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Title: Phenotypic Comparison of Thirty-eight Steelhead (Oncorhynchus mykiss) Populations from Coastal Oregon

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An aspect of the genetic structure of coastal Oregon steelhead was explored and found to gradually change in a north to south pattern for the allelic frequencies of several enzymes. Isocitrate dehydrogenase and superoxide dehydrogenase were the clearest examples of this pattern of variation. This pattern was most evident in populations from river basins larger than 350 km^2.

The area south of the Coos River was marked by a transition in the increase of at least four rare alleles, most notably variants of phosphoglucose isomerase 2 and malate dehydrogenase 3-4.

Populations from the largest (2000 km^2) basins had on average 10% more variants of the ME 3 common enzyme than did populations from the smallest (200 km^2) basins.

The genetic distance between the Nehalem hatchery stock and neighboring wild stocks appears to have narrowed since the reintroduction of wild fish to the hatchery.

In the decade since the last major electrophoretic work on coastal steelhead, most populations seemed little changed; however shifts in several isozyme frequencies were noted in populations from two Rogue

River tributaries and the Elk River. The Bandon Hatchery stock persisted in showing large departures from coastwide trends for many alleles.

A Phenotypic Comparison of Thirty-eight Steelhead (*Oncorhynchus mykiss*) Populations from Coastal Oregon

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A Phenotypic Comparison of Thirty-eight Steelhead (Oncorhynchus mykiss) Populations from Coastal Oregon

INTRODUCTION

Steelhead trout (Oncorhynchus mykiss, formerly Salmo gairdneri) generally return to their natal streams to spawn, so it is possible for populations to become locally adapted to their native streams. The identification of adapted stocks is important to fishery managers because it is commonly believed that hatchery releases in "foreign" streams generally result in poorer survival than releases in a brood stocks stock's source stream. (Montgomery 1977). If a detectable population structure has a basis in selection, then there may be genetic patterns of similarities and differences in populations from similar and different habitat types. Thus steelhead in similar environments would display similar phenotypes which could be related to descriptions of stream basins.

Hjort and Schreck (1982) suggested such a relationship for coastal Oregon coho salmon (Oncorhynchus kisutch). Coho stocks from large stream systems were more similar to each other than to stocks from smaller stream systems, independent of geographic proximity. However, for coastal steelhead stocks from 13 Northwest drainages, McIntyre (1976) found a strong negative correlation between a genetic similarity index developed by Rogers (1972) and the distance between the ocean mouths of

the drainages. Basing stock transfers primarily on geographic proximity may be ineffective if adaptive genetic differences exist within the distance of the transfer.

The demonstration of a stock's adaptation is beyond the scope of this study, but genetic differences between populations are detectable. Allelic frequencies of many isozyme loci are estimated by using electrophoretic separation of proteins and histochemical staining techniques (Smithies 1955). Allendorf and Utter (1979) defined alleles as alternative proteins coded by different deoxynucleic acid sequences that comprise synonymous genes occurring at the same locus. Although differences in isozyme frequencies alone cannot be attributed to the selective forces of differing environments, the differences found are accepted as evidence for defining stocks of fish (Utter et al. 1974). The use of isozyme data for stock definition implies that the isozymes used are selectively neutral, otherwise a truly panmictic population could appear as separate stocks after even one generations exposure to a selective environment (Gauldie 1984). Utter et al. (1980) described such use of protein data as the best existing single method for the definition of genetic population structure.

Steelhead population structure on a large scale has been described as including a coastal group ranging from Baja California to the Kamchatka peninsula, and an inland group found in the upper Skeena, Fraser and Columbia rivers. Wide differences in LDH-4 and SOD allelic frequencies distinguish these two groups, which are presumed to have separated in the last glacial era (Allendorf 1975, Parkinson 1984). Distinctions between

stocks from the Columbia river above the confluence the Snake River, and within the Snake River have been suggested (Milner 1977).

Study of the coastal group's structure has been fragmentary. In British Columbia, Parkinson (1984) detected unexpectedly uniform isozyme frequencies over three large coastal geographic areas (east and west coastal Vancouver Island, and mainland B.C. at the same latitudes). At the same time, electrophoretically distinct populations from adjacent streams were observed. Parkinson concluded that adaptive differentiation may occur on a small geographic scale, and that stabilizing selection may maintain similar phenotypes over a wider area. Populations of Washington coast steelhead, mostly from the Olympic Peninsula were genetically similar within drainages, and adjacent drainages were not significantly different in allele frequencies (Reisenbichler and Phelps 1989). Thirty-one populations of California coastal rainbow trout extending over 1000 km of California coast were electrophoretically very similar according to Berg and Gall (1988) who hypothesized that "geographic distance represents a porous barrier to gene flow by dispersal which is best described by a non-linear function of both an organism's vagility and migratory precision." Berg hypothesized these individual populations were once loosely tied together by gene flow which, over generational time, smoothed out excessive departures from panmictic allele frequencies, and that recent environmental degradation had fragmented the species distribution.

The objective of this study was to electrophoretically characterize stocks of steelhead found in the rivers and streams of coastal Oregon. Steelhead stocks were compared between north and south coastal

populations, among drainage basins of different sizes, between wild and hatchery populations and among populations from different estuary types. A stock of fish as used here is defined as a population which sustains itself over time in a definable area.

METHODS

Approximately 50 presumed steelhead of age 0+ and 1+ were collected from each selected stream by backpack electrofishing during times of low stream flow in 1984 and 1985. To minimize the collection of nonanadromous rainbow trout, samples were taken from areas where concentrations of steelhead were known to spawn annually.

To minimize the risk of collecting a sample of juveniles resulting from few parents, collection sites of individuals were spaced as widely as practical and equal numbers of each age class were collected when possible (Krueger and May 1987). Ages were estimated in the field by relative lengths, and verified by scale analysis of subsamples. The Sixes Rivers population was re-sampled in 1985 after preliminary dendrograms suggested the 1984 sample (N = 20) was not representative. Rogue River samples came from three different tributaries and totaled 147 fish. The fork length (tip of the snout to the fork of the caudal fin) of each fish was recorded along with the collection date and river kilometer of the collection site (Appendix Table 1).

Site selection

The streams and rivers selected for this project are depicted in Fig. 1. Some basin morphology and discharge characteristics of these study sites are listed in Table 1. The criteria for the selection of these sites were as follows:

1. Thirteen major drainages (greater than 250 km^2) were included to update existing knowledge of the genetic composition of their steelhead stocks. The two largest rivers, the Rogue and the Umpqua, were sampled only in tributaries of their lower reaches. Variation

within these basins was not detectable by this sampling design. Major basins not sampled due to time constraints or not meeting the second criteria included the Yaquina and Salmon Rivers.

2. Populations from sites believed to be least affected by hatchery outplanting were sampled. This determination was made by Oregon Department of Fish and Wildlife (ODFW) personnel (McHugh, N. personal communication, 1983). Populations from these rivers and streams probably have had some introgression from hatchery stocks, but the degree of this introgression has not been quantified. There were two exceptions to the above criterion. The Miami River, where a hatch-box planting program maintained by Salmon and Trout Enhancement Program (STEP) volunteers used eggs of hatchery origin and the Fishhawk Creek, Nehalem River collection. There are two Fishhawk Creeks, both tributaries of the Nehalem River, and the creek sampled was not the unstocked creek advised by the ODFW personnel. The collection of wild fish from the Salmonberry River, also a Nehalem tributary, served to represent the wild population.

3. Streams with basin areas smaller than 250 km^2, that met the second criterion were selected. Steelhead from streams of this size generally had not previously been studied electrophoretically. Table 2 lists the drainages by basin area.

4. All of coastal Oregon's steelhead hatchery stocks were sampled (Table 3). This study did not attempt to compare the hatchery stocks with their stocks of origin, but rather with the wild or natural stocks found at varying distances from the hatchery.

Sixty juvenile steelhead comprised each hatchery stock sample collected in the spring of their second year. This timing permitted the collecting of larger fish which are preferable for tissue extraction. Two of the stocks were not released into the rivers on which they were reared. Chetco River steelhead were reared at the Elk River Hatchery and returned to the Chetco River. The Elk River Hatchery did not propagate Elk River steelhead. The Rock Creek Hatchery on the Umpqua River reared transported Alsea winter steelhead for release into the South Umpqua, in addition to summer steelhead released to the Umpqua.

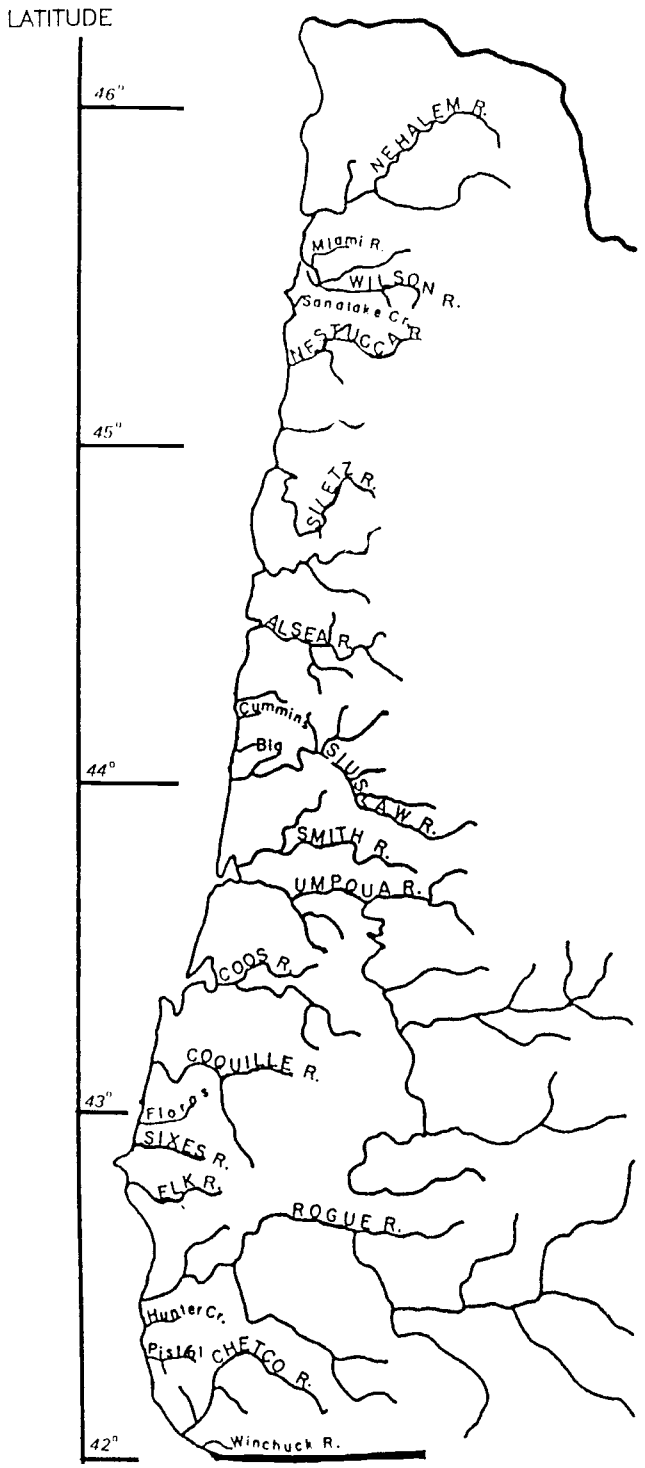

Fig. 1. The streams and rivers sampled in this study to determine isozyme frequencies in their steelhead populations.

