Columbia River White Sturgeon Genetics and Early Life History

Population Segregation and Juvenile Feeding Behavior

Final Report
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COLUMBIA RIVER WHITE STURGEON GENETICS AND EARLY LIFE HISTORY: POPULATION SEGREGATION AND JUVENILE FEEDING BEHAVIOR

Final Report

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Acknowledgments

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Abstract

Investigations in 1987 continued to examine genetic differences and life history characteristics of the Columbia River white sturgeon, for purposes of maintaining or developing this fisheries resource. Sturgeon populations in the reservoirs above Bonneville Dam may not be able to sustain themselves without enhancement measures taken to supplement natural recruitment. If sturgeon enhancement measures are to be employed in isolated reservoirs upstream of Bonneville, the genetic makeup of populations, and sturgeon juvenile life history must be understood to provide the background on which such programs can be based

The geographic area of the genetics study broadly covered the distribution range of sturgeon in the Columbia from below Bonneville Dam at Ilwaco to Lake Roosevelt, the Upper Snake River, and the Kootenai River. The two remote river sections provided data important for enhancement considerations. There was little electrophoretic variation seen among individuals from the Kootenai river . Upper Snake river sturgeon showed a higher percentage of polymorphic loci than the Kootenai fish, but lower than the other areas in the Columbia river we sampled. Sample size was increased in both Lake Roosevelt and at Ilwaco, and with the larger data set more variants at low frequencies were noted . Electrophoretic variation was specific to an individual sampling area in several cases and this shaped our conclusions.

The 1987 early life history studies concentrated on the feeding behavior of juvenile sturgeon. The chemostimulant components in prey attractive to sturgeon were examined, and the sensory systems utilized by foraging sturgeon were determined under different environmental conditions. These results were discussed with regard to the environmental changes that have occurred in the Columbia River. Under present river conditions, the feeding mechanism of sturgeon is more restricted to certain prey types, and their feeding range may be limited. In these situations, enhancement measures cannot be undertaken without consideration given to the introduction of food resources that will be readily available under present conditons.

Introduction

White sturgeon (Acipenser transmontanus) have been exploited for their roe and flesh for many years in the Columbia river. During the late 1800's when sturgeon were processed and shipped east for market, large fish averaging 150 lbs.were taken (Galbreath, 1983) until the catch could no longer be sustained. Subsequent to this turn of the century decline, the annual capture rate remained stable at well under a half-million pounds until 1970. In recent years the catch has gradually increased significantly and present harvest levels now exceed 3 million pounds. While the price attracted by sturgeon has generated heightened commercial involvement, the major factor responsible for the increase has been the growth of the sport fishery. The major fishing effort is expended in the lower river below the dams where sturgeon abundance is greatest, and it appears that the population has been able to sustain a harvest rate of 30,000 to 56,000 fish annually since 1979 (King, 1983). However, in the river and reservoirs above Bonneville Dam, where population strength is unknown and where productivity potential is limited, the situation is different. River access for anadromous fish has changed with the advent of hydroelectric development. Historically, thousands of sturgeon were able to feed in the rich marine environment adjacent to the river mouth and coastal areas, and move back upstream for spawning and early rearing. The effectiveness of spawning may now be limited by a number of factors, including the lack of riverine area or captive conditions created by the impoundments. Reproduction in some of the impoundments occurs, but how well sturgeon adapted to environmental changes there and what their long-range status will be is uncertain. Large increases in fishing effort may seriously endanger the sturgeon by limiting recruitment of reproductive fish.

Management decisions must reflect key elements related to the biology of sturgeon. The specificity of stocks within the Columbia River system needs to be defined,the life history of the species has to be understood, and the best habitat for good growth of sturgeon must be determined and preserved. These three elements need to be the basis of any enhancement program in the future.
The objectives of the present study were to:

1. Continue to examine genetic variability and isolation of white sturgeon populations in the Columbia River.

2. Identify the responses required by juvenile white sturgeon to feed successfully on prey items under different environment conditions.

This project addresses priority needs specified in section 903(e) of the Northwest Power Planning Council's Columbia River Fish and Wildlife program for resident fish.

TASK I

Genetic variability of Columbia River white sturgeon populations

Statement of the Problem

Successful enhancement of sturgeon must be based on mainaining the genetic discreteness of the populations targeted, unless sufficient evidence exists to the contrary The 1987 genetics sampling regime broadly covered the distribution range **of** white sturgeon in the Columbia River, in areas associated with the upriver pool, two large tributaries and the estuary. The mouth of the Columbia and the resultant estuarine environment at Ilwaco provide a very suitable habitat based on catch (King 1983), and has been used during this study as a base for comparison with other areas. The upper river was exclusively Lake Roosevelt, specifically the north end from the town of Marcus to just above the Canadian border. The Snake River included the area below Twin Falls downstream to Mountain Home. Kootenay Lake in Canada, was sampled at the entrance of the river. In both the Upper Snake and the Kootenai, large fish were the target and no fish under 3 feet were examined.

The genetic characteristics were assessed using starch gel electrophoresis. We examined in detail the enzyme systems which were polymorphic in an effort to provide evidence toward rejecting the null hypotheses that all sturgeon within the Columbia river are one stock of fish regardless of where they reside within the river system. The physical characteristics of snout shape and number of dorsal scutes present were investigated for trends between areas. The morphometric information was examined but not conclusive pending further evaluation. The dorsal scute counts were noticed to vary within an area during the initial sampling season (1985) and were subsequently recorded for substantiation of the variability. In the absence of clear genetic fixed differences, other species of closely related sturgeon have been segregated using morphometric and meristic information (Bailey and Cross, 1954). This was true in the case of pallid and shovelnose sturgeon which are two separate species based on physical character sets, but are electrophoretically very similar (Phelps and Allendorf, 1983). Because of their findings and our own observations we felt that an examination of white sturgeon physical characteristics might prove useful.

Objective: Examine genetic variability and degree of isolation of white sturgeon populations on the Columbia River

Null hypothesis: All sturgeon in the Columbia River system have the same genetic structure.

METHODS AND MATERIALS

Electrouhoresis

To collect tissue for genetic analysis, set line fishing and sampling of the sport and commercial fishery through interviews was conducted at the sampling locations on the river from March through October of 1987. Two major tissues, muscle and blood were collected for electrophoretic analysis from individual fish at field sampling locations. Since the fish were not sacrificed, a muscle plug was taken by inserting a steel cork borer into the area just below the dorsal ridge of scutes towards the posterior end of the fish (Fig 1). The tissue was then placed in a ziploc bag, set on dry ice for immediate freezing, and transferred back to the University of Washington. Blood was taken from the caudal artery near the tail of the fish. This was stored chilled until separation of the serum and clot occurred at which time the serum was put in another test tube. At the laboratory samples were stored at -85°C in a super cold freezer to prevent breakdown of tissue proteins.

Prior to electrophoresis, muscle tissue was slightly thawed and a l/4" by 1/8" by l/4" piece was cut off and put into a test tube. The test tube contained 0.3 ml of a tissue prepping solution (called PTP; Aebersold et al. , 1987) which enhances activity when some of the enzyme systems are stained. Test tubes were put into the super-freezer (-85°C) for storage. Each tissue type was kept in a separate rack in a specific ordered sequence, and the same sequence was repeated for every tissue. Tissues obtained from all individuals in each sample area were stored in the same test tube rack.

Starch gels were routinely prepared the day before electrophoresis was performed. Gels were poured using Sigma starch and the buffer solutions (Table 1). Test tube racks were removed from the freezer, and tubes centrifuged for 3 minutes to thaw the liquid. A paper wick was dipped in the test tube to absorb the protein slurry and placed across the cut face of the gel. Gels were placed on ice packs for cooling prior to placing the paper wicks against the cross-section cut in the slab. Electric current was run through the gel using a Heathkit power supply for 4-6 hours. Marker dye was placed on several paper wicks so that migration of the proteins through the gel could be monitored as the electric current was applied for the appropriate length of time. The starch gel was kept refrigerated with gel ice to prevent protein breakdown .

Laboratory procedures followed standard electrophoresis methods (Harris and Hopkinson 1976; May 1980; Utter et al. 1974; Aebersold et al., 1987). Gels are sliced and covered with agar and chemicals (for specific enzyme stains) which react to produce banding patterns. Each protein has a different mobility and banding pattern representing genotypes of individual fish.

The banding patterns were recorded as genotypes and used to calculate allele frequencies. Banding patterns were scored or rated by their migration distance from the point of origin. The most common homozygote band was assigned a 100. Bands for homomeric proteins of other alleles were given a number representing their migration distance as a percent in relation to the common band following protocol described by Utter et al. (1974). Horizontal starch gels were run with 35-40 individuals of one tissue type at a time. Gels were run utilizing tissue from muscle, liver, eye, and heart when available. Different buffers were employed to obtain the best resolution of the enzymes tested (Table 1). Once the analysis of enzyme systems began, photos were taken of the gels for later reference. Enzyme recipes were tried again using other buffer systems (Table 1) if resolution was not scorable on the first run. Systems which were defined

Figure 1. Muscle tissue sampling location on sturgeon.

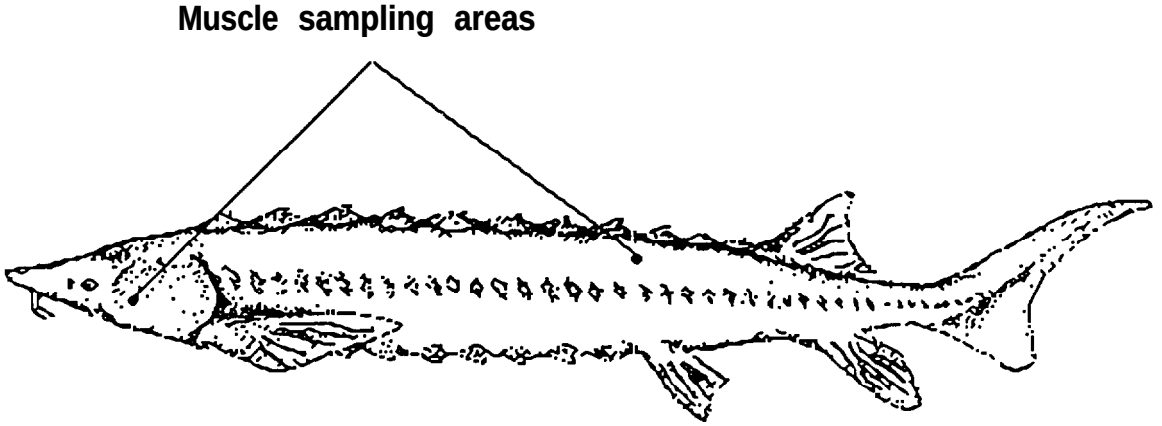


Table 1. Buffers used for sturgeon electrophoresis.

	Gel Buffer	Electrode Buffer	
1	.Tris-citrate (pH 8.7)	Lithium-borate (pH 8.0)	(Ridgway et al., 1970) (RW)
2.	Tris-borate (pH 8.7)	Tris-borate (pH 8.7)	(Aebersold et al., In Press) (TBE)
3.	Citric Acid (pH 6.5) * (pH 5.5)	Citric Acid (pH 6.5)	(Clayton and Tretiak, 1972) (AC)
	+ (NAD added to gel and cathcdal electrode tray)		
4.	Tris-citrate (pH 7.0)	Tris-citrate pH 7.0)	(Shaw and Prasad, 1970) (TC)
5.	Tris-phosphate (pH 8.2)	Tris-phosphate (pH 8.2)	(Busack et al., 1979) (TP)

enough for scoring purposes are listed in Table 2, with the tissue and buffer defined. Data were collected from each individual and analyzed with a Chi-square statistic between and within each area to determine if any frequency differences existed which would not conform to Hardy Weinburg expectations. In extrapolating to population genetic characteristics from a random sampling of individuals, genetic theory expectations are based on the assumption of Hardy Weinburg equilibrium conditions as defined in all basic genetic texts. Data collected in previous years were pooled to form a single database for analysis, so that sample sizes within two of the areas were increased. Genetic identity values calculated from the gene frequencies measured the closeness of the relationship between the sampling areas using the method of Nei (1978). The average heterozygosity was calculated within each sampling area for use assessing the degree of variation and for use with Hardy Weinburg equilibrium evaluations. Twenty-eight loci were scored overall, with some not scored for all areas or all individuals within an area. Analyses were performed using the BIOSYS (Swofford and Selander, 1981) program, Minitab, and SAS statistical packages on the University of Washington Cyber computer.

Mornhometics and Meristics

In an effort to further evaluate potential stock characteristics, morphometric and meristic information was collected at the time of tissue sampling so that any apparent physical or structural differences could be noted. It was hoped that differences would correlate with the genetic data collected through electrophoresis.

Snout shape was evaluated by multivariate statistical analysis of 13 measurements taken from photographs. Fish were placed on a white background and the head region photographed from above. A metric ruler was included in each photograph for a size reference (Fig 2). The positions of seven landmarks (Fig 3) were digitized from the photographs on an x-y grid using the technique of Winans (1984). Landmark 1 was tip of the snout; landmarks 4 and 5 were positions of the eyes along the body outline. Landmarks 2,3,6 and 7 were calculated. To calculate these landmarks, line 4-5 was drawn on the photograph. Then a line perpendicular to 4-5 that intersected landmark 1 was drawn. The length of this line is "x" Two lines perpendicular to this line were drawn at distances 0.25x and 0.50x from the snout, as indicated in Figure 3. The points of intersection of these two lines and the body outline constituted landmarks 2 and 7 (at 0.25x) and landmarks 3 and 6 (at 0.50x) We assumed that these landmarks were homologous from specimen to specimen.

Dorsal scutes are the plates which lie along the dorsal crest of the fish. Because casual observations during previous years showed variation in the total count among fish, dorsal scute counts were included as part of the sample routine for further comparative examination. Lengths of fish were not routinely noted and were thought to be of no influence on the total number of scutes observed. (Laboratory sturgeon 5 - 12 cm in length have shown the full range of scute counts, personal observation.) Data were then entered on a computer and tested against the snout data, and the electrophoretic data for any correlation between areas. The correlation analyses were performed using Minitab statistical program. Data were assembled so that the three character sets collected from each individual fish were aligned for comparison. Sample size of both the scute count and head shape data were smaller than the electrophoresis sample size. This was primarily due to the logistics of collecting data on other peoples fish during processing, and the tissue samples had priority.

Table 2. Listing of systems by tissue and buffer.

