

PHENOTYPIC DIFFERENCES AMONG STOCKS OF HATCHERY AND WILD COHO SALMON, *ONCORHYNCHUS KISUTCH*, IN OREGON, WASHINGTON, AND CALIFORNIA¹

R. C. HJORT AND C. B. SCHRECK²

ABSTRACT

Similarities in phenotypic characters (isozyme gene frequencies, life history, and morphology) among 35 stocks of coho salmon, *Oncorhynchus kisutch*, from Oregon, Washington, and California were compared by using agglomerative and divisive cluster analyses. Coho salmon stocks from similar environments were phenotypically similar. Five groups of stocks were identified by the agglomerative cluster analysis: 1) wild stocks from the northern Oregon coast, 2) wild stocks from the southern Oregon coast, 3) stocks from hatcheries that used wild coho salmon for an egg and sperm source, 4) stocks from large stream systems, and 5) hatchery stocks from the northern Oregon coast. Three trends were indicated by the clustering patterns: 1) stocks that were geographically close tended to be phenotypically similar, 2) stocks from large stream systems were more similar to each other than to stocks from smaller stream systems, independent of geographic proximity, and 3) hatchery stocks were more similar to each other than to wild stocks, and wild stocks were more similar to each other than to hatchery stocks. These trends may be useful to fishery managers for selecting donor stocks from hatcheries for transplanting to stream systems or transferring to other hatcheries. Individual phenotypic characters were correlated with characters of the stream systems. Results of two agglomerative cluster analyses, one of certain characters of the stocks and one of certain characters of the stream systems, demonstrated a lack of correspondence between stream types and stock phenotypes.

Genetic diversity among stocks of anadromous salmonids (Simon and Larkin 1970) is a biological characteristic that is more frequently discussed than used in fishery management. The tendency to return to native streams reduces gene flow among salmon populations and enables the individual stocks to adapt to the native stream systems. The mixing of stocks highly adapted to their native stream systems with other stocks, or transplanting them to other stream systems, may reduce the rate of return or survival rate of the donor stock (Ritter 1975³; Bams 1976). If the survival rate of a salmon stock is related to its degree of adaptation to its stream system, fishery managers may be able to increase survival of hatchery fish by planting them in recipient streams having native stocks geneti-

cally similar to the planted fish. Higher survival should be especially important during the first several generations, while the transplanted stock is adapting to the recipient environment. An additional advantage of using genetically similar stocks might be a reduction in the introgression of divergent hatchery genotypes into wild stocks (Reisenbichler and McIntyre 1977).

Genetic descriptions of salmon stocks could benefit salmon management by assisting fishery managers in selecting hatchery stocks and in protecting wild stocks. Obviously, determination of genetic similarity among stocks is not now possible for the entire genome; however, similarity can be estimated by comparing genetically related characters. Two biochemical characters that vary among stocks of coho salmon, *Oncorhynchus kisutch*, are transferrin (Utter et al. 1970) and phosphoglucose isomerase (PGI) (May 1975), the electrophoretic expressions both of which were established by breeding studies to be genetically determined. Life history and morphological characters also vary among salmonid stocks. Time of spawning (Roley 1973) and frequency of occurrence of jacks in the population (Feldmann 1974) both have a genetic basis in

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²Oregon Cooperative Fishery Research Unit, Oregon State University, Corvallis, OR 97331. Cooperators are Oregon State University, Oregon Department of Fish and Wildlife, and U.S. Fish and Wildlife Service.

³Ritter, J. A. 1975. Lower ocean survival ratio for hatchery reared Atlantic salmon (*Salmo salar*) stocks released in rivers other than their native streams. Int. Counc. Explor. Sea, Anadromous and Catadromous Fish Comm., C. M. 1975/M 26, 10 p.

coho salmon but probably have an environmental component as well. A genetic basis, as shown in rainbow trout, *Salmo gairdneri*, has also been established for numbers of vertebrae (Winter et al. 1980a), scales in the lateral series (Winter et al. 1980a), scale rows (Neave 1944), gill rakers (Smith 1969), branchiostegals (MacGregor and MacCrimmon 1977), and anal fin rays (MacGregor and MacCrimmon 1977). Ricker (1970) hypothesized that the meristic characters of salmonids probably have both genetic and environmental components. The difficulty of determining the importance of these phenotypic characters to the fitness of the stock does not preclude the possibility that they could, through selection or pleiotrophic effects, have a bearing on fitness as suggested by Barlow (1961).

The objective of this study was to characterize stocks of coho salmon by using enzyme gene frequencies, life history characters, and morphological characters. Secondly, we hoped this information would help provide a basis for selecting donor stocks in Oregon hatchery programs. The stocks were selected so that comparisons could be made among geographical areas and stream types and between hatchery and wild stocks. We calculated a measure of a phenotypic similarity and used cluster analysis to display the relationships among stocks. Because cluster analyses are arbitrary (Blackith and Reymont 1971), we used two clustering strategies. Factors affecting genetic similarity were hypothesized by determining environmental characteristics common to the similar stocks.

Although our analysis is primarily systematic, we correlated the phenotypic characters with variables characteristic of the stream systems. Although correlations do not prove a functional significance, they are included here because inferences and hypotheses can be developed from the correlations for future studies.

METHODS

Sampling

We evaluated 10 characters for 15 hatchery stocks (based on samples of 75-100 juvenile coho salmon of the 1976 brood from 14 hatcheries in Washington, Oregon, and California and 9 hatcheries from Oregon for the 1977 brood year) and 12 wild stocks (based on samples of 30-100 juvenile coho salmon of the 1976 and 1977 broods, collected by electrofishing from 12 Oregon

stream systems). (See Figure 1 for locations of hatcheries and stream systems.) Because some of the hatcheries have used nonnative egg sources, and stream systems have been stocked with juvenile and adult coho salmon, few pure native stocks remain. We did not use hatchery stocks or

