EVOLUTION OF BREEDING LIFE HISTORY AND MORPHOLOGY IN COHO SALMON (ONCORHYNCHUS KISUTCH)

by

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Evolution of Breeding Life History and Morphology in Coho Salmon

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ABSTRACT

This thesis examines the evolution of morphology and life history in female and male coho salmon (Oncorhynchus kisutch) in response to breeding competition, migration arduousness, and selection for egg size.

Morphology and life history were examined in 13 wild and 5 hatchery populations of coho salmon. Female secondary sexual characters, including kype (an extension of the upper jaw used in fighting) and body colouration, increased significantly with degree of female competition. By contrast, arduous spawning migrations appeared to select for increased body streamlining. Both breeding competition and the difficulty of migration, though nonsignificant, negatively effected ovarian investment. In hatcheries, where breeding competition is relaxed, characters associated with breeding competition and spawning performance were reduced. Moreover, there was an increase in egg weight.

Secondary sexual characters were highly dimorphic. Males had larger kypes, more intense colouration, and greater body depth. In addition, the size of the male dorsal fin, used in signals of courtship and aggression, exceeds that of females. The sexes also differed in morphology of propulsive fins, which may be related to sexual dimorphism in their risk assessment of foraging strategies. Male secondary sexual characters, like those of females, increased with breeding competition. Hatchery male morphology differed significantly from that of wild males, as predicted from the lack of breeding competition. These results reveal the importance of breeding competition, as well as migration, for understanding the evolution of life history and morphology in male and female salmon.

Several authors have demonstrated a positive latitudinal gradient in salmon fecundity. Using correction factors developed from a study of egg preservation, latitudinal variation in egg size was investigated here. Opposing latitudinal trends were found in fecundity and egg size, with the result that production of egg biomass was constant with latitude. This suggests that egg size, and not fecundity, may be the important determinant of latitudinal patterns. Egg size was often positively correlated with female body size, probably reflecting female access to different gravel qualities. Moreover, egg size decreased with spawning date among populations. Finally, hatchery fish had significantly larger eggs than their wild counterparts. Thus, egg size appears to be free to evolve according to local conditions. This suggests that egg size evolution may be responsible for latitudinal trends in fecundity.

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PART A

GENERAL INTRODUCTION

Life History Evolution

The intricate fit between organisms and their environments prompts us to ask adaptive questions (Williams 1966a). Adaptive questions are concerned with the way organisms are molded by their environment through natural selection. The purpose of this thesis is to examine differences in the breeding morphology and life history among populations of coho salmon (*Oncorhynchus kisutch*) as evolutionary responses to natural selection. As selective agents, I have focused on the competition that occurs during breeding and the difficulty of their migration to the breeding grounds. In addition, latitudinal patterns are examined in fecundity and egg size.

Life histories are an emergent property of organisms and reflect a compromise in their allocation of limited resources among reproduction, growth and maintenance (Fisher 1958). Theories of how selection affects the optimal partitioning of energy have been developed by Williams (1966a, b), Gadgil and Bossert (1970), Schaffer (1974), Stearns (1976) and others. By assuming that traits have heritability, the selective forces that shape populations can be identified. This can be done by using the comparative approach. The comparative approach, in which two or more groups from differing environments are contrasted, tests for associations that are suggested by hypotheses based on natural selection (e.g., Clutton-Brock and Harvey 1979, 1984, Harvey and Mace 1982, Jarman 1982, Ridley

1983). Comparisons among populations, rather than species, is an attractive method since the problem of genetic differences due to phylogeny is greatly reduced (Jarman 1982).

A major component of natural selection is sexual selection (Darwin 1859). Sexual selection operates on traits giving certain individuals an advantage over others of the same sex in obtaining successful matings. Bateman (1948) discovered that variance in reproductive success within the male sex is generally greater than within females. He proposed that the reproductive success of females is limited by their ability to garner resources to produce eggs and that male reproductive success is limited by access to females. Thus, males should evolve traits which maximize mating opportunities while females maximize egg production and survival.

In addition, to sexual selection on males and natural selection on females during breeding, there will be natural selection on both sexes due to migration costs. During freshwater migration to the spawning grounds, salmon must travel extensive distances through often turbulent waters. During this time no feeding occurs (Foerster 1968). Thus both migration and breeding competition should mold adaptations in adult salmon.

Sexual Characters in Salmon

Many fishes, including salmonids, show elaborate male secondary sexual characteristics (Breder and Rosen 1966). For instance, Foerster (1968, p. 105) remarked that

> "changes which take place in salmonoid fishes and in particular, the Pacific salmon, genus Oncorhynchus, are so great that were one not cognizant of the transformation which takes place, as the fish mature, one would not consider them the same species."

These changes include the growth of a kype or hooked snout, a humped back, thickening of the skin, absorption of scales and a dramatic alteration of colour. The kype is formed primarily by the elongation of the premaxillae, almost doubling in length in some species (pink salmon - Davidson 1935, Vladykov 1962). The structure of the back changes, the dorsal spines split to form a bar of cartilage about the supracarinales muscles creating the hump (Davidson 1935). The hump rises directly behind the head, reaching its maximum just anterior to the insertion of the dorsal fin and gradually tapers off toward the tail. Also at this time, the colouration changes from the silvery marine state to a breeding colouration which may be a brilliant red along the sides.

Darwin (1871) proposed that salmon secondary sexual characters evolved through sexual selection. The male kype, for example, functions as a specialized "weapon" evolved to aid in the competition for females (Gross 1984). The hump can serve as a shield against the attack by an opponent's kype (Schroder 1973). The bright colouration probably aids to attract females (Darwin 1871). Although the secondary sexual characters are less well developed in females (Davidson 1935), they do have kypes and some red colouration. Since females are not limited in access to mates (Sargent et al. 1986a), the traits must arise from the natural selection due to female competition for nest sites (van den Berghe and Gross 1986b).

Thesis Objectives

The purpose of this thesis was to examine the evolution of coho salmon breeding morphology and life history. I used a comparative approach, contrasting several wild and hatchery populations, and examined the importance of breeding competition, migration arduousness, and geographic latitude in molding breeding morphology and life history.

Part B describes the impact of the social environment, particularly female breeding competition, on population variation. I test several evolutionary predictions for the relationship between freshwater spawning migration, female breeding competition, and egg production.

Part C investigates sexual dimorphism in relationship to mating system. It compares how males have responded to the selection pressures already identified for females.

Part D examines the evolution of egg size. Using the correction factors developed from a study of egg preservation techniques (Appendix I), egg size data from coho salmon populations throughout North America are examined in light of evolutionary predictions.

Finally, Part E provides a general discussion and summary of the findings of this thesis, discusses implications for salmonid management and enhancement, and suggests ideas for future research.

PART B

LIFE HISTORY AND MORPHOLOGY OF FEMALE COHO SALMON

INTRODUCTION

Female reproductive success may be highly variable in nature as a consequence of female competition for breeding resources (e.g., Hrdy 1977, Reiter et al. 1981, Clutton-Brock et al. 1982, Wasser 1983, Robinson 1986, van den Berghe and Gross 1986b). Recently, van den Berghe and Gross (1986b) quantified the intensity of natural selection that may be generated by female breeding competition. They found that for a population of coho salmon the intensity of natural selection exceeded that reported for male sexual selection in other species (reviewed by Arnold and Wade 1984). The quantification of selection intensities, and the partitioning of selective forces, provides useful information for identifying selective agents and the potential for evolution. It does not, however, demonstrate an evolutionary response. The present study determines the degree to which female morphology and life history in the coho salmon is an evolutionary response to the selective force of breeding competition (the latter identified by van den Berghe and Gross [1986b]), as well as to the sometimes counteracting selection pressures from the physical environment.

Natural History

Pacific salmon are typically anadromous and semelparous, growing to maturity in the sea and spawning in small streams and tributaries, whereafter they die. In Washington State and southern British Columbia the female coho typically have a three-year life cycle (Drucker 1972, Schubert 1982). Adults spawn during the fall and winter, and eggs hatch in the spring. After one year in the freshwater streams, juveniles migrate to the ocean, where they spend one and a half years growing before returning to their natal stream to spawn. The secondary sexual characters, kype (an extension of the upper jaw used in fighting) and red body colouration (an apparent badge of social status; Schroder 1981), develop during the return migration (Davidson 1935). Hatchery populations differ from wild ones in that the former are captured at the completion of migration, gametes are stripped, eggs randomly fertilized, and fry reared until ready to migrate to the ocean for adult development.

The reproductive behaviour of coho females in the wild was described in detail by van den Berghe and Gross (1984, 1986a, b). Briefly, females establish territories in the stream, within which they sequentially construct nests. From one to seven nests are made, collectively referred to as the "redd". The redd is the minimum area necessary for oviposition of all eggs. Males neither take part in territory establishment nor parental care, but rather compete for access to females that are ovipositing, enter the nest to fertilize the eggs, and depart (Gross 1984, 1985). By contrast, females remain to guard their territory until death to prevent the destruction of their eggs by re-use of the site by later arriving females.

Salmon populations within each species differ considerably in their morphology and life history (e.g., Ricker 1972, Beacham 1984a, 1985, Carl and Healey 1984, Taylor and McPhail 1985a, Healey 1986). The evolution of population-specific morphology is facilitated by three factors. First, salmon "home" to their natal stream to spawn, thereby restricting gene flow among populations (Hasler and Scholz 1983, Quinn 1984). Second, stream differences create local selectional pressures. For example, spawning may occur in creeks as narrow as a meter or as wide as several hundred meters (e.g., Fraser River), and some Pacific salmon populations breed near the coast, while others migrate over 3,000 km (Aro and Shephard 1967) to reach their spawning grounds. Finally, many morphological traits in salmon have been shown to be heritable (Riddell et al. 1981, Taylor and McPhail 1985a) and thus the selectional differences among streams may evolutionarily shape differences in salmon populations.

Evolutionary Predictions

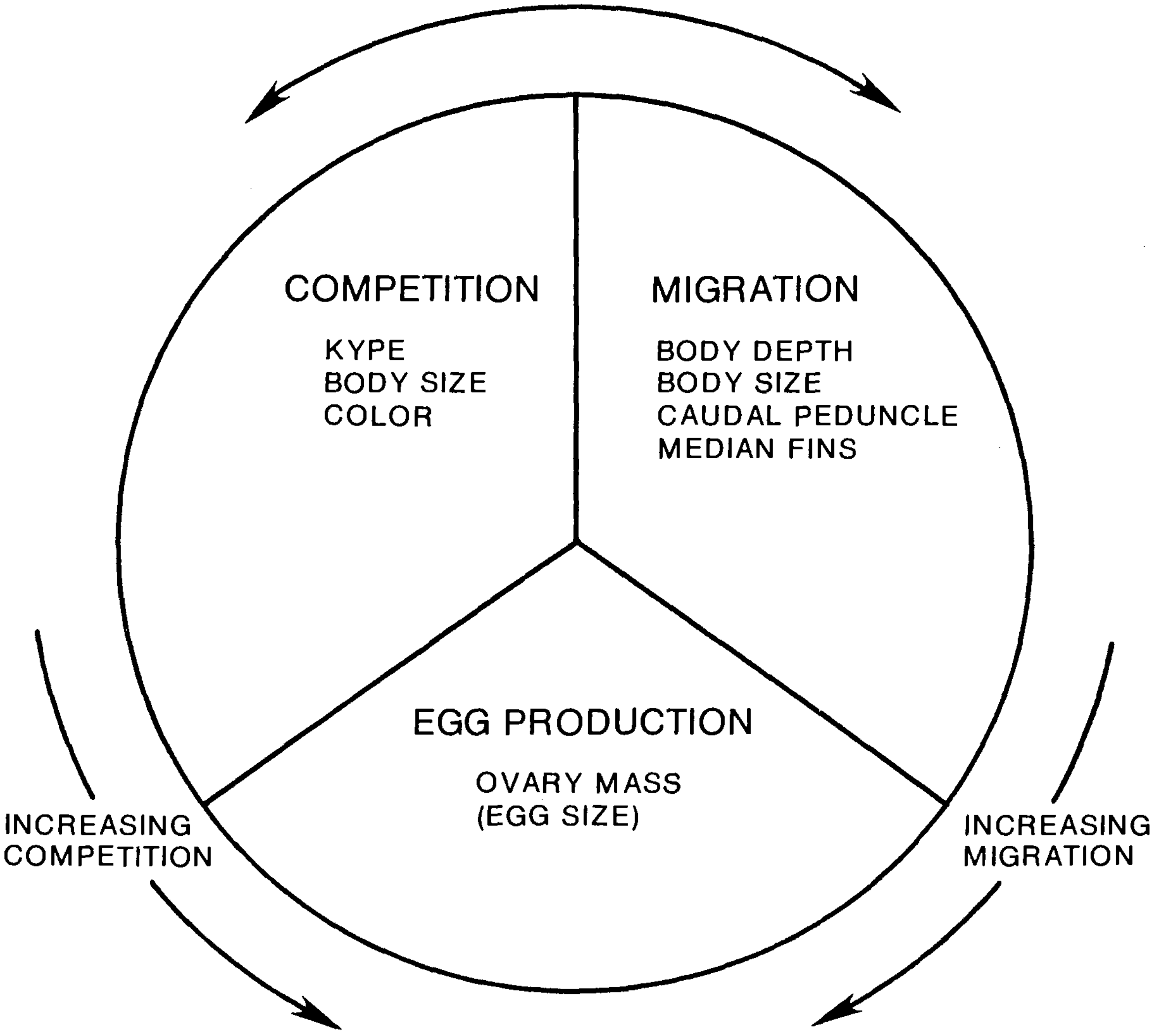
Here I apply a "comparative approach" to examine morphological and life history evolution among coho salmon populations. The intent was to contrast several environmental variables suggested to be of importance in molding the morphology and life history of salmon (e.g., Schaffer and Elson 1975, Riddell and Leggett 1981, Beacham 1984a, 1985, Taylor and McPhail 1985b), with the selection pressures of breeding competition identified by van den Berghe and Gross (1986b). I compared several wild populations differing in degree of breeding competition and difficulty of migration. In addition, I contrasted several hatchery populations with the wild ones. These hatcheries had no directed program of artificial selection, and by removing natural breeding competition and enhancing the survivorship of eggs and juveniles they provided a situation in which salmon populations could potentially respond to the relaxation of natural selection.

Given that resources are limited in nature, conflict will exist among investments and because of the law of conservation of energy, this will be irrefutable (Sibly and Calow 1986). Therefore, organisms should evolve an optimal allocation of resources (such as time and energy) in their life history program which maximizes the combined fitness benefit of growth, maintenance and reproduction (Williams 1966a, Cody 1966, Stearns 1976). Within the allocation of resources to reproduction, female salmon morphology and life history should reflect tradeoffs between egg production and two important selectional pressures - difficulty of freshwater migration and female breeding competition (Fig. 1).

Breeding Competition

The availability of high quality redd sites within a stream is often limited, resulting in female fighting, dig-up of previously spawned eggs, egg retention, and delayed spawning

Figure 1. The phenotype of adult female coho salmon faces an allocation tradeoff among egg production and success in breeding competition and migration. In this scenario energy which goes into one component of the life history cannot go into another. The optimal solution will be the allocation which maximizes lifetime reproductive success.


COMPETITION
KYPE
BODY SIZE
COLOR
MIGRATION
BODY DEPTH
BODY SIZE
CAUDAL PEDUNCLE
MEDIAN FINS
EGG PRODUCTION
OVARY MASS
(EGG SIZE)
INCREASING COMPETITION
INCREASING MIGRATION

(Schroder 1981, van den Berghe and Gross 1986b). Van den Berghe and Gross (1986b) showed that both redd quality and parental care through redd defense were important for the survival of embryos, accounting for 21% and 36% of the intensity of natural selection in Deer Creek Junior, WA. By contrast, female fecundity accounted for only 22% and post-emergent mortality for 25% of the total selection on females. The size of the kype, as well as the body, were of primary importance in successful acquisition of quality redd sites. After spawning, however, the survival of nests was primarily a function of body size, because larger females dug deeper nests and lived longer guarding their redds. Therefore, as suggested by van den Berghe and Gross(1986b), the degree of development of the kype, the size of the body, and the intensity of red colouration indicating social status (i.e., Rohwer 1975) are predicted to vary directly with the degree of competition among populations (Table 1).

As a consequence of investment through parental care into brood survival, ovary mass should decrease with increasing breeding competition (Fig. 1; Table 1). Furthermore, average egg size should decrease because: (1) smaller eggs survive better in poor quality gravel (van den Berghe and Gross 1986b), and with increasing competition a larger proportion of individuals will be forced into suboptimal nest sites; and (2) poorer average offspring survivorship selects for a smaller mean egg size (Sargent et al. 1986b).

Table 1. Evolutionary predictions of slopes of relationship between female morphological and life history traits, and variables specific to each population.

	Population Variables		
	Difficulty of Migration		
Character	Elevation	Distance	Breeding Competition
Body:			
Kype			positive
Colour			positive
Depth	negative	negative	
Caudal Peduncle	negative	negative	
Length	positive	positive	positive
Median Fins:			
Anal	negative	negative	
Dorsal	negative	negative	
Life History:			
Ovary Mass	negative	negative	negative
Egg Weight			negative

If my reasoning about tradeoffs among competition, ovary mass, and egg size is correct, then females should exhibit smaller kypes, less intense red colouration and larger ovary masses and egg weights in populations where competition is reduced. Such responses should be particularly evident in hatcheries, where natural breeding competition has been reduced.

Freshwater Migration

Both the migration distance and the elevation above sea level to reach the natal stream impose a major energetic demand on salmon (Idler and Clemens 1959, Gilhousen 1980), especially since salmon do not feed once they enter freshwater (Foerster 1968). Arduous migrations should select for body streamlining to reduce drag (Webb 1984, Taylor and McPhail 1985b), including a narrow caudal peduncle, a deep, narrow tail and a fusiform body shape (Webb 1984). However, such design is not effective for burst swimming, which facilitates spawning and escape from predators on the spawning grounds. Such burst swimming requires "thrust", which is maximized by depth in each propulsive element (Webb 1978, 1984). Therefore, characters associated with burst swimming (e.g., body depth, caudal peduncle depth, and median fin sizes) should be inversely related to freshwater migration distance and elevation (Taylor and McPhail 1985b; Table 1).

Arduous migrations were suggested by Schaffer and Elson (1975) to select for a large body size to meet energetic demands. However, migration arduousness should also affect energy that would otherwise be allocated to the ovary (Fig. 1; Table 1).

I examined hatchery populations which were established at the same location as their original brood stock. Therefore, selection for sustained swimming had not changed. However, selection for burst swimming was reduced, since both spawning and juvenile rearing occurred in controlled environments. Hatchery females, experiencing reduced selection for burst swimming, were therefore expected to evolve a more "streamlined" body shape, relative to wild females.

METHODS

Study Populations

Fully mature female coho salmon were collected during the 1984-85 spawning season from 18 different populations, 13 wild and 5 hatchery, from 4 geographic regions (Table 2, Fig. 2). The choice of wild populations was based on minimal historic disturbance by man to the stream environment, and the hatcheries for their proximity to natural populations and absence of planned artificial selection. The wild coho were caught on their spawning grounds by hand net, measured, and released undamaged to continue spawning. Emphasis on random sampling was assisted by the small size of the streams which allowed all habitats to be sampled. The hatcheries were chosen, in part, because of their lack of artificial selection programs; most of the returning fish are utilized. Our collections were made during normal spawning operations.