Enzyme	Buffer	Tissue
Aspartate aminotransferase (AAT) E.C. 2.6.1.1	TBE	mus, hrt*
Adenosine deaminase (ADA) E.C. 3.5.4.4	TP	mus
Aconitase hydratase (AH) E.C. 4.2.1.3	TBE	mus
Adenylate kinase (AK) E.C. 2.7.4.3	AC	mus
Fructose biphosphate aldolase (ALD) E.C. 4.1.2.13	AC+	mus
Creatine kinase (CK) EC. 2.7.3.2	AC+	mus, eye, hrt
Esterase (EST) E.C. 3.1.1.	AC	mus, liv
Glyceraldehyde-3-phosphate dehydrogenase (GAP) E.C. 1.2.1.12	TC	mus
Glycerate dehydrogenase (GD) E.C. 1.1.1.29	TP	mus
Glycerol-3-phosphate dehydrogenase (GPD) E.C. 1.1.1.8	TBE	mus
Glucose-6-phosphate isomerase (GPI) E.C. 5.3.1.9	RW	mus
Isocitric dehydrogenase (IDH) EC. 1.1.1.42	RW	mus
Lactate dehydrogenase (LDH) E.C. 1.1.1.27	AC	mus
Malic dehydrogenase (MDH) E.C. 1.1.1.37	AC	mus
Malic Enzyme (ME) E.C. 1.1.1.40	AC	mus
A-mannosidase (a-MAN) E.C. 3.2.1.24	RW	liv
Phosphogluconate dehydrogenase (PGD) E.C. 1.1.1.44	TBE	mus, liv
Phosphoglucomutase (PGM) E.C. 5.4.2.2	TBE	m u s
Superoxide dismutase (SOD) E.C. 1.15.1.1	RW	mus

* muscle = mus, heart = hrt, liver = liv

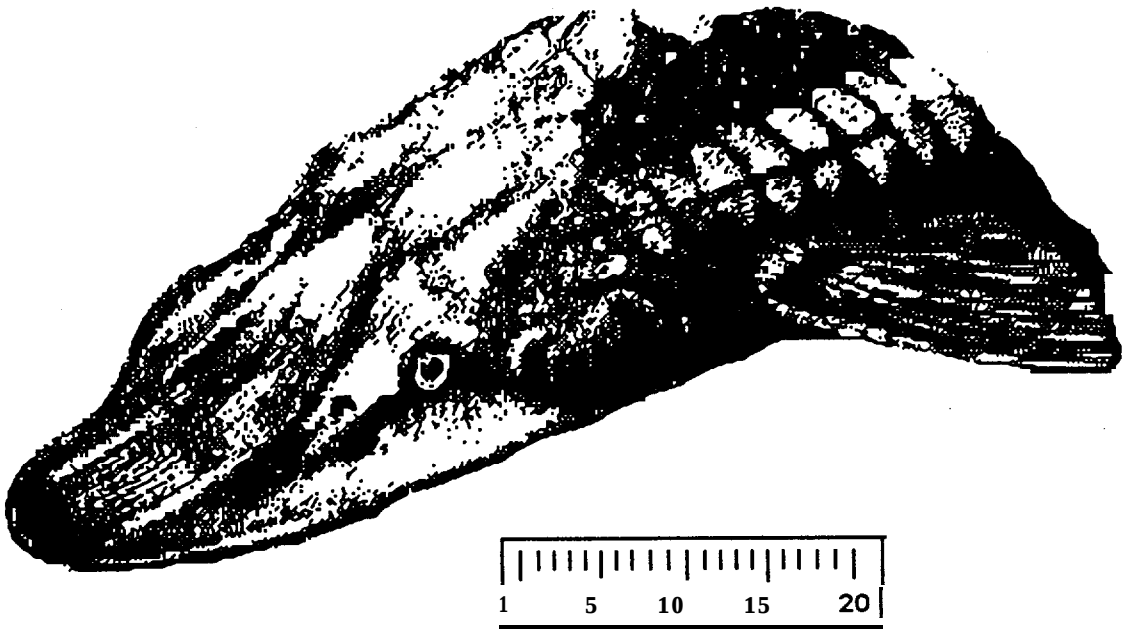


Figure 2. Position of Photo taken of head shape.

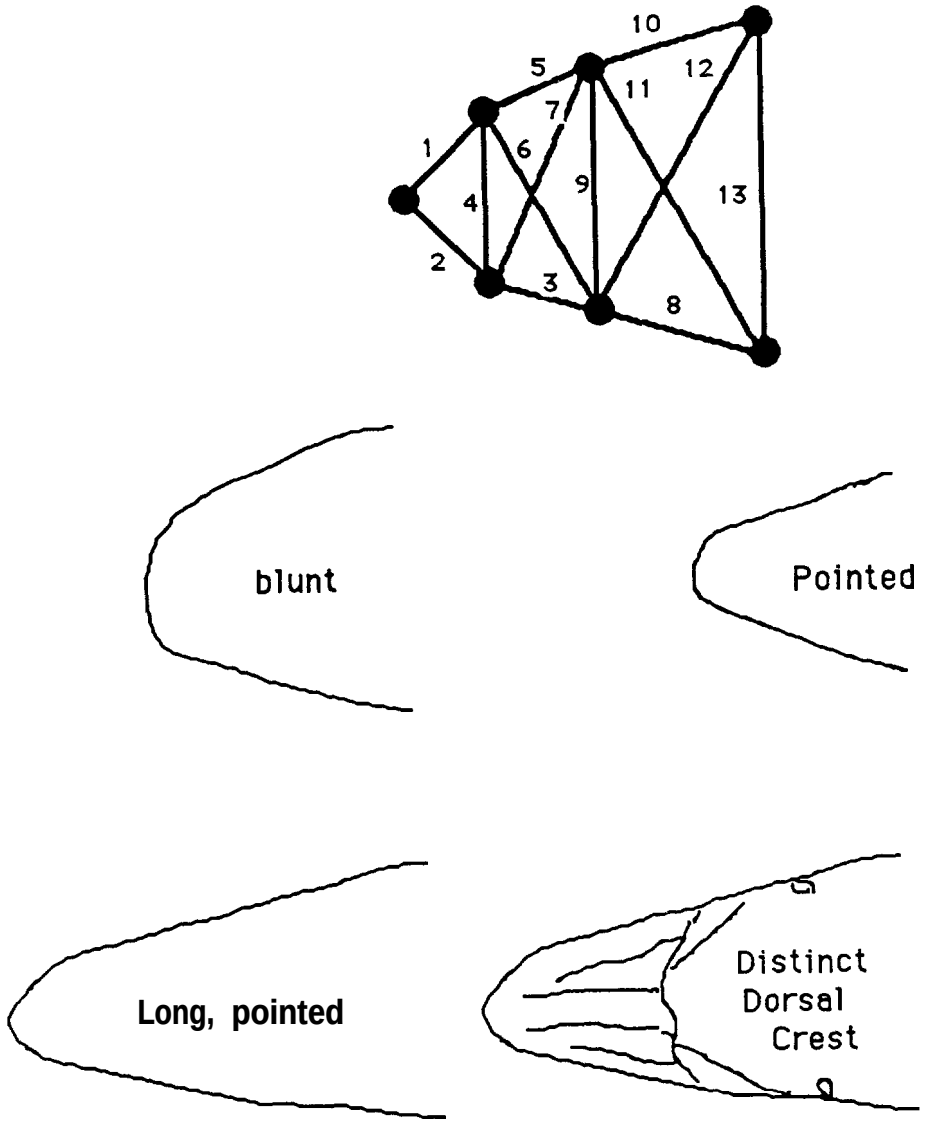


Figure 3. Landmarks used for head, and outlines of observed snout shape differences.

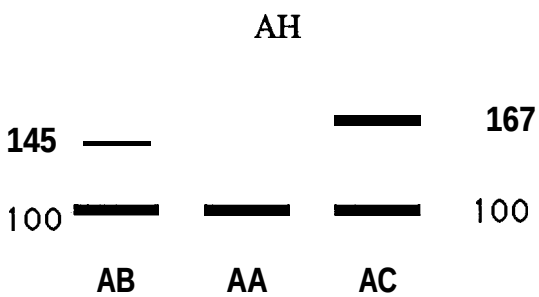
RESULTS

Electronhoresis

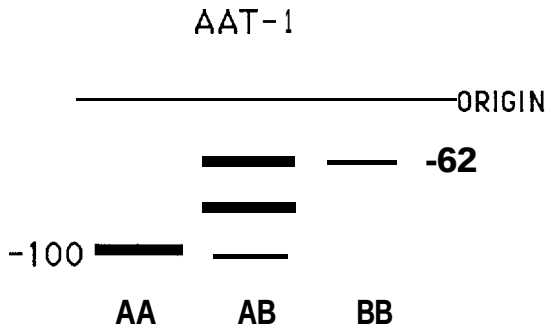
In the overall electrophoretic analysis of the present study, a total of twenty-seven loci showed banding patterns which could be scored (Table 2). Eighteen of the loci scored from the areas examined showed some variation, but only eleven were considered polymorphic ($p<.95$). The remaining seven systems were assumed to have shown a somewhat rare allelic variation. Enzyme systems which were evaluated at the four areas studied are listed below with a brief structural description. While the banding pattern for these enzyme systems based on their molecular structure has been defined (Harris and Hopkinson, 1972), the position of the loci and the number of loci are specific for white sturgeon. Each description is followed by a drawing showing the banding patterns obtained from the electrophoretic technique. The drawings show the most common allele found at each locus labeled as 100, and alternate alleles labeled according to their relative position. Data are reported for these systems from each individual fish by interpreting the banding patterns. The interpretation of the banding patterns into genotype descriptors is referred to as scoring.

Description of loci

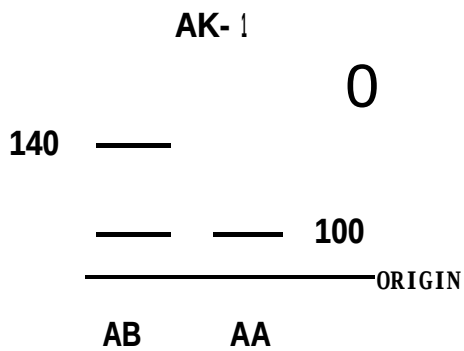
Aconitase hydratase (AH) was scored using a single locus model having two fast alleles. This system is polymorphic but was difficult to score. There was a super-fast allele which has been seen only in Roosevelt Lake, but in low frequencies.



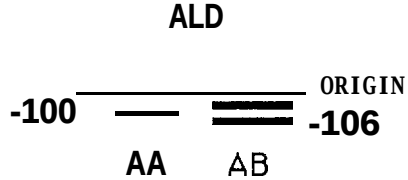
Aspartate aminotransferase (MT) showed a cathodal locus which was scored in muscle. I observed a fairly common slow allele at this locus in all areas.



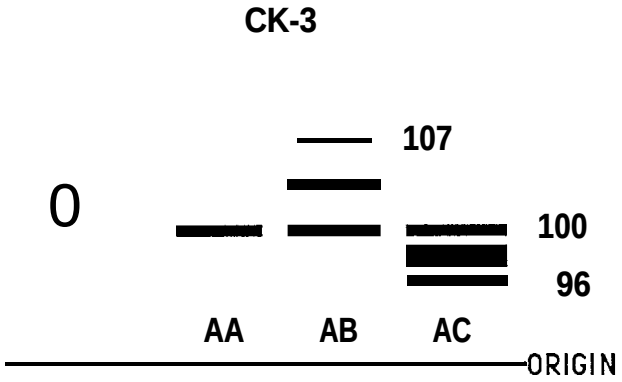
Adenylate kinase (AK) had one locus. There was a fast variant out of this locus (AK- 1) found only in the Ilwaco samples.



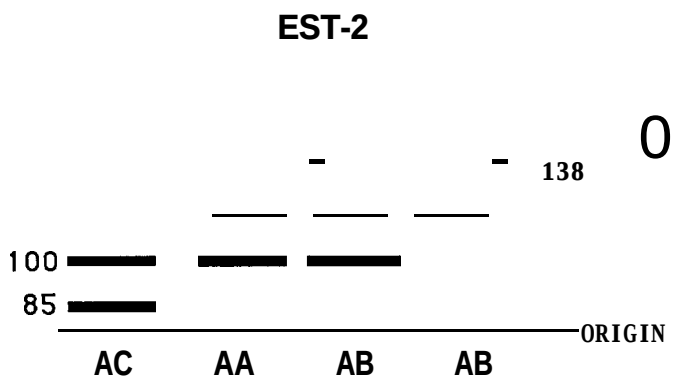
Fructose biphosphate aldolase (ALD) showed one locus in muscle which migrated anodally. There was a fast variant from this locus. There appears to be tissue specific isozymes which have different mobilities but show the same variation in this system. Observed banding patterns did not conform to expected structure, most likely due to the close affinity of their relative electrical charge.



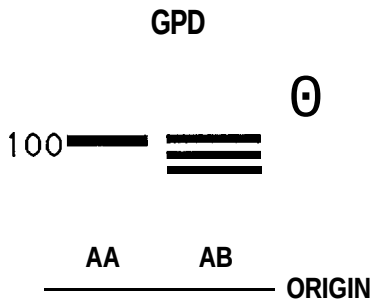
Creatine kinase (CK) had three loci of which CK-1 and CK-2 were both monomorphic. CK-3 was scorable in eye and heart and was polymorphic. We saw a fast allele in all areas scored, but a slow allele only in Roosevelt Lake.



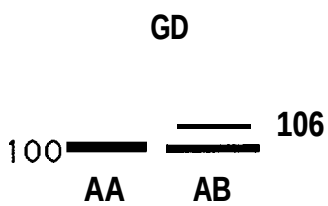
Esterase (EST-l) was monomorphic in all areas. EST-2 was polymorphic in Roosevelt Lake and the mid-Columbia areas in liver tissue. Liver was not available for testing from other locations.



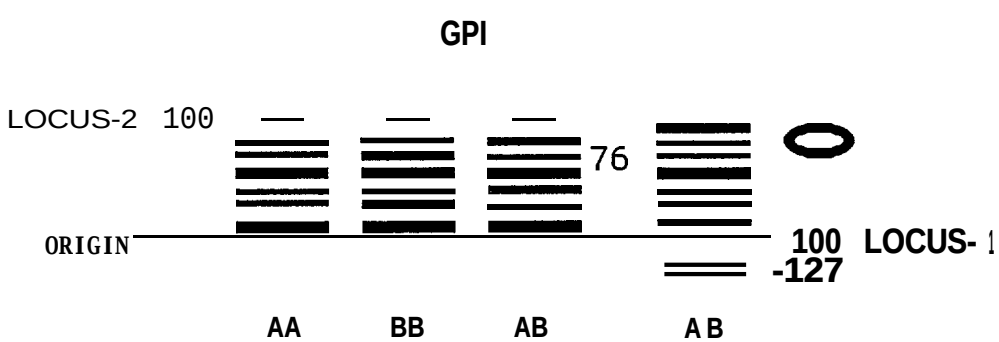
Glycerol-3-phosphate dehydrogenase (GPD) migrated anodally and had a slow variant. The variant was seen in all areas.



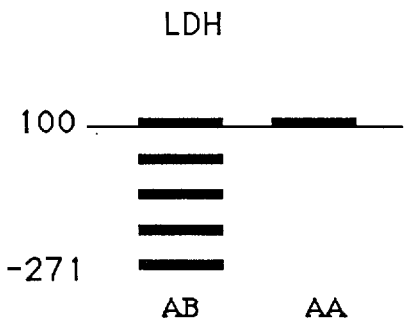
Glycerate dehydrogenase (GD) migrated anodally and showed a fast variant. This variant was only observed at Ilwaco.



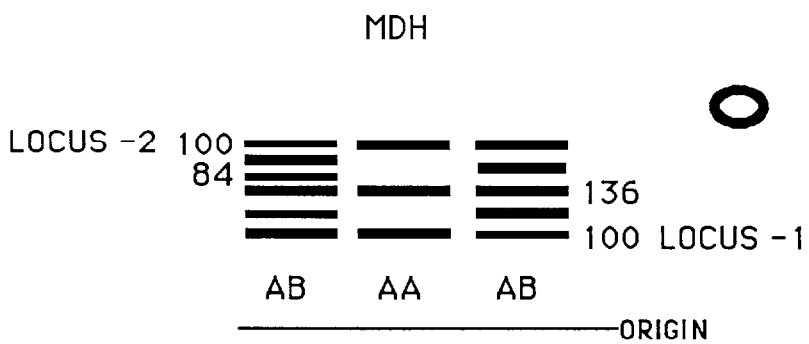
Glucose phosphate isomerase (GPI) was scored as being coded for by two loci with an interaction band The first locus was near the origin and had a variant that migrated cathodally and was seen only at Ilwaco. The second locus was anodal and also had a slow variant observed in all areas.. We could not reduce or eliminate the large number of shadow bands by treatment with either mercaptoethanol or reduced glutathione as thiol reagents.



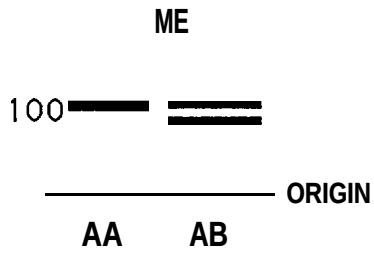
Lactate dehydrogenase (LDH) had one locus which was scored in muscle. The common allele was on the origin and a variant migrated cathodally. A high percentage of heterozygotes were seen in samples from most areas and this supported deviation from the expected Hardy-Weinburg proportion. The structure of LDH and MDH in Russian sturgeon has been described by Slynko (1976) and for other fish species by (Markert et al. 1975; Markert and Faulhaber,1965), a simple model was used for scoring. White sturgeon in the Columbia River appear to have other loci specific to heart and eye. The heart loci banding pattern seems to be expressed by muscle tissue better in older individuals when the muscle locus is no longer discernable (D. Bartley, personal communication).



