AN ABSTRACT OF THE THESIS OF

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Title: Quantitative Genetics of Chum Salmon, Oncorhynchus keta (Walbau

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Chum salmon from different stocks were bred together in two experiments. Three stocks contributed gametes to one experiment, two stocks to another. Sibling groups of eggs, alevins, and fry were maintained in a common environment. Variability of development rates, rearing performance, susceptibility to disease, and behavioral traits was partitioned into genetic and non-genetic components.

Embryonic development rate differed among the progeny of sires in crossbred groups. Its heritability was high in crossbred but not in purebred groups, and was correlated with geographical location of parental stocks and size of eggs. Size after rearing was affected by sires within parental groups indicating that its heritability is significant. It was also affected by egg size and geographical location of parental stock. Susceptibility to the marine disease vibriosis in

controlled and natural challenges differed among sires within parental stocks. It is probably heritable in these stocks. Behavioral response to a salinity gradient, and length of residence in a stream were not affected by sires or parental stocks. Evidence for interactive effects was lacking for all traits.

These observations lead to acceptance of the hypothesis that observed traits related to fitness (e.g., development rate) exhibit significant additive genetic variability in crossbred groups of salmon but not in purebred groups. Thus, the notion that crossbreeding may be advantageous cannot be excluded.

A conceptual model is described for assessing selection in either a wild or hatchery stock. Dynamics are simulated for a stock in which (1) the number of returns per spawner depends on the number of spawners, (2) the number of returns is reduced biennially (simulating competition from pink salmon), and (3) age of maturation is 3 or 4 years. When age of maturation is given high heritability (h^2=1) both average age and abundance cycle biennially; when heritability is low (h^2=0) average age but not abundance cycles biennially. The first pattern has been reported for chum salmon in places where pink salmon spawn in significant numbers biennially. This result suggests that chum salmon, by genetic regulation of their age structure, can avoid competition with pink salmon.

Quantitative Genetics of Chum Salmon, *Oncorhynchus keta* (Walbaum)

by

William Williams Smoker, B.A., M.S.

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James E. Lannan, Assistant Professor of Fisheries in charge of major

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Head of Department of Fisheries and Wildlife

Redacted for privacy

Dean of Graduate School

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I dedicate this thesis to my father, William Alexander Smoker, on the occasion of his retirement from the Director's office of Auke Bay Fisheries Laboratory. My earliest memories include going with him to watch chum salmon on their spawning beds; his continuing delight in the study of salmon has made it easy for me to undertake this work.

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INTRODUCTION

Chum Salmon, Fisheries and Culture

Chum salmon (*Oncorhynchus keta*) spawn in rivers and streams around the rim of the Pacific Ocean north of latitude 33° N, around the Bering Sea, and entering the Arctic Ocean from eastern Siberia, Alaska, and western Canada. Most populations spawn near the sea, but some spawn far upstream in large northern rivers such as the Amur, the Yukon, and the MacKenzie. Maturing fish feed in the subarctic Pacific Ocean and the Bering Sea from whence they return to their natal streams at ages ranging from two to six years. Unlike some congeners, fry do not reside in fresh water but proceed to sea immediately upon their emergence from their gravel redds. (Bakkala 1970 reviews much of the biological information concerning chum salmon.)

Populations of chum salmon are enormously valuable fishery resources. During 1972 through 1976 the annual harvest of chum salmon by fishermen in the United States attained an average of near 23 thousand tonnes (over 5 million fish). The average harvest of all salmon during those years was over 110 thousand tonnes. The average exvessel price per kg of chum salmon in 1980 was about

$1.03; that harvest was worth over $20 million to fishermen (Fisheries of the United States). The average of the annual harvests of chum salmon by Canada, the US, and Japan during 1972 through 1976 was over 100 thousand tonnes, 39% of the harvest of all Pacific salmon (Statistical Yearbooks of the North Pacific Commission). During the 1960s the USSR harvested 67 thousand tonnes of salmon each year of which about 40% were chum salmon (Konovalov 1980).

In the past thirty years the artificial culture of chum salmon embryos increasingly has become important in the total production of the species, because survival of embryos to the ocean-going fry stage can be much greater in artificial culture than in nature (McNeil 1976), and because natural spawning grounds have been lost to industrial development (Atkinson 1976). Particularly on the island of Hokkaido, Japan, the number of artificially produced chum salmon fry has been increased, from around 200 million in the early 1950's to 802 million in 1975, 523 million in 1976, and 1.1 billion in 1980 (Table I). The total run of chum salmon has increased from 2 to 4 million to between 9 and 26 million fish. Chum salmon fry have also been produced by Soviet hatcheries in increasing numbers: their Sakhalin Islands' hatcheries released 160 million fry in 1962; by 1974, 337 million

TABLE I

Size of Chum Salmon Runs in Hokkaido, Japan, 1950-1979. Number of Fry Released. Number of Returning Adults.[1]

Brood Year	Total Run (Thousands)	No. of Fry Released (Millions)	No. Returning Adults (Thousands)
1950	4,396	222.4	3,129
1951	2,923	189.1	2,770
1952	2,065	159.6	1,842
1953	2,209	170.6	1,990
1954	3,380	269.3	3,314
1955	2,416	247.9	2,008
1956	1,884	140.4	1,907
1957	2,618	361.6	3,060
1958	2,961	417.2	2,232
1959	1,781	313.5	3,166
1960	1,730	203.4	3,364
1961	2,942	359.4	5,937
1962	2,760	280.7	3,025
1963	3,768	272.1	4,983
1964	3,812	334.4	2,119
1965	4,749	549.2	2,572
1966	3,804	272.0	5,942
1967	4,500	434.7	8,110
1968	2,137	207.4	4,881
1969	4,173	361.5	8,737
1970	5,278	442.1	10,110
1971	7,652	575.9	12,913
1972	6,957	475.8	11,909
1973	8,321	445.5	9,036
1974	9,627	484.8	11,342
1975	15,774	801.9	
1976	8,805	523.3	
1977	10,207	692.6	
1978	13,147	778.9	
1979	18,903		

[1] Personal Communication from T. Minoda, Faculty of Fisheries, Hokkaido University, Hakodate, Japan, dated 12 September 1980; Dr. Minoda relied on O. Hiroi, Japan Fishery Agency, Sapporo, Hokkaido, Japan, for the correctness of these statistics.

fry were released from hatcheries in the Soviet far east (Atkinson 1976).

On the eastern side of the Pacific most artificial production of chum salmon has been in the state of Washington. Between 1.3 million and 5.6 million fry were released from all east Pacific hatcheries in the years between 1960 and 1972; releases increased in size to 29.6 million in 1975 (Wahle and Smith 1978).

In the past decade there has been a renaissance of activity in the artificial culture of salmon in Alaska; programs of hatchery construction are being undertaken by both the state government and private nonprofit corporations. The total present (1981) capacity of hatcheries, either completed or for which designs are complete, is 546 million eggs of which 452 million will be devoted to chum salmon as brood stock becomes available (McMullen and Kissel 1981). Chum salmon are considered ideal for these facilities because they have been increasingly valuable relative to other salmon (their roe is highly valued in Asia) and they are relatively easy to culture--chum salmon are released in the sea in the first spring following spawning, thus they do not require extended periods of fresh water rearing. In Oregon, where private corporations are beginning to operate "ocean ranches" for salmon, there is strong interest in committing production facilities to chum

salmon for these same reasons. (Interview, February 1980, with W. J. McNeil, General Manager, Oregon Aquafoods, Springfield, Oregon, USA.)

Genetic Variation

Qualitative variation. Our knowledge of genetic variation in chum salmon stocks, even though rudimentary, ought to be important in both managing fisheries and planning and operating hatchery programs for the purposes of minimizing the impacts on the productivity of wild populations and carrying out artificial breeding programs in the most effective way.

Most of the present information concerning salmon genetics has been gained by the study of qualitative traits, i.e., traits determined at a single genetic locus; nearly all of these traits have been the presence or absence of isoenzymes separated from tissue samples by electrophoresis (Allendorf and Utter 1979). These observations, since they are of immediate products of genes, imply the genotypes of salmon, and are used to estimate the frequencies of genes in populations. Gene frequencies in salmon stocks (populations) are used to estimate two important parameters, genetic distance between stocks (a measure of the number of different genes at loci in the genomes of different stocks) and heterozygosity (a measure of the genetic variability in a

stock, the proportion of loci for which the stock's genome has more than one allele). These are measures made in genotype space (Lewontin 1974), that is, they are derived from observations of genes or of the immediate products of genes.

Estimates of genetic distance should be important to the planning of a salmon hatchery because such estimates could help minimize the impact of the hatchery on wild populations. Helle (1976) and Calaprice (1969) have described the sort of risk that theory predicts might be involved in introducing an artificially cultured stock into the neighborhood of wild stocks: through the straying of returning adults from the hatchery to spawning grounds of wild stocks, genes of the artificially maintained stock might introgress into the wild stock, thereby reducing its fitness. This risk would be minimized if the stock chosen for the hatchery were close to the neighboring wild stock in genotype space.

Quantitative variation. Observations of the distance between stocks of salmon and of their heterozygosity or genetic variability can be made in phenotype space as well. Indeed, most observations of the morphology and biology of salmon stocks have been made in phenotype space. For example, the morphology of dermal scales, which reflect in their structure the growth

history of individuals, has been extensively used to recognize differences between stocks of salmon (Major et al. 1972). Scales from fish of different stocks reflect the different growth patterns characteristic of those stocks; as for any phenotype the differences between stocks are related to environmental as well as genetic differences between stocks. Ricker (1972) extensively reviews evidence that some differences of the biology and morphology of salmon stocks result from genetic differences beween stocks.

Heterozygosity in a segment of the genome of a stock results in a contribution of additive genetic variability to the total variability of whatever phenotypic traits are affected by that segment (Falconer 1960). The heritabilty of one of those traits, i.e., the proportion of the total variability that arises from additive genetic variability, is a measure made in phenotype space (Lewontin 1974).

The heritability of a trait can be used to predict the response of the trait in the stock to mass selection: if the heritability is high, i.e., if much of the trait's total variability is due to the additive effects of different genes in the stock, then the response of that trait to mass selection will be rapid. For instance, if the weights of salmon of a given age in a stock were to vary over an appreciable range and, if the heritability

of weight at that age were large, then the selection of larger individuals as breeders would result in a few generations in a stock comprised of heavier fish at that age. If, however, the heritability were low, the variability of weight having been caused largely by the members of the stock experiencing different environments and not by their possessing different genes, selection of heavier fish as breeders will have little effect. The weights of fish at that age would not change over generations.

The heritability of a trait can be estimated by experiments in which the correlation of the trait within and between related groups of individuals is observed. For instance, if the heritability of weight-at-age were large, then offspring would be more similar to parents than to other members of the stock and siblings would be more similar to each other than to other members. If heritability is low, there would be no special similarity between offspring and parents or between groups of siblings (see, for example, Falconer 1960; Kempthorne 1969).

Knowledge of the heritabilities of traits and of the related parameter, genetic correlation, which predicts the extent to which correlated traits respond jointly to the same selection, is necessary to a fish culturist who is carrying out an artifical breeding program in which

artificial selection of certain traits, either purposeful or not, might occur. Table II lists estimates of heritability that have been made for salmonid populations.

Estimates of heritability are important to fishery managers as well. There is a growing awareness that fisheries themselves may exercise artificial selection on stocks. Ricker et al. (1978) and Ricker (1980) for instance, suggest that size selection by gill nets may have been responsible for a historical decline in the size of pink (O. gorbuscha) and chum salmon in British Columbia. Favro, et al. (1979) suggest that fishing pressure may have been responsible through genetic change for changes of the distribution of sizes of brown trout (Salmo trutta) in the AuSable River, Michigan. Gwahaba (1975) attributes the change of size-at-maturity of Tilapia after a fishery began to exploit them in Lake George, Uganda, to the heritable response of the stock to selection of large fish by the fishery.

Allendorf and Utter (1979) point out that estimates of heterozygosity (which include the entire genome, and cannot strictly apply to the parts of the genome which code for a given trait) can, nevertheless, give some indication of the amount of genetic variability in the stock, of the general efficacy of selection in the stock.

TABLE II

Estimates of Heritability in Salmonid Populations.

Species	Trait	Heritability(h^2)	Reference
Oncorhynchus nerka	IHN Virus Tolerance	.30	McIntyre and Amend 1978
O. tshawytsca	Maturation Age	.24	Appendix V
O. gorbuscha	Date of Spawning	.26	Appendix V
Salmo salar	Vibrio Tolerance	.07-.12	Gjedrem and Aulstad 1974
S. salar	Smolting Age	.06	Refstie et al. 1977
S. gairdneri	Hatching Time	0,.23	McIntyre and Blanc 1973
S. gairdneri	Weight, post spawning	.20	Gall, 1975
	Egg size	.20	Gall, 1975
	Fecundity	.20	Gall, 1975
S. gairdneri	Fingerling Size	.17-.42	Aulstad et al. 1972
		.1-.2	Steine quoted in Gjedrem, 1976
		.26-.29	Kincaid 1972
		.26	Kincaid 1977
		0-.30	Moller 1976 quoted in Gall 1977
S. gairdneri	Number of Pyloric Carcae	.41	Chevassus et al. 1979
S. trutta	Vertebrae Number	.33,1	Schmidt 1922 (Appendix V)
S. trutta	Pylonic Caecae	.84	Bergot et al. 1976

Consideration of heterozygosity and heritability leads to another tactic that might be important in the successful beginning of a salmon culture enterprise, that of crossbreeding or hybridizing between stocks in order to obtain a highly heterozygous stock--one in which the heritability of important traits might be high and in which rapid progress toward high productivity could be made through selection. Experiments by Ayala (1968) demonstrated the potential of the tactic. He observed the growth in numbers, generation by generation, of populations of fruit flies (Drosophila) introduced into a new environment, glass jars containing food. He observed that populations known through knowledge of their chromosomes to be highly heterozygous grew more quickly and to higher ultimate numbers than did populations of low heterozygosity. Furthermore, populations that were started by hybridizing between strains of fruit flies performed in the same way as the heterozygous populations. They grew more quickly and to higher numbers than populations derived purely from one strain. Presumably the parental strains had different alleles present in their respective genomes at loci which effected the fitness, the ability of individuals to reproduce, of the offspring in the jars. These differences presumably were brought about either through the differing action of natural selection on the isolated

parental strains or through the processes of random genetic drift acting in the isolated parental strains. When the strains were hybridized the resulting population received all alleles from both parental strains and therefore presumably had a higher level of heterozygosity than populations descended from one or the other of the parental strains. Apparently those levels of heterozygosity correspond to levels of genetic variance of fitness in the new environment, for as predicted by the Fundamental Theorem of Natural Selection (Fisher [1930] 1958) the "hybrid populations [had] larger size, and, generally also greater productivity, than the corresponding parental populations" (Ayala 1968).

By analogy, one would expect that the best scheme for starting a new salmon stock in a new (hatchery) environment would involved crossbreeding or hybridizing between existing stocks. This is the obverse of the hypothetical problem foreseen by Helle (1976). Rather than reducing the average fitness of a stock which is naturally and presumably optimally adapted to its environment through artificially causing the hybridization of its genome with the genome of another stock, this scheme starts with the presumption that no naturally reproducing stock has the maximum fitness possible in the new, artificial, environment. Therefore it provides a new stock with as much genetic variability

as possible through crossbreeding between parental stocks. This new stock would be able to respond more quickly to the selection pressures in the new environment and would achieve greater productivity.

This scheme could also be applied to the enhancement of certain naturally reproducing stocks which are not optimally adapted to their environments and have small amounts of variability due, for instance, to having been reduced to small numbers by fishing. An increase in those stocks' genetic variability and ultimate productivity might well be brought about by the judicious introduction of foreign genomes to it.

Nature of gene action in chum salmon stocks. Whether or not a crossbreeding scheme such as the one proposed above is workable and whether or not introductions of exotic genes into wild stocks will seriously harm the fitness of those stocks depends to an extent on the nature of gene action in those stocks. If the high fitness of a fish is dependent on a particular combination of different genes interacting at different loci then crossbreeding or introductions could seriously disrupt those combinations and would cause fitness to be reduced in the stock. If, however, the fitness of a salmon is the resultant of several traits each acting independently of the other and each effected by genes that act additively--without interactions--mass selection

would efficiently eliminate any non-adaptive genotypes and adaptive genotypes would add to the fitness of the stock.

Another consequence of Fisher's ([1930] 1958) Fundamental Theorem is that in a stock which has adapted to its environment the heritability of fitness is low because natural selection has exhausted the available additive genetic variability of fitness. Lerner (1954) argues that a population retains an ability to regulate its average fitness, to keep it high in the face of a changing environment, through genetic homeostatic mechanisms that involve the interaction of genes, e.g., overdominance (heterozygote superiority) or epistatic interactions. One consequence predicted by Lerner is that fitness, or a trait closely allied to it, displays a large interactive component of genetic variability. This interactive component of genetic variability of fitness is not readily available to mass selection in the way that the additive component is available. (See, for example, Chapter Eight in Falconer, 1960, for a discussion of the several components of phenotypic variability-- environmental, interactive genetic, and additive genetic.) However, the interactive genetic variability of fitness-traits does allow the population to maintain a reserve of heterozygosity. When different environments are encountered by the population it will

heterozygosity which in the new environment can result in additive components of genetic variability thereby allowing the population to respond to new selection pressures. Lerner also predicts that metric traits, those which can be measured on a continuous scale, which are not closely allied to fitness are likely to display additive components of genetic variability. The heritability of those traits, therefore, might be appreciable.

A countervailing view is that of Williams (1975) who argues that in species characterized by great fecundity intense selection is experienced in each generation, i.e., "...a tremendous amount of genetic change can occur in one generation..." (p. 62); and that:

> Much selection is concerned with the elimination of low-fitness genotypes produced by mutation or recombination. It can be at a generally intense level, but vary so in direction and strength at different times or places that little cumulative change takes place. (p. 65.)

Under Williams' model the traits which determine fitness at different times or places sequentially operate to determine which infinitesimally small fraction of each generation's zygotes survive to become reproductive. Fitness is not a "canalized" trait, i.e., a trait whose value in the stock can be produced by a range of genotypes, but is a "sisyphean" trait, which depends on the individual having had a fortunate combination of many

different traits at different times and places in its life in order for it to reproduce and which must be re-formed in each generation. Highly fecund species depend on the reproduction of a great variety of genotypes in each generation, a very few of which will prove successful (the sisyphean types) in the highly variable environment. The component traits of fitness which act in a sequential fashion are each possessed of a high degree of additive genetic variability according to Williams' model. Powell and Taylor (1979) also find that high levels of genetic variability at fitness loci can be maintained in populations if there are many microhabitats in which different genotypes are favored.

THESIS

Pacific salmon have adapted to a large variety of spawning environments that differ in many ways, e.g., annual patterns of water flow, temperature, insolation, gravel sizes, distance from the ocean, etc. The adaptation of a stock to an environment is probably affected by the selection of alleles at loci which control certain key fitness traits of the stock such as the annual timing of spawning, the temperature dependent development rate of embryos and timing of emergence of larvae, the size of eggs, or the choosing of proper nest sites. If the variability of these fitness traits in the stock is at least partly due to additive genetic variability at the controlling loci then these traits can readily change in response to natural selection, allowing the stock to colonize new environments. For example, sockeye salmon spawn in tributaries of Mendenhall Lake near Juneau, Alaska; yet 60 years ago Mendenhall Glacier covered those spawning grounds. Or the variability allows the stock to adapt to changes in existing spawning habitats. For example, in 1964 an earthquake lifted land masses around Prince William Sound, Alaska, substantially altering the spawning habitat of many chum and pink salmon (O. gorbuscha) stocks (Noerenberg, 1971; Roys, 1971; Thorsteinsen, et al., 1971); but most of these

stocks have endured and are very productive.

Additive genetic variability at these fitness-controlling loci may not be very great: they are related to fitness and under Lerner's (1954) model that additive variability would be reduced by selection. If, however, Williams' (1975) model applies to chum salmon, there may be maintained high levels of additive genetic variability in the stock of traits related to fitness. Chum salmon and other species of Oncorhynchus whose fecundities range between 1,000 and 10,000 fall into Williams' category of medium fecundity. These fecundities may not be large enough to enable a stock to rely on the production of new sisyphean genotypes in each generation in order to maximize its fitness. However it is easy to speculate that chum salmon stocks derive greater fitness by producing a wide range of genotypes in each generation of which few survive to reproduce because many important aspects of their environment change unpredictably and appreciably from generation to generation, and because mortality before spawning is commonly very high. Parker (1962), for instance, estimated mortality at several stages in one stock:

Life Stage	Egg	Coastal Juvenile	Pelagic Subadult	Coastal Adult	Total
Mortality	0.922	0.946	0.434	0.070	0.998

Hypotheses

If gametes from different stocks of salmon are combined and the resulting populations are observed in a common environment, (1) the mean value of characteristics of crossbred populations (those groups of individuals which had a parent from each of two different stocks) will be intermediate between the mean values of the respective purebred populations (the groups of individuals which had two parents from one stock), (2) the additive genetic variability and the heritabilities of fitness-related characters of crossbred populations will be greater than the additive genetic variabilities and heritabilities of characters of purebred populations, and (3) interactions between parents will not affect the characteristics of the purebred or crossbred populations. Dominance (within locus) or epistatic (between locus) interactions should not occur for traits which must assort freely in the creation of sisyphean genotypes.

The genetic model by which I made these predictions is simple: one locus controls the characteristic; there are two alleles at the locus; stocks differ in the relative frequencies of those alleles. Under this model if there is no dominance: $M_i = a(1 - 2q_i)$ and $M = a(1 - 2q)$ where i =

1 for stock number 1 (or purebred population number 1)

2 for stock number 2 (or purebred population number 2)

C for the crossbred population,

M = the mean value of the characteristic

q = the frequency of one of the alleles in the population

a = half the difference between the value of an individual homozygous for one allele and the value of an individual homozygous for the other allele, and

$q_c = 1/2\ (q_1 + q_2)$ (Falconer 1960).

If there is complete dominance (heterozygotes have the same value as individuals which are homozygous for the dominant allele), Falconer (1960) evaluates the mean value of a trait as:

$$M = a\ (1 - 2q^2)$$

To predict the mean in a crossbred population, I let $M_i = a\ (1 - 2q_i^2)$ and compute M_c.

Figure 1 is a nomogram incorporating these equations. It can be entered either with the gene frequencies or mean values of the purebred populations (or of the parental stocks) and from which can be read the mean value of the crossbred population. The case of no dominance is shown by a dotted line, the case of complete dominance by a solid line.

Genetic components of variance can be predicted under this model as well: if there is no dominance: V_A =

$2p_iq_ia^2$ where V_A is the additive variance (Falconer 1960). Figure 2 is a nomogram incorporating these equations for the case in which there is no dominance. If there is dominance: $V_D = (2pqd)^2$, where V_D is the variance of dominance deviations and d is the value of the trait for an heterozygous individual. Figure 3 is a nomogram which incorporates the equation for V_D for the case in which there is complete dominance (d = a). The nomograms can be entered with the gene frequencies of the purebred populations (or of the parental stocks) and the genetic variances of the crossbred population can be read from the graph.

