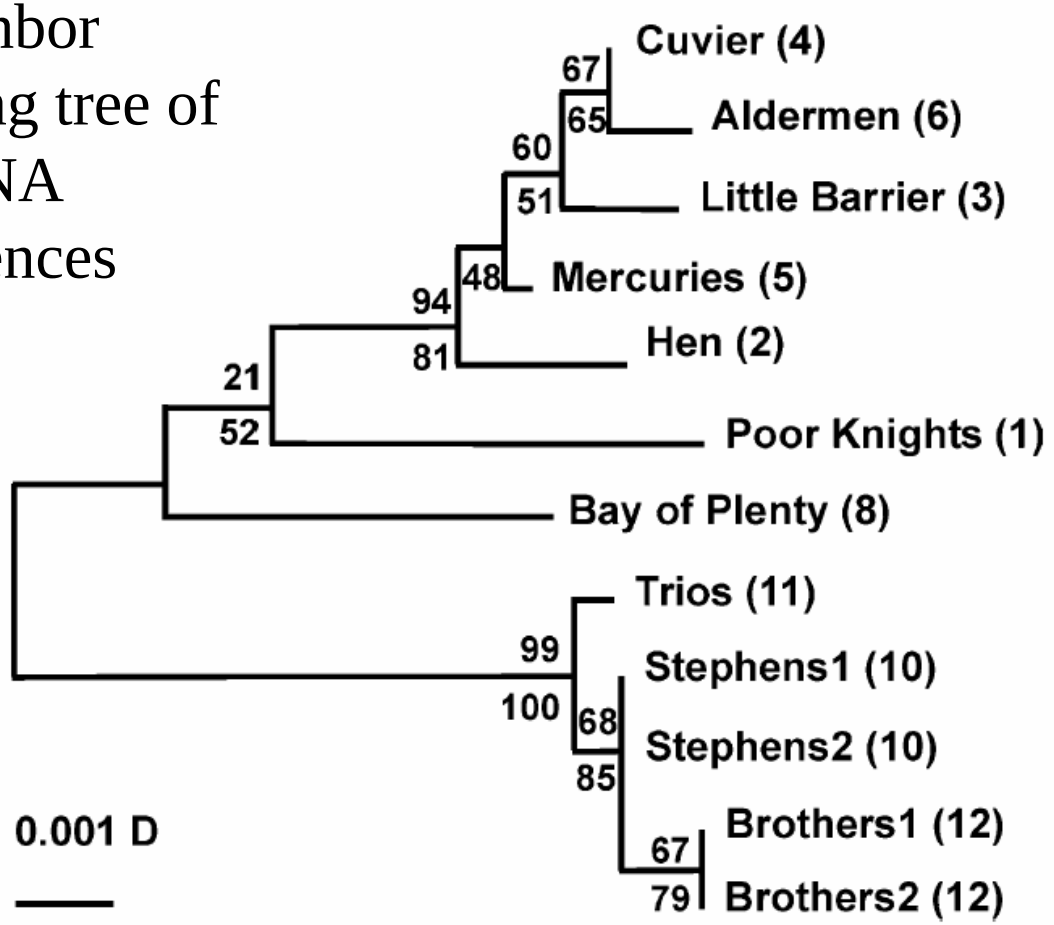
North Brother Island recognized as separate species

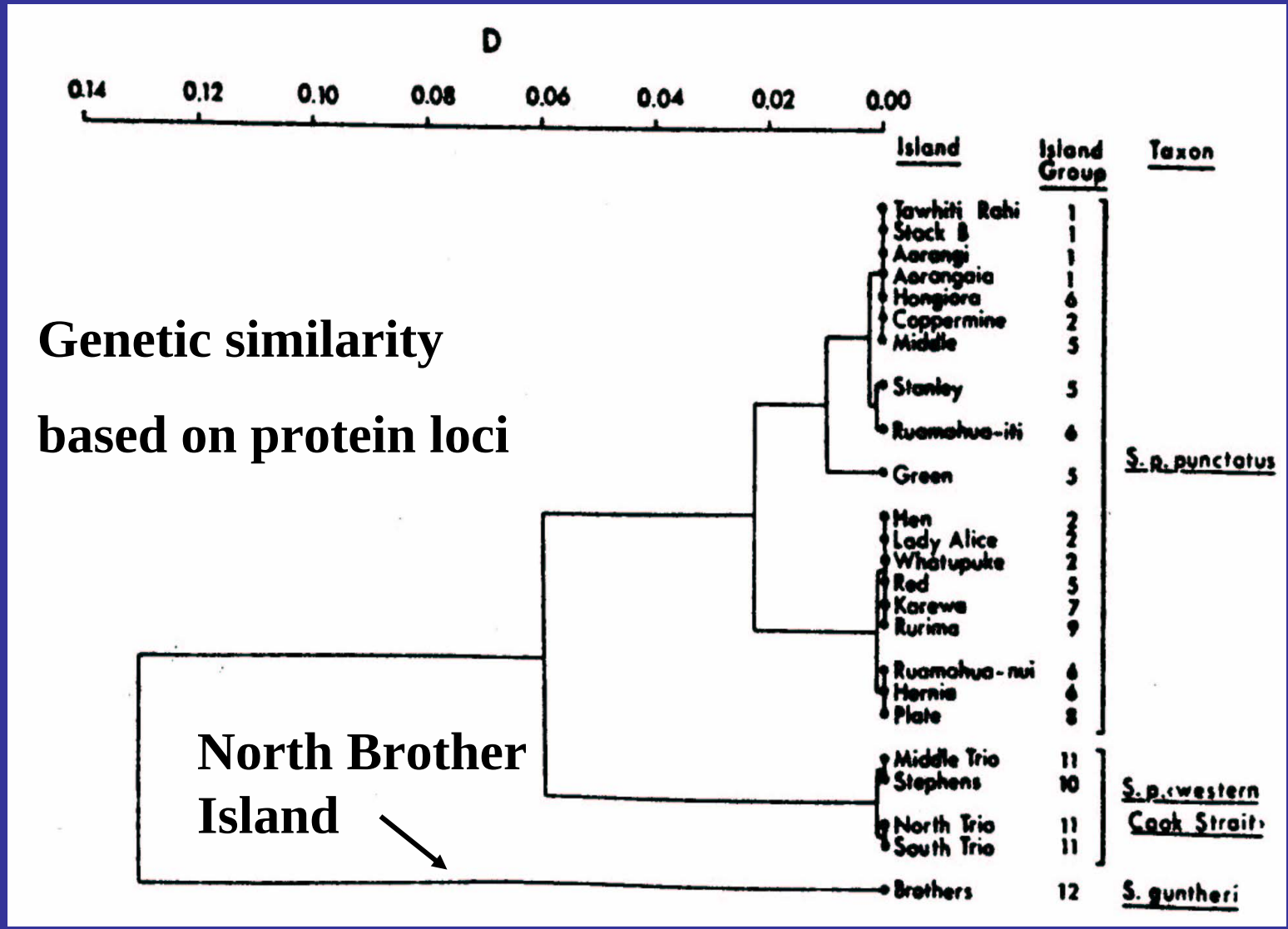
Low genetic divergence obscures phylogeny among populations of *Sphenodon*, remnant of an ancient reptile lineage

Jennifer M. Hay,[a,*] Charles H. Daugherty,[b] Alison Cree,[c] and Linda R. Maxson[d]

North Brothers have extremely low variation at microsatellite loci.

Neighbor joining tree of mtDNA sequences





Population Tree (cluster diagram, not a phylogeny)

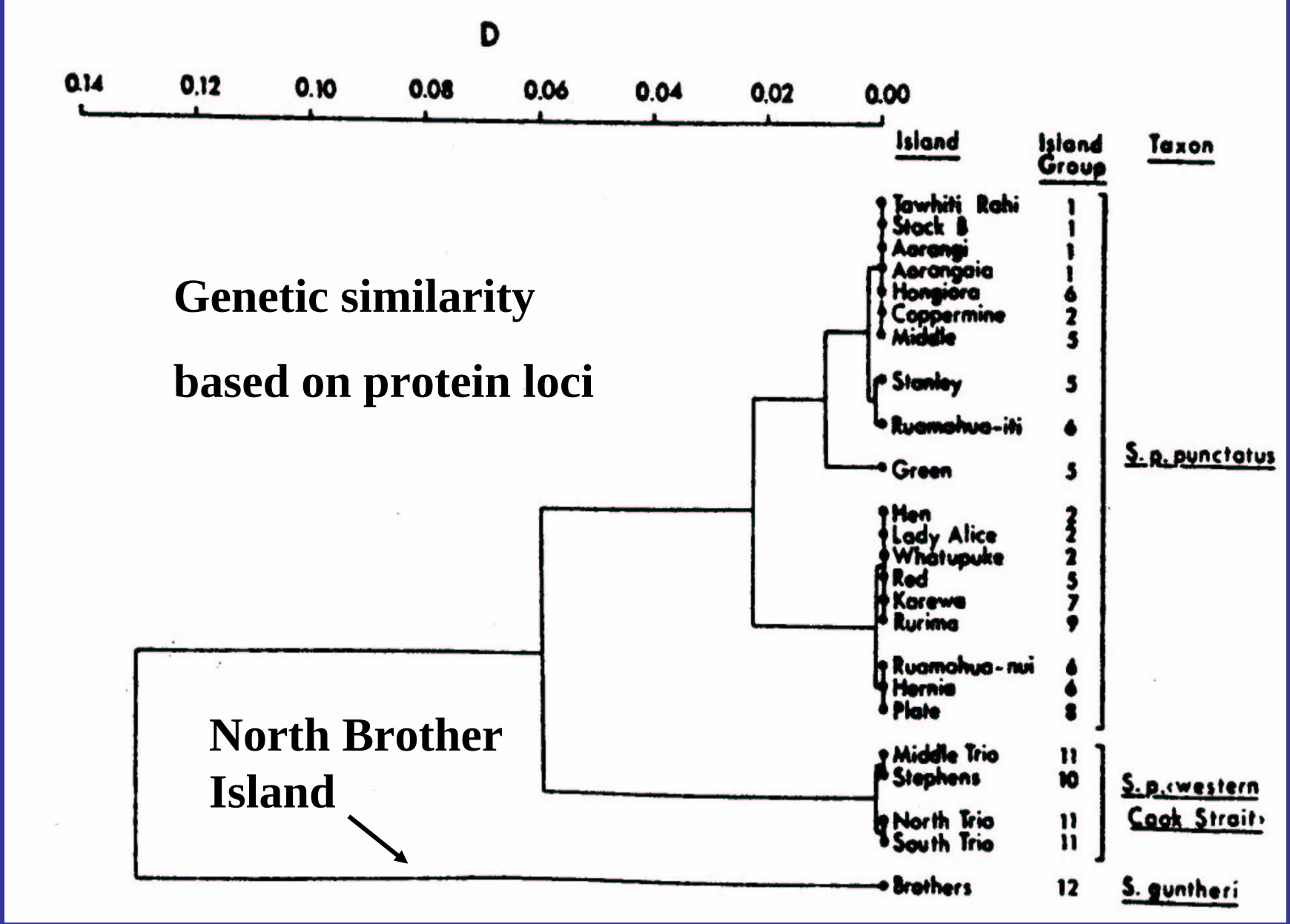
Groups together populations with similar allele frequencies; does not show relative time since common ancestor.

