# 2005 Arctic Yukon Kuskokwim Sustainable Salmon Initiative Project Final Report<sup>1</sup>

Genetic variation in Norton Sound chum salmon populations

# by:

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#### Abstract

The genetic health of Norton Sound chum salmon populations may have been impacted by the regional-level decline in chum salmon abundance that began in the mid 1990's. However, limited genetic data exist with which to evaluate these populations. In this study, 20 microsatellite loci were used to describe and evaluate factors influencing intra- and interpopulation genetic diversity in 15 populations from Norton and Kotzebue sounds. The microsatellite data provided evidence of statistically significant population structure within Norton Sound, overall and among ecoregions and fishing subdistricts, but not between every population pair. Despite their more rapid decline, chum salmon from the Nome Subdistrict exhibited levels of intra-population genetic diversity similar to those of other Norton Sound chum salmon. Early- and late-run chum salmon from Norton Sound exhibited levels of intra- and interpopulation genetic diversity similar to those of chum salmon from the Yukon River. Genetic divergence was positively correlated with the geographic distance between early-run populations however, temporal isolation (early versus late run timing) was the largest single factor influencing population structure. Assignment test results suggested that the two late-run populations may differ in the extent to which their spawn timing overlaps with early-run populations. Estimates of effective population size  $(N_e)$  in four early-run populations were relatively large and were not indicative of a high risk of short-term loss of genetic diversity. Nevertheless, estimates of the immigration fraction (*m*) suggested that gene flow is a key determinant of genetic diversity in these populations and their long-term genetic health depends upon persistent gene flow, especially during declines in abundance. Estimates of the effective number of breeders per year  $(N_b)$  and the assignment test results suggested that gene flow is relatively balanced among most populations, and the genetic health of the early-run population complex depends upon maintaining connectivity among all populations. Finally, the collective results suggested that the Inmachuk and Koyuk River chum salmon populations are the most vulnerable to loss of genetic diversity should the decline in chum salmon abundance continue.

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## Introduction

Norton Sound has suffered a progressive collapse in salmon populations since the mid 1960's, that greatly affected the lifestyle and culture of most residents. The decline began in the Nome Subdistrict, progressed through the Seward Peninsula, and by the late 1990's had affected the majority of summer (early)-run chum populations returning to spawn in western Alaska. Salmon populations reached such low levels that the Secretary of Commerce declared the region a Fisheries Disaster on August 8, 2000. Some communities in Norton Sound have relied on commercial fishing for income, yet most commercial salmon fishing is now closed. Similarly, regulations now dictate if and when local residents can fish, and how many fish they may take for subsistence, which changes the traditions and culture of the residents of Norton Sound. Norton Sound has more rivers designated as yield concerns (stocks with a chronic inability to maintain yields or harvestable surplus) than any other area in Alaska, and the Nome Subdistrict has the only Tier II (limited participation subsistence) fishery in the state (ADFG 2003a). Despite these management efforts by the Alaska Department of Fish and Game, the salmon stocks in Norton Sound continue to decline, and now many consider them to be in peril.

An adequate inventory of genetic variability and population structure is a critical component of conservation programs for Pacific salmon (Shaklee and Currens 2003). In addition to defining population structure to identify conservation or management units (e.g., Phelps et al. 1995; Johnson et al. 1997), genetic data can be used to quantify gene flow and population independence (e.g., Ford et al. 2004), to evaluate population health (Allendorf et al. 1997), and to evaluate the response of individual populations to management changes or habitat modifications (e.g., Beacham et al. 2000).

Genetic data have been an extremely important component in defining population structure of chum salmon throughout their range (Kondzela et al. 1994; Phelps et al. 1994; Seeb and Crane 1999; Wilmot et al. 1994; Winans et al. 1994). Over 42,000 chum salmon from 356 populations have been characterized at allozyme loci, including 6 populations from Norton Sound. These data have been used to create a database for estimating the origin of chum salmon sampled on the high seas and from local fisheries (Seeb et al. 2004). The database has been instrumental in 1) estimating genetic relationships and patterns of genetic diversity among chum salmon populations across the Pacific Rim and 2) validating and refining estimates of marine migration

patterns of chum salmon. For example, allozyme and minisatellite DNA data indicate that chum salmon from Southeast Alaska and the Pacific Northwest are distinct from chum salmon from the remainder of North America, and indicate that western Alaskan populations are more genetically similar to Asian populations (Seeb and Crane 1999; Taylor and Beacham 1994). The distinction of western Alaskan populations from the remainder of North America is also supported by mitochondrial DNA data (Sato et al. 2004). Gene diversity analysis using allozyme data also indicates that the level of genetic variation among populations of Northwest Alaska chum salmon (generally corresponding to the Artic-Yukon-Kuskokwim region) is the lowest of any Pacific Rim region (Seeb et al. 2004).

Studies within Alaska suggest that there are two major lineages of chum salmon in Alaska, which descended from chum salmon surviving Pleistocene glaciation in two refugia (Kondzela et al. 1994; Wilmot et al. 1994; Seeb and Crane 1999). Chum salmon in Norton Sound are part of a closely related complex of populations in coastal western Alaska that are likely descended from chum salmon persisting in the Bering refuge (unglaciated regions of western Alaska, the Bering Land Bridge, and Asia). Seeb and Crane (1999) showed that the degree of genetic population structure in Norton Sound chum salmon was lower than found in six regions of an eight region survey of western Alaska. No allele frequency heterogeneity was detected among rivers in Norton Sound in a hierarchical heterogeneity analysis conducted for western Alaska populations (Seeb and Crane 1999). However, this type of analysis has little power to detect genetic variation on fine geographic scales (Seeb and Crane 1999). Further, the low levels of polymorphism typical of allozyme loci limit their use for estimating population structure on small geographic scales (Wright and Bentzen 1994).

Though the allozyme data have greatly enhanced our understanding of chum salmon stock structure and migration patterns, higher resolution genetic data are needed for chum salmon populations in Norton Sound to evaluate the structure of this population complex and to understand the influence of factors such as gene flow on genetic diversity. Lack of resolution of genetic diversity within and among Norton Sound populations also limits the ability to monitor population responses to changes in management. Genetic variation at allozyme loci does not permit the identification of Norton Sound chum salmon in mixed-fishery samples (Seeb et al. 2004). Therefore, there is also a lack of data to estimate the origin of chum salmon sampled within Norton Sound that can be used to evaluate the timing, abundance, and migration patterns of juvenile chum salmon and adult returns (RRPNSS 2003).

Geographic/ecological region and runtime variation can significantly influence the genetic structure of salmon species (Waples et al. 2001). Multiple ecoregions and subtle run timing variation in chum salmon in Norton Sound make the presence of multiple populations of chum salmon likely. Two ecoregions have been described for Norton Sound (Nowacki et al. 2001). Streams south of the Koyuk River drainage occur in the Nulato Hills ecoregion. This region comprises an ancient, eroded, unglaciated mountain range characterized by a moist polar climate, with tundra vegetation on hilltops and willow/alder/birch or spruce/birch forests at lower elevations. Chum salmon in this region begin to enter freshwater in mid-June and run until mid-August, an earlier run that has a longer duration than chum salmon on the Seward Peninsula. The Seward Peninsula ecoregion is characterized by a moist polar climate and tundra vegetation with some willow and alder in lowland areas, and was glaciated at higher elevations. Chum salmon in this region begin to enter freshwater genetice and tundra vegetation with some willow and alder in lowland areas, and was glaciated at higher elevations. Chum salmon in this ecoregion enter rivers to spawn in early July and have a short spawning run. The run timing and habitat variation in Norton Sound may be important factors in limiting gene flow among chum salmon in rivers in this region, leading to multiple populations.

# Objectives

This project had 3 objectives:

*Objective 1 – Sample collection, summer 2005.* Collect 200 chum salmon samples from 12 rivers in Norton Sound (Agiapuk, Pilgrim, Snake, Nome, Eldorado, Niukluk, Kwiniuk, Koyuk, Inglutalik, Shaktoolik, Unalakleet and Pikmiktalik rivers), and 100-200 chum salmon samples from 2 rivers in Kotzebue Sound (Noatak and Inmachuk rivers).

Two hundred samples were collected from all but the Agiapuk (184), Niukluk (150), Fish (50), Koyuk (46), and Ungalik (54) rivers in Norton Sound. The Fish River was added because it is part of the same drainage as the Niukluk River. The Ungalik River was sampled in place of the neighboring Inglutalik River and the Kobuk River was sampled in place of the neighboring Noatak River because field logistics were more feasible. The 200 samples collected in 2005 from the Pilgrim, Snake, Eldorado and Pikmiktalik rivers were combined

with 200 samples collected in 2004 from each river to estimate the effective population size  $(N_e)$ . The 2004 samples were collected as part of other projects and sample collection was not funded by the AYK-SSI.

*Objective 2 – Laboratory analysis.* The U.S Fish and Wildlife Service, Conservation Genetics Laboratory (CGL) and the Canadian Department of Fisheries and Oceans (CDFO) genetics laboratory will genotype 100 samples from each population using 9 and 13 microsatellite loci, respectively. Of these 22 loci, two [*Oke3, Oki3*] will be used by both laboratories to assist with integrating the two data sets. Thus, each individual will be genotyped for 20 unique loci.

Of the 20 unique loci described in the proposal, two were not included in the analysis of genetic population structure. One locus (*One111*) was dropped because of an apparent null allele and one locus (*One103*) was dropped because it is the same microsatellite as *One101*. Primers for two of the remaining 18 loci each amplified two groups of independently segregating alleles that were treated as unique loci. Overall, data were taken for 20 microsatellites. The 20 microsatellite loci were used to genotype approximately 100 chum salmon from all but the Fish, Koyuk, and Ungalik rivers. Approximately 50 samples were collected from these rivers. Approximately 300 additional chum salmon from each of the Pilgrim, Snake, Nome, and Eldorado rivers were genotyped to provide adequate sample sizes for estimating *N<sub>e</sub>*.

*Objective 3* – *Genetic data analysis*. This objective has 5 parts: 1) estimate the extent of genetic variation within and among chum salmon populations in Norton Sound and compare to estimates of genetic variation reported for chum salmon in the Yukon River; 2) test if chum salmon populations in the Nome Subdistrict, which have declined more rapidly than other Norton Sound populations, have less variability than and are divergent from other Norton Sound chum salmon; 3) determine the population structure to identify conservation units for chum salmon in Norton Sound; 4) estimate patterns of gene flow using individual-based analyses and isolation-by-distance modeling; and 5) estimate the effective population size ( $N_e$ ) in order to evaluate the genetic health of Norton Sound chum salmon populations.

• Estimates of intra-population genetic variation including expected heterozygosity  $(H_e)$ , observed heterozygosity  $(H_o)$  and allele richness  $(A_r)$  were computed for each chum salmon population sample. Comparisons of intra- and inter-population genetic variation in Norton Sound and Yukon River chum salmon were made by comparing estimates of mean  $H_e$ ,  $A_R$ , and the relative measure of population structure ( $F_{st}$ ) from both regions. These statistics were also used to compare genetic variation of chum salmon in the Nome Subdistrict to genetic variation of other Norton Sound populations. Spatial and temporal population structure was assessed using hierarchical gene diversity analysis and phenetic clustering. Individual- and population-level analyses were used to evaluate patterns of gene flow. Estimates of  $N_e$  were computed using the temporal method (Waples 1990b; Wang and Whitlock 2003) for the Pilgrim, Snake, Eldorado, and Pikmiktalik rivers. The linkage-disequilibrium method (Hill 1981) was also used to estimate the effective number of breeders per year ( $N_b$ ) for all populations. However, this method is biased in age-structured species, so the values were used to evaluate the degree and pattern of genetic variation in Norton Sound chum salmon with respect to conservation. We did not, however, make recommendations regarding conservation boundaries because such recommendations must consider other factors (e.g., ecology, life history).

#### Methods

#### Study Area, sample collection, preparation, and genotyping

For the purpose of this study, Norton Sound is defined as the area extending from Port Clarence on the western end of the Seward Peninsula, Alaska, to the Pikmiktalik River east of the Yukon River flats (Figure 1). The area supports five species of Pacific salmon. Pink, chum and coho salmon are the most abundant while chinook and sockeye salmon occur in much smaller numbers. Forty-two key rivers have been identified as having spawning salmon (Rue et al. 1996 as cited in RRPNSS 2003). Commercial fisheries targeting Norton Sound salmon are managed in two fishing districts, Norton Sound and Port Clarence, and six subdistricts (Figure 1). Two ecoregions surround Norton Sound: Seward Peninsula and Nulato Hills (Figure 1, Nowacki et al. 2001).

Fin tissue samples for DNA analysis were collected in the summer of 2005 from adult chum salmon in 12 rivers in Norton Sound and 2 rivers in Kotzebue Sound (Figure 1, Table 1). The average sample size was 172, and in 10 of 15 rivers 200 samples were taken. Each individual

sample was preserved in 95% ethanol in a 2 ml vial labeled with the species, sampling location and year. Vial numbers were recorded on sample sheets to allow integration of genetic and biological data (e.g., sex, length). Archived fin tissue samples (N = 200) collected in the summer of 2004 from the Pilgrim, Snake, Eldorado, and Pikmiktalik rivers were added to the 2005 samples to allow estimation of the effective population size ( $N_e$ ).

The chum salmon in two rivers, the Agiapuk in Norton Sound and the Inmachuk in Kotzebue Sound, are considered late run, arriving in late July through August. The chum salmon in the other 13 rivers are considered early run (common), arriving in late June through early August.

For examination of genetic diversity, subsamples of approximately 100 individuals (the first 100 from each river) were genotyped at 20 microsatellites. If the sample size was less than 100, then all individuals were genotyped. Approximately 300 additional individuals were genotyped from the Pilgrim, Snake, Eldorado, and Pikmiktalik rivers for estimation of  $N_e$ .

Genotyping was conducted by the US Fish and Wildlife Service CGL and the CDFO genetics laboratory. Total genomic DNA was isolated from approximately 10-20mg of fin tissue by CDFO using a Promega Wizard SV96 Genomic DNA Purification system. Subsamples of DNA were sent to the CGL for their portion of the laboratory analysis.

The CGL examined 9 microsatellite loci: *Oke3*, *Oke4*, *Oke8*, and *Oke11* (Buchholz et al. 2001); *Oki1* and *Oki23.1* (Smith et al. 1998); *Ots2.1* and *Ots3.1*(Banks et al. 1999); and *Ots103* (Small et al. 1998). The microsatellites were amplified via PCR, size fractionated on denaturing polyacrylamide gels, and visualized and scored using a Li-Cor IR<sup>2®</sup> scanner with Li-Cor Saga<sup>TM</sup> GT ver 2.0 software (Lincoln, NE). Li-Cor 50-350bp and 50-700 size standards were loaded in the first and last lanes and at intervals of 14 lanes or less across each gel to estimate microsatellite fragment lengths. Positive controls, consisting of 2-10 alleles of predetermined size, were loaded in three lanes distributed evenly across the gels to ensure consistency of allele scores. The PCR primers for *Oki1* and *Ots2.1* each produced two groups of alleles. These alleles were determined to represent unlinked (independently segregating) loci and were treated as separate microsatellites (*Oki1U*, *Oki1L*, *Ots2.1U*, *Ots2.1L*) for analysis.

The CDFO examined 13 microsatellite loci: *Ots3* (Banks et al. 1999), *Oke3* (Buchholz et al. 2001), *Oki2* (Smith et al. 1998), *Oki100* (Miller et al. unpub), *Omy1011* (Bentzen, unpub.), *One101, One102, One103, One104, One111,* and *One114* (Olsen et al. 2000), *Ssa419* (Cairney

et al. 2000), and *OtsG68* (Williamson et al. 2002). The microsatellites were amplified via PCR, size fractionated in an ABI 3730 capillary DNA sequencer, and genotypes were scored by GeneMapper software 3.0 (Applied Biosystems, Foster City, CA) using an internal lane sizing standard in each lane. Microsatellite fragment lengths were estimated with Genescan 3.1 and Genotyper 2.5 software (PE Biosystems, Foster City, CA).

Multi-locus microsatellite genotypes from both laboratories were integrated and stored in an  $Excel^{TM}$  (Microsoft) spreadsheet for data analysis. Each population sample was examined at the following 20 loci: *Oke3*, *Oke4*, *Oke8*, *Oke11*, *Oki1U*, *Oki1L*, *Ots2.1U*, *Ots2.1L*, *Oki23.1*, *Ots103 Ots3*, *Oki2*, *Oki100*, *Omy1011*, *One101*, *One102*, *One104*, *One114*, *Ssa419*, and *OtsG68*. The locus *One111* was dropped because initial statistical evaluation suggested the presence of a null allele. The locus *One103* was dropped because it is the same microsatelite as *One101*.

# Genetic diversity within and among populations and population groups

Estimates of allele frequency, allele richness ( $A_r$ ), and observed and expected heterozygosity ( $H_o$ ,  $H_e$ ) were computed for each locus and population sample using the computer program FSTAT version 2.9.3 (Goudet 2001). These values were also computed for each cohort for the Pilgrim, Snake, Eldorado, and Pikmiktalik rivers. A randomization test of the statistic *f* (inbreeding coefficient) was used to test for conformity to Hardy-Weinberg equilibrium (HWE) for each locus and population combination. A randomization test of the log-likelihood *G*-statistic was used to test for genotypic disequilibrium among locus pairs over all populations. These tests were performed using FSTAT and the threshold for statistical significance ( $\alpha = 0.05$ ) was corrected ( $\alpha/k$ , Cooper 1968) for k-simultaneous tests using the sequential Bonferroni method (Rice 1989). Two values of k were used for the HWE test to evaluate each population over loci (k = 21) and each locus over populations (k = 15).

Estimates of mean  $A_r$  and mean expected heterozygosity ( $H_s$ ) over all loci were computed for two population groups in each of three grouping strategies: 1) run timing (early and late), 2) ecoregion (Seward Peninsula and Nulato Hills), 3) fishing subdistrict (Nome and all other). All 15 populations were included in group 1. Groups 2 and 3 examined Norton Sound populations excluding chum salmon from the Agiapuk and Koyuk rivers. Because these populations were genetically distinct, they would likely conceal the general trend of divergence among the remaining 11 early-run populations. Randomization tests implemented in FSTAT were used to test if these values differed significantly among groups within each grouping strategy.

Finally, estimates of mean  $A_r$  and  $H_s$  for chum salmon from Norton and Kotzebue sounds and chum salmon from the Yukon River were compared using FSTAT. Comparisons were made for all populations in each region and for early- and late-run populations, separately. For the purposes of this study we refer to the summer- and fall-run chum salmon from the Yukon River as early- and late-run. The timing of each run is defined for management purposes as the time of entry into the Yukon River which is June – July 15 and July 16 – August 31 for the summer- and fall-run, respectively (JTC 2005).

A *G*-test of genotypic frequency homogeneity was used to test for genetic divergence among all chum salmon population pairs and among cohorts from the Pilgrim, Snake, Eldorado, and Pikmiktalik rivers. Estimates of the degree population divergence based on the relative measure  $F_{st}$  were computed for all population pairs, over all loci, according to Weir and Cockerham (1984). Estimates of  $F_{st}$  were also computed for each population group listed above and a randomization test was used to evaluate differences in the degree of population structure in each group. These analyses were performed in FSTAT.

An analysis of molecular variation for diploid data (AMOVA, Michalakis and Excoffier 1996) was used to test for hierarchical structuring of genetic variation. The AMOVA tests were performed using ARLEQUIN version 3.01 (Schneider et al. 2000) to independently examine the three grouping strategies: run timing, ecoregion, and fishing subdistrict. For each analysis the estimate of  $F_{st}$  was partitioned into within-group ( $F_{sc}$ ) and between-group ( $F_{ct}$ ) genetic variation. Randomization was used to test if the estimates of  $F_{st}$ ,  $F_{sc}$ , and  $F_{ct}$  were significantly greater than zero.

Phenetic clustering was used to graphically evaluate the distribution of genetic diversity among the 15 populations. A pairwise genetic distance matrix of the Cavalli-Sforza and Edwards (1967) chord distance (CSE) was generated from allele frequency estimates using the program GENDIST in PHYLIP version 3.5c (Felsenstein 1995). The program NEIGHBOR in PHYLIP was used to construct an unrooted neighbor-joining (NJ) phenogram based on the CSE distance matrix. The NJ phenogram was visualized using the program TreeView version 1.6.6 (Page 1996).

#### Isolation by distance and time

Mantel tests (Mantel 1967) implemented in the computer program IBD version 1.52 (Bohonak 2002) were used to determine if genetic divergence increases with spatial separation among Norton Sound chum salmon populations. For comparison, Mantel tests were also used to evaluate the influence of temporal separation (here treated as a binary variable, early versus late run timing) on genetic divergence among pairs of chum salmon populations. Partial Mantel tests were also performed to assess the extent to which these two factors, run timing and spatial separation, influence each while influencing gene flow. Two measures of genetic divergence were computed for all population pairs. First, pairwise estimates of  $F_{st}$  from FSTAT were used to compute  $F_{st}/(1 - F_{st})$ : the measure of genetic divergence recommended by Rousset (1997) for populations in a primarily linear array. Second, estimates of the proportion of misassigned individuals derived from the computer program GeneClass2 (Piry et al. 2004) were used to compute the average proportion of misassigned fish between each population pair. This approach has been shown to reveal isolation by distance not apparent using a Mantel test of a populationlevel statistic like F<sub>st</sub> (Castric and Bernatchez 2004). Briefly, the Bayesian individual assignment method of Rannala and Mountain (1997) was used to assign individuals to populations based on multilocus genotype frequencies. Individuals that were assigned to a population other than the population from which they were taken were considered misassigned. Simulation was used to determine the probability distribution of genotypes in each population. If the genotype probability of the misassigned individual was less than 0.05 in the assigned population, then the individual was classified as unknown, representing a population not sampled.

Two series of Mantel tests and partial Mantel tests were performed at two spatial scales using both measures of genetic divergence. First, the influence of spatial and temporal isolation on genetic population structure was examined using all 15 populations (Norton and Kotzebue sounds). The second test excluded the two late run populations (Inmachuk, Agiapuk rivers) and the Koyuk River chum salmon. The third test excluded Kotzebue Sound and used all 13 Norton Sound populations. The fourth test excluded Kotzebue Sound and the Agiapuk and Koyuk rivers. For each test, geographic distance was the shortest coastline distance between river mouths.

#### Effective population size per generation

Waples (1990a) showed that the effective population size per generation ( $N_e$ ) for Pacific salmon is equal to the effective number of breeders per year ( $N_b$ ) multiplied by the mean generation length (g). We used two methods to estimate  $N_b$  from allele frequency data for 3 cohorts (1999, 2000, 2001) of chum salmon from the Pilgrim, Snake, Eldorado, and Pikmiktalik rivers. The first estimate of  $N_b$  ( $\hat{N}_{b(w)}$ ) assumes populations are isolated (no gene flow) and was derived using the temporal method modified for Pacific salmon (Waples 1990b). The standardized variance in allele frequency for the *j*th locus,  $\hat{F}_j$ , was computed using the formula

$$\hat{F}_{j} = \frac{1}{L-1} \sum_{i=1}^{L} \frac{(X_{i1} - X_{i2})^{2}}{(X_{i1} + X_{i2})/2},$$

where *L* is the number of alleles at locus *j* and  $X_{i1}$  and  $X_{i2}$  are the frequencies for allele *i* at the first and second temporal sampling. The weighted mean standardized variance in allele frequency,  $\hat{F}$ , was computed using the formula

$$\hat{F} = \frac{\sum [(L_j - 1)\hat{F}_j]}{\sum (L_j - 1)},$$

where  $L_j$  is the number of alleles at locus *j*. Because the adult data were partitioned by cohort,  $\hat{N}_{b(w)}$  was calculated using the sample plan II formula

$$\hat{N}_{b(w)} = \frac{b}{\{2[\hat{F} - (1/S)]\}}$$

where *b* is an empirically derived parameter that reflects the number of generations between the temporal samples (Waples 1990b; Tajima 1992) and S is the harmonic mean of the sample sizes of the two cohorts. This formula was used to compute a single estimate of  $N_b$  for each population by computing the average  $\hat{F}$  from all pairwise comparisons of temporal samples and then using the weighting scheme proposed by Waples (1990b) to estimate  $N_b$ .

The 95% confidence intervals for  $\hat{F}$  were computed from a chi-square distribution using the formula

$$\left[\frac{n\hat{F}}{X^{2}.025(n)},\frac{n\hat{F}}{X^{2}.975(n)}\right],$$

where *n* is equal to  $\sum (Lj-1)$ , the number of independent alleles among all loci. These values were used to derive 95% confidence intervals for  $\hat{N}_{b(w)}$ .

The second estimate of  $N_b$  ( $\hat{N}_{b(ml)}$ ) was derived using the computer program MLNE version 1.0 (Wang and Whitlock 2003). This program assumes gene flow among populations and uses maximum likelihood (ML) to simultaneously estimate  $N_b$  and the immigration fraction (*m*) for a single population (the focal population). Immigrants to the focal population are assumed to come from a single source population; however, Wang and Whitlock (2003) showed their ML method will work for other models of gene flow (e.g., island and stepping stone models). They recommend pooling potential source populations into a single sample for analysis. For this study, the source population was derived by pooling all Norton Sound populations except for the focal population. The number of generations between each sample (*b*) was estimated using the program of Tajima (1992). The estimates of *b* were rounded to the nearest integer as required for input into MLNE version 1.0.

 $\hat{N}_{e}$  was computed from  $\hat{N}_{b(w)}$  and  $\hat{N}_{b(ml)}$  using the formula

$$\hat{N}_e = g(\hat{N}_b),$$

where g is the mean generation length for each population.

Finally, we used the computer program NeEstimator version 1.3 (Peel et al. 2004) which uses the linkage-disequilibrium method of Hill (1981) to estimate  $N_b$  from single samples. This method is biased when applied to age-structured species (Waples 2004). Therefore, we assume the age structure and age class survival is the same for each population and we use the  $N_b$ estimates from each population for a relative comparison only. We feel these assumptions are reasonable given the geographic proximity and level of relatedness of the populations in this study.