My predictions of the outcomes of crossbreeding follow from this model if the trait is determined by the additive action of loci--if there is no interaction between loci. That is, the model depicted in Figure 1 predicts that at each locus in the crossbred population the contribution to the value of the trait will be intermediate between the contributions by the same locus in the purebred populations. The sum of a number of such loci will also be intermediate in a crossbred population. This holds true even if there are dominance (non-additive) interactions between alleles within a locus, but not if there is overdominance (heterosis) in some loci, i.e., greater contribution to value by heterozygotes than by either homozygote.

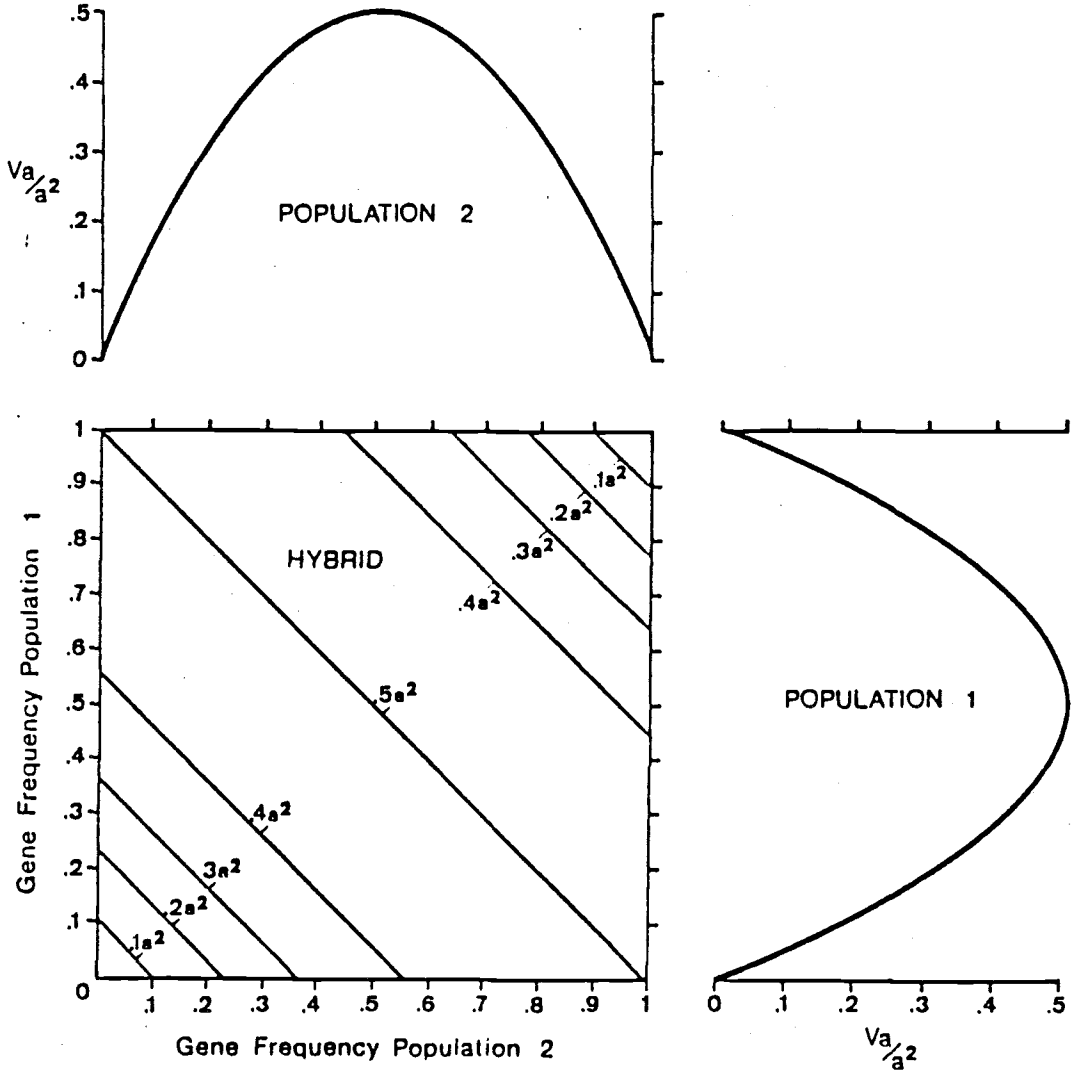

Figure 1. Nomogram giving mean values and gene frequencies of parental and hybrid populations for a simple two allele single locus trait.

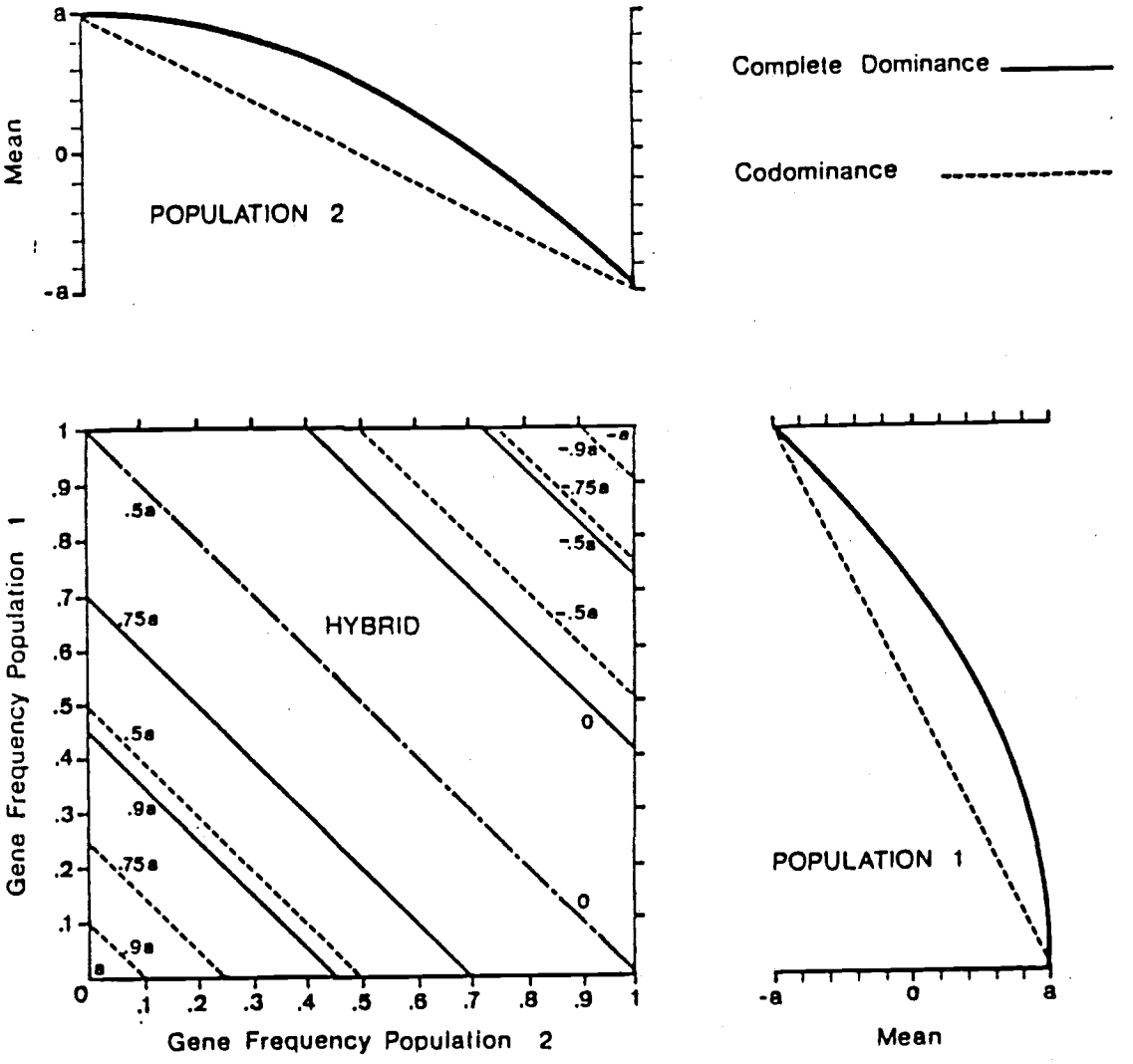

Figure 2. Nomogram giving additive variance of parental and hybrid populations for a simple two wllele single locus trait for which there is no dominance.

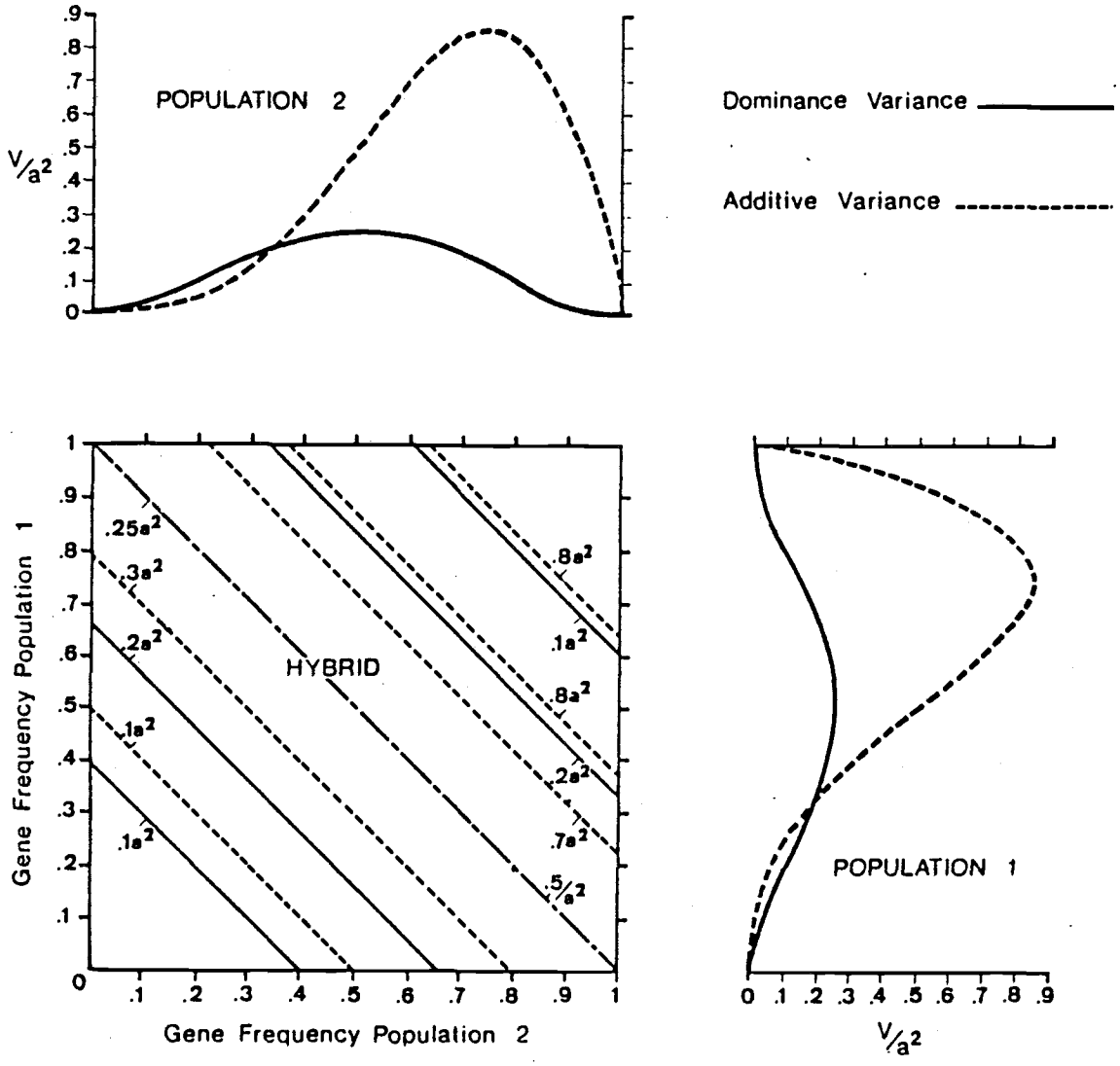

Figure 3. Nomogram giving additive and dominance variance of parental and hybrid populations for a simple two allele single locus trait for which there is complete dominance.

If alternate alleles are fixed in two parental stocks, the additive genetic variance will be greater in the crossbreds than in the purebreds, whether or not there are dominance interactions within loci. If the frequencies of the alternate alleles deviate from fixation in the two parental stocks, additive genetic variation will still be greater in the crossbreds than in either purebred population if the frequencies of the alternate alleles are symmetric about 0.5 (when there is no dominance) or about 0.7 (if there is complete dominance.)

The model's predictions about genetic variability in crossbred populations apply in the generations of random breeding which follow the first generation. However, in my tests of the model, and in some of the other experiments (cited below) which test it, observations have been made only in the first generation. In the instance in which alternate alleles are fixed at every locus in the purebred populations, the first generation of the crossbred population will, however, have no genetic variability--each individual will be a heterozygote at every locus. While the mean values of traits would follow the prediction of the model in that first generation, the amount of genetic variability would not. In the instance in which the same pairs of alternate alleles are present in the purebred

populations, the genetic variability would also be less in the first generation after crossbreeding than in later generations of random breeding due to an excess of heterozygotes. However, if, as is more likely, more than two alleles are present in the two purebred populations at some of the loci which effect the trait being modeled, the crossbred population will contain a larger array of genotypes than either of the purebred populations. Therefore the predictions of the model about genetic variability should be qualitatively met even in the first generation.

There already exists some evidence concerning my hypotheses from experiments with other Pacific salmon. Brannon (1972) observed that the mean value of rheotaxis in sockeye salmon (O. nerka) fry was intermediate in crossbreds: in one purebred population it was positive, in the other purebred population it was negative, but in the crossbred population it was indeterminate. Furthermore, in the crossbreds, the time which elapsed between fertilization and yolk absorption was intermediate between the elapsed times of the purebreds. However, the time which elapsed between spawning and the onset of migratory behavior was longer in the crossbreds; this may have been related to the size of the eggs involved. Brannon did not estimate components of variability of these traits.

Bams (1976) observed the homing abilities of a purebred population, a crossbred population and a parental stock of pink salmon. The parental stock was observed in its native environment, its performance was best; the purebred population was in an exotic environment, its performance was noticeably worst; the crossbred population was in its paternal stock's native environment, its performance was intermediate. Bams did not estimate components of variability of homing ability.

Hershberger (1976) observed that the growth of crossbred groups of coho salmon (O. kisutch) at hatcheries was greater than the growth of purebred populations, which is consistent with the notion of overdominance (heterosis). Refstie, et al. (1977) found greater variation of smoltification between stocks of Atlantic salmon (Salmo salar) than within stocks. Those results imply that there are differences in the genotypes of the stocks as they effect smoltification.

PART ONE

OBSERVATIONS OF QUANTITATIVE VARIATION IN AND BETWEEN STOCKS

Introduction

I conducted two breeding experiments each involving gametes from more than one chum salmon stock. Observations of the offspring provided tests of the hypotheses that the mean values and variabilities of traits would be different in purebred and crossbred groups. The 1975 experiment involved three widely spaced parental stocks but could not involve both purebred and their resultant crossbred groups in the same test environment. The 1976 experiment did test purebred and resultant crossbred groups in the same test environment, but there were only two parental stocks and in the wild they spawn nearby to one another.

Methods. Design of Experiments

Breeding experiment: Three stocks (1975 brood year). I collected and combined gametes from three different chum salmon hatchery stocks. All eggs came from four females randomly chosen from among ripe fish at the Oregon State University's Netarts Field Station (Whiskey Creek) on 19 November. Milt came from five males randomly chosen from the Whiskey Creek stock, from

five males chosen from the Nemah River stock near Willipa Bay, Washington, and from five males chosen from the Hood Canal (Hoodsport) stock on Puget Sound, Washington (Figure 4). Milt from the Nemah and Hoodsport stocks was collected and carried to the Netarts station on 19 November. The eggs from each female were divided into twenty approximately equal groups; each group of eggs was fertilized by one male's milt: five groups were fertilized by milt from Nemah males, five groups by milt from Hoodsport males, and ten groups of eggs were fertilized by milt from Whiskey Creek males. Among each female's eggs two groups of eggs were fertilized by each Whiskey Creek male's milt and one group of eggs by milt from each male from Nemah or Hoodsport. The 80 groups of fertilized eggs were randomly assigned to replicate incubators (Figure 5).

The design of the breeding experiment was a "nested factorial" in which four females were crossed with males from three populations; there were five males sampled from each population. Among these the crosses of the four females with the five males from Whiskey Creek were replicated. I chose this design because: 80 incubators were available; I wanted gametes from as many populations as possible; I wanted at least four parents of each sex in each sub-group of the experiment in order to achieve minimal statistical power; I wanted at least part of the

experiment to be replicated in order to provide an estimate of the within-cell variance, and because bringing exotic eggs to the Netarts Station was not practicable, i.e., I could not combine milt from Netarts males with eggs from the other stocks.

Breeding experiment: Two stocks (1976 brood year). In 1976 I combined gametes from two chum salmon stocks: that of the Netarts hatchery and a wild stock which spawns in a tributary (Coal Creek) of the Kilchis River. Both are in Tillamook County, Oregon (Figure 6). On 24 November I collected three females and three males from the Kilchis stock, brought them to the Netarts Station, and combined their gametes with those of three females and three males chosen from the Whiskey Creek stock. Each of six groups of eggs from each female was combined with one of six aliquots of milt from each male. Two 100-egg groups from each of the 36 matings were seeded into replicated incubators (Figure 7). These incubators were designed so that emigration would be behaviorally more distinct than in the incubators used in 1975.

In the 1975 experiment exotic sperm and indigenous gametes were used. In the 1976 experiment both exotic sperm and eggs were combined with indigenous Whiskey Creek gametes.

Parent salmon. I observed in 1975 each female's length (mid-eye to hypural plate, MEHP), age (years,

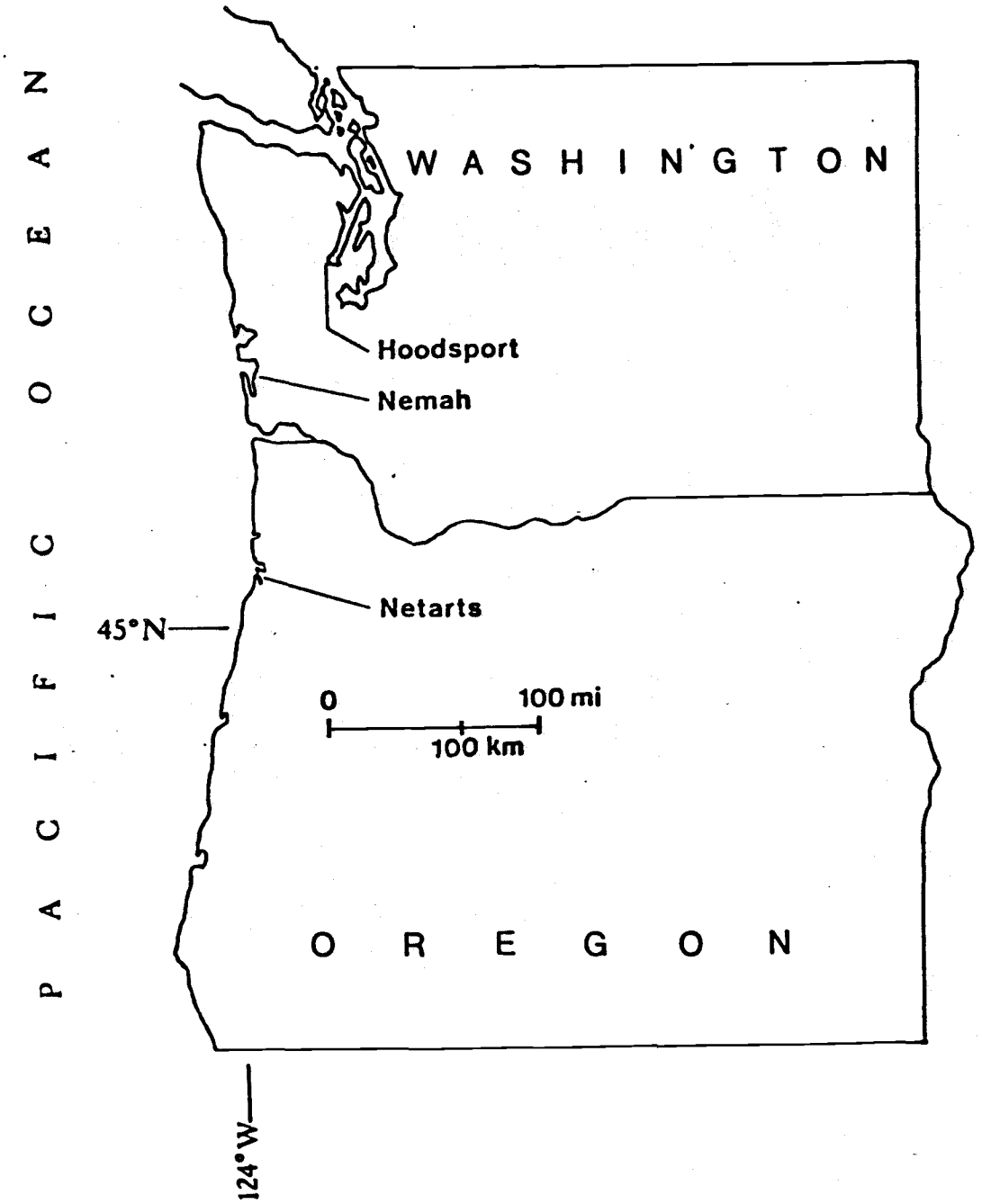

Figure 4. Map of Oregon and Washington showing the locations of the parental stocks of the 1975 experiment.