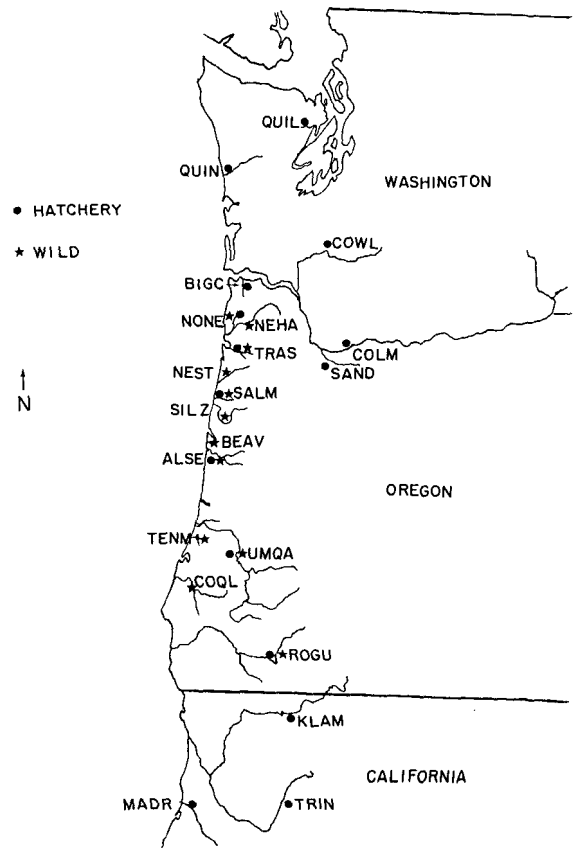


FIGURE 1.—Map indicating sample site locations of wild and hatchery coho salmon stocks. Location codes are as follows with the hatcheries in parentheses: ALSE, Alsea River (Fall Creek Hatchery); BEAV, Beaver Creek; BIGC, Big Creek (Big Creek Hatchery); COLM, Columbia River (Cascade Hatchery in 1976 and Bonneville Hatchery in 1977); COQL, Coquille River; COWL, Cowlitz River (hatchery stock reared at Cascade Hatchery in 1976 and Big Creek Hatchery in 1977); KLAM, Klamath River (Irongate Hatchery); MADR, Mad River (Mad River Hatchery); NEHA, Nehalem River; NEST, Nestucca River; NONE, North Nehalem River (North Nehalem River Hatchery); QUIN, Quilcene River (Quilcene River Hatchery); QUIN, Quinalt River Hatchery); ROGU, Rogue River (Cole Rivers Hatchery); SALM, Salmon River Hatchery); SAND, Sandy River (Sandy River Hatchery); SILZ, Siletz River; TENM, Tenmile Lakes; TRAS, Trask River (Trask River Hatchery); TRIN, Trinity River (Trinity River Hatchery); UMPQ, Umpqua River (hatchery stock collected from Smith River and reared at Cole Rivers Hatchery).

fish from tributaries of streams that had received a large supplement of a nonnative hatchery stock in the previous 6 yr. This was to ensure that characterization of the genotype would reflect environmental considerations rather than introgression of foreign stocks.

Morphological Characters

For each sample, 15 carcasses were frozen for later counts. Scales in the lateral series were counted in the second row above the lateral line, starting with the anteriormost scale and terminating at the hypural plate. Scales above the lateral line were counted from the anterior insertion of the dorsal fin to the lateral line. Anal ray counts did not include the short rudimentary anterior rays, and branched rays were counted as one. The total number of gill rakers on the first gill arch was recorded. Alizarin red was used to highlight rudimentary gill rakers. The total number of branchiostegal rays from both sides was counted. Vertebral counts, made on X-ray plates, included the last three upturned centra. Accuracy of morphological counts was checked by recounting two fish from each sample. If errors were found, additional fish from that sample were recounted to correct for any error.

Electrophoresis

Blood and white muscle samples were collected from the fish that were not used for morphological counts. The caudal peduncle was severed and the blood collected in heparinized microhematocrit tubes that were then centrifuged and stored at -10°C . White muscle samples (1 cm^3) were removed from the anterior dorsal portion of the frozen carcasses, homogenized with 2 or 3 drops of water, and then centrifuged to clear the supernatant. Only the blood serum and supernatant were used for electrophoresis.

The methodology for electrophoresis of transferrin and phosphoglucose isomerase followed the basic principles of May (1975) with some modifications by Solazzi.⁴ The gel and electrode buffers were described by Ridgway et al. (1970). Four genotypes of transferrin (AA, AC, CC, and BC) in the serum samples were interpreted ac-

ording to Utter et al. (1970). Transferrin was recorded as the frequency of the "A" allele, since the "B" allele was relatively rare. The variant allele for the second locus of phosphoglucose isomerase, first observed in white muscle tissue by May (1975), was recorded as the frequency of this variant allele.

Life History

The life history characters we used were time of peak spawning and proportion of females in the adult population. We estimated the peak spawning times on the basis of interviews with district fishery biologists and hatchery managers. Whenever possible, we verified the estimates with spawning ground survey records and hatchery records. We stratified the peak spawning times into five segments of 2 wk each.

The proportions of adult females (3 yr olds) were estimated from hatchery records and spawning ground surveys. This character is an indirect measure of the proportion of jacks (males that mature at 2 yr of age) in the population. Populations with high proportions of jacks in a given year should have relatively higher proportions of females returning the next year. A direct measure of the proportion of jacks cannot be used because body size differences between jacks and 3-yr-old adults affect the catch in gill net fisheries, retention in hatchery holding ponds, recovery of carcasses on spawning ground surveys, and catch rate in sport fisheries.

Environmental Data

Stream characteristics include distance upstream to spawning grounds, basin area, area and length of the estuary on the stream system, latitude, gradient, spring runoff, the presence or absence of the myxosporidan parasite, *Ceratomyxa shasta*, and the presence or absence of the following nine species of fish: carp, *Cyprinus carpio*; Oregon chub, *Hybopsis cramerii*; northern squawfish, *Ptycholcheilus oregonensis*; speckled dace, *Rhinichthys osculus*; reddsider shiner, *Richardsonius balteatus*; largescale sucker, *Catostomus macrocheilus*; brown bullhead, *Ictalurus nebulosus*; largemouth bass, *Micropterus salmoides*; and striped bass, *Morone saxatilis*. To separate the populations that have short and potentially long swimming distances to the spawning grounds, we measured spawning distances from the mouth of the stream sys-

⁴Solazzi, M. F. 1977. Methods manual for the electrophoretic analysis of steelhead trout (*Salmo gairdneri*). Oreg. Dep. Fish Wildl., Res. Sect., Inf. Rep. Ser. Fish. 77-7, 35 p.

tem to the upper limit of coho salmon spawning, as estimated from Anadromous Fish Distribution Maps⁵ and interviews with district fishery biologists. Inasmuch as, intuitively, latitude should be correlated with the temperature and flow regimes of the stream systems, we determined the latitude at the mouth of each stream system. Gradients were calculated from tide-water to the upper limit of coho spawning as a basis for estimating the difficulty of the spawning migration. Because estuary size and length is an estimate of exposure to vibriosis (Harrel et al. 1976) and potential richness of feeding grounds (Myers 1979), we measured the estuary lengths, stream elevations, and distances on United States Geographical Survey Quadrangle Maps. Inasmuch as high flows could have an effect on both the early life history and the smolting processes of juvenile coho salmon, we determined the presence of a spring runoff from snowmelt by interviewing district biologists. We obtained information on the distributions of other fish species in Oregon stream systems from C. E. Bond,⁶ and on the distribution of *Ceratomyxa shasta* from J. E. Sanders.⁷

We obtained temperature data from hatchery records to help interpret the morphological data for the hatchery stocks. The average temperature for the first month of incubation was used, because previous studies have indicated that this time is a period during ontogeny when morphological features may be most sensitive to the effects of temperature (Tåning 1952).

Statistics

We calculated averages for the morphological characters, enzyme gene frequencies, and the proportion of females for each stock, and used multivariate analysis of variance and Rao's (1970) test for additional information to determine whether morphological characters differed significantly among stocks. In Rao's test, the statistical significance of each morphological character is determined, given that the other morphological characters are already in the model. Because environmental data on spawn-

ing distance, estuary length, estuary size, basin area, and gradient were skewed, we transformed them to natural logarithms to stabilize the variance and improve normality. We standardized the stock characters ($\bar{z} = 0$, $S^2 = 1$) for the cluster analyses, using the standard normal standardization. This standardization expresses the stock character as standard deviations from the character means, thus giving equal weight to each character.