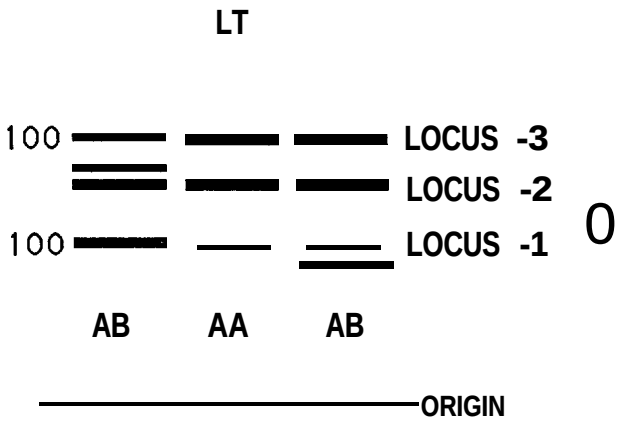
Malate dehydrogenase (MDH) showed two loci anodally, with both MDH-1 and MDH-2 being polymorphic. MDH-1 had a fast variant allele which fell on the heteropolymeric band between the two loci, and was found in all areas scored.. There was also a slow allele that showed itself out of MDH-2 in the Ilwaco area.



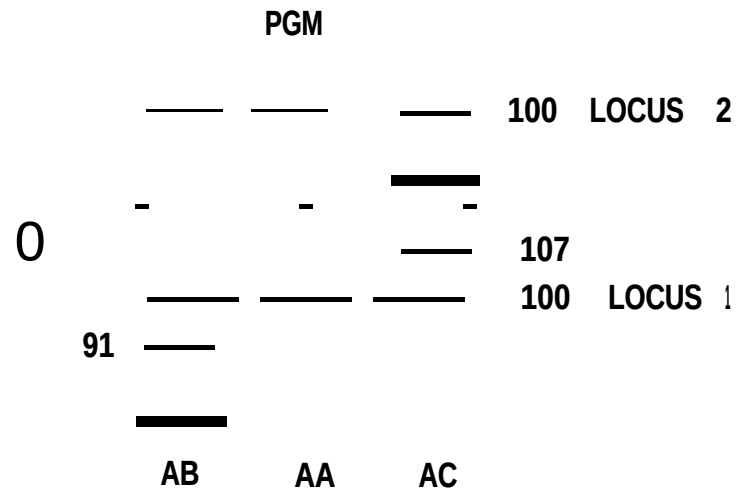
Malate dehydrogenase [-NADP] (ME) had one locus which was polymorphic. ME-l migrated cathodally and had a slow variant seen only in Ilwaco. While this is a tetrameric protein, the five bands expected from a heterozygote were not apparent.



Peptidase (PEP) showed three loci and two were polymorphic. PEP was scored from the peptide leucyl tyrosine (LT) which revealed three loci, two of which were scored. There was a slow variant out of LT-3 and LT-1. No variation was observed in Roosevelt Lake or the Snake River for LT-1. LT-2 was fainter and less discemable, and no data were collected.



Phosphoglucomutase (PGM-1+2) was scored in muscle tissue for two loci. Variation was seen in PGM-1. There was a rare fast allele seen in Roosevelt Lake and a slow allele seen frequently throughout all areas.



Adenosine deaminase (ADA- 1+2), Glycerakiehyde-3-phosphate dehydrogenase (GAP), A-Mannose (A-MAN), (CK-1+2), (PGM-2), Superoxide dismutase (SOD), Phosphogluconate dehydrogenase (PGD), were all monomorphic.

Polymorphic loci have been mentioned above and displayed with drawings. The relative mobility to the common allele of alternate alleles for each enzyme system are compiled and shown in Appendix Table 1. The allele frequencies are listed by system and area (Appendix Table 2) and are a summarization of the raw data obtained by area. All statistical calculations have been derived from this basic data and tested by system between areas for determination of any apparent separation .

In several enzyme systems, the observed banding pattern frequencies were slightly greater than expected within an area. A chi-square test for determination of Hardy-Weinburg equilibrium conditions pointed this out. There were two of these enzyme systems which perhaps suggests error in the scoring model. One possible explanation for the high number of heterozygotes observed in muscle LDH of white sturgeon may be an occurence of gene duplication.

Interesting systems (those polymorphic) are found throughout the river, but two that were particularly perplexing occurred in the upriver samples. Genotypic variation existed in both AH and PGM enzyme systems, but the model for the number of loci was unable to be verified, so the simplest model was assumed. PGM-1 appears to also suggest possible gene duplication with each having a different mobility, while AH may have two loci with the same mobility . This was not clarified by the use of fresh samples or the use of thiol reagents suggested by Harris and Hopkinson (1972). A single loci model for scoring this enzyme system (AH) was assumed. This allowed the allele found only in Lake Roosevelt to be scored separately from the other hetozygotic genotypes found elsewhere in the river. ALD showed tissue specificity because each tissue seems to have at least one specific locus, but the scoring appeared the same at each locus. The heterozygote did not show the full banding that would be expected of a tetrarneric enzyme, so the exact position

of the alternate is unclear.

The average heterozygosity by area was calculated as an index of the amount of variation (Selander and Johnson, 1973). Values ranged from 0.043 to 0.079. The percentage of loci which are heterozygous in an average individual is referred to as H (Hartl, 1980). Overall sturgeon samples H = 0.075 , this is slightly higher than the average values seen in fish (Nevo et al., 1984). There was little variation in the individual heterozygosity between areas (Table 3).

The observed and expected allele frequency values according to Hardy-Weinburg equilibrium were tested by loci within each of the five areas using a chi-square analysis. The systems where the observed frequencies did not fit Hardy-Weinburg expectations are shown with an asterisk in Appendix Table 3 by area. These are enzyme systems which have been discussed previously in regard to the high number of heterozygotes and the low frequency or lack of alterrnate homozygotes (LDH,GD). The Chi-square statistic did reject the null hypothesis that differences between observed and expected values by loci were the same. If either an excess or deficiency of alternate homozygote genotypes occurred in a particular enzyme system, the Chi-square statistic was significant at .001 < p< .025. Contingency Chi-square table evaluations provided evidence of differentiation between sampling areas. In enzyme systems where an allele did not occur in all areas or where the frequency of occurrence between areas varied, the test statistics were significant (Appendix Table 4) . Significance of the chi-square statistic for an enzyme system proved that the allelic frequencies between areas were indeed different. In essence this data formed the crux of our study from which we would draw our conclusions. Based on this test's results, we were able to conclude that there were some differences between areas which were significant.

Sample size was small in both the Kootenai (n=9) and Snake R. (n=8) for good statistical validation of the genetic differences observed. Still, it was large enough to yield a heterozygosity estimate which would probably fall within 1% of an estimate obtained from a large sample of fish since many loci were sampled (see: Gorman and Renzi, 1979). The number of loci tested is limited by the number of tissues available and the number of substrates which are being used to bring up the various stains, If samples are taken from a catch and release situation, a small muscle plug and blood sample allow limited testing. For instance, LDH can be scored in muscle, but there is another locus in heart, and probably another in eye (Bartley et al, 1987) which could be scored if the samples were attainable and the models were precise.

Genetic distance estimates were made from allele frequencies using an unbiased procedure (Nei, 1978). This method showed all areas to be very similar, which was not surprising since it is most useful in finding interspecies gene differences (Table 4). It was done to see if any trends of divergence were apparent genetically between the areas examined Genetic distance is sometimes related linearly with geographic distance or area (Nei, 1972). The calculation for genetic distance used the allele frequency data shown in Appendix Table 2. The values attained from this procedure suggest there has been little differentiation in white sturgeon within the river system Nei (1978) values for D, the genetic distance, were highest for the Kootenai River (D=0.012) and Ilwaco (D=0.010) when compared to the Upper Snake sturgeon sampled.

The sample size of 12 individuals from the Snake river was considered too small for accurate population estimation. No genotypic differences were found to indicate there is or has been the evolving of different genes specific to the present environment in the Sanke

Table 3. Average heterozygosity calculated by area.

	POPULATION	MEAN SAMPLE SIZE PER LOCUS	MEAN NO. OF ALLELES PER LOCUS	PERCENTAGE OF LOCI POLYMORPHIC*	MEAN HETEROZYGOSITY DIRECT-COUNT	MEAN HETEROZYGOSITY HDYWBG EXPECTED**
1	SNAKE	8.0 (1.0)	1.3 (.1)	25.0	.078 (.033)	.072 (.027)
2.	UPPER SNAKE	4.8 (.7)	1.2 (.1)	21.4	.076 (,037)	,062 (.028)
3.	ILWACO	216.3 (13.0)	1.8 (.1)	64.3	.071 (.014)	.078 (,016)
4.	LAKE ROOSEVELT	60.1 (3.1)	1.6 (.1)	46.4	.073 (.020)	.073 (.020)
5	MID-COLUMBIA	130.9 (7.5)	1.5 (.1)	46.4	.071 (.018)	.070 (.018)
6.	KOOTENAI	6.7 (.7)	1.1 (.0)	7.1	.028 (.024)	.021 (.018)

* A LOCUS IS CONSIDERED POLYMORPHIC IF MORE THAN ONE ALLELE WAS DETECTED

** UNBIASED ESTIMATE (SEE NEI. 1978)

Table 4. Genetic distance calculations.

BELOW DIAGONAL: NEI (1978) UNBIASED GENETIC DISTANCE

POPULATION	1	2	3	4	5	6
1 SNAKE						
2 UPPER SNAKE	.002					
3 ILWACO	,006	.010				
4 LAKE ROOSEVELT	.005	.003	.002			
5 MID-COLUMBIA	.004	.006	.001	.001		
6 KOOTENAI	.006	.012	.004	.005	.003	

River. The Upper Snake River samples appear more fixed than the sturgeon in the Columbia below the confluence of the two rivers. This is obvious from the allele frequencies (Appendix Table 2), the average heterozygosity (Table 3), and somewhat from the genetic distance.

Mornhometrics and Meristics

The computerized approach lent preciseness to the visual evidence for substantiating differences in snout shape. For assessment of this approach, fish were not categorized by area but evaluated as a variable group. Thirteen interlandmark distances from each fish were calculated between the seven landmarks illustrated in Figure 3. A variance-covariance matrix from log10 transformed data was subjected to a principal component analysis. The first two eigenvectors are presented in Table 5. Coefficients were relatively equal in size on the first component and separated fish by overall size. This component was not considered further. The second component (PCII) separated fish by snout shape. The signs of coefficients in PC II can be used to interpret the multicharacter relationship described by PC ll. Namely, four characters had positively -signed coefficients; the remaining characters had negatively-signed coefficients. This is simply interpreted to mean that the four outside characters contrast with the remaining characters. We interpreted the variation in PC II values as multivariate differences in snout elongation .

Head shape was broken up by area to see if any trends in snout shape were apparent. In the mid Columbia area , head shapes were categorized to fall into three empirical groupings. Lk. Roosevelt and Snake river fish represented the pointed-nosed and rounded-nosed snout categories. Kootenai River fish were representative of the pointed nose fish only. Ilwaco fish comprised 65% of the blunt nosed classification with both other categories represented. This may follow the rapid growth hypothesis suggested by Ruban and Sokolova (1986), which provides evidence that warmer temperatures during early development and the resultant faster growth may be instrumental in varying head shape characteristics. The estuarine area near IIwaco is thought to provide abundant food and warmer temperatures than areas further upstream in the Columbia. The quantity of fish harvested in this lower river stretch suggests optimal growing conditions (over 50,00 annually; Ring, 1983). Growth rates have been measured in the Snake river by Coon et al (1977) where water temperatures are colder and growth was shown to be slower than in areas of the lower Columbia river.

Dorsal scute counts varied throughout the river both between and within areas sampled (Table 6). Analysis of data showed no correlation between dorsal scute count and head shape. The number of dorsal scutes may vary due to water temperature during early rearing and may indicate more about early rearing conditions than genetic variability. Electrophoretic data were tested against the scute count data for correlation and no relationship was shown. One way analysis of variance was performed to test the variability between areas. Table 6 shows the test result, there was no significant difference between the areas sampled. Ventral scute counts were also evaluated, but no significant difference was found between areas. The mean and standard deviation are shown in Appendix Table 5.

Table 5. Eigenvector of PC 1 + PC2.

	PC 1	PC2
X 1	0.28	- 0.12
X 2	0.28	0.43
X 3	0.36	0.45
x 4	0.22	0.40
x 5	0.33	- 0.22
X 6	0.22	- 0.11
x 7	0.25	0.33
X 8	0.33	- 0.39
x 9	0.22	- 0.08
x10	0.33	0.23
x11	0.25	- 0.18
x12	0.26	- 0.11
x13	0.23	- 0.12

Table 6. Analysis of dorsal scute count data by area.

	Lk.Roosevelt	Mid Columbia	Ilwaco	Snake
Mean	12.133	11.803	11.853	12.083
StDev	0.915	1.112	1.077	2.109
(N)	15	66	34	12

Analysis of Variance

$H_O = \mu_1 = \mu_2 = \mu_3 = \mu_4$

$H_A = \mu_1 \neq \mu_2 \neq \mu_3 \neq \mu_4$

SOURCE	DF	ss	MS	F
FACTOR	3	1.87	0.62	0.43
ERROR	123	179.35	1.46	
TOTAL	126	181.23		

$F(0.25,3,123) = 2.68$ Do not reject Ho , ($p > .25$)

DISCUSSION

White sturgeon in the Columbia River were naturally anadromous. The identification of their population genetic structure in the Columbia depends on the ability to locate polymorphic enzymes with electrophoresis or other significant morphometric and meristic character variation. Allendorf and Phelps (1983) analyzed pallid and shovelnose sturgeon and found 3 polymorphic loci, but no statistically significant allele frequency differences between these species were detected at any of the variable loci. Bartley et al (1987) found 7 polymorphic loci in white sturgeon from four different river systems in the Pacific Northwest, but were limited by sample size to distinquish major differences. Carlson et al. (1982) found low genetic variability and slight suggestion of differentiation between geographically isolated populations of paddlefish. If different subgroups of white sturgeon migrated long distances upstream to reach ancestral habitat, dam construction has trapped them in various reservoirs along the river. A mixture of upriver subgroups may now be represented within the various reservoirs.

Evidence for intraspecific groups of sturgeon has been noted in the Delaware River (Dean, 1893) and the southern rivers of the USSR (Gerbil&ii, 1951). Both papers make reference to several peaks of migration and the condition of the gonads at the time of upstream migration. The early fish had immature gonads and were headed for the furthest upstream spawning sites. There was also a variation related to upper lethal temperature of the eggs of the fish from the various segments of a run (Systina et al., 1985). This shows that family Acipenseridae has been capable of adjusting to specific environmental conditions by varying timing of upstream migration. It seems not unrealistic to imagine that historically a similar type of biological race structure could have existed amongst white sturgeon in the Columbia river .

The construction of hydroelectric dams promoted a change in existing habitat and life history strategies of anadromous and resident fish. Sturgeon now reside totally in freshwater in the reservoirs of the Columbia River and with time unique adaptations will likely evolve. For instance, morphological variation could occur within different areas due to different prey items becoming available. This is particularly important if you compare the free flowing stretches to the reservoirs. The longer retention time of water in reservoirs favors different food chain ecosystems than a river system. If sturgeon now reside in lower velocities, one might expect some morphological changes to occur, and could be in the form of lost physical characters that are no longer utilized in the altered river environment.

Acipenserid subspecies have been shown to differ in snout length, mean dorsal and ventral scute counts and gill raker counts between three river systems (Artyukhin and Zarkua, 1986). Morphological character variation in the sterlet (Acipenser ruthenus) s been documented by Usynin (1980) . Hybrids have exhibited intermediate morphological and meristic characters between the beluga (Huso huso) and the sevryuga (Acipenser stellatus). Crass and Gray (1982) have documented that such morphological variation in snout shape exists among white sturgeon in the Columbia. How such a difference relates to genetics or life history strategies has not been identified. A genetic basis for the dimorphism is not supported by electophoric data.

The morphological characteristic of snout shape varies within the Columbia River. Snout dimorphism of white sturgeon has been reported by Crass and Gray (1980) and Brannon et al (1986) in the Columbia river . Stock specific differences in snout shape and length are observed in the Siberian sturgeon and also the sterlet (Sokolov et al. 1986)

suggesting this may be common for sturgeon species. Carlson et al (1985) have noted differences in snout shape of pallid and shovelnose sturgeon using a technique similar to the one employed for this study of principal component analysis.

Blunt nosed sturgeon are found primarily in the mid and lower reaches of the Columbia, while long, pointed snouts predominate upriver. White sturgeon in the Sacramento River are usually blunt-nosed resembling the fish of the lower reach of the Columbia River (Ken Beer, personal communication). This seems to lend credence to the theory that warmer water temperature and a faster growth rate may influence snout length as suggested by Ruban and Sokolov (1986).