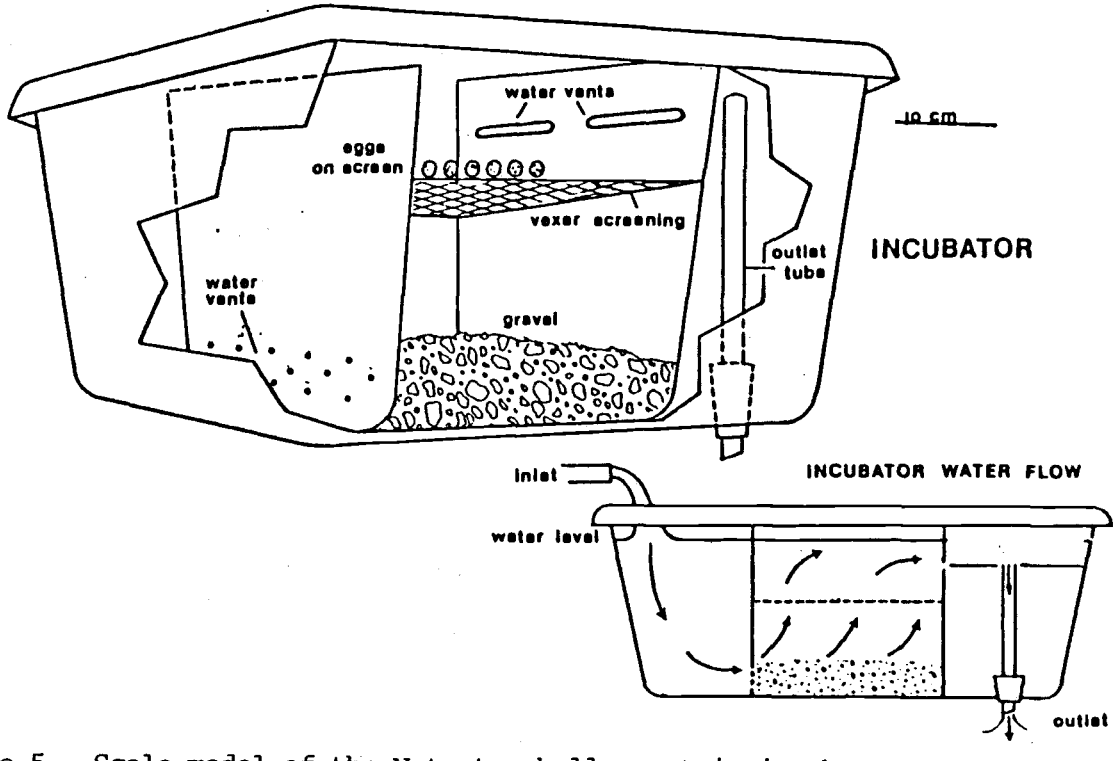

Figure 5. Scale model of the Netarts shallow matrix incubator.

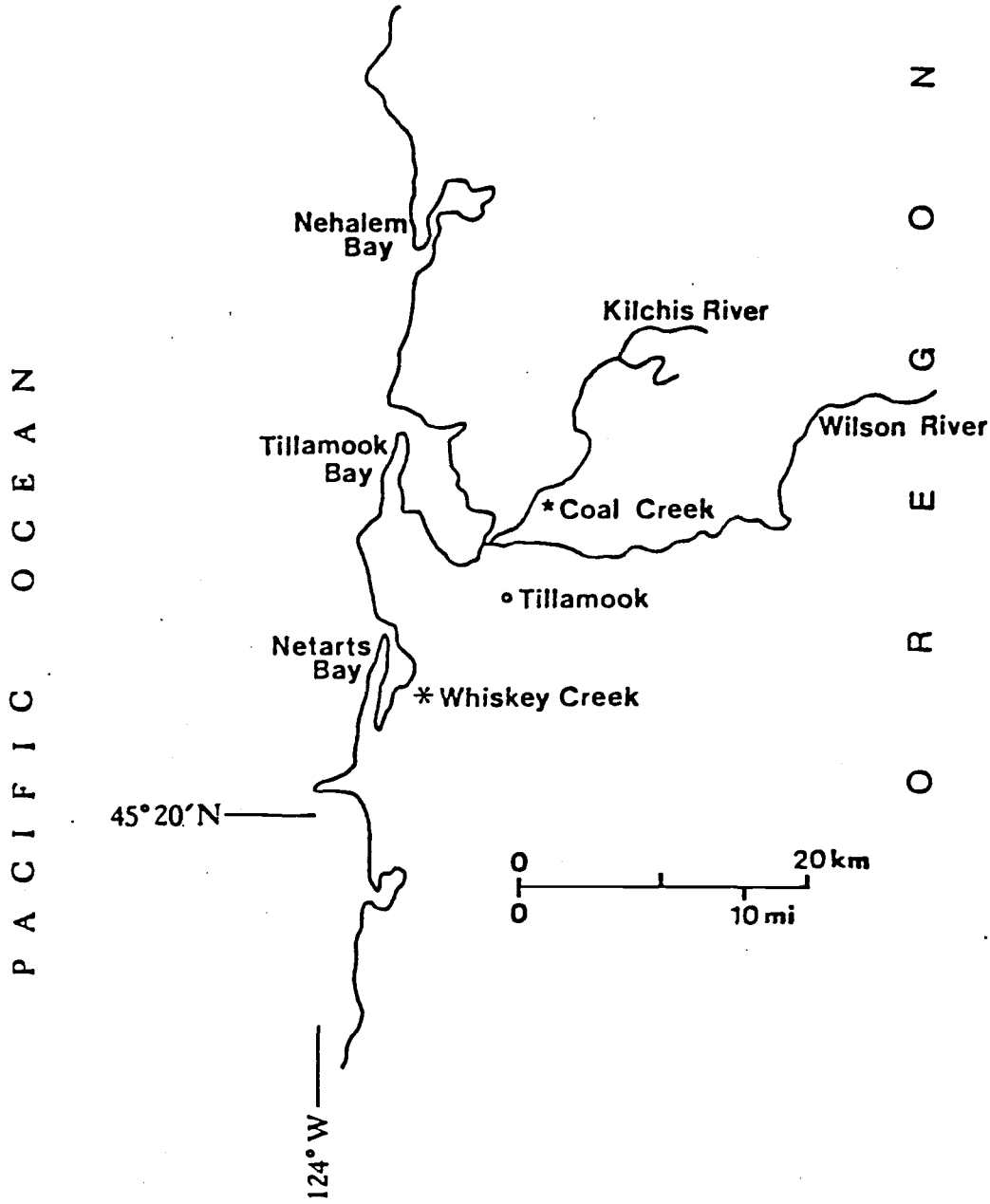

Figure 6. Map of part of Tillamook County, Oregon, showing the locations of the parental stocks of the 1976 experiment.

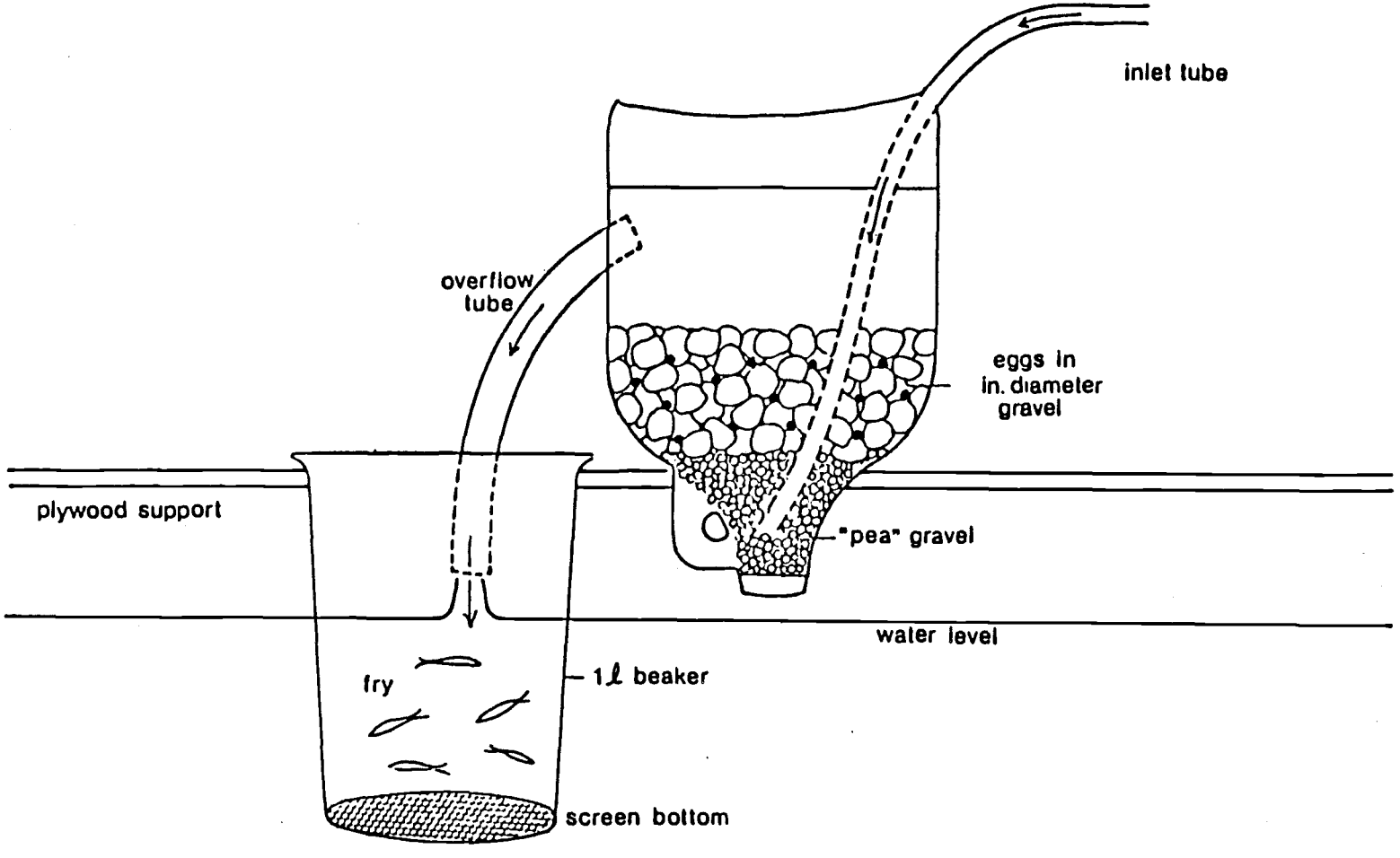

Figure 7. Scale model of a gravel substrate incubator and the trap for collecting emergent fry.

number of scale annuli plus one), weight after spawning and the weights of 25 to 30 of her eggs (green, unfertilized, not water-hardened). Similar data were collected from males from the Whiskey Creek stock; they were not collected from other males because their heads were taken off in the spawn-taking operations and because fungus infections made collection of their scales difficult. I weighed, measured, and determined the age (from a scale) of each parent in the 1976 experiment. These data are in Appendix VII.

Fish Culture Procedures

Incubation. All eggs were incubated in darkness, irrigated by Whiskey Creek water pumped to the hatchery. Appendix I is a record of temperatures observed once each day during incubation. After the eggs had developed visible eye pigment the number of eggs in each incubator was reduced to 110.

Figure 5 describes the incubator used in the 1975 experiment. It is a scale model of the shallow matrix gravel incubator used at the Netarts Station for producing chum salmon. The incubators were held in tiers five high; water was introduced to them individually at a rate of 300 ml/min.

Figure 7 describes the incubator used in the 1976 experiment. It was designed to provide a precise

observation of the emigration from the incubator. Unlike the other design, it did not allow observation of hatching. The incubators were provided an individual water supply of about 300 ml/min. They were fashioned from plastic gallon jugs.

Marking fry. In the 1975 experiment I marked by freeze-branding about 70 fish from each incubator group between 6 April and 10 April 1976. The emergent fry were anaesthetized (tricaine methane sulfonate) and marked with one or two (or no) dots above the lateral line anterior to their dorsal fins, and posterior to their dorsal fins on both their right and left sides. The dots were made with blunt dissecting probes chilled in liquid nitrogen. Each group was distributed among four tanks. When marking was complete there were four replicate tanks each with about 1400 fry in it. There was no mortality attributable to the trauma of marking. Other smaller lots of marked fry were made by clipping fins of anaesthetized fry. Pairwise combinations of fins were clipped to make several identifiable groups.

Feeding fry. Fry were fed Oregon Moist Pellet food according to the manufacturer's recommended feeding schedule which calls for rations that vary with the size of the fish and temperature of the water. The fish were fed in tanks which were similar in construction to those used by Brett, et al. (1969) i.e., oval in shape, about

200 liters capacity, supplied with about 5 liters per minute of water pumped from Whiskey Creek. Each contained about 1400 fry.

Observations

Embryonic development. I observed the span of time between spawning and hatching in the 1975 experiment by counting the number of unhatched eggs on the screen of each incubator on each day during the time when hatching occurred: 23 January through 5 February 1976. I observed the time span between spawning and emergence from each incubator in the 1975 experiment by counting the number of alevins which swam out over the downstream baffle (Figure 5) of each incubator each day beginning on 1 March 1976. Emergence of alevins from incubators was not complete when I began the next phase of the experiment--these observations were carried out only until about one half of the fish had emerged from the incubators.

In the 1976 experiment on every day between 7 March and 12 April 1977, I counted the number of fry which had swum into each incubator's fry trap (Figure 7).

Short Term Rearing

Size of fry. In the 1975 experiment the size distribution of fry in each of the incubator groups was

observed after the fry had been fed for about one month in two replicate groups of freeze-branded fry. I anaesthetized (tricaine methane sulfonate), weighed (.01g), measured (mm total length), and recorded the brand code of each fry. Fish in one tank were fed for about 28 days, those in the other tank for 33 days. I did not achieve a truly synoptic observation of the sizes of the fish because I intended to observe others of their traits and couldn't kill the fry.

Susceptibility to Disease (Vibriosis)

Artificial challenge. Twenty fry from each of 36 sibling groups were marked by fin clips according to the identity of their father in the 1975 experiment. The offspring of all four females and of three males from each of the stocks were involved. The offspring of each mother were fed in separate containers.

Two months after marking (1 June 1976), the fry were moved from the Netarts Station to the Oregon State University Fish Disease Laboratory at Corvallis. At that laboratory the fish could be exposed, in pathogen-free fresh water, to the marine bacterium Vibrio anguillarum in a controlled dose. Each of the four groups of half-siblings (each had a common mother) were housed in a separate tank.

Fish in each tank were exposed to 5 X 10^5 cells of V. anguillarum (LS 174 isolate, Department of Microbiology, Oregon State University) per ml for 15 min in quiet water after which the flow through the tank was resumed. Dead fish were collected from the tanks twice each day until mortality ceased. Each dead fish was examined: kidney tissue was aseptically streaked on Brain Heart Infusion agar medium and incubated at room temperature. Bacterial colonies which grew on the medium were tested by rapid slide agglutination against rabbit anti-LS174 serum. On 17 June, after 75% of the fry were dead and mortality had apparently ceased, I killed the survivors and examined them in the same way.

Natural challenge. In the 1975 experiment two groups of freeze-branded, reared, fry were moved from the Netarts Station to the OSU Marine Science Center at Newport, Oregon, where they were housed in two replicate seawater tanks. There they would be challenged naturally by waterborne Vibrio. The expected epizootic did not occur until after some of the brands had begun to heal (in the previous year a trial of this method had succeeded.) The parentage of dead fish could not be determined and no data could be taken.

In the 1976 experiment in order to to observe the susceptibility of different family groups to a natural, waterborne, challenge of vibriosis, I constructed live

cages out of plastic waste paper cans (Figure 8) which floated in a large tank supplied with seawater at the Marine Science Center in Newport. In these cages I could expose fry to a common pathogen environment while avoiding the requirement for an identifying mark on each fish to identify its parentage. On 6 April 1977 I moved 50 fry from each of the 35 sibling groups from Netarts to the cages at Newport. They were fed for about three weeks when the number of fry in each cage was reduced to 30 healthy fry (any 'pinhead' fry were selectively removed).

The expected epizootic began on 23 May 1977. I collected dead fish from the cages every twelve hours until 27 May when all the fish were dead. A presumptive diagnosis of vibriosis, based on morphology of colonies and sensitivity to Novobiocin and 0-129, was positive for each dead fish; the presence of Vibrio anguillarum (Serotype I) in the kidney of twelve dead fry was confirmed by rapid slide agglutination with rabbit anti-serum.

Preference for Seawater

In order to examine the variability of the age of onset of a preference for seawater, I made a device for observing the preference of fry for saline water. I constructed a trough by splitting a 35 cm diameter

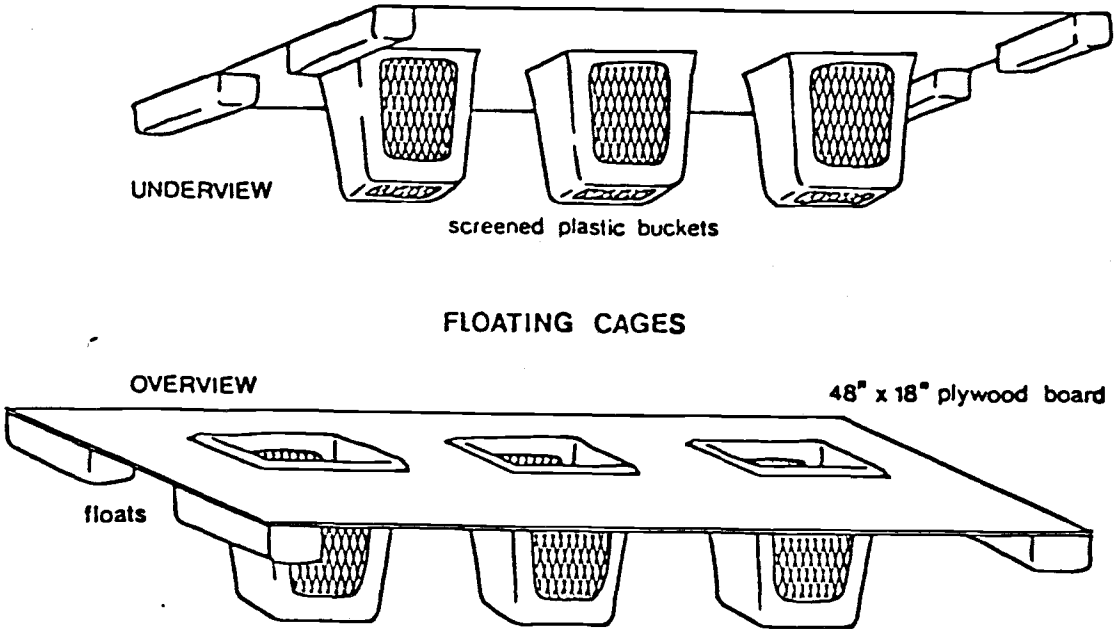

Figure 8. Live cages for culturing separate lots of fry in a common tank.

plastic pipe lengthwise. It was 90 cm long; I used baffles to close its ends and to divide it into three interconnected chambers. It had an overflow standpipe of 2.5 cm pipe at its center (Figure 9). Seawater from Netarts Bay was introduced at one end, freshwater from Whiskey Creek at the other; thus, the three chambers were characterized by three different salinities. If the flows of seawater and freshwater were equal the salinity of water in the center chamber was intermediate between zero and the salinity of the seawater (about 25 ppt).

I conducted a number of trials in which 20-100 fry, either chum salmon or coho salmon (O. kisutch), (ranging from newly-emerged to three weeks past emergence) were placed in the center chamber and left in darkness for lengths of time ranging from 15 minutes to 90 minutes.

Movement Through a Stream Channel

In the three stock experiment, I observed the time spent in a 25-foot stream channel by about 25 freeze-branded members of each of the original 80 incubator groups. About two weeks after marking, the fry were placed in an enclosure at the head end of an artificial stream. This raceway was about three feet wide, gravel lined, had vertical wooden walls, and water about 8 cm deep flowed through it at about 30 cm per

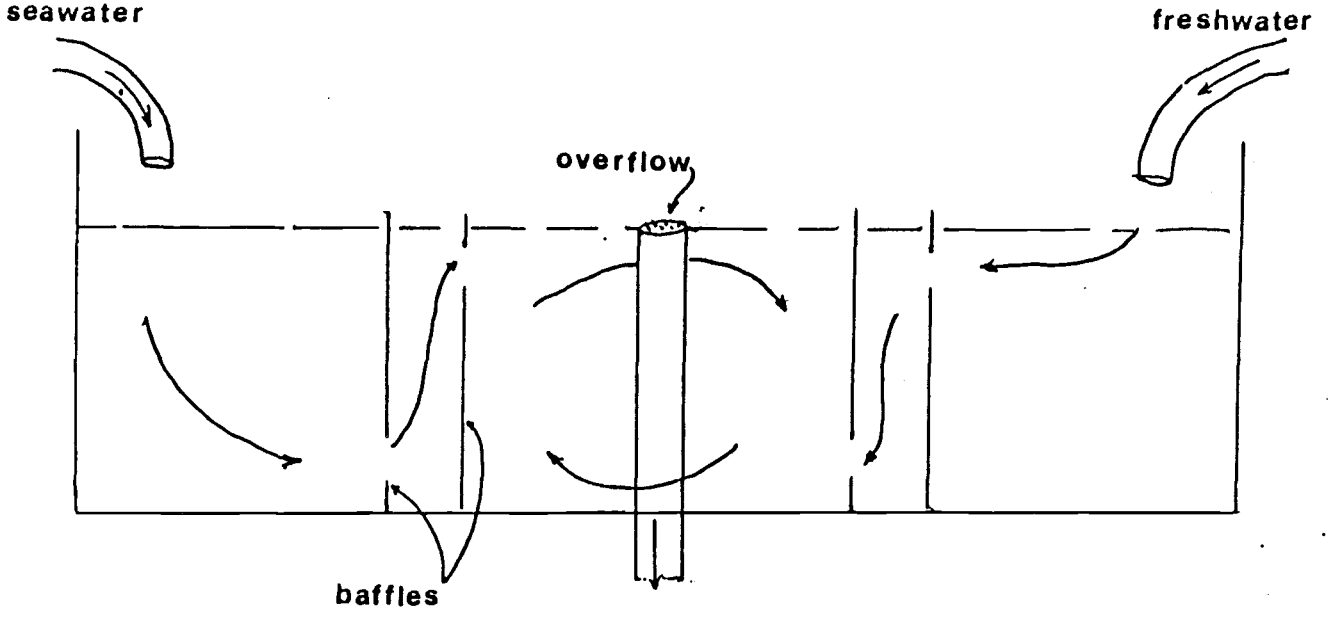

Figure 9. Trough for observing the behavior of fry in a salinity gradient.

second. After the fish had been enclosed for four days they were released at dusk. They moved from the enclosure downstream to a trap. I collected fry from the trap every half hour for seven hours, and at hourly intervals the next day. One final collection was made from the trap 36 hours after release.

Techniques of Analysis

For each set of observations, I analyzed the mean values in cells (incubator groups or sibling groups) rather than the values of individual fish in those groups. Two conditions caused me to sacrifice estimates of within cell variability: in several cases, the performances of individuals in a group were not independent of one another; and, in every case, the numbers of observations in the groups were not equal. If I had used a general least-squares technique (e.g. Harvey 1960) for analyzing these unbalanced sets of data, I would have given greater weight to the more numerous groups in the analysis. I estimated within cell variances from replicate observations of some groups: in observations of the 1975 experiments only one third of the array was replicated; I assumed that the replicate error estimated from that part applied to the entire experiment.

Transformations. When observations were of ratios (survival rates, etc.), I transformed them:

$$y = r/n;\ y' = \text{Arcsine } [(r + 1/4)/(n + 1/2)]^{1/2}$$

$$\text{or} \qquad y' = \text{Arcsine } [r/n]^{1/2}$$

where y is the observed and y' the transformed ratio. In order to satisfy the assumption that the variance was the same in each cell of an experiment, I analyzed the transformed data rather than the data themselves. The former transformation was used when y was near zero or near one.