Table 1. Environmental data for the sampled basins.

	ave cfs	max cfs	min cfs	length km.	elevation meters	slope m/km	area km.sqr.	mean rainfall cm/yr	max. rainfall cm/yr	latitude degrees
Nehalem	3635	43200	200	190	671	4	2192	216	381	45.68
Miami	174	N/A	N/A	21	518	25	93	229	381	45.56
Wilson	1108	32100	34	16	518	32	499	229	381	45.48
Sand	N/A	N/A	N/A	8	N/A	N/A	44	241	279	45.28
Nestucca	1228	24000	32	85	732	9	657	216	279	45.16
Siletz	1562	35600	48	116	869	7	797	178	457	44.93
Alsea	1949	41800	45	79	914	12	1227	152	279	44.43
Yachats	152	N/A	N/A	27	703	26	114	N/A	N/A	44.31
Cummins	N/A	N/A	N/A	N/A	754	N/A	29	N/A	N/A	44.27
Big	78	N/A	N/A	N/A	700	N/A	41	N/A	N/A	44.18
Siuslaw	2669	32300	31	190	914	5	2001	203	254	44.01
Umpqua 1	7435	265000	640	366	2290	6	11801	196	279	43.68
Coos	1613	5500	90	56	671	12	1566	127	254	43.36
Coquille	3478	8250	130	101	914	9	2738	127	279	43.11
Floras	243	N/A	N/A	N/A	732	N/A	207	152	279	43.01
Sixes	572	23800	18	50	274	5	334	152	279	42.85
Elk	388	14300	48	48	274	6	243	165	279	42.80
Rogue	11721	16200	1200	341	1585	5	13199	229	305	42.44
Hunter	268	N/A	N/A	32	914	28	116	N/A	N/A	42.39
Pistol	653	48	8	35	975	28	274	203	292	42.28
Chetco	2715	4000	130	93	1219	13	936	203	305	42.05
Winchuck	337	14	5	13	610	47	181	203	267	42.00

1 Umpqua flows measured at river km 91
N/A = Not Available

Table 2. An ordination by area of the coastal Oregon drainage basins sampled to determine isozyme frequencies. Drift Creek, the Wilson, Miami, and Smith Rivers are listed because they each empty into estuaries.

River (tributary or basin)	Area of basin in km^2
Rogue (Lawson, Saunders, Lobster)	13,198
Umpqua	11,801
Coquille	2,738
Nehalem (Salmonberry)	2,213
Siuslaw	2,001
Coos	1,566
Tillamook (Wilson, Miami)	1,397
Alsea	1,227
Siletz	967
Chetco	936
Smith (Umpqua)	898
Nestucca	833
Wilson (Tillamook)	499
Sixes	334
Pistol	274
Elk	243
New (Floras)	207
Winchuck	181
Drift Creek (Alsea)	179
Hunter	116
Yachats	114
Miami (Tillamook)	93
Sand Lake	44
Big	41
Cummins	29

Table 3. Coastal Oregon steelhead hatcheries sampled to determine isozyme frequencies in their steelhead populations. Lot numbers are ODFW designations which denote brood year and summer or winter run.

Hatchery	Stock	Lot No.
Nehalem	Nehalem	3284 StW
	Fish Hawk	9984 StW
Cedar Cr.	Siletz	3384 StS
	Cedar Cr.	4784 StW
Alsea	Alsea	4384 StW
Rock Cr.	Umpqua	5584 StS
	Alsea	4384 StW
Bandon	Coquille	4484 StW
Cole Rivers	Rogue	5284 StS
	Rogue	5383 StW
	Applegate	6283 StW
Elk River	Chetco	9684 StW

Electrophoretic analysis followed the methodology described by Aebersold et al. 1987, and was performed in the laboratory of the Oregon Cooperative Fisheries Research Unit, Corvallis, Oregon. Table 4 lists the enzyme systems screened.

Historical Data

Comparisons were made between previous analyses of coastal steelhead isozyme frequencies (McIntyre and Schreck 1976, McIntyre 1976) and the results of this study. The collection dates for these data sets span a decade, and comparisons were only possible between enzyme systems in use throughout that time interval. Some older enzyme systems were found not to be under genetic control and histochemical staining techniques developed since 1976 have made it possible to screen additional enzyme systems.

Meristics

Photographs were taken of 240 individuals for future morphometric comparisons. During this process, variation in the number of dark spots visible on the dorsal fin of the juvenile fish was noted. Because the spotting density seemed size related, fork length measurements were taken from the calibrated photographs using a digitizing pad. Each sample of fish was then classified as northern or southern, and two regression analyses were performed with fork length as the independent variable, and dorsal fin spot number as the dependent variable. The classification of northern or southern was made with Cape Blanco as a dividing point between these two regions and was based on interpretation of electrophoretic data. Regression lines with 95% confidence intervals were plotted.

Table 4. Enzyme systems screened on coastal Oregon steelhead. Author citations refer to rainbow trout descriptions. The E.C. number refers to the identification standards adopted by the International Union of Biochemistry (1984).*

Abbreviation	Name	tissue	buffer	E.C. #
ACO	Aconitate hydratase	liver	AC	4.2.1.3
ADH	Alcohol dehydrogenase	liver	RW	1.1.1.1
CK	Creatine kinase	muscle	RW	2.7.3.2
AGP	Glycerol-3-phosphate dehydrogenase	muscle	AC	1.1.1.8
PEPGL	Dipeptidase	eye	RW	3.4.13.11
PGI	Glucose-6-phosphate isomerase	muscle	RW	5.3.1.9
bGa-1	N-Acetyl-B-glucosaminidase	liver	RW	3.2.1.30
IDH	Isocitric dehydrogenase (Reinitz 1977)	muscle liver	AC AC	1.1.1.42
LDH	L-Lactate dehydrogenase (Williscroft and Tsuyuki 1970)	muscle liver	RW RW	1.1.1.27
MDH	Malate dehydrogenase (Bailey, et al. 1970)	liver muscle	AC AC	1.1.1.37
ME	Malate dehydrogenase (NADP)	muscle liver	AC AC	1.1.1.40
PGM	Phosphoglucomutase	liver muscle	AC AC	2.7.5.1
PMI	Mannose-6-phosphate isomerase	eye	AC	5.3.1.8
SOD	Superoxide dehydrogenase (Cederbaum and Yoshida 1972)	liver	RW	1.15.1.1

*The abbreviations used for these enzymes vary from lab to lab and over time. Some alternatives under current use are: AH and Ah-3 for ACO, G3PDH for AGP, DPEP for PEPGL, GPI for PGI, MDHp for ME, and MPI for PMI. bGa-1 resolution was so consistently poor, and it was dropped from further analysis.

Environmental data

Environmental data compiled included average, peak and minimum flows, length, elevation, slope, area, mean and maximum annual rainfall, and latitude, (ODFW, US Geological Survey quadrangle and Oregon State Water Resources Board maps).

Statistical Analysis

A standard procedure for the analysis of electrophoretic data as outlined by Avise (1974) was applied. Allelic frequencies were computed for each locus. Alleles were identified by their mobilities, (the distance traveled in a starch gel by an allele divided by the distance from the origin to the common allele, regardless of direction). Negative numbers refer to cathodal migration. Nei's genetic distance was calculated among all 38 sampled populations using all of the allelic frequency data in Appendix Table 4 (Nei 1977). The resulting genetic distance matrix was then used to hierarchically cluster the sampled populations using the unweighted pair group mean algorithm (Sneath and Sokal 1973). The relationship between estimated genetic similarity and geographic proximity among populations was illustrated by a dendrogram. The genetic distance measure was also used to directly compare the Nehalem River hatchery brood stocks to neighboring wild populations. Groups of steelhead stocks were compared on the basis of north and south geographical separation, among drainage basins of different sizes, between wild and hatchery populations, and among populations from different estuary types.

To determine if the above groups were separable, discriminant function analysis was utilized (BMDP, Dixon and Brown 1979). Input

variables for all of the discriminant analyses were the arcsine transformed frequencies of the common alleles for the most variable enzymes, namely SOD, MDH-3,4, PGM-1, PGM-2, IDH-3,4, LDH-4, PGI-2, PGI-3, AGP-1, ACO, ME-3, and ME-4. When any of the assigned classifications yielded distinct separations on a canonical variable, each population group was defined in terms of the presence or absence of a particular allele. The significantly different alleles were then identified using Chi-square contingency tables (Snedecor and Cochran 1980). Jackknife classification (the reassigning of populations to categories defined a priori) evaluated the distinctiveness of the groups.

RESULTS

North-South Clines

Frequencies of the SOD 100 allele were highest in the southern populations of the Oregon coast, with one Rogue River sample having a frequency of 84%. This contrasts with the 64% frequency found in the Nehalem population to the north. The transition between these two regions was gradual for populations from basins larger than 350 km^2 (Fig. 2). Populations from drainages smaller than 350 km^2 did not demonstrate as smooth a transition and were plotted with a different symbol in this graph. There were basically two ranges of SOD 100 frequency in the hatchery populations (Appendix Table 4). To the north, Cedar Creek and Nehalem stocks ranged from 60 to 63%. The mean SOD frequency of all hatcheries from the Alsea south was 82%, excluding the anomalous Bandon hatchery stock, which had an SOD frequency of 45%. A north-south cline in the frequency of the 71 allele of the IDH-3,4 loci was also evident (Fig. 3). Rogue River sample frequencies were as low as 10%, while samples from the north coast were as high as nearly 20%. There was a gradual, though less distinct, north-south transition in the frequency of this allele in the geographically intermediate rivers. These patterns were not evident when all of the data was used to produce a dendrogram (Fig. 4).

If only those basins larger than 350 km^2 are considered for the MDH-3,4 isozyme, another north-south pattern is observed (Appendix Table 4). All of those populations in larger rivers north of and including the Siuslaw had a 95 percent or higher frequency of MDH-3,4 common allele.

The populations from larger rivers south of and including the Coos had common allele frequencies of less than 90 percent.

The area south of the Coos River was marked by sharp transition in four different enzymes, including the MDH-3,4_{120} allele (Fig. 5). The 120 allele was detected at a level of up to nearly 10% in the south, and was virtually absent from populations north of the Sixes River. PGM-2 also varied between these two areas, the PGM-2_{140} allele was virtually absent north of the Coos River, while its frequency was 5.4% in one of three wild Rogue River samples. The Umpqua's Rock Creek Hatchery summer steelhead stock was the major exception to this pattern, with a high 11.4% frequency for the 140 allele. The only other northern detections of the allele were in the Sand Lake Creek and the Nestucca river populations (1.0% and 1.8%).

PGI-2_{133} and PGI-3_{120} also showed a level of specificity to the south coast. PGI-2_{133} was detected in nine populations south of the Coos River, and in only two to the north. PGI-3_{120} was detected in only three populations south of the Coos River, and was absent in all populations north of the Coos River.

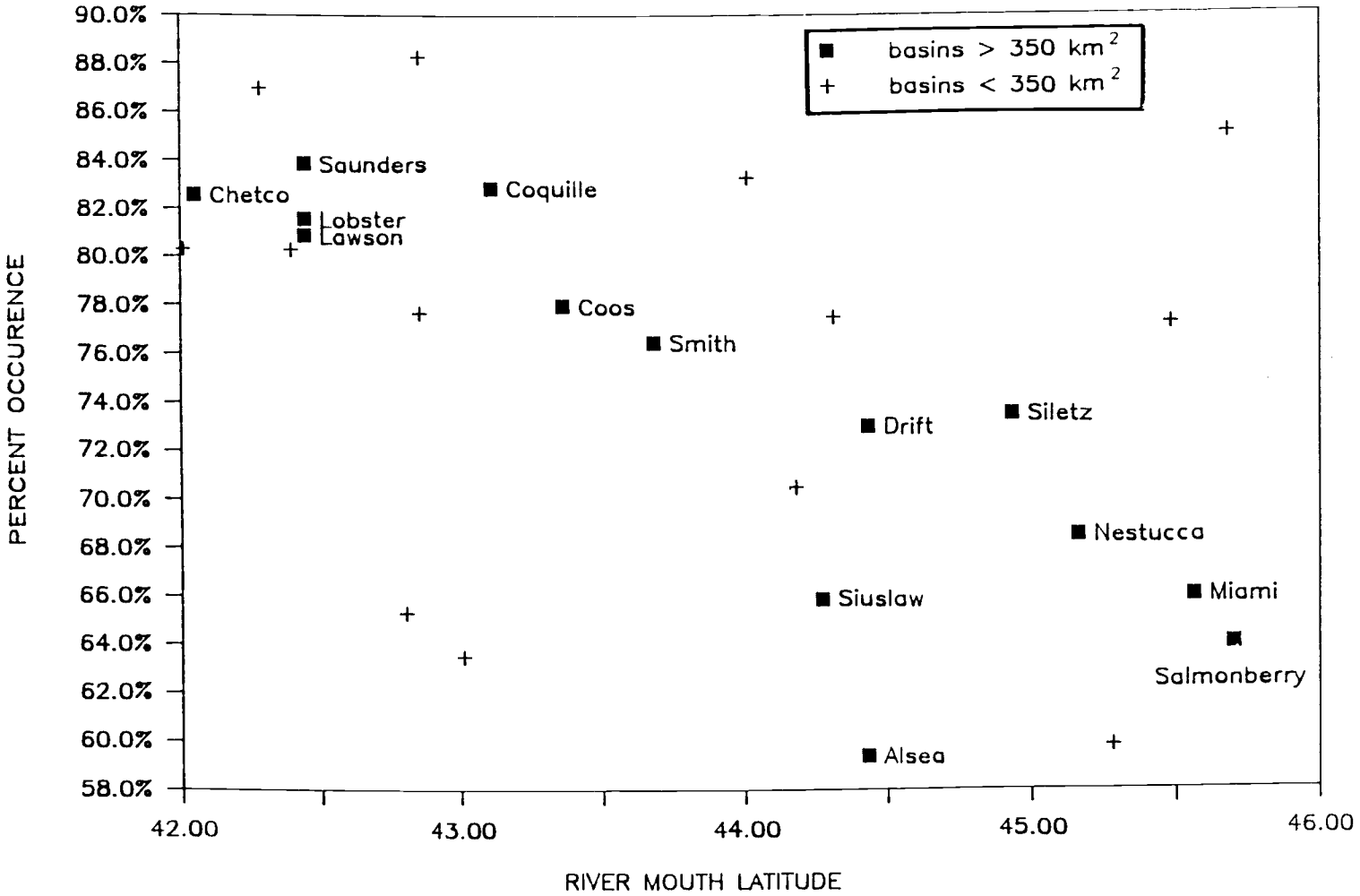

Fig. 2. SOD common allele frequencies for wild populations vs the latitude of their river's mouth.