Measurements

The 12 morphological characters in Figure 3 were measured with Vernier calipers to the nearest 0.1 mm, except for body (postorbital-hypural) length, fork length and body depth, which were measured to the nearest 1 mm. Any damaged characters were not measured. Body colouration was rated by eye on a scale of 1 to 6: 1 - silver (ocean colour), 2 - darkening (dull), 3 - dark,

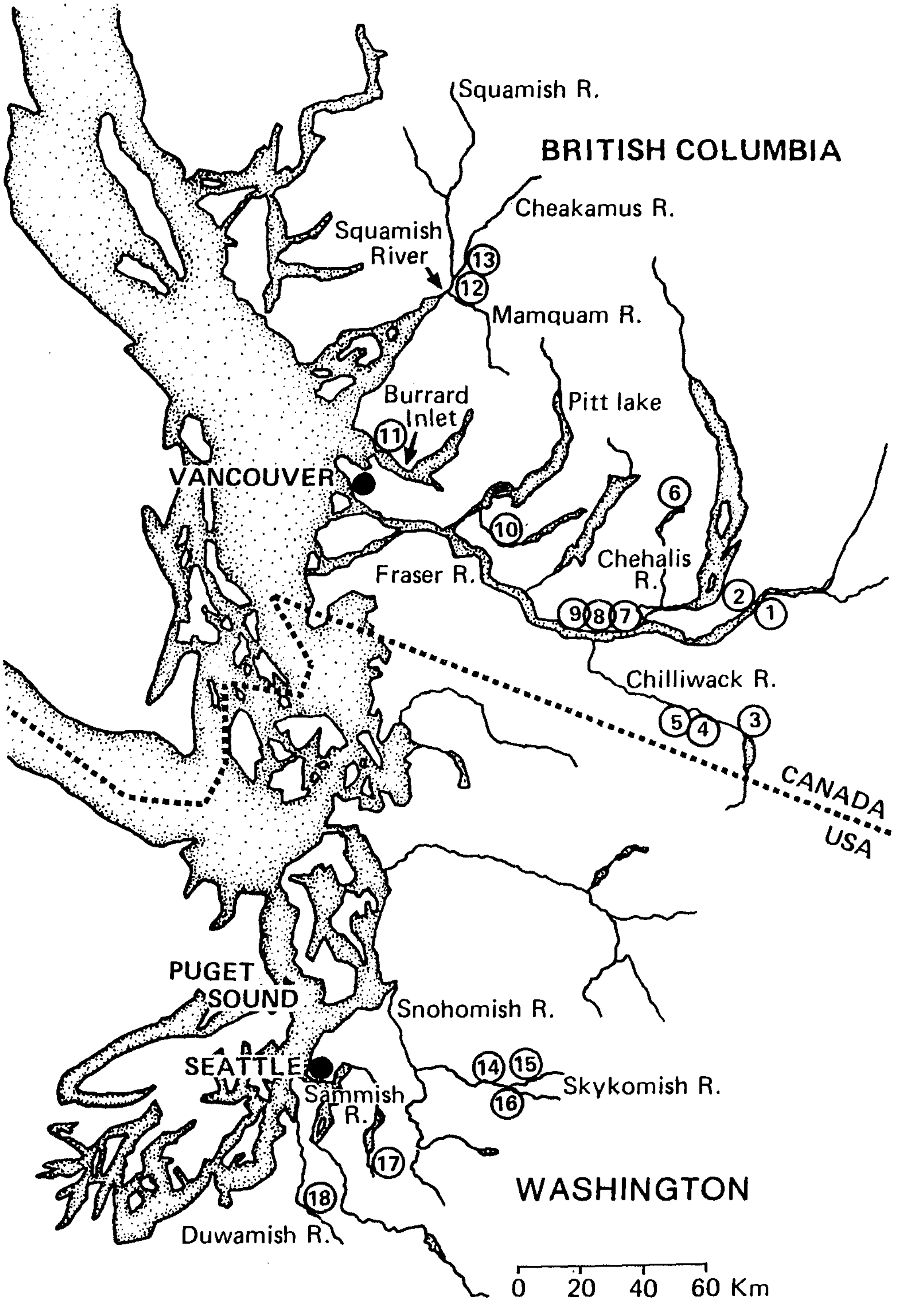
Table 2. Characteristics of the 18 coho salmon streams and hatcheries. Average competition is a measure of the average female spawning density, and episode competition is a measure of the average amount by which the female spawning capacity is exceeded.

Coho Salmon Population	Hatchery Age (years)	Freshwater Migration Distance (km)	Elevation Above Sea Level (m)	Spawnable Area (m^2)	No. Years Population Size Estimated	Competition Index	
						Average	Episode
Fraser River:							
Blaney Creek	-	52.2	30	778.5	36	2.83	1.77
Borden Creek	-	126.8	198	390.5	37	0.72	0.14
Chilliwack Hatchery	4	129.8	207	-	-	-	-
Cohoe Creek	-	136.3	220	593.8	29	1.25	0.97
Hicks Creek	-	133.6	35	374.3	13	3.53	2.40
Lorenzetta Creek	-	139.7	35	671.7	38	0.71	0.12
Post Creek	-	150.0	564	1440.3	7	0.21	0.00
Pye Creek	-	101.9	14	225.6	29	1.17	0.42
Siddle Creek	-	105.1	14	1008.0	34	0.81	0.20
Worth Creek	-	93.3	14	-	-	-	-

(cont'd)

Coho Salmon Population	Hatchery Age (years)	Freshwater Migration Distance (km)	Elevation Above Sea Level (m)	Spawnable Area (m^2)	No. Years Population Size Estimated	Competition Index	
						Average	Episode
Burrard Inlet:							
Capilano Hatchery	13	5.0	68	-	-	-	-
Squamish River:							
Mamquam River	-	6.5	23		-	-	-
Tenderfoot Creek	-	20.4	46	1485.0	8	1.31	0.47
Puget Sound:							
Deer Creek Junior	-	79.3	140	214.2	3	1.26	0.21
Green River Hatchery	83	55.3	21	-	-	-	-
Issaquah Hatchery	48	42.3	25	-	-	-	-
Peyton Creek	-	81.9	152	200.6	4	1.38	0.31
Skykomish Hatchery	67	63.9	49	-	-	-	-

Figure 2. Location of the 18 coho salmon populations. Fraser River: (1) Lorenzetta Creek, (2) Hicks Creek, (3) Post Creek, (4) Chilliwack Hatchery, (5) Borden Creek, (6) Cohoe Creek, (7) Siddle Creek, (8) Pye Creek, (9) Worth Creek, (10) Blaney Creek; Burrard Inlet: (11) Capilano Hatchery; Squamish River: (12) Mamquam River, (13) Tenderfoot Creek; Puget Sound: (14) Skykomish Hatchery, (15) Deer Creek Junior, (16) Peyton Creek, (17) Issaquah Hatchery, (18) Green River Hatchery.


Squamish R.
BRITISH COLUMBIA
Cheakamus R.
Squamish River
13
12
Mamquam R.
Burrard Inlet
11
Pitt lake
VANCOUVER
6
10
Chehalis R.
Fraser R.
2
1
9
8
7
Chilliwack R.
5
4
3
CANADA
USA
PUGET SOUND
Snohomish R.
SEATTLE
14
15
Skykomish R.
16
Sammish R.
17
WASHINGTON
18
Duwamish R.
0
20
40
60 Km

4 - rainbow stripe, 5 - widening stripe, 6 - bright red. Ten eggs were stripped from most females, preserved in Stockard's solution (Velsen 1980), and weighed to the nearest 0.1 mg wet weight. Total ovary wet weight, to the nearest 5 g, was obtained for a sub-sample of the females.

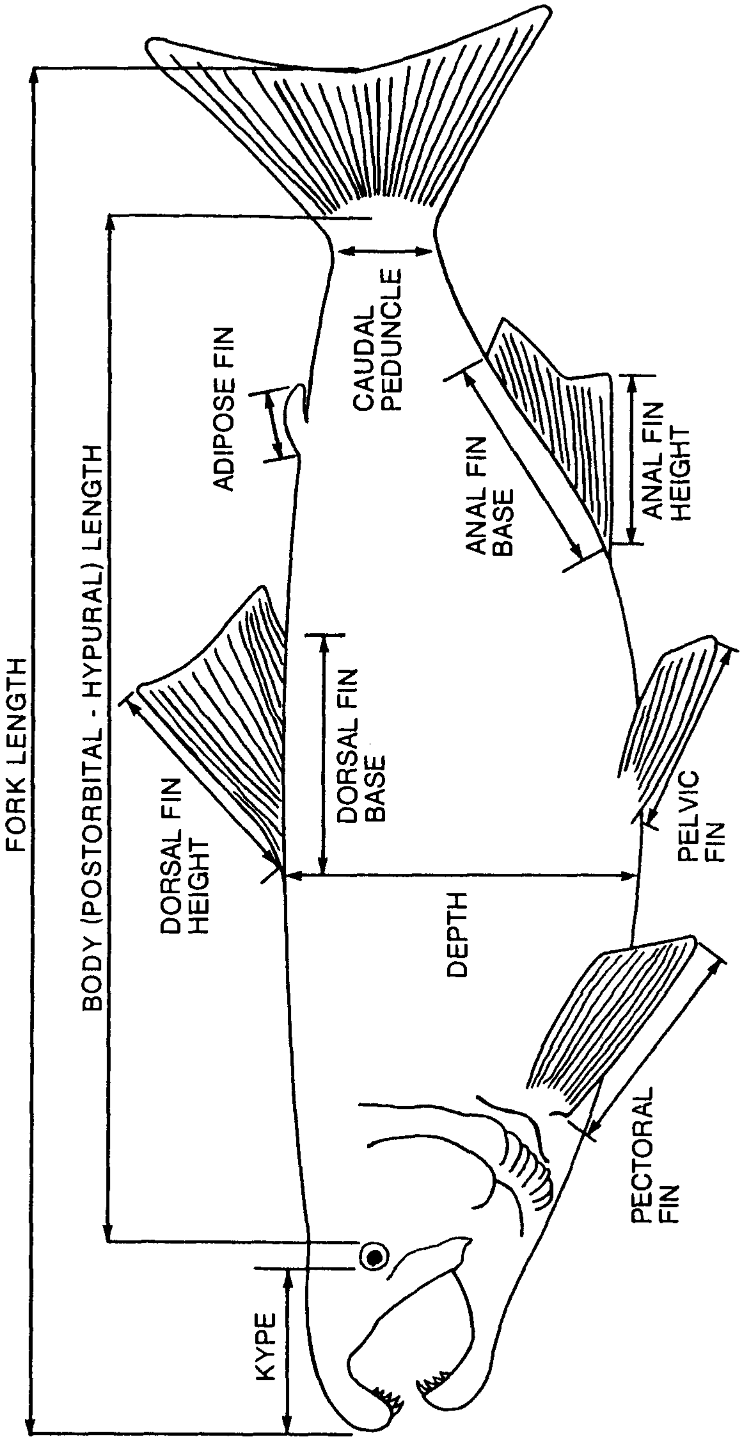
Population Parameters

Breeding competition, measured by population size and area of spawning habitat, was calculated for all wild populations except Mamquam River and Worth Creek, excluded because their variable and expansive spawning habitat prevented an accurate assessment of spawning area.

Population Size

Adult population size varies among years. Records of population size were from the Canadian Department of Fisheries and Oceans (DFO), the State of Washington Department of Fisheries (WDF) and van den Berghe and Gross (1986b). Because DFO foot surveys underestimate true population size (Cousens et al. 1982), I attempted a correction factor, by conducting comparative foot surveys on seven British Columbia populations. Following Ames (1984), my survey frequency of seven days was slightly shorter than the expected average length of breeding life of female coho, which is 9.6 ± 3.0 days (N = 5 populations; Willis 1954, Koski 1966, Crone and Bond 1976, van den Berghe and Gross 1986a). There was a significant difference between my

Figure 3. The twelve morphological characters measured on female coho salmon.


FORK LENGTH
BODY (POSTORBITAL - HYPURAL) LENGTH
KYPE
DORSAL FIN HEIGHT
ADIPOSE FIN
DORSAL FIN BASE
CAUDAL PEDUNCLE
DEPTH
ANAL FIN BASE
ANAL FIN HEIGHT
PELVIC FIN
PECTORAL FIN

estimates and those of the DFO for the same populations and year (t = 4.019, N = 7, P = 0.007). The DFO counts averaged 50% smaller (SD = 12.0), in agreement with Cousens et al. (1982) who found DFO foot survey counts to underestimate true population size by 30-50%. I therefore assumed the DFO counts were consistent and adjusted their foot survey data by a multiple of 2.1 (the average difference between my counts and theirs; see also Harrison [1984]). WDF counts, which were only used for Peyton Creek, were compared with our counts for Peyton Creek in 1983. They were found to be relatively accurate (8% smaller) and thus the three other years of counts were left unadjusted.

Three additional adjustments were made. The wild populations, Siddle, Post and Pye, contained some first generation hatchery reared coho (recognized by clipped adipose fins - a hatchery marking technique). Although mixing of the gene pool had not occurred, accurate estimates of the number of hatchery fish were not available, so the 4 years of hatchery planting were excluded from my analyses. Second, Blaney Creek coho competed for breeding territories with chum salmon, *O. keta*, and thus I calculated levels of competition from the combined size of coho and chum populations. At this time, there is no information available on the relative competitive abilities of theses species. Third, I assumed an equal sex ratio (Schubert 1982), and calculated female population size as 50% of total population size.

Spawning Habitat

Each stream was divided into 30 m sections, and the percentage of suitable spawning habitat was determined. The criteria for spawnable habitat was gravel size between 9 and 100 mm, less than 20% sand, and water flow faster than still and slower than turbulent (no white water; see Tagart 1976, Tappel and Bjornn 1983, Witzel and MacCrimmon 1983). These criteria, estimated by eye, were approximately equivalent to a minimum gravel quality of 3.5 on the Fredle Index and an expected embryo survivorship of 51% (Lotspeich and Everest 1981). Total spawning habitat for each stream, assumed to be stable across years, was the sum of the spawnable area in each section. These estimates appear to be quite accurate, since my estimate for Deer Creek Junior exceeded the relatively exacting measurements of van den Berghe and Gross (1986b) by only 4.5%.

Female Breeding Competition

Female breeding competition was estimated from the size of the female population, average redd size, and the total spawning habitat in the natal stream. Since redd size varies with female body size (Burner 1951, Tautz 1977), the average redd size was determined from the average female body size within each population. Following Tautz (1977) the average redd size was calculated as:

$$(FL/31)^2 \times 2358\ \text{cm}^2 \times 4 \times 0.7$$

where FL is the average fork length (cm) of females in the population, 4 is the modal number of nests per redd, the factor of 0.7 adjusts for nest overlap, and 2358 cm^2 represents the area used by a 31 cm female during nest construction. This equation, although developed from field measurements of sockeye salmon and steelhead trout (Tautz 1977), provides a redd size that closely approximates the existing data for coho salmon (e.g., Burner 1951, Crone and Bond 1976). The estimation of capacity is liberal because territory size is typically larger than the redd area itself (Burner 1951, Mathisen 1962), and because I do not exclude small areas which, as a result of redds surrounding them, are unusable.

Two indices of competition were used. (1) Average competition, calculated from the average female population size relative to the stream's spawning capacity. (2) Episode competition, calculated from the years in which the spawning capacity was exceeded (Table 2). In each such year the spawning capacity was subtracted from the population size. These differences were summed, and the sum was divided by the total number of years of available data (Table 2). This calculation was based upon the supposition that competition occurs primarily when the total spawning capacity of the stream is surpassed (cf. Wiens 1977).

Arduousness of Migration

The difficulty of migration was assessed from both the length and elevation of freshwater migration. River distance from the ocean to the natal stream was measured with a cartometer and elevation above sea level was read from topographic maps.

Statistical Analyses

Female morphology, ovary mass, and egg size were standardized to a grand sample mean body length of 489 mm (postorbital-hypural; N = 380) to minimize variability as a result of allometric growth and mean body size differences among populations. The data were transformed ($\log_{10}$) and regressed against the logarithm of body length and the resultant slopes used to calculate the standardized data set (Gould 1966). The transformation followed the equation of Ihssen et al. (1981),

$$M_t = M_o \times (L/L_o)^b$$

where M_t is the transformed character, M_o is the observed character, L is the grand sample mean body length of females, L_o is the observed body length and b is the regression coefficient of log M_o on log L_o within populations obtained from analysis of covariance.

Stepwise discriminant function analysis was used to define overall female morphological variation among the populations and identify which characteristics best distinguished individual populations. Egg weight and ovary mass were excluded from the discriminant analysis, since these data were not available for all individuals. Wilks' Lambda (SPSS Inc. 1983) and its approximate transformation to the F statistic tested for significant differences between population centroids. Homogeneity of sample covariance matrices was tested by Box's M test (SPSS Inc. 1983). Bayes' Rule was used for classification into groups (Tatsuoka 1971). A correlation coefficient was calculated between Euclidean distances (a measure of dissimilarity, Pimentel [1979]) among female character means, and geographic distances between populations. Stepwise discriminant function analysis also defined overall female morphological variation between wild and hatchery populations. Hierarchical agglomerative cluster analysis (Pimentel 1979) was used to display similarities among populations, based on female morphological characters. Female character means were calculated for each population. This reduced variation within each cluster, and facilitated discrimination between clusters. Therefore, quantitative comparisons of cluster discreteness were not made and only the general trends in the clustering patterns were emphasized. The population characters were standardized ($z = 0$, SD = 1). Squared Euclidean distance was used as the dissimilarity measure, and the clustering strategy was Ward's (Sneath and Sokal 1973).

Stepwise multiple regression determined the relationship between population character means and breeding competition and the difficulty of migration. Population character means were used rather than individual female character measures to avoid pseudoreplication (Hurlbert 1984). Only the eleven wild populations with competition indices were used, unless the analysis suggested that competition was unimportant in explaining female characters. Then a second stepwise regression was run with all 13 wild populations. (Because of small sample sizes the Lorenzetta Creek population was excluded from analyses involving anal and pectoral fin lengths.)

Tests of significance were one-tailed for all predicted character relationships. The probability level for significant differences was 0.05, unless otherwise specified. Analyses were performed with the Statistical Package for the Social Sciences (version SPSSx, SPSS Inc. 1983).

RESULTS

Variation Among Populations

Considerable interpopulation variation exists in the morphology and life history of females (Appendices 2 and 3). Each of the 12 morphological characters was significantly different among populations (by tests for univariate equality of population means, $P < 0.001$), with the kype, which ranged 25% in size, being most variable (range 40.5 - 50.6 mm, Wilks' Lambda $U = 0.543$).

Females from the 17 populations (Lorenzetta excluded) could be identified by discriminant analysis to their site of origin, based on morphology alone, with 52% accuracy. The most dissimilar from other populations was the Capilano Hatchery females (range $F = 12.50 - 36.00$, d.f. = 12, 340, $P < 0.001$), which was classified with 100% accuracy. Only the females of Cohoe Creek and Deer Creek Junior ($F = 1.52$, $P = 0.113$), Deer Creek Junior and Peyton Creek ($F = 1.51$, $P = 0.118$), and Pye and Worth Creeks ($F = 1.52$, $P = 0.116$) did not differ significantly from each other (other populations: range in $F = 2.23 - 36.00$, $P < 0.01$).

Geographical distance among the 17 populations was significantly correlated with morphological (Euclidean) distance ($r = 0.192$, $N = 136$, $P = 0.013$). Therefore, some relationship between neighboring populations can explain a small portion of the variation among populations.

Morphological Character Relationships

The two indices of competition, average and episode, were significantly correlated ($r = 0.957$, $P < 0.001$), and migration distance and elevation nearly so ($r = 0.467$, $P = 0.054$). The variables were analyzed with a multiple regression to identify the relative contributions of breeding competition and the difficulty of migration to female morphology (Table 3).

Breeding competition best described the variation among populations in female kype length (Fig. 4A) and body colouration (Fig. 4B, Table 3). Distance of freshwater migration was correlated with a decrease in body depth (Fig. 5A), caudal peduncle depth (Fig. 5B), body length (Fig. 5C) and dorsal fin base (Fig. 5D). In single parameter correlations dorsal fin base was also correlated with elevation ($r = -0.491$, $N = 13$, $P=0.044$). Natal stream elevation was negatively correlated with dorsal fin height (Fig. 6). Distance was also correlated with dorsal fin height in single parameter correlations ($r = -0.567$, $N=13$, $P = 0.022$).

Life History Character Relationships

A trend towards decreasing ovary weight existed with elevation, distance and average competition, although the trends

Table 3. Partial correlations and statistical probabilities (in parentheses) from stepwise multiple regression analyses of female coho salmon morphology. Multiple regressions are shown for average and episode competition when both were statistically significant.

Character	N	Elevation	Migration Distance	Competition	
				Average	Episode
Body:					
Kype	11	N.S.	N.S.	0.673 (P=0.012)	0.713 (P=0.007)
Colour	11	N.S.	N.S.	0.764 (P=0.003)	0.796 (P=0.002)
Depth	13	N.S.	-0.571 (P=0.021)	N.S.	N.S.
Caudal Peduncle	13	N.S.	-0.683 (P=0.005)	N.S.	N.S.
Length	13	N.S.	-0.772 (P=0.005)	N.S.	N.S.
Median Fins:					
Anal Height	12	N.S.	N.S.	N.S.	N.S.
Anal Base	13	N.S.	N.S.	N.S.	N.S.
Dorsal Height	13	-0.567 (P=0.022)	N.S.	N.S.	N.S.

(cont'd)

				Competition	
Character	N	Elevation	Migration Distance	Average	Episode
Dorsal Base	13	N.S.	-0.556 (P=0.024)	N.S.	N.S.

N.S. = notsignificant (P>0.05)

Figure 4. The relationships between average breeding competition and kype length (A), and colour intensity (B), for wild populations of female coho salmon. The numbers within the circles refer to the individual populations as identified in Figure 2.