Observations of the number of hours spent by fry in a stream channel were transformed by square roots.

Missing data. In some instances (e.g., 1976 Experiment, Susceptibility to Vibriosis), missing data were estimated by the formula

$$y = [sS + dD - T]/[(s - 1)(d - 1)]$$

where: S = sum of all cells with the same sire as the missing cell

D = sum of all cells with the same dam as the missing cell

T = grand sum of cells

s = number of sires

d = number of dams

(Snedecor and Cochran 1967).

Expected mean squares. In Appendix II are several tables which include expected mean squares for the

analyses I performed and from which I chose appropriate F tests and estimated components of variance. Approximate F tests and degrees of freedom were calculated according to the formulae in Snedecor and Cochran (1967, p. 369).

Heritability. I estimated values of heritabilities by appropriate ratios of components of variance by Kempthorne's method (1969, p. 423). In each instance heritabilities were estimated in the "narrow sense" and only from the sires' component of variance. Standard errors of these estimates were estimated according to Kempthorne's method (1969, p 246). In Appendix III, I have included the FORTRAN code by which I computed the standard errors.

In order to test the significance of differences between my estimates of heritabilities, I made a conservative estimate of a 90% confidence region around each estimate by adapting Broemeling's (1969) procedure for a hierarchical design to my factorial design (Appendix III). The confidence regions described by this technique, however, included zero and one in each case, indicating that my estimates are imprecise.

I also used a less conservative method to test the significance of differences between estimates of heritabilities by assuming that a linear combination of only three or four of such estimates would be normally distributed, computing the standard error of the

combination, forming the ratio of the linear combination and its standard error, and comparing that to a Z statistic (Snedecor and Cochran 1967).

Analysis of variance. All analyses of variance were computed using the program BMDP2V (Sampson 1975) and the Honeywell model 6600 computer operated by the University of Alaska at Fairbanks, Alaska. Wherever I have given the probability associated with a value of the F statistic, that probability has been computed using the program supplied by its manufacturer with the Tektronix model 4051 computer.

Tables of analyses of variance are included in Appendix II.

Results and Discussion

Analyses of the two experiments are summarized in Tables III and IV. The analyses of variance, tables of expected mean squares, and summaries of the observations are in Appendix II. Records of the vital statistics of the parents in the two experiments are in Appendix VII. Records of water temperature, observed each day during the incubation of eggs, are in Appendix I.

The summary tables (Tables III and IV) display the significance levels for several comparisons in the analyses, where the comparisons are possible, as well as estimates of heritabilities and their standard errors.

TABLE III

SUMMARY OF 1975 EXPERIMENT
MEAN VALUES, SIGNIFICANCE PROBABILITIES, AND HERITABILITIES

Trait	Reference Population	Mean Value	Significance of Comparisons							h^2 (SE)
			Paternal Stock (P)	Coast vs. Sound	Sires (S)	Dams (D)	Egg Size	Interaction	h^2Pure = h^2Cross	
Days Between Spawning and Hatching	Entire Experiment (2 replic)	69.306	.071 .103	.011 .039	.002 .000	.000 .000	.000 .000	PxD: .956 .640	.010	
	Purebred Whiskey Creek	69.509			.502	.003		SxD: .192		.0 (.2)
	Crossbred Nemah R.	69.548			.003	.002		SxD: insign.		1.4 (.7)
	Hoodsport	68.862			.016	.009		SxD: insig.		1.2 (.7)
Emergence From Incubators	Entire Experiment	.539	.571 .593	.358 .754	.424 .705	.047 .021	.086 .114	PxD: .229 .345	.900	
	Purebred Whiskey Creek	.534			.447	.033		SxD: .693		.0 (.2)

Table III
(continued)

Trait	Reference Population	Mean Value	Significance of Comparisons							h^2 (SE)
			Paternal Stock (P)	Coast vs. Sound	Sires (S)	Dams (D)	Egg Size	Interaction	h^2Pure = h^2Cross	
Emergence (cont.)	Crossbred									
	Nemah R.	.514			.379	.005		SxD: insign.		.2 (.4)
	Hoodsport	.573			.519	.049		SxD: insign.		.1 (.4)
Length After Feeding (two tanks) (two replicates of Whiskey Creek)	Entire Experiment	45.05 47.32	.077 .075	.032 .082	.129 .093	.036 .084	.012 .025	Tank x P: .258 .248 Tank x S: .202 .576 Tank x D: .001 .021 PxD: .779 .264 SxD: .022 .446	.100	
	Purebred									
	Whiskey Creek	45.06 47.63			.000	.099		Tank x S: .900 Tank x D: .197 SxD .410		.9 (.5)

Table III
(continued)

Trait	Reference Population	Mean Value	Significance of Comparisons					h^2 (SE)
			Paternal Stock (P)	Coast vs. Sound	Sires (S)	Dams (D)	Egg Size	Interaction	h^2Pure = h^2Cross
Length (cont.)	Crossbred								
	Nemah R.	44.69 46.53			.530	.036		TxS .034 TxD .024 SxD .077	.2 (.2)
	Hoodsport	45.39 47.47			.185	.036		TxS: .398 TxD: .091 SxD: .130	.3 (.3)
Hours Spent in a Stream Channel	Entire Experiment	12.61	.917 .542		.561 .522	.089 .065	.039 .035	PxD: .200 .234	
	Purebred								
	Whiskey Creek	13.29			.631	.005		SxD: .710	.0 (.2)
	Crossbred								
	Nemah R.	12.21			.597	.015		SxD: insign.	.1 (.3)
	Hoodsport	12.70			.430	.208		SxD: insign.	.0 (.6)

Table III
(continued)

Trait	Reference Population	Mean Value	Significance of Comparisons						h^2 (SE)
			Paternal Stock (P)	Coast vs. Sound	Sires (S)	Dams (D)	Egg Size	Interaction	h^2Pure = h^2Cross
Survival of Vibriosis	Entire Experiment	.25	.226		.037	.144		SxD: .335 PxD: .184	.320	
	Purebred								
	Whiskey Creek	.24			.127	.021				.5 (.6)
	Crossbred								
	Nemah R.	.19			.379	.589				.2 (1.0)
	Hoodsport	.29			.340	.689				.1 (1.0)

TABLE IV
SUMMARY OF 1976 EXPERIMENT
MEAN VALUES AND SIGNIFICANCE PROBABILITIES

Trait	Reference Population	Mean Value	Significance of Comparisons						h^2 (SE)
			Paternal Stock (P)	Sires (S)	Maternal Stock (M)	Dams (D)	Interaction	h^2Pure = h^2Cross	
Days Between Spawning and Emergence	Entire Experiement	121.095	.308	.284	.068	.352	SxD: .431 PxM: .132	.050	
	Purebred								
	Kilchis R.	120.673		.438		.445	SxD: .000		0.0 (1.1)
	Whiskey C.	120.396		.667		.966	SxD: .159		0.8 (1.1)
	Crossbred								
	Whiskey C. Sires	119.979		.021		.260	SxD: .702		2.2 (.8)
	Kilchis R. Sires	123.332		.550		.584	SxD: .714		.2 (.4)

Table IV
(continued)

Trait	Reference Population	Mean Value	Significance of Comparisons					h^2 (SE)
			Paternal Stock (P)	Sires (S)	Maternal Stock (M)	Dams (D)	Interaction	h^2Pure = h^2Cross
Survival of Vibriosis (natural challenge)	Entire Experiment	.46	.176	.014	.043	.015		.460
	Purebred							
	Kilchis R.	.47		.659		.060		-.2 (.3)
	Whiskey C.	.51		.260		.705		1.1 (1.3)
	Crossbred							
	Whiskey Cr. Sires	.28		.247		.336		1.8 (1.2)
	Kilchis R. Sires	.52		.545		.966		-.7 (2.0)

Where the word "insignificant" has been entered, I have compared the mean square value to a value of the error mean square estimated for a part of the experiment. In the 1975 experiment only some of the matings were observed in replicate, they provided an estimate of error mean square. Two comparisons were not planned in the design of the 1975 experiment. It so happened that two of the females had eggs which were 0.2 g in weight and the other two females had 0.3 g eggs. The comparison labeled Egg Size compares the offspring of these two pairs of females. Another comparison that was not planned in the design is that of offspring of the Hoodsport males with the offspring of the Nemah River and Whiskey Creek males; it is labeled Coast vs. Sound in Table III.

In the 1976 experiment one mating produced no live offspring. In analysis either all the data from that female were eliminated or the missing data were estimated.

Timing of Events in Chum Salmon Life Cycles

An important component of fitness in a chum salmon stock is the synchronization of events in the fish's life cycle with annual cycles of the environment. The emergence of fry from incubation gravels into nursery areas is critical. In the high latitudes at which chum

salmon spawn there are marked annual cycles of temperature and biological production, both important to the growth and survival of fry; successful fry must enter nursery grounds in synchrony with these annual cycles. Fry which emerge too early, before the onset of springtime warming, are likely to suffer high mortality as are fry which enter too late, after considerable opportunity for growth has passed (Taylor 1978, and Martin et al. 1981, have investigated the survival of emigrant pink salmon vis a vis the time of emigration and have found that the relationship between time of emigration and survival has a springtime maximum).

The time during the year at which a stock spawns is also critical because there are annual cycles of streamflow and temperature in their spawning environments. For instance, if adults enter a stream too early, they may encounter low levels of streamflow and high temperature; too late, and they may encounter floods or ice.

The date of emergence of fry is largely dependent on the date of spawning and on incubation temperature. Sheridan (1961, 1962) found that stocks of pink salmon which spawn in cold streams tend to spawn earlier in the year than stocks which spawn in warm streams so that all fry tend to emerge into nursery environments at the same time in the spring. The development rate of embryos

determines the number of days after spawning after which fry emerge. The development rate is strongly affected by temperature (see Alderdice and Velsen 1979 for a discussion of the functional relationship between temperature and development rate of salmon eggs, and Bakkala 1970 for a review of observations of chum salmon eggs) and, secondarily, by the availability of oxygen (Alderdice et al. 1958). There is evidence, however, that genetically mediated compensation does occur, allowing early spawning fish to achieve relatively slower development rates, or vice versa. Koski (1975) reports that fry from an early spawning stock of chum salmon in Big Beef Creek, Washington, emerge 35 days earlier than fry from a late spawning stock, but that their parents spawned 47 days apart, a compensation of about 12 days. There are two distinct spawning stocks of pink salmon in Auke Creek, Alaska, each year. One spawns in mid-August, one in mid-September; each spring, however, there is only one, unimodal, emigration of fry from Auke Creek indicating that embryos of the early stock experience a longer period of warmer water than those of the late stock.[2]

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[2]Records maintained by S. G. Taylor, Auke Bay Laboratory, Auke Bay, Alaska, U.S.A.

There is evidence that the annual timing of spawning of a pink salmon stock is itself a heritable trait in data gathered by Taylor (1977, 1978). In Appendix IV, I show calculations of an estimate of the heritability of spawning date in Auke Creek pink salmon of about one fourth.

Development rate of chum salmon embryos: time between spawning and hatching. The development rate of chum salmon eggs is heritable. I observed two indicators of development rate: the number of days between spawning and hatching, and the number of days between spawning and emigration of fry. Both were observed in fry which were incubated in a common water environment so that no effect of different temperatures was felt. According to Ballard (1973) in salmonoids the same orderly progression through embryonic stages from fertilization to hatching occurs at any tolerable temperature; the time between fertilization and hatching, therefore, is a good indicator of an underlying development rate for a given temperature regime. Similarly the time between fertilization and emigration from an incubator is closely related to the time which would elapse in nature between spawning and emergence. Emergence from incubation gravels is the adaptively important outcome of development rate. In the 1975 experiment, I observed that the mean time between fertilization and hatching was significantly different

for offspring of different paternal stocks (Table III). Furthermore, offspring of different mothers required significantly different lengths of time between spawning and hatching.

Some of these differences can be explained by the hypothesis that development rate is adaptively important to stocks and a comparison of the stocks' native environments. Two of the paternal stocks spawn in streams which drain west-facing coastal hills into shallow bays on the open Pacific Ocean coast: Nemah and Whiskey Creek; the other, Hoodsport, spawns in a tributary of Puget Sound that drains east-facing slopes of the Olympic Peninsula. The average temperature of the incubation water at Hoodsport between mid-November and the first of April is 6.7C, at Nemah 7.8C, and at Whiskey Creek 7.8C. (The average of the weekly average daily maxima and minima for Nemah and Hoodsport Hatcheries for the years 1969 through 1973 reported by Rasch 1974 and from similar records at Whiskey Creek.) One would expect, therefore, that the Hoodsport stock, adapted to a cooler incubation temperature, would have a quicker development rate at a given temperature than the other in order that fry would emerge after the same period of incubation. A comparison of Hoodsport with the others is labeled Coast vs. Puget Sound in Table III, and reveals a significant difference of development rate.

Differences of the size of eggs explain much of the difference between females. The larger eggs from females B and C developed significantly faster than the smaller eggs from females A and D. This comparison is labeled Egg Size in Table III.

The proportionate contribution of additive genetic variability was relatively greater in crossbred than in purebred groups. The offspring of Whiskey Creek fathers were a purebred group, those of the other paternal stocks were crossbred. The observations of the offspring of the three paternal stocks were analyzed separately. The heritability of hatching time was estimated for each group, as was the standard error of the estimate. I tested[3] the null hypothesis that heritabilities are the same for crossbred and purebred groups, and rejected that hypothesis. This supports the hypothesis that different alleles affecting development rate have been selected in the different paternal stocks.

In the analysis of offspring of Whiskey Creek sires (Appendix IIA), I was able to compute an Error term because each of the cells in this part of the experiment was duplicated. In this analysis the interaction of

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[3] $1/2h_N^2 + 1/2h_H^2 - h_W^2 = 1.29$

$SE = [1/4(SE_N)^2 + 1/4(SE_H^2 = (SE_W)^2]^{1/2} = 0.55$

$Pr[Z>(1.29/0.55 = 2.34)] = 0.0096$; (Selby 1971; p 577ff)

sires and dams is not significant; if I assume that the same error term applies to the other analyses, I find that again the interactions of sires and dams are insignificant. Applying this estimate of within cell variability to the analysis of the entire experiment (Appendix IIA3), I find that neither the interaction between paternal stock and dams nor that between sires within paternal stocks and dams is significant. These findings support the hypothesis that the action of alleles effecting development rate is largely additive, exhibiting little dominance or epistasis.

Time between spawning and emergence. After about half of all fry had emerged in the 1975 experiment, I computed the proportion emerged in each cell. Emergence from incubators was similar to hatching in that relatively more offspring of Hoodsport fathers emerged than of Whiskey Creek or Nemah fathers (Appendix IIB1). Among the females, however, the pattern was different than that exhibited by hatching time. Offspring of female A emerged in greater proportion than the others. Only the differences between offspring of different females were significant however (Table III and Appendix IIB2). Again, the comparison between egg sizes reveals a significant difference, but it is due to the anomalously large value for the offspring of female A.

Separate analyses of observations of offspring of different paternal stocks did not reveal any significant effect of sires implying that estimates of the heritability of emergence date would not be high (Table III and Appendix IIB3). Even though emergence date ought to be a reflection of the same underlying development rate as hatching time, it is not surprising that no differences between paternal stocks or between sires were found because of the comparatively imprecise manner in which I observed emergence. I cannot reject the hypothesis that heritabilities estimated in purebred and crossbred groups are the same.[4]

In the 1976 experiment, there were two purebred and two crossbred groups. Appendix IIC1 lists the mean number of days between fertilization and emergence for each group. There were no significant differences between paternal stocks, sires, or dams; maternal stocks may have produced a significant effect (Table IV, Appendix IIC3). These are not surprising findings considering that the parental stocks spawn nearby to one another, separated by only about 32 km of coastline (Figure 6), whereas the parental stocks in the 1975

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[4] $1/2h_N^2 + 1/2h_H^2 - h_W^2 = 0.063$

$SE = [1/4(SE_N)^2 + 1/4(SE_H)^2 + (SE_W)^2]^{1/2} = .374$

$Pr[Z>(0.063/0.374 = 0.168)] = 0.90$

experiment were separated by as much as 560 km (Figure 4). Presumably the ordinary amount of straying between nearby stocks would tend to eliminate differences between them and they are presumably adapted to similar environments.

In the two purebred groups the estimates of heritability of emergence were low, as predicted. In the crossbred groups, however, one estimate was high, and one was low. The standard errors of these estimates were rather large (Table IV, Appendix IIC4).

I tested and rejected with slight confidence (P = .05) the hypothesis that the heritabilities are the same in the purebred as in the crossbred groups.[5]

Qualities of Fry

Size of fry after feeding. Growth of fry in a tank on an artificial diet is probably not a trait closely related to the growth of fry in a wild state; it probably is correlated with growth of fry in an artificial production facility so that these observations have relevance to fish culture. Short-term rearing of chum

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[5] $(1/2h_{KK}^2 + 1/2h_{WW}^2) - (1/2h_{KW}^2 + 1/2h_{WK}^2) = -1.38$

$SE = [1/4(SE_{KK})^2 + 1/4(SE_{WW})^2 + 1/4(SE_{KW})^2 + 1/4(SE_{WK})^2]^{1/2} = 0.850$

$Pr[Z\ (1.38/0.85 = 1.62)] = 0.05$

salmon fry has become increasingly important to Japanese chum salmon aquaculturists where the practice has resulted in a doubling of survival rates (Moberly and Lium 1973; Kobayashi 1980). In Table I the greater survival rates since 1968 are associated with broods in which more than half the fry were released after short term rearing. It is not clear whether the higher survival of reared fry is due to their larger size at release or to the propitious delay of their entry into a wild environment, but there is evidence that chum salmon fry of a larger size are more likely to survive than are smaller fry (Levanidov, reported in Kanid'yev, et al. 1970; Hiyama, et al. 1972).

I fed two replicates of 80 groups of fry from the 1975 experiment for one month (Appendix IID1). Offspring of fathers from different paternal stocks were significantly different from one another, offspring of different sires were significantly different, and offspring of different dams were significantly different (Table III and Appendix IID3). The effect of egg size is important. The comparison of the offspring of coastal with those of Puget Sound paternal stocks revealed no significant difference. One interaction effect, that between tanks and dams, was significantly large in both versions of the analysis (each incorporating a different set of replicates of the Whiskey Creek portion of the

experiment). This interaction was apparently associated with the difference between the two pairs of dams which had different size eggs: (Females A and D had small, 0.2g, eggs; B and C had large, 0.3g, eggs; cf. Appendix VIIA.)

Dam	Length Difference Tank II - Tank I	Mean Length Tank I, Tank II
A	2.09	45.2
B	1.64	47.7
C	1.48	46.6
D	3.14	45.8

The smaller eggs produced smaller fry but showed larger between-tank differences. Since fish in Tank II were fed for a longer period before being measured, I would expect that groups of larger fish would show the greater differences because the rate of growth of fish ought to be size-specific.

Because the fish had been fed in Tank II for a longer period of time and under different feeding conditions during the final week before measurement, the weight-length relationship was significantly different in the two tanks. Regression of the logarithm of length (mm) on the logarithm of weight (g) gave

$$\text{weight} = 0.0030\ (\text{length})^{2.71}$$

in Tank I, and

$$\text{weight} = 0.0006\ (\text{length})^{3.15}$$

in Tank II. F-tests of hypotheses of equality of mean values and regression coefficients in the two tanks led to their rejection. Therefore I chose to analyze length observations as being less subject to the different environments in the two tanks; I reasoned that the length of a fish would not respond as quickly to a period of overfeeding as would weight.

There is no evidence that heterosis is important in the growth of these fry. The purebred groups were as large or larger than the crossbred groups.

These findings support a hypothesis of different, additively acting, alleles effecting growth in different stocks. In analyzing the offspring of different paternal stocks separately, however, I found the heritability of size to be high in the purebred group and low in the crossbred groups, a pattern contrary to that found for development rate characters (Table III). This pattern would be consistent with alleles at intermediate frequencies in the Whiskey Creek stock, but near fixation in the other paternal stocks (Figure 1, Figure 2). I tested the hypothesis that there is no difference between the heritability estimated in the purebred group and

those estimates made in the crossbred groups.[6] I rejected the hypothesis of no difference.

Residence in a stream channel. I observed the length of time spent in an artificial stream by differentially marked members of groups in the 1975 experiment hypothesizing that a tendency to migrate quickly out of the confined stream environment might be important to survival. These observations, transformed by square roots, are in Appendix IIE. The only significant differences are between dams (Table III, Appendix IIE2). A comparison of females A and D with B and C shows a significant difference between these two pairs; the groups descended from larger eggs, which presumably were of the larger fry, spent more time in the stream channel. Separate analysis of the offspring of different paternal stocks provided no evidence that the trait is heritable in either purebred or crossbred groups (Table III, Appendix IIE3).

Preference for seawater. In every trial chum salmon fry distributed themselves evenly through the salinity gradient; none of the groups showed preference for or aversion to seawater. Fry which were marked by fin-clips

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[6] $1/2h_N^2 + 1/2h_H^2 - h_W^2 = -0.68$

$SE = [1/4(SE_N)^2 + 1/4(SE_H)^2 + (SE_W)^2]^{1/2} = 0.54$

$Pr[Z>(0.68/0.54 = 1.266)] = 0.10$

according to their parentage (Whiskey Creek mother, Kilchis father; Whiskey Creek father, Kilchis mother; Whiskey Creek mother, Whiskey Creek father; Kilchis River mother, Kilchis River father) were distributed evenly in the trough. I was never able to observe any preference for either fresh- or seawater by chum salmon fry. Coho salmon (O. kisutch) fry (which are not ordinarily exposed to seawater in nature), however, clearly preferred the freshwater end of the trough: for instance after 90 minutes in the trough, of 20 fry which had been placed in the center chamber 18 moved to the freshwater end, and two remained in the center; not one moved to the seawater end. These observations of coho fry gave me confidence that the device worked, that groups of salmon fry would display a preference or aversion in it.

Susceptibility to vibriosis. Vibriosis is an infectious disease of marine fish caused by the cosmopolitan marine bacterium Vibrio anguillarum. It is a particularly troublesome disease of salmon when they are cultured in seawater, causing extensive mortality in infected lots of fish (Cisar and Fryer 1969; Evelyn 1971; Sawyer 1978.) Vibriosis can also infect and damage wild stocks of marine fish (National Marine Fisheries Service 1975). Descriptions of the disease, its etiology, pathology, diagnosis, and control are given by Fryer et al. (1972) and by Novotny et al. (1975). The importance

of vibriosis to stocks of wild salmon is not known.

If susceptibility to vibriosis is heritable in an artificially cultured stock of salmon the offspring of survivors of the disease ought to, be on the average, less susceptible than their parents' generation. In this way a resistant stock of salmon might be bred.