Scute counts are quite variable throughout the river but exhibit no obvious geographic pattern. Meristic traits were also examined by other researchers at the same time as morphometric charcteristics. Evidence supporting that warmer water culture causes changes in the total number of scute counts and fin ray counts has been documented for two Russian Acipenser species. A test of this theory is planned for white sturgeon in 1988 using two different incubation and early rearing water temperatures. Data collected for this study did not show that variability in scute counts is significant between the areas sampled . There is no indication that scute counts could be used as an indice for determining what area of the Columbia river a sturgeon resided.

Electrophoresis has identified some differential variation among stocks from different areas. The allelic frequency data in Appendix Table 2 shows the enzyme system and the degree of variability in gene frequencies by area. Variation is different between the areas sampled but the frequencies of the variants are low. Low frequencies depict rare alleles because the alternate genotype is not seen in more than 95% of the individuals from a given area. It should be mentioned that this technique can only detect a percentage of all the proteins which exist. However, electrophoretic analysis has been successful in differentiating fish populations by both species and stock (Allendorf et al., 1987).

Genetic changes are expected to occur as the environmental factors that dictate genetic characteristics change. If the environmental change is too rapid, the genetic response may not be fast enough and the population may be adversely affected In the present study, each isolated group will be responding in a different degree depending on the magnitude of environmental alteration. The low annual catch of sturgeon in certain areas of the Columbia is believed the result of altered environmental conditions which have reduced spawning area and diminished recruitment. We feel that the electrophoretic evidence compliled thus far is showing that genetic differences in populations between areas do exist. However,while variation was seen specific to individual sampling areas, it was apparent only as rare alleles or gene frequency differences. Based on this evidence, it is recommended that enhancement measures on the Columbia should be undertaken in such a manner as to maintain any discreteness that populations have acquired.

TASK II

The influence of the environmental factors associated with prey odor, substrate cover and water movement on the feeding success of juvenile white sturgeon.

Statement of the Problem

Successful enhancement of sturgeon must be based on an understanding of the effects of recent ecological changes in the Columbia River. Basic relationships between sturgeon and their biological and physical habitat have followed ancestral patterns that evolved with open access to the whole river system and marine environment. Entirely new habitat definition, reduced food resources, changes in community composition of the reservoirs and the introduction of new predator species may limit sturgeon potential in the river above Bonneville Dam.

Observations made on the general feeding behavior during the 1985 studies and tests in 1986 on their habitat requirements implicated the feeding mechanism of white sturgeon as a contributing factor to the difficulty they may have adapting to some upriver habitats in the Columbia. White sturgeon are non-visual feeders (Sbikin 1973; Buddington and Christofferson 1985; Brannon et al. 1986) whose feeding success is affected by the ability of prey species to avoid capture. As non-visual predators, sturgeon feeding success on some species of fish is dependant on the amount of light available for prey to detect their approach. Hydro developments have altered the turbidity in the river which enhances the ability of visually oriented prey items to avoid capture, and thus reduces their availability to non-visual predators. Sturgeon have several other well developed sensory systems (Disler 1971; Teeter et al. 1980) that can be used in feeding, and such non-visual predatory mechanisms undoubtedly have defined their present feeding niche, associated primarily with immobile benthic prey, and reduced access to fish and zooplankton.

Studies conducted in 1985 and 1986 at the University have indicated that juvenile white sturgeon are opportunistic feeders that would eat any aquatic animal that was presented to them, provided they could capture and ingest it. This was confirmed by examination of food habits which have shown that white sturgeon eat a relatively wide variety of prey types in numbers often reflecting their temporal and numerical abundance (McKechnie and Fenner, 1971; Radtke, 1966; Semakula and Larkin, 1968). The diet of the shortnose sturgeon A. brevirostrum, has shown changes in relative consumption of prey items that simply appear to be a reflection of changing benthos composition (Dadswell, 1979; Dadswell, 1984). A European sturgeon, the sterlet, A. ruthenus, also appears to be an opportunistic feeder and has been found to utilize as many as 69 different prey items (Zakora 1978). Like other species, the diet of the white sturgeon is probably just a reflection of the availability of easily captured food resources found in a particular area. Ancestrally, white sturgeon populations may have depended on huge populations of salmonid and other migratory fish species that annually brought large quantities of biomass from the ocean to the inland river systems and made it available in one form or another to all ages of sturgeon. Now that the ecology of the Columbia River has been altered by hydroelectric development and other human impacts, the food resources available to upstream sturgeon populations and any opportunity for seasonal migration to distant feeding areas has been severely reduced.

Environmental conditions associated with incubation and rearing of larvae is determined by parental spawning behavior. In rivers impacted by hydroelectric

facilities in the U.S.S.R. spawning only occurs in those sections where the natural hydrologic conditions have been retained. Hydroelectric operation alters the environmental cues necessary to induce spawning (Badenko,et al 1976; Votinov and Kas'yanov, 1979) leaving fewer suitable sites and concentrating spawning activity. Behavioral studies with juvenile sturgeon in the Soviet Union have used pikeperch as predators and found significant amounts of predation on sturgeon (Kasimov , 1970). Stomach analyses of yellow perch have yielded young shortnose sturgeon (Dadswell et al, 1984), and white sturgeon eggs have been found in white catfish (Radtke, 1966). Others report intraspecific predation on eggs in the Fraser River, British Columbia (Semakula and Larkin, 1968).

Studies conducted by the University on the early life history of white sturgeon have also provided information related to habitat requirements (Brannon et al. 1984; Brannon et al. 1986). Three basic behavioral stages have been identified and correlated to developmental timing. Studies conducted in 1986 were designed to provide information about the vulnerability of larvae to various predators found in the Columbia River. Findings indicate that at all three stages the young fish are vulnerable to high mortality. The hazards they experience, however, are related to the quality of habitat. The amount of available cover, light intensity, food density, and predators can have decisive influences on the health of sturgeon.

Investigations in 1985 led to an understanding of the roles current, substrate type, and photoperiod play in the behavioral responses of larvae and fry. White sturgeon larval behavior shows that cover; such as rocks, plants, detrital material and interstices in gravel, is critical during the hiding phase of their early life history. Next to egg mortality during incubation, predation is probably the largest source of mortality in larval sturgeon, but at present remains largely undocumented. Observations and preliminary tests in 1986 confirm that larvae and fry are vulnerable to predation depending on the habitat conditions. Larvae unable to discover the proper cover would be subject to extended periods of dispersion by water-flow and vulnerability to predation by other fish species. Cover provides a means for the larvae to end movement in the current and reduce susceptibility to predation until yolk absorption. After yolk absorption, the young leave the physical protection of cover, and apparently frequent areas of low light intensity which affords a measure of the same protection against predation. Sturgeon fry should not be vulnerable to visual predators in areas with minimal light penetration. With the reservoirs reducing river turbidity, increased light penetration may limit the effective range of young sturgeon within the reservoir and river environments.

Management, therefore, will have to consider enhancement efforts that include habitat improvements compatible with the opportunistic, non-visual feeding mechanism and early life history behavior of white sturgeon. To improve such habitat, we must first understand their predatory mechanisms on different prey species and determine the influence of abiotic factors of the various environments in the Columbia River system. In 1987, these research needs were segregated in two areas of examination. The first was a continuation of 1986 research characterizing juvenile feeding ability under different environmental conditions. The second area was sturgeon as prey for sturgeon and other fish species. Circumstances at the laboratory resulted in the postponement of the predation work until 1988.

Objective: To identify the responses required by juvenile white sturgeon to feed successfully on prey items under different environmental conditions.

Null hypothesis - Prey odor, cover, and water movement, have no significant influence on young white sturgeon feeding success.

Materials and Methods

Experiments to determine the habitat requirements of juvenile white sturgeon for successfull feeding were conducted at laboratory facilities located at the University of Washington. Behavioral assessments were made in observation arenas that simulated river environments. White sturgeon eggs were obtained from a commercial sturgeon hatchery on the lower Columbia River during late May of 1987, hatched in incubators at the laboratory, and placed in static aquaria (38-190 1) at room temperature (17.1-23.8 0 C). Also, larvae from a sturgeon farm in Galt, California, were obtained and held in aquaria as experimental stock. A 30-40 mm deep layer of mixed sand and small gravel was present in the aquaria and a photoperiod corresponding to ambient daylength was maintained using automatic timers. Yearling sturgeon held at the University laboratory were used as experimental stock for studies with larger fish.

Sturgeon fry were fed chopped tubifex worms. Larger juveniles (< 850 mm) were fed a wider range of live food including tubifex worms, carp larvae (Cyprinus *carpio),* chinook salmon eggs and alevins (Oncorhynchus *tschuwytscha),* coho salmon eggs and fry (0. *kisutch),* pink salmon fry (0. *gorbusca),* chum salmon fry *(0. keta),* and rainbow trout fry *(Salmo gairdneri).*

Observations on feeding behavior of juvenile sturgeon were made periodically during their growth, and recorded by video camera. Video recordings were made from a side view in the aquaria using a JVC model GR-ClU VHS video camera. Frame-by-frame analyses of close-up feeding events of larger solitary individuals (130-250 mm) in aquaria were used to determine methods of prey capture. The morphology of juvenile sturgeon was noted with regard to detection and capture mechansims.

Degree of yolk absorption and stomach fullness of the larvae and fry were assessed visually. Samples of these fish were preserved in 10% formalin and examined for degree of morphological development and yolk absorption. A camera lucida dissecting scope was used to make precise drawings of developmental stages and sensory structures of the head.

Three experimental manipulations were performed to provide further information about the white sturgeon feeding mechanism. Assessments were made on 1. the stimulatory components in feeds that elicite feeding responses, 2. the ability to detect and capture buried prey, and 3. the ability to detect and capture mobile prey.

Stimulatory Components of Feeds

Tubifex worms have been shown to be preferred food of white sturgeon (Buddington, 1984: Doroshov, 1983; Lindberg, 1986). Tubifex worms were chosen as the test food from which stimulatory components might be extracted, identified, and later synthesized artificially. Test materials were presented to the

sturgeon in 1.5 cm3 gelatin cubes. Tests for attractiveness of materials were determined by observing the behavior of test fish when the material was placed in two doughnut tanks, each occupied with six juvenile sturgeon (50-100 mm). Feeding behavior was assessed to occur when the sturgeon actively searched by sweeping back and forth across the substrate surface into the current and attempting to strike the gelatin cube. In contrast, passive behavior was when movement was away from the substrate and non-directional. Feeding activity was quanitified by counting the number of strikes at the gelatin cubes, one containing the test substance and the other the control, in a 10 minute period following their presentation. The following procedures were used to isolate and test materials for attractiveness to the sturgeon.

1. Live tubifex worms were chopped and tested.
2. Water was removed from the worms by freeze drying, and the dry material was tested.
3. The lipids were then extracted from the freeze-dried worms using the Bligh and Dyer method (1959). The lipid was tested by painting it onto the gelatin cubes presented to the sturgeon. The remaining fat-free fraction was evaporated with nitrogen to remove any solvents and tested
4. A portion of the fat-free fraction was ground and rehyrated in distilled water, centrifuged to separate out the water-soluble fraction, and the supematant tested for attractiveness. The remaining pellet was also tested.
5. A portion of the supematant was put in a vial in boiling water for 10 minutes to degrade that fraction which was not heat stable at 100°C. The resultant gelatinous material was mashed and tested.
6. The attractive material was profiled by putting tubifex worm exudate through a 0.45 millimicron filter to exclude molecules greater than 500 molecular weight, and injected into columns of a Bechman 18 cl amino acid analyzer calibrated for moles (Stone and Hardy, 1986). Using crystalline L-amino acids this profile was duplicated and tested at a 10° molar concentration in the gelatin cube. Also, a test solution was formulated using only those amino acids in the profile with 5 or fewer carbons. Finally, the three most prevalent amino acids were tested singly at 10" molar concentration.

Capture of Buried Prey

Tests on the ability of sturgeon to detect and capture benthic food items were scheduled to determine how effective yearling sturgeon were at feeding on items below the substrate surface. Experiments were performed in a flow-through doughnut-shaped tank (Brannon et al., 1985) in which continuous current was generated around the circle by positioning the inflow nozzle at an angle with the direction of flow. The tank was supplied with dechlorinated city water, 20 cm in depth, and had a 50-60 mm layer of sand and fine gravel on the bottom. A single 225 mm white sturgeon conditioned to feed on chinook salmon eggs and live rainbow trout fry, was used as the predator. The sturgeon was conditioned by placing partially buried eggs or stunned fry in the sand. Over a period of several days the prey were buried with less of their mass exposed, until they were completely buried. At that point the experimental protocol was initiated, which consisted of placing two plastic mesh partitions across the width of the channel, blocking off an area in which the prey could be buried without the sturgeon entering. After the prey was placed in the substrate, its depth was measured using a metal probe and the partitions were lifted to give the sturgeon access thoughout the tank. During each trial the sturgeon was observed until it either captured the buried prey or

passed over the prey several times without showing a response. Detection was assessed to have occurred when random movement of the sturgeon was replaced by bottom oriented searching behavior around or over the buried prey. Jaw protrusion to remove the prey item from the substrate was assessed as a capture response.

The experimental protocol called for tests on the sturgeon's response ability to detect live chinook salmon, *Oncorhynchus tschawytscha* eggs, stunned buried rainbow trout, *Salmo nairdneri*, fry, dead rainbow fry refrigrated for over 12 hours after death, and stunned fry inside a small sealed plastic bag. Responses to other buried objects were also measured including a 30 mm in long nail, and copper wire generating a small electric field in the substrate. The exposed ends of two insulated copper wires attached to AA and AAA 1.5 V batteries, were buried 15 mm apart and 20 mm deep in the sand. Sturgeon behavior was observed with the wires both connected and disconnected to the battery.

Capture of mobile prey

Sturgeon predation on mobile prey was undertaken as a continuation of 1986 studies to examine the predator ability of different sized sturgeon on different salmonid prey. Pink, *O. norbuscha*, and chum, *O. keta*, salmon fry were tested as prey. Tests were conducted in the doughnut-shaped observation arenas with current velocity of about 2-3 cm/set, 20 cm in water depth, and a uniform substrate composition of sand and small gravel. Four resident sturgeon (120-300 mm in length) were in each of two doughnut arenas. Both arenas were covered with black plastic to maintain darkness during the trials. Twenty chum fry (35 mm mean length) were added to one test arena, and twenty pink fry (32 mm mean length) were added to the second in partitioned chambers and acclimated to the tank for 2 hours before the partitions were removed and the sturgeon allowed to forage. After 24 hrs of exposure the number of fry remaining in each tank was recorded.

Larger sturgeon (700-850 mm) were tested for their ability to capture chinook salmon fry (43-47 mm) in 1.5 m circular tanks covered with black plastic. The tanks had water levels of 300 mm, center standpipes and dechlorinated city water inflows of about 5 l/min. These tests were designed to continue the1986 study on the influence of water movement on white sturgeon ability to capture rainbow trout fry (Brannon et al., 1986). Larger sturgeon were to be tested using chinook salmon fry.

In the first test, 20 chinook fry were netted from the holding tank, placed into a bucket and gently released into each of two tanks containing three sturgeon predators, and covered with black plastic to maintain darkness. One tank had a continuous current (10 cm/set) moving around the tank maintained by the direction of the inflow nozzle. The other tank had minimum water current by adjusting the inflow nozzle at an angle 90° to the wall of the tank. The number of fry remaining at 15,30,45, and 60 min was determined using a flashlight in both tanks, and capture success compared to determine the influence of current. Tanks with and without current were alternated throughout six paired tests.

The second test followed the same procedures as the first except 30 chinook fry were added to each tank, and the no current condition was altered to no inflow during the test period to eliminate the slight turbulence created by the 90" inflow pattern. The tanks in which current and no flow conditions were tested were alternated as above in four paired tests performed during the study. The number of

fry remaining after each of the test periods was compared between tanks using paired t-tests.

The study plan called for an examination of sturgeon feeding success and predator avoidance ability when exposed to different levels of light intensity, turbidity, and cover. During the early phase of the test period, a severe pH change was experienced in the dechlorinated city water supply, resulting in the immediate mortality of all larvae and several yearling sturgeon held as experimental stock. The loss altered the experimental design planned for the study, and postponed those portions of the plan requiring sturgeon larvae and fingerlings until the following spring.