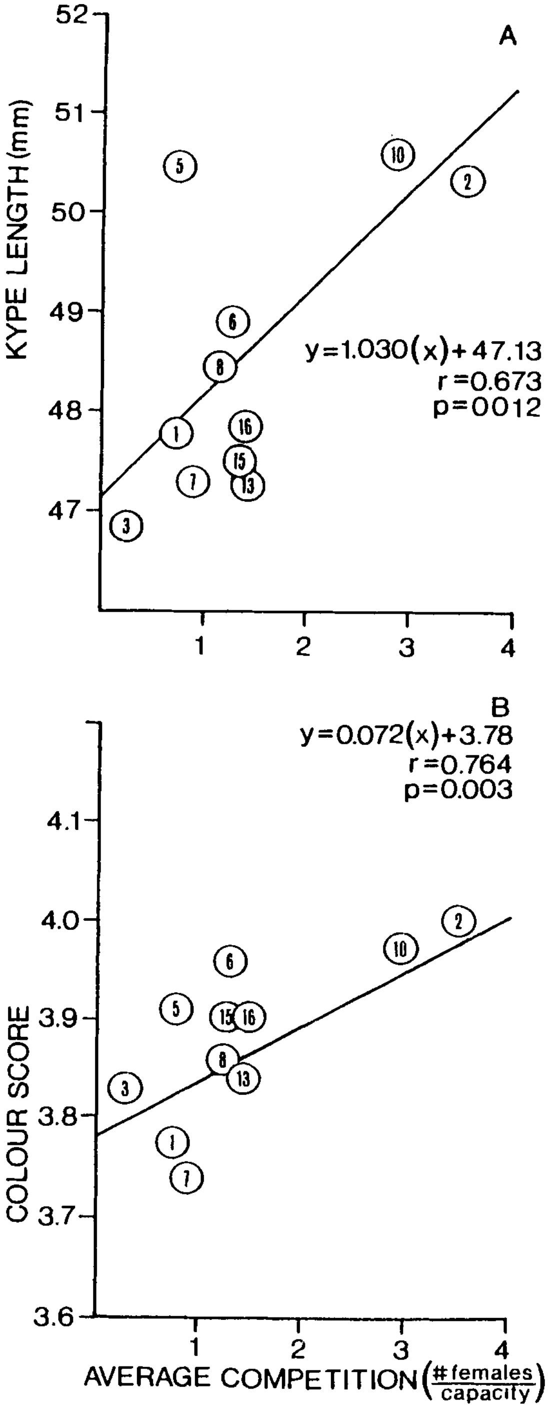
A
KYPE LENGTH (mm)
52
51
50
49
48
47
y=1.030(x)+47.13
r=0.673
p=0012
1
2
3
4
B
y=0.072(x)+3.78
r=0.764
p=0.003
COLOUR SCORE
4.1
4.0
3.9
3.8
3.7
3.6
1
2
3
4
AVERAGE COMPETITION (# females / capacity)
1
2
3
5
6
7
8
10
13
15
16

Figure 5. The relationships between distance of freshwater migration and body depth (A), caudal peduncle depth (B), body length (C), and dorsal fin base (D), for wild populations of female coho salmon. The numbers within the circles refer to the individual populations as identified in Figure 2.

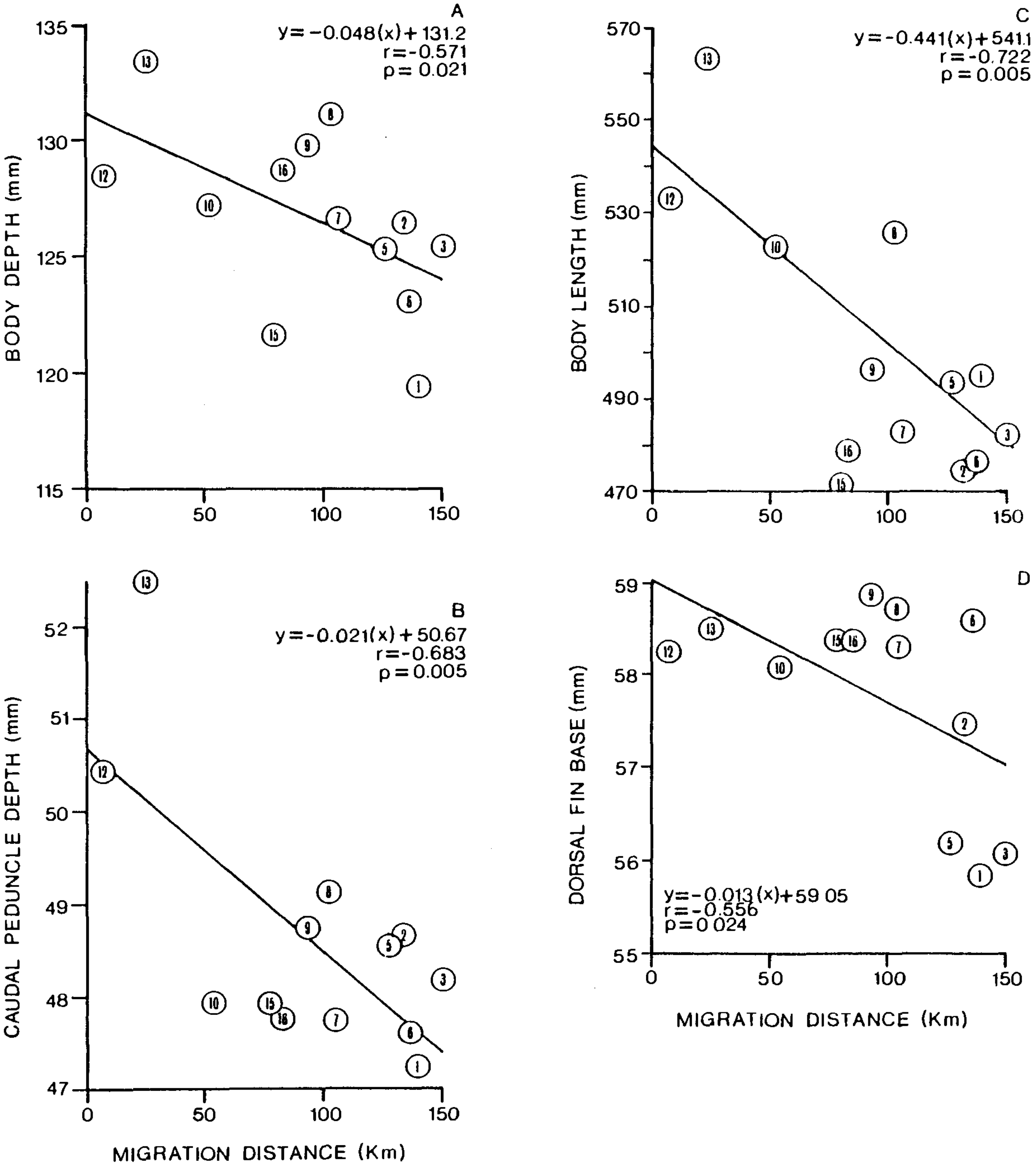
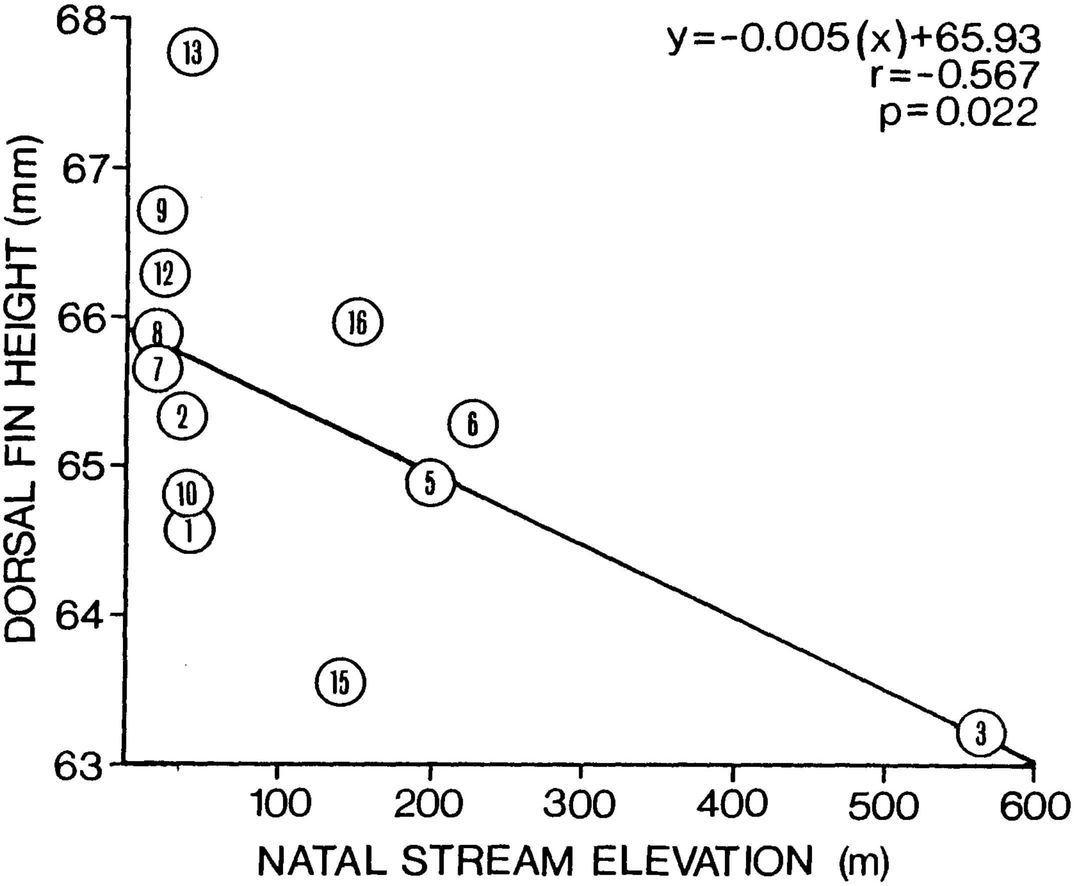

A
y= -0.048(x)+131.2
r=-0.571
p= 0.021
BODY DEPTH (mm)
135
130
125
120
115
0
50
100
150
13
12
10
16
9
8
7
5
2
3
6
15
1
C
y=-0.441(x)+541.1
r=-0.722
p=0.005
BODY LENGTH (mm)
570
550
530
510
490
470
0
50
100
150
13
12
10
8
9
5
1
3
7
16
2
6
15
B
y=-0.021(x)+50.67
r=-0.683
p=0.005
CAUDAL PEDUNCLE DEPTH (mm)
52
51
50
49
48
47
0
50
100
150
13
12
8
9
5
2
3
10
15
16
7
6
1
MIGRATION DISTANCE (Km)
D
DORSAL FIN BASE (mm)
59
58
57
56
55
0
50
100
150
9
8
6
13
15
16
7
12
10
2
5
3
1
y=-0.013(x)+59 05
r=-0.556
p=0 024
MIGRATION DISTANCE (Km)

Figure 6. The relationship between natal stream elevation and dorsal fin height for wild populations of female coho salmon. The numbers within the circles refer to the individual populations as identified in Figure 2.


y=-0.005(x)+65.93
r=-0.567
p=0.022
DORSAL FIN HEIGHT (mm)
NATAL STREAM ELEVATION (m)
68
67
66
65
64
63
100
200
300
400
500
600
13
9
12
8
7
2
10
1
16
6
5
15
3

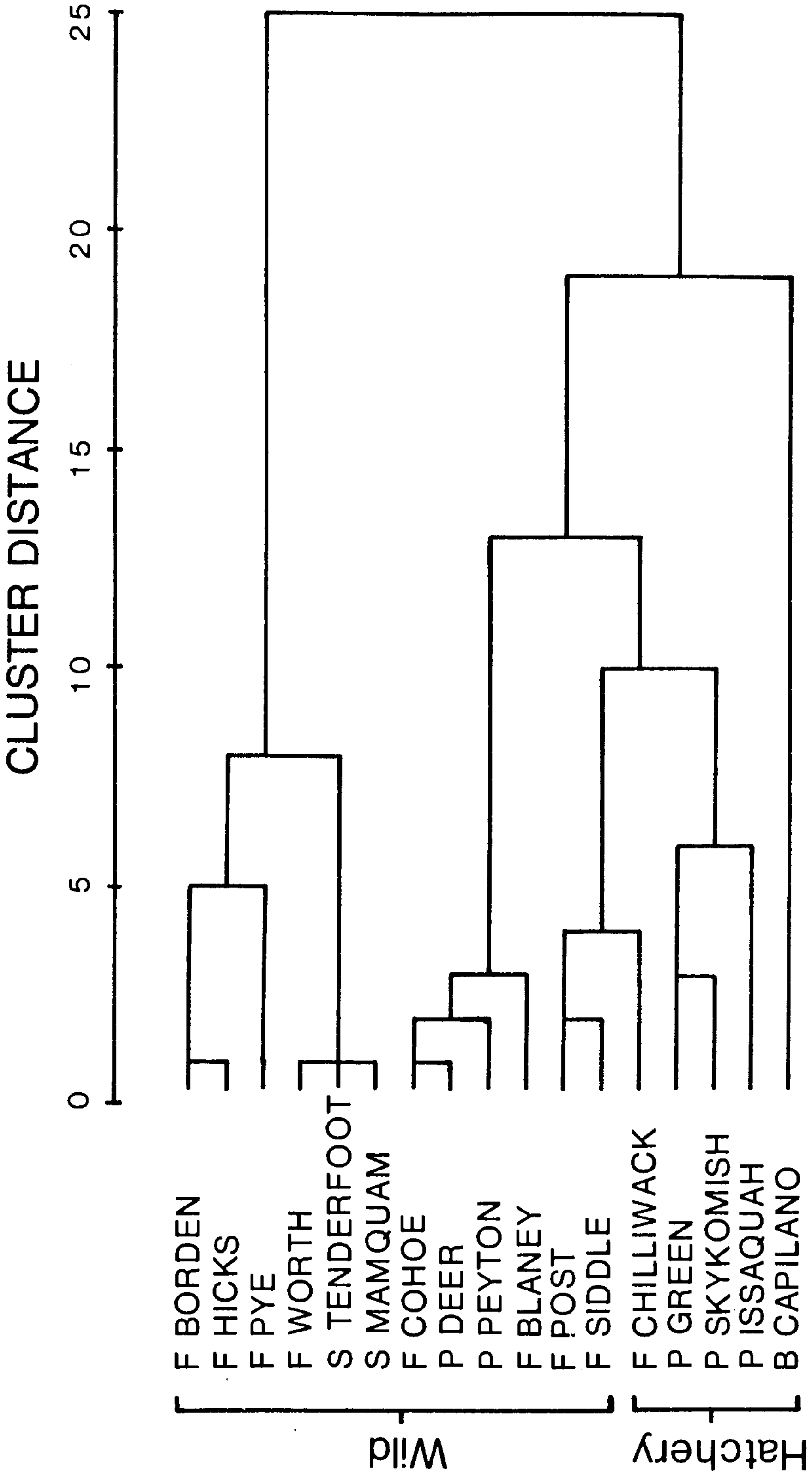
were not statistically significant(average competition: partial r = -0.749, N = 6, P = 0.185; elevation: partial r = -0.750, P = 0.185; distance: partial r = -0.549, P = 0.232; multiple r = 0.871, P = 0.300). Egg size was significantly correlated with spawning date across populations (r = -0.490, N = 13, P = 0.045), though nonsignificant with competition (average: r = -0.257, P = 0.223; episode: r = -0.271, P = 0.210).

Hatchery Versus Wild Populations

There was no significant difference between the wild and hatchery populations in either migration distance (t = 1.47, d.f. = 16, P = 0.160) or stream elevation (t = 0.55, d.f. = 16, P = 0.590).

An agglomerative cluster analysis resulted in four major groups of fish (Fig. 7): (1) a mixture of wild Fraser River and Squamish River populations; (2) a mixture of wild Fraser River and Puget Sound populations; (3) hatchery populations and two wild Fraser River populations; and (4) Capilano hatchery. Within cluster 3, there are two sub-clusters: (1) Puget Sound hatchery populations; and (2) Chilliwack hatchery (the youngest hatchery) and two wild Fraser River populations. The composition of groups suggests that while geographical regions may be a small source of difference, there are important differences between hatchery and wild populations.

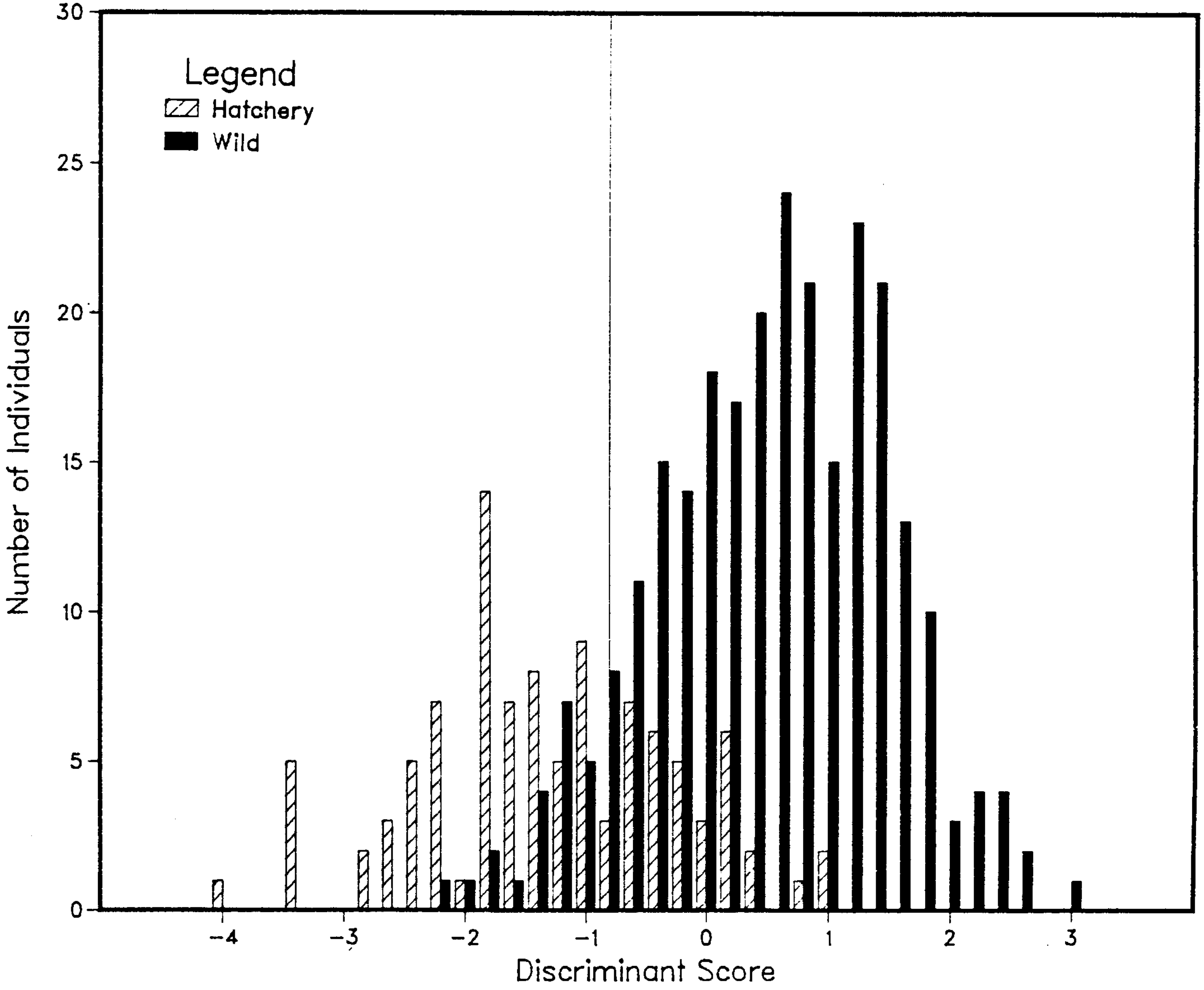
Figure 7. Cluster analysis (Ward's method) of female coho salmon populations based on squared Euclidean distance of twelve morphological characters. The four general regions, F = Fraser River, S = Squamish River, B = Burrard Inlet, and P = Puget Sound.


CLUSTER DISTANCE
0
5
10
15
20
25
F BORDEN
F HICKS
F PYE
F WORTH
S TENDERFOOT
S MAMQUAM
F COHOE
P DEER
P PEYTON
F BLANEY
F POST
F SIDDLE
F CHILLIWACK
P GREEN
P SKYKOMISH
P ISSAQUAH
B CAPILANO
Wild
Hatchery

A discriminant analysis of wild and hatchery females shows that there are significant differences based on morphology (Fig. 8, F = 15.50, d.f. = 5, 11, P < 0.001). Hatchery females exhibited smaller kypes (F = 9.62, d.f. = 1,15, P = 0.007) and body lengths (F = 8.65, P = 0.010) and less intense red body colouration (F = 23.42, P < 0.001). In addition, hatchery females had significantly smaller body depths (F = 4.66, P = 0.048), anal fin bases (F = 11.40, P = 0.004), dorsal fin heights (F = 12.15, P = 0.003), pelvic fins (F = 9.43, P = 0.008) and pectoral fins (F = 6.91, P = 0.019). Overall, females could be classified as being of hatchery or wild origin with an accuracy of 85%. Most misclassifications involved the youngest hatchery population (Chilliwack).

Hatchery coho had significantly larger egg weights than wild coho (t = 2.18, d.f. = 16, P = 0.020). Although wild coho tended to exhibit smaller ovary weights, no statistically significant difference existed (wild: 429.1 g; hatchery: 524.4 g; t = 1.52, d.f. = 9, P = 0.081).

