Genotypic Analyses and Parental Identifications of Hatchery-Origin Pallid Sturgeon in the Upper Missouri River

Phase I: Inheritance of Microsatellite, Nuclear DNA Markers

Final Report

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Patrick W. DeHaan, Donald E. Campton, and William R. Ardren
(Patrick_DeHaan@fws.gov; Don_Campton@fws.gov; William_Ardren@fws.gov)
U.S. Fish and Wildlife Service
Abernathy Fish Technology Center
Conservation Genetics Laboratory
1440 Abernathy Creek Road
Longview, WA 98632
TEL: 360-425-6072; FAX: 360-636-1855

Submitted to: Steven Krentz (Steven_Krentz@fws.gov)
U.S. Fish and Wildlife Service
Bismarck, North Dakota

Greg Pratschner (Greg_Pratschner@fws.gov)
U.S. Fish & Wildlife Service
Denver, Colorado

Genotypic Analyses and Parental Identifications of Juvenile and Sub-adult Pallid Sturgeon in the Upper Missouri River

Background

The U.S. Fish and Wildlife Service ("Service") listed pallid sturgeon (*Scaphirhynchus albus*) as endangered in 1990 under the U.S. Endangered Species Act (USFWS 1990). Pallid sturgeon are now considered highly endangered and on the verge of extinction in parts of their native range. This critical status is due largely to little or no natural reproduction or insufficient recruitment during the past 25-30 years.

As part of the Recovery Plan for pallid sturgeon, an artificial propagation program has been developed for fish inhabiting the upper Missouri River[1]. Each year wild adults are collected for broodstock by gill net sampling, spawned in a hatchery, and returned to the upper Missouri River in the general vicinity where they were trapped. Approximately 20-30 adults are trapped each year for broodstock. The juveniles are then reared in fish hatcheries prior to their release into the upper Missouri River.

Until recently, all hatchery-produced pallid sturgeon resulting from artificial spawning were given a *passive integrative transponder* (PIT) or elastomer tag prior to release. Full sibs resulting from each single pair (1 male: 1 female) mating were maintained together until they were large enough to be physically tagged. The need to tag all hatchery-produced pallid sturgeon constrained the number of fish that could be released each year, however. Previously, raising fish to a markable size has greatly increased the likelihood that pallid sturgeon irrdovirus will express and there has been reluctance to stocking fish that test positive for this virus. Additionally, because of hatchery space constraints, to maintain rearing densities it is often necessary to sacrifice juvenile fish before they have reached a markable size and can be stocked.

This report describes the results of a study designed to demonstrate the Mendelian genetic inheritance of microsatellite, nuclear DNA markers in pallid sturgeon. The long-term goal of this work is to use DNA markers as "genetic tags" to identify hatchery-produced pallid sturgeon (via parentage analysis) that are released and recaptured in the Missouri River. The

[1] The upper Missouri River is defined here as the region upstream from Fort Peck Dam and Reservoir and immediately below Fort Peck Dam, including the confluence of the Missouri and Yellowstone Rivers and the Yellowstone River.

use of DNA markers to identify hatchery-origin pallid sturgeon will supplement the need to physically tag individual fish prior to release. This will allow substantially greater numbers of fish to be released each year while at the same time reducing the risks that juvenile sturgeon will contract irrodovirus. Moreover, in contrast to physical tags, sturgeon don't shed "DNA tags" thus increasing substantially the probability of accurate identifications.

Objective 1. Identify a suite of microsatellite loci for distinguishing pallid and shovelnose sturgeon in the upper Missouri River with a 99% probability of correct assignment.

Tranah et al. (2004) used nine, *tetranucleotide-repeat* microsatellite loci to discriminate pallid and shovelnose sturgeon in the upper Missouri River with an 82 to 95% probability of correct assignment (Table 1). Four of those loci were developed from pallid/shovelnose sturgeon (McQuown et al. 2000), four were developed from lake sturgeon (*Acipenser fulvescens*) (May et al. 1997), and one from Atlantic sturgeon (*A. oxyrhynchus*) (King et al. 2001). Additional loci, or a different suite of loci, will be necessary to obtain a probability of correct assignment greater than 0.99.

In addition, Heist and Schrey (2004) used 11 *dinucleotide-repeat* microsatellite loci to discriminate pallid and shovelnose sturgeon in the upper Missouri and mid-Mississippi rivers. There was no overlap between the loci used in the Tranah (2004) paper and the loci used in the Heist and Schrey (2004) report. Using their set of 11 microsatellite loci, these latter investigators were able to correctly assign an individual to its morphological classification between 88 and 100% of the time for the middle Mississippi and upper Missouri Rivers.

Materials and Methods

We initially screened the following 27 microsatellite loci for their ability to amplify via the *polymerase chain reaction* (PCR) in pallid sturgeon: *Spl12, Spl15, Spl7, Spl18, Spl19, Spl26, Spl30, Spl34, Spl35, Spl36, Spl40, Spl53, Spl56, Spl60, Spl101, Spl105, Spl106, Spl115, Spl119, Spl158, Spl169, Spl173* (McQuown et al. 2000), *Afu19, Afu34, Afu57, Afu68* (May et al. 1997) and *Aox27* (King et al. 2001). This suite of loci included all the loci used by Tranah et al. (2004) and all the loci used by Heist and Schrey (2004). DNA from each specimen at each locus was amplified via PCR in 15ul volumes. Each reaction contained 2ul template DNA, 10X PCR

buffer, 0.2mM dNTPs, 0.5uM of the forward and reverse primers for that locus, and 0.2 units of *Taq* polymerase. Reactions were carried out over a DNA annealing temperature gradient ranging from 50^{o} C to 60^{o} C. We also tested two $MgCl_2$ concentrations: 1.5 mM and 2.0mM. PCR conditions were as follows: an initial DNA denaturation at 94^{o} C for 3 minutes, followed by 38 cycles of (a) denaturation at 94^{o} C for 30 seconds, (b) annealing at the gradient temperature for 30 seconds, and (c) primer extension at 72^{o} C for 30 seconds, followed by a final annealing and extension at 72^{o} C for seven minutes.

Following PCR, DNA products were visualized on agarose gels stained with ethidium bromide (EtBr). We added 2ul of 10X loading dye to our PCR products and then loaded 8ul of the PCR product onto 2% agarose gels for electrophoresis. Gels were run at 95V for 35 minutes. Following electrophoresis gels were visualized using UV light. We identified the optimal annealing temperature and $MgCl_2$ concentration for each locus and developed genotyping protocols for all loci that amplified using an ABI 3100 DNA analyzer (Applied Biosystems Inc.).

