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**Genetic analysis of coho salmon colonization in recently deglaciated
streams in Glacier Bay, Alaska**

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Abstract

Processes associated with the evolution of ecological communities or metapopulation complexes are seldom documented from initial colonization events. Combining molecular genetic and geomorphological data we examine stream colonization events for coho salmon (*Oncorhynchus kisutch*) breeding in recently deglaciated streams (50-230 yrs BP) in Glacier Bay National Park, Alaska. Population estimates of genetic diversity, coancestry and evidence of reproductive founder events were significantly related to stream age. Genetic relationships among populations correlated significantly with location and stream age. Knowledge gained of ecological processes of natural colonization, and how genetic and demographic characteristics of newly founded or repatriated populations change over time in response to successional changes in stream habitat have significant implications for restoration and conservation of declining or extirpated salmon populations in degraded habitats across their native range.

1. INTRODUCTION

Studies of postglacial colonization offer valuable perspectives into the roles evolutionary biotic and geomorphological processes have on species distributions and abundance (Hewitt 1996). Dispersal and colonization of vacant habitats have contributed to the genetic, phenotypic, and ecological diversity across populations of many species throughout North America and Europe, including anadromous salmon (Thomas *et al.* 1986; Labeile 1992; Nielsen 1999). Analyses of recently deglaciated habitats and of species and populations that have colonized them has led to important findings regarding the relative importance of extinction, recolonization and secondary contact, that contrast classical population genetic predictions for equilibrium populations (Comps *et al.* 2001). Findings from studies of natural colonization events and of ecological and successional changes in habitat (Milner & York 2001) that affect population demography and concomitantly population levels of genetic variability have important implications for conservation and restoration strategies for threatened or declining populations, including Pacific salmon.

Recently deglaciated environments in the Pacific Northwest of North America afford unique opportunities to better understand how time- and location-dependent successional processes create and alter stream habitats (Benda *et al.* 1992) and affect their colonization potential (Milner 1987; Milner & Bailey 1989). Biological complexity and ecosystem stability are often correlated with age, spatial heterogeneity and connectivity of habitats within ecological communities (Milner *et al.* 200). Studies of these relationships based on analyses conducted retrospectively by examination of streams representing ranges in known times since deglaciation can play important roles in the development of restoration strategies for extirpated or depleted populations (Dobson *et al.* 1997).

Most anadromous adult Pacific salmonids (genus *Oncorhynchus*) return to their natal streams to reproduce after 1-4 years at sea. However, straying and colonization are important components of the evolutionary history of this genus (Quinn 1993), impacting distributions in northern latitudes and forming the basis for genetic structuring among local breeding populations. Straying from natal streams is an evolutionarily adaptive strategy to protect populations against the loss of genetic diversity following environmental catastrophes, and provides a competitive advantage when colonists move into less populated areas (NRC 1996).

Among Pacific salmonids, coho salmon (*O. kisutch*) utilize a great diversity of freshwater habitats for spawning, including streams unsuitable for other salmon species (Aro & Shepard 1967). Coho salmon are early fish colonizers in many recently deglaciated habitats, including Glacier Bay National Park (GBNP), Alaska (Milner *et al.* 2000). Genetic surveys have documented strong evidence for geographic population structure at microgeographic (Small *et al.* 1998) and phylogeographic scales across the North Pacific Ocean (Milner *et al.* 1992; Weitkamp *et al.* 1995; Olsen *et al.* 2003).

Glacier Bay National Park (GBNP) covers 13,280 km² in Southeast Alaska. The last 250 years has been marked by a dramatic recession of glacial ice from Glacier Bay proper (Fig. 1), and subsequent rapid colonization of newly formed streams by freshwater organisms, including salmonid fishes (Milner & Bailey 1989). The glacial history of this area is well documented (Cooper 1937; Field 1947). Patterns of colonization and the development of stream communities have been described for this system (Milner 1987; Milner & Bailey 1989; Milner *et al.* 2000) and elsewhere (Milner & York 2001; Benda *et al.* 1992). Salmonid colonization patterns, stream composition and species diversity within the Glacier Bay ecosystem has been documented in relation to stream ecological characteristics related to stream geomorphology and glacial influence (Milner 1987; Milner & Bailey 1989; Milner *et al.* 2000; Milner & York 2001). Historical studies offer predictive potential of the timing of initial salmon colonization and of requisite stream conditions needed to support spawning adults and growth and survival of offspring. However, critical population information regarding number of colonizers and their geographic origins from streams of different ages and degrees of successional development and juxtaposition for the greater metapopulation within GBNP or other natural or anthropogenically altered systems remains unknown.