#### Results

# Genetic diversity within and among populations and population groups

The range in genetic variation among the 20 microsatellite loci was relatively large (Table 2). The mean estimates of allele richness ( $A_r$ ) and expected heterozygosity ( $H_e$ ) over all populations for each locus ranged from 2.0 (*Ots2.1L*) to 23.7 (*OtsG68*) and 0.08 (*Oke8*) to 0.94 (*Ots103*), respectively. Despite these differences among loci, the 21 microsatellites revealed similar levels of genetic diversity within most populations. The mean  $A_r$  and  $H_e$  over all loci for each population ranged from 9.8 (Inm) to 11.9 (Nom) and 0.64 (Inm) to 0.71 (Fish).

Multiple randomization tests of conformity to HWE for each locus and population revealed 14 tests where the *P*-value for the test statistic *f* was below 0.05 because of a deficit of heterozygotes (Table 2). These results were not common to any one locus or population and only one locus in one population (*Oke3* x Agi) was significant after the  $\alpha$ -level ( $\alpha = 0.05$ ) was adjusted ( $\alpha/k$ ) for multiple testing (k = 15 tests for each locus across all populations). No results remained significant after the  $\alpha$ -level was adjusted for k = 20 tests (each population across all loci).

Randomization tests for genotypic disequilibrium revealed 10 locus pairs with a *P*-value for the *G*-statistic below 0.05. These results were not judged significant when the  $\alpha$ -level was adjusted for 190 pairwise tests.

The estimates of genetic variation ( $\overline{A}_r$ ,  $\overline{H}_e$ ,  $\overline{H}_o$ ) within the Pilgrim, Snake, Eldorado, and Pikmiktalik rivers were similar among the cohorts used to estimate  $N_b$  and  $N_e$  (Table 3). Randomization tests of conformity to Hardy-Weinberg equilibrium revealed one cohort (Pilgrim River, 2000) where the *P*-value for the test statistic *f* was below 0.05 because of a deficit of heterozygotes. This result was not significant after the  $\alpha$ -level was adjusted ( $\alpha/k$ ) for k = 12 tests.

The estimates of  $A_r$ , mean gene diversity ( $H_s$ ) and  $F_{st}$  differed when all 15 populations were grouped by run timing (Table 4). The two late-run populations exhibited significantly lower (P < 0.05) values of  $A_r$  and  $H_s$  and higher  $F_{st}$  as compared to the 13 early-run populations. In contrast, these statistics did not differ when the Norton Sound populations (excluding Agi and Koy) were grouped by ecoregion and fishing subdistrict (Table 4). Estimates of  $A_r$  and  $H_s$  for all chum salmon populations from Norton and Kotzebue sounds were significantly (P = 0.01) larger than for Yukon River populations (Table 5). This difference, however, was likely due to the greater number of late-run populations (14) in the Yukon River sample. Late-run chum salmon populations in both regions exhibit significantly lower genetic diversity than early-run populations (Table 4, B. Flannery, USFWS, Anchorage, AK, pers. com.). When early- and late-run populations were examined separately, only  $A_r$  for early-run populations exhibited significant (P = 0.05) inter-regional difference. There was no evidence of interregional difference in  $A_r$  and  $H_s$  for late-run populations. Estimates of the degree of population structure ( $F_{st}$ ) in the two regions did not differ significantly (Table 5).

The AMOVA results indicated that, while most of the genetic variation is found within populations ( $\approx 97 - 99\%$ ), chum salmon from Norton and Kotzebue Sounds exhibit significant inter-population structure (Table 6). All values of  $F_{st}$ ,  $F_{ct}$  and  $F_{sc}$  were significantly greater than zero (P < 0.05), regardless of the population grouping strategy. When the inter-population variation was partitioned temporally, the AMOVA results indicated that run timing explains the greatest proportion ( $F_{ct} > 0.014 > F_{sc}$ ) of the observed genetic population structure. When only Norton Sound populations were partitioned spatially (excluding Agi and Koy), the ecoregion and fishing subdistrict explained a similar proportion ( $F_{ct} \approx 0.0004 - 0.0006$ ) of the observed genetic population structure (Table 6). Although significant, the amount of genetic variation between the spatial groupings was less than the amount of population structure within the groups ( $F_{sc}$ ).

When no grouping strategy was invoked, the estimate of  $F_{st}$  over all 15 populations was 0.011. Estimates of  $F_{st}$  for all population pairs confirms that the greatest divergence occurs between the early-run populations with the two late-run populations (Inm, Agi, Table 7). Pairwise estimates of  $F_{st}$  involving the Koyuk River population were also relatively large. The *G*-test of genotypic frequency homogeneity over all loci revealed *P*-values below 0.05 for 81 of the 105 population pairs (Table 7). Forty-nine population pairs differed significantly when the  $\alpha$ -level was adjusted for 105 pairwise tests.

With the exception of the Inmachuk River population, the individual assignment success was relatively low (Table 8). The proportion of correctly assigned individuals ranged from 0.02 (Fish) to 0.73 (Inm) and averaged 0.20. The proportion of individuals not meeting the statistical threshold for assignment (P < 0.05) and classified as unknown averaged 0.15.

The neighbor-joining phenogram supported the temporal and spatial trends observed in the evaluation of genetic diversity within and among population groups (Figure 2). The two late-run populations were distinct from the early-run populations and from each other. Two early-run population clusters corresponded weakly to Northern and Western geographic groups, consistent with the two ecoregions in Norton Sound. Finally, the Koyuk River population appeared unique from the late-run populations and from other early-run populations in Norton Sound.

#### Isolation by distance and time

The Mantel tests also revealed the importance of temporal isolation as a factor influencing gene flow among Norton and Kotzebue Sound chum salmon. When all 15 populations were examined, the correlation between genetic divergence  $[F_{st}/(1 - F_{st})]$  and geographic distance was not significant (P = 0.080, Figure 3A). When run timing was considered (independent of geographic distance), the correlation was highly significant (P = 0.009). The pairwise values for the Inmachuk River population formed a distinct cluster above 0.050 whereas the pairwise values for the Agiapuk River population were all less than 0.015. The partial Mantel test results showed a decrease in the test statistic (r) and an increase in the P-value when the influence of each variable (run time, geographic distance) was tested while controlling for the effect of the other variable. A highly significant correlation (P < 0.003) was also observed between genetic divergence and geographic distance for early-run populations including the Kobuk River when the late-run populations and the Koyuk River were removed (Figure 3A).

The scatter plots of genetic divergence  $[F_{st}/(1 - F_{st})]$  versus geographic distance for the 13 Norton Sound populations revealed the distinct Agiapuk and Koyuk River populations (Figure 4A). As above, the correlation between genetic divergence and geographic distance was not significant (P = 0.122), but when run timing was considered, the correlation was highly significant (P < 0.001). Also, when the Agiapuk and the Koyuk River populations were removed the correlation between genetic divergence and geographic distance was nearly significant (P = 0.058, Figure 4A). As above, the partial Mantel test results showed a decrease in the statistic rand an increase in the P-value for the primary variable when controlling for the effect of the secondary variable.

Replacing  $[F_{st}/(1 - F_{st})]$  with the misassignment proportion did not change the results of the Mantel tests and partial Mantel tests (Figure 3B, 4B). However, the distribution of pairwise

values did differ. The values that included late-run populations were less distinct in Figure 3B than in Figure 3A, and the values that included the Agiapuk and Koyuk River populations were less distinct in Figure 4B than in Figure 4A.

# Effective population size per generation

The two genetic estimators provided different values of the effective population size per generation ( $\hat{N}_e$ , Table 9). The estimates that assume isolation ( $\hat{N}_{e(w)}$ ) ranged from 5,304 (Eldorado River) to 10,058 (Pilgrim River). The upper bound of the 95% confidence interval for the four  $\hat{N}_{e(w)}$  values was infinite, indicating the sampling variance was high relative to the temporal variance in allele frequencies for this time period. The estimates that assume migration ( $\hat{N}_{e(ml)}$ ) ranged from 579 (Eldorado River) to 944 (Snake River, Table 9). The maximum likelihood estimates of the immigration fraction ( $\hat{m}_{(ml)}$ ) ranged from 0.09 (Snake River) to 0.26 (Eldorado River). All estimates of  $\overline{N}$  were larger than corresponding  $\hat{N}_{b(ml)}$  value.

The values of  $\hat{N}_b$  from the linkage-disequilibrium method ranged from 46 (Inmachuk River) to 604 (Nome River) and averaged 290 (Figure 5). The estimates of  $\hat{N}_b$  were above average for five of the six populations from Northwest Norton Sound (Pilgrim, Nome, Eldorado, Niukluk, Fish rivers) and were below average for the three populations from Norton Bay (Kwiniuk, Koyuk, Ungalik rivers). Of the two late-run populations, the chum salmon from the Inmachuk exhibited the lowest overall  $\hat{N}_b$  estimate , while the estimate for the Agiapuk River chum salmon was not statistically different (95% confidence intervals overlapped) from seven of the early-run populations.

#### Discussion

## Genetic variation within populations: Norton Sound with comparison to Yukon River

Of the three population grouping criteria, only one, adult return timing, was associated with intrapopulation genetic variation in chum salmon from Norton and Kotzebue sounds. The two laterun populations exhibited significantly lower allele richness and gene diversity than the 13 earlyrun populations. Lower genetic diversity in both late-run populations is likely the result of lower immigration because of temporal isolation from early-run populations, and because there are fewer late-run populations in the region. Of the two late-run populations, the estimates of genetic diversity are lowest for the Inmachuk River. The pairwise  $F_{st}$  values and assignment test results suggest that the level of temporal isolation (from early-run populations) may be greater for chum salmon from the Inmachuk River than the Agiapuk River. This possibility is discussed in more detail under patterns of gene flow, below. It is also possible the low genetic diversity in the Inmachuk River population (relative to the Agiapuk River population) is in part the result of a higher rate of genetic drift due to a smaller population size. The estimate of  $\hat{N}_b$  for the Inmachuk River chum salmon was significantly lower than the estimate for all other populations in this study (Figure 5). One explanation for the low  $\hat{N}_b$  value is that the Inmachuk River drainage was heavily impacted by mining activity 70 years ago (C. Lean pers. comm.) and this land alteration, visible today, may have reduced chum salmon spawning habitat relative to other rivers in the area.

Chum salmon from the Norton and Kotzebue Sound region exhibit levels of intra-population genetic diversity similar to those of the Yukon River chum salmon when grouped by return timing. This result provides some insight into the broad-scale (inter-regional) and fine-scale (intra-regional) factors influencing genetic variation in both regions of Western Alaska. First, it appears that the broad-scale factors underlying the recent decline in chum salmon in Western Alaska has not differentially impacted the genetic diversity in either region. Indeed, Yukon River chum salmon have experienced abundance shortfalls similar to those described for Norton Sound. As a result of these declines, some chum salmon populations in both regions have been classified as management concerns under the State of Alaska Sustainable Salmon Fisheries Policy (ADFG 2003b, ADFG 2004a, ADFG 2004b). Second, it is likely that the same intra-regional factors are, in part, responsible for the similarly low levels of genetic diversity in the late run populations in both regions. For example, the fall (late)-run chum salmon on the Yukon River spawn primarily in isolated upwelling habitat in the upper portion of the drainage whereas the summer (early)-run populations utilize much larger portions of tributaries and often spawn in nearly contiguous reaches (J. Bromaghin, pers. comm.). Because the late-run chum salmon tend to spawn in more isolated habitat, they likely experience lower rates of immigration than the early-run populations. In addition, some of the early-run populations on the Yukon River are very large (e.g., Anvik

River, JTC 2005) and likely experience lower rates of genetic drift (and loss of genetic diversity) than the late-run chum salmon.

#### Genetic variation within populations: Nome Subdistrict and ecoregions

The three early-run populations from the Nome Subdistrict exhibited levels of intra-population genetic diversity similar to those of other early-run populations from Norton Sound. Two tentative conclusions may be drawn from this result. First, it appears the general decline in chum salmon abundance in Norton Sound has not differentially impacted the genetic diversity of any group of populations despite the fact that the decline has been more pronounced in northern Norton Sound (ADFG 2006). Second, the subdistrict-based fishery management strategy employed by the Alaska Department of Fish and Game (ADFG 2003a) appears to have prevented escapements in the Nome Subdistrict from falling to a level that would result in rapid loss of genetic diversity. The minimum annual escapement goals for Nome Subdistrict rivers should assure that the effective population size (per generation) is well above 50, the value below which theoretical studies suggest that isolated populations are at risk of significant short-term loss of genetic diversity (Lande and Barrowclough 1987; Waples 1990a; Allendorf et al. 1997). It should be noted here that these populations are not isolated and that migration (gene flow) is also an important determinant of genetic diversity in these populations (see discussion on patterns of gene flow and effective population size, below). These conclusions are tentative because the chum salmon decline is relatively recent (~ 2-3 chum salmon generations). If the chum salmon abundance in the Nome Subdistrict does not increase, or continues to decline, then a detectable loss of genetic diversity could occur.

Intra-population genetic diversity did not differ among the early-run Norton Sound populations when grouped by ecoregion. This result suggests that the broad-scale habitat differences between the areas (Nowacki et al. 2001) are not differentially constricting population size or gene flow or both for chum salmon. Indeed, the values of  $\hat{N}_b$  for three of the four populations from the Nulato Hills ecoregion were similar to the values for the seven populations from the Seward Peninsula ecoregion (Figure 5). The estimates of the degree of population differentiation ( $\hat{F}_{st}$ ) within each area were the same (0.001, Table 4) suggesting similar levels of gene flow.

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# Population structure and conservation units

The AMOVA results indicate that population structure in Norton and Kotzebue sounds is influenced more by run timing than location (Table 6). This result is consistent with previous studies of chum salmon in the Yukon River and the Pacific Northwest and indicates that run timing is the primary barrier to gene flow at the intra-regional level in Western Alaska chum salmon (Phelps et al. 1994; Wilmot et al. 1994; Seeb and Crane 1999). The AMOVA result is supported by the phylogenetic analysis and pairwise tests of allele frequency homogeneity in which the two known late-run populations from the Agiapuk and the Inmachuk rivers are genetically distinct from all early-run populations and from each other. Interestingly, the Koyuk River chum salmon also appear quite distinct from other early-run populations. Although this river has been characterized as having early-run chum salmon, there is some indication that a late run exists (C. Lean pers. comm.). It is possible that the fish used in this study were from a late run, given that the river was sampled the end of July, at the same time that the Agiapuk River was sampled. It is also possible, however, that the unique nature of this sample is not due to run timing but to genetic drift in a relatively small population. The latter conclusion is consistent with other results from this study. The value of  $\hat{N}_{h}$  for the Koyuk River population is lower than all populations except the Inmachuk, but the degree of intra-population genetic diversity is more similar to the diversities of other early-run populations. An evaluation of both explanations will require more detailed information on run timing of chum salmon in the Koyuk River. This river is one of the largest in Norton Sound and it should be determined if multiple and temporally isolated populations spawn there.

The AMOVA results also indicate that significant spatial population structure exists among the Norton Sound early-run chum salmon. The degree of spatial population structure, however, is relatively low ( $F_{st} = 0.0017$ ) and similar to the value reported by Seeb and Crane (1999) from allozyme loci. Also, the *G*-test failed to detect allele frequency heterogeneity in 26 of 55 pairwise comparisons of the 11 populations (Koyuk River excluded). Despite this weak structure, some geographic patterns exist. Low, but significant, levels of population structure were detected when populations were grouped by ecoregion and fishing subdistrict (Nome versus others). The former grouping represents a clustering strategy based on habitat characteristics including climate, geology, and terrestrial vegetation (Nowacki et al. 2001). The latter grouping represents a clustering strategy based on a single scenario using the fishery management subdistricts. The AMOVA results indicate that the populations in the Nulato Hills are, as a whole, genetically distinct from populations on the Seward Peninsula and suggest that some local adaptation to the unique habitat features in each ecoregion may be restricting gene flow between populations from each ecoregion. This conclusion is supported by the neighbor-joining phenogram that revealed geographic coherence among early-run populations consistent with the two ecoregions. The AMOVA results also suggest that populations in the Nome Subdistrict are, as a whole, genetically distinct from other early-run populations in Norton Sound, which provides genetic support for the Nome Subdistrict as a management unit but not necessarily as a demographically independent conservation unit. In fact, the low values of  $F_{ct}$  observed for both grouping strategies suggests that gene flow between groups is relatively high and persistent and strongly influences genetic diversity.

This analysis of population structure provides some genetic support for both life history (e.g., run timing) and ecological (e.g., ecoregion) criteria that may be used in determining conservation units for Norton Sound chum salmon. Of these criteria, the support is very strong for two conservation units defined by run timing but weak for any further parsing of population groups based on ecological criteria. Identifying conservation boundaries, however, is controversial and requires a much more thorough analysis of biological and genetic data than was conducted here. Waples et al. (2001) described the approach used in the Pacific Northwest to define conservation units for five species of Pacific salmon, steelhead, and sea-run cutthroat trout for Endangered Species Act implementation. Their method included detailed evaluation of life history, ecological, and genetic data by review teams for each species in order to determine the relative weight to apply to the three criteria. A similar comprehensive approach was used by Halupka et al. (2003) to identify vulnerable populations of Pacific salmon in southeast Alaska. These kinds of methods should be used to determine conservation units for Western Alaska chum salmon.

# Patterns of gene flow

Multiple Mantel tests, partial Mantel tests, and the assignment test allowed us to unravel and evaluate the influence of run timing and spatial isolation on gene flow in chum salmon from Norton and Kotzebue sounds. The results of these analyses suggest that the two variables are largely, but not entirely, independent, which supports the two following general conclusions. First, gene flow between early-run populations is influenced by spatial separation. The Mantel tests revealed evidence of non-random, isolation-by-distance (IBD), gene flow among early-run chum salmon of Norton Sound. This pattern appears to extend from Norton to Kotzebue Sound as evidenced by the significant positive association between genetic divergence and geographic distance when the Kobuk River population was included with the 11 early-run Norton Sound populations (Figure 1A). Evidence of IBD is not uncommon among populations of anadromous salmonids in large river systems (e.g., Primmer et al. 2006) or along long, linear shorelines (e.g., Castric and Bernatchez 2004), but may be less likely among salmon populations distributed along non-linear shorelines (e.g., Olsen et al. 2003). The evidence of IBD in this study suggests that, despite the concave shape of Norton Sound, most early-run populations likely follow a similar migration route along the shoreline when returning to spawn. This result is consistent with the tagging results of Gaudet and Shaefer (1982), which suggested that returning chum salmon enter Norton Sound from the west along the north central shore and the majority follow the shoreline east and south toward the Yukon River while a minority travel west towards the Nome Subdistrict.

Second, gene flow is restricted, but occurs, among some early- and late-run populations and is, in some cases, influenced by spatial separation. The Mantel test results indicate that genetic divergence is associated with run timing of chum salmon populations from Norton and Kotzebue sounds. However, the two late-run populations appear to exhibit different patterns and levels of gene flow with respect to the early-run populations. For example, the distribution of pairwise values of  $F_{st}/(1 - F_{st})$  in Figure 3A suggest that the extent of isolation is greater between the earlyrun populations and chum salmon from the Inmachuk River than between the early-run populations and the Agiapuk River regardless of the degree of spatial separation. This trend is supported by the assignment test results that showed much higher assignment success for chum salmon from the Inmachuk River than the Agiapuk River (Table 8). In addition, no fish were misassigned to the Inmachuk River, but 28 fish were misassigned to the Agiapuk River from 12 other rivers. It is possible that the two late run populations differ in the extent to which their spawn timing overlaps with the early-run populations and consequently the extent to which genetic divergence is associated with geographic distance from the early-run populations. Indeed, the Agiapuk River samples were collected earlier (late July) than the Inmachuk River samples (mid August). The partial Mantel tests indicated that, by controlling for the effect of

spatial separation, geographic distance may influence gene flow between early-run populations and the Agiapuk River chum salmon but not the Inmachuk River chum salmon. The test result was significant (P = 0.014, Figure 3A) when both late-run populations were considered, but not significant (P = 0.055, Figure 4A) when the Inmachuk River population was removed. The slope of the least-squares linear regression describing the relationship between  $F_{st}/(1 - F_{st})$  and geographic distance was positive ( $2.0 \times 10^{-6}$ ) for the Agiapuk River and negative ( $-7.0 \times 10^{-6}$ ) for the Inmachuk River.

Other factors such as population size, local adaptation, and the level of spatial isolation may contribute to these differences in the pattern and level of gene flow for the two late-run populations. In particular, the Inmachuk River is more spatially isolated from other populations in this study; located on the opposite side of the Seward Peninsula from the Norton Sound populations and separated from the Kobuk River in Kotzebue Sound by the Baldwin Peninsula (Figure 1).

The two measures of genetic divergence ( $[F_{st}/(1 - F_{st})]$ , misassignment proportion) provided identical results with respect to the Mantel tests, but they differed in the distribution of pairwise population values. These early x late values were clearly distinct in the scatter plots of  $F_{st}/(1 - F_{st})$  but overlapped with early x early population values in the scatter plot of misassignment proportion. This difference reflects the level of analysis (population versus individual) and highlights the complementary insights obtained when using both approaches to examine gene flow. The estimates of  $F_{st}/(1 - F_{st})$  provides an indication of population-level distinctiveness and the effects of historic gene flow (among other factors), whereas, the misassignment proportion examines individuals and provides an indication of contemporary gene flow. The fact that the pairwise estimates of the misassignment proportion involving the Agiapuk River, but not the Inmachuk River, overlapped with those of early-run population pairs (Table 8, Figure 3B) suggests that contemporary gene flow between some early- and late-run populations may, in some years, exceed gene flow between some pairs of early-run populations. This insight was not apparent from the  $F_{st}/(1 - F_{st})$  values.

# Effective population size per generation

The minimum estimates (2.5% confidence interval) of effective population size per generation  $(\hat{N}_e)$  for the Pilgrim, Snake, Eldorado, and Pikmiktalik rivers ranged from 2,300 to 2,844

assuming isolation ( $\hat{N}_{e(w)}$ ) and 461 to 696 assuming migration ( $\hat{N}_{e(ml)}$ ). Although there are no strict criteria for evaluating the two estimators,  $\hat{N}_e$  values of 50 and 500 are considered general thresholds indicating significant threat of short- and long-term loss of genetic diversity, respectively, in *isolated* populations (Waples 1990a; Mace and Lande 1991; Allendorf et al. 1997). The fact that the  $\hat{N}_{e(w)}$  values (assuming isolation) were all well above 500 suggests that the recent decline in chum salmon abundance in Norton Sound has not seriously increased the risk of loss of genetic diversity in these populations. However, given the small spatial scale, the coastal distribution, the short stream lengths and the relatively low degree of genetic population structure, it is important to consider the role that migration may play in the genetic diversity of these populations. The  $\hat{N}_{e(m)}$  values (assuming migration) were 8 to 13 times smaller, however, the companion estimates of the immigration fraction  $(\hat{m}_{(ml)})$  suggests that intra-population genetic diversity may be influenced substantially by gene flow. These estimates imply that migration is a key determinant of genetic diversity in these populations and that their long-term genetic health may depend upon persistent migration, especially during declines in abundance. Maintaining connectivity and habitat health in this type of population complex is critical to long-term population health.

It should be noted that the Wang and Whitlock (2003) method of simultaneously estimating  $N_e$ and *m* has not been fully evaluated in Pacific salmon and further analysis is needed to verify the findings and conclusions above. Nevertheless, the values of  $\hat{m}_{(ml)}$  for this study (0.09 – 0.26) seem reasonable given the level of genetic population structure revealed by the AMOVA. For example, the estimates of  $F_{st}$  for the early-run Norton Sound chum salmon were 0.0016 and 0.0017 (Table 6). The estimates of  $F_{st}$  from the formula  $F_{st} = 1/(4N_em + 1)$ , where the values of  $\hat{N}_{e(ml)}$  and  $\hat{m}_{(ml)}$  were used to derive  $N_em$ , ranged from 0.0014 to 0.0029.

The estimates of  $\hat{N}_b$  from the linkage disequilibrium method provided no evidence of a single large population that may act as a source in a source-sink metapopulation model (Cooper and Mangel 1998; Manier and Arnold 2005). The largest value, 604, for the Nome River chum salmon was not statistically different from four other early-run populations in Norton Sound. This result suggests that, while gene flow is important to maintaining genetic diversity as suggested by the estimates of  $\hat{N}_{e(ml)}$  and  $\hat{m}_{(ml)}$  above, no single population is likely responsible for maintaining connectivity among Norton Sound chum salmon. Rather, gene flow is likely more balanced and the genetic health of the early-run population complex depends upon maintaining connectivity among all populations. Support for this conclusion also comes from the assignment test results where the average proportion of misassignments among early-run populations was similar, ranging from 0.048 (Snake River) to 0.074 (Fish River).

Estimates of  $\hat{N}_b$  for chum salmon from the Inmachuk and Koyuk rivers stood out as uniquely small. In addition, the assignment test results suggest that these two populations receive the lowest proportion of immigrants. The proportion of individuals misassigned to these populations (from other populations) was zero and 0.016 respectively compared to an average of 0.063 over all early-run populations. Collectively, these results suggest that these two populations (of the 15 populations surveyed) are likely the most vulnerable to loss of genetic diversity.

# Summary and recommendations

In summary for the Norton Sound chum salmon:

- Significant population structure exists, overall and among ecoregions and fishing subdistricts.
- Run timing is the largest single factor influencing population structure.
- Populations from the Nome Subdistrict exhibit levels of intra-population genetic diversity similar to levels observed in other Norton Sound populations.
- Early- and late-run populations from Norton Sound and the Yukon River exhibit similar levels of genetic diversity.
- Genetic divergence is positively correlated with geographic distance for early-run populations.
- Late-run populations may differ in the extent to which their spawn timing overlaps with early-run populations.
- Current effective population sizes are not indicative of a high risk of short-term loss of genetic diversity.

- Populations from the Inmachuk and Koyuk rivers appear to be the most vulnerable to loss of genetic diversity.
- Gene flow appears to be a key contributor to genetic diversity and the genetic health of the early-run population complex depends upon maintaining connectivity among populations.