We calculated correlation coefficients (Snedecor and Cochran 1967) between the stock characters and the environmental data for all stocks, and between the morphological characters and temperature data for hatchery stocks only. The levels of significance for the correlation coefficients were also calculated as described by Snedecor and Cochran (1967).

We used two cluster analysis programs to display similarities among stocks. One, a nonhierarchical divisive cluster analysis, minimized the total sum of squares between observations and the cluster means (McIntire 1973). In the other, a hierarchical agglomerative cluster analysis, Euclidean distance was used as the dissimilarity measure, and the clustering strategy was group average (see Sneath and Sokal [1973] or Clifford and Stephenson [1975] for terminology). Standardized data were used in both programs.

We used canonical variate analysis to investigate the relation among the clusters from the agglomerative cluster analysis (Clifford and Stephenson 1975). Canonical variate analysis produces canonical variables that project groups of multivariate data onto axes separating the groups as much as possible. We plotted the canonical variables against each other in two-dimensional space to determine the relationships among clusters and the discreteness of the clusters.

RESULTS AND DISCUSSION

Morphological Characters

Significant differences ($\alpha = 0.01$) for each morphological character (Tables 1-3) as indicated by multivariate analysis of variance and Rao's test of additional information existed among the 35 samples which consisted of wild and hatchery stocks from two brood years. When morphological characters for each stock between brood years were compared for each of the hatcheries that were sampled in both years of the study

⁵Anadromous Fish Distribution Maps. Oregon State Water Resources Board, Salem, Oreg.

⁶Carl E. Bond, Professor of Fisheries, Oregon State University, Corvallis, OR 97331, pers. commun. April 1979.

⁷James E. Sanders, Assistant Fish Pathologist, Oregon Dep. Fish Wildl., Corvallis, OR 97331, pers. commun. February 1979.

TABLE 1.—Means, standard errors (in parentheses), and ranges for the morphological characters of the 1976 brood year hatchery samples of juvenile coho salmon and the hatchery water incubation temperatures for the first month of incubation. Sample sizes were 15. The data are listed in north to south order of the sampling locations.

Stock and (in parentheses) incubation water tempera- tures (°C)	Scales in lateral series	Scales above lateral line	Anal rays	Gill rakers	Branchi- ostegals	Vertebrae
Washington:						
Quilcene River	126.93	28.13	14.07	22.33	27.87	64.40
Hatchery (7.3)	(.97)	(.38)	(.15)	(.19)	(.26)	(.13)
	116-132	25-30	13-15	21-23	26-30	64-65
Quinalt River	132.67	29.93	13.53	22.53	26.67	65.50
Hatchery (7.3)	(.48)	(.33)	(.16)	(.24)	(.21)	(.13)
	130-136	28-32	13-15	21-24	25-28	65-66
Oregon:						
Cascade Hatchery (6.9)	133.07	28.20	14.00	22.20	27.27	66.80
(Columbia River)	(.56)	(.40)	(.20)	(.35)	(.37)	(.22)
	128-135	26-32	12-15	20-25	25-29	66-68
Big Creek Hatchery (6.4)	132.67	28.80	14.31	22.87	26.07	65.80
(Columbia River)	(.57)	(.28)	(.13)	(.17)	(.30)	(.15)
	128-136	28-31	13-15	22-24	24-28	65-67
Cowlitz Hatchery stock,	133.60	27.87	13.80	22.20	28.13	64.47
Cascade Hatchery (6.9)	(.63)	(.24)	(.14)	(.26)	(.24)	(.22)
	131-137	26-29	13-15	21-24	27-30	65-68
Sandy River Hatchery (7.0)	133.13	28.27	14.33	22.07	28.20	66.07
(Columbia River)	(.72)	(.42)	(.13)	(.34)	(.26)	(.21)
	128-137	24-30	14-15	20-25	26-30	65-67
North Nehalem	131.93	28.33	14.00	22.67	26.73	65.80
River Hatchery (7.8)	(.64)	(.30)	(.14)	(.27)	(.32)	(.17)
	128-138	26-36	13-15	21-24	24-28	65-67
Trask River Hatchery (9.8)	132.13	28.80	13.93	22.13	26.40	66.07
	(.48)	(.47)	(.12)	(.31)	(.32)	(.18)
	128-135	26-32	13-15	20-24	24-29	65-67
Salmon River Hatchery (6.2)	129.40	27.00	13.60	22.13	25.40	64.93
	(.54)	(.59)	(.19)	(.24)	(.24)	(.30)
	125-132	23-33	13-15	21-24	24-27	62-66
Fall Creek Hatchery (5.7)	132.00	28.67	14.00	23.20	27.13	65.80
(Alsea River)	(.50)	(.29)	(.17)	(.20)	(.34)	(.17)
	129-135	27-31	13-15	22-25	25-29	65-67
Umpqua Hatchery stock	131.20	26.00	13.47	22.13	25.13	65.33
(Smith River), Cole	(.51)	(.34)	(.19)	(.22)	(.24)	(.23)
Rivers Hatchery (3.5)	127-134	24-28	13-15	21-23	24-26	64-67
California:						
Irongate Hatchery (5.3)	132.73	29.07	13.80	22.33	27.00	66.07
(Klamath River)	(.78)	(.18)	(.14)	(.25)	(.28)	(.30)
	129-138	28-30	13-15	21-24	25-28	64-68
Trinity River Hatchery (7.3)	130.87	28.27	13.60	22.00	26.00	66.00
(Klamath River)	(.75)	(.64)	(.13)	(.31)	(.59)	(.14)
	126-137	24-33	13-14	19-23	20-28	65-67
Mad River Hatchery (8.5)	129.20	25.27	13.40	20.93	23.47	65.60
	(.88)	(.37)	(.19)	(.33)	(.51)	(.31)
	121-134	22-27	12-15	19-23	20-27	63-68

(Table 4), the agreement between brood years was not particularly high, especially for scale rows and branchiostegal ray counts.

Although meristic counts and water temperatures during the incubation period of the eggs are usually correlated (Barlow 1961), we found that lateral series scale counts provided the only meristic character significantly ($\alpha = 0.05$) correlated with the temperature of the hatchery water during incubation. Under the extant environmental conditions, incubation temperatures may have little effect in determining the morphological characters of our stocks.

Among all possible statistically significant

correlations between morphological characters and the stream characteristics in Table 5, only vertebral number and estuary length, and vertebral number and spawning distance, had correlation coefficients $>r = 0.50$ (Table 6). All other correlations each accounted for $<25\%$ of the variation observed. Possibly we overlooked some important environmental gradients, or possibly the selective forces occur during periodic environmental extremes or pulses that were not accounted for in our environmental data. Each of the counts significantly correlated with at least two of the characters of the stream systems, suggesting that, if these characters are the

TABLE 2.—Means, standard errors (in parentheses), and ranges for morphological characters of the 1977 brood year hatchery samples of juvenile coho salmon and the hatchery water incubation temperatures for the first month of incubation. Sample sizes were 15. The data are listed in north to south order of the sampling location.