We estimate measures of genetic variation and coancestry within, and interrelationships among recently established coho salmon populations of recent common ancestry. Genetic data are combined with geomorphological data measured across streams within the recently deglaciated GBNP to infer colonization history and connectivity of spawning populations, and thus to chronicle past and ongoing ecological events that are otherwise difficult to document and interpret.

2. MATERIALS AND METHODS

(a) Study sites and field sampling

Streams were selected a priori based on surveys indicating absence of salmonid migration barriers within the watershed and presence of coho salmon. Streams were accessed by motorized vessel (boat, fixed-wing aircraft or helicopter). Sampling efforts focused specifically on juveniles. Samples of age 1 juveniles (total N=615) were collected over 0.1-0.7 km of each stream (N=17) using baited minnow traps and by electrofishing. Sampling during June-October was timed to target fish at ages that would minimize sampling bias [i.e., to avoid newly emerged fry (Waples 1998)].

Stream location refers to the general region within GPNP. Streams designated "Outside Bay" (with the exception of Salmon River (227 BP) were not glaciated during the last glacial advance (Milner 1992; Cooper 1937), and represent the most geographically proximal sources for colonization of streams within Glacier Bay proper. Streams designated as "Lower Bay" were the oldest streams in the deglaciated region of the bay (152-197 yr BP) and were located near the bay entrance. Streams designated as "Middle Bay" were of intermediate age (130-117 yr BP) and were situated in the park interior. Streams designated as "Upper Bay" were the youngest (50-68 yr BP) and were located in the upper reaches of recently deglaciated inlets (see Fig. 1 for stream location and location of glacial ice mass over recorded time).

Sampling of juvenile progeny rather than spawning adults inflate estimates of inter-population variance in gene frequency (Waples 1998). However, genetic characteristics of juveniles (e.g., gene diversity and coancestry) capture aspects of breeding events (e.g., effective number of breeding adults) during the previous year, which we hypothesized would be related to stream age and basin characteristics. Further, we anticipated that spawning adults in each stream would be composed of different age classes (overlapping generations) including some unknown proportion individuals produced in other streams.

(b) Molecular Methods

Data include one nuclear gene intron (GH-1, Forbes *et al.* 1994), one tetranucleotide (Oki1, Smith *et al.* 1998) and seven dinucleotide microsatellite loci (Oke4, Buchholz *et al.* 2001; Oki11, Smith *et al.* 1998; Omy77 Morris *et al.* 1996; One μ 3-1 and One μ 3-2, Scribner *et al.* 1996; Ots-1 and Ots-2, Banks *et al.* 1999). Loci were amplified using the polymerase chain reaction (PCR) as described in these references. Gel electrophoresis and visualization of microsatellite alleles were performed using a Li-COR Model 4200 automated fluorescent DNA sequencer and were analyzed using RFLPScan software (Scanalytics, Billerica, MA).

(c) Statistical Methods

A generalized Mantel test (Smouse *et al.* 1986) was used to determine relationships between inter-population differences in allele frequency (genetic distance,

Cavalli-Sforza & Edwards 1967) as the dependent variable, estimated based on nine polymorphic nuclear loci, and minimum geographic distance among streams and differences in stream age as independent variables. Network Analysis software and ArcView GIS were used to calculate minimum distances between sampled populations, from the stream mouth. Stream age was estimated as elapsed time since glacial ice recession from each stream mouth using published glacial records, historical documents and aerial and oblique photographs to determine timing, location, and movement of ice masses (Cooper 1937; Fields 1947). Significant associations between measures of inter-population genetic distance with stream proximity and age provide measures of spatial or temporal autocorrelation and colonization history.

Stream age and gross stream habitat features indicative of stages of ecosystem development conducive to coho salmon spawning and juvenile rearing may influence effective breeding numbers of adults and concomitantly, population measures of genetic diversity and coancestry of progeny. Effects of stream age, watershed area, stream order, and gradient were examined as independent variables to explain inter-population variation in allelic diversity (Petit *et al.* 1998), heterozygosity, and coefficients of relationship (r_{xy} ; Queller & Goodnight 1989).