Figure 8. Histogram of discriminant scores of morphological variation between wild (N=268) and hatchery (N=102) female coho salmon. The standardized canonical discriminant function is: 0.488(kype) + 0.201(colour) + 0.283(anal base) + 0.324 (dorsal height) + 0.138(pelvic) + 0.171(pectoral) - 0.195(caudal peduncle) + 0.484(body length) (r=0.622, P<0.001).


Legend
Hatchery
Wild
Number of Individuals
0
5
10
15
20
25
30
Discriminant Score
-4
-3
-2
-1
0
1
2
3

DISCUSSION

Morphology in the Wild

Breeding Competition

My results support the hypothesis of van den Berghe and Gross (1986b) that female morphology is related to female breeding competition. Kype length and body colouration, both involved in female breeding competition, were strongly correlated with competition intensity. However, I found no relationship between competition and body length. Since larger females provide superior parental care (van den Berghe and Gross 1986b), it was predicted that body size would evolve with breeding competition. Perhaps because each coho population has a different freshwater and ocean growing environment, the effects of differential competition are masked by the individual growing conditions of the populations.

"Episode" competition produced stronger statistical relationships with the secondary sexual characters than did "average" competition. Wiens (1977), Boag and Grant (1981) and Lande and Arnold (1983) suggested that natural selection may be sufficiently intermittent in nature that a few strong episodes of selection are responsible for most evolution. My results suggest that for female coho salmon, competition may increase more rapidly once the total spawning capacity is exceeded. Female salmon tend to select redd sites on a "relative quality" rather than "absolute quality" basis (van den Berghe and Gross 1986b), but the rate of increase in competition for nest sites may rise sharply as spawning capacity is exceeded.

Migration Arduousness

The distinctive trend of decreasing caudal peduncle width, body depth and median fin size (i.e., dorsal fin height and base) with increasing migration arduousness corresponds to the presumably increased selection for sustained relative to burst swimming performance. Similar trade-offs have been documented by Taylor and McPhail (1985a) for juvenile coho salmon and Riddell et al. (1981) for juvenile Atlantic salmon. Frictional drag has apparently been a major selectional pressure on the body morphology of all stages of salmonid development.

I found that female body length decreased with migration distance. The basis for the negative relationship is not, however, clear, and contradicts the Schaffer and Elson (1975) prediction of a positive relationship between migration distance and body size.

Life History in the Wild

Pacific salmon show considerable interpopulation variation in fecundity. However, only Healey and Heard (1984) and Healey (1986) have studied this variation in light of life history theory and then only in terms of the optimal age at maturity.

Most studies of variation in female gametic investment in fish have focused solely on the abiotic environment (e.g., Schaffer and Elson 1975, Leggett and Carscadden 1978), ignoring selection from breeding competition. The pattern of resource allocation to ovaries by female coho salmon suggests that both the difficulty of migration and breeding competition may mold female life history. Unfortunately, the small sample size makes it difficult to detect statistical significance. Swimming is known to use the majority of the fat and protein reserves of sockeye salmon during migration (Idler and Clemens 1959). Energy may be diverted from egg production (see sockeye data in Gilhousen [1980]). Leggett and Carscadden (1978) reached a similar conclusion concerning migration and egg production in the American shad (Alosa sapidissima).

Spawning date appears to be an important factor influencing egg size. The early spawning populations generally produced larger eggs than did the late spawning populations. Since fry emergence is usually synchronous (Koski 1966, Tagart 1976), eggs of early spawning populations may require more resources to sustain the embryo through a longer incubation. In chum salmon, Beacham and Murray (1986) also found that early spawning populations have larger eggs and longer incubation periods than late spawning populations, even within the same natal stream.

Although statistically nonsignificant, egg weight appears to decrease with increasing competition. Egg survival decreases more rapidly with decreasing gravel quality for large eggs than for small eggs (van den Berghe and Gross 1986b), presumably because large eggs have a smaller surface to volume ratio for the diffusion of oxygen. However, larger eggs produce larger fry (Fowler 1972, Beacham and Murray 1985a, Rombough 1985), which are competitively superior (Chapman 1962). Thus, there is a trade-off between egg and juvenile survivorship. Female size will directly affect the optimal solution to this trade-off, for female size dictates: (1) the quality of gravel the eggs will experience, as a consequence of female competition for redd sites; and, (2) the quality of female parental care in defense of the nest (van den Berghe and Gross 1986b, Sargent et al. 1986b). The nonsignificant result may, however, suggest that variation in the intensity of competition among populations is insignificant relative to success in competition within in populations due to body size.

Morphology and Life History in Hatcheries

The hatcheries provided an unusual opportunity to test the predictions about causality. Female coho originating in hatcheries exhibited a reduced expression of kype, body colour and body size, morphological characters associated with competition. Although body size was not significantly correlated with competition among wild populations, the comparison of wild populations against hatchery populations may control for the variation in growth potentials among streams. Thus, the reduction in body size in hatcheries supports the prediction of relaxation of selection due to breeding competition.

By contrast, hatchery coho had relatively larger ovary weights than wild coho, though the difference was marginally nonsignificant. The reduced breeding competition may permit more resources to be allocated to egg production in hatchery fish. Hatchery fish do exhibit significant larger eggs, probably because fry size is still important for juvenile competition and survival, but the constraint of gravel quality has been eliminated.

Characters that enhance steering and burst swimming performance were reduced in hatchery fish. Such swimming performance probably contributes to: (1) avoiding predation on the shallow spawning grounds, (2) success in intrasexual breeding competition, and (3) spawning itself. For example, thrust is critical in female nest construction because force is necessary to move gravel. Thus, as predicted, the absence of natural breeding and the possible importance of burst swimming to avoid predators appears to have allowed selection to streamline females for migration efficiency.

It is possible that the hatchery environment provides new selectional pressures. For example, juvenile agonistic behaviour (Abbott and Dill 1985) may well result in selection for smaller fins to avoid damage. Taylor and McPhail (1985a) demonstrated that population-specific traits in juveniles, such as fin shape, may be maintained in adults. The unintentional alteration of selectional pressures in the hatchery may therefore account for some of the differences found in adult fins. Furthermore, if selection on juvenile traits impacts negatively on the development of adult secondary sexual characters, this could explain some of the results as an environmental rather than an evolutionary response. Such negative interaction, though possible, seems unlikely because of the variety of secondary sexual traits developed and the fact that they do not appear until reproduction. The fact that the direction of response was predicted a priori further suggests that these are not simply environmental responses.

Finally, hatchery populations showed greater similarity to each other than to wild populations. Hjort and Schreck (1982) and Taylor (1986) also found that hatchery coho salmon in British Columbia, Washington, Oregon and California showed greater similarity to each other than to wild populations. The development of a "hatchery type" fish (cf., Helle 1981) due to the absence of natural breeding competition may be an inevitable result of hatchery conditions.

SUMMARY

Van den Berghe and Gross (1986b) demonstrated that female competition on the spawning grounds generates intense natural selection on the morphology and life history of coho salmon (Oncorhynchus kisutch). In the present study I examined the adaptation of female coho salmon to both breeding competition and their abiotic environment, by comparing morphology and ovarian investment among wild and hatchery populations. The results support the importance of breeding competition in molding female morphology and life history. Female secondary sexual characters, including body colouration and length of kype (an extension of the upper jaw used for fighting), increase significantly with degree of competition. In contrast, female investment into egg production (ovary mass and egg weight), though nonsignificant, generally decreases as competition increases. The difficulty of migration to the spawning grounds also appears to mold female morphology and life history. Salmon become more streamlined with increasing migration arduousness, and ovarian investment declines. In hatcheries, where breeding competition is relaxed, characters associated with breeding competition and spawning performance are reduced. However, there is an increase in egg weight. These results suggest that morphology and life history in salmon responds evolutionarily to the sometimes conflicting demands of both breeding competition and migration arduousness.

PART C

SEXUAL DIMORPHISM AND THE MORPHOLOGY OF MALE COHO SALMON

INTRODUCTION

Female reproduction is often limited by fertility and male reproduction by access to females (Bateman 1948). Therefore, males are selected to compete aggressively for access to females and females are selected to be cautious in their choice of males (Trivers 1972, Williams 1975). Where males can monopolize breeding access to several females there is likely to be intense interference competition, frequent aggressive interactions and large advantages to possessing traits that affect success in interactions (Wittenberger 1981, Thornhill and Alock 1983, Patridge and Halliday 1984). Reproductive success in male salmon (Oncorhynchus) is often closely related to fighting ability and depends upon body size, strength, or weapon development (Schroder 1982, Gross 1984, 1985). Female choice, through delayed nest construction, may also play a limited role in male reproductive success (Schroder 1981). Thus, these two types of sexual selection, in addition to natural selection, will produce sexual dimorphism in adult coho salmon morphology.

Salmon are sexually dimorphic in many traits (Davidson 1935, Beacham and Murray 1983, 1985b, Beacham 1984a, 1985). The purpose of this section is to examine sexual dimorphism in coho salmon in light of their mating system. This is done by examining differences in male morphology among populations as a result of breeding competition and migration arduousness, parameters shown to be important (Part B) in molding female morphology.

Male salmon do not provide parental investment for their young. Instead, they compete intensely for access to females that are about to oviposit. Males remain reproductively active for relatively long periods of time and move throughout the stream in search of these females (van den Berghe and Gross 1986a). There are generally fewer females ready to spawn than there are males seeking mates at any one time (Sargent et al. 1986a). As a consequence of this skewed operational sex ratio (OSR = # males/ # females that are ready to spawn), males aggregate about females and compete for proximity, because proximity dictates male mating success (Schroder 1981, Gross 1984, 1985).

Coho salmon exhibit two alternative male mating strategies. Small, precocious "jack" males (age 2) sneak matings, while large, "hooknose" males (age 3) fight for access to females (Gross 1984, 1985). It is the hooknose male whose fighting morphology should directly reflect the intensity of breeding competition, and it is these males I examine in this study.

Schroder (1973, 1981) found that a key factor in male competition in chum salmon was spawner density. Increased proportions of nonestablished females, as a consequence of competitive exclusion by other females, resulted in more highly skewed, male-biased operational sex ratios and thus increased male competition for females. Similarly, in coho salmon, van den Berghe and Gross (1986) found that the lifespan of hooknose males (age 3) decreased as their density, and thus presumably mate competition, increased on the spawning grounds. Since OSR was impossible to obtain from historical records of coho breeding, female "spawner density" was used as a correlated measure of male breeding competition. When spawner density or female number is high, male competition will be high since not all females will obtain nest sites and the OSR (assuming a 50-50 population sex ratio) will therefore be skewed towards males. The use of female spawner density, however, will probably be less reliable as a measure of competition for males than in females where resources are directly affected by numbers.

Intense male breeding competition should select for greater expression of male secondary sexual characters. However, as in females, these traits must be traded-off with selection for migration. I therefore compared breeding competition (average and episode) and migration arduousness (length and elevation of freshwater migration; see Table 2) as selective agents molding male morphology.

In general, male traits for competition should be larger than those of females. Females are more limited in resources available for investment into breeding competition than are males, since females are faced with an additional trade-off with egg production (Fig. 1). Not only should fighting traits be larger in males, but so too should traits associated with display. Males, unlike females, have stereotyped fighting stances or patterns (Schroder 1973) and the most common fighting posture displayed by males is the lateral display, in which the dorsal fin is held erect. The dorsal fin is also important in the male "quivering" mating display.

METHODS

Three to seven fully mature hooknose male coho salmon (age 3) were sampled from each of 12 wild study populations (Table 2, Fig. 2; Cohoe Creek excluded). In addition, one to nine hooknose males were collected from each of the 5 hatchery study populations (Table 2, Fig. 2). The smaller sample of males relative to females for each population was a consequence of the original objective of my study to examine the impact of breeding competition on females.

Male body colour and the 12 morphological characters identified in Figure 3 were measured following the method for females. The data were transformed to logarithms (log10) and regressed against the logarithm of body length and the resultant slopes from analysis of covariance were used to calculate the standardized data set (see Methods, Part B). Male and female morphologies were standardized to a grand sample mean body length of 482 mm (postorbital-hypural; N = 461) to compare the two sexes. When comparing among males, morphologies were standardized to the mean male body length of 451 mm (N = 93) using slopes determined from analysis of covariance.

Sexual dimorphism was examined by stepwise discriminant analysis, using Wilks' Lambda and its approximate transformation to the F statistic. Stepwise discriminant analysis was also used to determine the importance of the secondary sexual characters in discriminating between the sexes. The classification procedure used Bayes' Rule (Tatsuoka 1971). Stepwise multiple regressions determined if male morphological characters were sensitive to population parameters also important for female morphology. Only the ten populations with competition indices were used, unless the analysis suggested that competition was unimportant. Then a second stepwise multiple regression was performed with all 12 wild populations. Stepwise discriminant analysis determined overall morphological variation and also identified the characters important in distinguishing wild from hatchery males.

Analyses were performed using the Statistical Package for the Social Sciences (version SPSSx, SPSS Inc. 1983) and the probability level for significant differences was 0.05. One-tailed tests of significance were used for all predicted relationships.

RESULTS

Sexual Dimorphism

For each sex the regressions between the measured characters and body length were statistically significant (Table 4). Males and females were strongly dimorphic ($F_{10,450} = 237.47$, $P < 0.001$). Accuracy of classification to sex, based on the 12 morphological characters, was 99% (Fig. 9). Only anal fin height and base were not sexually dimorphic (Table 4). Kype exhibited the greatest sexual dimorphism, differing on average 33% between the sexes.

Discriminant analysis between the sexes based solely upon the secondary sexual characters - kype, body depth and colour was also highly significant ($F_{3,469} = 356.14$, $P < 0.001$). Ninety-six percent of the salmon were accurately classified to sex based only on these characters. Of the 17 male misclassifications, significantly more hatchery males were misclassified than wild males ($X^2 = 11.835$, d.f. = 1, $P < 0.01$). There was no significant difference in mean body length between males that were misclassified as females and those correctly classified as males ($t_{91} = 0.04$, $P = 0.966$).

Table 4. The means, standard deviations (in parentheses) and allometric regressions for the 12 morphological characters. The data are based on 93 males and 368 females. All measurements, except colour which is a rank score, are in mm and standardized to a postorbital-hypural (body) length of 482 mm, with the exception of body length itself. All allometric regressions are of the form, character = a(length)^b and are significant at a probability level of $P < 0.001$.

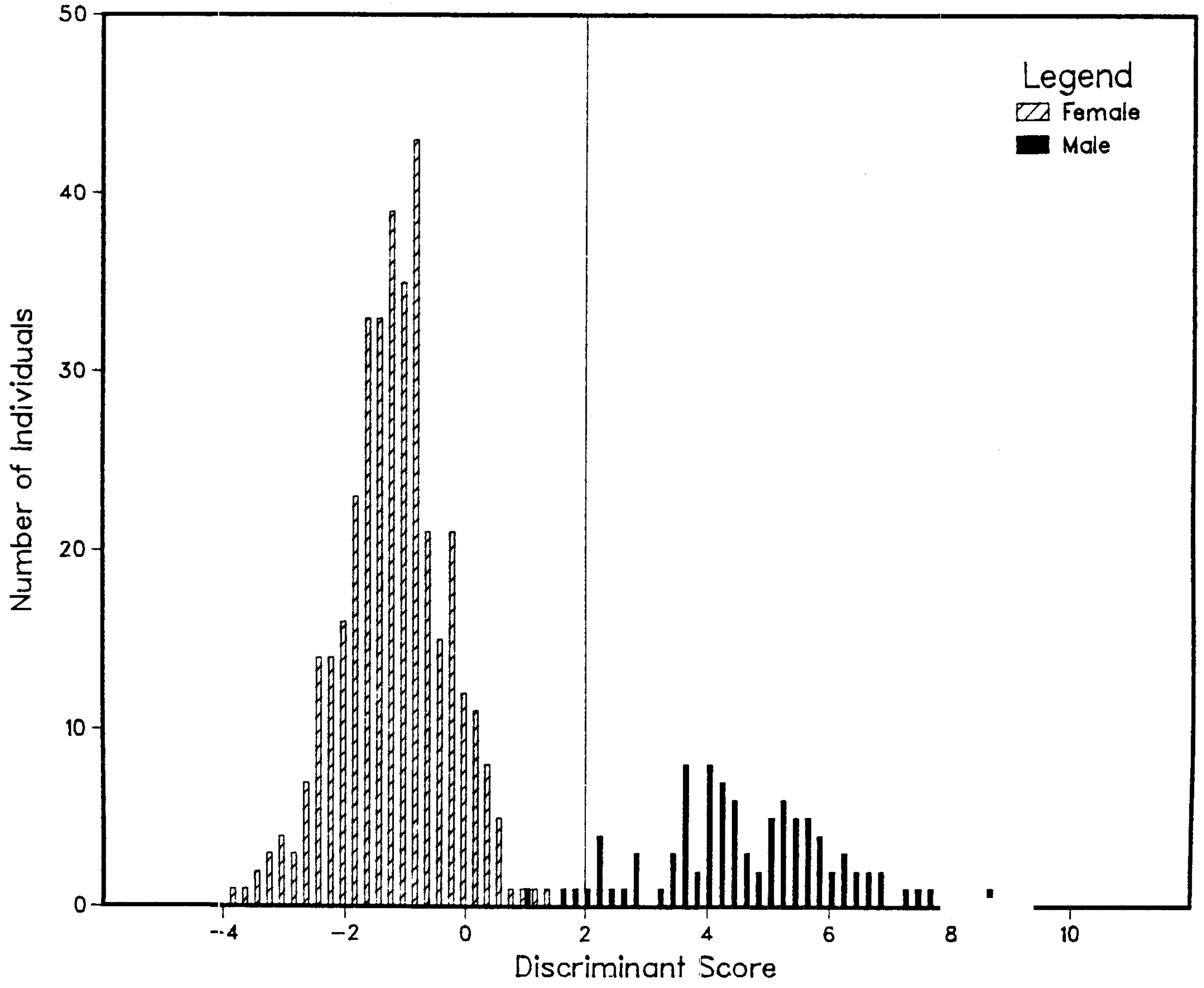
	Male				Female				Male vs. Female	
Character	Mean	a	b	r^*	Mean	a	b	r^*	$F_{1,459}$	P
Body:										
Kype	61.82 (6.25)	0.0024	1.644	0.910	46.42 (3.39)	0.0011	1.720	0.920	1036.0	<0.001
Colour	4.84 (0.71)	0.0078	1.038	0.695	3.70 (0.57)	0.0025	1.179	0.607	269.7	<0.001
Depth	131.08 (9.49)	0.0667	1.227	0.917	123.61 (6.96)	0.0300	1.347	0.919	73.0	<0.001
Caudal Peduncle	48.22 (2.46)	0.0649	1.070	0.943	47.79 (1.99)	0.0379	1.155	0.944	3.2	=0.072
Length	450.83 (61.91)	-	-	-	489.29 (50.49)	-	-	-	39.1	<0.001
Median Fins:										
Anal Height	60.74 (3.27)	0.0881	1.058	0.929	60.32 (2.77)	0.1350	0.988	0.907	1.6	=0.208

(cont'd)

Character	Male				Female				Male vs. Female	
	Mean	a	b	r*	Mean	a	b	r*	$F_{1,459}$	P
Anal Base	71.92 (4.02)	0.1171	1.039	0.929	71.75 (3.14)	0.0857	1.089	0.931	0.2	=0.673
Dorsal Height	70.29 (3.45)	0.1665	0.978	0.939	63.72 (2.80)	0.1400	0.991	0.914	370.7	<0.001
Dorsal Base	60.18 (3.70)	0.0943	1.045	0.917	56.94 (2.61)	0.0792	1.064	0.921	95.1	<0.001
Paired Fins:										
Pelvic	65.12 (3.28)	0.1991	0.938	0.933	60.52 (2.76)	0.1200	1.007	0.912	238.1	<0.001
Pectoral	87.95 (4.33)	0.3218	0.908	0.926	81.52 (3.15)	0.2487	0.937	0.923	262.5	<0.001
Adipose	39.90 (3.13)	0.0159	1.267	0.899	32.74 (2.43)	0.0150	1.244	0.852	571.2	<0.001

* correlation coefficient

Figure 9. Discriminant analysis of morphological variation between male (N=93) and female (N=368) coho salmon. The standardized canonical discriminant function is: 0.716(kype) + 0.070(colour) - 0.238(anal height) - 0.439(anal base) + 0.497(dorsal height) + 0.267(dorsal base) + 0.135 (pelvic) + 0.464(adipose) - 0.350(caudal peduncle) - 0.113(body length) ($r = 0.917$, $P < 0.001$)


Legend
Female
Male
Number of Individuals
0
10
20
30
40
50
-4
-2
0
2
4
6
8
10
Discriminant Score

Male Morphological Character Relationships

Breeding Competition

Breeding competition was significantly correlated with the variation among populations in male kype length, body depth and dorsal fin height (Table 5). Colour, however, was not significantly correlated with competition (average, $r=0.242$, $P=0.250$; episodes, $r=0.219$, $P=0.271$) or the other population parameters.

Migration Arduousness

Natal stream elevation was negatively correlated with anal fin base, while distance of freshwater migration was negatively correlated with body length (Table 5). The remaining characters were not significantly correlated with any population parameter, although, the median fins and caudal peduncle had negative relationships with migration arduousness.