Remember: Genetic drift has two primary effects on the genetic composition of populations:

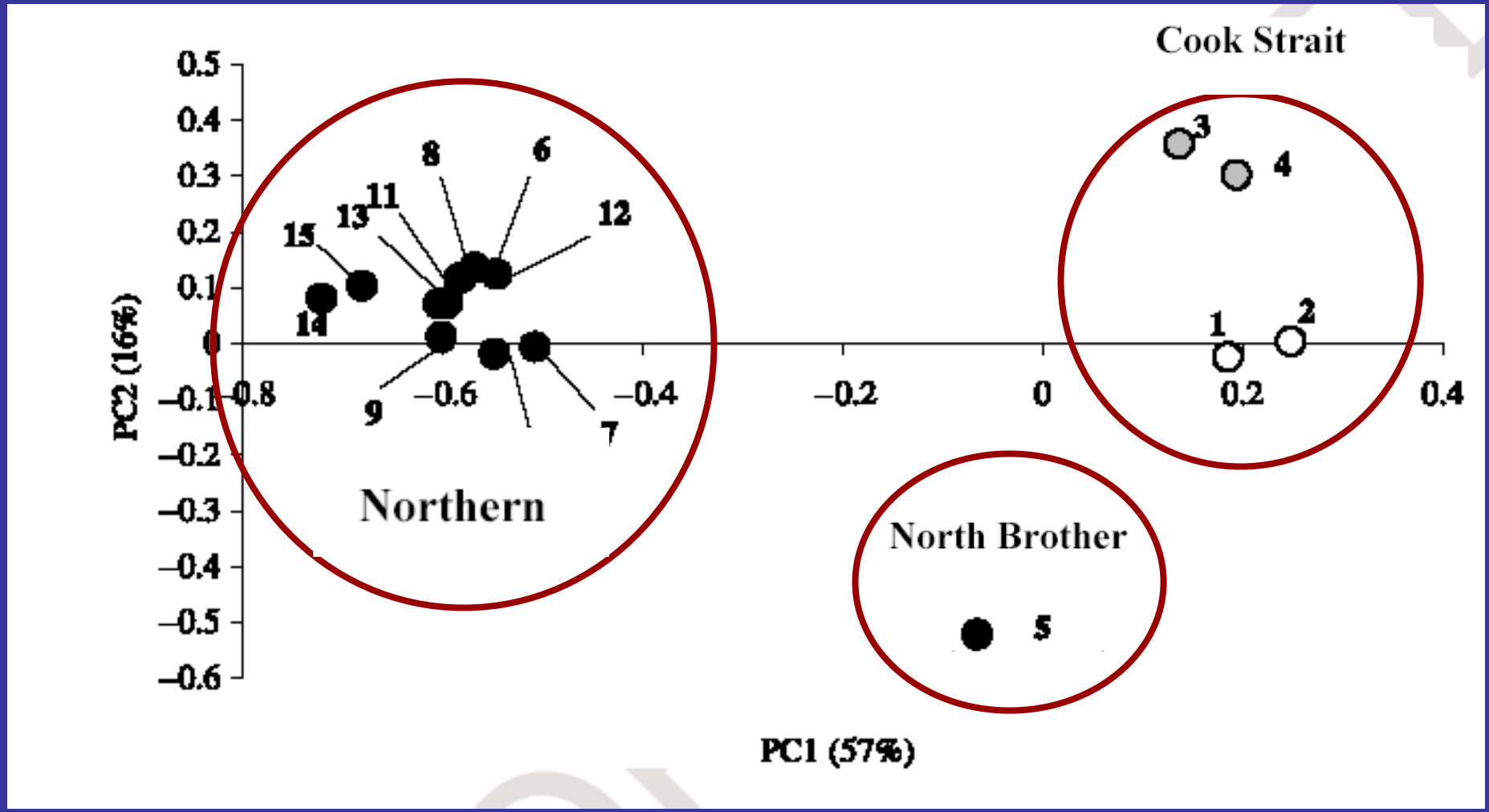
(1) Change in allele frequencies.

(2) Loss of genetic variation.

The small N_e of North Brother Island tuatara apparently has caused (1) an increase in genetic divergence and (2) the loss of substantial genetic variation.



Populations trees can be misleading.



Principle Component Analysis (PCA)

Represents allele frequency relations among populations in multiple dimension space.

Is the North Brother Island population of tuatara a separate species worthy of special protection or a small, inbred isolate of relatively low conservation priority?

What did Congress mean by a DPS?

Waples, R.S. 1991. Pacific salmon, *Oncorhynchus* spp., and the definition of "species" under the ESA. Marine Fisheries Review 53:11-22.

A stock of Pacific salmon is considered a DPS if it represents an evolutionarily significant unit (ESU) of a biological species. A stock must satisfy two criteria to be considered an ESU:

(1) It must be substantially reproductively isolated from other conspecific population units; and

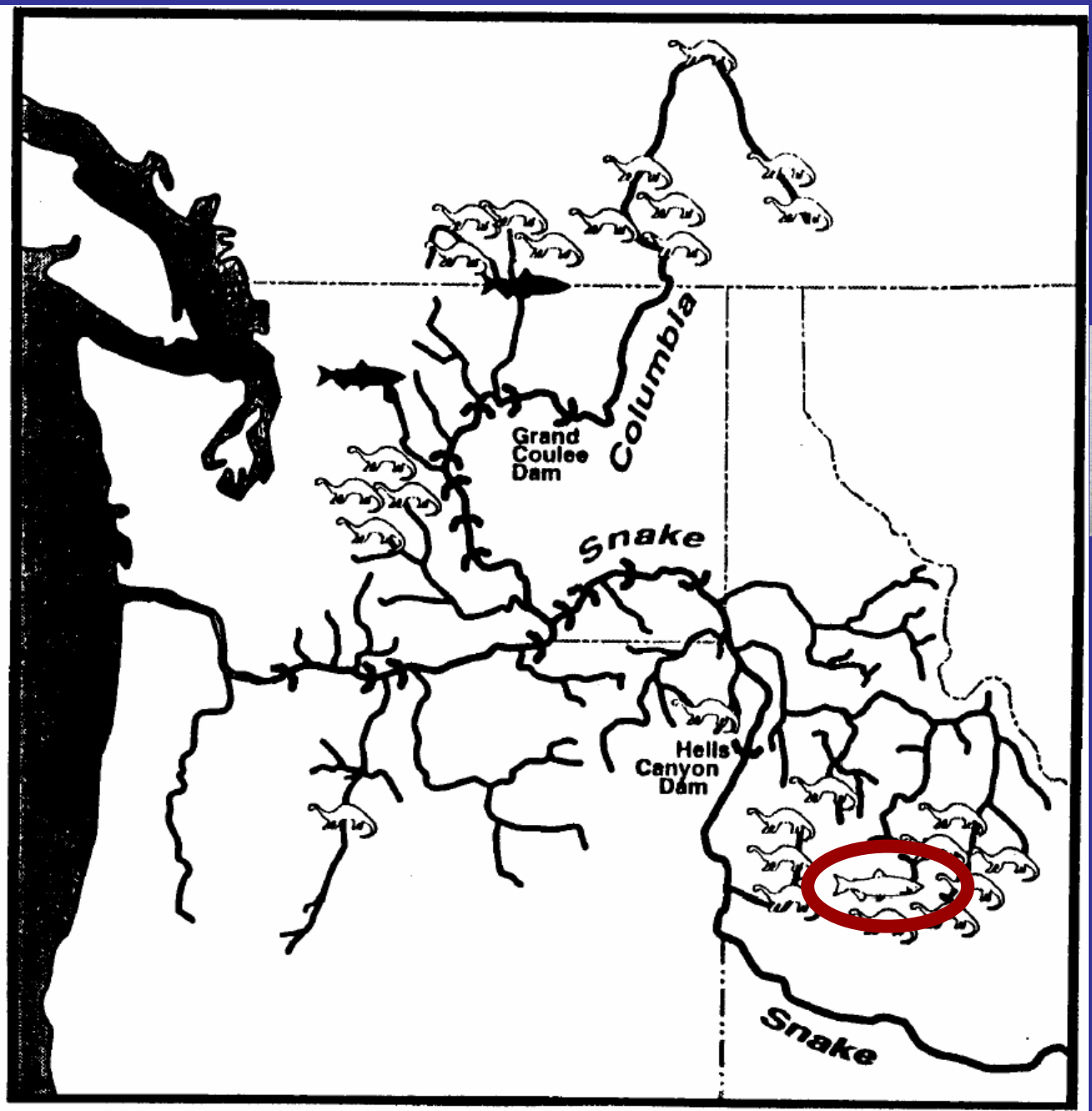
(2) It must represent a significant component in the evolutionary legacy of the species.