We utilized 4 watershed variables (stream age class, stream order, watershed size, and stream gradient) that proved to be independent based on 8 measured variables that might influence population measures of genetic diversity. Watershed area and gradient had been estimated from scanned USGS 1:63360 series topographic maps using ArcView GIS. Stream age was categorized into the afore mentioned classes because the oldest streams outside Glacier Bay were 2 orders of magnitude older than the streams inside Glacier Bay (Table 1) and, if treated as continuous variables, would have been biased by the extreme stream ages. Because there was possible confounding among stream age and watershed size (independent variables) and because all three dependent genetic variables were significantly correlated with each other, we used a multivariate analysis of variance (MANOVA) design.

Matrices summarizing differences in stream age and inter-stream geographic distance were correlated ($r=-0.347$, $P=0.007$) implying that stream age and location were confounded. We compare genetic distance among streams using a measure of difference between elements of the 2 standardized independent variable matrices (Dow & Cheverud 1985). Correlation coefficients obtained from Mantel tests indicated by sign whether inter-stream distance or age had a greater influence on inter-stream differences in allele frequency (and inferentially degree of straying or gene flow).

We further examined estimates of total gene diversity (Nei 1973) for the entire GBNP metapopulation (C_T ; Petit *et al.* 1986), partitioned into population-specific contributions associated with each k^{th} population's own diversity [$C_S(k)$] and that due to divergence from other populations [$C_D(k)$]. Effects of stream age class on each genetic diversity characteristic were tested separately using analysis of variance (ANOVA).

Tukey-Kramer least square means multiple comparisons were used to test for differences among stream age classes.

For selectively neutral loci, the number of alleles and their frequency distributions in natural populations result from a balance between mutations and genetic drift. When a bottleneck occurs, such as during a founding event following deglaciation, the effective population size can be severely reduced causing a reduction in allelic diversity and heterozygosity. Rare alleles are lost with high probability (Leberg 1992), leading to conditions where observed heterozygosity exceeds levels expected based on the number of alleles still segregating in the population. Degree of population bottleneck was estimated using estimates of heterozygosity excess (Cornuet & Luikart 1996) under the infinite alleles model (IAM.) and stepwise mutation model (SMM.). Results from both models are presented because different loci employed herein have been shown to evolve following each model. Significance of heterozygosity excess under each model was tested using a one-way Wilcoxon test. One assumption of the bottleneck test is that populations are closed (no immigration and without substructure). We assume that the adults that produced the age 1 juveniles sampled represented a random sample of successful breeding adults. Results from the bottleneck test should be representative of the juvenile population, and useful for inferring demographic history of the previous years spawning event.

3. RESULTS

Genetic distance among stream populations was significantly correlated with geographic distance ($r=0.435$, $P=0.007$) and stream age ($r=-0.281$, $P=0.007$). Accounting for the confounding effects of stream age and proximity, we found geographic distance to be more predictive of genetic relationships among stream populations ($r_{A, B-C}=-0.495$). Results from Mantel tests provided quantitative support for characterizations of genetic relationships among populations (Fig. 2), that clearly reveal a pattern of isolation by distance. Analyses reveal that gene flow occurs predominantly among streams of close proximity [i.e., among streams within each region of GBNP – Outside Bay, Lower Bay, Middle Bay and Upper Bay]. Tree topology suggests that colonization proceeded from oldest (outside the GBNP proper) to youngest streams (Fig.2).

The genetic diversity of progeny sampled (a function of the effective number of spawning adults) was significantly related to the 4 watershed variables examined. In the full model, stream age class had a significant effect on genetic diversity ($P=0.045$) whereas stream order ($P=0.692$), watershed size ($P=0.241$), and gradient ($P=0.131$) did not contribute significantly to the model. When stream order, watershed size, and gradient were eliminated from the model, the effect of stream age class on genetic diversity became highly significant ($P=0.003$).