RESULTS

Sensory Morphology and Foraging

When fry begin foraging, sensory structures of the head appear well developed (Fig. 4). White sturgeons have five major types of sensory receptors located on the head. Juveniles have large eyes on the dorsolateral surface of the head and anterior to each eye is a large olfactory rosette recessed in a shallow pit with large and small openings. There are four barbels anterior to the mouth on the underside of the rostrum and there appear to be numerous tastebuds on the fleshy lobes of the lips. Lateral line canals on the underside of the head extend from the snout tip posteriorly around the outside of the barbels to the side of the head about even with the mouth. Other canals may be located on the lateral and dorsolateral surface of the head (Disler, 1971). Finally, numerous apparent receptors are distributed over the lateral and ventral surfaces of the snout of white sturgeon in the same locations as the electroreceptors described in other species (Jorgenson, 1980; Teeter et al., 1980).

In the laboratory, white sturgeon fry constantly swam over the substrate with their barbels just above or contacting the substrate, once they left the hiding phase. When food was not present on the substrate, fry would regularly swim in the water column and move to another area before returning back down to the substrate. When odorous food was placed in the tank, the sturgeon responded by rapidly dropping to the substrate, intensifying movement, and searching back and forth or circling until they contacted the food. There was no indication that visual cues were used in feeding, and they often passed within mm of less odorous prey types, showing no response until they made contact with the prey later. In total darkness they fed successfully on benthic foods as well as salmonid fry.

Video and direct observations of feeding events indicated that contact with food by the barbels usually resulted in jaw protrusion. However, the jaws were sometimes protruded when strong chemosensory cues were encountered in the water column away from any prey items. Video observations indicated that the jaws were protruded considerably outside the head and prey items were rapidly sucked into the mouth. Suction pressure was created when the jaws were protruded, which pulled the prey well into the mouth. Such protrusions also appeared to be involved in forcing captured fry through the esophagus by gripping it and retracting the jaws. The roof of the mouth, which has ridges and two tooth patches on the inside surface, was protruded with the upper jaw outside the head. Similar ridges and teeth are found on the base of the gill arches. The two structures thus appear to form opposable surfaces used for gripping and manipulating captured prey.

Stimulatory Components of Feeds

Tests on the attractiveness of feed components showed good differentiation between test materials. When gelatin cubes containing chopped tubifex worms were presented to the sturgeon, active feeding behavior was observed. Freeze-dried worms and the residue from the lipid extraction were both attractive, but the extracted lipid elicited no response. When the residue remaining from the lipid extraction was separated into soluble and nonsoluble components, only the soluble fraction or supematant was attractive. Boiling the supematant and presenting the coagulate induced a feeding response, but it was less vigorous. The number of strikes evolked by the different materials summed for both tanks (Table. 7), showed

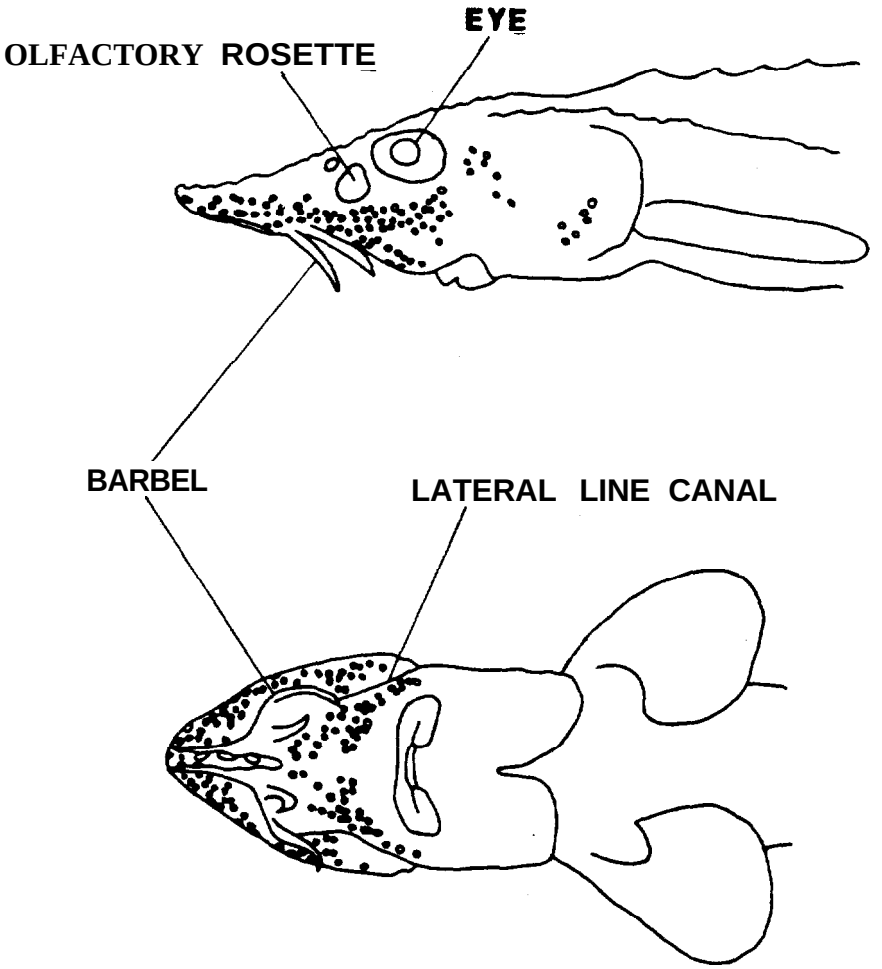


Figure 4. Lateral and ventral views of a white sturgeon showing the location of sensory receptors. Small circles represent electrical receptors.

Table 7. Attractiveness and number of strikes on tubifex worm fractions in gelatin cubes and control cubes by juvenile sturgeon.

Test Substance	Attractiveness	S tikes Test/Contol
Contol		0/0
Chopped worm	+	101/22
Freeze-dried	+	40/10
Lipids		0/0
Fat-free worm	+	16/6
Centrifuge		o/o
Supematant	+	51/13
Boiled supematant	+	20/4

Table 8. Free amino acid levels (Sulfosalicylic Acid Extract) of tubifex worm exudate (moles/l00 moles).

Amino Acid	Test #l	Test #2	Average
Alanine	51.6	50.0	50.80
Leucine	7.2	9.9	0.55
Glycine	7.9	7.6	7.75
Valine	6.9	8.3	7.60
Isoleucine	4.9	4.0	4.45
Aspartic Acid	2.7	2.7	2.70
Phenylalanine	2.2	3.1	2.65
Lysine	3:o	2.0	2.50
Proline	2.6	2.2	2.40
Tyrosine	3.4	1.4	2.40
Methionine	1.4	2.4	1.90
Serine	1.4	1:6	1.50
Glutamic Acid	1.5	1.4	1.45
Threonine	1.4	1.4	1.40
Cystine	.8	.8	.80
Histidine	.8	.8	.80
Arginine	.3	.4	.35

tubifex worms the most attractive, followed by the supematant, freeze-dried tubifex worms, boiled supematant, and fat free worms. Results indicated that the amino acid fraction was the attractive component, and when that was altered by treatment, it became less attractive.

When the free amino acid profile of tubifex exudate (Table 8) was synthesized with free crystalline L-amino acids and presented to sturgeon, it induced active feeding behavior. The amino acid profile showed Alanine the most dominant form present, and when it was tested it was attractive, but quickly abandoned. The other two most abundant amino acids were unattractive when presented singly.

Capture of Buried Prey

Buried prey tests indicated that white sturgeon are very capable of detecting prey beneath the substrate. The 225 mm sturgeon conditioned to feed on live salmonid fry was consistently able to detect stunned rainbow trout fry buried up to 20 mm below the surface of the sand. Fry buried deeper than 20 mm were not detected, or at least sensory cues were insufficient to evoke a capture response. When the sturgeon was unable get a grip on the fry during the first protrusion of their jaw, there were several subsequent protrusions until the fry was captured. Each protrusion sucked up sand through the mouth and ejected it out through the gill openings. The rapid series of protrusions served to remove sand above the fry until either the head or tail was pulled into the mouth of the sturgeon. Once the fry was gripped by the jaws it was pulled out of the sand and ingested.

Chinook fry buried under 10 mm of small gravel were also detected by the sturgeon. However, since the particle size of the gravel was too large to be ejected through the gill openings, the fry was not uncovered as easily because the gravel had to be spit back out of the mouth onto the general area above the prey. The difficulty in removing the overlying gravel often resulted in unsuccessful capture attempts., and the sturgeon would move on.

The 225 mm sturgeon was also able to detect and capture buried live chinook salmon eggs. The same digging technique used to capture buried fry was used to capture the eggs. However, the eggs could not be detected when buried deeper than about 10 mm. When buried less than 10 mm, the shape and smaller size of the salmon egg compared to the body of a fry enabled the sturgeon to capture the egg in one or two protrusions.

A variety of other experimental manipulations were performed to provide information about what sensory stimuli the sturgeon was using to detect buried prey. Stunned trout fry buried in a small zip-lock plastic bag were not detected at any depth. The plastic apparently prevented the odor cues from being emitted. Further evidence on the importance of odor in detecting prey was demonstrated with the use of dead trout fry. Dead fry elicited a response and were captured by the sturgeon when buried at depths similar to the stunned fry.

Tests with buried metal objects demonstrated that sturgeon were able to detect them several mm below the surface. Protrusions were consistently observed as the sturgeon past over a buried nail about 30 mm in length. Also strong responses consisting of several protrusions were illicited when a AAA or AA, 1.5 volt penlight battery was buried 20-40 mm beneath the substrate. These responses were interpreted as detection of some electrical field around the objects. Further evidence on the detection of electrical fields was demonstrated with buried copper wire. An

electric field was created by burying the exposed ends of two insulated copper wires (about 15 mm apart and 20 mm deep) connected to the terminals of a C size 1.5 volt battery. When the sturgeon passed over the area above the two wires, one or two protrusions were observed but it usually moved away from the area without further response. In contrast, no response was observed when the buried wires were disconnected from the battery.

Capture of Mobile Prey

White sturgeon (120-300 mm) were observed to be able to capture both pink and chum salmon fry in the doughnut arenas with equal ease. Under lighted conditions, the fry could avoid capture, but in darkness they were quickly captured, and demonstrated that chum and pink salmon fry were as easily captured as were rainbow trout in the 1986 studies. Quantitative tests with sturgeon in the doughnut arenas were not performed because of mortality caused by an influx of high pH water, but during the 24 hour tests 60% to 80% of the fry were eaten.

Larger sturgeon (700-850 mm), tested for differences in chinook fry capture ability when exposed to different levels of velocity, were shown to be very effective predators. The influence of velocity was detectable (Table 9). Gut of 20 fry the number captured by four sturgeon predators in tanks with current showed a slightly higher cumulative average number of fry captured at all the observation periods when compared to no current, with the first period showing the greatest differences (Fig 5). Differences in number of fry captured were only significant at the15 min { .025 < p(t6) < .05) and 30 min census periods {.01 c p(t6) < .025}

Greater differences were observed in four paired tests in which 30 chinook salmon fry were added and current was tested against no inflow (Table10). A comparison of the cumulative average number of fry captured during each census period is shown in (Fig 6). The number of fry captured were significantly different at the 15 min period { .005 < p(t4) < .Ol}, and both the 30, and 45 min census periods {.025 < p(t4) < .05}, but was not significantly different at the 60 min period.

Table 9. Cumulative average number of 20 (43-47 mm) chinook fry captured by 700-850 mm sturgeon in current/no current conditions under darkness during 60 minute exposure trials.

Minutes	Current	No Current
15	17.6	15.0
30	18.8	17.8
45	19.0	18.5
60	19.1	19.0

Table 10. Cumulative average number of 30 (43-47 mm) chinook fry captured by 700-850 mm sturgeon in current/no flow conditions under darkness during 60 minute exposure trials.

Minutes	Current	No Flow
15	24.5	21.0
30	28.5	24.5
45	29.5	25.7
60	29.7	27.0

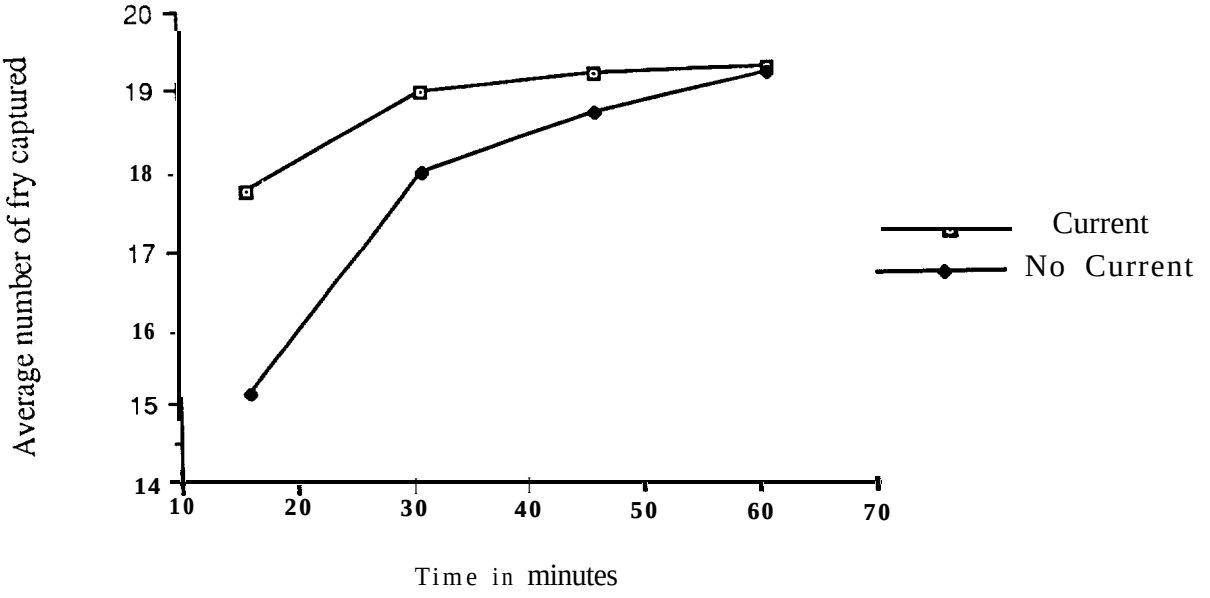


Figure 5. Cumulative average number of 20 (43-47 mm) chinook fry captured by 700-850 mm sturgeon in current/no current conditions under darkness during 60 minute exposure trials.

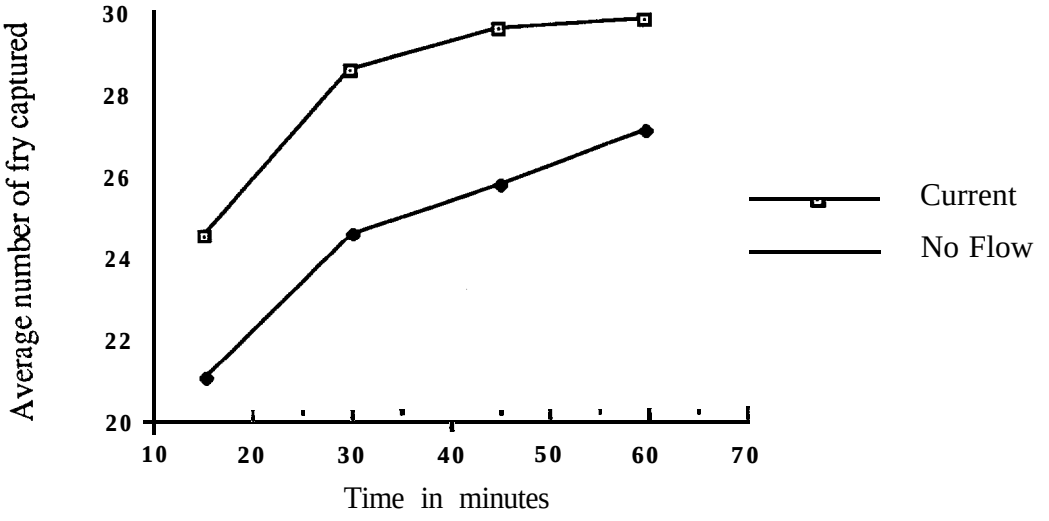


Figure 6. Cumulative average number of 30 (43-47 mm) chinook fry captured by 700-850 mm sturgeon in current/no flow conditions under darkness during 60 minute exposure trials.

