NATURAL SELECTION AND REPRODUCTIVE SUCCESS OF FEMALE COHO SALMON (ONCORHYNCHUS KISUTC): A STUDY IN FEMALE COMPETITION

by

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NATURAL SELECTION AND REPRODUCTIVE SUCCESS OF FEMALE COHO SALMON (ONCORHYNCHUS KISutch) : A STUDY IN FEMALE COMPETITION.

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ABSTRACT

This thesis looks at how reproductive behavior and life history traits evolve under female-female competition, in the coho salmon (Oncorhynchus kisutch). Previous studies of reproductive success in female fishes have ignored the contribution of behavior to reproductive success, and thus to natural selection.

Reproductive success of individual females was studied for two years in a wild population in Washington State, from the first spawning in November until fry emergence in April. Mature adults were tagged and followed until death. The position, depth, completion date, and eventual fate of each nest was known for most females in the population. Territory quality was quantified by examining survival of eggs to fry. The age and growth patterns are known from analyses of adult scales. My data are supplemented with additional sources on fecundity, and on post-emergent freshwater, ocean, and fishing mortalities.

Nest depth was strongly correlated with female body size (r=.778, P<.001), as was female breeding life (r=.65, P<.001) which ranged from 3 to 22 days. Females spent almost all of their breeding life guarding their territory to prevent other females from re-using it and thereby digging up the eggs. Variance in nest survival was due to competitive differences in guarding time, fighting ability, and nest depth among females of different body sizes. A total of 24% of all nests in the stream were lost.
Reproductive success differed by 25-fold among females. Based on theoretical models of selection intensity, fecundity differences account for only 20-23% of all natural selection on female body size, whereas 32-41% is contributed by differential nest destruction, 17-24% is due to territory quality, and 20-21% is due to a post-emergent advantage of fry produced from larger eggs. Thus female-female competition via nest destruction and territory quality contributes more than half of all selection for body size, making it, not fecundity, the major selective force for body size evolution in female coho salmon.
ACKNOWLEDGMENTS

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Dr. Mart R. Gross deserves special thanks for his midnight trips to the field at a moment's notice to help handle all the fish and for insight and discussion throughout the study and graduate school. Thanks also to Ronald Coleman, Ian Fleming, and Dr. Craig Sargent who made helpful suggestions, assisted in carrying out some of the experiments, and helped to make being part of this lab group a pleasure not soon forgotten.

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A. GENERAL INTRODUCTION

A major area of research in evolutionary biology today is understanding behavior and life history evolution. To properly understand the evolution of life history traits, however, requires a detailed knowledge of how fitness is affected at each stage in an organism's life history. To date, few studies have successfully measured the intensity of selection at different life-history stages (McCauley, 1983; Arnold and Wade, 1984b). Three major obstacles have prevented investigators from attaining these goals. First is the difficulty of following individuals throughout their lives in a field situation. Second is that the age structured populations which characterize most vertebrates make the calculations of lifetime reproductive success very difficult, because reproductive success changes with age. Third is the lack of theoretical models for separating the intensities of selection at different stages of the life history and for different components of the phenotype.

A further area of much current research is the role of female-female competition in natural selection (Wasser, 1983). During the past decade, most studies have focused on male-male competition as a major aspect of natural selection via sexual selection. However, it has recently become apparent that females may be sufficiently resource limited to compete aggressively among themselves and thus share many of the selective factors
previously thought to occur only in males (Lennington, 1980; Wasser, 1983).

Coho salmon are ideal for studies on reproductive competition because they only live a few weeks on their spawning grounds in small streams, and are readily observable. In addition, preliminary observations showed that female coho engage in prolonged fights over breeding territories, and that body size and jaw size may be important determinants of their fighting success. I therefore applied recently developed theoretical models of selection intensity (Arnold and Wade, 1984a,b) to measure selection for body size and jaw length across each stage of a female's life history.

The first two parts of this thesis identify and document the mechanisms which lead to differential female reproductive success and hence to selection for breeding adaptations. The third part documents the extent of female-female competition, calculates reproductive success, and separates natural selection into several components to compare the intensities of selection due to female competition, differential fecundity, and differential survival of the progeny. This study represents one of the first to have quantified lifetime reproductive success and to have measured the influence of female competition on reproductive success.

The study involved tagging all the adult fish in a small population as they arrived on their spawning grounds, and following these individuals for their entire breeding lives.
This yielded information on the breeding success of individuals, including the effects of female competition on territory quality and destruction of nests by dig-up. Additional information included their breeding lifespan, guarding time, nest depths, and behavioral interactions.

Territory quality was important for the survival of eggs and embryos. The locations of individual nests, and hence site characteristics, were known from the first part of the study. To find out precisely how site characteristics affect egg survival, I buried pouches of fertilized eggs in a range of sites in the stream. These eggs were monitored until April when natural fry emerged and the pouches were excavated. The data for post-emergent mortality were already available in the literature, and did not need to be measured in this study.

These various sources of mortality were used to identify the relative strength and direction of selection at each stage in the life of female coho salmon. The results were combined to give a comprehensive overview of female behavior and life-history evolution under natural selection.
B. FEMALE SIZE AND NEST DEPTH

I. Introduction

Female salmonids spawn into nests they construct in stream beds. Nests are excavated using a series of lateral body flexures, which produce a vortex, lifting gravel to be carried downstream by the current. After egg deposition, the female moves upstream and, with a similar digging motion, covers the nest (Foerster, 1968; McCart, 1967; Tautz and Groot, 1975). The function of egg burial is to increase brood survivorship by decreasing predation (Reed, 1967; Stuart, 1953, cited in Jones 1959), mechanical damage, and agitation, which is lethal during critical periods of brood development (Smirnov, 1955). The relationship between substrate characteristics and brood survivorship has been well studied (Coble, 1961; Dill and Northcote, 1970; and others). However, an important, but less well studied, factor for brood survivorship is nest depth. Increased depth will afford greater protection from mechanical damage and exposure when gravel is shifted by floods and when nests are superimposed by competing females. Superimposition, or re-use of nest sites by later spawning females, is a common phenomenon in salmonids and is responsible for considerable brood loss (McNeil, 1962; Schroder, 1973; and others).
Studies reporting nest depth give depths at which investigators encountered eggs in the course of excavating redds (e.g. Burner, 1951; Hawke, 1978). Such data may be inaccurate due to the frequent and often extensive gravel shifts associated with fluctuating water levels. McNeil (1962), for instance, showed gravel shifts in one season to exceed 25 cm at one third of his sites. Shifts of such magnitude would destroy many of the shallower nests thereby removing them from the sample. A further important shortcoming of the existing nest depth data is the lack of information on female size. Larger females make deeper nests in brown trout (Salmo trutta) (Ottaway et al., 1981) and possibly in salmon (Jones, 1959; Major and Craddock, 1962; Ricker, 1972). If so, the destructive effect of nest re-use and flooding will differentially affect females of different size; this would have important management implications for salmonid populations. Therefore, I measured nest depths of coho salmon of known body size at the time of spawning.
II. Methods

Data was collected on a small wild population of spawning coho salmon native to a tributary of Deer Creek, 1.8 km west of Index, Snohomish Co., Wa. During November-January of 1981-82 and 1982-83, all the returning fish were caught at a weir near the mouth of the stream. The fish were measured to the nearest half centimeter (fork length), sexed, and tagged using color-coded Petersen disk tags (Floy Tag Co., Seattle, Wa). Tagging permitted subsequent recognition of individual fish. All fish were released above the weir to spawn naturally.