Hatchery versus Wild

Discriminant analysis revealed a significant difference in morphology between hatchery and wild male coho salmon (Fig. 10; $F_{7,9} = 13.86$, $P < 0.001$). Wild coho had significantly larger kypes ($F_{1,15} = 5.13$, $P = 0.019$), colour ($F_{1,15} = 4.12$, $P = 0.030$), dorsal fin heights ($F_{1,15} = 4.58$, $P = 0.025$), and pelvic fin lengths ($F_{1,15} = 5.74$, $P = 0.030$). Overall classification accuracy was 80% for wild and hatchery males.

Table 5. Partial correlations and statistical probabilities (in parentheses) from stepwise multiple regression analyses of male coho salmon morphology. Regressions are shown for average and episode competition when statistically significant.

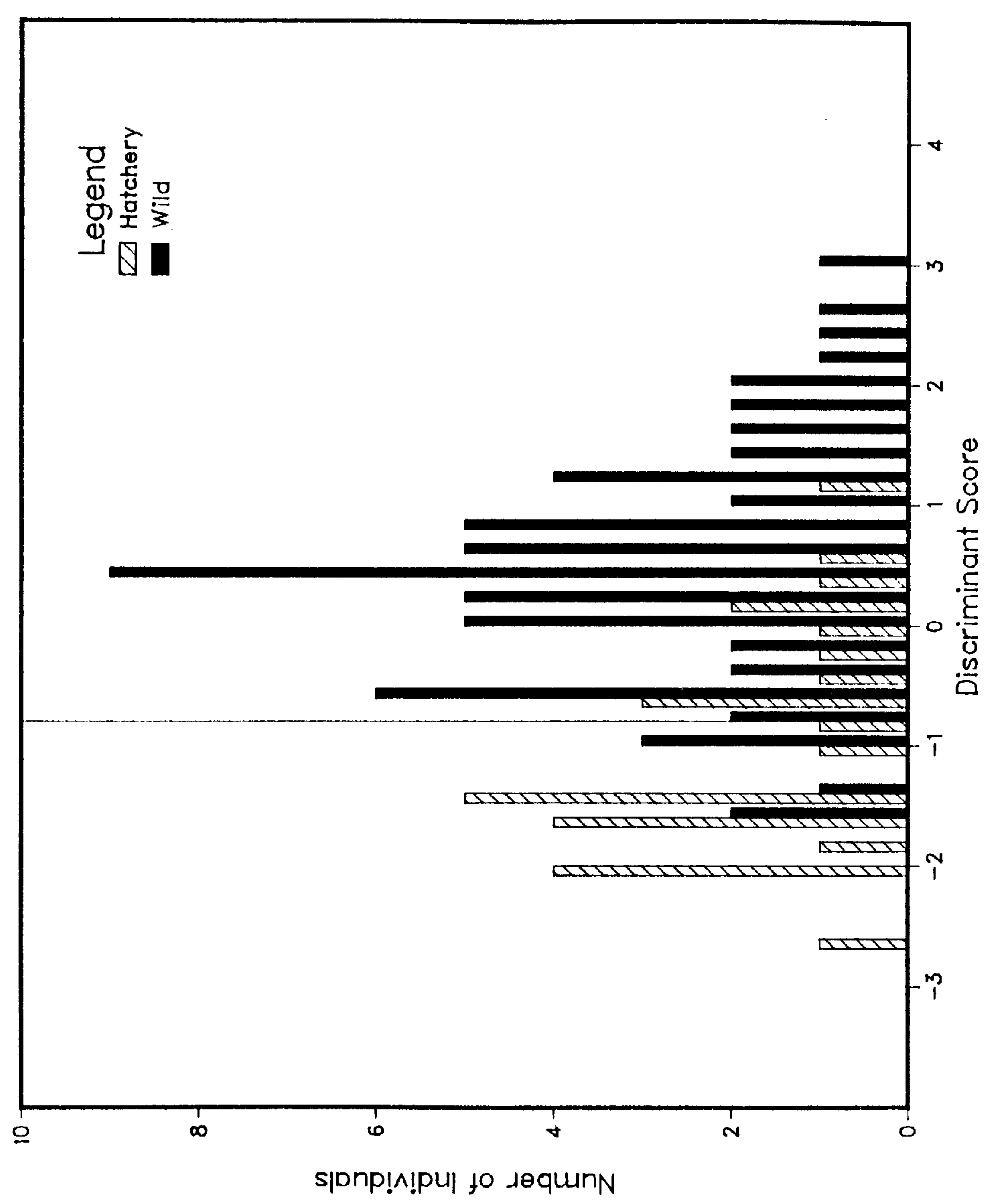
Character	N	Elevation	Migration Distance	Competition	
				Average	Episode
Body:					
Kype	10	N.S.	N.S.	0.690 (P=0.014)	0.673 (P=0.016)
Colour	12	N.S.	N.S.	N.S.	N.S.
Depth	10	N.S.	N.S.	0.599 (P=0.034)	0.610 (P=0.031)
Caudal Peduncle	12	N.S.	N.S.	N.S.	N.S.
Length	12	N.S.	-0.684 (P=0.007)	N.S.	N.S.
Median Fins:					
Anal Height	12	N.S.	N.S.	N.S.	N.S.
Anal Base	12	-0.690 (P=0.007)	N.S.	N.S.	N.S.
Dorsal Height	10	N.S.	N.S.	0.641 (P=0.023)	0.654 (P=0.020)

(cont'd)

Character	N	Elevation	Migration Distance	Competition	
				Average	Episode
Dorsal Base	12	N.S.	N.S.	N.S.	N.S.

N.S. = notsignificant (P>0.05)

Figure 10. Discriminant analysis of morphological variation between hatchery ($N=28$) and wild ($N=65$) male coho salmon. The standardized canonical discriminant function is: 0.795(kype) + 0.303(colour) + 0.413(anal base) - 0.307(dorsal base) + 0.529(pelvic) - 0.365(adipose) - 0.605(caudal peduncle) ($r = 0.550$, $P < 0.001$)


Legend
▨ Hatchery
■ Wild
Discriminant Score
-3
-2
-1
0
1
2
3
4
Number of Individuals
0
2
4
6
8
10

DISCUSSION

Sexual Dimorphism

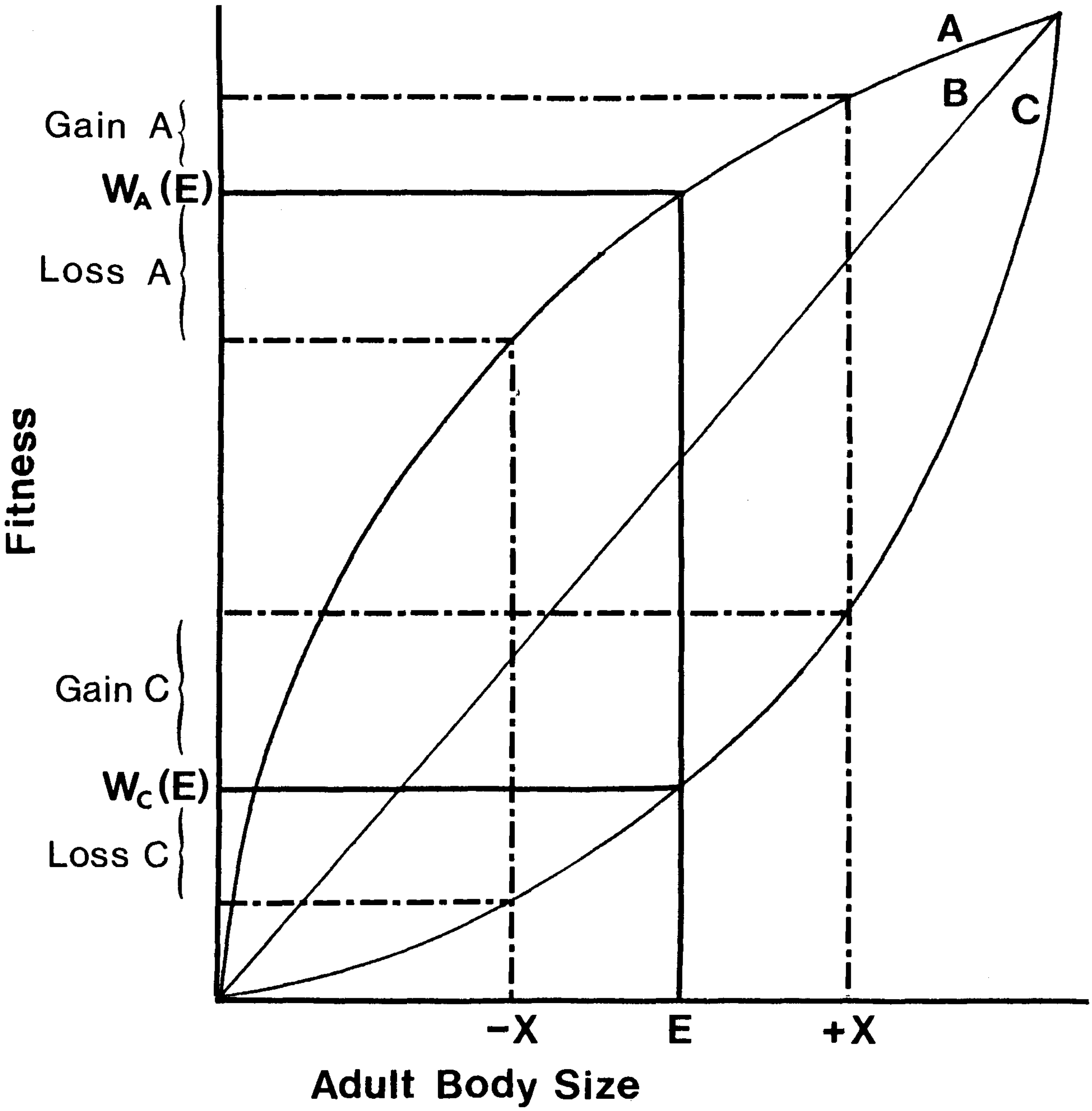
Coho salmon are strongly sexually dimorphic, especially in secondary sexual characters. Males have larger kypes and body depths (i.e., hump), and more intense red body colouration. The hump, which is the result of a bar of cartilage formed dorsally during maturation (Davidson 1935), is a secondary sexual character. It appears to function as a shield against attack by opponents which attempt to grasp the mid-body. The lack of a well developed hump in females is perhaps due to its energetic expense and its lesser worth, since female body girth already increases due to egg production. Males also exhibit larger dorsal fins, which function in male display.

The degree of sexual dimorphism in secondary sexual characters does not vary with male body size. Beacham and Murray (1985b) found that smaller pink and chum males are more likely to be mistaken for females than larger ones in discriminant analysis based upon body depth. They suggested that small males may be using an alternative mating tactic to reduce aggression and gain access to spawning females, by reducing the expression of the secondary sexual characters and thus mimicking females. However, it is unclear that mimicry can be successful in salmon, since mimics would incur female aggression. The question as to whether aggression from females is less of a hinderance to mating success than male aggression remains to be established. In coho salmon, there is no evidence that smaller males are similar to females.

Body size is critical for both male and female reproductive success (Gross 1985, van den Berghe and Gross 1986b). Investment of energy into growth by juveniles will, therefore, influence their future reproductive success as adults. The relationship between fitness and body size, however, will dictate the "risk proneness" of male and female foraging strategies (see Real 1980, Lacey et al. 1983, Real and Caraco 1986). In salmon, it is possible that the relationship between reproductive success and body size increases at a faster rate for males than females (Fig. 11). This is because the largest males may monopolize several females, while females can increase the number and survivorship of only their own clutch. If true, juvenile males should, therefore, "gamble" more during growth than juvenile females. Thus, some males should exhibit faster growth rates than obtained by any females, and males would be expected to have greater variation in body size at any given age.

A faster growth rate for juvenile males than females has been demonstrated in salmon (Sano 1966, Bakkala 1970, Hager and Noble 1976, Bilton et al. 1984). At maturity, males in some populations are larger on average and exhibit a greater variation (i.e., coefficient of variation) in body size than do females for a given age (Shapavolov and Taft 1954, Beacham and

Figure 11. Three hypothetical fitness curves (following Real [1980] and Real and Caraco [1986])for salmonid body size: (A) decelerating, (B) linear and (C) accelerating. Salmon may achieve an average adult body size (E), but there will always be some variation about the mean (± X). Juveniles with accelerating curves (C) should be selected to "gamble" for increased growth rates, since they have more to gain than lose in fitness (gain C > loss C). However, juveniles with decelerating curves (A) should be selected to do the opposite, for their loss of fitness would be greater than their gain (loss A > gain A). Therefore, juveniles with accelerating curves (C) may be selected to be "risk prone" and those with decelerating curves (A) may be selected to be "risk averse".


A
B
C
Gain A
W_A (E)
Loss A
Gain C
W_C (E)
Loss C
Fitness
−X
E
+X
Adult Body Size

Murray 1985b). Although, hooknose males do exhibit greater variation in length at maturity than females in this study (males: coefficient of variation = 13.73; females: coefficient of variation = 10.31), for an undetermined reason males were smaller in size.

Large pectoral, pelvic and dorsal fins and caudal peduncles are important for steering and burst swimming (Webb 1978, 1984) during foraging and predator avoidance, but expensive in terms of drag and stamina swimming efficiency. Greater investment into swimming morphology may be part of the more risk prone strategy of males to aid foraging and increase their growth rate. An alternative hypothesis is the larger fins of males may function to increase their swimming performance given the larger hump and kype which decrease efficiency.

By contrast, anal fin size is not sexually dimorphic. In addition to swimming performance for both males and females, this character functions in female nest construction. The anal fin is used to measure the depth and suitability of the nest pit (Tautz and Groot 1975, Schroder 1981). Therefore, this additional selection pressure favoring a large anal fin in females may explain why this character is the only one not larger in males.

Although the adipose fin is known to be sexually dimorphic in many species of Pacific salmon (Beacham and Murray 1983), no explanation can be given for why this sexual dimorphism exists.

The function of the adipose fin in the biology of salmon is not yet understood.

Male Morphology

Several important characters for male-male competition were significantly correlated with breeding competition. This includes kype length and body depth. The positive, but nonsignificant correlation of colour intensity could be due to the qualitative measurements and the small sample sizes obtained.

In addition, the significant correlation between dorsal fin height and competition is consistent with the importance of this character in ritualized male displays during breeding. Beacham (1985) found that in pink salmon the dorsal fin was the most sexually dimorphic of four characters studied.

The body colouration and hump in salmon have been suggested to serve in female mate choice (Darwin 1871, Davidson 1935). Schroder (1981) found that female chum salmon delay nest construction when being courted by subdominant or relatively small males. But the hump also appears to serve as a shield against attack by opponents. The hump, as Schroder (1973) demonstrated, is the region where the majority of attacks are directed. A large hump may prevent grasping about the mid-section by smaller opponents.

There were similar patterns of relationship between male morphology and migration arduousness as found for females. However, for males the relationships were often statistically nonsignificant, perhaps because of a considerably smaller data set.

Hatchery males were the most often misclassified fish in discriminant analysis of males and females. Like females (Part B), male coho originating from hatcheries exhibit reduced expression of the secondary sexual characters, kype, colour and body depth (though body depth was nonsignificant). Presumably, the energy savings from these characters are going in increasing survivorship, such as on the return migration. The kype is probably the most important character in male competition, and it is the most important character in discriminating hatchery and wild male coho. Male coho originating in hatcheries also exhibit reduced expression of characters that enhance burst swimming performance, especially the median fins. Therefore, as previously suggested, the unintentional alteration of selection pressures through the reduction of natural breeding competition in hatcheries may be resulting in the evolution of a "hatchery type" fish.

SUMMARY

Adult coho salmon are sexually dimorphic in many characters. However, this is especially true for the secondary sexual characters - kype, colour and body depth. The sexes also differ in fin morphology, which may be a consequence of different risk assessments in their foraging strategies. The only feature which is not relatively larger in males is the anal fin, which serves a special function in female reproductive behaviour.

The sexual dimorphism and morphology of adult male coho salmon may be understood as a response to the different selective pressures of breeding competition and migration. Populations experiencing greater competition have significantly larger male kypes, body depths and dorsal fin heights. Hatchery populations, where male competition is relaxed, have significantly smaller kypes and dorsal fin heights, and less intense body colouration. Migration arduousness appears to also influence fin shape, with negative trends, though sometimes nonsignificant, in the median fins and caudal peduncle. The body morphology of male coho salmon may, therefore, be understood in light of their mating system and natural selection for migration.

PART D

FECUNDITY AND EGG SIZE VARIATION

INTRODUCTION

Variation among populations in number of eggs produced has long interested evolutionary ecologists (Lack 1947, Svardson 1949). In particular, the increase in avian clutch size with geographic latitude has been the center of considerable controversy and speculation (e.g., Ricklefs 1980, Koenig 1984, Jarvinen 1986, Lima 1986). In addition to birds, however, a diverse array of organisms (Lord 1960, Berven 1982), including fishes (Svardson 1949, Rounsefell 1957) exhibit latitudinal clines in egg number (i.e., fecundity).

Rounsefell (1957) suggested that fecundity in Pacific salmon (Oncorhynchus) decreases with latitude. He ascribed this cline to faster growth rates and earlier maturity in southern populations. However, Rounsefell's data set was small, the geographic range he examined was limited, and the most southerly population was compared with all other populations for each species. In contrast, Drucker (1972), Crone and Bond (1976), Beacham (1982) and Healey and Heard (1984) found that fecundity increases with latitude. These authors provided little explanation for the trend, however, and it has remained an enigma in fishes just as in birds.

The purpose of this paper is to show that the understanding of clines in salmon egg number requires an understanding of egg size evolution. I present new data on fecundity variation in coho salmon (O. kisutch) and integrate these data with existing literature values to re-analyze latitudinal trends in fecundity. Moreover, I incorporate latitudinal variation in egg weight to show that the trends in fecundity may simply be a consequence of a negative relationship between latitude and egg weight.

Life History Theory

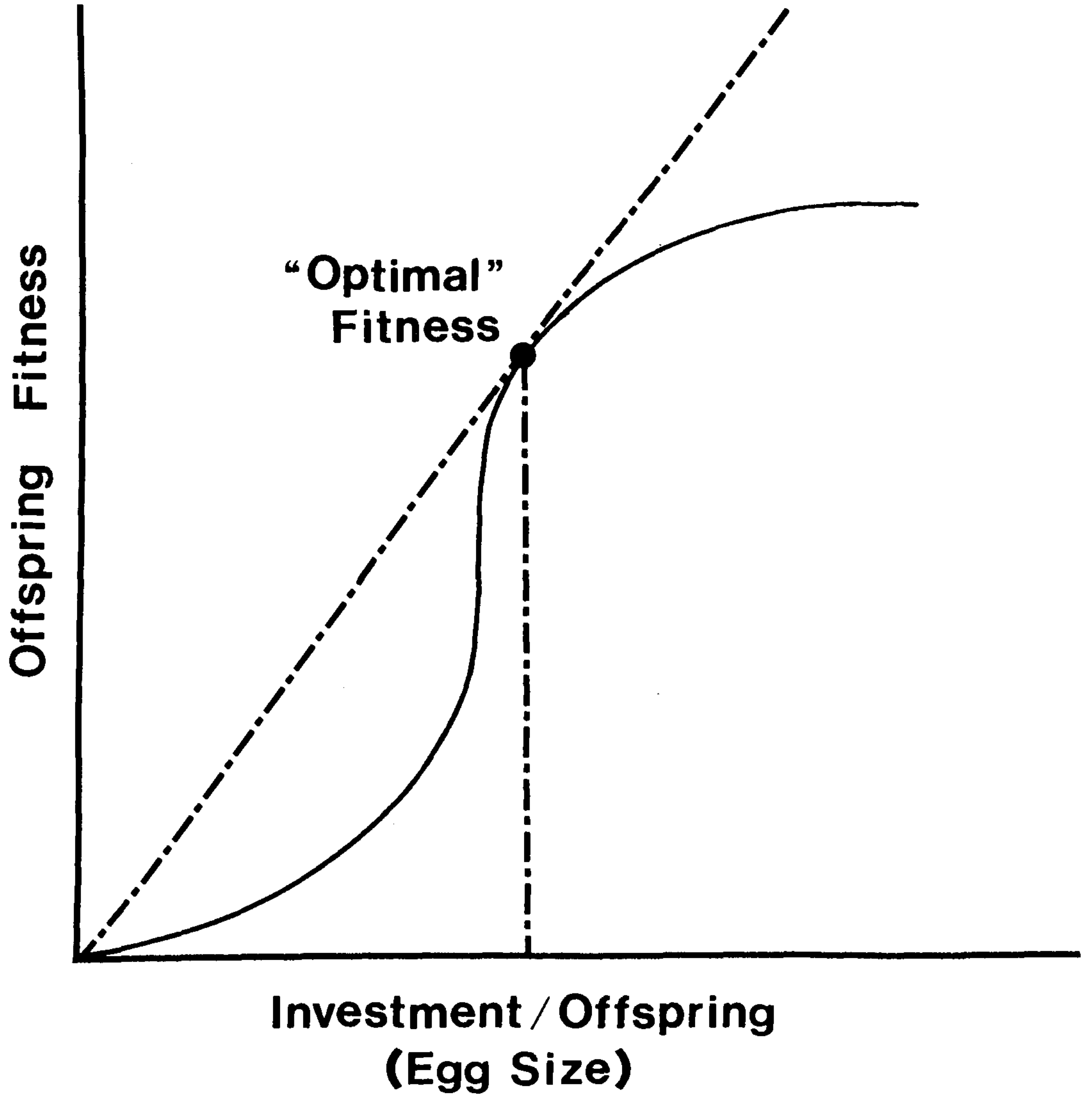
Life history theory proposes that the optimal allocation of resources to a life history program will maximize the combined fitness benefit of growth, maintenance and reproduction (Williams 1966a, Stearns 1976). A major component of a female's allocation to reproduction is egg production, defined as the product of egg number and egg weight. Egg weight and fecundity are opposing attributes - selection for one will be at the expense of the other if investment into egg production is fixed. Thus, all else equal, populations with low fecundities should have large eggs and populations with high fecundities should have small eggs.