These points support the following recommendations:

- Conservation and management actions should maintain connectivity among populations because gene flow appears to be an important factor in maintaining genetic diversity. For example, land use planners should avoid habitat impacts that alter salmon migration patterns and fishery managers must be aware that harvest strategies may alter gene flow patterns as well as the escapement number.
- Genetic diversity should be monitored in these populations with emphasis on the Inmachuk and Koyuk rivers. Periodic examination will help identify trends in genetic diversity that may compromise genetic health as well as help evaluate conservation and management actions.
- Use an approach similar to that described by Waples et al. (2001) and Halupka et al. (2003) to define conservation boundaries for western Alaska chum salmon. A comprehensive review of life history, ecology, and genetic variation of chum salmon will identify factors influencing population health and viability as well as focus monitoring efforts.
- Test for population structure and run timing variation in Koyuk River chum salmon. There is evidence that the Koyuk River may contain multiple populations that vary in run timing.

## References

- Alaska Department of Fish and Game (ADFG). 2003a. The 2003 Norton Sound Salmon Management Plan. Alaska Department of Fish and Game, Commercial Fisheries Division, Nome, Alaska.
- Alaska Department of Fish and Game (ADFG). 2003b. Norton Sound Nome subdistrict chum salmon stock status and action plan: a report to the Alaska Board of Fisheries. RIR no. 3A03-35. Alaska Department of Fish and Game, Commercial Fisheries Division,

Anchorage, Alaska.

- Alaska Department of Fish and Game (ADFG). 2004a. Yukon River fall chum salmon stock status and action plan: a report to the Alaska Board of Fisheries. RIR no. 3A04-05. Alaska Department of Fish and Game, Commercial Fisheries Division, Anchorage, Alaska.
- Alaska Department of Fish and Game (ADFG). 2004b. Yukon River summer chum salmon stock status and action plan: a report to the Alaska Board of Fisheries. RIR no. 3A04-03.
  Alaska Department of Fish and Game, Commercial Fisheries Division, Anchorage, Alaska.
- Alaska Department of Fish and Game (ADFG). 2006. 2006 Norton Sound salmon fisheries management plan. Alaska Department of Fish and Game, Commercial Fisheries Division, Nome, Alaska.
- Allendorf, F. W., D. Bayles, D. L. Bottom, K. P. Currens, C. A. Frissell, D. Hankin, J. A. Lichatowich, W. Nehlsen, P. C. Trotter, and T. H. Williams. 1997. Prioritizing Pacific salmon stocks for conservation. Conservation Biology 11:140-152.
- Banks, M. A., M. S. Blouin, B. A. Baldwin, V. K. Rashbrook, H. A. Fitzgerald, S. M.
  Blankenship, and D. Hedgecock. 1999. Isolation and inheritance of novel microsatellites in chinook salmon (*Oncorhynchus tshawytscha*). Journal of Heredity 90: 281-288.
- Beacham, T. D., K. D. Le, M. R. Raap, K. Hyatt, W. Luedke, and R. E. Withler. 2000.
   Microsatellite variation and estimation of stock composition of sockeye salmon,
   *Oncorhynchus nerka*, in Barkley Sound, British Columbia. Fishery Bulletin 98:14-24.
- Bohonak, A. J. 2002. IBD (isolation by distance): a program for analyses of isolation by distance. Journal of Heredity 93:153-144.
- Buchholz, W., S.J. Miller, and W.J. Spearman. (2001). Isolation and characterization of chum salmon microsatellite loci and use across species. Animal Genetics 32:160-167.
- Cairney, M., J. B. Taggart, and B. Hoyheim. 2000. Characterization of microsatellite and minisatellite loci in Atlantic salmon (*Salmo salar* L.) and cross-species amplification in other salmonids. Molecular Ecology 9:2175-2178.
- Castric, V., and L. Bernatchez. 2004. Individual assignment test reveals differential restriction to dispersal between two salmonids despite no increase of genetic differences with distance. Molecular Ecology 13:1299-1312.
- Cavalli-Sforza, L. L. and Edwards, A. W. F. 1967. Phylogenetic analysis: Models and estimation procedures. Evolution 21:550-570.

- Cooper, A. B., and M. Mangel. 1999. The dangers of ignoring metapopulation structure for the conservation of salmonids. Fishery Bulletin 97:213-226.
- Cooper, D. W. 1968. The significance level in multiple tests made simultaneously. Heredity 23:614-617.
- Felsenstein, J. 1995. PHYLIP version 3.57c. Department of Genetics, University of Washington, Seattle, WA.
- Ford, M. J., D. Teel, D. M. VanDoornik, D. Kuligowski, and P. W. Lawson. 2004. Genetic population structure of central Oregon coast coho salmon (*Oncorhynchus kisutch*). Conservation Genetics 5:797-812.
- Gaudet, D. M., and G. Schaefer. 1982. Migrations of salmon in Norton Sound, Alaska: determined by tagging in 1978-1979. Alaska Department of Fish and Game.
- Goudet, J. 2001. FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3). Available from http://www.unil.ch/izea/softwares/fstat.html.
- Halupka, K. C., M. F. Willson, M. D. Bryant, F. H. Everest, and A. J. Gharrett. 2003. Conservation of population diversity of pacific salmon in southeast Alaska. North American Journal of Fisheries Management 23:1057-1086.
- Hanski, I.A., and M.E. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. Biological Journal of the Linnean Society 42:3-16.
- Hill, W. G. 1981. Estimation of effective population size from data on linkage disequilibrium. Genetical Research 38:209-216.
- Johnson, O. W., W. S. Grant, R. G. Cope, K. Neely, F. W. Waknitz, and R. S. Waples. 1997. Status review of chum salmon from Washington, Oregon, and California. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-32, 280 p.
- Joint Technical Committee (JTC) of the Yukon River US/Canada Panel. 2005. Yukon River salmon 2004 season summary and 2005 season outlook. Fisheries and Ocean Canada, stock assessment and fisheries management section, Yukon transboundary area. Whitehorse, Yukon Territory.
- Kondzela, C. M., C. M. Guthrie, S. L. Hawkins, C. D. Russell, J. H. Helle, and A. J. Gharrett.
  1994. Genetic relationships among chum salmon populations in southeast Alaska and northern British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 51 (Suppl. 1):50-64.

- Lande, R., and G. F. Barraclough. 1987. Effective population size, genetic variation, and their use in population management. Pages 87-123 in M. E. Soulé, editor. Viable populations for conservation. Cambridge University Press, New York.
- Manier, M., and S. J. Arnold. 2005. Population genetic analysis identifies source-sink dynamics for two sympatric garter snake species (*Thamnophis elegans* and *Thamnophis sirtalis*).
   Molecular Ecology 14:3965-3976.
- Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research 27:209-220.
- Michalakis, Y. and Excoffier, L. 1996. A generic estimation of population subdivision using distances between alleles with special reference for microsatellite loci. Genetics 142: 1061-1064.
- Nowacki, G., P. Spencer, T. Brock, M. Fleming, and T. Jorgenson. 2001. Narrative descriptions for the ecoregions of Alaska and neighboring territiories. U.S. Geological Survey, available at http://alaska.usgs.gov/ecoregions expl.html.
- Olsen, J. B., S. L. Wilson, E. J. Kretschmer, K. C. Jones, and J. E. Seeb. 2000. Characterization of 14 tetranucleotide microsatellite loci derived from Atlantic salmon. Molecular Ecology 9:2155-2234.
- Olsen, J.B., S.J. Miller, W.J. Spearman, and J.K. Wenburg. 2003. Patterns of intra- and interpopulation genetic diversity in Alaskan coho salmon: Implications for conservation. Conservation Genetics 4: 557-569.
- Page, R. D. M. 1996. TREEVIEW: An application to display phylogenetic trees on personal computers. Computer Applications in the Biosciences 12: 357-358.
- Peel, D., J. R. Ovenden, and S. L. Peel. 2004. NeEstimator: software for estimating effective population size, Version 1.3. Queensland Government, Department of Primary Industries and Fisheries.
- Phelps, S. R., L. L. LeClair, S. Young, and H. L. Blankenship. 1994. Genetic diversity patterns of chum salmon in the Pacific Northwest. Canadian Journal of Fisheries and Aquatic Sciences 51 (Suppl. 1):65-83.
- Phelps, S., J. Uehara, D. Hendrick, J. Hymer, A. Blakley, and R. Brix. 1995. Genetic diversity units and major ancestral lineages for chum salmon in Washington. Technical Report Number RAD95-02, Washington Department of Fish and Wildlife, Fish Management

Program, Resources Assessment Division, Olympia, Washington.

- Piry, S., A. Alapetite, J.-M. Cornuet, D. Paetkau, L. Budouin, and A. Estoup. 2004. GeneClass2: A Software for Genetic Assignment and First-Generation Migrant Detection. Journal of Heredity 95:536-539.
- Primmer, C. R., A. J. Veselov, A. Zubchenko, A. Poututkin, I. Bakhmet, and M. T. Koskinen. 2006. Isolation by distance within a river system: genetic population structuring of Atlantic salmon, *Salmo salar*, in tributaries of the Varzuga River in northwest Russia. Molecular Ecology 15:653-666.
- Rannala, B., and J. L. Mountain. 1997. Detecting immigration by using multilocus genotypes. Proceedings of the National Academy of Sciences USA 94:9197-9201.
- Raymond, M., and F. Rousset. 1995. GENEPOP Version1.2: Population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248-249.
- Research and Restoration Plan for Norton Sound Salmon, Draft (RRPNSS). 2003. Prepared by the Scientific Technical Committee for the Norton Sound Steering Committee. Available at: http://www.cf.adfg.state.ak.us/region3/proposals/nsrr/nsrrp.pdf
- Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43: 223-225.
- Rousset, F. 1997. Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. Genetics 145: 1219-1228.
- Rue, F. 1996. Norton Sound/Bering Strait regional comprehensive salmon plan 1996-2010. Alaska Department of Fish and Game, Commercial Fisheries Division, Juneau, Alaska.
- Sato, S., H. Kojima, J. Ando, H. Ando, R. L. Wilmot, L. W. Seeb, V. Efremov, L. LeClair, W. Buchholz, D.-H Jin, S. Urawa, M. Kaeriyama, A. Urano, and S. Abe. 2004. Genetic population structure of chum salmon in the Pacific rim inferred from mitochondrial DNA sequence variation. Environmental Biology of Fishes 69:21-37.
- Schneider, S., Roessli, D., and Excoffier, L. 2000. ARLEQUIN version 2.0: A software for population genetics data analysis. Genetics and Biometry Laboratory, Dept. of Anthropology and Ecology, University of Geneva, CP 511, 1211 Geneva 24, Switzerland.
- Seeb, L. W., P. A. Crane, C. M. Kondzela, R. L. Wilmot, S. Urawa, N. V. Varnavskaya, and J. E. Seeb. 2004. Migration of Pacific Rim chum salmon on the high seas: insights from genetic data. Environmental Biology of Fishes 69:21-36.
- Seeb, L.W. and P.A. Crane. 1999. High genetic heterogeneity in chum salmon in western Alaska,

the contact zone between northern and southern lineages. Transactions of the American Fisheries Society 128:58-87.

- Shaklee, J. B., and K. P. Currens. 2003. Genetic stock identification and risk assessment. Pp. 291-328 in E. Hallerman (ed.) Population genetics: principles and applications for fisheries scientists. American Fisheries Society, Bethesda.
- Small, M.P., T.D. Beacham, R.E. Withler, and R.J. Nelson. 1998. Discriminating coho salmon (*Oncorhynchus kisutch*) populations within the Fraser River, British Columbia, using microsatellite DNA markers. Molecular Ecology 7: 141-155.
- Smith, C.T., B.F. Koop, and R.J. Nelson. 1998. Isolation and characterization of coho salmon (*Oncorhynchus kisutch*) microsatellites and their use in other salmonids. Molecular Ecology 11: 1614-1616.
- Tajima, F. 1992. Statistical method for estimating the effective population size in salmon. Journal of Heredity 83:309-311.
- Taylor, E. B., and T. D. Beacham. 1994. Population structure and identification of North Pacific
   Ocean chum salmon (*Oncorhynchus keta*) revealed by an analysis of minisatellite DNA.
   Canadian Journal of Fisheries and Aquatic Sciences 51:1430-1442.
- Wang, J. and M. C. Whitlock. 2003. Estimating effective population size and migration rates from genetic samples over space and time. Genetics 163:429-446.
- Waples, R. S. 1990a. Conservation genetics of pacific salmon. II. Effective population size and the rate of loss of genetic variability. Journal of Heredity 81:267-276.
- Waples, R. S. 1990b. Conservation genetics of pacific salmon. III. Estimating the effective population size. J. Hered. 81:277-289.
- Waples, R. S., R. G. Gustafson, L. A. Weitkamp, J. M. Myers, O. W. Johnson, P. J. Busby, J. J.
  Hard, G. J. Bryant, F. W. Waknitz, K. Neely, D. Teel, W. S. Grant, G. A. Winans, S.
  Phelps, A. Marshall, and B. M. Baker. 2001. Characterizing diversity in salmon from the Pacific Northwest. Journal of Fish Biology 59:1-41
- Waples, R. 2004. Salmonid insights into effective population size. Pages 295-314 *in* A. P.
   Hendry and S. C. Stearns, editors. Evolution illuminated: salmon and their relatives. Oxford University Press, New York.
- Weir, B. S., and C. C. Cockerham. 1984. Estimating F-statistics for the analysis of population structure. Evolution 38: 1358-1370.

- Williamson, K. S., J. F. Cordes, and B. P. May. 2002. Characterization of microsatellite loci in chinook salmon (*Oncorhynchus tshawytscha*) and cross-species amplification in other salmonids. Molecular Ecology Notes 2:17-19.
- Wilmot, R.L., R.J. Everett, W.J. Spearman, R. Baccus, N.V. Varnavskaya, and S.V. Putivkin.
  1994. Genetic stock structure of western Alaska chum salmon and a comparison with Russian Far East stocks. Canadian Journal of Fisheries and Aquatic Sciences 51(Suppl. 1): 84-94.
- Winans, G. A., P. B. Aebersold, S. Urawa, and N. V. Varnavskaya. 1994. Determining continent of origin of chum salmon (*Oncorhynchus keta*) using genetic stock identification techniques: status of allozyme baseline in Asia. Canadian Journal of Fisheries and Aquatic Sciences 51(Suppl. 1): 95-113.
- Wright, J. M., and P. Bentzen. 1994. Microsatellites: genetic markers for the future. Reviews in Fish Biology and Fisheries 4:384-388.

# Deliverables

The following deliverables disseminate the findings from this study: 1) one progress report and a final report available through the AYKSSI program or from the authors; 2) an oral report of preliminary findings presented to Kawerak staff and Norton Sound residents in April 2006; 3) a poster summarizing the project findings distributed to Norton Sound communities; 4) genotype and allele frequency data in a Excel (Microsoft Office version 11) spreadsheet available from the authors and on the Conservation Genetics Laboratory Website (http://alaska.fws.gov/fisheries/genetics/data.htm; and 5) a manuscript in preparation for submission to a peer-reviewed journal.

# **Project Data**

The primary data for this study is the individual genotype data (for each locus and individual) for each population and for each cohort (Pilgrim, Snake, Eldorado, and Pikmiktalik rivers only). This data is available from the authors in an Excel spreadsheet (Microsoft Office version 11). Allele frequency data for each cohort is available in Appendices 1 and 2 of this report and on the Conservation Genetics Laboratory Website (http://alaska.fws.gov/fisheries/genetics/data.htm.
The primary author can be contacted at: Conservation Genetics Laboratory, U.S. Fish and Wildlife Service (USFWS), 1011 East Tudor Road, Anchorage AK, 99503. (907) 786-3858. jeffrey\_olsen@fws.gov.

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## **Press Release**

Data from microsatellite DNA was used to describe and evaluate genetic diversity in chum salmon from Norton Sound following the regional-level decline in abundance that began in the mid 1990's. The study provided five results that have important conservation and management implications. First, the primary factor influencing population structure in Norton Sound chum salmon is run timing. The data suggests early- and late-run populations have limited opportunity of genetic exchange, providing support for two conservation units based on run timing.

Second, location also influences population structure but not as much as run timing. Early-run populations in the Nome Subdistrict are genetically distinct from other early-run populations in Norton Sound, and early-run populations in the Nulato Hills ecoregion are distinct from early-run populations in the Seward Peninsula ecoregion. The significant but low level of geographic structure between fishing subdistricts and ecoregions provides genetic support for distinct management units but not demographically independent conservation units. Additional ecological and life-history distinctions would be needed to characterize these geographic groups as conservation units.

Third, the level of genetic diversity in chum salmon from the Nome Subdistrict is similar to that of other Norton Sound chum salmon despite the fact that the decline in abundance has been more pronounced in northern Norton Sound. This is likely due to a high level of immigration among populations as well as the subdistrict-based fishery management strategy employed by the Alaska Department of Fish and Game.

Fourth, the genetic data suggests that Norton Sound chum salmon populations are not at high risk of immediate loss of genetic diversity. Given the recent decline in abundance, however, these populations should be monitored. Periodic genetic examination will help identify trends in diversity that may compromise genetic health as well as help evaluate conservation and management actions. The data suggests the populations from the Inmachuk and Koyuk rivers are most vulnerable and warrant emphasis in monitoring.

Finally, gene flow (migration) appears to be relatively high among early-run populations. Conservation and management actions should maintain connectivity among populations because gene flow appears to be an important factor in maintaining genetic diversity. For example, land use planners should avoid habitat impacts that alter salmon migration patterns and fishery managers must be aware that harvest strategies may alter gene flow (migration) patterns as well as the escapement number.

## **Non-discrimination Statement**

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Figure 1. Map of Seward Peninsula showing population sample locations in Kotzebue and Norton sounds, commercial fishing subdistricts and ecoregions.



Figure 2. Unrooted neighbor-joining phenogram generated from the CSE distance matrix for chum salmon from Kotzebue (Kob, Inm) and Norton Sounds. Sample abbreviations are as indicated in Table 1. The open circles show population clusters from Northern (1) and Western (2) Norton Sound.



Figure 3. Scatter plot of two measures of genetic divergence versus geographic distance for chum salmon from Kotzebue and Norton sounds ( $\diamond = \text{early/late}, \bullet = \text{early/early}, \text{excluding Koyuk}$  River,  $\Box = \text{Koyuk/early}$ ). Mantel test results for isolation by distance (IBD) and time (IBT) are shown for all 15 populations. Partial Mantel test results (controlling for run time and geographic distance) are shown in parentheses. IBD<sub>12</sub> is the Mantel test result after excluding the two late-run populations and the Koyuk River. The linear regression line and least-squares equation for these 12 populations is shown.



Figure 4. Scatter plot of two measures of genetic divergence versus geographic distance for chum salmon from Norton Sound (NS,  $\Diamond = Agiapuk/early$ ,  $\Box = Koyuk/early$ ,  $\blacklozenge = early/early$ ). Mantel test results for isolation by distance and time are shown for the 13 populations (IBD<sub>13</sub>, IBT<sub>13</sub>). Partial Mantel test results (controlling for time and geographic distance) are shown in parentheses IBD<sub>11</sub> is the Mantel test result after excluding the Agiapuk and Koyuk populations. The linear regression line and least-squares equation for these 11 populations is shown.



Figure 5. Estimates of the effective number of breeders ( $\hat{N}_b$ ) for 15 chum salmon populations using the linkage-disequilibrium method. Sample abbreviations are as indicated in Table 1.

Sample	Abbr.	RT	Year	Date	п
Kotzebue Sound					
Kobuk R	Kob	Е	2005	7/18-8/05	200
Inmachuk R	Inm	L	2005	8/08-8/23	200
Norton Sound					
Agiapuk R	Agi	L	2005	7/25-7/30	184
Pilgrim R	Pil	Е	2004	7/04-7/20	200
			2005	6/29-7/27	200
Snake R	Sna	Е	2004	7/03-7/19	200
			2005	6/29-7/26	200
Nome R	Nom	Е	2005	7/15-8/01	200
Eldorado R	Eld	Е	2004	7/02-7/17	200
			2005	6/28-7/29	200
Fish R	Fis	Е	2005	7/15-7/21	50
Niukluk R	Niu	Е	2005	7/03-8/03	150
Kwiniuk R	Kwi	Е	2005	7/19-7/24	200
Koyuk R	Koy	Е	2005	7/30-7/31	46
Ungalik R	Ung	Е	2005	7/17-7/19	54
Shaktoolik R	Sha	Е	2005	7/23	200
Unalakleet R	Una	Е	2005	7/20-8/02	200
Pikmiktalik R	Pik	Е	2004	7/05-8/03	200
			2005	7/02-7/28	200

Table 1. Summary of chum salmon population samples collected from Kotzebue and Norton Sound in  $2004^{a}$  and  $2005^{b}$ .

<sup>a</sup>the 2004 samples were collected as part of other projects not funded by the AYK-SSI. <sup>b</sup>Abbr. – sample abbreviation; RT – relative adult return timing, E – early, L – late; n – sample size.

							Po	opulatic	ons						
Locus	Kob	Inm	Agi	Pil	Sna	Nom	Eld	Niu	Fis	Kwi	Koy	Ung	Sha	Una	Pik
Oki23															
n	89	90	96	90	87	89	92	77	48	88	42	48	93	86	91
$H_e$	0.21	0.25	0.24	0.25	0.21	0.18	0.18	0.22	0.28	0.25	0.29	0.17	0.26	0.24	0.31
$H_o$	0.19	0.29	0.21	0.23	0.23	0.19	0.16	0.25	0.31	0.25	0.24	0.19	0.29	0.23	0.34
$A_r$	2.6	2.4	2.9	2.9	3.0	3.0	3.3	2.9	3.0	3.6	3.0	2.7	3.6	3.0	3.0
Oke8															
n	84	87	93	89	86	89	90	76	48	88	42	47	92	85	89
$H_e$	0.11	0.01	0.02	0.07	0.08	0.07	0.05	0.09	0.08	0.08	0.05	0.10	0.10	0.12	0.16
$H_o$	0.10	0.01	0.02	0.07	0.08	0.07	0.06	0.09	0.08	0.08	0.05	0.11	0.11	0.11	0.15
$A_r$	2.0	1.4	1.6	2.3	2.6	2.3	1.9	2.4	2.0	2.0	2.0	2.0	2.0	2.0	2.0
Oke3															
n	82	85	91	85	85	88	88	72	46	86	40	47	89	80	84
$H_e$	0.77	0.72	0.80	0.77	0.79	0.74	0.76	0.76	0.75	0.74	0.73	0.75	0.78	0.73	0.75
$H_o$	0.72	0.67	0.68*	0.76	0.79	0.77	0.75	0.85	0.76	0.76	0.73	0.83	0.79	0.64	0.80
$A_r$	7.2	6.3	6.7	6.7	6.5	7.0	7.2	6.9	5.9	6.0	5.8	7.0	7.5	7.2	6.9
Oke4															
n	80	87	91	87	86	88	89	75	46	78	40	46	86	81	85
$H_e$	0.05	0.02	0.11	0.07	0.20	0.13	0.17	0.14	0.15	0.10	0.10	0.08	0.12	0.10	0.02
$H_o$	0.05	0.02	0.11	0.07	0.17	0.14	0.18	0.15	0.15	0.10	0.10	0.09	0.13	0.07	0.02
$A_r$	2.2	1.8	2.6	2.5	3.0	2.7	2.9	2.8	3.6	2.6	2.9	2.0	2.9	2.7	1.6
Ots2.1L															
n	88	88	97	89	88	90	92	77	48	87	42	48	94	85	85
$H_e$	0.07	0.06	0.03	0.11	0.11	0.10	0.14	0.13	0.17	0.11	0.18	0.12	0.09	0.11	0.10
$H_o$	0.07	0.06	0.03	0.11	0.11	0.10	0.15	0.14	0.19	0.11	0.14	0.13	0.10	0.09	0.11
$A_r$	1.9	1.9	1.7	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0
<i>Ots2.1U</i>															
п	89	88	97	87	88	88	87	76	48	84	42	47	95	84	83
$H_e$	0.66	0.37	0.63	0.62	0.61	0.61	0.61	0.62	0.58	0.57	0.52	0.63	0.57	0.57	0.57
$H_o$	0.69	0.36	0.67	0.67	0.61	0.53	0.59	0.57	0.67	0.55	0.55	0.51	0.58	0.55	0.57
$A_r$	5.2	4.6	4.7	3.9	3.0	4.8	3.4	3.8	4.4	3.8	3.8	6.0	3.9	4.7	3.9
Okel l															
п	84	83	94	88	88	88	86	74	47	78	41	46	88	79	86
$H_e$	0.63	0.70	0.58	0.47	0.57	0.61	0.59	0.58	0.61	0.52	0.56	0.49	0.55	0.61	0.51
$H_o$	0.55	0.66	0.56	0.49	0.51	0.59	0.60	0.62	0.55	0.50	0.41	0.50	0.48	0.53	0.45
$A_r$	6.0	5.7	5.4	5.3	5.6	6.0	5.4	5.0	5.0	4.8	5.8	4.9	5.5	5.0	4.9
Ots103															
n	87	86	79	88	88	80	89	41	45	83	33	48	81	83	88
$H_e$	0.94	0.88	0.93	0.94	0.94	0.95	0.94	0.94	0.95	0.94	0.95	0.95	0.95	0.95	0.95
$H_o$	0.94	0.87	0.90	0.97	0.95	0.93	0.94	0.90	0.96	0.93	1.00	0.98	0.96	0.93	0.95
$A_r$	23.0	17.9	20.8	23.2	21.5	23.8	21.5	22.0	25.1	22.4	25.0	25.9	23.0	24.7	25.1

Table 2. Genetic diversity at 20 microsatellite loci in 15 chum salmon population samples from Kotzebue and Norton Sounds: n = sample size,  $H_e =$  expected heterozygosity,  $H_o =$  observed heterozygosity<sup>a</sup>,  $A_r =$  allele richness<sup>b</sup>. Sample abbreviations are as indicated in Table 1.

Table 2. cont.