NMFS DPS policy

Isolation does not have to be complete but must allow evolutionary important differences to accrue.

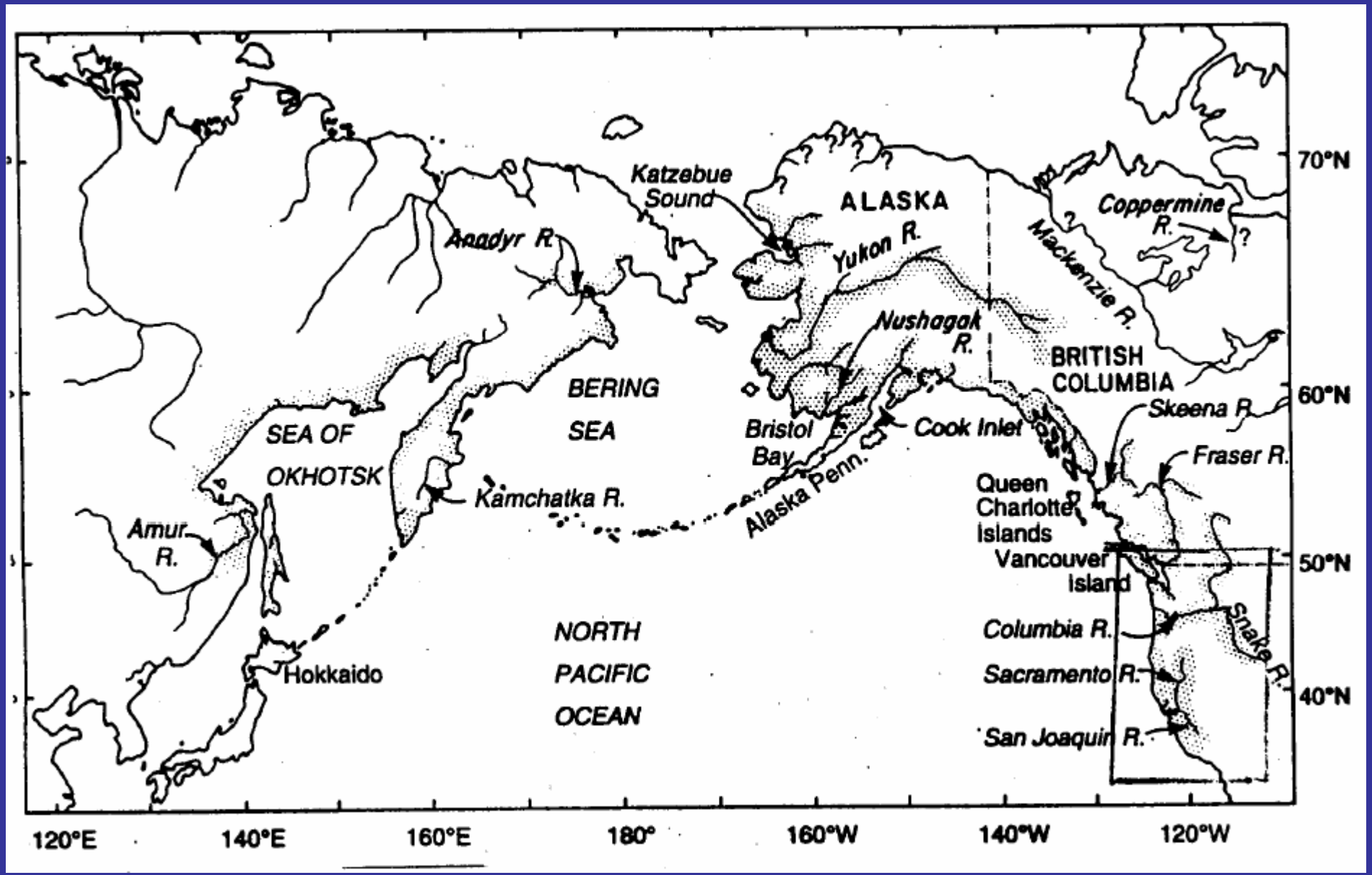
Neutral genetic markers are proxies for adaptive differences.

However, local natural selection can maintain important adaptive differences between populations even when there is substantial gene flow as indicated with molecular markers.



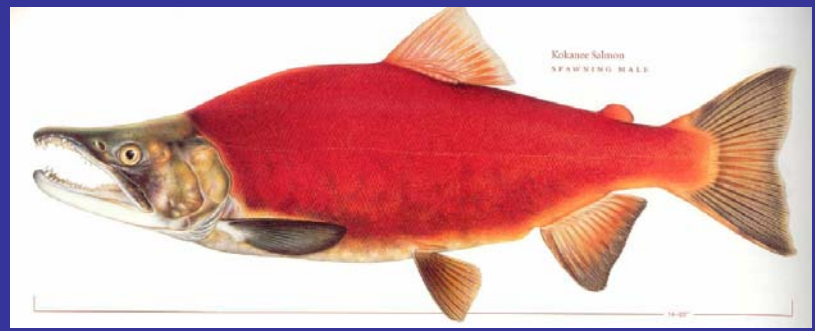
Listed as Endangered in 1991

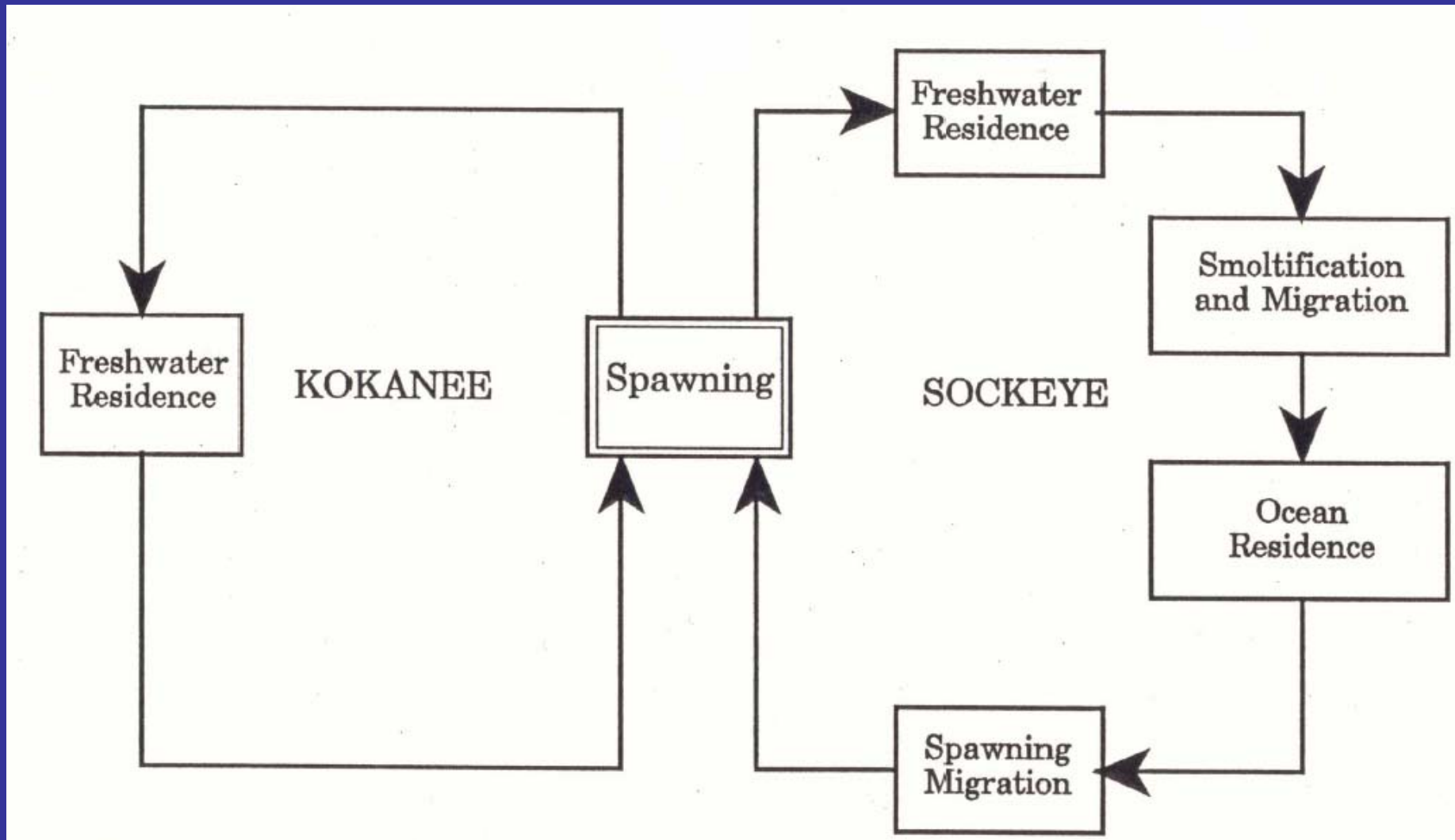
Redfish Lake sockeye salmon


Katzebue Sound
ALASKA
Anadyr R.
Yukon R.
Coppermine R.
Mackenzie R.
Nushagak R.
BRITISH COLUMBIA
BERING SEA
SEA OF OKHOTSK
Bristol Bay
Cook Inlet
Skeena R.
Fraser R.
Kamchatka R.
Alaska Penn.
Queen Charlotte Islands
Vancouver Island
Amur R.
Columbia R.
Snake R.
Sacramento R.
San Joaquin R.
Hokkaido
NORTH PACIFIC OCEAN
70°N
60°N
50°N
40°N
120°E
140°E
160°E
180°
160°W
140°W
120°W