In the evolution of egg production, selection should first adjust egg size (Fig. 12; Smith and Fretwell 1974, Sargent et al. 1986b). This is because fitness is maximized by the optimization of returns on energetic investment per offspring. Therefore, organisms are selected to vary their energy allocation to each reproductive episode. Thus understanding fecundity lies in understanding (i) the optimal egg size, and (ii) the trade-off between present and future allocation for the adult (Williams 1966a)

Salmon are semelparous organisms and thus have no future after they have spawned. The reproductive effort trade-off for female reproductive success is therefore between allocations to migration survival, parental care, competition for breeding sites and total egg production. Since egg size is fixed first, variation in fecundity among populations must be due to (i) variation in parental care, migration costs, and reproductive competition, and (ii) variation in the optimal egg size.

However, it is unlikely that parental care, migration costs or reproductive competition are latitudinal in salmon. Parental care and reproductive competition are a function of breeding density in relation to available nest sites (van den Berghe and Gross 1986b) and there is no evidence that breeding density is latitudinal (Part B). In addition, migration costs are unlikely to be latitudinal since river lengths are extremely variable at all latitudes (see Aro and Shephard [1967]).

Figure 12. Relationship of offspring fitness to the amount of parental investment per individual offspring (see Brockleman 1975 for justification of the nonlinear shape). Maximum rate of conversion of parental resources into aggregate offspring fitness occurs at the point tangent to the line extending from the origin. The diagonal line is an adaptive function (Smith and Fretwell 1974) of equal parental fitness, because the ratio of parental fitness to total investment per clutch is constant.


"Optimal" Fitness
Offspring Fitness
Investment / Offspring
(Egg Size)

METHODS

Field Collections

Eggs from fully mature female coho salmon were collected during the 1984-85 spawning season in British Columbia and Washington State. Collections were made in 13 wild and 5 hatchery populations (see Part B). For each female, postorbital-hypural (POH) length was recorded to the nearest 1 mm and 10 eggs were stripped, preserved in Stockard's solution and weighed to the nearest 0.1 mg wet weight. Egg weight is used as the measurement of egg size because it is the most accurate (Appendix 1). For some females the ovary wet weight was measured to the nearest 5 g.

Literature Data

Literature data on egg size were obtained for 8 populations of coho salmon on the Pacific Coast, ranging from California to Alaska, and 6 populations in the Great Lakes. For some it was necessary to convert body weight or length measurements to postorbital-hypural body length (POH). Weight measurements of Great Lakes data were converted to total length (TL) using the regression relationships of Stauffer (1976). The following equations were used to convert total length (TL), standard length (SL), fork length (FL) and mid-eye fork length (ME) to POH length:

$$(1)\ POH = 36.9 + 0.703\ TL\ (r^2 = 0.97,\ N = 32)$$

$$(2)\ POH = 28.3 + 0.858\ SL\ (r^2 = 0.99,\ N = 359)$$

$$(3)\ POH = 28.8 + 0.774\ FL\ (r^2 = 0.99,\ N = 359)$$

$$(4)\ POH = 21.8 + 0.93\ ME\ (r^2 = 0.98,\ N = 52)$$

Equation 1 is from female coho in Hicks Creek, B.C. and equations 2 and 3 are from measurements of the 18 study populations described above. Equation 4 is from Beacham (1982).

Latitude

Latitude of the natal stream spawning areas was determined to the nearest degree minutes from topographic maps. Populations for which the three variables - fecundity, egg size and ovarian investment - could be calculated were used to examine the effect of latitude (Table 6).

If either fecundity or ovary weight did not exist, fecundity was determined by dividing ovary weight by egg weight, and ovary weight by multiplying fecundity by egg weight.

Statistical Analyses

The egg size data were converted to fresh egg weights using the statistical relationships developed in Appendix 1. Populations with raw data were examined statistically. Egg weight, fecundity and ovary weight were standardized to a POH

Table 6. Location, latitude and regression equations of ovary weight (OV) and fecundity (F) on female body length (postorbital-hypural [POH; mm]) for coho salmon populations examined for latitudinal clines.

Population	Latitude	N	Regression Equation	r	P	Reference
Washington:						
Deer Cr. Jr.	47°49′	6	$OV = 7.35\times10^{-7}(POH)^{3.28}$	0.97	<0.001	present study
		6	$F = 3.18\times10^{-4}(POH)^{2.54}$	0.97	0.002	
Green R.	47°18′	60	$OV = 3.32\times10^{-6}(POH)^{3.03}$	0.94	<0.001	Allen (1958)
		60	$F = 1.25\times10^{-3}(POH)^{2.35}$	0.94	<0.001	
Green R.	47°18′	20	$OV = 1.18\times10^{-6}(POH)^{3.22}$	0.89	<0.001	present study
		20	$F = 2.66\times10^{-2}(POH)^{1.83}$	0.80	<0.001	
Issaquah	47°31′	15	$OV = 3.21\times10^{-5}(POH)^{2.68}$	0.90	<0.001	present study
		15	$F = 4.37\times10^{-1}(POH)^{1.36}$	0.67	0.007	
Soleduck R.	48°03′	11	$OV = 1.20\times10^{-9}(POH)^{4.29}$	0.95	<0.001	Tagart (1976)
		11	$F = 1.81\times10^{-3}(POH)^{2.29}$	0.86	<0.001	
Skykomish R.	47°52′	20	$OV = 4.64\times10^{-8}(POH)^{3.79}$	0.89	<0.001	present study
		20	$F = 4.62\times10^{-5}(POH)^{2.90}$	0.70	<0.001	
British Columbia:						
Capilano R.	49°21′	19	$OV = 2.34\times10^{-6}(POH)^{2.98}$	0.91	<0.001	present study
		19	$F = 1.12\times10^{-2}(POH)^{2.00}$	0.85	<0.001	

(cont'd)

Population	Latitude	N	Regression Equation	r	P	Reference
Chilliwack R.	49°04′	19	$OV = 2.34\times10^{-7}(POH)^{3.46}$	0.90	<0.001	present study
		19	$F = 4.44\times10^{-4}(POH)^{2.53}$	0.76	<0.001	
Mamquam R.	49°44′	23	$OV = 3.45\times10^{-7}(POH)^{3.40}$	0.86	<0.001	present study
		23	$F = 1.10\times10^{-2}(POH)^{2.04}$	0.61	0.002	
Pye Cr.	49°12′	6	$OV = 9.49\times10^{-7}(POH)^{3.23}$	0.96	0.001	present study
		6	$F = 5.55\times10^{-5}(POH)^{2.83}$	0.77	0.075	
Post Cr.	49°06′	20	$OV = 1.91\times10^{-8}(POH)^{3.87}$	0.96	<0.001	present study
		20	$F = 1.44\times10^{-4}(POH)^{2.73}$	0.88	<0.001	
Siddle Cr.	49°13′	7	$OV = 3.23\times10^{-6}(POH)^{3.05}$	0.97	<0.001	present study
		7	$F = 1.56\times10^{-3}(POH)^{2.34}$	0.91	0.005	
Tenderfoot Cr.	49°50′	23	$OV = 5.00\times10^{-6}(POH)^{2.98}$	0.91	<0.001	present study
		23	$F = 1.78\times10^{-3}(POH)^{2.33}$	0.86	<0.001	
Alaska:						
Karluk R.	57°27′	25	$OV = 6.42\times10^{-8}(POH)^{3.58}$	0.82	<0.001	Drucker (1972)
		25	$F = 9.52\times10^{-5}(POH)^{2.81}$	0.88	<0.001	

length of 488 mm (meand length of populations examined) following the methods outlined in Part B. The analyses focused on examining regional, temporal and hatchery (environmental) influences on egg weight. Analysis of variance was used to compare egg weight among years and regions. Great Lakes populations, which had been transplanted from Oregon, were used for these analyses, but not to test latitudinal relations and differences between hatchery and wild fish. A multiple regression analysis was used to test whether spawning date contributed to egg weight independently of latitude. The relationships of standardized fecundity, egg weight, and ovary weight with latitude were examined by regression. The probability level for significant differences was 0.05. Analyses were performed with the Statistical Package for the Social Sciences (version SPSSx, SPSS Inc., 1983).

RESULTS

Egg Size Within Populations

Egg weight within populations varied as much as 255% from smallest to largest egg (Table 7). Egg weight was often positively correlated with female length (18 [69%] of 26 populations), although the form of this relationship differed among populations (Table 7). Body length explained 78% of variation in egg weight in one population, and on average 40% (Fisher's z transformation: z = 0.634). There was no correlation between egg weight and spawning date in two populations that spawned over an extended period, 11 weeks (Borden Creek: r = 0.177, N = 23, P = 0.237; Hicks Creek: r = 0.097, N = 30, P = 0.618). Also egg weight generally did not vary across years. The Capilano hatchery coho exhibited no significant annual variation in egg weight (F = 0.06, d.f. = 1, 23, N = 2 years, P = 0.805), as did the Platte River coho (F = 2.68, d.f. = 2, 68, N = 3 years, P = 0.076). However, coho which originated from the Green River hatchery in 1950 (Allen 1958), exhibited significantly smaller egg weights than the Green River hatchery coho of 1984 (F = 81.33, d.f. = 1, 78, P < 0.001).

Table 7. The data on coho salmon populations, including location, year sampled, postorbital-hypural body length, and egg weight (standard deviations in parentheses). Regression coefficients (r) and statistics of egg weight = a + b(length).

Location	Year	Sample Size	Mean Length (mm)	Mean Egg Weight (mg)	Regression Statistics a	b	r	P	Reference
California:									
Scott Creek Hatchery	1935-36	4	521[1]	212.3(11.5)	-	-	-	-	Shapovalov & Taft (1954)
Washington:									
Soleduck River	1973	11	559.7(44.5)	207.3(38.0)	-173.1	0.68	0.796	0.003	Tagart (1976)
Green River Hatchery[2]	1953	61	518.8(59.1)	200.1(27.7)	73.5	0.24	0.520	<0.001	Allen (1958)
Green River Hatchery	1984	20	451.3(39.6)	214.9(44.8)	-96.5	0.69	0.610	0.004	present study
Deer Creek Junior	1984	7	462.6(40.4)	198.5(46.7)	-274.2	1.02	0.884	0.008	present study
Peyton Creek	1984	8	474.4(31.4)	195.7(21.9)	-71.5	0.56	0.809	0.015	present study
Issaquah Hatchery	1984	15	456.9(50.2)	236.5(46.1)	-77.6	0.69	0.749	0.001	present study
Skykomish River Hatchery	1984	20	474.7(26.9)	177.1(25.3)	39.2	0.34	0.302	0.195	present study
British Columbia:									
unknown	-	-	-	187.6	-	-	-	-	Groot & Alderdice (1985)
Wade Creek	1982	2	444.4(43.4)	159.2(85.8)	-	-	-	-	Taylor & McPhail (1985c)
Morrison Creek	1982	3	431.6(26.0)	228.8(122.1)	-	-	-	-	Taylor & McPhail (1985c)
Qualicum River Hatchery	1970	3	591.7(56.2)	247.3(3.5)	-	-	-	-	Beacham et al. (1985b)
Chilliwack River Hatchery	1984	28	472.2(31.2)	165.8(20.8)	12.9	0.32	0.486	0.009	present study
Blaney Creek	1984	1	485	167.2	-	-	-	-	present study
Borden Creek	1984	23	495.8(55.6)	172.6(33.9)	120.0	0.11	0.174	0.427	present study
Capilano River Hatchery	1984	19	439.0(45.4)	161.4(33.3)	-22.1	0.15	0.570	0.011	present study
	1985	6	447.5(23.4)	168.4(35.8)	-53.0	0.49	0.671	0.145	present study
Cohoe Creek	1984	10	470.0(46.8)	215.4(46.7)	1.0	0.46	0.659	0.038	present study
Hicks Creek	1984	30	474.8(41.4)	146.6(29.4)	12.5	0.28	0.399	0.029	present study
Lorenzetta Creek	1984	6	476.8(43.1)	177.9(48.1)	-245.0	0.89	0.795	0.059	present study

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(cont'd)

Location	Year	Sample Size	Mean Length (mm)	Mean Egg Weight (mg)	Regression Statistics a	b	r	P	Reference
Mamquam River	1984	23	532.9(33.7)	167.4(29.5)	-61.3	0.43	0.489	0.018	present study
Pye Creek	1984	17	517.9(35.2)	206.9(24.2)	154.1	0.10	0.148	0.571	present study
Post Creek	1984	23	479.5(44.0)	158.4(31.5)	-64.4	0.47	0.649	<0.001	present study
Siddle Creek	1984	11	484.0(48.7)	170.7(22.8)	38.7	0.27	0.582	0.060	present study
Tenderfoot Creek	1984	24	563.0(51.5)	177.1(25.3)	64.5	0.20	0.407	0.048	present study
Worth Creek	1984	21	486.3(29.7)	177.3(30.2)	2.2	0.36	0.354	0.116	present study
Alaska:									
Karluk River	1966	25	552.6(34.4)	97.3(15.5)	35.6	0.11	0.249	0.231	Drucker (1972)
Lake Ontario:									
Salmon River	1982	10	569.6[1]	182.3	-	-	-	-	Morrison et al. (1985)
Credit River	1982	10	565.7[1]	166.0	-	-	-	-	Morrison et al. (1985)
Lake Erie:									
Trout Run	1982	10	485.9[1]	158.4	-	-	-	-	Morrison et al. (1985)
Lake Michigan:									
Platte River	1969	17	514.8(54.4)	211.4(30.6)	-4.1	0.42	0.749	<0.001	Stauffer (1976)
	1970	30	487.5(55.8)	189.2(27.4)	3.9	0.38	0.773	<0.001	Stauffer (1976)
	1972	24	492.2(43.3)	180.0(24.2)	20.6	0.34	0.609	0.002	Stauffer (1976)
	1982	10	458.9[1]	157.9	-	-	-	-	Morrison et al. (1985)
Lake Superior:									
Anna River	1970	32	400.2(44.5)	112.7(26.0)	-60.0	0.43	0.527	0.002	Stauffer (1976)
Huron River	1970	16	391.1(31.3)	125.5(20.2)	-57.3	0.47	0.726	0.002	Stauffer (1976)
	1982	10	458.9[1]	157.9	-	-	-	-	Morrison et al. (1985)

[1] length not recorded from same females as eggs

[2] adults were Green River progeny which were transplanted to the University of Washington, Seattle

Egg Size Among Populations

There was as much variation among populations as within populations. Mean egg weight varied up to 254% ($F = 30.89$, d.f. = 23, 506, $P < 0.001$). Among regions the descending order of egg weight was: Washington State, British Columbia, Great Lakes and Alaska ($F = 8.80$, d.f. = 3, 20, $P < 0.001$).

Hatchery populations produced larger eggs than wild populations ($F = 3.51$, d.f. = 1, 18, $P = 0.039$), while controlling for the covariate latitude, which was also significant ($F = 32.33$, d.f. = 1, 18, $P < 0.001$).

Egg weight was negatively correlated with spawning date among populations ($r = -0.541$, $N = 21$, $P = 0.007$), while controlling for latitude

Egg Size, Fecundity and Latitude

As reported by other researchers, there is a significant latitudinal trend in fecundity (Fig. 13). However, there is an opposite latitudinal trend in egg weight (Fig. 14). The importance of this result is that ovary weight and thus total egg production are not significantly correlated with latitude (Fig. 15).

The outlying population of extreme in latitude, Karluk River (57°27'), when analyzed by Spearman rank correlation (Siegel

Figure 13. The relationship between latitude and coho salmon fecundity, standardized to a female body length of 488 mm.

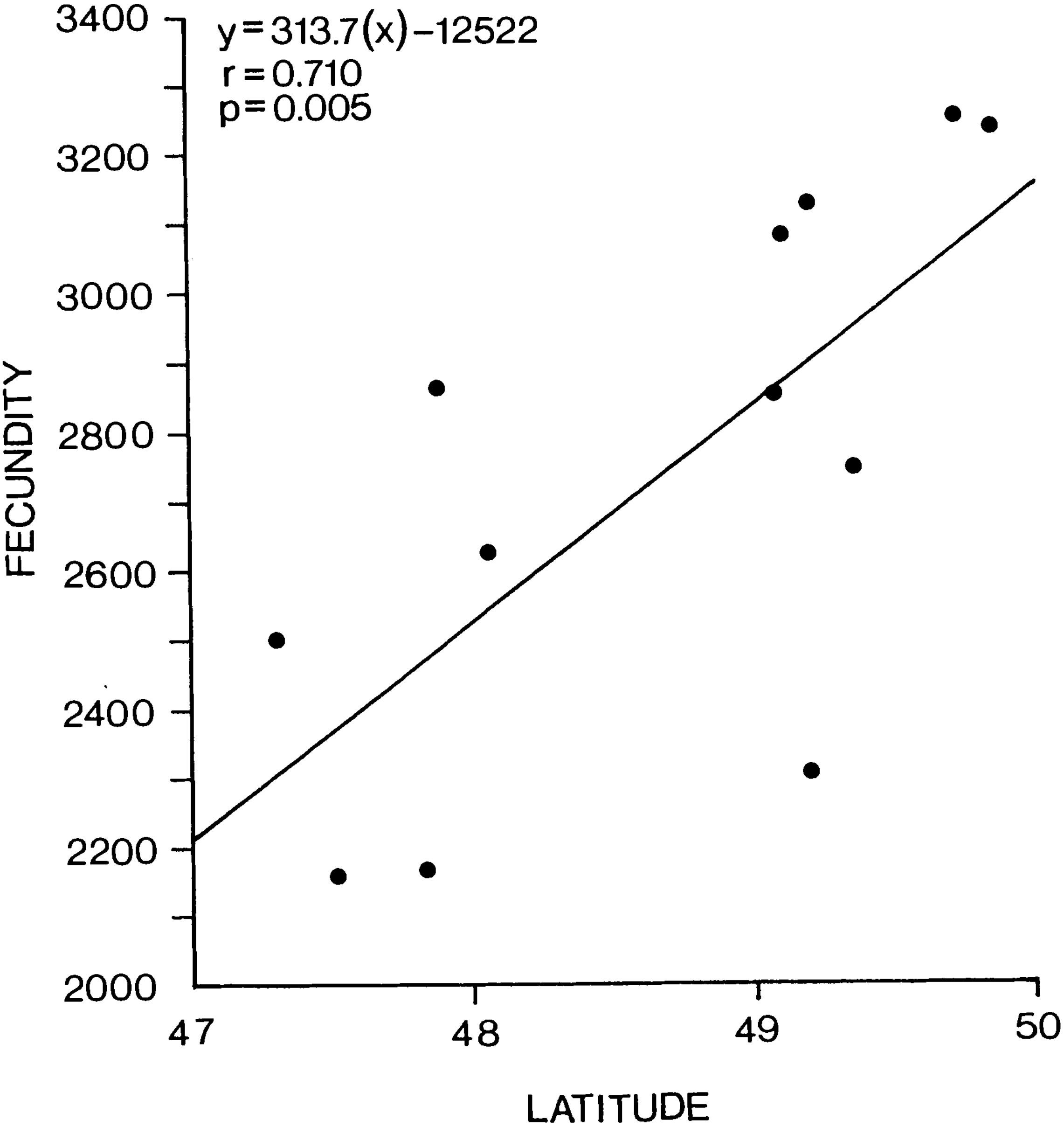

y=313.7(x)-12522
r=0.710
p=0.005
FECUNDITY
3400
3200
3000
2800
2600
2400
2200
2000
47
48
49
50
LATITUDE

Figure 14. The relationship between latitude and the size of eggs produced by coho salmon, standardized to a body length of 488 mm.