Results

All loci except *Spl7* and *Spl115* produced PCR products for pallid sturgeon. We currently have optimized all the loci used by both Tranah et al. (2004) and Heist and Schrey (2004) plus three additional loci (*Spl119, Spl158* and *Spl169* (McQuown et al. 2000)) and now have a total of 25 microsatellite loci for distinguishing these two species. We have genotyped and calculated allele frequencies for a total of 93 adult pallid sturgeon from the Upper Missouri River at these 25 loci (Table 2). These 93 individuals represent adult pallid sturgeon captured in the upper Missouri River for broodstock from 2000 to 2004. At this point we have only genotyped a small number of shovelnose sturgeon at these loci (n=15). We have contacted USFWS personnel who will be collecting pallid sturgeon in the Upper Missouri River this spring/summer and have made arrangements to obtain at least 50 shovelnose sturgeon in order to expand our genetic baseline for this species.

Given that we have optimized a suite of 25 loci that have been shown to distinguish between pallid and shovelnose sturgeon with a high degree of accuracy, we feel confident that we will be able to perform this analysis. At this point our baseline data set for shovelnose sturgeon is too small (n=15 fish) to perform a jackknifing procedure to test the power of our baseline to distinguish between these two species. Once we have obtained additional shovelnose

sturgeon samples and incorporated them into our baseline dataset, we will be able to fully test our ability and statistical power to distinguish these two species genetically.

Objective 2: Identify a suite of loci for correctly identifying the parents of hatchery-produced pallid sturgeon, and test the Mendelian inheritance of microsatellite alleles.

Recent developments in genetic technology and methods for parentage analysis make the process of genetic tagging a very robust procedure (Jones and Ardren 2003). Genetic tagging using microsatellite loci has been successfully used to reassign unknown progeny to their parental pairs in aquaculture settings for a number of species including; rainbow trout (*Oncorhynchus mykiss*) (Estoup et al. 1998, Ferguson and Danzmann 1998), turbot (*Scophthalmus maximus*) (Estoup et al. 1998), channel catfish (*Ictalurus punctatus*) (Waldbeiser and Wolters 1999), sea bass (*Dicentrarchus labrax*) (Garcia de Leon et al., 1998), and Atlantic salmon (*Salmo salar*) (O'Reilly et. al 1998). There are also numerous examples of the successful application of microsatellite data for parentage analysis in natural fish populations (e.g., Seamons et al. 2004, Fiumera et al. 2002, Garant et al. 2001). A recent paper by Rodzen et al. (2004) also provides documentation that microsatellite loci can be used to accurately estimate parentage and relatedness in white sturgeon (*Acipenser transmontanus*).

The application of microsatellite based genetic studies has been delayed in many species of sturgeon due to genome duplications (Rodzen et al. 2004). These delays are associated with complex inheritance patterns. For example, inheritance patterns for microsatellite loci in white sturgeon (8N) include disomic, tetrasomic and higher levels (Rodzen and May 2002). These inheritance issues are prevalent in *Acipenser*.

Blacklidge and Bidwell (1993) documented shovelnose sturgeon are ancestral tetrapolid (4N). We are unaware of a study documenting the ploidy level in pallid sturgeon. However, because the level of genetic differentiation between pallid and shovelnose sturgeon is extremely small (Campton et al. 2000), we assume pallid sturgeon are also 4N.

McQuown et al. (2000) observed disomic banding patterns for microsatellite loci in *Scaphirhynchus* species, but the true mode of inheritance was not documented via an inheritance study. If pallid sturgeon have undergone a re-diploidization, as suggested by McQuown et al. (2000), it is critical to validate this finding via an inheritance study. Confirming pallid sturgeon

microsatellite loci have inheritance patterns consistent with disomic expectations allows us to utilize the many parentage methods that have been developed for this class of markers (reviewed by Jones and Ardren 2003).

Materials and Methods

Optimization of microsatellite loci

Biologists from the USFWS Garrison Dam National Fish Hatchery and Missouri River Fish and Wildlife Management Assistance Office provided us with fin clips from 52 pallid sturgeon that represented the progeny of adults artificially spawned in 2004. We used Qiagen DNeasy kits to extract whole genomic DNA from each of the 52 individuals following the manufacturer's protocol.

We initially screened the following 22 microsatellite loci, initially developed in shovelnose sturgeon, for their ability to amplify via the *polymerase chain reaction* (PCR) in pallid sturgeon: *Spl12, Spl15, Spl7, Spl18, Spl19, Spl26, Spl30, Spl34, Spl35, Spl36, Spl40, Spl53, Spl56, Spl60, Spl101, Spl105, Spl106, Spl115, Spl119, Spl158, Spl169, Spl173* (McQuown et al. 2000). DNA from each specimen at each locus was amplified by PCR in 15ul volumes. Each reaction contained 2ul template DNA, 10X PCR buffer, 0.2mM dNTPs, 0.5uM of the forward and reverse primers for that locus, and 0.2 units of *Taq* polymerase. Reactions were carried out over a DNA annealing temperature gradient ranging from 50^{o} C to 60^{o} C. We also tested two $MgCl_2$ concentrations: 1.5 mM and 2.0mM. PCR conditions were as follows: an initial DNA denaturation at 94^{o} C for 3 minutes, followed by 38 cycles of (a) denaturation at 94^{o} C for 30 seconds, (b) annealing at the gradient temperature for 30 seconds, and (c) primer extension at 72^{o} C for 30 seconds, followed by a final annealing and extension at 72^{o} C for seven minutes.

Following PCR, DNA products were visualized on agarose gels stained with ethidium bromide (EtBr). We added 2ul of 10X loading dye to our PCR products and then loaded 8ul of the PCR solution onto 2% agarose gels for electrophoresis. Gels were run at 95V for 35 minutes. Following electrophoresis gels were visualized using UV light. We identified the optimal annealing temperature and $MgCl_2$ concentration for each locus. All loci except *Spl7* and *Spl115* produced PCR products for pallid sturgeon.

Genotypic determinations of parent and progeny pallid sturgeon

We obtained fin clips from all pallid sturgeon adults collected for broodstock in 2004 (n=26; fin clips provided by Bernie May, Department of Animal Science, University of California, Davis). In addition, biologists from the USFWS Garrison Dam National Fish Hatchery, Missouri River Fish and Wildlife Management Assistance Office and one of us (William Ardren) collected fin clips from 50 progeny from each of six full-sib families at the Garrison Dam National Fish Hatchery. Those 300 pallid sturgeon juveniles represented six full-sib families produced from the artificial spawning of six male-female pairs in 2004.