In the 1975 experiment, I observed mortality after an artificial, controlled exposure to Vibrio of the offspring of matings of four females with three males from each of the parental stocks. Appendix IIF1 summarizes those observations. The differences between the groups' offspring of different parental stocks were not significant; but differences between the offspring of different sires from the same parental stocks were significant (Table III, Appendix IIF2). It may be that the survival rate of offspring of Nemah sires (0.17) is significantly different from that of the offspring of Hoodsport fathers (0.29); the Least Significant Difference (Snedecor and Cochran 1967, p. 272) between the mean survival rates of offspring of different paternal stocks is 0.10. However, since the effect of paternal stocks is not significant, the use of this criterion is questionable. The finding of significant differences between offspring of different dams is trivial because the effects of tanks and of dams were confounded in the experiment and a significant difference

between tanks is to be expected. In order to compare heritabilities determined by separate analysis of the data from the paternal stocks, I assumed that sire by dam interactions were negligible. To make that assumption, I analyzed a subsample of these data (in order to have equal numbers of fish in each cell of the analysis) and used the binomal estimate of within cell variance (Snedecor and Cochran 1967, p. 494). This analysis, Appendix IIF3, does not indicate interaction between sires and dams. The separate analyses of the survival rates of offspring of different paternal stocks are given in Appendix IIF4. I cannot reject the hypothesis that the heritability of susceptibility to vibriosis is different in the purebred groups than it is in the crossbred groups.[7]

In the 1976 experiment, I observed the survival of offspring of different maternal and paternal stocks in a natural epizootic of vibriosis. In this experiment, all groups experienced the same mortality (total); I recorded, however, the mortality in each group at a time during the epizootic when about one half of all fish were dead (Appendix IIG2). Implicit in the analysis of these

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[7] $1/2h_N^2 + h_H^2 - h_W^2 = -.0.42$

$SE = [1/4(SE_N)^2 + 1/4(SE_H)^2 + (SE_W)^2]^{1/2} = 0.913$

$Pr[Z>(0.42/0.913 = 0.456)] = 0.32$

data is the assumption that less susceptible fish succumbed later in the epizootic than more susceptible fish.

Analysis of variance (Table IV, Appendix IIG3) revealed a significant difference between maternal stocks, and possibly a significant difference between paternal stocks (the probability associated with the F statistic for this test is only 0.176). There were significant differences between dams. I analyzed the two purebred and two crossbred groups individually (Table IV, Appendix IIG4) and estimated heritability in each group. Again I could not reject the hypothesis of no difference between the heritabilities in the purebred and crossbred groups.[8]

These observations of susceptibility to vibriosis, either in an artifical challenge or in a natural epizootic, neither support nor contradict my hypothesis predicting greater variability in crossbred groups of salmon. It is unlikely that liability to vibriosis is an important component of the fitness of chum salmon stocks;

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[8] $(1/2h_{KK}^2 + 1/2h_{WW}^2) - (1/2h_{KW}^2 + 1/2h_{WK}^2) = -0.119$

$SE = [1/4(SE_{KK})^2 + 1/4(SE_{WW})^2 + 1/4(SE_{KW})^2 + 1/4(SE_{WK})^2]^{1/2} = 1.36$

$Pr[Z > (0.119/1.36 = 0.087)] = 0.46$

in nature they probably do not encounter the warm temperatures coupled with the stressors of artificial culture that are associated with epizootics of vibriosis. It is unlikely therefore, that different stocks would be adapted to different "vibriosis environments." The significant differences between sires within the paternal stocks revealed by the analysis of the entire experiment indicate that selection could have a positive effect in increasing resistence to vibriosis in a hatchery stock.

Summary

Of all the traits which I observed, the one that is probably most correlated with an adaptively important trait of wild stocks and that was observed with the greatest precision--time elapsed between fertilization and hatching--provided observations which most strongly support the hypothesis that different alleles affecting the trait are selected in different stocks. If selection for quicker or slower development rate were an important consideration for a hatchery, stocking the hatchery with crossbred individuals would be a useful practice.

The differences between Whiskey Creek and Nemah or Hoodsport stocks are apparently greater than the differences between the Whiskey Creek and Kilchis River stocks. This is to be expected if genetic distance and geographic distance are related--straying of occasional

members of a stock to a neighboring stock, which probably occurs in chum salmon, would tend to cause such a relationship.

Since for several traits I found that genetic variability is relatively greater in crossbred groups, I would expect that crossbred groups will adapt more quickly to a new (artificial culture) environment. Managers of new chum salmon hatcheries can benefit by initially stocking a facility with crossbred stocks because these stocks will more quickly respond to the selection imposed by the new environment. They should, however, use such a practice within limits, and recognize that it is probably more important to choose broodstock from ecologically similar, nearby stocks.

Two other traits which could be important to domesticating chum salmon, size after short-term feeding and susceptibility to disease, exhibit significant differences between sires generally. This indicates that progress can be made through selection based on these traits. Low values of heritability of the second and the lesser significance of differences in disease susceptibility indicate that progress through mass selection would be slow.

The general lack, in these experiments, of significant interactions between sires and dams (Tables III, IV) supports an additive model of gene action. It

does not easily support a model such as Lerner's (1954) which predicts important interactive effects for traits which are important to fitness.

Evidence for maternal effects apparently related to egg size is noteworthy but not surprising. Evidence for significant genotype-environment interactions is found in the significant tank-by-stock and tank-by-parent interactions in the 1975 feeding experiment.

PART TWO

APPLICATION OF QUANTITATIVE GENETICS TO THE BIOLOGY OF CHUM SALMON STOCKS

Introduction. A Conceptual Model of the Response of a Typical Chum Salmon Population to Selection

The life history of chum salmon is complex, they endure environments ranging from freshwater stream beds to the open ocean. Each environment imposes a significant mortality on a cohort as it matures. Different stocks are adapted to different sets of environments and therefore exhibit different adaptations to their environments; for instance, some stocks spawn early in the year, and some late; some stocks mature at young ages, others at older ages; etc. An understanding and prediction of the genetic response of a chum salmon stock to changes of management practice requires, therefore, an understanding of its adaptation to its environments and its response to changes of its environments. Furthermore, this understanding requires knowledge of the many relationships between different aspects of the biology of chum salmon; many of these relationships are paradoxical, making understanding and prediction difficult.

Here are some examples of relationships and the questions they raise: the determinants of maturation age

are related to growth. Chum salmon that grow fast at early ages tend to mature at younger ages; however, fish that grow more slowly at early ages, which mature at older ages, tend to be larger at maturity than their faster-growing counterparts because of their advanced age. (Ricker 1980; Helle 1979a). What, then, would be the effect of choosing large fish to breed?

Larger fry released from a hatchery late in the spring may be retarded in growth (Martin et al. 1981) but large fry released early in the spring may mature at younger ages because of their head start on growth (Helle 1979b, reporting Asian experiences). How, therefore, should a hatchery manager schedule the release of fry?

Larger females are more fecund (Helle 1979a; Koski 1975) but older females of a size are probably not more fecund.[9] Fecundity and egg size are inversely related in females of a given size;[9] egg size correlates with the size of fry (Koski 1975) which correlates with survival

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[9]Koski (1975) finds, in Appendix Table 2, that the correlation between fecundity and age is significant ($p = 0.05$). However, computing from Koski's statistics the partial correlation (Snedecor and Cochran, 1967 p. 402) between age and fecundity over all lengths, I find $r = 0.05$ which is not a significant value. Similarly Koski found that fecundity and egg size are not significantly correlated, but computing, with his data, the partial correlation coefficient between egg size and fecundity overall lengths I find there is a significant ($p = 0.01$) negative correlation between fecundity and egg size ($r = -0.99, -0.80$ for observations of the Hoodsport stock of chum salmon made in 1971 and 1970).

(Hiyama et al. 1972; etc.). Should the hatchery manager select larger or more fecund fish as breeders?

Early-spawning fish in a run are likely to be older (Helle 1960, 1979a; Thorsteinson et al. 1963) but males, which tend to be younger (Helle 1979a, Sano 1966), predominate among earlier fish in a spawning run (Gilbert 1922, Marr 1943, Henry 1954, Semko 1954, all reported in Bakkala 1970). What will be the outcome of allowing only earlier or only later fish to breed?

Survival of eggs to become spawning adults is related to the size of parents; the size of spawners is related to the sea temperature they experience in their final growing season as well as to their age; the age of spawners is related to their growth during their second growing season (Helle 1979a). Will the average age of a stock change in response to selection of older or younger breeders, or will it only reflect ocean conditions?

These relationships, and others, can be collectively used to understand and predict the response of a stock to environmental or managerial change only within the framework of a model that incorporates all of the important relationships between aspects of the biology of chum salmon and between chum salmon and their environments. The conceptual model presented here (Figure 10) provides such a framework in a way that

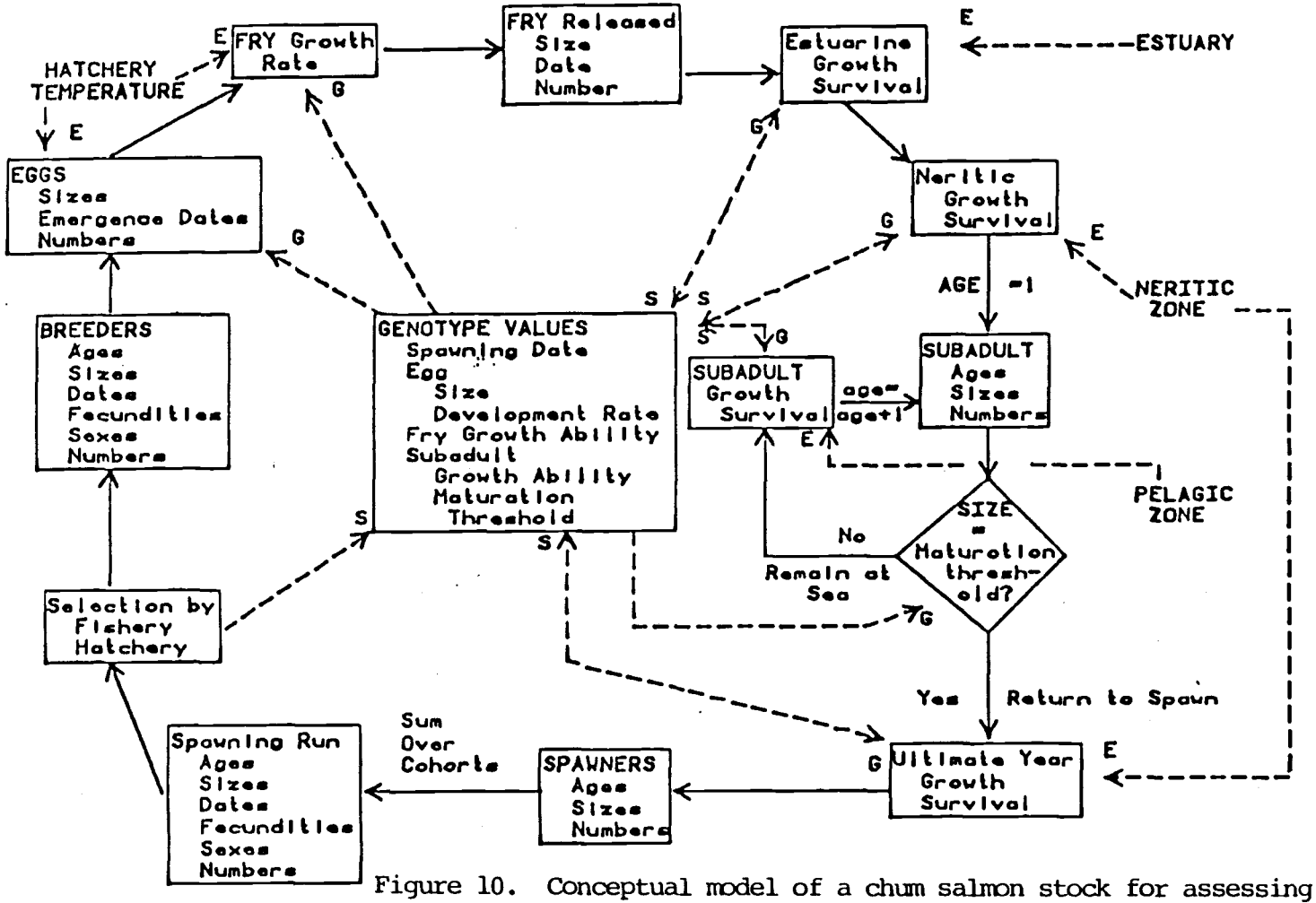

Figure 10. Conceptual model of a chum salmon stock for assessing the effects of selection.

permits explicit consideration of genetic responses to either environmental or managerial pressures.

The model's goal and point of view. The conceptual model's goal is to assess the differences in the performance of a stock of chum salmon, both heritable and not, associated with alternative management practices or with different biotic and abiotic environmental states. Performance may be measured in several ways, e.g., age, size, fecundity, etc. It answers the question, "What change in the collective genotype of a stock and consequently in the performance of the stock will be brought about by a change of conditions, particularly the employment of different management practice?"

The model operates from the point of view of a manager, either the manager of a hatchery who makes decisions about which members of the population breed and about certain features of the environment of their early life, or the manager of a fishery who makes decisions which affect the breeding structure of the population and who needs to understand the relationships between environmental conditions and the productivity of the population.

The manager of a hatchery must decide, for instance, when and at which size fry emigrate to the sea, whether larger fish should predominate among the breeders, or whether early members of the spawning immigration should

comprise the breeding population (should incubators be filled with eggs from the first available females to reach the hatchery?). The manager of a fishery also makes decisions concerning the size distribution of spawners by establishing the size-selectivity of gear. For instance, Ricker (1980) found that gill net fishermen in northern British Columbia have selectively fished smaller chum salmon in recent decades because of the size of the meshes of their nets. A fishery manager also can affect the distribution of spawning times by setting the season of harvest either early or late during the spawning run.

Responses to selection and correlated responses. Prediction of the population's heritable response to these management practices is not a simple matter of applying estimates of the heritability of age, size, fecundity, etc., and the intensities of selection on each of them caused by a management practice. Although nothing is known about the genetic correlation between characters in any chum salmon stock, undoubtedly such correlations exist: selection applied to a trait may elicit a correlated response of other traits as well. For instance, selection of age or size might result in a change of the fecundity in the stock; selection of timing of spawning might result in a change of the distribution of ages or sex in the stock.

Knowledge of correlated responses to selection (Falconer 1960, Chapter 19) is doubly important in the prediction of a stock's response to management practice. Responses of traits nominally different from the trait under selection must be considered, and since environments change any trait must be regarded as two different, correlated, traits in succeeding generations. This is a paradox: estimates of heritability or genetic correlation presume that the environment does not change, yet the environment of a chum salmon population does change from year to year in ways that probably cannot be understood fully. We could assume that environmental changes are unimportant, that a trait measured in one generation is genetically highly correlated with the same trait measured in a succeeding generation even though the environment is changed. Or we could assume that simple characterizations of environmental change can explain changes of a trait; e.g., that growth is simply related to sea surface temperature, so that known environmental changes could be factored-out in predicting the stock's response. This latter is the approach taken here; it implicitly assumes that there is no genotype-environment interaction.

State variables and forcing functions. The state variables of the conceptual model (Table V) include

TABLE V

State Variables and Forcing Functions of the Conceptual Model

STATE VARIABLES

- Fry
  - Number
  - Size
- Estuarine Juveniles
  - Number
  - Size
- Neritic Juveniles
  - Number
  - Size
- Pelagic Subadults
  - Number
  - Size
  - Age
  - Maturation threshold
- Ultimate Year Subadult
  - Number
  - Size
  - Age
- Adult
  - Number
  - Size
  - Age
  - Sexes
  - Fecundities
  - Spawning Date
- Breeders
  - Number
  - Size
  - Age
  - Sexes
  - Fecundities
  - Spawning Date
- Eggs
  - Size
  - Number
- Genotype
  - Spawning Date
  - Egg Size
  - Egg Development Rate
  - Fry Growth Rate
  - Juvenile Growth Rate
  - Subadult Growth Rate
  - Maturation Threshold

FORCING FUNCTIONS

- Environmental
  - Fluvial/Hatchery
    - Temperature
    - Oxygen Content
    - Predation/Competition
  - Estuary
    - Temperature
    - Food
    - Predation/Competition
  - Neritic
    - Temperature/Upwelling
    - Food
    - Predation/Competition
- Managerial
  - Date and Size of
    - Fry Release
  - Selection of Breeders
    - Date
    - Size

the number and size distributions of members of the stock at each of eight life stages: fry, estuarine juveniles, neritic juveniles, pelagic subadults, ultimate year subadults, adults, breeders, and eggs. In addition the subadult stages are characterized according to age distribution, the pelagic subadult stage to maturation threshold, and the adults and breeders according to distributions of age, sex, fecundity, and spawning date. Other state variables are distributions of genotype values in the stock for spawning date, egg size and development rate, growth rates of fry, juveniles, and subadults, and maturation thresholds.

Forcing functions are of two kinds, environmental and managerial. The environmental functions include both biotic and abiotic forces; the environment is categorized as fluvial or hatchery, estuarine, neritic, and pelagic. Managerial forces are affected by such decisions as those which determine the date and size of release of fish from a hatchery, and the selection of the size and spawning date of breeders.

Functional relationships. At each of the life stages, the number of fish is functionally related to the number of the preceding stage by a survival rate. The distribution of sizes at each stage is related to that in the previous stage by growth rates. Survival rates between stages are determined by (a) the sizes of

individuals in the earlier stage and (b) by environmental conditions. Growth rates of individuals from stage to stage are determined (a) by the genotypic values, (b) by environmental conditions, and (c) by the sizes of individuals.

Maturation age. Each cohort of fry can contribute to the run of returning spawners in several different years at ages II through VI. The relative contributions of a cohort to different years' spawning runs depend on the ages at which members of the cohort mature. The age of maturation of an individual is determined in the model by comparing its size as a subadult to a threshold size. The threshold size is specific to the age of the subadults, and it increases with age. Ricker (1964, 1980) and Helle (1979a) described inverse relationships between rate of growth and age of maturity of chum salmon by back-calculating lengths-at-age of mature salmon. Mature fish aged five years were found to have been smaller at younger ages than those aged four, etc. Helle's work further demonstrates that growth attained by chum salmon during their first summer is not correlated to age of maturity, but that growth attained during the second (and probably succeeding) summer is negatively related to age of maturity which implies that the "decision" to enter maturity is made by most of the fish after their penultimate growing season--the majority

mature at either three or four years of age. Other Pacific salmon also exhibit this relationship between maturation age and growth rate (Ricker 1980; Childs and Law 1972).

Because there is considerable overlapping of the size distributions of mature chum salmon of different ages, the determination of spawning age in chum salmon is probably not simply related to growth rate. In the model there are two traits underlying maturation age: growth rate and maturation threshold size. The model tests each fish each year against a threshold size specific to the age of the fish. If the fish exceeds the threshold size, it joins the spawners at the end of the succeeding year; if it does not exceed that size, it undergoes another comparison after the next year's growth against another maturation threshold. Maturation threshold sizes specific to older ages are larger than those specific to younger ages. Each of these underlying traits varies between individuals--each is heritable.

For each spawning year, the population of adults is the aggregate of all the constituent ages. The time distribution of spawning is determined by the genotype of the stock and such aspects of the environment as tide cycles, ocean temperatures, and the discharge of the spawning stream.

Genetic selection. The central feature of the model is an array of genotypic values. These values, key determinants of the stock's bionomic performance, are distributed normally over the stock. They determine, along with environmental influences, traits of the stock. Certain important other traits are derived from them, e.g., fecundity is determined by size and egg size.

The array of genotype values is changed by selection whenever mortality is related to a trait of the stock, e.g., whenever size-related mortality occurs. Artificial selection acts on the array of genotype values when the manager of either a hatchery or fishery selects part of the run to breed; e.g., by allowing an early or late portion of the run to breed or by taking larger or smaller fish to breed. Each trait may be genetically correlated with any other trait so that selection which changes the genotypic values of one trait could change the values of all the other traits according to the extent of the correlations between them. There may be no correlation between some pairs of traits.

Thus the model allows characteristics of the stock to change in response to selection. The number, size, age, and spawning date of the breeders takes into account these selection processes. The fecundity of the females is a function of their size, their age, and the genotypically influenced size of eggs. The sex ratio is

influenced by the age of the spawners and their dates of spawning. The number of eggs is simply a product of the number of breeders, their sex ratio, and fecundity. The size of eggs is genotypically influenced. The development rate of eggs is genotypically influenced and is related to the size of eggs; it is also affected by the temperature of the incubation water. The number, size, and emigration date of fry are derived from the number, size, spawning date and development rate of eggs; if a hatchery stock is being modeled, the high survival of eggs and the controlled release date can be included; if a wild stock is being modeled, a survival rate of eggs which depends on various environmental factors can be included. If the variability of the genotypic values of a trait is appreciable, it will change and in the next generation the mean value of the trait will have changed.

The variability of genotype values in stocks of chum salmon will not be easily measured, but estimates of the heritabilities of traits will provide information about the relative contribution of genotype variability to the total variability. If the contribution of environmental variability to the total variability of the trait remains constant from generation to generation then estimates of heritability can be applied in the model to predict genetic change. If another trait is correlated with the trait under selection, its genotypic value will change

commensurately. In the model this is accomplished in a simplified way: the genotype value is the mean of values achieved over the range of environments experienced by the stock; environments are characterized by simple measurements (temperature, upwelling indices, numbers of competitors, etc.) and actual mean values of traits are determined by adding these contributions. This is tantamount to assuming that there is no genotype-environment interaction for these traits; for instance, that growth at one temperature has a large genetic correlation with growth at another temperature.

Environmental relationships. Sea surface temperature has been shown by Helle (1979a) to correlate with growth of individuals in a chum salmon stock. Helle found that the amount of growth in the penultimate year of life is important in determining the age at which maturation is achieved and that growth in the final year is important in determining the ultimate size of spawners which, in turn, is highly correlated with the number of returning offspring produced by those spawners. Ricker (1978, 1980) found that changes of ocean temperature failed to entirely account for secular changes of mean sizes of pink and chum salmon which spawn in British Columbia. The sea surface temperature records he examined, however, were from coastal stations and from Ocean Station Papa (50° north latitude, 145° west

longitude), near the extreme edges of the ocean range of British Columbia chum salmon (Childerhose and Trim 1979) and may not adequately represent the temperature environment of those stocks. Temperature is easy to measure and is a characteristic of the environment for which long-term records exist. It may only be a simply measured indicator of other qualities of the environment, or it may be a primary effector of growth and survival; in either case, it can be used effectively in the model as a measure of the influence of the ocean environment on traits of chum salmon. Our knowledge of the relationships between water temperature and the rates of development and growth of salmon embryos and fry in artificial culture is more precise; positive correlations are well known (e.g., Alderdice and Velsen 1978; Brett et al. 1969).

Variations of other environmental indices have been used to explain variations in the productivity of salmon stocks. For instance, Gonsolus (1978) found that upwelling indices on the Oregon Coast (Bakun 1973) were highly correlated to growth and survival of coho juveniles in their first summer of foraging in the ocean. However, Helle (1979a) found no correlation between upwelling indices and the productivity of a chum salmon stock from the Gulf of Alaska.