Substrate samples, each consisting of about 4 kg of material, were collected with a shovel at 2-m intervals in midstream along the entire spawning ground. This provided samples to a depth of 25 cm which I considered representative of the depth affected by the fishes' digging. Examination of the stream substrate showed no significant layering to that depth (analysis of six samples taken at 0-5, 10-15, and 20-25 cm; MANOVA (Nie et al., 1975) P=0.699, 0.908, 0.821, and 0.560 for comparisons between depths). All gravel in the stream was of a smooth rounded texture. The substrate samples were analyzed in the laboratory, and Fredle indices were calculated (Lotspeich and Everest, 1981). Nest sites were characterized by superimposing the Fredle scores on a grid map locating the nests. To minimize the effects of spatial heterogeneity in gravel, only those nests with centers within 50 cm of a gravel sampling locality were used.
Nest depth was defined as the maximum depth to which a female excavated her nest. This was calculated as the maximum distance from the top of the water column to the deepest place in the nest, minus the distance to the top of the undisturbed substrate around the nest. Series of nest measurements were taken between digging episodes and immediately following the spawning. The greatest observed depth is used here as the nest depth. Measurements were made from shore using a meterstick attached at right angles to a pole; this minimized spawning disturbance. Records were kept on 83 of 160 females that spawned in the stream. Of these, measurements were obtained during daylight hours for nests of 42 females. Observation periods of individual fish were of variable duration because the moment of egg release is often unpredictable. Although the females could not be observed at night, nest locations and the identity of the females were rarely in doubt, since digging was often initiated during the daytime and covering frequently continued long after sunrise. Gravel disturbed for new nests also contrasted strongly with the algae covered substrate in the surrounding areas, and females rarely abandoned their completed nests prior to dying. It was therefore possible to obtain reliable data on the number of nests they constructed.
III. Results

The females which were studied ranged in length from 40.5 to 76 cm, which was representative of the size range in the stream. They constructed an average of 2.07 ± 0.84 nests with 20 (28.6%), 27 (38.6%), 21 (30.0%), and 2 (2.8%) fish making 1, 2, 3, and 4 nests, respectively. Larger females dug significantly more nests than did smaller ones (comparing female size categories > 70, 61-70, 51-60, and < 50 cm, N=70, Chi square=20.4, df=3, P<0.01). Depths of first nests for individual females did not differ significantly from those of nests they excavated last (paired t test, t=0.695, N=13, P=0.5)(Table 1). Females spawned into each nest they dug. Nests were roughly cone shaped, with the smallest diameter at the bottom where the eggs were laid.

Nest depth averaged 13.7 ± 4.0 cm (N=42); however, nest depth was strongly correlated with female size (r=0.778, P<0.001)(Fig. 1). Large females buried their eggs as much as 2.5 fold deeper than did small females. This could result from (1) larger females selecting nest sites that are easier to excavate, (2) larger females having greater strength or a mechanical advantage for lifting gravel, or (3) the greater fecundity of large females necessitating deeper nests. The third alternative is ruled out because the greater egg volume of large females is divided among more nests resulting in similar numbers of eggs in nests of large and small fish (see also Hawke, 1978). To examine the first two alternatives, I regressed nest depth on both female size and gravel size. The multiple regression (Nie et
Table 1: Nest depths of the first and last nests made by 13 female coho salmon. Last row of data is mean ±SE.

<table>
<thead>
<tr>
<th>Female size (cm)</th>
<th>First nest (cm)</th>
<th>Last nest (cm)</th>
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<tr>
<td>46.5</td>
<td>8.9</td>
<td>11.4</td>
</tr>
<tr>
<td>50</td>
<td>14.0</td>
<td>15.2</td>
</tr>
<tr>
<td>53</td>
<td>11.4</td>
<td>14.0</td>
</tr>
<tr>
<td>53.5</td>
<td>12.7</td>
<td>14.0</td>
</tr>
<tr>
<td>56</td>
<td>12.7</td>
<td>11.4</td>
</tr>
<tr>
<td>56</td>
<td>9.0</td>
<td>11.4</td>
</tr>
<tr>
<td>58</td>
<td>10.5</td>
<td>12.5</td>
</tr>
<tr>
<td>61.5</td>
<td>14.0</td>
<td>17.8</td>
</tr>
<tr>
<td>65.5</td>
<td>22.8</td>
<td>23.4</td>
</tr>
<tr>
<td>67</td>
<td>15.2</td>
<td>15.2</td>
</tr>
<tr>
<td>68</td>
<td>17.8</td>
<td>16.5</td>
</tr>
<tr>
<td>69</td>
<td>20.3</td>
<td>17.8</td>
</tr>
<tr>
<td>74</td>
<td>26.7</td>
<td>21.6</td>
</tr>
<tr>
<td><strong>59.8±8.3</strong></td>
<td><strong>15.1±5.2</strong></td>
<td><strong>15.5±3.7</strong></td>
</tr>
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al., 1975) revealed that 71% of the variance in nest depth is explained by female body size alone (P<0.001) and only 5% is explained by gravel size (P=0.57). Therefore, the second explanation appears to be most plausible.

IV. Discussion

I have shown that larger females dig deeper nests. The analysis suggests that the difference in nest depth is due to a mechanical or energetic advantage from larger body size. Approximately one quarter of the variance in nest depth among females is not explained by body size; however, female energy reserves probably varied considerably. Oceanic ectoparasites were still attached to some of the fish, suggesting that these came directly from the sea. By contrast, some coho were observed in the main river near the mouth of the stream in early September, 2 months prior to spawning activity. Such disparity in river residence time probably causes considerable variation in energy reserves. Current velocity may account for some variance in nest depth; however, if currents had a major influence, gravel size would have been more strongly correlated with depth, since gravel size is strongly related to current velocity (Novak, 1973).

Female salmonids compete aggressively among themselves for nest sites, and eggs are often dug up by females that arrive later (Hanson and Smith, 1967; McNeil, 1962; Schroder, 1973; and others). Since larger females bury their eggs as much as
Figure 1: Nest depth as a function of female size in coho salmon.
y = -10.44 + 0.411 x
r = 0.778
N = 42  P < 0.001
2.5-fold deeper, their broods will be less susceptible to damage from superimposition because fewer competitors dig deep enough. Furthermore, due to the cone-shaped nature of the nests, the area disturbed by digging decreases with increasing depth. Shallow nests are thus vulnerable to females excavating off center, whereas deep nests are vulnerable only if subsequent nests are precisely centered. Shallower nests are also subject to a higher probability of destruction by gravel movement during heavy runoff. By contrast, mortality costs of deeper burial are probably negligible over the range of depths found in nature. Hatching success and alevin mortality have not been found to differ over a range of gravel depth to 30.5 cm (Dill and Northcote 1970). Managers of salmon populations should recognize that there is a selective advantage to larger bodied females resulting from their ability to dig nests deeper.
C. FEMALE SIZE AND BREEDING LIFE

I. Introduction

Few data are available on a significant aspect of salmonid reproductive biology: the length of adult life on the spawning grounds. Because individuals vary in body size and presumably in energy reserves, larger individuals may well survive longer than smaller ones. However, published data on duration of spawning give only population means (e.g. Killick, 1955; Schroder, 1973). Therefore, I studied the breeding life of individually marked male and female coho salmon (Oncorhynchus kisutch) of different sizes during two breeding seasons. This study was carried out on a small wild population in the Snohomish River system, Wa., U.S.A., and is an extension of a study by van den Berghe and Gross (1984a). The results show, for the first time, that there is a significant positive correlation between body size and length of life on the spawning grounds for mature adult salmon.
II. Methods

The study population occupied a tributary to Deer Creek, locally known as Deer Creek Junior, 1.8 km west of Index, Snohomish Co. Wa. Adults were caught at a weir near the stream mouth during November to January of 1981-82 and 1982-83; they were measured (fork length), sexed, and tagged using color-coded Petersen disk tags (Floy Tag Co., Seattle, Wa.). Scales were removed for aging, and all fish of the study reported here were age 3 (one freshwater year and two ocean years). I checked the weir at 0800, 1600, and 2300 daily and released all fish above it, where 90% of spawning areas were located. I also checked the stream for dead and dying fish at these times, recorded the stream water level at 0800 daily, and recorded water temperature on unusually warm and cold days. More frequent surveys were made when fish activity was high. Dying fish (those too weak to maintain an upright position) were checked frequently to determine the interval between cessation of guarding and death to within one hour. Fish were declared dead when they ceased to respire. Spawning and mortality data were not collected between the hours of 2300 and 0800. I used only the fish for which time intervals were known within one hour for my analyses.