Stock and (in parentheses) incubation water tempera- tures (°C)	Scales in lateral series	Scales above lateral line	Anal rays	Gill rakers	Branchi- ostegals	Vertebrae
Bonneville Hatchery (5.4) (Columbia River)	133.33 (.61) 129-138	26.73 (.27) 25-29	13.93 (.12) 13-15	22.53 (.29) 21-25	27.00 (.32) 25-29	65.80 (.15) 65-67
Big Creek Hatchery (7.2)	133.60 (.46) 130-136	27.20 (.33) 26-30	13.53 (.13) 13-14	23.13 (.22) 22-25	25.60 (.24) 23-27	66.07 (.21) 65-67
Cowlitz Hatchery stock (7.2) (Big Creek Hatchery)	132.20 (.40) 129-135	26.60 (.41) 25-30	13.60 (.13) 13-14	21.80 (.22) 20-23	26.00 (.34) 24-28	65.67 (.16) 65-67
North Nehalem Hatchery (7.7)	130.93 (.42) 128-134	27.73 (.25) 26-29	13.73 (.15) 13-15	23.07 (.27) 21-24	26.13 (.29) 24-28	65.27 (.18) 64-66
Trask River Hatchery (9.9)	130.33 (.42) 128-133	25.53 (.32) 23-27	13.67 (.13) 13-14	22.73 (.23) 21-24	25.60 (.32) 24-28	65.40 (.24) 63-66
Salmon River Hatchery (7.8)	130.53 (.59) 127-135	26.80 (.28) 25-29	13.67 (.16) 13-14	22.40 (.16) 22-24	26.27 (.25) 25-29	65.53 (.19) 64-66
Fall Creek Hatchery (7.4) (Alsea River)	131.53 (.68) 127-136	26.20 (.33) 24-28	13.80 (.17) 13-15	22.53 (.27) 21-24	26.07 (.23) 25-28	66.13 (.19) 65-67
Umpqua Hatchery stock (8.6) (Smith River)	129.07 (.37) 126-131	26.40 (.32) 24-29	13.40 (.13) 13-14	21.47 (.17) 21-23	25.87 (.24) 24-28	65.40 (.13) 65-66
Cole Rivers Hatchery	126-131	24-29	13-14	21-23	24-28	65-66
Cole Rivers Hatchery (8.6) (Rogue River)	130.33 (.66) 125-134	26.20 (.33) 24-28	13.80 (.17) 13-15	22.20 (.30) 20-24	26.20 (.24) 25-28	65.20 (.26) 64-67

result of selection, several interacting selective forces were involved.

Life History Characters

Earlier peak spawning times (Table 7) were strongly associated with the northern stream systems and with stream systems having large estuaries (Table 6). However, the correlation of peak spawning time with size of estuary may be biased by the large number of samples from Columbia River hatcheries: spawning times of stocks from the Columbia River are earlier than those of coastal stocks, and the Columbia River has a large estuary. Selection for earlier spawning times through hatchery practices may be the cause for the differences in spawning times between hatchery and wild stocks in the North Nehalem, Trask, and Alsea Rivers. Selection for earlier spawning times has been observed in a steelhead trout hatchery program (Millenbach 1973). At hatcheries using wild stocks as sources for eggs and sperm, peak spawning times were similar to those of naturally spawning fish in the respective stream system.

The proportion of females (Table 7) appeared to be higher in the southern stream sys-

tems, suggesting that jacks were more common there. The effective sex ratio, including jacks, at the time of spawning should be close to 1:1 (Fisher 1930). If only 3-yr-old males and females are counted, the proportion of females should be >0.50 , the margin above 0.50 depending on how many jacks returned in the previous year. However, the proportion of males was higher than that of females in stocks from the Quilcene, Quinault, Sandy, North Nehalem, Nehalem, Trask, Salmon, Alsea, Umpqua, and Rogue Rivers. Nikolskii (1969) reviewed several possible causes for sex ratios departing from 1:1; however, the reason for the high proportion of males in these stocks is not known.

Isozyme Gene Frequencies

Transferrin gene frequencies (Figs. 2, 3), correlated significantly with six of the stream characters (Table 6). The best model from stepwise multiple regression explained only 68% of the variation in gene frequencies. Analysis of the relationships of the "A" allele frequencies with basin area (Fig. 4) and latitude (Fig. 5) explained the variation more simply than did the stepwise regression model. These correlations showed

TABLE 3.—Means, standard errors (in parentheses), and ranges of morphological characters for 1977 brood year samples of wild juvenile coho salmon. Sample size was 12 for all stream systems except Tenmile Lakes and Coquille River (15 each). The data are listed in north to south order of the sampling locations.

Stream system	Scales in lateral series	Scale rows above lateral core	Anal fin rays	Gill rakers	Branchiostegals	Vertebrae
North Nehalem River	132.25 (.88)	27.75 (.33)	13.58 (.15)	23.25 (.37)	26.75 (.25)	65.50 (.26)
	126-137	26-30	13-14	22-25	26-28	63-66
Nehalem River	132.50 (.77)	26.67 (.35)	13.75 (.13)	23.00 (.25)	27.33 (.22)	65.75 (.25)
	127-136	25-29	13-14	22-24	26-28	64-67
Trask River	131.17 (.47)	26.50 (.31)	14.00 (.12)	22.92 (.31)	26.58 (.26)	65.83 (.11)
	128-133	24-28	13-15	21-24	25-28	65-66
Nestucca River	132.17 (.68)	26.83 (.40)	14.00 (.12)	22.92 (.34)	27.25 (.28)	65.58 (.19)
	128-136	25-29	13-15	21-25	26-29	65-67
Salmon River	131.83 (.61)	26.92 (.31)	13.67 (.14)	23.08 (.29)	26.67 (.19)	65.00 (.17)
	128-135	24-28	13-14	22-25	26-28	64-66
Siletz River	130.33 (.61)	27.08 (.29)	13.58 (.15)	23.00 (.21)	27.50 (.23)	65.25 (.28)
	128-135	26-29	13-14	22-24	26-29	63-67
Beaver Creek	132.27 (.49)	27.33 (.38)	13.27 (.20)	23.27 (.36)	27.18 (.30)	65.33 (.14)
	130-135	25-29	12-14	21-25	26-29	65-66
Alsea River	131.25 (.37)	27.17 (.30)	13.67 (.19)	23.17 (.34)	26.83 (.30)	65.25 (.18)
	129-134	26-29	12-14	21-25	26-28	64-66
Umpqua River	131.75 (.70)	26.83 (.40)	13.25 (.13)	22.92 (.19)	27.00 (.28)	65.83 (.27)
	128-136	25-30	13-14	22-24	26-29	65-68
Tenmile Lakes	131.73 (.58)	26.20 (.28)	13.47 (.13)	22.53 (.19)	26.60 (.31)	65.73 (.25)
	128-136	25-29	13-14	21-24	25-28	64-67
Coquille River	131.67 (.43)	26.27 (.43)	13.27 (.18)	22.40 (.19)	26.47 (.27)	65.93 (.21)
	129-134	24-30	13-14	21-24	24-28	65-67
Rogue River	132.75 (.59)	26.58 (.26)	14.00 (.17)	22.50 (.31)	26.92 (.40)	65.42 (.15)
	131-137	25-28	13-15	21-25	24-29	65-66

TABLE 4.—Hatchery stocks of coho salmon in which differences in morphological characters occurred between the 1976 and 1977 brood years as determined by a two-sample test.