Blackbourn (1980) reported a very high correlation ($r = 0.999$) between marine survival of chum salmon fry spawned at Big Beef Creek on Hood Canal in Puget Sound, Washington, and the discharge during June of the Snohomish River which empties into northern Puget Sound. He also reported a high correlation between the survival of pink salmon fry (returns per spawner) from Kodiak Island and sea surface temperatures in the Gulf of Alaska.

Biological relationships. The early survival of fry is enchanced by the increased size of fry which enter into the marine environment. Parker (1971) found this to be true for pink salmon and Hiyama et al. (1972) demonstrated greater survival among larger chum salmon fry released into a river. The size of fry at release is larger if eggs are larger (Koski 1975). Larger eggs, however, may be gotten at some cost in fecundity (see footnote 19). The size of fry at release is also larger if fry are reared before release. The growth of fry being reared will be enchanced (within limits) by warmer temperatures (Brett et al. 1969) and by extending the period of rearing. Rearing periods can be longer without arbitrarily extending them past the preferred release date if the date of spawning is earlier, the incubation temperature is warmer (Alderice and Velsen 1978), or if the temperature specific rate of embryonic development is

faster. Rearing periods could be extended past the preferred release date but survival probably would be poorer (Martin et al. 1981).

Evidences of relationships between growth, size, and age at maturity have been reviewed above.

The ratio of sexes in a spawning stock is related to the ages of the spawners. Sano (1966) and Helle (1979a) found that males tend to predominate among younger spawners and females among older so that the net result is a ratio of one. Males also tend to predominate among earlier spawners in a run and females among later spawners (Helle 1979a, Gilbert 1922, Marr 1943, Henry 1954, Semko 1954 all cited in Bakkala 1970). This would lead us to expect younger fish in the early part of a run; contrarily Helle (1979a) found that among males and among females older individuals tend to spawn earlier in the run.

Evidence for interspecific competition between chum and pink salmon is provided by Gallagher (1979). He demonstrates odd-year, even-year patterns in the size of chum salmon runs and age at return of chum salmon in Puget Sound that are apparently related to the odd-year presence of spawning pink salmon in Puget Sound. Pink salmon are virtually absent in even-numbered years. He also demonstrates that the survival of pink salmon fry is negatively related to the abundance of chum salmon.

These relationships he explains by competition between fry and fingerlings of the two species during their early sea life in Puget Sound. Helle (1979a), however, reported that the numbers of pink and chum salmon as adults in a spawning year are inversely related implying that competition between the species may occur in the ocean during the final year of their life cycles.

Ricker (1980) examined chum salmon catch statistics from British Columbia for evidence of both intraspecific and interspecific competition. Instead of the expected negative relationships between sizes of chum salmon and numbers of chum salmon, which would be expected if there were density dependent effects on the size of individuals, he discovered a small but significant positive relationship. He explains this as an artifact of the progression of especially large or of especially small year-classes through the history of the stocks. Instead of the negative relationship between sizes of chum salmon and the numbers of all species of salmon, which would be expected if there were interspecific competitive inhibitions of the growth of chum salmon, he found insignificant positive relationships.

Table VI summarizes these relationships in the order in which they are used in the model.

Summary. The model has been designed to incorporate a number of known features of chum salmon biology as it

TABLE VI. Functional Relationships in the Conceptual Model of a Chum Salmon Stock

Dependent Variable	Relationship	Independent Variable(s)	Reference, Comments
Egg Size	negative	Fecundity	Koski (1975)
	positive	Adult Size	"
Emergence Date	positive	Spawning Date	
	negative	Development Rate	
	positive	Hatchery Temperature	Alderdice and Velsen (1978), etc.
Fry Growth Rate	positive	Hatchery Temperature	Brett, et al. (1969)
	positive	Inherent Ability	
Size of Fry at Release	positive	Fry Growth Rate	
	positive	Date of Release	
	negative	Emergence Date	
Number of Fry at Relase	negative	Date of Release	Longer rearing periods incur greater risk of epizootic mortality (Martin, et al., 1981)
	positive	Number of Eggs	
Early Survival of Fry	positive	Size of Fry at Release	Parker (1971)
	hump-shaped (not monotonic)	Date of Release	Hiyama, et al. (1972) Time window important, probably month of May (Martin, et al., 1981)
Ocean Growth Rate	positive	Inherent Ability	
	positive	Ocean Conditions	
		Temperature	Helle (1979[a])
		Upwelling	Gonsolus (1978)
	negative	Number of Competitors	Ricker (1980)

TABLE VI
(continued)

Dependent Variable	Relationship	Independent Variable(s)	Reference, Comments
Breeders' Fecundity	positive	Breeders' Size	Helle (1979[a])
Egg Number	negative	Breeders' Sex Ratio	
	positive	Breeders' Fecundity	
Selection Differential	positive	Breeders' Sex Ratio --less the--	Use to predict the response to selection
Size-at-Age	positive	Far Ocean Growth Rate	Helle (1979[a])
	negative	Date of Release	Martin
Age at Maturity	negative	Size-At-Age	Ricker (1964)
	negative		Helle (1979[a])
Survival in Ocean	positive	Ocean	Blackbourn (1980)
	negative	Number of Competitors	Helle (1979[a])
Size	positive	Age at Maturity	Helle 1960, 1979)
	negative	Spawning Date	Skud (1958)
	positive		Helle (1979[a])
Fecundity of Breeders' Sex Ratio males:females	positive	Size at Maturity	Koski (1975)
	negative	Spawning Date of Breeders	

TABLE VI
(continued)

Dependent Variable	Relationship	Independent Variable(s)	Reference, Comments
Breeders' Spawning Date	positive or negative	Selection Differential of Spawning Date	Selection may be of early or of late spawners
Selection Differentials	negative	Number of Immigrants	Minimum number of breeders must be chosen
Breeders' Age	positive	Breeders' Size	Helle (1979[a]) etc.
Breeders' Size	positive or negative	Selection Differential of Size	
Selection Differential (age)	positive	Breeders' Age —less the— Average Age	Use to predict the response to selection

is affected by artificial management. It can incorporate greater survival of eggs and alevins in culture than in nature, greater survival of fry which have been reared for a short term, for instance. Of interest, however, are any predictions that have not been observed in the practice of chum salmon biology, that foretell future problems, or that explain changes that have occurred but haven't been understood. Of course, none of the predictions of genotypic change can be precisely made without good estimates of heritability and of genetic correlations of traits in the stock under consideration; at present these predictions must be based largely on intuition and knowledge of other species. The estimates of heritability made in this study can rightfully only apply to the Whiskey Creek stock of chum salmon, and even in this study no estimates of genetic correlation have been made.

Method. Application of the Conceptual Model

Simulation of the dynamics of a chum salmon stock. Gallagher (1979) suggests that a genetic mechanism may be responsible for the odd-year, even-year cycles of abundance and of average age in chum salmon stocks in Puget Sound. In his model if offspring of even-year spawners mature at an average age of 3.65 years (65% age IV, 35% age III) and if offspring of odd-year spawners

(those that compete with pink salmon fry during their residence as juveniles in Puget Sound) mature at an average age of 3.5 years (50% age IV, 50% age III), there will result a stable cycling of the abundance and age of spawners between even and odd years. The strict correlation between the average ages of parents and of their offspring causes the cycling of mean ages and abundance from year to year. In Gallagher's model the number of returns per spawner is always 1.0.

In a constant environment such a correlation of the ages of parents and offspring might indicate that spawning age is highly heritable; since, however, the environment cycles in precisely the same manner as average age or abundance of chums (pink salmon competitors are present in even-year springtimes only) spawning age may not be at all heritable but may be induced environmentally--by the alternate-year occurrence of pink salmon. It is difficult to imagine, however, how the presence of pink salmon competitors during the first few months of their lives could induce chums to mature at an earlier age; if competition acts to retard the growth of fry but not to increase mortality of fry, I would expect that fry which experience competition should mature at older ages because of their failure to attain maturation threshold size at younger ages. While the advantage for chums from odd-numbered brood years to

spawn at even numbered ages is evident (their offspring will avoid competition from pink salmon and their fitness will be commensurately greater), it is not evident as Gallagher points out (1979, pp. 95-96) whether genetic or environmental mechanisms bring about the cyclings of age and abundance.

A simulation model of the Puget Sound chum salmon stock can help explain the phenomenon. This simulation model incorporates several features of the conceptual model. It simplifies the conceptual model in that chum salmon in the modeled stock mature at only three or four years of age, all of the survival rates of the conceptual model are summarized by a density dependent survival function, a "Ricker Curve," in particular the one found by Helle (1979a) to best fit his observations[10], and that completion with pink salmon years during the estuarine fry state in alternate years causes a ten percent reduction of survival of fry. The effect of this competition on the genotype of the stock can then be explored by simulating the dynamics of the stock either assuming that age of maturation is heritable or that it is not. Appendix VI contains the Fortran codes by which

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[10] $R/S = 1.76\exp(-0.0427S)$, where S is the number of spawners in a year and R is the number of adult offspring they produce.

two such simulations were made, one assuming that the heritability of maturation age is great--that the ages of parents and offspring are highly correlated--and the other assuming that the heritability is zero--that ages of offspring are just as likely to be three as four no matter the parent's ages.

In each simulation the number of returns is computed for each year using the survival function and the number of spawners. In alternate years the number of returns is then reduced by 10 percent, simulating competition from pink salmon. In the next step of the simulation the number of returns is allocated to the two brood years which follow the year in question by three or four years. Thus, each brood year has spawners in it which are returns to parent spawners of years three or four years earlier.

The rule by which the number of returns is allocated to brood years is different for the two cases in which age of maturation is either completely heritable or not heritable at all. No account is taken of the added mortality suffered by older spawners in their additional year of residence at sea. When age of maturation is completely heritable (i.e., heritability = 1), the allocation rule is that the returns have the same age structure as their parents. When age is not heritable (heritability = 0), the rule is that the returns will

mature equally as three and four year olds.

Result. Dynamics of a Stock Which Competes with Pink Salmon in Alternate Years

When age at maturation is not heritable, the simulation shows a stable cycling of the mean age of the stock from year to year but not a cycle in the size of the run (Table VIA). Historical observations of odd year/even year cycling of the ages and abundance of Puget Sound chum salmon stocks are not, therefore, explained by an environmental reduction of the survival of fry in every second brood year when maturation age is not heritable.

If, however, we construct the model so that there is a strict correlation between the ages of parents and of offspring--that maturation age is highly heritable and is not affected by environmental changes--the simulation shows a cycling of both mean age and of abundance from year to year (Table VIB).

In each simulation, the stock began at the size at which R/S = 1.0 in Helle's (1979a) model and at an average age of 3.5 years. Each simulation proceeded for 50 years. Notice that the simulated stock approached an equilibrium at which R/S is near one in all years and that fewer age four fish spawn with pinks, thus avoiding competition.

TABLE VIIA

Simulated changes of number (in thousands), ages, and the rate of returns per spawner in a chum salmon stock in which age of maturity is not heritable (h^2=0) and pink salmon compete (reduce survival) in every other (odd-numbered) brood year.

YEAR	Numbers (Thousands)				RETURNS PER SPAWNER
	Age III	Age IV	Run Total	Mean Age	
1	6.613	6.613	13.225	3.500	0.901
2	6.613	6.613	13.225	3.500	1.001
3	6.613	6.613	13.225	3.500	0.901
4	5.955	6.613	12.568	3.526	1.029
5	6.617	5.955	12.572	3.474	0.929
6	5.955	6.617	12.572	3.526	1.029
7	6.467	5.955	12.422	3.479	0.936
8	5.839	6.467	12.306	3.526	1.041
9	6.468	5.839	12.307	3.474	0.941
10	5.810	6.468	12.278	3.527	1.042
11	6.403	5.810	12.213	3.476	0.945
12	5.788	6.403	12.191	3.525	1.046
13	6.396	5.788	12.184	3.475	0.946
14	5.769	6.396	12.166	3.526	1.047
15	6.375	5.769	12.144	3.475	0.948
16	5.764	6.375	12.138	3.525	1.048
17	6.368	5.764	12.132	3.475	0.948
18	5.756	6.368	12.124	3.525	1.049
19	6.361	5.756	12.117	3.475	0.949
20	5.753	6.361	12.114	3.525	1.049
21	6.358	5.753	12.111	3.475	0.949
22	5.750	6.358	12.108	3.525	1.050
23	6.355	5.750	12.105	3.475	0.950
24	5.749	6.355	12.104	3.525	1.050
25	6.353	5.749	12.102	3.475	0.950
26	5.748	6.353	12.101	3.525	1.050
27	6.353	5.748	12.100	3.475	0.950
28	5.747	6.353	12.100	3.525	1.050
29	6.352	5.747	12.099	3.475	0.950
30	5.747	6.352	12.098	3.525	1.050
31	6.351	5.747	12.098	3.475	0.950
32	5.746	6.351	12.098	3.525	1.050
33	6.351	5.746	12.098	3.475	0.950
34	5.746	6.351	12.097	3.525	1.050
35	6.351	5.746	12.097	3.475	0.950
36	5.746	6.351	12.097	3.525	1.050
37	6.351	5.746	12.097	3.475	0.950
38	5.746	6.351	12.097	3.525	1.050

TABLE VII A
(continued)

YEAR	NUMBERS (THOUSANDS)				RETURNS PER SPAWNER
	Age III	Age IV	Run Total	Mean Age	
39	6.351	5.746	12.097	3.475	0.950
40	5.746	6.351	12.097	3.525	1.050
41	6.351	5.746	12.097	3.475	0.950
42	5.746	6.351	12.097	3.525	1.050
43	6.351	5.746	12.097	3.475	0.950
44	5.746	6.351	12.097	3.525	1.050
45	6.351	5.746	12.097	3.475	0.950
46	5.746	6.351	12.097	3.525	1.050
47	6.351	5.746	12.097	3.475	0.950
48	5.746	6.351	12.097	3.525	1.050
49	6.351	5.746	12.097	3.475	0.950
50	5.746	6.351	12.097	3.525	1.050

TABLE VIIB

Simulated changes in a stock in which age of maturity is completely heritable ($h^2 = 1.0$).

	Numbers (Thousands)				
YEAR	AGE III	AGE IV	TOTAL	MEAN AGE	RETURNS PER SPAWNER
1	6.613	6.613	13.225	3.500	0.091
2	6.613	6.613	13.225	3.500	1.001
3	6.613	6.613	13.225	3.500	0.901
4	5.955	6.613	12.568	3.526	1.029
5	6.617	5.955	12.572	3.474	0.929
6	5.955	6.617	12.572	3.526	1.029
7	6.128	5.955	12.084	3.493	0.951
8	6.146	6.085	12.951	3.525	1.012
9	6.127	5.532	11.659	3.474	0.970
10	5.826	6.808	12.633	3.539	1.026
11	6.222	5.661	11.883	3.476	0.960
12	5.942	6.889	12.831	3.537	1.018
13	5.978	5.365	11.343	3.473	0.984
14	5.971	6.986	12.957	3.539	1.012
15	6.047	5.432	11.479	3.473	0.978
16	5.885	7.010	12.895	3.544	1.015
17	6.043	5.281	11.324	3.466	0.985
18	5.914	7.071	12.985	3.545	1.011
19	5.972	5.313	11.285	3.471	0.987
20	5.954	7.114	13.068	3.544	1.007
21	5.979	5.203	11.181	3.465	0.992
22	5.894	7.148	13.042	3.548	1.008
23	5.998	5.224	11.242	3.466	0.989
24	5.930	7.166	13.096	3.547	1.006
25	5.944	5.160	11.104	3.465	0.995
26	5.932	7.208	13.140	3.549	1.004
27	5.966	5.187	11.153	3.465	0.993
28	5.917	7.210	13.127	3.549	1.005
29	5.957	5.137	11.094	3.463	0.996
30	5.925	7.239	13.164	3.550	1.003
31	5.945	5.151	11.097	3.464	0.996
32	5.933	7.245	13.178	3.550	1.003
33	5.944	5.116	11.060	3.364	0.998
34	5.920	7.262	13.182	3.551	1.002
35	5.948	5.130	11.078	3.463	0.997
36	5.930	7.264	13.193	3.551	1.002
37	5.935	5.103	11.038	3.462	0.999
38	5.929	7.280	13.208	3.551	1.001
39	5.941	5.113	11.054	3.463	0.998
40	5.926	7.268	13.204	3.551	1.001
41	5.936	5.096	11.032	3.462	0.999
42	5.928	7.289	13.217	3.551	1.001
43	5.935	5.101	11.036	3.462	0.999

TABLE VIIB
(continued)

YEAR	AGE III	AGE IV	TOTAL	MEAN AGE	RETURNS PER SPAWNER
44	5.929	7.289	13.218	3.551	1.001
45	5.934	5.090	11.023	3.462	0.999
46	5.927	7.296	13.223	3.552	1.001
47	5.935	5.094	11.029	3.462	0.999
48	5.929	7.295	13.225	3.552	1.001
49	5.931	5.086	11.017	3.462	1.000
50	5.929	7.301	13.230	3.552	1.000

Other Applications of the Conceptual Model

Size at release. The model can account for changes associated with rearing of fry before they are released. Since greater probabilities of survival accrue to large fry at release the genotype of the stock should change to increase the ability of fry to grow in culture. These sorts of change were reported in Brook Trout (Salvelinus malma) by Vincent (1960). This might involve a lessening of the stressful response of the fry to the stressors of artificial culture making them better able to withstand disease and to assimilate food, etc. The model would predict that the ability to grow would increase--whatever composes that ability, that the size of eggs (a predeterminant of fry size) would increase, and that spawning date would be earlier and development rate faster (both tending to allow for longer periods of rearing, hence larger size).

There is little evidence pertinent to these predictions. The high, over 2%, survival rates associated with reared chum salmon at Japanese hatcheries (Moberly and Lium 1977) and the high survival rates of marked pink salmon fry in Alaskan experiments (Kerns 1980; MacDaniel and Blackett 1980; Martin et al. 1981; all reported greater survival rates in experimental groups which had been reared for short periods before

release) argue that the deterioration of fitness-related traits reported by Vincent (1960) would not occur in stocks of artificially reared chum salmon. There have not been many generations of experience of rearing chum salmon fry, however.

Selection of size. Selection of breeders, by either a hatchery manager or a fishery manager, is most likely to take the form of size selection (fishing gear selectivity or conscious selection for bigger fish by spawn takers) or of selection for spawning date (setting of fishing seasons vis a vis the timing of the stock's spawning run or filling egg incubators as the run arrives at the hatchery thereby choosing the breeders from the first part of the run). In the model selection of breeders by size results also in selection by age: choice of larger breeders is also choice of older breeders, on the average. The size distributions of each age group are combined, the larger fish are chosen as breeders, and the resultant distribution of ages in computed. If there is great overlap of size distributions for fish of different ages the selection for age will be lesser; if there is no overlap of size distributions size will act as a surrogate for age in selection. The ability of subadults to grow and the maturation thresholds of subadults respond to this selection--in each age class the individuals with larger

maturation thresholds and greater growth ability will be preferentially chosen to breed.

There is some evidence that selection of larger or smaller fish by a fishery can affect genetic change in a stock. Gwahaba (1975) found that Tilapia nilotica in Lake George, Uganda, matured at smaller sizes than they did before commercial fishing exploited the population, a change he attributes to size selection and genetic change. Silliman (1975) experimentally demonstrated that Tilapia can genetically respond to size selection by fishing. Favro, et al. (1979) explain changes of growth of a trout stock in the AuSable River, Michigan, by means of a model that incorporates genetic change in response to size selection. Ellis and Noble (1960) present evidence that maturation age in a chinook stock is heritable (see Appendix Vb).

Ricker et al. (1978) and Ricker (1980) found that British Columbia stocks of pink and chum salmon have been selectively fished so that smaller pink salmon and larger chum salmon have been allowed to reproduce the stocks; genetic changes are suggested to be responsible for part of the decline since 1951 of the average size of pink salmon in British Columbia. Chum salmon, however, have not gotten larger over this period of selection for larger size, but have become smaller. Their average age has become greater. Ricker (1980) believes that both of

these changes of British Columbia chums may be the result of genetic change brought about by the selection by the fishery of larger fish as breeders: age increased because older (larger) fish were allowed to breed, size decreased because older (slower growing) fish were allowed to breed.

The conceptual model, however, predicts that selection of larger chums as breeders will result in older fish and larger fish: size is positively correlated with maturation threshold sizes (selection results in older ages in later generations) and size is positively correlated with growth ability (selection results in larger fish at each age in later generations). Selection of larger fish not only selects for older breeders, but within each age group selects for faster growers. Ricker's paradoxical observation of increasing age and smaller size of chums would be predicted by the model if there had been a long-term worsening of the pelagic environment causing a decline in growth rates and the concomitant failure of a greater and greater proportion of the population to exceed maturation thresholds at younger ages. Ricker tested the hypothesis that change of ocean temperature explains the change of chum salmon size and found that it does not. However, Ricker's records of ocean temperature may not adequately represent temperatures of the ocean range of chum salmon.

In the eastern subarctic Pacific Ocean there have been long-term trends of sea surface temperature:

> ... warming over the 1930s and into the 1940s as well as between the 1st half of the 1950s and early 1960s. Cooling occurred during the 1940s and into the first half of the 1950s, but the most recent decline in temperature since the 1960s seems more pronounced. (Pella 1979 p.36.)

Pulsating changes with periods of five to six years have been shown to be superimposed on these long-term trends (Favorite and McLain 1973 quoted in Favorite et al. 1977). Favorite and Ingraham's (1976) figure depicting historical patterns of change of mean sea surface temperature over several areas of the subarctic Pacific records these phenomena (Figure 75 in Favorite et al. 1977).

If the recent period of cooling were to have retarded the growth of chum salmon, either by direct effect on the growth of the fish or by depressing the productivity of the ocean, this model predicts that chums would have become smaller (due to slower growth) and older (because individuals were not able to reach younger maturation thresholds). Blackbourn (1980) suggests that recorded changes of sea surface temperature in the northern Gulf of Alaska can explain all of the recent historical decline of British Columbia pink salmon sizes reported by Ricker et al. (1978); if chums are affected in the same way these

changes of temperature may explain changes of chum size as well.

I cannot therefore attribute either the decline of chum salmon size or the increase of chum salmon age to one or the other force--environmental change or size selection by the fishery. Both probably have operated to produce change. More precise knowledge of the functional relationships of the conceptual model would allow a better understanding of the forces.

Selection of spawning date. The other selective force most likely to be imposed by a fishery or hatchery manager is directed at the timing of the stock's spawning run. The model predicts that if, for instance, early fish in the run comprise the breeding population that the run will occur on earlier and earlier dates over the years. That the timing of the stock's spawning run is likely to change in response to such selection is supported by the evidence in Taylor's (1977; 1978) work that run timing in a pink salmon stock is heritable (Appendix V) and by experience such as that reported by Millenbach (1973) in which a run of steelhead trout at a hatchery in Washington achieved a two month advance of maturation date over 14 years during which the early fish in each run comprised the brood stock.

Selection for earlier or later spawners in a stock may produce some correlated responses of other traits.