The total time alive on the spawning ground is known for 83 of 160 females (52%) that entered the stream in the two seasons. Of these, 4 (5%) died of predation, and 15 (18%) had signs of previous spawning below the weir (i.e. frayed caudal fin from
digging and thin abdomen indicating that most eggs were missing). These 19 fish were omitted from the analysis of natural breeding life, leaving a sample of 64. The mean body size of omitted fish was not significantly different from the population mean (t=0.61; P>0.5; in 1981-2 and t=0.42; P>0.5 in 1982-3), suggesting they were a random subsample of the stream population. In addition to total time alive, the approximate time to establishing a territory and time of territory abandonment were recorded for females.

Life on the spawning ground is known for 96 (47%) of 205 age three males that entered the stream. Some of these males may have spawned in lower reaches of the stream (Deer Creek) before entering Deer Creek Junior; however, this could not be accurately determined and all 96 fish are included in the analyses. Sub-intervals in spawning time were not collected for males, because males moved extensively between female territories, and neither helped in nest construction nor guarded nests after spawning. "Seasonal" regression analyses are based on the entry dates onto the spawning ground, relative to the date when the first fish entered for that year.

Results are expressed as arithmetic mean ± 1 SE unless otherwise specified. Multiple regression analyses are based on Nie et al. (1975).
III. Results

The average life on the spawning grounds was 9.0±0.52 days for females (N=64, range=3-17 days), and 9.4±0.61 days for males (N=96, range=2-30 days). These times were not significantly different (t-test; t=0.51; v=156; P>0.5). In both sexes, breeding life was significantly correlated with body size (Fig. 2a,b). Regression slopes and adjusted means were not significantly different between years; I therefore pooled the data for subsequent analyses. For females, a multiple regression analysis of days alive on the spawning grounds against body size, average water level during residence, and season measured in days from the date of entry of the first female revealed that water level and female size had a strong positive interaction (R²=0.54; P<0.001). Total explained variance for females was 54%, of which 41% was due to body size alone (P<0.001) and an additional 13% could be explained by water level (P<0.001). No significant seasonal effect was found in either year (1981-82: r= -0.16; P=0.19; 1982-83: r= +0.22; P=0.12).

In males, the same factors accounted for only 29% of variance in breeding life. Body size made a 14% contribution (P<0.001), and season made a 13% contribution (P=0.004). The contribution by water level was small and not statistically significant (2%; P=0.62).

For females, the average time to starting the first nest after passing the weir was 10.8±1.9 hours (N=25). The mean time
Figure 2: Body size and number of days alive on the spawning ground for coho salmon (Deer Creek Junior, Wa., U.S.A.). Double circles represent two fish. a) female data: $N=64$, $r=.65$, $P<.001$, $Y = -9.0 + .314 X$. b) male data: $r=.33$, $N=96$, $P<.001$, $Y = -1.4 + .203 X$. 
between leaving the redd and death was 8.7±1.6 hours (N=19). There was no significant difference for females larger or smaller than the mean female body size in starting or leaving their redd (large versus small females: time to starting the first nest, \( t=0.072; 23\text{df}; P>0.5 \) and absence from the redd until death \( t=0.147; 17\text{df}; P>0.5 \)). The time interval when females were not associated with their nest was about one day, thus female guarding lasts from about 2 to 16 days for the smallest and largest females respectively. It is possible that disturbance from capture and tagging slightly prolonged the time to starting nests; however, this should be independent of female size.
IV. Discussion

I have shown for the first time that larger salmon live longer on the spawning grounds than do smaller ones. Of the variables measured, size has the most important affect on breeding lifespan. However there was a considerable difference in the explained variance: body size made a much greater contribution to female than male variance in length of breeding life. The contribution of body size may have been reduced in males because some males probably spawned prior to arrival at the weir. Another factor which may be important is male fighting. Although females fight (Schroder, 1981), males are much more aggressive among themselves and sustain major injuries. The chance nature of injuries and the variability in male fighting may also account for the higher variance in male breeding life.

The correlation between water level and breeding life in females, but not in males, is probably due in part to water level constraints on digging for larger females. By contrast, males were able to spawn at all water levels. It is less clear why later males tended to live longer. Although water temperatures decreased seasonally, which could increase breeding life, it is unclear why females would not exhibit a similar trend.
The residence time of salmon on their spawning grounds has at least two implications for stock management. First, since most females spend less than 24 hours out of 9 days not associated with their redd, larger females guard their nests as much as 10 fold longer than do small ones. This longer period of parental care in larger females will, on average, improve egg survival because guarding reduces the likelihood of redd re-use (see part D), considered to be a significant source of brood mortality (Ginetz, 1977; McNeil, 1966; Neilson and Banford, 1983). The second implication is that estimates of population size from spawner counts could be improved by incorporating fish size. One of the more common techniques for spawner enumeration is to make periodic counts of fish on the spawning grounds, and to adjust these to an average lifespan (Craddock, 1958; Neilson and Geen, 1981). My results, however, show that larger fish will be overrepresented by this technique, since they live longer than the average; the converse is true for smaller fish. Averages may also give misleading data if fish sizes vary among years. As an example, the mean size and consequently survivorship of coho in Deer Creek Junior was significantly different in 1981-82 from 1982-83. If the average survivorships from these two years were combined and used to estimate the population size in 1982-83, the estimate would be 48% too high.
D. COMPETITION, LIFE-TIME REPRODUCTIVE SUCCESS, AND THE INTENSITY OF NATURAL SELECTION IN FEMALE COHO SALMON

I. Introduction

Nearly all studies on reproductive success and sexual selection have until recently focused exclusively on male-male competition because males generally possess the more exaggerated secondary sexual characters and because the non-limiting sex (usually males) should compete for access to the limiting one (usually females) (Trivers, 1972). It has also long been recognized that sexual selection may act on females if the sex roles (in terms of parental investment) are reversed, because males are then limiting (Williams, 1975; Petrie, 1983). However, the role of female-female competition in natural selection of non-role-reversed species has recently generated considerable interest. Several studies on a variety of taxa have now shown that, when they are sufficiently resource limited, females too may compete aggressively, thereby sharing many of the selective factors previously thought unique to males. Li and Owings (1978) have evidence of both male and female mate choice in sticklebacks in that males do not court all females, nor do all courted females spawn with the courting male. Li and Owings further document that dominant females in aquaria may interrupt
courtship of subordinates and force subordinate individuals to shed eggs away from nests. Wasser (1983) has shown that dominant wild female baboons with very young progeny will systematically harass subordinate individuals that come into estrus, presumably to prevent them from reproducing. Dublin (1983) similarly shows reproductive competition in female African elephants, and Lennington (1980) showed competition among female redwing blackbirds over nesting territories. Although these studies demonstrate that the existence of female competition is widespread, the present study is the first to measure the selective pressure generated by female-female competition, thereby clarifying the importance of female-female competition as an evolutionary mechanism.