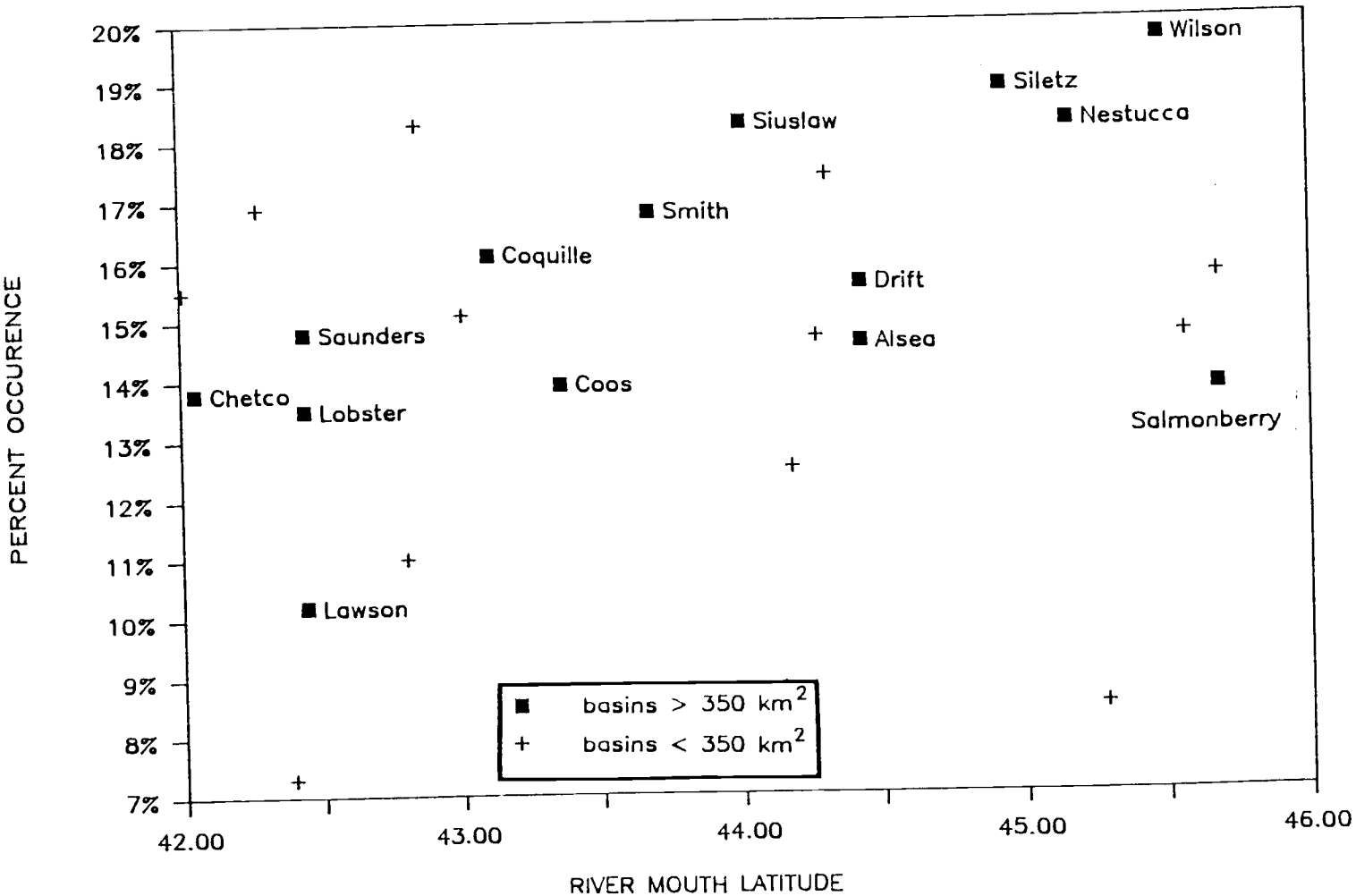

Fig. 3. IDH 3-4$_{71}$ allele frequencies for all sampled populations vs the latitude of their river's mouth.

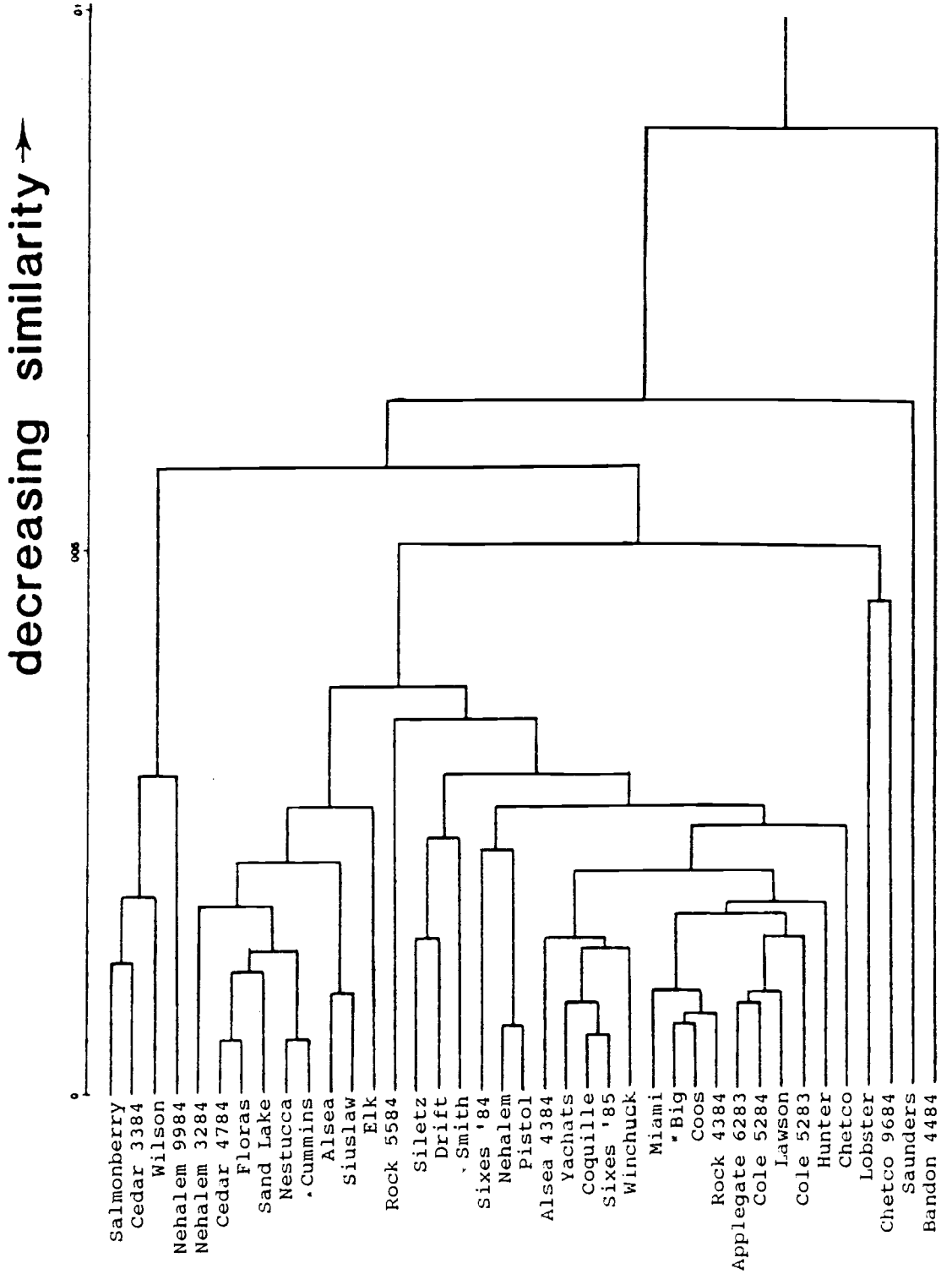

Fig. 4. Dendrogram of all populations based on the allele frequency data in Appendix Table 4. A matrix of Nei's genetic distances (Nei 1977) was hierarchically clustered using the unweighted pair group mean algorithm (Sneath and Sokal 1973). Hatchery samples are followed by their four digit lot numbers, listed in Table 3.

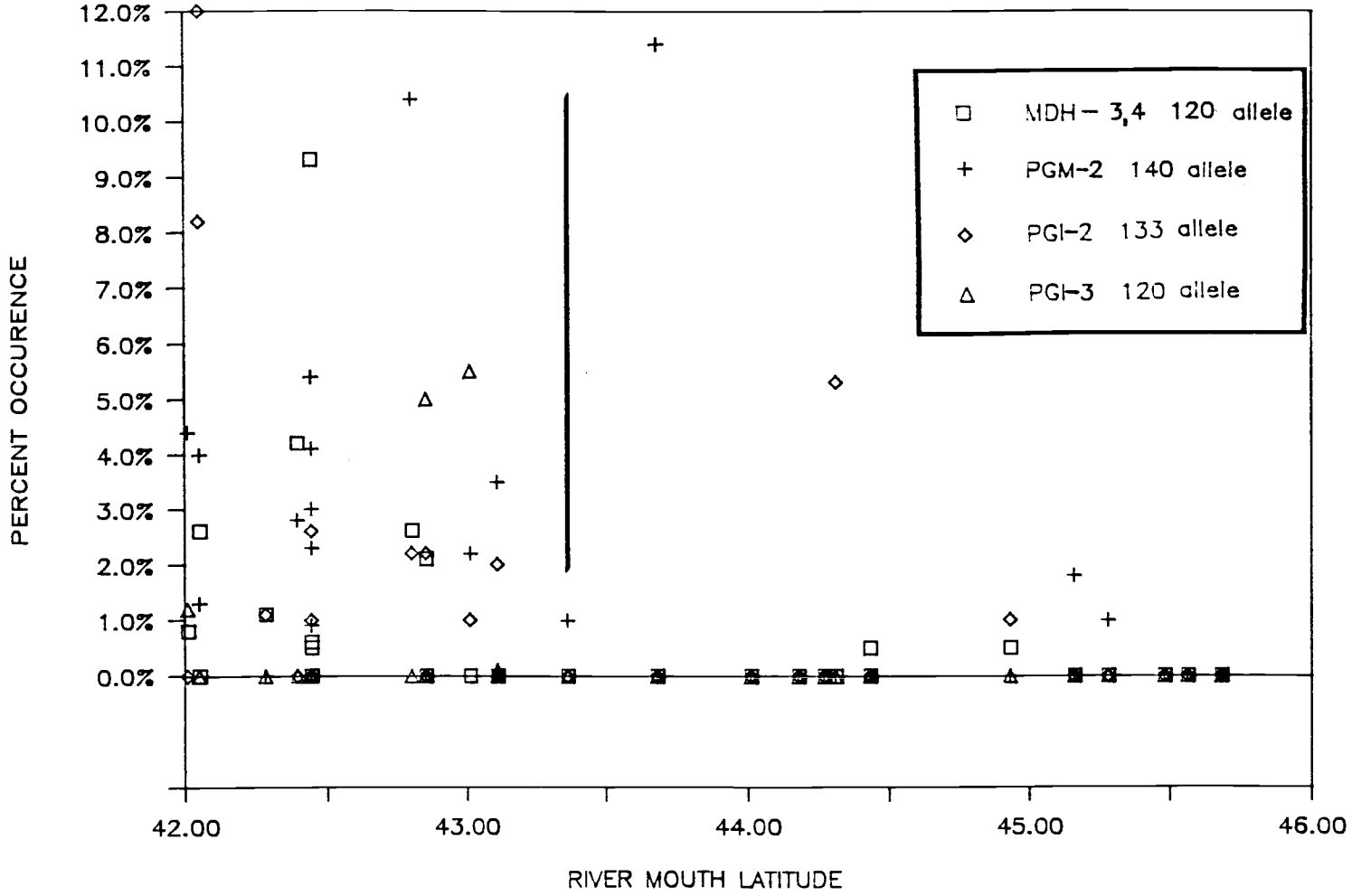

Fig. 5. Four allele frequencies for wild populations from basins larger than 350 km^2 vs the latitude of their river's mouth. These alleles became quite rare north of the Coos River (indicated by the vertical line).