We used Qiagen DNeasy kits to extract whole, genomic DNA from all adult and progeny sturgeon described above. We performed PCR reactions for the 20 loci described above (excluding *Spl7* and *Spl115)* using the conditions identified during optimization. All forward primers were labeled with one of four fluorescent dyes for detecting and quantifying PCR products on an ABI 3100 DNA analyzer (Applied Biosystems Inc.). PCR conditions were as follows; 94 ^{o} C for 3 minutes followed by 35 cycles of 94 ^{o} C for 30 seconds, primer specific annealing temperature for 30 seconds and 72 ^{o} C for 30 seconds with a final extension at 72 ^{o} C for 7 minutes.

PCR products were pooled into four groups and diluted for electrophoresis on our *ABI 3100* DNA analyzer. Automated electrophoresis was carried out following the manufacturer's protocols with the G5 filter set to produce electropherograms, and electrophoresis data were analyzed using the program Genescan (Applied Biosystems Inc.). Genotypes were then determined for each individual at each locus using the Genotyper Software package (Applied Biosystems, Inc.).

Statistical analyses

We used the program CERVUS v2.0 (Marshall *et al.* 1998) to generate genetic summary statistics, including observed and expected heterozygosities and numbers of alleles at each locus. CERVUS was also used to estimate the exclusion probability of each of the 20 loci using the sample of 93 adult pallid sturgeon from Objective 1 of this report. These 93 adults represent the potential parents of all the hatchery produced offspring that have been released into the Upper Missouri River since 2000. We used the program GENEPOP v3.4 (Raymond and Rousset 1995)

to test the distribution of genotypes at each locus for conformance to Hardy-Weinberg expectations.

Parental and progeny genotypes representing each of the six full-sib families were collated by locus and family groups in a Microsoft EXCEL spreadsheet. We used GENEPOP to calculate the numbers of each genotype we observed for each family at each locus and we then compared the observed number of each genotype within each family to the expected number assuming Mendelian rules of inheritance. Chi-square *goodness of fit* tests were used to determine conformance to Mendelian rules of inheritance for each family at each locus. We used the program LINKMFEX (R.G. Danzmann, www.uoguelph.ca/~rdanzman/software/LINKMFEX) to test each pair of loci for linkage and to calculate recombination rates between each pair of loci.

To evaluate the effect that juveniles from un-sampled (wild) parents would have on parentage assignments, we used the program PAPA v2.0 (Duchesne et al. 2002) to simulate data sets of 1000 offspring composed of sampled (adults spawned in a hatchery) and un-sampled (wild) parents based on our observed population allele frequencies. We established 3 different mating scenarios:

1) 1000 offspring were generated from 10 sampled females and 30 sampled males PLUS 1 un-sampled female and 3 un-sampled males
2) 1000 offspring were generated from 10 sampled females and 30 samples males PLUS 10 un-sampled female and 30 un-sampled males
3) 1000 offspring were generated from 10 sampled females and 30 samples males PLUS 100 un-sampled female and 300 un-sampled males

For each of these mating scenarios we generated 6 data sets with varying proportions of offspring produced from sampled (adults spawned in a hatchery) and un-sampled (wild) parents. The 6 data sets contained; 100% hatchery origin and 0% natural origin fish, 80% hatchery origin and 20% natural origin fish, 60% hatchery and 40% natural origin fish, 40% hatchery and 60% natural origin fish, 20% hatchery origin and 80% natural origin fish and 0% hatchery origin and 100% natural origin fish. This resulted in a total of 18 separate data sets of 1000 offspring (3

mating scenarios X 6 sets of hatchery and natural origin offspring per mating scenario). We then used PAPA to determine our assignment success for each dataset.

Results

Nineteen of the 20 optimized loci were polymorphic for 93 adult pallid sturgeon tested (Tables 2 and 3; see also Appendix 1 for compilation of multi-locus genotypes for each fish). Genotypes among the 93 individuals conformed to Hardy-Weinberg expected proportions at all loci except at *Spl18* where a deficit of heterozygotes was observed ($P < 0.001$). Overall, observed and expected heterozygosities averaged 0.647 and 0.634, respectively. Based on the genotypes and resulting allele frequencies for those 93 adults, predicted parental exclusion probabilities per locus for the first parent (2^{nd} parent assumed unknown) ranged from 0.108 (*Spl173*) to 0.558 (*Spl26*). The overall predicted probability of exclusion of the first parent (other parent unknown) based on all 20 loci was 0.998. This probability increases to >0.9999 if the genotype of the first parent is assumed known (last column, Table 3).

Our initial genotyping analysis showed that nearly all observed progeny genotypes were consistent with Mendelian genetic predictions based on their parental genotypes. Of the approximately 5,500 progeny genotypes scored among six families and 19 polymorphic loci, we initially scored 24 individuals (<0.5%) with genotypes not predicted by their parents. Unpredicted progeny genotypes at a particular locus typically represented one individual within a family. All individuals that showed unpredicted genotypes were re-analyzed and after re-analyzing these individuals we determined that all but one of these unpredicted genotypes was caused by a genotyping error. The one unresolved individual was PCR amplified two additional times and consistently showed the same genotype. We therefore concluded this individual had a mutation at the locus *Spl169*, giving us a mutation rate of 8.7×10^{-5}. This mutation rate is within the range reported for microsatellites (Jarne and Lagoda 1996) but is slightly lower than reports for microsatellites in other fish species (e.g. Crane et al. 2004 ($\mu = 2.1 \times 10^{-3}$ to 4.4×10^{-3}), Jones et al. 1999 ($\mu = 2.0 \times 10^{-3}$ to 2.7×10^{-3})).

Chi-squared tests showed that progeny genotypic proportions for each of the six full-sib families (families A through F) conformed to Mendelian expectations based on the genotypes of their parents following a sequential Bonferroni correction (Rice 1989) where data for each of the six families was treated statistically as an independent test of the same Mendelian hypothesis for

a locus (Table 4). We were unable to perform Chi-squared tests for the locus *Spl53* because this locus failed to amplify consistently in the offspring, therefore we will drop this locus (4th lowest exclusionary power). For the locus *Spl169* in family F, we excluded the one individual that showed a mutation from our Chi-squared test.