	Populations														
Locus	Kob	Inm	Agi	Pil	Sna	Nom	Eld	Niu	Fis	Kwi	Koy	Ung	Sha	Una	Pik
Oki1L															
n	89	91	96	90	88	89	92	77	45	82	43	49	94	86	92
$H_e$	0.35	0.51	0.24	0.37	0.34	0.38	0.42	0.41	0.42	0.31	0.49	0.41	0.33	0.41	0.41
$H_o$	0.37	0.51	0.23	0.33	0.38	0.43	0.33	0.35	0.44	0.33	0.60	0.39	0.33	0.41	0.39
$A_r$	2.8	2.6	2.7	2.9	2.8	3.0	2.9	3.0	3.0	3.0	3.0	2.7	3.0	2.9	2.8
Oki1U															
n	87	88	96	88	89	84	88	74	45	79	41	48	92	83	88
$H_e$	0.92	0.78	0.89	0.92	0.90	0.92	0.92	0.91	0.92	0.89	0.91	0.91	0.92	0.92	0.92
$H_o$	0.91	0.78	0.89	0.90	0.85	0.90	0.90	0.96	0.89	0.89	0.98	0.98	0.91	0.93	0.94
$A_r$	15.5	11.6	13.3	15.6	14.8	15.7	14.1	15.1	15.3	14.2	16.1	15.3	16.2	16.2	15.4
Oki100															
n	88	91	95	91	90	88	93	76	48	88	43	49	93	87	91
$H_e$	0.90	0.77	0.88	0.90	0.91	0.92	0.90	0.90	0.92	0.92	0.89	0.90	0.90	0.89	0.91
$H_o$	0.85	0.78	0.91	0.93	0.92	0.94	0.92	0.97	0.94	0.86	0.84	0.84	0.85	0.92	0.92
$A_r$	15.8	11.1	14.5	15.0	15.6	18.2	17.1	15.6	18.8	16.8	16.4	15.7	15.6	16.5	16.5
Oki2															
п	88	86	86	87	88	89	91	73	45	85	42	48	90	86	91
$H_e$	0.89	0.74	0.89	0.89	0.88	0.90	0.90	0.90	0.89	0.90	0.91	0.88	0.91	0.90	0.90
$H_o$	0.92	0.72	0.92	0.91	0.89	0.87	0.90	0.92	0.89	0.87	0.95	0.85	0.87	0.90	0.87
$A_r$	11.2	10.7	11.2	12.1	11.3	12.8	11.7	11.7	12.6	12.4	11.6	12.9	11.6	12.5	10.7
Omy101															
n	88	89	95	90	91	89	93	77	48	86	43	49	94	86	91
$H_e$	0.92	0.93	0.89	0.90	0.94	0.92	0.93	0.91	0.93	0.94	0.87	0.92	0.93	0.92	0.91
$H_o$	0.89	0.93	0.87	0.89	0.92	0.93	0.94	0.90	1.00	0.90	0.88	0.94	0.94	0.93	0.89
$A_r$	18.0	17.9	16.3	18.9	19.1	18.7	18.2	17.8	19.3	20.4	17.1	18.9	19.5	18.1	16.9
One101			2.4					- /		~ <b>-</b>		10	~ -	0.6	
n	88	90	96	91	88	89	91	76	47	87	41	49	95	86	90
H <sub>e</sub>	0.89	0.89	0.89	0.90	0.88	0.91	0.90	0.87	0.89	0.89	0.83	0.92	0.91	0.90	0.92
$H_o$	0.84	0.89	0.85	0.84	0.92	0.88	0.89	0.87	0.98	0.92	0.76	0.98	0.88	0.90	0.90
$A_r$	18.1	14.0	15.3	18.7	16.9	18.9	19.7	16.7	18.5	18.0	16.4	18.8	18.9	19.1	19.4
One102	00	0.1	07	0.0	01	0.0	0.0	70	40	0.0	41	47	0.5	0.4	01
n	89	91	9/	90	91	90	89	/8	48	80	41	4/	95	84	91
H <sub>e</sub>	0.90	0.89	0.91	0.91	0.90	0.91	0.91	0.91	0.89	0.90	0.92	0.91	0.91	0.92	0.91
$H_o$	0.90	0.8/	0.86	0.84	0.89	0.93	0.83	0.90	0.90	0.86	0.88	0.96	0.88	0.88	0.89
$A_r$	13.2	12.5	13.2	14.7	13.8	14.3	13.0	13.1	12.7	11.7	14.5	13.9	13.0	14.3	14.2
One104	00	0.1	07	00	00	00	02	77	16	07	26	47	0.4	0.1	01
n	88	91	9/	90	90	90	93	//	46	8/	36	4/	94	81	91
H <sub>e</sub>	0.93	0.89	0.93	0.93	0.94	0.94	0.94	0.92	0.95	0.94	0.91	0.93	0.93	0.93	0.93
$H_o$	0.97	0.89	0.90	0.94	0.94	0.89	0.95	0.95	0.96	0.98	0.97	0.96	0.94	0.98	0.92
$A_r$	18.3	14.4	1/.4	19.5	18./	19.7	20.2	19.6	20.1	18.3	18.6	18.1	18.2	18.7	19.4
One114	07	0.1	0.6	00	0.0	00	02	76	40	07	42	40	0.4	07	07
n	87	91	96	90	88	89	93	/6	48	8/	43	49	94	86	8/
H <sub>e</sub>	0.92	0.89	0.94	0.93	0.92	0.93	0.93	0.92	0.93	0.92	0.92	0.92	0.93	0.95	0.93
$H_o$	0.92	0.89	0.92	0.91	0.92	0.98	0.97	0.89	0.90	0.95	0.95	0.92	U.87	0.94	0.92
$A_r$	18.1	17.5	18.0	18.3	16.5	19.4	17.3	18.6	17.3	17.3	18.4	15.1	17.0	18.6	17.2

Table 2. cont.

							Pe	opulatio	ons						
Locus	Kob	Inm	Agi	Pil	Sna	Nom	Eld	Niu	Fis	Kwi	Koy	Ung	Sha	Una	Pik
Ots3															
n	88	89	97	90	91	88	93	77	47	81	41	49	95	85	90
$H_e$	0.71	0.78	0.80	0.73	0.79	0.77	0.77	0.77	0.71	0.79	0.80	0.75	0.78	0.76	0.77
$H_o$	0.69	0.80	0.86	0.66	0.79	0.77	0.78	0.77	0.72	0.78	0.76	0.88	0.80	0.78	0.72
$A_r$	8.0	9.6	10.4	9.5	11.4	10.5	10.1	9.8	10.6	11.6	11.1	11.8	11.5	10.4	9.4
Otsg68															
n	89	87	96	90	91	89	92	77	48	86	43	49	93	85	90
$H_e$	0.93	0.90	0.93	0.95	0.94	0.95	0.95	0.93	0.94	0.95	0.95	0.93	0.94	0.94	0.94
$H_o$	0.97	0.87	0.94	0.96	0.95	0.96	0.96	0.97	0.98	0.92	0.93	0.92	0.97	0.95	0.96
$A_r$	23.7	21.9	21.4	24.3	23.5	25.5	24.7	21.9	26.0	23.6	24.1	26.1	24.0	22.9	22.3
Ssa419															
n	87	89	97	90	90	90	93	77	48	88	43	48	93	86	89
$H_e$	0.86	0.83	0.88	0.85	0.87	0.85	0.85	0.85	0.86	0.88	0.87	0.87	0.86	0.83	0.87
$H_o$	0.82	0.80	0.87	0.86	0.90	0.80	0.85	0.84	0.85	0.80	0.81	0.81	0.88	0.74	0.88
$A_r$	10.4	9.7	11.4	9.6	10.9	10.7	10.5	10.3	9.6	12.8	9.9	11.4	10.6	10.0	11.9
Avg															
n	87	88	94	89	89	88	91	74	47	84	41	48	92	84	89
$\overline{H}_{e}$	0.68	0.64	0.67	0.67	0.69	0.68	0.69	0.68	0.69	0.68	0.68	0.68	0.68	0.68	0.68
$\overline{H}_{o}$	0.67	0.63	0.66	0.67	0.69	0.68	0.68	0.69	0.71	0.67	0.68	0.69	0.68	0.67	0.68
$\overline{A}_{-}$	11.2	9.8	10.6	11.4	11.1	11.9	11.4	11.1	11.7	11.3	11.4	11.7	11.5	11.6	11.3

<sup>a</sup>A bold value indicates P < 0.05 that the sample/locus conforms to Hardy-Weinberg expectation. An asterisk (\*) indicates *P*-value was judged significant when the  $\alpha$ -level (0.05) was adjusted for simultaneous tests (see text). <sup>b</sup>Allele richness estimates are based on a minimum sample size of 33 diploid individuals.

Sample	Year	Cohort	Abbr	п	$\overline{A}_r$	$\overline{H}_e$	$\overline{H}_{o}$	f
Eldorado R.	2004-05	1999	99Eld	85	13.2	0.68	0.68	-0.002
		2000	00Eld	108	13.6	0.69	0.69	-0.007
		2001	01Eld	139	13.1	0.69	0.68	0.010
Pilgrim R.	2004-05	1999	99Pil	90	13.5	0.69	0.68	0.016
0		2000	00Pil	83	13.7	0.68	0.67	0.024
		2001	01Pil	134	13.3	0.68	0.68	0.004
Snake R.	2004-05	1999	99Sna	100	12.6	0.69	0.68	0.014
		2000	00Sna	116	12.5	0.68	0.68	0.004
		2001	01Sna	139	13.0	0.69	0.69	-0.002
Pikmiktalik R.	2004-05	1999	99Pik	75	13.6	0.69	0.68	0.002
		2000	00Pik	86	13.2	0.68	0.68	0.002
		2001	01Pik	189	13.2	0.69	0.69	0.003
ax 7 1	0.1	. 1 1	1 0		411		1	

Table 3. Genetic diversity in chum salmon cohorts used to estimate  $N_b$  and  $N_e^{a,b}$ .

<sup>a</sup>Year – sample year; Cohort – individuals of same age; Abbr – sample abbreviation; n – sample size;  $\overline{A}_r$  – allele richness per locus;  $\overline{H}_e$  – expected heterozygosity per locus;  $\overline{H}_o$  – observed heterozygosity per locus; f – index of heterozygote deficit. A bold value indicates P < 0.05 that the sample conforms to Hardy-Weinberg expectation.

<sup>b</sup>allele richness estimates are based on a minimum sample size of 70 diploid individuals.

Table 4. Comparison of genetic diversity [allele richness  $(A_r)$ , gene diversity  $(H_s)$ , and  $F_{st}$ ] among groups of N populations for three grouping strategies. The *P*-value for each pair of estimates indicates the probability that the true values are the same.

Grouping					
Strategy	Group	N	$A_r$	$H_s$	$F_{\rm st}$
Run Timing <sup>a</sup>	Late run	2	10.2	0.655	0.054
(all samples)	Early run	13	11.4	0.681	0.002
		Р	0.020	0.034	0.028
Ecoregion <sup>b</sup>	Seward P.	7	11.4	0.681	0.001
(NS only)	Nulato Hills	4	11.5	0.683	0.001
		Р	0.880	0.898	0.974
Fishing district <sup>c</sup>	Nome SD	3	11.5	0.686	0.001
(NS only)	Other SD	8	11.4	0.680	0.001
		Р	0.890	0.568	0.968

<sup>a</sup>Late run (Inm, Agi); Early run (Kob, Pil, Sna, Nom, Eld, Niu, Fis, Kwi, Koy, Ung, Sha, Una, Pik).

<sup>b</sup>Seward Peninsula (Pil, Sna, Nom, Eld, Niu, Fis, Kwi); Nulato Hills (Ung, Sha, Una, Pik).

<sup>c</sup>Two groups: Nome Subdistrict (Sna, Nom, Eld); all other subdistricts (Pil, Niu, Fis, Kwi, Ung, Sha, Una, Pik).

Table 5. Comparison of genetic diversity [allele richness $(A_r)$ ,
gene diversity $(H_s)$ , and $F_{st}$ ] among Norton Sound/Kotzebue
Sound (NS/KS) and Yukon River chum salmon (data from B.
Flannery). The <i>P</i> -value for each pair of estimates indicates the
probability that the true values are the same

Grouping	Region	N	$A_r$	$H_s$	$F_{\rm st}$
Overall	NS/KS	15	9.1	0.677	0.011
	Yukon River	29	8.0	0.665	0.017
		Р	0.010	0.010	0.550
Early Run	NS/KS	13	9.2	0.681	0.002
	Yukon River	15	8.6	0.674	0.007
		Р	0.050	0.262	0.648
Late Run	NS/KS	2	8.2	0.655	0.054
	Yukon River	14	7.4	0.658	0.015
		Р	0.250	0.790	0.280

Table 6. Hierarchical gene diversity	analysis of chum salmon population samples using three grouping
strategies. An asterisk (*) denotes P	< 0.05 the value is not greater than zero; ct = between groups; sc =
within groups; NS = Norton Sound.	
Crowning	Dereant

Grouping			Percent			
Strategy	Source of variation	$\sigma^2$	of total	$F_{\rm st}$	$F_{\rm ct}$	$F_{\rm sc}$
Run Timing <sup>a</sup>	Total	6.928	100.00			
(all samples)	Within populations	6.781	97.88			
	Between populations	0.147	2.13	0.0213*		
	Between groups	0.099	1.43		0.0143*	
	Between populations within groups	0.049	0.70			0.0071*
Ecoregion <sup>b</sup>	Total	6.837	100.00			
(NS only)	Within populations	6.826	99.84			
	Between populations	0.011	0.16	0.0016*		
	Between groups	0.003	0.04		0.0004*	
	Between populations within groups	0.008	0.11			0.0011*
Fishing district <sup>c</sup>	Total	6.837	100.00			
(NS only)	Within populations	6.826	99.83			
	Between populations	0.012	0.17	0.0017*		
	Between groups	0.004	0.06		0.0006*	
	Between populations within groups	0.007	0.11			0.0011*

<sup>a</sup>Two groups: late run (Inm, Agi); early run (Kob, Pil, Sna, Nom, Eld, Niu, Fis, Kwi, Koy, Ung, Sha, Una, Pik).

<sup>b</sup>Two groups: Seward Peninsula (Pil, Sna, Nom, Eld, Niu, Fis, Kwi); Nulato Hills (Ung, Sha, Una, Pik). <sup>c</sup>Two groups: Nome Subdistrict (Sna, Nom, Eld); all other subdistricts (Pil, Niu, Fis, Kwi, Ung, Sha, Una, Pik).

Table 7. Pairwise estimates of  $F_{st}$  (below diagonal) and *G*-test results (above diagonal) for chum salmon population samples from Kotzebue (Kob, Inm) and Norton Sounds. Sample abbreviations are as indicated in Table 1. An asterisk denotes P < 0.05 of allele frequency homogeneity. A double asterisk denotes  $P \le 0.00048$ , the table-wide  $\alpha$ -level. NS denotes not significant (P > 0.05).

	Kob	Inm	Agi	Pil	Sna	Nom	Eld	Niu	Fis	Kwi	Koy	Ung	Sha	Una	Pik
Kob		**	**	NS	**	*	**	*	*	**	**	*	*	*	**
Inm	0.055		**	**	**	**	**	**	**	**	**	**	**	**	**
Agi	0.008	0.055		**	**	**	**	**	**	**	**	**	**	**	**
Pil	0.003	0.056	0.010		**	*	*	NS	NS	*	**	NS	*	*	**
Sna	0.004	0.053	0.009	0.004		*	*	*	*	**	**	*	**	**	**
Nom	0.003	0.053	0.009	0.001	0.001		NS	NS	NS	NS	**	NS	NS	NS	**
Eld	0.004	0.049	0.011	0.003	0.001	-0.001		NS	*	*	**	*	*	*	**
Niu	0.003	0.055	0.010	0.001	0.001	-0.001	-0.001		NS	NS	**	NS	*	NS	*
Fis	0.003	0.053	0.011	0.001	0.004	0.000	0.001	0.000		NS	*	NS	NS	NS	*
Kwi	0.006	0.059	0.010	0.002	0.003	0.000	0.002	0.002	0.002		**	NS	*	*	*
Koy	0.008	0.051	0.016	0.007	0.010	0.008	0.009	0.008	0.005	0.010		*	**	**	**
Ung	0.003	0.054	0.011	0.001	0.004	-0.001	0.001	0.000	0.001	0.002	0.008		NS	NS	*
Sha	0.003	0.051	0.008	0.001	0.002	-0.001	0.001	0.001	0.000	0.000	0.008	0.001		NS	*
Una	0.004	0.048	0.011	0.002	0.004	0.000	0.001	0.000	0.001	0.002	0.009	0.001	0.000		*
Pik	0.006	0.051	0.013	0.003	0.005	0.001	0.002	0.002	0.002	0.003	0.010	0.001	0.001	0.001	

Table 8. Proportion of chum salmon from Kotzebue (Kob, Inm) and Norton Sounds that are assigned to each river. Values in bold are the proportion assigned to their sample river. Abbreviations are as indicated in Table 1. "unk" denotes the proportion of individual genotypes with frequencies less than 5% of all genotypes in the assigned population.

	Assi	gned t	0													
Sample	Kob	Inm	Agi	Pil	Sna	Nom	Eld	Niu	Fis	Kwi	Koy	Ung	Sha	Una	Pik	unk
Kob	0.20	0.00	0.04	0.03	0.02	0.04	0.08	0.07	0.04	0.03	0.04	0.04	0.03	0.04	0.08	0.18
Inm	0.01	0.73	0.01	0.01	0.02	0.02	0.01	0.00	0.02	0.00	0.01	0.00	0.00	0.01	0.02	0.12
Agi	0.05	0.00	0.46	0.05	0.05	0.02	0.05	0.01	0.00	0.02	0.01	0.02	0.04	0.03	0.02	0.15
Pil	0.09	0.00	0.01	0.09	0.04	0.09	0.08	0.05	0.08	0.02	0.00	0.05	0.05	0.10	0.13	0.11
Sna	0.07	0.00	0.03	0.02	0.24	0.09	0.10	0.03	0.01	0.05	0.01	0.01	0.02	0.05	0.07	0.19
Nom	0.04	0.00	0.01	0.09	0.06	0.09	0.09	0.04	0.08	0.06	0.02	0.07	0.07	0.09	0.02	0.18
Eld	0.06	0.00	0.03	0.09	0.12	0.06	0.10	0.10	0.05	0.06	0.02	0.04	0.04	0.03	0.03	0.15
Niu	0.08	0.00	0.01	0.06	0.08	0.06	0.12	0.13	0.08	0.08	0.03	0.06	0.08	0.05	0.03	0.06
Fis	0.02	0.00	0.00	0.10	0.06	0.08	0.02	0.19	0.02	0.02	0.02	0.04	0.08	0.10	0.08	0.15
Kwi	0.03	0.00	0.01	0.05	0.06	0.06	0.08	0.05	0.09	0.22	0.00	0.02	0.08	0.06	0.09	0.11
Koy	0.07	0.00	0.00	0.02	0.05	0.05	0.05	0.00	0.07	0.07	0.19	0.05	0.05	0.02	0.07	0.26
Ung	0.06	0.00	0.00	0.08	0.06	0.06	0.08	0.08	0.02	0.06	0.02	0.08	0.06	0.08	0.12	0.12
Sha	0.06	0.00	0.01	0.04	0.06	0.12	0.06	0.03	0.02	0.04	0.03	0.05	0.17	0.07	0.06	0.16
Una	0.05	0.00	0.01	0.11	0.05	0.05	0.08	0.05	0.05	0.05	0.01	0.03	0.08	0.13	0.10	0.16
Pik	0.03	0.00	0.01	0.05	0.03	0.04	0.09	0.09	0.03	0.04	0.00	0.08	0.10	0.04	0.21	0.15

Table 9. Genetic estimates of the effective number of breeders per year (  $\hat{N}_b$  ) and effective population size per generation ( $\hat{N}_e$ ) using the temporal method of Waples (1990,  $\hat{N}_{b(w)}$ ,  $\hat{N}_{e(w)}$ ) and Wang and Whitlock (2003,  $\hat{N}_{b(ml)}, \ \hat{N}_{e(ml)})^{a}.$ 

			Isol	ation		Migration	
Sample (cohort)	g <sup>b</sup>	$\overline{N}$ c	<i>Ñ<sub>b(w)</sub></i> (95%CI)		<i>Ñ<sub>b(ml)</sub></i> (95%CI)	<i>Ñ<sub>e(ml)</sub></i> (95%CI)	<i>m̂<sub>(ml)</sub></i> (95%CI)
Eldorado R.	4.0.5	0156	1010	5204	100		0.04
(99-01)	4.35	9156	(529 - inf)	5304 (2300 - inf)	133 (106 - 170)	579 (461 - 740)	0.26 (0.20 - 0.34)
Pilgrim R.		L					
(99-01)	4.40	1739 <sup>ª</sup>	2286 (646 - inf)	10058 (2844 - inf)	179 (133 - 252)	788 (585 - 1108)	0.23 (0.16 - 0.31)
Snake R.							
(99-01)	4.35	1526	1709 (644 - inf)	7433 (2803 - inf)	217 (160 - 311)	944 (696 - 1353)	0.09 (0.06 - 0.14)
Pikmiktalik R.							
(99-01)	4.35	N/A	1874 (620 - inf)	8150 (2699 - inf)	168 (128 - 229)	731 (557 - 996)	0.17 (0.12 - 0.24)

<sup>a</sup>The method of Waples (1990) assumes populations are isolated. The method of Wang and Whitlock (2003) allows estimation of  $N_b$  assuming isolation or migration. When migration is assumed, *m* (the immigration fraction) is also estimated.

<sup>b</sup>mean generation time in years <sup>c</sup>  $\overline{N}$  – arithmetic mean adult count per year. <sup>d</sup>data available for 1999 and 2000 only.

Appendix 1. Table of allele frequencies at each locus for each population. Abbreviations are as indicated in Table 1. A dash indicates the allele was not present.

Locus																
∖allele		Kob	Inm	Agi	Pil	Sna	Nom	Eld	Niu	Fis	Kwi	Koy	Ung	Sha	Una	Pik
Oki23																
1	117	0.139	0.107	0.120	0.111	0.063	0.056	0.054	0.097	0.073	0.085	0.143	0.083	0.081	0.093	0.110
1	129			0.010										0.011		
1	137	0.856	0.882	0.865	0.861	0.885	0.904	0.902	0.877	0.844	0.864	0.833	0.906	0.855	0.866	0.819
1	139							0.005			0.011					
1	141	0.006	0.011	0.005	0.028	0.052	0.039	0.038	0.026	0.083	0.040	0.024	0.010	0.054	0.041	0.071
Oke8																
1	185	0.006	0.060	0.011	0.028	0.023	0.028	0.028	0.039	0.042	0.040	0.024	0.053	0.054	0.065	0.084
]	197	0.994	0.940	0.989	0.966	0.959	0.966	0.972	0.954	0.958	0.960	0.976	0.947	0.946	0.935	0.916
]	199				0.006	0.017	0.006		0.007							
01.0																
Oke3	227		0.010	0.016	0.007		0.011	0.011	0.007		0.007			0.000	0.005	0.010
4	237		0.012	0.016	0.006		0.011	0.011	0.007		0.006			0.022	0.025	0.012
4	250	0.018	0.049	0.0/1	0.059	0.035	0.045	0.051	0.049	0.033	0.076	0.063	0.043	0.062	0.031	0.095
4	263	0.088	0.329	0.269	0.335	0.24/	0.284	0.176	0.250	0.326	0.285	0.400	0.298	0.2/5	0.256	0.244
4	2/0	0.24/	0.079	0.2/5	0.135	0.194	0.09/	0.119	0.111	0.098	0.140	0.038	0.0/4	0.140	0.100	0.101
4	289	0.170	0.293	0.181	0.288	0.294	0.398	0.392	0.3/5	0.304	0.390	0.250	0.383	0.331	0.419	0.393
-	50Z	0.429	0.185	0.104	0.141	0.1/0	0.130	0.210	0.100	0.217	0.093	0.238	0.11/	0.118	0.131	0.131
-	213	0.029	0.043	0.082	0.029	0.041	0.011	0.023	0.042	0.022	0.012	0.013	0.033	0.028	0.031	0.012
-	520	0.012	0.012		0.000	0.012	0.017	0.017	0.007				0.052	0.017	0.000	0.012
Oke4																
Oke4	228		0.006													
	230	0.006	0.000	0 044	0.011	0 064	0.051	0.062	0.053	0.022	0.038	0.025		0.035	0.031	0.012
	246	0.000	0.017	0.945	0.966	0.004	0.031	0.002	0.035	0.022	0.050	0.025	0.957	0.035	0.051	0.988
-	248	0.006		0.011	0.023	0.047	0.017	0.028	0.020	0.043	0.013	0.025	0.043	0.029	0.019	
-	250									0.011						
-										0.011						
Ots2.1	L															
1	112	0.028	0.034	0.015	0.056	0.057	0.050	0.076	0.071	0.094	0.057	0.095	0.063	0.048	0.059	0.053
1	130	0.972	0.966	0.985	0.944	0.943	0.950	0.924	0.929	0.906	0.943	0.905	0.938	0.952	0.941	0.947
Ots2.1	U															
1	142	0.790	0.483	0.515	0.529	0.528	0.557	0.540	0.533	0.583	0.595	0.655	0.521	0.595	0.601	0.608
]	146		0.011													
]	148	0.011	0.011	0.005			0.011						0.011		0.012	
1	150			0.010									0.011		0.006	0.024
]	152	0.074	0.180	0.191	0.213	0.205	0.176	0.195	0.224	0.167	0.167	0.131	0.138	0.168	0.190	0.175
1	154	0.057	0.275	0.258	0.236	0.267	0.227	0.259	0.224	0.229	0.226	0.202	0.287	0.221	0.179	0.193
]	156						0.006			0.010	0.006		0.011	0.005		
1	158	0.068	0.039	0.021	0.023		0.023	0.006	0.020	0.010	0.006	0.012	0.021	0.011	0.012	

Oke11

89 0.024 0.060 0.053 0.074 0.063 0.091 0.099 0.081 0.085 0.096 0.085 0.043 0.051 0.070 0.052 91 0.024 0.054 0.011 0.045 0.063 0.063 0.058 0.074 0.053 0.032 0.085 0.109 0.034 0.076 0.076

Appendix 1 cont.