Hatchery	Lateral series scales	Scales above lateral line	Anal rays	Gill rakers	Branchiostegal rays	Vertebrae
Cascade-Bonneville	
Cowlitz stock	
Big Creek				
Trask River
Salmon River					.	
Alsea River		..			.	
Umpqua River	

* $P < 0.05$; ** $P < 0.01$.

that the stocks from large stream systems and the southernmost stream systems had high frequencies of the "A" allele, whereas the frequencies in the smaller stream systems and northern stream systems were highly variable. Combining these two relationships helps explain the pattern of transferrin gene frequencies. Fre-

quencies of the "A" allele were high in stocks from large stream systems regardless of latitude, and in southern stocks regardless of stream size. Stocks from smaller stream systems on the northern Oregon coast and in Washington had higher frequencies of the "C" allele.

The factors affecting the patterns of transferrin gene frequencies in coho salmon stocks are not known. However, Utter et al. (1980) suggested that the frequencies may be influenced by bacteriostatic properties associated with the different transferrin alleles. Genotypes of transferrin had differential mortality when exposed to bacterial kidney disease in studies by Suzumoto et al. (1977) and Winter et al. (1980b), and to vibriosis, cold-water disease, and furunculosis in a study by Pratschner (1978). Transferrin genotype was also related both to differences in juvenile growth rates and to propensity to return as jacks (McIntyre and Johnson 1977).

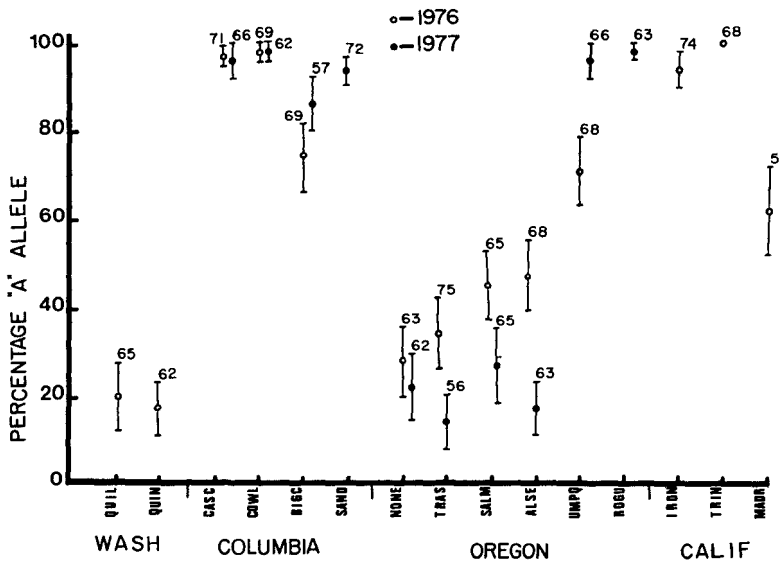


FIGURE 2.—Transferrin gene frequencies of hatchery coho salmon. Samples are arranged from north to south. Vertical lines represent 95% confidence intervals; numbers above the line show sample sizes. Location codes are as in Figure 1.

TABLE 5.—Environmental data for the stream systems sampled in this study.

Stream system	Spawning distance (km)	Latitude	Estuary area (ha)	Estuary length (km)	Gradient (m/km)	Runoff in spring	Basin area (km ²)
Washington							
Quilcene River	13	47.75	¹ 512	3.2	19.2	yes	² 179
Quinault River	92	47.33	¹ 64	3.2	2.8	yes	² 1,123
Oregon							
Columbia River							
Cascade-							
Bonneville Hatcheries	235	46.25	¹ 37,513	236.5	0	yes	³ 51,769
Cowlitz Hatchery stock	193	46.25	¹ 37,513	109.4	0.8	yes	⁶ 6,418
Big Creek Hatchery	60	46.25	¹ 37,513	43.4	14.2	no	² 88
Sandy River Hatchery	270	46.25	¹ 37,513	194.7	7.1	yes	² 1,299
North Nehalem River	45	46.25	⁴ 1,128	11.3	8.6	no	¹ 233
Nehalem River	195	45.68	⁴ 1,128	24.1	2.4	no	² 2,192
Trask River	72	45.52	³ 480	20.9	9.5	no	⁵ 455
Nestucca River	76	45.16	⁴ 400	12.9	7.7	no	² 657
Salmon River	29	45.05	⁴ 82	6.4	13.0	no	⁶ 194
Siletz River	122	44.93	⁴ 475	37.0	3.4	no	² 797
Beaver Creek	21	44.52	¹ 3	3.2	4.3	no	¹ 31
Alsea River	93	44.43	⁴ 858	19.3	3.2	no	⁶ 1,227
Umpqua River	372	43.68	² 2,285	45.0	1.9	yes	⁶ 11,801
Smith River ⁷	122	43.68	² 2,285	24.1	2.5	no	² 898
Tenmile Lakes	24	43.57	¹ 1	1.6	3.2	no	² 54
Coquille River	138	43.11	⁴ 308	66.0	3.4	no	⁶ 2,738
Rogue River	249	42.44	⁴ 251	6.4	1.9	yes	⁶ 13,199
California							
Klamath River	293	41.58	¹ 200	3.2	2.2	yes	⁶ 31,314
Trinity River	235	41.58	¹ 200	3.2	2.4	yes	⁷ 7,383
Mad River	72	40.95	¹ 200	6.4	6.5	no	⁶ 1,255

¹ Provided by district biologists.

² Pacific Northwest River Basins Commission. 1966, 1967, 1968, 1969, 1972. River Mile Indices. Hydrol. Hydraul. Comm.

³ Personal estimate of area utilized by coho in the Columbia drainage.

⁴ Gaumer, T., D. Demory, and L. Osis. 1973. Estuary resources use study. Fish Comm. Oregon, Div. Manage. Res.

⁵ Water Resources Board of Oregon. 1969. Oregon long range requirements for water. Salem, Oregon, 397 p.

⁶ Wisley and Ham Incorp. 1974. Estuarine resources of the Oregon coast. A natural resource inventory report to the Oregon Coastal Conservation and Development Commission, Portland, Oregon, 233 p.

⁷ Source of Umpqua Hatchery stock.

⁸ United States Geological Survey. 1977. Water resources data for California water year 1977. Water Data Rep. CA 77-2.

Therefore, diseases, life history characteristics, and other factors may play a role in maintaining the patterns of transferrin gene frequencies.

Transferrin gene frequencies were in good

agreement between the two year classes of Oregon coast wild stocks, despite the small size of some of the samples (Fig. 3). The heterogeneity between year classes was greater for the Oregon

FIGURE 3.—Transferrin gene frequencies of wild coho salmon stocks for 1976 and 1977 brood years. Stocks are arranged from north to south. Bars represent 95% confidence intervals and the sample sizes are above the bars. Location codes are as in Figure 1.