In this study I look at the influence of female competition on the reproductive success of coho salmon (Oncorhynchus kisutch) and estimate the selective pressure exerted by female competition. To compute selection from field measurements, I have incorporated recent developments in the measurement of natural selection (Arnold and Wade, 1984a,b). These advances have made it possible for evolutionary behavioral ecologists to study individual adaptations and identify the direction as well as intensity of natural selection at each stage in life. Although selection intensities for one or more life history stages are known for some organisms (Howard, 1983; McCauley, 1983; Trivers in: Arnold and Wade, 1984b), selection throughout the animal's life-history has never been measured.
Fecundity has generally been assumed a good indicator of female reproductive success in fish. However, fecundity does not incorporate any behavioral competition or other processes which cause differential offspring survivorship. Offspring survival is itself the product of changing selectional pressures throughout life. To learn how selection acts at various points in life, I have divided reproductive success into stages or episodes of selection, which can be analyzed separately. Thereby I take into consideration the chance of a given female's progeny surviving 1) nest destruction by competing females to the end of the current spawning season, 2) development in the substrate to emergence, and 3) predation to maturity.

Theory

It is important to distinguish clearly at this point between selection and response to selection (Haldane, 1954). Selection depends simply on differential reproduction and occurs within a generation. A response to selection occurs between generations and depends on inheritance. The intensity of selection is measured as a theoretical shift in character mean. This is done by treating the character as if it were 100% heritable, and calculating changes in the character mean via changes in the relative representations of individuals in the population. My objective here is to measure selection for specific breeding adaptations in salmon, not to measure the
response. Measuring the intensity of selection can tell us what features of the environment and life history give rise to selection for specific adaptations.

Measuring selection intensity involves separating overall selection into stages or episodes in life to reveal changes in the direction and strength of selection throughout life. Arnold and Wade (1984a,b) use "selection differentials" to compare the influence of different selective agents and stages. Selection differentials provide a means of comparing the relative intensity of selection. They compare the representation of the original individuals by character size before and after each stage of selection and can be applied to any morphological character. The differences in character distribution means are the selection differentials, and their magnitudes are directly proportional to the intensity of selection. Selection for all components can thus be directly compared by the index of selection differentials. Note that the shifts in size distributions are not intended to imply that characters in progeny will in fact be shifted (that implies heredity), rather, they are a tool to compare the importance of each component on overall selection.

Two characters were chosen for analysis; body size and jaw length. I focus on these because of their importance in competition and because they apply to two distinct types of evolutionary questions. Selection for body length is of interest for life history evolution, whereas jaw length is of interest
for the evolution of secondary sexual characters. Jaw length is one of a suite of secondary sexual characters which develop in salmon as they mature (Davidson, 1935) (Fig. 3). These characters cannot be explained by sex role reversal (Williams, 1975) because male salmon do not provide parental care, nor are males a limiting resource for females (Gross, 1984). Rather, the use of secondary characters in fighting with other females and their development just prior to reproduction suggest that they are selected for reproductive competition with other females.

**Natural History**

Coho salmon are one of five species of Pacific salmon in the genus *Oncorhynchus* which are native to North America. These species are all semelparous and have similar anadromous life-histories. They all spawn in freshwater, migrate to the ocean and return to the stream in which they were born. The species differ, however, in their length of freshwater residence, ocean residence, and age at maturation.

Iteroparity, overlap of mature reproductive generations, and changes in reproductive success with age, have been major stumbling blocks in other studies of lifetime reproductive success (e.g. Howard, 1983). These are not a problem in coho because coho are semelparous and in most populations only one female age class reproduces. In addition, coho salmon often spawn in small streams only two or three meters wide, with populations limited to a few hundred individuals.
Figure 3: Secondary sexual characters of female coho salmon. The ocean morphology (top) lacks secondary sexual characters present on the spawning grounds (bottom). These include 1) greatly elongated jaws 2) enlarged teeth, 3) skin color changes, 4) subdermal cartilagenous deposits and 5) dorsally and ventrally thickened skin. Cross sections are taken at the dotted lines just anterior of the dorsal fin.
Coho salmon generally spawn from November to January in small Pacific coast streams. As is typical of fishes, fecundity increases with body size in coho salmon (Allen, 1958; Ivankov and Andreyev, 1969; Stauffer, 1976), however egg size has also been reported to increase with body size (Allen, 1958). The life history is summarized in Figure 4. The young emerge from the gravel about three months after oviposition, and most stay in freshwater where they maintain feeding territories (Chapman, 1962) for one year before migrating to the ocean. There, they feed and grow for two more years before returning to spawn and die in their natal stream. Adult females compete vigorously among themselves for nesting territories. Females prepare nests which consist of an oval depression ranging from 9-24cm deep and 50-70cm wide in the gravel substrate (van den Berghe and Gross 1984a). On average, these territories require about 2.8m² of substrate area (Burner, 1951). Eggs are released into the bottom of the nest where they are fertilized by one or more males (Schroder, 1981; Gross, 1984), and are then covered with gravel by the female. Each female makes from one to four closely spaced nests within her territory, and then guards the territory until her death (Mathisen, 1955; Hanson and Smith, 1967; Schroder, 1973). Female guarding is an attempt to prevent re-use of the territory by subsequent females. Guarding lasts eight days on average but may range from two to sixteen days, and is positively correlated with body size (van den Berghe and Gross, 1984b). A shortage of suitable territories leads to intense
Figure 4: The life history of coho salmon.
female competition and frequent re-use of nest sites. This may result in the "dig-up" and destruction of some broods laid by earlier females (McNeil, 1962, 1964; Mattson et al., 1964; Hoopes, 1972; Ginetz, 1977).

An important component of territory quality is the composition of the gravel substrate. Several studies have shown that embryo mortality is correlated with the amount of fine sediment in the substrate (e.g. Coble, 1961; Dill and Northcote, 1970). Fine sediments impede intragravel current flows, thereby restricting oxygen availability, and may also preclude physical emergence of the fry. Inadequate gravel composition in territories has been estimated to kill 46% to 87% of the eggs deposited by coho (Koski, 1966). Thus territory quality is an important component of female reproductive success.

The larger eggs produced by large females confer two advantages on fry after hatching. Fowler (1972) found that larger eggs result in larger fry at emergence \( (r=.98) \) and faster growth for at least the first three months \( (r=.72) \), at which time his work terminated. The advantages of this are 1) faster growth rate may increase the eventual size at adulthood, and 2) larger fry may suffer lower predation rates (Parker, 1962; Mathews and Buckley, 1976; Bilton, 1984). Hatchery releases of marked chinook \( (O. tsawyitscha) \) show a strong increasing curvilinear relationship between percent survivorship and size at migration to the ocean \( (r^2=.88; \) Bilton, 1984). Coho show a similar relationship (Parker, 1962; Mathews and Buckley, 1976).
Thus the egg size differences may carry over into later differential growth and mortalities.

II. Methods and Materials

Study Site and Population

The study site is located on a small tributary to Deer Creek, 1.8 km West of Index, Snohomish Co., Wa. This tributary is locally known as Deer Creek Junior (DCJ). It was monitored daily from November through January, in 1981 and 1982, and once a week thereafter, through March 1983. DCJ has a native spawning population of about 200 adult coho (231 in 1981, 186 in 1982). The limited useable spawning area (180 square meters) enabled me to monitor all breeding activity. Observations were readily obtainable as the stream is only about three meters wide with a mid-channel depth that varies between 10 and 25cm in normal water conditions. Water level was measured daily at a fixed point in the stream.