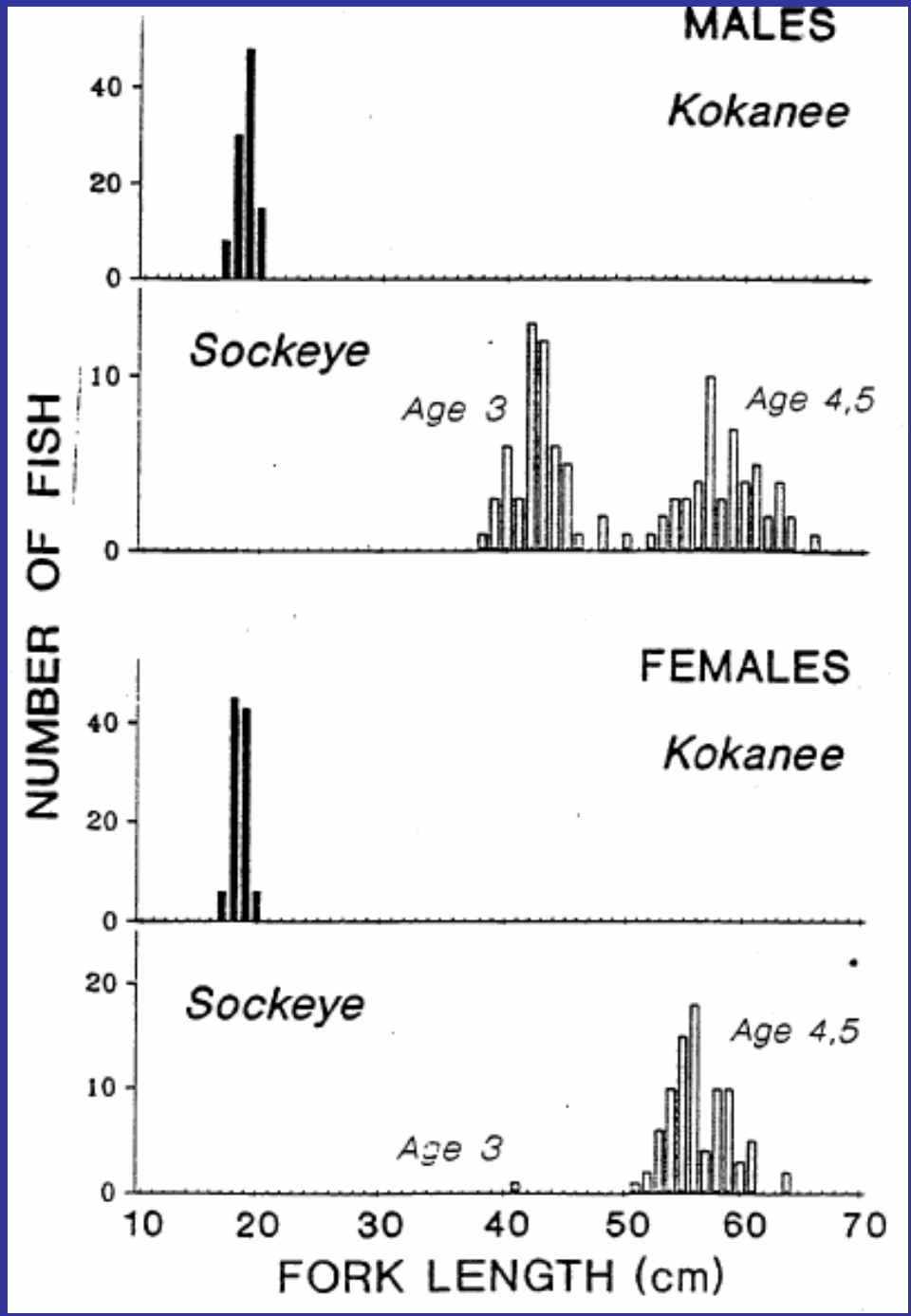

Sockeye Salmon
Oncorhynchus nerka
Sockeye Salmon
SPAWNING MALE
21–26"

Kokanee


Kokanee Salmon
SPAWNING MALE


Freshwater Residence
KOKANEE
Spawning
SOCKEYE
Freshwater Residence
Smoltification and Migration
Ocean Residence
Spawning Migration


Sockeye Salmon
Oncorhynchus nerka


MALES
Kokanee
Sockeye
Age 3
Age 4,5
FEMALES
Kokanee
Sockeye
Age 4,5
Age 3
NUMBER OF FISH
FORK LENGTH (cm)
0
10
20
30
40
50
60
70


Sockeye Salmon
Oncorhynchus nerka

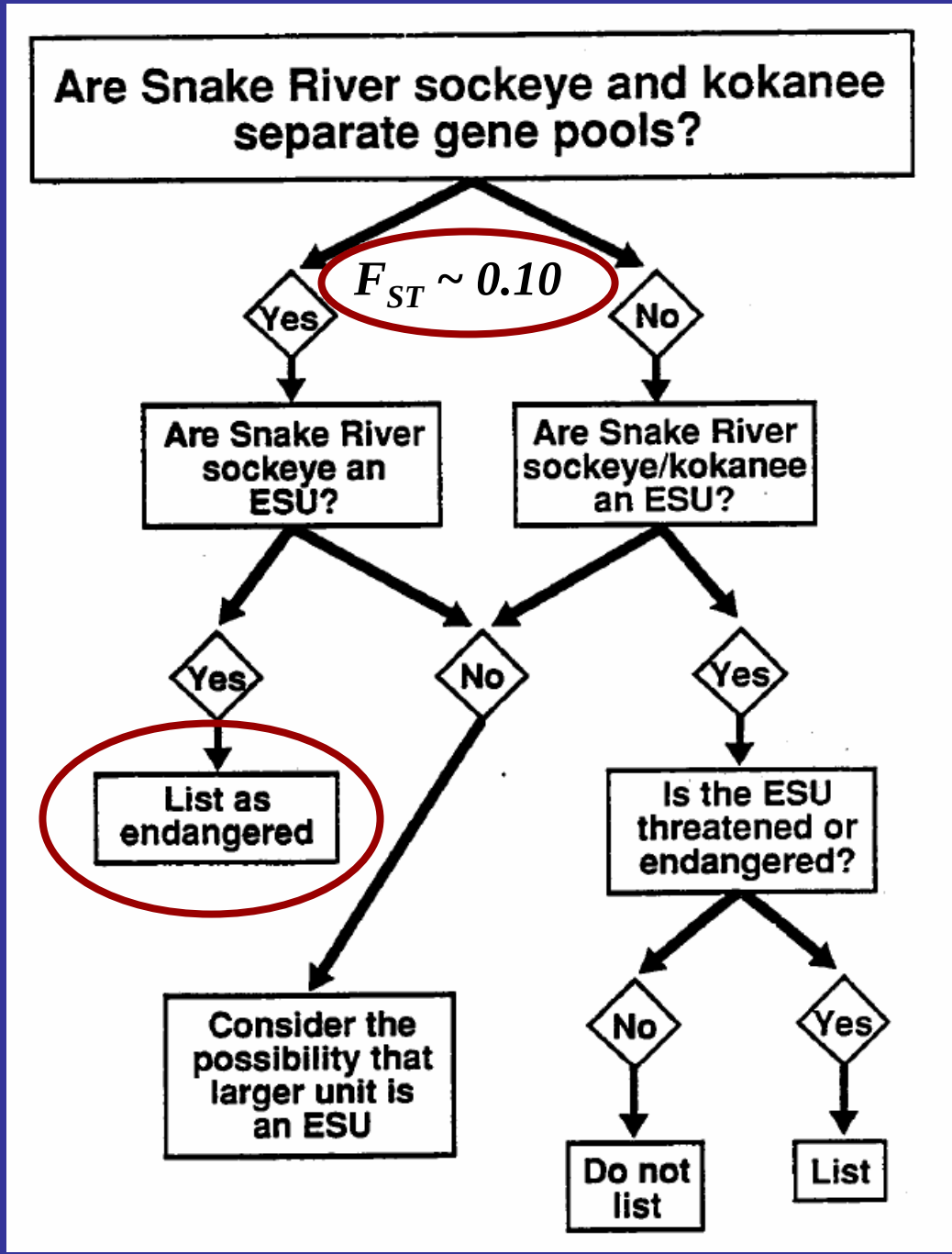
(1) Isolated?

Yes.

(2) Significant?

Yes.

Resident sockeye salmon



NMFS DPS policy

Isolation does not have to be complete but must allow evolutionary important differences to accrue.

Neutral genetic markers are proxies for adaptive differences.

However, local natural selection can maintain important adaptive differences between populations even when there is substantial gene flow as indicated with molecular markers.