Basin Size

Discriminant function analysis suggested that frequencies of the ME-3_{100} allele were related to basin size, the smallest basin populations having higher frequencies of the common allele (Table 5). A Chi-square test showed these frequency differences were most significant between the largest and smallest size groups ($P < 0.005$). The large and medium size classes were not significantly different.

Table 5. Means and standard deviations for the frequencies of the ME-3_{100} allele in three classes of basin size.

x=Basin Size	N	Mean	Standard Deviation in km^2
x>2000	8	81%	0.108
200<x<2000	12	85%	0.036
x<200	7	92%	0.041

Rare alleles of the AGP-1 enzyme showed a relation to basin size as well. Rare alleles were detected in 57% of the populations from large (>2000 km^2) basins and in none of the populations from basins less than 200 km^2 in size. The 200 to 2000 km^2 category was found to hold these rare alleles in 38% of the populations. The jackknife routine of the discriminant function analysis was able to correctly reassign 86 percent of the small basin populations to the small basin category defined by actual data. These results are illustrated by a histogram of the first canonical variable (Fig. 6). A north-south pattern in ME variation was not evidenced by this study.

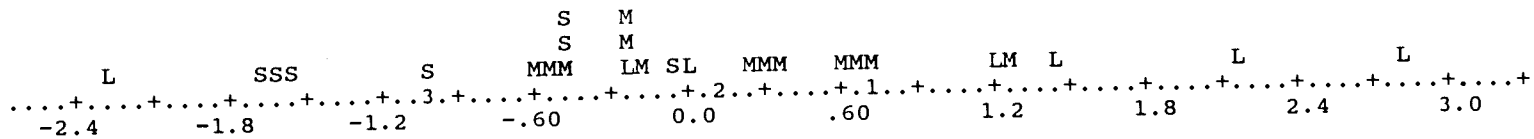

Fig. 6. Discriminant function analysis for populations categorized by basin size, a histogram of the first canonical variable. S = small basins less than 200 km^2, M = medium basins 200 to 2000 km^2, and L = large basins greater than 2000 km^2.

Hatchery-Wild Comparisons

Steelhead from hatcheries tended to reflect isozyme frequencies found in neighboring wild populations, (excepting the Bandon stock). Slight hatchery-wild differences were detected in the rare alleles of two enzymes. Variants of the PGM-1 locus were detected much more frequently (58% of the time) in the hatchery populations than in wild populations (19% of the time). A Chi-square test of the PGM-1 frequency difference between all hatcheries pooled and all wild populations pooled was significant ($P < 0.005$, Table 6), even though the PGM-1 variants were never detected above a level of 6%.

A second enzyme, ME-4, showed an opposite pattern. Variants of the common allele were detected in only one of the 12 hatchery stocks, while 6 of the 26 wild samples showed variation from the common allele ($P = 0.10$, Table 6). A discriminant function analysis separated 7 of the 12 hatchery stocks, (and 5 of 26 wild stocks) from the rest of the populations on the canonical variable (Fig. 7).

Average heterozygosities were comparable between hatchery and wild populations (9.57% and 9.51%). The summer steelhead stock at the Cole Rivers Hatchery on the Rogue River had the lowest heterozygosity of any coastal stock (6.48% vs 9.97% for the Cole Rivers winter stock, Appendix Table 6.

Table 6. Allelic frequency differences between hatchery and wild steelhead populations sampled in coastal Oregon. All 12 hatchery populations pooled compared to all 26 wild populations pooled.

Enzyme (allele)	Allele Frequency	Chi square value	Degrees Freedom	Significance 'P'
ME-4 (100)	hatchery:100% wild: 99%	2.84	1	0.1
ME-4 (110)	hatchery:0.08% wild:0.64%	2.71	1	0.1
PGM-1 (100)	hatchery: 98% wild:100%	13.61	1	0.005
PGM-1 (85)	hatchery:1.72% wild:0.21%	12.30	1	0.005

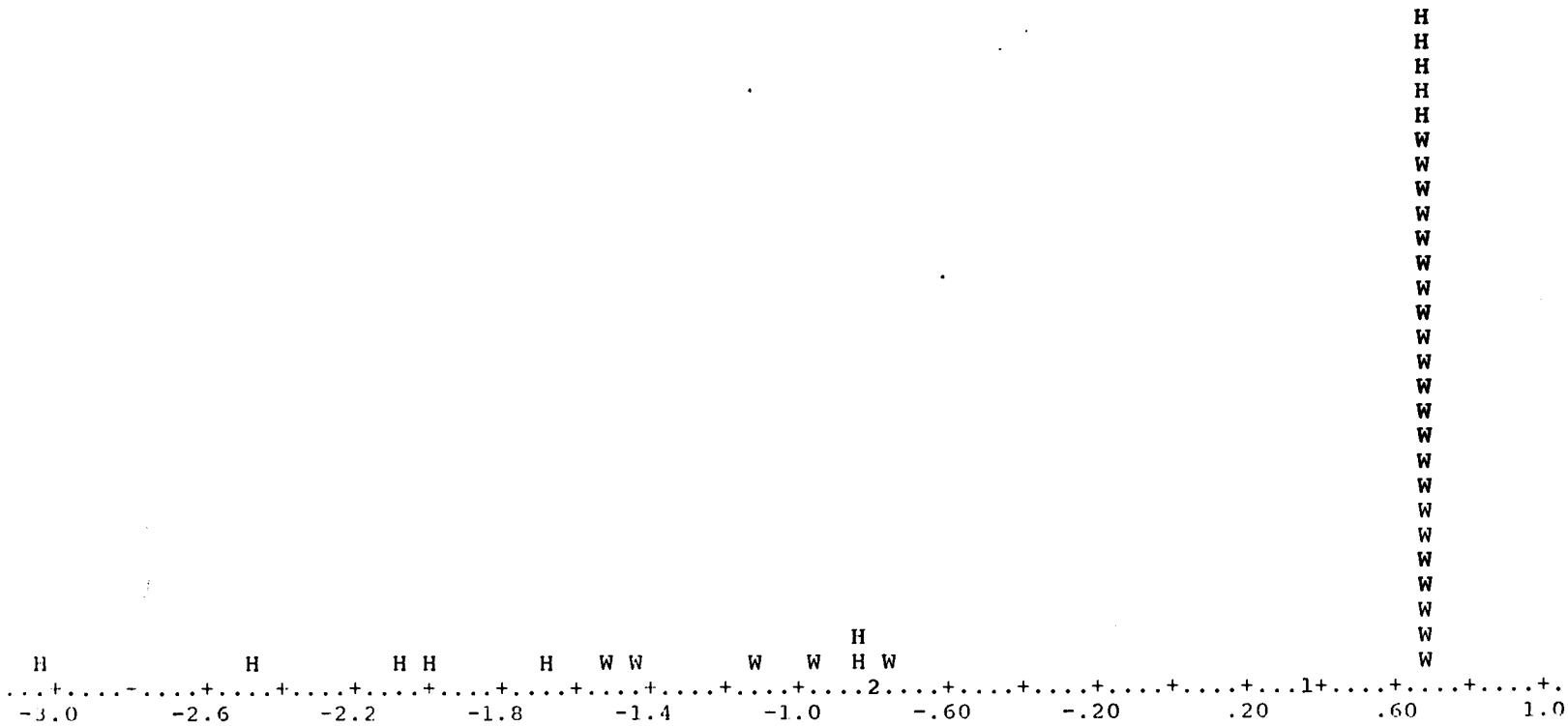

Fig. 7. Discriminant function analysis for hatchery vs wild populations. A histogram of the canonical variable. H = hatchery populations, W = wild populations.

Hatchery Brood Selection

Using wild fish to start a new Nehalem hatchery brood stock increased the genetic similarity of the hatchery stock with neighboring wild stocks (Fig. 8). The degree of genetic relatedness among the four Nehalem area stocks was measured by Nei's genetic distance (Nei 1977). The larger the number in this table, the larger the allelic frequency differences in the populations. The wild Salmonberry River population was most like the neighboring Wilson River population, (genetic distance of 0.00115) less similar to the new wild based Nehalem hatchery stock, (genetic distance of 0.00392) and least like the old Nehalem Hatchery stock (genetic distance of 0.00683). The Wilson River wild fish were similarly related to the two hatchery stocks (Fig. 8).

Meristics

Northern and southern populations of juvenile steelhead differed in spotting pattern on the dorsal fin, the more southern fish tending to be more densely spotted than northern fish (Fig. 9). Cape Blanco was selected as the dividing line in this analysis after consideration of the electrophoretic results. The fork length of the fish was found to account for 18 percent of the variability in spot number for fish from the north, and 28 percent of the variability in the south.

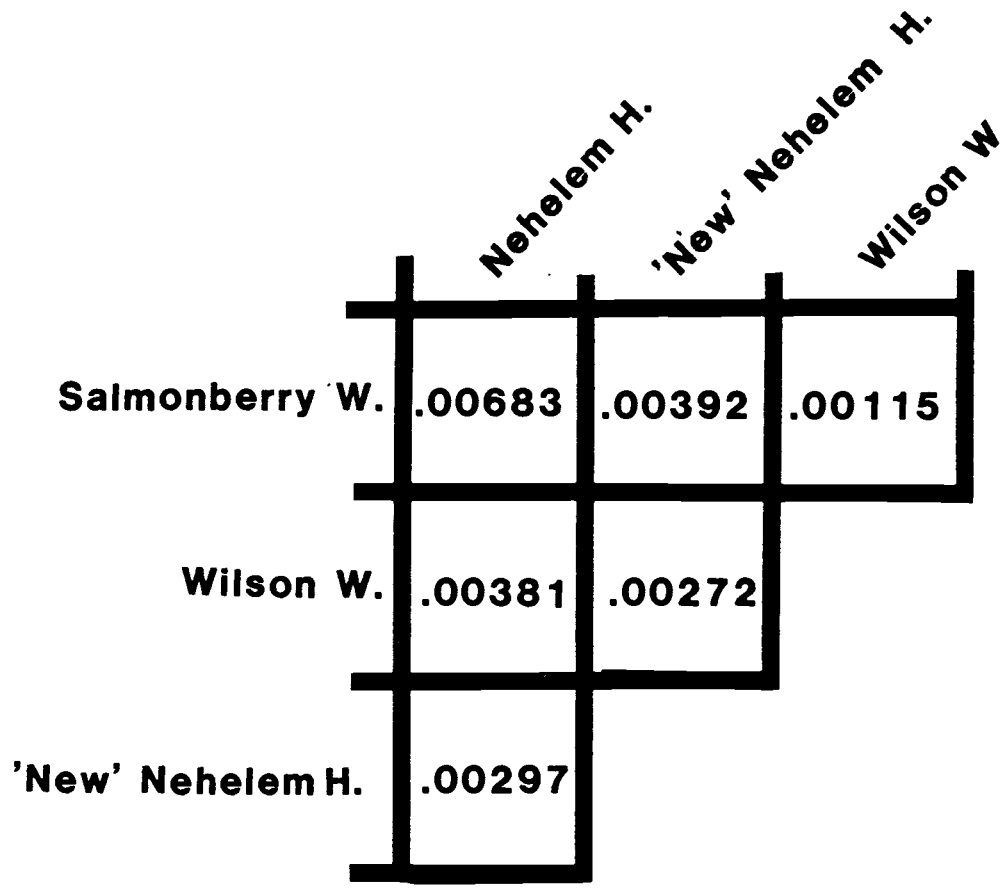

Fig. 8. The degree of genetic relatedness between two wild and two hatchery stocks of the Nehalem River area. The 'New' Nehalem Hatchery stock was being developed from trapped wild fish. The greater the numeric value of Nei's genetic distance, the larger are the allelic frequency differences between two populations (Nei 1977).