Results of the program LINKMFEX showed that two loci, *Spl35* and *Spl169*, showed a significant linkage relationship. The LOD values for this pair of loci ranged from 10.881 to 14.75 for the six families. This relationship was observed when both the male and the female was used as the mapping parent. The recombination frequency between these two loci ranged from 0.000 to 0.023, thus indicating that they are tightly linked on the same chromosome. Given that *Spl35* and *Spl169* showed a significant linkage relationship, we will drop *Spl169* from our parentage analysis since it has fewer alleles and has a lower exclusionary power (2nd lowest out of 19 polymorphic loci) than *Spl35*.

When we performed parentage assignments for our simulated data sets of 1,000 offspring, we found that in every instance we were able to correctly assign parentage for hatchery produced fish but fish produced from un-sampled parents (natural origin fish) did not assign back to any parents in any instance. This shows that if we do have juveniles that were produced by un-sampled parents (i.e. natural origin juveniles), we are confident that they will not be erroneously assigned to parents we have sampled.

The suite of 17 loci that we optimized for parentage analysis show a high degree of exclusionary power for assigning parentage in pallid sturgeon. Exclusion power for these 17 loci for the first parent (other parent unknown) was 0.996. This probability increases to >0.9999 if the genotype of the first parent is assumed known. The low genotyping error rate and relatively low mutation rate for the microsatellite loci used in this study make the set of 17 loci ideal for parentage analysis. In the future, juvenile pallid sturgeon captured in the upper Missouri River will be genotyped at these 17 loci and we will conduct parentage analysis using the all individuals crossed in a hatchery to date as the potential parent pool. If we can successfully assign parentage to an offspring and hatchery records indicate that those particular fish have been spawned with one another in the past, we will assume an individual is of hatchery origin. If we cannot successfully assign a pair of hatchery spawned parents to an individual then we will assume that individual represents the result of natural reproduction.

Future parentage analyses for juveniles of unknown origin will employ a likelihood based method for calculating parentage that provides a simulation-based assessment of confidence in assignments. Employing a likelihood based method allows us to overcome the very minor source of error associated with mutations and genotyping errors (see below), provided accurate estimates of both sources of error are available (Jones and Ardren 2003, Marshall *et al.* 1998). We do have robust estimates of these two sources of error based on the rigorous ground truthing of the 17 loci conducted in this study allowing for extremely accurate parentage analysis in pallid sturgeon populations in the Upper Missouri River. Thus, we believe the DNA markers described here provide a valid, complementary alternative to physical tags for identifying the progeny of hatchery-spawned adults, particularly when one also considers the rate at which physical tags might be shed (Clugston 1996).

Objective 3: Conduct a blind test of the accuracy of the methods developed under Objectives 1 and 2.

Materials and Methods

In order to test the accuracy of our ability to identify the parents of hatchery produced pallid sturgeon and differentiate between pallid and shovelnose sturgeon, we conducted a "blind test" of the methods developed in Objectives 1 and 2 of this project. To test our ability to assign parentage, we randomly selected 36 juvenile pallid sturgeon (6 from each of the 6 families we had available) and re-labeled fin clips from these samples so that the parents of these individuals were unknown to the personnel that spawned the adults to produce these progeny. We then sent these samples to the Missouri River Fish and Wildlife Management Assistance Office where USFWS personnel changed the IDs of the samples and kept the new IDs confidential from AFTC personnel. The personnel at Garrison Dam NFH and the Missouri River Fish and Wildlife Management Assistance Office also took fin clips from an additional 20 fish (both pallid and shovelnose sturgeon) in order to test our ability to distinguish the two species. The species ID of these 20 samples was also kept confidential from AFTC personnel. All 56 samples were then returned to AFTC for genetic analysis.

Upon receiving the samples from the Missouri River Fish and Wildlife Management Assistance Office we genotyped all 56 unknown samples at the 25 loci that we optimized in objectives 1 and 2. Presently we are unable to distinguish the species of the 20 unknown fish that

we received due to our inadequate genetic baseline for shovelnose sturgeon. Once we receive more shovelnose sturgeon samples and expand our baseline for this species, we are confident that we will be able to assign each of these 20 samples to their correct species. Any of these 20 individuals that we identify as pallid sturgeon we will then use CERVUS to determine if these individuals are progeny from hatchery crosses.

Results

For the 36 individuals that we knew were from crosses made in 2004, we used the computer program CERVUS to assign parentage. For each offspring we determined the most likely parental pair. Once we had determined the identity and the parents of these 36 individuals, we sent our results to a third party to verify our assignments. Upon reviewing our data and comparing it to the data provided by Missouri River Fish and Wildlife Management Assistance Office personnel, the third party reviewer determined our accuracy of parentage assignment for these 36 individuals was 100% (Table 5). This initial test strongly supports our ability to use genetic markers to assign parentage for pallid sturgeon of unknown origin.

Error Analysis

We used the data generated for the "Blind test" (Objective 3) to estimate our genotyping error rate. 36 samples were analyzed once as a part of Objective 2 of this project and were re-extracted and re-genotyped without us knowing their ID as a part of Objective 3. To estimate our error rate we simply compared the two genotypes generated for each fish. The comparison showed we had 12 mis-typed alleles out of 1224. Therefore, we estimated our error rate to be 12/1224 = 0.98% (12 mistyped alleles/(36 fish*17 loci * 2 alleles per locus)). These errors were all attributed to allelic dropout and 6 of the 12 errors were attributed to a single locus, *Spl40*. It is important that we maintain a low level of genotyping error to ensure that we do not mis-identify the parents of any juvenile sturgeon captured in the future.

Future Work

One important future goal of this project is to standardize genotypes among the different labs working on pallid sturgeon genetics. Presently multiple labs have performed work on pallid

sturgeon genetics, however, multiple sets of loci have been used and allelic designations have yet to be standardized. Standardization of loci will allow for the combination of pallid sturgeon genetic data sets from across the species range and will facilitate range-wide genetic analysis. At the present time we have been able to standardize our genetic data with genetic data generated by Dr. Bernie May's lab at UC Davis. We would also like to standardize our data with the data generated by Dr. Ed Heist's lab at University of Southern Illinois. Further standardization among labs will require that a common set of samples be run at the same loci in each lab involved in standardization. We suggest that the U.S Fish and Wildlife Service take a strong leadership role in coordinating these standardizations.

In order for the genetic marking program to be successful, it is absolutely essential that we obtain and analyze genetic samples from all pallid sturgeon adults that are hatchery-spawned in the future. Also in order to identify sources of error inherent in genetic tagging (null alleles, upper allele dropout) each year we will genotype 20-30 fry per family to in order to ground truth our loci and ensure that the progeny genotypes are consistent with their parents. For example, this "ground truthing" is necessary to ensure that germline mutations had not occurred in the developing ovaries or testes of hatchery-spawned adults that would affect all, or a significant fraction of, the genotypes of their resulting progeny.