There was a significant effect of watershed age on allelic richness, expected heterozygosity, and r_{xy} (MANOVA $P=0.003$). Allelic richness, expected heterozygosity,

and mean coancestry (r_{xy}) differed significantly from youngest to oldest streams (Table 1). Total allele richness was significantly less in streams <75 yrs than in streams >230 yrs ($P=0.004$) and significantly less in streams 75-150 yrs than in streams >230 yrs ($P=0.017$). Expected heterozygosity was significantly less in streams <75 yrs than in streams 75-150 yrs ($P=0.013$), 150-230 yrs ($P=0.0164$), and >230 yrs ($P=0.002$). Coefficients of relatedness (a measure of coancestry) were significantly greater in juveniles from streams <75 yrs than in streams 75-150 yrs ($P=0.008$), 150-230 yrs ($P=0.003$), and >230 yrs ($P=0.002$).

Juvenile coho salmon produced in streams of young age and smaller basin area had significantly lower levels of genetic diversity [expected heterozygosity ($P=0.002$), and allelic richness ($P=0.004$)] and higher coefficients of relatedness ($P=0.001$) than were observed in juvenile coho salmon from older stream systems within GBNP, and in unglaciated areas immediately outside the bay (Table 1). Results suggest that the effective number of breeding adults differed significantly, and in a consistent manner among streams of different age. We also observed strong evidence of population bottlenecks in juveniles from young small stream systems (Table 1).

Successionally younger streams are likely predisposed to have low effective numbers of breeding adults and variable inter-annual recruitment. In GBNP and in other degraded systems that are also of low carrying capacity, sources of recruitment will be needed from other more stable populations of the metapopulation. Given that population transfers designed to rebuild depleted populations have often failed (NRC 1996), our results highlight the importance of recruitment from immigrating adults (straying) from established populations.

Populations were not extreme in levels of genetic divergence from other populations (range in pair-wise estimates of $G_{st}=0.017-0.049$ and Fig. 2). Most contributions to total gene diversity stem from levels of diversity within each population (Fig. 3). However, samples from streams outside the bay and in the lower bay regions contribute disproportionately to overall metapopulation levels of gene diversity. Contributions to total gene diversity reflect geographic stream location within GBNP and stream age (Fig. 3). In streams of young age (or in altered systems undergoing recovery) small numbers of adults likely breed successfully and spawner recruitment is likely to be realized from straying of adults from adjacent source populations.

4. DISCUSSION

Many populations within the GBNP metapopulation are not in genetic or demographic equilibrium. Founder effects associated with reproductive events in the year prior to sampling were evidenced by reduced levels of allelic diversity and heterozygosity, and high estimates of coefficients of relationship for progeny from populations sampled from the most recently deglaciated streams (Table 1). Genetic characteristics of these natural populations and interrelationships among them likely

reflect comparable evolutionary trajectories of stream systems where restoration efforts are ongoing or planned.

Gene flow among GBNP streams is a function of geographic proximity from other potential sources, implying both homing of returning adults to specific geographic regions of GBNP and active migration of adults among populations within each region. Propensity for movements among populations after initial colonization events may be an important consideration for long-term restoration planning.

Evolutionary changes in GBNP stream communities are gradual, and stable habitats conducive to all phases of salmonid life cycle (e.g., spawning and juvenile rearing) take long periods of time (decades to centuries) to develop (Milner & Bailey 1998; Milner & York 2001). Long-term availability of recruitment from larger source populations is critical. We observe evidence for founder events and consequently high levels of relatedness in juveniles inhabiting streams of comparatively young age. Analogies to recovering stream systems in other areas of the Pacific Northwest are evident.

Introductions of salmon into vacant habitats provide opportunities to study rates and patterns of evolutionary change within and among salmon populations (Burger *et al.* 2000; Hendry *et al.* 2000). Inferences drawn from introduced populations have been used to offer recommendations for salmon restoration or reintroduction. However, predicting the success of ecological restoration programs based on results from anthropogenically mediated introduction events may not reflect outcomes of natural colonization, nor are they likely to be generalizable to conservation efforts in other areas (Burger *et al.* 2000). Predictability of the outcome of directed introductions or of suites of characteristics correlated with success or adaptation, may be lacking due to complexities associated with timing of releases, origins of source populations, and numbers introduced. Reasons underlying introduction failures may be related to biological incompatibilities between life history adaptations of the donor populations and the geographic, hydrologic, or ecological characteristics of recipient environments (Milner *et al.* 2000; Burger *et al.* 2000). To increase understanding of habitat effects on success of salmon colonization into vacant environments, knowledge of similarities and differences between directed and natural colonization events are necessary to broaden our understanding of problems to be overcome by ecological restoration.