Local adaptation

	mN						
	0.5	1	2	5	10	25	N
			F_{ST}				
Expected	0.3333	0.2000	0.1111	0.0476	0.0244	0.0099	
t=0.00	0.3070	0.2043	0.1245	0.0418	0.0198	-	25
	0.3350	0.1826	0.1077	0.0484	0.0264	0.0120	50
	0.3216	0.1884	0.1061	0.0437	0.0251	0.0095	100
t=0.01	0.3343	0.1703	0.1070	0.0556	0.0220	-	25
	0.2979	0.1192	0.1000	0.0381	0.0256	0.0099	50
	0.2997	0.1850	0.1146	0.0354	0.0229	0.0105	100
t=0.05	0.3560	0.1857	0.1204	0.0497	0.0217	-	25
	0.4618	0.2679	0.1489	0.0550	0.0265	0.0113	50
	0.5950	0.4230	0.1982	0.0632	0.0207	0.0118	100
t=0.10	0.4700	0.2446	0.1632	0.0473	0.0289	-	25
	0.6242	0.3653	0.2611	0.0771	0.0356	0.0128	50
	0.8054	0.6575	0.4432	0.1589	0.0632	0.0193	100

Pacific Salmon Diversity

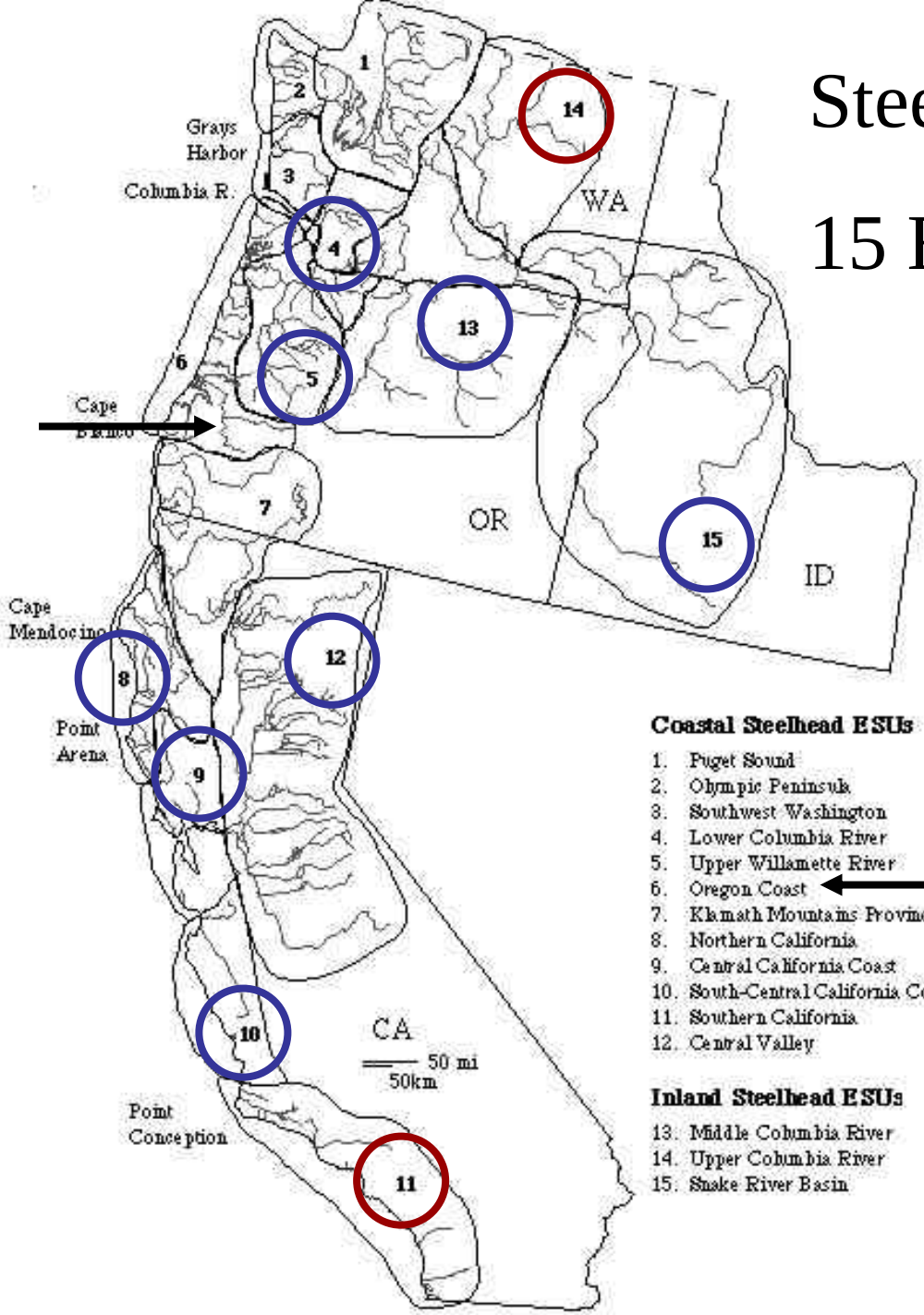
Species	Number of Major Diversity Groups				ESUs
	Ecology	Life History	Genetics	Total	
Pink	2	1	2	5	2
Chum	4	1	2	7	4
Sockeye	4	6	9	19	7
Coho	6	1	2	9	7
Chinook	11	7	10	28	17
Steelhead	11	7	7	25	15

Robin Waples, NMFS (NOAA Fisheries)

SPECIES	ESU	STATUS
Chinook salmon	**Sacramento River Winter-run**	**E**
	Snake River Fall-run	T
	Snake River Spring/Summer-run	T
	Central Valley Spring run	T
	California Coastal	T
	Puget Sound	T
	Lower Columbia River	T
	Upper Willamette River	T
	Upper Columbia River Spring-run	**E**
Chum salmon	Hood Canal Summer-run	T
	Columbia River	T
Coho salmon	Central California	T
	Southern OR/Northern CA Coasts	T
	Oregon Coasts	T
Sockeye salmon	Ozette Lake	T
	Snake River	**E**

Steelhead (rainbow trout)

15 ESU's



Coastal Steelhead ESUs

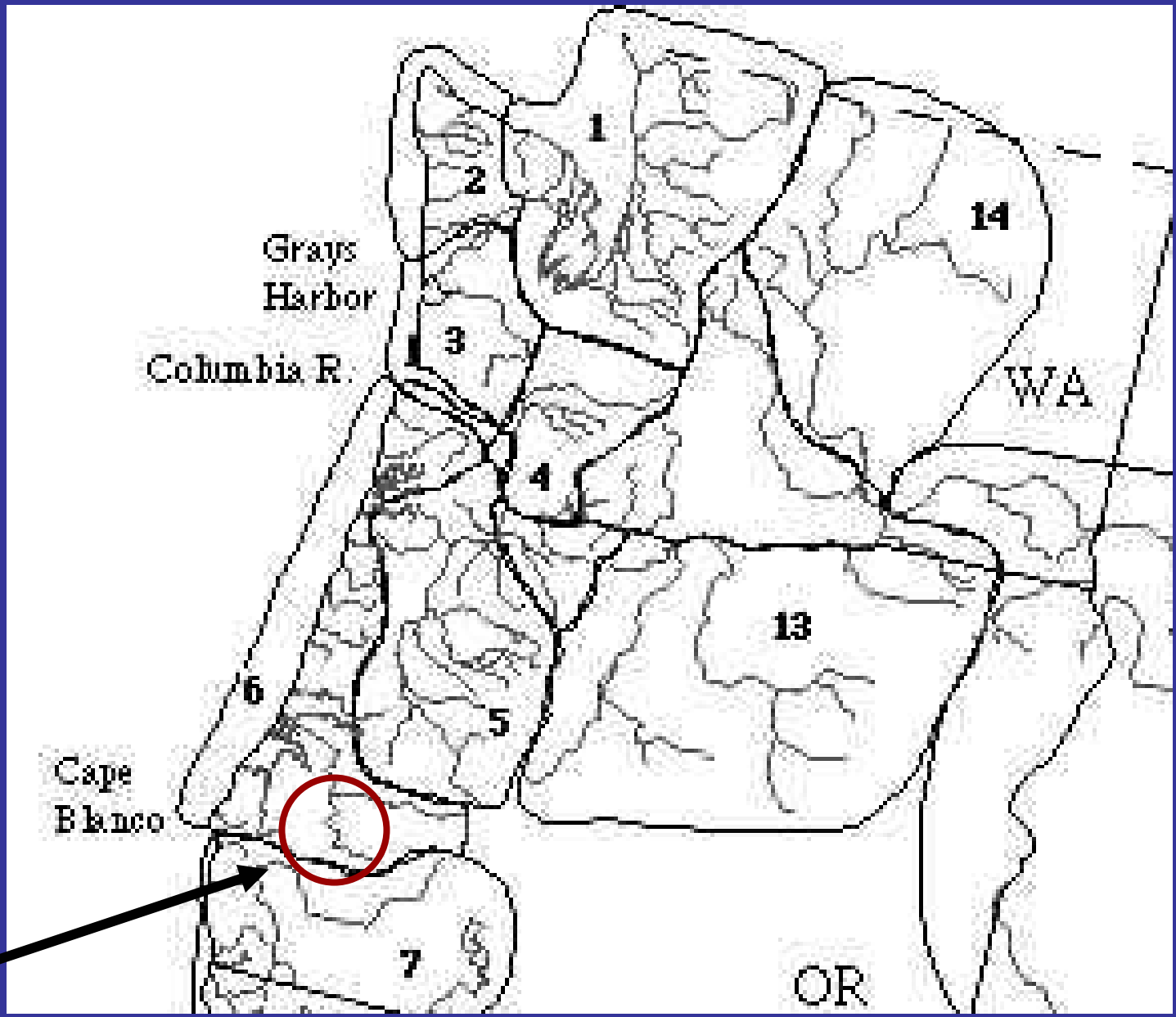
1. Puget Sound
2. Olympic Peninsula
3. Southwest Washington
4. Lower Columbia River
5. Upper Willamette River
6. Oregon Coast
7. Klamath Mountains Province
8. Northern California
9. Central California Coast
10. South-Central California Coast
11. Southern California
12. Central Valley

Inland Steelhead ESUs

13. Middle Columbia River
14. Upper Columbia River
15. Snake River Basin

Endangered: 11
14

Threatened: 4,
5,
8,
9,
10
12
13
15



South Fork Umpqua River rainbow trout

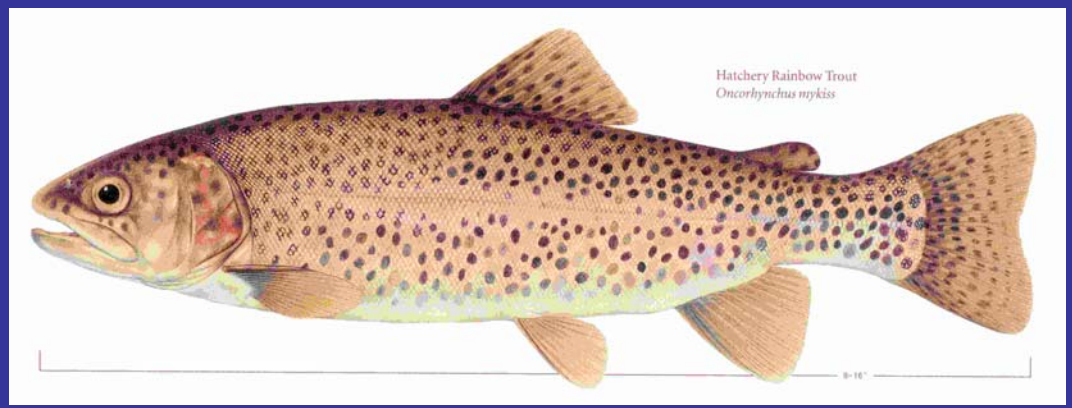
Geographical and life history diversity

1 Species (*Oncorhynchus mykiss*)
2 Subspecies (*O. mykiss mykiss*) (coastal)
3 ESU (Oregon Coast)
4 Gene Conservation Group (Mid and North Coast)
5 Major River Basin (Umpqua River)
6 Major tributary (South Fork Umpqua River)
7 Life history form (Resident)
7 Life history form (Anadromous)
8 Life history form (Summer run)
8 Life history form (Winter run)