DISCUSSION

Food habits studies have suggested that the white sturgeon is an opportunistic predator on benthic and free-swimiming aquatic animals. Adults in San Pablo and Suisun Bays of the Sacramento-San Joaquin River estuary were found to feed on several species of clams throughout the year, with barnacles, crabs, shrimp, herring eggs, and several fish species seasonally important in the diet (Mckechnie and Fenner, 1971). Stomach analysis of smaller white sturgeon (190-1020 mm) captured in the Sacramento-San Joaquin Delta showed that amphipods (Corohpium) and mysid shrimps (Neomysis) were the primary food items (Radtke, 1966). Other observations showed that *Corophium*, Tendipedidae larvae, and *Neomysis* had been eaten by juveniles (Schreiber, 1962). Simenstad (1984) found that *Corophium* was abundant in the lower Columbia River and estuary, where it was found to be the most important food item in the diet of juvenile white sturgeon (R. J. McConnell, pers. comm.). Its importance was reduced for larger individuals, especially in the lower estuary where a wider range of prey (including fishes) were eaten. Fishes were found in half the stomachs of adults during the summer in the Lower Fraser River (Semakula and Larkin, 1968). In May, eulachon (Thaleichthys pacificus) were spawning in the Fraser and were the main food item. Invertebrates such as crayfish, and chironomid and stonefly larvae were also eaten by adults during the summer.

Sturgeon have a variety of sensory systems that can be used to detect food sources. The eyes of sturgeons are in a poor position to provide precise information about the location of prey relative to the ventrally positioned jaw, and are probably used primarily as light intensity, shadow, and movement sensors. Similarly the dorsally located nares are in a poor position for close field prey detection, but have a major role in distant field orientration to prey odors. Mechanoreceptors, chemoreceptors, and electroreceptors, however, are well positioned on the underside of the head for near field detection of prey. Lateral line receptors on the underside of the snout may detect prey movement before contact with the barbels. If chemostimuli are contacted by the barbels only a slight movement forward is required before the jaws is protruded for prey capture (Fig 7). Electroreceptors on the underside and lateral edges of the snout appear similar to those of other species of sturgeon which have been shown to detect weak electric fields (Teeter et al., 1980; New and Bodznick, 1985). These receptors appear to be structurally (Jorgensen, 1980) and physiologically (Teeter et al., 1980) similar to the ampullae of Lorenzini of elasmobranchs, which have been shown to be sensitive to electric fields of prey animals (Kalmijn, 1971). Sturgeon may be able to detect the electrical stimuli of benthic prey types hidden in sediment or epiphytes that could not be detected by other senses.

The present feeding behavior study demonstrated that sturgeon use a variety of these feeding mechanisms, and they appear able to adapt to different feeding situations. Tubifex supernatant clearly indicated that the rapid directional movements of fry towards food could be induced by olfactory cues in the absence of food. Olfactory cues are believed best described as a chemostimulant composite picture of amino acids, some of which are not singly attractive.

Buried prey experiments demonstrated that white sturgeon were able to detect and capture prey beneath the surface of the substrate, implicating chemosensory and electrosensory systems. Buried prey most likely give off some odor components that are detected by foraging sturgeon through olfaction. Such odors may leach up

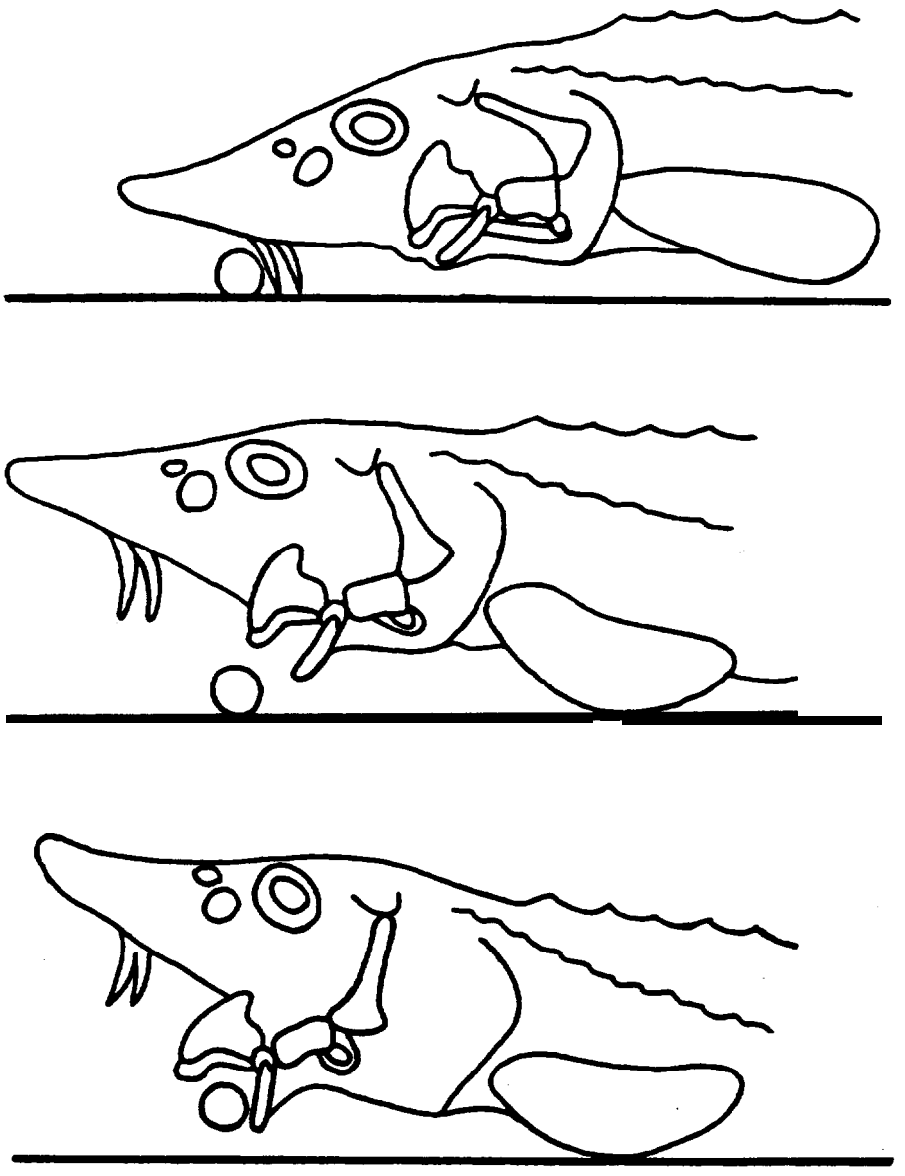


Figure 7. A sequential diagrammatic representation of barbels triggering jaw protrusion and subsequent capture of a salmon egg.

through the sand and elicite an initial strike. Subsequent prey related chemostimuli present on the disturbed substrate would induce further intensified attempts at capture, via gustation. Detection and capture of buried dead fry suggests that chemosensory cues (odor and taste) are used in initial detection of buried prey. Similarly, the observation that the sturgeon did not respond at all to fry buried in a small plastic bag, suggested that the plastic blocked transmission of chemosensory cues. However, an electrical field generated by live fry may also have been altered by plastic.

Experimental manipulations indicated that sturgeon are able to detect the electrical field of potential prey. They responded to buried metal objects as if they were food items suggesting that the metal must provide some stimuli similar to those of the actual prey, and the only characteristic metal objects and live prey probably have in common would be a weak electric field. Similarly, sturgeon responded to the buried ends of two wires connected to a 1.5 V battery, but showed no response to the area when the wires were disconnected from the battery, indicating sensitivity was to the electric field. It is possible that sturgeon used in these experiments were detecting an electric field around the buried fry and salmon eggs. The maximum depth at which the sturgeon could detect the prey might have been the maximum distance at which the electric field was detectable. The results indicate that both electroreception and chemoreception are sensory mechanisms that juvenile sturgeon may use when foraging.

Capture of mobile prey appears dependent on near field chemosensory abilities. Tests on the ability of white sturgeon to capture chinook salmon fry are congruent with previous tests of the same nature with rainbow trout (Brannon, et al., 1986). Salmonid fry were able to avoid predation except in darkness, clearly suggesting that a visually mediated escape response enables salmonids to avoid predation by sturgeon under lighted conditions. However, any factors that increased turbulence around the prey, also improved the sturgeons ability to capture it. In the absence of visual cues fry or other prey items must rely on mechanoreception to detect approaching sturgeon, and water movement over these receptors will tend to mask such mechanostimuli. In this regard, white sturgeon predatory success on visually oriented fish in reduced current of the Columbia River is expected to be limited compared to their historical success in the open river.

In conclusion, the white sturgeon feeding mechanism is remarkably adaptable to a wide range of prey types, but in the present conditions in the Columbia River system the ability appears to be restricted to certain habitat conditions for capturing fish and some crustaceans. Prey odors, cover, and water movement combined with the absence of light are major influences on the ability of juvenile sturgeon to capture prey. Introduction of prey resources for sturgeon should be given consideration in any enhancement program on the river. Under conditions of decreased velocity and increased light penetration characteristic of impoundment environments on the Columbia, benthic organisms would be recommended for introduction, especially those that have chemosensory attractants similar to the amino acid profile of tubifex supematant. The non-visual nature of their predatory mechanism is the primary limitation on their ability to utilize available food resources, and must be taken into consideration when evaluating their enhancement potential under the present conditions on the Columbia.

Summary and Conclusions

Sturgeon from two geographically isolated areas were examined in 1987 and evaluated for genetic structure using electrophoresis. The Kootenai and Upper Snake rivers were both evaluated from a relatively small sample size. The other areas, Lake Roosevelt (n=70) and Ilwaco (n=240) supplemented data previously collected in these areas. We find more variation as the sample size increases within an area, but of course at low frequencies. These are often the variants distinct to a given area. We feel that the sample size in both the Kootenai and Upper Snake rivers should be increased to approximate genetic composition most accurately.

Contingency chi-square tests on goodness of fit show some differences exist between the areas examined using electrophoresis. Morphometric and meristic data have not shown any correlation with the genetic data, although the sample size examined was low. Snout shape is the most promising characteristic for some correlation since it seems to show some geographic specificity. Scute counts vary consistently throughout the river.

Our early life history feeding studies have shown that amino acids play a role in attracting young sturgeon to food. While the most effective combination of amino acids was not able to be determined, it does imply that sturgeon use distant field chemostimuli to locate food by olfaction. Capture of mobile prey appears dependent on near field chemoreception. Tests on the ability of white sturgeon to capture chinook salmon fry confirm that visually oriented prey are able to avoid predation by sturgeon under the presence of light. However, any factors that increased turbulence around the prey, also improved the sturgeons ability to capture it. In the absence of visual cues fry or other prey items must rely on mechanoreception to detect approaching sturgeon, and water movement over these receptors will tend to mask such mechanostimuli.

In the present conditions in the Columbia River system the ability of white sturgeon to feed most successfully appears to be restricted to certain habitat conditions if they target fish and certain crustaceans as prey. Introduction of prey resources for sturgeon should be given consideration in any enhancement program on the river. Under conditions of decreased velocity and increased light penetration characteristic of impoundment environments on the Columbia, benthic organisms with a chemosensory stimulant would be recommended for introduction. The non-visual nature of their predatory mechanism is the primary limitation on their ability to utilize available food resources under altered river conditions related to hydro development, and this must be taken into consideration when evaluating their enhancement potential.

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Appendix Table 1. List by system of mobility of alternate alleles.

System	Allele 1	Allele 2	Allele 3
AAT-1	-100	-62	
AH-1	100	145	167
AK-1	100	140	
ALD-1	-100	-106	
CK-3	100	107	96
EST-2	100	138	85
GAP-l	-100	-12	
GD- 1	100	106	
GPD- 1	100	94	
GPI- 1	100	-127	
GPI-2	100	76	
LDH-1	-100	-271	
LT-1	100	88	
LT-3	100	92	
MDH-1	100	136	
MDH-2	100	84	
ME-l	100	44	
PGM- 1	100	91	107

**The common allele is designated as 100 and alternate alleles are a measure of their percent migration distance in proportion with the common.

Appendix Table 2. Allele frequency data by area.

KEY TO POPULATIONS

POP. NO.	POPULATION NAME
1	SNAKE
2	UPPER SNAKE
3	I LWACO
4	LAKE ROOSEVELT
5	MID-COLUMBIA
6	KOOTENAI

	POPULATION					
LOCUS	1	2	3	4	5	6
AAT-1						
(N)	12	8	240	70	133.	9
A	.917	.938	.900	.957	.083	0.000 1.000
B	.083	.063	.100	.043		
ADA-1						
(N)	12	1	90	72	84	9
A	1.000	1.000	1.000	1.000	1.000	1.000
ADA-2						
(N)	12	1	91	72	84	9
A	1.000	1.000	1.000	1.000	1.000	1.000
AH-1						
(N)	12	8	191	68	77	6
A	.792	.938	.903	.882	.964	.667
B	0.000	0.063	.097	.096	0.000	.333
C			0.000	.022		0.000
AK-1						
(N)	1	8	243	66	164	6
A	1.000	1.000	.967	1.000	1.000	1.000
B	0.000	0.000	.033	0.000	0.000	0.000
ALD-1						
(N)	1	8	210	71	150	9
A	1.000	.938	910	.951	.913	1.000
B	0.000	.063	: 090	.049	.087	0.000
CK-1						
(N)	1	8	243	72	164	9
A	1.000	1.000	1.000	1.000	1.000	1.000
CK-2						
(N)	1	1	243	52	164	1
A	1.000	1.000	1.000	1.000	1.000	1.000
CK-3						
(N)	1	1	182	49	102	1
A	1.000	1.000	.876	.867	.892	1.000
B	0.000	0.000	.118	.071	.108	
C	0.000	0.000	0.000	.061	0.000	0.000 0.000
D	0.000	0.000	.005	0.000	0.000	0.000

Appendix Table 2 (cont.). Allele frequency data by area.

LOCUS	POPULATION 1	2	3	4	5	6
EST-I						
(N)	12	1	283	70	164	9
A	1.000	1.000	1.000	1.000	1.000	1.000
EST-2						
(N)	1	1	35	33	48	1
A	1.000	1.000	.814	.833	.854	1.000
B	0.000	0.000	.157	.136	.115	0.000
C	0.000	0.000	,029	.030	.031	0.000
GAP-1						
(N)	12	8	283	70	111	9
A	1.000	1.000	1.000	1.000	1.000	1.000
GD- 1						
(N)	l i	8	is2	65	50	9
A	.833	1.000	.922	1.000	1.000	1.000
B	.167	0.000	.078	0.000	0.000	0.000
GPD-1						
(N)	12	8	263	63	164	9
A	1.000	1.000	.981	.952	.966	1.000
B	0.000	0.000	.019	.048	.034	0.000
GPI-1						
(N)	12	8	283	74	134	9
A	1.000	1.000	.975	1.000	.993	1.000
B	0.000	0.000	.025	0.000	.007	0.000
GPI-2						
(N)	12	8	283	71	134	9
A	.792	.625	.898	.768	.877	.944
B	.208	.375	.102	.232	,123	.056
IDH-1						
(N)	12	1	184	49	164	1
A	1.000	1.000	1.000	1.000	1.000	1.000
LDH-1						
(N)	12	8	283	72	164	9
A	.625	.563	.949	.847	.841	1.000
B	.375	.438	.051	.153	.159	0.000
LT- 1						
(N)	12	1	283	70	149	9
A	1.000	1.000	.956	.986	.980	1.000
B	0.000	0.000	.044	.014	.020	0.000
LT- 3						
(N)	11	1	124	1	71	1
A	.955	1.000	.923	1.000	.930	1.000
B	.045	0.000	.077	0.000	.070	0.000

Appendix Table 2 (cont.). Allele frequency data by area.