A fence was erected near the stream mouth to prevent new fish from entering the stream until they had been tagged. Fish were caught using dip nets, sexed, fork lengths were taken, jaw lengths recorded (upper jaw, tip to anterior orbit of the eye), and they were tagged before release above the weir to spawn
naturally. Color coded 2 cm diameter Petersen disk tags (Floy Tag Co., Seattle, Wa.) allowed individual recognition of fish without apparent disturbance to spawning. Behaviors were recorded during approximately 700 hours of observation, and the progress of about 95% of the females was followed for their entire breeding lives. The location and fate of each nest was recorded on a detailed grid map of the spawning grounds.

**Fecundity**

Females were collected after their natural death to examine their ovaries for unspawned eggs. Any such remaining eggs were retained to correlate female size with egg size. Data on fecundity were available in Allen (1958) and Salo and Bayliff (1958) for a wild population of coho with body sizes similar to those of the DCJ fish. Thus, fecundity was not sampled in the DCJ population because this would affect population size and thereby alter the level of competition observed. It is unlikely that the fecundity relationship within the study population is different from that reported by Allen (1958) and Salo and Bayliff (1958), since slopes of regressions of fecundity with body size for populations from several regions in the state are not significantly different (Allen, 1958).
The re-use of previous nest sites was evident from the grid maps which showed precise nest locations. Nest destruction was assumed if 1) there was greater than 50% overlap and 2) the new female was larger than the previous one, because larger females make deeper nests ($R^2 = .76$; van den Berghe and Gross, 1984a). Actual destruction was verified by the presence of numerous partially developed eggs which lay exposed in eddies below destroyed nests before the eggs were preyed upon by birds and fish. I assumed that brood mortality was 100% if eggs appeared in downstream eddies, indicating that a subsequent female had surpassed the previous female's burial depth. This binary assumption, either total mortality or no mortality, was made to facilitate replicability, and because it appears to provide a reasonable approximation of actual losses. Although some instances of minor losses probably went undetected using the 50% overlap criterion, it is also likely that estimates of total destruction were sometimes too high. Small errors either way probably occurred for females of all sizes and are unlikely to have yielded a systematic bias, except in so far as this would reduce statistical variance.
**Territory Quality and Brood Survival**

For present purposes, territory quality was not measured in terms of the probability that the brood would be dug-up. Rather, territory quality was measured by the composition of the gravel substrate (e.g. Coble, 1961). To estimate variance in territory quality within DCJ, I collected gravel samples in midstream along the spawning grounds just prior to and following the spawning season. Samples consisted of 3-4 kg of substrate taken at 2m intervals from midstream and passed through 1mm, 6mm, 12mm, 25mm and 50mm diameter mesh screens. Fredle indices (Lotspeich and Everest, 1981) were calculated for each sample, and provide a measure of gravel quality based on geometric mean particle size as well as on dispersion around the mean. Fredle indices are well correlated with egg to fry survival in coho (Lotspeich and Everest, 1981). I quantified the mortalities for different gravels and egg sizes (van den Berghe and Gross, in prep.) using 24 nylon mesh bags buried in the stream substrate. Each bag contained 100 fertilized eggs and was buried to a depth of 15cm, to be excavated when natural fry emerged, about three months later. Seven sets of three bags containing small (7.10±.43mm), medium (8.05±.25mm), and large (8.89±.23mm) eggs were buried in different gravels, and an eighth set that was not buried served as a control. The survivorship data for the different egg sizes and fredle indices in DCJ then allow territories to be scored for egg survival. Since gravel
composition becomes important for territory quality only if nests survive through the spawning season, only those nests remaining after dig-up are included in the analysis.

Post Emergent Growth Rates and Mortality

Scales were collected from dead adults to determine the relationship between early freshwater growth, subsequent ocean growth, and adult size (Bagenal and Tesch, 1978). Scales were removed from just above the lateral line in the region near the dorsal fin, as suggested by Scarnecchia (1979). Annual growth intervals were measured using an ocular micrometer. Minor scale resorption occurred at spawning, however this only affected the latest growth, and did not affect calculations. Conversions of scale size to fish size in Marr (1943) enabled me to back-calculate the approximate size of fry at the time they entered the ocean.

To estimate the migratory and ocean mortality for progeny of different sized mothers, I used mortality data reported in the literature. These include studies of fry released at various sizes (Parker, 1962; Senn, In: Mathews and Buckley, 1976; and Bilton, 1984). The studies estimate fry survivorships of 1-3% to age 3 years for coho and chinook fry (Oncorhynchus tshawytscha) of the sizes migrating in the study population. For my calculations, I use the reported size dependent mortalities for chinook given in Bilton (1984) because these are the most
precise and because there are no problems associated with times of release which occur in the coho studies. In my calculations of differential fry mortalities, I assume that, on average, the larger fry originated from the larger females and vice versa (this seems reasonable because the larger females produced larger eggs which produce larger, faster growing progeny). The estimated mortality rate yields a curvilinear relationship with endpoints of .9% and 2.7% for the smallest and largest fry respectively (Bilton, 1984).

Results are given as mean ± SE unless otherwise specified. Analyses are based on Nie et al. (1975).

III. Results

Female Body Size

A total of 83 and 78 females entered DCJ in 1981 and 1982 respectively. Data were obtained for 80 and 77 respectively, or about 95%. All females were three years of age, yet there was a large range in female size within each year: female length ranged from 39.5 to 76cm with a mean of 54.98 ± .87cm in 1981 and 63.06 ± .74cm in 1982 (Fig. 5). The difference in mean size between years is statistically significant (t=18.85, 155df, P<.001). Scale data obtained for the two years show significant differences in both total scale radius (1981 females: 2.431 ±
Figure 5: Body size distributions of female coho in Deer Creek Junior in 1981 (top) and 1982 (bottom).
and 3rd year growth (1981: .877 + .191 mm; 1982: 1.258 + .197 mm, t=3.96, 32df, P<.001). However, when third year growth is removed, the remaining growth difference is no longer significant (t=1.14, 32df, P>.1). Furthermore, there were no significant differences in first or second year scale growth when these were evaluated individually (first year: 1981= 1.03 + .02; 1982= 1.10 + .02; t=1.18, 32df, P>.1; second year: 1981= 3.40 + .22; 1982= 3.07 + .36; t=1.40, 32df, P>.1). This suggests that the size difference between years can be accounted for by ocean growth conditions in the third year of life. Since ocean conditions are not under control of the fish, this is probably a stochastic environmental effect on body size.

Female Entry to Spawning Grounds

There were distinct peaks in the number of adults entering the stream during the breeding season. These peaks coincided with raised stream flow levels (Fig. 6). In both years, water level when the fish entered was significantly correlated with female size (1981: r=.53, N=66,1 P<.001 ; 1982: r=.42, N=77, P<.001). The larger females entered at peak discharge, and progressively smaller ones entered as waters receded. By contrast, there was no such trend in males (r=.13, N=85, P>.1). There was no significant trend for female entry during the

1. 1981 water level and morphological data were not collected for the first two weeks of the study, thus sample sizes for these items in 1981 are only 66.
Figure 6: Water level, female entry and residence on the spawning grounds, and nest locations in the Fall and Winter of 1981-82. Note that the scale for the stream width is 2X that for length to accommodate the nest sites.
season with respect to body size (1981: $r = -0.15$, $N=80$, $P>0.05$, and 1982: $r=0.22$, $N=77$, $P>0.05$). Thus neither small or large females were more likely to enter particularly early or late in the season.