Fig. 9. The standard fork length in cm vs the number of dorsal fin spots for individual fish collected either south (solid dots) or north (open dots) of Cape Blanco. Regression lines and 95% confidence limits for the mean response at a given value of x are also plotted. The data for this graph is listed in Appendix Table 2.

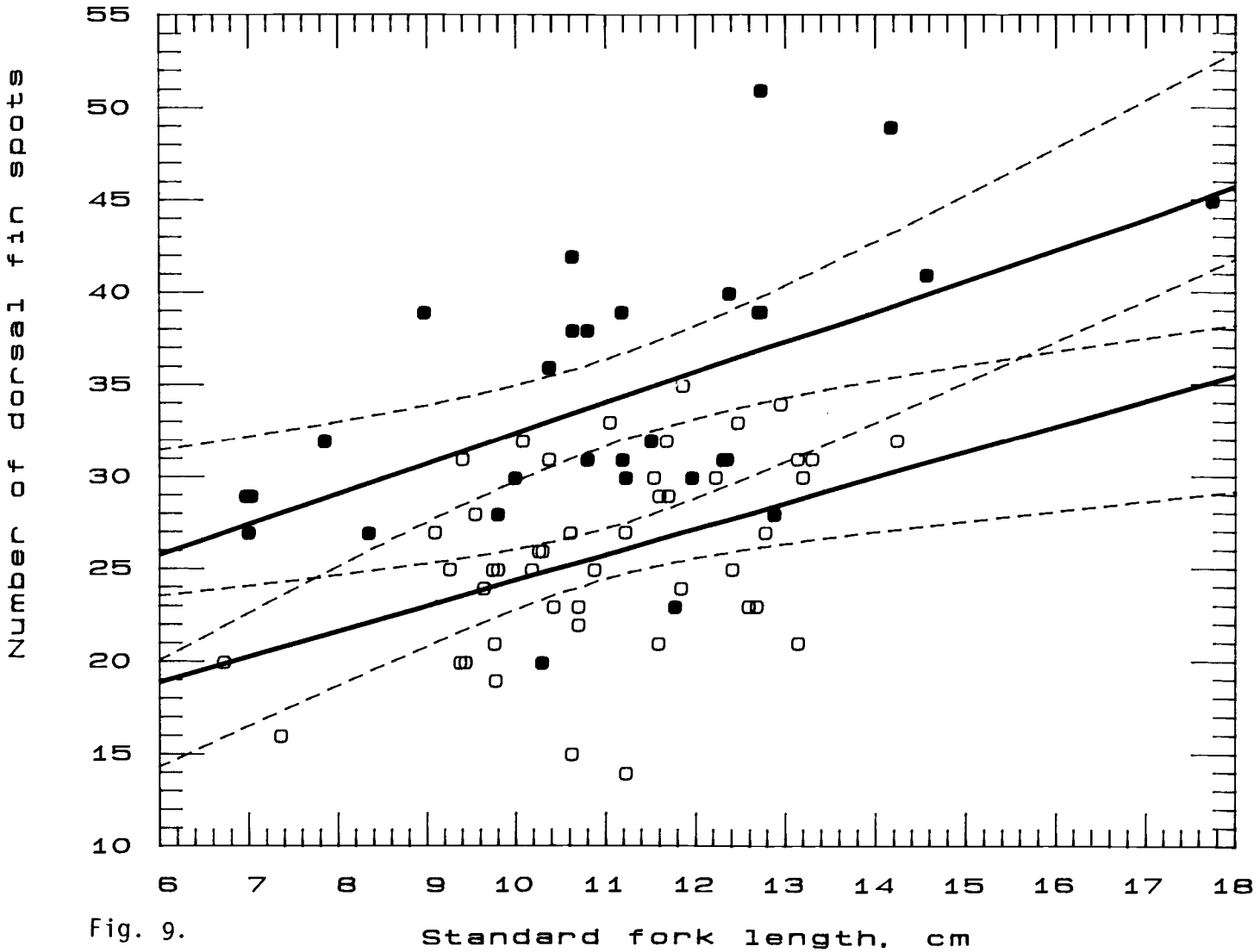
Number of dorsal fin spots
55
50
45
40
35
30
25
20
15
10
6
7
8
9
10
11
12
13
14
15
16
17
18
Standard fork length, cm

Fig. 9.

Estuaries

Each of the study streams were categorized by estuary type according to the system of Bottom et al. (1979). These estuary types differ largely in salinity and sediment regimes. Discriminant function analysis could not distinguish among populations from the three resulting categories of estuary type. If steelhead were to follow a population structure analogous to that theorized by Nicholas and Hankin (1988) for coastal Oregon chinook, some level of discrimination would have been expected. Nicholas and Hankin based their classification of stocks on observed differences in estuarine life history.

In summary, there are several north-south clines in isozyme frequency for populations of steelhead from the larger basins of coastal Oregon. The SOD and IDH enzyme systems are clearest examples, (Fig. 2 and Fig. 3). These patterns were not evident when all of the data was used to produce a dendrogram (Fig. 4). An area of transition south of the Coos River was marked by the increasing presence of four alleles; most notable were PGM-2 and MDH-3,4 variants (Fig. 5). An inverse relationship was noted between basin size and the occurrence of ME-3 variants (Table 5), and a hatchery stock and neighboring wild stocks appear to have become more similar electrophoretically after the reintroduction of wild fish to the hatchery (Fig. 8).

DISCUSSION

Electrophoretically detected phenotypic differences among populations related to basin size were slight compared to regional differences, but they were statistically significant. Several postulates are possible. One is that random genetic drift has occurred. Another is that there has been selection by differing freshwater or marine environments.

Random Drift

Smaller streams generally have lower carrying capacities, and smaller populations are more susceptible to random drift. The probability of small populations becoming fixed for rare alleles is higher than in larger populations. In this study many smaller stream populations were void of rare alleles that were detected in populations from larger streams and rivers. Such drift could also explain why the coast-wide patterns observed in isozyme frequency were not apparent in the small stream populations (Fig. 4). Such a pattern of nonconformity in small or isolated populations was also observed by Krueger and May (1987) and Campton and Utter (1987). It is difficult to quantify the role drift plays in the observed isozyme frequencies of small coastal systems because the effective population sizes of these systems are not known. Periodic population crashes and resulting genetic drift via the founder effect would seem more probable in a small, relatively isolated coastal stream. A basin-wide population disruption would seem less probable in a large river with a dendritic system of spawning grounds. When localized depressions in large river populations occur, perhaps intrabasin straying buffers the system from the major changes postulated for the small

stream populations. This hypothesis requires the assumption that populations from small streams draining into the ocean are relatively isolated from other river populations, which is reasonable if straying is a distance related phenomenon.

Natural Selection

An alternative explanation for the observed genetic variation between large and small basin populations would be that the difference is a result of natural selection. Steelhead from small streams that drain directly into the ocean are not exposed to the range of habitats available to populations from large river drainages. The adaptations needed for these differing environment might therefore differ too. If geographic variation in an environmental trait (in this case, basin size) correlates with a genetic trait, then natural selection is suggested, but methods other than correlation are required to demonstrate that the observed frequencies have any adaptive value (Endler 1986).

The geographic variable latitude was shown to vary in parallel with several isozymes, and this too suggests natural selection. Many environmental variables are associated with latitude and sorting out one that influences SOD or IDH allele frequencies could be difficult, especially if these enzymes are selectively neutral and selection is actually occurring on something not directly observable. It is known that there is SOD variation on a much larger geographic scale, the SOD 100 allele ranges from fixation (100%) in Mexico (Berg 1987) to at least 49% in the samples from the Kamchatka peninsula (Okazaki 1984). The pattern of several alleles ending their detectable Oregon presence just north of Cape Blanco suggests that there is a less than average amount

of straying between the populations north and south of this feature. Given that the area offshore of Cape Blanco has had weak upwelling (Fig. 10), perhaps there is a degree of stock isolation, based on marine migrational differences just prior to freshwater entry. Actively feeding adult steelhead may stray less frequently across this relatively nutrient poor zone. High seas stock segregation does not appear to be occurring based on tagging studies and pelagic recoveries (Light et al. 1989). Ocean recoveries of coded wire tags have shown ocean segregation of southerly and northerly migrating chinook and coho stocks on the Oregon coast (Nicholas and Hankin 1988). These authors separated fall chinook into two major production areas, divided between the Elk and the Rogue Rivers. Coho production areas were divided between the Coos and Coquille Rivers. While stock differences in isozyme frequency are generally considered to be related to freshwater adaptation, perhaps they are also influenced by marine migration patterns.

There are life history differences between northern and southern Oregon coastal steelhead populations (Bali 1959). Based on adult scale analysis Bali found south coast steelhead tend to emigrate from freshwater a larger size, spend less time in the ocean, and mature at an earlier age than northern steelhead. South coast steelhead also produced nearly twice the frequency of repeat spawners and had sex ratio of nearly two females to each male, (northern populations were nearly balanced in sex ratio). Bali's northern populations included Sand Creek and the Necanicum, Nehalem, Wilson, Trask, Nestucca, Salmon and Siletz Rivers. His southern populations included the Coos, Coquille, Sixes, Elk, Chetco and Winchuck Rivers.

Historical Data

Gene frequency data for comparable populations sampled by earlier researchers (McIntyre 1976, McIntyre and Schreck 1976) are listed in Appendix Table 3. Notable relationships between this study and the earlier data sets included the following:

a) The Bandon Hatchery stock had the lowest frequency (59%) of the SOD 100 allele in 1974, and in this study as well (45%). The highest frequencies for the allele were found in Rogue river populations in both cases.

b) Variation in the PGM-2 locus was detected primarily in south coast populations in the 1970's and the same pattern was detected in this study (Fig. 4). The Siletz, Alsea, and Umpqua population samples were void of PGM-2 variation both in past and in this study. In 1975 the only PGM variation in northern populations was detected in Trask River or Slickrock Creek samples (4 out of 1603 fish screened). In this study it was detected only in the nearby Miami River, Nestucca River, and Sand Lake Creek populations (9 out of 923 northern fish).

c) Past studies detected PGI-2 enzyme variation mostly in the Rogue River, with only two out of 1589 fish showing variation north of Cape Blanco (both from the Trask River). In this study only three out a 1040 fish showed PGI-2 variation north of the Coquille River (one Siletz and two Yachats fish). PGI-2 variation was detected in eight new south coast populations in this study (Fig. 5), mostly in populations previously unscreened for this enzyme.

Changes appear to have taken place in three south coast populations whose isozyme frequencies have shifted away from those reported the earlier studies. These populations were Saunders and Lobster Creeks of the Rogue River, and the Elk River. Evidence against these differences having been sampling artifacts is that they were repeated in up to four different enzyme systems:

a) The ME-3 enzyme frequencies were little changed over time in most stocks, with the exception of two Rogue river samples. The Saunders Creek sample showed an increase in the 93 allele of 20%. In this study, the 85 allele was not detected in the Lobster Creek population, whereas it occurred at this site at a level of 20% in the past.

b) While LDH-4 variation was similar in populations from the Tillamook, Siletz, Alsea and Umpqua basins, large shifts (11% and 12%) in frequency were detected in populations from Saunders Creek on the Rogue and the Elk River. The Bandon Hatchery population also changed in LDH frequency; this population lacked LDH-4 variation in 1975, but contained it at a frequency of seven percent in this study.

c) IDH-3,4 frequencies were generally similar in both studies, but three populations showed large increases in the occurrence of the common allele. The Elk River, Lobster and Saunders Creek populations all increased at least 12% in common allele frequency.

d) The SOD 100 allele frequency increased 17% over past observations of the Saunders Creek population.