Locus															
\allele	Kob	Inm	Agi	Pil	Sna	Nom	Eld	Niu	Fis	Kwi	Koy	Ung	Sha	Una	Pik
93	0.120	0.274	0.223	0.136	0.159	0.153	0.186	0.155	0.266	0.179	0.134	0.130	0.205	0.190	0.157
95	0.458	0.542	0.601	0.710	0.625	0.597	0.605	0.622	0.564	0.667	0.646	0.696	0.636	0.589	0.680
97	0.120	0.054	0.090	0.028	0.080	0.080	0.047	0.068	0.032	0.026	0.037	0.022	0.063	0.076	0.035
99	0.253	0.012	0.021	0.006	0.011	0.011	0.006				0.012		0.011		
101		0.006				0.006									
Ots103															
92		0.011	0.032	0.006	0.006		0.017	0.012					0.006	0.006	
96	0.017	0.017	0.070	0.011	0.028	0.013	0.011		0.056	0.012				0.012	0.006
100	0.285	0.006	0.044	0.006	0.034	0.056	0.011	0.012			0.030	0.031	0.037	0.048	0.023
104	0.070	0.029	0.032	0.045	0.045	0.038	0.039	0.061	0.078	0.012	0.015	0.042	0.043	0.078	0.017
108	0.070	0.092	0.070	0.091	0.091	0.094	0.090	0.098	0.067	0.048	0.015	0.083	0.043	0.060	0.045
112	0.012	0.034	0.006	0.051	0.051	0.056	0.079	0.061	0.100	0.048	0.106	0.031	0.062	0.036	0.051
116	0.035	0.098	0.082	0.085	0.068	0.063	0.045	0.085	0.089	0.072	0.061	0.052	0.105	0.072	0.057
120	)	0.029	0.025	0.028		0.056	0.045		0.022	0.018		0.031	0.025	0.030	0.011
124	0.017	0.017	0.013	0.006	0.017	0.025	0.011		0.011	0.006	0.015	0.021	0.006	0.012	0.023
128	0.012	0.006		0.011	0.006	0.006		0.012	0.022		0.030		0.019	0.012	0.051
132	0.006	0.011		0.011	0.011	0.006	0.006		0.022	0.012		0.010	0.006	0.012	
136	,			0.006		0.006	0.006				0.015				
140	)	0.011		0.006		0.006									0.006
144		0.011	0.006	0.017	0.011			0.012	0.022	0.006	0.091	0.010	0.012	0.024	0.034
148			0.019	0.011	0.011	0.006	0.006			0.012	0.015		0.006	0.018	0.023
152	0.035	0.017		0.017	0.006	0.006	0.022		0.022	0.012	0.015	0.031	0.037	0.030	0.023
156	0.006	0.006			0.011		0.017	0.012		0.018		0.021	0.006	0.012	0.011
160	0.076	0.006	0.006	0.045	0.017	0.019	0.011	0.037	0.011	0.042		0.010	0.012	0.024	0.011
164	0.006	0.011	0.006		0.006	0.013		0.012	0.011	0.012	0.015	0.021	0.012	0.006	
168	0.023	0.080	0.057	0.040	0.080	0.044	0.034	0.037	0.022	0.072	0.045	0.021	0.025	0.024	0.017
172	0.076	0.075	0.038	0.102	0.097	0.050	0.084	0.061	0.056	0.078	0.091	0.083	0.117	0.084	0.114
176	0.081	0.103	0.108	0.085	0.114	0.075	0.124	0.146	0.122	0.114	0.091	0.125	0.074	0.072	0.068
180	0.029	0.098	0.165	0.108	0.085	0.056	0.096	0.073	0.067	0.127	0.045	0.094	0.049	0.108	0.097
184	0.017	0.069	0.057	0.040	0.063	0.100	0.067	0.061	0.011	0.072	0.061	0.073	0.056	0.054	0.080
188	0.012	0.029	0.006	0.028	0.017	0.056	0.056		0.033	0.042	0.045	0.010	0.080	0.042	0.040
192	0.081	0.011	0.051	0.017	0.006	0.025	0.028	0.061	0.022	0.030	0.061	0.042	0.019	0.012	0.034
196	0.017	0.023		0.011	0.034	0.031			0.011	0.018	0.015	0.021	0.037	0.030	0.028
200	0.006	0.040	0.013	0.040	0.011	0.013	0.034	0.037	0.022	0.048	0.045	0.031	0.049	0.012	0.023
204		0.017	0.032		0.011	0.013		0.037	0.022	0.006		0.031		0.018	0.011
208	0.006	0.006		0.023		0.006	0.006	0.024	0.011	0.006	0.015	0.010	0.006	0.018	0.017
212			0.006	0.011		0.006	0.011		0.022	0.006	0.015	0.010	0.006	0.006	0.011
216		0.006		0.011		0.006				0.018		0.010	0.012		0.006
220	0.006	0.006		0.006				0.012		0.006		0.010	0.012	0.012	0.028
224		0.017	0.019	0.023	0.045	0.025	0.022	0.012	0.022	0.018	0.030	0.010	0.019		0.011
228		0.006	0.025		0.011	0.019	0.017	0.012		0.006		0.010		0.006	0.011
232			0.006		0.006	0.006	0.006	0.012	0.011						0.011
236	,										0.015				
240	)		0.006									0.010		0.006	
244									0.011						

Appendix 1 cont.

Locus																
\allele		Koh	Inm	Agi	Dil	Sna	Nom	FId	Niu	Fig	Kwi	Kov	Una	Sha	Una	Dik
ancie		KUU	111111	Agi	1 11	Sila	NOIII	Liu	Iviu	1 15	IX WI	КОУ	Ung	blia	Ulla	1 IK
Oki11																
OMIL (	96	0 4 8 4	0 202	0.120	0 206	0 193	0 197	0 245	0 201	0 244	0 140	0 267	0 265	0 160	0.250	0.250
1(	0	0.505	0.202	0.120	0.200	0.790	0.157	0.245	0.201	0.722	0.140	0.663	0.203	0.100	0.230	0.230
1(	)4	0.000	0.017	0.005	0.028	0.017	0.704	0.723	0.058	0.033	0.043	0.005	0.724	0.005	0.023	0.022
10	7	0.011	0.017	0.010	0.020	0.017	0.057	0.055	0.050	0.055	0.045	0.070	0.010	0.057	0.025	0.022
Oki1U																
18	82						0.006	0.006			0.006	0.012		0.022		
18	86	0.023	0.040		0.074	0.051	0.065	0.108	0.054	0.044	0.025	0.098	0.031	0.076	0.042	0.085
19	90	0.034	0.023	0.047	0.028	0.028	0.018	0.011	0.007	0.022	0.013	0.012	0.021	0.027	0.024	0.023
19	94	0.176	0.132	0.120	0.102	0.191	0.107	0.125	0.081	0.056	0.101	0.159	0.073	0.071	0.066	0.085
19	98	0.074	0.034	0.078	0.125	0.101	0.083	0.068	0.142	0.089	0.076	0.098	0.125	0.060	0.072	0.091
20	02	0.023	0.092	0.063	0.045	0.067	0.060	0.057	0.061	0.056	0.070	0.037	0.021	0.065	0.102	0.068
20	)6	0.040	0.092	0.063	0.074	0.062	0.048	0.091	0.081	0.067	0.095	0.024	0.073	0.027	0.042	0.085
2	10	0.068	0.109	0.167	0.080	0.090	0.107	0.108	0.101	0.100	0.222	0.061	0.135	0.141	0.139	0.114
2	14	0.420	0.086	0.172	0.131	0.107	0.125	0.119	0.108	0.089	0.133	0.110	0.115	0.130	0.139	0.125
2	18	0.028	0.103	0.135	0.108	0.135	0.155	0.085	0.122	0.156	0.120	0.159	0.167	0.114	0.102	0.085
22	22	0.040	0.080	0.026	0.085	0.039	0.065	0.091	0.115	0.156	0.063	0.085	0.115	0.082	0.060	0.091
22	26		0.040	0.042	0.017	0.051	0.048	0.034	0.014	0.044	0.019	0.012	0.021	0.038	0.060	0.040
23	30		0.006	0.042	0.011	0.022	0.018	0.006	0.020	0.011	0.013	0.024	0.010	0.027	0.024	0.034
23	34	0.017	0.063	0.010	0.040	0.011	0.018	0.051	0.014	0.044	0.013	0.024	0.010	0.049	0.012	0.017
23	38		0.040	0.016	0.028	0.011	0.006	0.023	0.014		0.006	0.049	0.042	0.005	0.048	0.017
24	12	0.051	0.006	0.005	0.011	0.006	0.024		0.007	0.011	0.006		0.021	0.016	0.018	0.017
24	46	0.006	0.023	0.005	0.017	0.000	0.021	0.006	0.027	0.033	0.006	0.012	0.021	0.016	0.012	0.011
24	50		0.023	0.010	0.017	0.006	0.021	0.000	0.027	0.022	0.006	0.012		0.033	0.012	0.006
2.	54		0.025	0.010	0.006	0.000	0.024	0.011	0.027	0.022	0.000	0.024	0.010	0.055	0.024	0.000
2.	58		0.006		0.000	0.000									0.012	
2.			0.000													
Oki100																
	2	0.016	0.028	0.016	0.099	0.078	0.045	0.070	0.099	0.052	0.114	0.023	0.031	0.038	0.040	0.038
	3	0.335	0.239	0.216	0.203	0.167	0.176	0.226	0.217	0.177	0.136	0.186	0.245	0.210	0.259	0.181
	4	0.005			0.005	0.017	0.011	0.011	0.013	0.010	0.017	0.012		0.005	0.023	0.033
	5		0.028	0.026	0.044	0.028	0.017	0.016	0.026	0.021	0.011		0.010		0.029	0.011
	6	0.022	0.057	0.005	0.115	0.067	0.051	0.059	0.053	0.083	0.045	0.012	0.061	0.113	0.063	0.099
	7	0.011	0.068	0.032	0.027	0.106	0.068	0.091	0.020	0.073	0.074	0.105	0.071	0.070	0.046	0.077
	8	0.038	0.102	0.158	0.088	0.056	0.108	0.054	0.125	0.115	0.119	0.163	0.102	0.075	0.103	0.071
	9	0.159	0.085	0.063	0.104	0.111	0.125	0.118	0.099	0.146	0.136	0.070	0.102	0.102	0.109	0.176
	10	0.308	0.102	0.158	0.088	0.117	0.074	0.091	0.059	0.073	0.063	0.198	0.082	0.113	0.075	0.071
1	11	0.005	0.063	0.074	0.038	0.072	0.040	0.032	0.053	0.021	0.023	0.035	0.010	0.070	0.040	0.016
	12	0.027	0.085	0.079	0.055	0.028	0.074	0.038	0.033	0.021	0.023	0.047	0.051	0.027	0.057	0.044
	13	0.011	0.034	0.063	0.038	0.050	0.034	0.043	0.033	0.042	0.051	0.035	0.082	0.038	0.029	0.027
	14	0.027	0.028		0.027	0.022	0.028	0.038	0.046	0.031	0.080	0.023	0.051	0.038	0.023	0.033
	15		0.023	0.016	0.016	0.044	0.040	0.022	0.079	0.010	0.034		0.051	0.038	0.034	0.038
-	16	0.005	0.011	0.016	0.027	0.011	0.011	0.016	0.020	0.021	0.017	0.023	0.010	0.011	0.006	0.033
-	17	0.005	0.006	0.016	0.005		0.006	0.022					0.010	0.005	0.006	0.022
	18	0.016	0.011	0.021	0.011	0.006	0.011	0.016		0.021	0.011		0.010	0.011		0.005
-	19		0.011	0.032		0.006	0.023	0.016	0.007	0.031	0.011	0.012		0.005		0.011
-	20		0.006	0.005		0.006	0.006			0.010	0.017	0.012	0.010		0.023	
						-	-									

Appendix 1 cont.