Female Competition

Because females require approximately 2.8 m² (Burner, 1951) for their nests, the population in DCJ needed in excess of 200 m². However, only about 90 m² of suitable spawning substrate existed. As a result, there was intense competition for spawning substrate among females (Fig. 6). Body size did not determine ability to lay eggs, in spite of the competition. Only two females of 50 sampled had laid less than 99% of their estimated egg number. These two exceptions were both large females; one of these had sustained a gill injury during handling and the other had a large tumor in the body cavity.

Competition among females involved either fighting and active displacement from a territory, or passive take-over of a territory when the guarding female died. In either case, nests were likely to be dug up. There were 82 cases of nest site re-use over the two seasons. Of these, 48 involved dig-up of the eggs. In 1981, 29% of 97 nests were destroyed and in 1982, 18% of 113 were destroyed. Eggs exposed by site re-use were eaten within hours by a variety of predators including dippers Cinclus mexicanus, rainbow trout Salmo gairdneri (a 25 cm specimen had
Figure 7: The relationship between female size and the proportion of nests remaining undisturbed throughout the season. Points represent the mean survival values for 3 cm female body size ranges (number of nests in the sample next to each point). r = .85, y = -28.26 + 1.47x, P < .001.
64 partially developed eggs in its stomach), cutthroat trout *Salmo clarki* and dolly varden *Salvelinus malma* (26 partially developed eggs in a 41 cm specimen).

Female size and territory quality (fredle index) were significantly correlated for nests remaining at the end of the season ($r = .37$, $P = .005$, $N = 47$, $Y = -6.50 + .177X$). Since gravel composition is only an important component of territory quality and female success if the nest survives dig-up, only those nests remaining after dig-up were included in this analysis. This correlation is a consequence of larger females successfully defending their territories against smaller rivals. Smaller intruders were often quickly repulsed, but larger intruders usually displaced the resident female after a lengthy fight (Table 2). The proportion of territories re-used did not differ significantly for large and small females ($t = 0.08$, 1 d.f., $P > .5$). This was because small females sometimes used the territories of larger females that had died instead of just using the less desirable territories. However destructive re-use of a female's nest was inversely correlated with her size (Fig. 7), because both large and small fish destroyed shallow nests while only big fish destroyed the deep ones characteristic of large females (van den Berghe and Gross, 1984a). As a result larger females had a two to three-fold nest survivorship advantage over the smaller females in the population (Fig. 7).
Table 2: Female-female fighting in coho salmon. A comparison of resident (R) and intruder (I) female body size, and the outcome of female-female competition over a territory. Short fights were defined as lasting less than five minutes. Long ones usually lasted from twenty minutes to several hours. No fights of intermediate duration were observed.

<table>
<thead>
<tr>
<th>Size (cm)</th>
<th>Size (cm)</th>
<th>Winner (R,I)</th>
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<tr>
<td>short</td>
<td></td>
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</tr>
<tr>
<td>68.5</td>
<td>68</td>
<td>R</td>
</tr>
<tr>
<td>69</td>
<td>55.5</td>
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<td>fights</td>
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<td>71</td>
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</tr>
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<td>64</td>
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<td></td>
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<tr>
<td>67.6±2.6</td>
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</tr>
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<td>long</td>
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</tr>
<tr>
<td>61.5</td>
<td>72.5</td>
<td>I</td>
</tr>
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<td>67.5</td>
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<tr>
<td>64.0±3.6</td>
<td>69.4±1.7</td>
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</table>

Resident Intruder Winner
Offspring Size, Growth Rate and Survival to Adulthood

The egg burial experiment (van den Berghe and Gross, in prep.) showed that egg survivorship during development, egg size, and gravel quality were significantly correlated ($R^2=.87$, $N=10$, $P<.001$). Smaller eggs were more likely to survive to fry emergence than were large ones in the same substrate, apparently because the latter required more oxygen. Female size and egg size were also strongly correlated ($r=.84$, $y=-150 + 5.2x$, $P<.001$, Figure 8), thus territory quality was not a constant measure for all females. Instead, survival of eggs depended on the size of eggs as well as the composition of substrate into which the eggs were laid. Mortality estimates incorporating egg size and substrate composition ranged from means of 24% for the smallest females to 15% for the largest. Figure 9 compares the actual mortalities in different substrates to those found for a single egg size across gravels (Lotspeich and Everest, 1981). The three measured values in Figure 9 are each based on only one replicate because the experimental design results in only one bag of each egg size buried in the gravel size expected by each female.

The scale measurements from DCJ adults also show that the early freshwater growth of coho is positively correlated with subsequent growth in the ocean (1981 females: $r=.73$, $y=1.46 + 4.9x$, $N=28$, $P<.001$, Fig. 10). Thus the fry size advantage conferred by large eggs at birth and in early growth (Fowler, 1962) tends to be carried into adulthood. Back-calculations of
Figure 8: Female coho body size and egg diameter. Each point represents the mean egg size of an individual. Intra-individual variance was less than 0.4mm and is incorporated in the regression.
Figure 9: Measured mortalities in different gravel compositions when egg size is constant (bottom) or varies with female size (top). Survival in poor gravel is greatly improved by the smaller egg size of smaller females.
fry size from scale diameter at entry into the ocean reveal that Deer Creek Junior fry enter the ocean at a range of sizes from 6 to 10 g. To estimate natural migratory and ocean mortality, I use reported mortalities of fry released at these sizes (see Methods). This gives estimates of 0.9% and 2.7% (Bilton, 1984) for the migratory and ocean survival of progeny from the smallest and largest females respectively. Note that this excludes about 7 months of possible differential mortality in freshwater prior to migration to the ocean, because no data were available on fish too small to tag.

Summary of Mortality

The natural sources of mortality at various stages from egg to adult are summarized in Figure 11. Starting with the expected baseline fecundities (top line) (Salo and Bayliff, 1958), I first subtract losses due to nest re-use (from Fig. 7). This is followed by losses due to territory quality and egg size (from Fig. 9). This leaves the expected number of offspring surviving to emergence. Note that while the actual number of fry dying due to inadequate territory quality is lower for small females, the proportion of brood lost due to territory quality is higher. Finally, the differential survivorship attributable to different progeny sizes and growth rates (0.9 to 2.7% of those surviving to emergence) is included to arrive at the expected number of progeny surviving to adulthood (number of adults remaining has not been corrected for the fishing harvest imposed by man). It
Figure 10: The relationship between first year freshwater growth and the remaining 19-22 months of ocean growth. Growth rates are from scales of 28 females collected after death in 1981.
FRESH WATER GROWTH
(scale radius mm)

OCEAN GROWTH
(scale radius mm)

FRESHWATER GROWTH
(scale radius mm)
should be noted that all values used to compose this figure are the expected means from regressions, and considerable individual variation exists.

**Intensities of Selection**

A. Body Size

Selection differentials were calculated separately for the two years of study to give independent measures of the relative intensities of selection. The results are presented graphically in Figure 12; calculations appear in Appendix A. Dividing individual "S" values (selection differentials) by the standard deviation of the character gives an idea of the relative intensities of selection "i" (i=S/SD of population before selection). These can be converted to percent by taking the ratio of individual i's to the sum of i values (this is equivalent to S/ΣS since %i=(S/SD)/Σ(S/SD)). The individual contributions of the various stages are summarized in Table 3. Note the similarity between years in the contribution of mortality factors despite very different female sizes. Note also that fecundity contributes less than one quarter of the selection pressure favoring increased female body size. By contrast, female competition expressed in "dig up" and "territory quality" accounts for over half of all natural selection on female body size.
Figure 11: Summary of expected reproductive success for females of a given size.
Figure 12: Selection for body size in female coho salmon. The $Z$ values represent the theoretical mean body size of the population based on the representation of females and their progeny. $Z_0$ is the size of the adult females, and $Z_1$ through $Z_4$ represent progeny at various stages of selection. $Z_1$ incorporates fecundity differences, $Z_2$ dig up, $Z_3$ substrate quality, and $Z_4$ migratory and ocean mortality. Increasing values of $Z$ indicate directional selection for larger body size. $S$ values are the selection differentials and can be found by subtracting $Z$ values; these provide a direct measure of selective pressure.
Table 3: Selection intensities on female body size in coho salmon (see Appendix A for calculation of selection intensity).