Declines of Pacific salmon across the Pacific Northwest have led to numerous mitigation projects designed to increase species distributions and abundance (Nehlsen & Williams 1991; Young 1999). Population persistence in the face of low effective size and limited reproductive success is a major factor in salmonid conservation and recovery. Studies of natural colonization within a large natural metapopulation composed of streams of varying size and age can provide critical information to aid in restoration planning.

5. CONCLUSION

Colonization of Alaskan watersheds by Pacific salmon can provide a predictive model for rebuilding and conserving threatened and endangered populations elsewhere in the Pacific Northwest. Implicit in this model is developing understanding about the minimal population requirements of habitat, straying rates and sources of immigration which are tied to stages of successional development, and levels of genetic diversity necessary to sustain wild salmon populations. Clearly, the natural loss and recovery of Alaska habitats by glaciers differs substantially from the incremental and multifaceted degradation of more southerly landscapes. However, areas of early colonizing events such as GBNP, provide important comparative research sites to determine the requisite constituents of transitory salmon ecosystems, and to identify critical processes and mechanisms that must be understood to guide and evaluate restoration efforts.

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Table 1. Summary of genetic characteristics of coho salmon (*Oncorhynchus kisutch*; N=615) and the physical and ecological features of streams surveyed within Glacier Bay National Park (GBNP), Alaska. Stream location refers to the general region within the park (Fig. 1).

| Population (number) | N | Geological/Ecological Variables | | | Genetic Variables | | | Heterozygosity Excess (32) | |
|-------------------------|----|---------------------------------|------------|-----------------------------------|-------------------|------------------|-----------------|----------------------------|----------------|
| | | Stream Location | Stream Age | Watershed Size (km ²) | Expected Het. | Allelic Richness | r _{xy} | IAM (Prob.) | SMM (Prob.) |
| Seclusion River (1) | 20 | Outside Bay | >14,000 | 93.2 | 0.496 | 19.9 | 0.044 | 0.716 (0.013) | 0.123 (0.326) |
| Excursion River (2) | 28 | Outside Bay | >14,000 | 190.6 | 0.519 | 27.3 | -0.034 | 0.553 (0.082) | -0.412 (0.590) |
| Carolus River (3) | 44 | Outside Bay | > 1,350 | 57.0 | 0.534 | 23.0 | -0.024 | 0.881 (0.050) | 0.053 (0.500) |
| Salmon River (4) | 27 | Outside Bay | 227 | 115.2 | 0.480 | 21.2 | 0.046 | 0.526 (0.082) | -0.208 (0.082) |
| Bartlett River (5) | 38 | Lower Bay | 197 | 117.9 | 0.500 | 22.5 | 0.017 | 0.634 (0.023) | -0.285 (0.410) |
| North Berg Stream (6) | 37 | Lower Bay | 167 | 26.8 | 0.506 | 19.9 | 0.018 | 0.795 (0.010) | 0.064 (0.285) |
| South Berg Stream (7) | 24 | Lower Bay | 167 | 18.6 | 0.515 | 19.5 | 0.007 | 0.810 (0.014) | 0.251 (0.150) |
| NPS Stream 200 (8) | 38 | Lower Bay | 197 | 22.0 | 0.461 | 20.5 | 0.111 | 0.491 (0.125) | -0.424 (0.590) |
| NPS Stream 141 (9) | 33 | Lower Bay | 152 | 17.0 | 0.492 | 18.7 | 0.017 | 0.873 (0.024) | 0.220 (0.125) |
| North Vivid Stream (10) | 51 | Middle Bay | 127 | 21.6 | 0.492 | 16.4 | 0.040 | 1.104 (0.005) | 0.577 (0.024) |
| Reid Creek (11) | 47 | Middle Bay | 117 | 17.4 | 0.492 | 16.3 | 0.086 | 1.006 (0.007) | 0.564 (0.065) |
| N. Sebree Creek (12) | 51 | Middle Bay | 130 | 2.5 | 0.494 | 18.3 | 0.060 | 0.970 (0.005) | 0.370 (0.150) |
| Ice Valley River (13) | 20 | Middle Bay | 127 | 18.5 | 0.514 | 20.8 | -0.016 | 1.009 (0.002) | 0.329 (0.019) |
| NPS Stream 317.5 (14) | 21 | Upper Bay | 57 | 0.8 | 0.442 | 16.7 | 0.177 | 0.897 (0.005) | 0.457 (0.102) |
| NPS Stream 318 (15) | 51 | Upper Bay | 50 | 0.6 | 0.441 | 17.4 | 0.176 | 0.689 (0.010) | 0.237 (0.213) |
| Wolf Point Creek (16) | 26 | Upper Bay | 68 | 30.8 | 0.480 | 17.4 | 0.103 | 1.210 (0.002) | 0.819 (0.002) |
| Gull Creek (17) | 59 | Upper Bay | 57 | 9.4 | 0.444 | 15.3 | 0.291 | 0.859 (0.014) | 0.401 (0.082) |