Phenotypic correlations between spawning date and age, size, and sex have been reported (Thorsteinson et al. 1963; Helle 1960, 1979a). If these correlations reflect a genetic correlation the conceptual model predicts that, for instance, selection of earlier spawners would result in selection for older fish and for a predominance of males, but since males tend to be younger the net outcome may be for younger, more predominantly male spawning runs. Helle (1979b) reports that at the Yakumoh Hatchery on Hokkaido's west coast the chum stock has been getting younger and more predominantly male over the past twenty years. This is attributed to both the practice of feeding fry before release (which, according to the conceptual model would allow them to reach maturation thresholds earlier because of their head start on growth) and the selection of early fish as spawners. Helle reports that both Japanese and Soviet "experiments in selecting early spawners for brood stock produced a larger percentage of males." (Helle 1979b, p.66).

Conclusion

This conceptual model provides a method for the analysis of the relative contributions of a chum salmon stock's environment and genome to its productivity. The analysis by simulation of the response of age and abundance of a chum salmon stock to competition from pink

salmon in alternate years is an example of the kind of analysis of which the conceptual model will be more fully capable when more knowledge of the functional relationships in the model and of heritabilities and genetic correlations of traits has been gained. Even without such knowledge, however, the use of this model allows managers to better understand the consequences of policy. It is particularly important in that it points up the possibility of correlated responses of allied traits to selection exercised on certain traits. Free lunches don't exist; gains in the value of a trait that is important to the manager may well be offset by correlated losses of other traits. Gains in average size might be at the expenses of longer generations. On the other hand it may well be possible for the manager to rearrange the characteristics of his stock to better suit the management situation. Changing the timing of the stock's spawning immigration could avoid mixed-stock harvests, for instance, with the only cost being maintenance of the stock by artificial culture.

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APPENDICES

Appendix IA. Temperature and accumulated temperature units of incubation water recorded each morning at the Netarts Field Station during the 1975 Experiment.

DATE	TEMPERATURE	CUMULATIVE TEMPERATURE UNITS
20 November 1975	7.3°C	7
21	8.0	15
22	8.0	23
23	8.0	31
24	9.0	40
25	9.0	49
26	9.0	58
27	7.0	65
28	6.0	71
29	5.5	77
30	6.0	83
1 December	9.5	93
2	10.0	103
3	10.0	113
4	9.0	122
5	7.0	129
6	7.0	136
7	8.0	144
8	9.5	153.5
9	9.5	163
10	9.0	172
11	8.0	180
12	5.5	185.5
13	5.5	191
14	6.0	197
15	8.0	205
16	8.5	213.5
17	8.0	221.5
18	6.0	227.5
19	6.0	233.5
20	6.0	239.5
21	5.5	246
22	7.0	252
23	7.5	259.5
24	8.0	267
25	8.0	275
26	8.0	283
27	8.0	291
28	8.0	299
29	9.0	308
30	8.0	316
31	6.5	322.5

Appendix IA (Continued).

DATE	TEMPERATURE	CUMULATIVE TEMPERATURE UNITS
1 January 1976	5.5°C	329
2	6.0	335
3	7.0	342
4	8.0	350
5	8.0	358
6	7.0	365
7	7.0	372
8	7.0	379
9	7.5	386.5
10	7.5	394
11	8.0	402
12	7.0	409
13	7.0	416
14	7.0	423
15	9.0	432
16	9.0	441
17	9.0	450
18	7.0	457
19	6.5	463.5
20	6.5	470
21	6.0	476
22	7.0	483
23	7.0	490
24	6.0	496
25	4.0	500
26	5.0	505
27	7.5	512.5
28	8.0	529.5
29	7.5	528
30	6.5	534.5
31	7.0	541.5
1 February	7.0	548.5
2	7.0	555.5
3	6.5	562
4	6.0	568
5	3.0	571
6	3.0	574
7	3.0	577
8	3.5	580.5
9	5.5	586
10	5.5	591.5
11	5.5	597
12	7.0	604
13	8.0	612
14	7.5	619.5
15	8.0	627.5

Appendix IA (Continued).

DATE	TEMPERATURE	CUMULATIVE TEMPERATURE UNITS
16	9.5°C	637
17	8.0	645
18	8.0	653
19	8.0	661
20	8.0	669
21	8.0	677
22	8.0	675
23	8.0	683
24	8.0	691
25	8.0	699
26	8.0	707
27	7.0	714
28	6.0	720
29	7.0	726
1 March 1976	5.5	732
2	5.0	737
3	5.0	742
4	5.0	747
5	5.0	752
6	5.0	757
7	6.0	763
8	5.0	768
9	7.0	775
10	6.0	781
11	6.0	787
12	6.0	793
13	7.0	800
14	8.0	807
15	8.0	815
16	9.0	824
17	10.0	834
18	9.5	844
19	7.0	851
20	8.0	859
21	7.5	866
22	9.0	875
23	7.5	883
24	8.0	891
25	8.0	899
26	8.0	907
27	7.0	914
28	7.0	921
29	8.0	929
30	9.0	938
31	8.0	946
1 April	8.0	954
2	7.0	961
3	7.0	968

Appendix IB. Temperature and accumulated temperature units of incubation water at the Netarts Field Station during the 1976 Experiment.

DATE	TEMPERATURE	TEMPERATURE UNITS
24 November 1976	13.0°C	13
25	12.0	25
26	12.0	37
27	11.0	10
28	10.5	58.5
29	10.2	68.7
30	9.5	78.2
1 December 1977	9.5	87.8
2	4.5	92.2
3	4.5	96.7
4	5.0	101.7
5	5.5	107.2
6	7.0	114.2
7	8.0	122.2
8	10.0	132.2
9	10.0	142.2
10	8.3	150.5
11	6.5	157.0
12	5.5	162.5
13	8.0	170.5
14	8.4	178.9
15	9.0	187.9
16	9.0	196.9
17	9.0	205.9
18	8.0	214
19	7.0	221
20	6.0	227
21	6.5	234.5
22	6.5	241.0
23	7.4	248.4
24	6.1	254.5
25	8.0	262.5
26	9.2	271.7
27	5.0	473.2
28	4.2	477.4
29	4.2	481.6
30	4.0	485.6
31	6.0	491.6
1 February	7.0	498.6
2	6.5	505.1
3	7.0	512.1
4	8.0	520.1

Appendix IB (Continued).

DATE	TEMPERATURE	TEMPERATURE UNITS
5 February	7.0	527.1
6	7.8	534.9
7	7.5	542.4
8	8.1	550.4
9	8.5	558.9
10	9.0	567.9
11	10.2	578.1
12	9.0	587.1
13	8.0	595.1
14	7.5	602.6
15	7.5	610.1
16	9.5	619.6
17	9.0	628.6
18	9.0	637.6
19	8.0	645.6
20	8.8	654.4
21	10.0	664.4
22	8.0	672.4
23	6.8	679.2
24	6.9	686.1
25	7.1	693.2
26	8.0	701.2
27	9.0	710.2
28	10.0	720.2
1 March	10.0	730.2
2	8.0	738.2
3	7.5	745.7
4	7.8	754.5
5	7.0	761.5
6	7.5	769
7	8.5	777.5
8	9.0	786.5
9	8.8	795.5
10	8.5	803.8
11	8.5	812.6
12	7.5	820.1
13	6.0	826.1
14	6.5	832.4
15	7.8	840.4
16	6.5	846.9
17	7.8	854.7
18	8.0	862.7
19	9.0	872
20	8.0	880
21	8.0	888
22	8.0	896
23	9.0	905

Appendix IB (Continued).

DATE	TEMPERATURE	TEMPERATURE UNITS
24 March	8.0	913
25	8.0	921
26	8.0	929
27	7.5	936.5
28	7.5	944
29	7.5	951.5
30	7.5	958
1 April	8.0	964
2	8.0	972
3	8.5	980.5
4	8.5	989
5	9.0	998
6	9.0	1007
7	9.0	1016
8	9.0	1025
9	9.0	1034
10	8.0	1042
11	8.5	1050.5
12	9.0	1059.5
13	9.0	1068.5
14	9.0	1077.5
15	9.0	1086.5
16	9.0	1095.5
17	8.0	1103.5
18	8.0	1111.5
19	9.0	1120.5

APPENDIX II A 1

Days to hatching. 1975 Experiment.

		Paternal Stocks			
		Whiskey	Nemah	Hoodsport	Female Mean
Females	A	70.188	70.358	69.568	70.076
	B	69.023	69.104	68.590	68.935
	C	69.041	69.067	68.324	68.868
	D	69.785	69.663	68.967	69.550
Paternal Stock Mean		69.509	69.548	68.862	

APPENDIX II A 2

Expected Mean Squares,

1975 Experiment

Source of Variation	Entire Experiment, Replicate one or two of Whiskey Creek	Whiskey Creek Fathers	Nemah or Hoodsport Fathers
Paternal Stock (P)	$\sigma^2 + \sigma_{SD}^2 + 5\sigma_{PD}^2 + 4\sigma_S^2 + 20\sigma_P^2$		
Sires in Paternal Stock (S)	$\sigma^2 + \sigma_{SD}^2 + 4\sigma_S^2$	$\sigma^2 + 2\sigma_{SD}^2 + 8\sigma_S^2$	$\sigma^2 + \sigma_{SD}^2 + 4\sigma_S^2$
Dams (D)	$\sigma^2 + \sigma_{SD}^2 + 5\sigma_{PD}^2 + 15\sigma_D^2$	$\sigma^2 + 2\sigma_{SD}^2 + 10\sigma_D^2$	$\sigma^2 + \sigma_{SD}^2 + 5\sigma_D^2$
P X D	$\sigma^2 + \sigma_{SD}^2 + 5\sigma_{PD}^2$		
S X D	$\sigma^2 + \sigma_{SD}^2$	$\sigma^2 + 2\sigma_{SD}^2$	$\sigma^2 + \sigma_{SD}^2$
Error		σ^2	

APPENDIX II A 3

Analysis of Variance

Days to Hatching. 1975 Experiment.

A. Incorporating replicate number 1 of Whiskey Creek matings.

Source	df	Mean Square	F(df)	Probability
Paternal Stock	2	2.9860	3.272(2,13)†	.071
Coast vs. Puget Sound	1	5.9602	8.692(1,13)†	.011
Sires (in paternal stocks)	12	.9277	3.453(12,36)	.002
Dams	3	4.5383	67.635(3,6)†	.000
Large vs. Small eggs	1	10.8536	161.753(1,6)†	.000
PxD	6	.0671	0.249(6,36)	.956
SxD	36	.2687		

B. Incorporating replicate number 2 of Whiskey Creek matings

Paternal Stock	2	2.9498	2.655(2,15)†	.103
Coast vs. Puget Sound	1	5.8809	5.095(1,15)†	.039
Sires (in populations)	12	1.0300	4.317(12,36)	.000
Dams	3	5.2966	30.974(3,6)†	.000
Large vs. Small eggs	1	13.3399	78.011(1,6)†	.000
PxD	6	.1710	0.717(6,36)	.640
SxD	36	.2386		

† Approximate

APPENDIX II A 4

Analysis of Variance

Days to Hatching. 1975 Experiment.

A. Whiskey Creek Fathers Only
(2 replicates)

Source of Variation	Degrees of Freedom	Mean Square	F(df)	Probability
Sires	4	.3644	0.883(4,12)	0.502
Dams	3	3.3113	8.023(3,12)	0.003
SxD	12	.4127	1.534(12,20)	0.192
Error	20	.2690		

Heritability (sires) (h^2) = 0.0 SE = 0.2

B. Nemah River Fathers Only

Sires	4	1.4653	7.254(4,12)	.003
Dams	3	1.8287	9.053(3,12)	.002
SxD	12	0.2020		

h^2 = 1.4 SE = 0.7
(using 0.269 as estimate of Mean Square Error from A above)

C. Hoodsport Fathers Only

Sires	4	1.1259	4.754(4,12)	.016
Dams	3	1.4549	6.142(3,12)	.009
SxD	12	.2369		

h^2 = 1.2 SE = 0.7
(using 0.269 as estimate of Mean Square Error from A above)

APPENDIX II B 1

Emergence* On 30 March. 1975 Experiment.

		Paternal Stock			
		Whiskey Creek	Nemah River	Hoodsport	Female Mean
	A	.695	.778	.868	.759
	B	.549	.396	.447	.485
	C	.342	.543	.592	.455
	D	.550	.340	.384	.456
Male Population Mean		.534	.514	.573	/.539

*Number emerged /Number of alevins surviving incubation, [Sine (Arcsine (Y) ½)]

Appendix II B 2

Analysis of Variance

Emergence* from Incubators on 30 March

1975 Experiment

A. Incorporating replicate number 1 of Whiskey Creek matings.

Source	df	Mean Square	F(df)	Probability
Paternal Stock Coast vs. Puget Sound	2 1	0.0964 0.1536	0.843(7,14)† 1.105(2,14)	0.571 0.358
Sires (in paternal stocks)	12	0.0925	1.055(12,36)	0.424
Dams Large vs. Small eggs	3 1	0.6178 0.5283	4.911(3,6)† 4.200(1,6)†	0.047 0.086
PxD	6	0.1258	1.434(6,36)	0.229
SxD	36	0.0877		

B. Incorporating replicate number 2 of Whiskey Creek matings

Paternal Stock Coast vs. Puget Sound	2 1	0.0576 0.0521	0.861(11,13)† 0.589(7,13)	0.593 0.754
Sires (in populations)	12	0.0664	0.739(12,36)	0.705
Dams Large vs. Small eggs	3 1	0.7521 0.3582	7.170(3,6)† 3.415(1,6)†	0.021 0.114
PxD	6	0.1049	1.167(6,36)	0.345
SxD	36	0.0899		

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* Arcsine $\left[\text{No. emerged/No. surviving}\right]^{\frac{1}{2}}$

† Approximate

APPENDIX II B 3

Analysis of Variance

Emergence* from Incubators on 30 March

1975 Experiment

A. Whiskey Creek Fathers

Source of Variation	Degrees of Freedom	Mean Square	F(df)	Probability
Sires	4	.0739	0.996(4,12)	.447
Dams	3	.3002	4.046(3,12)	.033
SxD	12	.0742	0.747(12,20)	.693
Error	20	.1003		

h^2 (Heritability) = 0.0

SE = .2

B. Nemah River Fathers

Sires	4	.0589	1.153(4,12)	.379
Dams	3	.2785	7.250(3,12)	.005
SxD	12	.0384		

h^2 = 0.2

SE = 0.4

C. Hoodsport Fathers

Sires	4	.1108	0.853(4,12)	.519
Dams	3	.4584	3.528(3,12)	.049
SxD	12	.1299		

h^2 = -0.1

SE = 0.4

*Arcsine $\left[\frac{\text{No. emerged}}{\text{No. surviving}}\right]^{\frac{1}{2}}$

APPENDIX II C 1

Number of Days Between
Spawning and Emigration

1976 Experiment

	Whiskey Creek Females	Kilchis River Females	Paternal Stock Mean
Whiskey Creek Males	120.396	119.979	120.187
Kilchis River Males	123.332	120.673	122.003
Maternal Stock Mean	121.864	120.326	121.095

APPENDIX II C 2

Expected Mean Squares. 1976 Experiment.

Omitting observations of one Female's Offspring

Source of Variation	Expected Mean Squares
Sires (S)	$\sigma^2 + 2\sigma_{SD}^2 + 10\sigma_S^2$
Dams (D)	$\sigma^2 + 2\sigma_{SD}^2 + 12\sigma_D^2$
SxD (SD)	$\sigma^2 + 2\sigma_{SD}^2$
Error	σ^2

APPENDIX II C 3

Expected Mean Squares

Missing Data Estimated

1976 Experiment

Source of Variation	Expected Mean Squares
Paternal Stock (P)	$\sigma^2 + 2\sigma_{SD}^2 + 12\sigma_S^2 + 36\sigma_P^2$
Maternal Stock (M)	$\sigma^2 + 2\sigma_{SD}^2 + 12\sigma_D^2 + 36\sigma_M^2$
P X M	$\sigma^2 + 2\sigma_{SD}^2 + 18\sigma_{PM}^2$
Sires Within Paternal Stocks (S)	$\sigma^2 + 2\sigma_{SD}^2 + 12\sigma_S^2$
Dams Within Maternal Stocks (D)	$\sigma^2 + 2\sigma_{SD}^2 + 12\sigma_D^2$
S x D	$\sigma^2 + 2\sigma_{SD}^2$
Error	σ^2

APPENDIX II C 4

Expected Mean Squares

1976 Experiment

Purebred or Crossbred Groups only.

Missing Data Estimated

Source of Variation	Expected Mean Squares
Sires	$\sigma^2 + 2\sigma_{SD}^2 + 12\sigma_S^2$
Dams	$\sigma^2 + 2\sigma_{SD}^2 + 12\sigma_D^2$
S x D	$\sigma^2 + 2\sigma_{SD}^2$
Error	σ^2

Missing Data Omitted

Sires	$\sigma^2 + 2\sigma_{SD}^2 + 10\sigma_S^2$
Dams	$\sigma^2 + 2\sigma_{SD}^2 + 12\sigma_D^2$
S x D	$\sigma^2 + 2\sigma_{SD}^2$
Error	σ^2

APPENDIX II C 5

Analysis of Variance

Days Between Spawning and Emigration

1976 Experiment

A. Omitting data of one female for which data were incomplete

Source of Variation	Degrees of Freedom	Mean Square	F(df)	Probability
Sires	5	42.3448	1.351(5,20)	0.284
Kilchis vs Netarts (Paternal Stocks)	1	34.3723	1.096(1,20)	0.308
Dams	4	36.8355	1.175(4,20)	0.352
Kilchis vs Netarts (Maternal Stocks)	1	116.8420	3.726(1,20)	0.068
SxD	20	31.3546	1.062(20,30)	0.431
Error	30	29.5257		
Paternal x Maternal Stocks	1	72.7300	2.404(1,30)	0.132

B. Estimating Missing Data

Paternal Stocks	1	59.3320	0.884(1,4)	0.400
Maternal Stocks	1	42.5811	1.105(1,4)	0.352
Sires within Paternal Stocks	4	67.0834	1.327(4,16)	0.302
Dams within Maternal Stocks	4	38.5362	0.762(4,16)	0.565
PxM	1	22.6150	0.447(1,16)	0.513
SxD	24	33.7022	1.060(24,35)	0.429
Residual	35	31.7885		

APPENDIX II C 6

Analysis of Variance

Days Between Spawning and Emigration
Missing Data Included by Estimation

Kilchis River Parent Only

Source of Variation	Degrees of Freedom	Mean Square	F(df)	Probability
Sires	2	72.7220	1.010(2,4)	0.438
Dams	2	71.2798	0.999(2,4)	0.445
SxD	4	71.3196	17.961(4,8)	0.000
Error	8	3.9707		

$h^2 = 0.0$
SE = 1.1

Whiskey Creek Parents Only

Sires	2	46.7456	0.448 (2,4)	0.667
Dams	2	3,7006	0.035 (2,4)	0.966
SxD	4	104.2877	2.200 (4,8)	0.159
Error	9	47.3986		

$h^2 = 0.8$
SE = 1.1

Whiskey Creek Sires, Kilchis River Dams

Sires	2	81.1836	11.951(2,4)	0.021
Dams	2	13.0411	1.920(2,5)	0.260
SxD	4	6.7928	0.555(4,8)	0.702
Error	8	12.2409		

$h^2 = 2.2$
SE = 0.8

APPENDIX II C 6
(continued)

Kilchis River Sires, Whiskey Creek Dams

Sires	2	13.8317	0.698 (2,4)	0.550
Dams	2	12.2334	0.617 (2,4)	0.584
SxD	4	19.8127	0.5352 (4,9)	0.714

$h^2 = -0.2$
SE = .40

APPENDIX II D 1

Lengths (mm) After One Month of Feeding
1975 Experiment

Paternal Stock

		Whiskey Creek Replicate 1	Whiskey Creek Replicate 2	Nemah River	Hoodsport	Female Mean	
Female	A	44.38	44.12	43.64	44.47	44.15	TANK I
		46.56	47.36	45.07	46.05	46.26	TANK II
	B	45.82	45.81	45.83	46.45	46.98	TANK I
		48.87	47.83	47.85	48.81	48.34	TANK II
	C	45.49	46.44	46.51	46.04	45.84	TANK I
		47.53	47.72	46.54	47.47	47.32	TANK II
	D	44.23	44.24	43.88	44.59	44.23	TANK I
		47.18	48.00	46.73	47.56	47.37	TANK II
Male Population Mean		44.98	45.15	44.69	45.39	45.05	TANK I
		47.53	47.73	46.53	47.47	47.32	TANK II

APPENDIX II D 2

Expected Mean Squares

Analysis of Lengths

1975 Experiment

Source of Variation	Expected Mean Squares
Tanks (T)	$\sigma^2 + \sigma_{TSD}^2 + 5\sigma_{TPD}^2 15\sigma_{TD}^2 4\sigma_{TS}^2 + 20_{TP}^2 + 60\sigma_T^2$
Paternal Stock (P)	$\sigma^2 + \sigma_{TSP}^2 + 5\sigma_{TPD}^2 + 2\sigma_{SD}^2 + 10\sigma_{PD}^2 + 4\sigma_{TS}^2 + 20\sigma_{TP}^2 + 40\sigma_P^2$
Sires in Paternal Stocks (S)	$\sigma^2 + \sigma_{TSD}^2 + 2\sigma_{SD}^2 + 4\sigma_{TS}^2 + 8\sigma_S^2$
Dams (D)	$\sigma^2 + \sigma_{TSD}^2 + 5\sigma_{TPD}^2 + 2\sigma_{SD}^2 + 10\sigma_{PD} + 15\sigma_{TD}^2 + 30\sigma_D^2$
T x P	$\sigma^2 + \sigma_{TSD}^2 + 5\sigma_{TPD}^2 + 2\sigma_{SD}^2 + 4\sigma_{TS}^2 + 20\sigma_{TP}^2$
T x S	$\sigma^2 + \sigma_{TSD}^2 + 4\sigma_{TS}^2$
T x D	$\sigma^2 + \sigma_{TSD}^2 + 5\sigma_{TPD}^2 + 15\sigma_{TD}^2$
P x D	$\sigma^2 + \sigma_{TSD}^2 + 5\sigma_{TPD}^2 + 2\sigma_{SD}^2 + 10\sigma_{PD}^2$
S x D	$\sigma^2 + \sigma_{TSD}^2 + 2\sigma_{SD}^2$
TPD	$\sigma^2 + \sigma_{TSD}^2 + 5\sigma_{TPD}^2$
TSD	$\sigma^2 + \sigma_{TSD}^2$