<table>
<thead>
<tr>
<th></th>
<th>1981</th>
<th>1982</th>
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<tbody>
<tr>
<td>Fecundity</td>
<td>i1 = 0.290</td>
<td>23.5%</td>
</tr>
<tr>
<td>Dig Up</td>
<td>i2 = 0.404</td>
<td>31.8%</td>
</tr>
<tr>
<td>Territory Quality</td>
<td>i3 = 0.305</td>
<td>23.9%</td>
</tr>
<tr>
<td>Post-emergent</td>
<td>i4 = 0.263</td>
<td>20.7%</td>
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i = selection intensity
B. Jaw Length

The same techniques used to look at the intensity of selection for body size can also be used to look at selection for secondary sexual characters. The only episodes of importance for selection are those in which the characters are expressed, specifically the two stages of competition on the spawning grounds. Figure 13 shows the measured selection for jaw elongation, one of the more prominent fighting characters of female coho salmon (calculations in Appendix B). Selection for jaw length (.44 SD shift) was about one third that for body size but still strong. Thus intrasexual behavioral competition for limited resources that affect reproduction may select for secondary sexual characters in females.

Jaw length was less important in determining success in territorial defense (39% contribution) than it was in determining the quality of the territory she obtained (61% contribution). This is in contrast to selection for body size where the most important episode was "dig-up," and territory quality was of secondary importance.

Two analyses were conducted to separate the contributions of body size and jaw length to selection. In one analysis, I regressed both jaw length and body size on nest destruction via "dig up;" in the other, jaw length and body size were regressed on territory quality. This was done to separate the partial regression of fitness on the characters, termed "selection
Figure 13: Selection for jaw elongation. Selection for jaw length occurs in 1) territorial defense (selection measured in "dig up"), and 2) in the quality of the territory that is defended successfully (selection measured in territory quality). Jaw length was not collected in 1982.
gradient" (Arnold and Wade, 1984a). In both analyses, the contributions of jaw length and body size were highly correlated with each other, and either alone explained almost the same variance as did both jaw and body length together. Body size was more important than jaw length in losses via "dig-up," and accounted for 82% of the selection gradient. Jaw length was the more important variable for the quality of the territory that was defended successfully, with jaw length alone accounting for 78% of the selection gradient. Actual explained variance in this analysis was only about 10% of "dig-up" and 5% of "territory quality," owing to a reduced sample and lower body size variation, since I was limited to those 1981 females on which I had complete data sets (n=21). What is more important for the strength of selection, however, are the slopes of the regressions, rather than the explained variance itself.

IV. Discussion

One of the interesting findings of this study is the intense selective pressure generated by competition between females. Fecundity, which is generally assumed to be an accurate indicator of female reproductive success, only accounted for about one quarter of the selection on body size; whereas competition between females for spawning sites accounted for more than half of all selection on body size. The actual strength of selection measured in standard deviations of character shift (see Arnold and Wade, 1984b) is stronger than
those reported for males in other studies of sexual selection (McCauley, 1983; Arnold and Wade, 1984b).

Although small females are disadvantaged on the spawning grounds, they use several tactics to improve their situation. Without these, they would do worse than the present results indicate. One tactic is to enter the spawning grounds at times different from those of large females. The largest females entered the stream only at high water following heavy rainfall, and finished spawning about four days after entry (van den Berghe and Gross, 1984b.), but remained guarding their redds. Smaller females, by entering only as the water receded, tended to get the remaining, poorer, sites which reduced the probability of being displaced by a larger fish. Mortality for the eggs of smaller females in poor sites is much lower than expected from other studies (e.g. Lotspeich and Everest, 1981) because the smaller eggs survive better than would large ones in poor sites.

The question arises whether, given the strong selection observed, females might be evolving larger body sizes. While there may be some variance in the genetic growth potential, the most important variables for growth in organisms with indeterminate growth are age and food availability. Delaying maturation by large three year olds to achieve very large size, would be of dubious value as this entails the cost of 1) an additional year of natural ocean and fishing mortality, 2) reduced maneuverability on the spawning grounds, 3) fever
suitable hiding places to escape predators on spawning grounds, 4) higher egg mortality, and 5) fewer suitable nest sites. Although all these costs are not readily estimated, there are few benefits to be gained as the large fish suffer few losses in competition to begin with. It would therefore be expected that the costs of delaying maturation for large females would exceed benefits in the study population. By contrast, the benefits of delayed maturation for small females could be enormous (up to 25 fold in DCJ) whereas costs, excepting the additional year of ocean mortality, are probably small, since the small 3 year olds returning at age 4 would not be much larger than the large 3 year old fish. Data from other species indicate that the cost of an additional year of ocean and fishing mortality would only add about 20% beyond the mortality suffered by three-year olds (Ricker, 1976). Given this apparent imbalance in known costs and potential benefits, it is unclear why delayed maturation to achieve larger size is not occurring in the smaller fish.

Interestingly, variability does exist in some populations such as the Karluk R. (Alaska) where spawning coho are predominantly four and five years old (Drucker, 1972).

By contrast, a response to selection on female size is suggested by the fact that no females mature at age 2 in the study population. A recent study by Healy and Heard (1984) based on fecundity and mortality tradeoffs (not including female competition) suggests that for chinook salmon, (O. tshawytscha), the mean female age at maturity is above the theoretical
optimum. This suggests the observed age of maturation is already a response to female competition.

In addition to age of maturation, food availability appears to be very important for coho salmon. Despite the correlation between early and late growth \((r=.73, \text{Fig 10})\), there is considerable scatter in the eventual fish size given the first year scale size. The projected effects of this scatter on the expected size distributions of progeny are shown in Figure 14. The progeny distributions are derived by normally distributing the expected number of progeny for each female size (from Appendix A). The mean of each such distribution is the size of the females in that category, and the SD is determined by variance in eventual adult size as calculated from scale growth. The overall expected progeny distribution is then the sum of the progeny distributions across female size categories. The mean offspring size thus produced is about 2cm larger than the original females. This increase is much less than the 7-10 cm shift indicated by the calculations of selection differentials (Appendix A). However the remaining theoretical 2cm increase still does not mean that body size should necessarily increase, even if there is genetic variance. In this century, fishing mortality has become a major selective factor which has not been incorporated into the calculations. The opportunity for selection by the fishery is substantial since the fishery currently takes about 80% of the mature fish (Washington Dept. of Fisheries, unpubl.); in other words, the fishery makes up the
Figure 14: The size distributions of breeding females in DCJ and the expected size distribution of their progeny at maturity.
numerical difference between parent and offspring distributions in Figure 14. Studies on the fishery selectivity for sockeye salmon (*O. nerka*) show a decrease of approximately 2cm in mean fish size on days when gillnets fished a river (Peterson, 1954). It is also known that the mean size of adult coho has been declining fairly regularly over the last few decades in Pacific waters (Ricker, 1981). This may be in response to selective fishing techniques such as gillnets and minimum size limits which make smaller individuals less vulnerable. Thus artificial selection by the fishery appears to be favoring fish smaller than the natural balance between selection for and cost of larger female body size.