The cause of these allele frequency changes is unknown, but several things suggest genetic drift. In the earlier studies the Saunders Creek population was atypical in two to the above mentioned enzymes when compared to other local populations. In this study it was atypical in two new ways. Immigration does not seem likely as a cause for the shift in ME-3_{100} allele frequency because no population surveyed has the allele frequencies likely to have such an effect. Not only does this population change in allele frequency, but these changes cause it to be atypical of the prevailing enzyme frequencies in the area. The small nature of this tributary, and its proximity to the City of Gold Beach (a source of harvest) suggest a very low effective population size. Genetic drift also seems likely to have caused the isozyme shifts in the Lobster Creek population. Lobster Creek was atypical both in the past and in this study.

The Elk River population frequency changes may have a cause other than genetic drift. High frequencies of the LDH-4_{76} allele, and the PGM-2_{140} allele might have been influenced by the return to Elk River of Chetco River stock. These fish are reared, but not released at the Elk River Hatchery and are high in both of the alleles needed to have brought about the observed change.

Regional and Adjacent Population Differences

The two coastal clines in SOD and IDH allele frequency demonstrate that while differences between adjacent coastal steelhead populations may be imperceptible, within the 430 km length of coastal Oregon these differences accumulated to significant levels. These latitudinal rates of isozyme frequency change may have bearing on the interpretation of studies outside the region if they are representative of natural population structure.

Steelhead populations from adjacent drainages were found to be significantly different in Canada (Parkinson 1984). Three major groups were also identified, upper Fraser, upper Skeena, and coastal, though Parkinson cautioned that even major differences in few loci should not be taken to represent a fundamental subdivision of a species without additional evidence. Large areas within these major groups were unexpectedly uniform, a finding attributed to stabilizing selection. The significant differences between adjacent streams was attributed to a limited interchange of individuals. Geographic distance between two stocks was not considered by Parkinson to be a measure of genetic similarity. Parkinson sampled on average 58 individuals in all but the upper Fraser (as reported for LDH sample sizes).

Adjacent populations from the west coast of the Olympic Peninsula were not significantly different (Reisenbichler and Phelps 1989). This finding was attributed to the effects of hatchery production since the 1940's. These authors concluded that there was less gene flow among populations in British Columbia than along the north coast of Washington.

Most of the Washington studies fish were collected within 70 kilometers of coastline and up to 494 individuals were collected from one basin.

In California, all isozyme differences among rainbow trout populations were attributed to temporal fluctuations around the panmictic allele frequencies of the greater global population (Berg 1988). Berg viewed the invocation of selection as an effector of interpopulational gene diversity as simply unnecessary. Berg did not observe a consistent relationship between genetic similarity and geographic proximity. His study area covered over 1100 km of coastline, and sampled an average of 44 individuals in just six rivers outside of the Sacramento basin (where 698 samples were collected).

In the Olympic Peninsula study, the absence of significant differences in adjacent populations was speculated by the authors to be due to a homogenizing affect of hatcheries. If it were true that hatchery strays and off station releases were capable of homogenizing even the remote wilderness streams of the Olympic National Park, then this effect might have been expected in Oregon where propagation has been successful as long as anywhere else. The fact Oregon populations showed significant regional differences absent even in pristine Canadian populations suggests that hatcheries have not had a homogenizing effect. If the geographic scale appropriate for describing Oregon's coastal steelhead isozyme variation were applicable to the Olympic Peninsula populations, then perhaps significant adjacent drainage differences could not have been expected within the 70 kilometers of Washington coastline where most fish were collected. The absence of wild population isozyme frequency

data predating Olympic peninsula hatcheries makes a certain answer to the question of hatchery impacts unlikely.

This studies pattern of small basin populations diverging from coastal isozyme frequency clines suggests a partial explanation for the significant differences observed in adjacent British Columbian steelhead populations. Many of the populations sampled in Parkinson's study were from small, ocean draining basins of a scale similar to that suspected to drift in isozyme frequency in coastal Oregon. It is difficult to say how frequently larger adjacent Canadian coastal populations might have appeared homogeneous if sampled over many broods, and as intensively as in the Washington study.

The Canadian result of uniform isozyme frequencies among three large geographic areas (easterly and westerly Vancouver Island, and mainland British Columbia at the same latitudes) was interpreted by Parkinson as evidence for stabilizing selection for similar phenotypes over a wide geographic area. The absence of regional isozyme uniformity in Oregon would suggest the absence of stabilizing selection, and possibly directional selection. The Californian theory of a globally panmictic population wouldn't be changed by this or any of the other steelhead studies because regardless of the resulting patterns, recent isolation, or high gene flow could be invoked as causal factors. The difficulty in knowing if sampled natural populations represent pre-supplementation conditions remains a problem in these types of studies.

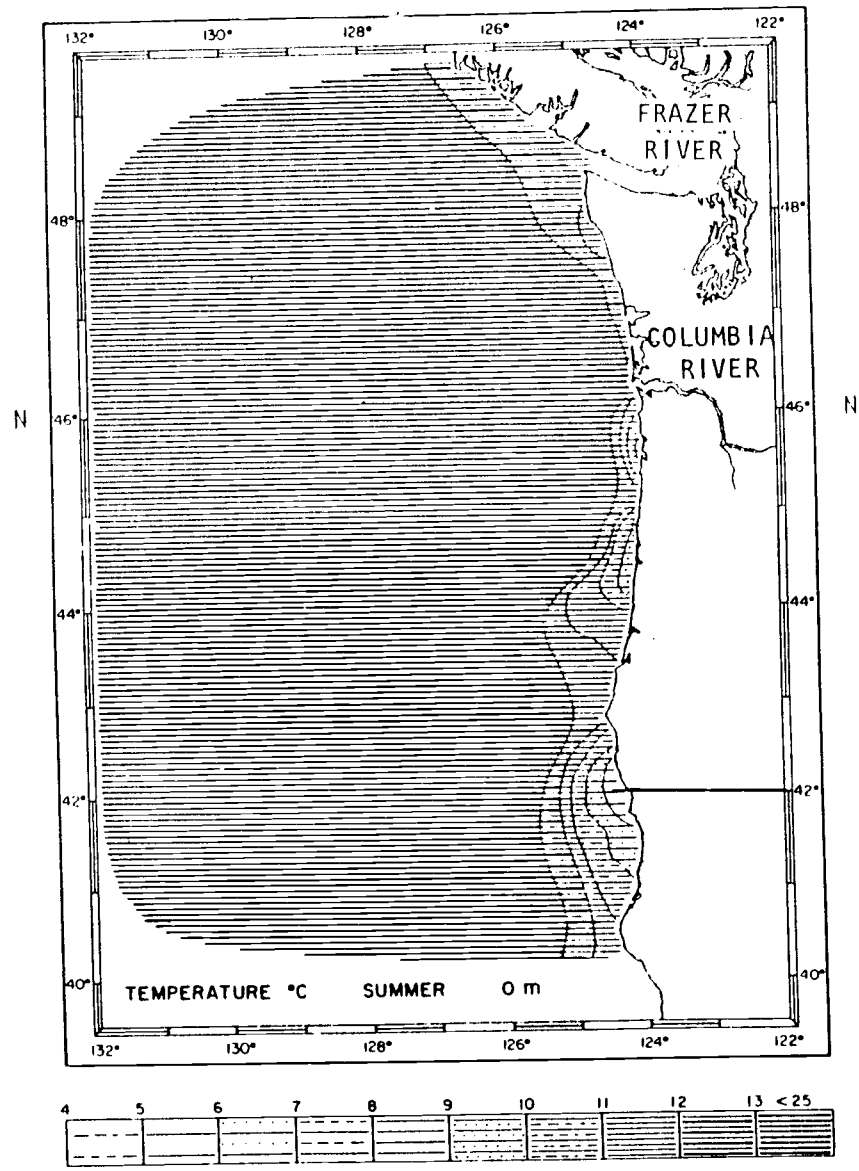

Fig. 10. Summer temperature at the surface, offshore Northern California, Oregon, and Washington. Distribution shown is averaged from data obtained during summer months of 1961, 1962, and 1963 (McGary 1971).

CONCLUSION

Steelhead allelic frequencies for several isozymes gradually change in a north to south pattern in populations along the Oregon coast. This postulated structure is in agreement with earlier electrophoretic work (McIntyre 1976) and clarifies the population structure postulated by Bali (1959) who studied life history characteristics but lacked mid-coastal samples. Electrophoresis can be used to measure genetic characteristics of a population and is a useful tool for steelhead management. Although the importance of naturally occurring genetic diversity is largely unquantified, efforts to preserve such diversity are being made and should continue. Hatchery management can effectively reduce the divergence between long isolated brood stocks and wild populations by brood stock maintenance programs of the type shown effective at the Nehalem Hatchery.

This study has demonstrated techniques which may be further developed and used to aid managers in the defining of steelhead stocks. With these tools, managers will better be able to assure that the genetic diversity of assisted populations will be maintained. These tools may also be utilized to help determine if stocking programs are appropriate to the assisted basin.

Small basin populations were shown to have some distinct differences from the large basin populations. While the cause of the differences is not known, the effects of genetic drift on these small, relatively isolated populations is suggested. The genetic pattern of apparent allelic fixation in small basin populations provides a warning to managers that any population isolated and low in numbers (such as a depressed stock or a micro hatchery) may be subject to detrimental genetic change.

Artificial propagation is but one way a native population may be altered. Environmental degradation reduces the quantity and quality of available habitat. This serves to reduce a population's size, making it susceptible to the random drift or inbreeding characteristics which may have been observed in this study's small basin populations and the Bandon Hatchery stock. Environmental degradation in coastal Oregon has been significant. In the Siuslaw National Forest, for example, fish habitat productivity is estimated to have been reduced by forty-three percent between 1940 and 1979 (U.S. Forest Service 1979).

The maintenance of genetic diversity in coastal salmonids is not just a management concern involving where or if hatchery production should be released off station. To be effective it should be one of maintaining large natural and hatchery populations. The effective population size of a stock should be a great concern to managers. Local brood stock programs should be developed and maintained from as many locally adapted individuals as possible, not just the number available at the most convenient trap site. Managers should consider the genetic consequences of efforts to isolate a depressed wild stock from even the most closely related donor stock because the costs of insularism may outweigh its benefits.

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APPENDICES

Appendix Table 1. Collection sites and dates for field collections of juvenile steelhead. River kilometers are estimated (PNRBC 1968).

	Collection areas	Collection mo/yr
NEHALEM	Fishhawk Cr. Falls, west of Jewel	08-84
SALMONBERRY	N. Fork 0-15 rk & mainstem at N. Fork	10-85
WILSON	Mainstem rk 10, Jones Cr. & Elk Cr.	08-84
MIAMI	Mainstem rk 3, rk 8, and Ross Cr.	08-84
SAND	0.2-3 rk	10-84
NESTUCCA	Mainstem rk 50, Bear Cr., and Elk Cr.	08-84
SILETZ	Euchre Cr. & Rock Cr.	09-85
DRIFT	Williams place, Willams spur, Gopher Cr, & Uppermost 1000 line bridge crossing	10-85
ALSEA	At all 3 Five Rivers road crossings, & E. Fork Lobster Creek	09-85
YACHATS	North Fork & South Fork	07-84 & 08-84
SIUSLAW	Indian Cr., 0-16 rk	10-84
CUMMINS	0-3 rk	07-84 & 08-84
BIG	river kilometers 0.8, 5 & 10	08-84
SMITH	North Fork and upper mainstem	08-85
COOS	Tioga Cr., Fall Cr., & Millicomb R. at Gold & Silver Park	08-84
COQUILLE	Mid Fork at Bear Cr., S. Fork at Elk Cr.	08-85
		08-85
FLORAS	N. Fork at rk .8, Mainstem below North and South Forks confluence	08-84
SIXES '84	Dry Creek	07-84
SIXES '85	Dry Creek & Elephant Cr.	08-85
ELK	Bald Mt. Cr. rk 0 & 4, & Red Cedar Cr. 0-1 rk	08-84
SAUNDERS	0.2-5 rk	08-84
LOBSTER	Lobster Cr. 0-25 rk, Fall Cr. & Upper Fall Cr.	08-84
LAWSON	0-7 rk	05-85
HUNTER	0.8-2 rk S. Fork Hunter Cr.	06-84
PISTOL	0-0.8 rk Deep Cr.	06-84
CHETCO	Mainstem at rk <5 and Little Redwood Cr.	08-85
WINCHUCK	Fourth of July Cr.	07-84

Appendix Table 2. The collection site, fork length in cm, and number of dorsal fin spots for steelhead trout collected north and south of Cape Blanco.