Presently we are screening additional microsatellite loci developed in lake sturgeon (see Welsh et al. 2003) to identify any additional loci that may be useful for pallid sturgeon. We have also been in contact with Dr. Tim King of the U.S. Geological Survey who is currently developing new microsatellite loci for shortnose sturgeon (*Acipenser brevirostrum*). Dr. King has agreed to screen these loci for pallid sturgeon as well and we anticipate that some of these loci will be informative for pallid sturgeon. In short, we have established a team of collaborators who are working with us to achieve the objectives of the work described in this proposal.

Conclusion

Our results to date confirm the capability of using a suite of microsatellite, nuclear DNA loci as "genetic tags" to identify, via parentage analyses, hatchery-origin pallid sturgeon subsequent to their release into the upper Missouri River. We are confident that once we develop a baseline dataset for shovelnose sturgeon in the upper Missouri River, we will be able to accurately distinguish these two species, thus fully completing the first objective of this

project. Future success of this program will be contingent upon collection and analysis of genetic samples from all pallid sturgeon whose offspring are produced in a hatchery and released into the upper Missouri River.

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Table 1. Allele frequencies and sample sizes (N) for pallid sturgeon (P), shovelnose sturgeon (S), and morphologic hybrids (H) from the Missouri River (MR) and the Atchafalaya River (AR). Data from Tranah et al. (2004). "Other" refers to the sum of two or more low-frequency alleles. Alleles with frequency differences greater than 0.30 for pallid and shovelnose sturgeon in the upper Missouri River or Atchafalaya River are highlighted.

Locus	Allele	P-MR	S-MR	P-AR	S-AR	H-AR
Afu 19	(N)	19	18	10	18	10
	122	0.66	0.64	1.00	0.89	0.45
	125	0.34	0.36	0.00	0.11	0.55
Afu 34	(N)	19	19	10	18	10
	139	0.18	0.13	0.00	0.03	0.15
	147	**0.45**	**0.76**	0.80	0.81	0.80
	159	0.29	0.05	0.15	0.17	0.00
	Other	0.08	0.06	0.05	0.09	0.05
Afu 68	(N)	19	19	10	18	10
	117	0.00	0.13	0.10	0.03	0.15
	121	0.00	0.05	0.20	0.22	0.15
	125	**0.16**	**0.53**	0.15	0.36	0.20
	129	0.16	0.05	0.20	0.11	0.05
	137	**0.61**	**0.08**	0.15	0.06	0.25
	141	0.08	0.13	0.15	0.17	0.20
	Other	0.00	0.03	0.05	0.05	0.00
Afu 57	(N)	17	19	10	17	9
	144	**0.06**	**0.55**	**0.10**	**0.53**	0.39
	147	**0.94**	**0.45**	**0.90**	**0.47**	0.61
Aox 27	121	0.31	0.29	0.50	0.28	0.40
	125	0.66	0.50	**0.10**	**0.58**	0.30
	129	0.03	0.21	0.40	0.14	0.30
Spl 101	(N)	17	18	10	18	10
	286	**0.50**	**0.08**	0.45	0.36	0.30
	290	0.21	0.06	0.10	0.14	0.25
	294	**0.18**	**0.53**	0.25	0.28	0.20
	298	0.00	0.22	0.20	0.00	0.05
	310	0.12	0.03	0.00	0.11	0.05
	Other	0.00	0.08	0.00	0.11	0.15

Table 1. Continued

Locus	Allele	P-MR	S-MR	P-AR	S-AR	H-AR
Spl 105	(N)	18	19	10	18	10
	128	0.33	0.45	0.45	0.28	0.45
	132	0.61	0.53	0.35	0.36	0.35
	Other	0.06	0.02	0.20	0.36	0.20
Spl 106	(N)	18	16	10	18	10
	234	0.00	0.22	0.10	0.14	0.00
	238	**0.61**	**0.19**	0.40	0.19	0.30
	246	0.31	0.28	0.35	0.28	0.25
	Other	0.08	0.31	0.15	0.39	0.45
Spl 173	(N)	18	19	8	18	9
	180	0.00	0.29	0.06	0.28	0.00
	184	0.22	0.03	0.19	0.19	0.00
	188	0.39	0.42	0.31	0.14	0.72
	192	0.03	0.13	0.38	0.08	0.06
	196	0.17	0.08	0.06	0.14	0.06
	200	0.17	0.05	0.00	0.08	0.17
	204	0.03	0.00	0.00	0.08	0.00

Table 2. Allele frequencies at 25 microsatellite loci for 93 adult pallid sturgeon captured in the upper Missouri River for broodstock from 2000 to 2004.

Locus	Size	Frequency
Spl12	174	1.000

Locus	Size	Frequency
Spl15	193	0.180
	195	0.579
	197	0.011
	206	0.129
	208	0.045
	212	0.011
	225	0.045

Locus	Size	Frequency
Spl18	239	0.017
	240	0.111
	241	0.594
	243	0.222
	245	0.039
	247	0.017

Locus	Size	Frequency
Spl19	233	0.005
	235	0.005
	237	0.185
	239	0.250
	241	0.304
	243	0.239
	255	0.005
	257	0.005

Locus	Size	Frequency
Spl26	294	0.092
	296	0.165
	298	0.281
	302	0.012
	304	0.012
	308	0.061
	310	0.098
	312	0.006
	314	0.006
	316	0.024
	323	0.012
	325	0.098
	327	0.079
	329	0.031
	331	0.012
	333	0.012

Locus	Size	Frequency
Spl30	239	0.006
	249	0.055
	255	0.703
	257	0.077
	259	0.006
	261	0.011
	263	0.137
	265	0.006

Locus	Size	Frequency
Spl34	316	0.006
	318	0.006
	332	0.308
	334	0.357
	336	0.006
	338	0.170
	342	0.093
	344	0.006
	346	0.050

Locus	Size	Frequency
Spl35	230	0.066
	232	0.088
	234	0.104
	236	0.374
	238	0.115
	250	0.198
	252	0.039
	254	0.006
	256	0.011

Locus	Size	Frequency
Spl36	351	0.319
	353	0.275
	355	0.050
	357	0.050
	361	0.017
	367	0.231
	369	0.011
	371	0.017
	373	0.033

Locus	Size	Frequency
Spl40	219	0.028
	221	0.062
	227	0.326
	229	0.174
	231	0.107
	233	0.242
	235	0.062