Figure Legends

Fig. 1. Locations of streams within Glacier Bay National Park (GBNP) and approximate locations of the glacial ice sheet during the past 300 years.

Fig. 2. Neighbor-joining tree showing population relationships based on pair-wise estimates of genetic distance among coho salmon populations. Numbers on branches correspond to bootstrap support estimated based on 2000 replicates.

Fig. 3. Contribution ($C_T\%$) to total diversity (h) of each coho salmon populations ($N=17$) subdivided into components associated with diversity and degree of differentiation. Data are arrayed by geographic location within the bay (Fig. 1).

Coho Salmon Genetics Study

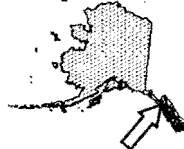
Glacier Bay National Park



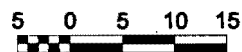
Sampled streams (estimated age)

- < 75 y
- ◆ 76- 150 y
- ▲ 151 - 230 y
- > 230 y
- Existing ice cover
- ∩ Historic extent of glaciation
- ∞ Perennial streams
- Bathymetry (depth scaled to color intensity)

Map Location

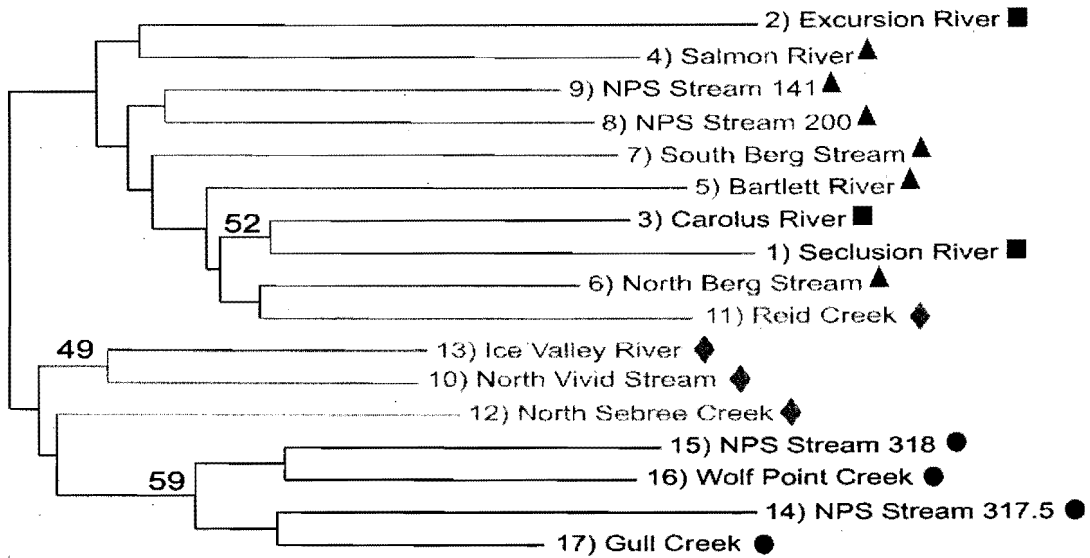


Kilometers



Plot date: December 22, 2000 k:\eco_data\data\glbe\salm\genetics\gle\coho gen study 1a.apr

Neighbor Joining Tree Generated by CornuetNJTree Program, resampling loci, 2000 replicates.



Cavalli-Sforza and Edwards 1967 chord distance



● 0 - 75 years old ◆ 76 - 150 years old ▲ 151 - 230 years old ■ > 230 years old