Waples (in press)

Anadromous rainbow trout (steelhead; SH)

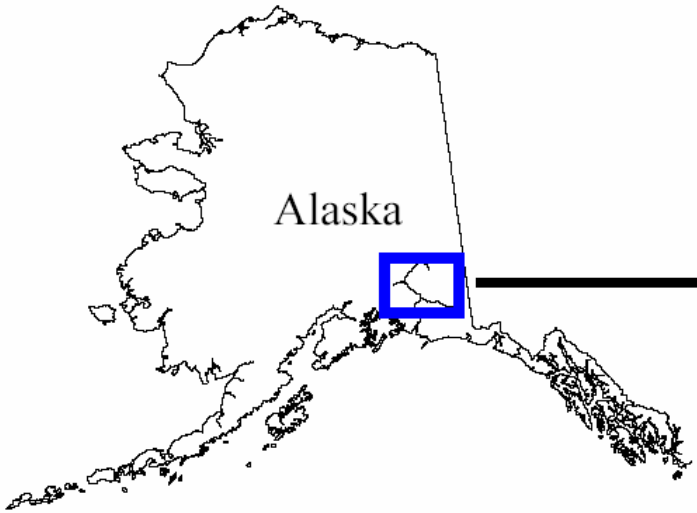
Resident rainbow trout (RR)



*Population Structure of Anadromous And Resident Rainbow Trout (*Oncorhynchus mykiss*) in the Copper River, Alaska*

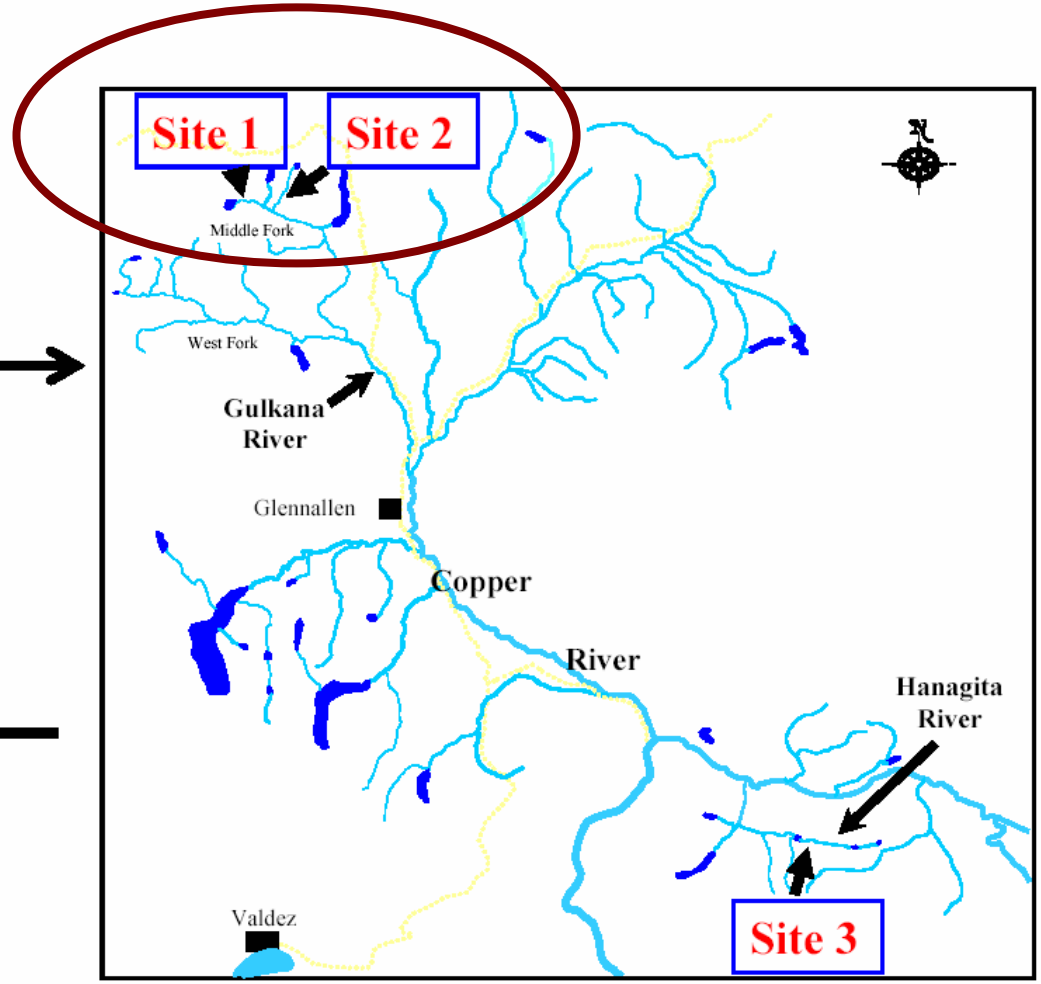
Jeffrey B. Olsen, Doug Fleming, Klaus Wuttig, and John K. Wenburg