Locus	Size	Frequency
Spl53	217	0.006
	219	0.006
	221	0.581
	229	0.156
	233	0.250

Locus	Size	Frequency
Spl56	211	0.022
	223	0.071
	225	0.137
	227	0.275
	229	0.451
	231	0.044

Locus	Size	Frequency
Spl60	197	0.011
	199	0.478
	201	0.378
	203	0.133

Locus	Size	Frequency
Spl101	269	0.050
	277	0.028
	281	0.143
	285	0.258
	289	0.462
	293	0.060

Locus	Size	Frequency
Spl105	121	0.139
	125	0.050
	133	0.494
	137	0.267
	146	0.044
	150	0.006

Table 2 Continued

Locus	Size	Frequency
Spl106	214	0.125
	218	0.011
	222	0.267
	226	0.023
	230	0.489
	234	0.063
	250	0.011
	254	0.011

Locus	Size	Frequency
Spl119	228	0.335
	248	0.040
	256	0.102
	258	0.006
	260	0.381
	268	0.136

Locus	Size	Frequency
Spl158	203	0.163
	207	0.017
	211	0.056
	215	0.275
	223	0.225
	227	0.208
	231	0.056

Locus	Size	Frequency
Spl169	181	0.006
	189	0.062
	193	0.056
	197	0.725
	201	0.135
	203	0.006
	205	0.011

Locus	Size	Frequency
Spl173	205	0.277
	214	0.041
	218	0.671
	222	0.006
	226	0.006

Locus	Size	Frequency
Afu19	124	0.861
	130	0.139

Locus	Size	Frequency
Afu68	113	0.007
	121	0.039
	125	0.169
	129	0.039
	133	0.623
	137	0.117
	141	0.007

Locus	Size	Frequency
Afu57	120	0.345
	128	0.338
	132	0.317

Locus	Size	Frequency
Aox27	114	0.051
	118	0.943
	128	0.006

Locus	Size	Frequency
Afu34	136	0.203
	146	0.532
	154	0.013
	156	0.184
	160	0.063
	164	0.006

Table 3. Summary statistics for 20 microsatellite loci observed in 93 adult pallid sturgeon trapped for broodstock in the upper Missouri River (near Fort Peck Res.). Samples were collected from 2000 to 2004.

Locus	Alleles	H_{obs}[a]	H_{exp}[b]	P[c]	Excl(1)[d]	Excl(2)[e]
Spl12	1	0	0	NA	0	0
Spl15	7	0.584	0.615	0.378	0.216	0.391
Spl18	6	0.4	0.586	0.000*	0.187	0.349
Spl19	8	0.696	0.758	0.312	0.34	0.516
Spl26	16	0.841	0.86	0.030	0.558	0.718
Spl30	8	0.484	0.48	0.177	0.125	0.284
Spl34	9	0.791	0.742	0.201	0.332	0.507
Spl35	9	0.791	0.788	0.123	0.417	0.598
Spl36	9	0.791	0.767	0.909	0.371	0.547
Spl40	7	0.787	0.79	0.147	0.409	0.588
Spl53	5	0.575	0.579	0.800	0.169	0.315
Spl56	6	0.78	0.699	0.896	0.286	0.459
Spl60	4	0.656	0.615	0.097	0.19	0.326
Spl101	6	0.681	0.697	0.027	0.285	0.46
Spl105	6	0.644	0.664	0.103	0.248	0.416
Spl106	8	0.625	0.673	0.660	0.261	0.432
Spl119	6	0.773	0.716	0.921	0.298	0.469
Spl158	7	0.843	0.802	0.111	0.422	0.6
Spl169	7	0.506	0.452	0.941	0.109	0.262
Spl173	5	0.482	0.465	0.250	0.108	0.222
Overall		0.6365	0.637	0.3935	0.9986	0.9999

[a] H_{obs}, observed heterozygosity

[b] H_{exp}, expected heterozygosity

[c] P, probability level for Hardy-Weinberg equilibrium.

[d] Exclusion probability. Probability of excluding a single unrelated candidate parent from parentage of a given offspring at a locus.

[e] Exclusion probability assuming one parent is known, the exclusion probability is calculated taking account of alleles that are unambiguously descended from the known parent.

* Significantly deviated from Hardy-Weinberg expectations at the $p < 0.05$ level after sequential Bonferroni adjustments for simultaneous tests.

Table 4. Chi-squared test statistics and associated degrees of freedom in parentheses for each of the 6 full sib families for 18 loci. The locus *Spl12* was monomorphic and was excluded and the locus *Spl53* failed to amplify consistently in the juveniles and was also excluded.

	Spl15	Spl18	Spl19	Spl26	Spl30	Spl34	Spl35	Spl36	Spl40	Spl56	Spl60	Spl101	Spl105	Spl106	Spl119	Spl158	Spl169	Spl173
FamA	0.86(1)	0.86(2)	2.00(3)	0.48(3)	0.00(1)	0.86(2)	0.86(3)	0.86(3)	2.00(3)	0.10(1)	0.00(1)	1.62(3)	3.52(3)	0.29(3)	2.76(3)	1.62(1)	0.86(3)	0.22(1)
FamB	1.68(3)	0.72(1)	1.28(1)	2.14(2)	2.00(1)	0.08(1)	1.20(3)	0.00(1)	4.31(3)	1.65(1)	0.08(1)	0.72(1)	2.88(1)	4.24(3)	0.02(1)	2.18(3)	0.08(1)	0.00(1)
FamC	0.02(1)	3.65(3)	1.28(1)	6.87(3)	0.08(1)	2.83(2)	2.17(3)	2.11(3)	2.83(3)	1.49(3)	2.92(2)	2.28(3)	2.88(1)	0.91(3)	0.91(3)	3.83(3)	2.64(2)	0.00(1)
FamD	9.31(3)	0.20(1)	8.48(3)	0.18(3)	0.24(2)	0.46(3)	0.59(2)	3.40(2)	1.24(3)	2.69(1)	2.20(3)	2.38(3)	0.81(3)	1.93(2)	11.62(3)	2.76(3)	0.73(2)	0.00(1)
FamE	6.42(1)	0.36(1)	0.00(1)	1.93(3)	6.33(3)	1.80(1)	1.88(1)	0.42(30	2.81(1)	2.69(1)	1.09(1)	0.60(3)	0.20(1)	1.67(3)	7.18(3)	2.00(3)	6.36(3)	0.10(1)
FamF	2.36(3)	0.08(1)	0.00(1)	2.00(1)	2.00(1)	1.19(3)	0.26(3)	6.92(3)	2.96(3)	4.50(3)	1.53(3)	1.09(1)	2.62(3)	3.69(30	0.02(1)	0.10(3)	0.04(1)	0.04(1)

Table 5. Pallid sturgeon parentage "blind test" results. The column labeled "New ID Numbers" represents the Blind Test ID given to each sample by USFWS Garrison Dam NFH personnel. The column labeled "USFWS Bismarck BT Sample ID" represents the ID that AFTC personnel deduced from running the blind test. The IDs in these two columns match in every instance.