LOCUS	POPULATION 1	2	3	4	5	6
MAN- 1						
(N)	1	1	170	52	164	1
A	1.000	1.000	1.000	1.000	1.000	1.000
MDH- 1						
(N)	1	8	243	48	164	9
A	1.000	.813	.940	.885	.945	1.000
B	0.000	.188	.060	.115	.055	0.000
MOH-2						
(N)	1	1	210	48	164	9
A	1.000	1.000	.990	1.000	1.000	1.000
B	0.000	0.000	.010	0.000	0.000	0.000
M E - 1						
(N)	12	8	283	71	152	9
A	1.000	1.000	.988	1.000	1.000	1.000
B	0.000	0.000	.007	0.000	0.000	0.000
C	0.000	0.000	.005	0.000	0.000	0.000
PGD-1						
(N)	1	1	149	40	164	6
A	l.ooo	1.000	.977	.975	1.000	l.ooo
B	0.000	0.000	.023	.025	0.000	0.000
PGM-1						
(N)	12	8	275	71	134	9
A	.833	1.000	.935	.972	.929	1.000
B	.167	0.000	.065	.021	.071	0.000
C	0.000	0.000	0.000	.007	0.000	0.000
PGM-2						
(N)	12	8	283	70	164	9
A	1.000	1.000	l.ooo	.964	1.000	1.000
B	0.000	0.000	0.000	.021	0.000	0.000
C	0.000	0.000	0.000	.014	0.000	0.000
SOD-1						
(N)	12	1	214	52	84	1
A	1.000	l.ooo	1.000	1.000	1.000	1.000

Appendix Table 3. Hardy-Weinburg Chi-square statistics.

POPULATION: UPPER SNAKE

LOCUS	CLASS	OBSERVED FREQUENCY	EXPECTED FREQUENCY	CHI-SQUARE	DF	P
AAT-1						
	A-A	7	7.031			
	A-B	1	.938			
	B-0	0	.031	.036	1	.850
AH- 1						
	A-A	7	7.031			
	A-B	1	.938			
	B-B	0	.031	.036	1	.850
ALD-1						
	A-A	7	7.031			
	A-B	1	.938			
	B-B	0	.031	,036	1	.850
GPI-2						
	A-A	3	3.125			
	A-B	4	3.750			
	B-B	1	1.125	.036	1	.850
LDH- 1						
	A-A	1	2.531			
	A-B	7	3.938			
	B-B	0	1.531	4.840	1	.028
MDH- 1						
	A-A	5	5.281			
	A-B	3	2.438			
	B-0	0	.281	.426	1	.514

Appendix Table 3 (cont.). Hardy-Weinburg Chi-square statistics.

POPULATION: SNAKE

LOCUS	CLASS	OBSERVED FREQUENCY	EXPECTED FREQUENCY	CHI-SQUARE	DF	P
AAT-1						
	A-A	10	10.083			
	A-B	2	1.833			
	B-B	0	.083	.099	1	.753
AH-1						
	A-A	7	7.521			
	A-B	5	3.958			
	B-B	0	.521	.831	1	.362
GD-1						
	A-A	8	8.333			
	A-B	4	3.333			
	B-B	0	.333	.480	1	.488
GPI-2						
	A-A	8	7.521			
	A-B	3	3.958			
	B-0	1	.521	.703	1	.402
LDH-1						
	A-A	3	4.688			
	A-0	9	5.625			
	B-B	0	1.688	4.320	1	.038
LT-3						
	A-A	10	10.023			
	A-B	1	.955			
	B-B	0	.023	.025	1	.875
PGM-1						
	A-A	9	8.333			
	A-0	2	3.333			
	B-B	1	.333	1.920	1	.166

Appendix Table 3 (cont.). Hardy-Weinburg Chi-square statistics.

POPULATION: ILWACO

LOCUS	CLASS	OBSERVED FREQUENCY	EXPECTED FREQUENCY	CHI - SQUARE	DF	P	
AAT-1							
	A-A	196	194.400				
	A-B	40	43.200				
	B-B	4	2.400	1.317	1	.251	
AH- 1							
	A-A	154	155.792				
	A-B	37	33.416				
	B-B	0	1.792	2.197	1	.138	
AK- 1							
	A-A	228	227.263				
	A-B	14	15.473				
	B-B	1	.263	2.203	1	138	
ALD-1							
	A-A	174	173.719				
	A-B	34	34.562				
	B-B	2	1.719	.056	1	.814	
CK- 3							
	A-A	140	139.782				
	A-B	37	37.684				
	A-D	2	1.753				
	B-B	3	2.540				
	B-D	0	.236				
	O-D	0	.005	.373	3	.946	
EST-2							
	A-A	25	23.207				
	A-B	5	8.957				
	A-C	2	1.629				
	0-B	3	.864				
	B-C	0	.314				
	c-c	0	.029	7.592	3	.055	
GD- 1							
	A-A	166	163.172				
	A-B	22	27.656				
	B-B	4	1 172	8.031	1	.005	*
GPO- 1							
	A-A	253	253.095				
	A-B	10	9.810				
	B-B	0	,095	.099	1	.753	
GPI-1							
	A-A	269	269.173				
	A-B	14	13.654				
	0-B	0	.173	. 182	1	.670	

Appendix Table 3 (cont.). Hardy-Weinburg Chi-square statistics.

ILWACO

GPI-2						
	A-A	230	227.972			
	A-B	48	52.057			
	B-B	5	2.972	1.718	1	.190
LDH- 1						
	A-A	254	254.743			
	A-B	29	27.514			
	B-B	0	.743	.825	1	.364
LT- 1						
	A-A	260	258.552			
	A-B	21	23.896			
	B-B	2	.552	4.156	1	.041
LT- 3						
	A-A	107	105.728			
	A-B	15	17.544			
	B-B	2	.728	2.608	1	. 106
MDH- 1						
	A-A	214	214.865			
	A-B	29	27.270			
	B-B	0	.865	.979	1	.323
MDH-2						
	A-A	206	206.019			
	A-6	4	3.962			
	B-B	0	.019	.019	1	.889
ME- 1						
	A-A	276	276.043			
	A-B	4	3.951			
	A-C	3	2.963			
	B-B	0	.014			
	B-C	0	.021			
	c-c	0	.008	.044	3	.998
PGD- 1						
	A-A	142	142.082			
	A-B	7	6.836			
	B-B	0	.082	.086	1	.769
PGM- 1						
	A-A	240	240. 178			
	A-B	34	33.644			
	B-B	1	1.178	.031	1	.861

Appendix Table 3 (cont.). Hardy-Weinburg Chi-square statistics.

POPULATION: LAKE ROOSEVELT

LOCUS	CLASS	OBSERVED FREQUENCY	EXPECTED FREQUENCY	CHI-SQUARE	DF	P	
AAT-1							
	A-A	64	64. 129				
	A-B	6	5.743				
	B-B	0	.129	.140	1	.708	
AH- 1							
	A-A	52	52.941				
	A-B	13	11.471				
	A-C	3	2.647				
	B-B	0	.621				
	B-C	0	.287				
	c-c	0	.033	1.209	3	.751	
ALD- 1							
	A-A	64	64.173				
	A-B	7	6.655				
	B-B	0	.173	,191	1	.662	
CK- 3							
	A-A	38	36.862				
	A-B	3	6.071				
	A-C	6	5.204				
	B-B	2	.250				
	B-C	0	.429				
	c-c	0	184	14.573	3	.002	*
EST-2							
	A-A	23	22.917				
	A-B	7	7.500				
	A-C	2	1.667				
	B-B	1	.614				
	B-C	0	273				
	c-c	0	: 030	.647	3	.886	
GPD- 1							
	A-A	57	57.143				
	A-B	6	5.714				
	B-B	0	.143	. 158	1	.691	
GPI-2							
	A-A	43	41.835				
	A-B	23	25.331				
	B-0	5	3.835	.601	1	.438	

Appendix Table 3 (cont.). Hardy-Weinburg Chi-square statistics.

LAKE ROOSEVELT

LDH-1						
	A-A	50	51.681			
	A-B	22	18.639			
	B-B	0	1.681	2.341	1	.126
LT- 1						
	A-A	68	68 014			
	A-0	2	1 971			
	B-0	0	014	.015	1	.903
MDH-1						
	A-A	37	37.630			
	A-B	11	9.740			
	B-B	0	.630	.804	1	.370
PGD-1						
	A-A	38	38.025			
	A-B	2	1.950			
	B-B	0	.025	.026	1	.871
PGM-1						
	A-A	67	67.056			
	A-B	3	2.915			
	A-C	1	972			
	B-B	0	: 032			
	B-C	0	.021			
	c-c	0	.004	.060	3	.996
PGM-2						
	A-A	65	65.089			
	A-B	3	2.893			
	A-C	2	1.929			
	B-B	0	.032			
	B-C	0	.043			
	c-c	0	.014	.096	3	.992

Appendix Table 3 (cont.). Hardy-Weinburg Chi-square statistics.

POPULATION: MID-COLUMBIA

LOCUS	CLASS	OBSERVED FREQUENCY	EXPECTED FREQUENCY	CHI-SQUARE	DF	P
AAT-1						
	A-A	111	111.910			
	A-B	22	20.180			
	B-B	0	.910	1.081	1	,298
AH- 1						
	A-A	57	57.432			
	A-B	19	18.136			
	B-B	1	1.432	.175	1	,676
ALD-1						
	A-A	125	125.127			
	A-B	24	23.747			
	B-B	1	1.127	.017	1	.896
CK- 3						
	A-A	83	81.186			
	A-B	16	19.627			
	B-B	3	1.186	3.484	1	.062
EST-2						
	A-A	35	35.021			
	A-B	9	9.396			
	A-C	3	2.563			
	B-B	1	.630			
	B-C	0	.344			
	c-c	0	.047	.699	3	.873
GPD- 1						
	A-A	154	153.184			
	A-0	9	10.631			
	B-B	1	184	3.861	1	.049
GPI-1						
	A-A	132	132.007			
	A-B	2	1.985			
	B-B	0	.007	.008	1	.931
GPI-2						
	A-A	104	103.032			
	A-B	27	28.937			
	B-B	3	2.032	.600	1	.439

Appendix Table 3 (cont.). Hardy-Weinburg Chi-square statistics.

MID-COLUMBIA

LDH-1							
	A-A	112	116.122				
	A-B	52	43.756				
	B-B	0	4.122	5.821	1	.016	*
LT- 1							
	A-A	143	143.060				
	A-0	6	5.879				
	B-B	0	.060	.063	1	.802	
LT- 3							
	A-A	61	61 .352				
	A-B	10	9 296				
	B-B	0	352	.407	1	.523	
MOH-1							
	A-A	146	146 494				
	A-B	18	17 012				
	B-B	0	494	.553	1	.457	
PGM-1							
	A-A	115	115 674				
	A-B	19	17 653				
	B-B	0	674	.780	1	.377	

Appendix Table 3 (cont.). Hardy-Weinburg Chi-square statistics.

POPULATION: KOOTENAI

LOCUS	CLASS	OBSERVED FREQUENCY	EXPECTED FREQUENCY	CHI-SQUARE	OF	P
AH-1						
	A-A	2	2.667			
	A-B	4	2.667			
	B-B	0	.667	1.500		.221
GPI-2						
	A-A	a	8.028			
	A-B	1	.944			
	B-B	0	.028	.031	1	.860

Appendix Table 4. Contingency chi-square results for the entire river.

LOCUS: AAT-1

POPULATION		ALLELE A	ALLELE B
SNAKE	OBS (O)	22.000	2.000
	EXP (E)	21.992	2.008
	(O-E)**2 / E	.OOO	0 0 0
UPPER SNAKE	DBS (O)	15.000	1 .ooo
	EXP (E)	14.661	1.339
	(O-E)**2 / E	.008	.086
ILWACO	OBS (O)	432 .000	48.000
	EXP (E)	439.831	40. 169
	(O-E)**2 / E	.139	1 ,526
LAKE ROOSEVELT	OBS (O)	134.000	6.000
	EXP (E)	128.284	11.716
	(O-E)**2 / E	.255	2.789
MID-COLUMBIA	OBS (O)	244.000	22.000
	EXP (E)	243.739	22.261
	(O-E)**2 / E	.000	.003
KOOTENAI	OBS (O)	18.000	0.000
	EXP (E)	16.494	1.506
	(D-E)**2 / E	1 3 8	1.506

CI-II-SQUARE = 6.450
D.F. = 5
P = .26483

Appendix Table 4 (cont.). Contingency chi-square results for the entire river.

LOCUS: AH- 1

POPULATION		ALLELE A	B	C
SNAKE	OBS (O)	19.000	5.000	0.000
	EXP (E)	21.215	2.685	.099
	(O-E)**2 / E	.231	1.996	.099
UPPER SNAKE	DBS (O)	15.000	1.000	0.000
	EXP (E)	14.144	1.790	.066
	(O-E)**2 / E	.052	.349	.066
I LWACO	OBS (O)	345.000	37.000	0.000
	EXP (E)	337.680	42.738	1.583
	(O-E)**2 / E	.159	.770	1.583
LAKE ROOSEVELT	OBS (O)	120.000	13.000	3.000
	EXP (E)	120.221	15.215	564
	(D-E)**2 / E	.000	.323	10: 534
MID-COLUMBIA	OBS (O)	133.000	21.000	0.000
	EXP (E)	136. 133	17.229	.638
	(O-E)**2 / E	.072	.825	.638
KOOTENA I	OBS (O)	8.000	4.000	0.000
	EXP (E)	10.608	1.343	.050
	(O-E)**2 / E	.641	5.260	.050

CHI-SQUARE = 23.649
D.F. = 10
P = .00859

Appendix Table 4 (cont.). Contingency chi-square results for the entire river.

LOCUS: AK- 1

POPULATION		ALLELE A	ALLELE B
SNAKE	OBS (O)	2.000	0.000
	EXP (E)	1.967	.033
	(O-E)**2 / E	.001	.033
UPPER SNAKE	OBS (O)	16.000	0.000
	EXP (E)	15.738	.262
	(O-E)**2 / E	.004	.262
ILWACO	OBS (O)	470.000	16.000
	EXP (E)	478.033	7.967
	(O-E)**2 / E	.135	8.099
LAKE ROOSEVELT	OBS (O)	132.000	0.000
	EXP (E)	129.836	2.164
	(O-E)**2 / E	.036	2.164
MID-COLUMBIA	OBS (O)	328.000	0.000
	EXP (E)	322.623	5.377
	(O-E)**2 / E	.090	5.377
KOOTENAI	OBS (O)	12.000	0.000
	EXP (E)	11.803	.197
	(O-E)**2 / E	.003	.197

CHI-SQUARE = 16.401
D.F. = 5
P = .00579

Appendix Table 4 (cont.). Contingency chi-square results for the entire river.

LOCUS: ALD-1

POPULATION		ALLELE A	ALLELE B
SNAKE	OBS (O)	2.000	0.000
	EXP (E)	1.840	160
	(O-E)**2 / E	.014	160
UPPER SNAKE	OBS (O)	15.000	1.000
	EXP (E)	14.717	1.283
	(O-E)**2 / E	.005	.062
ILWACO	OBS (O)	382.000	38.000
	EXP (E)	386.325	33.675
	(D-E)**2 / E	.048	.556
LAKE ROOSEVELT	OBS (O)	135.000	7.000
	EXP (E)	130.615	11.385
	(O-E)**2 / E	.147	1.689
MID-COLUMBIA	OBS (O)	274.000	26.000
	EXP (E)	275.947	24.053
	(O-E)**2 / E	.014	.158
KOOTENAI	OBS (O)	18.000	0.000
	EXP (E)	16.557	1.443
	(O-E)**2 / E	. 126	1.443

CHI-SQUARE = 4.423
D.F. = 5
P = .49030

Appendix Table 4 (cont.). Contingency chi-square results for the entire river.

LOCUS: CK- 3

POPULATION		ALLELE A	B	C	D
SNAKE	OBS (O)	2 000	0.000	0.000	0.000
	EXP (E)	1.762	.214	.018	.006
	(O-E)**2 / E	.032	.214	.018	.006
UPPER SNAKE	OBS (O)	2.000	0.000	0.000	0.000
	EXP (E)	1.762	.214	.018	.006
	(O-E)**2 / E	,032	.214	.018	.006
ILWACO	OBS (O)	319.000	43.000	0.000	2.000
	EXP (E)	320.667	39.000	3.250	1.083
	(O-E)**2 / E	.009	.410	3.250	.776
LAKE ROOSEVELT	OBS (O)	85.000	7.000	6.000	0.000
	EXP (E)	86.333	IO.500	.875	.292
	(O-E)**2 / E	.021	1.167	30.018	.292
MID-COLUMBIA	OBS (O)	182.000	22.000	0.000	0.000
	EXP (E)	179.714	21 .857	1.821	.607
	(O-E)**2 / E	.029	.001	1.821	.607
KOOTENAI	OBS (O)	2.000	0.000	0.000	0.000
	EXP (E)	1.762	214. .	.018	.006
	(O-E)**2 / E	.032	.214	.018	.006

CHI-SQUARE = 39.211
D.F. = 15
P = .00060

Appendix Table 4 (cont.). Contingency chi-square results for the entire river.