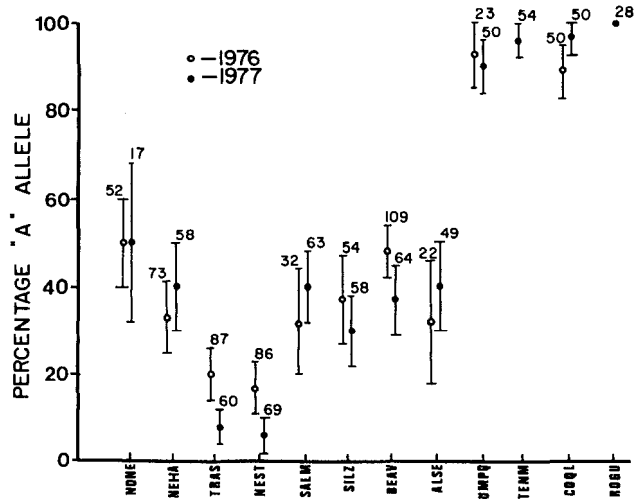


TABLE 6.—Statistically significant correlation coefficients between the characteristics of the coho salmon stocks and the environmental characteristics of their respective stream systems. $r = 0.28$ at $\alpha = 0.05$ and 0.37 at $\alpha = 0.01$.

Characteristics		
Stock	Environmental	Correlation
Scales in lateral series	Spawning distance	0.418
	Estuary size	0.341
	Estuary length	0.430
	Gradient	-0.368
Scale rows	Latitude	0.360
	Spring runoff	0.315
Anal rays	Estuary size	0.414
	Latitude	0.382
Gill rakers	Latitude	0.346
	Basin area	-0.353
Branchiostegals	Spring runoff	-0.319
	Latitude	0.431
	Spring runoff	0.381
Vertebrae	Estuary size	0.350
	Basin area	0.445
	Gradient	-0.432
	Spawning distance	0.549
Proportion of females	Estuary length	0.533
	Latitude	-0.426
	Estuary size	-0.613
Time of peak spawning	Spring runoff	-0.345
	Estuary length	-0.391
	Latitude	-0.702
Phosphoglucose isomerase	Spring runoff	-0.410
	Estuary length	0.326
Transferrin	Latitude	-0.381
	Spawning distance	0.590
	Basin area	0.588
	Spring runoff	0.528
	Gradient	-0.596

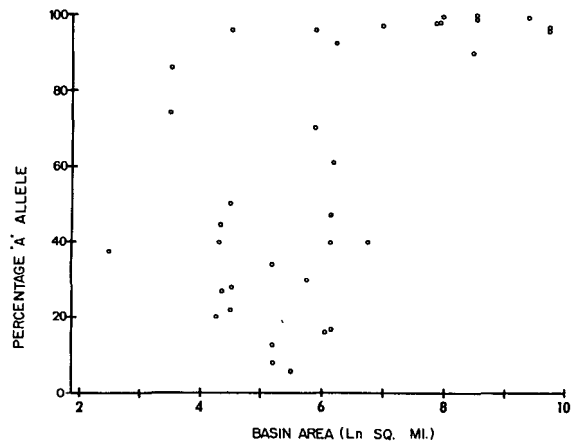


FIGURE 4.—Transferrin gene frequencies for wild and hatchery coho salmon stocks arranged by basin area, in square miles.

fish in hatcheries, then the transferrin gene frequency of a given year class could be altered without affecting the other two year classes.

The phosphoglucose isomerase variant (Table 7) was present only in samples from Oregon stocks—particularly those from the northern Oregon coast. May (1975) reported this variant in Washington stocks.

Similarity of Stocks

The groups of stocks of coho salmon found to be most similar by the agglomerative cluster analysis (Fig. 6) were composed of northern

coast hatchery stocks (Fig. 2). The gene frequencies of hatchery stocks may have been altered by earlier importing of stocks with different gene frequencies, or by disease epizootics. If fish with certain transferrin genotypes have different resistances to diseases, and if epizootics are more severe because of the higher densities of

TABLE 7.—Proportion of females, time of peak spawning, and gene frequency, 95% confidence interval (CI), and sample size of phosphoglucose isomerase variant of wild and hatchery stocks of coho salmon. Years of data used to estimate proportion of females are in parentheses. The data are listed in north to south order of the sampling locations.

Stream system	Proportion of females ¹	Years	Time of peak spawning ¹	Proportion of females	Years	Time of peak spawning ¹	1977			1976			1977		
							Frequency	95% CI	Sample size	Frequency	95% CI	Sample size	Frequency	95% CI	Sample size
Washington:															
Quilcene Hatchery				0.41	1972-78	Oct. 15-30				0	—	36			
Quinalt Hatchery				0.37	1973-75	Oct. 15-30				0	—	40			
Oregon:															
Columbia River															
Cascade-Bonneville Hatchery				0.51	1970, 72-76	Nov. 1 -15				0	—	40	0	—	60
Cowlitz Hatchery stock				0.50	(²)	Nov. 1 -15				0	—	40	0	—	60
Big Creek Hatchery				0.55	1970-76	Nov. 1 -15				0	—	40	0	—	40
Sandy River Hatchery				0.45	1970-76	Nov. 1 -15				0	—	40			
North Nehalem River	0.43	(³)	Dec. 1 -15	0.43	1970-76	Nov. 1 -15	0.05	0.08	19	0.05	0.04	44	0.08	0.04	60
Nehalem River	0.43	1949-69	Dec. 1 -15				0.11	0.06	64						
Trask River	0.33	1949-69	Dec. 1 -15	0.43	1970-76	Nov. 1 -15	0.06	0.04	62	0.08	0.06	40	0.20	0.08	60
Nestucca River	0.56	1949-69	Dec. 1 -15				0.03	0.04	59						
Salmon River	0.46	1975-77	Dec. 1 -15	0.46	1975-77	Dec. 1 -15	0.01	0.02	64	0	—	40	0	—	60
Siletz River	0.54	1949-69	Dec. 1 -15												
Beaver Creek	0.58	1949-69	Dec. 15-31				0	—	32						
Alsea River	0.53	1949-69	Dec. 1 -15	0.42	1970-76	Nov. 16-30	0.01	0.02	49	0.05	0.04	40	0.15	0.06	60
Umpqua River	0.63	1949-69	Dec. 1 -15	0.49	1977-78	Dec. 1 -15	0	—	41	0	—	40	0	—	60
Tenmile Lake	0.65	*1954-74	Dec. 15-31				0	—	50						
Coquille River	0.55	1949-69	Dec. 1 -15				0.01	—	59						
Rogue River	0.44	(³)	Dec. 1 -15	0.44	1974, 75, 77 & 78	Dec. 1 -15	0	—	29				0		60
California:															
Klamath River															
Irongate Hatchery				0.53	1969-78	Dec. 1 -15				0		40			
Trinity Hatchery				0.53	1966-78	Dec. 1 -15				0		40			
Mad River				0.62	1971-78	Dec. 1 -15				0		36			

¹Three-year-old fish only.