Northern Basins	fork length cm.	number of spots	Southern Basins	fork length cm.	number of spots
Sand Lake	10.62	15	Elk	8.34	27
Sand Lake	10.30	26	Elk	8.97	39
Sand Lake	9.43	20	Elk	12.38	40
Sand Lake	9.64	24	Elk	6.97	29
Sand Lake	11.05	33	Elk	7.03	29
Sand Lake	9.76	21	Elk	7.00	27
Wilson	7.36	16	Elk	7.85	32
Wilson	6.72	20	Pistol	9.80	28
Wilson	9.37	20	Pistol	12.31	31
Siletz	11.84	24	Pistol	10.37	36
Siletz	13.20	30	Pistol	11.51	32
Siletz	13.14	21	Pistol	14.17	49
Siletz	12.41	25	Pistol	10.63	42
Siletz	12.59	23	Pistol	9.99	30
Siletz	12.78	27	Pistol	10.80	31
Siletz	14.24	32	Pistol	11.19	31
Cummins	12.47	33	Pistol	12.73	39
Cummins	9.80	25	Hunter	12.73	51
Cummins	9.77	19	Hunter	10.29	20
Cummins	9.40	31	Hunter	11.23	30
Cummins	9.54	28	Hunter	11.77	23
Cummins	10.08	32	Hunter	12.88	28
Cummins	11.23	14	Hunter	10.63	38
Yachats	10.70	23	Hunter	10.80	38
Yachats	9.74	25	Hunter	12.35	31
Yachats	11.59	21	Rogue	11.96	30
Yachats	9.26	25	Rogue	14.57	41
Yachats	10.61	27	Rogue	11.18	39
Yachats	10.18	25	Rogue	17.75	45
Yachats	11.60	29	Rogue	12.70	39
Yachats	11.54	30			
Yachats	10.26	26			
Yachats	13.30	31			
Yachats	11.22	27			
Yachats	11.86	35			
Yachats	10.37	31			
Miami	9.09	27			
Miami	10.88	25			
Miami	10.42	23			
Miami	11.68	32			
Nehalem	11.70	29			
Nehalem	10.70	22			
Big	12.23	30			
Big	13.14	31			
Big	12.95	34			
Big	12.68	23			

Appendix Table 3. Steelhead trout isozyme frequencies derived from McIntyre and Schreck (1976) and McIntyre (1976).

	MDH 3-4				PGM-2		ME-3	
	100	83	75	120	100	-140	100	93
TRASK	0.926	0	0.065	0.010	0.996	0.004		
SLICKROCK	0.936	0	0.065	0	0.969	0.031		
NESKOWIN	0.933	0.027	0.041	0	1.000	0		
SILETZ	0.934	0.054	0.014	0	1.000	0		
ALSEA	0.970	0.023	0.008	0	1.000	0	0.930	0.070
CROOKED	0.956	0.008	0.033	0.004	1.000	0	0.885	0.115
LOBSTER	0.931	0.041	0.022	0.007	1.000	0	0.835	0.165
MILL	0.938	0.062	0	0	1.000	0	0.890	0.110
BIG	0.924	0.023	0.047	0.007	1.000	0		
ROCK CR. H.	0.852	0.132	0.017	0			0.871	0.129
BANDON H.	0.882	0.104	0.016	0	1.000	0	0.798	0.202
ELK	0.882	0.070	0.039	0.009	0.960	0.040	0.890	0.110
ROGUE	0.906	0.061	0.012	0.022	0.982	0.019		
LOBSTER	0.883	0.018	0.128	0.023	0.985	0.015	0.800	0.200
SAUNDERS	0.900	0.045	0.005	0.050	1.000	0	0.875	0.125
ILLINOIS	0.902	0.088	0.010	0	1.000	0	0.875	0.125
HUNTER	0.910	0.058	0.020	0.012	0.983	0.017	0.924	0.076

	SOD			PGI-2		LDH-4		IDH 3-4			
	100	152	48	100	133	100	76	100	40	120	71
TRASK	0.725	0.265	0.010	0.992	0.008	0.874	0.126				
SLICKROCK	0.688	0.261	0.051			0.889	0.141				
NESKOWIN	0.671	0.329	0	1.000	0	0.847	0.153				
SILETZ	0.615	0.385	0	1.000	0	0.980	0.020	0.713	0.098	0.037	0.152
ALSEA	0.675	0.325	0	1.000	0	0.935	0.065	0.589	0.155	0.045	0.202
CROOKED	0.622	0.376	0	1.000	0	0.885	0.115	0.631	0.100	0.131	0.239
LOBSTER	0.695	0.306	0	1.000	0	0.878	0.122	0.620	0.130	0.050	0.210
MILL	0.671	0.324	0.006	1.000	0	0.920	0.081	0.738	0.069	0.026	0.166
BIG	0.727	0.270	0.005	1.000	0	0.940	0.060				
ROCK CR. H.	0.750	0.246	0.005			0.939	0.062	0.683	0.076	0.006	0.236
BANDON H.	0.590	0.410	0	1.000	0	1.000	0	0.760	0.110	0.000	0.130
ELK	0.689	0.307	0.045			0.960	0.040	0.718	0.087	0.035	0.160
ROGUE	0.781	0.208	0.012	0.964	0.037	0.945	0.055	0.813	0.135	0.007	0.042
LOBSTER	0.775	0.215	0.010	1.000	0	0.915	0.085	0.665	0.113	0.028	0.175
SAUNDERS	0.665	0.225	0.120	1.000	0	0.865	0.135	0.640	0.195	0.048	0.118
ILLINOIS	0.880	0.130	0	0.965	0.035	0.930	0.070	0.815	0.075	0.018	0.093
HUNTER	0.720	0.170	0	1.000	0	0.926	0.074	0.750	0.067	0.046	0.135

Appendix Table 4. Isozyme frequencies as determined by electrophoresis.

	AGP-1		PGM-2			ME-3		ME-4			SOD		
	100	130	100	-140	-80	100	93	100	82	110	100	152	48
NEHELEM	1.000	0	1.000	0	0	0.765	0.235	1.000	0	0	0.351	0.149	0
NE 9984	1.000	0	1.000	0	0	0.908	0.092	1.000	0	0	0.632	0.368	0
NE 3284	1.000	0	1.000	0	0	0.924	0.076	1.000	0	0	0.615	0.385	0
SALMONBERRY	1.000	0	1.000	0	0	0.721	0.279	0.980	0	0.020	0.640	0.350	0.010
WILSON	0.988	0.012	1.000	0	0	0.820	0.180	1.000	0	0	0.660	0.340	0
MIAMI	0.989	0.011	0.948	0	0.052	0.870	0.130	1.000	0	0	0.772	0.228	0
SAND	1.000	0	0.970	0.010	0.020	0.960	0.040	0.980	0.020	0	0.598	0.402	0
CE 4784	1.000	0	1.000	0	0	0.896	0.104	1.000	0	0	0.620	0.380	0
CE 3384	1.000	0	1.000	0	0	0.770	0.230	1.000	0	0	0.600	0.400	0
NESTUCCA	1.000	0	0.982	0.018	0	0.893	0.107	1.000	0	0	0.685	0.315	0
SILETZ	1.000	0	1.000	0	0	0.816	0.184	0.970	0.030	0	0.735	0.265	0
DRIFT	1.000	0	1.000	0	0	0.778	0.222	0.960	0	0.040	0.730	0.270	0
ALSEA	1.000	0	1.000	0	0	0.837	0.163	0.990	0	0.010	0.594	0.406	0
AL 4384	1.000	0	1.000	0	0	0.966	0.034	1.000	0	0	0.800	0.200	0
RK 4384	1.000	0	1.000	0	0	0.940	0.060	1.000	0	0	0.810	0.190	0
YACHATS	1.000	0	1.000	0	0	0.922	0.078	1.000	0	0	0.775	0.225	0
SIUSLAW	0.975	0.025	1.000	0	0	0.782	0.218	1.000	0	0	0.659	0.341	0
CUMMINS	1.000	0	1.000	0	0	0.889	0.111	1.000	0	0	0.705	0.295	0
BIG	1.000	0	1.000	0	0	0.889	0.111	1.000	0	0	0.833	0.167	0
RK 5584	1.000	0	0.886	0.114	0	0.893	0.107	1.000	0	0	0.833	0.167	0
SMITH	0.988	0.011	1.000	0	0	0.872	0.128	1.000	0	0	0.765	0.235	0
COOS	0.990	0.010	0.990	0.010	0	0.886	0.114	0.950	0	0.050	0.780	0.220	0
COQUILLE	0.993	0.007	0.965	0.035	0	0.858	0.142	1.000	0	0	0.829	0.171	0
BA 4484	1.000	0	1.000	0	0	0.815	0.185	1.000	0	0	0.449	0.531	0.020
FLORAS	1.000	0	0.978	0.022	0	0.957	0.043	1.000	0	0	0.635	0.365	0
SIXES '84	1.000	0	1.000	0	0	0.842	0.158	1.000	0	0	0.883	0.118	0
SIXES '85	0.989	0.011	1.000	0	0	0.872	0.128	0.989	0	0.011	0.777	0.223	0
ELK	1.000	0	0.896	0.104	0	0.813	0.188	0.967	0.033	0	0.653	0.347	0
SAUNDERS	0.986	0.014	0.977	0.023	0	0.679	0.321	1.000	0	0	0.839	0.161	0
LOBSTER	1.000	0	0.946	0.054	0	1.000	0	1.000	0	0	0.816	0.105	0.079
LAWSON	0.982	0.019	0.991	0.009	0	0.873	0.127	1.000	0	0	0.809	0.191	0
AP 6283	1.000	0	0.970	0.030	0	0.926	0.074	1.000	0	0	0.844	0.156	0
CO 5383	0.970	0.030	0.959	0.041	0	0.867	0.133	0.990	0	0.010	0.720	0.280	0
CO 5284	1.000	0	1.000	0	0	0.939	0.061	1.000	0	0	0.800	0.200	0
HUNTER	1.000	0	0.972	0.028	0	0.861	0.139	0.958	0	0.042	0.803	0.182	0.015
PISTOL	1.000	0	1.000	0	0	0.833	0.167	1.000	0	0	0.870	0.130	0
CHETCO	1.000	0	0.960	0.040	0	0.895	0.105	1.000	0	0	0.826	0.174	0
CH 9684	0.937	0.063	0.870	0.130	0	0.871	0.129	1.000	0	0	0.920	0.080	0
WINCHUCK	1.000	0	0.956	0.044	0	0.963	0.037	0.988	0.012	0	0.803	0.197	0

Appendix Table 4. cont.