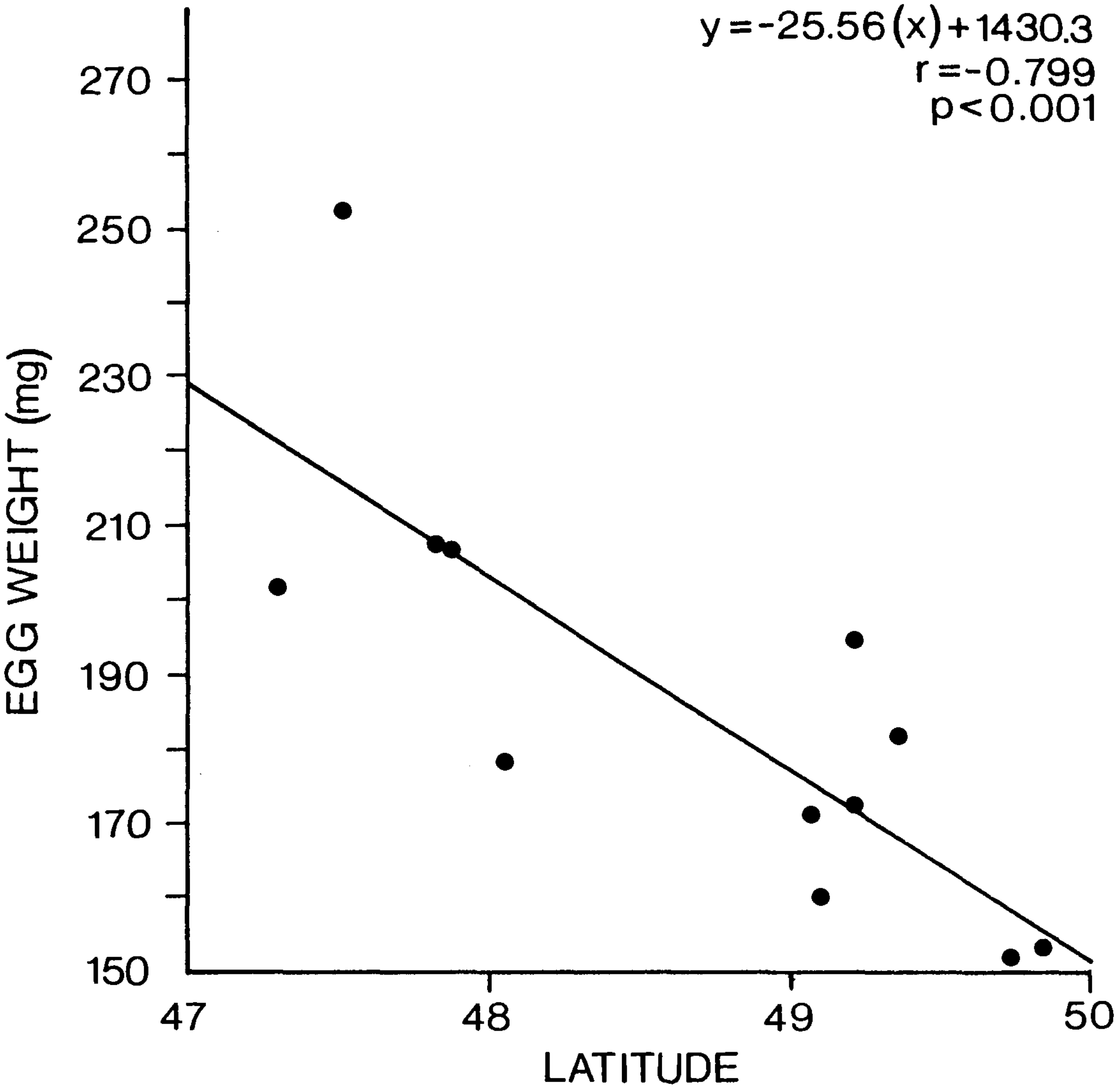
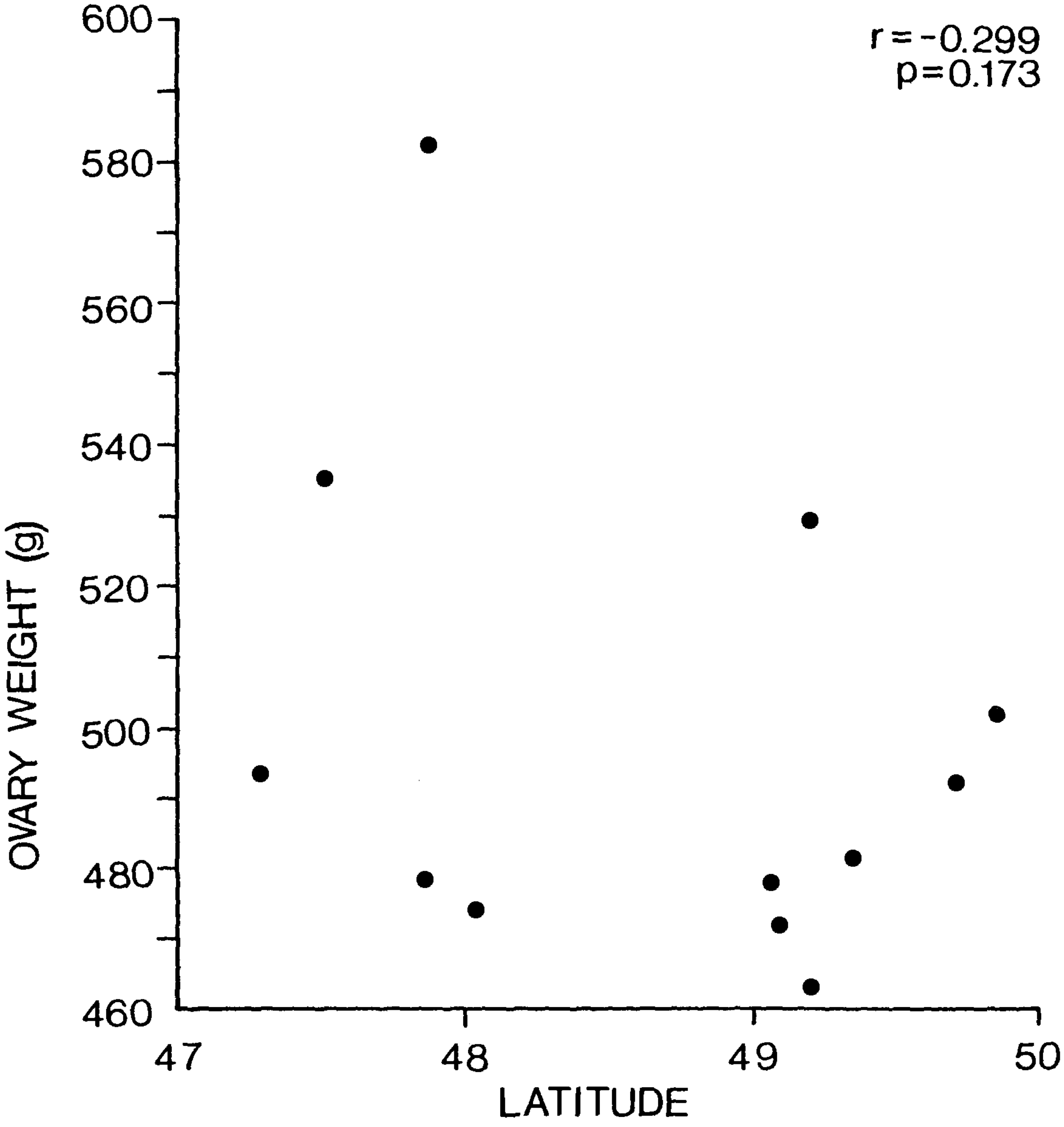

y=-25.56(x)+1430.3
r=-0.799
p<0.001
EGG WEIGHT (mg)
270
250
230
210
190
170
150
47
48
49
50
LATITUDE

Figure 15. The relationship between latitude and egg production (ovary weight in grams) for female coho salmon, standardized to a body length of 488 mm.


r = -0.299
p=0.173
OVARY WEIGHT (g)
600
580
560
540
520
500
480
460
LATITUDE
47
48
49
50

1956) to correct for the lack of bivariate normality, adds further support to these trends. When included in the analysis the statistical relationships with latitude are further strengthened (fecundity: r = 0.791, N = 13, P = 0.001; egg weight: r = -0.783, N = 13, P < 0.001; ovary mass: r = -0.313, N = 13, P = 0.297). Thus, the positive latitudinal cline in fecundity, the negative cline in egg weight, and the lack of a cline in egg production are further supported.

DISCUSSION

The variation which exists in salmon egg weight within, as well as among, populations should reflect the different advantages of egg size in various environments. A spawning stream is a heterogeneous environment of gravel quality, and intense competition occurs among females for quality gravel nest sites (van den Berghe and Gross 1986b). The survival of large eggs decreases more rapidly with decreasing gravel quality than that of small eggs (van den Berghe and Gross 1986b). However, a positive correlation exists between egg size and juvenile size (Fowler 1972, Beacham and Murray 1985a), and larger juveniles are competitively superior (Chapman 1962). Female size contributes to success in nest site competition (van den Berghe and Gross 1986b). Therefore, both female size and the intensity of competition among populations may directly affect the optimal solution to the trade-off between egg and juvenile survivorship (Sargent et al. 1986b, van den Berghe and Gross 1986b, Part B).

In hatcheries the eggs of all females experience similar incubation environments, thus the constraint of gravel quality has been eliminated and average offspring survivorship increased. This alteration of the selectional environment by the elimination of breeding competition in hatcheries, appears to have resulted in the evolution of significantly larger egg weights than that found in wild coho. Similar results were found by Leitritz (1959) for rainbow trout. The fact that egg weight changed significantly in only 10 generations of hatchery (Green River) rearing, even without direct selection for egg size, suggests that egg size can evolve under different environmental conditions.

Egg size also reflects the temporal environment. Egg weight among populations varied inversely with spawning date. Beacham and Murray (1986) found a similar relationship in chum salmon, with late-spawning populations having smaller eggs and shorter incubation periods than early-spawning populations. They suggested that this may be a mechanism for regulating the time of fry emergence. But in the present study, for the two populations where spawning lasted over two months, there was no relationship between egg weight and spawning date within populations. The lack of a relationship within populations may be a consequence of the smaller range in spawning dates than occurs across populations.

Annual variation in egg weight is apparently slight in the wild, supporting the contention that natural selection first determines the optimal egg size for an environment and then varies egg number about this. Scott (1962) and Wootton (1973) have found that changes in diet effect growth rate and clutch size, but egg size remains unaltered.

The well-known positive relationship between fecundity and latitude in Pacific salmon (Drucker 1972, Crone and Bond 1976, Beacham 1982, Healey and Heard 1984) appears to be a consequence of latitudinal variation in egg weight. The constriction of growing seasons in the northern latitudes, increased productivity at the time of hatching, and fewer juvenile competitors and size-selective predators could reduce the selective advantage of large egg size. Egg size and clutch size for a variety of zooplankton (McLearn et al. 1969, Allan 1976), marine invertebrates (Sastry 1966) and fish (Shrode and Gerking 1977), have been shown to vary directly with temperature. Therefore, the explanation for the latitudinal cline in fecundity may be found in understanding the latitudinal trend in egg size. It is clear that life history studies must not only consider fecundity, but also egg size when investigating interpopulation variation in egg production.

SUMMARY

Clutch size variation in Pacific salmon has remained an enigma since Rounsefell (1957) noted a latitudinal cline. However, clutch size is one of two components of egg production, the other being egg size. Coho salmon exhibit significant latitudinal variation in clutch size. However, they also have significant egg weight variation both within and among populations. As a consequence of an opposing cline in egg weight, no latitudinal cline exists in total biomass of egg production.

To understand trends in clutch size we must examine the selective forces acting upon egg size. Egg weight is often correlated with female body length, explaining 40% of the variation on average by this variable. It appears that egg size can rapidly evolve since the altered selectional environment of hatcheries has resulted in significantly larger egg weights than found in wild coho. The temporal environment also appears to have molded egg size; egg weight is significantly correlated with spawning date among populations. These and other factors which influence selection for egg size may be the basis for understanding why latitudinal clines exist in salmon fecundity.

PART E

GENERAL DISCUSSION AND SUMMARY OF THESIS

The importance of breeding competition for explaining variation in morphological and life history traits among populations of salmon has never been tested. This thesis provides the first comparative examination of the role of breeding competition in shaping salmon populations.

Breeding competition appears to result in:

(1) The molding of female secondary sexual characters, including kype and colour, through natural selection.

(2) Decreased investment into egg production; both ovary mass and egg weight.

(3) Increased investment into male fighting characters, kype and hump, through sexual selection.

(4) The molding of characters associated with male display, colour and dorsal fin.

(5) Sexual dimorphism in secondary sexual characters.

By contrast, selection for swimming efficiency appears to result in:

(1) Increased body streamlining (i.e., smaller median fins, body depth and caudal peduncle depth) with increasing migration arduousness, to aid stamina swimming performance.

(2) Increased body robustness (i.e., larger median fins, body depth and caudal peduncle) for burst swimming performance during spawning and freshwater residence.

This thesis also provides insights into the enigma of clutch size variation (i.e., fecundity) in Pacific salmon.

(1) Clutch size in coho salmon varies directly with latitude.

(2) However, egg size varies inversely with latitude.

(3) Therefore, no latitudinal cline exists in total egg production.

(4) Because selection tends to adjust egg size first and then vary clutch size, the basis for understanding latitudinal clines in salmon fecundity may lie in understanding latitudinal clines in egg size.

Suggestions For Future Research

This research has thus provided us with a greater appreciation of the selective forces, particularly breeding competition, and the evolutionary tradeoffs which shape many populations. But it has also simultaneously prompted several new questions and extensions.

(1) Pink salmon have a two year brood cycle, with no gene flow between brood lines. Genetic differences are often greater between brood lines, even if from the same river, than among populations within each brood line (Aspinwall 1974, Johnson 1979, McGregor 1983, Beacham et al. 1985a). Yet, the two brood lines within a river are more similar morphologically to one another, than to brood lines in other rivers (Beacham 1985). This indicates that the environments experienced within a river are similar for the two brood lines. But, there is an important difference. The number of adults returning to spawn is commonly

greater in one brood line than the other. In southern British Columbia the odd-year brood line of pink salmon is dominant while in northern British Columbia the even-year brood line is dominant (Beacham 1984b). Therefore, one would predict that the expression of secondary sexual characters should be greater in the odd-year brood line in the south and vice versa in the north. These results would further confirm the general importance of breeding competition in molding salmon morphology and life history.

(2) Compare the mating systems and environmental preferences of all five Pacific salmon species to determine their evolutionary response to the selective pressures outlined in this thesis. Such research should involve the investigation of such life history traits as the optimal age of reproduction and differential investment into breeding competition. The modelling of the optimal age of reproduction should incorporate selection due to breeding competition, which has often been left out of previous analyses (e.g., Healey and Heard 1984).

(3) Sexual dimorphism in fin size might be a consequence of sexual dimorphism in "risk proneness" of foraging strategies as juveniles. Sexual dimorphism in adult morphology and behaviour is well known, but that in juveniles is poorly understood. When juvenile development influences the expression of adult reproductive traits, juveniles should exhibit sexual dimorphism in development. Different patterns of risk assessment by the sexes due to different relationships between adult body size and

fitness, as discussed in Part C, should affect both growth rate and body size at maturity. Investigating the degree of sexual dimorphism in juvenile risk assessment and growth rate may provide us with a better understanding of juvenile life histories and morphologies, as they impact upon adult reproductive success.

(4) A closer examination should be made of the actual benefits of some of the secondary sexual characters important in breeding competition. This would best be done in a controlled stream channel, where one could select individuals to interact based upon their morphologies and determine their reproductive success. For instance, we could identify the importance of kype size in intrasexual competition by forcing individuals of similar body size and condition to compete for a resource (i.e., nest site or mate) and determine success. A further extension of this would be to examine the reproductive success of wild versus hatchery fish on the spawning grounds. The results of this thesis suggest that due to the alteration of natural selection in hatcheries, hatchery fish should be less successful in breeding competition than their wild counterparts.

Management Implications

Lawton and May (1984) noted that evolutionary ecology can provide powerful insights into some of the biological problems that confront fisheries managers. This thesis provides several such insights.

(1) The competitive ability and reproductive potential of salmon on the spawning grounds is closely correlated with body size. The typical harvesting practice used is to set limits on the minimum size of fish which can be harvested, thus primarily allowing the smaller fish to replenish the fishery. The result of such a practice would be selection against large body size (Ricker 1981), and thus the evolution of a less suitable fish. An alternative to this practice would be to set an upper limit on body size, thereby selecting for a more suitable body size, as well as reducing the abundance of escapement needed to replenish the population. Since the largest fish have the greatest competitive ability and reproductive potential, this would potentially allow an increase in the size of the fishery.

(2) Adult morphologies and life histories are closely adapted to their natal stream environment. This observation has profound implications for transplanting salmon from one location to another. The extent to which interbreeding between transplanted and native fish is detrimental to the adapted wild population is not yet fully understood. However, it is clear that transplants will be relatively unsuccessful because of the unique adaptations of existing native populations. Therefore, if transplants are necessary, they should be made among environmentally similar areas with similar levels of competition.

(3) To maintain genetic constitution of natural populations, yet increase numbers of fish produced, artificial spawning channels, where some form of competition still occurs, should be preferred over hatcheries. For example, Mead and Woodall (1968) have found that hatchery fry are inferior to natural fry in many characteristics for the stream environment, while fry from artificial spawning channels are equivalent to natural fish.

(4) In addition to reducing breeding competition, those hatcheries which rear juveniles for a long period of time (i.e., chinook salmon, coho salmon and steelhead trout), should hasten the production of "hatchery type" fish (Greene 1952, Flick and Webster 1964, 1976, Reisenbichler and McIntyre 1977, Rosentreter 1977, Fraser 1981). The divergence of the hatchery population from the natural state could be minimized, however, by resampling from the wild.

(5) By contrast to the above, the production of a "hatchery type" fish may be ideal for hatcheries, where one of the main goals is to produce large numbers of individuals for the fishery. The comparisons in this thesis between hatchery and wild females clearly suggests the extent of adaptation that occurs within hatcheries.

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PART F

APPENDICES 1 - 3

APPENDIX 1 - PRESERVATION AND MEASUREMENT OF SALMON EGGS

Introduction

Egg size data are important for salmon management and life history research. The size of eggs can influence estimation of female fecundity, the optimum time to initiate feeding (Rombough 1985), and stock identification (Craig 1985). Understanding variability in egg size can also shed light on life history evolution and variability in female fecundity (e.g., Part D).

However, studies of salmon egg size have been riddled with methodological inconsistencies. Eggs have been collected at various states of gonad maturity, and various preservation techniques and measures of egg size have been used, with varying degrees of accuracy.

The purpose of this paper, therefore, is to experimentally determine a suitable preservation method for salmon eggs, which minimizes the alteration of natural egg size. In addition, I develop empirical relationships which allow the comparative use of existing literature data on egg size.

Methods

Egg Collection and Preservation

Eggs were stripped from six reproductively mature female coho salmon (Oncorhynchus kisutch) of the November 1985 brood stock of the Capilano River Hatchery, North Vancouver, B.C. Within two hours, 90 eggs per female were individually weighed to the nearest 0.1 mg wet weight, grouped into random lots of 5 and placed into one of 18 preservation treatments (see Table 8). Immediately after the initial weighing, fertilization and waterhardening were conducted. Eggs were fertilized for 5 minutes with a random mixture of sperm from 4 males, then rinsed and waterhardened. Waterhardening involved placing eggs in standing river water until preservation. Waterhardened and fertilized-waterhardened eggs were then reweighed immediately prior to preservation. Preservation solutions were: (a) 5% neutral formalin (50 ml formaldehyde, 4.0 g sodium phosphate monobasic, and 6.5 g sodium phosphate dibasic, made to 1 l with distilled water; Velsen 1980), or (b) Stockard's solution (50 ml formaldehyde, 40 ml glacial acetic acid, 60 ml glycerin, and 850 ml distilled water; Velsen 1980). The eggs were reweighed seven days after preservation.

Eggs were also stripped from six reproductively mature female chum salmon (O. keta) of the Chehalis River Hatchery stock, Harrison Mills, B.C. in November 1985. Within 2 hours, 40 eggs per female were individually weighed, grouped into

Table 8. The 18 preservation treatments for coho salmon eggs.

Egg State	Preservative Solution	Time Before Applying Preservative (hours)
Fresh	Stockard's	3
		7
		24
	Formalin	3
		7
		24
Unfertilized-Waterhardened	Stockard's	3
		7
		24
	Formalin	3
		7
		24
Fertilized-Waterhardened	Stockard's	3
		7
		24
	Formalin	3
		7
		24

random lots of 10, and placed into one of four treatments: (1) 5% neutral formalin, (2) Stockard's solution, (3) waterhardened and 5% neutral formalin, and (4) waterhardened and Stockard's solution. Fertilization had no significant effect on coho egg weight (see below), and was, therefore, not performed with chum salmon. Eggs in treatments 3 and 4 were waterhardened immediately following initial weighing. Eggs were preserved 3 hours after their last manipulation, and reweighed seven days after preservation.

Egg diameters, both long and short axis, were measured to 0.02 mm using a dissecting microscope at a power of 12x for a subsample of coho and chum eggs.