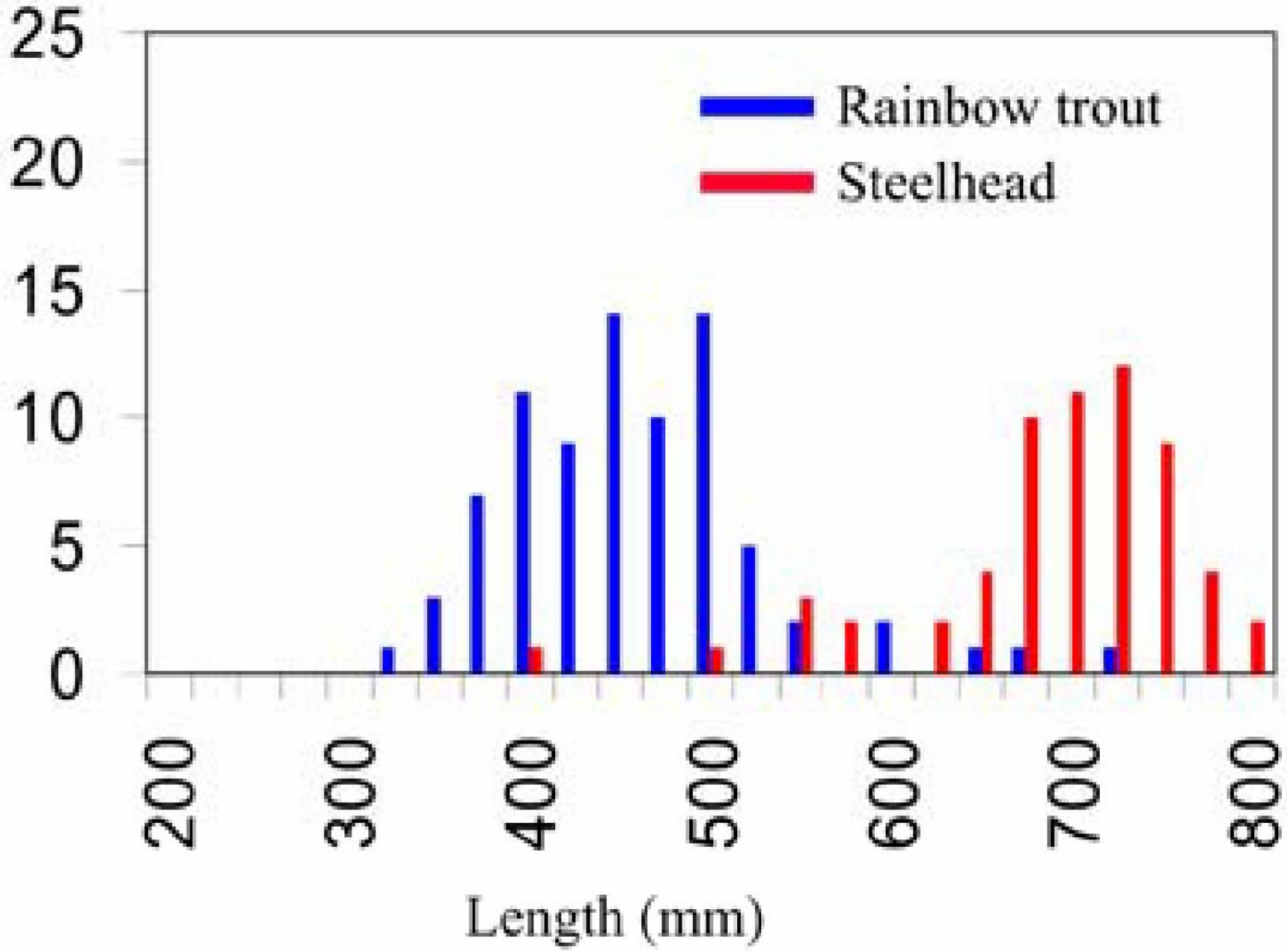
USFWS, Anchorage, Alaska

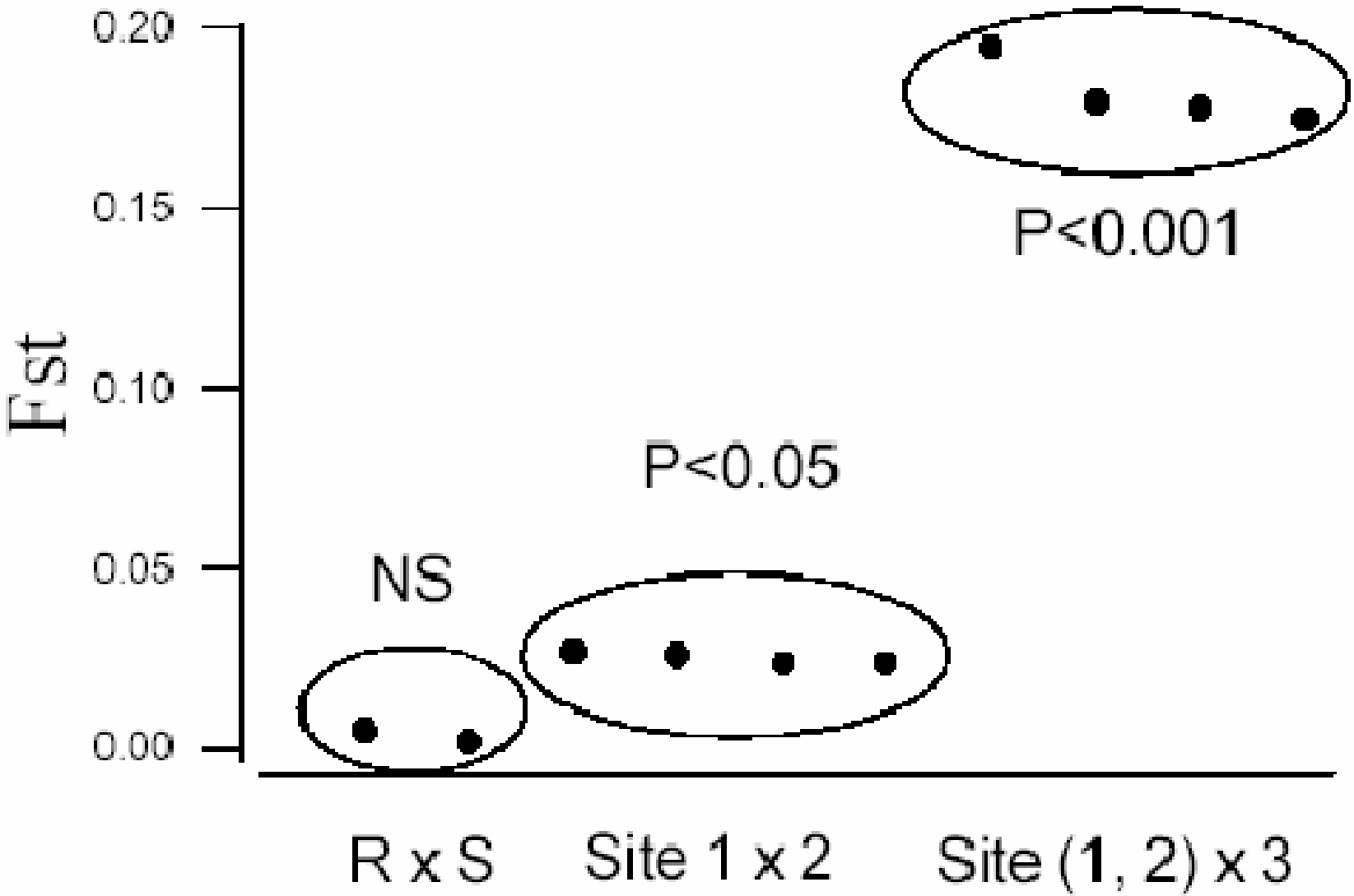


Life History

	Type	N
Site 1	SH	54
	RR	67
Site 2	SH	55
	RR	55
Site 3	SH	55




25
20
15
10
5
0
Rainbow trout
Steelhead
200
300
400
500
600
700
800
Length (mm)

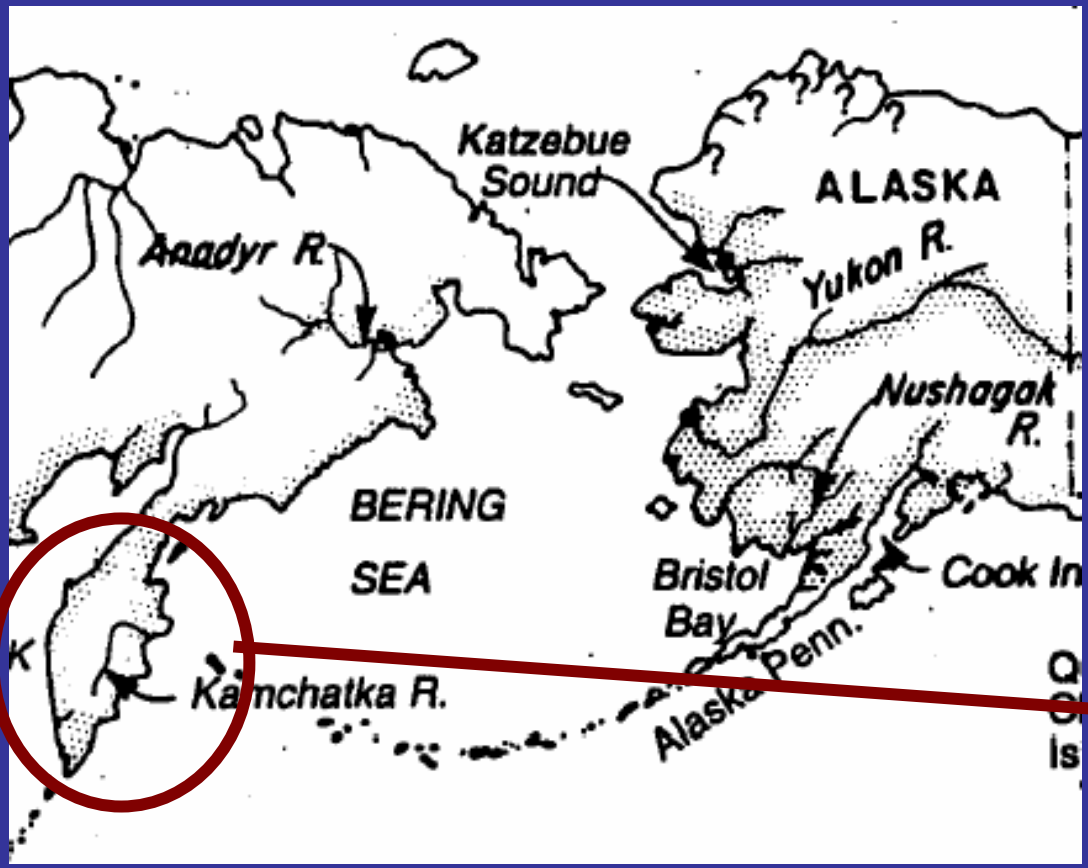


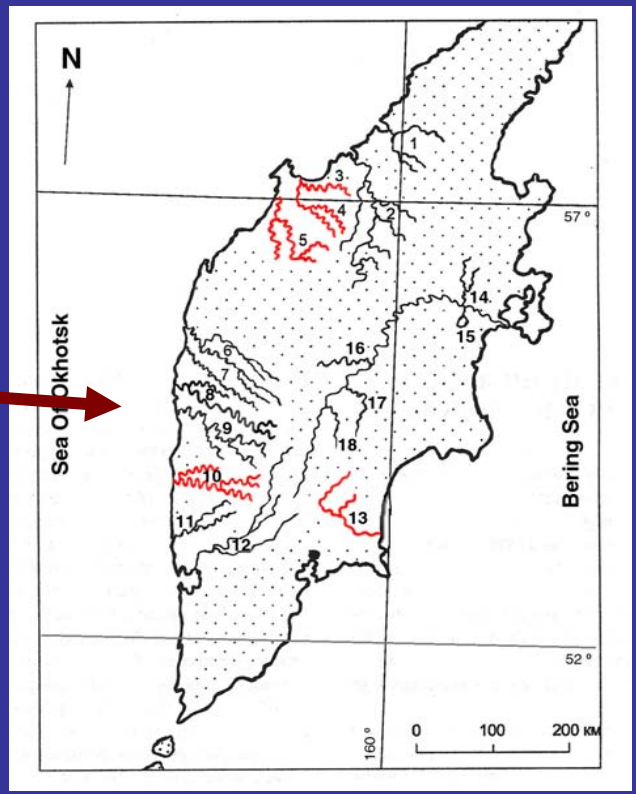
Genetic divergence at 13 microsatellite loci

Otolith microchemistry analysis

Progeny	Mother RR	Mother SH	Population
RR	38	0	Deschutes River
SH	0	20	
RR	7	2	Babine River
SH	1	23	

Chris Zimmerman & Reeves (2000)