²Estimated by hatchery manager.

³Estimated from hatchery data.

*Except 1959.

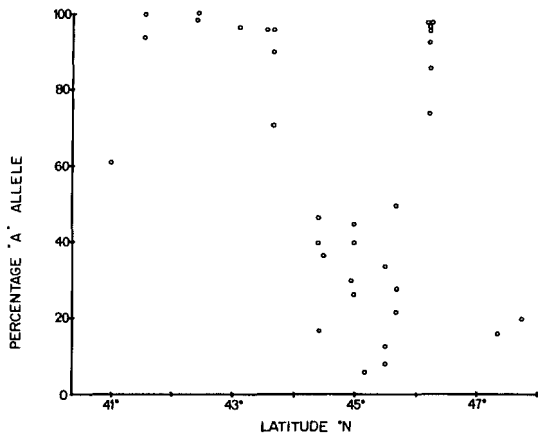


FIGURE 5.—Transferrin gene frequencies for wild and hatchery coho salmon stocks arranged by latitudes.

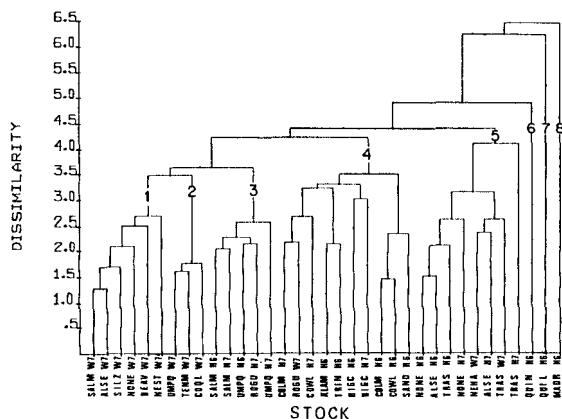


FIGURE 6.—Dendrogram of the agglomerative cluster analysis for all stocks of wild and hatchery coho salmon of two brood years, 1976 and 1977. Euclidean distance was the dissimilarity measure and group average was the clustering strategy. Location codes are as in Figure 1. The other codes are as follows: H6, hatchery stock of the 1976 brood year; H7, hatchery stock of the 1977 brood year; and W7, wild stock from the 1977 brood year.

Oregon coast wild stocks (cluster 1), southern Oregon coast wild stocks (cluster 2), stocks from hatcheries that used wild stocks for the egg source (cluster 3), stocks from large river systems (cluster 4), hatchery stocks and two wild stocks from the northern Oregon coast (cluster 5), and three individual hatchery stocks from California and Washington (clusters 6-8).

Canonical variate analysis on the five larger clusters produced three canonical variables that

were significant ($\alpha = 0.05$). When these three variables were plotted against each other, only clusters 1 and 5 (consisting of wild stocks and hatchery stocks, both from the northern Oregon coast) were not completely separate in three-dimensional space. The other three clusters were discrete, suggesting that intercluster differences were stronger than between clusters 1 and 5. Statistical testing for differences between the clusters would not be valid because the necessary assumption of randomness of data is violated.

The results of the canonical variate analysis must be interpreted with caution because the variation within each cluster was reduced by our using the averages of the morphological characters. This reduction of variation facilitates discrimination between clusters by canonical variate analysis, so that quantitative comparisons of cluster discreteness cannot be made. Individual phenotypes undoubtedly overlap between stocks or between clusters; however, the multivariate analysis of variance did indicate that significant differences existed among the stocks for each of the morphological characters. We characterized the stocks by the average phenotypes in order to estimate the phenotypes typical for each stream system, and on that basis the results of the canonical variate analysis suggested that there were discrete differences between all clusters except 1 and 5.

The results of the agglomerative and divisive cluster analyses were similar. At the 13-cluster level of the divisive analysis (Table 8), all but two clusters were identical with clusters from the agglomerative cluster analysis dendrogram. The results of these analyses should be interpreted cautiously, because they are based on only 10 characteristics—a small number compared with the total number of genetically related characteristics possible. If other characteristics had been used, the results might have differed. Thus, we did not emphasize the exact order or the levels of dissimilarity at which any two clusters joined together; rather, we observed only general trends in the clustering patterns.

Three general trends are apparent in the clustering patterns of the agglomerative cluster analysis dendrogram. First, the stocks from the larger stream systems (Columbia, Rogue, and Klamath Rivers) were more similar to each other than to the stocks from smaller streams. The only exceptions to this trend were wild stock from the Umpqua River and the Umpqua and Rogue hatchery stocks. The Umpqua wild stock was

TABLE 8.—Coho salmon stocks at the 13 cluster level of the divisive cluster analysis. "Wild" denotes wild stocks.

Cluster no.	Divisive cluster analysis stock	Brood year
1	Cascade Hatchery	1976
	Cowlitz Hatchery	1976
	Sandy Hatchery	1976
2	Salmon River Hatchery	1976, 1977
	Rogue River Hatchery	1977
	Umpqua River Hatchery	1976, 1977
3	North Nehalem wild	1977
	Nestucca River wild	1977
	Salmon River wild	1977
	Siletz River wild	1977
	Beaver Creek wild	1977
	Alsea River wild	1977
4	Quilcene Hatchery	1976
5	Nehalem River wild	1977
	Trask River wild	1977
6	Mad River Hatchery	1976
7	North Nehalem Hatchery	1976, 1977
	Trask Hatchery	1976
	Alsea Hatchery	1976
8	Umpqua River wild	1977
	Tenmile Lake wild	1977
	Coquille River wild	1977
9	Trask Hatchery	1977
	Alsea Hatchery	1977
10	Quinalt Hatchery	1977
11	Bonneville Hatchery	1977
	Cowlitz Hatchery	1977
	Rogue wild stock	1977
12	Trongate Hatchery	1976
	Trinity Hatchery	1976
13	Big Creek Hatchery	1976, 1977

associated with the other southern Oregon coast wild stocks, and the Rogue and Umpqua hatchery stocks were in the cluster with other hatcheries that used wild stocks as egg sources.

The second trend observed in the dendrogram was geographical clustering. Three stocks from Washington and California were dissimilar to the Oregon stocks, and the Oregon wild stocks clustered into two groups, northern and southern coastal stocks.

The third trend in the dendrogram was for hatchery and wild stocks to cluster independently. One of the clusters was composed entirely of wild stocks from the northern Oregon coast, and another included all but one of the northern Oregon coast hatchery stocks, in addition to two wild stocks from the northern Oregon coast. The hatchery stock excluded from this cluster (no. 5) was from the Salmon River, a stock developed from eggs of wild coho salmon; both brood years of this stock were in the cluster of hatcheries that used wild stocks as an egg source. The rest of the northern Oregon coast hatcheries used returning hatchery-reared adults for egg sources. The two wild stocks in this cluster were from the Trask and Nehalem Rivers. They are also simi-

lar to the other wild stocks; however, because of the mechanics of the group-average clustering strategy, they both clustered first with the hatchery stocks. The average Euclidean distance between the Nehalem wild stock and the other wild stocks was less than that between the Nehalem wild stock and the hatchery stocks of cluster 5. The close relationships of the stocks in clusters 1 and 5 were also apparent in the results of the canonical variate analysis, which showed these two clusters to be continuous.