AFTC Original ID	AFTC BT Sample ID:	USFWS Bismarck BT Sample ID:	Mother Genetic ID	Mother PIT Tag Number	Father Genetic ID	Father PIT Tag Number	New ID Numbers	PIT Tag female	PIT Tag male
17-Sal-158-05	17-Sal- BT-01	17-Sal-BT-23	17-PF0411	114476216A	17-PF0406	430E452777	17-Blind Test - 23		
17-Sal-158-07	17-Sal- BT-02	17-Sal-BT-11	17-PF0411	114476216A	17-PF0406	430E452777	17-Blind Test - 11		
17-Sal-158-08	17-Sal- BT-03	17-Sal-BT-36	17-PF0411	114476216A	17-PF0406	430E452777	17-Blind Test - 36		
17-Sal-158-20	17-Sal- BT-04	17-Sal-BT-30	17-PF0411	114476216A	17-PF0406	430E452777	17-Blind Test - 30		
17-Sal-158-25	17-Sal- BT-05	17-Sal-BT-05	17-PF0411	114476216A	17-PF0406	430E452777	17-Blind Test - 05		
17-Sal-158-45	17-Sal- BT-06	17-Sal-BT-15	17-PF0411	114476216A	17-PF0406	430E452777	17-Blind Test - 15		
17-Sal-158-60	17-Sal- BT-07	17-Sal-BT-20	17-PF0411	114476216A	17-PF0408	7F7E55466D	17-Blind Test - 20		
17-Sal-158-67	17-Sal- BT-08	17-Sal-BT-27	17-PF0411	114476216A	17-PF0408	7F7E55466D	17-Blind Test - 27		
17-Sal-158-72	17-Sal- BT-09	17-Sal-BT-32	17-PF0411	114476216A	17-PF0408	7F7E55466D	17-Blind Test - 32		
17-Sal-158-84	17-Sal- BT-10	17-Sal-BT-07	17-PF0411	114476216A	17-PF0408	7F7E55466D	17-Blind Test - 07		
17-Sal-158-91	17-Sal- BT-11	17-Sal-BT-10	17-PF0411	114476216A	17-PF0408	7F7E55466D	17-Blind Test - 10		
17-Sal-158-93	17-Sal- BT-12	17-Sal-BT-28	17-PF0411	114476216A	17-PF0408	7F7E55466D	17-Blind Test - 28		
17-Sal-159-05	17-Sal- BT-13	17-Sal-BT-03	17-PF0410	454910202B	17-PF0416	220F0F7677	17-Blind Test - 03		
17-Sal-159-11	17-Sal- BT-14	17-Sal-BT-26	17-PF0410	454910202B	17-PF0416	220F0F7677	17-Blind Test - 26		
17-Sal-159-18	17-Sal- BT-15	17-Sal-BT-19	17-PF0410	454910202B	17-PF0416	220F0F7677	17-Blind Test - 19		
17-Sal-159-24	17-Sal- BT-16	17-Sal-BT-09	17-PF0410	454910202B	17-PF0416	220F0F7677	17-Blind Test - 09		
17-Sal-159-35	17-Sal- BT-17	17-Sal-BT-06	17-PF0410	454910202B	17-PF0416	220F0F7677	17-Blind Test - 06		
17-Sal-159-45	17-Sal- BT-18	17-Sal-BT-34	17-PF0410	454910202B	17-PF0416	220F0F7677	17-Blind Test - 34		
17-Sal-159-55	17-Sal- BT-19	17-Sal-BT-02	17-PF0405	15555495A	17-PF0401	431565767B	17-Blind Test - 02		
17-Sal-159-67	17-Sal- BT-20	17-Sal-BT-13	17-PF0405	15555495A	17-PF0401	431565767B	17-Blind Test - 13		
17-Sal-159-75	17-Sal- BT-21	17-Sal-BT-18	17-PF0405	15555495A	17-PF0401	431565767B	17-Blind Test - 18		
17-Sal-159-85	17-Sal- BT-22	17-Sal-BT-17	17-PF0405	15555495A	17-PF0401	431565767B	17-Blind Test - 17		
17-Sal-159-89	17-Sal- BT-23	17-Sal-BT-35	17-PF0405	15555495A	17-PF0401	431565767B	17-Blind Test - 35		
17-Sal-159-95	17-Sal- BT-24	17-Sal-BT-16	17-PF0405	15555495A	17-PF0401	431565767B	17-Blind Test - 16		
17-Sal-160-01	17-Sal- BT-25	17-Sal-BT-29	17-PF0422	454B380D60	17-PF0409	7F7F065834	17-Blind Test - 29		
17-Sal-160-11	17-Sal- BT-26	17-Sal-BT-04	17-PF0422	454B380D60	17-PF0409	7F7F065834	17-Blind Test - 04		
17-Sal-160-25	17-Sal- BT-27	17-Sal-BT-33	17-PF0422	454B380D60	17-PF0409	7F7F065834	17-Blind Test - 33		
17-Sal-160-35	17-Sal- BT-28	17-Sal-BT-14	17-PF0422	454B380D60	17-PF0409	7F7F065834	17-Blind Test - 14		