After five months of preservation, a subsample of coho and chum eggs were reweighed, to determine if further changes in egg size had occurred.

Finally, to determine the effect of freezing on egg weight, 6 coho and 19 chum eggs were weighed fresh and then frozen in individually sealed vials at a temperature of $-10^{\circ}C$. The eggs were thawed and reweighed one month later.

Statistical Analyses

The coho salmon data were analyzed by analysis of variance, with egg state (N = 3), solution (N = 2), and time (N = 3) treated as fixed effects and fish (N = 6) treated as a random effect. Since some preservation techniques resulted in the destruction of up to two eggs per fish, the unbalanced data set was balanced by randomly selecting three eggs per fish from each cell (N = 18). The full statistical model, including all first, second, and third order interactions, was fitted to the ratio of preserved to initial weight. Residual analysis revealed that the variance of the residuals increased as the ratio increased. Therefore, log-transformed data were used.

The chum data were analyzed with egg state (N = 2), and solution (N = 2) as fixed effects, fish (N = 6) as a random effect and 9 replicates per cell. The chum data were also compared to the coho data using a mixed, nested model (fish nested in species). This analysis of variance had two egg states, two solutions, two species, six fish, one time and three replicates per cell. Again, log-transformed data and the ratio of preserved to fresh weight were used.

Regression models were developed for egg diameter on weight. Tests of coincidence were conducted between regression lines for chum and coho salmon, and among treatments using a multiple regression model with dummy variables.

Results

Coho salmon eggs ($\bar{x}$ = 168.1 mg, SD = 33.5, n = 540) were smaller than chum salmon eggs ($\bar{x}$ = 209.7 mg, SD = 11.7, n = 270), as were the females from which they came (coho: $\bar{x}$ = 547.5 mm postorbital-hypural body length, SD = 48.6; chum: $\bar{x}$ = 633.5, SD = 21.2).

Coho

In general, coho salmon eggs increased from 0 to 48 % in size after preservation (Table 9). Time before preservation had minimal effect on the size of eggs, while egg state, solution and individual fish were highly significant (Table 10). I therefore reduced the model by eliminating the time effects.

Fertilization had no significant effect on the size of waterhardened eggs ($t = -0.12$, d.f. = 10, $P = 0.907$), although waterhardening itself significantly increased egg size ($t = 13.15$, d.f. = 10, $P < 0.001$). Even after preservation, waterhardened and fresh eggs differed significantly (Stockard's: $t = 23.87$, d.f. = 13, $P < 0.001$; formalin: $t = 11.26$, d.f. = 8, $P < 0.001$).

The preservatives, Stockard's and formalin, differed in their effects on egg size ($t = 11.59$, d.f. = 5, $P < 0.001$). This difference was mainly a consequence of the fertilized-waterhardened ($t = 13.13$, d.f. = 8, $P < 0.001$) and

Table 9. The means and standard deviations (in parentheses) of the ratios of preserved to initial fresh egg weights for coho and chum salmon.

		Treatment						
	Time Before Applying Preservative	Fertilized Waterhardend		Unfertilized Waterhardened		Fresh		
Species	(hours)	Stockard's	Formalin	Stockard's	Formalin	Stockard's	Formalin	Waterhardened
Coho	3	1.481 (0.156) N=26	1.180 (0.052) N=29	1.488 (0.136) N=29	1.167 (0.062) N=30	1.055 (0.031) N=32	0.999 (0.019) N=31	1.266 (0.058) N=111
	7	1.448 (0.121) N=29	1.184 (0.053) N=29	1.466 (0.140) N=28	1.177 (0.055) N=29	1.055 (0.031) N=29	0.997 (0.016) N=31	1.255 (0.054) N=115
	24	1.466 (0.138) N=30	1.188 (0.048) N=34	1.499 (0.135) N=28	1.184 (0.058) N=30	1.057 (0.031) N=29	1.004 (0.019) N=31	1.245 (0.052) N=113
	Combined	1.464 (0.137) N=85	1.184 (0.050) N=92	1.484 (0.136) N=85	1.176 (0.058) N=89	1.055 (0.030) N=90	1.000 (0.018) N=93	1.255 (0.055) N=339
Chum	3	-	-	1.358 (0.054) N=68	1.120 (0.014) N=68	1.048 (0.013) N=65	1.003 (0.010) N=70	1.170 (0.023) N=136
Combined		1.464 (0.137) N=85	1.184 (0.050) N=92	1.428 (0.125) N=153	1.152 (0.052) N=157	1.052 (0.024) N=155	1.001 (0.015) N=163	1.231 (0.062) N=475

unfertilized-waterhardened egg states ($t = 14.29$, d.f. = 8, $P < 0.001$). The preservative effect was much reduced for fresh eggs ($t = 3.23$, d.f. = 8, $P = 0.012$), where both solutions produced a nonsignificant increase in egg weight (Stockard's: $t = 2.15$, d.f. = 10, $P = 0.057$; formalin: $t = 0.06$, $P = 0.957$). Not only did the two solutions have different effects on egg weight, but Stockard's solution resulted in significantly more burst eggs during preservation (Chi-square = 14.41, d.f. = 1, $P < 0.001$).

The individual fish effect and its related interactions were all highly significant across the experiment. When individual fish were isolated and tested, however, the general results were unchanged.

Chum

Egg state, solution and fish had statistically significant effects on the size of chum salmon eggs (Table 11).

Coho and Chum

When the chum and coho data were compared the main species effect and the second order species interaction were not significant at 5%, and the first order species interactions were not significant at 1% (Table 12). A direct comparison of the chum and coho data showed no significant difference in preservation response ($t = 2.096$, d.f. = 10, $P = 0.063$).

Table 10. Full model analysis of preservation techniques on the size of coho salmon eggs. The analysis compares preserved egg weight with initial fresh egg weight.

Effect	Degrees of Freedom	F	Probability
State	2,10	114.35	<0.001
Solution	1,5	134.34	<0.001
Fish[1]	5,216	385.42	<0.001
Time	2,10	3.94	=0.055
State-Soln	2,10	110.36	<0.001
State-Fish	10,216	52.89	<0.001
State-Time	4,20	1.33	=0.292
Soln-Fish	5,216	44.90	<0.001
Soln-Time	2,10	6.45	=0.016
Fish-Time	10,216	1.84	=0.056
State-Soln-Fish	10,216	6.44	<0.001
State-Soln-Time	4,20	1.71	=0.188
State-Fish-Time	20,216	1.83	=0.019
Soln-Fish-Time	10,216	0.67	=0.755
State-Soln-Fish-Time	20,216	1.76	=0.026

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[1] individual females

Table 11. Analysis of preservation techniques on the weight of chum salmon eggs.

Effect	Degrees of Freedom	F	Probability
State	1,5	690.52	<0.001
Solution	1,5	231.12	<0.001
Fish[1]	5,192	16.52	<0.001
State-Soln	1,5	94.65	<0.001
State-Fish	5,192	13.06	<0.001
Soln-Fish	5,192	15.33	<0.001
State-Soln-Fish	5,192	14.89	<0.001

[1] individual females

Table 12. Combined analysis of coho and chum egg preservation.

Effect	Degrees of Freedom	F	Probability
Species	1,10	4.40	=0.062
State	1,10	300.34	<0.001
Solution	1,10	584.59	<0.001
Fish[1]	10,96	32.28	<0.001
Species-State	1,10	8.45	=0.016
Species-Soln	1,10	8.32	=0.016
State-Soln	1,10	126.63	<0.001
State-Fish	10,96	16.14	<0.001
Soln-Fish	10,96	3.42	<0.001
Species-State-Soln	1,10	3.46	=0.093
State-Soln-Fish	10,96	5.68	<0.001

---

[1] individual females

There was no significant change in egg weight between the first measure of preserved weight at 7 days and that at 5 months under any preservation technique, except waterhardened Stockard's which resulted in an average decrease of 1.2 mg (0.5%) (t = 3.40, d.f. = 19 P = 0.003).

Measurement of egg diameter did not provide a completely accurate measure of egg size as determined by weight (Table 14). Eggs varied in shape. The relationship between egg diameter measured along the longest axis and that measured along the shortest axis was not very strong and varied among preservation techniques. The best linear correlate to egg weight was the average of the shortest and longest axis diameters (Table 13). As with fresh egg weight, egg diameter was not altered by preservation in 5% formalin (average diameter: t = 0.046, df = 9, P = 0.964).

Freezing caused significant shrinkage in egg weight, averaging 2.5% (t = 2.33, d.f. = 24, P = 0.028).

Table 13. Regressions equations for the relationships between egg diameters, and egg diameter and egg weight, under different preservation treatments. Coho and chum salmon were combined, as were eggs preserved fresh in formalin and those preserved fresh in Stockard's, because no significant differences ($P>0.05$) existed between these regressions.

Dependent Variable	Independent Variable	Treatment	Regression Equation	N	R Squared	Probability
Shortest Axis Diameter	Longest Axis Diameter	Preserved Fresh	$y = 0.68 + 0.894(x)$	60	0.922	<0.001
		Waterhardened Formalin	$y = 0.75 + 0.847(x)$	40	0.786	<0.001
		Waterhardened Stockard's	$y = -0.01 + 0.897(x)$	40	0.674	<0.001
Weight	Shortest Axis Diameter	Preserved Fresh	$y = 0.64(x)^{2.937}$	60	0.971	<0.001
		Waterhardened Formalin	$y = 0.94(x)^{2.751}$	40	0.940	<0.001
		Waterhardened Stockard's	$y = 3.46(x)^{2.101}$	40	0.857	<0.001
Weight	Longest Axis Diameter	Preserved Fresh	$y = 0.88(x)^{2.971}$	60	0.954	<0.001
		Waterhardened Formalin	$y = 0.82(x)^{2.744}$	40	0.909	<0.001
		Waterhardened Stockard's	$y = 0.88(x)^{2.668}$	40	0.915	<0.001
Weight	Average Diameter	Preserved Fresh	$y = 0.69(x)^{2.889}$	60	0.978	<0.001
		Waterhardened Formalin	$y = 0.65(x)^{2.901}$	40	0.976	<0.001
		Waterhardened Stockard's	$y = 1.19(x)^{2.587}$	40	0.966	<0.001

(cont'd)

Dependent Variable	Independent Variable	Treatment	Regression Equation	N	R Squared	Probability
Weight	Volume[1]	Preserved Fresh	$y = 5.35 + 1.034(x)$	60	0.978	<0.001
		Waterhardened Formalin	$y = 8.84 + 1.000(x)$	40	0.975	<0.001
		Waterhardened Stockard's	$y = 33.02 + 0.881(x)$	40	0.924	<0.001

[1] conversion from diameter to volume following Alderdice et al. (1979)

Discussion

I found that commonly used preservation techniques altered fresh egg weight by 0.1% to 46.4%, averaging 21.6%. Stockard's solution generally produced the greatest alteration in egg weight and was the least consistent in terms of degree of alteration. Stockard's also resulted in the destruction of significantly more eggs. The greatest alteration in egg weight occurred when eggs were waterhardened before placement in Stockard's solution. Although Velsen (1980) recommended the use of Stockard's solution for external examination of egg development, it is clearly not ideal for studies of egg size variation.

Buffered formalin produced significantly less alteration in egg weight than Stockard's solution and was generally more consistent in the degree of alteration. The best preservation technique, which produced no significant alteration in egg weight, was to place fresh eggs directly into 5% buffered formalin. Although some investigators have used higher concentrations of formalin, for example 10%, it is unlikely that this will improve preservation (Tucker and Chester 1984).

Waterhardening caused major changes to fresh egg weight, averaging a 23% increase. Although fertilization had no significant effect on waterhardened egg weight (Bilton [1970] also found no effect of fertilization on sockeye salmon eggs), preservation method did. Preservation in Stockard's solution after waterhardening resulted in a further 17% increase in egg weight. Preservation in 5% formalin, however, caused a 5% decrease in egg weight. It is unclear why Heming and Preston (1981) found no significant alteration in fertilized-waterhardened chinook salmon egg weight when preserved in 5% buffered formalin.

There was no species difference in the reaction of eggs to the preservation techniques, except that coho eggs tended to absorb a slightly greater percentage of water than chum eggs relative to egg weight.

Researchers have used various measures and methods of determining egg size without attempting to standardize their procedures. Egg diameter, the most commonly reported measure in the literature, is relatively inaccurate. The relationship between long-axis and short-axis egg diameter has considerable residual variance and is not well correlated with egg weight. Egg weight provides a more consistent and accurate measure of egg size. The use of egg weight also provides information for life history studies. I therefore recommend that salmonid egg measurements are made by weight on fresh eggs or fresh eggs preserved directly into a 5% buffered formalin solution. Finally, the data in Tables 9 and 13 can be used as correction factors for egg preservation and measurement techniques.

Summary

I compared the suitability of several popular methods of egg preservation for studies of salmon egg size. The use of egg weight as a measure of egg size was apparently more accurate and consistent than linear measures of diameter. There was no general difference in the response of coho (*Oncorhynchus kisutch*) and chum (*O. keta*) salmon eggs to preservation. Preservation of eggs in Stockard's solution, especially after waterhardening, greatly altered their weight. Moreover, Stockard's solution gave inconsistent results between fresh and preserved egg weight. In contrast, fresh eggs preserved in 5% buffered formalin were not significantly altered, even after 5 months of preservation, suggesting this was the most suitable technique for egg preservation. Some empirical relationships for correcting published data on preserved egg weight are presented.

Appendix 2. The means and standard deviations (in parentheses) of female coho salmon morphological characters. All measurements, except colour which is a rank score, are in mm and are standardized to a postorbital-hypural (body) length of 489 mm, with the exception of body length itself.

Population	N	Kype	Colour	Depth	Anal Height	Anal Base	Dorsal Height	Dorsal Base	Pelvic	Pectoral	Adipose	Caudal Peduncle	Body Length
Blaney	15	50.64	3.97	127.26	58.08	75.67	64.76	58.08	60.40	80.97	35.64	47.97	520.33
		(2.04)	(0.41)	(5.39)	(2.08)	(2.14)	(1.81)	(1.70)	(1.51)	(1.67)	(2.26)	(1.16)	(36.04)
Borden	26	50.46	3.91	125.34	62.26	73.97	64.82	56.13	62.32	83.73	32.45	48.64	493.65
		(3.13)	(0.52)	(6.06)	(2.82)	(3.40)	(2.52)	(3.01)	(3.04)	(2.95)	(2.32)	(1.75)	(52.51)
Capilano'	19	40.47	3.34	114.52	63.36	71.81	65.24	59.93	59.65	76.21	29.92	45.26	439.00
		(2.09)	(0.66)	(4.96)	(2.58)	(2.96)	(2.35)	(2.93)	(2.17)	(3.25)	(2.36)	(1.20)	(45.45)
Chilliwack'	28	44.12	3.34	127.55	60.97	69.90	63.90	57.60	61.71	83.16	30.68	47.96	472.60
		(3.02)	(0.51)	(5.29)	(2.57)	(2.91)	(2.60)	(2.21)	(2.10)	(2.60)	(2.05)	(1.42)	(31.24)
Cohoe	25	48.92	3.96	123.01	60.58	75.31	65.27	58.58	60.95	84.27	34.31	47.67	475.76
		(2.81)	(0.47)	(5.26)	(2.42)	(2.56)	(2.44)	(2.64)	(2.16)	(2.70)	(2.23)	(1.40)	(40.08)
Deer	10	47.45	3.89	121.65	59.63	74.83	63.59	58.39	59.82	80.78	34.61	47.84	470.08
		(2.43)	(0.37)	(2.59)	(1.32)	(2.32)	(2.27)	(2.27)	(2.46)	(2.38)	(2.00)	(1.14)	(42.20)
Green'	20	47.22	3.77	123.61	57.84	70.84	59.86	56.76	58.46	79.48	34.08	47.86	451.30
		(2.18)	(0.48)	(7.55)	(2.75)	(2.98)	(2.68)	(2.27)	(2.84)	(3.44)	(1.93)	(1.56)	(39.61)
Hicks	32	50.37	4.03	126.36	61.72	73.30	65.31	57.41	62.32	83.30	31.83	48.68	475.50
		(3.38)	(0.61)	(6.46)	(2.75)	(2.77)	(2.52)	(2.44)	(2.67)	(2.82)	(2.18)	(1.71)	(40.19)
Issaquah'	15	46.04	3.36	121.47	61.25	70.32	62.12	55.78	58.38	80.64	35.26	47.66	456.93
		(2.26)	(0.80)	(5.63)	(2.70)	(2.37)	(3.25)	(2.39)	(3.45)	(3.01)	(2.49)	(1.45)	(50.22)

(cont'd)

Population	N	Kype	Colour	Depth	Anal Height	Anal Base	Dorsal Height	Dorsal Base	Pelvic	Pectoral	Adipose	Caudal Peduncle	Body Length
Lorenzetta	*	47.76	3.77	119.44	**	72.81	64.73	55.84	60.26	**	35.24	47.22	495.50
		(2.95)	(0.31)	(5.27)		(2.94)	(2.82)	(1.98)	(1.13)		(2.23)	(1.06)	(51.43)
Mamquam	23	47.23	3.73	128.41	62.41	72.72	66.27	58.22	63.23	83.74	33.60	50.48	532.87
		(2.26)	(0.41)	(4.77)	(2.51)	(1.86)	(2.90)	(2.46)	(2.20)	(2.26)	(1.81)	(1.64)	(33.67)
Peyton	15	47.83	3.89	128.64	61.39	74.69	66.91	58.37	59.30	80.96	35.47	47.71	478.60
		(2.17)	(0.59)	(4.95)	(1.77)	(2.76)	(2.00)	(2.30)	(1.70)	(2.11)	(1.88)	(1.36)	(34.57)
Post	30	46.79	3.83	125.44	60.70	70.86	63.23	56.04	61.45	83.04	32.08	48.11	482.27
		(3.21)	(0.52)	(5.48)	(2.43)	(2.45)	(1.85)	(2.43)	(2.40)	(2.81)	(2.19)	(1.38)	(40.65)
Pye	24	48.41	3.85	131.08	62.28	74.89	65.84	58.73	63.31	84.81	32.76	49.09	526.00
		(2.86)	(0.34)	(5.24)	(2.48)	(2.30)	(2.11)	(1.92)	(2.20)	(2.17)	(1.74)	(1.79)	(35.68)
Siddle	19	47.28	3.74	126.83	59.97	71.15	65.70	58.34	62.12	83.79	33.38	47.73	482.79
		(2.08)	(0.48)	(6.46)	(2.24)	(2.84)	(2.53)	(2.17)	(2.51)	(2.52)	(2.01)	(1.66)	(42.06)
Skykomish'	20	48.17	3.73	126.75	58.35	72.76	62.07	57.07	59.34	82.55	36.47	49.92	474.70
		(2.11)	(0.75)	(5.36)	(2.48)	(2.32)	(1.81)	(2.12)	(3.27)	(2.17)	(1.36)	(1.94)	(26.92)
Tenderfoot	24	47.38	3.83	133.41	61.95	73.26	67.76	58.53	62.71	82.56	34.12	52.51	562.96
		(2.88)	(0.34)	(5.48)	(2.55)	(2.91)	(2.46)	(2.39)	(2.02)	(2.47)	(2.75)	(2.19)	(51.53)
Worth	23	48.67	4.13	129.77	63.11	74.23	66.66	58.81	63.64	84.93	31.67	48.74	496.78
		(2.60)	(0.61)	(5.99)	(3.32)	(3.14)	(2.44)	(2.52)	(2.56)	(3.07)	(2.04)	(1.71)	(45.05)

' hatchery

* the sample size for anal base is 11, dorsal height 5, dorsal base 10, adipose 10, caudal peduncle 11

** no data

Appendix 3. The means and standard deviations of female coho salmon life history traits. All measurements are standardized to a postorbital-hypural (body) length of 489 mm.

	Egg Weight (mg)			Ovary Weight (g)		
Population	N	Mean	Standard Deviation	N	Mean	Standard Deviation
Blaney	1	177.4	-	0	-	-
Borden	23	180.5	37.6	0	-	-
Capilano'	19	189.1	31.4	19	485.2	66.8
Chilliwack'	28	180.3	20.2	19	481.0	59.1
Cohoe	10	235.9	27.4	0	-	-
Deer	7	218.7	38.0	6	481.7	49.2
Green'	20	244.3	41.4	20	529.6	79.4
Hicks	30	159.1	30.5	0	-	-
Issaquah'	15	265.5	37.3	15	534.6	87.9
Lorenzetta	6	189.9	42.9	0	-	-
Mamquam	23	161.3	25.2	23	494.9	57.3
Peyton	8	212.0	15.6	0	-	-
Post	23	169.4	27.2	20	472.3	55.5

(cont'd)

	Egg Weight (mg)			Ovary Weight (g)		
Population	N	Mean	Standard Deviation	N	Mean	Standard Deviation
Pye	17	206.1	25.7	6	466.0	30.2
Siddle	11	182.1	22.2	7	533.1	48.1
Skykomish[1]	20	218.1	32.1	20	591.7	83.4
Tenderfoot	24	166.2	21.6	23	504.4	65.8
Worth	21	187.6	30.1	0	-	-

[1] hatchery