Locus																
\allele		Kob	Inm	Agi	Pil	Sna	Nom	Eld	Niu	Fis	Kwi	Koy	Ung	Sha	Una	Pik
	21					0.011	0.017	0.011		0.010	0.006			0.016		
	22		0.006		0.005		0.023	0.011	0.007		0.006	0.023	0.010	0.011	0.017	
	23	0.005	0.006				0.011		0.013	0.021	0.006			0.005	0.017	0.005
	24											0.012				0.005
	25									0.010						
	26			0.005								0.012				
Oki2																
	1						0.006			0.011	0.006		0.010			
	2		0.011	0.006	0.006		0.011	0.005	0.007	0.011	0.024	0.012	0.010	0.022	0.029	0.005
	3	0.012				0.006	0.006							0.006		
	4	0.448	0.045	0.047	0.017	0.023	0.039	0.038	0.048	0.033	0.053	0.012	0.031	0.078	0.087	0.055
	5	0.215	0.108	0.134	0.115	0.153	0.129	0.159	0.144	0.178	0.153	0.107	0.219	0.111	0.128	0.148
	6	0.058	0.097	0.064	0.103	0.040	0.118	0.110	0.110	0.156	0.118	0.107	0.104	0.094	0.087	0.121
	7	0.035	0.119	0.163	0.126	0.125	0.180	0.170	0.110	0.111	0.147	0.095	0.094	0.128	0.163	0.077
	8	0.087	0.182	0 1 1 6	0.132	0.142	0.112	0.099	0 1 1 0	0.078	0 1 1 8	0 1 3 1	0 188	0 144	0.122	0.099
	9	0.023	0.125	0.128	0.207	0.119	0.073	0.099	0 1 4 4	0.133	0 100	0 1 1 9	0.083	0.089	0.122	0.137
	10	0.035	0.040	0.023	0.052	0.028	0.062	0.088	0.048	0.100	0.047	0.083	0.031	0.100	0.052	0.044
	11	0.029	0.085	0.020	0.069	0.020	0.079	0.000	0.055	0.011	0.088	0.005	0.031	0.078	0.052	0.132
	12	0.029	0.005	0.157	0.009	0.068	0.084	0.060	0.082	0.067	0.059	0.060	0.083	0.078	0.070	0.082
	12	0.027	0.100	0.076	0.000	0.000	0.067	0.000	0.002	0.007	0.055	0.000	0.003	0.070	0.070	0.002
	11	0.017	0.000	0.070	0.040	0.100	0.007	0.075	0.021	0.007	0.005	0.075	0.075	0.007	0.070	0.005
	14		0.011	0.012	0.029	0.011	0.022	0.022	0.021	0.011	0.016	0.151	0.021	0.000	0.029	0.005
	15				0.000	0.011		0.011	0.007	0.011	0.000		0.010		0.017	
	17			0.006	0.006		0.011									
	17			0.006	0.006		0.011									
	17 18 20	 0.006		0.006	0.006 0.006		0.011									
	17 18 20	0.006 0.006	 	0.006	0.006 0.006 	 	0.011	 	 	 	 	 	 	 	 	 
Omvl	17 18 20	0.006 0.006	 	0.006	0.006 0.006 		0.011	 	 	 		 				
Omy1	17 18 20 01	0.006 0.006	 	0.006	0.006 0.006		0.011	 	 	 	  0.006	 				
Omy1	17 18 20 01 1 2	0.006 0.006	  0.011	0.006	0.006 0.006 	 	0.011	 	 	 	  0.006	 	 	 	 	
Omy1	17 18 20 01 1 2 3	0.006 0.006	  0.011	0.006	0.006 0.006 	   0.011	0.011	 	   0.013	   0.031	  0.006	 	   0.010	   0.016	   0.017	   0 011
Omy1	17 18 20 01 1 2 3	0.006 0.006	  0.011 0.006 0.006	0.006	0.006 0.006  0.011 0.006	  0.011	0.011	   0.032	  0.013 0.032	  0.031	  0.006  0.012 0.023	   0.012	   0.010 0.020	  0.016	  0.017	  0.011 0.005
Omy1	17 18 20 01 1 2 3 4 5	0.006 0.006   0.017	  0.011 0.006 0.006 0.034	0.006	0.006 0.006  0.011 0.006 0.011	  0.011 0.027	0.011	   0.032	  0.013 0.032 0.045	  0.031 0.010 0.021	  0.006  0.012 0.023 0.017	   0.012 0.047	  0.010 0.020 0.082	  0.016 0.011	   0.017 0.006 0.029	  0.011 0.005
Omy1	17 18 20 01 1 2 3 4 5 6	 0.006 0.006   0.017 0.067	  0.011 0.006 0.006 0.034 0.125	0.006  0.005 0.011 0.005 0.011	0.006 0.006  0.011 0.006 0.011	  0.011 0.027 0.071	0.011   0.006 0.028 0.034	   0.032 0.011	  0.013 0.032 0.045	  0.031 0.010 0.021 0.135	  0.006  0.012 0.023 0.017 0.110	   0.012 0.047 0.116	  0.010 0.020 0.082 0.163	  0.016 0.011 0.059	  0.017 0.006 0.029 0.087	  0.011 0.005 0.060 0.150
Omy1	17 18 20 01 1 2 3 4 5 6 7	 0.006 0.006   0.017 0.067	  0.011 0.006 0.006 0.034 0.125	0.006  0.005 0.011 0.005 0.011 0.258	0.006 0.006  0.011 0.006 0.011 0.106	  0.011 0.027 0.071 0.099	0.011   0.006 0.028 0.034 0.169	  0.032 0.011 0.124	  0.013 0.032 0.045 0.149	  0.031 0.010 0.021 0.135	  0.006  0.012 0.023 0.017 0.110 0.116	   0.012 0.047 0.116	  0.010 0.020 0.082 0.163 0.184	  0.016 0.011 0.059 0.144	  0.017 0.006 0.029 0.087	  0.011 0.005 0.060 0.159
Omy1	17 18 20 01 1 2 3 4 5 6 7	 0.006 0.006   0.017 0.067 0.084 0.056	  0.011 0.006 0.006 0.034 0.125 0.199	0.006  0.005 0.011 0.005 0.011 0.258 0.132	0.006 0.006  0.011 0.006 0.011 0.106 0.250	  0.011 0.027 0.071 0.099 0.132	0.011   0.006 0.028 0.034 0.169 0.152	   0.032 0.011 0.124 0.167	  0.013 0.032 0.045 0.149 0.208	  0.031 0.010 0.021 0.135 0.177	  0.006  0.012 0.023 0.017 0.110 0.116	   0.012 0.047 0.116 0.279 0.025	  0.010 0.020 0.082 0.163 0.184	  0.016 0.011 0.059 0.144 0.138	  0.017 0.006 0.029 0.087 0.198	  0.011 0.005 0.060 0.159 0.176
Omy1	17 18 20 01 1 2 3 4 5 6 7 8	 0.006 0.006   0.017 0.067 0.084 0.056	 0.011 0.006 0.006 0.034 0.125 0.199 0.045	0.006  0.005 0.011 0.005 0.011 0.258 0.132 0.074	0.006 0.006  0.011 0.006 0.011 0.106 0.250 0.050	  0.011 0.027 0.071 0.099 0.132 0.071	0.011   0.006 0.028 0.034 0.169 0.152 0.051	   0.032 0.011 0.124 0.167 0.038	  0.013 0.032 0.045 0.149 0.208 0.052	  0.031 0.010 0.021 0.135 0.177 0.042	 0.006  0.012 0.023 0.017 0.110 0.116 0.064	   0.012 0.047 0.116 0.279 0.035	  0.010 0.020 0.082 0.163 0.184 0.051	  0.016 0.011 0.059 0.144 0.138 0.043	  0.017 0.006 0.029 0.087 0.198 0.093	  0.011 0.005 0.060 0.159 0.176 0.060
Omy1	17 18 20 01 1 2 3 4 5 6 7 8 9	 0.006 0.006   0.017 0.067 0.084 0.056 0.011	 0.011 0.006 0.006 0.034 0.125 0.199 0.045 0.063	0.006  0.005 0.011 0.005 0.011 0.258 0.132 0.074 0.058	0.006 0.006  0.011 0.006 0.011 0.106 0.250 0.050 0.017	  0.011 0.027 0.071 0.099 0.132 0.071 0.033	0.011  0.006 0.028 0.034 0.169 0.152 0.051 0.039	  0.032 0.011 0.124 0.167 0.038 0.075	  0.013 0.032 0.045 0.149 0.208 0.052 0.045	  0.031 0.010 0.021 0.135 0.177 0.042 0.052	 0.006  0.012 0.023 0.017 0.110 0.116 0.064 0.052	   0.012 0.047 0.116 0.279 0.035 0.070	  0.010 0.020 0.082 0.163 0.184 0.051 0.031	  0.016 0.011 0.059 0.144 0.138 0.043 0.043	  0.017 0.006 0.029 0.087 0.198 0.093 0.052 0.052	  0.011 0.005 0.060 0.159 0.176 0.060 0.022
Omy1	17 18 20 01 1 2 3 4 5 6 7 8 9 10	 0.006 0.006   0.017 0.067 0.084 0.056 0.011 0.034	 0.011 0.006 0.006 0.034 0.125 0.199 0.045 0.063 0.074	0.006  0.005 0.011 0.005 0.011 0.258 0.132 0.074 0.058 0.021	0.006 0.006  0.011 0.006 0.011 0.106 0.250 0.050 0.017 0.039	  0.011 0.027 0.071 0.099 0.132 0.071 0.033 0.049	0.011  0.006 0.028 0.034 0.169 0.152 0.051 0.039 0.084	  0.032 0.011 0.124 0.167 0.038 0.075 0.054	  0.013 0.032 0.045 0.149 0.208 0.052 0.045 0.058	  0.031 0.010 0.021 0.135 0.177 0.042 0.052 0.083	 0.006  0.012 0.023 0.017 0.110 0.116 0.064 0.052 0.052	  0.012 0.047 0.116 0.279 0.035 0.070 0.012	  0.010 0.020 0.082 0.163 0.184 0.051 0.031 0.071	  0.016 0.011 0.059 0.144 0.138 0.043 0.043 0.048	  0.017 0.006 0.029 0.087 0.198 0.093 0.052 0.058	  0.011 0.005 0.060 0.159 0.176 0.060 0.022 0.060
Omy1	17 18 20 01 1 2 3 4 5 6 7 8 9 10 11	 0.006 0.006   0.017 0.067 0.084 0.056 0.011 0.034 0.022	 0.011 0.006 0.006 0.034 0.125 0.099 0.045 0.063 0.074 0.057	0.006  0.005 0.011 0.005 0.011 0.258 0.132 0.074 0.058 0.021 0.047	0.006 0.006  0.011 0.006 0.011 0.106 0.250 0.050 0.017 0.039 0.089	  0.011 0.027 0.071 0.099 0.132 0.071 0.033 0.049 0.033	0.011   0.006 0.028 0.034 0.169 0.152 0.051 0.039 0.084 0.073	  0.032 0.011 0.124 0.167 0.038 0.075 0.054 0.038	  0.013 0.032 0.045 0.149 0.208 0.052 0.045 0.058 0.039	  0.031 0.010 0.021 0.135 0.177 0.042 0.052 0.083 0.083	 0.006  0.012 0.023 0.017 0.110 0.116 0.064 0.052 0.052 0.105	  0.012 0.047 0.116 0.279 0.035 0.070 0.012 0.105	  0.010 0.020 0.082 0.163 0.184 0.051 0.031 0.071 0.020	  0.016 0.011 0.059 0.144 0.138 0.043 0.043 0.048 0.037	  0.017 0.006 0.029 0.087 0.198 0.093 0.052 0.058 0.087	  0.011 0.005 0.060 0.159 0.176 0.060 0.022 0.060 0.077
Omy1	17 18 20 01 1 2 3 4 5 6 7 8 9 10 11 12	 0.006 0.006   0.017 0.067 0.084 0.056 0.011 0.034 0.022 0.045	 0.011 0.006 0.006 0.034 0.125 0.199 0.045 0.063 0.074 0.057 0.034	0.006  0.005 0.011 0.005 0.011 0.258 0.132 0.074 0.058 0.021 0.047	0.006 0.006  0.011 0.006 0.011 0.106 0.250 0.050 0.017 0.039 0.089 0.050	  0.011 0.027 0.071 0.099 0.132 0.071 0.033 0.049 0.033 0.027	0.011  0.006 0.028 0.034 0.169 0.152 0.051 0.039 0.084 0.073 0.034	  0.032 0.011 0.124 0.167 0.038 0.075 0.054 0.038 0.038	  0.013 0.032 0.045 0.149 0.208 0.052 0.045 0.058 0.039 0.032	  0.031 0.010 0.021 0.135 0.177 0.042 0.052 0.083 0.083 0.031	 0.006  0.012 0.023 0.017 0.110 0.116 0.064 0.052 0.052 0.052	  0.012 0.047 0.116 0.279 0.035 0.070 0.012 0.105 0.012	  0.010 0.020 0.082 0.163 0.184 0.051 0.031 0.071 0.020 0.041	  0.016 0.011 0.059 0.144 0.138 0.043 0.043 0.048 0.037 0.069 0.053	  0.017 0.006 0.029 0.087 0.198 0.093 0.052 0.058 0.087 0.041	  0.011 0.005 0.060 0.159 0.176 0.060 0.022 0.060 0.077 0.022
Omy1	17 18 20 01 1 2 3 4 5 6 7 8 9 10 11 12 13	 0.006 0.006   0.017 0.067 0.084 0.056 0.011 0.034 0.022 0.045 0.096	 0.011 0.006 0.006 0.034 0.125 0.045 0.045 0.074 0.057 0.034 0.045	0.006  0.005 0.011 0.005 0.011 0.258 0.032 0.074 0.058 0.021 0.047 0.058	0.006 0.006  0.011 0.006 0.011 0.106 0.250 0.050 0.017 0.039 0.089 0.050 0.039	  0.011 0.027 0.071 0.099 0.132 0.071 0.033 0.049 0.033 0.027 0.044	0.011  0.006 0.028 0.034 0.169 0.051 0.039 0.084 0.073 0.039	  0.032 0.011 0.124 0.167 0.038 0.075 0.054 0.038 0.038 0.011	  0.013 0.032 0.045 0.045 0.052 0.045 0.058 0.039 0.032 0.013	  0.031 0.010 0.021 0.135 0.177 0.042 0.042 0.042 0.042 0.083 0.083 0.083 0.031	 0.006  0.012 0.023 0.017 0.110 0.116 0.064 0.052 0.052 0.052 0.052 0.035	  0.012 0.047 0.116 0.279 0.035 0.070 0.012 0.0012 0.012 0.023	  0.010 0.020 0.082 0.163 0.082 0.163 0.051 0.031 0.071 0.020 0.041	  0.016 0.011 0.059 0.144 0.037 0.043 0.043 0.043 0.043 0.043 0.043 0.043	  0.017 0.006 0.029 0.087 0.198 0.093 0.052 0.058 0.087 0.041 0.064	  0.011 0.005 0.060 0.159 0.176 0.060 0.022 0.060 0.077 0.022 0.038
Omy1	17 18 20 01 1 2 3 4 5 6 7 8 9 10 11 12 13 14	 0.006 0.006   0.017 0.067 0.084 0.056 0.011 0.034 0.022 0.045 0.096	 0.011 0.006 0.006 0.034 0.125 0.199 0.045 0.045 0.074 0.034 0.045 0.034	0.006  0.005 0.011 0.005 0.011 0.258 0.021 0.074 0.058 0.021 0.047 0.058 0.058	0.006 0.006  0.011 0.006 0.011 0.106 0.250 0.050 0.050 0.039 0.039	  0.011 0.027 0.071 0.099 0.132 0.071 0.033 0.049 0.033 0.027 0.044 0.049	0.011  0.006 0.028 0.034 0.169 0.152 0.051 0.039 0.084 0.073 0.034 0.039	  0.032 0.011 0.124 0.167 0.038 0.075 0.054 0.038 0.038 0.038 0.011 0.059	  0.013 0.032 0.045 0.045 0.045 0.052 0.045 0.058 0.039 0.032 0.013 0.058	  0.031 0.010 0.021 0.135 0.177 0.042 0.042 0.042 0.042 0.083 0.083 0.083 0.031 0.021	 0.006  0.012 0.023 0.017 0.110 0.116 0.064 0.052 0.052 0.052 0.035 0.076	  0.012 0.047 0.116 0.279 0.035 0.070 0.012 0.0012 0.012 0.023 0.023	  0.010 0.020 0.082 0.163 0.082 0.051 0.031 0.071 0.020 0.041 	  0.016 0.011 0.059 0.144 0.037 0.043 0.043 0.043 0.043 0.043 0.043 0.043 0.043 0.043	  0.017 0.006 0.029 0.087 0.198 0.093 0.052 0.058 0.093 0.052 0.058 0.087 0.041 0.064	  0.011 0.005 0.060 0.159 0.176 0.060 0.022 0.060 0.077 0.022 0.038 0.049
Omy1	17 18 20 01 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15	 0.006 0.006   0.017 0.067 0.084 0.056 0.011 0.034 0.022 0.045 0.045 0.045	 0.011 0.006 0.006 0.034 0.125 0.199 0.045 0.063 0.074 0.057 0.034 0.045 0.057	0.006  0.005 0.011 0.005 0.011 0.258 0.132 0.074 0.058 0.021 0.047 0.058 0.058 0.005 0.021	0.006 0.006  0.011 0.006 0.011 0.106 0.250 0.050 0.050 0.039 0.039 0.039 0.039	  0.011 0.027 0.071 0.099 0.132 0.071 0.033 0.049 0.033 0.027 0.044 0.049	0.011  0.006 0.028 0.034 0.169 0.051 0.039 0.084 0.073 0.034 0.039 0.028 0.034	  0.032 0.011 0.124 0.167 0.038 0.075 0.054 0.038 0.038 0.038 0.011 0.059	  0.013 0.032 0.045 0.045 0.045 0.045 0.045 0.045 0.045 0.039 0.032 0.032 0.013 0.058 0.052	  0.031 0.010 0.021 0.135 0.177 0.042 0.052 0.083 0.083 0.031 0.021 0.031 0.021	 0.006  0.012 0.023 0.017 0.110 0.116 0.064 0.052 0.052 0.052 0.052 0.035 0.076 0.041	  0.012 0.047 0.116 0.279 0.035 0.070 0.012 0.0012 0.012 0.023 0.023 0.023 0.023	  0.010 0.020 0.082 0.163 0.082 0.031 0.071 0.020 0.041  0.051 0.031	  0.016 0.011 0.059 0.144 0.037 0.043 0.043 0.043 0.043 0.053 0.027 0.059 0.059	  0.017 0.006 0.029 0.087 0.198 0.093 0.052 0.058 0.087 0.041 0.064 0.041 0.047	  0.011 0.005 0.060 0.159 0.176 0.060 0.022 0.060 0.077 0.022 0.038 0.049 0.038
Omy1	17 18 20 01 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16	 0.006 0.006   0.017 0.067 0.084 0.056 0.011 0.034 0.022 0.045 0.045 0.096 0.045 0.140 0.034	 0.011 0.006 0.006 0.034 0.125 0.199 0.045 0.063 0.074 0.057 0.034 0.045 0.057	0.006  0.005 0.011 0.005 0.011 0.258 0.132 0.074 0.058 0.021 0.047 0.058 0.058 0.005 0.021 0.068	0.006 0.006  0.011 0.006 0.011 0.106 0.250 0.050 0.050 0.039 0.039 0.039 0.039 0.039	  0.011 0.027 0.071 0.099 0.132 0.071 0.033 0.049 0.033 0.027 0.044 0.049 0.060	0.011  0.006 0.028 0.034 0.169 0.152 0.051 0.039 0.084 0.073 0.034 0.039 0.028 0.034	  0.032 0.011 0.124 0.167 0.038 0.075 0.054 0.038 0.011 0.059 0.032 0.032	  0.013 0.032 0.045 0.045 0.045 0.045 0.045 0.045 0.045 0.039 0.032 0.032 0.013 0.058 0.052 0.032	  0.031 0.010 0.021 0.135 0.177 0.042 0.052 0.083 0.083 0.031 0.021 0.031 0.042 0.031	 0.006  0.012 0.023 0.017 0.110 0.016 0.052 0.052 0.052 0.052 0.035 0.076 0.041 0.047	  0.012 0.047 0.116 0.279 0.035 0.070 0.012 0.0012 0.012 0.023 0.023 0.023 0.023	  0.010 0.020 0.082 0.163 0.082 0.031 0.031 0.020 0.041  0.051 0.031	  0.016 0.011 0.059 0.144 0.037 0.043 0.048 0.037 0.069 0.053 0.027 0.059 0.043 0.043	  0.017 0.006 0.029 0.087 0.093 0.052 0.058 0.058 0.087 0.041 0.064 0.041 0.047 0.047	  0.011 0.005 0.060 0.159 0.176 0.060 0.022 0.060 0.077 0.022 0.038 0.049 0.038 0.044
Omy1	$\begin{array}{c} 17\\18\\20\\\\01\\1\\2\\3\\4\\5\\6\\7\\8\\9\\10\\11\\12\\13\\14\\15\\16\\17\\\end{array}$	 0.006 0.006   0.017 0.067 0.084 0.056 0.011 0.034 0.022 0.045 0.045 0.045 0.045 0.045 0.140 0.034	 0.011 0.006 0.006 0.034 0.125 0.099 0.045 0.063 0.074 0.057 0.034 0.057 0.051 0.040 0.051	0.006  0.005 0.011 0.005 0.011 0.258 0.03 0.074 0.058 0.021 0.047 0.058 0.058 0.005 0.021 0.068 0.063	0.006 0.006  0.011 0.006 0.011 0.106 0.250 0.050 0.039 0.089 0.039 0.039 0.039 0.039 0.039	 0.011 0.027 0.071 0.099 0.132 0.071 0.033 0.049 0.033 0.027 0.044 0.049 0.060 0.071 0.071	0.011  0.006 0.028 0.034 0.169 0.051 0.039 0.084 0.073 0.034 0.039 0.034 0.039 0.028 0.034	  0.032 0.011 0.124 0.167 0.038 0.075 0.054 0.038 0.038 0.038 0.011 0.059 0.032 0.038 0.091	  0.013 0.032 0.045 0.045 0.045 0.052 0.045 0.039 0.032 0.013 0.058 0.052 0.032 0.052	  0.031 0.010 0.021 0.135 0.177 0.042 0.052 0.083 0.083 0.031 0.021 0.031 0.042 0.031	 0.006  0.012 0.023 0.017 0.110 0.016 0.052 0.052 0.052 0.052 0.052 0.035 0.076 0.041 0.047 0.029	  0.012 0.047 0.116 0.279 0.035 0.070 0.012 0.0012 0.023 0.023 0.023 0.023 0.151	  0.010 0.020 0.082 0.163 0.082 0.163 0.031 0.020 0.041  0.051 0.031 0.051	  0.016 0.011 0.059 0.144 0.138 0.043 0.043 0.048 0.037 0.069 0.053 0.027 0.059 0.043 0.048 0.053	  0.017 0.006 0.029 0.087 0.198 0.093 0.052 0.058 0.087 0.041 0.041 0.041 0.047 0.047 0.029	  0.011 0.005 0.060 0.159 0.176 0.060 0.022 0.060 0.077 0.022 0.060 0.077 0.022 0.038 0.049 0.038 0.044 0.071
Omy1	$\begin{array}{c} 17\\18\\20\\\end{array}\\ 01\\1\\2\\3\\4\\5\\6\\7\\8\\9\\10\\11\\12\\13\\14\\15\\16\\17\\18\\\end{array}$	 0.006 0.006   0.017 0.067 0.084 0.056 0.011 0.034 0.022 0.045 0.045 0.045 0.045 0.045 0.045 0.045 0.034	 0.011 0.006 0.006 0.034 0.125 0.099 0.045 0.063 0.074 0.057 0.034 0.057 0.051 0.040 0.051 0.045	0.006  0.005 0.011 0.258 0.031 0.074 0.058 0.021 0.047 0.058 0.058 0.005 0.021 0.068 0.063 0.063 0.058	0.006 0.006  0.011 0.006 0.011 0.106 0.250 0.050 0.050 0.039 0.039 0.039 0.039 0.039 0.044 0.039	 0.011 0.027 0.071 0.099 0.132 0.071 0.033 0.049 0.033 0.027 0.044 0.049 0.060 0.071 0.071 0.071	0.011  0.006 0.028 0.034 0.169 0.152 0.051 0.039 0.084 0.073 0.034 0.039 0.028 0.034 0.034 0.045 0.045 0.045	  0.032 0.011 0.124 0.167 0.038 0.075 0.054 0.038 0.038 0.038 0.038 0.038 0.038 0.038 0.032 0.038 0.032	  0.013 0.032 0.045 0.045 0.045 0.052 0.045 0.032 0.032 0.032 0.032 0.052 0.032 0.071 0.019	  0.031 0.010 0.021 0.135 0.177 0.042 0.042 0.083 0.083 0.031 0.021 0.031 0.021 0.031 0.021 0.031 0.021 0.031 0.042 0.031 0.042 0.031	 0.006  0.012 0.023 0.017 0.110 0.016 0.052 0.052 0.052 0.052 0.052 0.035 0.076 0.041 0.047 0.029 0.035	  0.012 0.047 0.116 0.279 0.035 0.070 0.012 0.012 0.023 0.023 0.151 	  0.010 0.020 0.082 0.163 0.082 0.163 0.051 0.031 0.051 0.031 0.051 0.031 0.051	  0.016 0.011 0.059 0.144 0.138 0.043 0.043 0.043 0.053 0.043 0.043 0.043	  0.017 0.006 0.029 0.087 0.093 0.052 0.058 0.087 0.041 0.041 0.047 0.047 0.047 0.029 0.035	  0.011 0.005 0.060 0.159 0.176 0.060 0.022 0.060 0.077 0.022 0.038 0.049 0.038 0.049 0.038 0.044
Omy1	17 18 20 01 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 10 10 10 10 10 10 10 10 10 10	 0.006 0.006   0.017 0.067 0.084 0.056 0.011 0.034 0.022 0.045 0.096 0.045 0.096 0.045 0.096 0.045 0.034 0.056 0.056 0.056	 0.011 0.006 0.006 0.034 0.125 0.045 0.045 0.045 0.045 0.057 0.034 0.045 0.057 0.051 0.040 0.045 0.045 0.045	0.006  0.005 0.011 0.005 0.011 0.258 0.032 0.074 0.058 0.021 0.047 0.058 0.025 0.021 0.068 0.063 0.058 0.005	0.006 0.006  0.011 0.006 0.011 0.006 0.050 0.050 0.050 0.039 0.039 0.039 0.039 0.039 0.039 0.039 0.044 0.039	  0.011 0.027 0.071 0.099 0.132 0.071 0.033 0.049 0.033 0.027 0.044 0.049 0.060 0.071 0.022 0.033	0.011  0.006 0.028 0.034 0.169 0.051 0.039 0.084 0.073 0.034 0.039 0.034 0.039 0.028 0.034 0.035 0.045 0.045 0.051 0.051	  0.032 0.011 0.124 0.167 0.038 0.075 0.054 0.038 0.011 0.059 0.032 0.038 0.011 0.059 0.032	  0.013 0.032 0.045 0.045 0.052 0.045 0.052 0.032 0.013 0.058 0.052 0.032 0.013 0.052 0.032 0.013 0.052 0.032	  0.031 0.010 0.021 0.135 0.177 0.042 0.042 0.083 0.031 0.021 0.021 0.031 0.021 0.031 0.021 0.031 0.021 0.031 0.042 0.031 0.042 0.031 0.042	 0.006  0.012 0.023 0.017 0.110 0.116 0.064 0.052 0.052 0.052 0.052 0.035 0.035 0.076 0.041 0.047 0.029 0.035 0.023	  0.012 0.047 0.116 0.279 0.035 0.070 0.012 0.023 0.023 0.023 0.023 0.023 0.023 0.023 0.023 0.023 0.023	  0.010 0.020 0.082 0.163 0.082 0.082 0.051 0.031 0.020 0.041  0.051 0.031 0.051 0.031 0.061 0.041	  0.016 0.011 0.059 0.144 0.037 0.043 0.043 0.027 0.059 0.043 0.043 0.043 0.043 0.043 0.043 0.043 0.043 0.043 0.043	  0.017 0.006 0.029 0.087 0.198 0.093 0.052 0.058 0.087 0.041 0.064 0.041 0.047 0.047 0.047 0.029 0.035 0.029	  0.011 0.005 0.060 0.159 0.176 0.060 0.022 0.060 0.077 0.022 0.038 0.049 0.038 0.044 0.071 0.060 0.016

Appendix 1 cont.

Locus																
\allele		Kob	Inm	Agi	Pil	Sna	Nom	Eld	Niu	Fis	Kwi	Koy	Ung	Sha	Una	Pik
	21	0.051	0.006	0.005	0.022	0.049	0.034	0.043	0.013	0.010	0.047	0.023	0.010	0.011	0.006	0.005
	22		0.011		0.011	0.011			0.006	0.010	0.006		0.010	0.021	0.006	
	23		0.006		0.011		0.006	0.022			0.006	0.012		0.005	0.012	0.011
	24	0.006				0.005	0.006				0.017	0.012		0.011		
	25	0.022				0.005									0.006	0.005
	26	0.017		0.011	0.011			0.005					0.010			
	27			0.011	0.011		0.006				0.012		0.010			
	28	0.006					0.006			0.010	0.0012			0.005		
	20	0.000					0.000	0.005		0.010	0.000			0.005		
	2)							0.005								
Onalo	1															
Onero	1									0.011						
	1			0 177	0.165	0.244		0.220	0.217	0.011	0.220	0 124	0 1 5 2	0.170	0.200	
	2	0.089	0.199	0.1//	0.165	0.244	0.180	0.220	0.217	0.213	0.230	0.134	0.153	0.1/9	0.209	0.189
	3	0.150	0.017			0.028	0.011	0.022	0.007	0.032	0.006	0.03/	0.020	0.021	0.012	0.017
	4							0.005								
	5	0.006			0.005	0.006										
	6	0.178	0.199	0.203	0.209	0.125	0.152	0.132	0.145	0.181	0.201	0.354	0.153	0.153	0.186	0.106
	7	0.078	0.074	0.089	0.060	0.051	0.062	0.082	0.053	0.074	0.063	0.049	0.112	0.100	0.099	0.089
	8	0.017	0.148	0.109	0.115	0.159	0.140	0.143	0.224	0.149	0.092	0.146	0.122	0.116	0.081	0.083
	9	0.033	0.080	0.099	0.077	0.102	0.096	0.077	0.072	0.074	0.052	0.049	0.082	0.100	0.070	0.122
	10					0.006	0.022		0.013	0.021	0.006	0.012		0.016	0.029	0.011
	11	0.094	0.011	0.010	0.033	0.034	0.022	0.005	0.013		0.052	0.024	0.020	0.026	0.012	0.022
	12	0.083	0.023	0.026	0.033	0.028	0.017	0.022	0.046	0.032	0.006	0.012	0.061	0.016	0.029	0.011
	13		0.006	0.005	0.022	0.034	0.051	0.022	0.007	0.021	0.029	0.012	0.020	0.032	0.006	0.067
	14		0.023	0.005	0.011	0.040	0.017	0.022		0.011	0.017	0.024	0.010	0.005	0.017	0.011
	15		0.011	0.010	0.005		0.011	0.011		0.011			0.020	0.016		0.017
	16	0.006	0.023	0.010	0.033	0.006		0.027	0.020		0.017	0.012	0.031	0.032	0.017	0.056
	17	0.006	0.023	0.031	0.033	0.023	0.017	0.016	0.013	0.032	0.011	0.012	0.010	0.032	0.041	0.028
	18	0.000	0.025	0.051	0.033	0.025	0.017	0.010	0.015	0.032	0.023	0.012	0.010	0.052	0.073	0.020
	10		0.000	0.010	0.022	0.023	0.028	0.011	0.040	0.021	0.023		0.051	0.011	0.023	0.028
	20	0.006	0.011	0.016	0.027	0.025	0.011	0.022	0.007	0.011	0.004	0.012	0.020	0.005	0.027	0.022
	20	0.000	0.023	0.010	0.027	0.000	0.000	0.011	0.007	0.011	0.000	0.012	0.020	0.020	0.017	0.022
	21	0.006	0.034	0.120	0.044		0.022	0.022	0.015	0.011	0.017		0.020	0.021	0.023	0.011
	22	0.000	0.011	0.005	0.011		0.011	0.022	0.007	0.011	0.022	0.027	0.051	0.020	0.023	0.000
	23	0.017	0.006	0.005	0.016	0.006	0.01/	0.005	0.013	0.021	0.023	0.037	0.020	0.011	0.006	0.022
	24	0.178	0.011	0.005	0.022	0.006	0.006	0.016	0.007	0.021	0.029	0.012	0.010	0.011	0.023	0.011
	25	0.006		0.026	0.005	0.011	0.034	0.022	0.013	0.021	0.017	0.049		0.021	0.006	
	26	0.006	0.023	0.010	0.016	0.011	0.011	0.022	0.007		0.011				0.006	0.011
	27		0.006		0.005	0.034	0.022	0.022	0.039	0.021	0.046		0.020	0.016	0.017	0.022
	28	0.022	0.017	0.010	0.016			0.016	0.007		0.006	0.012		0.005		0.011
	29	0.006	0.011		0.005		0.034	0.011	0.007						0.006	
	30	0.017	0.006	0.016				0.011			0.006		0.010		0.006	
	31					0.006									0.006	
	32					0.006			0.007					0.005		0.006
	34				0.005	0.006										
One10	2															
	2				0.006		0.006		0.006	0.010						
	3					0.005										
	5					5.000										

Appendix 1 cont.

Locus																
\allele		Kob	Inm	Agi	Pil	Sna	Nom	Eld	Niu	Fis	Kwi	Koy	Ung	Sha	Una	Pik
	4	0.005	0.006		0.006	0.005				0.010				0.005		0.005
	5	0.121	0.006	0.041	0.022	0.022	0.011	0.006	0.013	0.010	0.006	0.012		0.016	0.030	0.011
	6	0.066	0.039	0.088	0.061	0.049	0.039	0.039	0.058	0.010	0.013	0.012	0.021	0.026	0.042	0.038
	7	0.192	0.073	0.113	0.056	0.077	0.067	0.096	0.077	0.073	0.106	0.049	0.106	0.105	0.095	0.077
	8	0.126	0.140	0.149	0.072	0.115	0.111	0.118	0.141	0.146	0.131	0.098	0.106	0.111	0.143	0.159
	9	0.137	0.101	0.098	0.106	0.066	0.106	0.096	0.135	0.208	0.138	0.110	0.106	0.089	0.083	0.099
	10	0.038	0.118	0.036	0.061	0.159	0.117	0.067	0.083	0.031	0.088	0.134	0.160	0.079	0.089	0.115
	11	0.126	0.101	0.077	0.189	0.165	0.139	0.118	0.083	0.125	0.125	0.061	0.053	0.168	0.113	0.115
	12	0.027	0.118	0.119	0.100	0.099	0.061	0.124	0.071	0.125	0.100	0.110	0.117	0.084	0.089	0.088
	13	0.071	0.140	0.072	0.117	0.071	0.128	0.124	0.128	0.094	0.094	0.049	0.074	0.105	0.095	0.071
	14	0.016	0.062	0.072	0.061	0.044	0.056	0.045	0.083	0.073	0.031	0.061	0.085	0.074	0.065	0.055
	15	0.044	0.028	0.052	0.072	0.055	0.067	0.084	0.077	0.052	0.100	0.049	0.074	0.079	0.083	0.044
	16	0.011	0.028	0.041	0.028	0.044	0.039	0.039	0.026	0.031	0.056	0.159	0.043	0.032	0.024	0.077
	17	0.011	0.028	0.036	0.017	0.011	0.028	0.034	0.013		0.013	0.024	0.011	0.021	0.012	0.005
	18		0.006	0.005	0.006	0.005	0.006	0.006				0.049	0.021	0.005	0.018	0.016
	19											0.024	0.011		0.006	0.011
	20	0.005	0.006		0.017		0.011	0.006	0.006				0.011		0.006	0.011
	21				0.006	0.005	0.011									
	22														0.006	
One10-	4															
	3		0.006	0.005	0.006	0.006		0.027	0.006	0.022	0.017	0.014			0.012	0.005
	4		0.006	0.005	0.006	0.056	0.056	0.011	0.032	0.054	0.029		0.074	0.032	0.025	0.022
	5	0.176	0.074	0.093	0.144	0.128	0.133	0.124	0.143	0.109	0.092	0.083	0.138	0.085	0.123	0.143
	6	0.170	0.153	0.072	0.133	0.117	0.128	0.124	0.182	0.087	0.103	0.097	0.138	0.128	0.173	0.143
	7	0.027	0.045	0.036	0.050	0.028	0.061	0.043	0.052	0.087	0.098	0.056	0.096	0.074	0.031	0.033
	8		0.023	0.010	0.028	0.033	0.044	0.032	0.032	0.043	0.063	0.028	0.011	0.043	0.056	0.038
	9	0.005	0.028	0.026	0.039	0.022	0.022	0.027	0.039	0.043	0.029	0.042	0.043	0.011	0.031	0.038
	10	0.038	0.006	0.098	0.033	0.050	0.044	0.043	0.026	0.076	0.034	0.069	0.043	0.090	0.037	0.038
	11	0.082	0.063	0.010	0.028	0.006	0.011	0.027	0.013	0.022	0.006	0.009	0.013	0.032	0.019	0.033
	12	0 181	0.034	0.088	0.022	0.061	0.011	0.027	0.026	0.011	0.029	0 1 3 9	0.021	0.027	0.043	0.027
	13	0.016	0.057	0.041	0.039	0.028	0.067	0.059	0.032	0.033	0.040	0.028	0.032	0.027	0.031	0.027
	14	0.016	0.051	0.021	0.037	0.020	0.039	0.054	0.052	0.033	0.086	0.020	0.032	0.059	0.068	0.027
	15	0.027	0.017	0.021	0.056	0.030	0.028	0.048	0.032	0.043	0.000	0.042	0.032	0.016	0.000	0.027
	16	0.033	0.125	0.057	0.056	0.067	0.033	0.022	0.026	0.054	0.052	0.028	0.053	0.074	0.043	0.060
	17	0.071	0.063	0.037	0.050	0.061	0.067	0.022	0.020	0.076	0.092	0.020	0.043	0.128	0.062	0.000
	18	0.060	0.005	0.021	0.000	0.001	0.007	0.021	0.058	0.070	0.092	0.042	0.045	0.120	0.002	0.045
	19	0.000	0.023	0.021	0.050	0.072	0.050	0.070	0.030	0.003	0.034	0.042	0.003	0.032	0.074	0.033
	20	0.060	0.023	0.072	0.033	0.033	0.033	0.054	0.013	0.022	0.021	0.014	0.032	0.052	0.025	0.033
	20	0.000	0.025	0.072	0.022	0.017	0.039	0.027	0.013	0.022	0.046	0.014	0.032	0.037	0.025	0.055
	$\frac{21}{22}$	0.011	0.020	0.041	0.022	0.017	0.037	0.022	0.013	0.033	0.040	0.028	0.045	0.037	0.025	0.033
	22	0.001	0.040	0.005	0.020	0.011	0.011	0.011	0.010	0.055	0.000	0.020		0.001	0.051	0.055
	23 24	0.005	0.000	0.005	0.011	0.000	0.011	0.011	0.019		0.011		0.011	0.005		0.011
	24 25		0.023	0.005		0.022	0.022	0.010	0.019				0.011	0.010		0.005
	25 26	0.005			0.006			0.005								0.005
	20 27	0.005			0.000		0.011		0.006							
	∠/ 28						0.011	0.005	0.000	0.011						
	29				0.006		0.006									
					0.000		0.000									

Appendix 1 cont.