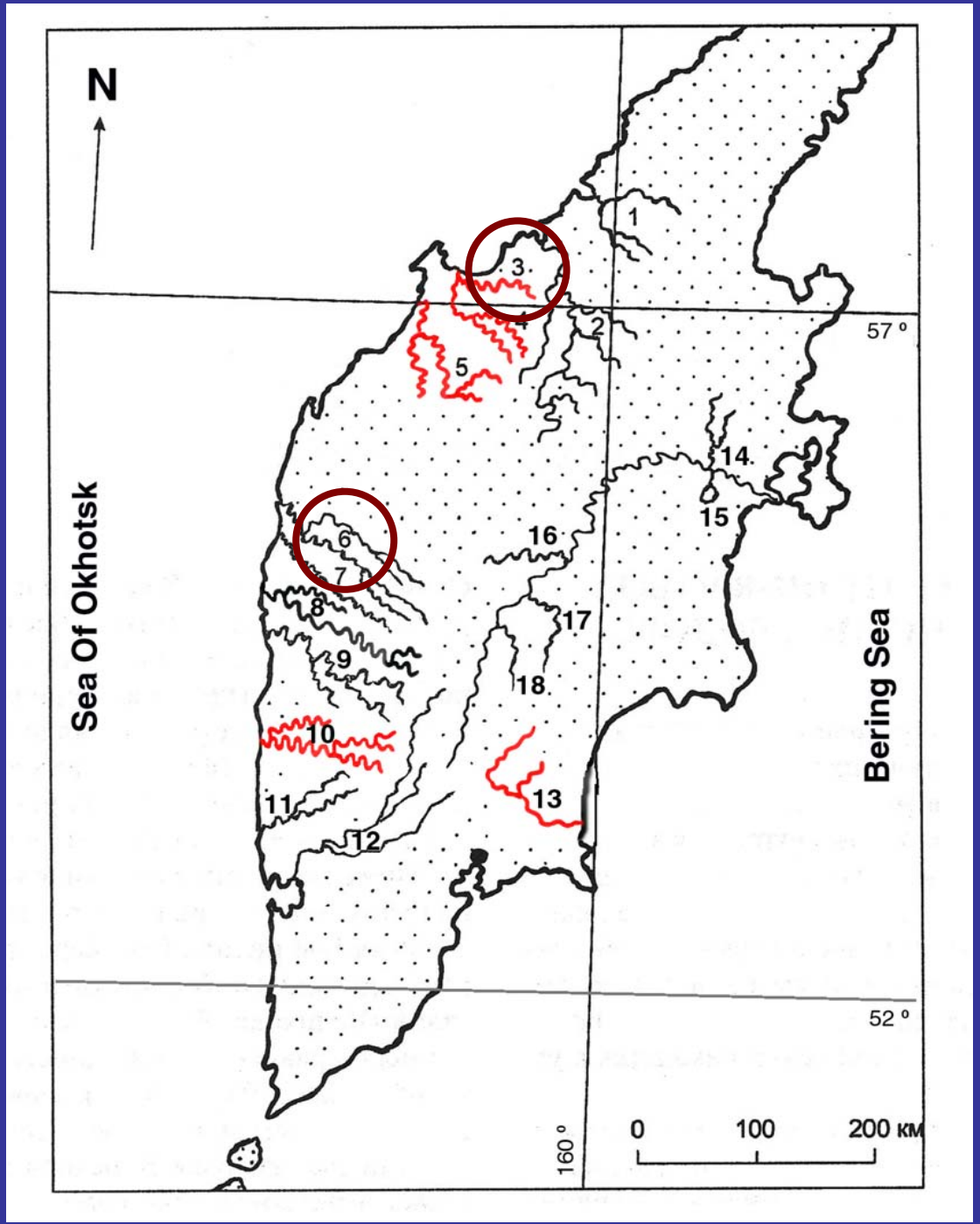


Salmon Rivers Ecology Project (Kamchatka Steelhead Project)

Jack Stanford

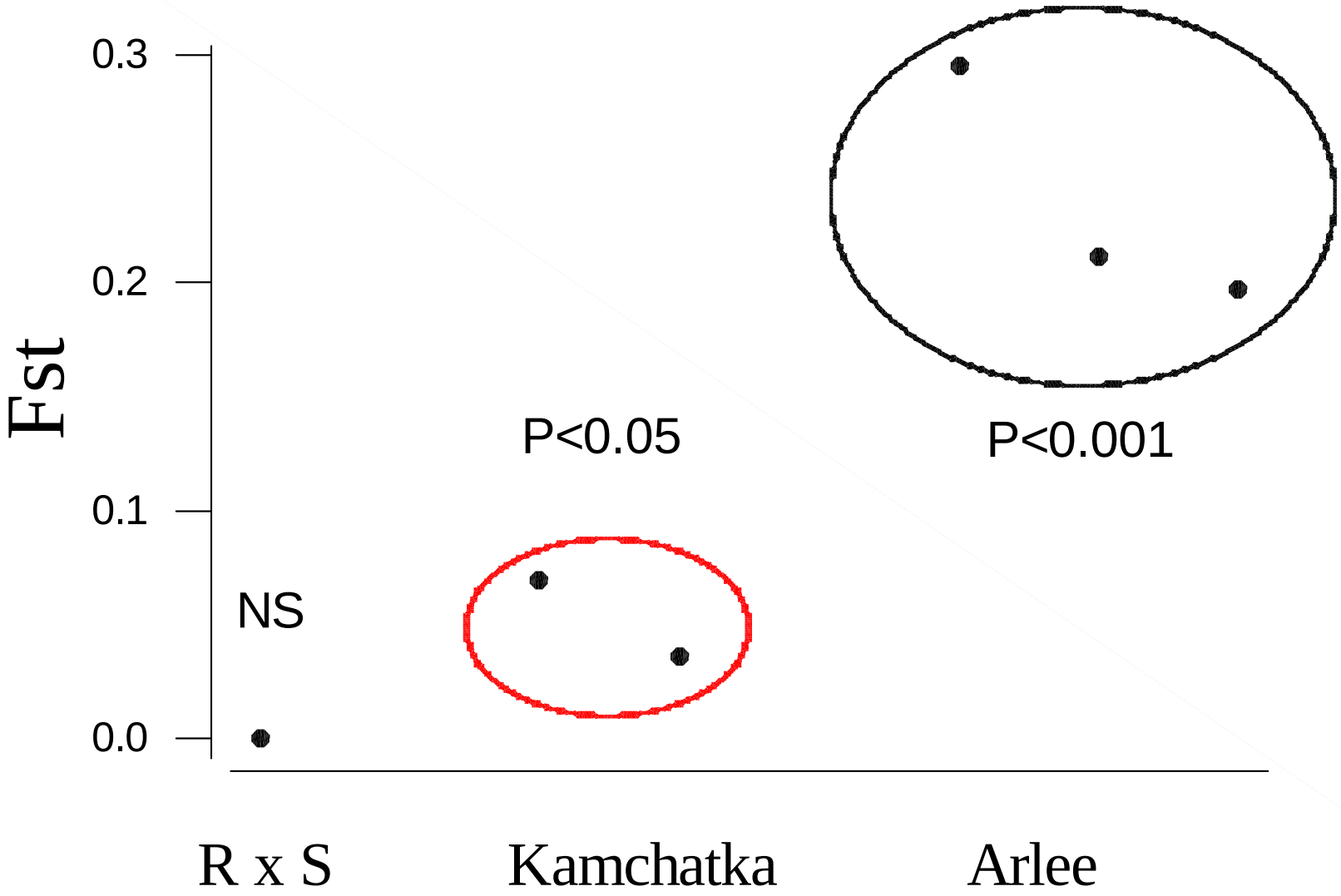
Snatylvayam

Sopochnaya



Samples analyzed at 10 microsatellite loci

		N	female	male
Arlee hatchery	RT			
Snatalovayam	SH	39	28	11
Sopochnaya	SH	19	15	4
Sopochnaya	RR	13	1	12


0.3
0.2
0.1
0.0
Fst
P<0.05
P<0.001
NS
R x S
Kamchatka
Arlee

CONCLUSION: RR and SH are part of the same "reproductive unit", and should be considered as part of the same DPS under the ESA.

This result is the opposite of the sockeye/kokanee situation.

Should a ESU in which only the anadromous life history is imperiled be listed under the ESA?

ESA

(20) The term ‘‘threatened species’’ means any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range.

The loss of the anadromous life history form would result in the loss of rainbow trout from throughout a major portion of its range (the North Pacific Ocean).

November 4, 2005

Proposal to apply "Distinct Population Segment" Policy to 10 Pacific steelhead stocks

Background

In June 2004, NOAA Fisheries Service proposed listing 9 steelhead stocks in Washington, Idaho Oregon, and California as "threatened" (South-Central California, Central California Coast, California Central Valley, Northern California, Upper Willamette River, Lower Columbia River, Middle Columbia River, Snake River Basin, and Upper Columbia), and one in southern California as "endangered" under the Endangered Species Act (ESA). The proposed listings utilized the "Evolutionary Significant Unit" or "ESU" Policy; (56 FR 58612; November 20, 1991), originally proposed for Pacific salmon to define population groups of West Coast *O. mykiss*. NOAA Fisheries Service proposed that anadromous *O. mykiss* (steelhead) and resident, fresh water *O. mykiss* (rainbow trout) where they co-occur should be included as part of the same ESU. Under the ESU policy, the biological ESU is considered to be a "distinct population segment" (DPS) and thus a "species" under the ESA.

On June 7, 2005, the U.S. Fish and Wildlife Service (FWS) wrote to NOAA Fisheries Service, stating its concerns about the factual and legal bases for our proposed listing determinations for 10 *O. mykiss* ESUs, specifying issues of substantial disagreement regarding the relationship between anadromous and resident *O. mykiss*. On June 28, 2005, NOAA Fisheries Service published a notice in the *Federal Register* announcing the ESA statutory 6-month extension of the final listing determinations for the subject *O. mykiss* ESUs to resolve the substantial disagreement regarding the sufficiency or accuracy of the available data relevant to the determinations.

New Proposal

After considering information provided by the FWS and from several public comments, NOAA Fisheries Service has reconsidered its earlier proposal to apply the Pacific salmon ESU Policy to these steelhead and rainbow trout stocks and seek comment on the proposed application of the joint NOAA Fisheries Service and FWS "Policy Regarding the Recognition of Distinct Vertebrate Population Segments under the Endangered Species Act" (DPS Policy) in delineating *O. mykiss* DPSs for listing consideration. The joint DPS Policy adopts similar but slightly different criteria from the ESU Policy for determining when a group of organisms constitutes a DPS. Despite the apparent lack of substantial reproductive isolation between steelhead and rainbow trout within a given population or group of populations, under the DPS Policy these two life forms may not warrant delineation as part of the same DPS. Consequently, we are re-opening the comment period to consider whether the final rule should delineate ten steelhead-only DPSs.

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Ruling that sympatric steelhead and resident rainbow trout are different DPS's would mean that full-sibs (brothers & sisters) would be in separate DPSs.