LOCUS: EST-2

POPULATION		ALLELE A	B	C
SNAKE	OBS (O)	2.000	0.000	0.000
	EXP (E)	1.681	.261	.059
	(O-E)**2 / E	.061	.261	.059
UPPER SNAKE	OBS (O)	2.000	0.000	0.000
	EXP (E)	1.681	.261	.059
	(O-E)**2 / E	.061	.261	.059
ILWACO	OBS (O)	57.000	11.000	2.000
	EXP (E)	58.824	9.118	2.059
	(O-E)**2 / E	.057	,389	.002
LAKE ROOSEVELT	OBS (O)	55.000	9.000	2.000
	EXP (E)	55.462	8.597	1.941
	(O-E)**2 / E	.004	.019	.002
MID-COLUMBIA	OBS (O)	82.000	11.000	3.000
	EXP (E)	80.672	12.504	2.824
	(O-E)**2 / E	.022	181	.011
KODTENA I	OBS (O)	2.000	0.000	0.000
	EXP (E)	1.681	.261	.059
	(D-E)**2 / E	.061	.261	.059

CHI-SQUARE = 1.825
D.F. = 10
P = .99751

Appendix Table 4 (cont.). Contingency chi-square results for the entire river.

LOCUS: GD- 1

POPULATION		ALLELE A	ALLELE B
SNAKE	OBS (O)	20.000	4.000
	EXP (E)	22.786	I.214
	(O-E)**2 / E	.341	6.391
UPPER SNAKE	DBS (O)	16.000	0.000
	EXP (E)	15.190	.810
	(O-E)**2 / E	.043	.810
ILWACO	OBS (O)	354.000	30.000
	EXP (E)	364.571	19.429
	(O-E)**2 / E	.307	5.752
LAKE ROOSEVELT	OBS (O)	130.000	0.000
	EXP (E)	123.423	6.577
	(O-E)**2 / E	.351	6.577
MID-COLUMBIA	OBS (O)	100.000	0.000
	EXP (E)	94.940	5.060
	(O-E)**2 / E	.270	5.060
KOOTENAI	OBS (O)	18.000	0.000
	EXP (E)	17.089	.911
	(O-E)**2 / E	.049	.911

CHI-SQUARE = 26.859
D.F. = 5
P = .00006

Appendix Table 4 (cont.). Contingency chi-square results for the entire river.

LOCUS: GPO-I

POPULATION		ALLELE A	ALLELE B
SNAKE	OBS (O)	24.000	0.000
	EXP (E)	23.376	.624
	(O-E)**2 / E	.017	.624
UPPER SNAKE	OBS (O)	16.000	0.000
	EXP (E)	15.584	.416
	(O-E)**2 / E	.011	.416
ILWACO	oss (O)	516.000	10.000
	EXP (E)	512.318	13.682
	(O-E)**2 / E	.026	.991
LAKE ROOSEVELT	OBS (O)	120.000	6.000
	EXP (E)	122.723	3.277
	(O-E)**2 / E	.060	2.262
MID-COLUMBIA	OBS (O)	317.000	11.000
	EXP (E)	319.468	8.532
	(O-E)**2 / E	.019	.714
KOOTENA I	OBS (O)	18.000	0.000
	EXP (E)	17.532	.468
	(O-E)**2 / E	.013	.468

CHI-SQUARE = 5.621
D.F. = 5
P = .34481

Appendix Table 4 (cont.). Contingency chi-square results for the entire river.

LOCUS: **GPI-1**

POPULATION		ALLELE A	ALLELE B
SNAKE	OBS (O)	24.000	0.000
	EXP (E)	23.631	.369
	(O-E)**2 / E	.006	.369
UPPER SNAKE	OBS (O)	16.000	0.000
	EXP (E)	15.754	246
	(O-E)**2 / E	.004	: 246
ILWACO	OBS (O)	552 .000	14.000
	EXP (E)	557.292	8.708
	(O-E)**2 / E	.050	3.217
LAKE ROOSEVELT	OBS (O)	148.000	0.000
	EXP (E)	145.723	2.277
	(O-E)**2 / E	.036	2.277
MID-COLUMBIA	OBS (O)	266.000	2.000
	EXP (E)	263 .a77	4.123
	(O-E)**2 / E	.017	1.093
KOOTENAI	OBS (O)	18.000	0.000
	EXP (E)	17.723	.277
	(O-E)**2 / E	.004	.277

CHI-SQUARE = 7.596
O.F. = 5
P = .17996

Appendix Table 4 (cont.). Contingency chi-square results for the entire river.

LOCUS: GPI-2

POPULATION		ALLELE A	ALLELE B
SNAKE	OBS (O)	19.000	5.000
	EXP (E)	20.843	3.157
	(O-E)**2 / E	.163	1.076
UPPER SNAKE	OBS (O)	10.000	6.000
	EXP (E)	13.896	2.104
	(O-E)**2 / E	1.092	7.211
ILWACO	OBS (O)	508.000	58.000
	EXP (E)	491.555	74.445
	(O-E)**2 / E	.550	3.633
LAKE ROOSEVELT	OBS (O)	109.000	33.000
	EXP (E)	123.323	18.677
	(O-E)**2 / E	1.664	10.984
MID-COLUMBIA	OBS (O)	235.000	33.000
	EXP (E)	232.750	35.250
	(O-E)**2 / E	.022	.144
KOOTENAI	OBS (O)	17.000	1.000
	EXP (E)	15.632	2.368
	(O-E)**2 / E	.120	.790

CHI-SQUARE = 27.448
O.F. = 5
P = .00005

Appendix Table 4 (cont.). Contingency chi-square results for the entire river.

LOCUS: LOH-1

POPULATION		ALLELE A	ALLELE B
SNAKE	OBS (O)	15.000	9.000
	EXP (E)	21.394	2.606
	(O-E)**2 / E	1.911	15.690
UPPER SNAKE	OBS (O)	9.000	7.000
	EXP (E)	14.263	1.737
	(O-E)**2 / E	1.942	15.943
I LWACO	OBS (O)	537.000	29.000
	EXP (E)	504.546	61.454
	(O-E)**2 / E	2.088	17.139
LAKE ROOSEVELT	OBS (O)	122.000	22.000
	EXP (E)	128.365	15.635
	(O-E)**2 / E	.316	2.591
MID-COLUMBIA	OBS (O)	276.000	52.000
	EXP (E)	292.387	35.613
	(O-E)**2 / E	.918	7.540
KOOTENAI	OBS (O)	18.000	0.000
	EXP (E)	16.046	1.954
	(O-E)**2 / E	.238	1.954

CHI-SQUARE = 68.271
D.F. = 5
P = 0.00000

Appendix Table 4 (cont.). Contingency chi-square results for the entire river.

LOCUS: LT- 1

POPULATION		ALLELE A	ALLELE B
SNAKE	OBS (O)	24.000	0.000
	EXP (E)	23.244	.756
	(O-E)**2 / E	.025	.756
UPPER SNAKE	OBS (O)	2.000	0.000
	EXP (E)	1.937	.063
	(O-E)**2 / E	.002	.063
ILWACO	OBS (O)	541 .ooo	25.000
	EXP (E)	548.177	17.823
	(O-E)**2 / E	.094	2.891
LAKE ROOSEVELT	OBS (O)	138.000	2.000
	EXP (E)	135.592	4.408
	(O-E)**2 / E	.043	1.316
MID-COLUMBIA	OBS (O)	292.000	6.000
	EXP (E)	288.616	9.384
	(O-E)**2 / E	.040	1.220
KOOTENA I	OBS (O)	18.000	0.000
	EXP (E)	17.433	.567
	(O-E)**2 / E	.018	.567

CHI-SQUARE = 7.033
D.F. = 5
P = .21817

Appendix Table 4 (cont.). Contingency chi-square results for the entire river.

LOCUS: LT- 3

POPULATION		ALLELE A	ALLELE B
SNAKE	OBS (O)	21.000	1.000
	EXP (E)	20.421	1.579
	(O-E)**2 / E	.016	.212
UPPER SNAKE	OBS (O)	2.000	0.000
	EXP (E)	1.856	.144
	(O-E)**2 / E	.011	.144
ILWACO	OBS (O)	229.000	19.000
	EXP (E)	230.201	17.799
	(O-E)**2 / E	.006	.081
LAKE ROOSEVELT	OBS (O)	2.000	0.000
	EXP (E)	1.856	.144
	(O-E)**2 / E	.011	.144
MID-COLUMBIA	OBS (O)	132.000	10.000
	EXP (E)	131.809	10.191
	(O-E)**2 / E	.000	.004
KOOTENAI	OBS (O)	2.000	0.000
	EXP (E)	1.856	.144
	(O-E)**2 / E	.011	.144

CHI-SQUARE = .784
D.F. = 5
P = .97806

Appendix Table 4 (cont.). Contingency chi-square results for the entire river.

LOCUS: MDH-1

POPULATION		ALLELE A	ALLELE B
S N A K E	OBS (O)	2.000	0.000
	EXP (E)	1.871	.129
	(O-E)**2 / E	.009	. 129
UPPER SNAKE	OBS (O)	13.000	3.000
	EXP (E)	14.968	1.032
	(O-E)**2 / E	259	3.755
I LWACO	OBS (O)	457.000	29.000
	EXP (E)	454.662	31.338
	(O-E)**2 / E	.012	.174
LAKE ROOSEVELT	OBS (O)	85.000	11.000
	EXP (E)	89.810	6.190
	(O-E)**2 / E	.258	3.737
MID-COLUMBIA	DBS (O)	310.000	18.000
	EXP (E)	306.850	21.150
	(O-E)**2 / E	.032	.469
KOOTENAI	OBS (O)	18.000	0.000
	EXP (E)	16.839	1.161
	(O-E)**2 / E	.080	1.161

CHI-SQUARE = 10.075
D.F. = 5
P = .07314

Appendix Table 4 (cont.). Contingency chi-square results for the entire river.

LOCUS: MDH-2

POPULATION		ALLELE A	ALLELE B
SNAKE	OBS (O)	2.000	0.000
	EXP (E)	1.991	.009
	(O-E)**2 / E	.000	.009
UPPER SNAKE	OBS (O)	2.000	0.000
	EXP (E)	1.991	.009
	(O-E)**2 / E	.000	.009
ILWACO	OBS (O)	416.000	4.000
	EXP (E)	418.060	1 ,940
	(O-E)**2 / E	.010	2.188
LAKE ROOSEVELT	OBS (O)	96.000	0.000
	EXP (E)	95.557	.443
	(O-E)**2 / E	.002	.443
MID-COLUMBIA	OBS (O)	328.000	0.000
	EXP (E)	326.485	1.515
	(O-E)**2 / E	.007	1.515
KOOTENAI	OBS (O)	18.000	0.000
	EXP (E)	17.917	,083
	(O-E)**2 / E	.000	.083

CHI-SQUARE = 4.267
D.F. = 5
P = .51160

Appendix Table 4 (cont.). Contingency chi-square results for the entire river.

LOCUS: ME- 1

POPULATION		ALLELE A	B	C
SNAKE	OBS (O)	24.000	0.000	0.000
	EXP (E)	23.843	.090	.067
	(O-E)**2 / E	.001	.090	.067
UPPER SNAKE	OBS (O)	16.000	0.000	0.000
	EXP (E)	15.895	.060	.045
	(O-E)**2 / E	.001	.060	.045
ILWACO	OBS (O)	559.000	4.000	3.000
	EXP (E)	562.297	2.116	1.587
	(O-E)**2 / E	.019	1.678	1.258
LAKE ROOSEVELT	OBS (O)	142 .OOO	0.000	0.000
	EXP (E)	141.071	.531	.398
	(O-E)**2 / E	.006	.531	.398
MID-COLUMBIA	OBS (O)	304.000	0.000	0.000
	EXP (E)	302.011	1.136	.852
	(O-E)**2 / E	.013	1.136	.852
KOOTENAI	OBS (O)	18.000	0.000	0.000
	EXP (E)	17.882	.067	.050
	(O-E)**2 / E	.001	.067	.050

CHI-SQUARE = 6.274
D.F. = 10
P = .79172

Appendix Table 4 (cont.). Contingency chi-square results for the entire river.

LOCUS: PGO-1

POPULATION		ALLELE A	ALLELE B
SNAKE	OBS (O)	2.000	0.000
	EXP (E)	1.975	,025
	(O-E)**2 / E	.000	,025
UPPER SNAKE	OBS (O)	2.000	0.000
	EXP (E)	1.975	.025
	(O-E)**2 / E	.000	.025
ILWACO	OBS (O)	291.000	7.000
	EXP (E)	294.285	3.715
	(O-E)**2 / E	.037	2.906
LAKE ROOSEVELT	OBS (O)	78.000	2.000
	EXP (E)	79.003	.997
	(O-E)**2 / E	.013	1.008
MID-COLUMBIA	OBS (O)	328.000	0.000
	EXP (E)	323.911	4.089
	(O-E)**2 / E	.052	4.089
KOOTENAI	OBS (O)	12.000	0.000
	EXP (E)	11.850	.150
	(O-E)**2 / E	.002	.150

CHI-SQUARE = 8.306
D.F. = 5
P = 14018

Appendix Table 4 (cont.). Contingency chi-square results for the entire river.

LOCUS: PGM-1

POPULATION		ALLELE A	ALLELE B	ALLELE C
SNAKE	OBS (O)	20.000	4.000	0.000
	EXP (E)	22.515	1.462	.024
	(O-E)**2 / E	.281	4.408	.024
UPPER SNAKE	OBS (O)	16.000	0.000	0.000
	EXP (E)	15.010	.974	.016
	(O-E)**2 / E	.065	.974	.016
ILWACO	OBS (O)	514.000	36.000	0.000
	EXP (E)	515.963	33.497	.540
	(O-E)**2 / E	.007	.187	.540
LAKE ROOSEVELT	OBS (O)	138.000	3.000	1.000
	EXP (E)	133.212	8.648	.139
	(O-E)**2 / E	.172	3.689	5.309
MID-COLUMBIA	OBS (O)	249.000	19.000	0.000
	EXP (E)	251.415	16.322	.263
	(O-E)**2 / E	.023	.439	.263
KOOTENAI	OBS (O)	18.000	0.000	0.000
	EXP (E)	16.886	1.096	.018
	(O-E)**2 / E	.073	1.096	.018

CHI-SQUARE = 17.585
D.F. = 10
P = .06237

Appendix Table 4 (cont.). Contingency chi-square results for the entire river.

LOCUS: PGM-2

POPULATION		ALLELE A	B	C
SNAKE	OBS (O)	24.000	0.000	0.000
	EXP (E)	23.890	.066	.044
	(O-E)**2 / E	.001	,066	.044
UPPER SNAKE	OBS (O)	16.000	0.000	0.000
	EXP (E)	15.927	.044	.029
	(O-E)**2 / E	.000	.044	.029
ILWACO	OBS (O)	566.000	0.000	0.000
	EXP (E)	563.408	1.555	1.037
	(O-E)**2 / E	.012	1.555	1.037
LAKE ROOSEVELT	OBS (O)	135.000	3.000	2.000
	EXP (E)	139.359	.385	.256
	(O-E)**2 / E	136	17.785	11.856
MID-COLUMBIA	OBS (O)	328.000	0.000	0.000
	EXP (E)	326.498	.901	.601
	(O-E)**2 / E	.007	.901	.601
KOOTENAI	OBS (O)	18.000	0.000	0.000
	EXP (E)	17.918	.049	.033
	(O-E)**2 / E	.000	.049	.033

CHI-SQUARE = 34.156
D.F. = 10
P = .00017

Appendix Table 5. Mean values of left and right ventral scute counts of white sturgeon from the Columbia River.

	Areas			
Scute region	Mid-Columbia	Ilwaco	Lake Roosevelt	Upper Snake
Left ventral	9.60±0.97	9.41±1.31	9.58±1.17	9.14±0.89
Right ventral	9.52±1.07	9.28±1.24	9.32±0.75	9.14±0.89