There are still two remaining sources of potential variation in reproductive success which have not been incorporated. The more important of these is fry competition from a few weeks after emergence to downstream migration. There is likely to be some selection favoring larger fish during this 7 month interval due to advantages of larger fry in territory defense and reduced predation. Incorporation would further exaggerate differences between large and small females.

Secondly, larger male juveniles are more likely to mature one year early, at age 2, thereby suffering about 20% less mortality than their 3 year old counterparts. I have not taken the possible overproduction of two year old males by large females into account here because their effect on female fitness is negligible since they represent only about 6-7% of mature
fish in the study population, and 2) because their survival advantage is balanced by a mating disadvantage to yield approximately equal fitness with 3 year old males (Gross, in press).

I have thus calculated lifetime reproductive success from field measurements and from data in the literature, and computed selection for body size as well as jaw morphology. The analysis has shown that more than half of the very strong measured selection on female body size is due to intrasexual competition between females over spawning sites. In addition, the competition over spawning sites has selected for elongated jaws and may also explain the other correlated secondary sexual characters in females. Finally, competition also appears to have selected for behavioral tactics in smaller females.
E. Appendices

Appendix A

The intensities of selection (i) for 1981 and 1982 are calculated in separate tables on the following pages using the methods of Arnold and Wade (1984). Identical procedures were used for all tables. The column labelled "female size" is a list of the female size categories used in calculations across rows. Size categories are used rather than individual female sizes so that general trends will become apparent. The 3cm range in each category draws a balance between a reasonable sample from which to compute means, and a maximum number of categories. These are the same intervals used in Figure 7. The column labelled "N" gives the number of females in each category.

Po is the proportion of females in the population which appear in each category. W1 is the average expected fecundity in each category, based on Salo and Bayliff (1958). P1 is the proportion of eggs in the population produced by the observed number of females in each category. The change from Po to P1 is the measure of selection exerted by differential fecundities. P1 is calculated for each size category by multiplying (W1) times (Po) and dividing by the sum of all W1Po. The sum of any P column should always be 1.000 except for rounding errors.

W2 is the proportion of nests surviving dig-up (from Fig. 7). Thus W1W2 is fecundity times the proportion surviving dig-up. This assumes that, on average, individual surviving and
destroyed nests contained similar numbers of eggs for females of a given size. P2, P3, and P4 are the relative representations for the categories after the corresponding selective factor. These are calculated following the formula \((Pn-1)(Wn) / \text{sum of}[(Pn-1)(Wn)]\). W3 is the percent of young surviving in the substrate. W4 is the expected migratory and ocean survival to adulthood. Note that the P columns are population representations, and the W columns are eggs and later offspring per female.

The values below the tables are population means. W1...W4 are mean numbers of progeny expected to survive at each stage. Zo is the starting population mean of adult females, and Z1 ... Z4 are the mean progeny size representations corresponding to the P distributions.

S values are the differences in population mean population size before and after selection. These are measured from the theoretical shifts in body size represented by Zo through Z4; e.g. \(S1 = Z1 - Zo\). Note that these shifts are not intended to imply that the offspring will be larger. The differentials are used to measure selection, not the result of selection. Finally, the intensity of selection, \((i)\), for each stage is equal to \(S/SD\) of Zo. The in/sum of \(i\) is the percent of total selection accounted for by the nth stage.
Appendix A.1
1981

<table>
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<th>Female Size</th>
<th>N</th>
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<th>W1</th>
<th>P1</th>
<th>W1W2</th>
<th>P2</th>
<th>W1W2W3</th>
<th>P3</th>
<th>W1W2W3W4</th>
<th>P4</th>
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<td>.0625</td>
<td>800</td>
<td>.027</td>
<td>528</td>
<td>.009</td>
<td>322</td>
<td>.002</td>
<td>2.6</td>
<td>.000</td>
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<td>44-47</td>
<td>9</td>
<td>.1125</td>
<td>1050</td>
<td>.064</td>
<td>656</td>
<td>.027</td>
<td>426</td>
<td>.007</td>
<td>3.8</td>
<td>.001</td>
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<td>1300</td>
<td>.079</td>
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<td>.035</td>
<td>476</td>
<td>.011</td>
<td>4.7</td>
<td>.002</td>
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<td>1550</td>
<td>.126</td>
<td>1096</td>
<td>.089</td>
<td>778</td>
<td>.042</td>
<td>8.9</td>
<td>.013</td>
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<td>.1375</td>
<td>1800</td>
<td>.134</td>
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<td>.071</td>
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<td>.095</td>
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80 1.000  .996  .999  1.000  1.000  
W1=1735  W1W2=1543  W1W2W3=1501  W1-W4=15.0

Zo=54.98±7.78cm  SD  Z1=57.30  Z2=60.44  Z3=62.81  Z4=64.86
S1=2.32  S2=3.14  S3=2.37  S4=2.05
i1=.290  i2=.404  i3=.305  i4=.263
=23.5%  =31.8%  =23.9%  =20.7%

W1=Fecundity  W2=Dig up  W3=Site quality  W4=Migration & Ocean survival
Po=population distribution before selection.
Pn= " " " after nth episode = (Pn-1)(Wn)
Z=mean body size of population.
Zn= " " " " after nth episode = Σ[(Pn-1)(Z)]
S=selection differential  Sn=(Zn)-(Zn-1)
i= selection intensity = S/SD of Zo
### Appendix A.2

#### 1982

<table>
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<tr>
<th>Size</th>
<th>Female N</th>
<th>Po</th>
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<th>P1</th>
<th>W1W2</th>
<th>P2</th>
<th>W1W2W3</th>
<th>P3</th>
<th>W1W2W3W4</th>
<th>P4</th>
<th>Size</th>
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<td>-</td>
<td>-</td>
<td>-</td>
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<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>-</td>
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<td>1550</td>
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<td>-</td>
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<td>0.026</td>
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<td>10.6</td>
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<th>1.000</th>
<th>1.000</th>
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<td>W1W2=1935</td>
<td>W1W2W3=1568</td>
<td>W1-W4=26.2</td>
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<td></td>
</tr>
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<td>Zo=63.06±6.45cm</td>
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<td>Z2=67.44</td>
<td>Z3=68.71</td>
<td>Z4=70.21</td>
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<td>S3=1.27</td>
<td>S4=1.50</td>
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</tr>
<tr>
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<td>i2=.457</td>
<td>i3=.197</td>
<td>i4=.233</td>
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</tr>
<tr>
<td>=20.0%</td>
<td>=41.3%</td>
<td>=17.8%</td>
<td>=20.0%</td>
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</table>
Appendix B

Selection for jaw length. Jaw length is measured as the distance from the anterior of the occipital orbit to the tip of the upper jaw. Jaw measurements were made in 1981 only.

<table>
<thead>
<tr>
<th>Jaw Length (cm)</th>
<th>N</th>
<th>Po (W1)</th>
<th>Dig Up (W1)</th>
<th>P1 (W1W2)</th>
<th>P2 (W1W2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.0-2.5</td>
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<td>.67</td>
<td>.0807</td>
<td>.55</td>
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<td>.0794</td>
<td>.27</td>
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<td>.50</td>
<td>.1504</td>
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<td>.74</td>
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</table>

Z₀=3.79±.98 cm SD  Z₁=3.96 cm  Z₃=4.23 cm
S₁=.17 cm  S₂=.27 cm
i₁=.39  i₂=.61
39%  61%

66


Dublin, H.T. 1983. Cooperation and competition among female


----- 1964. Redd superimposition and egg capacity of pink salmon


Scarnecchia, D.L. 1979. Variation of scale characteristics of coho salmon with sampling location on the body. Prog. Fish Cult. 41:132-134.