APPENDIX II D 3

Analysis of Variance

Lengths after 1 month of feeding

1975 Experiment

A. Incorporating replicate number 1 of Whiskey Creek mating

Source of Variance	Degrees of Freedom	Mean Square	F(df)	Prob. of greater F
Tanks	1	140.740	29.528(1,6)*	0.002
Paternal Stock	2	7.303	4.235(3,5)*	0.077
Coast vs Sound	1	6.503	4.927(1,42)*	0.032
Sires (in paternal stocks)	12	1.730	1.527(18,42)*	0.129
Dams	3	27.756	8.118(3,4)*	0.036
Egg Size: Large vs Small	1	65.647	19.152(1,4)*	0.012
TxP	2	1.241	1.356(5,47)*	0.258
TxS	12	0.587	1.418(12,36)	0.202
TxD	3	3.143	25.762(3,6)*	0.001
PxD	6	0.291	0.751(26,42)*	0.779
SxD	36	0.817	1.973(36,36)	0.022
TPD	6	0.122	0.295(6,36)	0.936
TSD	36	0.414		

*Approximate

APPENDIX II D 3

(Continued)

Analysis of Variance

Lengths after 1 month of feeding

1975 Experiment

B Incorporating Replicate Number 2 of Whiskey Creek Matings

Source of Variance	Degrees of Freedom	Mean Square	F(df)	Probability
Tank	1	141.911	21.127(1,6)*	0.004
Paternal Stock	2	8.898	3.116(3,10)*	0.075
Coast vs Sound	1	4.293	3.192(1,39)*	0.082
Sires (in population)	12	3.146	1.596(24,39)*	0.093
Dams	3	22.640	4.035(3,5)*	0.084
Egg Size	1	56.652	9.929(1,5)*	0.025
TxP	2	1.347	1.337(10,37)*	0.248
TxS	12	0.733	0.878(12,36)	0.576
TxD	3	4.608	7.100(3,6)*	0.021
PxD	6	1.163	1.312(16,24)*	0.264
SxD	36	0.873	1.047(36,36)	0.446
TxPxD	6	0.649	0.778(6,36)	0.592
TxSxD	36	0.834		

*Approximate

APPENDIX II D 4

Analysis of Variance

Lengths after 1 month of feeding

1975 Experiment

Whiskey Creek Fathers Only

Source of Variance	Degrees of Freedom	Mean Square	F(df)	Probability
Tanks	1	131.531	49.447(1,4)*	0.002
Sires	4	6.615	7.922(6,16)*	0.000
Dams	3	9.858	3.53(4,5)*	0.099
TxS	4	0.261	0.196(4,12)	0.900
TxD	3	2.426	1.821(3,12)	0.197
SxD	12	0.742	0.931(12,12)	0.410
TxSxD	12	1.332	0.157(12,40)	0.111
Error	40	0.797		

h^2 (Heritability, Sires) = 0.9
SE = 0.50

Nemah Fathers Only

Tanks	1	34.588	13.435(1,7)*	0.008
Sires	4	1.485	0.901(6,10)*	0.530
Dams	3	11.025	5.031(3,7)*	0.036
TxS	4	1.171	3.729(4,12)	0.034
TxD	3	1.427	4.545(3,12)	0.024
SxD	12	0.827	2.633(12,12)	0.077
TxSxD	12	0.315		

h^2 = .2

SE = .2

APPENDIX II D 4
(continued)

Hoodsport Fathers Only

Source of Variance	Degrees of Freedom	Mean Square	F(df)	Prob. of greater F
Tanks	1	43.559	24.194(1,5)*	0.004
Sires	4	2.099	1.718(6,15)*	0.185
Dams	3	10.111	4.668(3,8)*	0.036
TxS	4	0.525	1.105(4,12)	0.398
TxD	3	1.295	2.716(3,12)	0.091
SxD	12	0.973	2.048(12,12)	0.1
TxSxD	12	0.475		

$h^2 = 0.3$

SE = 0.3

*Approximate

APPENDIX II E 1

Time* Spent in Stream Channel

1975 Experiment

			Whiskey Creek	Nemah River	Hoodsport	Female Mean
Females	A	Rep 1	3.42576	3.31086	3.04567	3.26076
		Rep 2	3.29890			
	B	Rep 1	3.39913	3.28095	3.90796	3.52768
		Rep 2	3.62873			
	C	Rep 1	4.01583	3.98296	3.70546	3.90141
		Rep 2	3.96547			
	D	Rep 1	3.54918	3.40524	3.59838	3.51760
		Rep 2	3.89185			
Paternal Stock Mean		Rep 1	3.59622	3.49500	3.56437	
		Rep 2	3.69624			

* Time = (Hours)$^{\frac{1}{2}}$

APPENDIX II E 2

Analysis of Variance

Time Spent in Stream Channel

1975 Experiment

Source of Variance	Degrees of Freedom	Mean Square	F(df)	Probability
A. Incorporating replicate number of of Whiskey Creek matings				
Paternal Stock	2	0.05358	0.528(25,13)*	0.917
Sires in Paternal Stock	12	0.17479	0.894(12,36)	0.561
Dams	3	1.04343	3.515(3,6)	0.089
Egg Size	1	1.58797	5.350(1,6)	0.039
P x D	6	0.29681	1.518(6,36)	0.200
S x D	36	0.19556		
B. Incorporating replicate number 2 of Whiskey Creek matings				
Paternal Stock	2	0.20899	0.886(7,14)*	0.542
Sires in Paternal Stock	12	0.18008	0.938(12,36)	0.522
Dams	3	1.3374	4.161(3,6)	0.065
Egg Size	1	1.53703	5.640(1,6)	0.035
P x D	6	0.27250	1.419(6,36)	0.234
S x D	36	0.19198		

* Approximate

APPENDIX II E 3

Analysis of Variance

Time* Spent in Stream Channel

Whiskey Creek Fathers

Source of Variance	Degrees of Freedom	Mean Square	F	Probability
Sires	4	0.06676	0.661	0.631
Dams	3	0.74304	7.361	0.005
SxD	12	0.07347	0.728	0.710
Error	20	0.10094		

h^2 (Heritability) = 0.0
SE = .2

Nemah River Fathers

Sires	4	0.07353	0.716	0.597
Dams	3	0.54314	5.288	0.015
SxD	12	0.10272		

h^2 = 0.2
SE = .3

Hoodsport

Sires	4	0.39898	1.032	0.430
Dams	3	0.68028	1.760	0.208
SxD	12	0.38645		

h^2 = 0.0

SE = 0.6

---

* Time = (Hours) $^{1/2}$

APPENDIX II F 1

Survival After Artificial Challenge by

Vibrio anguillarum

1975 Experiment

		Paternal Stock Whiskey Creek	Nemah River	Hoodsport	Female Mean
Females	A	.38	.17	.36	.30
	B	.05	.11	.28	.15
	C	.27	.22	.28	.26
	D	.27	.19	.25	.24
Paternal Stock		.24	.19	.29	.25

APPENDIX II F 2

Analysis of Variance

Survival* After Challenge by Vibrio anguillarum.

1975 Experiment

Source of Variance	Degrees of Freedom	Mean Square	F	Probability
Paternal Stock	2	0.05921	1.668(3,12)†	0.226
Sires (in paternal stock)	6	0.02044	2.895(6,18)	0.037
Dams - Tanks	3	0.0617	2.634(3,6)	0.144
PxD	6	0.02342	1.676(6,18)	0.184
SxD	18	0.01397		

*Survival = Arcsine $\left[\frac{r + 0.25}{n + 0.50}\right]^{\frac{1}{2}}$ where r = number of survivors and n = number of fish challenged.

†Approximate

APPENDIX II F 3

Analysis of Variance

Survival* After Challenge by Vibrio anguillarum.

Subsample+ of 1975 Experiment

Source of Variance	Degrees of Freedom	Mean Square	F(df)	Probability
Paternal Stock	2	.05312	0.954(4,9)§	0.477
Sires in Paternal Stock	6	.03630	1.691(6,12)	0.206
Dams - Tanks	2	.09820	2.344(2,4)§	0.212
PxD	4	.04189	2.205(4,324)	0.130
SxD	12	.02149	1.130(12,324)	0.335
Error #	324	.01924		

*Survival = Arcsine $\left[\frac{r}{n}\right]^{\frac{1}{2}}$

Where r = number of survivors
n = number of fish challenged

+Dams, B, C, D; 13 offspring per mating

#$\frac{0.25009}{n} = \frac{0.25009}{13}$

§Approximate

APPENDIX II F 4

Analysis of Variance

Survival* After Challenge by Vibrio anguillarum.

1975 Experiment

Whiskey Creek Fathers Only

Source of Variance	Degrees of Freedom	Mean Square	F(df)	Probability
Sires	2	0.02339	2.971(2,0)	0.127
Dams	3	0.05633	7.158(3,6)	0.021
SxD	6	0.00787		
	$h^2 = 0.6$ SE = 0.6			

Nemah River Sires Only

Sires	2	0.01834	1.145(2,6)	0.379
Dams	3	0.01112	0.694(3,6)	0.589
SxD	6	0.01602		
	$h^2 = 0.2$ SE = 0.1			

Hoodsport Sires Only

Sires	2	0.01875	1.107(2,6)	0.340
Dams	3	0.00866	0.511(3,6)	0.689
SxD	6	0.01694		
	$h^2 = 0.1$ SE = 1			

*Survival = Arcsine $\left[\frac{r + 0.25}{n + 0.50}\right]^{\frac{1}{2}}$

Where r = number of survivors
n = number of fish challenged

APPENDIX II G 1

Survival* in a Natural Epizootic of Vibriosis

1976 Experiment+

		Paternal Stock Whiskey Creek	Paternal Stock Kilchis River	Maternal Stock Mean
Maternal Stock	Whiskey Creek	.51	.52	.52
	Kilchis River	.28	.47	.38
Paternal Stock Mean		.42	.50	.46

*Survival - Number of surviving / initial Number (30) at the time when on-half (.46) of all fish remained alive.

+Observation of 1 female's offspring were incomplete and are omitted.

APPENDIX II G 2

Analysis of Variance

Survival* in a Natural Epizootic of Vibriosis.

1976 Experiment+

Source of Variance	Degrees of Freedom	Mean Square	F(df)	Probability
Sires	5	.15153	3.767(5,20)	0.014
Paternal Stocks	1	.07930	1.971(1,20)	0.176
Dams	4	.16149	4.014(4,20)	0.015
Maternal Stocks	1	.18700	4.648(1,20)	0.043
Sires X Dams	20	.04023		

*Survival = Arcsine $\left[\frac{\text{Number Surviving (When .46 of total remained alive)}}{\text{Initial Number (=30)}}\right]^{\frac{1}{2}}$

+Observations of 1 female's offspring were incomplete and are omitted.

APPENDIX II G 3

Analysis of Variance

Survival in a Natural Epizootic of Vibriosis

1976 Experiment

A. Whiskey Creek Parents Alone

Source of Variance	Degrees of Freedom	Mean Square	F(df)	Probability
Sires	2	.1363	1.925(2,4)	0.260
Dams	2	.0271	0.383(2,4)	0.705
SxD	4	.0708		

$h^2 = 1$

SE = 1

B. Kilchis River Parents Alone

Sires	2	.01301	0.519(2,2)	0.659
Dams	1	.32878	15.097(1,2)	0.060
SxD	2	.02509		

$h^2 = -0.2$

SE = 0.3

APPENDIX II G 3
(continued)

C. Whiskey Creek Fathers, Kilchis River Mothers

Source of Variance	Degree of Freedom	Mean Square	F(d,f)	Probability
Sires	2	.17252	3.051(2,2)	0.247
Dams	1	.08943	1.581(1,2)	0.336
SxD	2	.05655		

$h^2 = 1.8$

SE = 1.2

D. Kilchis River Fathers, Whiskey Creek Mothers

Sires	2	.03267	0.710(2,4)	0.545
Dams	2	.00161	0.035(2,4)	0.966
SxD	4	.04606		

$h^2 = 0.7$

SE = 2

APPENDIX III

Confidence intervals for heritability estimates. I adapted Broemeling's (1969) method for a hierarchical experimental design to a factorial design for which the analysis is:

Source	Mean Squares	Expected Means Squares
1) Sires	S_1	$\sigma^2 + k_1\sigma_1^2$
2) Dams	S_2	$\sigma^2 + k_2\sigma_2^2$
3) Error	S_e	σ^2

Assuming interaction effects are negligible.

Let $h_1 = 4\sigma_1^2/\sigma^2 + \sigma_1^2 + \sigma_2^2$

$h_2 = \sigma_2^2/\sigma^2 + \sigma_1^2 + \sigma_2^2$

F = the value of the F statistic of significance .

S_1, S_2, S_e are the appropriate mean squares from the analysis.

Then

$$Pr\left\{F_{1-\alpha_1/2} < S_1/[1 + k_1 h_1/(4-h_1-h_2)]S_e < F_{\alpha_1/2},\right.$$

$$\left.F_{1-\alpha_2/2} < S_2/[1+k_2 h_2/(4-h_1-h_2)]S_e < F_{\alpha_2/2}\right\}$$

$$= (1-\alpha_1)(1-\alpha_2)$$

Substituting in these inequalities values from the analysis for Sl, Sl, Se, kl, k2 and tabulated values of F, and letting h_2 vary between zero and one, a

APPENDIX III
(continued)

range of values of h_1 can be computed. These values of h_1 can be inspected and the confidence limits with $P=(1-\alpha_1)(1-\alpha_2)$ can be determined.

When I follow this procedure, using, for instance, the analysis of the mean number of days between spawning and hatching of offspring of Whiskey Creek fathers in the 1975 Experiment I found the maximum value of h_1 (h^2 estimated from sires) to be well in excess of one (68.47) and the minimum to be less than zero (-1.7).

APPENDIX III
(continued)

FORTRAN code used to compute heritability estimates, their standard errors, and lower confidence limit.

```
      REAL MSS, MSSD, MSE, MSD, H2, LIM, K1
10    READ(5,101,END=999) A,B,C,MSS,MSSD,MSD,MSE,DFS,DFD,
           DFSD,DFE
      X=(4/A)*(MSS-MSSD)
      Y=(MSS-MSSD)/A (MSD-MSSD)/B (MSSD-MSE)/C MSE
      VMSS=2*(MSS 2)/(DFS+2)
      VMSD=2*(MSD 2)/(DFD+2)
      VMSSD=2*(MSSD 2)/(DFSD+2)
      VMSE=2*(MSE 2)/(DFE+2)
      VARX-((4/A) 2)*(VMSS+VMSSD)
      VARY=((1/A) 2)*VMSS+(((1/C)-(1/C)-(1/A)-(1/B)) 2)*VMSSD
     &  +(((C-1)/C) 2*VMSE+((1/B) 2)*VMSD
      COVXY-(4/A*(1/A*VMSS+(4/A)*((1/C)-(1/A)-(1/B))*VMSSD
      VARH2=(VARX)/(Y 2)-2*X*COVXY/(Y 3)+(X 2)*VARY/(Y 4)
      H2+X/Y
      SE+SQRT(VARH2)
      WRITE(6,101)   "HERITABILITY'", H2
      WRITE(6,101)   "SE =", SE
      GO TO 10
101   FORMAT   (V)
999   STOP
      END
```

Where A,B,C, are the coefficients of the expected mean squares for sires, dams and the sire X dams interaction.

MSS, MSSD, MSD, MSE are the Mean Squares for sires, sire X dam interaction, dams, and error.

DFS, DFD, DFSD, DFE are degrees of freedom for sires, dams, sire X dam interaction, and error.

APPENDIX IV

Heritability Estimates

A. Number of vertebrae in Brown Trout (Salmo trutta L.). Schmidt (1922) reported the average number of vertebrae in fifty offspring of each of four female and three male brown trout; and he reported the number of vertebrae in each parent. I analyzed the mean number of vertebrae in each sibling group by analysis of variance:

Source of Variation	Degrees of Freedom	Mean Square
Males	2	0.5329
Females	3	4.3969
Residual	6	0.0017

Assuming no effect of interactions between males and females I computed the heritability of vertebra number as:

$$\frac{0.5329}{\frac{0.5329}{4} + \frac{4.3969}{3} + 0.0017} = 0.33$$

By regression analysis I regressed the number of vertebra in the sibling groups on the mean of the number of vertebrae in each group's parents and found the regression coefficient (the estimate of heritability which is made by this method) to be 1.314, i.e., heritability is estimated as one.

B. Age at maturity of chinook salmon (O. tshawytscha). Ellis and Noble (1961) reported the age of maturation of the offspring of crosses between two-year-old males, three-year-old males, and three-year-old females in the Deschutes River, Washington, stock of chinook salmon. The average age of the offspring of the two-year-old fathers was 2.3 years for males and 3.7 years for females; the average age of the offspring of three-year-old fathers was 3.9 years for females and 3.15 years for males. Taking the midpoints between the average ages of the sexes in each offspring group and "regressing" them on the midpoints of the parental ages I get a slope or heritability estimate of .24.

C. Date of spawning immigration of pink salmon. In 1974 in an investigation of the survival of early and late migrating fry, Taylor (1977, 1978) marked over 79,000 fry that were the offspring of some of the latest adults to enter Auke Creek, Alaska, in 1973. In 1973 the mean date of entry into the creek of adults in the later of the two stocks was September "4.164" (SE = .085). The mean date of entry of the parents of the marked fish is not precisely known, but it was certainly later, probably seven days* . In 1975 the mean date of entry of progeny of all the 1973 late-stock adults was September "7.048" (SE = .048)

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*S. G. Taylor, U. S. National Marine Fisheries Service, Auke Bay Laboratory, Box 155, Auke Bay, Alaska, 99821.

and that of the marked fish September "8.886" (SE = .050). If this is regarded as a selection experiment the response to selection was 8.886 - 7.048 = 1.84 days; if the selection differential is taken to have been seven days (the difference between the mean dates of entry into Auke Creek of the entire stock in 1973 and of the parents of the marked fish), the heritability of time of entry into the creek is 1.84/7 = 0.26. (Falconer 1960 p. 189). Some of this correlation between parents and offspring must be due to assortative mating; fish characterised by a given date of entry into a stream must spawn preferentially with fish of a similar phenotype.

APPENDIX V A

FORTRAN code used to simulate the change in numbers of a chum salmon stock in which age of maturity is not heritable, i.e. $h^2 = 0$.

```
C Establish year-age cells, five for four year olds, four for
C three year olds.
DIMENSION FO(5), TH(4)
C Set number of fish in each cell at 6.6125 thousand
DO 5 I=1,5
FO(I)=6.6125
5 CONTINUE
DO 6 I=1,4
TH(I)=6.6125
6 CONTINUE
C Set counter at year 1
K=1
C Define  Size of Run as sum of number of age threes and number of age
C             fours in cell 1
C         Mean age of run as the average age of fish in cell 1
C       Rate of return per spawner (RPS) according to Ricker Curve
10 RUN=FO(1)+TH(1)
AGE=(4*FO(1)+3*TH(1))/RUN
RPS=1.76*EXP(-.0427*RUN)
C In years of competition with pink salmon cause RPS to be 90% of RPS
C in years of non-competition.
IF(FLOAT(K)/2.GT.(K/2))RPS=RPS-.1
C Set total number of surviving offsping from the run.
GET=RPS*RUN
C Apportion those offspring between two ages of maturation.  Since
C heritability is zero, the portions in each age are equal.
TH(4)=GET/2
FO(5)=GET-TH(4)
C List for the current year:
C   Size of the Run
C   Average Age of the Run
C   Rate of return to be experienced by offspring of the Run.
WRITE(6,101)K,TH(1),FO(1),RUN,AGE,RPS
101 FORMAT (' ',I2,5(5X,F8.3))
C Cause the population to age one year:  move the numbers of
C fish in each year-age cell to the next lower-numbered cell.
DO 20 I=1,4
FO(I)=FO(I+1)
20 CONTINUE
DO 25 I=1,3
TH(I)=TH(I+1)
C Repeat fifty times--simulate fifty yr.
25 CONTINUE
IF(K.EQ.50) GO TO 999
K=K+1
GO TO 10
999 STOP
END
```

APPENDIX V B

FORTRAN code used to simulate the change in numbers of a chum salmon stock in which age of maturity is greatly heritable, i.e. $h^2 = 1.0$.

```
C Establish year-age cells, five for four year olds, four for
C three year olds.
DIMENSION FO(5), TH(4)
C Set number of fish in each cell at 6.6125 thousand
DO 5 I=1,5
FO(I)=6.6125
5 CONTINUE
DO 6 I=1,4
TH(I)=6.6125
6 CONTINUE
C Set counter at year 1
K=1
C Define  Size of Run as sum of number of age threes and number of age
C             fours in cell 1
C         Mean age of run as the average age of fish in cell 1
C       Rate of return per spawner (RPS) according to Ricker Curve
10 RUN=FO(1)+TH(1)
AGE=(4*FO(1)+3*TH(1))/RUN
RPS=1.76*EXP(-.0427*RUN)
C In years of competition with pink salmon cause RPS to be 90% of RPS
C in years of non-competition.
IF(FLOAT(K)/2.GT.(K/2))RPS=RPS-.1
C Set total number of surviving offsping from the run.
GET=RPS*RUN
C Apportion those offspring between two ages of maturation.  Since
C heritability is one, the portions in each age are the same
C as the portions in the current year.
TH(4)=GET*(4-AGE)
FO(5)=GET-TH(4)
C List for the current year:
C   Size of the Run
C   Average Age of the Run
C   Rate of return to be experienced by offspring of the Run.
WRITE(6,101)K,TH(1),FO(1),RUN,AGE,RPS
101 FORMAT (' ',I2,5(5X,F8.3))
C Cause the population to age one year:  move the numbers of
C fish in each year-age cell to the next lower-numbered cell.
DO 20 I=1,4
FO(I)=FO(I+1)
20 CONTINUE
DO 25 I=1,3
TH(I)=TH(I+1)
C Repeat fifty times--simulate fifty yr.
25 CONTINUE
IF(K.EQ.50) GO TO 999
K=K+1
GO TO 10
999 STOP
END
```

APPENDIX VI A
Description of Whiskey Creek Parents
1975 Experiment

	MEHP* mm	Weight pounds	Age+ Years	Egg Weight# grams Mean	SE of Mean	N
Males						
1	525	5	3			
2	655	14	4			
3	630	12	4			
4	535	6	3			
5	525	6	3			
Females						
A	555	6	3	23.22	0.44	28
B	630	8	4	30.17	0.25	24
C	615	9	4	31.85	0.28	33
D	590	8	3	22.83	0.20	23

*Mid eye to hypural plate, Length

+Years since parents of these fish spawned, number of scale annuli plus one.

#Mean, standard error of mean, number of eggs weighed. Eggs to be weighed were not fertilized, were not exposed to water, were not preserved or frozen. They were kept in closed polyethylene bags under refrigeration and weighed within eight hours of spawning.

APPENDIX VI B

Description of Parents 1976 Experiment

Parent	MEHP Length mm	Weight kg	Age Yr
Males			
Kilchis R.			
1	628	28.6	4
2	582	22.2	3
3	526	14.5	3
Whiskey Cr.			
1	606	24.2	3
2	531	14.7	3
3	580	16.5	4
Females			
Kilchis R.			
A	574	17.3	3
B	595	19.1	4
C	544	15.7	3
Whiskey Cr.			
A	624	20.4	4
B	621	17.6	3
C	600	17.6	4