	MDH-3,4				ACO-2				IDH-3,4				PGM-1			
	100	83	75	120	100	79	66	120	100	40	120	71	80	100	85	115
NEHELEM	0.951	0.006	0.046	0	0.934	0.013	0.053	0	0.790	0.041	0.012	0.157	0	1.000	0	0
NE 9984	0.935	0	0.065	0	0.720	0.260	0	0.020	0.723	0.112	0	0.165	0	0.990	0.010	0
NE 3284	0.860	0.045	0.095	0	0.902	0.098	0	0	0.755	0.071	0	0.174	0	1.000	0	0
SALMONBERRY	0.939	0	0.061	0	0.810	0.180	0.010	0	0.670	0.154	0.037	0.138	0	1.000	0	0
WILSON	0.985	0	0.015	0	0.846	0.106	0.048	0	0.755	0.048	0	0.197	0	1.000	0	0
MIAMI	0.941	0.020	0.039	0	0.861	0.116	0.023	0	0.756	0.032	0.064	0.147	0	1.000	0	0
SAND	0.917	0.021	0.063	0	0.957	0.022	0.022	0	0.799	0.049	0.067	0.085	0	1.000	0	0
CE 4784	0.929	0.020	0.051	0	0.949	0.051	0	0	0.699	0.082	0.031	0.189	0	0.990	0.010	0
CE 3384	0.960	0.020	0.020	0	0.810	0.190	0	0	0.685	0.145	0.025	0.145	0	0.969	0.031	0
NESTUCCA	0.964	0	0.036	0	1.000	0	0	0	0.769	0.029	0.019	0.183	0	1.000	0	0
SILETZ	0.910	0.040	0.045	0.005	0.802	0.128	0.058	0.012	0.765	0.036	0.010	0.189	0	1.000	0	0
DRIFT	0.945	0.005	0.050	0	0.854	0.073	0.010	0.063	0.703	0.099	0.042	0.156	0	1.000	0	0
ALSEA	0.938	0.021	0.036	0.005	0.936	0.053	0.011	0	0.755	0.052	0.047	0.146	0	1.000	0	0
AL 4384	0.940	0.018	0.042	0	1.000	0	0	0	0.693	0.063	0	0.245	0	0.976	0.024	0
RK 4384	0.935	0.035	0.030	0	0.853	0.102	0.045	0	0.794	0.028	0.022	0.156	0	1.000	0	0
YACHATS	0.891	0.026	0.083	0	0.975	0.025	0	0	0.758	0.046	0.008	0.174	0.015	1.000	0	0
SIUSLAW	0.950	0.019	0.031	0	0.985	0.015	0	0	0.787	0.018	0.012	0.183	0	1.000	0	0
CUMMINS	0.968	0.008	0.024	0	0.909	0.055	0.036	0	0.795	0.049	0.009	0.147	0	1.000	0	0
BIG	0.885	0.039	0.077	0	0.908	0.041	0.051	0	0.790	0.080	0.005	0.125	0	1.000	0	0
RK 5584	0.803	0.059	0.138	0	0.820	0.160	0.020	0	0.714	0.107	0	0.179	0	1.000	0	0
SMITH	0.910	0.005	0.085	0	0.898	0.051	0.020	0.031	0.636	0.136	0.060	0.168	0	0.980	0.020	0
COOS	0.904	0.026	0.070	0	0.872	0.096	0.032	0	0.794	0.056	0.011	0.139	0	1.000	0	0
COQUILLE	0.898	0.035	0.067	0	0.958	0.014	0.007	0.021	0.719	0.109	0.011	0.161	0	0.979	0.021	0
BA 4484	0.832	0.020	0.148	0	0.990	0	0.010	0	0.730	0.100	0	0.170	0	1.000	0	0
FLORAS	0.933	0.050	0.017	0	0.910	0.090	0	0	0.729	0.099	0.021	0.151	0	1.000	0	0
SIXES '84	0.875	0.056	0.069	0	0.964	0.036	0	0	0.909	0.023	0.046	0.023	0	1.000	0	0
SIXES '85	0.883	0.043	0.053	0.021	0.947	0.053	0	0	0.729	0.112	0.027	0.133	0	1.000	0	0
ELK	0.880	0.063	0.031	0.026	0.929	0.071	0	0	0.848	0.031	0	0.110	0.012	1.000	0	0
SAUNDERS	0.826	0.105	0.064	0.006	0.814	0.140	0.047	0	0.778	0.051	0.023	0.148	0	0.988	0	0.012
LOBSTER	0.800	0.100	0.007	0.093	0.926	0.015	0.059	0	0.811	0.054	0	0.135	0	1.000	0	0
LAWSON	0.891	0.091	0.018	0	0.946	0.055	0	0	0.832	0.031	0.005	0.102	0.031	0.991	0.009	0
AP 6283	0.940	0.050	0.005	0.005	0.950	0.020	0	0.030	0.804	0.049	0.087	0.060	0	0.957	0.043	0
CO 5383	0.910	0.075	0.015	0	0.910	0.075	0.015	0	0.832	0.117	0.010	0.041	0	0.940	0.060	0
CO 5284	0.885	0.089	0.026	0	0.978	0.011	0	0.011	0.867	0.090	0.016	0.027	0	0.967	0.033	0
HUNTER	0.896	0.028	0.036	0.042	0.900	0	0.040	0.060	0.807	0.040	0.081	0.073	0	0.986	0	0.014
PISTOL	0.946	0.005	0.038	0.011	0.913	0.033	0.054	0	0.767	0.064	0	0.169	0	1.000	0	0
CHETCO	0.906	0.047	0.021	0.026	0.883	0.011	0.106	0	0.676	0.074	0.112	0.138	0	1.000	0	0
CH 9684	0.961	0.039	0.000	0	0.948	0.010	0.042	0	0.760	0.094	0.026	0.120	0	1.000	0	0
WINCHUCK	0.808	0.050	0.133	0.008	0.963	0.024	0.012	0	0.716	0.061	0.068	0.155	0	1.000	0	0

Appendix Table 4. cont.

	PGI-1			PGI-2		PGI-3		LDH-4	
	100	130	25	100	133	100	120	100	76
NEHELEM	1.000	0	0	1.000	0	1.000	0	0.837	0.163
NE 9984	1.000	0	0	1.000	0	1.000	0	0.880	0.120
NE 3284	1.000	0	0	1.000	0	1.000	0	0.980	0.020
SALMONBERRY	1.000	0	0	1.000	0	1.000	0	0.770	0.230
WILSON	1.000	0	0	1.000	0	1.000	0	0.800	0.190
MIAMI	1.000	0	0	1.000	0	1.000	0	0.936	0.036
SAND	0.990	0	0.010	1.000	0	1.000	0	0.873	0.128
CE 4784	1.000	0	0	1.000	0	1.000	0	0.870	0.130
CE 3384	1.000	0	0	1.000	0	1.000	0	0.870	0.130
NESTUCCA	1.000	0	0	1.000	0	1.000	0	0.919	0.089
SILETZ	1.000	0	0	0.990	0.010	1.000	0	0.920	0.080
DRIFT	1.000	0	0	1.000	0	1.000	0	0.910	0.080
ALSEA	0.958	0.042	0	1.000	0	1.000	0	0.959	0.041
AL 4384	1.000	0	0	1.000	0	1.000	0	0.880	0.120
RK 4384	1.000	0	0	1.000	0	1.000	0	0.900	0.100
YACHATS	1.000	0	0	0.947	0.053	1.000	0	0.888	0.113
SIUSLAW	0.988	0.012	0	1.000	0	1.000	0	0.988	0.012
CUMMINS	1.000	0	0	1.000	0	1.000	0	0.891	0.109
BIG	1.000	0	0	1.000	0	1.000	0	0.930	0.070
RK 55	1.000	0	0	1.000	0	1.000	0	0.918	0.082
SMITH	0.929	0.071	0	1.000	0	1.000	0	0.960	0.040
COOS	1.000	0	0	1.000	0	1.000	0	0.939	0.061
COQUILLE	1.000	0	0	1.000	0	0.999	0.001	0.875	0.125
BA 44	1.000	0	0	0.980	0.020	1.000	0	0.930	0.070
FLORAS	1.000	0	0	0.990	0.010	1.000	0	0.870	0.130
SIXES '84	1.000	0	0	1.000	0	0.950	0.050	0.875	0.125
SIXES '85	1.000	0	0	0.978	0.022	1.000	0	0.883	0.117
ELK	1.000	0	0	0.978	0.022	1.000	0	0.850	0.150
SAUNDERS	1.000	0	0	1.000	0	1.000	0	0.989	0.011
LOBSTER	1.000	0	0	0.974	0.026	1.000	0	0.855	0.145
LAWSON	1.000	0	0	1.000	0	1.000	0	0.891	0.109
AP 6283	1.000	0	0	1.000	0	1.000	0	0.910	0.090
CO 5383	1.000	0	0	0.990	0.010	1.000	0	0.920	0.080
CO 5284	1.000	0	0	1.000	0	1.000	0	0.940	0.060
HUNTER	1.000	0	0	1.000	0	1.000	0	0.944	0.056
PISTOL	1.000	0	0	0.978	0.011	1.000	0	0.859	0.141
CHETCO	1.000	0	0	0.918	0.082	1.000	0	0.850	0.150
CH 9684	1.000	0	0	0.880	0.120	1.000	0	0.910	0.090
WINCHUCK	1.000	0	0	1.000	0	0.988	0.012	0.890	0.110

Appendix Table 5. The number of resolvable electrophoretic patterns for each isozyme and population.

	Number of fish in sample	AGP-1	PGM-2	ME-3	ME-4	SOD	MDH 3-4	ACO	IDH 3-4	PGM-1	PGI-1	PGI-2	PGI-3	LDH-4
NEHELEM	50	45	49	34	48	47	41	21	38	46	46	46	46	46
NE 9984	50	49	50	49	50	38	50	50	47	50	50	50	50	50
NE 3284	50	45	50	46	47	48	41	41	46	48	50	50	50	50
SALMONBERRY	50	46	49	43	50	50	49	50	47	39	50	50	50	50
WILSON	50	40	50	50	50	47	50	48	47	50	41	41	41	50
MIAMI	57	47	48	54	57	46	52	43	39	57	56	56	43	53
SAND	51	50	50	50	50	46	48	46	41	50	49	49	49	51
CE 4784	50	50	50	49	50	50	49	49	49	50	43	43	43	50
CE 3384	50	50	50	50	49	50	50	50	50	48	50	50	50	46
NESTUCCA	28	28	28	28	28	27	28	24	26	10	27	27	27	28
SILETZ	50	46	48	38	50	49	50	43	49	50	50	50	50	50
DRIFT	50	50	50	45	50	50	50	48	48	50	50	50	50	50
ALSEA	49	49	49	46	49	48	48	47	48	49	48	48	48	49
AL 4384	50	35	50	50	50	50	50	50	48	42	50	50	50	50
RK 4384	50	50	50	50	50	50	44	44	45	50	50	50	50	50
YACHATS	40	40	40	32	42	38	39	40	33	40	38	38	38	40
SIUSLAW	42	39	48	39	42	42	40	33	41	42	41	41	41	42
CUMMINS	64	61	64	63	64	61	62	55	56	64	64	64	64	64
BIG	50	50	50	45	50	45	39	49	50	46	50	50	50	50
RK 5584	50	28	44	50	50	48	50	50	49	50	45	45	45	49
SMITH	50	45	50	47	50	49	50	49	46	50	50	42	42	50
COOS	50	50	50	44	50	50	39	47	45	50	50	50	50	49
COQUILLE	72	70	72	67	72	70	72	72	72	67	71	71	71	72
BA 4484	50	50	49	50	50	49	50	50	50	50	50	50	50	50
FLORAS	35	43	46	47	50	48	45	50	48	35	50	50	50	50
SIXES '84	20	20	20	19	20	17	18	14	11	11	20	20	20	20
SIXES '85	47	47	47	47	47	47	47	47	47	47	46	46	46	47
ELK	50	50	48	48	45	49	48	49	41	50	46	46	46	50
SAUNDERS	49	34	44	42	42	28	43	43	44	43	44	44	44	44
LOBSTER	44	43	37	37	37	38	35	34	37	31	38	38	38	38
LAWSON	55	55	55	55	55	55	55	55	49	53	50	50	50	55
AP 6283	50	48	50	47	50	48	50	50	46	47	50	50	50	50
CO 5383	50	50	49	45	50	50	50	49	49	50	50	50	50	50
CO 5284	50	43	50	49	46	46	48	45	47	46	50	50	50	50
HUNTER	36	36	36	36	36	33	36	25	31	36	36	36	36	36
PISTOL	46	34	45	45	46	46	46	46	43	45	46	46	46	46
CHETCO	50	45	50	43	50	43	48	47	47	45	49	49	49	50
CH 9684	50	40	50	35	50	50	45	43	48	50	50	50	50	50
WINCHUCK	41	34	34	41	41	40	30	41	37	30	41	41	41	41

Appendix Table 6. Average heterzygosities of sampled populations.

	Average Heterozygosity
Nehalem	0.08550
NE 9984	0.11097
NE 3284	0.08671
Salmonberry	0.12920
Miami	0.09667
Wilson	0.10705
Sand	0.08857
CE 4784	0.09425
CE 3384	0.11729
Nestucca	0.07346
Siletz	0.11745
Drift	0.10691
Alsea	0.09278
AL 4384	0.07635
RK 4384	0.11193
Yachats	0.08422
Siuslaw	0.07994
Cummins	0.08434
Big	0.08000
RK 5584	0.11193
Smith	0.10317
Coos	0.09557
Coquille	0.09324
BA 4484	0.10351
Floras	0.09182
Sixes '85	0.09507
Sixes '84	0.07368
Elk	0.11322
AP 6283	0.07381
Saunders	0.10658
Lawson	0.08287
CO 5284	0.06482
CO 5383	0.09969
Lobster	0.09199
Hunter	0.09971
Pistol	0.09177
CH 9684	0.09789
Chetco	0.10874
Winchuck	0.09390