Locus	,															
Vallele	•	Koh	Inm	Δσi	Pil	Sna	Nom	Fld	Niu	Fis	Kwi	Kov	Unσ	Sha	Una	Pik
unere	30	KOU		1161	0.006	Silu		Liu	Itiu	1 15	IX WI	ROy	0115	Silu	Ond	I IK
	50				0.000											
One1	14															
Oner	1			0.010		0.023	0.006	0.005	0.007		0.006	0.012			0.006	0.006
	2	0.011	0.006	0.036	0.011	0.017	0.006	0.027	0.026		0.000	0.012		0.011		0.017
	3	0.016	0.000	0.063	0.044	0.017	0.000	0.032	0.013	0.042	0.046	0.058	0.041	0.011	0.047	0.029
	4				0.011		0.011				0.006					0.02
	5	0.005			0.006									0.011	0.012	0.011
	6	0.016	0.052	0.010	0.028	0.023	0.022	0.011	0.013	0.042	0.006	0.035	0.020	0.037	0.012	0.040
	7	0.055	0.046	0.031	0.050	0.040	0.051	0.075	0.033	0.042	0.040	0.023	0.061	0.069	0.064	0.063
	8	0.220	0.075	0.078	0.061	0.040	0.062	0.070	0.059	0.042	0.069	0.023	0.112	0.080	0.047	0.002
	9	0.033	0.103	0.063	0.001	0.148	0.135	0.140	0.178	0.094	0.138	0.151	0.082	0.144	0.110	0.132
	10	0.066	0.063	0.003	0.139	0.136	0.084	0.059	0.079	0.135	0.132	0.128	0.061	0 101	0.145	0.086
	11	0.060	0.075	0.078	0.117	0.063	0.079	0.091	0.046	0.125	0.086	0.120	0.163	0.090	0.116	0.086
	12	0.060	0.167	0.078	0.100	0.108	0.079	0.070	0.105	0.104	0.000	0.047	0.051	0.085	0.105	0.057
	13	0.022	0.075	0.073	0.083	0.040	0.067	0.075	0.086	0.104	0.092	0.035	0.092	0.090	0.052	0.092
	14	0.022	0.098	0.031	0.028	0.097	0.045	0.086	0.079	0.042	0.063	0.093	0.092	0.043	0.023	0.023
	15	0.077	0.029	0.063	0.044	0.074	0.112	0.070	0.046	0.042	0.005	0.023	0.092	0.064	0.052	0.025
	16	0.038	0.075	0.052	0.072	0.102	0.073	0.081	0.079	0.073	0.034	0.105	0.082	0.069	0.076	0.052
	17	0.011	0.023	0.115	0.033	0.017	0.034	0.038	0.046	0.042	0.017	0.012	0.002	0.016	0.023	0.029
	18	0.016	0.017	0.063	0.022	0.028	0.034	0.022	0.033	0.010	0.040	0.012	0.061	0.032	0.029	0.023
	19				0.022		0.006	0.022	0.033	0.010	0.011				0.012	
	20	0.022	0.023		0.011		0.000		0.013	0.021	0.006	0.012		0.005	0.012	0.011
	21	0.005	0.025	0.005		0.006		0.005						0.005	0.0012	
	22	0.005	0.000	0.000		0.000	0.017	0.005	0.013	0.010			0.010	0.005	0.006	
	23	0.198	0.006	0.026				0.000	0.013		0.006	0.012	0.020			
	23	0.005	0.000				0.006									
	25	0.005	0.011	0.010	0.006	0.006	0.000	0.005			0.006	0.023		0.011	0.012	0.006
	26	0.005	0.006	0.005		0.006	0.006	0.011			0.006	0.023			0.006	
	27		0.000											0.005	0.012	
	28									0.010						
	29		0.006		0.011						0.006					
	30				0.006											
	33						0.011		0.007							
	34			0.005												
	35						0.006									
	36				0.006											
	37								0.007	0.010						
	38										0.006					
	40														0.012	
	41				0.006		0.006									
	42															0.006
	43								0.007					0.005		
	rJ								0.007					0.005		
Ots3																
- 13 J	1			0.005												
	2					0.005					0.006	0.012		0.005	0.006	
	3	0.079		0.021	0.022	0.060	0.034	0.043	0.026		0.019	0.024	0.031		0.035	0.006

Appendix 1 cont.

Locus																
\allele		Kob	Inm	Agi	Pil	Sna	Nom	Eld	Niu	Fis	Kwi	Kov	Ung	Sha	Una	Pik
	4		0.006	0.015	0.028	0.016		0.005		0.011	0.006			0.005		0.006
	5		0.006	0.015	0.006	0.022	0.006	0.011	0.006	0.011			0.010	0.021	0.012	
	6	0.017	0.063	0.041	0.039	0.027	0.040	0.038	0.058	0.043	0.049	0.098	0.010	0.037	0.035	0.044
	7	0.051	0.011	0.031			0.011			0.011	0.006		0.010	0.011	0.006	0.006
	8	0.371	0.449	0.335	0.372	0.324	0.341	0.344	0.325	0.394	0.284	0.366	0.357	0.305	0.282	0.300
	9	0.028	0.011	0.129	0.028	0.044	0.028	0.048	0.039	0.032	0.037	0.085	0.031	0.047	0.006	0.017
	10	0.011	0.006	0.010	0.033	0.016	0.023	0.011	0.026	0.032	0.012	0.024	0.010	0.021	0.018	0.033
	11	0.213	0.176	0.186	0.089	0.121	0.108	0.151	0.136	0.053	0.080	0.085	0.092	0.142	0.182	0.161
	12	0.006	0.006	0.005		0.011	0.028	0.016	0.006		0.062	0.012	0.020	0.011	0.018	0.022
	13	0.180	0.233	0.191	0.350	0.302	0.324	0.296	0.318	0.362	0.346	0.220	0.347	0.316	0.359	0.339
	14				0.006	0.027					0.012		0.010	0.016	0.006	
	15	0.022	0.006	0.005		0.011	0.011	0.011	0.006	0.021	0.006	0.012	0.010		0.006	
	16	0.017		0.005		0.005	0.040	0.011	0.026	0.021	0.043	0.012	0.041	0.032	0.018	0.022
	17	0.006	0.028	0.005	0.022	0.005		0.016	0.026	0.011	0.031	0.049	0.020	0.021	0.012	0.044
	19				0.006									0.011		
	21						0.006									
Otsg68																
	5	0.006	0.011	0.010	0.017	0.022	0.006		0.006	0.010						0.006
	6	0.006						0.011	0.006	0.010	0.006	0.012		0.005	0.012	
	7	0.006	0.011		0.039	0.016	0.006	0.016	0.013	0.010			0.010		0.012	0.022
	8	0.017	0.028	0.010	0.028	0.022	0.039	0.038	0.019	0.021	0.023	0.023	0.020	0.048	0.024	0.033
	9	0.052	0.067	0.016	0.039	0.126	0.062	0.033	0.065	0.073	0.070	0.047	0.020	0.081	0.065	0.100
	10	0.052	0.157	0.177	0.094	0.088	0.079	0.043	0.104	0.156	0.093	0.105	0.082	0.097	0.129	0.100
	11	0.115	0.146	0.120	0.133	0.121	0.124	0.109	0.149	0.094	0.128	0.081	0.214	0.129	0.135	0.083
	12	0.040	0.079	0.089	0.083	0.121	0.079	0.109	0.149	0.125	0.093	0.035	0.051	0.113	0.088	0.122
	13	0.034	0.062	0.036	0.050	0.033	0.039	0.065	0.084	0.042	0.058	0.140	0.020	0.043	0.082	0.039
	14	0.011	0.011	0.016	0.028	0.027	0.017	0.043	0.032	0.021	0.023	0.023	0.010	0.022	0.029	0.028
	15	0.276	0.006	0.052	0.017	0.016	0.022	0.016	0.006	0.010	0.012	0.012	0.010	0.005	0.006	0.033
	16	0.023	0.056	0.089	0.011	0.044	0.028	0.016	0.006	0.010	0.017	0.023	0.031	0.011	0.006	0.022
	17	0.029	0.017	0.005	0.039	0.011	0.039	0.033	0.013	0.042	0.017	0.023	0.020	0.027	0.018	0.017
	18	0.006			0.006		0.006	0.016	0.006		0.017	0.012		0.022	0.024	0.039
	19	0.052					0.006	0.011	0.006	0.010			0.010	0.011	0.012	
	20		0.006	0.031	0.006	0.011	0.028			0.021	0.029	0.023	0.010	0.005	0.006	
	21	0.034	0.006	0.010			0.006		0.006	0.021	0.006	0.047	0.010	0.005	0.018	0.017
	22	0.006	0.006	0.005	0.006	0.016	0.011	0.016	0.006		0.006		0.031	0.022	0.006	0.006
	23	0.011	0.028	0.042	0.033	0.044	0.006	0.027	0.013	0.010	0.017	0.035	0.031	0.022	0.024	0.011
	24	0.029	0.011	0.031	0.022	0.016	0.011	0.011	0.013	0.042		0.023	0.010	0.011	0.006	0.017
	25		0.011	0.021	0.011	0.022	0.034	0.033	0.026		0.058	0.023	0.041	0.022	0.024	0.017
	26	0.017	0.017	0.016	0.022	0.022	0.039	0.033	0.026	0.031	0.017	0.012	0.010	0.011	0.029	0.006
	27	0.023	0.006	0.047	0.011	0.049	0.028	0.011		0.021	0.023	0.023	0.010	0.011	0.018	
	28	0.006	0.045	0.010	0.033	0.011	0.039	0.049	0.065	0.021	0.052	0.070	0.041	0.027	0.006	0.056
	29	0.023	0.028	0.031	0.044	0.033	0.051	0.049	0.026	0.031	0.064	0.035	0.041	0.038	0.047	0.061
	30		0.039	0.052	0.083	0.027	0.056	0.109	0.065	0.021	0.041	0.070	0.061	0.038	0.082	0.067
	31		0.011	0.005	0.033	0.016	0.045	0.016	0.006	0.042	0.029	0.035	0.071	0.065	0.035	0.033
	32	0.006	0.017	0.005	0.039	0.016	0.017	0.022	0.019	0.021	0.023	0.012	0.031	0.011	0.006	0.011
	33		0.011		0.017	0.005	0.011	0.011	0.013	0.021	0.012		0.010	0.005	0.012	0.017
	34			0.005	0.006	0.005		0.011		0.021	0.017		0.041	0.027		

Appendix 1 cont.

Locus																
\allele		Kob	Inm	Agi	Pil	Sna	Nom	Eld	Niu	Fis	Kwi	Koy	Ung	Sha	Una	Pik
	35	0.006			0.011	0.011	0.006	0.005	0.013	0.021			0.010	0.011	0.012	0.006
	36	0.017					0.006	0.016	0.013		0.006	0.047	0.020	0.027	0.018	0.022
	37		0.022	0.021	0.006	0.016	0.011	0.005			0.006	0.012		0.022	0.006	0.006
	38	0.017	0.011	0.005	0.006		0.011		0.006		0.023			0.005		
	39	0.006	0.022	0.031			0.011									0.006
	40		0.022	0.005	0.011	0.022	0.006	0.005	0.013	0.010	0.006					
	41	0.006	0.006			0.005	0.017						0.010			
	42	0.057	0.011	0.005	0.017			0.011					0.010	0.005	0.006	
	43	0.011	0.011								0.006					
	44									0.010						
Sec. 410	)															
554419	′ 1		0.006													
	2		0.000								0.034					
	3								0.006							
	4	0.006		0.005						0.010				0.005	0.006	
	5		0.006	0.005	0.006	0.022	0 044	0.016	0.013	0.021	0.006		0.010	0.005	0.000	0.034
	6	0 1 5 2	0.080	0.072	0.050	0.083	0.067	0.091	0.039	0.063	0.063	0.058	0.073	0.081	0.047	0.039
	7	0 101	0.253	0.196	0.0278	0.005	0.007	0.263	0.059	0.005	0.005	0.020	0.260	0.001	0.291	0.039
	8	0 146	0 144	0 186	0 161	0.167	0 189	0.172	0.182	0.229	0.125	0.116	0.156	0.172	0.209	0.197
	9	0.129	0.132	0.149	0.139	0.139	0.139	0.134	0.156	0.115	0.136	0.151	0.115	0.097	0.163	0.067
	10	0.022	0.075	0.077	0.100	0.083	0.089	0.097	0.104	0.104	0.102	0.081	0.125	0.145	0.110	0.112
	11	0.028	0.092	0.103	0.089	0.117	0.072	0.113	0.091	0.156	0.097	0.116	0.083	0.081	0.058	0.079
	12	0.067	0.132	0.082	0.094	0.039	0.078	0.027	0.078	0.042	0.068	0.116	0.094	0.081	0.023	0.096
	13	0.309	0.034	0.036	0.044	0.044	0.011	0.032	0.032	0.052	0.040	0.070	0.042	0.032	0.058	0.039
	14	0.022	0.034	0.005	0.033	0.061	0.022	0.038	0.026		0.023	0.023	0.010	0.016	0.012	0.034
	15	0.017		0.057	0.006	0.017	0.011	0.011	0.006		0.017	0.023	0.010	0.027	0.006	0.039
	16		0.006	0.010		0.006	0.006	0.005			0.028		0.010			0.017
	17			0.005												0.006
	19			0.010												
	20						0.006				0.011		0.010			
	22										0.006					

Appendix 2. Table of allele frequencies at each locus for population cohorts used to estimate  $N_{e}$ . Abbreviations are as indicated in Table 3. A dash indicates the allele was not present.

Locus

\allele		99Eld	00Eld	01Eld	99Pil	00Pil	01Pil	99Sna	00Sna	01Sna	99Pik	00Pik	01Pik
Oki23							<b>.</b> -		1				
	1	0.090	0.080	0.080	0.097	0.062	0.095	0.088	0.071	0.048	0.133	0.118	0.136
	2				0.006							0.006	
	3 ⊿	0 0 0 5	0.000	0.850	0.860	0.014	0.874	0.856	0.976	0.807	0.820	0.000	0.700
	4	0.005	0.900	0.850	0.809	0.914	0.0/4	0.830	0.870	0.097	0.820	0.071	0.799
	6	0.026	0.020	0.011	0.028	0.025	0.031	0.057	0.053	0.055	0.047	0.006	0.064
	U	0.020	0.020	0.020	0.020	0.025	0.051	0.007	0.000	0.000	0.017	0.000	0.001
Oke8													
	1	0.026	0.067	0.053	0.075	0.051	0.050	0.059	0.046	0.030	0.047	0.038	0.064
	2										0.007		
	3	0.974	0.933	0.947	0.914	0.936	0.946	0.941	0.950	0.947	0.947	0.962	0.936
	4				0.011	0.013	0.004		0.005	0.023			
Oke3													
	1	0.014	0.021	0.004	0.006	0.013	0.004	0.022			0.021	0.007	0.003
	2	0.014	0.059	0.064	0.083	0.099	0.048	0.043	0.037	0.028	0.068	0.046	0.106
	3	0.270	0.245	0.189	0.315	0.283	0.315	0.228	0.296	0.299	0.281	0.270	0.276
	4	0.081	0.138	0.114	0.095	0.092	0.141	0.109	0.106	0.165	0.116	0.099	0.098
	5	0.412	0.335	0.348	0.345	0.368	0.310	0.391	0.356	0.291	0.3/7	0.368	0.348
	0	0.189	0.144	0.250	0.119	0.125	0.125	0.152	0.181	0.1/3	0.110	0.158	0.144
	/ 0	0.014	0.045	0.019	0.050	0.007	0.052	0.045	0.025	0.055	0.014	0.040	0.014
	0	0.007	0.010	0.011	0.000	0.015	0.024	0.011		0.008	0.007	0.007	0.011
Oke4													
one r	2	0.082	0.036	0.065	0.042	0.025	0 048	0.065	0 041	0 075	0 041	0.018	0.029
	3	0.904	0.943	0.912	0.935	0.911	0.929	0.880	0.917	0.862	0.959	0.976	0.963
	4	0.014	0.021	0.023	0.024	0.051	0.024	0.054	0.032	0.059		0.006	0.009
	5								0.009	0.004			
	6					0.013							
Ots2.1	L												
	1	0.048	0.086	0.058	0.063	0.048	0.057	0.060	0.044	0.054	0.034	0.071	0.069
	2	0.952	0.914	0.942	0.938	0.952	0.943	0.940	0.956	0.946	0.966	0.929	0.931
0.01													
Ots2.1	U	0.5(0	0 5 4 4	0.565	0.550	0 5 40	0.521	0 5 4 5	0.521	0.500	0.567	0.570	0.506
	1	0.568	0.544	0.365	0.558	0.549	0.531	0.545	0.531	0.529	0.56/	0.572	0.596
	2	0.006		0.004		0.006			0.004	0.004	0.015		
	3 1	0.000		0.004		0.000	0.004		0.004	0.004		0.006	0.011
	+ 5	0 1 2 3	0 1 8 0	0 185	0 151	0 160	0.004	0 235	0 212	0 213	0 102	0.163	0.167
	6	0.123	0.100	0.105	0.131	0.272	0.204	0.200	0.212	0.215	0.195	0.103	0.220
	7	0.006	0.005		J.27J	0.006			0.004				
	8	0.019	0.010	0.008	0.017	0.006	0.023	0.020	0.004	0.007	0.013	0.006	0.006
	9		0.005										

Appendix 2 cont.

Locus												
\allele	99Eld	00Eld	01Eld	99Pil	00Pil	01Pil	99Sna	00Sna	01Sna	99Pik	00Pik	01Pik
Oke11												
	1 0.110	0.085	0.077	0.132	0.093	0.080	0.071	0.044	0.069	0.056	0.077	0.047
	2 0.128	0.065	0.069	0.040	0.056	0.042	0.051	0.044	0.053	0.111	0.065	0.069
	3 0.146	0.190	0.169	0.167	0.185	0.153	0.194	0.248	0.141	0.215	0.226	0.185
	4 0.567	0.620	0.631	0.586	0.574	0.679	0.622	0.602	0.637	0.583	0.542	0.666
	5 0.043	0.030	0.050	0.069	0.086	0.042	0.056	0.062	0.088	0.028	0.089	0.028
	6 0.006	0.010	0.004	0.006	0.006	0.004	0.005		0.011	0.007		0.006
Ots103												
	1	0.005										
	2 0.006	0.005	0.015	0.011	0.007	0.004	0.010	0.005	0.004		0.006	
	3 0.025	0.024	0.015			0.011	0.010	0.027	0.023	0.007	0.012	0.003
	4 0.013		0.011	0.006	0.033	0.004	0.020	0.036	0.034			0.023
	5 0.076	0.078	0.042	0.051	0.053	0.030	0.100	0.050	0.053	0.007	0.012	0.031
	6 0.063	0.092	0.098	0.084	0.059	0.095	0.110	0.095	0.102	0.063	0.059	0.051
	7 0.063	0.058	0.061	0.067	0.046	0.053	0.065	0.032	0.053	0.069	0.041	0.062
	8 0.044	0.049	0.027	0.084	0.086	0.072	0.070	0.109	0.071	0.056	0.076	0.051
	9 0.019	0.019	0.027	0.028	0.020	0.027	0.010	0.005	0.008	0.035	0.012	0.014
	10 0.013	0.024	0.004	0.006	0.007	0.015		0.005	0.011	0.021	0.024	0.028
1	11 0.006	0.010	0.008	0.017	0.013	0.011			0.008	0.014	0.012	0.045
	12 0.019	0.015	0.008	0.006	0.007	0.019		0.009	0.011			0.003
	13 0.006		0.008			0.008	0.015	0.009	0.004		0.006	0.003
	14		0.008	0.011	0.007	0.008						0.006
	15				0.026	0.015	0.005	0.005	0.004	0.028	0.012	0.028
	16 0 019	0.024	0.004	0.028	0.013	0.015			0.015	0.035	0.024	0.023
-	17 0 013	0.019	0.004	0.028	0.013	0.015	0.010	0.014	0.011	0.021	0.024	0.023
	18	0.005	0.023	0.011		0.004	0.005		0.011	0.007		0.017
	19 0 013	0.015	0.004	0.011	0.007	0.027	0.010	0.014	0.008	0.014		0.006
	20 0 013	0.010	0.004		0.026	0.0027	0.005	0.005	0.000	0.021	0.012	0.003
-	20 0.013	0.010	0.034	0.034	0.020	0.038	0.005	0.005	0.004	0.021	0.012	0.005
-	21 0.044	0.010	0.009	0.004	0.020	0.050	0.040	0.132	0.075	0.020	0.055	0.023
4	22 0.114	0.027	0.078	0.090	0.052	0.000	0.090	0.152	0.004	0.007	0.155	0.085
4	23 0.003	0.121	0.140	0.101	0.000	0.127	0.100	0.071	0.107	0.137	0.000	0.003
4	240.002	0.112	0.100	0.075	0.092	0.045	0.005	0.000	0.071	0.063	0.053	0.070
-	250.127	0.049	0.070	0.090	0.092	0.043	0.070	0.045	0.071	0.003	0.033	0.079
4	200.013	0.034	0.049	0.045	0.020	0.023	0.035	0.030	0.011	0.003	0.047	0.031
4	27 0.052	0.024	0.013	0.000	0.020	0.013	0.023	0.014	0.004	0.007	0.033	0.023
4	200.000	0.010	0.008	0.022	0.020	0.025	0.015	0.003	0.025	0.014	0.047	0.028
4	290.023	0.010	0.034	0.011	0.039	0.019	0.023	0.025	0.013	0.014	0.018	0.040
-	50 0.015	0.005		0.011		0.011	0.030	0.018	0.008	0.021	0.024	0.000
-	01 U.U32	0.005	0.015	0.017	0.020	0.02/	0.005	0.005	0.004		0.012	0.014
-	52 U.UU6	0.010	0.008	0.01/	0.007	0.004			0.004	0.014		0.011
-	33 24 0 00C	0.010			0.00/	0.008	0.010	0.005			0.006	0.003
-	54 0.006	0.005				0.004	0.015			0.021	0.012	0.011
-	35 0.006	0.029	0.019	0.011	0.033	0.015	0.015	0.045	0.041			0.011
-	36 0.019	0.010	0.023		0.007	0.004	0.010	0.014	0.011	0.021	0.018	0.006
-	5/	0.005	0.004	0.011	0.013			0.005	0.004	0.007	0.006	0.006
	38			0.006						0.007		

Appendix 2 cont.

Locus												
\allele	99Eld	00Eld	01Eld	99Pil	00Pil	01Pil	99Sna	00Sna	01Sna	99Pik	00Pik	01Pik
3	39									0.007		
4	0		0.004									
<i>Oki1L</i>												
	1 0.256	0.255	0.210	0.233	0.207	0.194	0.222	0.224	0.211	0.295	0.244	0.210
	2 0.714	0.722	0.732	0.744	0.762	0.761	0.742	0.737	0.767	0.699	0.744	0.766
	3 0.030	0.019	0.054	0.022	0.030	0.045	0.035	0.039	0.023	0.007	0.012	0.024
	4	0.005	0.004									
	-											
0ki1U												
	1						0.010					
	2		0.012							0.036		
	$\frac{1}{3}$ 0 044	0.054	0.062	0.097	0.095	0.080	0.062	0.040	0.038	0 121	0.095	0.075
	4 0 025	0.020	0.019	0.028	0.025	0.027	0.031	0.018	0.015	0.007	0.018	0.011
	5 0 101	0.108	0.127	0.063	0.082	0.088	0.134	0.173	0.178	0.064	0.107	0.098
	6 0 044	0.127	0.058	0.001	0.095	0.107	0.093	0.080	0.114	0.093	0.060	0.075
	7 0 057	0.098	0.054	0.057	0.057	0.073	0.067	0.080	0.068	0.043	0.054	0.075
	8 0 076	0.039	0.001	0.068	0.063	0.076	0.007	0.058	0.053	0.129	0.021	0.095
	9 0 108	0.057	0.096	0.000	0.003	0.070	0.119	0.000	0.035	0.064	0.137	0.115
1	0.0.130	0.137	0.123	0.100	0.005	0.130	0.119	0.075	0.123	0.004	0.119	0.119
1	1 0 165	0.137	0.125	0.123	0.104	0.103	0.130	0.120	0.114	0.130	0.117	0.12)
1	2 0 1 2 2	0.142	0.119	0.114	0.120	0.105	0.139	0.102	0.100	0.057	0.107	0.000
1	2 0.133	0.009	0.000	0.131	0.070	0.093	0.098	0.093	0.001	0.037	0.107	0.105
1	4 0 006	0.020	0.031	0.025	0.038	0.023	0.031	0.022	0.042	0.030	0.030	0.040
1	5 0 0 1 1	0.010	0.015	0.017	0.015	0.008	0.020	0.022	0.025	0.050	0.018	0.034
1	5 0.044	0.054	0.050	0.051	0.032	0.038	0.010	0.031	0.008	0.014	0.024	0.011
1	0.000	0.025	0.019	0.011	0.006	0.019	0.005	0.027	0.011	0.014	0.012	0.017
1	0.0.005	0.025	0.004		0.006	0.008		0.004	0.004	0.007	0.012	0.017
1	8 0.025	0.025	0.012	0.006	0.025	0.019	0.015	0.022	0.027	0.021	0.036	0.009
1	9 0.013	0.010	0.008	0.011	0.013	0.015	0.005	0.009	0.008	0.007	0.018	0.006
2	20				0.006	0.004	0.005		0.004			0.003
2	.2								0.004			
01.100												
<i>Oki100</i>	1										0.000	
	1	0.120									0.006	
	2 0.054	0.120	0.083	0.060	0.058	0.081	0.073	0.080	0.09/	0.014	0.043	0.035
	3 0.196	0.120	0.230	0.196	0.173	0.223	0.120	0.119	0.180	0.214	0.185	0.187
	4 0.012	0.009	0.018	0.006	0.013	0.008			0.022	0.036	0.025	0.029
	5 0.030	0.032	0.018	0.036	0.019	0.042	0.031	0.018	0.029	0.021	0.019	0.016
	6 0.060	0.046	0.072	0.119	0.083	0.108	0.073	0.071	0.054	0.071	0.080	0.096
	7 0.060	0.074	0.076	0.095	0.064	0.023	0.104	0.093	0.119	0.029	0.068	0.051
	8 0.119	0.125	0.072	0.071	0.090	0.104	0.083	0.071	0.065	0.086	0.068	0.075
	9 0.101	0.120	0.097	0.101	0.103	0.112	0.135	0.124	0.122	0.114	0.167	0.147
1	0 0.107	0.111	0.104	0.077	0.058	0.085	0.068	0.119	0.076	0.093	0.074	0.078
1	1 0.036	0.028	0.040	0.024	0.071	0.046	0.042	0.093	0.072	0.057	0.031	0.027
1	2 0.024	0.009	0.032	0.071	0.038	0.046	0.052	0.027	0.014	0.050	0.056	0.045
1	3 0.042	0.069	0.040	0.036	0.032	0.027	0.042	0.035	0.047	0.043	0.031	0.032
1	4 0.065	0.014	0.043	0.036	0.064	0.019	0.026	0.035	0.022	0.050	0.037	0.043
1	5 0.024	0.046	0.018	0.024	0.045	0.023	0.089	0.035	0.043	0.029	0.037	0.027

Appendix 2 cont.