AFTC Original ID	AFTC BT Sample ID:	USFWS Bismarck BT Sample ID:	Mother Genetic ID	Mother PIT Tag Number	Father Genetic ID	Father PIT Tag Number	New ID Numbers	PIT Tag female	PIT Tag male
17-Sal-160-46	17-Sal- BT-29	17-Sal-BT-01	17-PF0422	454B380D60	17-PF0409	7F7F065834	17-Blind Test - 01		
17-Sal-160-48	17-Sal- BT-30	17-Sal-BT-25	17-PF0422	454B380D60	17-PF0409	7F7F065834	17-Blind Test - 25		
17-Sal-160-55	17-Sal- BT-31	17-Sal-BT-12	17-PF0418	115551683A	17-PF0421	7FD3C555D	17-Blind Test - 12		
17-Sal-160-65	17-Sal- BT-32	17-Sal-BT-21	17-PF0418	115551683A	17-PF0421	7FD3C555D	17-Blind Test - 21		
17-Sal-160-75	17-Sal- BT-33	17-Sal-BT-08	17-PF0418	115551683A	17-PF0421	7FD3C555D	17-Blind Test - 08		
17-Sal-160-83	17-Sal- BT-34	17-Sal-BT-24	17-PF0418	115551683A	17-PF0421	7FD3C555D	17-Blind Test - 24		
17-Sal-160-90	17-Sal- BT-35	17-Sal-BT-22	17-PF0418	115551683A	17-PF0421	7FD3C555D	17-Blind Test - 22		
17-Sal-160-91	17-Sal- BT-36	17-Sal-BT-31	17-PF0418	115551683A	17-PF0421	7FD3C555D	17-Blind Test - 31		
							17-Blind Test - 37	220E345E09	1F4A111C6A
							17-Blind Test - 38	7F7F06672B	115631222A
							17-Blind Test - 39	220E345E09	1F4A27214F
							17-Blind Test - 40	220E345E09	1F4A111C6A
							17-Blind Test - 41	RPA #2 PXS	
							17-Blind Test - 42	2777	216A
							17-Blind Test - 43	2777	216A
							17-Blind Test - 44	216A	446D
							17-Blind Test - 45	495A	767B
							17-Blind Test - 46	6452	1445
							17-Blind Test - 47	202B	6357
							17-Blind Test - 48	216A	014F
							17-Blind Test - 49	202B	374A
							17-Blind Test - 50	683A	555D
							17-Blind Test - 51	216A	446D
							17-Blind Test - 52	683A	116A
							17-Blind Test - 53	202B	6357
							17-Blind Test - 54	216A	767B
							17-Blind Test - 55	0D60	5834
							17-Blind Test - 56	216A	3A65

Appendix 1: Microsatellite genotypes for all pallid sturgeon used in this study at 20 loci.

Pallid Sturgeon Genotypes at 20 microsatellite loci generated by Patrick DeHaan and Danielle Warner Abernathy Fish Technology Center, March 2005

Spl12
Spl15
Spl18
Spl19
Spl26
Spl30
Spl34
Spl35
Spl36
Spl40
Spl53
Spl56
Spl60
Spl101
Spl105
Spl106
Spl119
Spl158
Spl169
Spl173

POP = 2000 Adults
17-Sal-00-01 , 174174 195208 241243 237239 296296 255255 332342 236250 351351 227235 000000 211229 201201 277293 133133 222222 228256 207215 181197 218218
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17-Sal-01-05 , 174174 000000 241241 239241 000000 255263 334338 236236 000000 000000 000000 223225 199201 281289 000000 000000 000000 000000 000000 000000
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17-Sal-02-18 , 174174 195195 243243 237243 296310 255255 332334 236238 353373 229233 221229 225227 201203 281289 137137 222230 228268 203203 197197 205218
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POP = 2004 Adults
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POP = 2004 Offspring

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17-Spl-01-19 , 174174 000000 243243 239241 329331 255259 330340 236250 353355 223231 000000 205215 199201 277281 133133 000000 256256 203231 000000 000000
17-Spl-01-20 , 174174 193195 241243 241243 325325 255255 340340 236244 355359 227231 000000 209227 199199 281289 133133 226234 252260 207215 189201 000000
17-Spl-01-21 , 174180 197197 241243 237237 300327 255259 318340 236236 361367 225227 000000 209223 201201 273281 133133 214230 256260 203203 000000 000000
17-Spl-01-22 , 174180 195195 241241 237237 000000 255261 000000 234238 353353 000000 000000 225227 199201 269281 121133 000000 000000 215227 000000 000000
17-Spl-01-23 , 000000 000000 000000 255257 000000 000000 000000 000000 000000 000000 000000 000000 199199 000000 000000 000000 000000 000000 000000 000000
17-Spl-01-24 , 174174 000000 241243 237241 000000 255259 000000 228236 347351 000000 000000 000000 199207 277277 133146 000000 252264 000000 000000 000000
17-Spl-01-25 , 000000 000000 000000 255255 000000 000000 000000 000000 000000 000000 000000 241247 201201 000000 000000 000000 000000 000000 000000 000000
17-Spl-01-26 , 174174 193206 243243 237241 294327 261261 340340 228244 373373 227233 217229 209229 199199 277289 121133 226230 228254 195215 000000 218226
17-Spl-01-27 , 000000
17-Spl-01-28 , 174180 197203 241243 237243 294316 259261 340346 236244 355357 231231 000000 217229 199201 281281 133137 230230 258258 195207 000000 210218
17-ST-FPR11 , 174174 000000 241241 237241 000000 255259 000000 000000 353355 000000 000000 223227 199199 277281 133133 000000 000000 207215 000000 000000
17-ST-FPR13 , 174180 195195 241247 237241 321329 259263 316316 230242 349353 225231 000000 199219 201201 269293 133133 234234 258264 215215 181197 226226
17-ST-FPR14 , 174174 193206 243243 237241 000000 261261 000000 000000 000000 000000 000000 209229 195199 277289 000000 000000 000000 000000 000000 000000
17-ST-FPR15 , 000000
17-ST-FPR16 , 174180 197203 241243 237243 294294 259261 340346 236244 355357 000231 000000 217229 199201 281281 133137 230230 000000 195207 000000 000000
17-ST-FPR18 , 174174 193193 243243 243255 000000 000000 000000 000000 000000 231000 217221 211219 201201 269289 133133 000000 000000 000000 000000 000000
17-ST-FPR21 , 000000 000000 000000 249255 000000 000000 000000 000000 000000 000000 000000 000000 000000 000000 000000 000000 000000 000000 000000 000000
17-ST-FPR25 , 000000 000000 000000 255265 000000 000000 000000 000000 000000 000000 000000 000000 000000 000000 000000 000000 000000 000000 000000 000000
17-ST-FPR4 , 174180 193193 243243 237243 327342 255263 332334 228246 351353 227231 000000 209211 199201 281289 133133 218230 228256 203207 189197 222226
17-ST-FPR8 , 174174 000000 241243 000000 000000 255255 000000 000000 000000 000000 000000 241243 000000 000000 121121 000000 000000 000000 000000 000000
POP = Hybrid
17-Hyb-01-17 , 174180 000000 241243 237237 000000 253255 000000 248256 353373 000000 000000 000000 201201 289289 000000 000000 000000 195223 000000 000000
17-Hyb-02-01 , 174174 197208 240243 237237 327329 255255 328332 236236 353373 231231 221221 223223 201201 281293 000000 210222 228258 207227 189197 214218