The three trends in the clustering pattern indicated that coho salmon stocks from similar environments had similar phenotypes. These trends provide some guidance for the transfer of coho salmon stocks. Geographical clustering indicates that the phenotypic or perhaps genetic similarity between stocks probably decreases as the distance between stocks increases. McIntyre⁸ showed a strong negative correlation for the distance between stream systems and the genetic similarity of the steelhead trout stocks in those stream systems. If a similar relation between phenotype and distance exists among coho salmon stocks, survival rate would be expected to vary inversely with the distance that the stock is transferred from its native stream. The crucial question from the management standpoint, assuming the relationships we found are real, is how far stocks can be transferred before decreasing survival rate and the increasing genetic impact on the native stocks reduce the practicality of such transfers.

Although geographical distance can be an important factor in selecting a donor stock, other considerations must also be taken into account. The difference between stocks from large and small stream systems illustrates a problem in basing stock transfers primarily on geographical distance. Stocks from large stream systems were more similar to stocks in distant large systems than to stocks in small stream systems that were geographically close. Other environmental variables may also differ, affecting the phenotypes of geographically close stocks. Characteristics such as time of peak spawning or transferrin genotype may be closely related to flow and temperature regimes or to disease organisms present in the stream systems. These characteristics and others not included in this

⁸McIntyre, J. D. 1976. The report of interbreeding of artificially propagated and native stocks of steelhead trout. *Oreg. Dep. Fish Wildl., Res. Sect., Steelhead Annu. Rep.*, 22 p.

study all should play a role in choosing stocks for transfer to other stream systems.

The third trend mentioned (that of hatchery and wild stocks diverging toward different phenotypes) presents a problem to managers who must choose the best stock for transfer to other stream systems. The separate clustering of hatchery and wild stocks suggests that hatchery stocks have become dissimilar to wild stocks—even those that inhabit the same drainage. Studies with steelhead trout indicated that hatchery fish survived better in hatchery ponds, whereas wild fish had higher survival in streams (Reisenbichler and McIntyre 1977). The dissimilarity between hatchery and wild stocks may play a role in reducing the survival of hatchery-reared coho salmon when they are released into a stream system.

Similarity of Stream Systems and Wild Stocks

Because coho salmon appear to have similar phenotypes in similar environments, one could possibly relate phenotypes of stocks with descriptions of their stream basins (Tables 5, 9). However, comparisons of an agglomerative cluster analysis of wild stocks (Fig. 7) with a cluster analysis of stream characters (Fig. 8) indicated that they were less similar than we had anticipated—although we expected some differences because the stream characters were not necessarily related to taxonomic characters used in this study.

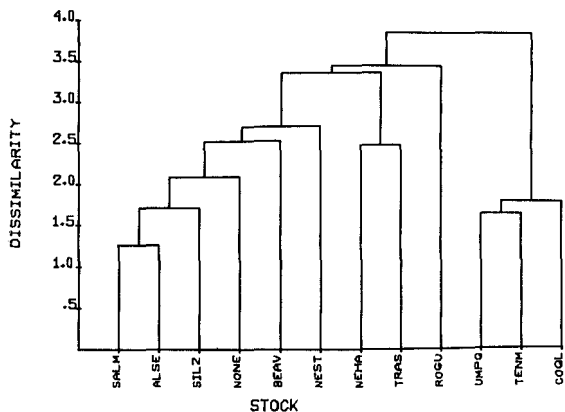


FIGURE 7.—Dendrogram of the agglomerative cluster analysis for wild coho salmon stocks with a Euclidean distance dissimilarity measure and group average clustering strategy. Location codes are as in Figure 1.

CONCLUSIONS

Individual characters of the stocks examined by us showed a variety of responses to stream characters. Time of peak spawning was strongly correlated with latitude, whereas other characters were significantly correlated with several environmental gradients, suggesting that interactions determining stock phenotypes are complex. The variability of the stock character may also change along environmental gradients, as demonstrated by the transferrin genotype (Figs. 4, 5).

The results of the cluster analysis indicate that stocks that are geographically close are similar, that stocks from large stream systems are similar to each other, that stocks from coastal stream systems are similar to each other, and that hatch-

TABLE 9.—Fish species and myxosporidan parasite, *Ceratomyxa shasta*, present in the Oregon stream systems. X = present.

Stream systems	Carp	Oregon chub	Squawfish	Redside shiner	Catostomus sp.	Speckled dace	Striped bass	Brown bullhead	Largemouth bass	<i>Ceratomyxa shasta</i>
Nehalem River					X				X	X
Trask River										
Nestucca River						X				
Salmon River										
Siletz River						X		X		
Beaver Creek						X				
Alsea River						X				
Smith River		X	X	X	X		X	X		
Umpqua River		X	X	X	X	X	X	X		
Tenmile Lake						X		X	X	
Coquille River					X	X	X	X		
Rogue River	X			X	X		X	X		X

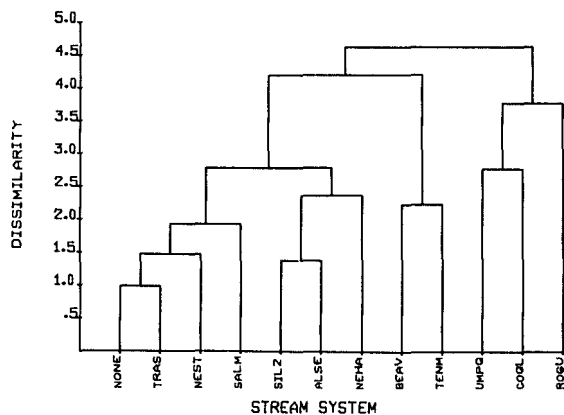


FIGURE 8.—Dendrogram of the agglomerative cluster analysis for stream systems with a Euclidean distance measure and group average clustering strategy. Location codes are as in Figure 1.

ery and wild stocks are dissimilar. In general, coho salmon stocks from similar environments appear to have similar phenotypes; however, groupings obtained from cluster analyses of coho salmon stocks and corresponding stream systems were dissimilar. This dissimilarity may be a result of our using only a small number of characters for analysis. As additional characters are considered, additional trends may become evident. The characters in this study, in concert with other characters, should be used in future evaluations of genetic similarities between stocks for an eventual characterization of stocks that will ensure effective transplantation.

In addition to providing information which may be useful for selecting donor stocks for hatchery programs, the results of this study also suggest a potential weakness in hatchery supplementation. Selection through hatchery environment and hatchery practices may be changing the overall phenotype of hatchery stocks, as well as the between-year variability of individual genotypes (as we found for transferrin). If these changes result in reduced performance of the donor stocks in other stream systems, practices designed to increase hatchery production must be weighed against the actual benefits to wild production.

We believe that this study demonstrates a relationship between phenotypic characters and certain habitat types. The differences in phenotype that are attributable to hatchery or wild origin, geographic proximity, and small or large stream systems may provide a first basis for judging the advisability of stock transfers.

ACKNOWLEDGMENTS

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