Locus													
\allele		99Eld	00Eld	01Eld	99Pil	00Pil	01Pil	99Sna	00Sna	01Sna	99Pik	00Pik	01Pik
	16	0.030	0.014	0.014	0.018	0.026	0.023		0.027	0.022	0.014	0.019	0.032
	17		0.005	0.014		0.013	0.008	0.010	0.013		0.029		0.043
	18	0.012	0.005	0.014	0.006	0.015	0.012	0.021	0.013	0.014	0.027	0.012	0.011
	10	0.012	0.010	0.014	0.000	0.000	0.012	0.021	0.004	0.014	0.007	0.012	0.011
	19	0.000	0.019	0.004	0.000	0.000		0.010	0.018		0.021	0.023	0.003
	20		0.009							0.004	0.014	0.019	0.011
	21	0.006	0.023	0.004		0.013	0.008		0.009				0.003
	22	0.018	0.005	0.007	0.012	0.013		0.005	0.009				0.003
	23				0.006	0.013	0.004	0.005					0.003
	24										0.007		0.003
	25							0.005					
Oki2													
	2	0.006	0.014	0.026	0.006	0.030				0.004			0.008
	3				0.006			0.005		0.007			0.005
	4	0 024	0.033	0.048	0.034	0.043	0.020	0.015	0.013	0.022	0.033	0.019	0.052
	5	0.224	0 1 8 0	0 141	0.155	0.165	0 1 1 3	0.153	0 1 8 0	0.156	0 147	0.156	0.142
	6	0.1220	0.00/	0 1 1 0	0.155	0.001	0.125	0.087	0.057	0.079	0 1 1 2	0.112	0.127
	7	0.122	0.094	0.119	0.009	0.091	0.123	0.087	0.037	0.078	0.113	0.113	0.137
	/	0.091	0.100	0.150	0.107	0.140	0.132	0.179	0.149	0.130	0.115	0.000	0.090
	8	0.091	0.108	0.096	0.121	0.104	0.102	0.102	0.088	0.122	0.120	0.113	0.123
	9	0.171	0.118	0.107	0.161	0.165	0.156	0.071	0.110	0.104	0.133	0.100	0.126
	10	0.037	0.038	0.074	0.063	0.061	0.047	0.046	0.053	0.022	0.087	0.063	0.038
	11	0.085	0.066	0.081	0.063	0.049	0.113	0.087	0.145	0.078	0.100	0.094	0.101
	12	0.049	0.047	0.059	0.063	0.079	0.086	0.097	0.083	0.070	0.060	0.169	0.087
	13	0.061	0.090	0.096	0.046	0.055	0.051	0.122	0.105	0.163	0.053	0.050	0.077
	14	0.018	0.028	0.019	0.034	0.006	0.016	0.020	0.004	0.011	0.040	0.038	0.011
	15	0.018	0.005	0.004	0.006		0.008	0.015	0.009	0.007			0.003
	16					0.006							
	17		0.005		0.006		0.012		0.004				
	18		0.005										
	10		0.002										
Omv1	01												
Siny1	ົາ 2	0.012	0.010	0.007	0.017	0.013	0.008	0.026	0.018	0.025	0.042	0.024	0.022
	1	0.012	0.010	0.007	0.017	0.013	0.000	0.020	0.010	0.020	0.042	0.024	0.022
	4	0.029	0.010	0.022	0.017	0.052	0.013	0.020	0.020	0.029	0.014	0.018	0.008
	2	0.041	0.019	0.022	0.022	0.05/	0.019	0.041	0.048	0.008	0.077	0.0004	0.054
	6	0.124	0.143	0.081	0.129	0.114	0.124	0.112	0.083	0.098	0.092	0.108	0.113
	7	0.135	0.167	0.152	0.197	0.133	0.244	0.148	0.211	0.123	0.190	0.145	0.172
	8	0.088	0.033	0.052	0.056	0.089	0.034	0.051	0.075	0.076	0.021	0.060	0.059
	9	0.018	0.052	0.093	0.039	0.006	0.011	0.031	0.022	0.033	0.028	0.036	0.043
	10	0.071	0.071	0.052	0.062	0.076	0.049	0.061	0.075	0.051	0.063	0.054	0.048
	11	0.112	0.067	0.059	0.045	0.082	0.083	0.046	0.057	0.054	0.042	0.066	0.083
	12	0.035	0.014	0.048	0.067	0.044	0.038	0.041	0.026	0.022	0.042	0.048	0.043
	13	0.035	0.019	0.019	0.011	0.013	0.034	0.051	0.022	0.036	0.021	0.012	0.035
	14	0.018	0.071	0.048	0.073	0.044	0.030	0.066	0.039	0.043	0.042	0.048	0.051
	15	0.041	0.071	0.041	0.034	0.038	0.034	0.051	0.057	0.076	0.070	0.060	0.048
	16	0.029	0.043	0.044	0.022	0.044	0.053	0.051	0.035	0.069	0.049	0.042	0.038

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Appendix 2 cont.

Locus	5												
\allele	;	99Eld	00Eld	01Eld	99Pil	00Pil	01Pil	99Sna	00Sna	01Sna	99Pik	00Pik	01Pik
	20	0.024	0.019	0.033	0.028	0.019	0.019	0.005	0.009	0.007	0.021	0.012	0.013
	21	0.041	0.057	0.041	0.022	0.019	0.034	0.046	0.022	0.047	0.021	0.012	0.008
	22		0.005		0.011	0.019	0.008		0.018	0.007	0.007	0.024	0.005
	23			0.019	0.006	0.006	0.004		0.009	0.004	0.014	0.006	0.005
	24	0.006								0.004	0.007	0.006	0.005
	25			0 004								0.006	0.003
	26			0.004		0.006	0.004						
	27						0.011	0.005		0 004	0.007		
	28							0.005					
	20			0.007									
	2)			0.007									
()no11	01												
oner		0 232	0.236	0 204	0 176	0 198	0 201	0 1 7 0	0 177	0 191	0 196	0 235	0.182
	3	0.036	0.052	0.019	0.034	0.170	0.011	0.025	0.040	0.037	0.120	0.018	0.019
	4	0.050	0.052	0.017	0.054	0.012	0.011	0.025	0.040	0.057	0.020	0.010	0.017
	- - -		0.005	0.004			0.004	0.005		0.004	0.007		
	6	0 137	0.005	0.148	0.216	0 1 7 9	0.004	0.005	0.181	0.004	0.007	0.124	0.106
	7	0.137	0.157	0.140	0.210	0.179	0.223	0.175	0.101	0.100	0.108	0.124	0.100
	0	0.077	0.032	0.074	0.057	0.050	0.004	0.050	0.071	0.040	0.034	0.100	0.079
	0	0.101	0.125	0.107	0.133	0.142	0.129	0.200	0.101	0.131	0.120	0.100	0.109
	10	0.000	0.085	0.078	0.008	0.080	0.001	0.145	0.095	0.092	0.101	0.071	0.109
	10				0.000	0.019	0.004	0.025	0.009	0.007	0.027	0.006	0.011
	11		0.019	0.011	0.01/	0.012	0.011	0.025	0.035	0.029	0.014	0.006	0.022
	12	0.060	0.014	0.030	0.028	0.049	0.019	0.025	0.022	0.022	0.068	0.024	0.038
	13	0.018	0.019	0.030	0.006	0.012	0.019	0.030	0.040	0.011	0.034	0.041	0.049
	14		0.014	0.022	0.011	0.012	0.011	0.035	0.027	0.040		0.012	0.016
	15	0.006	0.009	0.007		0.006	0.019			0.004	0.014	0.012	0.014
	16	0.036	0.009	0.022	0.023	0.025	0.034	0.005	0.013	0.011	0.068	0.024	0.043
	17	0.024	0.024		0.023	0.031	0.038	0.015	0.009	0.022	0.014	0.041	0.027
	18	0.006	0.009	0.015	0.011	0.037	0.011	0.010			0.041	0.029	0.022
	19	0.018	0.019	0.026	0.011	0.012			0.004	0.018	0.007	0.012	0.024
	20		0.009	0.007	0.011	0.019	0.019		0.004	0.004	0.007		0.014
	21	0.030	0.019	0.011	0.011	0.006	0.038		0.004	0.011	0.007	0.024	0.016
	22	0.006	0.028	0.030	0.011	0.019	0.004	0.005	0.009	0.004	0.014		0.016
	23	0.030	0.005	0.004	0.006	0.025	0.011	0.010	0.018	0.011	0.007	0.006	0.019
	24	0.012	0.019	0.007	0.034		0.027	0.015	0.031	0.011	0.014	0.029	0.008
	25	0.012	0.019	0.022	0.017	0.012		0.020	0.009	0.026		0.018	0.005
	26	0.006	0.009	0.015	0.011	0.006	0.011	0.010		0.015	0.020	0.012	0.011
	27	0.018	0.038	0.019	0.034	0.012	0.011	0.015	0.013	0.040	0.020	0.024	0.019
	28	0.018	0.005	0.011	0.011	0.006	0.011	0.010				0.018	0.014
	29		0.005	0.011			0.008						
	30		0.009	0.004							0.007		
	31				0.006				0.004				
	32		0.009							0.004		0.006	0.008
	33			0.004	0.006	0.006			0.004	0.007	0.007		
Onall	0.2												

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1	 	0.006	 0.004	0.005	 	 0.006	
2	 		 		 0.004	 	

Appendix 2 cont.

Locus	

\allele	99	9Eld	00Eld	01Eld	99Pil	00Pil	01Pil	99Sna	00Sna	01Sna	99Pik	00Pik	01Pik
	3 0.	012				0.006	0.004			0.004	0.007	0.006	0.005
	4 0.	006	0.019	0.008	0.011	0.019	0.041	0.020	0.043	0.011	0.020	0.041	0.013
	5 0.	065	0.065	0.045	0.050	0.043	0.067	0.035	0.026	0.040	0.014	0.041	0.040
	6 0.	113	0.121	0.125	0.089	0.086	0.075	0.095	0.112	0.076	0.095	0.081	0.091
	7 0.	149	0.117	0.140	0.117	0.123	0.116	0.140	0.112	0.133	0.162	0.122	0.160
	8 0.	083	0.107	0.072	0.117	0.099	0.108	0.105	0.086	0.068	0.088	0.076	0.102
	90.	131	0.075	0.083	0.117	0.074	0.067	0.115	0.138	0.147	0.115	0.099	0.128
	10 0.	137	0.121	0.102	0.111	0.136	0.123	0.090	0.116	0.133	0.074	0.093	0.083
	11 0.	113	0.079	0.106	0.117	0.086	0.116	0.095	0.129	0.119	0.142	0.105	0.078
	12 0.	083	0.107	0.098	0.122	0.117	0.082	0.100	0.091	0.086	0.115	0.081	0.083
	13 0.	042	0.056	0.042	0.067	0.074	0.075	0.090	0.039	0.036	0.041	0.081	0.080
	14 0.	036	0.061	0.083	0.033	0.049	0.056	0.085	0.056	0.079	0.047	0.076	0.048
	15 0.	012	0.047	0.049	0.017	0.043	0.037	0.010	0.017	0.036	0.034	0.052	0.045
	16 0.	018	0.019	0.034	0.017	0.019	0.019	0.015	0.026	0.014	0.020	0.023	0.011
	17	-	0.005	0.008		0.006	0.004		0.009	0.004	0.007	0.006	0.016
	18	-									0.020	0.012	0.008
	19	-		0.004	0.011	0.006	0.007			0.007			0.008
	20	-				0.012				0.004			
One10	)4												
	2	-											0.003
	3 0.	006	0.019	0.014	0.006		0.008	0.010	0.009	0.015	0.007		0.005
	4 0.	018	0.009	0.022	0.023	0.025	0.015	0.081	0.083	0.059	0.047	0.042	0.032
	5 0.	071	0.097	0.129	0.165	0.144	0.126	0.126	0.096	0.121	0.196	0.095	0.139
	60.	153	0.139	0.129	0.148	0.100	0.118	0.136	0.162	0.125	0.115	0.149	0.134
	7 0.	059	0.060	0.047	0.045	0.031	0.088	0.025	0.039	0.029	0.054	0.048	0.056
	8 0.	012	0.032	0.018	0.006	0.025	0.027	0.025	0.031	0.029	0.007	0.054	0.035
	90.	029	0.019	0.032	0.063	0.031	0.053	0.025	0.009	0.026	0.041	0.030	0.032
	10 0.	047	0.032	0.043	0.045	0.063	0.050	0.010	0.048	0.029	0.027	0.030	0.035
	11 0.	024	0.028	0.032	0.028	0.019	0.031	0.005	0.004	0.015	0.007	0.012	0.024
	12 0.	035	0.037	0.036	0.051	0.069	0.015	0.005	0.035	0.037	0.034	0.024	0.032
	13 0.	041	0.032	0.043	0.051	0.025	0.034	0.035	0.044	0.022	0.034	0.030	0.024
	14 0.	088	0.056	0.072	0.034	0.050	0.038	0.056	0.026	0.048	0.014	0.042	0.040
	15 0.	018	0.037	0.040	0.028	0.031	0.053	0.025	0.044	0.037	0.074	0.083	0.061
	16 0.	029	0.065	0.025	0.040	0.069	0.038	0.111	0.079	0.081	0.047	0.089	0.070
	17 0.	106	0.088	0.086	0.063	0.044	0.042	0.076	0.048	0.070	0.101	0.054	0.067
	18 0.	065	0.069	0.061	0.057	0.094	0.076	0.051	0.057	0.074	0.061	0.048	0.056
	19 0.	065	0.060	0.047	0.040	0.069	0.050	0.071	0.070	0.110	0.034	0.060	0.040
	20 0.	047	0.046	0.047	0.028	0.050	0.046	0.066	0.031	0.033	0.027	0.030	0.037
	21 0.	024	0.009	0.018	0.017	0.019	0.046	0.015	0.039	0.011	0.027	0.024	0.029
	22 0.	012	0.023	0.018	0.023	0.013	0.019	0.005	0.004	0.011	0.020	0.030	0.035
	23 0.	006	0.005	0.007	0.011	0.025	0.011	0.010	0.013	0.004		0.006	0.011
	24 0.	024	0.028	0.022	0.017	0.006		0.020	0.022	0.015	0.014	0.012	
	25 0.	012	0.005	0.004	0.011		0.004	0.005			0.014	0.006	0.003
	26 0.	006	0.005	0.004			0.004	0.005					
	27 0.	006							0.004				
	28	-		0.004									
	29	-					0.004						

Appendix 2 cont.

Locus	5												
\allele	e 99	9Eld	00Eld	01Eld	99Pil	00Pil	01Pil	99Sna	00Sna	01Sna	99Pik	00Pik	01Pik
	30	-					0.004					0.006	
Onel	14												
	1 0.	012	0.005	0.004	0.006			0.010	0.013	0.015		0.012	0.014
	2 0.	042	0.037	0.014	0.022	0.019	0.008	0.030	0.039	0.038	0.029	0.012	0.014
	3 0.	012	0.014	0.025	0.056	0.038	0.042	0.040	0.022	0.008	0.043	0.049	0.043
	4 0.	018				0.013	0.008				0.021	0.006	0.008
	5 0.	006	0.005				0.004	0.005		0.004	0.014	0.006	0.016
	6 0.	048	0.019	0.014	0.028	0.032	0.019	0.015	0.039	0.019	0.007	0.030	0.027
	70.	036	0.056	0.050	0.039	0.032	0.046	0.030	0.048	0.038	0.050	0.055	0.043
	8 0.	089	0.103	0.072	0.083	0.070	0.073	0.085	0.087	0.038	0.136	0.134	0.095
	90.	119	0.107	0.144	0.100	0.127	0.156	0.110	0.178	0.174	0.100	0.067	0.116
	10 0.	101	0.089	0.079	0.072	0.101	0.118	0.100	0.074	0.125	0.136	0.122	0.105
	11 0.	.095	0.084	0.122	0.111	0.070	0.099	0.095	0.104	0.068	0.064	0.104	0.081
	12 0.	071	0.093	0.065	0.078	0.089	0.073	0.090	0.096	0.080	0.057	0.061	0.089
	13 0.	083	0.112	0.083	0.106	0.070	0.065	0.060	0.074	0.068	0.050	0.067	0.076
	14 0.	036	0.061	0.061	0.039	0.063	0.061	0.070	0.057	0.072	0.036	0.037	0.032
	15 0.	048	0.037	0.076	0.050	0.051	0.061	0.090	0.052	0.068	0.071	0.091	0.084
	16 0.	083	0.075	0.108	0.056	0.076	0.057	0.070	0.057	0.114	0.057	0.073	0.062
	17 0.	024	0.042	0.029	0.028	0.019	0.034	0.030	0.013	0.019	0.029	0.037	0.038
	18 0.	018	0.019	0.011	0.017	0.044	0.023	0.030	0.026	0.019	0.029	0.006	0.019
	19 0.	018	0.009	0.007	0.006	0.019	0.008	0.005		0.008	0.014		0.005
	20 0.	006	0.005	0.004	0.017	0.006	0.008	0.025	0.004		0.014		0.008
	21	-		0.007	0.011	0.006	0.015			0.008	0.007	0.006	
	22	-	0.005		0.011			0.005	0.004	0.011		0.006	
	23 0.	006		0.004								0.006	
	24	-	0.005										
	25 0.	006		0.004	0.033	0.013	0.004	0.005	0.004	0.004	0.007	0.006	0.005
	26 0.	012		0.007	0.017	0.025	0.004		0.009	0.004			
	27	-										0.006	0.003
	29	-			0.006	0.006	0.008						
	31	-	0.005										
	32 0.	012	0.005	0.011			0.004						
	33	-			0.006						0.007		0.003
	35	-				0.006							
	36	-			0.006								
	39	-				0.006							
	40	-									0.014		0.005
	41	-	0.005										0.005
	42	-					0.004						
	43	-									0.007		0.003
	44	-	0.005										
Ots3	-									0.00.			
	2	-								0.004			
	30.	018	0.033	0.043	0.006	0.042	0.015	0.075	0.043	0.050	0.027	0.035	0.008
	4	-	0.024	0.004	0.011	0.012	0.019		0.004	0.011			0.003

Appendix 2 cont.

Locus												
\allele	99Eld	00Eld	01Eld	99Pil	00Pil	01Pil	99Sna	00Sna	01Sna	99Pik	00Pik	01Pik
6	0.024	0.009	0.040	0.056	0.030	0.038	0.020	0.030	0.029	0.055	0.041	0.054
7	'	0.005		0.028	0.006				0.004		0.006	0.005
8	0.335	0.396	0.349	0.361	0.416	0.352	0.320	0.323	0.349	0.295	0.343	0.325
9	0.041	0.024	0.050	0.039	0.024	0.030	0.005	0.022	0.043	0.027	0.023	0.011
10	0.018	0.009	0.018	0.011	0.048	0.019	0.015	0.022	0.018	0.021	0.041	0.032
11	0.153	0.080	0.126	0.083	0.054	0.117	0.145	0.147	0.119	0.103	0.140	0.140
12		0.009	0.014	0.006	0.012	0.008	0.015	0.017	0.011	0.007	0.047	0.024
13	0.365	0.349	0.313	0.367	0.319	0.337	0.290	0.306	0.284	0.411	0.302	0.325
14	0.012	0.014	0.004			0.011	0.035	0.039	0.014	0.007	0.006	0.005
15	0.006	0.014	0.004	0.006	0.006		0.005	0.004	0.011	0.007		0.003
16	0.012	0.014	0.007	0.017	0.006	0.008	0.020	0.026	0.025	0.021	0.017	0.022
17	0.018	0.014	0.022	0.006	0.024	0.023	0.040	0.009	0.014	0.021		0.043
18				0.006		0.004						
19	)						0.005					
Otsg68												
1		0.005	0.004			0.015		0.022	0.022			0.003
2		0.005	0.007									
3	0.024		0.007	0.017	0.024	0.026	0.015	0.004	0.007	0.021	0.018	0.024
4	0.006	0.037	0.040	0.028	0.012	0.038	0.010	0.027	0.007	0.014	0.012	0.030
5	0.089	0.111	0.059	0.050	0.049	0.038	0.092	0.106	0.101	0.100	0.065	0.111
6	0.054	0.037	0.055	0.150	0.152	0.094	0.071	0.093	0.094	0.093	0.112	0.095
7	0.101	0.083	0.114	0.089	0.067	0.117	0.199	0.146	0.115	0.100	0.088	0.111
8	0.077	0.097	0.103	0.067	0.091	0.086	0.082	0.137	0.086	0.071	0.135	0.092
9	0.042	0.088	0.066	0.044	0.061	0.071	0.071	0.027	0.043	0.036	0.018	0.046
10	0.024	0.028	0.033	0.044	0.024	0.034	0.031	0.027	0.036	0.036	0.006	0.019
11	0.024	0.019	0.015	0.028	0.030	0.011	0.010	0.009	0.014	0.014	0.018	0.016
12	0.018	0.023	0.015	0.033	0.012	0.019	0.041	0.022	0.043	0.043	0.035	0.011
13	0.036	0.042	0.033	0.044	0.049	0.045	0.031	0.022	0.036	0.007	0.012	0.024
14	0.030	0.005	0.011			0.004	0.015	0.009	0.014	0.021	0.029	0.022
15	0.006	0.005	0.007	0.011	0.012					0.007		
16	0.006	0.005		0.011		0.004		0.009	0.011		0.006	0.003
17	'				0.006						0.018	0.016
18	0.006	0.028	0.022	0.011	0.030	0.004	0.005	0.022	0.004	0.029	0.012	0.005
19	0.030	0.028	0.018	0.011	0.012	0.026	0.020	0.027	0.029	0.014	0.024	0.014
20	0.024	0.009	0.015	0.022	0.024	0.008	0.010	0.013	0.029	0.014	0.012	0.027
21	0.089	0.028	0.044	0.022	0.012	0.019	0.031	0.013	0.025	0.014	0.024	0.022
22	0.018	0.042	0.033	0.022	0.012	0.026	0.026	0.022	0.029	0.014		0.016
23	0.024	0.009	0.018	0.017	0.037	0.008	0.056	0.058	0.040	0.043	0.024	0.014
24	0.071	0.051	0.059	0.044	0.030	0.034	0.020	0.022	0.029	0.036	0.059	0.038
25	0.036	0.023	0.055	0.022	0.030	0.056	0.036	0.027	0.047	0.050	0.018	0.068
26	0.089	0.056	0.077	0.050	0.055	0.049	0.041	0.066	0.032	0.086	0.106	0.043
27	0.006	0.032	0.015	0.028	0.043	0.053	0.010	0.022	0.025	0.071	0.041	0.038
28	0.012	0.009	0.026		0.012	0.038	0.036	0.004	0.022	0.007	0.029	0.014
29	0.006	0.009		0.039	0.037	0.011	0.005	0.013	0.014	0.014	0.006	0.014
30	)	0.005	0.007	0.011	0.006	0.004		0.004	0.007		0.006	0.008
31		0.005	0.004	0.006	0.012	0.015	0.020	0.009	0.007	0.014	0.024	0.022
32		0.009	0.007	0.011	0.012		0.005				0.024	0.030
Appendix 2 cont.

Locus													
∖allele	;	99Eld	00Eld	01Eld	99Pil	00Pil	01Pil	99Sna	00Sna	01Sna	99Pik	00Pik	01Pik
	33	0.012	0.009	0.011	0.011	0.006	0.019	0.010	0.009	0.011	0.021	0.006	0.003
	34	0.012	0.009			0.024							0.003
	35	0.006	0.009		0.011	0.012			0.004				0.003
	36	0.012	0.014	0.015	0.017		0.008			0.018			
	37		0.005		0.006					0.004		0.006	
	38	0.006	0.019	0.004			0.011		0.004			0.012	
	39	0.006	0.005		0.022		0.004						
	40						0.004						
	41										0.007		
	42						0.004						
S410													
55441	່າ												0.005
	2 1	0.012						0.005					0.005
		0.012		0.014	0.017		0.004	0.005	0.030	0.018	0.007	0.018	0.027
	6	0.010	0.079	0.014	0.017	0.043	0.004	0.020	0.057	0.010	0.007	0.010	0.027
	7	0.351	0.079	0.005	0.051	0.043	0.004	0.072	0.050	0.005	0.041	0.268	0.040
	8	0.149	0.131	0.200	0.182	0.130	0.154	0.097	0.232	0.145	0.176	0.161	0.137
	9	0.145	0.126	0.147	0.165	0.150	0.117	0.027	0.174	0.145	0.101	0.137	0.113
	10	0.095	0.120	0.079	0.063	0.111	0.113	0.138	0.096	0.058	0.101	0.054	0.097
	11	0.060	0.103	0.108	0.005	0.111	0.115	0.092	0.090	0.098	0.095	0.083	0.097
	12	0.077	0.098	0.036	0.045	0.074	0.117	0.051	0.007	0.051	0.095	0.107	0.091
	13	0.054	0.051	0.054	0.045	0.074	0.034	0.051	0.039	0.033	0.001	0.060	0.030
	14	0.018	0.001	0.036	0.068	0.012	0.026	0.000	0.009	0.072	0.020	0.030	0.050
	15	0.006	0.019	0.025	0.023		0.020	0.020	0.005	0.018	0.020	0.012	0.032
	16	0.006	0.009				0.004	0.010		0.004	0.007		0.019
	17										0.014		0.003
	18				0.006		0 004	0.005					
	10				0.000		0.004	0.000					